

2023

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[10.1007/s00227-023-04192-6](https://doi.org/10.1007/s00227-023-04192-6)

Webster, C., Lavery, P. S., O'Dea, C., Sánchez Alarcón, M., Salgado Kent, C., & McMahon, K. (2023). The influence of abiotic and biotic conditions on lifecycle stages is critical for estuarine seagrass resilience. *Marine Biology*, 170(4), Article 48. <https://doi.org/10.1007/s00227-023-04192-6>

This Journal Article is posted at Research Online.
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The influence of abiotic and biotic conditions on lifecycle stages is critical for estuarine seagrass resilience

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Received: 4 October 2022 / Accepted: 20 February 2023 / Published online: 18 March 2023
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Abstract

Abiotic and biotic factors influence seagrass resilience, but the strength and relative importance of the effects are rarely assessed over the complete lifecycle. This study examined the effects of abiotic (salinity, temperature, water depth) and biotic (grazing by black swans) factors on *Ruppia* spp. over the complete lifecycle. Structures were set up in two estuaries (−33.637020, 115.412608) that prevented and allowed natural swan grazing of the seagrasses in May 2019, before the start of the growing season. The density of life stage(s) was measured from June 2019 when germination commenced through to January 2020 when most of the seagrass senesced. Our results showed that swans impacted some but not all life stages. Seedling densities were significantly higher in the plots that allowed natural grazing compared to the exclusion plots (e.g. 697 versus 311 seedlings per m²), revealing an apparent benefit of swans. Swans removed ≤ 10% of seagrass vegetation but a dormant seedbank was present and new propagules were also observed. We conclude that grazing by swans provides some benefit to seagrass resilience by enhancing seedling recruitment. We further investigated the drivers of the different lifecycle stages using general additive mixed models. Higher and more variable salinity led to increased seed germination whilst temperature explained variation in seedling density and adult plant abundance. Bet-hedging strategies of *R. polycarpa* were revealed by our lifecycle assessment including the presence of a dormant seedbank, germinated seeds and seedlings over the 8-month study period over variable conditions (salinity 2–42 ppt; temperatures 11–28 °C). These strategies may be key determinants of resilience to emerging salinity and temperature regimes from a changing climate.

Keywords Lifecycle · Herbivory · Salinity · Temperature · Colonising seagrass

Introduction

Identifying the drivers of resilience of foundation plant species, that have a key role in structuring ecosystems, is complex but projecting resilience to future conditions is even harder (Thrush et al. 2008; Duarte et al. 2009; Lefcheck et al. 2017). Understanding the conditions required for each life stage and for species to complete their lifecycles could improve these predictions (Radchuk et al. 2013). The increased emergence of extreme events is shifting the timing and duration of favourable conditions for the different stages

of the lifecycle across global ecosystems (Wetz and Yoskowitz 2013; Hallett et al. 2018). Environmental changes are occurring more rapidly in shallow estuarine ecosystems with the potential to disrupt the lifecycles of foundation plant species (Oczkowski et al. 2015; Scanes et al. 2020). These disruptions can erode the resilience of foundation plant species and lower the amount and/or quality of ecosystem goods and services (Preen and Marsh 1995; Kendrick et al. 2019).

As foundation plant species play a significant role in determining ecosystem function, changes to their ecological resilience have major implications for the whole ecosystem (Kendrick et al. 2019). Ecological resilience is an emergent property that allows structure and function to be maintained following disturbances via two key processes: resistance and recovery (Levin and Lubchenco 2008). These processes of resistance and recovery manifest in different lifecycle stages, that enable populations to resist and/ or recover and ultimately, survive and reproduce (Brock 1982). Generally,

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more is known about the conditions that enable adult life stages to persist compared to earliest life stages (Kuiper-Linley et al. 2007). However, the conditions that enable the earliest life stages to transition are important to understand to clarify predictions about population dynamics and resilience with climate change (Duncan et al. 2019). Each life stage and/or transition can have distinct environmental requirements, meaning a suite of biotic and abiotic factors are likely to be important for completing the lifecycle and building resilience (Ren et al. 2012). Such knowledge can lead to more effective management actions such as optimisation of fire regimes for the longevity of plants in fire-prone regions (Bradstock and Auld 1995; Gordon et al. 2017). The combined performance of individual lifecycle stages in the context of the complete lifecycle will determine population persistence (Radchuk et al. 2013). This understanding for marine plant species, many of which depend on sexual reproduction for resilience, is presently lacking (Kendrick et al. 2022).

Colonising seagrass species commonly dominate estuaries and typically exhibit annual lifecycles, making substantial investment in sexual reproduction to produce dormant seeds (Kilminster et al. 2015). Seeds must transition through dormancy to germinate, and the seedlings go through multiple life history stages to reach maturity. Whether the plants complete their lifecycle and reproduce can be regulated by the differing responses of each life-history stage to abiotic and biotic factors (Strazisar et al. 2015), yet whether a factor is considered a key driver of resilience is commonly based on its effect on a single life stage (Rodríguez-Pérez and Green 2006; Tatu et al. 2007). However, the strength of effect of different stressors can differ (Mitchell and Wass 1996), they may interact (Bell et al. 2019) and positive effects on some life stages may compensate for negative effects on others. Thus, conclusions based on single life-history stages and stressors should be treated with caution; assessing effects across multiple life history stages is likely to be more accurate for determining whether these factors are key driver(s) of resilience (Hootsmans et al. 1987; Strydom et al. 2017).

In highly seasonal estuaries, the growing season for seagrasses can coincide with periods of intense fluctuations in both abiotic and biotic factors (Cho and Poirrier 2005). To cope with such variability, plant life cycles are generally annual, with rapid plant development to maximise sexual reproductive output and high densities of seeds (Brock 1983). Salinity and temperature changes are primary factors controlling seed germination, seedling establishment and growth (Xu et al. 2016; Cumming et al. 2017). Seagrasses are a major food source for herbivorous waterfowl so grazing might also influence the life cycle but often depends upon which part of the plant is consumed (Congdon and McComb 1981). For example, if leaves remain after grazing,

then plants can still photosynthesize, grow and reproduce but if all parts are removed, then recovery will proceed via germination of seeds (Jacobs et al. 1981; Nakaoka and Aioi 1999). If enough seeds germinate, complete their life cycle and reproduce, then the reductions of adults may not be negative for overall resilience. Most studies regarding grazing effects on seagrass have focussed on the response of adults, and so the impacts to earlier life stages, which could potentially compensate for the negative effects at the adult stage, are less well known (Lee et al. 2007; Rodríguez-Pérez and Green 2006; Bakker et al. 2016). Understanding the relative importance of plant–herbivore interactions and environmental conditions can inform conservation management actions for ecologically significant ecosystems supporting seagrasses and grazing waterfowl but is hampered by limited collection of in situ data (Rodríguez-Pérez and Green 2006; Tatu et al. 2007).

Southwestern Australia (SWA) has a Mediterranean climate and climate change effects are rapidly progressing in many of its estuaries (Hallett et al. 2018), raising concern for the ecosystems within them. Estuaries in the region are characterised by seasonal and inter-annual variation in environmental conditions which are expected to become more extreme under future conditions (Hallett et al. 2018). The estuaries are also habitat for herbivorous waterfowl (Choney et al. 2014) whose grazing pressure can be expected to interact with changes in abiotic conditions. There has even been speculation that drying of regional wetlands will force waterfowl to retreat to estuaries as refugia, intensifying grazing pressure (O'Dea et al. 2022). Whilst seagrasses are subjected to both abiotic and biotic pressures, phenological studies are relatively scarce and so the importance of these factors for the ability of species to complete their lifecycle remains unknown. In this study, we examined the response of several sequential life history stages of two seagrass species, *Ruppia megacarpa* and *Ruppia polycarpa*, to a range of abiotic and biotic factors in two seasonally hypersaline estuaries in Southwestern Australia. The goal was to understand the key drivers of resilience. Low biomass of *Ruppia* spp. in the estuaries in the past led to the proposal that swan grazing is a potential stressor of seagrasses (Chambers and Paice 2018). Using a manipulative field experiment, we quantified the effects of abiotic (surface and porewater salinity, water depth, temperature) and biotic (swan grazing) factors on the complete lifecycle of *Ruppia* spp. Plots were set up that excluded and allowed natural swan grazing and we collected data on the phenology of *Ruppia* spp. and environmental conditions over an annual cycle. We hypothesised that salinity and temperature would have the greatest impact on seeds and seedlings, and swan grazing would have the greatest negative impact on adults. Overall, we considered that the implications for resilience would depend on the successful completion of the life cycle.

Methods

The Vasse Wonnerup Wetland System (VWWS) comprises two seasonally hypersaline microtidal estuaries (i.e. the Vasse and the Wonnerup, Fig. 1) characterised by eutrophic and variable water quality conditions that are expected to worsen under future warming (Tweedley et al. 2019; McCallum et al. 2021). Both estuaries are shallow (≤ 1.5 m depth) and characterised by dramatic fluctuations in water levels (0.2–1 m) driven primarily by inundation from rainfall and river flow in the wet season and evaporation rates in the dry but also influenced by flood gate operation which allows intermittent opening to the ocean (Chambers and Paice 2018, Fig. 1). In 1990, the VWWS was listed as a wetland of international significance under the RAMSAR convention due to the abundance and diversity of waterbirds that use the wetland to feed and breed including the largest breeding colony of black swans in SWA (Wetland Research and Management 2007). In the VWWS, *R. polycarpa* dominates and co-occurs with *R. megacarpa* and are preferred food sources for black swans (Kissane 2019). To assess the influence of environmental conditions and grazing on each life-cycle stage, a grazing exclusion experiment was conducted with regular sampling extending through the period from

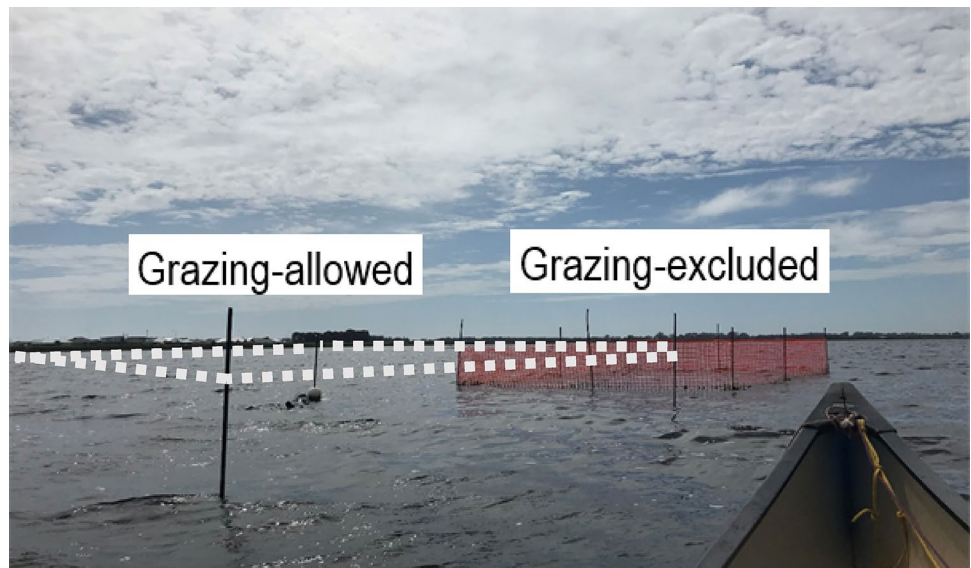
winter to summer at three sites in the Vasse estuary and three sites in the Wonnerup estuary (Fig. 1), to capture environmental variability between estuaries and amongst sites within each estuary. Sites within each estuary were selected to represent the range of seagrass distribution, where swans have been recorded feeding and to capture a range of water quality conditions; e.g. that vary with distance from flood gates (Chambers and Paice 2018). The estuaries are generally more dry and saline in summer and autumn, and more so in the upper sections that dry out over this period (March–May) resulting in salinity and temperature values of 90–132 ppt and 30 °C, respectively (Lane et al. 2011; Tweedley et al. 2014). There is usually broader variation in salinity within a year in the Vasse (e.g. annual range in 2016 was 0–99 ppt) compared to the Wonnerup (e.g. annual range in 2016 was 0–82 ppt) but Wonnerup generally has a higher median salinity (Online Resource Fig. 1). The variation in salinity may be due to a range of factors including differences in river flow with the Vasse estuary that is fed by three rivers (Sabina, Abba and Vasse) compared to the Wonnerup estuary which is fed by a single river, the Ludlow (Fig. 1).

In May 2019 at each site, two plots (7 × 5 m) separated by 1 m were established; one plot was ‘grazing-excluded’ to exclude swans from grazing based on the design of Tatu et al. (2007), and the other to act as a control

Fig. 1 Vasse Wonnerup estuaries located in Southwestern Australia within which seagrass monitoring sites (sites 1, 2, 3 in each estuary, $n=6$) and where sediment cores (to measure porewater salinity) were collected



Fig. 2 Photo of experimental plots set up at each site to evaluate the influence of access to grazing by black swans (grazing-allowed) or absence of grazing (grazing-excluded) on the abundance of seagrass lifecycle stages over time. Note that dashed lines have been overlaid on the image to make the boundaries of the ‘grazing-allowed’ plot more distinguishable



where grazing could occur, hereafter, ‘grazing-allowed’ (Fig. 2). The small addition of nutrients from swans would be unlikely to affect effect on the seagrass in the nearby plot as the estuaries are highly eutrophic (McCallum et al. 2021) and being shallow (< 1 m depth), highly susceptible to wind-driven forces such that inputs from birds would quickly become a dispersed input rather than localised. The plot perimeter was marked with ten metal reinforcing bars inserted into the sediment with barrier fencing composed of plastic barricade mesh secured onto the bars of the ‘grazing-excluded’ plot to prevent swans entering (Fig. 2). The fencing extended 1 m above the water surface to approximately 15 cm below the water surface when installed. Whilst black swans can feed on seagrass up to a depth of 1 m, 15 cm below the water surface was selected in favour of maintaining water flow and minimising the accumulation of plant matter that could break the fencing. Grazing scars were not observed within the plot areas suggesting that 15 cm below the water surface was an effective prevention. Plant debris accumulated on the barrier was removed during each monthly sampling trip to allow water flow but ensure swans could not enter. The height was modified when water levels changed. The ‘grazing-allowed’ plots lacked barrier mesh, allowing swans to enter and graze (Fig. 2). Sites were monitored monthly from June 2019, just prior to winter rainfall which was expected to be a trigger for germination (Vollebergh and Congdon 1986, pers comm Kath Lynch), to January 2020 when very little seagrass remained. During each monthly monitoring trip, measurements were taken in both plots at each site to estimate the density and state of different lifecycle stages: sediment seedbank, germinated seed and seedling density, canopy height, canopy cover, plant volume inhabited (PVI) and biomass. The presence

or absence of flowering and reproductive shoots was also recorded. Swans were observed entering and feeding in all grazing-allowed plots.

Seagrass cover, canopy height and percent volume inhabited (PVI)

Discriminating between *R. polycarpa* and *R. megacarpa* could only be done from seeds and seedlings so all measures relating to adult plants combine both species. Another macrophyte, *Stuckenia pectinata*, was also present and was included in the cover, canopy height and PVI measurements due to difficulties with distinguishing it from *Ruppia* in situ but was excluded for biomass. Snorkellers entered the plots on flotation boards to avoid disturbing or damaging the benthic habitat. Ten replicate measurements of cover and canopy height (20×30 cm) were taken haphazardly in each plot. Macrophyte cover (%) was estimated visually in 5% increments but on three monitoring trips, visual assessment of cover could not be used due to zero visibility, so the amount of seagrass was estimated by feeling the amount attached to the sediment within the 20×30 cm area. Maximum canopy height (cm) was measured on the longest leaf of an individual plant selected at random to the nearest 5 mm. Water depth was recorded in the middle of each plot to the nearest cm. Canopy height, cover and water depth measurements per 0.06 m² area were used to calculate ‘plant volume inhabited’ (PVI). PVI (m³) describes relative plant habitat to water volume, as per Canfield et al. (1984):

$$\text{PVI} = \frac{H \times C}{d} \times \frac{1}{A}$$

where *H* is canopy height (m), *C* is cover (%), *d* is the water depth (m) and *A* is the sample area (m²). When canopy

height was greater than the water depth, it was adjusted to the water depth measure so that PVI values never exceeded 100% of the water volume.

Seagrass seedbank and seedling density

Seedbank (the number of ungerminated seeds with intact seed coat), germinated seed and seedling densities were estimated from ten replicate cores (4.8 cm inside diameter, 15 cm depth) collected haphazardly in each plot at each time. Seagrass measurements in subsequent months were unlikely to be affected as the area sampled by the ten cores (0.06 m^2) amounted to 0.001% of the experimental plot area (35 m^2). Each sample was stored in a ziplock bag at 4°C until processing, then flushed with freshwater through a $710 \mu\text{m}$ sieve to capture *Ruppia* spp. seeds that are typically $> 1 \text{ mm}$ in length (Brock 1982). Following Mason (1967), seeds and seedlings were identified to species. Germinated seeds were categorised as those that had an emerging cotyledon ($> 1 \text{ mm}$ but $< 10 \text{ mm}$) whilst seedlings were those in which the leaf was longer than 1 cm and adventitious roots were present, indicative of successful establishment (Gu et al. 2018).

Seagrass biomass

Cores for seagrass biomass estimates were collected monthly from October 2019 to January 2020 to capture the pre-peak, peak biomass (generally November) and die-off periods (Chambers and Paice 2018). These cores were collected after the canopy height and cover measurements. To ensure the same area was never sampled more than once, each plot was divided into $35 \times 1 \text{ m}^2$ squares, a unique set of five random numbers was generated using the RAND function in Excel and assigned for each month. Each core (9.6 cm \varnothing , 3 cm depth) was 'threaded' over the seagrass to capture all biomass originating from within the core area. Above ground (leaves, branches, flowers if present) and below ground (rhizomes, roots) material were stored in calico bags and, where possible, macroalgae was removed in situ. In the laboratory, epiphytic material was removed from the leaves by gently scraping with a microscope slide and any remaining macroalgae was also removed. *Ruppia* spp. was separated from other macrophytes and separated into above and below ground parts and dried at 60°C for 48 h to achieve a constant weight. These dry weight (DW) values were standardised to m^{-2} for comparison with other studies.

Environmental parameters: benthic salinity and temperature, water depth and porewater salinity

At each site from June 2019 to January 2020, benthic salinity and temperature were measured continuously and

discrete measures of water depth were taken at each site once per month. Discrete measures of porewater salinity were obtained but due to logistical reasons, measurements were commenced in July 2019 and measured once per month until January 2022.

To measure porewater salinity, one sediment core (9.6 cm \varnothing) was collected each month (June 2019 to January 2020) at each site just outside the plot area. The core was pushed into the sediment to a depth of 15 cm and then a bung was placed immediately at the bottom of the core, surface water was removed by siphoning and another bung was placed at the top of the core. Cores were secured upright and transported back to Edith Cowan University for processing. Within 48 h of collection, cores were sliced at 5 cm intervals and each slice was placed in a separate sealed bag and stored at 4°C prior to processing. Porewater was extracted with a Wild-coTM sediment squeezer with $100 \mu\text{m}$ mesh and measuring salinity using a conductivity metre. Benthic salinity and temperature were measured at hourly intervals using loggers (HOBOTM U24-002-C) that were attached at the sediment water interface to a reinforcement bar reflecting the conditions seagrass was growing in at each site (hereafter, benthic salinity and temperature). The logging periods at Vasse site 2 (from July 2019) and Wonnerup site 2 (from August 2019) were shorter than at other sites due to logistical issues with initial deployment. Each logger was placed into a PVC pipe cover with holes to allow water flow but reduce biofouling according to the manufacturer's datasheet for logger deployment. Each month additional in situ water temperature and salinity measurements were taken with a Thermoscientific multimeter placed next to the logger for data calibration, and the loggers were cleaned and data retrieved. Each deployment's data set was calibrated with the in situ measurements from the beginning and the end of the deployment period using the non-linear, seawater compensation based on the PSS-78 scale via from the HOBOWare® Pro Conductivity Assistant. The calibrated subsets of data were combined to create a dataset for each site for the available period and checked for quality by plotting the hourly salinity and temperature data. Additional information outlining the methods are given in the Online Resource (Tables 1 & 2).

Statistical analyses

For each lifecycle stage, there were ten measurements per plot in each of the eight time periods giving $N=960$ for each variable, except biomass with five measurements per plot collected from October to January ($N=240$). For each month, the measurements were averaged to create a value for each site within each estuary ($n=3$ per estuary per month). Sites were considered the experimental units. To assess the effects of swan grazing on the density of each lifecycle stage, separate permutational analysis of variance was conducted

Table 1 Timing of lifecycle stages of *Ruppia* spp. observed (1- dormant seedbank, seed germination, seedlings, 2- peak seedling density, 3- flowering, 4- peak biomass/ abundance and 5- senescence) and associated minimum and maximum environmental conditions

Life stage	Months	Benthic salinity (ppt)		Porewater salinity (ppt)		Benthic temperature (°C)		Water depth (m)	
		Min	Max	Min	Max	Min	Max	Min	Max
1	Jun to Jan	2	42	7	38	12	28	0.2	0.9
1	Jun to Jan	9	42	13	45	11	28	0	0.9
2	Jun	40	63	n.s.	n.s.	12	16	0.3	0.4
	Sep	2	4	5	10	14	23	0.7	0.7
	Jan	n.d.	n.d.	39	45	n.d.	n.d.	0.2	0.2
2	Jun	32	39	n.s.	n.s.	12	16	0.4	0.5
	Nov	12	22	15	24	17	28	0.6	0.7
3	Oct	16	24	2	14	16	24	0.7	0.7
3	Sep to Nov	10	22	13	17	14	28	0.6	0.9
4	Oct to Nov	2	8	7	11	16	28	0.6	0.7
4	Nov	12	22	15	24	17	28	0.6	0.7
5	Jan	21	46	33	45	20	25	0.2	0.2
5	Jan	34	44	36	67	23	27	0	0.1

Data shaded grey are for the Vasse estuary and data in white are for the Wonnerup estuary. Estuaries are located in Southwestern Australia. *n.s.* not sampled, *n.d.* no data. Timing was determined by either in situ observation during monthly sampling or from pairwise comparisons of 'Site x Month'.

Benthic salinity and temperature data collected by loggers deployed at three sites within each estuary ($n=3$) whilst porewater salinity and water depth were discrete monthly measures taken at each site per estuary ($n=3$)

with estuary, plot type (two levels: grazing-allowed, grazing-excluded) and month as fixed factors. Analyses for seedbank, germinated seeds and seedlings were conducted for both species combined. The analyses for variables relating to adult plants (canopy height, cover, PVI, biomass) were for both species combined. For cover measures that were greater than 0% but less than 5% cover, a value of 2.5% was assigned for the statistical analysis. Prior to conducting the analyses, the assumption of homogeneity of dispersions was confirmed using PERMDISP (p -values < 0.05) on the raw data and if assumptions were not met, then transformations were attempted. If after transformation, the PERMDISP was still not met, the α -value was adjusted to 0.01. Following a significant main effect or interaction, post hoc pairwise tests were used to identify where those differences occurred. The aforementioned analyses were performed using PRIMER v7 multivariate software package with the PERMANOVA + add-on module (Clarke and Gorley 2006; Anderson et al. 2008).

To investigate which environmental variables best explained the spatial and temporal patterns in the different life history stages, generalised additive mixed models (GAMMs) were used. GAMMs offer the flexibility of being able to analyse a range of distribution and data types (e.g. continuous and categorical) and are useful for capturing non-linear relationships that frequently exist in ecology (Murase et al. 2009; Beatty 2019). Because each life history stage is a reflection of environmental conditions leading up to the time of sampling, we assessed the relationship between the abundance of the relevant life history stage and

environmental variables integrated over different preceding time periods: long term (≈ 32 days prior to the seagrass sampling) or short term (fortnight before sampling) at each sampling time (July–December 2019) (Online Resource 1, Table 2). Although seagrass sampling occurred in June 2019 and January 2020, no environmental data were collected in May and there was extensive logger malfunction in January so these periods were excluded from the analyses. Response variables were the densities of ungerminated and germinated seeds and seedlings, which were combined for both *Ruppia* spp., seagrass PVI and biomass. For each site, the response variable was represented by the mean of the ten measurements collected in each 'grazing-excluded' plots only, to remove the effects of grazing. This resulted in $N=6$ for the short-term and long-term timesteps for each variable, matching the replication in the environmental data.

Water depth, salinity and temperature environmental data were selected for their influence on the distribution and abundance of *Ruppia* spp. (Brock 1986; Santamaría and Hootsmans 1998; Carruthers et al. 1999). Given the availability of continuous salinity and temperature data, we were able to calculate several metrics including: minimum, mean, maximum, variation (standard error) and rate of change. The mean of an environmental variable may not be the driver causing variability in the response variable but rather its variation, the rate of change or the maximum value (Ralph 1999; Steward et al. 2006; Fernández-Torquemada and Sánchez-Lizaso 2011; Griffin and Durako 2012). Of 22 possible variables considered, 17 were excluded due to strong collinearity ($r_s \geq 0.7$, Online Resource Table 3). The

Table 2 PERMANOVA Mains test for the effects of location, plot type and month on seedling density and percent volume inhabited of *Ruppia* spp in the Vasse and Wonnerup estuaries, Southwestern Australia

	Seedling density			PVI		
	df	SS	P	df	SS	P
Location	1	599	0.0080	1	0.14	0.3048
Plot type	1	816	0.0024	1	0.27	0.1588
Month	7	7015	0.0001	7	67	0.0001
Lo × Pl	1	455	0.0206	1	0.06	0.5205
Lo × Mo	7	2123	0.0017	7	6	0.0001
Plot type × Month	7	2881	0.0002	7	0.33	0.9232
Lo × Pl × Mo	7	736	0.2506	7	0.76	0.5798
Residual	64	5057		64	8	
Total	95	19,682		95	83	
<i>Seedbank density</i>				<i>Germinated seed density</i>		
Location	1	5324	0.0321	1	84	0.0940
Plot type	1	320	0.6050	1	82	0.0952
Month	7	6712	0.5549	7	459	0.0413
Lo × Pl	1	755	0.4280	1	8	0.5815
Lo × Mo	7	2801	0.9239	7	461	0.0389
Plot type × Month	7	4911	0.7395	7	72	0.9266
Lo × Pl × Mo	7	1174	0.9940	7	363	0.1043
Residual	64	72,863		64	1844	
Total	95	94,860		95	3372	
<i>Canopy height</i>				Cover ($\alpha=0.01$)		
Location	1	0.06	0.004	1	0.10	0.0008
Plot type	1	0.02	0.1381	1	0.005	0.4332
Month	7	4	0.0001	7	2	0.0001
Lo × Pl	1	0.0002	0.5816	1	0.0006	0.7884
Lo × Mo	7	0.1	0.0146	7	1	0.0001
Plot type × Month	7	0.05	0.45	7	0.02	0.9069
Lo × Pl × Mo	7	0.08	0.1758	7	0.12	0.0456
Residual	64	0.5		64	0.5	
Total	95	4		95	4	
<i>Biomass</i>						
Location	1	77	0.0158			
Plot type	1	3	0.6812			
Month	3	216	0.0021			
Lo × Pl	1	14	0.3531			
Lo × Mo	3	171	0.0050			
Plot type × Month	3	6	0.9469			
Lo × Pl × Mo	3	13	0.8504			
Residual	32	436				
Total	47	935				

Statistically significant factors are indicated in bold (unless otherwise stated: $\alpha=0.05$)

variables retained were water depth, long-term (monthly) average temperature, long-term rate of change in temperature, long-term average salinity and coefficient of variation in salinity which were considered surrogates for the collinear variables. To reduce model overfitting and aid in data interpretation, the maximum number of predictors was limited to three, pairwise correlation tests were run automatically and models with correlated predictors (>0.28) were included in

each model set but never in the same model (Graham 2003). The GAMMs analyses were run in the R Language for Statistical Computing (version 4.0.5 Core Team 2021). The full subsets ‘FSSgam’ package (Fisher et al. 2018) was used and is based on the ‘mgcv’ (Wood 2011) and ‘gamm4’ packages (Wood and Scheipl 2016). The Akaike Information Criteria corrected for small samples sizes (AICc) and adjusted r^2 were considered during model selection. Models within two

Table 3 Outputs of the generalised additive mixed model analyses for predicting the condition of seagrass variables each month (July 2019–January 2020)

Response variable	Models (sig. of predictor)	AICc	delta.AICc	wi.AICc	r^2	r^2 -sq-adj	# Basis functions (k)	Deviance explained (%)
Germinated seeds	Average salinity ($p=0.012$)	233.70	0.00	0.41	0.18	0.147	3	17.20%
	Average salinity + coefficient of variation in salinity (0.3126)	234.64	0.93	0.26	0.20	0.10	3	19.70%
Seedlings	Average temperature ($p=0.0003$) + rate of change temperature ($p=0.11$)	257.23	0.00	0.47	0.42	0.329	3	42.10%
	Average temperature ($p=7.7e-5$)	257.61	0.38	0.39	0.37	0.282	3	37.30%
Percent volume inhabited	Average temperature ($p=2e-16$) + rate of change temperature ($p=0.005$)	119.05	0.00	0.87	0.81	0.78	3	82.50%

AICc Akaike Information Criterion corrected for small sample sizes, delta. AICc AIC differences, wi.AICc- model weights, and coefficient of determination (r^2). The most parsimonious model with the best predictive power is shaded and best supported models are within 2 delta. AICc. Family = Gaussian, link = identity

AICc of the lowest AICc (or best fit model) were considered (Burnham and Anderson 2002). The importance of each predictor was calculated by summing the AIC weights across all best-fitting models involving that variable (Burnham et al. 2011). In GAMMs, errors are assumed to be mutually independent; however, time series of environmental data may be autocorrelated. Therefore, models were also tested for temporal autocorrelations using the ‘acf’ and ‘pacf’ functions, which revealed low autocorrelation removing the need for an autocorrelation term in the models. Model quality was also assessed using the ‘gam.check’ function within the mgcv package.

Separate GAMMs models were tested for each lifecycle stage (seedbank, germinated seeds, seedlings and adult plants). The null model (null.terms) included site specified as a random effect. Model coefficients were estimated using restricted maximum likelihood (REML) method. All response variables were square root transformed except for biomass which was $\log(X+1)$ transformed. The distribution of the predictor variables was visually inspected, and square root transformations were applied to all of them except for the rates of change which were not transformed. Based on the distribution of the response variables, a Gaussian error distribution with an identity link function was selected for the GAMMs.

Results

Environmental conditions and phenology of *Ruppia* species

Environmental conditions varied over the annual cycle with distinct trends for each variable (Online Resource 1, Fig. 2). Average temperature increased progressively over the study period in both estuaries (15 °C in June to 27 °C in January). Benthic salinity was highest in June with values of 60 ppt and 40 ppt in the Vasse and Wonnerup and then declined reaching a minimum of 2 ppt in September in the Vasse and 5 ppt in the Wonnerup in October before increasing progressively for the remaining months (Fig. 3). Porewater salinity followed a similar pattern to benthic salinity but the range was less, from 6 to 48 ppt. Water depth followed an inverse pattern to benthic salinity. It increased from June, ~0.4 m to maximums in August, September (0.85 m) and then declined to January (0–0.9 m) and some sites in the Wonnerup had completely dried out (Fig. 4).

The phenology of *Ruppia* spp. was generally similar in the two estuaries. Seedlings were absent during a reconnaissance survey in autumn (May) but were observed in winter (June) when salinity was high and temperature was low (42 ppt, 12 °C, Table 1). Germinated seeds and seedlings were observed for all remaining time periods under a variety of conditions (Table 1) but the time of peak seedling densities differed slightly between estuaries: in the Wonnerup, this was winter (June) during high salinity–low temperature conditions and again in spring (November) in low salinity–high temperature conditions (Table 1); whilst in Vasse, this was also winter and spring (June, September) but additionally in January under high salinity–temperature conditions (Table 1). Thus, seedling emergence occurred under a wide range of environmental conditions. From September,

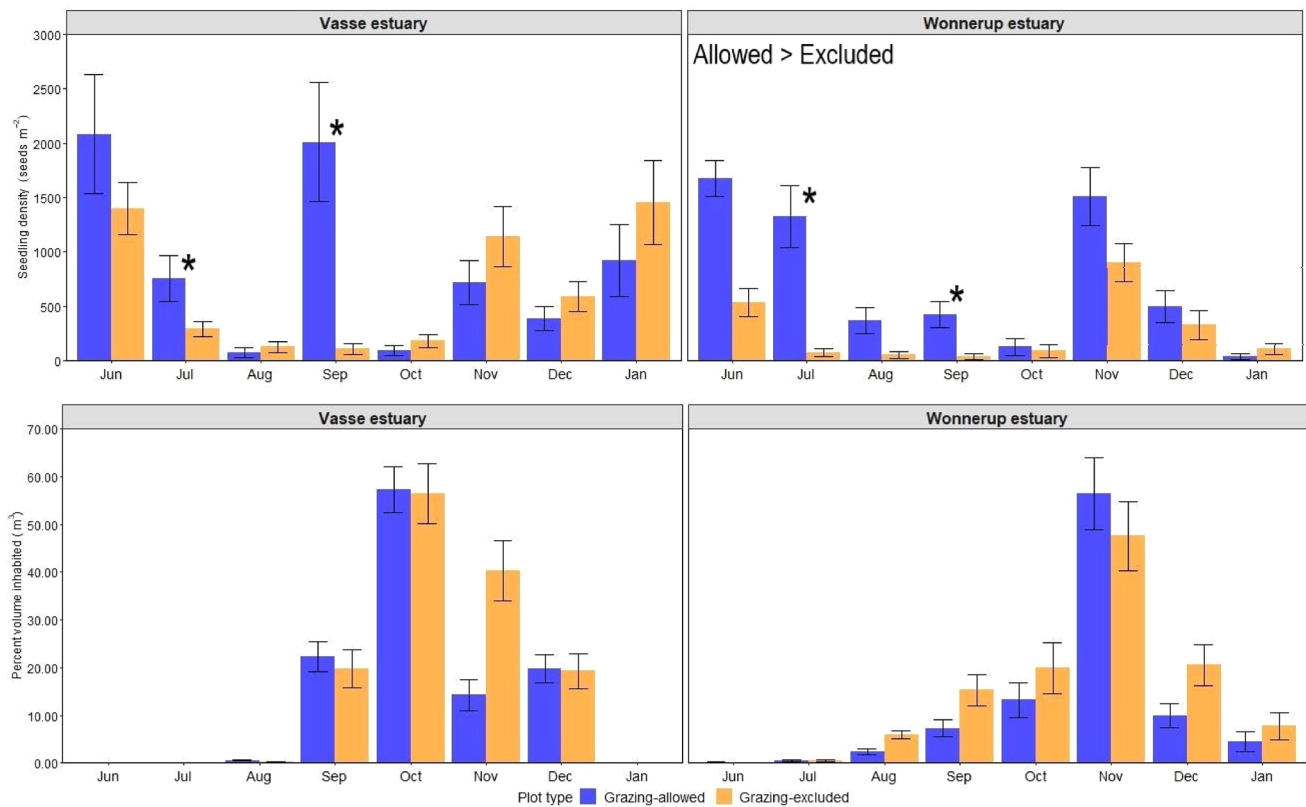


Fig. 3 Seedling density (top panels) and PVI (bottom panels) of *Ruppia* spp. measured in plots that allowed grazing ('Grazing-allowed') and where grazing was excluded ('Grazing-excluded') between June 2019–January 2020 in sites in the Vasse and Wonnerup estuaries,

Southwestern Australia. Stars indicate the month that significant differences between plot types occurred (pairwise tests; $p < 0.05$). Values are average (\pm SE)

extensive branching was observed amongst plants in both estuaries and in some cases, plant length reached or exceeded the top of the water column (0.6–0.7 m depth). Flowering and production of seed-bearing shoots began in September for the Wonnerup and in October for the Vasse, for a duration of 2–3 months. Flowers and seed-bearing shoots coincided with minimum benthic and porewater salinity (16 ppt; 1.5 ppt in the Vasse and 10 ppt; 13 ppt in the Wonnerup), maximum water depth (0.75–0.92 m) and temperatures between 18.5 and 20 °C (Table 1). Vegetation peaked mid-spring (October) in the Vasse and late-spring (November) in the Wonnerup when salinity had increased but was still low (~10 ppt) and temperature was still increasing (22.6 °C, Table 1). Early senescence began as water levels dropped at the start of summer (December) and was completed by mid-January when sites had either dried out or were very shallow (<0.25 m, Table 15). By then, temperatures exceeded 27 °C and porewater salinities were 45 ppt and 67 ppt in the Vasse and Wonnerup, respectively (Table 1). The lifecycle duration of *Ruppia* spp. from seed germination to senescence was 7 months with a seed dormancy period of at least 5 months. These stated durations are approximate based on monthly

sampling from June to January and the observation that no seedlings were present in May when the initial site visit was conducted.

Effects of grazing on lifecycle stages of *Ruppia*

Grazing scars were observed at all sites in the 'grazing-allowed' plots from September to January, inclusive. The seedbank (17,574 total), germinated seeds (142 total) and seedlings (1110 total) were dominated by *R. polycarpa*, by 78%, 96% and 81% of the total, respectively. Of *R. megacarpa* found, all germinated seeds and > 60% of seeds and seedlings were found in the Wonnerup. Average seedling density ranged from 37 ± 26 to 2081 ± 547 seedlings m⁻² (Fig. 5) with significant interactive effects of location and plot type (Lo \times Pl, $p < 0.05$). For the Wonnerup estuary, seedling density was significantly higher in the grazing-allowed (746 ± 72) plot compared to the grazing-excluded plot (267 ± 38) (Fig. 3). There was also a significant interactive effect of plot type and month, with pairwise comparisons indicating significantly higher seedling densities in the grazing-allowed plot compared to the

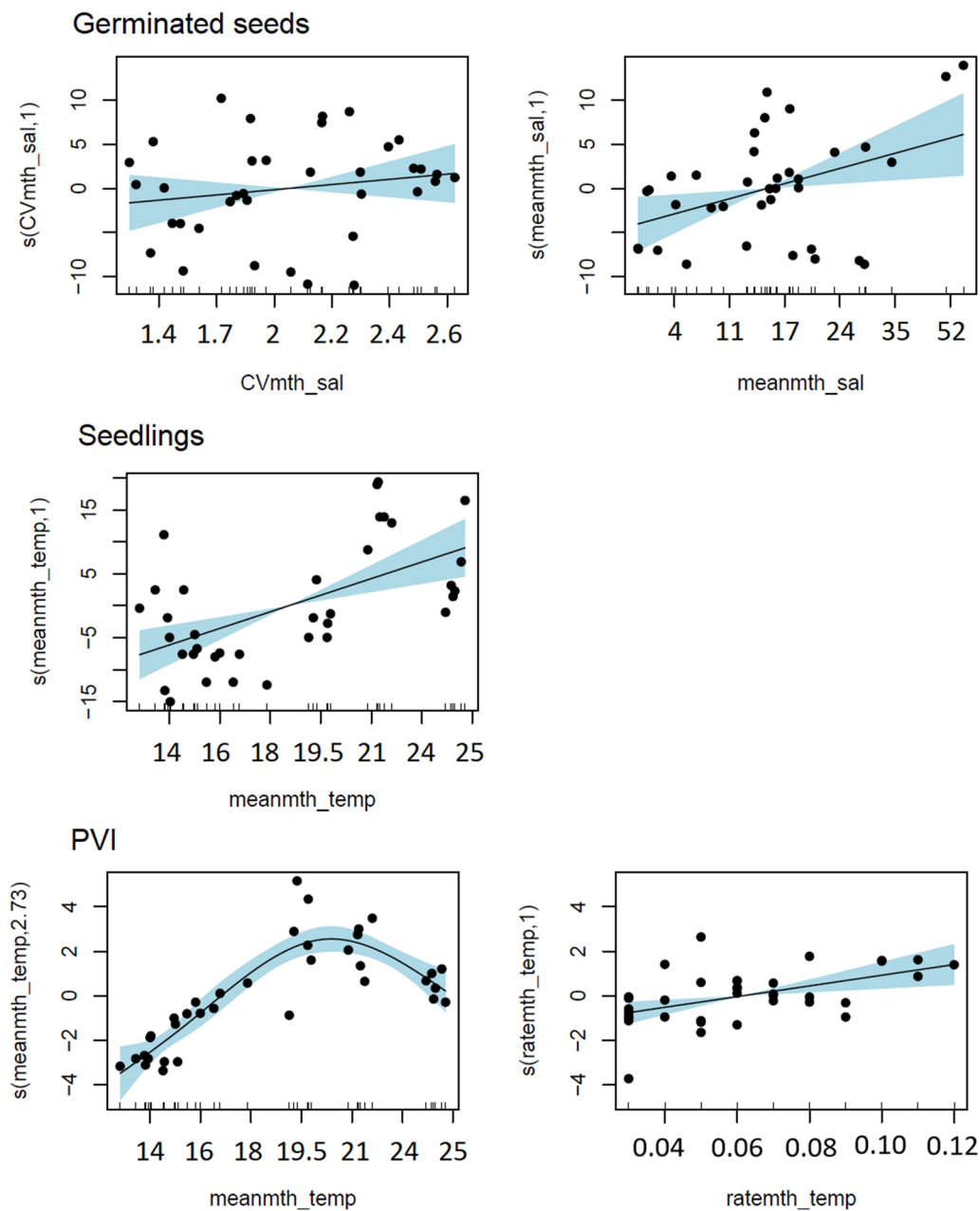


Fig. 4 Generalised additive mixed models (GAMMs) relating the smoothed effects of environmental variables on seagrass germinated seed density, seedling density and percent volume inhabited. Shaded regions indicate 95% confidence intervals

grazing-excluded plot in July (1041 ± 181 versus 184 ± 41) and September irrespective of Estuary (PTxMo, $p < 0.05$, Table 2; Fig. 3). PVI increased from June, peaked in October in the Vasse ($57 \pm 5 \text{ m}^3$) and in November in the Wonnerup ($\sim 56 \pm 8 \text{ m}^3$) and then declined with little remaining in January (Fig. 3). Month had a significant effect on PVI ($p < 0.05$) and no other factors were significant (Table 2). Plot type, or the interaction with any other factors, was not significant for the remaining seagrass variables. There was no effect of grazing on seedbank density, germinated

seeds or biomass. Seedbank density varied significantly between estuaries (Table 2), with the density in the Vasse estuary being significantly greater than the Wonnerup ($10,906 \pm 336$ versus $9322 \pm 417 \text{ seeds m}^{-2}$). Location and month interacted to affect germinated seed densities, cover, canopy and biomass; significant differences occurred between the estuaries in some months and not others (Table 2). For instance, biomass was significantly higher in the Vasse compared to the Wonnerup in October (36 ± 11 versus $19 \pm 30 \text{ g DW m}^{-2}$).

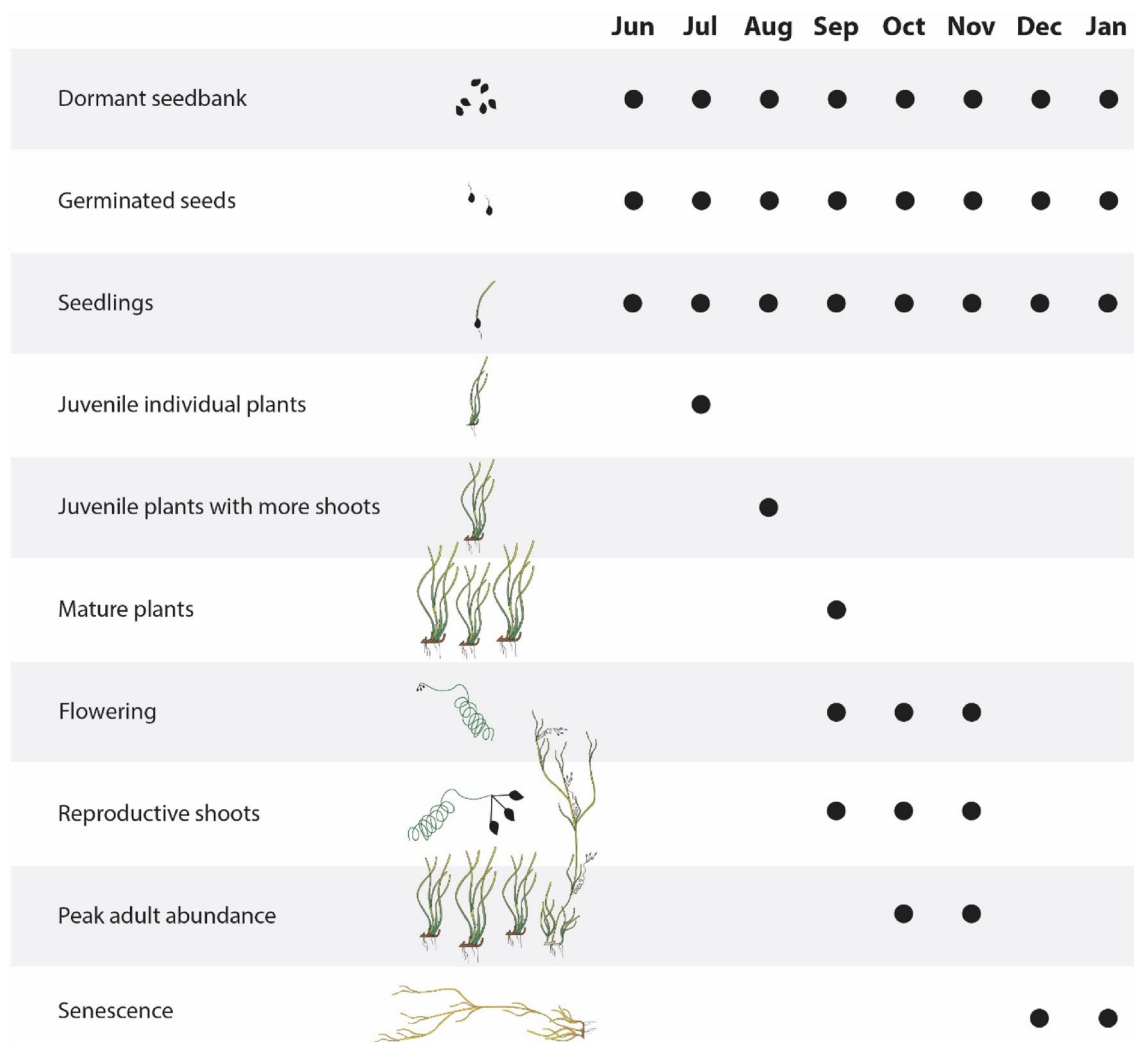


Fig. 5 Conceptual diagram with timing, presence and duration of the lifecycle stages of *Ruppia polycarpa* indicated by ● observed between June 2019 and January 2020 in the Vasse and Wonnerup estuaries, Southwestern Australia

Effects of environmental conditions on *Ruppia* lifecycle stages

Temperature and salinity metrics (average, rate of change, variation) best explained the spatial and temporal patterns in seagrass response variables apart from seedbank density and biomass where no models were supported (Table 3). Either one or two models were best supported.

Two models predicted the germinated seed density. The first model included average salinity which explained 17.2% of the total deviance ($p=0.012$, r^2 -sq-adj=0.147, Table 3). The second model included variation in salinity and explained 19.7% of the deviance in germinated seeds ($p=0.019$, r^2 -sq-adj=0.10, Table 3). There was a positive effect of increasing average salinity on the density of germinated seeds between 2 and 52 ppt (Fig. 4). Similarly, higher densities of germinated seeds were associated with more

variation in salinity with a change in salinity from +0.2 to 1.4 ppt day⁻¹ (Fig. 4). Average salinity was a slightly stronger predictor (0.372) than the variation in salinity (0.325) with the remaining predictors assigned low importance (<0.1, Table 3).

For seedling abundance, a model including the average temperature and rate of change in temperature was supported but the latter was not a significant predictor ($p=0.11$, Table 3). Average temperature on its own was the next top model, explaining 37.3% of the deviance in seedling abundance (r^2 -sq-adj=0.354, Table 3). Increasing average temperatures between 13.6 and 24.7 °C was associated with greater seedling abundances (Fig. 4). Average temperature and rate of change in temperature were assigned equal importance (0.534, Table 4).

Average temperature and rate of change in temperature were significant predictors of average PVI explaining

Table 4 Variable importance of environmental predictors from the generalised additive mixed model (GAMMs) analyses for predicting various lifecycle stages of *Ruppia* spp. (*Ruppia polycarpa* and *Ruppia megacarpa*) in Southwestern Australia.

Response variable	Water depth	Average salinity	Variation in salinity	Average temperature	Rate of change temperature
Germinated seeds (sqrt)	0.075	0.674	0.293	0.104	0.053
Seedlings (sqrt)	0.001	0	0.135	0.861	0.474
PVI (sqrt)	0	0	0.027	0.973	0.871

Colour scale indicates relative importance: most important = purple to least important = light yellow

82.5% of the deviance (Table 3) but average temperature was more important (0.973 versus 0.871, Table 4). There was a positive effect of increasing average temperatures on PVI but only up to 21 °C after which further increases caused reductions in PVI (Fig. 4). Higher PVI was associated with increased changes in temperature between +0.03 and 0.12 °C day⁻¹ (Fig. 4).

Discussion

This study represents the first complete lifecycle assessment of the key habitat former *Ruppia* for two variable estuaries, demonstrating that grazing, temperature and salinity influenced different stages of the lifecycle, but not always as expected. Swan grazing did not have a significant negative impact on adult plants. Seedling abundance increased in the presence of natural swan grazing in one estuary across time and only during some months in the other estuary. These results reveal a benefit for seagrass resilience since more seedlings can enhance population recovery (Olesen et al. 1994). Our approach that considered grazing effects at all life stages provided increased confidence that swan grazing was not a major stressor to seagrasses in this system and at this time. We also found evidence that *Ruppia* is likely to be resilient to the changes in salinity associated with climate change as germinated seeds and seedlings were present over a broad range of salinity, temperature and water depth conditions. This is indicative of bet hedging. Studies in variable terrestrial (Fan et al. 2018) and aquatic environments (Vollebergh and Congdon 1986) suggest these bet-hedging strategies are critical for the resilience of annual plant populations over multiple generations.

Swan grazing benefits seagrass resilience

The relative importance of herbivores in seagrass ecosystems can be difficult to predict due to the influence of multiple factors including grazing intensity (Dos Santos et al. 2013). We hypothesised that if swan grazing was a major stressor of seagrasses, then the abundance of each or more lifecycle stages would be significantly greater without grazing. Unexpectedly, plots grazed by swans had significantly higher seedling densities which could be related to grazing scars created by swans which form 'pits' in the sediment and

that were observed during most months (September–January). It is possible that more seeds became 'trapped' in the pits created by swans in the 'grazing-allowed' plot meaning there were simply more seeds available to germinate (Zipperle et al. 2010). It is also possible that swans may have moved seeds up the sediment profile but this could not be substantiated as we did not measure the change in burial depth of seeds. Ailstock et al. (2010) showed that seeds at shallower depths are more likely to germinate and become established seedlings but this was not evaluated in relation to grazing. Despite the grazing scars observed in the plots, there was no effects of grazing, and seagrasses would likely have been able to recover from grazing, given vegetative material was retained, a dormant seedbank was present and new seeds were produced (Jacobs et al. 1981). Overall, our results highlight that swan grazing is not a major stressor of seagrass in this system but rather, at least at the current intensities, is beneficial for seagrass resilience since seedling recruitment aids seagrass recovery (Olesen et al. 1994). It may be important to consider these results in the context of variability in swan abundance, both within and amongst estuaries. Swan numbers varied substantially over the sampling period and in all previous sampling seasons. During the study period (June 2019–January 2020), the average number of swans observed across the entire system was higher (342) than in most other seasons (158–232) (Online Resource Table 5). It is possible that the positive effects of swan grazing on seagrass may not be as strong when swan numbers are lower, or negative effects may be significant at higher swan numbers (Dos Santos et al. 2013).

Waterfowl abundance and grazing intensity could increase on permanent waterbodies as the extent and number of ephemeral wetlands decline under a drying climate (Roshier et al. 2001). Other studies have shown that increasing grazing intensity can reduce resilience (Dos Santos et al. 2013). To explore the potential for grazing to have negative effects in the future, we calculated the time it would take for swans to completely graze or remove 20% of seagrass biomass, a percentage loss associated with a decline in resistance (Dos Santos et al. 2013). An average seagrass consumption rate was not available for *Ruppia* spp. and so a rate of 394 g dry mass (DM) swan⁻¹ d⁻¹ was used based on data for grazing of *Zostera* which also exhibits colonising characteristics (Dos Santos et al. 2013). Based on seagrass biomass and swan abundance in November (2018–2019), the peak time for both

attributes, we estimated it would take 2,411 swans 39 days to graze 20% of the biomass or 197 days to graze out both estuaries entirely (Online Resource 1, Table 6). Swans migrate seasonally to the VWWS to breed, so it is unlikely that such a high number of swans remain in the system over an annual cycle and swan count data from 2015 to 2020 clearly supports this (Online Resource 1, Fig. 3). Alternatively, it would take 3,122 swans 1 month to graze out 20% of the biomass (Online Resource 1, Table 6). The average densities of swans in December 2018 and 2019 was 3,204 suggesting this scenario may be more plausible. However, in this system, a 20% reduction in biomass may not necessarily equate to a reduction in resilience in the following season because the biomass of *Ruppia* spp. is reduced to zero over each annual cycle anyway and especially if seeds are produced and a seedbank is present. On the other hand, Lekammudiyanse et al. (2022) found that grazing which occurred prior to flowering caused significant reductions in flowering densities of *Z. muelleri* and concluded that this likely reflects the re-allocation of resources away from reproduction towards vegetative growth. Reductions in flowering would likely impact seed set. Recruitment and ongoing persistence of *Ruppia* can depend on recurrent seed set (Strazisar et al. 2016). We conclude that it is unlikely that grazing pressure would result in significant loss of *Ruppia* from the VWWS, but the potential complexity of outcomes warrants further investigation, with emphasis on sexual reproductive stages of the life cycle and ideally, extending over multiple annual cycles where seasonal variation in environmental factors, consumption and herbivory can be taken into account (Ren et al. 2012; Heck et al. 2021).

Salinity and temperature are important drivers of the lifecycle of *Ruppia*

Note that less than 5% of the total number of germinated seeds found were *R. megacarpa*, making it difficult to draw conclusions about the germination requirements of this species (although freshwater has been reported as a requirement (Brock 1982)), and so the remainder of this discussion pertains to *R. polycarpa*. Low salinities generally promote germination of estuarine seagrass seeds (Orth et al. 2000), seedling growth and survival (Strazisar et al. 2013). Germinated seeds of *R. polycarpa* were first observed in June when conditions were hypersaline and remained present at all sites over the entire experiment, with surface water salinities ranging from 1 to 60 ppt. The number of germinated seeds also rose with both increasing average salinity and when there was more variation in salinity over a month. Similarly, Vollebergh and Congdon (1986) observed in situ germination of *R. polycarpa* when salinity was 40‰ TDS in autumn which was the start of the growing season. The authors concluded that the ability to germinate under

hypersaline conditions had important implications for population persistence since seeds that germinated early in the season would be exposed to favourable conditions for longer, be more likely to mature and reproduce. Early stages of the lifecycle, including seed germination and seedling establishment, are vital for species persistence (Donohue et al. 2010). We predict that early timing of germination and the ability to germinate over a broad range of salinities could increase the resilience of *R. polycarpa* to higher and more variable salinities associated with a drying climate.

Temperature is recognised as an important regulatory factor for seagrass growth (Lee et al. 2007) and we assumed that it would control adult plant abundance (Moore et al. 2014). Seedling density increased with rising average temperatures from ~ 14 to 25 °C. This wide optimal range for seedling emergence is beneficial, given temperatures continuously rise over the growing season. Variation in seedling emergence is another form of bet hedging as it spreads the risk of seedling failure and increases the likelihood of a proportion surviving and reproducing in habitats characterised by temporal unpredictability (Fan et al. 2018). Gu et al. (2018) reported 30 °C as being optimal for seedling establishment of *R. sinensis* so it is possible that seedlings of *R. polycarpa* may tolerate higher temperatures than were observed here. The abundance of adult plants rose with increasing average temperature and increasing variation in temperature and then declined at temperatures ≥ 21 °C suggesting the temperature for optimum growth may be closer to 20 °C. This is similar to the values reported for *R. maritima* (Koch and Dawes 1991) and *R. drepanensis* (Santamaría and Hootsmans 1998). We do not consider the apparent sensitivity of the adults to temperature concerning for resilience as the plants grew rapidly, reached sexual maturity within 3 months and were able to set seed before the negative effects of warming became evident. However, sexual reproduction can be inhibited by temperature and the ability of *R. polycarpa* to reproduce under warmer temperatures associated with climate change will likely be a key determinant for resilience. For *R. drepanensis*, the optimal temperature for flowering and seed production was 20 °C with no flowers produced at 14 °C and only a few flowering at 30 °C but no seeds produced after approximately 4 months (Santamaría and Hootsmans 1998). We recommend that future studies investigate the likelihood of seeds and/or seedlings transitioning to become reproductive adults under different temperature scenarios.

Complete lifecycle assessment reveals bet-hedging strategies of *Ruppia*

In habitats characterised by fluctuating environmental conditions, survival and reproduction are likely to be greatest for individuals able to complete their lifecycles quickly and over

a broad range of environmental conditions (Brock 1982). Early life history stages, including dormant seeds, germinated seeds and seedlings, were present over the entire study period (Fig. 5) and under different combinations of salinity, temperature and water depth: high salinity/low temperature/high water depth, low salinity/high temperature/high water depth and high salinity/high temperature/low water depth. Prolonged germination and seedling emergence under multiple combinations of conditions reduce the risk of losing an entire cohort when conditions suddenly change (Cohen 1966) and is proposed to maintain shoots, and overall fitness, during fluctuations with seasonal wetting and drying (Manino and Graziano 2016). These strategies are indicative of bet hedging and may confer resilience to more persistent hypersaline conditions associated with drying, but for this to be realised, the resultant juveniles must survive and reproduce. Seed set occurred between September and November (Fig. 5) under conditions of low salinity–warm temperatures and, combined with the rapid decline of adults from November onwards, suggests that reaching sexual maturity during early spring (September) may be critical for the persistence of *R. polycarpa* populations. This could be due to the sensitivity of flowering and seed production to temperature, as has been reported for *R. drepanensis* (Santamaría and Hootsmans 1998). Sim et al. (2006) observed higher adult mortality under increased salinity conditions. The same individuals were not tracked in our study; however, we did observe adult senescence when temperature and salinity had both increased in December and January (Fig. 5). The conditions in this study likely do not represent those predicted to emerge under a more extreme climate so we stress the need for experiments to be designed with these scenarios in mind and with more focus on determining the salinity and temperature thresholds that enable sexual reproduction. Experiments should use the same individuals from the start, through each transition, to completion of the lifecycle to determine the overall response to climate change (Radchuk et al. 2013).

Conclusion

By examining the complete lifecycle, our results confirmed that swan grazing does not negatively impact seagrass resilience. We revealed a benefit of swan grazing through enhanced seedling recruitment that was not previously known as assessments tend to focus swan grazing effects on later life stages. The continuous seed germination and seedling emergence of *R. polycarpa* over the study period, linked to a broad range of salinity and temperature conditions, indicates bet-hedging strategies that increase resilience to variable environmental conditions. Since early life stages are often key determinants of population persistence,

these results, in combination with rapid growth and seed set of adult plants, imply that *R. polycarpa* may be well placed to cope with drier and warmer conditions. These findings lay the foundation for examining how emerging salinity and temperature regimes may impact seagrasses. Gathering information pertaining to abiotic and biotic thresholds for each lifecycle stage is recommended as part of the toolbox for predicting seagrass response to climate change.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s00227-023-04192-6>.

Acknowledgements We are very grateful to the Department of Water and Environmental Regulation (DWER) for the funding provided to support the Industry Engagement Scholarship, and also to ECU staff and volunteers for fieldwork assistance and use of equipment. We thank DWER staff including Kath Lynch, Joanna Browne and Linda Kalnejais for fieldwork assistance and information regarding management of the system. Thanks to DBCA staff including Simone Strydom and Molly Moustaka for their expert advice and reviews. Thanks to Terry McFarlane for assistance with species identification and Kim Williams and Christine Taylor for the swan abundance data.

Author contributions C.W., K. M. and P.L. conceived the study idea, contributed critically to the concepts and review of the manuscript drafts. C. W. carried out the data collection and analysis and led the writing of the manuscript. C. S. K. provided advice and critically reviewed statistical analyses and reviewed the manuscript. C.O. and M. S. provided advice on the study design concepts, the data collection and reviewed manuscript drafts.

Funding Open Access funding enabled and organized by CAUL and its Member Institutions. Funding for this project was supported through an Industry scholarship provided by Edith Cowan University and supported by the Department of Water and Environmental Regulation and research funding provided by Kathryn McMahon and Paul Lavery.

Data/code availability Metadata for the dataset is now available at Edith Cowan University's repository online via the link: <https://ro.ecu.edu.au/datasets/109/>

Data availability The datasets generated during and/or analysed during the current study are available in the Edith Cowan University Research Online Institutional repository, link: <https://doi.org/10.25958/K1VE-GM19>.

Declarations

Conflict of interest The authors have no conflicts of interest to declare that are relevant to the content of this article.

Ethics approval Ethics approval was provided by Edith Cowan University (Reference # 19952).

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References

- Ailstock MS, Shafer DJ, Magoun AD (2010) Effects of planting depth, sediment grain size, and nutrients on *Ruppia maritima* and *Potamogeton perfoliatus* seedling emergence and growth. *Restor Ecol* 18:574–583
- Anderson MJ, Gorley RN, Clarke KR (2008) PERMANOVA+ for PRIMER: Guide to software and statistical methods
- Bakker ES, Wood KA, Pagès JF, Veen GF, Ciska, Christianen MJA, Santamaría L, Nolet BA, Hilt S (2016) Herbivory on freshwater and marine macrophytes: a review and perspective. *Aquat Bot* 135:18–36. <https://doi.org/10.1016/j.aquabot.2016.04.008>
- Beatty SJ (2019) Drivers of spatial and temporal movement patterns of *Acanthopagrus butcheri* through an estuarine surge barrier
- Bell SY, Fraser MW, Statton J, Kendrick GA (2019) Salinity stress drives herbivory rates and selective grazing in subtidal seagrass communities. *PLoS ONE* 14:1–13
- Bradstock RA, Auld TD (1995) Soil temperatures during experimental bushfires in relation to fire intensity: consequences for legume germination and fire management in South-Eastern Australia. *J Appl Ecol* 32:76
- Brock MA (1982) Biology of the salinity tolerant genus *Ruppia* L. in saline lakes in South Australia I. Morphological variation within and between species and ecophysiology. *Aquat Bot* 13:219–248
- Brock MA (1983) Reproductive allocation in annual and perennial species of the submerged aquatic halophyte *Ruppia*. *Ecology* 71:811–818
- Brock MA (1986) Adaptation to fluctuations rather than to extremes of environmental parameters. *Limnology*
- Burnham KP, Anderson DR (2002) Model selection and inference: a practical information—theoretic approach, 2nd edn. Springer, New York. <https://doi.org/10.1007/b97636>
- Burnham KP, Anderson DR, Huyvaert KP (2011) AIC model selection and multimodel inference in behavioral ecology: Some background, observations, and comparisons. *Behav Ecol Sociobiol* 65:23–35
- Canfield DE, Shireman JV, Colle DE, Haller WT, Watkins CE, Macaina MJ (1984) Prediction of chlorophyll a concentrations in Florida lakes: importance of aquatic macrophytes. *Can J Fish Aquat Sci* 41:497–501
- Carruthers TJB, Walker DI, Kendrick GA (1999) Abundance of *Ruppia megacarpa* mason in a seasonally variable estuary. *Estuar Coast Shelf Sci* 48:497–509
- Chambers JM, Paice R (2018) Vasse Wonnerup 2006–2016 An overview of the ecological condition of the Vasse-Wonnerup
- Cho HJ, Poirrier MA (2005) Seasonal growth and reproduction of *Ruppia maritima* L. s.l. in Lake Pontchartrain, Louisiana, USA. *Aquat Bot* 81:37–49
- Choney GE, McMahon K, Lavery PS, Collier N (2014) Swan grazing on seagrass: Abundance but not grazing pressure varies over an annual cycle in a temperate estuary. *Mar Freshw Res* 65:738–749
- Clarke KR, Gorley RN (2006) PRIMER v6: User Manual/Tutorial (Plymouth Routines in Multivariate Ecological Research). Primer-E, Plymouth
- Cohen D (1966) Optimizing reproduction in a randomly varying environment. *J Theor Biol* 12:119–129
- Cumming E, Jarvis JC, Sherman CDH, York PH, Smith TM (2017) Seed germination in a southern Australian temperate seagrass. *PeerJ* 2017:1–19
- Congdon ARA, McComb AJ (1981) The vegetation of the Blackwood River Estuary, South-West Australia. *J Ecol* 69:1–16
- Donohue K, Rubio de Casas R, Burghardt L, Kovach K, Willis CG (2010) Germination, postgermination adaptation, and species ecological ranges. *Annu Rev Ecol Evol Syst* 41:293–319
- Dos Santos VM, Matheson FE, Pilditch CA, Elger A (2013) Seagrass resilience to waterfowl grazing in a temperate estuary: A multi-site experimental study. *J Exp Mar Bio Ecol* 446:194–201. <https://doi.org/10.1016/j.jembe.2013.05.030>
- Duarte CM, Conley DJ, Carstensen J, Sánchez-Camacho M (2009) Return to Neverland: Shifting baselines affect eutrophication restoration targets. *Estuaries Coasts* 32:29–36
- Duncan C, Schultz N, Lewandowski W, Good MK, Cook S (2019) Lower dormancy with rapid germination is an important strategy for seeds in an arid zone with unpredictable rainfall. *PLoS ONE* 14:1–19
- Fan B, Zhou Y, Ma Q, Yu Q, Zhao C, Sun K (2018) The bet-hedging strategies for seedling emergence of *Calligonum mongolicum* to adapt to the extreme desert environments in northwestern China. *Front Plant Sci* 9:1–7
- Fernández-Torquemada Y, Sánchez-Lizaso JL (2011) Responses of two Mediterranean seagrasses to experimental changes in salinity. *Hydrobiologia* 669:21–33
- Fisher R, Wilson SK, Sin TM, Lee AC, Langlois TJ (2018) A simple function for full-subsets multiple regression in ecology with R. *Ecol Evol* 8:6104–6113
- Gordon CE, Price OF, Tasker EM, Denham AJ (2017) Acacia shrubs respond positively to high severity wildfire: Implications for conservation and fuel hazard management. *Sci Total Environ* 575:858–868. <https://doi.org/10.1016/j.scitotenv.2016.09.129>
- Graham MH (2003) Confronting multicollinearity in ecological multiple regression. *Ecology* 84:2809–2815
- Griffin NE, Durako MJ (2012) The effect of pulsed versus gradual salinity reduction on the physiology and survival of *Halophila johnsonii* Eiseman. *Mar Biol* 159:1439–1447
- Gu R, Zhou Y, Song X, Xu SSSS, Zhang X, Lin H, Xu SSSS, Zhu S (2018) Effects of temperature and salinity on *Ruppia sinensis* seed germination, seedling establishment, and seedling growth. *Mar Pollut Bull* 134:177–185. <https://doi.org/10.1016/j.marpollbul.2017.08.013>
- Hallett CS, Hobday AJ, Tweedley JR, Thompson PA, McMahon K, Valesini FJ (2018) Observed and predicted impacts of climate change on the estuaries of south-western Australia, a Mediterranean climate region. *Reg Environ Chang* 18:1357–1373
- Heck KL, Samsonova M, Poore AGB, Hyndes GA (2021) Global patterns in seagrass herbivory: why, despite existing evidence, there are solid arguments in favor of latitudinal gradients in seagrass herbivory. *Estuaries Coasts* 44:481–490
- Hootsmans MJM, Vermaat JE, Van Vierssen W (1987) Seed-bank development, germination and early seedling survival of two seagrass species from The Netherlands: *Zostera marina* L. and *Zostera noltii* Hornem. *Aquat Bot* 28:275–285
- Jacobs RPWM, Den Hartog C, Braster BF, Carriere FC (1981) Grazing of the seagrass *Zostera noltii* by birds at Terschelling (Dutch Wadden Sea). *Aquat Bot* 10:241–259
- Kendrick GA, Orth RJ, Sinclair EA, Statton J (2022) Effect of climate change on regeneration of seagrasses from seeds. *Inc*. <https://doi.org/10.1016/B978-0-12-823731-1.00011-1>
- Kendrick GA, Nowicki RJ, Olsen YS, Strydom S, Fraser MW, Sinclair EA, Statton J, Hovey RK, Thomson JA, Burkholder DA, McMahon KM, Kilminster K, Hetzel Y, Fourqurean JW, Heithaus MR, Orth RJ (2019) A systematic review of how multiple stressors from an extreme event drove ecosystem-wide loss of resilience in an iconic seagrass community. *Front Mar Sci*. <https://doi.org/10.3389/fmars.2019.00455>

- Kilminster K, McMahon K, Waycott M, Kendrick GA, Scanes P, McKenzie L, O'Brien KR, Lyons M, Ferguson A, Maxwell P, Glasby T, Udy J (2015) Unravelling complexity in seagrass systems for management: Australia as a microcosm. *Sci Total Environ* 534:97–109. <https://doi.org/10.1016/j.scitotenv.2015.04.061>
- Kissane Z (2019) Temporal and spatial use of resources by black swans (*Cygnus atratus*) on the Vasse-Wonnerup wetlands.
- Koch EW, Dawes CJ (1991) Influence of salinity and temperature on the germination of *Ruppia maritima* L. from the North Atlantic and Gulf of Mexico. *Aquat Bot* 40:387–391
- Kuiper-Linley M, Johnson C, Lanyon J (2007) Effects of simulated green turtle regrazing on seagrass abundance, growth and nutritional status in Moreton Bay, south-east Queensland, Australia. *Mar Freshw Res* 58:492–503
- Lane JAK, Clarke AG, Winchcombe YC (2011) Depth, Salinity and Temperature Profiling of Vasse - Wonnerup Wetlands in 1998–2000.
- Lee KS, Park SR, Kim YK (2007) Effects of irradiance, temperature, and nutrients on growth dynamics of seagrasses: A review. *J Exp Mar Bio Ecol* 350:144–175
- Lefcheck JS, Wilcox DJ, Murphy RR, Marion SR, Orth RJ (2017) Multiple stressors threaten the imperiled coastal foundation species eelgrass (*Zostera marina*) in Chesapeake Bay, USA. *Glob Chang Biol* 23:3474–3483
- Lekammudiyanse MU, Saunders MI, Flint N, Irving AD, Jackson EL (2022) Simulated megaherbivore grazing as a driver of seagrass flowering. *Mar Environ Res* 179:105698. <https://doi.org/10.1016/j.marenvres.2022.105698>
- Levin SA, Lubchenco J (2008) Resilience, robustness, and marine ecosystem-based management. *Bioscience* 58:27–32
- Mannino AM, Graziano M (2016) Differences in the growth cycle of *Ruppia cirrhosa* (Petagna) Grande in a Mediterranean shallow system. *Plant Biosyst* 150:54–61. <https://doi.org/10.1080/11263504.2014.906511>
- Mason R (1967) The species of *Ruppia* in New Zealand. *New Zeal J Bot* 5:519–531
- McCallum R, Eyre B, Hyndes G, McMahon K, Oakes JM, Wells NS (2021) Importance of internal dissolved organic nitrogen loading and cycling in a small and heavily modified coastal lagoon. *Biogeochemistry*. <https://doi.org/10.1007/s10533-021-00824-5>
- Mitchell SF, Wass RT (1996) Grazing by black swans (*Cygnus atratus* Latham), physical factors, and the growth and loss of aquatic vegetation in a shallow lake. *Aquat Bot* 55:205–215
- Moore KA, Shields EC, Parrish DB (2014) Impacts of Varying Estuarine Temperature and Light Conditions on *Zostera marina* (Eelgrass) and its Interactions With *Ruppia maritima* (Widgeongrass). *Estuaries Coasts* 37:20–30
- Murase H, Nagashima H, Yonezaki S, Matsukura R, Kitakado T (2009) Application of a generalized additive model (GAM) to reveal relationships between environmental factors and distributions of pelagic fish and krill: A case study in Sendai Bay, Japan. *ICES J Mar Sci* 66:1417–1424
- Nakaoka M, Aioi K (1999) Growth of seagrass *Halophila ovalis* at dugong trails compared to existing within-patch variation in a Thailand intertidal flat. *Mar Ecol Prog Ser* 184:97–103
- O'Dea CM, Lavery PS, Webster CL, McMahon KM (2022) Increased extent of waterfowl grazing lengthens the recovery time of a colonizing seagrass (*Halophila ovalis*) with implications for seagrass resilience. *Front Plant Sci* 1–16
- Oczkowski A, McKinney R, Ayvazian S, Hanson A, Wigand C, Markham E (2015) Preliminary evidence for the amplification of global warming in shallow, intertidal estuarine waters. *PLoS ONE* 10:1–18
- Olesen B, Sandjensen K, Sand-jensen K (1994) Patch dynamics of eelgrass *Zostera marina*. *Mar Ecol Prog Ser* 106:147–156
- Orth RJ, Harwell MC, Bailey EM, Bartholomew A, Jawad JT, Lombana AV, Moore KA, Rhode JM, Woods HE (2000) A review of issues in seagrass seed dormancy and germination: Implications for conservation and restoration. *Mar Ecol Prog Ser* 200:277–288
- Preen A, Marsh H (1995) Response of dugongs to large-scale loss of seagrass from Hervey Bay, Queensland Australia. *Wildl Res* 22:507–519
- R Development Core Team (2021) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org/>
- Radchuk V, Turlure C, Schtickzelle N (2013) Each life stage matters: The importance of assessing the response to climate change over the complete life cycle in butterflies. *J Anim Ecol* 82:275–285
- Ralph PJ (1999) Photosynthetic response of *Halophila ovalis* (R. Br.) Hook. f. to combined environmental stress. *Aquat Bot* 65:83–96
- Ren H, Schönbach P, Wan H, Gierus M, Taube F (2012) Effects of Grazing Intensity and Environmental Factors on Species Composition and Diversity in Typical Steppe of Inner Mongolia, China. *Plos One* 7:e52180
- Rodríguez-Pérez H, Green AJ (2006) Waterbird impacts on widgeongrass *Ruppia maritima* in a Mediterranean wetland: comparing bird groups and seasonal effects. *Oikos* 112:525–534
- Roshier DA, Whetton PH, Allan RJ, Robertson AI (2001) Distribution and persistence of temporary wetland habitats in arid Australia in relation to climate. *Austral Ecol* 26:371–384
- Santamaría L, Hootsmans MJM (1998) The effect of temperature on the photosynthesis, growth and reproduction of a Mediterranean submerged macrophyte, *Ruppia drepanensis*. *Aquat Bot* 60:169–188
- Scanes E, Scanes PR, Ross PM (2020) Climate change rapidly warms and acidifies Australian estuaries. *Nat Commun* 11:1–11. <https://doi.org/10.1038/s41467-020-15550-z>
- Sim LL, Chambers JM, Davis JA (2006) Ecological regime shifts in salinised wetland systems. I. Salinity thresholds for the loss of submerged macrophytes. *Hydrobiologia* 573:89–107
- Steward JS, Virnstein RW, Lasi MA, Morris LJ, Miller JD, Hall LM, Tweeddale WA (2006) The impacts of the 2004 hurricanes on hydrology, water quality, and seagrass in the central Indian River Lagoon, Florida. *Estuaries Coasts* 29:954–965
- Strazisar T, Koch MS, Madden CJ, Filina J, Lara PU, Mattair A (2013) Salinity effects on *Ruppia maritima* L. seed germination and seedling survival at the Everglades-Florida Bay ecotone. *J Exp Mar Bio Ecol* 445:129–139. <https://doi.org/10.1016/j.jembe.2013.02.045>
- Strazisar T, Koch MS, Madden CJ (2015) Seagrass (*Ruppia maritima* L.) Life History Transitions in Response to Salinity Dynamics Along the Everglades-Florida Bay Ecotone. *Estuaries Coasts* 38:337–352
- Strazisar T, Koch MS, Frankovich TA, Madden CJ (2016) The importance of recurrent reproductive events for *Ruppia maritima* seed bank viability in a highly variable estuary. *Aquat Bot* 134:103–112. <https://doi.org/10.1016/j.aquabot.2016.07.005>
- Strydom S, McMahon K, Lavery PS (2017) Response of the seagrass *Halophila ovalis* to altered light quality in a simulated dredge plume. *Mar Pollut Bull* 121:323–330. <https://doi.org/10.1016/j.marpolbul.2017.05.060>
- Tatu KS, Anderson JT, Hindman LJ, Seidel G (2007) Mute Swans' Impact on Submerged Aquatic Vegetation in Chesapeake Bay. *J Wildl Manage* 71:1431–1439
- Thrush SF, Halliday J, Hewitt JE, Lohrer AM (2008) The effects of habitat loss, fragmentation, and community homogenization on resilience in estuaries. *Ecol Appl* 18:12–21
- Tweedley JR, Keleher J, Cottingham A, Beatty SJ, Lymbery AJ (2014) The fish fauna of the Vasse-Wonnerup and the impact of a substantial fish kill event. *Rep GeoCatch, Murdoch Univ Perth, West Aust* 113

- Tweedley JR, Dittmann SR, Whitfield AK, Withers K, Hoeksema SD, Potter IC (2019) Hypersalinity: Global Distribution, Causes, and Present and Future Effects on the Biota of Estuaries and Lagoons. In: Coasts and Estuaries: The Future. pp 523–46.
- Vollebergh P, Congdon RA (1986) Germination and growth of *Ruppia polycarpa* and *Lepilaena cylindrocarpa* in ephemeral saltmarsh pools, Westernport Bay, Victoria. *Aquat Bot* 26:165–179
- Wetland Research & Management (2007) Ecological Character Description Vasse-Wonnerup Wetlands Ramsar Site. :237. http://www.dpaw.wa.gov.au/images/documents/conservation-management/wetlands/ramsar/ECD_Vasse_Wonnerup.pdf
- Wetz MS, Yoskowitz DW (2013) An ‘extreme’ future for estuaries? Effects of extreme climatic events on estuarine water quality and ecology. *Mar Pollut Bull* 69:7–18. <https://doi.org/10.1016/j.marpollbul.2013.01.020>
- Wood SN (2011) Generalized additive models : an introduction with R. Boca Raton SE - XVII, [1], 392 s. : il. ; 24 cm.: Chapman & Hall/CRC
- Wood S, Scheipl F (2016) gamm4: Generalized additive mixed models using ‘mgcv’ and ‘lme4’. R package version 0.2-4. <https://CRAN.R-project.org/package=gamm4>
- Xu S, Zhou Y, Wang P, Wang F, Zhang X, Gu R (2016) Salinity and temperature significantly influence seed germination, seedling establishment, and seedling growth of eelgrass *Zostera marina* L. *PeerJ* 2016:1–21
- Zipperle AM, Coyer JA, Reise K, Stam WT, Olsen JL (2010) Waterfowl grazing in autumn enhances spring seedling recruitment of intertidal *Zostera noltii*. *Aquat Bot* 93:202–205. <https://doi.org/10.1016/j.aquabot.2010.05.002>

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