

Habitat modelling of key submergent macrophytes
within the Lower Lakes,
South Australia



Matthew Linn
Student ID: 211294695
School of Life and Environmental Sciences
Deakin University

Submitted in partial fulfilment of the degree of
Bachelor of Environmental Science (Honours)
October 2014

Statement of Responsibility

This thesis is submitted in accordance with the regulations of Deakin University in partial fulfilment of the requirements of the degree of Environmental Science Honours. I, Matthew Linn, hereby certify that the information presented in this thesis is the result of my own research, except where otherwise acknowledged or referenced, and that none of the material has been presented for any degree at another university or institution.

A handwritten signature in black ink, appearing to read 'm. linn', followed by a long horizontal flourish.

Date: 27/10/2014

Front cover: Site photo Point Sturt (site 6)

Abstract

The Murray-Darling Basin in south-eastern Australia is subject to the compounding effects of river regulation and extraction. The recent decade-long Millennium Drought saw large-scale changes in environmental conditions, degrading ecological communities and reducing species occurrence. With limited recovery of many communities post-drought, predictive habitat models were developed and field-validated to investigate the relationship between two key submergent macrophytes (*Myriophyllum salsugineum* and *Vallisneria australis*) and the environmental variables influencing their occurrence, using the Lower Lakes as a case study. Telemetered records of logged environmental data were paired with vegetation monitoring data to develop non-parametric multiplicative regression models. The influence of the intra-seasonal variation in conductivity and water temperature from these telemetered records in conjunction with water pH from field surveys was found to define the habitat envelope for those species, and therefore, potentially limiting species occurrence post-drought. These findings provide managers with regional predictions of species responses that can be incorporated into management decisions to ensure submergent macrophyte assemblages remain viable into the future, while providing a proof of concept for a modelling approach that can be undertaken to describe similar relationships for other key taxa within the Murray-Darling Basin and abroad.

Key words: Non-parametric multiplicative regression, habitat modelling, post-drought, macrophytes

Acknowledgements

I wish to thank my two tireless supervisors Dr Rebecca Lester and Dr Jan Barton sincerely, for their unwavering encouragement and support throughout the entire honours year. Their wealth of knowledge and readiness to discuss, share and develop thoughts and ideas has made what was a challenging year, a really enjoyable and rewarding experience. I would also like to kindly acknowledge Dr Jason Nicol (with a special mention for field assistance and plant identification) and the South Australian Research and Development Institute, as well as Jason Higham, Peta Hansen and the Department of Environment Water and Natural Resources, South Australia, for their generous contribution of time, effort, expertise, along with the provision of data. Additionally, I wish to thank Michael Diplock, Laurie Rankine Junior and the Ngarrindjeri Nation for their enthusiastic involvement in the present study. I also acknowledge the Elliott Newspaper Group, The Murray-Darling Foundation and The Murray-Darling Freshwater Research Centre for their generous contribution to the project through the awarding of the Elliot Newspaper Group scholarship. It is an honour to receive this prize and to have the study recognised for its role in enhancing the sustainability of river systems within the Murray-Darling Basin. David Dodemaide is greatly acknowledged and thanked for his ongoing support during the field work as well as throughout the entire process. Alex Pearse is also thanked for his assistance with lab work. I wish to acknowledge Deakin University and the Warrnambool School of Life and Environmental Sciences staff who have, fostered a study environment full of passion and desire to share knowledge that I am yet to see matched. I also acknowledge the funding provided by Deakin to support my study. Finally, I wish to acknowledge the support of friends, family and the 2014 honours cohort who have been supportive, compassionate and understanding throughout the year.

Table of Contents

Statement of Responsibility	i
Abstract	ii
Acknowledgements.....	iii
List of Abbreviations	vi
Introduction.....	1
Materials and Methods.....	7
Study area.....	7
Vegetation monitoring data.....	9
Telemetered environmental data.....	9
Developing preliminary habitat envelope models	12
Likelihood of occurrence	13
Vegetation assessment	16
Site characteristics	18
Statistical analyses	21
Refined models	21
Results.....	23
Preliminary habitat envelope model	23
Models predicting likelihood of occurrence	25
<i>Myriophyllum salsgineum</i> and <i>Vallisneria australis</i> abundance	27
Testing the preliminary models	28

Vegetation assemblages	29
Water quality and other site characteristics	33
Refined models	34
Discussion	36
Modelling approach and proof of concept	36
Pairing data from telemetered sites and monitoring to enable key species modelling	40
Influence of ranges to capture intra-seasonal variation	41
Consistency of predictors	44
Conductivity and water temperature	46
Water pH	47
Management within the system	48
Conclusion	50
References	51
Appendices	i

Marine & Freshwater Research example publication

<http://www.publish.csiro.au/?paper=MF13163>

Marine & Freshwater Research Author guidelines

<http://www.publish.csiro.au/nid/129/aid/434.htm>

List of Abbreviations

NPMR - Non parametric multiplicative regression

SARDI - South Australian Research and Development Institute

DEWNR - Department of Environment Water and Natural Resources

EC - Electrical conductivity ($\mu\text{S cm}^{-1}$ @ 25 °C)

AHD - Australian height datum (approximates mean sea level)

Introduction

Freshwater environments are dynamic and complex ecosystems with energy and nutrient pathways linking aquatic systems with their terrestrial surrounds (Likens and Bormann, 1974). These aquatic systems provide important ecosystem services depending on the health and function of these systems (Rapport and Costanza 1998). However freshwater systems around the globe have been altered, with an estimated two thirds of the world's flowing fresh water obstructed by dams on route to the sea (Nilsson et al. 2005). Regulating the flows of rivers with dams, weirs, locks and barrages has created reliable water resources for power production, agriculture and domestic use out of otherwise variable freshwater systems, shaping surrounding communities and industries (Grey and Sadoff 2007).

The environmental cost of regulation, and often over-extraction from, freshwater ecosystems has included shifts in diversity and abundance in biota. Natural lake level fluctuation plays a crucial role in freshwater aquatic ecosystem structure and function (Leira and Cantonati 2008), with native taxa having life histories adapted to a variable hydrological regimes. Water regulation has greatly affected fish, aquatic vegetation and invertebrate communities (Blanch et al. 1999; Ning et al. 2013; Bice et al. 2014). In addition, it has also affected water quality, influencing conductivity, turbidity and nutrient loads within these systems (Ahearn et al. 2005; Mosley et al. 2012).

In drought-prone aquatic ecosystems, native taxa have adaptive life histories to persist and recover post-drought (Ning et al. 2013). Within regulated systems, these drought events can be exacerbated by water extraction and the natural resilience of taxa can be altered by deviations from natural conditions pre-drought (Lake et al. 2011). Drought places taxa under increasing stress via a progressive loss of resources, further reduced water quality and increased biotic interactions within a diminishing habitat, having deleterious consequences on many taxa (Bond

et al. 2008). With the natural cycle of drought linked with flood and subsequent recovery, recovery in regulated systems post-drought has been seen to vary among taxa (Boix et al. 2010) and in time frame (Rapport and Whitford 1999). With loss of natural variability, the synergistic effects of drought and subsequent loss in resilience of these systems, natural resource managers around the globe are dealt the challenging responsibility of ensuring ecosystem health into the future, whilst managing the demands of water-dependent industries.

Managers have recognised the value of controlled releases of additional water for environmental purposes (environmental watering) as a management tool to enhance ecosystem health and resilience in altered freshwater systems (Lind et al. 2007). Large water releases over time have been used to mimic natural cycles and pre-regulation condition, whilst other environmental watering programs have focused on targeted outcomes such as improving physicochemical characteristics (e.g. electrical conductivity), clearing periphyton off substrate in stream beds, clearing sediment deposits, reducing algal blooms, induce fish spawning, connecting fragmented habitat, inundating floodplains or restoring littoral vegetation and ecological communities (Kashaigili et al. 2005). As the targets of environmental flows have varied, so has the success of these actions (Tonkin and Death, 2014). Justifying further watering, particularly in regions with multiple competing interests for water resources, requires knowledge of the likely outcomes of watering actions (King 2006).

Large-scale flow regulation and over-extraction for irrigation has been occurring in the Murray-Darling Basin for well over a century (Murray Darling Basin Authority 2013). The River Murray is Australia's largest river, draining 14 % of the total land mass of the continent (CSIRO 2008) but, when compared internationally to other rivers with similar catchment areas, the natural flow characteristics are low and sporadic, typical of semi-arid zone rivers (Puckridge et al. 1998). As a result of regulation, the River Murray has seen a loss in hydrological variability, seasonality and a reduction in annual flow volumes (Maheshwari et

al. 1995). This shift in hydrology from its natural state has been in favour of a productive and extensive system of water-intensive irrigation agriculture (Quiggin 2001). The Lower Murray system ranges from freshwater lakes to saline and hypersaline lagoons with diverse fringing wetlands, with a complex conductivity gradient balanced by freshwater inflows from the River Murray channel. This reliance on upstream flows leaves the Lower Murray system vulnerable to the effects of regulation and over-extraction (Mosley et al. 2012). The Lower Murray region contains a number of Ramsar-listed wetlands of international importance which support populations of nationally- and internationally-significant flora and fauna. However many macroinvertebrates, water birds, fish and aquatic vegetation within the region are in decline (Frahn et al. 2013; Wedderburn et al. 2012; Paton et al. 2009). The two Lower Lakes, Lakes Alexandrina and Albert, mark the freshwater extent of the River Murray, with barrages in the south of the system preventing salt water intrusion. Prior to regulation, the conductivity gradient in the Lower Lakes was naturally maintained with flushing river flows (Mosley et al. 2012). During the Millennium Drought (1997-2009), the Lower Lakes saw water levels drop, conductivities rise and acid sulphate soils exposed along lakeshores and surrounding channels (Mosley et al. 2012).

Research examining the response of a range of taxa to environmental variables within the Lower Murray system has identified conductivity and water regime as the two major variables influencing species occurrence and abundance (Wedderburn et al. 2007; Kefford et al. 2007; Ning et al. 2013). Increasing conductivity, reduced flows and a changed water regime are symptoms of regulation and water management exacerbated by drought, therefore understanding how each affect a wide range of taxa within the system is crucial to its future management. In order to undertake effective management, natural resource managers require evidence-based and location-specific tools for assessing and accurately inferring ecosystem responses (Pace 2001). Researchers from Australian, and more recently international,

universities have been working with state and national government authorities to develop such tools for this region (Lester et al. 2013). This collaborative work has focused on developing tools to assess the large-scale ecosystem responses to changing environmental conditions. Accurately forecasting the ecosystem response of a complex river system requires detailed knowledge of how organisms respond, at a community and species level.

Habitat encapsulates the biotic and abiotic features of an environment within which a species can occur. Species have definable habitat requirements or a habitat niche (Whittaker et al. 1973) and organisms are limited by the availability of resources and their tolerances to environmental conditions (Grinnell 1917). Changes in the suitability of habitat can result in changes in the distribution or occurrence of species, as is the case with the changes evident in the Lower Lakes in recent years. Habitat modelling uses environmental and associated biological data to determine what environmental characteristics define a given species habitat (Soberón 2010). Depending on spatial scale of these models, they can be used to predict the extent of species distributions geographically, looking at the large-scale biogeographic characteristics that limit their distribution. At a finer scale, habitat models have been used to predict species occurrence using readily measurable and changing environmental variables such as physicochemical variables (Wedderburn et al. 2007). Using a combination of historical data and field validations, the spatial and temporal ranges of taxa within the Lower Murray system can be identified. This allows ecologists to not only assess the size and quality of habitat, but to further predict how this provision of habitat will change as these variables change through time. Developing habitat models to identify the spatial and temporal distribution of key aquatic taxa within the Lower Lakes will assist managers to infer the future response of the taxa in question to predicted environmental conditions. Such knowledge can inform decisions regarding water allocation and environmental flows.

Non-parametric regression analysis (NPMR) is a flexible modelling approach that has many advantages over more traditional methods. For example, the predictors are not predetermined as they are in parametric regression but are constructed according to information derived from within the analysed data. Furthermore, the variables are able to be applied multiplicatively as opposed to additively (McCune 2006) which is beneficial because the effect of each variable can interact with others. Based on the understanding that species respond to multiple interacting factors within their environment, this method allows these interactions to be modelled with their natural complexity intact (McCune 2006).

NPMR has been widely used to model the response of a range of taxa to various environmental gradients at differing spatial scales and with differing outcomes. It has been used to quantify geographic ranges of bird communities post fire disturbance, Grundel and Pavlovic (2007) and finding an optimal fire frequency to be incorporated as management targets. DeBano et al. (2010) examined the outbreak of insect pests in crops in Northwest United States, suggesting that warmer seasonal temperatures and lower elevations intensified outbreaks in crops, therefore enabling targeted mitigation measures to be developed. Habitat distribution modelling using NPMR has been undertaken within the Lower Murray system, providing insight into how species respond within their changed and changing environments. Wedderburn et al. (2007) utilised NPMR modelling to determine differences in the distribution of two similar small-bodied Arthenidae fish species within the River Murray that share similar geographic ranges yet are rarely found to coexist. Rogers and Paton (2009) used the same approach to examine the decline in the range of *Ruppia tuberosa*, a key submergent macrophyte within the South Lagoon of the River Murray estuary. NPMR modelling was successfully used to determine what variable, or combination of variables, best explained the distribution of the target species in both these studies. Wedderburn et al. (2007) found conductivity to be the most influential predictor of species occurrence for both of the species in question, with the

separation in range described by differing predicted responses to a conductivity gradients within the system. For *Ruppia tuberosa*, increased conductivity was identified as the driver for the observed diminishing range Rogers and Paton (2009). Such studies highlight the importance of establishing not only what drives occurrence at a species level, but to also understand the type of response that each shows to measurable environmental gradients, so as to accurately predict habitat use.

This study focused on the submerged macrophytes *Myriophyllum salsugineum* and *Vallisneria australis* which were previously common within the system (Frahn et al. 2013). The two species were studied as individual taxa and also as potential surrogates for submerged macrophyte assemblages as a whole. Submerged macrophytes form important littoral habitat for invertebrate and fish species (Bice et al. 2014) and provide food and foraging sites for aquatic birds (Paton and Rogers 2009). They are also important in nutrient cycling within aquatic ecosystems (Carpenter and Lodge, 1986). As sediment-rooted species, *M. salsugineum* and *V. australis*, are limited by water depth and are subject to desiccation and the effects of water quality and turbidity (Middelboe and Markager 1997; Deegan et al. 2007). Despite recruiting in the system post-drought, neither species has returned to historic abundance levels (Frahn et al. 2013).

The factors limiting the resurgence of submergent macrophytes post drought are currently unknown. This study aimed to identify the environmental drivers limiting *M. salsugineum* and *V. australis* within the Lower Murray system by quantifying the environmental requirements for each species using predictive models. A secondary aim of the project was to field-test these models to assess the degree of success of each in predicting species occurrence in the Lower Lakes. The developed and validated models will provide natural resource managers in the region with decision-making tools to assist in the development of targeted management actions to achieving specific positive ecological outcomes within the system.

Materials and Methods

Study area

The study area comprised Lakes Alexandrina and Albert and the adjoining Goolwa Channel in the River Murray catchment, South Australia (Fig. 1). The three connected freshwater bodies are shallow, turbid and eutrophic (Mosley et al. 2012) and can be collectively described as the Lower Lakes system (Fig. 1)

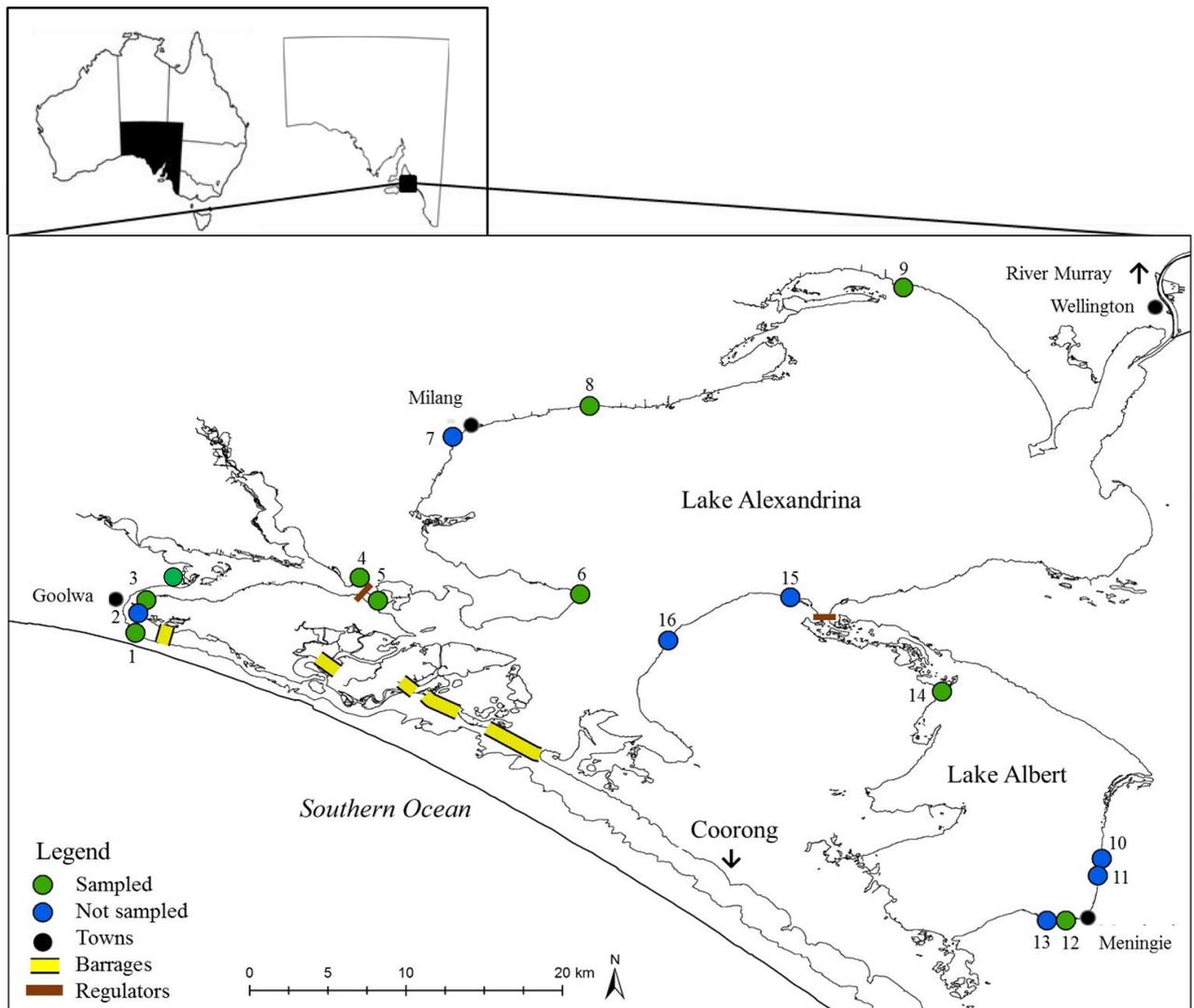


Fig. 1. Map showing the sixteen lakeshore vegetation monitoring sites monitored by SARDI (2008-2014) from within Lake Alexandrina, Lake Albert and the Goolwa Channel (south-eastern Australia) used to develop predictive models. All vegetation sites shown were used in the development of models, the selection of sites sampled during field testing of models shown in green, sites not sampled shown in blue. Major influences of hydrological disconnection include the barrages (permanent) and temporary regulators in operation during focal time period (2008-2014).

The Lower Lakes system is located above the Murray Mouth and the Coorong estuary, at the terminal end of the Murray-Darling Basin. The delineation between the freshwater Lower Lakes and the estuarine and saline Coorong is artificially maintained by a series of barrages constructed along the southern margins of Lake Alexandrina and the Goolwa Channel (Fig. 1).

In the Lower Lakes system, the three focal water bodies differ in hydrology, geomorphology and management. Lake Alexandrina is the largest (662 km²) and deepest (2.8 m average depth) and receives inflow directly from the River Murray to the north of the lake (Fig. 1). It also receives inflow from the Eastern Mount Lofty Ranges via the Angas and Bremer Rivers near Milang (Fig. 1) and can receive input from the Goolwa Channel. To the east, the shallower (1.7 m average depth) and smaller (177 km²) Lake Albert is connected to Lake Alexandrina by a narrow (200-300 m) channel (named the Narrows). The Goolwa Channel is a narrow (600-900 m) western extension of Lake Alexandrina and the junction of the Finnis River and Currency Creek tributaries, to the south the Goolwa channel is separated from the estuarine Coorong lagoon by the Goolwa Barrage (Fig. 1)

The focal time period for my study (2008-2014) encompassed the final years of the decade-long Millennium Drought in the Murray-Darling Basin which resulted in large-scale changes in water levels, conductivities, turbidity and water chemistry within the Lower Lakes system (Mosley et al. 2012). The focal time period also includes drought-breaking flooding that occurred in 2010 (Mosley et al. 2012). During the Millennium Drought, record low lake levels exposed acid sulphate soils along the lake margins of the three water bodies of the Lower Lakes system. In response, lake level regulators were constructed disconnecting the Goolwa Channel (Clayton Regulator, constructed in 2009) and Lake Albert (Narrung Bund, constructed in 2008) from Lake Alexandrina to enable the water level in each section to be managed independently and minimise the impact of acidification. The water bodies were later reconnected as the Lake Alexandrina rose with high flow levels in 2010 (Mosley et al. 2012).

Vegetation monitoring data

The South Australian Research and Development Institute (SARDI) monitor macrophyte species abundance at 16 lakeshore sites within the Lower Lakes. For my study, vegetation data were available from spring 2008 to autumn 2013, covering ten sampling periods. These biannual vegetation assessments re-survey the same sites at set elevations at each sampling period, providing species cover abundance scores for each elevation. The monitoring program includes 106 species and results have shown that submergent vegetation has not returned in comparable abundances and diversity since the Millennium Drought (Frahn et al. 2013). Through consultation with the SARDI Plant Ecology Sub-program Leader (pers. comm. J. Nicol, 2014), two species were selected for initial modelling, *Myriophyllum salsugineum* and *Vallisneria australis*, as being representative of the submerged vegetation assemblage of the region. They were selected as the target of modelling so as to identify the factor or factors limiting their recovery within the system which was of interest to the management agency responsible for biodiversity in the region (the South Australian Department of Environment and Natural Resources; DEWNR).

Telemetered environmental data

Vegetation assessment sites were matched with corresponding available telemetered environmental sites. Environmental data were provided by DEWNR from 26 telemetered real-time water monitoring stations within the Lower Lakes system. These moored telemetry stations vary with respect to the variables that are recorded and duration of records available. In total, data were available for up to six variables, recorded from the telemetry stations within the Lower Lakes between January 2006 and March 2014. Of these, three variables were sufficiently spatially and temporally complete for use in modelling: Electrical conductivity (EC, $\mu\text{S cm}^{-1}$ @ 25 °C), water temperature (°C) and lake level (m above the Australian Height

Datum [AHD], which approximates mean sea level) (Appendix 1). These three variables were recorded across the focal time period at eight of the 26 telemetry stations throughout the Lower Lakes. Six of these eight stations had recorded all three variables whilst two of the eight did not record lake level and so lake level was aliased from the nearest lake level recorder, taking into account any potential hydrological disconnection when deciding on pairs (Fig. 1). The six complete stations and two stations with aliased lake level provided eight telemetered sites covering the focal period. These were then matched to 16 vegetation sites by proximity, again taking into account any hydrological disconnection that may exist within the water bodies (Fig. 2; Table. 1).

Table 1. Paired telemetry sites matched vegetation sites from within the Lower Lakes used to model habitat characteristics for two key macrophytes, *Myriophyllum salsugenum* and *Vallisneria australis*

Site number	Telemetric site name	Vegetation site number	Vegetation monitoring site names
T1	b20/23GC	1,2,3	Goolwa South, Hindmarsh Island Bridge 1 and Hindmarsh Island Bridge 2
T2	Beacon 65	4	Clayton Bay
T3	b78/Point McLeay	5	Clayton Upstream of Regulator
T4	Beacon 97	6,15,16	Point Sturt & Narrung, Terrenge
T5	Milang Jetty	7,8	Milang & Bremer Mouth
T6	Near Mulgundawa	9	Lake Reserve Road
T7	Near Waltowa	10,11,14	Browns Beach 1, Browns Beach 2 and Nurra Nurra
T8	Warringee Point	12,13	Warrenge 1 and Warrenge 2

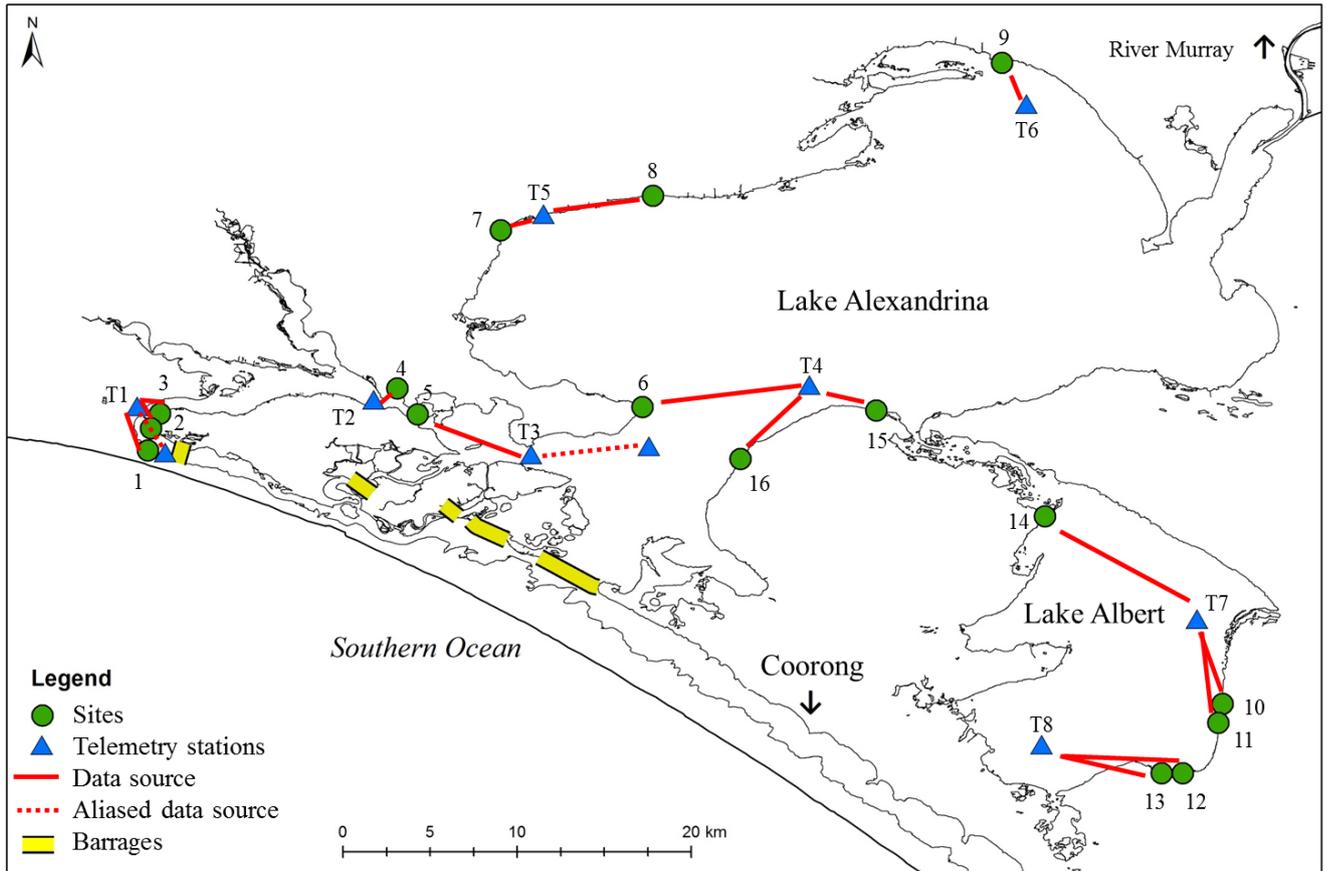


Fig. 2. Map of the Lower Lakes, showing telemetered sites (blue triangles) matched with lakeshore vegetation monitoring sites (green circles). Connections between the telemetered sites and the lakeshore vegetation monitoring sites shown as solid red lines. The aliasing of lake level data from nearby lake level recorder used in the absence of lake level recording at the telemetered site to allowing for complete records is indicated by dashed red lines.

The archived data from these eight sites were initially checked against site status codes provided by DEWNR. Status codes provided dates of faults with either unknown or known causes that resulted in values outside of expected ranges or errors with logging of data. Site data were compared among all eight sites for each recorded variable of focus (EC, water temperature and lake level) and data listed as containing errors were excluded. Daily averages for each variable were plotted against their date of recording. Deviation from trends were observed and compared to the recent history and management of the region. For the Goolwa Channel and Lake Albert, the management interventions of the construction of the Clayton Regulator and Narrung Bund explained differences from trend in lake levels and conductivities observed during this time period and these data were included in the modelling. Seasonal

means, maxima, minima and ranges were calculated for each variable from each telemetered site (summer, autumn, winter and spring). Seasons were only included when they had a minimum of 60 records to minimise bias due to unverified records or faults in data recording. These eight telemetered sites were found to have sufficient data to calculate seasonal statistics across the focal time period.

Developing preliminary habitat envelope models

Non-parametric Multiplicative Regression (NPMR) was undertaken using HyperNiche (ver. 1.0, McCune, 2006) to model the interactions between the response variables of species occurrence for each of the two focal species and the environmental predictor variables of EC, water temperature and lake level, from the eight paired telemetry stations (Fig. 2). A Gaussian weighting function with a local mean estimator was used, because a Gaussian distribution assumes a smooth and continuous response to predictor variables (McCune 2006) which matched the expected response of submerged macrophytes within the system (Gehrig and Nicol 2010) and had been used for a similar study of a submergent species within the region (Rogers and Paton 2009). Models were first developed using environmental data from a selection of 13 of the available 16 vegetation sites, corresponding with the most complete telemetered records, allowing for the inclusion of up to two lag years and eight lag seasons as predictor variables.

An additional series of four separate models were developed with differing lengths of record and numbers of sites to encompass all available data. This series of models were constructed including up to all 16 sites, however was limited to the inclusion of one lag season (the season previous), with lag years excluded. The most spatially-inclusive model of this series contained all 16 available sites covering eight seasons (spring 2010- spring 2012) while the most temporally inclusive model included 13 sites and 18 seasons (autumn 09 – spring 2013) (Appendix 2).

Model evaluation was undertaken by determining model fit to the response variables, defined by cross-validated R-squared values (xR^2). Unlike traditional R-squared values, xR^2 values are calculated using a leave-one-out-cross-validated approach, whereby the data point used in the estimate of the response from that point is left out. This consequently means that the residual sum of squares can exceed the total sum of squares resulting in a negative xR^2 value for weak models and is undertaken to reduce over fitting (McCune 2006). The predictors used within each of the best-fitting models were evaluated using sensitivity and tolerance analysis. Sensitivity analysis undertaken during the model evaluation stage used small nudges ($\pm 5\%$ of predictor value) to the value against observed changes in the response variable. Evaluating the relative importance of each predictor, higher sensitivities indicate a higher influence within the model (McCune 2006). The tolerance of continuous predictors used in the models is inversely related to the importance of a variable, with variables that have high tolerance using a larger neighbourhood of data points to make a prediction, suggesting a wider tolerance to that predictor variable (McCune 2006). The model's ability to explain a significant proportion of the variation within the response variables was tested using Monte Carlo random runs.

Likelihood of occurrence

To form predictions of occurrence for the two target species, four categories were calculated describing the likelihood of occurrence based on the best models for each species (high, moderate, low and very low). The models were used to generate an estimate of expected abundance per site and per time period (season). These predictions of abundances were averaged for the last available year (2013) to be applied to the sites selected for field surveys in 2014. The predicted annual averages were divided into the four categories using the quartiles of the estimates of predicted abundance. Due to a small number of observations, categories were compiled into two broader categories for statistical testing using Fishers Exact test. A

Fishers Exact test allowed a test of the relationship between predictions and observations, using likely present (high and moderate) and likely absent (low and very low) as the potential outcomes and the recorded observations from field survey in June 2014 as the observed outcomes.

Field validation of model predictions

Field surveys were undertaken in the Lower Lakes to test the quantitative predications of the preliminary models, comparing submerged macrophyte coverage with predictions of occurrence based on point-in-time environmental conditions. Field surveys were undertaken in July 2014 at nine existing vegetation monitoring sites used in modelling (as described below; Fig. 3). Of these nine sites, six sites were selected because *M. salsugineum* or *V. australis* had been recorded at those sites over the monitoring period. The remaining three out of a possible 10 sites, where the target species were less likely to be present, were selected at random. Two of the nine sites, Clayton Upstream and Bremer Mouth, were selected for their recorded presence of *M. salsugineum* and *V. australis* during the monitoring program. They had not been included in the most complete modelled datasets due to gaps in the paired telemetered dataset not allowing for the inclusion of lagged season and years. So, these two sites were not categorised by likelihood of occurrence and did not provide a test for the predictive models. They did, however, allow for the variation of lakeshore sites to be assessed, although not formally analysed or used in the refined models.

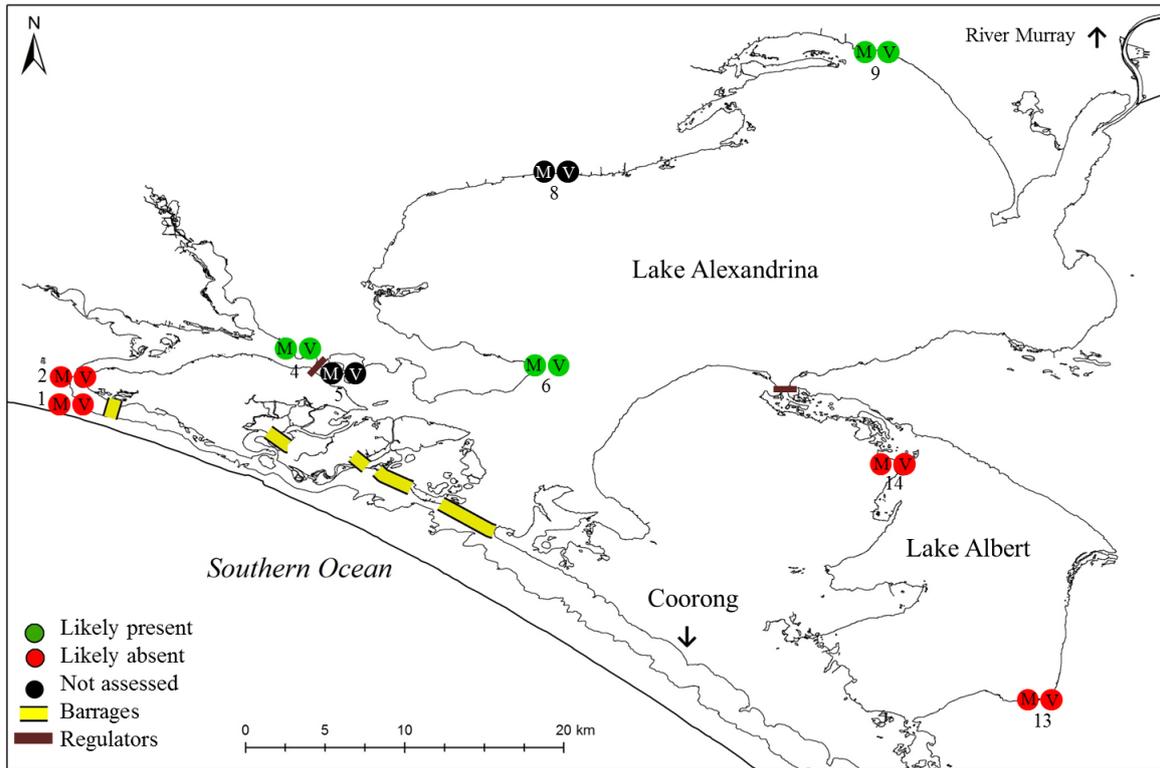


Fig. 3. Map showing predicted likelihood of occurrence categories for the nine lakeshore vegetation monitoring sites resampled in July 2014 testing the accuracy of the best developed models. Species depicted as circles *Myriophyllum salsaugineum* (M) and *Vallisneria australis* (V) with categories likely present (green), likely absent (red) and not assessed (black)

Vegetation assessment

In the field, detailed habitat assessments were conducted at each site to test the influence of a wider range of site characteristics than had been surveyed by SARDI, which had focused predominantly on vegetation. Sites were located using GPS and vegetation coverage assessments were conducted in accordance with the methods described in Frahn et al. (2013), for consistency with the monitoring data used in modelling. Verification of consistency with the SARDI vegetation assessment methods and assistance with identification of species was provided by the SARDI Plant Ecology Subprogram Leader, Dr Jason Nicol on the first day of sampling. At each site, vegetation assessments involved sampling three replicate transects running perpendicular to the shoreline separated by 1-m intervals. At each transect, five quadrats (1 x 3 m) were established at set elevations of +0.8, +0.6, +0.4, +0.2, and 0.0 m AHD (Fig. 4), with elevations kept consistent across sites.

Real-time telemetered data from the closest lake level station were accessed and, using lake level as a reference point, the elevations were established during the field survey for each site. A Leica Geo-systems NA720 automatic level and surveyor's staff were used to determine elevations above the water level, whilst depth of water was used to determine the elevations below that level. Macrophyte species were identified in the field (Sainty and Jacobs 2003) or photographed for later identification, whilst percent coverage was estimated for species present within each quadrat. The logistical constraints of water depth at the lowest elevation (-0.5 m AHD) prevented vegetation and habitat assessments and this elevation was excluded from analysis.

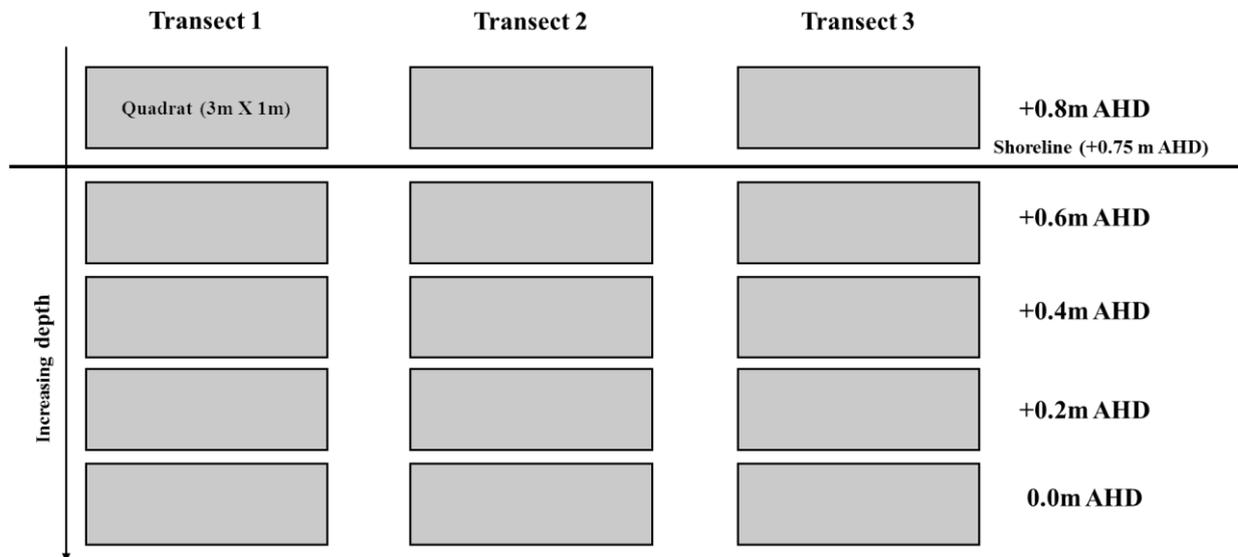


Fig. 4. Vegetation sampling protocol for lakeshore sites undertaken by SARDI and repeated for this study. The plan view shows the placements of quadrats relative to the shoreline. The shoreline is shown at 0.75m AHD at the current (2014) lake level target.

Site characteristics

Site characteristics were recorded at the time of vegetation assessments to be used as additional predictor variables in the secondary modelling. Fourteen additional variables were selected for their potential influence on macrophytes assemblages (Table 2). Water quality measurements were taken from mid-water depth (10-40 cm depth), standing at the shore line with aid of a sampling pole, with replicates at each of the three vegetation transects (Table 2). All measurements were taken prior to entering the water to avoid disturbing the water column. Dissolved oxygen, EC, pH and temperature were all measured using an YSI Pro Plus Multi-Parameter Water Quality Meter calibrated before each field day. Water clarity was measured using a secchi disc, measuring the depth at which the quadrants on the disc were no longer visible.

A rapid VISOCOLOUR® ECO Photometer nutrient test kit was used to measure concentrations of nitrate (NO_3^-), ammonium (NH_4^+), nitrite (NO_2^-) and phosphate (PO_4^{3-}). For each replicate transect, one 50-ml water sample was taken (a total of three per site) using a sampling pole to avoid disturbance of the water column. Samples were placed in rinsed collection vials before being stored on ice. Samples were stored for a maximum of 10 hours prior to analysis. Upon analysis, samples were homogenised and 10-ml sub-samples were taken and filtered (with a pore size of 0.2 μm) to remove particulates before for each test.

The slope of the shoreline was calculated based on measurements taken between the distances between each sampled elevation using a surveyor's tape held parallel to the water's surface. Exposure to wind was estimated using a clinometer, adding the measured angles of inclination of the horizon taken at each of eight compass points. Three measurements of sediment pH, sediment temperature and redox were measured from each site, one quadrat per replicate transect that was selected at random. Sediment pH was measured using an Inoculo soil pH kit. Sediment redox and temperature were measured with a HANNAH HI98120 ORP/Temperature

meter submersed in the sediment for two minutes, allowing the reading to stabilise before the measurement was recorded. Sediment particle size estimates were undertaken by visual and physical examination of surface sediments from each quadrat.

Table 2. Quantitative site characteristics recorded during field surveys from nine sites within the Lower Lakes in June 2014, indicating the unit for each variable measured, the level of replication (transect, site, quadrat, elevation, core/quadrat), the number of observations taken and inclusion as predictor variables in development of refined models (yes/no)

Water quality	Units	Replicate level	Replicates per site	Total replicates	Included in modelling
Temperature	°C	Transect	3	27	Yes
Dissolved O ₂	%	Transect	3	27	No
pH	-	Transect	3	27	Yes
EC @ 25°C	µS cm ⁻¹	Transect	3	27	Yes
Water clarity (secchi depth)	cm	Transect	3	27	Yes
Nutrients					
Total Phosphorous	mg L ⁻¹	Site	1	9	No
Nitrate	mg L ⁻¹	Site	1	9	No
Nitrite	mg L ⁻¹	Site	1	9	No
Ammonia	mg L ⁻¹	Site	1	9	No
Physical characteristics					
Water height above quadrat	cm	Quadrat	15	135	Yes
Slope of bank (distance between elevations)	m	Transect	3	27	Yes
Wind exposure (angle of inclination of horizon)	degrees	Site	1	9	Yes
Sediment characteristics					
Oxidation reduction potential (redox)	mV	Transect	3	27	Yes
Particle size estimate	%	Elevation	5	45	Yes

Statistical analyses

Prior to secondary modelling, a statistical analysis of the field-assessed variables was undertaken to complement NPMR modelling. Multivariate analyses were performed using PRIMER v. 6.0 (Clarke et al. 2006) with the PERMANOVA + add on (Anderson 2007). Non-metric multidimensional scaling (MDS) plots allowed for differences and variability among sites and likelihood of occurrence categories (likely present and likely absent) to be visualised. This was undertaken for each of the site characteristics, water quality, sediment characteristics, macrophyte assemblages and macrophyte species coverage, with permutation-based multivariate analysis of variance (PERMANOVA) used to test these differences. A two-factor PERMANOVA design was used with sites (random factor) nested within likelihood of occurrence categories (fixed factor). Environmental data were normalised to account for the differing scales of measurement and then a Euclidian distance similarity matrix was constructed before a MDS plot was used to visualise patterns. Coverage data underwent no pre-treatment and a Bray-Curtis resemblance matrix with dummy variable (of 1) was constructed, with the dummy variables added to account for the influence of zero abundance values within the dataset.

Refined models

To refine the models, the same telemetered and vegetation monitoring datasets (i.e. including lag seasons and years) were used, with the addition of measured site characteristics from the field surveys. The site characteristics that were included as potential predictor variables in the refined models excluded dissolved oxygen and soil temperature (Table 2), as changes in these variables were likely to be influenced by the presence of macrophytes (Carpenter & Lodge 1986) as opposed to those variables influencing macrophyte occurrence. The eleven site characteristics included were water pH, measured EC, water clarity, average water depth, wind

exposure, bank slope, sediment pH, sediment redox and the percentage contribution of sand, gravel, cobble and boulders to the sediment (Table 2).

These additional eleven predictor variables were applied to the seven resampled sites (from the best models for both species) as site averages expressed over all time periods. The models again were developed using HyperNiche, using a Gaussian weighting function with a local mean estimator. The models developed were then evaluated based on their fits to model dataset defined by the xR^2 value and best fitting models were selected, as described for the preliminary model development above. Sensitivity and tolerance analyses were again undertaken to investigate the relative importance of each selected predictor variable within these best selected models. Validation of the predictions of these models was not undertaken as was undertaken for the preliminary models, as these models were derived from observation from the field data and a new round of sampling would be required to quantify the accuracy of predictions, which was outside the scope of this project.

Results

Preliminary habitat envelope model

All sixteen vegetation sites were included in modelling, using the eight telemetered sites to identify habitat envelopes for the two target vegetation species. The best models for *M. salsugineum* and *V. australis* were developed from models including 13 of these sites and lagged seasons and up to two lagged years. These models showed a moderate ability to represent vegetation distributions with xR^2 values ranging from 0.30 to 0.66 (Table 3). The best model for *M. salsugineum* ($xR^2 = 0.66$) used four predictor variables: Average EC for the season sampled; Range of EC for the previous season, Average lake level for two seasons previous; and Range of EC for three seasons previous (Table 3). For *V. australis* ($xR^2 = 0.30$), the best model included Average EC for the season sampled, Range of EC for the season sampled, Range of lake level for the season sampled and Average lake level for two years previous (Table 3). Based on Monte Carlo random runs, the model for *M. salsugineum* explained a significant proportion of the variation recorded in *M. salsugineum* abundance ($P(MC) = 0.047$), as did the model for *V. australis* ($P(MC) = 0.047$).

Table 3. The best preliminary models derived from 13 vegetation sites that were matched with the most temporally-complete telemetered records allowing for the inclusion of lagged seasons (e.g. -1 season) and the inclusion of lagged years (e.g. -2 years). xR^2 describes the model fit and $p(MC)$ denoting the result of Monte Carlo tests ($\alpha = 0.05$). Predictor variables included in best models are each listed in order of the sensitivity, representing the influence of each predictor within the modelled data set. The tolerance shown for each predictor included in the best models for each species shows the impact of each predictor on the response variable.

Model	Predictor	Sensitivity	Tolerance
<i>Myriophyllum</i>	Range of EC, - 1 season	0.759	633.750
<i>salsugineum</i>	Average Lake level, -2 season	0.160	0.061
$xR^2=0.656$	Range of EC, - 3 season	0.092	2108.700
$P(MC)=0.047$	Average EC, current	0.079	1637.045
<i>Vallisneria</i>	Range of EC, current	0.169	1449.400
<i>australis</i>	Range in Lake level, current	0.138	0.077
$xR^2=0.302$	Average lake level, - 2 years	0.111	0.229
$P(MC)=0.047$	Average EC, current	0.043	777.532

When a series of models were developed using sub-sets of the available sites and years to maximise the data included (Appendix 2), all had lower correlations than those described for the overall model (i.e. $xR^2 < 0.2$) but the predictor variables of average EC and average lake level that were common among these models were similar to the predictors identified from the best single models selected for *M. salsugineum* and *V. australis*, as described above.

Sensitivity analysis for the best model for *M. salsugineum* showed that the Range of EC for one season previous (sensitivity = 0.759) was the most important predictor within the model (Table 3). Higher sensitivities indicate that larger changes in the response variable as a result of changes in the predictor variable. Tolerance values are not directly comparable among the predictor variables like sensitivity analysis, as data were not normalised, but they represent the species range of tolerance to predictor variable with higher tolerances equating to wider species tolerance to variables. For *V. australis*, the most important predictor for describing abundance

was Range of EC of the current season (sensitivity = 0.169), as defined by sensitivity, with this predictor variable also having the highest tolerance value within the model.

Models predicting likelihood of occurrence

Three of the sixteen modelled sites were not categorised by these best models, derived from the 13 sites with the most temporally complete telemetered records. Likelihood of occurrence, based on the best models for *M. salsugineum* and *V. australis*, predicted the same four categories for each of the thirteen sites for the two species. However, the predicted abundances for each site from the best models varied between the two species. *M. salsugineum* was predicted in the highest abundance at Clayton Bay (0.30 % coverage averaged across site) with the highest abundance of *V. australis* predicted at Lake Reserve Road (0.16 % coverage averaged across site). Quartiles of predicted abundances were used to derive the categories resulting in two sites that were predicted to have high abundances for both species, three moderate, two low and six where abundance was predicted to be very low or absent (Table 4).

Table 4. Predicted abundances used to categorise likelihood of occurrence for *Myriophyllum salsugineum* and *Vallisneria australis* among the 16 lakeshore vegetation monitoring sites derived by the best preliminary models. Likelihood of occurrences were derived from quartiles of predicted abundances predicted the same likelihood categories (High, Moderate, Low, Very low) for both species at all sites. Sites not included in the best preliminary models (i.e. 13-site model with lagged seasons and lagged years) were unable to be categorised (Bremer Mouth, Clayton upstream and Milang). *denotes sites resampled in July 2014.

Likelihood of occurrence	Site number	Site	Predicted abundance % cover of <i>M. salsugineum</i>	Predicted abundance % cover of <i>V. australis</i>
High	4	*Clayton Bay	0.299	0.0192
	9	*Lake Reserve Road	0.051	0.1612
Moderate	15	Narrung	0.047	0.0045
	6	*Point Sturt	0.041	0.0045
	16	Terrenge	0.047	0.0045
Low	13	Warringie 1	0.013	0.0004
	12	*Warringie 2	0.013	0.0004
Very low	14	*Nurra Nurra	0.010	0.0003
	10	Brown Beach 1	0.010	0.0003
	11	Brown Beach 1	0.010	0.0003
	1	*Goolwa South	0.000	0.0000
	3	Hindmarsh Island Bridge 1	0.000	0.0000
	2	*Hindmarsh Island Bridge 2	0.000	0.0000
Not categorised	8	*Bremer Mouth	No prediction	No prediction
	5	*Clayton upstream	No prediction	No prediction
	7	Milang	No prediction	No prediction

Myriophyllum salsugineum and *Vallisneria australis* abundance

From the nine resampled sites the target species, *M. salsugineum* and *V. australis* were found within Lake Alexandrina and the Goolwa Channel (Fig. 5). No submergent macrophyte species were recorded at sites within Lake Albert (Nurra Nurra & Warrengie). The four sites at which *M. salsugineum* were recorded at were Clayton Bay (predicted to have a high likelihood of occurrence), Goolwa South (predicted low likelihood), Bremer Mouth (not categorised) and Clayton Upstream (not categorised) (Fig.5). *V. australis* were recorded at three sites: Point Sturt (predicted moderate likelihood); Clayton Upstream (not categorised) and Bremer Mouth (not categorised).

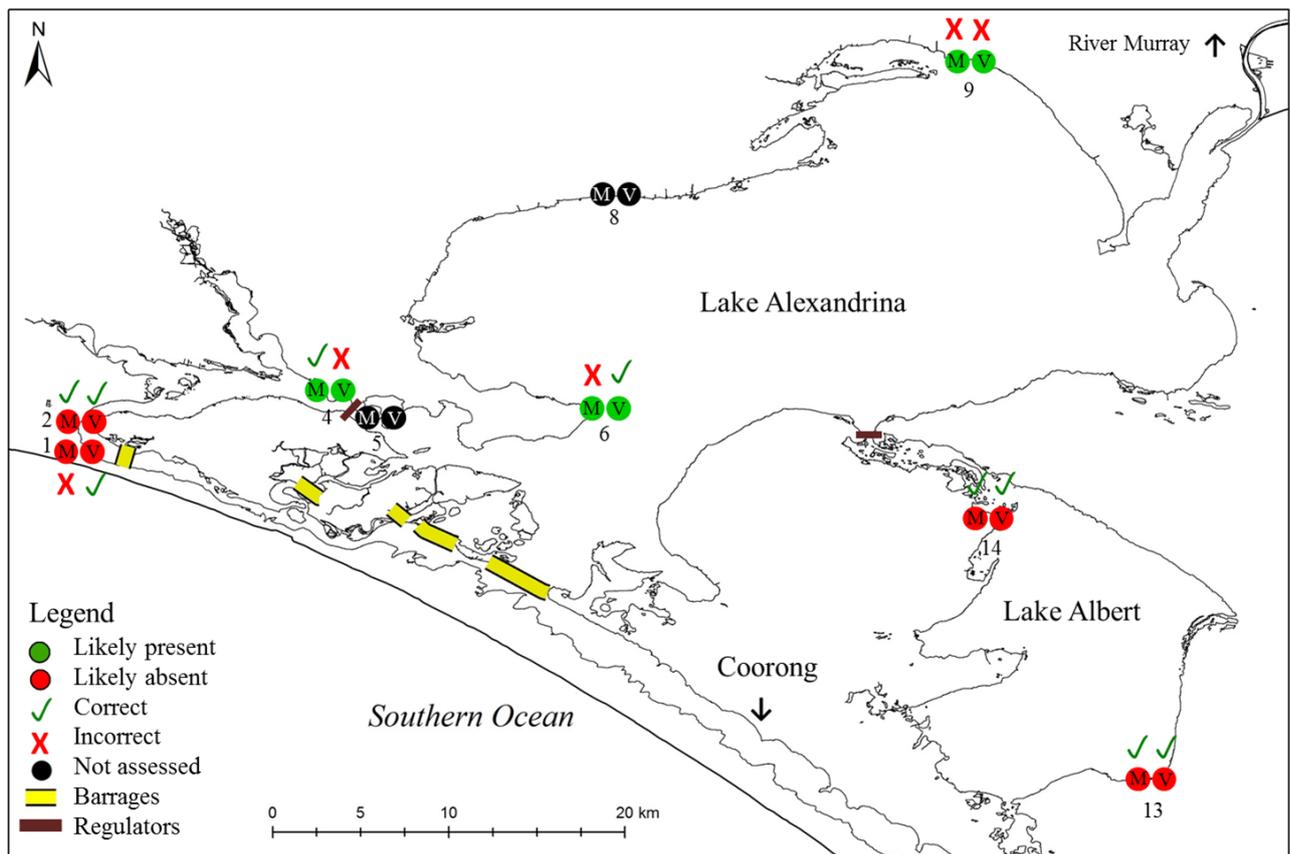


Fig. 5. Map showing predicted likelihood of occurrence categories for the nine lakeshore vegetation monitoring sites that were sampled in July 2014 to test the accuracy of the best developed models. Species are depicted as circles labelled *Myriophyllum salsugineum* (M) and *Vallisneria australis* (V) with likelihood categories shown as likely present (green), likely absent (red) and not assessed (black). The four correct predictions for *Myriophyllum salsugineum* are shown as ticks and the three incorrect predictions are shown as crosses. Site 1 (Goolwa South) was the only site predicted likely absent that was found to have either species present. For *Vallisneria australis*, again the five sites predicted correctly are shown with ticks and the two incorrect predictions are shown as crosses.

The percent coverage of *M. salsugineum* and *V. australis* averaged over the 15 quadrats at these sites ranged between 1.0 and 2.4 % for *M. salsugineum* and 0.4 to 3.3 % for *V. australis*, much higher than the predictions of the models. There was little difference in the elevation and water depth at which these two species were recorded. *M. salsugineum* was recorded at four of the five sampled elevations (+0.8, +0.6, +0.2 and 0.0 m AHD) in water depths up to 76 cm at 0.0 m AHD. The shallowest occurrence was at 0.8 m AHD, at the water's edge (i.e. 5 cm). *V. australis* was recorded at the same range of elevations (+0.8, +0.6, +0.4 m and 0.0 m AHD) with a similar range of water depths, of wetted edge at 0.8m AHD up to 79 cm deep at 0.0 m AHD. Three other submergent macrophyte species, *Potamogeton crispus*, *P. pectinatus* and *Ceratophyllum demersum* were identified during sampling. *P. crispus* was found at Bremer Mouth (not categorised). *C. demersum* was found at four sites, including Clayton Upstream (not categorised), Bremer Mouth (not categorised), Clayton Bay (predicted high likelihood for the two target species) and Hindmarsh Island Bridge 2 (predicted very low likelihood for the two target species), and *P. pectinatus* was found at Point Sturt (predicted moderate likelihood for the two target species).

Testing the preliminary models

The best preliminary model for *M. salsugineum* (Table 5) correctly predicted the occurrence at site which had the highest abundance, Clayton Bay (predicted high likelihood), but was poor at predicting occurrences at the other six categorised sites. In total, *M. salsugineum* was recorded at only one site that was categorised as high likelihood (Clayton Bay) and one that had been categorised as very low likelihood (Goolwa South). *V. australis* was recorded at one site that had been categorised as a moderate likelihood site (Point Sturt) but was absent at all other categorised sites (Table 5).

Table 5. Comparison of the likelihood of occurrence categories (High, Moderate, Low and Very low) and the observed presence or absence of *Myriophyllum salsugineum* and *Vallisneria australis* during field surveys in June 2014.

Likelihood of occurrence	Site number	Site	<i>M. salsugineum</i>	<i>V. australis</i>
High	4	Clayton Bay	Present	Absent
	9	Lake Reserve Road	Absent	Absent
Moderate	6	Point Sturt	Absent	Present
Low	12	Warringie 2	Absent	Absent
Very low	14	Nurra Nurra	Absent	Absent
	1	Goolwa South	Present	Absent
	3	Hindmarsh Island Bridge 2	Absent	Absent

Contingency tables of the likely occurrence categories for both species were tested using a Fishers Exact Test, grouping the high and moderate likelihood categories (likely present) and low and very low categories (likely absent). The ability of the model to accurately predict the likelihood of occurrence (based on the proportion of the predicted present or predicted absence categories that were correct) was not statistically significant for either species (*M. salsugineum*, $P = 1.00$ and *V. australis*, $P = 0.43$).

Vegetation assemblages

Field vegetation assessments identified 34 macrophyte species in total (Appendix 3) comprising of seven functional groups (Frahn et al. 2013). The most frequent and abundant species among sites was *Phragmites australis*, recorded at all sites and covering an average $12 \pm 21\%$ of all of the area sampled (Fig. 6). Emergent species were the most abundant functional group at all sites, covering an average $32 \pm 30\%$ of the sampled area at sites. Terrestrial plants

made up the most diverse functional group, with 8 species recorded covering an average of $3 \pm 6\%$ at sites sampled (Fig. 6).

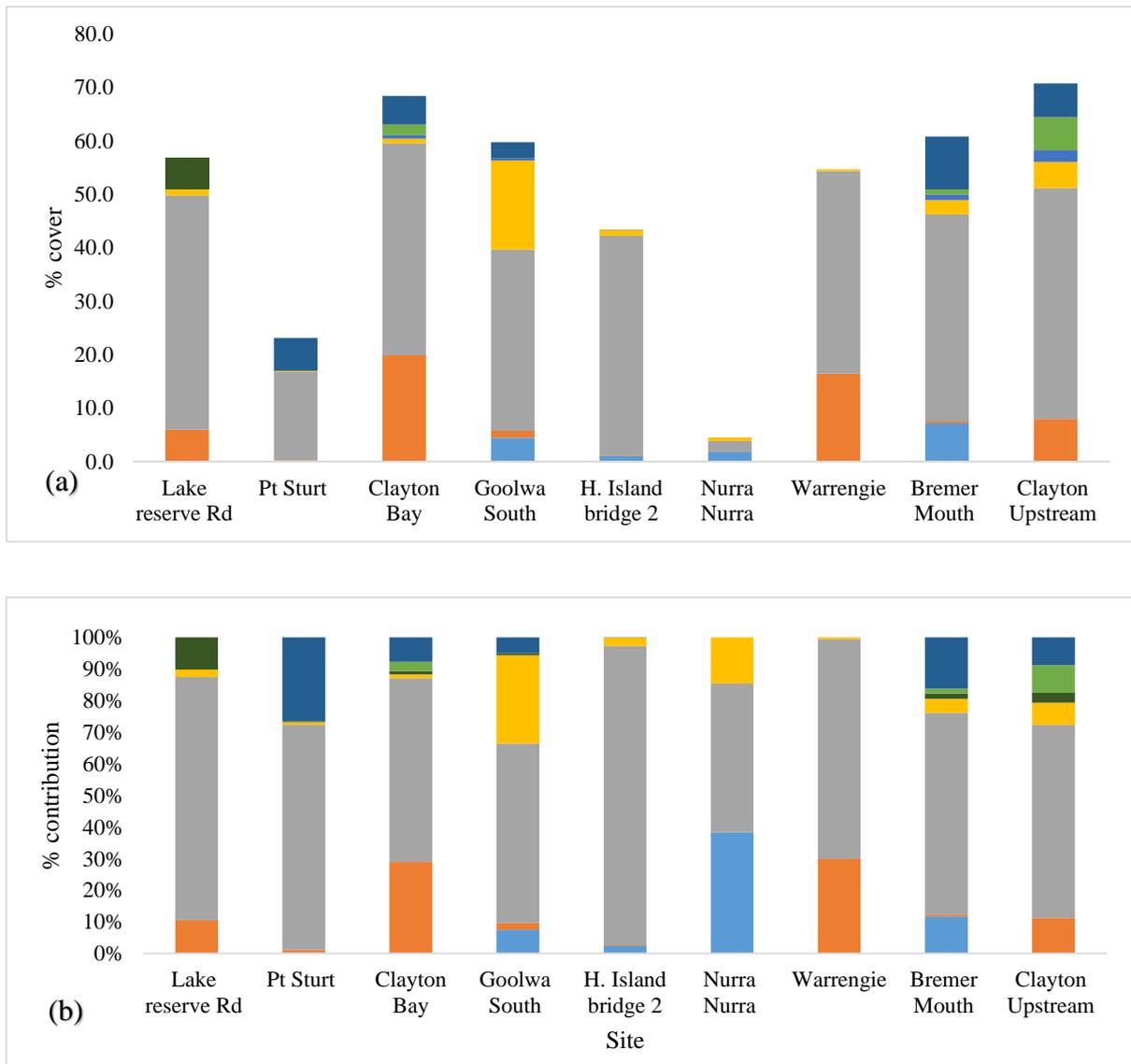


Fig. 6 (a) The variation of average percent coverage of macrophyte functional groups among the nine resampled sites and (b) the percentage contribution of macrophyte functional group coverage at each site observed during field surveys in June 2014.

When considering whether sites were predicted to be likely present or likely absent, vegetation assemblages at the seven resampled categorised sites were not significantly different between the two categories for species percent coverage (pseudo- $F_{1,5} = 0.94$ $P = 0.46$; Table 5) or the seven functional groups (Fig. 6) (pseudo- $F_{1,5} = 0.83$, $P = 0.505$; Appendix 4). In contrast, there were significant differences among sites nested within the likelihood categories for species percent coverage (pseudo- $F_{5,28} = 2.83$, $P = 0.001$; Appendix 4) and functional groups (pseudo- $F_{5,28} = 2.00$, $P = 0.007$; Appendix 4), indicating that there were high levels of variability at small spatial scales that was not explained by the preliminary model predictions.

Water quality and other site characteristics

EC was the most variable water quality parameter recorded, ranging from 858 $\mu\text{s cm}^{-1}$ at Lake Reserve Road (predicted high likelihood of occurrence) to 8866 $\mu\text{s cm}^{-1}$ near the Coorong estuary at Goolwa South (predicted low likelihood), with an average among sites of $2900 \pm 5966 \mu\text{s cm}^{-1}$ (Table 6). Dissolved oxygen and water clarity also had wide ranges, of 10.8 to 103.2 % and 4 to 46 cm, respectively. Water pH ranged between 6.9 and 8.4, in contrast, temperature which was the most consistent variable among sites, with a range of 8.6 to 10.3 °C. Nitrogen and phosphorus, as measured using the test kit, were below detection limits for 23 of the 36 nutrient tests, with total nitrogen recorded as $<2.0 \text{ mg L}^{-1}$ and total phosphorus was above detection limits $>15.0 \text{ mg L}^{-1}$. Given these results, nutrient concentrations were not included in any further analysis.

Table. 6 Site characteristics recorded from field surveys in June 2014 that were then included in the development of refined models. The unit for each variable measured is indicated, with measurements reported as site means. * denotes sites that were not included in the refined models.

Site Name	Units	*Clayton Upstream	Goolwa South	Hindmarsh Island Bridge 2	Nurra Nurra	Warrenegie	Pt Sturt	*Bremer Mouth	Lake Reserve Road	Clayton Bay
<i>Water Quality</i>										
Temperature	°C	8.8	11.7	10.5	9.2	9.6	10.5	9.6	11.9	9.7
pH	-	7.0	7.6	7.5	8.3	7.6	8.2	7.1	8.2	7.3
Electric Conductivity	µS cm ⁻¹	1239.3	8841.7	4714.7	2575.3	3820	1207.7	1748.7	858.7	1470.7
Water clarity	cm	27.7	32.3	44.7	5.3	9.3	7.7	34.3	11.7	25
<i>Physical Characteristics</i>										
Water depth	cm	36.3	38.7	32.0	38.0	35.0	30.0	26.0	32.0	30.0
Slope of bank	m	43.6	17.0	34.6	39.0	44.8	33.6	21.4	3.1	38.5
Wind exposure	degrees	48	73	22	19	57	46	29	18	71
<i>Sediment Characteristics</i>										
Soil redox	mV	30.7	-37.0	16.7	44.3	-83.7	120.3	-85.3	-90.7	1.7
Sediment grain size	% contribution									
Clay/silt		97.9	81.4	52.1	8.7	74.2	2.7	53.4	97.9	97.9
Sand		0.5	17.3	34.3	89.8	24.3	82.0	41.3	0.5	0.5
Gravel		0.5	0.4	2.4	0.5	0.5	1.6	4.4	0.5	0.5
Cobble		0.5	0.4	10.6	0.5	0.5	12.1	0.5	0.5	0.5
Boulders		0.5	0.4	0.5	0.5	0.5	1.6	0.5	0.5	0.5

Sediments at all sites largely consisted of clay/silt (<0.06 mm) and sand (0.06-2 mm). Gravel (2-64 mm) was predominant at Bremer Mouth, Hindmarsh Island Bridge 2 and Point Sturt. Cobble (65-256 mm) and boulders (>256 mm) were found at Hindmarsh Island Bridge 2 and Pt Sturt. Wind exposure (angle of inclination of the horizon) varied within predicted likelihood occurrence categories, with Lake Reserve Road (predicted high likelihood) and Nurra Nurra (predicted very low likelihood) being the most exposed sites. In contrast, Goolwa South (predicted very low likelihood) and Clayton Bay (predicted high likelihood) were the most sheltered sites. Slope of bank varied among the sites, the steepest sloping site with a 0.170 m gradient being Lake Reserve Road (predicted high likelihood) and the shallowest gradient with 0.007 m at Goolwa South (predicted very low likelihood) (Appendix 5). Soil pH was consistent with water pH, Clayton Bay (pH 7.0) and Clayton upstream (pH 6.5) were the most acidic recorded and Nurra Nurra (pH 8.5) and Warrengie 2 (pH 8) the most alkaline. Soil redox varied among sites, with the highest being Point Sturt (120 mV) and the lowest being Lake Reserve Road (-90 mV).

There were no significant differences between the predicted likelihood of occurrence categories of *M. salsugineum* and *V. australis* when examining water quality (pseudo- $F_{1, 5} = 0.86$, $P(\text{MC}) = 0.47$; Appendix 4) or physical site characteristics (pseudo- $F_{1, 5} = 0.75$, $P(\text{MC}) = 0.589$; Appendix 4). However, similar to the tests of vegetation assemblages, there were significant differences among sites nested within categories for both water quality (pseudo- $F_{5, 14} = 81.49$, $P = 0.03$; Appendix 4) and physical characteristics (pseudo- $F_{5, 28} = 1.6259$, $P = 0.001$; Appendix 4). Again, this suggests that the variation among recorded site variables were not described by the categories of likelihood predicted by the best preliminary vegetation models.

Refined models

Following the field validation of the original models, refined models for both *M. salsugineum* and *V. australis* were developed. The refined models were developed using the seven categorised sites that were surveyed in the field, the telemetry records used in the development of the previous best preliminary models and water quality and site characteristics from the field survey. The best refined models, again defined by the xR^2 value, both used three predictor variables and had increased fits to the previous best preliminary models. For *M. salsugineum*, the refined model had an excellent fit ($xR^2 = 0.936$), as did the model for *V. australis* ($xR^2 = 0.9743$) and both were found to describe a significant proportion of the variation in the modelled data (*M. salsugineum*, $P = 0.046$ and *V. australis*, $P = 0.046$). Akin to the preliminary models, the refined models did not vary in predictor variables used between the two target vegetation species, however the relative importance of each did vary within the model, as did the period of influence of the predictor. For *M. salsugineum*, the most important variable (again defined by sensitivity) was Range in EC for one previous season (sensitivity = 0.20), followed by Range in water temperature for the current season (sensitivity = 0.10) and Water pH from the resampling event in June 2014 (sensitivity = 0.02). The most influential predictor of *V. australis* abundance was Range in water temperature two years previous (sensitivity = 0.08), with Water pH having similar influence within the model (sensitivity = 0.07) and finally, Range in EC for the current season (sensitivity = 0.02).

Table 7. The best refined models derived from 13 vegetation sites that were matched with the most temporally-complete telemetered records, allowing for the inclusion of lagged seasons (e.g. -1 season) and the inclusion of lagged years (e.g. -2 years). xR^2 describes the model fit, $p(\text{MC})$ denoting the result of Monte Carlo tests ($\alpha = 0.05$). Predictor variables included in best models are listed in order of the sensitivity of each, representing the influence of each predictor within the modelled data set. The tolerance shown for each predictor included in the best model for each species, showing the impact of each predictor on the response variable.

Model	Predictor	Sensitivity	Tolerance
<i>Myriophyllum salsugineum</i> $xR^2=0.956$ $P(\text{MC}) = 0.046$	Range in EC, -1 season	0.199	2112.500
	Range WT	0.099	1.396
	Water pH	0.021	0.124
<i>Vallisneria australis</i> $xR^2=0.9743$ $P(\text{MC}) = 0.046$	Range in water temp, -2 years	0.082	0.794
	Water pH	0.066	0.249
	Range in EC	0.018	9058.750

Discussion

The current state of reduced diversity and coverage of submergent macrophytes within the Lower Lakes represents a loss of complex and crucial littoral habitat for birds, macroinvertebrates, small-bodied and larval fish (Ning et al. 2013; Paton and Rogers 2009; Wedderburn et al. 2012). Thus, there is a need to identify the factors that are limiting the recovery of submergent macrophytes within the Lower Lakes post-drought (Frahm et al. 2013), so as to inform the future recovery of this region, but also other large lake ecosystems that may be affected by drought around the world. This study was able to identify and quantify the drivers of occurrence for two key submergent species using a non-parametric multiplicative regression (NPMR) modelling technique (McCune 2006). The preliminary individual models developed for each of the target species were then field-tested and refined to include the site-specific variables measured during the field surveys. This project was able to make a significant contribution to the management capability within the Lower Lakes system by quantifying a strong relationship between conductivity, temperature and pH and the occurrence of two key macrophyte species. This study has therefore provided the managers of the Lower Lakes system with a tool enabling them to predict the response of these species under potential future scenarios. Furthermore, this method can now be further applied across a range of taxa within the system and abroad, to enable similar predictive capacity for other key species.

Modelling approach & proof of concept

The NPMR approach was successful in enabling the development of preliminary predictive models for *Myriophyllum salsugineum* and *Vallisneria australis*, using only three telemetered predictor variables: conductivity; water temperature; and lake level. The models for *M. salsugineum* and for *V. australis* both had good modelled fits to the species coverage data sets available (*M. salsugineum* $xR^2 = 0.656$, *V. australis* $xR^2 = 0.330$). The ability to fit models

based on a narrow selection of available predictor variables is likely to be, in part, due to the fact that those environmental variables are known to influence submergent macrophyte abundance, growth and survivorship (Carruthers et al. 1999; Frazer et al. 2006; Roger and Paton 2009). The good fit was also likely to be due to the manner in which these variables were applied within the preliminary modelling, so as to encompass temporal variation. The potential predictor variables included in the preliminary modelling included averages to encompass seasonal trends, ranges to quantify extremes within seasons, and lags to include the potential influence of conditions in previous seasons. All three expressions of the variables were found to be influential predictors within the developed models. A similar impact of seasonal averages, ranges and lagged variables have been found to be influential in previous multiple regression models of species coverage. Greve and Jensen (2004) modelled the occurrence of the marine eel grass *Zostera marina*, and found that temporal delays of up to two years for turbidity and water depth were critical in predicting species coverage. Carruthers et al. (1999) using generalised linear models examined the abundance of an estuarine species *Ruppia megacarpa* in response to recorded conductivities, depth and turbidity, and found that ranges of these variables at a seasonal scale best-described abundance.

NPMR has already been successfully applied within the region, being able to explain the declines in *Ruppia tuberosa* in the Coorong (Roger and Paton 2009) and differential habitat use of two similar small bodied Atherinidae species in River Murray fringing wetlands (Wedderburn et al. 2007). Both these two studies found conductivity as the most influential driver, influencing the decline of *Ruppia tuberosa* (Roger and Paton 2009) and limiting the distribution. Abroad, this approach has been used in a wider context to examine predicted responses of interacting effects, examining localised pollution and predicted climate change scenarios on a lichen species (Binder and Ellis 2008) and across a range of different ecosystems and target species, examining understory vegetation in tropical rain forests (Lindenmayer and

Likens 2011) and macroinvertebrates in response to drawdown events within water storages (Miller and Wooster 2007). This project adds to the list of successful applications of the approach. The value of this modelling method, and its ability to be broadly applied, stems from the way in which NPMR modelling can be used to represent the influence of multiple complex interacting factors in a simple manner, thus describing the important predictors underlying a species occurrence or abundance (McCune 2006).

This research project included field validation of preliminary predictions and the collection of site-specific characteristics to be included as predictors in refined models. Lester et al. (2011) stressed the importance of independent field validation, testing models with new data before they can be used by natural resource managers. This step was shown to be a valuable inclusion in the project, as testing the models and examining the site-specific characteristics identified statistically-significant differences among the sites in terms of the water quality, vegetation assemblages and habitat characteristics at each. However, there were no significant differences among these characteristics within groups of sites for which the occurrence of the two macrophytes was predicted likely present compared with those where they were predicted likely absent. As such, the observed site-to-site differences did not correlate with the predicted likelihood of the macrophyte species, suggesting that the preliminary predictive models had not captured the observed site-to-site variability that may have been influential in driving the occurrence of the target species. Istvánovics et al. (2008) examined the impact of site-to-site variability on the occurrence of mixed submergent vegetation communities including *Myriophyllum* spp. and *Potamogeton* spp, within a large lake in Hungary, finding that the small-scale site characteristics of sediment composition and exposure to wind-driven wave action were the most influential factors limiting distributions within the lake. The inclusion of site-specific variables as model predictors in my study did not point to physical site characteristics from the field surveys being influential, with vegetated sites exhibiting a range

in bank slope, wind exposure and sediment particle sizes. Instead, the predictors in the refined model indicated that these species were influenced by the water pH at these sites. This suggests that small-scale differences in water quality may have been influencing patterns in submerged vegetation assemblages in the Lower Lakes. This is consistent with studies by Roelofs (1983) and Biniet et al. (1999), who both found that pH was influential at a site-to-site scale in determining submergent macrophyte occurrence among small lake bodies. The inclusion of water quality variables in the refined models led to excellent, and improved, model fits compared with the preliminary modelling.

This project provides a proof of concept within the Murray-Darling Basin for modelling the occurrence of key species based on paired telemetered environmental data and biological monitoring data. Telemetered sites, which undertake remote water-quality monitoring, provide valuable data in near real-time. These comprehensive data are then available for a range of applications, such as the development of hydrological models, assessment of management thresholds, early warning for anoxic conditions (i.e. where dissolved oxygen is measured, for example) and flood risk (Glasgow et al. 2004). Such data have been shown useful in providing contextual environmental data for ecological studies within the system (Vilizzi et al. 2014; Frahn et al. 2013) and in other similar systems (Riis and Hawes 2002). Furthermore, the approach of linking the two data sources has already been used within the same region as the Lower Lakes, in the downstream estuarine Coorong, to model the distribution of the key submergent macrophyte, *Ruppia tuberosa*, using a hydrological model that was also developed from, these telemetered records (Paton and Rogers 2009). However, this modelling approach differed in how this data was applied as predictors, directly matching data from telemetered sites to monitoring sites for individual key species. The direct approach of pairing monitored biological data and continuously-recorded water quality data holds great appeal within the Murray-Darling Basin, given the large number of monitoring projects being undertaken within

the Murray-Darling Basin (Murray–Darling Basin Authority 2011). Birds, macroinvertebrates and fish are comprehensively monitored within the system and telemetered stations are located throughout the Basin, meaning that this modelling approach has the potential to be applied to a wide range of key species within the region, adding value to existing datasets by the development of tools for natural resource management and providing predictions for responses of a range of taxa.

Pairing data from telemetered sites & monitoring to enable key species modelling

From the best preliminary models for *M. salsugineum* and *V. australis*, developed solely from the variables provided by telemetered sites, the lakeshore sites used were categorised by likelihood of occurrence of each of the key species. These categories were then used to test the models' accuracy at predicting the occurrence of the target species, by undertaking targeted field surveys at sites that were categorised as likely to have the two species, and at those where the species were unlikely to occur. The predicted likelihood of occurrence categories were found to be accurate at four of the seven categorised sites for the *M. salsugineum* model and were slightly more accurate for *V. australis*, with five of the seven sites correctly predicted. These categories were not found to represent a statistically-significant ability to correctly categorise sites for either species. The inclusion of site-to-site variability, based on variables collected during the field surveys, produced refined models with closer fits to the modelled datasets. These refined models identified water pH as an influential predictor for both species, as well as further highlighting the importance of range of conductivity and range of water temperature during the focal time period (2008-2014).

These refined models had close fits, represented by very high xR^2 values, suggesting the potential for over-fitting of the models. Procedures used in this project attempted to minimise the likelihood of over-fitting by using conservative approaches such as a leave-one-out cross-

validation method of correlation, providing an xR^2 as opposed to the traditional R^2 method (McCune 2006). However, it remains important to further validate the refined models, with future field surveys to ensure that they can be relied upon to provide robust predictions (Elith and Leathwick 2009). Thus, the refined models should now be further tested by including additional modelled sites and validating over multiple time periods to provide a stronger test of the predictive power of the models. Repeating the validation procedure in the same manner as the field surveys undertaken as a part of this project will be important for developing confidence in the predictions arising from the refined models. This would involve re-assessing each site for the likelihood of occurrence based on the refined model, and then re-surveying. When undertaking these tests, care needs to be taken if applying such predictions outside of the bounds of the spatial range of original data set (Elith and Leathwick 2009) Such a validation should be easily undertaken, as both the biological and environmental data sources come from ongoing monitoring projects, so these models will be able to be further developed and refined at little additional cost, increasing the value of the existing monitoring projects.

Influence of ranges to capture intra-seasonal variation

A key finding from this study was the consistent influence that ranges, rather than average values, had throughout all the models produced. These predictor variables were calculated from daily averages and encapsulated the upper and lower extremes of each variable for a given season. The most influential predictor from the preliminary models for both species was the range in conductivity and for the refined models for both species, ranges were again the most important variables in the model. The refined model for *M. salsugineum* continued to show the range in conductivity as the most important variable, while for *V. australis*, the range in water temperature was the most important variable. This suggests that changes in environmental conditions at a seasonal scale may be a factor that is limiting species occurrences within the

system for submerged vegetation species. This finding addressed the primary aim of this study, which was to identify the factors limiting the resurgence of these species post-drought.

Measures such as ranges in environmental variables can often be overlooked in ecological studies, often to their detriment, because the averages that are commonly measured are less likely than extreme events to shape ecosystem structure (Gaines and Denny1993). Ranges encompassing extreme events, in this case at a seasonal scale, are important as organisms can have definitive limits to environmental variables that, if crossed, result in the loss of that organism from the environment, independent of how favourable or not conditions for that variable are post-disturbance (Gaines and Denny1993). Both *M. salsugineum* and *V. australis* are prone to desiccation and have definite observed conductivity tolerances (Gehrig and Nicol 2010; Bailey et al. 2002). So, given that the focal time period encompassed the Millennium Drought, any extreme deleterious events were expected to be important predictors. Furthermore, ranges proved an important inclusion in these models as the maximum and minimum values of a given predictor were often significantly correlated with seasonal averages for that variable and so were excluded from the models to reduce issues with collinearity. There was, however, a trade-off associated with capturing the range of these variables as there was a loss in the directionality in the shift (i.e. it was not possible to tell if conductivity was increasing or decreasing over a season, for example) that may have influenced the observed response within the modelled datasets. Nonetheless, by including ranges, averages and using the known history of the system during the time period to interpret the results, the shifts in directionality are often able to be inferred.

The effect of each of the predictors within the best refined models was examined independently, to assess the likely limits of occurrence for each of the key species. For conductivity, the highest predicted abundance for both species was for seasons with narrow ranges of conductivities, whereby the range in values observed through the season was small.

When the range in conductivity exceeded $12,000 \mu\text{S cm}^{-1}$ at a given site, the model predicted the absence of both species. A shift in conductivity of more than $12,000 \mu\text{S cm}^{-1}$ within a season represents a very large change of conductivity within a freshwater system (Nielson et al. 2003) and has been observed to occur at localised sites within the Lower Lakes system, particularly close to the barrages, with salt water intrusion from Coorong estuary occurring during low-flow events. Such a phenomenon has been observed at the southern end of the Goolwa Channel in the modelled data set, for example. A similar response in submergent macrophyte assemblages to large and rapid changes in conductivity has also been observed in a spring-fed tidally-influenced bay in Florida, USA (Frazer et al. 2006). Kings Bay is inhabited by similar species of freshwater submergent macrophytes, with *Vallisneria americana* and *Myriophyllum spicatum* the predominant species (Frazer et al. 2006). This system is influenced by rapid storm-induced conductivity pulses caused by wind and tidally-driven surges from the coast. The associated increases of conductivity have been recorded to be up to $25,000 \mu\text{S cm}^{-1}$ in the space of a few days, a change that is greater than that observed within the Lower Lakes. Furthermore, the changes in conductivity at Kings Bay persist over short durations of up to a week, compared to the drought and low-flow induced changes in conductivity within the Lower Lakes system that persisted for longer periods. Such short, pulse disturbances were found to reduce biomass and increase mortality of *V. americana* and *M. spicatum* in experimental treatments after a minimum of two days' exposure to conductivities above $25,000 \mu\text{S cm}^{-1}$ (Frazer et al. 2006). Such an acute response in a similar species to the same variable (i.e. conductivity) supports the model predictions generated in this study that the extremes of a variable within a time period of interest was influencing species occurrence (Gaines & Denny 1993).

Consistency of predictors

In this study the most influential telemetered variables from the refined models for *M. salsugineum* and *V. australis* were ranges in conductivity and in water temperature, respectively. The only site-specific predictor variable that was selected for inclusion in the refined models was water pH, despite the inclusion of a long list of site characteristics that were recorded during the field surveys as potential predictors. Interestingly, the three predictors identified in the refined models were consistent between the models for each of the two species. This consistency of predictor variables between the species is another important outcome from this project.

Given this consistency, it is of interest to understand why these environmental variables were important for the two key species included here. Firstly, there are likely to be broad similarities in the requirements of the two species. Both of the species that were selected for inclusion in this project, *M. salsugineum* and *V. australis*, are considered to fall within the same *k*-selected submergent macrophyte group classification used for vegetation within the system (Frahm et al. 2013). This group is defined by the known requirement of permanent water for more than a year to germinate or to reproduce vegetatively described by Brock and Casanova (1997) and was adapted for the lower lakes Gehrig and Nicol (2010). The similarity of the response exhibited by these *k*-selected submergent macrophytes supports the use of this functional group classification when comparing the composition of vegetation types at a coarse scale through time, as is undertaken in the Lower Lakes vegetation condition monitoring program. As a result, this study supports the current monitoring efforts within the Lower Lakes.

The findings of this study also holds promise for the use *M. salsugineum* and *V. australis* as indicators of suitable habitat for other *k*-selected submergent macrophytes within the region. In a North American example, a study in Wisconsin lakes was able to quantify the colonisation risk of the invasive *Myriophyllum spicatum* by the occurrence of native species within the

lakes, because of similarities in the environmental requirements (Buchan and Padilla 2000). This habitat envelope mapping approach, in conjunction with further refinement of the resultant predictive models, could be used to predict the likely areas of colonisation for the submergent macrophytes species that have not yet recovered to pre-drought coverage levels within the lake system, such as the native *Myriophyllum caput-medusae*. Such an approach is further supported by this study that the other *k*-selected submergent species *Potamogeton pectinatus* and *Potamogeton crispus* were observed during field surveys at sites where the target submerged macrophytes were predicted to occur.

Despite the consistency in the variables predicting the occurrence of the submergent macrophytes, there were inconsistencies in the time period of influence for each. Within the best refined models, the most influential variables had time periods of influence that ranged between the current season for *M. salsugineum* and up to two years previous for *V. australis*. This variability of the timing of response was observed in the monitoring dataset, with the post-drought resurgence for *M. salsugineum* recorded as early as spring 2010, whilst *V. australis* was not recorded until the following year in spring 2011. The disparity in the timing of resurgence may relate to seed bank viability post-drought, the different conditions required to germinate for the two species or differences in growth and reproductive output (Nicol and Ward 2010a). Previous mesocosm experiments have suggested that conductivity and temperature affect seed germination for *V. australis* (Salter et al. 2010). Two seed-bank emergence studies from within the Lower Lakes found that the time to germinate for *M. salsugineum* and *V. australis* was influenced by conductivity (Nicol and Ward, 2010a, 2010b). Thus, this study has important implications given the consistency of the predictors between the two species, but the inconsistency of the time period of influence may provide insight into why many species of submergent macrophytes have yet to return in abundance post-drought.

Conductivity & water temperature

The highest recorded tolerance to conductivity recorded within the monitoring dataset, averaged over a season, was 7302 $\mu\text{S cm}^{-1}$ for *M. salsugineum*, with the largest seasonal range for an occurrence of that species recorded as 15,110 $\mu\text{S cm}^{-1}$. These observations fall within the observed tolerances for this species reported in the literature, of up to 15,000 $\mu\text{S cm}^{-1}$ (Gehrig and Nicol 2010). For *V. australis* occurrence, the highest observed seasonal average was markedly lower at 860 $\mu\text{S cm}^{-1}$ with a range of 1068 $\mu\text{S cm}^{-1}$, recorded at the same site (Clayton Bay). As for *M. salsugineum*, these recorded values are well within the reported tolerances of this species in the literature, with *V. australis* reported to suffer a reduction in biomass at 6660 $\mu\text{S cm}^{-1}$ and extensive mortality at 13,320 $\mu\text{S cm}^{-1}$ (Bailey et al. 2002). Conductivity values higher than both known thresholds were found within the dataset, but not where either species occurred. The relatively low maximum conductivity for *V. australis* occurrence, relative to the observed tolerances may be due to impact of interacting stressors that were likely to be found within the Lakes during the drought. These may include desiccation as these lakeshore sites dried as lake levels decreased, increased turbidity, reducing light availability, and the exposure of acid sulphate soils, leading to widespread acidification of sediments in many regions (Mosley et al. 2012). The interaction of conductivity and water regime has been shown to inhibit *V. australis* growth and survivorship (Salter et al. 2008), but the same studies have not been undertaken for *M. salsugineum*, to my knowledge.

Large seasonal ranges in water temperature corresponded with the occurrence of both species. The largest seasonal range of water temperature that corresponded with an occurrence of both species occurred at Clayton Bay, with a range of 12.6 °C over the season. Growth and germination of the similar species *Vallisneria americana* have been shown to be influenced by temperature changes (Kimber et al. 1995). Therefore, responses in growth and

reproductive output may explain why water temperature from two years previous was the most influential predictor within the refined model for *V. australis*. The ability of the plant to produce seed or propagules in previous years can have a strong influence on the persistence of perennial vegetation into the future, as was found by Brock et al. (2003) who examined the role of seeds as a means of persistence and as insurance against adverse conditions such as drought. Similar studies have not been undertaken for *M. salsugineum* to my knowledge, however growth experiments of the invasive *Myriophyllum spicatum* have found a similar growth response to temperature to that of *V. americana* (Barko et al. 1982). Further investigation is needed into this growth response for *M. salsugineum*, as well as to quantify the more complex response of seed production in relation to water temperature for both *M. salsugineum* and *V. australis*.

Water pH

Water pH from the field surveys was inversely related with the abundance of both species, suggesting that the species were more likely to be found at lower pH values. The difference in pH tended to be small, with sites for which both species had been predicted to be likely present had a water pH of 7.2 ± 0.15 compared with the average across all sites of 7.7 ± 1.34 . This inverse relationship is contrary to existing literature that suggests that acidification in freshwater systems limits submerged macrophytes occurrences (Mauricio et al. 1999; Roelofs 1983). Within this study in the Lower Lakes, this result is likely to be influenced by the high coverage of emergent macrophytes recorded at the Clayton Bay and Point Sturt sites sampled, where the pH was lower than at some other sites. This may be representative of local-scale adaptation favouring slightly more acidic environments than elsewhere, which may have developed as a response to the large-scale acidification of lakeshores that occurred during the Millennium Drought (Mosley 2012). Alternatively, it is possible that those two sites had high

concentrations of organic matter in the soil and that the resulting decomposition may have influenced water pH (Carpenter and Lodge 1986). Further investigation into the influence of pH will need to be undertaken, to determine its cause and influence.

Management within the system

Given the relationships identified during this study, relating the occurrence of the two key submerged macrophyte species to changes in conductivity and temperature at a seasonal scale, it should be possible for the management of the Lower Lakes system to incorporate the likely response of these species when considering future actions. For example, DEWNR is currently examining management actions to reduce conductivity within the body of Lake Albert, in response to sustained high conductivities post-drought (DEWNR 2014). The approach that received the greatest public support, and required no infrastructure upgrades or construction, was to cycle water between the two lakes by varying water levels in the larger, connected Lake Alexandrina (DEWNR 2014). Such draw-down events are intended to be undertaken when there is sufficient upstream water stored within the River Murray to influence water levels via the use of environmental flows. The draw-down events are achieved by opening the barrages to lower lake levels by 0.25 m, then subsequently refilling the Lakes via the use of environmental flows, thus filling the shallow Lake Albert with comparatively fresh water. This approach is currently being assessed, with its potential to stimulate ecological processes considered to be an advantage (DEWNR 2014). However, there are uncertainties associated with the approach, including the fact that the ideal time frame for undertaking this action is not known, nor are any effects that this may have on submergent macrophytes within the Lakes. Based on this research, the potential for abrupt changes in conductivity and water temperature would need to be further investigated, and

these results suggest that changes in conductivity should not exceed the values of 12,000 $\mu\text{S cm}^{-1}$ to sustain populations of submergent macrophytes within the Lakes.

An additional management recommendation arising from this study is that pH could be included in the ongoing vegetation monitoring project. Such an inclusion would represent an inexpensive and efficient method of adding value to the data collected by the ongoing monitoring project. This is particularly important, given the influence that pH has as a predictor within the refined models and the need for further investigation of that effect. Finally, the predictor variables from the refined models (range in conductivity and range in water temperature) support the use of telemetered data sources in future modelling work, highlighting the importance of continuing the program, whilst the inclusion of pH in the refined models confirms the need encompass site-to-site variability that may not be expressed by the telemetered data.

For natural resource managers outside of the Lower Lakes region, the research highlights the value of NPMR for representing complex interacting factors influencing species recovery post-drought. This approach will be able to be applied to predict environmental requirements of key taxa and guide the design of environmental flows and other actions in similar systems. The finding of differences in the time period of influence for describing the response of the two species is important in recovering systems, as the perception of success and failure of environmental flows is subject to public scrutiny (Richter 2010). With the predicted delays in response, the benefit of environmental flows to this system may not be immediately apparent and so,

. a model is needed to guide expectations. As a result, this modelling approach gives not only a predictive tool for managers but can also be a communication tool to help explain the value of environmental flows to the general public.

Conclusion

This study provides a proof of concept for a robust approach to model species occurrence, using a combination of telemetered data and biological monitoring long-running datasets. This study focused on submergent macrophytes, given the poor response to post-drought conditions and lack of recovery following the record Millennium Drought in the case-study region. The models developed for the two key submergent macrophyte species identified ranges in conductivity and water temperature along with water pH as the key drivers of occurrence, following validation and model refinement. The refined models will be valuable tools to assist with the management of the system. Such tools, once validated, can be used to identify likely responses of key species to future drought events or management actions. This study suggested that changes in conductivity should not exceed the values of $12,000 \mu\text{S cm}^{-1}$ in order to sustain populations of submergent macrophytes within the Lakes. The inconsistency of the time period of influence may provide insight into why many species of submergent macrophytes have yet to return in abundance post-drought. Furthermore, the models identified likely mechanisms for response by these species, highlighting areas for future research, and add value to existing monitoring datasets. Thus, these models provide a tool for predicting the response of an important littoral habitat for fish, bird and macroinvertebrates and can be used to infer responses of those faunal assemblages within the system to future environmental conditions.

References

- Ahearn, D. S., Sheibley, R. W., and Dahlgren, R. A. (2005). Effects of river regulation on water quality in the lower Mokelumne River, California, *River Research and Applications* **21**, 651–670.
- Anderson, M. J. (2007). 'Primer V6: User Manual - Tutorial.' (Plymouth Marine Laboratory, Plymouth).
- Bailey, P., Boon, P., and Morris, K. (2002). 'Australian Biodiversity - Salt Sensitivity Database' (Land and Water Australia, Canberra)
- Barko, J. W., Hardin, D. G., and Matthews, M. S. (1982). Growth and morphology of submersed freshwater macrophytes in relation to light and temperature, *Canadian Journal of Botany* **60**, 877–887.
- Bice, C. M., Gehrig, S. L., Zampatti, B. P., Nicol, J. M., Wilson, P., Leigh, S. L., and Marsland, K. (2014). Flow-induced alterations to fish assemblages, habitat and fish-habitat associations in a regulated lowland river, *Hydrobiologia* **722**, 205–222.
- Binder, M. D., and Ellis, C. J. (2008). Conservation of the rare British lichen *Vulpicida pinastris*: changing climate, habitat loss and strategies for mitigation, *The Lichenologist* **40**, 63–79.
- Bini, L. M., Thomaz, S. M., Murphy, K. J., and Camargo, A. F. M. (1999). Aquatic macrophyte distribution in relation to water and sediment conditions in the Itaipu Reservoir, Brazil, *Hydrobiologia* **415**, 147–154.
- Blanch, S. J., Ganf, G. G., and Walker, K. F. (1999). Tolerance of riverine plants to flooding and exposure indicated by water regime, *Regulated Rivers: Research and Management* **15**, 43–62.
- Boix, D., García-Berthou, E., Gascón, S., Benejam, L., Tornés, E., Sala, J., Benito, J., Munné, A., Solà, C., and Sabater, S. (2010). Response of community structure to sustained drought in Mediterranean rivers, *Journal of Hydrology* **383**, 135–146.
- Bond, N. R., Lake, P. S., and Arthington, A.H. (2008). The impacts of drought on freshwater ecosystems: an Australian perspective, *Hydrobiologia* **600**, 3–16.
- Brock, M. A., and Casanova, M. T. (1997). Plant life at the edge of wetlands: ecological responses to wetting and drying patterns. In 'Frontiers in Ecology: Building the Links'. (Eds Klomp, N. and Lunt, I.). (Elsevier, London.)
- Buchan, L. A. J., and Padilla, D. K. (2000). Predicting the likelihood of Eurasian watermilfoil presence in lakes, a macrophyte monitoring tool, *Ecological Applications* **10**, 1442–1455.
- Buchanan, C., Moltz, H. L. N., Haywood, H. C., Palmer, J. B., and Griggs, A. N. (2013). A test of The Ecological Limits of Hydrologic Alteration (ELOHA) method for

- determining environmental flows in the Potomac River basin, U.S.A, *Freshwater Biology* **58**, 2632–2647.
- Carpenter, S. R., and Lodge, D. M. (1986). Effects of submersed macrophytes on ecosystem processes, *Aquatic Botany* **26**, 341–370.
- Carruthers, T. J. B., Walker, D. I., and Kendrick, G. A. (1999). Abundance of *Ruppia megacarpa* Mason in a Seasonally Variable Estuary, *Estuarine, Coastal and Shelf Science* **48**, 497–509.
- Clarke, K. R., Gorley, R. (2006). ‘PRIMER v6: User Manual/Tutorial.’ (*PRIMER-E*: Plymouth).
- CSIRO (2008). Water Availability in the Murray-Darling Basin A report from CSIRO to the Australian Government. CSIRO Land and Water, Canberra
- DeBano, S. J., Hamm, P. B., Jensen, A., Rondon, S. I., and Landolt, P. J. (2010). Spatial and temporal dynamics of potato tuberworm (Lepidoptera: Gelechiidae) in the Columbia Basin of the Pacific Northwest, *Environmental Entomology* **39**, 1–14.
- Deegan, B. M., White, S. D., and Ganf, G. G. (2007). The influence of water level fluctuations on the growth of four emergent macrophyte species, *Aquatic Botany* **86**, 309–315.
- Department of Environment Water and Natural Resources (2014). ‘Lake Albert Scoping Study Options Paper’ (Government of South Australia, Adelaide).
- Elith, J., and Leathwick, J. R. (2009). Species distribution models: Ecological explanation and prediction across space and time, *Annual Review of Ecology, Evolution, and Systematics* **40**, 677–697.
- Frahn, K., Gehrig, S., Nicol, J., and Marsland, K. (2013). Lower Lakes Vegetation Condition Monitoring 2012 / 2013. South Australian Research and Development Institute (Aquatic Sciences) No. 707, Adelaide.
- Frazer, T. K., Notestein, S. K., Jacoby, C. A., Littles, C. J., Keller, S. R., and Swett, R. A. (2006). Effects of storm-induced salinity changes on submersed aquatic vegetation in Kings Bay, Florida, *Estuaries and Coasts* **29**, 943–953.
- Gaines, S. D., and Denny, M. W. (1993). The Largest, Smallest, Highest, Lowest, Longest, and Shortest: Extremes in Ecology, *Ecology* **74**, 1677.
- Gehrig, S., and Nicol, J. (2010). Aquatic and Littoral Vegetation of the Murray River Downstream of Lock 1, the Lower Lakes , Murray Estuary and Coorong . A Literature Review. South Australian Research and Development Institute (Aquatic Sciences), No. 482.

- Glasgow, H. B., Burkholder, J. M., Reed, R. E., Lewitus, A. J., and Kleinman, J. E. (2004). Real-time remote monitoring of water quality: a review of current applications, and advancements in sensor, telemetry, and computing technologies, *Journal of Experimental Marine Biology and Ecology* **300**, 409–448.
- Greve, T. M., and Krause-Jensen, D. (2004). Predictive modelling of eelgrass (*Zostera marina*) depth limits, *Marine Biology* **146**, 849–858.
- Grey, D., and Sadoff, C. W. (2007). Sink or Swim? Water security for growth and development, *Water Policy* **9**, 545.
- Grinnell, J. (1917). Field tests of theories concerning distributional control, *American Society of Naturalists* **51**, 115–128.
- Grundel, R., and Pavlovic, N. B. (2007). Response of bird species densities to habitat structure and fire history along a midwestern open-forest gradient, *The Condor* **109**, 734–749.
- Istvánovics, V., Honti, M., Kovács, Á., and Osztóics, A. (2008). Distribution of submerged macrophytes along environmental gradients in large, shallow Lake Balaton (Hungary), *Aquatic Botany* **88**, 317–330.
- Kashaigili, J. J., Kadigi, R. M. J., Lankford, B. A., Mahoo, H. F., and Mashauri, D. A. (2005). Environmental flows allocation in river basins: Exploring allocation challenges and options in the Great Ruaha River catchment in Tanzania, *Physics and Chemistry of the Earth, Parts A/B/C* **30**, 689–697.
- Kefford, B. J., Fields, E. J., Clay, C., and Nuggeoda, D. (2007). Salinity tolerance of riverine microinvertebrates from the southern Murray–Darling Basin, *Marine and Freshwater Research* **58**, 1019.
- Kimber, A., Owens, J. L., and Crumpton, W. G. (1995). Light availability and growth of wildcelery (*Vallisneria americana*) in upper Mississippi River backwaters, *Regulated Rivers: Research and Management* **11**, 167–174.
- King, J. C., (2006). Environmental flows: Striking the balance between development and resource protection. *Ecology and Society* **11**, 2-26.
- Lake, P. S. (2011). 'Drought and Aquatic Ecosystems: Effects and Responses', (J. W. and Sons: United Kingdom.)
- Leira, M., and Cantonati, M., (2008). 'Ecological Effects of Water-Level Fluctuations in Lakes'. (Springer, Netherlands)
- Lester, R. E., Fairweather, P. G., Webster, I. T., and Quin, R. A. (2013). Scenarios involving future climate and water extraction: ecosystem states in the estuary of Australia's largest river, *Ecological Applications* **23**, 984–998.
- Lester, R. E., Webster, I. T., Fairweather, P. G., and Young, W. J. (2011). Linking water-resource models to ecosystem-response models to guide water-resource planning - an

- example from the Murray-Darling Basin, Australia, *Marine and Freshwater Research* **62**, 279.
- Likens, G. E., and Bormann, F. H. (1974). Linkages between terrestrial and aquatic Ecosystems, *BioScience* **24**, 447–456.
- Lind, P. R., Robson, B. J., and Mitchell, B. D. (2007). Multiple lines of evidence for the beneficial effects of environmental flows in two lowland rivers in Victoria, Australia, *River Research and Applications* **23**, 933–946.
- Lindenmayer, D. B., and Likens, G. E. (2011). Direct measurement versus surrogate indicator species for evaluating environmental change and biodiversity loss, *Ecosystems* **14**, 47–59.
- McCune, B. (2006). Non-parametric habitat models with automatic interactions, *Journal of Vegetation Science* **17**, 819–830.
- Middelboe, A. L., and Markager, S. (1997). Depth limits and minimum light requirements of freshwater macrophytes, *Freshwater Biology* **37**, 553–568.
- Miller, S. W., Wooster, D. and Li, J. (2007). Resistance and resilience of macroinvertebrates to irrigation water withdrawals, *Freshwater Biology* **52**, 2494–2510.
- Mosley, L. M., Zammit, B., Leyden, E., Heneker, T. M., Hipsey, M. R., Skinner, D., and Aldridge, K. T. (2012). The impact of extreme low flows on the water quality of the Lower Murray River and Lakes (South Australia), *Water Resources Management* **26**, 3923–3946.
- Murray Darling Basin Authority (2013). The Living Murray Annual Environmental Watering Plan 2013 – 14. Murray–Darling Basin Authority, No. 16/13, Canberra
- Murray–Darling Basin Authority (2011). The Living Murray Story- One of Australia's Largest River Restoration Projects . Murray–Darling Basin Authority, No. 157/11, Canberra
- Nicol, J., and Ward, R. (2010a). Seed Bank Assessment of Dunn's and Shadow's Lagoons, South Australian Research and Development Institute (Aquatic Sciences), No.478, Adelaide.
- Nicol, J., and Ward, R. (2010b). Seed Bank Assessment of Goolwa Channel , Lower Finnis River and Lower Currency Creek. South Australian Research and Development Institute (Aquatic Sciences), No. 489, Adelaide.
- Nielsen, D. L., Brock, M. A., Rees, G. N., and Baldwin, D. S. (2003). Effects of increasing salinity on freshwater ecosystems in Australia, *Australian Journal of Botany* **51**, 655–665.
- Nilsson, C., Reidy, C. A., Dynesius, M., and Revenga, C. (2005). Fragmentation and flow regulation of the world's large river systems, *Science* **308**, 405–8

- Ning, N. S. P., Gawne, B., Cook, R. A., and Nielsen, D. L. (2013). Zooplankton dynamics in response to the transition from drought to flooding in four Murray-Darling Basin rivers affected by differing levels of flow regulation, *Hydrobiologia* **702**, 45–62.
- Pace, M. L. (2001). Prediction and the aquatic sciences, *Canadian Journal of Fisheries and Aquatic Sciences* **58**, 63–72.
- Paton, D. C., and Rogers, D. J. (2009). Condition Monitoring of Indicator Bird Species in the Lower Lakes , Coorong and Murray Mouth Icon Site : Coorong and Murray Mouth Estuary 2009. CSIRO: Water for a Healthy Country National Research Flagship, Canberra.
- Puckridge, J. T., Sheldon, F., Walker, K. F., and Boulton, A. J. (1998). Flow variability and the ecology of large rivers, *Marine and Freshwater Research* **49**, 55-72.
- Quiggin, J. (2001). Environmental economics and the Murray-Darling river system, *The Australian Journal of Agricultural and Resource Economics* **45**, 67–94.
- Rapport, D. J., Costanza, R., and McMichael, A. J. (1998). Assessing ecosystem health, *Trends in Ecology and Evolution* **13**, 397–402.
- Rapport, D. J., and Whitford, W. G. (1999). How ecosystems respond to stress, *BioScience* **49**, 193-203
- Richter, B. D. (2010). Re-thinking environmental flows: from allocations and reserves to sustainability boundaries, *River Research and Applications* **26**, 1052–1063.
- Riis, T., and Hawes, I. (2002). Relationships between water level fluctuations and vegetation diversity in shallow water of New Zealand lakes, *Aquatic Botany* **74**, 133–148.
- Roelofs, J. G. M. (1983). Impact of acidification and eutrophication on macrophyte communities in soft waters in The Netherlands: Field observations, *Aquatic Botany* **17**, 139–155.
- Rogers, D. J., and Paton, D. C. (2009). Changes in the distribution and abundance of *Ruppia tuberosa* in the Coorong. CSIRO: Water for a Healthy Country National Research Flagship, Canberra.
- Sainty, G.R., and Jacobs, S. W. L. (2003). ‘Waterplants in Australia.’ 4th Edn. (Sainty and Associates: Darlinghurst)
- Salter, J., Morris, K., and Boon, P. I. (2008). Does salinity reduce the tolerance of two contrasting wetland plants, the submerged monocot *Vallisneria australis* and the woody shrub *Melaleuca ericifolia*, to wetting and drying?, *Marine and Freshwater Research* **59**, 291-303
- Soberón, J. M. (2010). Niche and area of distribution modeling: a population ecology perspective, *Ecography* **33**, 159–167.

- Tonkin, J. D., and Death, R. G. (2014). The combined effects of flow regulation and an artificial flow release on a regulated river, *River Research and Applications* **30**, 329–337.
- Vilizzi, L., Thwaites, L. A., Smith, B. B., Nicol, J. M., and Madden, C. P. (2014). Ecological effects of common carp (*Cyprinus carpio*) in a semi-arid floodplain wetland, *Marine and Freshwater Research* **65**, 802.
- Wedderburn, S. D., Hammer, M. P., and Bice, C. M. (2012). Shifts in small-bodied fish assemblages resulting from drought-induced water level recession in terminating lakes of the Murray-Darling Basin, Australia, *Hydrobiologia* **691**, 35–46.
- Wedderburn, S. D., Walker, K. F., and Zampatti, B. P. (2007). Habitat separation of *Craterocephalus* (Atherinidae) species and populations in off-channel areas of the lower River Murray, Australia, *Ecology of Freshwater Fish* **16**, 442–449.
- Whittaker, R. H., Levin, S. A., and Root, R. B. (1973). Niche, Habitat, and Ecotope, *The American Naturalist* **107**, 321–338.

Appendices

Appendix 1. Eight telemetric sites from within the Lower Lakes used in the development of predictive models. Seasonal recordings for the focal time period (2008-2014) are shown with X = >60 daily averaged observations per season, the threshold to be included in modelling. Telemetered station codes are shown for variable recorded (EC, Water temperature and Lake Level) *denotes a variable aliased form nearby site, allowing for complete records.

		Milang Jetty	b78/Point McLeay	Warringee Point	Near Waltowa	Beacon 97	Beacon 65	b20/23GC	Mulgundawa
EC		A4261004	A4261129	A4261155	A4261153	A4261133	A4261124	A4261123	A4261032
Water temp		A4261004	A4261129	A4261155	A4261153	A4261133	A4261124	A4261123	A4261032
Lake level		A4261004	*A4261156	A4261155	A4261153	A4261133	A4261124	*A4261122	A4261032
Season	Season ref.								
Spring 08	1	X	X		X	X	X	X	X
Summer 08/09	2	X	X	X	X	X	X	X	X
Autumn 09	3		X	X	X	X	X	X	X
Winter 09	4		X	X	X	X	X	X	X
Spring 09	5		X	X	X	X	X	X	X
Summer 09/10	6		X	X	X	X	X	X	X
Autumn 10	7	X	X	X	X	X	X	X	X
Winter 10	8	X	X	X	X	X	X	X	X
Spring 10	9	X	X	X	X	X	X	X	X
Summer 10/11	10	X	X	X	X	X	X	X	X
Autumn 11	11	X	X	X	X	X	X	X	X
Winter 11	12	X	X	X	X	X	X	X	X
Spring 11	13	X	X	X	X	X	X	X	X
Summer 11/12	14	X	X	X	X	X	X	X	X
Autumn 12	15	X	X	X	X	X	X	X	X
Winter 12	16	X	X	X	X	X	X	X	X
Spring 12	17	X	X	X	X	X	X	X	X
Summer 12/13	18	X	X	X	X	X	X	X	X
Autumn 13	19	X		X	X	X	X	X	X
Winter 13	20	X		X	X	X	X	X	X
Spring 13	21	X		X	X	X	X	X	X
Summer 13/14	22	X		X	X	X	X	X	X
Autumn 14	23			X	X	X	X	X	X

Appendix. 2 The range of preliminary models developed from telemetered records and vegetation monitoring sites. The best developed models with the inclusion lagged seasons and years are shown (a), as well as the most temporally-complete models (b) and the most spatially-complete models (c). * denotes the best preliminary model for each species. The length of modelled time period (seasons), number of sampling events within time period (sampling events), number of lagged season included (Lag seasons) and number of lagged years (Lag years) are shown. The best predictors for each developed model are listed in order of influence defined by sensitivity analysis with predictor codes listed below.

(a) **Models incorporating seasons & lag years**

Modelling run	13 sites 1 lag year, 4 lag seasons		13 sites 2 lag years 8 lag seasons	
Number of sites	13		13	
Seasons	Autumn 2010 - Spring 2013		Autumn 2011 -Spring 2013	
Sampling events	7		5	
Lag seasons	4		8	
Lag years	1		2	
Species	<i>M. salsugineum</i>	<i>V. australis</i>	<i>M. salsugineum</i>	<i>V. australis</i>
Best predictor	AvEC	RgLL	AvEC	AvEC
2nd predictor	RgEc S-1	AvEc S-2	AvLL	RgEC
3rd predictor	AvLL S-2	AvWT S-2	RgLL	RgLL
4th predictor	RgEC S-3	RgEC S-2	RgLL S-2	AvLLYr-2
best model xR ²	xR ² = 0.656 *	xR ² = 0.141	xR ² = 0.378	xR ² = 0.302 *

(b) **Temporally-complete models**

Modelling run	13 sites, 18 seasons		14 sites, 14 seasons	
Number of sites	13		14	
Seasons	Autumn 2009 – Spring 2013		Autumn 2009 – Spring 2012	
Sampling events	10		8	
Lag seasons	1		1	
Lag years	-		-	
Species	<i>M. salsugineum</i>	<i>V. australis</i>	<i>M. salsugineum</i>	<i>V. australis</i>
Best predictor	AvEC	AvEC	AvEC	AvEC
2nd predictor	RgEC	RgEC	RgEC	-
3rd predictor	AVEC S-1	AvLL S-1	AvLL S-1	-
4th predictor	AvLL S-1	RgLL S-1	RgEC S-2	-
best model xR ²	xR ² = 0.1529	xR ² = 0.0414	xR ² = 0.1635	xR ² =- 0.0181

(c) **Spatially complete models**

Modelling run	15 sites, 12 seasons		16 sites, 8 seasons	
Number of sites	15		16	
Seasons	Spring 2010- Spring 2013		Spring 2010- Spring 2012	
Sampling events	6		4	
Lag seasons	1		1	
Lag years	-		-	
Species	<i>M. salsugineum</i>	<i>V. australis</i>	<i>M. salsugineum</i>	<i>V. australis</i>
Best predictor	RgEC	AvEC	AvEC	AvWT
2nd predictor	AvEc S-1	AvEc S-1	AvLL	RgWT
3rd predictor	RgEC S-1	AvLL S-1	RgEC	-
4th predictor	RgWT S-1	RgLL S-1	AvLL S-1	-
best model xR ²	xR ² =0.1247	xR ² =0.0839	xR ² =0.1528	xR ² =-0.0262

Code	Season Variable
AvEC	Average EC
AvLL	Average lake level
AvWT	Average water temperature
RgEC	Range EC
RgLL	Range lake level
RgWT	Range water temperature
Y-1	One year previous
Y-2	Two years previous
S-1	One season previous
S-2	Two season previous
S-3	Three season previous

Appendix 3. Table of 34 species (categorised by functional group) recorded during field surveys of the seven resampled lake shore vegetation monitoring sites in June 2014. The target species *Myriophyllum salsugineum* and *Vallisneria australis* are shown in bold.

Functional group	Macrophytes	Lake Alexandrina				Lake Albert		Goolwa Channel			Total number of sites
		Point Sturt	Lake Reserve Road	Clayton Upstream	Bremer Mouth	Warrengeie	Nurra Nurra	Hindmarsh Island Bridge 2	Goolwa South	Clayton Bay	
Amphibious fluctuation responder-plastic	<i>Centella asiatica</i>									X	1
	<i>Hydrocotyle verticillata</i>				X						1
	<i>Limosella australis</i>		X								1
	<i>Persicaria lapathifolia</i>			X	X						2
	<i>Rorippa nasturtium-aquaticum</i>				X						1
<i>Rumex bidens</i>	X							X		2	
Amphibious fluctuation tolerator-emergent	<i>Calystegia sepium</i>				X	X		X	X	X	5
	<i>Juncus kraussii</i>	X	X		X				X		4
	<i>Lycopus australis</i>			X					X	X	3
	<i>Lythrum hyssopifolium</i>								X		1
	<i>Menhtha</i> sp.							X			1
	<i>Ranunculus tribolus</i>					X					1
	<i>Schoenoplectus pungens</i>	X				X		X			3
Emergent	<i>Berula erecta</i>		X		X						2
	<i>Phragmites australis</i>	X	X	X	X	X	X	X	X	X	9
	<i>Schoenoplectus validus</i>				X		X			X	3
	<i>Triglochin procerum</i>			X						X	2
	<i>Typha domingensis</i>	X		X	X	X		X	X	X	7
Floating	<i>Azolla filiculoides</i>			X	X					X	3
	<i>Lemna</i> sp.			X						X	2
Submergent k-selected	<i>Ceratophyllum demersum</i>			X	X			X		X	4
	<i>Myriophyllum salsugineum</i>			X	X				X	X	4
	<i>Potamogeton crispus</i>				X						1
	<i>Potamogeton pectinatus</i>	X									1
	<i>Vallisneria australis</i>	X		X	X						3
	<i>Paspalum distichum</i>	X	X	X	X	X		X	X	X	8
Terrestrial damp	<i>Lactuca serriola</i>				X						1
	<i>Pennisetum clandestinum</i>				X	X	X	X			4
	<i>Plantago lanceolata</i>							X			1
	<i>Scabiosa atropurpurea</i>							X			1
	<i>Stenotaphrum secundatum</i>								X		1
	<i>Tetragonia tetragonioides</i>								X		1
	<i>Trifolium</i> sp.	X					X				2
	Unknown terrestrial shrub								X		1
Total species diversity	9	5	11	19	5	5	9	12	12		

Appendix 4. PERMANOVA results, showing pre-treatment (normalised), degrees of freedom (*d.f.*) with significance ($\alpha = 0.05$) shown in bold

Variable	Pre-treatment	factor	<i>d.f.</i>	<i>pseudo-F</i>	<i>P(perm)</i>
Species abundance	none	Likelihood categories	1,5	0.94	0.460
		Sites (categories)	5,28	2.83	0.001
Functional groups	none	Likelihood categories	1,5	0.83	0.505
		Sites (categories)	5,28	2.00	0.007
Water Quality	normalised	Likelihood categories	1,5	0.86	0.470
		Sites (categories)	5,14	81.49	0.030
Physical characteristics	normalised	Likelihood categories	1,5	0.75	0.589
		Sites (categories)	5,14	1.63	0.001

Appendix.5 The variation in bank slope measured as the distance between the known elevations of sampled quadrats (0.8, 0.6, 0.4, 0.2, 0.0m AHD) for the nine sites resampled in June 2014

