

The growth of aquatic macrophytes (*Ruppia tuberosa* spp. and *Althenia cylindrocarpa*) and the filamentous algal community in the southern Coorong

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Aboriginal people are the First Peoples and Nations of South Australia. The Coorong, connected waters and surrounding lands have sustained unique First Nations cultures since time immemorial.

The Goyder Institute for Water Research acknowledges the range of First Nations' rights, interests and obligations for the Coorong and connected waterways and the cultural connections that exist between Ngarrindjeri Nations and First Nations of the South East peoples across the region and seeks to support their equitable engagement.

Aboriginal peoples' spiritual, social, cultural and economic practices come from their lands and waters, and they continue to maintain their cultural heritage, economies, languages and laws which are of ongoing importance.

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Executive Summary

The Coorong, located at the downstream end of the Murray-Darling Basin, was listed as a Ramsar wetland of international importance in 1985. Ramsar listed wetlands are recognised for the significant ecosystem services that they provide, with the Convention requiring a site to remain in the same ecological condition it was at the time of its listing. The Coorong has experienced declining ecological health over recent decades and is currently exhibiting signs of ecological stress, indicated by changes in biological communities including reduced numbers or absence of fish, invertebrates and birds, through hyper salinity and eutrophication.

The Coorong itself is a shallow, narrow saline to hypersaline lagoon with a narrow constriction in the central section separating the northern and southern sections. The central section, where constriction occurs, provides a barrier to the exchange of water, sediments and nutrients, leading to different system scale dynamics either side of this area. The Coorong South Lagoon, south of this constriction area from Parnka Point, is the region under the greatest ecological stress, which is exemplified by the presence of large scale filamentous algal blooms and high-water column chlorophyll *a* concentrations.

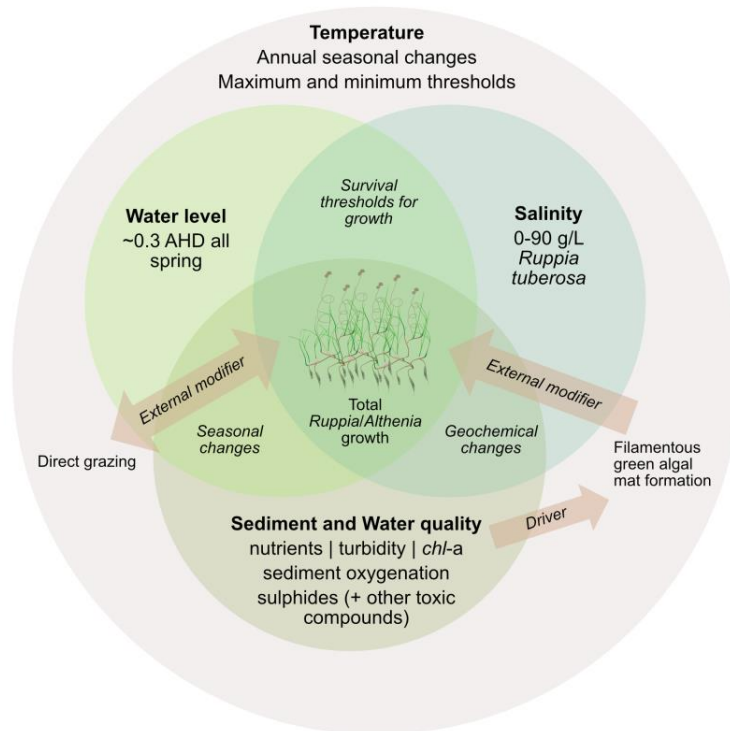
The dominant submerged aquatic macrophyte community of the Coorong central and South Lagoon is often a 'mixed' community of *Ruppia tuberosa* and *Althenia cylindrocarpa* (referred to as *R. tuberosa/Althenia* herein). This community is a major food source of the tens of thousands of waterbirds, including migratory shorebirds, that inhabit the Coorong. *Ruppia tuberosa* is recognised as a keystone species in the Coorong.

Although it is recognised that the ecological health of the Coorong was in decline prior to the Millennium Drought (2001–2010), the system was dramatically changed because of this period of extreme conditions. Hydrological changes in the River Murray combined with high evaporation rates caused low water levels in the Coorong. In addition, it is hypothesised that increased nutrient loads have accumulated in the system, leading to eutrophication. Lower water levels and reduced inputs and exchange between the Coorong North and South Lagoons have also resulted in higher salinities that have reached extreme-hyper salinities towards the end of the drought and periodically since.

The Millennium Drought led to conditions that caused seed bank depletion and almost the complete loss of the *R. tuberosa/Althenia* community in the South Lagoon. However, consistent seasonal water levels above 0.3 m, during the *R. tuberosa/Althenia* critical reproductive life cycle stage since 2016 (excluding 2018), has resulted in improved environmental conditions and the instigation of the recovery of the *R. tuberosa/Althenia* community. However, it is hypothesised that excess nutrients have led to the formation of filamentous algae blooms. When these blooms coincide with the critical reproductive life stage of *R. tuberosa/Althenia*, where flowers and developing fruits are floating in the water column, seed set is impacted. This has a significant effect on the annual recovery cycle, and more importantly, the formation of a resilient *R. tuberosa/Althenia* community in the long term.

The growth of *R. tuberosa/Althenia* in the South Lagoon is limited by the combined and interacting effects of temperature, water level, salinity, nutrients loads (water and sediment) and their flow on effects to the system and external modifiers such as filamentous algae formation and grazing (figure below). Environmental parameters (i.e., salinity, temperature, light, water level and algal biomass) suitable to supporting the seasonal growth of *R. tuberosa/Althenia* through different life stages in the South Lagoon are variable. Identifying the optimal conditions, based on the available literature, recent observations and key findings provide an improved framework for predicting optimal habitat suitability for *R. tuberosa/Althenia* in the Coorong.

The presence of the large scale filamentous algal blooms in the South Lagoon is representative of changes in the dominant primary producers where significant production is in the form of high turnover species. The return of *R. tuberosa/Althenia*, with their longer-term fixed carbon, is required to improve ecosystem health. The co-benefits of returning *R. tuberosa/Althenia* would be the potential return of macroinvertebrates and foraging species of fish and birds if accompanied by appropriate hydrological and physical conditions, principally lower salinities.



Key knowledge and information gaps that if addressed will support the achievement of improved ecological outcomes for the Coorong include:

- Development of an updated distribution of *R. tuberosa/Althenia* in the central Coorong and South Lagoon that will provide a critical baseline for future assessments of change and augment long term monitoring data sets such as those generated for The Living Murray Program.
- A review of the available data to determine the optimal water depths for abundance, distribution, growth and survival of *R. tuberosa* (including reproductive state/s). These values will play a significant role in the development of modelling for the Habitat Suitability Index for *R. tuberosa* in the South Lagoon and may change priorities for management.
- The nutrient allocations to different primary producers. This is poorly understood and in particular the interaction between the growth of *R. tuberosa/Althenia*, water column phytoplankton, benthic algal communities and other sediment and water column the microbiota. These other organisms likely represent a higher than desired proportion of the current productivity of the Coorong ecosystem.
- The formation of filamentous algae blooms during the critical reproductive life stage of *R. tuberosa/Althenia*. This stage has significant effect on the restoration and maintenance of the seagrass community in the South Lagoon. As the filamentous green algae have been found to have overlapping survival thresholds with *R. tuberosa*, and presumably *Althenia*, alternative interventions or management regimes that will reduce filamentous algae growth in the Coorong need to be identified.
- The impacts of the long-term exposure of *R. tuberosa/Althenia* seed banks to sediments with high concentrations of organic matter, sulfides and other breakdown compounds (organic sludge). This may lead to reduced seed viability or inhibit germination and remains untested.
- The impact of organic sludge sediments on the biogeochemistry and how this directly effects *R. tuberosa/Althenia* productivity and growth.
- The composition of the macrophyte community. *R. tuberosa* and *Althenia* are indistinguishable unless flowering, and as a result *R. tuberosa* was long believed to be the only species present in the South Lagoon. A majority of the aquatic macrophyte research in the Coorong has focused on *R. tuberosa*. *Althenia* appears to have similar thresholds as *R. tuberosa* for optimal growth, abundance

and distribution. However, this is an assumption made on based on their mixed presence in the Coorong and similar life cycle stages and a more detailed understanding of the relative proportions of *R. tuberosa* or *Althenia* in current populations is important for determining the need to document life history traits management of viable populations of the latter.

Based on available knowledge regarding, requirements to support and/or restore a healthy submerged macrophyte community in the South Lagoon include: a variable annual salinity, with highest levels in summer due to evaporation and lower levels in winter-early spring due to freshwater inputs. The Coorong ecosystem also requires water depths where plants remain in a moderate photic zone but do not get exposed to drying out before the completion of the reproductive cycle. The expected optimum annual mean water surface elevation for the growing season (April–December) is currently estimated at 0.3 m AHD but this requires updating based on the current physical structure of the system.

The previously robust mixed submerged angiosperm community (e.g., *R. tuberosa* and *Althenia*) in the Coorong has been assessed as being in a vulnerable state by an expert panel review. It will be critical, in any attempt to recover the system through management intervention solutions must therefore support the critical life cycle stages of *R. tuberosa*. In addition to management of salinity and water levels, options for reducing filamentous algal loads, will likely improve the rate of *R. tuberosa* recovery in the Coorong ecosystem from its current state.

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1 Context

The Coorong is culturally, environmentally and economically important at local, national and international scales but has experienced a long-term decline in its ecological condition due to reductions in inflows from the River Murray. The Millennium Drought from 2001 to 2010 caused severe reductions to inflows to the Coorong and resulted in a decline in its ecological condition, particularly in the South Lagoon (Figure 1) which experienced extreme salinisation (up to five times seawater salinity (Mosley et al. 2020)), widespread loss of aquatic vegetation and declines in the diversity and abundance of fish and waterbirds (Brookes et al., 2018). While there has been recovery in components of the Coorong ecosystem such as fish (Ye et al., 2015) associated with increased inflows to the North Lagoon since the Millennium Drought, the recovery of the Coorong South Lagoon has not returned to the levels expected (Nicol et al., 2018). For example, the Coorong South Lagoon was once dominated by aquatic plants such as *Ruppia tuberosa* and *Althenia cylindrocarpa* (referred herein as *R. tuberosa/Althenia*), that formed extensive areas, but the system has now switched to one dominated by filamentous algae and frequent phytoplankton blooms during warmer months. This has resulted in decreased submerged aquatic plant abundance and habitat quality and subsequent impacts on invertebrate, fish and waterbird communities (Brookes et al., 2018). The shift to an algal dominated system has been associated with eutrophication (nutrient enrichment), the cause of which is poorly understood (Mosley et al., 2020; Waycott et al., 2020b).

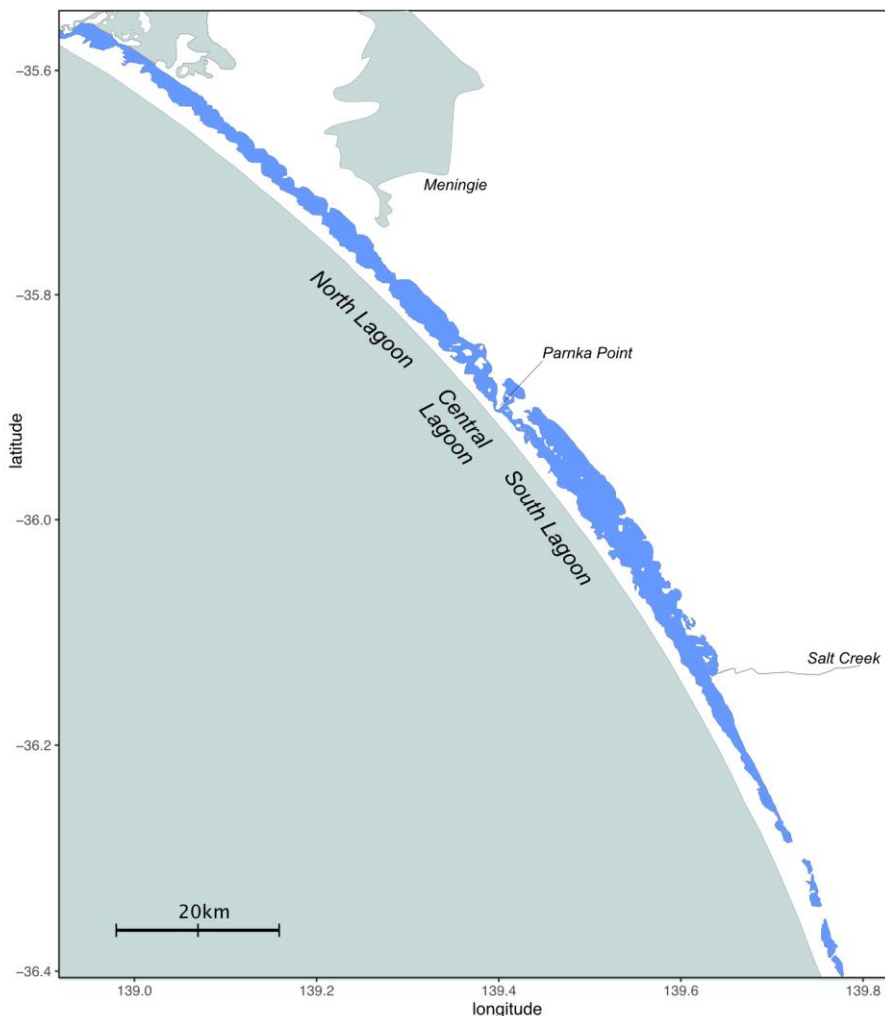


Figure 1. Map of the Coorong region indicating the general locations of areas used throughout this report.

The profound ecosystem changes and poor trajectory in recovery of the overall Coorong ecosystem is likely caused by a number of complex, interacting factors. This lack of knowledge impedes our ability to robustly forecast and predict the ecological response of Coorong aquatic plant communities to future management scenarios that seek to restore the health of the Coorong and prevent further impacts to the functioning of the ecosystem. This diminishes the capacity of decision makers to identify potential management interventions that can minimise/mitigate risks, maintain ecological values and/or prevent further ecosystem decline and/or the complete loss of highly value ecological functions.

The Phase One Trials and Investigations (T&I) Project of the Healthy Coorong Healthy Basin (HCHB) program consists of a series of integrated components that will collectively provide knowledge to inform the future management of the Coorong. *Component 2 – Investigating the drivers and control of filamentous algae and restoration of aquatic plants in the Coorong* forms part of the T&I Project. The overall objective of this project is to support ongoing management of the Coorong as an element of the Coorong, Lakes Alexandrina and Albert Wetland of International Importance under the Ramsar Convention as outlined in the Ecological Character Description by Phillips and Muller (2006) that was updated to the 2015 ecological character of the system (DEW 2015). In particular, the project aims to assist in delivering outcomes that maintain the health of the Coorong by undertaking research to address the issues outlined in the Ecological Character Description for *Ruppia tuberosa* (Paton et al. 2015). To achieve this, the approach has been to design components of research supporting the management of the Coorong such that it will:

- avoid the permanent loss of ecological values of the Coorong South Lagoon;
- restore the ecological values for the Coorong South Lagoon; and
- create an ecosystem that maintains the ecological values under climate change.

The primary focus for this component is to investigate how to reduce the extent of dominance of algae over seagrasses and other aquatic macrophytes during warmer months. Through improved understanding of *R. tuberosa* and its requirements, this research will contribute to several overarching management actions:

- 1) How to optimise the use of existing infrastructure to limit filamentous algal growth?
- 2) How to restore aquatic plant (i.e., *R. tuberosa*) distribution and abundance?
- 3) What are the additional management interventions required to assist with this recovery?

1.1 Aims

The overarching aim of Activity 2.1.1 “Knowledge synthesis report” is to collate and summarise available knowledge on the factors influencing the growth of aquatic macrophytes (*R. tuberosa* and *Althenia*) and filamentous algae in the Coorong South Lagoon. The relatively recent review of *R. tuberosa* and algae in the Coorong ecosystem by Collier et al. (2017), through the *Optimising Coorong R. tuberosa Habitat Project*, serves as a basis for this review, which extends the scope to include more recent studies and early stages of work completed in the HCHB Program.

This technical report is a contractual deliverable for the T&I project and meets the reporting requirements specified in the *Component 2 – Investigating the drivers and control of filamentous algae and restoration of aquatic plants in the Coorong* Project Plan. This report presents the results of work completed during the period from July to November 2020.

2 Aquatic macrophytes of the Coorong South Lagoon

2.1 Prior to the Millennium Drought

Historically there has been a persistent mixed sea grass community in the Coorong, which has included species such as *Ruppia megacarpa*, *R. polycarpa*, *R. tuberosa*, and *Althenia* (*syn. Lepilaena*) *cylindrocarpa* (Collier et al., 2017; Nicol 2005). The historical changes in the distribution of submerged aquatic macrophytes/seagrasses in the Coorong appear to have been associated with the ability to tolerate and thrive under the hyper-salinity conditions. *Ruppia tuberosa* is the most tolerant of such conditions, followed by *R. megacarpa* and another primarily estuarine seagrass species, *Zostera muelleri* (Collier et al., 2017). Changes in water level combined with increased salinity (including the lack of freshwater pulses at key times) led to the loss of seed banks and other propagules and subsequent changes in the abundance and distribution of *R. tuberosa* throughout the Coorong (Whipp 2010). The research conducted by Dick et al. (Dick et al., 2011) through radio-isotopic dating at Villa Dei Yumpa determined that *R. megacarpa* was dominant historically (>1000 years ago) in the Coorong South Lagoon. Its modern absence most likely resulted from a shrinking distribution following European settlement and the alteration of the River Murray flows which affected salinity and water level (Dick et al., 2011).

Other features of the different species of submerged aquatic plants that have been observed historically in the Coorong include differences in seed size. The seeds of *Ruppia tuberosa*, *R. megacarpa*, *R. polycarpa*, *Althenia cylindrocarpa* and *Zostera muelleri* vary in size and shape and the way that seeds are attached to the inflorescence peduncle (the spiral stem attaching the flowers to the main plant) (Waycott et al., 2014). *Ruppia tuberosa* has the smallest seeds which have a very short or non-existent point of attachment to the flowering stem (peduncle) that joins the seeds forming a star shaped hand when mature. Larger smooth coated seeds typically are from *R. megacarpa* and more easy to observe in sediments when present. These differences in seed types could be used in monitoring but have been not discussed in the literature.

Since the early 1970s, a changing Coorong aquatic plant community has been well documented (Geddes 1987; Geddes and Butler 1984; Noye 1973; Womersley 1975). These changes to the aquatic plant community are attributed to the changing environmental conditions (Figure 2). The main factors limiting the growth of submerged aquatic plants in the Coorong include: water depths, salinity levels, light availability and sediment type. In brief, high salinity has significant effects on seed and turion germination, flower and seed production, and shoot abundance of *R. tuberosa* in the Coorong (Kim et al., 2015; Kim et al., 2013), while optimal water levels are critical for completion of the *R. tuberosa* life cycle (Collier et al., 2017; Ye et al., 2016).

In the Coorong North Lagoon, which is less saline than the South Lagoon, *R. megacarpa* was dominant in the 1970s to mid-1990s. It has not been officially recorded by routine monitoring since 1995 and seeds in sediments have not been observed (Nicol 2005). It should be noted that the current monitoring targets the expected range of *R. tuberosa* in hypersaline waters that occur annually in the southern end of North and the South Lagoon (Paton et al., 2017b). *Zostera muelleri* was at times present in the North Lagoon, towards the ocean influenced waters where it survived in the Coorong (Nicol 2005). Characterised as a historical component of the Coorong (Phillips and Muller 2006), *Z. muelleri* requires modest salinities (marine ~35 ppt) and relatively stable water levels to persist.

2.2 Since the Millennium Drought

The Millennium Drought (2001—2010) resulted in large-scale losses of the *R. tuberosa* and *Althenia* plant communities in the Coorong (Collier et al., 2017; van Dijk et al., 2013). The drought was one of the driest periods recorded for southeast Australia and inflows to the Coorong were reduced (Ferguson et al., 2013). The reduced flow, combined with high evaporation rates, resulted in water levels in the South Lagoon dropping below a threshold for *R. tuberosa* tolerance (+0.2 m AHD) early in the growing season, thereby limiting the completion of its annual life cycle (Collier et al., 2017; Ye et al., 2016). It is expected that the

distribution and abundance of *Althenia* followed a trajectory given its current co-association with *R. tuberosa* in the Coorong, although this has not been established and little research has been conducted to date on the environmental conditions that are favourable for its life-cycle.

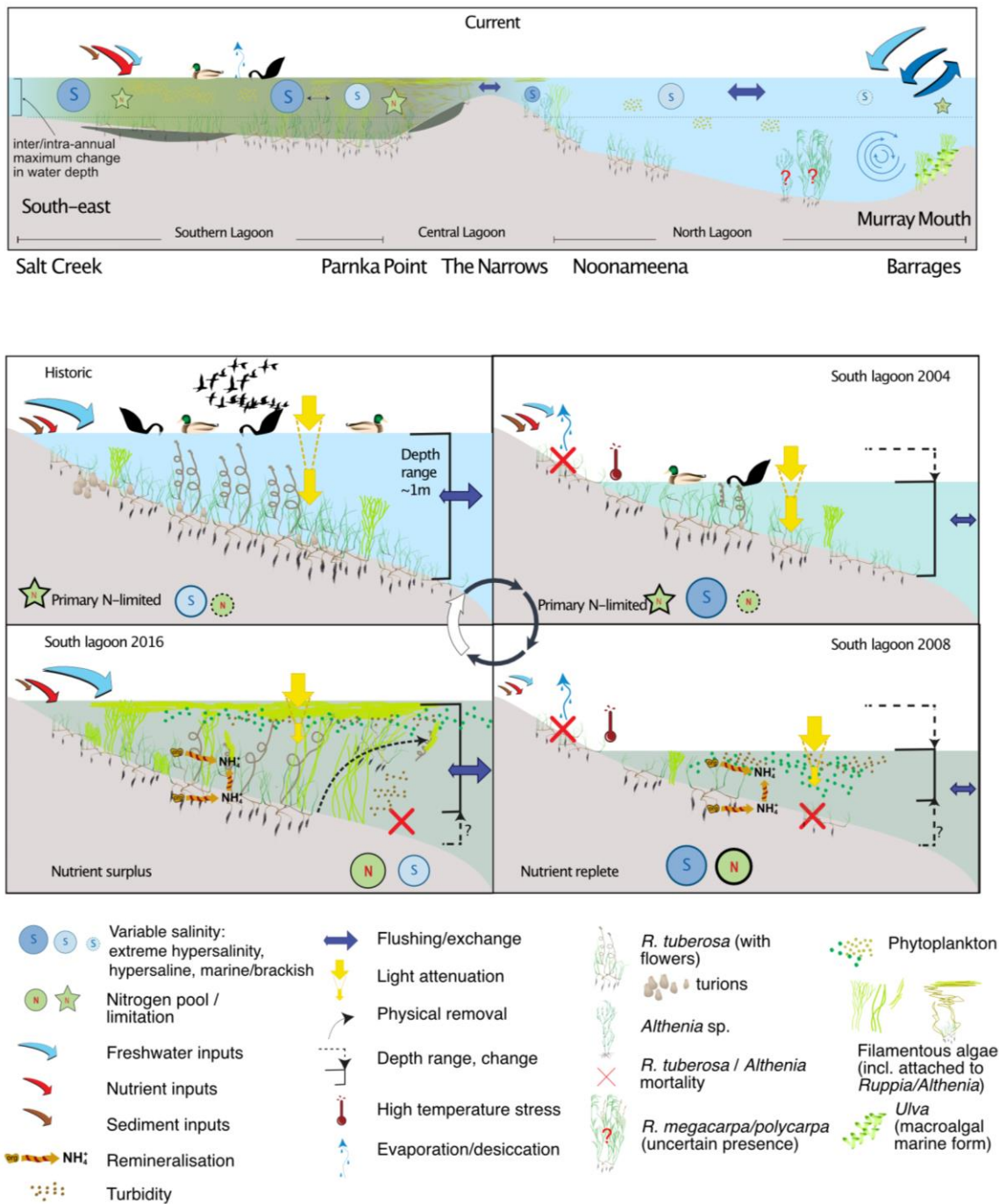


Figure 2. Conceptual diagram summarising the current and four historical states of the Coorong based on observed ecological conditions. Legend for icon use in lowest panel. Adapted from Collier et al. (2017).

2.3 Current Status

The current submerged aquatic macrophyte community in the central and southern sections of the Coorong (Figure 1) is composed of *R. tuberosa* and *A. cylindrocarpa* (Paton et al., 2020; Waycott et al., 2020b). These macrophytes appear able to tolerate highly variable conditions from fresh through to hypersaline conditions (Brock 1982a; Collier et al., 2017; Vollebergh and Congdon 1986). However, despite their presence

historically, there have been no observations of *R. megacarpa* and *R. polycarpa* in the South or North Lagoons of the Coorong since the mid-1990's (Dick et al., 2011; Nicol et al., 2018; Nicol 2005; Phillips and Muller 2006). *Ruppia megacarpa*, with its lower salinity tolerance (0–30 g/L) (Brock 1982a; Collier et al., 2017; Dick et al., 2011; Kim et al., 2013; Womersley 1975), has the potential to occur in restricted locations and seasons in the Coorong's North Lagoon. However, the presence of *R. megacarpa* has not been confirmed in the Coorong lagoons for several years despite being commonly found in the Lower Lakes (Lake Alexandrina and Lake Albert) and Goolwa boating channels (D. Cunningham, herbarium specimen, provided 2014). Similarly, while collections of *R. polycarpa* associated with the Coorong predate the 1980's (Nicol et al., 2018; Nicol 2005), it has been collected from surrounding lakes and wetlands, with some having salinities greater than seawater (see avh.chah.org.au), indicating *R. polycarpa* potentially may potentially return to the system if conditions change.

Ruppia tuberosa is considered a keystone species of the South Lagoon, underpinning the ecological functioning of the system (Phillips and Muller 2006); maintaining water quality, trapping and stabilising sediment, providing habitat for invertebrates and fish and food for waterbirds (Paton et al., 2016; Rogers and Paton 2009). *Ruppia tuberosa* appears to exhibit the widest salinity tolerance of any submerged aquatic angiosperm (Nicol 2005). However, historical changes to the environmental conditions of the Coorong have negatively impacted the distribution, abundance and viability of the *R. tuberosa* population in the Coorong.

The presence of *Althenia cylindrocarpa* (previously placed in the genus *Lepilaena*) has often been overlooked in the published monitoring literature (Paton et al., 2020), presumably because of its patchy distribution and the difficulty of discriminating *Althenia* plants from *R. tuberosa* when not in flower or fruit. *Althenia* has been widespread in the South Lagoon since at least 2015 (Collier et al., 2017; Waycott et al., 2020b), although observations of its frequency of occurrence and biomass is often lower than *R. tuberosa*. Determining the extent and the relative contribution that *Althenia* makes to the overall aquatic plant community in the Coorong, will be important in evaluating the total productivity and resource availability in the system.

The current state of the previously robust mixed species community of submerged aquatic macrophytes (e.g. *R. tuberosa* and *Althenia*) in the Coorong has been described as being in a vulnerable state by an expert panel (Brookes et al., 2018), requiring significant effort to restore its resilience. The status of the community continues to be routinely monitored (e.g. most recently Paton et al., 2020), and conceptual models have been developed depicting the alternative ecosystem states and providing a frame of reference for understanding ongoing changes (i.e. Figure 2). The importance of aquatic macrophytes in the Coorong, along with recognition of the environmental drivers and ecological character of the South Lagoon, in particular, have been well documented (Brock 1986; Brock 1982a; b; 1983; Brookes et al., 2018; Collier et al., 2017; Kim et al., 2015; Nicol 2005; Paton et al., 2015; Paton et al., 2019a; Paton et al., 2020; Phillips and Muller 2006; Rogers and Paton 2009; Waycott et al., 2020b; Womersley 1975). The past 20 years of research and monitoring of the Coorong aquatic plant communities has helped to characterise a highly variable system recovering from almost complete loss of a *R. tuberosa* dominated aquatic plant community following the Millennium Drought (Collier et al., 2017; Frahn and Gehrig 2015; Nicol 2005; Paton and Bailey 2014; Paton et al., 2020; Rogers and Paton 2009; van Dijk et al., 2013; Waycott et al., 2020b). The loss of *R. tuberosa* and *Althenia* vegetation significantly affects the invertebrates, fish and migratory waterbird populations for which it provides food and/or habitat.

2.4 Growth of *R. tuberosa*

Ruppia tuberosa and *Althenia* are important primary producers in the Coorong, providing ecological services to the fish and waterbird community (Dick et al., 2011; Kim et al., 2015; Paton et al., 2011). Classed as seagrasses (Kilminster et al., 2015), both *R. tuberosa* and *A. cylindrocarpa* are recognised as colonising species exhibiting characteristics that enable rapid recovery from frequent perturbations. *Ruppia tuberosa* and *Althenia* exhibit extraordinary tolerances for extreme environmental conditions, including the hypersaline and extreme-hypersaline conditions of the Coorong. As a result of the persistent extreme-hypersaline conditions of the Coorong (Mosley et al., 2020), *R. tuberosa* and *Althenia* have become the dominant angiosperms in the system, presumably out-competing *R. megacarpa* and *R. polycarpa* (Geddes and Butler 1984; Haynes et al., 2018; Nicol et al., 2018; Nicol 2005; Paton 2010; Rogers and Paton 2009). *Althenia* has

not been regularly recorded in routine surveys, as previously mentioned, and therefore an understanding of its distribution and relative competitive ability still remains a knowledge gap.

Ruppia tuberosa is often referred to as an annual species that occurs in salinities ranging from 13–230 g/L and reproduces both sexually and asexually through seeds and turions, respectively (Brock 1982a; Collier et al., 2017; Kim et al., 2013). However the current observations of *R. tuberosa* in the Coorong suggests there is a perennial form of this species, where vegetative growth continues over summer (Waycott 2020). *Ruppia polycarpa* and *R. tuberosa* are the only *Ruppia* species known to produce turions, with two types (Type I and II) recognised for *R. tuberosa* (Brock 1982a; b; Vollebergh and Congdon 1986). *Ruppia tuberosa* has a continuous life cycle (Figure 3), spanning from the austral autumn to summer. Initial life cycle stages (e.g. seed germination or turion sprouting) begin in mid to late autumn (March to May) and are followed by active growth (vegetative colonisation), development of reproductive structures (flowers or turions) and then propagule dispersal or deposition (e.g. seed bank production or turion formation) by late spring to early summer (Figure 4) (Brock 1982b; Collier et al., 2017; Paton et al., 2018). Dormant *R. tuberosa* reproductive propagules (i.e., seeds and turions) will survive through summer and germinate or sprout in the subsequent autumn if rewetting occurs. However, seed bank germination appears to persist over several growing seasons as a result of sporadic seed germination (Brock 1982b; Kim et al., 2013).

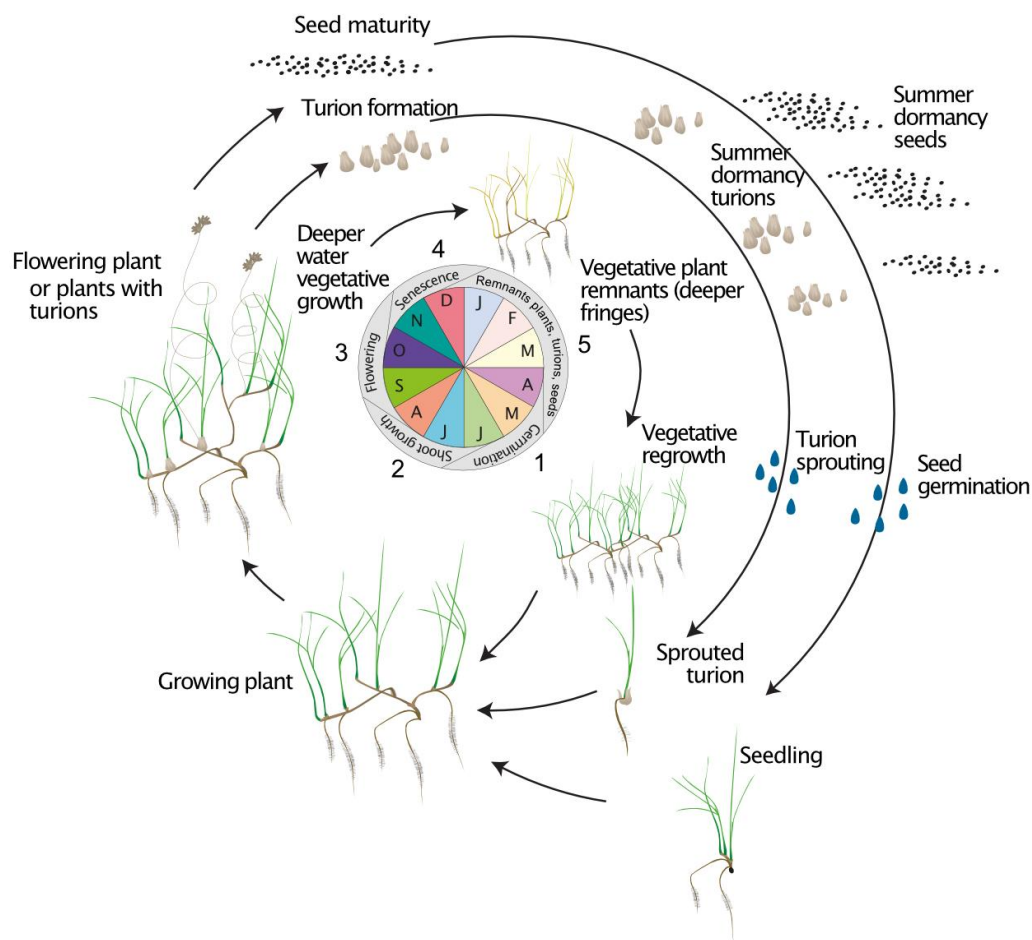


Figure 3. Conceptual diagram of the *R. tuberosa* five-stage life cycle showing annual growth through three possible life cycle pathways; whole plants, seeds and turions. Updated from Collier et al (2017) to include more complete view of the *R. tuberosa* life cycle including three potential growth modes: vegetative (whole plant survival); asexual persistence (turions); sexual (seed bank).

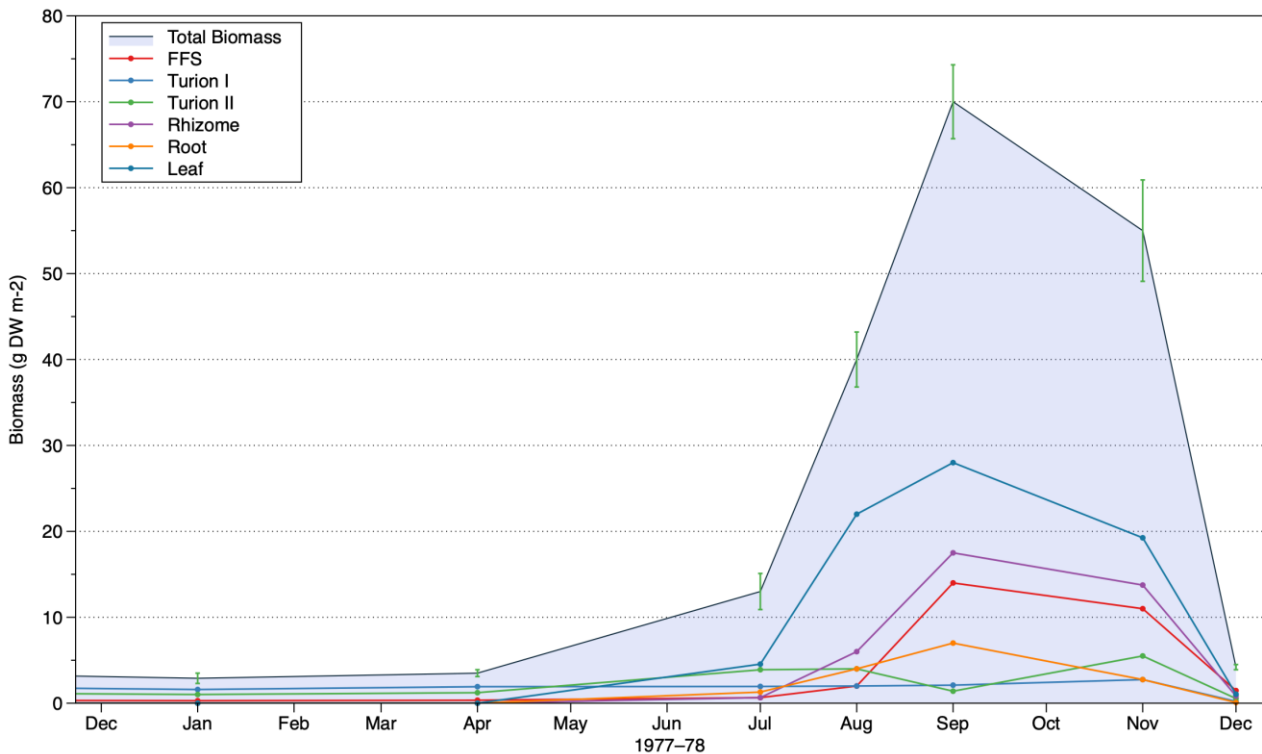


Figure 4. Seasonal life cycle of *R. tuberosa* in the Coorong, indicative changes in the biomass from leaves, rhizomes, roots, FFS (flowers and seed) and turions over a year. Data source: (Brock 1983).

2.4.1 Seasonality and *R. tuberosa* growth in the Coorong

The biology of the aquatic macrophytes that persist in the Coorong, in particular the South Lagoon, is dominated by strong seasonal cycles that also vary inter-annually, consistent with temporal changes in conditions within the Coorong. The hydrological conditions vary over the annual cycle of the Coorong system (Gibbs et al., 2018) and, along with the seasonal changes in temperature, wind and resulting system net evaporation, lead to a natural cycle of extreme water level and salinity changes. Of the dominant aquatic plants in the Coorong and the region, our understanding of the life cycle of *R. tuberosa* is best known. Brock (1982a; 1983; 1986) captured critical features of macrophyte life cycles and documented conditions favourable for the growth of *R. tuberosa*. It is worth noting that data is very limited for *Althenia*. There are a number of factors that influence the five stages of *R. tuberosa* (Figure 3). Further detail on each stage and the risks to progression to the next life stage are presented in section 3. Here we focus on the importance of one of the primary drivers associated with the seasonal growth cycle of *R. tuberosa*: salinity. Salinity is correlated with freshwater inputs in autumn and winter, with inputs lowering salinities. As water temperatures rise, evaporation increases and water levels drop, leading to higher salinity levels at the closure of the growing season. These combined factors, for which salinity is a surrogate, influence the major transitions in the life cycle of *R. tuberosa*.

Annual life cycle stage 1: Germination and recruitment

Germination

Salinity in the Coorong South Lagoon falls when the water levels rise with the increase in water inflows and rainfall and is lowest towards early spring (Gibbs et al., 2018). Long-term monitoring data shows that peak salinity occurs late March, after the very high evaporation rate and reduced connection with the Coorong North Lagoon in Summer (Gibbs et al., 2018). Seeds and turions have been documented to germinate or sprout upon inundation (Brock 1982b).

The range of salinities for seed germination has been determined experimentally for *R. tuberosa* to be between 0–90 g/L (Kim et al., 2013). In contrast, the upper salinity threshold for *R. megacarpa* germination is considerably lower, with a range of 0–30 g/L (Kim et al., 2013). This difference in upper germination salinity threshold is a significant difference between the tuberous and large seeded form of the two *R. tuberosa* forms (Kim et al., 2013). In addition to the experimental evidence, monitoring activities have detected *R. tuberosa* growing in a range of salinities (Paton et al., 2011; Paton and Bailey 2010; Paton and Bailey 2012; Paton et al., 2020; Waycott et al., 2020b) and this has been used to infer that *R. tuberosa* can also tolerate a wide range of salinities. There are no data available on what other factors may inhibit germination of *R. tuberosa* in anoxic or sulfidic sediments. This is a notable knowledge gap as sediments with high organic contents has been observed in the Coorong (Teasdale et al., 2020) in many areas where *R. tuberosa* seeds are deposited (Waycott 2020). *In situ* data documenting the conditions required for germination of *R. tuberosa* seeds in the Coorong also remain a knowledge gap.

Detailed experimental studies of turion germination (resprouting) (Brock 1982b; 1983; Kim et al., 2015; Kim et al., 2013) determined turion germination was highest between salinities of 70–125 g/L (14–74% germination rate; Figure 4). The time to germination following inundation of turions was also found to be longer as salinities increased, particularly above 120 g/L (Kim et al., 2013).

Recruitment (establishment)

Factors affecting the transition from seed germination or turion sprouting to recruitment, which can be defined as the stage when the seedling becomes capable of functioning as more than a single independent ramet (shoot), are currently unknown. It should be noted the dynamics of this process will differ for seedlings and sprouted turions as the resource allocation varies significantly (Brock 1983).

One of the critical components of the life history of plants that rely heavily on annual growth is the number of recruits that survive each growing season. The factors that influence the production, viability, germination/sprouting rates and seedling survival of seeds and turions are not fully understood. These factors are important for an improved understanding of the how many seeds are required to lead to viable seed stocks for *R. tuberosa* (Collier et al., 2017; Hipsey et al., 2020) that supports a reliant *R. tuberosa* population. There is currently a Condition Monitoring target of 2000 seeds m⁻² for with seed banks in the Coorong (Paton et al., 2017b), however we do not know if these numbers are adequate to regenerate or expand the current populations.

Annual life cycle stage 2: Shoot growth and vegetative expansion

Following germination from seeds or turions, there are likely a number of factors (e.g., timing) that influence the rate of patch growth and the resulting *R. tuberosa* meadow coverage and biomass for the senescent period over summer. The driving factors remain unknown in the Coorong, or elsewhere for *R. tuberosa*. Increased salinity has been observed to reduce the abundance and distribution of *R. tuberosa*, particularly in less salinity tolerant species (Sim et al., 2006).

It is well recognised that typically abundance is correlated negatively with salinity in *R. megacarpa* (Carruthers et al., 1999) and *R. polycarpa* (Sim et al., 2006). Optimal salinities for *R. tuberosa* shoot abundance have been observed to be between 19–70 g/L, supported by experiments and long term monitoring (Brock 1982b; Collier et al., 2017; Frahn and Gehrig 2015; Geddes 1987; Nicol 2005; Paton et al., 2020; Rogers and Paton 2009). Experimental evidence has shown increased *R. tuberosa* shoot abundance at salinities 19–70 g/L, declines between salinities of 70–109 g/L, but increases between 116 and 124 g/L, the latter most likely a stress response and a potential precursor to turion formation (Kim et al., 2015). Shoot abundance in *R. tuberosa* shows strong variability seasonally; abundance being highest in winter and spring, lowest in summer (Brock 1983) (Figure 4).

Annual life cycle stage 3: Flowering , propagule formation and turion formation

Factors affecting flowering and propagule/turion formation may include photoperiod, temperature (diurnal, seasonal), drought, salinity and nutrient availability, including relative proportions of macro and micro

nutrients (Bidwell 1979). In *R. tuberosa* flowering occurs in spring and summer (August – November) in the Coorong and other regional salt lakes (e.g. Lake Cantara, Lake George) (Brock 1982b). Evidence for this is flower abundance was highest at salinities between ~47 and 62 g/L and flower abundance was lowest at >70 g/L and <47 g/L (Brock 1982b; 1983; Kim et al., 2015; Kim et al., 2013; Nicol 2005; Paton and Bailey 2010). The observed reduction in *R. tuberosa* flowering with increasing salinity results in a decrease in the outputs of sexual reproduction (seeds).

There is a measurable increase in asexual reproduction (turions) for *R. tuberosa* in the Coorong compared to other habitats, associated with higher levels of salinity, particularly when salinity is elevated (estimated >70 g/L) early in spring (Collier et al., 2017; Kim et al., 2015; Paton et al., 2019b). The highest *R. tuberosa* turion densities in the Coorong and nearby Lake Cantara have been observed when salinity was greater than ~124 g/L (Kim et al., 2015) and up to 160 g/L and are most likely to occur where salinities are over 70 g/L (Kim 2014; Kim et al., 2015), although suboptimal at the lower and higher values that turions have been recorded. It is worth noting that once formed, turions are more vulnerable to extreme salinities than seeds due to a specific ion toxicity (Kim et al., 2013). Consequently, persistence of turions can decline at these higher concentrations when seeds may survive (Kim et al., 2015; Kim et al., 2013).

Annual life cycle stage 4: Senescence and maturation

The life cycle stage associated with completion of seed set in *R. tuberosa* has a high risk of reproductive failure in the Coorong. The flowers and setting seeds of *R. tuberosa* (and *Althenia*) form on an inflorescence that has a long peduncle forming spirals as the fruit matures (Jacobs and Brock 1982). These flowering structures can be up to 80 cm long (Jacobs and Brock 1982), however they are fragile and flexible, readily becoming caught up in anything floating towards the surface (Collier et al., 2017).

Once mature, seeds are released and sink to sediments, but they may be mobilised at this stage through sediment movement or ingestion by birds (Collier et al., 2017). The majority of seeds are likely to become incorporated into the local seed bank and persist for years buried in the sediments. Limited evidence for this is based on the observations by Rogers and Paton (2009) of reduced seed viability with sediment depth, most likely associated with the age of seed deposits.

For *R. tuberosa* there are two types of the asexual propagules (turions): type I and type II. These different types perform different functions relating to vegetative persistence (Brock 1982b). For instance, type I turions can be a resource for supporting ongoing plant growth. Persistence of type 1 turions is limited if fully exposed to the air when water levels recede (Brock 1982b). Type II turions are larger, more resistant to drying (i.e. and can survive several months of exposure) and extreme summer hyper-saline conditions (Paton et al., 2011). Type I turions are unlikely to function as a persistent propagule bank when water levels expose sediments during the summer months (Paton et al., 2011). The maturation of type II turions is critical for over-summer persistence of some populations, particularly if salinities become too high early in the seasonal cycle, or if exposure occurs before turions are fully formed (Paton et al., 2015). The primary threat to completion of turion formation appears to be the interaction between falling water levels and consequent exposure of plants. When the timing of higher salinities relative to the opportunity of plants to invest in flowering or turion initiation occurs too late for plants to allocate their reproductive effort, turion formation is likely to fail (Collier et al., 2017; Paton et al., 2015).

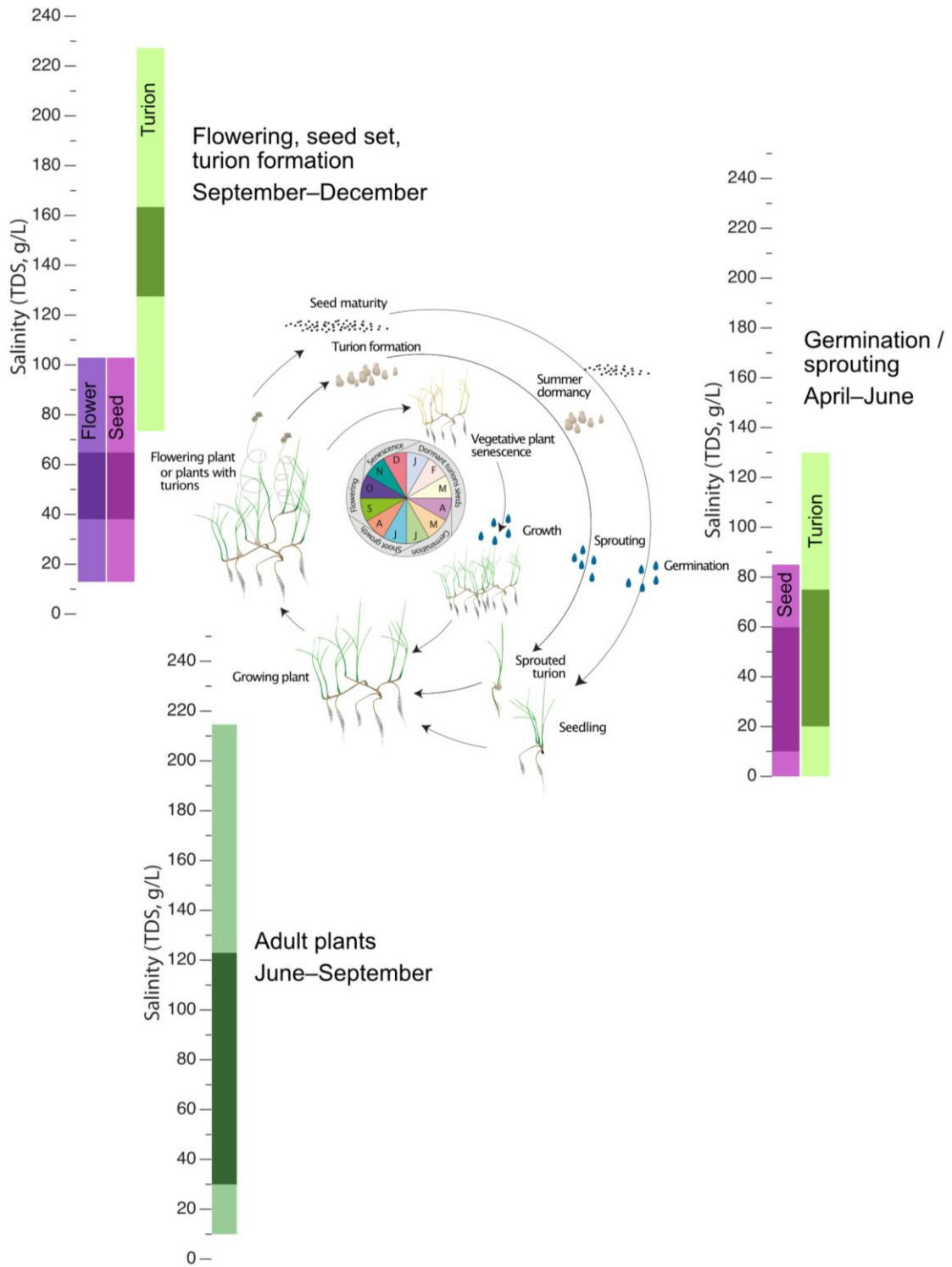


Figure 5. Summary of the optimal and extreme salinity ranges depicted on the life cycle model for *R. tuberosa*. Optimal conditions are shaded darker, lighter shades indicate sub-optimal conditions.

Annual life cycle stage 5: Propagule dormancy and vegetative persistence

For successful *R. tuberosa* growth in the Coorong it is essential that propagules survive potentially extreme summer conditions. *Ruppia tuberosa* exhibits key adaptations to persist through the high temperatures, exposure to drying out and hyper salinity, including hard coated seeds and the formation of turions (Brock 1982b; Kim 2014). Water levels and salinities must be maintained for a long enough period following the initiation of flowering to complete seed set or turion maturation. If this does not occur the seeds and turions will not go into dormancy but will most likely die before the next season. Dormancy is a feature of the life cycle pathways for seeds and turions and persistence is possible for vegetative plant remnants and turions.

Vegetative plant remnants

In deeper waters, *R. tuberosa* has been observed to persist over summer in some years (Waycott et al., 2020b). In shallower regions where water depth allows *R. tuberosa* persistence, such as the central Coorong constriction zone, water temperature and salinity may exceed tolerances. Finer scale data on these areas are not available to test this concept. Nevertheless, when historical salinity levels were lower, a deeper water aquatic plant community persisted when light availability was not limited (Dick et al., 2011; Geddes and Butler 1984; Haynes et al., 2018; Nicol et al., 2018; Nicol 2005; Paton 2010; Whipp 2010; Womersley 1975).

Speculatively, *R. tuberosa* plants will persist under extreme conditions, when minimal light requirements are met and extremes in water temperatures and salinities do not occur. Estimates of these conditions based on available information are: minimal light availability should be above 5% photosynthetically active radiation (PAR) (Collier et al., 2017); temperatures below 40°C in sediments; and salinities below 120 g/L.

Turions

As water levels drop and temperatures rise, salinities become concentrated and sediments dry, forcing dormancy of turions. Turions form, without any evidence of flowering, in the salt ponds and lakes surrounding the Coorong (Brock 1982b; Waycott and Nicol 2020). Turions that are fully formed type II structures with large reserves and several layers of shoot bases protecting their external interface, are able to persist for months in a dormant state (Paton et al., 2011). Experiments on the ability of turions to sprout after different periods of exposure support the survivorship for type II turions, albeit limited duration (resprouting after 4 months but not 7 months) and no survivorship for type I turions (Paton et al., 2011). Higher, temperatures are likely to cause the turion reserves to become depleted or the tissues to degrade physiologically leading to their death.

Seed bank

While seed banks are formed annually, *R. tuberosa* and *Athenia* seedbank dynamics, their long-term viability and inter-annual persistence are unknown (Rogers and Paton 2009), although seedbank depletion for *R. tuberosa* during the Millennium Drought took several years (Rogers and Paton 2009). The seed banks of the different forms of *R. tuberosa* are known to have a variable tolerance to exposure and drying out (Brock 1982a; Gu et al., 2018). Experimental testing of seeds from higher salinities indicate that lower viability occurs over 70 g/L

The chemical composition of surrounding sediments is likely to affect the long term viability of seeds, particularly where high organic load, black, anoxic sediments have formed (Mosley and Hipsey 2019). Data is currently not available on these factors.

3 Abiotic factors limiting the primary productivity of *R. tuberosa* and *Althenia* in the Coorong

The restoration and maintenance of a robust and resilient *R. tuberosa/Althenia* community in the Coorong is dependent on a variety of co-dependent environmental and physical factors including:

- Water depth
- Light availability
- Water quality
 - Nutrients
 - Salinity
 - Turbidity
 - Sediment biogeochemistry
- Disturbance through grazing
- Competition with filamentous green algae

Plant distribution through the southern Coorong is contingent on successful completion of all life cycle stages (Kim et al., 2015). If environmental conditions are not suitable, failure to set a seed bank or the formation of viable turions (for *R. tuberosa*) will result in reduced abundance and distribution of the *R. tuberosa/Althenia* community in subsequent seasons. The following section outlines the factors known to limit the condition of *R. tuberosa* and *Althenia* in the Coorong.

3.1 Water depth

Water depth is one of the primary factors driving the distribution of *R. tuberosa* and *Althenia* in the southern Coorong (Collier et al., 2017; Ye et al., 2014). Reproduction of the macrophyte community in the Coorong relies on the *R. tuberosa* and *Althenia* plants completing their life cycle by setting seeds (sexual) or forming turions (asexual) in late spring to early summer (see section 2.1.1) (Paton et al., 2018). The presence of water of sufficient depth to cover plants for the time needed to complete all their life cycle stage is necessary for the growth of *R. tuberosa* and *Althenia* s. The highest density of flowering and mature turion formation (for *R. tuberosa*) has been observed in water depths from 0.1 to 0.4 m and seed density of mature plants declines at depths greater than 0.4 m (Kim et al., 2015).

Plants are observed to grow in the Coorong at elevations from 0.1 m to 1.0 m Australian height datum (AHD) but to achieve the greatest density and extent when water levels are between 0.2 m and 0.7 m AHD (Collier et al., 2017). The community structure of the vegetation changes with water depth; *R. tuberosa* typically extends from 0.2 m to 0.6 m AHD (Brock 1982b; Kim et al., 2015). Historically, *R. megacarpa* had a wider depth range when present and was observed at 0.25 m, 0.35 m and 0.45 m AHD, but was most extensive between 0.55 m and 0.75 m AHD (Brock 1982b). *Althenia* has been observed in water elevations between 0.10 m to 0.5 m AHD (Brock 1982b).

Ruppia tuberosa plants (and presumably *Althenia*) growing in a water depth of less than 0.3 m are prone to desiccation, but above 0.6 m may become light limited. Water levels below the 0.3 m AHD threshold has previously resulted in poor *R. tuberosa* (and presumably *Althenia*) colonisation in the southern Coorong (Paton et al., 2018). Over the past 30 years water depths in the southern Coorong have fluctuated from less than 0 m AHD to greater than 1.0 m AHD but have only fallen below the optimal water threshold (above 0.3 m AHD) for the whole of the spring period in two of the years (2014, 2015) post the Millennium drought (Figure 6). Desiccation during the reproductive window (spring/summer) prevents seed bank and turion

production, reducing the resilience and regeneration of the population in subsequent growing seasons (Collier et al., 2017; Frahn et al., 2012; Nicol 2005; Paton et al., 2018).

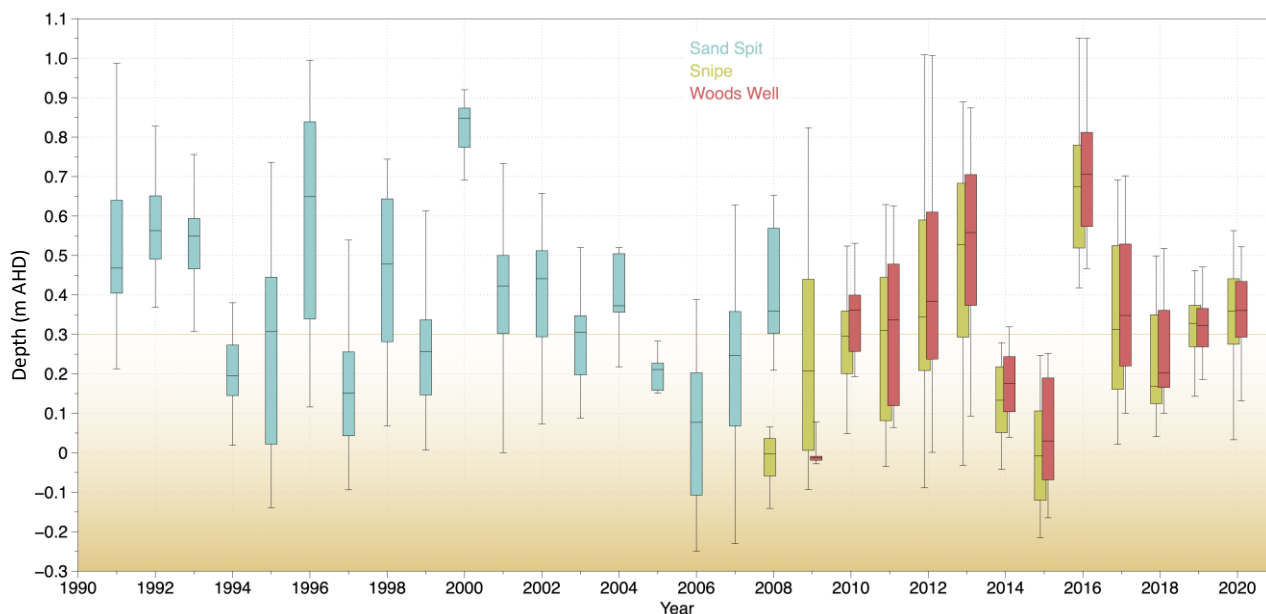


Figure 6. Box plots of water depths (m Australian height datum, AHD) for the spring months depth (Sept–Nov) from 1990 to 2020 in the Coorong. Sites shown are Sand Spit (Blue), Snipe (Yellow) and Woods Well (Orange) (note changeover between Sand Spit and Snipe Island has partial data sets at each end of the season (Sand Spit early September, Snipe Island November)). Data source: waterconnect.sa.gov.au (A4260634—Coorong, Sand Spit Point, -36.14458481, 139.63342461; A4261165—Coorong, NW Snipe Island, -36.10874032 139.6082716; A4261209—Coorong, near Woods Well, -36.01022037 139.529373).

3.2 Water quality

The Coorong is currently in a persistently hypersaline and hypereutrophic condition that appears to be unfavourable for the sustained, long term viability of *R. tuberosa/Althenia* communities (Mosley et al., 2020). Salinity and total nutrient levels in the Coorong are influenced by the hydrology of the River Murray and inputs from local catchments. Lack of flow during the Millennium Drought exacerbated the salinity and total nutrient levels of the South Lagoon (Auricht et al., 2018; Brookes et al., 2018; Mosley et al., 2020). The South Lagoon now remains in a hypersaline state, with a trophic index (TRIX) of >8, representative of a highly eutrophic environment (see Figure 2 (2020)). These conditions have caused a shift in the dominant primary producer of the system from *R. tuberosa/Althenia* to phytoplankton and filamentous green algae, as the high nutrient levels are favourable to their growth rather *R. tuberosa* (Brookes et al., 2018). The growth rate and expansion of the *R. tuberosa/Althenia* community in the Coorong is dependent upon the access and availability of nutrients and light, while distribution and abundance will depend on salinity and water levels (Collier et al., 2017). A strong north to south gradient exists in the Coorong, with increasing salinity levels, total nitrogen (TN), total phosphorus (TP), chlorophyll-*a* concentrations and turbidity with greater distance from the Murray Mouth towards the South Lagoon (Mosley et al., 2020). In addition, high temporal variability of salinity, TN, TP, chlorophyll-*a* and turbidity is also observed (Mosley et al., 2020).

3.2.1 Nutrients

Increased nutrients in the Coorong’s water column have contributed to the excessive growth of phytoplankton and filamentous green algae (see section 3.4) (Brookes et al., 2018). Filamentous algal blooms in the Coorong coincide with the critical reproductive life stage period of the *R. tuberosa/Althenia* community (Collier et al., 2017; Nicol et al., 2018; Nicol 2005; Paton et al., 2011; Paton et al., 2015; Paton et al., 2020;

Waycott et al., 2020b). Large aggregates of algae appear to interfere with *R. tuberosa* and *Althenia* flower heads (see section 3.4 for details). An increase in electrical conductivity (EC) beyond seawater values (>55 mS/cm) also corresponds with an increase in TN, TP, chlorophyll-*a* and TRIX values (Mosley et al., 2020). The DIN levels in the Coorong are highly variable. Ammonium (NH₄) and filterable reactive phosphorus (FRP) were found to be significantly elevated compared to previous years in the South Lagoon from 2007–2010 (Mosley et al., 2020). In contrast, since 2011 NH₄, FRP and oxidised nitrogen (NO_x) have been elevated in the North Lagoon as a result of increased flows from the River Murray and Lower Lakes (Mosley et al., 2020). Reactive silica concentrations have followed a similar pattern across both lagoons, but concentrations are often higher in the South Lagoon (Mosley et al., 2020).

Algae and *R. tuberosa* tissues collected from the Coorong in 2017 were found to be nitrogen limited (Collier et al., 2017). These results suggest that the total nutrient pools are mostly organic and less bioavailable, as is supported by the low dissolved inorganic nutrient (DIN) concentrations found in the South Lagoon.

3.2.2 Salinity

Salinity is another primary factor driving the distribution and abundance of *R. tuberosa* and *Althenia* in the southern Coorong (Collier et al., 2017). The Coorong has a natural salinity gradient that increases from north to south and reaches hypersaline (EC > 100 mS/cm or > 80 practical salinity units; PSU) conditions in the South Lagoon (Jeffries et al., 2011; Kim et al., 2015; Mosley et al., 2020). From 2008 to 2010, as a result of the Millennium Drought, conditions in the South Lagoon were extremely hypersaline (around 150 – 200 mS/cm) (Mosley et al., 2020). Between 2011 and 2013, and again in late 2016 after a small spike (reaching almost 150 mS/cm), conditions returned to pre-drought levels (>50 – <150 mS/cm) (Mosley et al., 2020). Salinity levels of the South Lagoon regularly exceed the salinity tolerance of *R. tuberosa* occurrence (19–70 g/L for highest abundance), flowering (between 47 and 64 g/L for highest abundance), and seed germination (0–90 g/L) but are currently within range of turion germination (0–125 g/L) (see Figure 5, section 2 for more details) (Collier et al., 2017; Kim et al., 2015; Kim et al., 2013; Mosley et al., 2020).

3.2.3 Light and turbidity

Ruppia tuberosa is a high light adapted species, requiring more than 5% of sunlight (relative to long term shading) to see significant improvements in total shoot biomass (Figure 7) (Collier et al., 2017). As a result, the greatest abundance of *R. tuberosa* occurs in depths less than 0.6 m, providing suitable light availability and signs of deterioration are observed in depths beyond 0.8 m (Kim et al., 2015; Paton et al., 2018). Source waters from the Lower Lakes into the North Lagoon can cause high turbidity in the Coorong, while Salt Creek inflows causes a localised reduction in turbidity at the southern end of the South Lagoon (Mosley et al., 2020). Turbidity in the Coorong is generally higher in the South Lagoon than the North Lagoon (Mosley et al., 2020). Increased turbidity (and salinity) in the Coorong has coincided with a shift of the dominant seagrass community in the Coorong from *R. megacarpa* to *R. tuberosa* (Carruthers et al., 1999). *Ruppia tuberosa* has higher salinity tolerance than *R. megacarpa*, but also has greater light requirements (Brock 1982b). The decline in *R. tuberosa* abundance in the Coorong has caused a loss of sediment stability, further increasing turbidity and facilitating the shift to phytoplankton dominance (Krull et al., 2008). When present, the roots and dense above ground biomass of the *R. tuberosa* and *Althenia* facilitate the trapping and stability of sediments. Turbidity was lower during the Millennium Drought but has since increased, particularly in the South Lagoon (Mosley et al., 2020). Dominance of phytoplankton and filamentous algae mats reduce light availability by blanketing water surfaces and increasing turbidity which can be detrimental to *R. tuberosa* shoot density in the southern Coorong. *Ruppia tuberosa* biomass has been found to reduce significantly with increasing degrees of shading over prolonged periods (>8 weeks) (Figure 7; Collier et al., 2017). Based on general field observations, the smothering of *R. tuberosa*/*Althenia* patches by filamentous green algae and phytoplankton in spring/summer, was found to reduced available light by around 80%.

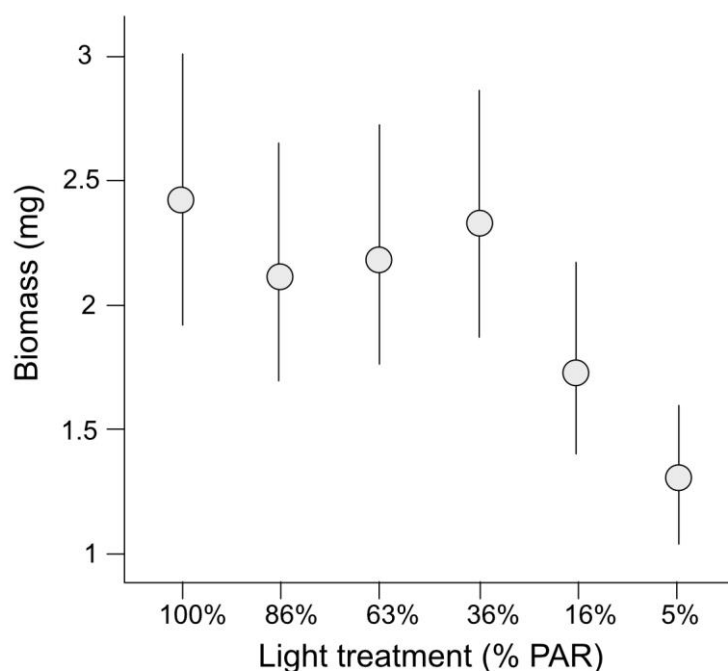


Figure 7. Total biomass of *R. tuberosa* exposed to shade treatments ranging from 5 to 100% of full sunlight over an 8-week period. $n=10 \pm$ S.E. Data source: Collier et al. (2017).

3.2.4 Sediment biogeochemistry

Information pertaining to Coorong sediment biogeochemistry and its impacts on *R. tuberosa* is limited. A comprehensive study was conducted in 2005 on sediments collected across the length of the Coorong and provides the best understanding of sedimentary conditions to date (Krull et al., 2008). The study compared the chronologies of carbon (C), nitrogen (N) and phosphorus (P) content; isotopes; and the chemical composition of organic matter (OM) in sediments from the Coorong's North and South Lagoons. Sediments from the North Lagoon exhibited increasing TN, TP, organic and inorganic carbon concentrations towards the South Lagoon, and so was correlated with spatial trends in salinity (Krull et al., 2008). The sediments exhibited progressive ecological degradation from the north to the south Coorong (Krull et al., 2008). The sources of organic matter (OM) were found to vary in line with the environment history of the Coorong and may provide a fundamental understanding of its environmental decline (Krull et al., 2008). The N to P (N:P) and C to P (C:P) ratios increased along the north-west to south-east axis of the North Lagoon and continued to increase within the South Lagoon which suggested P limitation of sediments, contrasting to nitrogen limitation in the water column (Krull et al., 2008; Mosley et al., 2020). The C to N (C:N) ratio of clay particles (<2 μ m) decreased along the major axis of the North Lagoon and into the South Lagoon, suggesting increasing contribution of phytoplankton to sedimentary OM in the southern Coorong (Krull et al., 2008). The North Lagoon has an average C:N of 8.6 compared to 7.6 for the South Lagoon, and phytoplankton has a C:N of ~6 which would account for the declining C:N towards and within the South Lagoon (Krull et al., 2008). A strong spatial gradient in the ecology and biogeochemical cycling of nutrients in the North Lagoon, which becomes more prominent towards the south, is further indication of nutrient limitation in sediments towards the South Lagoon, which existed prior to the 1950s and is continually increasing (Krull et al., 2008).

Chronological assessment of Coorong sediments revealed continued decline in their condition since the 1950s and loss of *R. tuberosa* as the dominant primary producer, a significant factor in the ongoing decline of the ecosystem (Krull et al., 2008). Stable carbon isotope analysis indicates a significant shift (>4%) in the source of OM that coincides with the first appearance of *Pinus* (pine) pollen in both the upper and lower North Lagoon and South Lagoon samples (Krull et al., 2008). The appearance of *Pinus* pollen in the sediments and a shift in the isotopic signature of Coorong sediments from heavy to light is indicative of more terrestrially derived OM and a decline in autochthonous material (Krull et al., 2008). The supply of sediments associated with the nutrients and salts from catchments provide an ongoing flux of sediments to estuarine

systems that can accelerate after human settlement (Gell 2017). Organic matter was comprised of lipids, carbohydrates and proteins in roughly equal proportions, however lipids increased in the lower North and South Lagoon (around Parnka Point) and corresponded with the increase in salinity (Figure 8; Krull et al., 2008). The biomolecules present in the Coorong sediments don't support an increase in terrestrially derived OM as suggested by isotope analysis (i.e., higher proportion of lignin generally assumed to be of terrestrial origin) (Figure 8; Krull et al., 2008). However, the lignin rich OM present in sediments dated pre-1950s in the North Lagoon that also had light $\delta^{13}\text{C}$ signatures is potentially driven by contribution of *R. megacarpa* tissues (Figure 8; Krull et al., 2008).

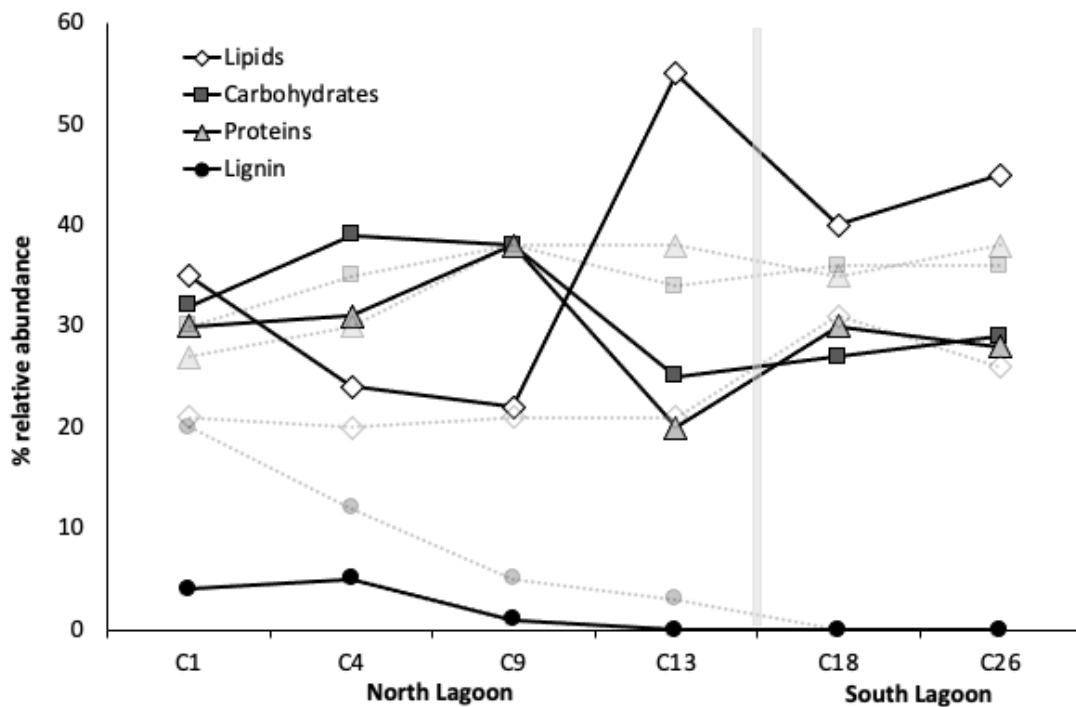


Figure 8. Spatial variation of major biomolecules (based on ^{13}C NMR and application of the molecular mixing model) pre- (transparent) and post- 1950s (solid). The grey line represents the boundary between the North and South Lagoons. Data Source: Krull et al., (2008). ©Springer Science + Business Media B.V. 2008.

There was little resemblance between sedimentary OM spectra and the spectra of potential sources (e.g., algae, aquatic plants, reeds, halophytes, plankton and soil) but phytoplankton had the greatest similarity in chemical composition (Figure 9; Krull et al., 2008). This may be representative of less decomposable material accumulating in sediments but as plankton is one of the most bioavailable materials, it is a valid assumption that plankton have become a major source of OM in the Coorong sediments (Krull et al., 2008).

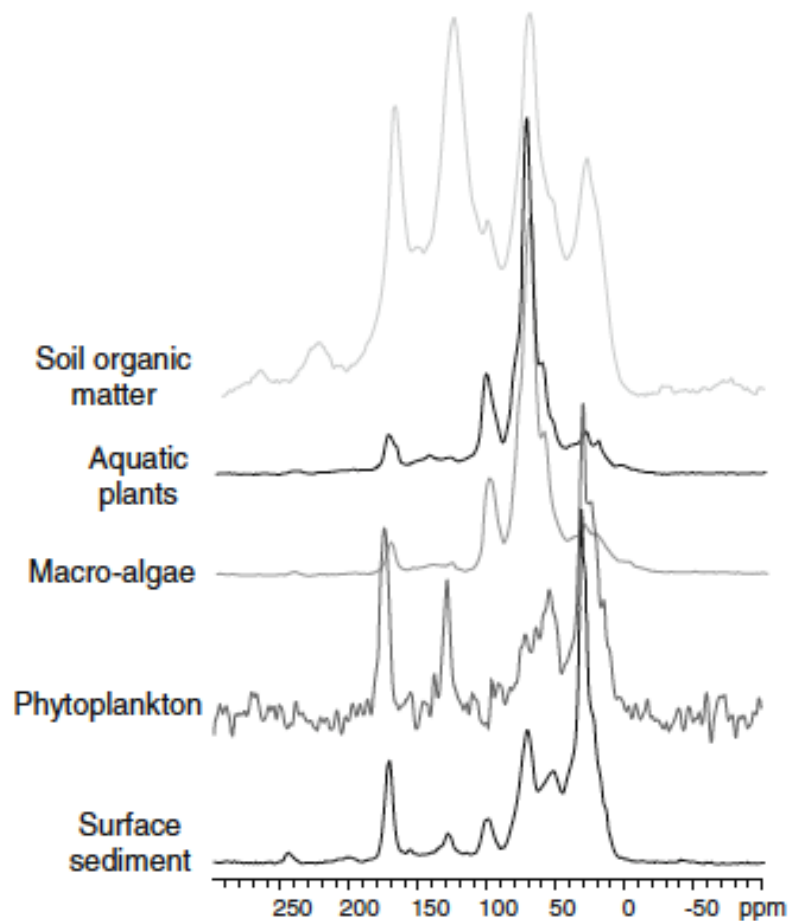


Figure 9. ^{13}C -NMR spectra of organic matter in the uppermost sediment in the Coorong and spectra of selected potential sources. Source: Krull et al., (2008). ©Springer Science + Business Media B.V. 2008.

Changes in the biogeochemistry of the Coorong sediments pre and post the 1950s are reflected in the aquatic ecology (Krull et al., 2008). The most substantial change in diatom assemblage occurring after the first appearance of *Pinus* in the sediments (Gell 2017; Krull et al., 2008). The shift in diatom assemblage saw thalassic species (strong marine influence and salinities between 5 and >35 g/L) replaced by tycho planktic taxa that are adapted to turbid low light environments (Gell 2017). The abundance of these species in post 1950s sediments across the Coorong is an indicator of increased turbidity and development of a semi-closed system (Gell 2017; Krull et al., 2008). The biogeochemical trend observed in sediments (in 2008) is correlated with the salinity gradient observed with increased proportion of hypersaline tolerant taxa towards the South-East of the North Lagoon (Krull et al., 2008).

3.3 Disturbance—grazing

In addition to shading, external stressors such as grazing can affect the morphology and biomass of *R. tuberosa* in the Coorong (Collier et al., 2017). Recent observations suggest that waterfowl grazing activity on *R. tuberosa* has declined from 80% in years prior to 2017 to an average of 57% in 2018. This is thought to be the result of high algae loads causing reduced access to plants (Paton et al., 2017a; Paton et al., 2018). In the most recent monitoring survey, 72% of *R. tuberosa* cores were grazed, relative shoot length being approximately one third of the ungrazed shoot lengths (Paton et al., 2020).

Research on *R. tuberosa* grazing by birds in Argentina, showed that the exclusion of bird grazing in *in situ* experimental treatment plots resulted in a 8.2% increase in above ground biomass but a 8.2% decrease in the below ground biomass (Bortolus et al., 1998). Exclusion of grazing had no significant effect on total biomass but changed the allocation of plant biomass to above ground, rather than below ground structures

(Bortolus et al., 1998). Foliar length of non-grazed *R. tuberosa* was significantly larger than grazed plants (Bortolus et al., 1998; Paton et al., 2018). The increase in below ground biomass with grazing pressure may lead indirectly to increased sediment stability and facilitate the lateral expansion of *R. tuberosa* (Bortolus et al., 1998), although this remains untested in the Coorong.

3.4 Filamentous green algae in the Coorong

Eutrophication in the Coorong (Mosley et al., 2020) has resulted in excessive filamentous algal growth, which is most obvious in late spring and over summer, that negatively impacts the ecological functioning of the Coorong (e.g. Collier et al., 2017; Paton et al., 2020; Waycott et al., 2020b). Filamentous algal mat forming species, such as *Ulva paradoxa*, *Cladophora* sp. and *Rhizoclonium* sp., gain an advantage over the *R. tuberosa/Althenia* community through the combined and complex interactions of nutrient availability, salinity, water temperature and water level (Collier et al., 2017; Waycott et al., 2019). Surface mats formed by the filamentous green algae shade submerged plants and entangle the *R. tuberosa* and *Althenia* flowers, causing flowers to break away from stems, which results in the failure of the plants sexual reproduction (Paton et al., 2018). Failure to reproduce, and in particular set seed, leads to depleted seedbanks and lowers the resilience of the *R. tuberosa/Althenia* community in the Coorong.

Filamentous green algal blooms form annually and across many locations in the Coorong. These algal blooms have been documented spanning over 10's of square kilometres, with blooms significantly increasing in size since 2010 (Waycott et al., 2019). High biomass and extensive coverage of filamentous green algae is symptomatic of the declining ecological state of the Coorong (see section 3.2 for more details). Algal blooms are associated with the increasing nutrients availability and have contributed to the significant loss of large areas of *R. tuberosa/Althenia* in the system (Brookes et al., 2018; Collier et al., 2017; Mosley et al., 2020; Waycott et al., 2020b). A study on the conditions required to support the restoration of *R. tuberosa* showed that filamentous algal growth outcompeted *R. tuberosa/Althenia* production as the Coorong recovered from the Millennium Drought, i.e. with reduced salinities and elevated water levels (Paton et al., 2011). Excessive filamentous algae leads to reduced light availability, smothering, and reduced density and diminished condition of *R. tuberosa* and *Althenia* (Paton et al., 2011; Paton et al., 2018; Waycott et al., 2019). The occurrence algal growth across large areas of the Coorong is indicative of a shift in the composition of the primary producer community across the ecosystem (Brookes et al., 2018; Collier et al., 2017; Waycott et al., 2020b). The growth rates of the filamentous green algal community that currently dominates the aquatic plant productivity in the central and southern Coorong are controlled by the combination of salinity and temperature under conditions of excess nutrients (Brookes et al., 2018; Collier et al., 2017; Mosley et al., 2020; Waycott et al., 2020b).

Recent investigations documented in Collier et al., (2017) found the upper salinity threshold for filamentous algal growth is 90 g/L. As such, filamentous algal growth is almost completely inhibited in the South Lagoon as its salinities routinely exceed the 90 g/L threshold (see section 3.2.2) (Mosley et al., 2020). In addition, experimental testing has identified that 30°C is the optimum water temperature for the growth of the filamentous green alga *Ulva paradoxa* in salinities ranging between 35–90 g/L (Waycott et al., 2019). The implication of these findings is that algae growth in the Coorong will be fastest as water temperatures approach 30°C (summer periods), where salinities remain below 90 g/L. Alternatively, where salinities exceed 90 g/L growth rates of the filamentous green algae are reduced (Waycott et al., 2019). At salinities below 35 g/L, algal communities appear resilient to a wide range of temperatures and nutrient availability (Collier et al., 2017).

The presence of extensive filamentous green algae in the Coorong has led to the formation of anoxic sediments, particularly in the areas with high biomass blooms, across more than 27% of the central Coorong (Waycott et al., 2020b). Anoxic sediments are a direct result of decomposing algal blooms deposited on the Coorong floor and limiting the oxygen availability (Figure 6) (Collier et al., 2017; McGlathery et al., 2007; Waycott et al., 2020a). It is now also recognised that the *R. tuberosa/Althenia* community provide a physical substrate for the filamentous algae to attach and become established (Waycott et al., 2020b). When the

larger aggregates of algae are of sufficient density, they can cause flowers and fruit to become detached from the parent plants before they are mature. Without this, the algae may not bloom to a high biomass. The impact of excessive filamentous algal growth is significant, with flow-on effects suppressing the long-term recovery of the ecosystem and the distribution of *R. tuberosa/Althenia* (Collier et al., 2017).

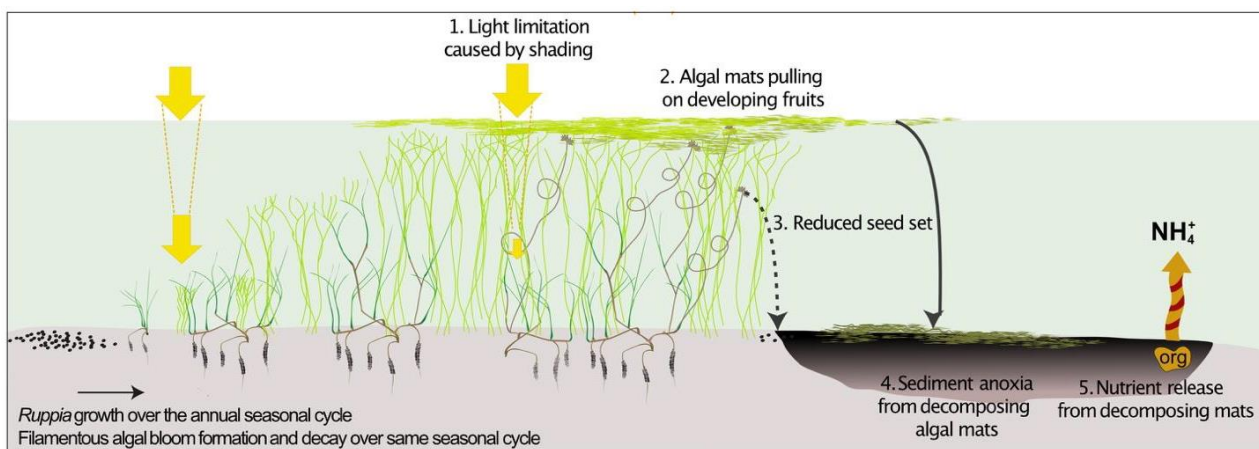


Figure 10. Conceptual diagram depicting the formation and decay of filamentous algal blooms highlighting the observed impacts of the blooms on *R. tuberosa/Althenia* in the Coorong. Source: Waycott et al., (2020a).

3.4.1 Monitoring for management of filamentous green algae blooms in the Coorong

Application of remote sensing techniques allows for understanding how, when and why algal mats form in the Coorong (Auricht et al., 2019). The technique has proved successful at detecting filamentous algal mats during their peak growth periods (November–January) in the Coorong (Auricht et al., 2019). In addition, it can be used in conjunction with system monitoring to help explain impacts of extreme events (e.g. droughts and flooding) and how they exacerbate the system (Auricht et al., 2019). Indexes, such as the Normalised Difference Vegetation Index (NDVI) and the Floating Algae Index (FAI), can be applied to satellite imagery to investigate the presence and vigour of vegetation in an aquatic environment (Auricht et al., 2019; Hu 2009). The use of remote sensing techniques in the Coorong has its challenges, however, as it is difficult to distinguish algal mats from aquatic vegetation, sand bars and elevated background chlorophyll-*a* levels (Auricht et al., 2019). Therefore in environments such as the Coorong it is best to combine imagery analysis with *in situ* field data for validation (Auricht et al., 2019). Regardless, remote sensing may help to inform models that can predict periods of high risk to algal blooms and prompt interventions to prevent or limit future algal blooms (Auricht et al., 2019). Early intervention and the management of algal blooms in the Coorong could assist in the recovery of *R. tuberosa/Althenia* in the system. However, the type of interventions that may assist in filamentous algae growth in the Coorong remains a knowledge gap.

4 The condition and distribution of *R. tuberosa*/*Althenia* in the southern Coorong

To evaluate the condition of an ecological community such as the aquatic macrophytes of the Coorong, the long-term variability in water levels, salinity and seasonal growing time are significant factors to consider. Previous reviews (Collier et al., 2017; Nicol et al., 2018; Nicol 2005; Paton 2010; Paton et al., 2015; Womersley 1975) all note the inherent variability of the Coorong. In a system such as the Coorong the suite of organisms that have adapted to survive its perturbations have developed life cycle strategies that are particularly resilient (as described for *R. tuberosa*/*Althenia* in section 2). However, extreme disruptions to ecological processes, such as large scale disturbances in climate (e.g. extended periods of drought), change multiple elements of an ecosystem's ecological processes that can have long term impacts (e.g. van Dijk et al., 2013).

In the Coorong, significant change was observed during the period of the Millennium Drought (Kingsford et al., 2011; Webster 2010). Drought related pressures on the ecological functioning of the Coorong were additive pressures to an already modified system as a result of the longer term decreased water availability in the Murray-Darling Basin (Geddes 1987; Geddes and Butler 1984). The flow on effects between the presence of abundant aquatic macrophytes in the Coorong, *R. tuberosa* in particular, and the dependent community of fish and birds, have been of increasing concern because abundance is declining (Brookes et al., 2018; Paton and Bailey 2010; Paton et al., 2009; Phillips and Muller 2006).

Long term monitoring of Coorong *R. tuberosa* populations has been undertaken to assess condition relative to the ecological objectives, one of which is the condition of *R. tuberosa* (methods outlined in Paton et al., 2017b). The monitoring is used to assess several Ecological Objectives. Monitoring data from some sites is available from 1998 and here we present plots of the monitoring data (up to summer 2019; source: data.gov.au). The data demonstrates the trends in shoot abundance in winter (early in the *R. tuberosa* growing season), turion and seed abundance in the summer of the following season (Figure 11).

The formation of turions follows an expected pattern, with higher counts of turions (mean \pm S. E) corresponding with lower counts of seeds (i.e., fewer smaller seedbanks were formed) (e.g., Figure 11a N19E; N12E; Figure 13b S06E). Note that the large standard errors (S.E) suggest a high degree of variability is evident in the associated data for each sample type.

The variability of the ecosystem is reflected in variable estimates of condition, in particular the variability in the maximum counts of *R. tuberosa* shoots, seeds and turions from year to year. The plots demonstrate that where sampling occurred over the Millennium Drought period (e.g., Figure 11b graph S06E, VDY) a decline in *R. tuberosa* condition occurred, based on the mean number of shoots per core, but has since begun to recover. Unfortunately, the long- term data was collected in different seasons (winter rather than summer for seed banks), preventing direct comparisons between sites.

There has been a widespread occurrence of *R. tuberosa* in recent years. A recently completed field survey of the central and southern Coorong (J. Nicol, M. Waycott and E. O'Loughlin pers. obs.) found widespread *R. tuberosa* meadows beyond the currently surveyed monitoring sites. These data, along with remote sensing data compiled last season (2019), will be used to validate a baseline map of the distribution and extent of the *R. tuberosa*/*Althenia* community of the central Coorong and South Lagoon. High flowering densities have been observed this season (M. Waycott pers. obs., 2020) and although filamentous algae was present, the algae was lower in density than previous years (Paton et al., 2020; Waycott et al., 2020c). It may be possible for seasonal conditions to yield higher than average seed set in the 2020/21 flowering season, enhancing the resilience of *R. tuberosa* in the Coorong (Paton et al., 2020).

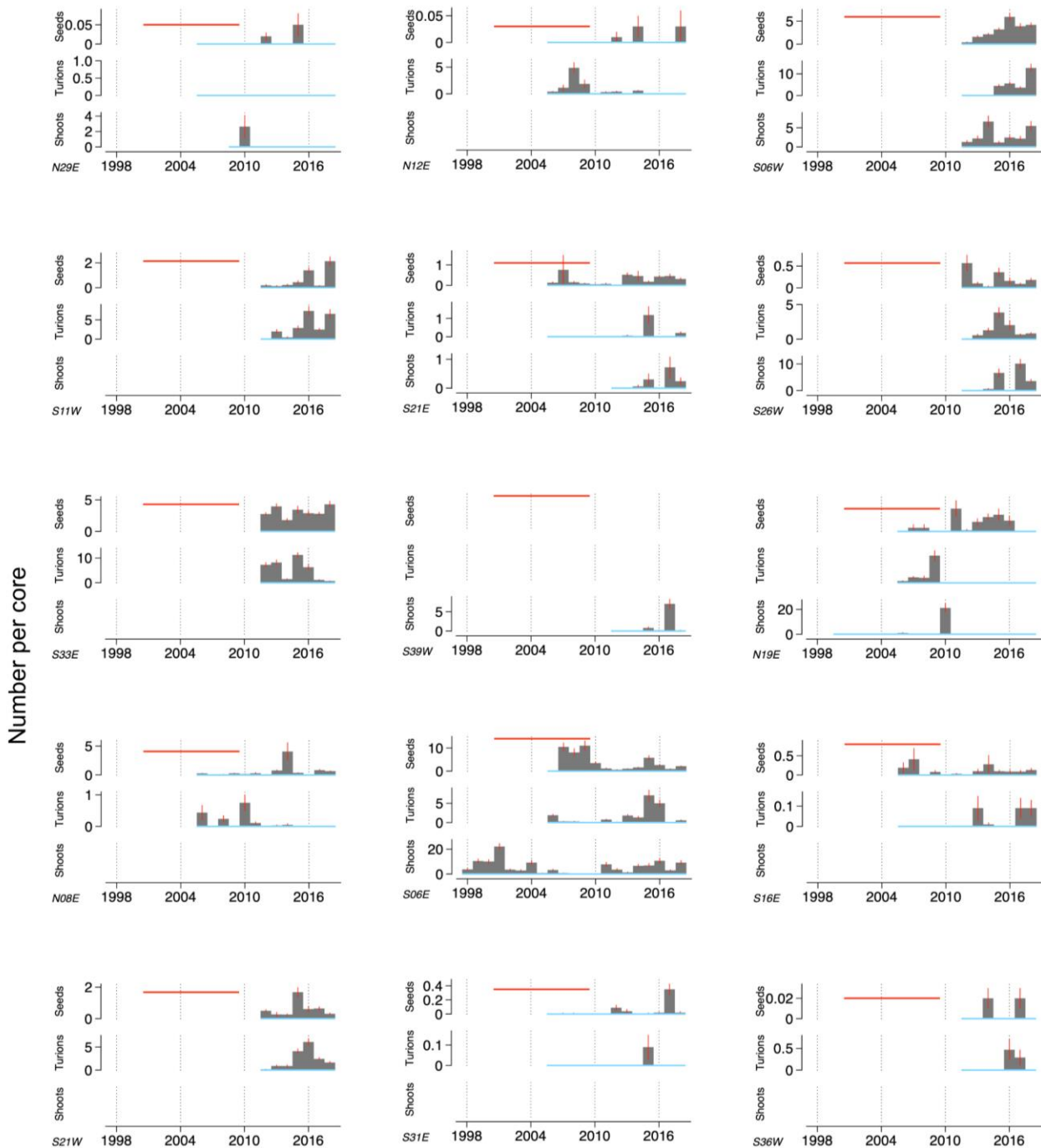


Figure 11a. Mean counts \pm S.E. ($n=25-100$) of shoots, turions and seeds from 7.5 cm diameter cores across 24 locations collected during the long-term annual monitoring of *R. tuberosa* in the South Lagoon (sites N29E–S36W). Shoot counts were made during winter sampling, turion and seed counts were made during the following summer. Red line indicates the period referred to as the Millennium Drought, the blue lines indicate the period of sampling. Note the scale on the y-axes vary depending on the maximum values for the site. Data source: (data.gov.au; Paton et al., 2017a).

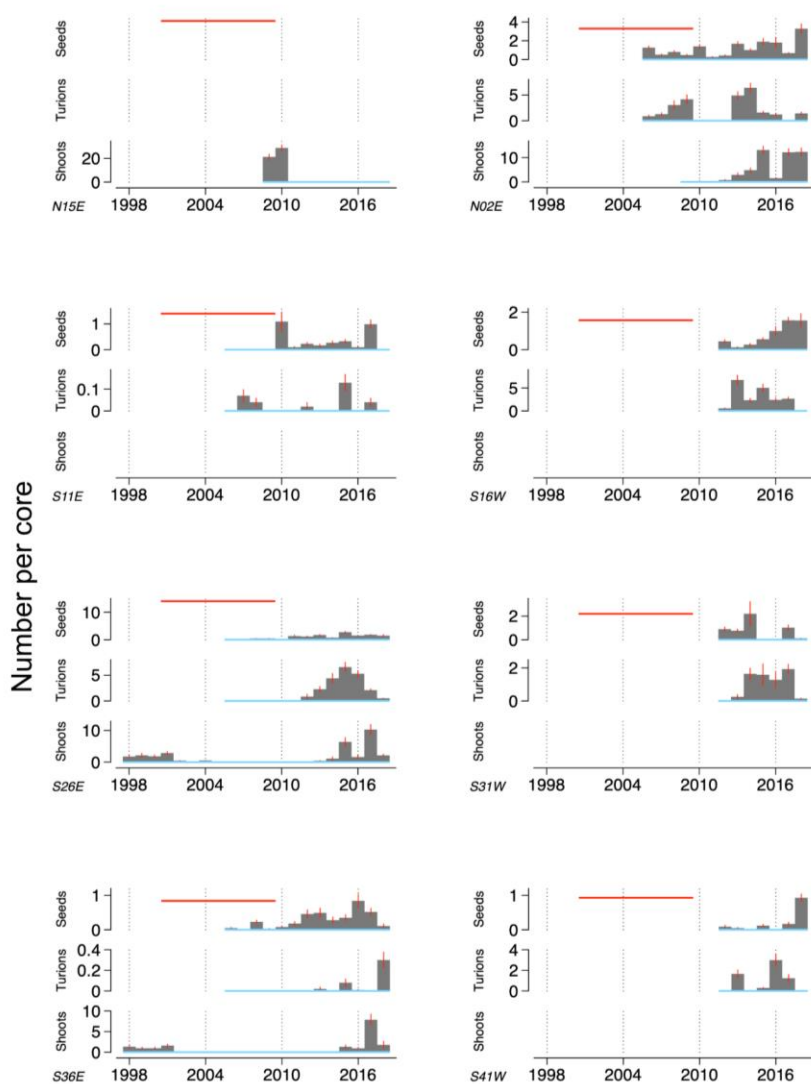


Figure 11b. Mean counts \pm S.E. ($n=25-100$) of shoots, turions and seeds from 7.5 cm diameter cores across 24 locations collected during the long-term annual monitoring of *R. tuberosa* in the South Lagoon (sites S11E–S41W) . Shoot counts were made during winter sampling, turion and seed counts were made during the following summer. The yellow lines define the sites on the same page for which graphs are plotted. Red line indicates the period referred to as the Millennium Drought, the blue lines indicate the period of sampling. Note the scale on the y-axes vary depending on the maximum values for the site. Data source: (data.gov.au; Paton et al., 2017a).

5 Microbial communities in the Coorong

In addition to macrophytes, the microbial community (microorganisms with a common living space i.e., in the soils and sediments) that plays a crucial role in maintaining ecosystem functions, such as maintaining chemical cycles and high turnover primary productivity (Jeffries et al., 2011; Leterme et al., 2018). The structure of a microbial community is determined by a combination of complex factors including historical conditions of the environment, the niche they occupy, their habitat characteristics and its physical structure as well as nutrient availability (Jeffries et al., 2011). In the Coorong, few studies have investigated the diversity of microbiota (Leterme et al., 2018); however, a high diversity of micro-organisms exist in the Coorong system, including phytoplankton. Although routine measures of chlorophyll-*a* concentrations have been undertaken, which provide an indication of the total water column load of phytoplankton, the changing community responsible for the chlorophyll-*a* concentrations in the Coorong is not measured routinely.

Increasing salinity is associated with an increase in the abundance of Coorong's microbial community, but a decrease in the diversity (Jeffries et al., 2011). These authors reported a 31- fold increase in heterotrophic bacteria and 28-fold increase in virus abundance along the Coorong salinity gradient. Bacteria dominated the sequences derived from Coorong sediment extractions, with the phylum *Proteobacteria* representing over 50% of the taxonomic composition across all four salinity profiles (Figure 12) (Jeffries et al., 2011). *Cyanobacteria* were abundant in the hypersaline environments (132 and 136 PSU) (Jeffries et al., 2011). In addition, the microbiota community composition shows an affinity for the water column or a solid substrate, as opposed to salinity or geographic location (Jeffries et al., 2011). Further changes to nutrients or substrate in the Coorong will be reflected in the microbiota.

Research into the relative productivity of the different microbiota versus the macrophyte productivity will support determining the characteristics that encourage the state change needed to shift primary production to forms that capture nutrients over the longer term, support the food webs of the system, support enhanced food resources for grazers and provide habitat for other ecosystem components.

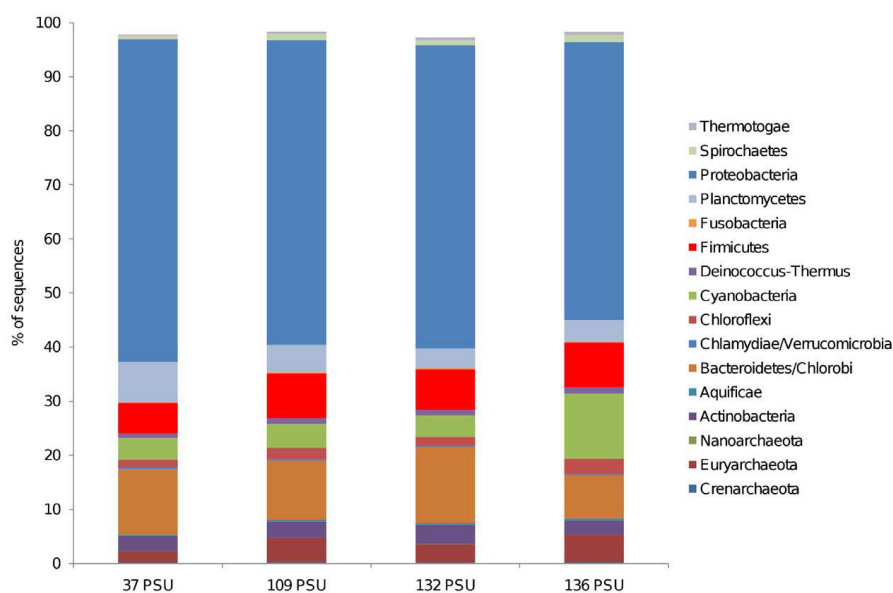


Figure 12. Taxonomic composition (Phyla level) of four phytoplankton DNA based analysis of all species present in Coorong lagoon sediments. Source: Jeffries et al. (2011).

6 Interactions that limit growth of *R. tuberosa*/*Althenia* in the southern Coorong

The growth of *R. tuberosa* and *Althenia* in the southern Coorong is limited by the combined and interacting effects of temperature, water level, salinity, nutrients loads (water and sediment) and external modifiers such as filamentous algae formation and grazing (Figure 13). Collier et al., (2017) summarised the known environmental parameters (i.e., salinity, temperature, light, water level, and algal biomass) and their suitability functions for supporting the seasonal *R. tuberosa*/*Althenia* life stages in the southern Coorong. The optimal conditions, based on the current literature (Collier et al., 2017), for optimising the *R. tuberosa*/*Althenia* community in the Coorong during its critical life stage (reproduction) in the most recent model are:

- Sexual reproduction, i.e., flowering and seed bank production (August – December):
 - Salinity: 35 – 62 g/L and 26 – 62 g/L, respectively
 - Temperature: 10 – 20°C, for both
 - Light: >24 % luminous Intensity, for both
 - Water level: 0.1 – 0.4 m AHD and >0.1 m AHD, respectively
 - Algal biomass: <25 grams dry weight per meter square
- Asexual reproduction, i.e., turion production (August – December):
 - Salinity: 124 – 160 g/L
 - Temperature: 10 – 20°C
 - Light: >24 % luminous Intensity
 - Water level: >0.1 meters AHD

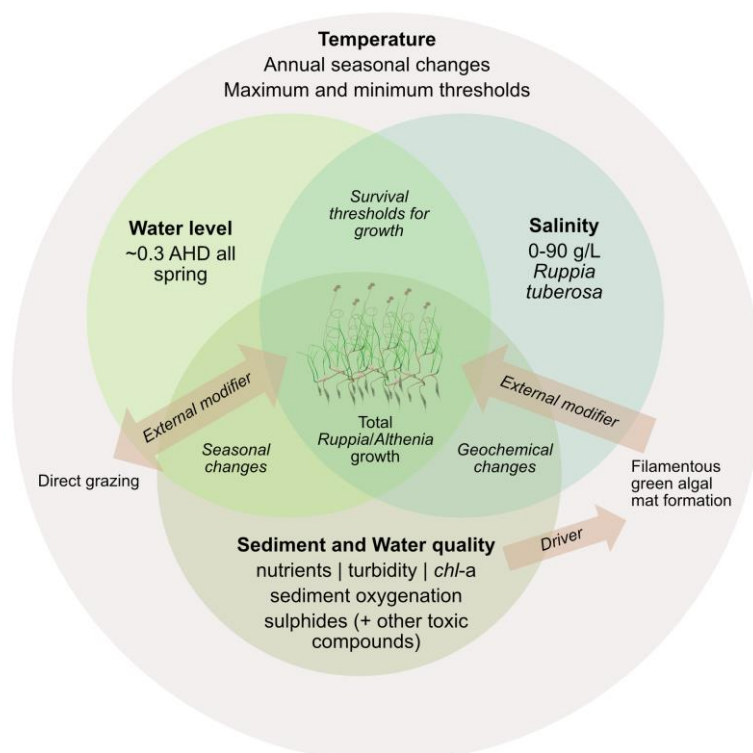


Figure 13. Overview of the interactions between the conditions that control *R. tuberosa* and *Althenia* growth in the southern Coorong and two specific types of external modifiers, grazing and filamentous algal bloom formation that form feedback mechanisms to the community composition.

Since the end of the Millennium Drought, the distribution of the *R. tuberosa/Althenia* community across the Coorong demonstrate a positive trajectory of ecological recovery (see section 4). However, large areas of the central and southern Coorong continue to be dominated by highly productivity algal species. These result from in interactions of available water levels, salinity within suboptimal and optimal ranges in the presence of bioavailable nutrients. At the same time, other typical components of the ecosystem, such as macroinvertebrates and foraging species of fish and birds are absent. There has been a resulting shift of the dominant primary producers in the central and southern Coorong from more persistent and biomass accumulating aquatic plant species (i.e., *R. tuberosa* and *Althenia*) with a slower organic matter turnover rather than fast turnover algae. Improvement to ecosystem health will require reversal of the relative balance of the algae versus *R. tuberosa/Althenia* community (McGlathery et al., 2007). This would facilitate a return of macroinvertebrates and foraging species of fish and birds if accompanied by appropriate hydrological and physical conditions.

Water level in the Coorong is dependent on the elevation band (0.2–0.6 m) occupied by the *R. tuberosa/Althenia* community. The optimal water level required for growth, to prevent desiccation, and to successfully complete reproduction for *R. tuberosa*, and presumably *Althenia*, is 0.3 m AHD (e.g. Paton et al., 2018; Ye et al., 2016). However, there exists conflicting information regarding the optimal water level requirements for *R. tuberosa* growth, which presumably also applies to *Althenia*. Paton et al., (2018) reports water levels for optimal growth and for *R. tuberosa/Althenia* to prosper in the Coorong are at 0.3 m AHD to prevent desiccation, and to successfully complete reproduction. Whereas, the critical water depth for *R. tuberosa* survival, but not optimal growth/distribution, is reported at 0.2 m AHD by Ye et al. (Ye et al., 2016).

The optimal salinity thresholds for *R. tuberosa* are well documented. It is presumed the co-occurrence of *Althenia* under the same conditions at least in some locations. Salinity is secondary to the presence of adequate water levels as a deterministic factor in the decline and recovery of *R. tuberosa* in the southern Coorong (Collier et al., 2017). Salinities for *R. tuberosa* growth in the southern Coorong vary dramatically and appears to dictate the plant life cycle pathways followed each seasonal cycle: annual or vegetative, sexual or asexual domination of the reproductive cycle. In addition, salinity influences the presence of and intensity of excessive filamentous algal growth. The life stages most affected by elevated salinities are flowering, turion formation, seed germination and turion sprouting.

The eutrophic state of the Coorong's southern lagoon (see section 3.2.1) promotes seasonal growth of filamentous green algae that has resulted in co-dominance of the seagrass (*R. tuberosa/Althenia*) and the algal communities (see section 3.4). The seasonal growth of the algae (spring–summer) in the Coorong coincides with the reproductive life stage of the *R. tuberosa* (and presumably the *Althenia*). The reproductive stage of the life cycle is critical to the establishment of the seed beds (or turions) that will facilitate the next year's growth of the *R. tuberosa/Althenia* community in the system.

Routine visits to the Coorong during critical (reproductive) life stage times of *R. tuberosa/Althenia* have observed that algae does not grow in areas without seagrasses present. Further observations have highlighted that algae uses the *R. tuberosa/Althenia* flowers as an anchor point to the Coorong floor. As a result, when the filamentous algae blooms rise to the surface during mat formation the *R. tuberosa/Althenia* flowers are broken away leaving them unviable for germination and seed bank setting for future generations.

7 Summary of knowledge gaps

The growth, distribution and abundance of *R. tuberosa/Althenia* in the Coorong is driven by the temperature (seasonality), water level, salinity and water and sediment quality, and their interactions (Figure 13). However, the optimal conditions required for a thriving and persistent *R. tuberosa/Althenia* community in the Coorong remains uncertain and requires further investigation. Key knowledge gaps and data sets that will enable improved outcomes for the ecological health of the Coorong include:

- Development of an updated distribution of *R. tuberosa/Althenia* in the central Coorong and South Lagoon that will provide a critical baseline for future assessments of change and augment long term monitoring data sets such as those generated for The Living Murray Program.
- A review of the available data to determine the optimal water depths for maximising abundance, distribution, growth and survival of *R. tuberosa* (including reproductive state/s). These values will play a significant role in the development of modelling for the Habitat Suitability Index for *R. tuberosa* in the South Lagoon and may change priorities for management.
- The nutrient allocations to different primary producers. This is poorly understood and in particular the interaction between the growth of *R. tuberosa/Althenia*, water column phytoplankton, benthic algal communities and other sediment and water column the microbiota. These other organisms likely represent a higher than desired proportion of the current productivity of the Coorong ecosystem.
- The formation of filamentous algae blooms during the critical reproductive life stage of *R. tuberosa/Althenia*. This stage has significant effect on the restoration and maintenance of the seagrass community in the South Lagoon. As the filamentous green algae have been found to have overlapping survival thresholds with *R. tuberosa*, and presumably *Althenia*, alternative interventions or management regimes that will reduce filamentous algae growth in the Coorong need to be identified.
- The impacts of the long-term exposure of *R. tuberosa/Althenia* seed banks to sediments with high concentrations of organic matter, sulfides and other breakdown compounds (organic sludge). This may lead to reduced seed viability or inhibit germination and remains untested.
- The impact of organic sludge sediments on the biogeochemistry and how this directly effects *R. tuberosa/Althenia* productivity and growth.
- The composition of the macrophyte community. *R. tuberosa* and *Althenia* are indistinguishable unless flowering, and as a result *R. tuberosa* was believed to be the only species present in the South Lagoon. A majority of the aquatic macrophyte research in the Coorong has focused on *R. tuberosa*. *Althenia* appears to have similar thresholds as *R. tuberosa* for optimal growth, abundance and distribution. This is an assumption made on the basis of their mixed presence in the Coorong and similar life cycle stages. Therefore, more detailed understanding of the relative proportion of *R. tuberosa* or *Althenia* in current populations will be important to determining the need to document life history traits of *Althenia*. As *Althenia* likely plays important ecological functions in the Coorong, an understanding of its abundance and life history traits will support the management of viable populations.

This review provides a basis for evaluating the responses of *Ruppia tuberosa* and associated community of aquatic plants (particularly *Althenia cylindrocarpa*) and algae (filamentous and microbial) to changing conditions in the Coorong South Lagoon. The interacting effects of water level, salinity, nutrients, sediment condition and season as modifiers of habitat suitability for *Ruppia tuberosa* are complex and highly variable. It will be crucial to understand the responses of these highly resilient submerged aquatic plants and their community to expected changes to their environment to facilitate and support effective management and decision making.

Glossary

AHD	Australian height datum. Note: the mean sea level for 1966-1968 was assigned a value of 0.000m on the Australian Height Datum (AHD) at 30 tide gauges around the coast of the Australian continent (Geosciences Australia).
Benthic	Of or associated with the sediment at the bottom of an estuarine or marine system.
Biomass	The total mass of sampled organisms, measured as wet or dry and for a particular sampled area such as m ² .
Central Coorong	The central part of the Coorong stretching from the Needles to Hack Point connecting the North Lagoon and the South Lagoon.
Chlorophyll a (<i>chl a</i>)	One of the photosynthetic pigments of plants that is used as an indicator of the eutrophic state of water bodies. One of the symptoms of degraded water quality condition is the increase of algae biomass as measured by the concentration of chlorophyll a. Waters with high levels of nutrients from fertilizers, septic systems, sewage treatment plants and urban runoff may have high concentrations of chlorophyll <i>a</i> and excess amounts of algae (epa.gov).
Eutrophication	The increase in the supply of organic matter to an ecosystem. Eutrophic systems are typically characterised by excessive plant and algal growth due to the increased availability of one or more limiting plant growth factors needed for photosynthesis including light, carbon dioxide, and nutrients.
EC	Electrical conductivity, the ability for a material to conduct electricity. The international standard term, commonly 'conductivity' used interchangeably. Conductivity is usually measured in microSiemens (µS/cm) at 25°C. In water quality, EC often is the way salinity is recorded.
Filamentous algae	The green filamentous algal community which occurs in the Coorong, consisting of <i>Ulva paradoxa</i> , <i>Rhizoclonium sp.</i> and <i>Cladophora sp.</i> defined in Collier et al. 2017.
Genet	The genetic individual that include all parts derived from a single zygote or seed.
HCHB	Healthy Coorong Healthy Basin
HSI	Habitat Suitability Index
Intra-annual	Within a year
Inter-annual	Between years
Laboratory detection limits	The smallest amount or concentration of an analyte that can be reliably distinguished from the baseline
Life history stages	The different growth stages of an organism that reflect investments in growth, reproduction and survivorship. For <i>R. tuberosa</i> , an organism goes through during its lifetime, i.e., seed, seedling, vegetative growth of mature plant, flowering, fruiting, turion formation, senescing plant.
Meristem	A formative plant tissue capable of dividing indefinitely and giving rise to similar cells or to cells that differentiate to produce the definitive tissues and organs. Shoot meristems give rise to new shoots and in the case of <i>R. tuberosa</i> and <i>Althenia</i> , rhizomes, root meristems give rise to roots.

Macrophyte	Aquatic plant visible with the naked eye that grows in, or near, water and is either emergent, submerged or floating.
Phenology	The transition and timing of each of the different stages of the life cycle.
Plant morphology	Physical form, shape and external structure of the aquatic plants
Primary productivity	The conversion of light energy to organic compounds through photosynthesis, can be referred to as carbon fixation.
Ramet	An independently operating unit within a genet.
<i>R. tuberosa</i>/Althenia	The truncated phrase used to describe the mixed submerged aquatic plant community that includes <i>R. tuberosa</i> and <i>Althenia cylindrocarpa</i> throughout this report. Where otherwise stated, the phrasing will be referring to either species independently or the genus.
Salinity	Water salinity when measured by passing an electric current between the two electrodes of a salinity meter in water. Salts increase the ability of a solution to conduct an electrical current, so a high EC value indicates a high salinity level. Commonly reported at ppt (parts per thousand) equivalent to g/kg Historically salinity was calculated as <i>salinity=1.80655*chlorinity (ppt or g/kg)</i>
Salinity – EC – TDS conversion	Conductivity in microSiemens ($\mu\text{S}/\text{cm}$) = 1000 i.e., EC = 1000 EC 1000 Converts to TDS of 555 ppm (or mg/L) Converts to salinity of 0.555 g/L $\text{TDS (mg/L)} = 3\text{E-}06 \times \text{EC}^2 + 0.5517 \times \text{EC}$ (for high TDS samples)
Sampling core ‘Cores’	A standard core referred to will be a sampled taken that is 7.5 cm diameter and 10 cm deep, including all above and below ground plant community as well as sediment. The device used to take a care is typically a cylinder (such as plumping pipe) with a mark made at 10 cm to indicate depth that can be pushed into the sediment to isolate the area to be sampled.
Seedbank	<i>R. tuberosa</i> or other aquatic flowering plants (e.g. <i>Althenia</i>) seeds which are dormant in the sediment (usually over dry summer periods)
Southern Coorong	The part of the Coorong south of Hack Point, sometimes including the central region
Spatial	Refers to the dimension of space or area.
T&I	Trials and Investigations Project
TDS	Total Dissolved Solids, the amount of substances that have been dissolved in the liquid. The most commonly used method of determining TDS is measuring specific conductivity to detect the presence of ions in water (EC), although this is an estimate not a direct measure. TDS is generally measured in parts per million (ppm) or mg/L.
Temporal	Refers to the dimension of time
Trophic	Feeding and nutrition of plants and animals and where they fit into niches and levels of the food web.

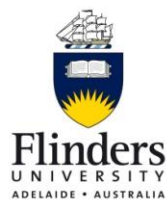
TSS	Total Suspended Solids. Particles larger than 2 microns found in the water column.
Turion	Reproductive structure that <i>R. tuberosa polycarpa</i> (Type I) and <i>R. tuberosa</i> (Type I and Type II) produce underground that is capable of forming into a new plant.

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