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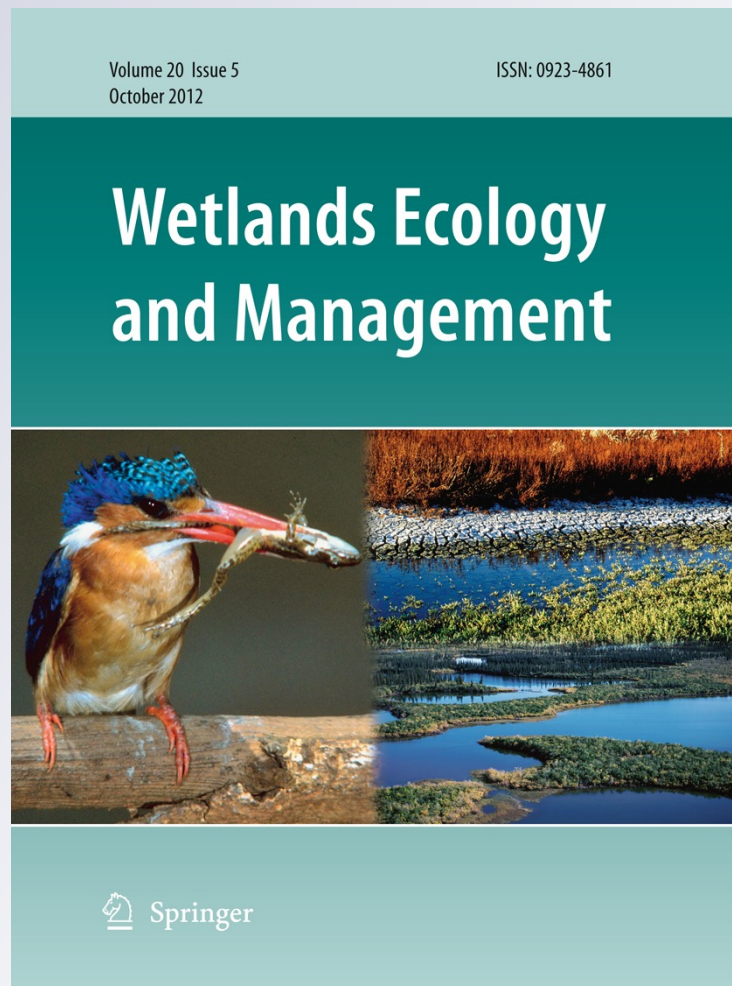
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Aquatic plant dynamics of Waituna Lagoon, New Zealand: trade-offs in managing opening events of a Ramsar site

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Abstract Coastal lagoons are at risk internationally due to impacts associated with human-induced land use change. The resilience of aquatic macrophytes in these systems is threatened by altered hydrological regimes, elevated nutrient loading, and increased dominance of nuisance species. We describe the aquatic plant dynamics of the Waituna Lagoon Ramsar Site, a 1,350 ha lagoon frequently opened to the sea for flood mitigation which is characterised by fluctuating water levels and salinity. The shallow lagoon supports a macrophyte community dominated by *Ruppia megacarpa* and *R. polycarpa*. Repeated survey of 48 sites across the lagoon during late summer in 2009, 2010 and 2011 were applied to describe aquatic plant composition and abundance. This period coincided with three opening events (winter 2008; winter 2009; spring 2010) when the lagoon switched from a predominantly fresh-brackish system to being influenced by tidal exchange and lower water levels. The lagoon experienced a period of 43 days open to the sea in 2008–2009, 67 days in

2009–2010 and 181 days in 2010–2011, during which macrophytes were subject to saline conditions in excess of 10 ppt. We observed a decline in the occurrence of *Ruppia* from 2009 (69 % sites) to 2011 (23 % sites). The shift in productivity was associated with the duration of the open phase and the period plants were subject to saline conditions >20 ppt and low water levels. The resilience of the system is also at risk from increased algal-dominance due to the intensification of agricultural land use occurring in the Waituna Lagoon catchment. While lagoon opening events cause extreme changes in water depth and salinity that can limit macrophyte growth, they also provide a mechanism to reduce the effects of eutrophication. Understanding these trade-offs is pivotal in management decisions regarding the likely impact of opening events on the ecological character of coastal lagoons.

Keywords *Ruppia* · Macrophytes · Salinity · Water management

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Introduction

Shallow lakes within catchments not subject to large-scale changes in land use often exhibit low nutrient loads, high water clarity and extensive macrophyte beds. As nutrient concentrations and phytoplankton

productivity increases in these systems, water clarity declines and competition for light limits macrophyte growth and reproduction. A complete switch from an unmodified macrophyte-dominated state to one of phytoplankton dominance has been reported for numerous sites (Moss 1990; Scheffer 1998; Scheffer et al. 2001; Morris et al. 2003; Scheffer and van Nes 2007). Coastal lagoons that intermittently open and close to the ocean are similarly vulnerable to land use change, and the effects of eutrophication can be exacerbated by the fluctuating water levels and ion concentrations (salinity) that characterises them (Cloern 2001). That is, in addition to the altered trophic interactions initiated by nitrogen or phosphorus loading, aquatic biota in coastal lagoons have to tolerate or adapt to variations in hydrological regime and salinity (Sanders 1968; Walker and McComb 1992; Carruthers et al. 1999).

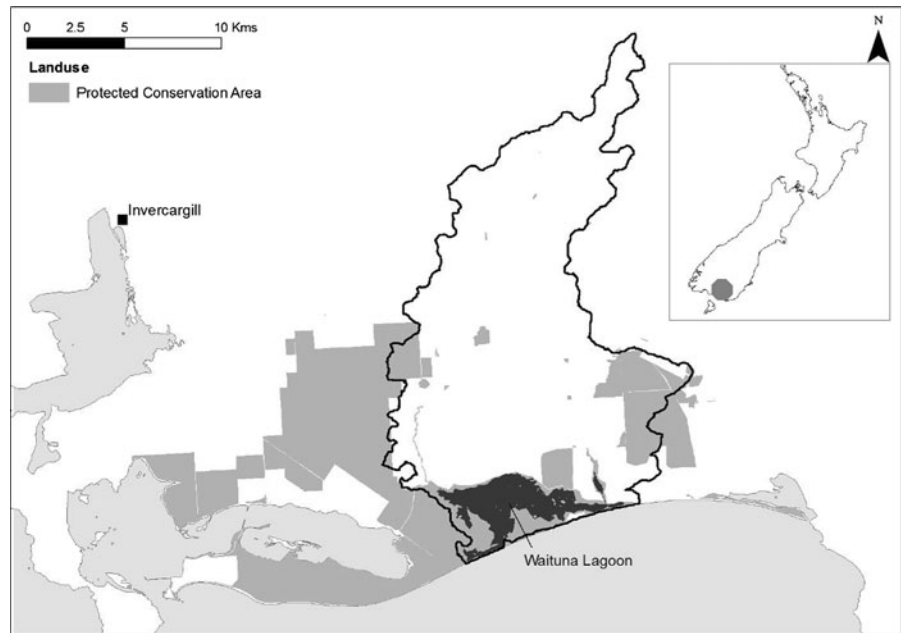
Human-induced changes in the frequency of coastal lagoon opening may disrupt ecological functioning by inhibiting critical life-history phases such as germination of aquatic plants (Nicol 2005; Viaroli et al. 2008). In New Zealand, a number of coastal lakes and lagoons have deteriorated in ecological integrity due to land use change and altered opening procedures (Hughey and Taylor 2009; Schallenberg and Sorrell 2009). Lake Ellesmere/Te Waihora in the South Island, for instance, underwent a switch from being dominated by submerged macrophytes (including *Ruppia* spp.) to a turbid, phytoplankton-dominated system (Gerbeaux and Ward 1991). Interestingly, a key driver for the change observed in Lake Ellesmere/Te Waihora is thought to be a significant storm event in 1968, which uprooted much of the macrophyte beds. Gerbeaux and Ward (1991) listed the main reasons for why the macrophytes failed to re-establish following this event as; (1) insufficient light reaching the bed of the lake, (2) moderately saline conditions due to frequent openings preventing germination, (3) uprooting of germinating seedlings by wind and wave action, and (4) exposure of seedlings and mature plants to drying out when lake levels are low when open to the sea.

This study examines the status and vulnerability of aquatic plants in Waituna Lagoon (46°34'S, 168°36'E), a shallow (depth 1–3 m) opened and closed coastal lake. Waituna Lagoon forms part of an extensive (18,900 ha) Ramsar site located on the Southland coast between Bluff Harbour and the Mataura River, 20 km

south-east of Invercargill, Southland, New Zealand (Fig. 1). Ramsar designation (1976) recognises the outstanding values of the wetlands and lagoon, which include; trans-equatorial migrating and wading birds, a diverse fish assemblage, and unimpeded sequences of wetland vegetation (Robertson et al. 2009). The aquatic plant community is characterised by an extensive population of *Ruppia megacarpa* and *R. polycarpa* (Johnson and Partridge 1998). This distinguishes the site from other intermittently open and closed coastal systems in New Zealand many of which have lost their submerged macrophytes (e.g. Gerbeaux and Ward 1991). Other aquatic plants include; *Myriophyllum triphyllum*, the charophytes *Lamprothamnium macropogon* and *Nitella* sp. and filamentous algae *Bachelotia antillarum* and *Enteromorpha* sp. (Johnson and Partridge 1998; Robertson and Stevens 2007; de Winton personal communication, 2011). *Ruppia* is considered a keystone species because of its importance as a habitat or food source for herbivorous water fowl, invertebrates and fish (Thompson and Ryder 2003; Schallenberg and Tyrell 2006; Atkinson 2008; Duggan 2010). Furthermore, *Ruppia* and other functionally-equivalent aquatic plants have a role in regulating water quality through competition for nutrients to prevent phytoplankton dominance and maintaining water clarity as plant roots, especially in dense beds, stabilise sediment that would otherwise be resuspended by wave action (e.g. Gerbeaux 1989; Scheffer 1998; Cronk and Fennessy 2001).

Coastal lagoons of this type generally remain closed and experience low to moderate inputs of freshwater from tributary creeks (Kirk and Lauder 2000). Waituna Lagoon is separated from the sea by a long narrow gravel beach that allows some slow percolation of the lagoon water. Opening of the lagoon to the sea occurs artificially on average once a year by local community removing material from the gravel barrier using a small digger. This artificial regime is implemented to prevent inundation of surrounding low-lying agricultural land. Surface water regularly exceeds salinity of 8 parts per thousand (ppt) with a recorded range of 0.7–33.6 ppt. During closed conditions salinity decreases due to the increasing volume of freshwater to stabilise around 4 ppt (Schallenberg et al. 2010). Prior to human intervention, drainage to the sea is likely to have occurred less frequently, when there was a combination of very high water levels and strong westerlies to cause a break out. These

Fig. 1 Location of Waituna Lagoon and associated catchment, Southland, New Zealand



conditions are predicted to have supported prolonged freshwater phases with higher water levels interrupted by sudden opening events (Waghorn and Thomson 1989; Kirk and Lauder 2000; Cosgrove 2011).

Water level management in Waituna Lagoon and its associated impacts on surface water salinity is thought to be a key driver of aquatic plant germination, growth and survival. The upper salinity tolerance of most freshwater aquatic plants is 4 ppt, above which the plant community is replaced by halophytic species (Nielsen et al. 2003). The genus *Ruppia* (Potamogetonaceae) consists of both annual and perennial species that occur in lacustrine and estuarine habitats. In New Zealand, two *Ruppia* species have been described *R. megacarpa* R.Mason and *R. polycarpa* R.Mason (Johnson and Brooke 1998). *Ruppia* are obligate aquatic plants and will desiccate rapidly if exposed to the air (Brock 1982a; Nicol 2005). *R. megacarpa* behaves more like a perennial species and is typically found in permanently inundated habitats, compared to *R. polycarpa* that is an annual species common in sites with fluctuating water levels where it is able to germinate rapidly following desiccation (Brock 1982a, b; Gerbeaux 1989). Although *Ruppia* species have the widest salinity tolerance of any submergent angiosperms (Brock 1982a, b; Kantrud 1991), salinity exhibits a strong influence on productivity (Brock 1982a; Carruthers et al. 1999). For

instance *Ruppia* dominance declined as a result of reduced freshwater inflows into the Coorong lagoons, south-east Australia (Nicol 2005). Optimal salinities for *Ruppia* establishment and growth in New Zealand have been reported to be between 4 and 8 ppt (Gerbeaux 1989). Another factor limiting *Ruppia* productivity is light availability, which varies depending on water levels, suspended solids and competition with phytoplankton (Gerbeaux 1989; Kantrud 1991). While low water levels will reduce light limitation, the associated wind-induced re-suspension of sediment may make conditions less favourable for *Ruppia* and other aquatic plants (Hamilton and Mitchell 1996).

An increase in the trophic state of Waituna Lagoon has been observed in recent years with nutrient and chlorophyll a concentrations high (Environment Southland 2009) relative to national guidelines (ANZECC and ARMCANZ 2000). Eutrophication is attributed to elevated sediment and nutrient loads in inflow streams from land use intensification (Thompson and Ryder 2003; Schallenberg et al. 2010). Robertson et al. (2011) suggested the system is at risk of ‘flipping’ to an algal-dominated state with subsequent loss of *Ruppia*. In a review of studies on the response of coastal ecosystems to eutrophication, however, Cloern (2001) noted that system-specific attributes and seasonality affects their sensitivity to nutrient enrichment. For the conservation of systems

such as Waituna Lagoon, where maintaining the dominance of indigenous aquatic plants is a key objective, site-scale information on community dynamics in response to multiple stressors is subsequently required.

In this paper we examine the status of the aquatic plant community in Waituna Lagoon. The vulnerability of the *Ruppia*-dominated ecosystem to shifting to an altered state dominated by phytoplankton or benthic algae is of particular concern. Through an investigation of key environmental drivers, the study aims to develop understanding of the resilience of *Ruppia* to opening and closing events and improve the management of coastal lagoons.

Methods

We examined the status of the aquatic plant community in Waituna Lagoon by comparing changes in composition and distribution between 2009 and 2011. Prior to our research programme a survey of macrophyte distribution was undertaken (Robertson and Stevens 2007). This used high resolution aerial photographs to identify areas dominated by macrophytes and subsequently verified by inspection to produce a map of macrophyte distribution and abundance. The 2007 map indicated macrophytes were widely distributed across the lagoon bed and this provided the basis for our survey design. We established a total of 48 geo-referenced sample sites on 10 transects in Waituna Lagoon (Fig. 2), with site locations stratified to incorporate variation in lagoon bathymetry.

A total of 192 benthic grab samples (48 sites \times 4 sub-samples) were collected for three consecutive years of monitoring, February 2009, February 2010 and March 2011. That is, four sub-samples of lagoon sediment and attached or rooted macrophytes were removed at each site. Grab samples have previously been applied for the survey of *Ruppia* in similar environments (e.g. Comin et al. 1990; Rogers and Paton 2009). Use of underwater cameras and diving to measure macrophyte abundance was not practical due to frequent poor water clarity. The benthic grab was a modified flat plate (dimensions 10 \times 10 cm) fixed on a 2 m pole that allowed retrieval of an intact sample (of approximately 4 cm depth) of surface vegetation and roots. Sub-samples were collected from a random

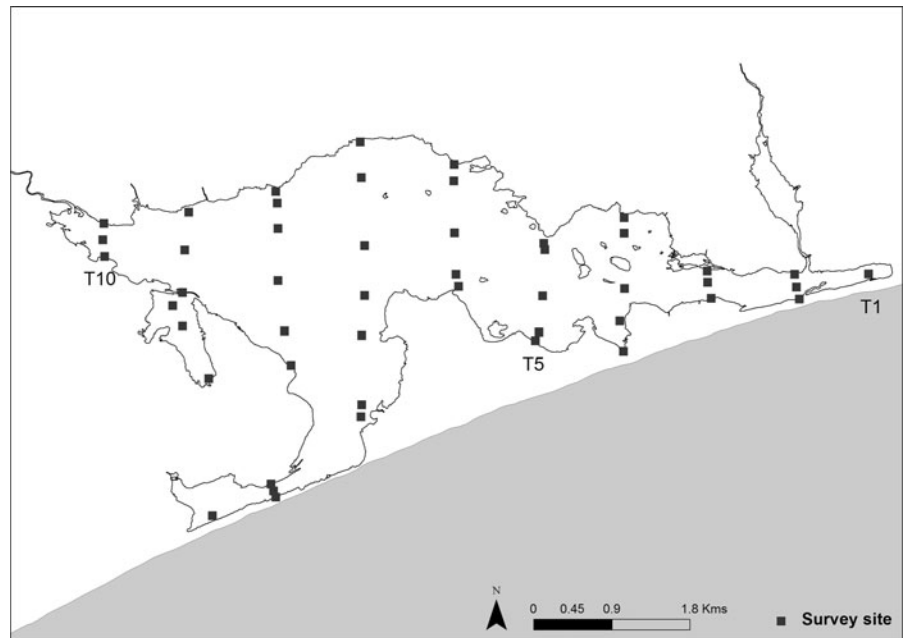
location at least 3 m from the nearest sub-sample. Homogeneity of sub-samples was checked by comparing the frequency of occurrence of target species (*R. megacarpa* and *R. polycarpa*) between sub-samples.

All aquatic plants collected from the benthic grab were identified to species. Measurements of the cover-abundance (percent cover), average height (cm) and life-history state (vegetative, flowering, seed-set) were recorded. Seven categories of cover-abundance were applied to reduce observer bias; 0 % (not present), <1–5 %, 5–10 %, 10–20 %, 20–50 %, 50–80 %, 80–100 % and each sub-sample individually photographed. At each site measurements of water temperature ($^{\circ}$ C), conductivity (ms/cm), water clarity (secchi disc visibility in cm), water depth (cm), and dissolved oxygen (mg/l) were also collected.

Monthly water quality data from four sites in Waituna Lagoon for the period February 2008 through May 2011 was provided by the Regional Council (Environment Southland, personal communication 2011). Parameters included salinity (ppt), the concentration of total and biologically available nutrients (TN, TP, NO_3 , DRP; mg/l), total suspended sediment (mg/l), turbidity (NTU), dissolved oxygen (mg/l) and chlorophyll a concentration (mg/l). Daily water level records for Waituna Lagoon measured at Waghorn's Bridge were supplied by Environment Southland for the period January 2008 to May 2011. These datasets have been previously described (e.g. Schallenberg et al. 2010) but have not been specifically applied to examine the status and vulnerability of *Ruppia* or other macrophyte populations. We described monthly variations of mean water quality measurements during open and closed conditions and relative to the key life cycle phases for both *Ruppia* species (1 August–31 March). The growing season was defined from previous studies (Brock 1982b; Gerbeaux 1989; Nicol 2005; Sim et al. 2006) in the absence of specific studies for the Southland region of New Zealand (Latitude 46° S, mean annual rainfall 1,000 mm, mean air temperature 10° C).

To describe the status of the macrophyte community we analysed changes in plant composition and abundance between 2009 and 2011. For each species, site occupancy (presence/absence) and the mean cover-abundance was used to examine the proportion of survey sites dominated by different taxa. The vulnerability of the macrophyte community,

Fig. 2 Location of the 48 sample sites distributed across 10 transects (T1–T10) in Waituna Lagoon for the 2009–2011 surveys



particularly *Ruppia*, to changes in water levels and salinity was also examined. Surface water in Waituna Lagoon is generally well mixed and salinity is assumed to be similar across sites. However, salinity is known to change with time due to lagoon opening and closing (Schallenberg et al. 2010). We examined the variation in salinity during the growing season for *Ruppia*, and calculated the proportion of time salinity was greater than 8 ppt, previously identified as the level over which *Ruppia* germination and growth are negatively impacted (Gerbeaux 1989; Nicol 2005).

The effect of fluctuating water depth on the abundance of *Ruppia* was examined by calculating the number of days during the growing season that each survey site had no water (0 cm) or moderate-high water depth (>100 cm). These water depth thresholds relate to the degree of bed exposure and light limitation. To validate the use of water depth as a surrogate for light limitation we calculated the average light attenuation depth over a range of conditions in Waituna Lagoon. Light meters (Onset HOBO Pendant Temp/Light Logger) were deployed in duplicate at two sites. One meter was located near the bottom substrate and the other 40 cm higher in the water column. These loggers measured light intensity (lux) at 15 min intervals between 3 December 2009 and 23 February 2010. The

difference in light intensity between meters was used to estimate light attenuation depth following Kirk (1994) where kd is the diffuse attenuation coefficient, I_0 is the measured light intensity near the surface, I_z is the measured light intensity near the substrate and Z is the distance in metres between light meters (1). We then calculated the 10 % light attenuation depth (D_{10}), a light intensity previously reported to affect *Ruppia* productivity (Congdon and McComb 1979), applying the constant 2.3025 (2).

$$kd = (\ln I_0 - \ln I_z) / Z \quad (1)$$

$$D_{10} = 2.3025 / kd \quad (2)$$

All 48 survey sites were allocated to eight elevation categories to analyse differences in macrophyte abundance between sites with contrasting degrees of bed exposure and light limitation based on water depth. Average daily water depth was extrapolated from the Waituna Lagoon gauge, and the percentage of the growing season sites subjected to light limitation or exposure then calculated. Spatial variability in wind-induced resuspension, phytoplankton abundance and other particulate matter is likely to occur in some areas, however, for this analysis light attenuation is assumed to be constant.

Results

Status of aquatic plant community

The Waituna Lagoon Ramsar site supported widespread populations of *R. megacarpa* and *R. polycarpa*. Other taxa recorded were *M. triphyllum*, charophytes (*Nitella* sp.) and the macroalgae *Enteromorpha* sp. and *B. antillarum*. The observed aquatic plant community was spatially and temporally dynamic. A decline in site occupancy of *R. polycarpa* was observed from 2009 to 2011 (Fig. 3). During the same time period *R. megacarpa* occupied between 5 and 11 % of survey sites. The overall number of sites with any *Ruppia* species present decreased from 69 % (2009), to 52 % (2010) and then 23 % (2011). We also observed annual variation in the frequency of other macrophytes and macroalgae. Charophytes were observed at six sites in 2009 and were not observed in the subsequent two years (Fig. 3). The brown filamentous algae *B. antillarum* was widespread, recorded at 45 sites in 2009 and 41 sites in 2010. In 2011, after a prolonged tidal phase when the lagoon was open to the ocean the marine alga *Ulva intestinales* was also recorded.

Aquatic plant abundance varied across the lagoon and between years. In 2010, the areas that supported the highest abundance of *R. megacarpa* were in the south west arm of Waituna Lagoon (20–50 % average cover abundance), *R. polycarpa* occurred in highest abundance, albeit with patchy distribution, in the eastern arm (20–50 %), while *M. triphyllum* was

abundant in Shand Bay a sheltered embayment along the western arm of the lagoon (50–80 %). This pattern was also observed in 2009, although with greater sites dominated by *R. polycarpa*. The sites with no occurrences of *Ruppia* or *M. triphyllum* were in central, exposed areas and near the south-eastern shoreline of the lagoon (Fig. 2). Substantial growth of *B. antillarum* and associated organic matter coincided with the later site during 2010. Figure 4 summarises the variation in the cover abundance of the *Ruppia* species between survey periods. *R. megacarpa* abundance ranged considerably between years, in 2009 only 8 % of sites exhibited 25–50 % foliage cover but this increased to 12 % in 2010 and 14 % in 2011 (Fig. 4a), although few sites supported a high abundance of *R. megacarpa*. In contrast *R. polycarpa* showed a decreasing trend in abundance across all cover classes (Fig. 4b). At sites where *Ruppia* were present the average cover abundance for *R. megacarpa* and *R. polycarpa* in 2009 was 17 and 30 % respectively, 17 and 23 % in 2010, and 11 and 4 % in 2011, reiterating the observed decline in abundance of both species during the three years of monitoring.

Vulnerability of *Ruppia* to changes in lagoon conditions

Environmental conditions in Waituna Lagoon were substantially altered during the study period as it coincided with three opening events when the lagoon switched from a predominantly fresh-brackish system

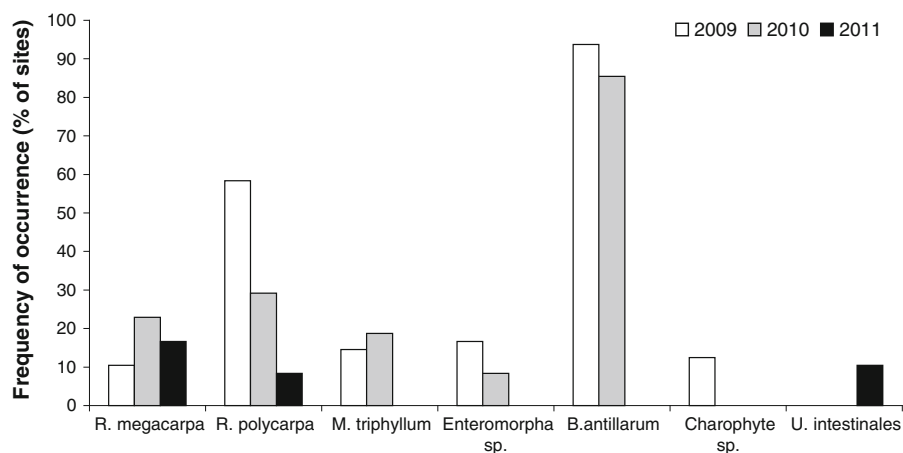
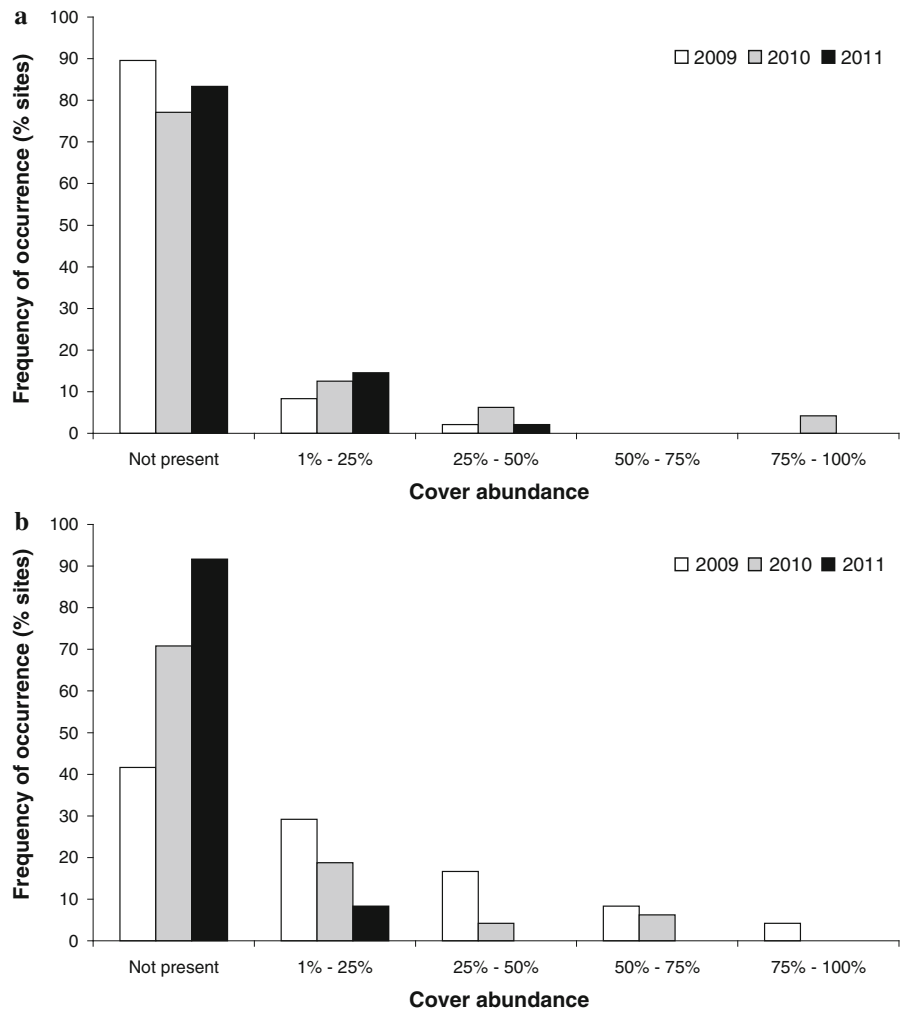


Fig. 3 Frequency of occurrence of macrophytes and macroalgae in Waituna Lagoon between 2009 and 2011

Fig. 4 Frequency of occurrence of *R. megacarpa* (a) and *R. polycarpa* (b) across cover abundance classes between 2009 and 2011



to being influenced by tidal exchange and lower water levels. The lagoon experienced a period of 43 days open to the sea in 2008–2009, 67 days in 2009–2010 and 181 days in 2010–2011, during which aquatic plants were subject to saline conditions in excess of 25 ppt (Table 1). Water clarity (turbidity), total nitrogen and nitrate concentrations were also affected by the change in water levels and seawater mixing associated with lagoon opening. Salinity concentrations and turbidity showed marked increases when the lagoon was open, with total nitrogen and nitrate higher during closed periods (Table 1). These comparisons, however, were somewhat limited due to the low frequency of samples during open periods. In addition, because the water quality sampling occurs monthly the range in turbidity is considered indicative due to the

potential for significant fluctuations related to wind-induced resuspension.

The timing and duration of fresh (<4 ppt) and saline (>8 ppt) periods provided opportunity to assess the resilience of macrophytes to fluctuating water chemistry (Fig. 5). During 2008–2009 and 2009–2010 the lagoon experienced similar opening and closing times, opening in winter and closing early October. In 2010–2011 the lagoon opened during September and remained open throughout the spring–summer period. This corresponded to a prolonged period with salinity concentration >20 ppt during the growing season for *Ruppia* in 2010–2011 (Fig. 5). Whereas, for the 2008–2009 growing season salinity >8 ppt was recorded on a single occasion (September) and by late November mean salinity was <5 ppt. In the 2009–2010

Table 1 Summary of water quality (mean \pm SE) in Waituna Lagoon during open and closed lagoon periods

| Variable | 2008–2009 | | 2009–2010 | | 2010–2011 | |
|--|--|-----------------------|--|-----------------------|---|-----------------------|
| | Open ($n = 1$) (25/08/08–7/ 10/08) | Closed ($n = 6$) | Open ($n = 2$) (29/07/09–4/ 10/09) | Closed ($n = 4$) | Open ($n = 6$) (28/09/10–27/ 03/11) | Closed ($n = 3$) |
| Duration open/closed (% growing season) | 18 % (43 days) | 82 % (200 days) | 26 % (64 days) | 74 % (179 days) | 74 % (181 days) | 26 % (62 days) |
| Salinity (ppt) | 28.0 | 2.8 (0.5) | 29.5 (3.5) | 7.9 (2.4) | 30.2 (2.1) | 0.4 (0.1) |
| Turbidity (NTU) | 5.8 | 10.1 (2.0) | 13.8 (10.2) | 5.4 (1.0) | 4.6 (1.3) | 8.3 (2.7) |
| pH | 8.0 | 7.5 (0.2) | 7.85 (0.05) | 7.8 (0.1) | 8.0 (0.1) | 7.5 (0.1) |
| Temperature ($^{\circ}$ C) | 9.6 | 14.7 (0.8) | 10.7 (0.8) | 15.0 (1.3) | 15.8 (0.8) | 7.43 (0.6) |
| Chl <i>a</i> (mg/l) | <0.01 | 0.01 (<0.01) | <0.01 (<0.01) | <0.01 (<0.01) | <0.01 (<0.01) | <0.01 (<0.01) |
| TN (mg/l) | 0.33 | 1.08 (0.21) | 0.49 (0.14) | 0.64 (0.18) | 0.37 (0.09) | 1.76 (0.01) |
| NO ₃ (mg/l) | 0.03 | 0.26 (0.21) | 0.07 (0.07) | 0.05 (0.05) | 0.06 (0.06) | 0.91 (0.04) |
| TP (mg/l) | 0.02 | 0.05 (0.01) | 0.06 (0.04) | 0.03 (<0.01) | 0.02 (<0.01) | 0.06 (0.02) |
| DRP (mg/l) | <0.01 | <0.01 (<0.01) | <0.01 (<0.01) | <0.01 (<0.01) | <0.01 (<0.01) | 0.01 (<0.01) |
| TN:TP | 17:1 | 22:1 | 8:1 | 21:1 | 19:1 | 29:1 |

Mean calculated for period encapsulating the key life cycle phases for *R. megacarpa* and *R. polycarpa* 1 August–31 March (243 days)

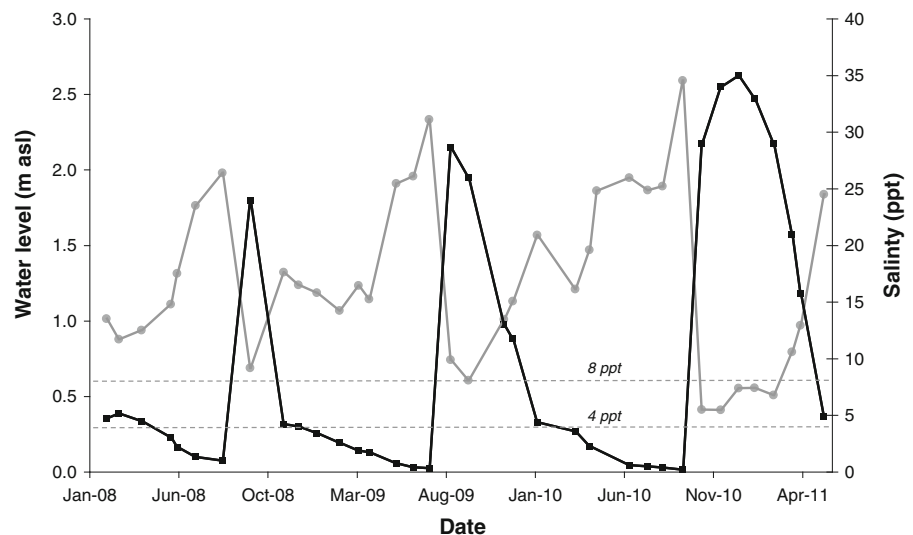
Source: Environment Southland monthly water samples collected from Waituna Lagoon

growing season, salinity was recorded >8 ppt for four sampling periods from early September to mid December, equivalent to 50 % of the growing period outside of optimal growing conditions in comparison to about 25 % of the time in the previous year (Fig. 5).

Variation in water levels during open and closed lagoon phases also alters the degree of light limitation

(high water levels) and bed exposure (low water levels). The proportion of time that each site was affected by light limitation, and exposed due to low water levels, is described (Table 2). Use of a 10 % light attenuation depth (D_{10}) of 1.0 m was based on observations of light attenuation at two sites over both calm and wind-affected conditions. The D_{10} varied

Fig. 5 Variation in salinity (black line) in Waituna Lagoon between 2008 and 2011 relative to changes in water level (grey line). Periodic increase in salinity corresponds to lagoon opening events and intrusion of sea water



from 0.4 to >2.5 m. Mean D_{10} was 1.40 m (SE \pm 0.08) at Site 1 and 0.98 m (SE \pm 0.07) at Site 2. We subsequently extrapolated the D_{10} (1.0 m) to daily water level measurements to estimate the proportion of the growing season *Ruppia* affected by light limitation, where deeper sites are more vulnerable to prolonged periods of low light. Prior to the 2009 macrophyte survey a high number of sites experienced light limitation due to high water levels, with deep sites (A–C) likely to experience light limitation for the entire (100 %) growing season. These regions correspond to sites where *R. polycarpa* is absent or in very low abundance (Table 2). Prior to the 2010 macrophyte survey there was reduced likelihood of light limitation. For example, at mid elevation sites (D) the percentage of the growing season affected light limitation decreased from 82 % in 2009 to 67 % and in this depth range (D) *R. megacarpa* abundance increased (Table 2). Aquatic plants were exposed to prolonged drawdown events after lagoon opening prior to 2010 and 2011. High elevation sites that occupy the lagoon margins (G) were exposed for 21 % of the growing season in 2010, and 56 % in 2011. *Ruppia* abundance as expected was correspondingly low on the lagoon margins (Table 2). In addition to the interrupted growing season due to the prolonged exposure of the lagoon bed in 2011, a co-factor explaining the overall low abundance of *R. megacarpa* and *R. polycarpa* is the prolonged periods of high salinity (Fig. 5).

Discussion

Factors influencing macrophyte resilience

Waituna Lagoon was recognised as New Zealand's first wetland of international importance (Ramsar site) for the pristine nature of the coastal lagoon and the native aquatic species it supported. Recent literature highlight concerns regarding intensification of land use in the catchment and the impact of lagoon opening on ecosystem processes (e.g. Schallenberg et al. 2010; Robertson et al. 2011). We established surveys of the aquatic plant community to examine the ecosystem status and resilience to perturbation. The assessment revealed a dynamic system where physical–chemical properties and plant community composition is altered or interrupted on a frequent basis, characterised by a patchy distribution of *Ruppia* and other plant species. The macrophytes and macroalgae appear to transition through rapid periods of growth and decline, which results in variable species composition (Fig. 3) and macrophyte beds that do not form dense stands (Fig. 4). The annual shift in plant composition indicates that many sites in the lagoon may support *Ruppia* with patterns observed largely driven by variation in salinity (Fig. 5), light availability and water level (Table 2).

The lagoon was subjected to a human-induced opening regime for a period of 43 days in 2008–2009, 67 days in 2009–2010 and 181 days in 2010–2011.

Table 2 Relationship between lagoon depth, the proportion of time sample sites were subject to light limitation or bed exposure, and *Ruppia* abundance

| Depth category (mean ground elevation relative to msl) | No. sites (total = 48) | % growing season ^a light limiting (WL > 1 m) ^b | | | % growing season ^a bed exposed (no water) | | | <i>Ruppia</i> abundance (mean % cover abundance) | | | | | |
|---|---------------------------|--|------|-------|--|------|------|--|------|------|---------------------|------|------|
| | | | | | | | | <i>R. megacarpa</i> | | | <i>R. polycarpa</i> | | |
| | | 2009 | 2010 | 2011 | 2009 | 2010 | 2011 | 2009 | 2010 | 2011 | 2009 | 2010 | 2011 |
| A (–1,450 mm) | 1 | 100.0 | 99.2 | 100.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| B (–1,180 mm) | 2 | 100.0 | 99.2 | 99.2 | 0.0 | 0.0 | 0.0 | 12.4 | 0.0 | 0.0 | 8.8 | 0.0 | 0.0 |
| C (–800 mm) | 2 | 86.4 | 76.5 | 35.8 | 0.0 | 0.0 | 0.0 | 4.5 | 0.0 | 1.5 | 0.0 | 0.0 | 0.0 |
| D (–610 mm) | 7 | 82.3 | 67.1 | 24.3 | 0.0 | 0.0 | 0.0 | 0.0 | 21.6 | 5.1 | 28.2 | 0.0 | 0.0 |
| E (–360 mm) | 9 | 43.2 | 35.0 | 24.3 | 0.0 | 0.8 | 0.0 | 1.0 | 5.2 | 0.0 | 23.4 | 15.0 | 1.6 |
| F (–130 mm) | 11 | 13.2 | 11.5 | 23.9 | 0.0 | 1.2 | 2.5 | 4.0 | 10.1 | 4.6 | 25.3 | 5.6 | 0.0 |
| G (130 mm) | 15 | 10.3 | 0.0 | 23.9 | 11.5 | 20.6 | 56.4 | 0.0 | 1.7 | 0.0 | 10.4 | 7.5 | 0.0 |
| H (250 mm) | 1 | 10.3 | 0.0 | 23.9 | 14.4 | 25.5 | 68.3 | 0.0 | 0.0 | 0.0 | 46.7 | 3.8 | 0.0 |

^a Growing season (1 August–31 March) includes the key phases of life-cycle

^b 1 m light limitation depth estimated from pilot study

This tidal connection resulted in a significant drop in water levels and increase in salinity (Table 1). The duration and timing of these events were observed to directly influence the germination and growth of *R. megacarpa*, *R. polycarpa* and other macrophytes. Previous research from Lake Ellesmere/Te Waihora (Gerbeaux 1989, 1993) and the Coorong, Australia (Nicol 2005), noted fluctuations in salinity are linked to lethal and sub-lethal impacts on the life-cycles of *Ruppia*. Charophytes were also absent from the survey in 2010 (Fig. 3) that is potentially correlated to the prolonged duration of saline conditions. The preferred germination and growth range for *Ruppia* observed in New Zealand is between 4 and 8 ppt (Gerbeaux 1989). This compares with the optimal germination range of *R. polycarpa* in Australia being between 0 and 6 ppt (Sim et al. 2006). It has been noted that adult plant survival declines above 45 ppt (Sim et al. 2006; Nicol 2005). Salinity concentrations in Waituna Lagoon did not exceed 45 ppt, however concentrations >8 ppt were regularly recorded. The critical period for *Ruppia* germination is likely to be September to November (Gerbeaux 1989; Nicol 2005). Salinity was recorded >8 ppt over this entire period in both the 2009–2010 and 2010–2011 seasons, which may explain the recorded down trend in *Ruppia* abundance, both in terms of site occupancy and foliage cover.

Some *Ruppia* species have been identified as “sun or high light” plants (Kantrud 1991). As the productivity of submerged macrophytes is dependent on adequate light penetration (e.g. Schwarz et al. 2002; Squires et al. 2002) the light environment therefore controls the depth distribution of *Ruppia*. The underwater light environment in the South Lagoon of the Coorong, Australia, is a major determinant of the distribution of *R. tuberosa*. High turbidity prevented *R. tuberosa* from growing at depths greater than 1 m (Paton 2001; Paton and Bolton 2001). Light requirements of *R. megacarpa* and *R. polycarpa* are not as well understood. Studies from the Coorong suggest *R. megacarpa* is uncommon in water deeper than 1 m and absent from water deeper than 2 m (Geddes 1987). Our estimation of the 10 % light attenuation depth (D_{10}) for Waituna Lagoon suggested that at water depths >1 m *Ruppia* will be somewhat affected by low light levels. This was corroborated as sites that spent the entire growing season at depths >1 m had little *Ruppia* growth (Table 2). Schallenberg and Tyrell (2006) applied a conceptual light model to Waituna

Lagoon and explored different water level scenarios. They predicted macrophyte growth is confined to zones between the lowest water level and the depth where light limitation causes plants to die off. They recommended that the duration of high water levels >1.8 m should not exceed two months. Our findings suggest that *Ruppia* may be able to withstand up to 30–40 % of the growing season in a moderately-stressed light environment (>1.0 m deep) (Table 2).

The depth distribution of *Ruppia* was also driven by exposure to desiccation. The minimum average water depth of sites that support *R. megacarpa* in Waituna Lagoon is approximately 0.5 m. This aligns with studies of *R. tuberosa* in the Coorong (Freebairn 1998; Australian Water Environments 2003) and *R. cirrhosa* in South Africa (Adams and Bate 1994) that similarly observed these species at depths between 0.4 and 0.8 m, sufficient to avoid desiccation. *R. polycarpa* in contrast occupied the high elevation sites susceptible to drying out during opening events. The observed decline in *R. polycarpa* at these sites in 2011 corresponded to the prolonged opening event and bed exposure (Table 2). *R. polycarpa* is often found in ephemeral habitats where it germinates from seed after inundation (e.g. Nicol 2005). According to Sim et al. (2006) not all viable seeds germinate at once in these habitats. In coastal systems where exposure from tidal influences is experienced this reproductive strategy may also occur, enabling rapid establishment after lagoon closure and re-wetting of habitat with declining salinity concentrations from freshwater inflows. Further investigation of the response and long-term viability of the seed bank is advocated to compare the impacts of alternative hydrological regimes on *Ruppia* reproductive strategies (Casanova and Brock 1990; Riddin and Adams 2009). This will help inform predictive models of *R. polycarpa* and *R. megacarpa* germination and growth in Waituna Lagoon.

Elevated loads of nitrogen and phosphorus are reported for the study region. Eutrophication of coastal lagoon systems is often a precursor for switching to an algal-dominated community (Cloern 2001). Monthly water samples from Waituna Lagoon during the study period recorded low chlorophyll concentration (Table 1) indicating relatively low abundance of phytoplankton. However, increased loading of TN and TP (Robertson et al. 2011) and the presence of benthic macroalgae such as *B. antillarum* identifies a further potential stressor to

the ecological character of the coastal lagoon. Scheffer et al. (2001) noted that while many systems experience gradual shifts in climate, nutrients and other stressors, stochastic events can lead to sudden shifts in ecosystem state. Gradual loss of the resilience of aquatic plants in Waituna Lagoon through elevated nutrient concentrations may render the lagoon vulnerable to stochastic fluctuations associated with opening events. Our findings suggest the key drivers of *Ruppia* productivity in Waituna Lagoon, and the resultant variation in macrophyte abundance, as being directly related to hydrological changes associated with opening and closing. The decline in *Ruppia* site occupancy from 69 % in 2009 to 23 % in 2011 is largely attributed to the prolonged period of salinity >20 ppt during key life cycle stages, and the increase in bed exposure from low water levels.

Implications for coastal lagoon management

One of the global challenges for conservation is to maintain the biological diversity and ecosystem services provided by aquatic environments, particularly freshwater and brackish ecosystems (Silk 2005). A change in the ecological character of Waituna Lagoon resulting from the decline of aquatic macrophytes is a primary concern for the wetland managers. While caution is required in making conclusions on cause-effect relationships in dynamic wetland ecosystems, our study observed a decline in *Ruppia* over a three year period and highly variable water properties. The increased understanding of key ecosystem drivers enables identification of indicators to inform management decisions. We suggest three measures for tracking the aquatic plant community response to management; water properties (% growing season subject to low/high salinity; chlorophyll a; nutrients), hydrological change (change in water levels during growing season) and aquatic plant composition [species diversity; frequency of occurrence (% sites); *Ruppia* cover abundance].

Opening events have occurred for >80 years at Waituna Lagoon to protect surrounding agricultural land from inundation, and throughout this time the aquatic plant community has persisted. In the future, opening events are likely to be utilised as a management tool to reduce eutrophication and the rate of sediment deposition. During open phases the lagoon nutrient concentrations (e.g. TN) are typically much

lower than during corresponding closed, freshwater phases (Table 1). In the longer-term the viability of lagoon opening events to flush nutrients and sediment may also become compromised due to climate change as higher sea-levels reduce outflow volumes. Optimising management to protect the integrity of the *Ruppia* community requires clear understanding of the trade-offs involved with alternative lagoon management scenarios. If being used to mitigate the pressure of eutrophication on the ecosystem, these scenarios must consider the resilience of the macrophyte community to prolonged exposure to salinity and desiccation.

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