

2021

Population-specific resilience of *Halophila ovalis* seagrass habitat to unseasonal rainfall, an extreme climate event in estuaries

Chanelle L. Webster

Kieryn L. Kilminster

Marta Sánchez Alarcón

Katherine Bennett

Simone Strydom

See next page for additional authors

Follow this and additional works at: <https://ro.ecu.edu.au/ecuworkspost2013>



Part of the [Environmental Sciences Commons](#), and the [Terrestrial and Aquatic Ecology Commons](#)

10.1111/1365-2745.13648 Webster, C. L., Kilminster, K. L., Sánchez Alarcón, M., Bennett, K., Strydom, S., McNamara, S., ... McMahon, K. M. (2021). Population-specific resilience of *Halophila ovalis* seagrass habitat to unseasonal rainfall, an extreme climate event in estuaries. *Journal of Ecology*. Advance online publication. <https://doi.org/10.1111/1365-2745.13648>

This Journal Article is posted at Research Online.

Authors

Chanelle L. Webster, Kieryn L. Kilminster, Marta Sánchez Alarcón, Katherine Bennett, Simone Strydom, Sian McNamara, Paul S. Lavery, and Kathryn M. McMahon

RECONCILING RESILIENCE ACROSS
ECOLOGICAL SYSTEMS, SPECIES AND SUBDISCIPLINES

Journal of Ecology



Research Article

Population-specific resilience of *Halophila ovalis* seagrass habitat to unseasonal rainfall, an extreme climate event in estuaries

Chanelle L. Webster¹ | Kierny L. Kilminster^{2,3} | Marta Sánchez Alarcón² |
Katherine Bennett² | Simone Strydom^{1,4} | Sian McNamara¹ | Paul S. Lavery¹ |
Kathryn M. McMahon¹

¹School of Science & Centre for Marine Ecosystem Research, Edith Cowan University, Joondalup, WA, Australia

²Department of Water and Environmental Regulation, Joondalup, WA, Australia

³School of Biological Sciences, University of Western Australia, Crawley, WA, Australia

⁴Department of Biodiversity, Conservation and Attractions, Kensington, WA, Australia

Correspondence

Chanelle L. Webster
Email: chanelle.webster@ecu.edu.au;
clwebst@hotmail.com

Funding information

Edith Cowan University

Handling Editor: Dan Friess

Abstract

1. Extreme climate events are predicted to alter estuarine salinity gradients exposing habitat-forming species to more frequent salinity variations. The intensity and duration of these variations, rather than the mean salinity values ecosystems are exposed to, may be more important in influencing resilience but requires further investigation.
2. Precipitation, including the frequency, intensity and timing of occurrence, is shifting due to climate change. A global analysis on the timing of rainfall in estuarine catchments was conducted. In 80% of the case studies, the maximum daily rainfall occurred in the dry season at least once over the 40-year period and could be classified as an extreme event.
3. We selected an estuary in southwestern Australia and investigated the effects of an extreme rainfall event in 2017 resulting in an excess discharge of freshwater on seagrass *Halophila ovalis*. Adapting an approach applied for marine heatwaves using salinity data, we quantified metrics and characterised the event along the estuarine gradient. We assessed seagrass resilience by calculating resistance times based on the comparisons of biomass and leaf density data prior to, and during the event, and recovery times through assessment against historical condition.
4. Where salinity is historically more variable, reductions in biomass were lower (higher resistance via plasticity in salinity tolerance) and meadows recovered within 9–11 months. Where salinity is historically more stable, loss of biomass was greatest (low resistance) post-event and recovery may exceed 22 months, and potentially due to the rapid decline in salinity (–3 PSU/day).
5. As estuaries become more hydrologically variable, these metrics provide a baseline for retrospective and future comparisons. Our results suggest seagrass resilience to hyposalinity is population specific. This understanding enables more

[The copyright line for this article was changed on 30 April 2021 after original online publication.]

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2021 The Authors. *Journal of Ecology* published by John Wiley & Sons Ltd on behalf of British Ecological Society

accurate predictions about ecological responses to climate change and identifies which populations may 'future proof' ecosystem resilience.

6. *Synthesis*. Following an extreme rainfall event, we found seagrass populations that are exposed to variable salinities recovered while those from a stable salinity environment were unable to recover within the study time frame. These findings expand upon existing evidence, derived primarily from other ecosystems, that show new sources of resilience may be uncovered by accounting for between-population variation.

KEYWORDS

climate change, foundation species, hierarchical metric, hyposalinity, plant–climate interactions, resilience, unseasonal precipitation

1 | INTRODUCTION

The occurrence of extreme climate events (ECEs) has increased since 1950, a trend projected to continue to the end of the century (Christensen & Christensen, 2004; IPCC, 2014; Trenberth & Fasullo, 2012). Smith (2011) defined an ECE 'as an episode or occurrence in which a statistically rare or unusual climatic period alters ecosystem structure and/or function well outside the bounds of what is considered typical or normal variability'. Thus, both the driver (climate event) and the response (ecological effect) must be assessed against long-term background data. An ongoing challenge for ecologists is to predict how these climate events influence ecological responses. For example, different metrics related to sea surface temperatures during a marine heatwave explained the single largest reduction in seagrass extent (~1,310 km²) to date in Shark Bay, Western Australia (Strydom et al., 2020). Unseasonal and extreme warming altered the community structure of subarctic vegetation (Bokhorst et al., 2012) highlighting the importance of timing of ECEs in predicting ecological response.

Research into climatic extremes has largely focused on heatwaves, anomalously warm events usually of a specified duration (e.g. ≥5 days) with temperatures exceeding the 90th percentile based on a climatological period, in both terrestrial and marine systems (Hobday et al., 2016; Hoover et al., 2014; Wernberg, 2020) and progressed to a point where hotspots, high probability of extreme ecological responses, have been identified (Smale et al., 2019). Other environmental drivers, for example, rising sea levels and wildfires, are also likely to exhibit extremes outside the bounds of 'normal variability', but the confidence around the predictions is not as great as for temperature (IPCC, 2014). One potential climatic extreme is severe precipitation events in many regions (Adler et al., 2018; IPCC, 2007; Trenberth, 2011) that can have significant ecological (Campbell & McKenzie, 2004), political and social consequences (Echendu, 2020; Zhou et al., 2011).

Changes in precipitation are a consequence of anthropogenic climate change due to higher levels of moisture in the atmosphere associated with rising global temperatures (Trenberth & Fasullo, 2012). These changes will not be uniform across the globe (IPCC, 2014; Power et al., 2017), regions that are already wet are

expected to become wetter and dry regions are forecast to become drier (Trenberth, 2011). Combined with these changes in total precipitation, the timing is also predicted to vary. For example, annual precipitation in Europe has declined overall, but the occurrence of extreme summer precipitation events has increased (Christensen & Christensen, 2004) and this is forecast to continue (IPCC, 2014). Extreme precipitation has been identified as a potential threat to global ecosystems but especially those in Mediterranean climate regions (Hallett et al., 2018; Kim et al., 2019).

Ecosystem impacts from changing precipitation, particularly unseasonal rainfall, are likely to be most apparent in estuaries. Ecosystem function in estuaries is structured by the salinity gradient which is usually characterised by predictable seasonal patterns that influence the presence, growth and reproductive cycles of different biota (Gasith & Resh, 1999; Largier et al., 1997; Thompson et al., 2016). Rapid and large declines in salinity occur following heavy precipitation (Steward et al., 2006), and such modifications can result in significant ecological responses such as the loss of aquatic species (Nicol, 2005) and impaired ecosystem functioning (Whitfield, 2017). While extreme rainfall can affect a number of critical environmental parameters in estuaries, including salinity and light, changes in salinity may be a useful way of characterising these extreme rainfall events because of the predictable relationship with freshwater and comprehensive spatial and temporal coverage of data for this variable (Boyer et al., 2005; Durack & Wijffels, 2010).

The ecosystem response to changes in salinity will depend on the resilience of estuarine biota to this pressure (Darr et al., 2014; Nche-Fambo et al., 2015). Resilience comprises resistance and recovery. During resistance, structure and function is upheld following a disturbance, and recovery implies the partial or full return to some pre-disturbance condition (Walker et al., 2004). For instance, most estuarine biota will be resistant to some fluctuations in salinity via phenotypic plasticity in salinity tolerance, so the ecosystem resilience will depend upon the ability to resist and/or recover from the disturbance. This in turn is dependent upon the characteristics of the disturbance such as the direction, intensity, magnitude of change and the duration of exposure (Kültz, 2015; Lee & Petersen, 2003). Scientists are using frameworks to define ECEs such as marine heatwaves (Hobday et al., 2016), and to understand

and predict ecosystem response and resilience, for example, in coral reefs (Hughes & Stachowicz, 2004; Kayanne, 2017), seagrass (Strydom et al., 2020) and forest ecosystems (Tatarinov et al., 2016). But such a framework for extreme rainfall events, and the associated changes in environmental conditions and ecosystem responses in coastal and marine ecosystems, has not been developed.

Seagrasses are foundation species in estuaries (Lefcheck et al., 2017), serve as bioindicators of environmental change and, being sessile, are vulnerable to disturbances (Kemp et al., 2004; Kim et al., 2013). Estuarine seagrass of the genera *Halophila*, *Zostera* and *Ruppia* is generally considered to have broad salinity tolerances (Brock, 1982; Tyerman, 1982). However, recent evidence suggests resilience can vary at multiple scales of biological organisation and time. Populations that are exposed to environmental regimes similar to those brought about by ECEs may be more resilient. This has been observed for different seagrass species in relation to hyposalinity, for example, *Zostera marina* (Salo & Pedersen, 2014) and *H. johnsonii* (Gavin & Durako, 2014) as well as for arctic diatoms (Wolf et al., 2018) and common ant species (Pelini et al., 2012) in connection with rising temperatures. Other factors may also be important in determining ecosystem resilience to the ECEs including the timing of the change and if it is gradual or rapid (Dietrich et al., 2018; Fernández-Torquemada & Sánchez-Lizaso, 2011; Griffin & Durako, 2012). Therefore, some populations may be more prone to localised extinctions from changing environmental regimes than others, but this could depend on the characteristics of the change.

There were three key aspects to this study. Firstly, an assessment to identify the likelihood of unseasonal rainfall events in estuaries across the globe, and if these could be considered extreme events defined by being statistically rare following the definition of Smith (2011). For example, if the amount of rainfall exceeds the 90th percentile. Secondly, development of metrics to characterise the environmental change in estuaries from unusual rainfall events following the approach of Hobday et al. (2016) for marine heatwaves, but using salinity rather than temperature. Finally, we applied this metric approach to an unseasonal and large summer rainfall event that occurred in a temperate estuary in 2017 and assessed the ecosystem response using a resilience framework. Here we tested two hypotheses: (a) the resistance and recovery of the seagrass *Halophila ovalis* R. Brown would vary among meadows distributed along the estuarine salinity gradient; and (b) that a longer duration and higher magnitude of freshwater exposure and faster rate of decline in salinity would negatively impact the resistance and recovery of seagrass meadows.

2 | MATERIALS AND METHODS

2.1 | Global assessment of the likelihood of unseasonal rainfall as extreme events

A conceptual model was developed to empirically test if unseasonal heavy rainfall could be considered an extreme climate event based

on the definition of Smith (2011). A first requirement is a dry season with relatively low rainfall compared to other times of the year. Then a second requirement is an extreme daily rainfall event occurring in that dry season which could potentially rapidly change salinity in the estuary. Daily precipitation values were used as these are more representative of large rainfall events that are usually short term in nature but with disproportionate impact (Jentsch et al., 2007) compared to total monthly rainfall which is an accumulation of a number of events over the month. We selected estuaries from the Global Estuary Database (Adler, 2003; Watson et al., 2004), five from each climate region (northern temperate, northern subtropics, tropics, southern subtropics and southern temperate regions) following the classifications of the IPCC (2014; Table S1) to represent different climate settings and the global distribution of estuaries. Background rainfall data (1 January 1979–30 December 2019) were extracted for each estuary from the CPC global unified gauge-based analysis of precipitation provided by the NOAA/OAR/ESRL PSL, Boulder, Colorado, USA (<https://psl.noaa.gov/>). As the rainfall data are available in 0.5° latitude × 0.5° longitude grids (89.75 N–89.75 S and 0.25 E–359.75 E), these were overlaid with the polygon of each estuary and its catchment and data from the most appropriate grid (highest overlap) extracted. The presence of seasonal patterns of rainfall in each estuary was assessed with boxplots of monthly rainfall generated from the 40-year period (Figures S1–S26). Months with much lower rainfall than others were selected by visual analysis to represent the dry season (Figures S1–S26). A dry season was identified in 20 of the 25 estuaries and the seasonality quantified by calculating the mean monthly rainfall for the dry season period and expressing it as a proportion of the mean annual rainfall. These estuaries were assessed further for the likelihood of extreme daily rainfall in the dry season. The time of the maximum daily precipitation for each year across the 40-year period was identified for each estuary. Then the number of annual maximum daily precipitation events that occurred in the dry season were tallied. For these events, the value of the annual maximum daily rainfall was expressed as a percentile of the entire 40 years of daily rainfall data. We considered rainfall in the summer or dry season that exceeded the 90th percentile to be an extreme rainfall event following Smith (2011). These events are likely to create a rapid change in salinity and lead to significant ecosystem impacts constituting an extreme event (Levinton et al., 2011).

2.2 | Flood metric development and ecosystem response

2.2.1 | Study site

The Swan-Canning is a shallow micro-tidal (<1 m) estuary that covers approximately 40 km² and flows through Perth, the capital city of Western Australia (Figure 1). Like estuaries world-wide, the Swan-Canning shows increasing signs of eutrophication including more frequent fish kills and algal blooms (Huang et al., 2019). Around 50% of the Perth population occupies the coastal catchments, so the lower

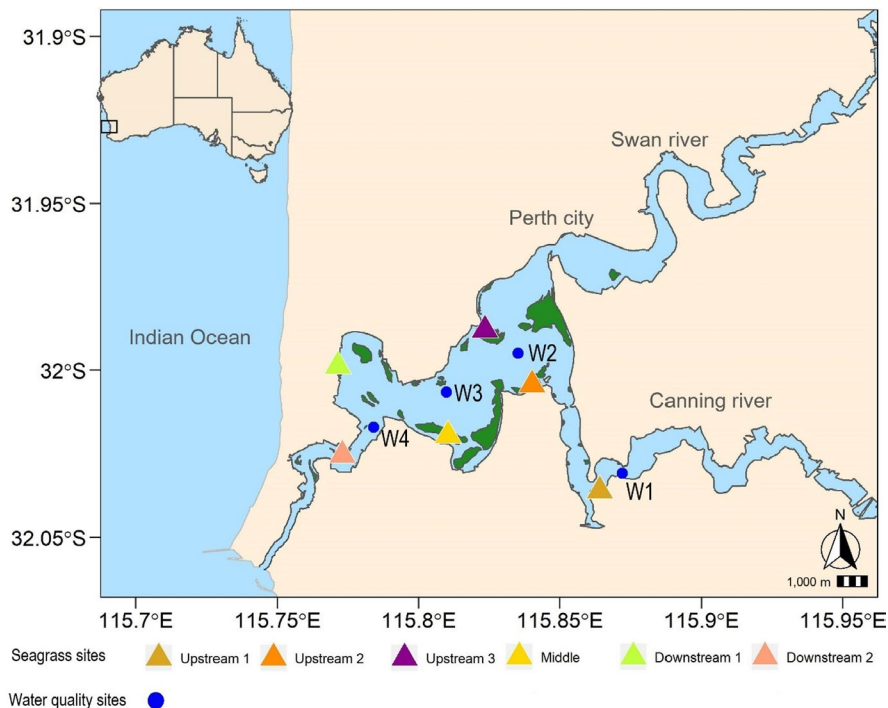


FIGURE 1 The distribution of the dominant seagrass, *Halophila ovalis* R. Brown in the Swan-Canning Estuary, southwestern Australia according to a 2010–2011 survey. Also shown is the location of six seagrass and four water quality monitoring sites (W1–W4) used to investigate the impact of an extreme summer rainfall event in February 2017

and middle estuarine reaches receive nutrients from urban sources while nutrient inputs to the upper estuary and river zones originate from agriculture and light industrial activities (Kelsey et al., 2010). Approximately 81% of inflows into the estuary come from both the Swan river and its major tributary the Avon river and 7% from the Canning river (Thomson et al., 2001) while the Indian Ocean enters the estuary through the permanently open mouth (Figure 1). Typical of estuaries in Mediterranean-climate regions that exhibit strong seasonality, the hydrological conditions in the estuary are characterised by distinct seasonal stratification and salt-wedge dynamics (Hodgkin, 1987). Summer (defined as December to March) is characterised by hot daily maximum air temperatures of between 29 and 31°C and low rainfall (62.4 mm total; retrieved from <http://www.bom.gov.au>, station: 009225). In winter (June to August), temperatures decline (18–19.5°C, retrieved from <http://www.bom.gov.au>, station: 009225) while the majority of annual rainfall (~80%) occurs (1993–2019 winter average: 397.8 mm, retrieved from <http://www.bom.gov.au>, station: 009225) generating high river flow throughout the estuary. This estuary was included in the unseasonal rainfall analysis described above.

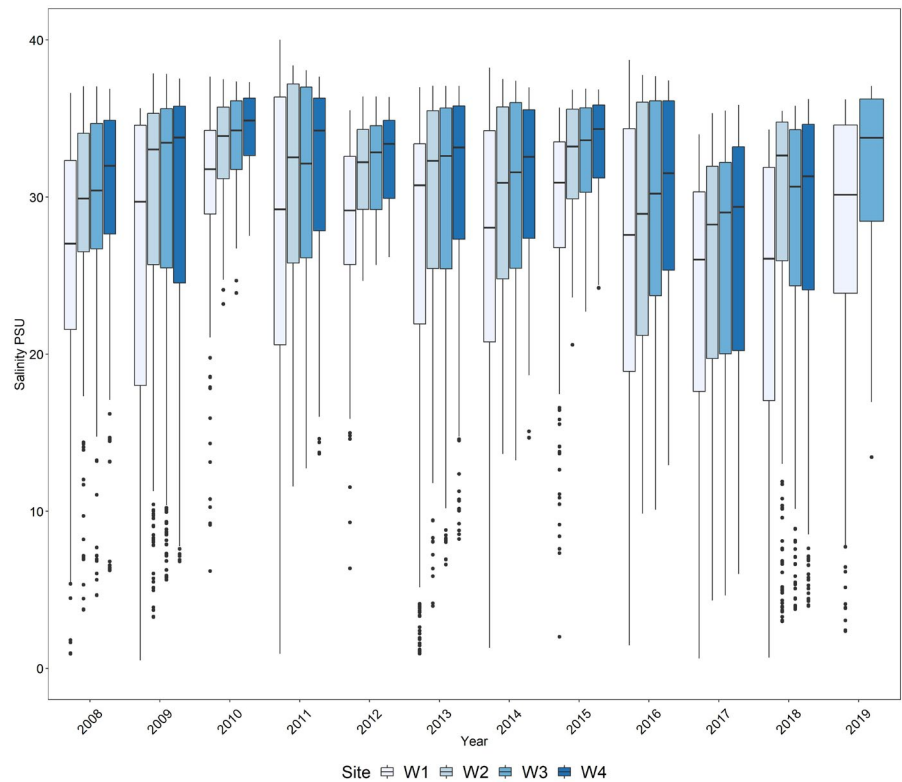
The seagrass, *H. ovalis*, is the dominant habitat in the system and covers approximately 4 km² of the estuary occurring primarily in the shallows (≤2 m depth; Figure 1; Kilminster & Forbes, 2014). Salinity, light and temperature are the major environmental factors affecting the growth of *H. ovalis* in this system (Hillman et al., 1995). The Department of Water and Environmental Regulation (DWER) has monitored water quality at four sites with monitoring of the most recent site starting in 2000 (Figure 1) and seagrass at six different sites during summer from 2011 to 2018 (Kilminster & Forbes, 2014). Monitoring was conducted at seagrass sites that represent *H. ovalis* distribution (Figure 1) and across a range of environmental conditions that occur throughout the estuary. Each site covers ~10 m² area but the meadows may extend beyond this. There

are three upstream seagrass sites, one in the Canning river (Upstream 1) and two in the Swan river (Upstream 2 and 3), one in the middle basin of the estuary (Middle) and two in the downstream part of the estuary (Downstream 1 and 2; Figure 1). Monitoring occurred monthly between December and March to coincide with *H. ovalis* peak growth and reproductive period. Data used in this study were from the seagrass monitoring program and additional samples that were collected outside the monitoring period (April, May, August to November 2017).

The salinity regime varies across the upstream (W1, W2), middle (W3) and downstream (W4) sections of the estuary (Figure 2). Generally, salinity is highly variable in the upstream section of the Canning river due to the small size and shallow nature of this river (W1, Figure 2). The variation in salinity in both upstream sections (W1, W2) is primarily influenced by seasonal changes in freshwater inflow. For instance, lower river flow in summer and increased evaporation increases salinities to maxima of 36–40 PSU then high river flow following winter rainfall results in salinities of 0–10 PSU (Figure 2). Comparatively, in the middle (W3) and downstream sections (W4), the influence of the marine environment is stronger causing salinity to be more stable and typically around 35–37 PSU in summer then declining to minima of approximately 28 PSU in winter (Figure 2).

A tropical low-pressure system in northwest Australia in late January to early February 2017 resulted in unseasonal summer rainfall in Perth totalling 216.4 mm. This total included a substantial rainfall event when 114 mm fell in 1 day in February exceeding the previous record that occurred in the summer of 1954/1955 (Bureau of Meteorology, 2017). These high intensity rainfall events are forecast to increase in summer in this region (Hallett et al., 2018). Most of the rain fell in the Swan-Avon catchment and approximately 270 GL of water discharged from the Avon river into the Upper Swan estuary between 1 February 2017 and 12 March 2017.

FIGURE 2 Annual salinity ranges including the minimum, 25th percentile, median, 75th percentile and maximum salinities from 2008 to 2018. The whiskers extend to the minimum and maximum data points which is no more than the 1.5 times the interquartile range, and outliers are values that exceed this. Data collected during water quality monitoring conducted weekly upstream in the Canning river (W1), upstream in the Swan river (W2), middle-Swan (W3) and downstream (W4) sections (Refer Figure 1 for site locations. Source: Department of Water and Environmental Regulation (<http://wir.water.wa.gov.au/Pages/Water-Information-Reporting.aspx>))



2.2.2 | Quantifying the Swan river extreme event: Flood metrics

The salinity changes associated with the 2017 flood were quantified in this study by adapting the hierarchical approach used for marine heatwaves (Hobday et al., 2016). Primary metrics relate to the event duration and intensity, secondary metrics reflect how the event changes over space and time and tertiary metrics describe the preceding conditions and are generally system specific. The event is compared to background conditions from the same time from years preceding the event. We explored how these metrics varied along the estuarine gradient at the six seagrass sites (Figure 1). Salinity was used since it is rapidly modified by freshwater inputs from extreme rainfall (Steward et al., 2006), is a critical determinant of structural and functional characteristics of aquatic biota in estuaries, including seagrasses (Hillman et al., 1995) and can be a useful climate change indicator (Durack & Wijffels, 2010). The flood was defined as an excess discharge of freshwater following extreme rainfall resulting in hyposalinisation where salinity decreased by $\geq 5\%$ from background salinity levels for 5 or more consecutive days following the marine heatwave definition of Hobday et al. (2016). This period of days was chosen as damage from freshwater exposure to the photosystems of *H. ovalis* can occur within 24 hr and in extreme cases, leaf senescence within 4 days (Ralph, 1998).

To quantify temporal and spatial changes in salinity at each seagrass site, we used two datasets: data when the flood definition applied, and data capturing background salinity levels for the same portion of the year but during a year when no extreme rainfall occurred (background). The datasets were generated using data

derived from a numerical water quality model and from a long-term water quality monitoring program. The flood definition applied from February to May 2017, so we set the background period as February to May 2015 and 2016, 2 years of data. This background period was much shorter than the 30 years used by Hobday et al. (2016) to define background periods heatwave assessments, but was selected to match the availability of daily salinity data for each seagrass site, essential for calculation of high-resolution metrics, for example, rate of change in salinity (Hobday et al., 2016). Longer term salinity data are available from the water quality monitoring program but for sites located further away from the seagrass sites and at weekly intervals, limiting the number of metrics that could be calculated. However, to assess whether salinity during our background years we used was representative of the longer term background, we used salinity data from the long-term water quality monitoring program to compare mean weekly salinity from December to May in 2014/2015 and 2015/2016 against the long-term mean from 2000 to 2016. At the four water quality sites, the mean background used in this study was always within 1 standard deviation of the longer term background mean (2000–2016) and giving confidence that our background dataset was representative (Figure S27).

Daily salinity data extracted from the Swan-Canning Estuary Response Model (SCERM v2; Huang et al., 2019) for each site were strongly correlated with in situ data collected by DWER, providing further confidence in the model and associated outputs (Figure S28). Salinity data generated by the model were used for the following periods: December–May (2014/2015 and 2015/2016; 'background') and February to March 2017 ('event'). Model data were not available for April and May 2017, so data

from the DWER long-term water quality monitoring program were used to predict the daily salinity data at each seagrass site. The water quality data were collected weekly from four water quality monitoring sites (depth ranging from 3.5 to 18 m, Figure 1) that are closest to each seagrass monitoring site and only the top 2 m of salinity data were used, reflecting the depth in which most seagrasses in the estuary grow. Then, over the period when both model data and DWER water quality data existed, regressions were performed to develop predictive relationships. Data were non-normal and therefore, a nonparametric Spearman correlation test was used to assess the relationship between the two datasets. In all cases, the datasets were significantly correlated ($p < 0.05$) in a positive direction ($r_s \geq 0.7$), so we concluded that this was still an appropriate method for predicting salinity (Figure S28). The same weekly value was used for each 7-day period. Flood metrics were calculated following Hobday

et al. (2016) but some of the metrics were modified from the original equation due to changes in the direction of salinity following a flood (i.e. lowered salinity) versus increased temperature during a heatwave (Table 1; Figure 3a).

While salinity was the focal environmental factor of this study, related changes in temperature and light from the flood could also have been important in inducing seagrass change. To test whether salinity was an appropriate proxy for daily changes in temperature and light, daily temperature ($^{\circ}\text{C}$) and light ($\text{mol m}^{-2} \text{day}^{-1}$) were correlated against daily salinity (using R Language for Statistical Computing version 4.0.1, R Core Team, 2020). For each of the seagrass sites, an Odyssey logger was deployed [calibrated against Li COR quantum 2π sensor in air (Shaffer & Beaulieu, 2012) and adjusted for water medium by applying a correction factor of 1.33 as per Kirk (1994)] with an in situ wiper to measure photosynthetic active radiation (PAR)

TABLE 1 Definitions of primary (before dashed line) and secondary (after dashed line) metrics adapted from their use to define marine heatwaves (Hobday et al., 2016) to describe flood events with a specific start and end date. Equations denoted by * are modified due to changes in the direction of response with a flood event (e.g. lowered salinity vs. increased temperature during a heatwave)

Metrics	Description of metric	Formula	Units
S_m	Climatological mean: calculated over a reference period to which all values are relative (reference period = $y_s - y_e$ = January 2015–June 2016)*	$\sum y_s \sum y_e \frac{S(d,y)}{(y_s - y_e)}$, where $S(d, y)$ is daily surface salinity on day d of year y , y_s and y_e are the start and end of the climatological base period respectively	PSU
t_s	Start of the flood where (Salinity 2016 – Salinity 2017) \geq 5%	t_s is the time, t , when: [[$(S_{\text{BACKGROUND}} - S_{\text{FLOOD}})/S_{\text{BACKGROUND}}$] \times 100] \geq 5%	days
S_{ts}	Salinity at start of flood or t_s	Salinity measured at t_s	PSU
t_{s-1}	Date before start of flood	(Date of t_s) – 1	days
S_{ts-1}	Salinity measured 1 day before the start of flood or at [(Date of t_s) – 1]		PSU
t_e	Date of end of flood	t_e is the time, t , when: [[$(S_{\text{BACKGROUND}} - S_{\text{FLOOD}})/S_{\text{BACKGROUND}}$] \times 100] \geq 5%	days
S_{te}	Salinity at end of flood	Salinity measured at t_e	PSU
$i_{\max} \Delta^*$	Highest salinity anomaly (difference) between background salinity conditions and those during the February flood event	$i_{\max} \Delta = \max(S_{tm} - S_{tmin})$	PSU
i_{mean}^*	Mean salinity anomaly during the flood plume event	$i_{\text{mean}} = \overline{(S_{tm} - S_{tmin})}$, where the overbar indicates time mean	PSU
i_{var}	Variation in salinity anomalies over the duration of the February flood, that is, when salinity following the flood differs from background by more than 5%	$i_{\text{var}} = \sigma$ when [[$(S_{\text{BACKGROUND}} - S_{\text{FLOOD}})/S_{\text{BACKGROUND}}$] \times 100] \geq 5%	PSU
S_{tmin}^*	Minimum salinity measured following the flood, at t_{\max}		PSU
t_{min}	The date when S_{tmin} occurred		days
Duration	The consecutive number of days between the start (t_s) and end of flood (t_e)	$D = t_s - t_e$	days
R_{onset}^*	Rate of decline in salinity from the start of the flood (t_s) to the minimum salinity reached during the flood	$\frac{S_{ts} - S_{tmin}}{\text{number of days taken to reach } S_{tmin}}$	PSU/day
R_{return}^*	Rate of salinity increase from the maximum intensity (S_{tmax}) to the end of the flood event (S_{te})	$\frac{S_{te} - S_{tmax}}{\text{number of days taken to reach } S_{te}}$	PSU/day
i_{cum}^*	Cumulative measure of the daily differences in salinity anomalies between t_s and t_e where: [[$(S_{\text{BACKGROUND}} - S_{\text{FLOOD}})/S_{\text{BACKGROUND}}$] \times 100] \geq 5%	$i_{\text{cum}} = \sum [[[(S_{\text{BACKGROUND}} - S_{\text{FLOOD}})/S_{\text{BACKGROUND}}] \times 100]]$ that are \geq 5%	PSU/days

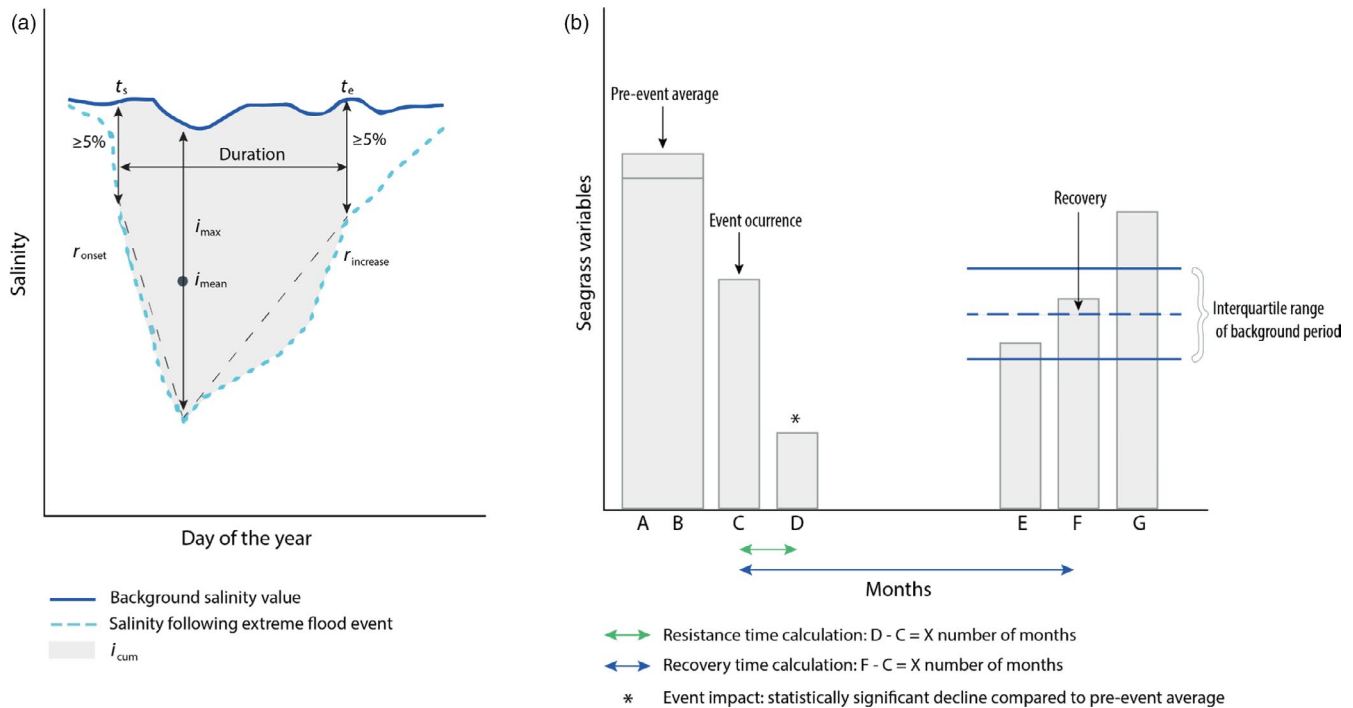


FIGURE 3 Schematic of metrics derived from salinity data to characterise an extreme rainfall event (a, left) based on an approach developed for marine heatwaves (Hobday et al., 2016). A flood is defined as an excess discharge of freshwater following extreme rainfall resulting in hyposalinisation where salinity decreased by $\geq 5\%$ from background salinity levels. Table 2 defines all flood metrics including i_{cum} , i_{mean} , i_{max} , Δ , r_{onset} and $r_{increase}$. Methods to assess resilience of seagrass meadows following the February 2017 flood (b, right). The resistance period is the amount of time (months) for a statistically significant decline to be detected compared to a pre-event average. The recovery period is the amount of time (months) for meadows to increase within the median levels of a background period during which no event occurred

integrated over 10-min periods, and a Hobo Tidbit V2 was used to measure temperature at 20-min intervals from December to March during each monitoring season. Data were pooled across the sites for each water quality variable. Correlations were performed at weekly intervals prior to and following the flood. Following Zuur et al. (2007), normality was assessed using the Shapiro–Wilk test and if satisfied, then the linear-based Pearson correlation was used. If data were non-normal, scatterplots were used to assess the relationship. If monotonic, then the nonparametric Spearman correlation was used which is based on the rank of observations. If non-monotonic, then the nonparametric Kendall correlation was used.

To further assess the changes in light following the flood, the hours above saturating irradiance (H_{sat}), where the saturating light intensity for photosynthesis of *H. ovalis* was set to $200 \mu\text{mol m}^{-2} \text{s}^{-1}$ (Hillman et al., 1995), were compared in the year prior to the flood and also before and after during the year of the flood. Light data were available from the DWER seagrass monitoring dataset from December 2015 to March 2016 in the year before the flood, and December 2016 to March 2017 in the year that the flood occurred, and data were summarised as Background (December–February), Background (February–March), Event year Pre-flood (December–February), Event year During flood (February–March). Mean H_{sat} (hours per day) and the number of consecutive days when H_{sat} was zero were calculated for each site in these periods.

2.2.3 | Seagrass resilience: Resistance to and recovery from the flood

The resistance and recovery of the six seagrass meadows to the flood in February 2017 was assessed by using seagrass biomass and leaf density. Indicators that reflect changes in growth, including biomass and leaf density, are common measures of hyper- and hyposalinity stress due to impacts on photosynthesis (Fernández-Torquemada & Sánchez-Lizaso, 2011; Hillman et al., 1995; Ralph, 1998). The same six seagrass sites were sampled monthly prior to (December 2016, January 2017) and after the flood (February 2017–March 2018); however, no sampling was conducted in June and July 2017 due to logistical constraints. Fruit and seed bank densities were also measured to indicate the recovery potential via seed banks.

At each site, biomass, leaf, fruit and seed bank densities were estimated from five replicate samples, randomly stratified within the seagrass meadow. A pilot study with 10 replicates from all sites showed that the coefficient of variation declined significantly from three to four replicates and then was similar up to 10 replicates supporting the use of five replicates to capture the variability at each site. Each replicate comprised two cores (9.6 cm diameter) placed side by side into the sediment to a depth of ~ 15 cm to ensure collection of most of the root material, which were then subsequently pooled. Plant material was separated from the sediment using a

1.5-mm mesh sieve and stored in a -20°C freezer prior to processing. The sediment was collected in a calico bag. Plant material was rinsed of excess sediment, and epiphytes removed using a blade, and discarded along with dead leaves and dead rhizomes. Above- (leaves, petioles, fruit, flowers) and below-ground (roots, rhizomes) material was separated, and the number of leaves and fruit counted. All plant material was placed in a 60°C oven for 48 hr to a constant dry weight and then weighed. The sediment samples were placed on a $750\text{-}\mu\text{m}$ sieve which trapped *H. ovalis* seeds that are 1 mm in diameter (Kuo & Kirkman, 1992) and flushed with seawater. Total biomass was calculated as the sum of the above- and below-ground dry weights and converted to a meadow scale measure ($\text{g DW}/\text{m}^2$). Leaf, fruit and seed bank densities were expressed m^{-2} .

Resistance and recovery times were defined in months based on the sampling frequency of the monitoring program; however, it is possible that either may have occurred on a shorter time-scale. Resistance was defined as the time taken (months) following the flood for a seagrass metric (biomass, leaf density) to show a statistically significant decline compared to the 2 months preceding the flood (December 2016 and January 2017). Significance was determined using a permutational univariate analysis of variance using PRIMER v7 and PERMANOVA + software (PRIMER-E). Data were tested for homogeneity of variance (PERMDISP) before the analysis was conducted. There were two factors: Site (fixed, six levels) and Month (fixed, 13 levels) and an interactive term (Site \times Month). As the interaction (Site \times Month) was significant, pairwise tests were conducted for each site to assess when the seagrass metric was lower than the background period. If homogeneity of variance was met, the p -value for determining statistical significance was set to 0.05, and if it was not met then this was set to 0.01. Resistance time (months) was calculated as the time between the flood and the first post-sampling time that biomass or leaf density was statistically significantly lower to the background period (Figure 3b). Further significant declines were considered after the initial significant decline and detected from the pairwise tests between each month.

Recovery was then defined as the time taken after the flood (months) for the seagrass metric to be equal to or greater than the median in the background period (Figure 3b). Because there is substantial inter-annual variability in seagrass biomass and leaf density (Kilminster & Forbes, 2014), it would be inappropriate to define the recovery period on the previous season's values alone. Instead, data were available from five seasons of historical summer monitoring (2011/2012, 2013/2014, 2014/2015, 2015/2016, data provided by DWER) and were used to represent the background period. Seagrass metric data were pooled from these years and the median plus inter-quartile ranges calculated.

As the production of fruit and seed banks can facilitate meadow recovery (Rasheed et al., 2014), these variables were assessed for recovery potential. Generally, fruit production of *H. ovalis* in the Swan-Canning estuary occurs in summer months, between January and March (Kilminster & Forbes, 2014), and based on preliminary trials, seed germination may occur in spring, around October (K. Kilminster, pers. commun., July 2020). If fruit were produced during and after

the flood, it was considered there was potential for recovery from recently produced seed banks in spring following the flood, when seeds are likely to germinate. If there was a seed bank present at a site following the flood, then it was considered that there was potential to recover from seed banks. Only viable seeds were counted, defined as those that remained firm following light squeezing between the forefinger and thumb with an intact seed coat and which sank when placed in seawater (Marion & Orth, 2010). The average fruit and viable seed bank densities were calculated for each month of sampling and plotted as heat maps.

To investigate the relationship between the flood metrics and either seagrass change following the event or seagrass recovery times, scatterplots were drawn to visualise the relationships and correlation tests conducted in R. The p -value for determining the statistical significance of the correlation was set to 0.05. Seagrass resistance time was 1–2 months across the sites and therefore, due to this lack of variation, was not assessed. The correlation tests followed what was previously described for examining the relationship between water quality variables.

3 | RESULTS

3.1 | Global assessment of unseasonal rainfall as extreme climate events

Of the 25 case studies across all climate regions, 20 estuaries had seasonal rainfall and had daily maximum precipitation that occurred during the dry season which exceeded the 90th percentile, and in most cases, the 99th percentile (Table 2; Tables S1 and S2; Figures S1–S25). The percentage of rainfall occurring in the dry season ranged from 1.5% to 15.4% with an average across estuaries of 6% (Table 2). The annual daily maximum rainfall occurred in the dry season at least once over the 40-year period in 16 of the 20 estuaries with seasonal rainfall. In eight out of the 20 estuaries this was rare, occurring only once in 40 years (Table 2). For the remaining estuaries it occurred up to seven times, while still rare, equivalent to about $\sim 0.05\%$ of the time. Dry season rainfall was assessed in the Swan-Canning estuary and extreme rainfall was identified on seven separate occasions (1982, 1986, 1990, 1992, 2000, 2017 and 2018) and for the 2017 event described below the rainfall received equated to the 99.98th percentile of the maximum daily rainfall data (Tables 1 and 2).

3.2 | Swan-Canning estuary—Extreme rainfall event

3.2.1 | Salinity as a proxy for changes in other water quality variables following the flood

The flood generated widespread runoff and distinct changes in light (Figure 4; Figure S29). Salinity and light declined reaching minimum values in ≤ 7 days while temperature increased and remained stable for around 4 weeks (Figure S30). There was a significant ($p < 0.05$)

TABLE 2 Estuaries across various climatic regions (NT, northern temperate; NS, northern subtropics; T, tropics; SS, southern subtropics; ST, southern temperate) identified in areas with strong seasonal rainfall patterns that are most likely to be impacted by extreme rainfall events that occur during the dry season. The distribution of daily maximum precipitation (d_{\max}) is expressed as a percentile to understand if it can be considered a climate extreme following the guidelines of Smith (2011)

Name of estuary	Climatic region	Dry season months	Mean annual rainfall (mm)	% of rainfall in dry season	Range of annual d_{\max} values (min-max)	Number of times d_{\max} occurs in the dry season	Range of d_{\max} values (mm)	Percentile value of d_{\max}
San Francisco Bay	NT	6–9	2,195	2.0%	55–332	0	0	N/A
Mondego	"	7, 8	3,231	2.8%	99–322	1	148	99.79
Ebro	"	6, 7	1,310	8.2%	63–263	2	122–151	99.74–99.86
Rio de Vigo	"	6–8	5,422	9.5%	130–356	1	169	99.53
Nile	NS	6–9	424	1.9%	22–139	1	56	99.83
Bahia	"	2–4	5,440	8.7%	130–697	1	195	99.1
Yangtze	"	10–12	4,467	13.8%	144–556	4	205–518	99.53–99.99
Colorado	"	5, 6	334	2.1%	6–737	1	18	98.88
Amazon	T	8–11	7,624	3.1%	161–574	1	427	99.99
Mwache	"	1, 2	3,866	4.5%	117–541	5	192–371	99.41–99.98
Cameroon	"	1,2,12	11,381	4.6%	190–983	1	738	99.97
Cambridge gulf	"	5–9	3,739	1.5%	81–794	0	0	N/A
Guayas	"	7–11	9,319	8.5%	165–1,019	0	0	N/A
Zambezi	SS	8–10	3,825	5.2%	153–1,187	1	277	99.85
Hervey Bay	"	9–12	894	13%	52–525	4	190–450	99.90–99.99
Shark Bay	"	10–12, 1–3	1,283	15.4%	64–363	7	77–315	99.27–99.99
Mania	"	5–11	3,183	7.9%	115–905	0	0	N/A
Swan-Canning	ST	1–3	3,033	6.2%	98–402	7	98–402	99.95–100
Murray Darling	"	1–3	1,864	11.4%	34–208	5	66–198	99.27–99.99
Rio de la Plata	"	6	4,558	5.0%	158–464	2	165–200	99.01–99.49

FIGURE 4 Water quality and seagrass condition observed at site Upstream 2 of the Swan River before (left) and after the flood including leaf senescence (right). Note: the 'After flood' image redness was due to CDOM absorption



positive correlation between salinity and light 1 week ($r_s = 0.60$), 4 weeks ($r_s = 0.42$) and 7 weeks after the flood ($r_s = 0.50$; Table S2). There was a significant ($p < 0.05$) negative correlation between salinity and temperature only 1 week ($r_k = -0.60$) and 4 weeks ($r_k = -0.44$) after the flood (Table S1). Based on these patterns, we considered salinity to be an appropriate proxy for predicting the overall effects of light and temperature. Other water quality variables, such as nutrients, would also have been impacted by the flood but we limit the focus to light and temperature as two major environmental factors, in addition to salinity, that can impact seagrass resilience (Hillman et al., 1995) and given the availability of site-specific data.

The hours of saturating irradiance (H_{sat}) were much lower during the flood event in 2017 compared to 2016 at four of the five sites where data were available (Table 3). The average H_{sat} declined by $\geq 50\%$ across all sites except the Middle site where the average H_{sat} before the flood was 9 hr and similar at 7 hr after (Table 3). The greatest difference in the mean H_{sat} before and after the flood occurred at Upstream 3 where it was 10 hr before and only 1 hr after the flood (Table 3). At Upstream 2 and 3, there was only 1 and 2 days, respectively, when H_{sat} was equal to zero in 2016 compared to 31 and 40 consecutive days in 2017 (Table 3). Similar trends were observed at both downstream sites, but the number of consecutive days when

TABLE 3 Average hours of daily saturating irradiance (H_{sat} , hr/day) before and after the flood in 2017 and in the same period in the background (2015/2016) when there was no flood. The number of consecutive days that daily H_{sat} was equal to zero in 2016 and 2017 are also shown

Variable	Year	Period	Upstream				Downstream	
			Months	1	2	3	Middle	1
H_{sat} hours	2015/2016	December–February	8	9	10	11	7	10
H_{sat} hours	2016/2017	December–February	6	5	10	9	5	6
H_{sat} hours	2016	February–March	5	8	8	10	No data	9
H_{sat} hours	2017	February–March ^a	2	2	1	7	1.1	3
# of days $H_{\text{sat}} = 0$	2015/2016	December–March	11	1	2	0	7	0
# of days $H_{\text{sat}} = 0$	2016/2017	December–March ^a	13	31	40	3	27	21

^aIndicates period of extreme rainfall.

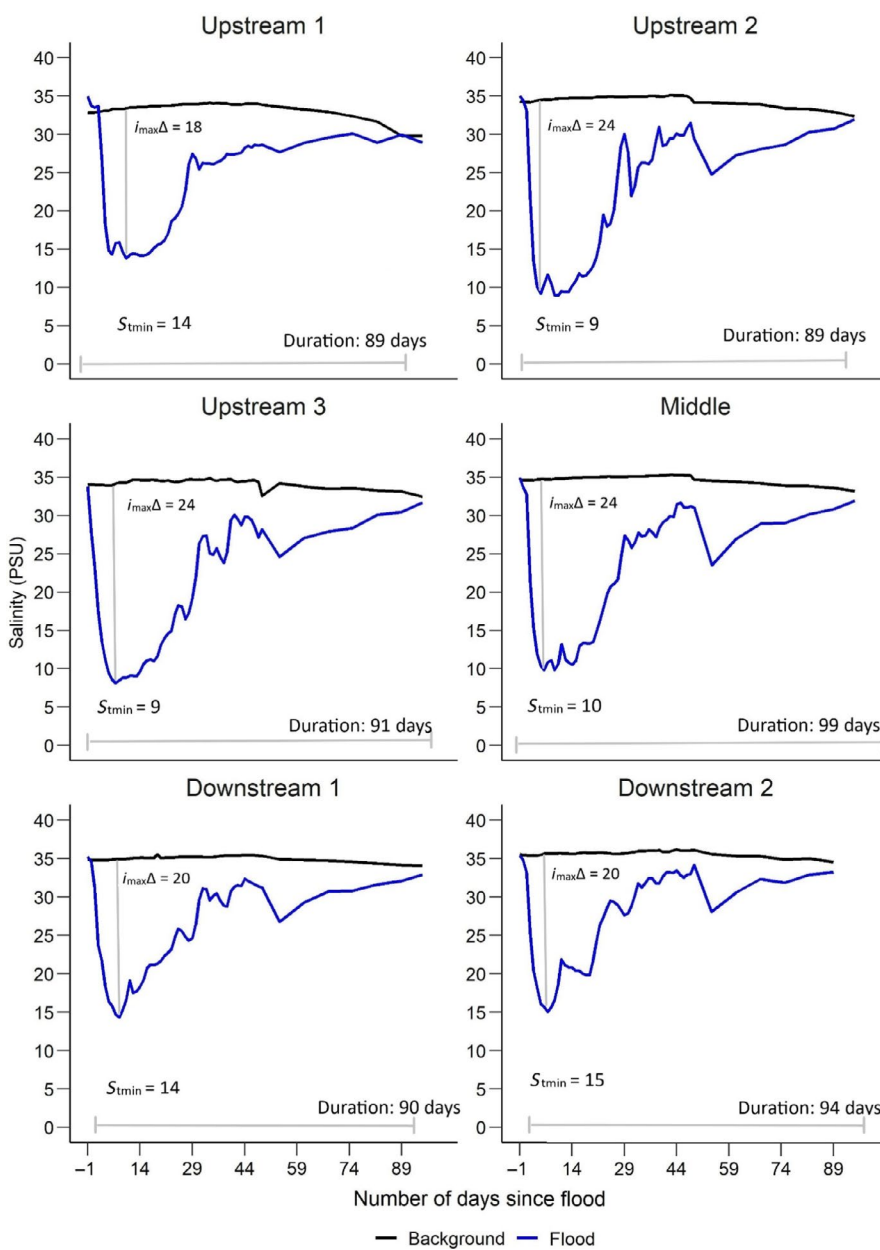


FIGURE 5 Daily changes in salinity (PSU) from background (black) following average summer rainfall and the wettest summer on record in 2017 (blue) which caused flooding in the Swan-Canning Estuary, southwestern Australia. A flood is defined here as the period during which salinity differed from background salinity conditions $\geq 5\%$. Magnitude of the flood ($i_{\text{max}}\Delta$), the lowest salinity reached (S_{tmin}) and the flood duration are also indicated (Table 3)

H_{sat} was equal to zero was not as high (Table 3). The light environment was least impacted at the Middle site in 2017 which had only three consecutive days of H_{sat} being zero compared to no days in 2016 (Table 3).

3.2.2 | Flood metrics characterise spatial and temporal changes in salinity

Marine salinities (~35 PSU) were recorded in January 2017 across the estuary and were similar to background values, then a large decline was evident following the flood in February 2017 (Figure 5). There was no consistent pattern in the flood metrics along the estuarine gradient. At the Upstream site 2 and 3 and Middle, the magnitude of the flood was highest with a reduction in salinity ($i_{\text{max}}\Delta$) of 24 PSU (Table 4). At Upstream 1 and both sites downstream, $i_{\text{max}}\Delta$ was lower ranging between 18 and 20 PSU (Table 4). The flood duration was similar, ranging between 89 and 94 days, among the upstream and downstream sites but persisted for 99 days at the site in the middle

basin (Table 4). The flood was most intense at Downstream 2 with mean daily salinity declining rapidly by 3 PSU/day (r_{onset}) to reach the minimum salinity ($S_{\text{tmin}} = 15$ PSU) within 6 days (Table 4). It took an additional 1–2 days to reach the minimum salinity at Upstream 2 and 3 and Middle site, but it was more extreme ($S_{\text{tmin}} = 9$ PSU) and low salinities persisted for approximately 2 weeks (Figure 5). The cumulative exposure to low salinity waters was greatest at Upstream 3 (822) and was lowest at Downstream 2 (482; Table 4). The flood ended in May 2017 and by then, salinity was between 30 and 33 PSU across all sites and within the typical range for that time of year (Table 4).

3.2.3 | Resistance and recovery of seagrass meadows to flood impacts

Seagrass biomass was highly variable among sites ranging from 50 to 500 g DW/m² before the flood (Figure 6). The minimum biomass for each site was reached by April, about 2 months after the flood,

TABLE 4 Primary and secondary flood metrics calculated using salinity data to understand the temporal and spatial changes in salinity adapted from the approach of Hobday et al. (2016). Not applicable (n.a.) refers to instances where a flood impact was not detected so a resistance or recovery time could not be determined

Location	Upstream				Downstream	
	1	2	3	Middle	1	2
Primary metrics						
S_m	32	33	33	34	34	35
t_s	13/2/17	12/2/17	10/2/17	11/2/17	11/2/17	11/2/17
S_{ts}	26.7	21.5	27.8	32.8	31.3	33.2
t_{s-1}	12/2/17	11/2/17	9/2/17	10/2/17	10/2/17	10/2/17
$S_{(ts-1)}$	33.67	33.13	33.83	33.73	34.53	34.84
t_e	13/5/17	12/5/17	12/5/17	31/5/17	12/5/17	15/5/17
Salinity _(te)	29.98	31.96	31.71	29.12	32.74	34.34
$i_{\text{max}}\Delta$	18.1	24.5	24.2	24	19.9	20
i_{mean}	11.25	13.95	14.68	13.39	10.02	9.28
i_{var}	5.97	72.55	67.42	65.58	32.9	35.24
t_{max}	20/2/17	20/2/17	23/2/17	19/2/17	18/2/17	
S_{tmin}	13.8	9	9	9.8	14.4	15.1
Duration (days)	89	89	91	99	90	94
Secondary metrics						
r_{onset}	-1.8	-1.6	-2.8	-2.9	-2.4	-3.0
r_{increase}	0.20	0.19	0.19	0.20	0.30	0.20
i_{cum}	596	741	822	728	535	482
Seagrass resilience metrics						
Resistance time (months)						
Biomass	n.a.	2	1	n.a.	1	2
Leaf density	2	1	1	n.a.	n.a.	1
Recovery time (months)						
Biomass	—	11	9	n.a.	10	>22
Leaf density	10	9	9	n.a.	n.a.	>22

with the greatest reductions of 82% recorded at Downstream 2 (Figure 6). The resistance time for biomass (i.e. the time to a statistically significant reduction) was one month at Upstream 2 and 3 and both downstream sites (Figure 6; Table 5).

No impacts to biomass occurred at Upstream 1 or the Middle site, so resistance and recovery times were not assessed (Figure 6). For the remaining sites, recovery time for biomass was variable, taking

9 months at Upstream 2, 11 months at Upstream 3 and 10 months at Downstream 1 (Figure 6). Recovery was not detected at Downstream 2 (Figure 6), and we estimate that the time will exceed 22 months (March 2017–January 2019) since meadows naturally decline from April following the onset of autumn before achieving peak biomass around January. Similar trends in resistance and recovery times for leaf density were observed following the flood (Figure S31).

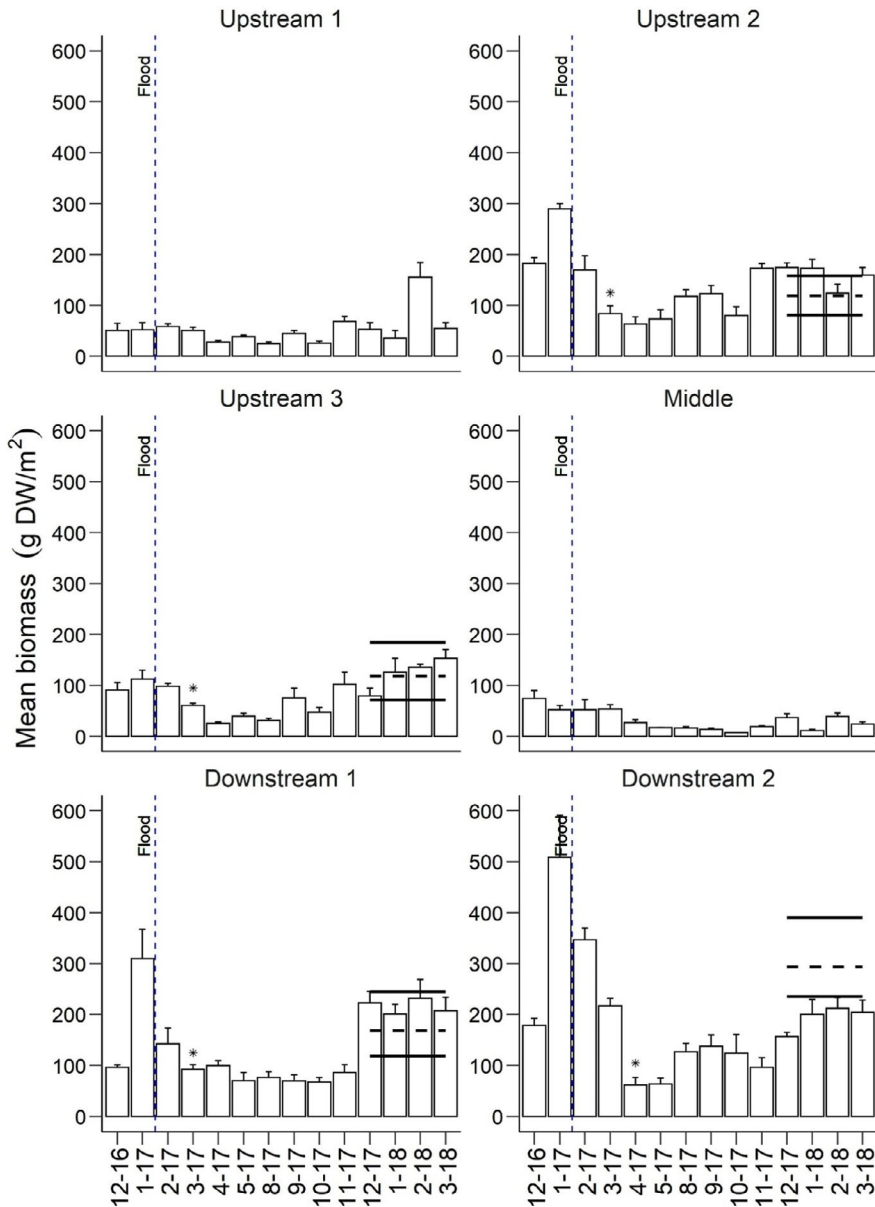


FIGURE 6 Impact to and recovery of average total biomass (g DW/m² ± SE) of *Halophila ovalis* seagrass at six sites from an extreme flood event in February 2017 in the Swan-Canning Estuary, southwestern Australia. Significant declines are indicated (*). Upper, median (dashed) and lower interquartile ranges of seagrass performance during background years without flooding represented by black lines. Note that June and July 2017 were not sampled

TABLE 5 PERMANOVA statistical outputs from examining the spatial (site) and the temporal (site × month) differences in total biomass (g DW/m²) and leaf density (leaves/m²) across sites ($p = 0.01$)

Source of variation	df	F-value		p-value		Unique perms	
		Biomass	Leaf	Biomass	Leaf	Biomass	Leaf
Site	5	197.7	150.6	0.0001	0.0001	9,932	9,953
Month	12	31.5	44.4	0.0001	0.0001	9,915	9,932
Site × Month	59	4.2	4.6	0.0001	0.0001	9,874	9,866

TABLE 6 Monthly average fruit (above dashed line, # m⁻²) and seed bank densities (below dashed lines, # m⁻²) at seagrass meadows with colour gradient applied to higher values (dark green) and lower values (light green to yellow) within the range across all sites prior to and after the February 2017 in the Swan-Canning estuary, Western Australia. Before the flood (◇), during the flood (■) and after the flood (□). Note that no sampling was conducted in June and July 2017 due to logistical constraints. Site legend: U1, Upstream 1; U2, Upstream 2; U3, Upstream 3; M, Middle; D1, Downstream 1; D2, Downstream 2

	2016		2017								2018				
	◇ D	◇ J	■ F	■ M	■ A	■ M	□ A	□ S	□ O	□ N	□ D	□ J	□ F	□ M	
U1	0	28	9	7	0	0	0	0	0	0	0	0	41	0	
U2	0	553	774	313	111	0	0	0	0	0	0	235	677	787	
U3	0	0	9	94	0	0	0	0	0	0	0	0	0	41	
M	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
D1	0	28	90	267	0	0	0	0	0	0	0	0	0	787	
D2	0	235	207	1,013	0	0	0	0	0	0	0	14	497	249	
U1	124	124	101	50	138	69	41	180	221	41	1,243	14	193	207	
U2	1,492	1,382	870	368	787	262	276	290	138	815	1,078	1,188	2,280	677	
U3	124	124	101	50	138	69	41	180	221	41	1,243	14	193	207	
M	0	28	46	7	0	14	0	28	0	14	0	14	138	7	
D1	207	1,755	456	368	304	290	470	318	1,050	138	55	1,755	83	470	
D2	4,587	6,452	290	5,149	332	884	608	926	622	249	2,653	1,188	1,989	1,934	

TABLE 7 Correlation coefficient (r) indicating the direction of the relationship between flood metrics ($i_{\max}\Delta$, r_{onset} , duration) and seagrass metrics (biomass change (Δ) and maximum recovery) for five meadows where significant impacts to biomass or leaf density were detected following a flood. Note that the Pearson correlation method was used when both data sources followed a normal distribution (all biomass change tests) and Spearman correlation method was used when one or both data sources followed a non-normal distribution (all max recovery tests)

	$i_{\max}\Delta$		r_{onset}		Duration	
	r	p -value	r	p -value	r	p -value
Biomass Δ	-0.61	0.27	0.49	0.39	-0.07	0.90
Max recovery time	-0.15	0.80	-0.97	0.005	0.36	0.55

3.2.4 | Recovery potential of seagrass meadows

At all sites, apart from the Middle site, fruiting was present during the normal fruiting time in summer (January–March) and occurred during and after the flood event (Table 6). The density of fruit did vary over time and among sites with the highest densities at Upstream 2 and both downstream sites (Table 6). Except for the Middle site, a seed bank was present at all sites at all times and densities were greatest at Upstream 2 and both downstream sites (Table 6). Despite the lack of fruiting at the Middle site, as all sites had a seed bank there was potential for recovery via seed germination.

3.2.5 | Relationship between flood metrics and changes in seagrass condition

The maximum decline in salinity ($i_{\max}\Delta$) was co-correlated ($r_p > 0.6$) with i_{mean} , i_{var} , S_{tmin} and i_{cum} , so we did not test the relationship between these metrics and changes in seagrass condition or seagrass recovery time. For the five sites that showed significant declines in biomass or leaf density, the change in seagrass biomass was best

associated with the flood metrics $i_{\max}\Delta$ and r_{onset} ; however, these relationships were not significant (Table 7). There was a negative relationship between biomass with $i_{\max}\Delta$ ($r_p = -0.61$) where greater declines in salinity during the flood resulted in more seagrass loss, with the exception of Downstream 2 (Table 7; Figure 7a). Downstream 2 had the greatest seagrass loss but one of the lowest changes in salinity ($i_{\max}\Delta$). There was a non-significant positive correlation with the rate of decline in salinity (r_{onset}) where, for the majority of seagrass meadows, the more rapid the decline in salinity during the flood the greater the decline in biomass. But in this case, the exception was Upstream 2, where there was a slow rate of change but a relatively high reduction in biomass (Table 7; Figure 7b). There was a significant negative relationship between the maximum seagrass recovery time and r_{onset} ($r_s = -0.97$, $p = 0.005$, Figure 7c), with a more rapid decline in salinity ($r_{\text{onset}} < -3$ PSU/day) there was slower recovery (>22 months) but when the r_{onset} was greater than -3 PSU/day recovery was quicker and more similar among sites, 10–11 months (Figure 7c). Recovery was generally shorter with longer durations of freshwater exposure but was non-significant (Table 7). There were no significant relationships between change in leaf density and flood metrics.

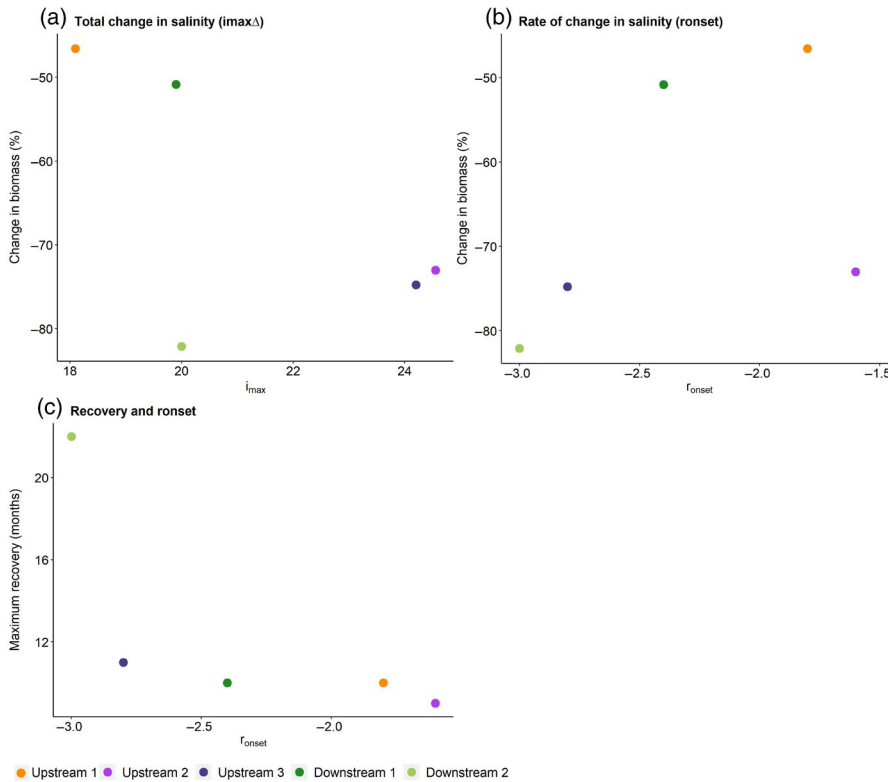


FIGURE 7 Relationship between reduction in salinity ($x = i_{max}\Delta$) and change in biomass (y) at five seagrass meadows where significant impacts to biomass or leaf density were detected following a flood (a); between rate of decline in salinity ($x = r_{onset}$) and change in biomass (y) (b); between rate of decline in salinity ($x = r_{onset}$) and maximum recovery time in months (y) at five seagrass meadows where significant impacts to biomass or leaf density were detected following a flood (c). Correlation coefficients (r) indicate strength and direction of relationship and statistical significance ($p = 0.05$)

4 | DISCUSSION

Extreme climate events, that are increasing in frequency and/or magnitude driven by climate change, are resulting in significant ecological change (Paerl et al., 2019). This has been well-documented for heatwaves (Smale et al., 2019) but our global analysis has identified that unseasonal rainfall events are another extreme climate event with the potential for significant ecological impacts, particularly in estuarine ecosystems, and they occur across all climate regions. As these events are predicted to increase in the future, consideration of the relevant environmental drivers and ecological impacts is warranted. The specific case study we investigated, the unseasonal 2017 summer rainfall event in the Swan-Canning estuary was extreme, exceeding the 99th percentile. The metrics we developed to define this extreme event varied along the estuary. Despite the climate event being extreme, the dominant *H. ovalis* seagrass habitat in the Swan-Canning estuary survived. The resilience of seagrass meadows to the extreme event varied among populations highlighting intraspecific differences that could be used to 'future proof' this ecosystem from continued climate events.

4.1 | Occurrences of extreme rainfall in the dry season

Our findings have revealed that across the globe, in regions with seasonal rainfall, extreme rainfall events have a very low likelihood of occurrence in the drier season ($\leq 0.05\%$) but when they

do occur, the values exceed the 90th percentile and can be considered extreme (Smith, 2011). This confirms the observed trend in increasing rainfall anomalies even where total precipitation is decreasing (Trenberth, 2011). Estuarine systems are susceptible to unseasonal rainfall because in the drier season salinity is typically elevated due to high evaporation, low rainfall and warm temperatures (Largier et al., 1997; Snow & Taljaard, 2007). Therefore, extreme precipitation will cause sudden changes in salinity and other drivers disturbing the community (Breux et al., 2019) and the provisioning of ecosystem services (Dolbeth et al., 2011). Increases in the frequency of heavy precipitation events have already been linked to regime shifts in estuarine ecosystems in the United States (Paerl et al., 2019). How estuaries can be managed to ensure resilience to extreme events is a complex and ongoing issue for scientists and managers where achieving a balance between economic and social interests against ecological objectives is even more complex (Gaylard et al., 2020; Jackson, 2010; Lotze et al., 2006; Wells et al., 2019). However, there is evidence to suggest that even small actions, such as the management of local scale non-climatic human impacts (e.g. elevated nutrients), can increase the resilience of benthic communities to climate change and retain their ability to provide ecosystem services which have economic and social benefits (Ateweberhan et al., 2013; Russell et al., 2009). For example, vegetation associated with coastal and marine habitats reduces erosion following extreme rainfall events protecting coastlines which are usually highly populated and could save lives (Morris et al., 2018; Narayan et al., 2017; Sale et al., 2014).

4.2 | Metrics as a monitoring tool for salinity changes following extreme rainfall

Our flood metrics characterised the temporal and spatial impacts on salinity following the 2017 extreme rainfall event and revealed the prolonged duration of low salinity conditions, where the change was most rapid and had the highest magnitude of change in salinity (Table 4). These metrics did not follow predictable patterns along the estuarine gradient highlighting the value of these metrics to characterise spatial variation and potential ecological response to extreme events. In this instance most of the rain fell in the Swan and not in the Avon catchment, and the most upstream site more closely associated with the Avon catchment had less change in salinity. The ongoing monitoring of salinity throughout estuaries can be progressed further using metrics to predict the risk of extreme rainfall events on foundation species. For instance, NOAA's Coral Reef Watch program (<http://coralreefwatch.noaa.gov/satellite/index.php>) collects sea surface temperature data, among other variables, from a variety of sources to predict mass coral bleaching events usually associated with marine heatwaves based on metrics (e.g. degree heating week) and thermal threshold information for corals (Kayanne, 2017). These metrics could be used to assess how unseasonal rainfall events vary in different places under different conditions and the range in ecological responses (Fraser et al., 2014; Wong et al., 2010). Considering estuaries are usually highly impacted from human activities (Wells et al., 2019), multiple pressures could compromise resilience further.

4.3 | Seagrass resilience varied temporally and spatially across the estuary

We documented survival but low resistance of seagrass meadows to the flood impact assessed by declines in seagrass biomass and leaf density. These observations confirm the general sensitivity of seagrasses to hyposalinity and associated flood impacts including light reduction (Lirman & Cropper, 2003; Longstaff & Dennison, 1999; Salo & Pedersen, 2014; Wetz & Yoskowitz, 2013) and aligns with observations in wetland ecosystems (Pan et al., 2012). Most meadows fully recovered within the time frame of this study except for the meadow furthest downstream. Here, we show resilience can vary at a smaller scale (i.e. within an estuary) than previous work that found marine *Halophila* spp. to be less resilient to hyposalinity than estuarine plants (Benjamin et al., 1999; Gavin & Durako, 2014). This information can be used to improve predictions of the responses of estuarine foundation species to increased hydrological variability associated with climate change (King et al., 2018). Similar observations of population-specific resilience have been recorded in other marine macrophytes such as *Fucus vesiculosus* (Nygård & Dring, 2008) and *Pinus pinaster* forests (Sánchez-Salguero et al., 2018). Overall, as the habitat was not lost and with the exception of the downstream site, the seagrass condition did not exceed the typical margins of variation, according to Smith (2011), we cannot consider that the Swan-Canning estuary had an extreme ecological response. However, as

more regular and intense precipitation events are forecast in the future (IPCC, 2014), the lack of recovery at the meadows furthest downstream may provide an early indication of potential disruptions to ecosystem structure and function (Kendrick et al., 2019).

The rate of change in salinity may have contributed to the variation in seagrass recovery as demonstrated by the significant nonlinear relationship and a rapid increase in recovery time at a rate of change 3 PSU/day. Salinity declined (r_{onset}) gradually at Upstream 2 (recovery time: 9 months), more rapidly at Downstream 1 (recovery time: 10 months) and at Upstream 3 (recovery time: 11 months) and most rapidly at Downstream 2 (recovery time: >22 months). As the site with the most rapid change in salinity actually had less reductions in light, salinity may be a bigger driver of recovery times. Gradual changes in salinity can increase the hyposalinity tolerance and survival of plants (Griffin & Durako, 2012), so this may explain the faster recovery and reduced flood impacts at Upstream 2 and 3 and Downstream 1, compared to Downstream 2. Rapid declines in salinity can impair physiological mechanisms that support growth (Fernández-Torquemada & Sánchez-Lizaso, 2011; Sola et al., 2020) and may have contributed to the lack of recovery at the downstream meadows or be due to the longer time required to recover from a greater loss (~80%) of biomass. A reduction in seagrass may have reduced the sediment stabilisation capacity of these meadows potentially increasing turbidity and decreasing light available for growth, creating a negative feedback loop that impeded recovery (Moksnes et al., 2018). However, this explanation was not supported by the light data and requires further investigation. No impacts to biomass or leaf density were observed at the Middle site following the flood although the event metrics indicated that changes in salinity were similar to impacted meadows. As the light environment at this site was minimally impacted, being the shallowest site, the higher light levels may have buffered against the significant seagrass loss. The pre-flood biomass and leaf density levels were also very low and could have made detecting further change associated with the flood difficult.

Other factors for the upstream meadows may have been important in influencing their resilience to the flood. In addition to the broader salinity regime, the water is also frequently more turbid at the upstream meadows. The leaves are generally larger and wider at the upstream meadows (in situ observations, Kilminster & Forbes, 2014) indicative of morphological responses to enhance photosynthesis (Bulthuis, 1987; Lee & Dunton, 1997). For *Zostera muelleri* meadows in Moreton Bay, Queensland, similar factors determined their resilience to severe flooding. Greater phenotypic plasticity including increased chlorophyll content and leaf height post-flood to maintain and/or increase photosynthesis was detected at meadows exposed to poorer water quality (Maxwell, 2014). The pressure exerted by this historical environmental regime appears to have selected for genotypes which make these meadows more adapted and able to survive or recover more quickly (Connolly et al., 2018). Potentially, the ability of the upstream meadows in this study to recover quicker reflects a combination of prior acclimations to low salinity and low light and/or the presence of genotypes that promote resilience. Where multiple environmental factors contribute to an extreme event, future research should aim to consider several

water quality variables in the development of metrics to increase their ecological relevance and be compared against a suite of seagrass indicators.

4.4 | Mechanism of recovery

The observed fruit production and seed bank densities during the flood and in the following spring and summer suggest minimal impact of the flood on *Halophila ovalis* phenology. The absence of a seed bank prevented the recovery of shallow meadows of *Halophila* spp. in north Queensland following storm impacts (Rasheed et al., 2014). However, this is unlikely to explain the absence of recovery we observed at Downstream 2, as seeds were present when germination would normally occur and water temperature conditions in spring 2017 (17–21.6°C) and summer of 2018 (24°C; <http://wir.water.wa.gov.au/Pages/Water-Information-Reporting.aspx>) were optimal for germination (Statton et al., 2017). Hyposalinity can reduce the resources available for sexual reproduction in favour of vegetative growth (Collier et al., 2014) which will be sustained provided salinity changes gradually (Fernández-Torquemada & Sánchez-Lizaso, 2011; Griffin & Durako, 2012). Thus, the differences in recovery may be due to greater growth upstream where the salinity change was more gradual. Alternatively, intrinsic differences in the capacity for growth may be responsible, with a more variable salinity environment (upstream), possibly selecting for plants that can make osmotic adjustments and grow faster (Benjamin et al., 1999). Our results suggest that measuring changes to growth, rather than standing biomass, is important to understand the impact of hydrological changes on estuarine seagrass resilience (Kilminster & Forbes, 2014; Roca et al., 2016).

4.5 | Management implications and future research directions

The upstream meadows fully recovered congruent with the high capacity for recovery among species of *Halophila* (Kilminster et al., 2015; Marbà & Duarte, 1998). The identification of these resilient meadows has implications for evolving management practices, which aim to reinforce or redefine populations by increasing their resilience to emerging future conditions (Coleman et al., 2020). These practices involve the identification of species and/or individuals within a species that have demonstrated the capacity to resist and/or recover from events that are representative of future scenarios. These locations possibly represent the 'must protect' locations of the future (e.g. York et al., 2017). The lack of recovery at the downstream meadows may be indicative of lower resilience to unseasonal and extreme rainfall-induced stress, so these meadows could be appropriate candidates for restoration aimed at 'future proofing' (Wood et al., 2019). Controlled experiments could aim to delineate interactive or synergistic effects from flood events (e.g. changes in salinity and light) that may impact ecosystem response, including effects at different life-history stages

(Kahn & Durako, 2005; Strazisar et al., 2013; Strydom et al., 2017). This consideration is relevant across marine and terrestrial ecosystems and can help to identify the environmental regimes that enhance or impact ecological resilience from climate change-related pressures (Pelini et al., 2012; Wolf et al., 2018).

5 | CONCLUSIONS

The study contributed to our knowledge of extreme climate events through the identification of extreme unseasonal rainfall events across a range of climate regions. The characterisation of the magnitude of these events (exceedance of 90th percentile) as extreme can inform subsequent ecological responses associated with salinity variations in estuaries following the event. The event metrics showed that the temporal and spatial patterns of salinity variation can be quantified, and they do not follow predictable patterns along an estuarine gradient. These metrics could be used to understand the impacts in estuaries where salinity data are readily available. We found resilience to the combination of hyposalinity and reduced light varied among seagrass populations within an estuary. Considering resilience on multiple scales will facilitate more accurate predictions of the fate of major habitat-forming species to more severe and frequent rainfall events. We predict that seagrass meadows and other estuarine benthic habitat that are exposed to more marine salinities, such as those located close to the ocean environment with consistent oceanic exchange, will be less resilient to these changes. The overall ecosystem trajectories will, therefore, depend on there being more resilient populations. The influence of environmental history in inducing variation in resilience is an exciting direction for future research.

ACKNOWLEDGEMENTS

The authors thank the three anonymous referees for their insight which greatly improved the manuscript. They thank the Department of Water and Environmental Regulation (DWER) for facilitating collaborative work and the provision of seagrass and water quality data in-kind co-funded by both DWER and Department of Biodiversity, Conservation and Attractions. They also thank the University of Western Australia, particularly Dr Matthew Hipsey and Brendan Busch, for the provision of salinity data generated by the Swan-Canning Emergency Response Model that made calculating accurate flood metrics possible. They appreciate the review and advice provided by Molly Moustaka and Nicole Said for refining this work, and Caitlyn O'Dea and Tash Dunham for extensive assistance in the field and laboratory. They are grateful to the Edith Cowan University, School of Science PhD and Honours grant and Western Australian Naturalist Club Serventy memorial award 2016 which funded this research.

AUTHORS' CONTRIBUTIONS

K.M.M. conceived the idea, and C.L.W. carried out the data collection and analysis and led the writing of the manuscript; K.M.M. and P.S.L. contributed critically to the concepts and drafts, and S.S. contributed especially to the revised manuscript including the global rainfall analysis; K.L.K., M.S.A., K.B. and S.M. were involved in the collection of the

majority of seagrass and water quality data and provided advice on the concepts and drafts. All the authors gave final approval for publication.

PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/1365-2745.13648>.

DATA AVAILABILITY STATEMENT

Data files associated with this article will be accessible via Edith Cowan University's Institutional Repository <https://doi.org/10.25958/49p6-na70> (Webster et al., 2021).

ORCID

Chanelle L. Webster  <https://orcid.org/0000-0002-8227-9791>

Marta Sánchez Alarcón  <https://orcid.org/0000-0003-0831-6539>

Katherine Bennett  <https://orcid.org/0000-0002-7710-7645>

Sian McNamara  <https://orcid.org/0000-0001-9330-0712>

Paul S. Lavery  <https://orcid.org/0000-0001-5162-273X>

REFERENCES

- Adler, J. (2003). Putting the coast in the 'Sea Around Us'. *The Sea around us Newsletter*, 15, 1–2. Retrieved from <http://seararoundus.org/newsletter/Issue15.pdf>; <http://data.unep-wcmc.org/datasets/23> (version 2.0).
- Adler, R. F., Sapiano, M. R. P., Huffman, G. J., Wang, J. J., Gu, G., Bolvin, D., Chiu, L., Schneider, U., Becker, A., Nelkin, E., Xie, P., Ferraro, R., & Shin, D. B. (2018). The Global Precipitation Climatology Project (GPCP) monthly analysis (new version 2.3) and a review of 2017 global precipitation. *Atmosphere (Basel)*, 9. <https://doi.org/10.3390/atmos9040138>
- Ateweberhan, M., Feary, D. A., Keshavmurthy, S., Chen, A., Schleyer, M. H., & Sheppard, C. R. C. (2013). Climate change impacts on coral reefs: Synergies with local effects, possibilities for acclimation, and management implications. *Marine Pollution Bulletin*, 74, 526–539. <https://doi.org/10.1016/j.marpolbul.2013.06.011>
- Benjamin, K. J., Walker, D. I., McComb, A. J., & Kuo, J. (1999). Structural response of marine and estuarine plants of *Halophila ovalis* (R. Br.) Hook. f. to long-term hyposalinity. *Aquatic Botany*, 64, 1–17. [https://doi.org/10.1016/S0304-3770\(98\)00103-X](https://doi.org/10.1016/S0304-3770(98)00103-X)
- Bokhorst, S., Bjerke, J. W., Tømmervik, H., Preece, C., & Phoenix, G. K. (2012). Ecosystem response to climatic change: The importance of the cold season. *Ambio*, 41, 246–255. <https://doi.org/10.1007/s13280-012-0310-5>
- Boyer, T. P., Levitus, S., Antonov, J. I., Locarnini, R. A., & Garcia, H. E. (2005). Linear trends in salinity for the World Ocean, 1955–1998. *Geophysical Research Letters*, 32, 1–4. <https://doi.org/10.1029/2004GL021791>
- Breaux, N., Lebreton, B., Palmer, T. A., Guillou, G., & Beseres Pollack, J. (2019). Ecosystem resilience following salinity change in a hypersaline estuary. *Estuarine, Coastal and Shelf Science*, 225, 106258. <https://doi.org/10.1016/j.ecss.2019.106258>
- Brock, M. A. (1982). Biology of the salinity tolerant genus *Ruppia* L. in saline lakes in South Australia I. Morphological variation within and between species and ecophysiology. *Aquatic Botany*, 13, 219–248. [https://doi.org/10.1016/0304-3770\(82\)90062-6](https://doi.org/10.1016/0304-3770(82)90062-6)
- Bulthuis, D. A. (1987). Effects of temperature on photosynthesis and growth of seagrasses. *Aquatic Botany*, 27, 27–40. [https://doi.org/10.1016/0304-3770\(87\)90084-2](https://doi.org/10.1016/0304-3770(87)90084-2)
- Bureau of Meteorology. (2017). *Special Climate Statement 60 – Heavy rainfall and flooding in southwest Western Australia*. Bureau of Meteorology. <https://www.bom.gov.au/climate/current/statements/scs60.pdf>
- Campbell, S. J., & McKenzie, L. J. (2004). Flood related loss and recovery of intertidal seagrass meadows in southern Queensland, Australia. *Estuarine, Coastal and Shelf Science*, 60, 477–490. <https://doi.org/10.1016/j.ecss.2004.02.007>
- Christensen, O. B., & Christensen, J. H. (2004). Intensification of extreme European summer precipitation in a warmer climate. *Global and Planetary Change*, 44, 107–117. <https://doi.org/10.1016/j.gloplacha.2004.06.013>
- Coleman, M., Wood, G., Filbee-Dexter, K., Minne, A., Goold, H., Vergés, A., Marzinelli, E., Steinberg, P., & Wernberg, T. (2020). Restore or re-define: Future trajectories for restoration. *Frontiers in Marine Science*, 7, 1–12. <https://doi.org/10.3389/fmars.2020.00237>
- Collier, C. J., Villacorta-Rath, C., Van Dijk, K. J., Takahashi, M., & Waycott, M. (2014). Seagrass proliferation precedes mortality during hypo-salinity events: A stress-induced morphometric response. *PLoS ONE*, 9, 15–19. <https://doi.org/10.1371/journal.pone.0094014>
- Darr, A., Gogina, M., & Zettler, M. L. (2014). Functional changes in benthic communities along a salinity gradient – A western Baltic case study. *Journal of Sea Research*, 85, 315–324. <https://doi.org/10.1016/j.seares.2013.06.003>
- Dietrich, C. C., Kreyling, J., Jentsch, A., & Malyshev, A. V. (2018). Intraspecific variation in response to magnitude and frequency of freeze-thaw cycles in a temperate grass. *AoB Plants*, 10, 1–13. <https://doi.org/10.1093/aobpla/plx068>
- Dolbeth, M., Cardoso, P. G., Grilo, T. F., Bordalo, M. D., Raffaelli, D., & Pardal, M. A. (2011). Long-term changes in the production by estuarine macrobenthos affected by multiple stressors. *Estuarine, Coastal and Shelf Science*, 92, 10–18. <https://doi.org/10.1016/j.ecss.2010.12.006>
- Durack, P. J., & Wijffels, S. E. (2010). Fifty-Year trends in global ocean salinities and their relationship to broad-scale warming. *Journal of Climate*, 23, 4342–4362. <https://doi.org/10.1175/2010JCLI3377.1>
- Echendu, A. J. (2020). The impact of flooding on Nigeria's sustainable development goals (SDGs). *Ecosystem Health and Sustainability*, 6. <https://doi.org/10.1080/20964129.2020.1791735>
- Fernández-Torquemada, Y., & Sánchez-Lizaso, J. L. (2011). Responses of two Mediterranean seagrasses to experimental changes in salinity. *Hydrobiologia*, 669, 21–33. <https://doi.org/10.1007/s10750-011-0644-1>
- Fraser, M. W., Kendrick, G. A., Statton, J., Hovey, R. K., Zavala-Perez, A., & Walker, D. I. (2014). Extreme climate events lower resilience of foundation seagrass at edge of biogeographical range. *Journal of Ecology*, 102, 1528–1536. <https://doi.org/10.1111/1365-2745.12300>
- Gasith, A., & Resh, V. H. (1999). Streams in mediterranean climate regions: Abiotic influences and biotic responses to predictable seasonal events. *Annual Review of Ecology and Systematics*, 30, 51–81.
- Gavin, N. M., & Durako, M. J. (2014). Population-based variation in resilience to hyposalinity stress in *Halophila johnsonii*. *Bulletin of Marine Science*, 90, 781–794. <https://doi.org/10.5343/bms.2013.1056>
- Gaylard, S., Waycott, M., & Lavery, P. (2020). Review of coast and marine ecosystems in temperate Australia demonstrates a wealth of ecosystem services. *Frontiers in Marine Science*, 7, 1–15. <https://doi.org/10.3389/fmars.2020.00453>
- Griffin, N. E., & Durako, M. J. (2012). The effect of pulsed versus gradual salinity reduction on the physiology and survival of *Halophila johnsonii* Eiseman. *Marine Biology*, 159, 1439–1447. <https://doi.org/10.1007/s00227-012-1923-8>
- Hallett, C. S., Hobday, A. J., Tweedley, J. R., Thompson, P. A., McMahon, K., & Valesini, F. J. (2018). Observed and predicted impacts of climate change on the estuaries of south-western Australia, a Mediterranean climate region. *Regional Environmental Change*, 18, 1357–1373. <https://doi.org/10.1007/s10113-017-1264-8>
- Hillman, K., McComb, A. J., & Walker, D. I. (1995). The distribution, biomass and primary production of the seagrass *Halophila ovalis* in the

- Swan/Canning Estuary, Western Australia. *Aquatic Botany*, 51, 1–54. [https://doi.org/10.1016/0304-3770\(95\)00466-D](https://doi.org/10.1016/0304-3770(95)00466-D)
- Hobday, A. J., Alexander, L. V., Perkins, S. E., Smale, D. A., Straub, S. C., Oliver, E. C. J., Benthuyzen, J. A., Burrows, M. T., Donat, M. G., Feng, M., Holbrook, N. J., Moore, P. J., Scannell, H. A., Sen Gupta, A., & Wernberg, T. (2016). A hierarchical approach to defining marine heatwaves. *Progress in Oceanography*, 141, 227–238. <https://doi.org/10.1016/j.pocean.2015.12.014>
- Hodgkin, E. P. (1987). The hydrology of the Swan River estuary: Salinity the ecological master factor. In J. John (Ed.), *The swan river estuary ecology and management* (pp. 34–44). Curtin University of Technology.
- Hoover, D. L., Knapp, A. K., & Smith, M. D. (2014). Resistance and resilience of a grassland ecosystem to climate extremes. *Ecology*, 95(9), 2646–2656. <https://doi.org/10.1890/13-2186.1>
- Huang, P., Trayler, K., Wang, B., Saeed, A., Oldham, C. E., Busch, B., & Hipsey, M. R. (2019). An integrated modelling system for water quality forecasting in an urban eutrophic estuary: The swan-canning estuary virtual observatory. *Journal of Marine Systems*, 199, 103218. <https://doi.org/10.1016/j.jmarsys.2019.103218>
- Hughes, A. R., & Stachowicz, J. J. (2004). Genetic diversity enhances the resistance of a seagrass ecosystem to disturbance. *PNAS*, <https://doi.org/10.1073/pnas.0402642101>
- IPCC (Intergovernmental Panel on Climate Change). (2007). Climate change 2007: Impacts, adaptation and vulnerability. Fourth Assessment Report—Summary for Policy-makers. WG II, IPCC (pp. 1–23).
- IPCC (Intergovernmental Panel on Climate Change). (2014). Climate change 2014: Impacts, adaptation, and vulnerability. In V. R. Barros, C. B. Field, D. J. Dokken, M. D. Mastrandrea, K. J. Mach, T. E. Bilir, M. Chatterjee, K. L. Ebi, Y. O. Estrada, R. C. Genova, B. Girma, E. S. Kissel, A. N. Levy, S. MacCracken, P. R. Mastrandrea, & L. L. White (Eds.), *Part B: regional aspects*. Contribution of working group II to the fifth assessment report of the intergovernmental panel on climate change. Cambridge University Press. <https://doi.org/10.1017/cbo9781107415386.001>
- Jackson, J. B. C. (2010). The future of the oceans past. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365, 3765–3778. <https://doi.org/10.1098/rstb.2010.0278>
- Jentsch, A., Kreyling, J., & Beierkuhnlein, C. (2007). A new generation of events, not trends experiments. *Frontiers in Ecology and the Environment*, 5, 365–374. [https://doi.org/10.1890/1540-9295\(2007\)5\[365:ANGOCE\]2.0.CO;2](https://doi.org/10.1890/1540-9295(2007)5[365:ANGOCE]2.0.CO;2)
- Kahn, A. E., & Durako, M. J. (2005). The effect of salinity and ammonium on seed germination in *Ruppia maritima* from Florida Bay. *Bulletin of Marine Science*, 77, 453–458.
- Kayanne, H. (2017). Validation of degree heating weeks as a coral bleaching index in the northwestern Pacific. *Coral Reefs*, 36, 63–70. <https://doi.org/10.1007/s00338-016-1524-y>
- Kelsey, P., Hall, J., Kitsios, A., Quinton, B., & Shakya, D. (2010). Hydrological and nutrient modelling of the Swan-Canning coastal catchments, Water Science technical series. Report no. 14, Department of Water, Western Australia.
- Kemp, W. M., Batiuk, R., & Bartleson, R. (2004). Habitat requirements for submerged aquatic vegetation in Chesapeake Bay: water quality, light regime, and physical-chemical factors. *Estuaries*, 27, 363–377.
- Kendrick, G. A., Nowicki, R. J., Olsen, Y. S., Strydom, S., Fraser, M. W., Sinclair, E. A., Statton, J., Hovey, R. K., Thomson, J. A., Burkholder, D. A., McMahon, K. M., Kilminster, K., Hetzel, Y., Fourqurean, J. W., Heithaus, M. R., & Orth, R. J. (2019). A Systematic review of how multiple stressors from an extreme event drove ecosystem-wide loss of resilience in an iconic Seagrass community. *Frontiers in Marine Science*, 6. <https://doi.org/10.3389/fmars.2019.00455>
- Kilminster, K., & Forbes, V. (2014). Seagrass as an indicator of estuary condition in the Swan-Canning estuary, Water Science Technical Series. Report no. 62, Department of Water, Western Australia.
- Kilminster, K., McMahon, K., Waycott, M., Kendrick, G. A., Scanes, P., McKenzie, L., O'Brien, K. R., Lyons, M., Ferguson, A., Maxwell, P., Glasby, T., & Udy, J. (2015). Unravelling complexity in seagrass systems for management: Australia as a microcosm. *Science of the Total Environment*, 534, 97–109. <https://doi.org/10.1016/j.scitotenv.2015.04.061>
- Kim, D. H., Aldridge, K. T., Brookes, J. D., & Ganf, G. G. (2013). The effect of salinity on the germination of *Ruppia tuberosa* and *Ruppia megacarpa* and implications for the Coorong: A coastal lagoon of southern Australia. *Aquatic Botany*, 111, 81–88. <https://doi.org/10.1016/j.aquabot.2013.06.008>
- Kim, G. U., Seo, K. H., & Chen, D. (2019). Climate change over the Mediterranean and current destruction of marine ecosystem. *Scientific Reports*, 9, 1–9. <https://doi.org/10.1038/s41598-019-55303-7>
- King, N. G., McKeown, N. J., Smale, D. A., & Moore, P. J. (2018). The importance of phenotypic plasticity and local adaptation in driving intraspecific variability in thermal niches of marine macrophytes. *Ecography (Cop.)*, 41, 1469–1484. <https://doi.org/10.1111/ecog.03186>
- Kirk, J. (1994). *Light and photosynthesis in aquatic ecosystems*. Cambridge University Press.
- Kültz, D. (2015). Physiological mechanisms used by fish to cope with salinity stress. *Journal of Experimental Biology*, 218, 1907–1914. <https://doi.org/10.1242/jeb.118695>
- Kuo, J., & Kirkman, H. (1992). Fruits, seeds and germination in the Seagrass *Halophila ovalis* (Hydrocharitaceae). *Botanica Marina*, 35, 197–204. <https://doi.org/10.1515/botm.1992.35.3.197>
- Largier, J. L., Hollibaugh, J. T., & Smith, S. V. (1997). Seasonally hypersaline estuaries in Mediterranean-climate regions. *Estuarine, Coastal and Shelf Science*, 45, 789–797. <https://doi.org/10.1006/ecss.1997.0279>
- Lee, C. E., & Petersen, C. H. (2003). Effects of developmental acclimation on adult salinity tolerance in the freshwater-invading copepod *Eurytemora affinis*. *Physiological and Biochemical Zoology*, 76, 296–301. <https://doi.org/10.1086/375433>
- Lee, K. S., & Dunton, K. H. (1997). Effects of in situ light reduction on the maintenance, growth and partitioning of carbon resources in *Thalassia testudinum* Banks ex König. *Journal of Experimental Marine Biology and Ecology*, 210, 53–73. [https://doi.org/10.1016/S0022-0981\(96\)02720-7](https://doi.org/10.1016/S0022-0981(96)02720-7)
- Lefcheck, J. S., Wilcox, D. J., Murphy, R. R., Marion, S. R., & Orth, R. J. (2017). Multiple stressors threaten the imperiled coastal foundation species eelgrass (*Zostera marina*) in Chesapeake Bay, USA. *Global Change Biology*, 23, 3474–3483. <https://doi.org/10.1111/gcb.13623>
- Levinton, J., Doall, M., Ralston, D., Starke, A., & Allam, B. (2011). Climate change, precipitation and impacts on an estuarine refuge from disease. *PLoS ONE*, 6, 1–8. <https://doi.org/10.1371/journal.pone.0018849>
- Lirman, D., & Cropper, W. P. (2003). The influence of salinity on seagrass growth, survivorship, and distribution within Biscayne Bay, Florida: Field, experimental, and modeling studies. *Estuaries*, 26, 131–141. <https://doi.org/10.1007/BF02691700>
- Longstaff, B. J., & Dennison, W. C. (1999). Seagrass survival during pulsed turbidity events: The effects of light deprivation on the seagrasses *Halodule pinifolia* and *Halophila ovalis*. *Aquatic Botany*, 65, 105–121. [https://doi.org/10.1016/S0304-3770\(99\)00035-2](https://doi.org/10.1016/S0304-3770(99)00035-2)
- Lotze, H. K., Lenihan, H. S., Bourque, B. J., Bradbury, R. H., Cooke, R. G., Kay, M. C., Kidwell, S. M., Kirby, M. X., Peterson, C. H., Jackson, J. B. C., & Bay, M. (2006). Coastal seas. *Science*, 312, 1806–1809.
- Marbà, N., & Duarte, C. M. (1998). Rhizome elongation and seagrass clonal growth. *Marine Ecology Progress Series*, 174, 269–280. <https://doi.org/10.3354/meps174269>
- Marion, S. R., & Orth, R. J. (2010). Innovative techniques for large-scale seagrass restoration using *Zostera marina* (eelgrass) seeds. *Restoration Ecology*, 18, 514–526. <https://doi.org/10.1111/j.1526-100X.2010.00692.x>

- Maxwell, P. (2014). *Ecological resilience theory: Application and testing in seagrass ecosystems*. Thesis (PhD doctorate). Griffith University. <https://doi.org/10.25904/1912/143>
- Moksnes, P., Eriander, L., Infantes, E., & Holmer, M. (2018). Local regime shifts prevents natural recovery and restoration of lost eelgrass beds along the Swedish West coast. *Estuaries and Coasts*, 41(6), 1712–1731. <https://doi.org/10.1007/s12237-018-0382-y>
- Morris, R. L., Konlechner, T. M., Ghisalberti, M., & Swearer, S. E. (2018). From grey to green: Efficacy of eco-engineering solutions for nature-based coastal defence. *Global Change Biology*, 24, 1827–1842. <https://doi.org/10.1111/gcb.14063>
- Narayan, S., Beck, M. W., Wilson, P., Thomas, C. J., Guerrero, A., Shepard, C. C., Reguero, B. G., Franco, G., Ingram, J. C., & Trespalacios, D. (2017). The value of coastal wetlands for flood damage reduction in the northeastern USA. *Scientific Reports*, 7, 1–12. <https://doi.org/10.1038/s41598-017-09269-z>
- Nche-Fambo, F. A., Scharler, U. M., & Tirok, K. (2015). Resilience of estuarine phytoplankton and their temporal variability along salinity gradients during drought and hypersalinity. *Estuarine, Coastal and Shelf Science*, 158, 40–52. <https://doi.org/10.1016/j.ecss.2015.03.011>
- Nicol, J. (2005). *The ecology of Ruppia spp. in South Australia, with reference to the Coorong*. The ecology of Ruppia spp. in South Australia, with reference to the Coorong. South Australian Research and Development Institute (Aquatic Sciences). SARDI Aquatic Sciences Publication Number RD04/0247-2. 44 pp.
- Nygård, C. A., & Dring, M. J. (2008). Influence of salinity, temperature, dissolved inorganic carbon and nutrient concentration on the photosynthesis and growth of *Fucus vesiculosus* from the Baltic and Irish Seas. *European Journal of Phycology*, 43, 253–262. <https://doi.org/10.1080/09670260802172627>
- Paerl, H. W., Hall, N. S., Hounshell, A. G., Luettich, R. A., Rossignol, K. L., Osburn, C. L., & Bales, J. (2019). Recent increase in catastrophic tropical cyclone flooding in coastal North Carolina, USA: Long-term observations suggest a regime shift. *Scientific Reports*, 9, 1–9. <https://doi.org/10.1038/s41598-019-46928-9>
- Pan, Y., Xie, Y., Chen, X., & Li, F. (2012). Effects of flooding and sedimentation on the growth and physiology of two emergent macrophytes from Dongting Lake wetlands. *Aquatic Botany*, 100, 35–40. <https://doi.org/10.1016/j.aquabot.2012.03.008>
- Pelini, S. L., Diamond, S. E., MacLean, H., Ellison, A. M., Gotelli, N. J., Sanders, N. J., & Dunn, R. R. (2012). Common garden experiments reveal uncommon responses across temperatures, locations, and species of ants. *Ecology and Evolution*, 2, 3009–3015. <https://doi.org/10.1002/ece3.407>
- Power, S. B., Delage, F. P. D., Chung, C. T. Y., Ye, H., & Murphy, B. F. (2017). Humans have already increased the risk of major disruptions to Pacific rainfall. *Nature Communications*, 8. <https://doi.org/10.1038/ncomms14368>
- R Core Team. (2020). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. <https://www.r-project.org/>
- Ralph, P. J. (1998). Photosynthetic responses of *Halophila ovalis* (R. Br.) Hook. f. to osmotic stress. *Journal of Experimental Marine Biology and Ecology*, 227, 203–220. [https://doi.org/10.1016/S0022-0981\(97\)00269-4](https://doi.org/10.1016/S0022-0981(97)00269-4)
- Rasheed, M. A., McKenna, S. A., Carter, A. B., & Coles, R. G. (2014). Contrasting recovery of shallow and deep water seagrass communities following climate associated losses in tropical north Queensland, Australia. *Marine Pollution Bulletin*, 83, 491–499. <https://doi.org/10.1016/j.marpolbul.2014.02.013>
- Roca, G., Alcoverro, T., Krause-Jensen, D., Balsby, T. J. S., Van Katwijk, M. M., Marbà, N., Santos, R., Arthur, R., Mascaró, O., Fernández-Torquemada, Y., Pérez, M., Duarte, C. M., & Romero, J. (2016). Response of seagrass indicators to shifts in environmental stressors: A global review and management synthesis. *Ecological Indicators*, 63, 310–323. <https://doi.org/10.1016/j.ecolind.2015.12.007>
- Russell, B. D., Thompson, J. A. I., Falkenberg, L. J., & Connell, S. D. (2009). Synergistic effects of climate change and local stressors: CO₂ and nutrient-driven change in subtidal rocky habitats. *Global Change Biology*, 15, 2153–2162. <https://doi.org/10.1111/j.1365-2486.2009.01886.x>
- Sale, P. F., Agardy, T., Ainsworth, C. H., Feist, B. E., Bell, J. D., Christie, P., Hoegh-Guldberg, O., Mumby, P. J., Feary, D. A., Saunders, M. I., Daw, T. M., Foale, S. J., Levin, P. S., Lindeman, K. C., Lorenzen, K., Pomeroy, R. S., Allison, E. H., Bradbury, R. H., Corrin, J., ... Sheppard, C. R. C. (2014). Transforming management of tropical coastal seas to cope with challenges of the 21st century. *Marine Pollution Bulletin*, 85, 8–23. <https://doi.org/10.1016/j.marpolbul.2014.06.005>
- Salo, T., & Pedersen, M. F. (2014). Synergistic effects of altered salinity and temperature on estuarine eelgrass (*Zostera marina*) seedlings and clonal shoots. *Journal of Experimental Marine Biology and Ecology*, 457, 143–150. <https://doi.org/10.1016/j.jembe.2014.04.008>
- Sánchez-Salguero, R., Camarero, J. J., Rozas, V., Génova, M., Olano, J. M., Arzac, A., Gazol, A., Caminero, L., Tejedor, E., de Luis, M., & Linares, J. C. (2018). Resist, recover or both? Growth plasticity in response to drought is geographically structured and linked to intraspecific variability in *Pinus pinaster*. *Journal of Biogeography*, 45, 1126–1139. <https://doi.org/10.1111/jbi.13202>
- Shaffer, J. M., & Beaulieu, J. J. (2012). Calibration of the OdysseyTM photosynthetic irradiance RecorderTM for absolute irradiance measures. *Journal of Freshwater Ecology*, 27, 599–605. <https://doi.org/10.1080/02705060.2012.711259>
- Smale, D. A., Wernberg, T., Oliver, E. C. J., Thomsen, M., Harvey, B. P., Straub, S. C., Burrows, M. T., Alexander, L. V., Benthuisen, J. A., Donat, M. G., Feng, M., Hobday, A. J., Holbrook, N. J., Perkins-Kirkpatrick, S. E., Scannell, H. A., Sen Gupta, A., Payne, B. L., & Moore, P. J. (2019). Marine heatwaves threaten global biodiversity and the provision of ecosystem services. *Nature Climate Change*, 9, 306–312. <https://doi.org/10.1038/s41558-019-0412-1>
- Smith, M. D. (2011). An ecological perspective on extreme climatic events: A synthetic definition and framework to guide future research. *Journal of Ecology*, 99, 656–663. <https://doi.org/10.1111/j.1365-2745.2011.01798.x>
- Snow, G. C., & Taljaard, S. (2007). Water quality in South African temporarily open/closed estuaries: A conceptual model. *African Journal of Aquatic Science*, 32, 99–111. <https://doi.org/10.2989/AJAS.2007.32.2.1.198>
- Sola, J., Sorrell, B. K., Olesen, B., Søndergaard Jørgensen, M., & Lund-Hansen, L. C. (2020). Acute and prolonged effects of variable salinity on growth, gas exchange and photobiology of eelgrass (*Zostera marina* L.). *Aquatic Botany*, 165, 103236. <https://doi.org/10.1016/j.aquabot.2020.103236>
- Statton, J., Sellers, R., Dixon, K. W., Kilminster, K., Merritt, D. J., & Kendrick, G. A. (2017). Seed dormancy and germination of *Halophila ovalis* mediated by simulated seasonal temperature changes. *Estuarine, Coastal and Shelf Science*, 198, 156–162. <https://doi.org/10.1016/j.ecss.2017.08.045>
- Steward, J. S., Virnstein, R. W., Lasi, M. A., Morris, L. J., Miller, J. D., Hall, L. M., & Tweedale, W. A. (2006). The impacts of the 2004 hurricanes on hydrology, water quality, and seagrass in the central Indian River Lagoon, Florida. *Estuaries and Coasts*, 29, 954–965. <https://doi.org/10.1007/bf02798656>
- Strazisar, T., Koch, M. S., Madden, C. J., Filina, J., Lara, P. U., & Mattair, A. (2013). Salinity effects on *Ruppia maritima* L. seed germination and seedling survival at the Everglades-Florida Bay ecotone. *Journal of Experimental Marine Biology and Ecology*, 445, 129–139. <https://doi.org/10.1016/j.jembe.2013.02.045>
- Strydom, S., McMahon, K., Kendrick, G. A., Statton, J., & Lavery, P. S. (2017). Seagrass *Halophila ovalis* is affected by light quality across different life history stages. *Marine Ecology Progress Series*, 572, 103–116. <https://doi.org/10.3354/meps12105>

- Strydom, S., Murray, K., Wilson, S., Huntley, B., Rule, M., Heithaus, M., Bessey, C., Kendrick, G. A., Burkholder, D., Holmes, T., Fraser, M. W., & Zdunic, K. (2020). Too hot to handle: Unprecedented seagrass death driven by marine heatwave in a World Heritage Area. *Global Change Biology*, 26(6), 3525–3538. <https://doi.org/10.1111/gcb.15065>
- Tatarinov, F., Rotenberg, E., Maseyk, K., Ogée, J., Klein, T., & Yakir, D. (2016). Resilience to seasonal heat wave episodes in a Mediterranean pine forest. *New Phytologist*, 210, 485–496. <https://doi.org/10.1111/nph.13791>
- Thompson, C., Kilminster, K., Hallett, C., Valesini, F., Hipsey, M., Trayler, K., Gaughan, D., Summers, R., Syme, G., & Seares, P. (2016). *Research and information priorities for estuary management in South-west Western Australia: Consultation Draft*. Western Australian Institute of Marine Science (WAMS).
- Thomson, C. E., Rose, T., & Robb, M. (2001). Seasonal water quality patterns in the Swan River Estuary, 1994–1998, technical report. Swan River Trust, Western Australia.
- Trenberth, K. E. (2011). Changes in precipitation with climate change. *Climate Research*, 47, 123–138. <https://doi.org/10.3354/cr00953>
- Trenberth, K. E., & Fasullo, J. T. (2012). Climate extremes and climate change: The Russian heat wave and other climate extremes of 2010. *Journal of Geophysical Research – Atmospheres*, 117, 1–12. <https://doi.org/10.1029/2012JD018020>
- Tyerman, S. (1982). Water relations of seagrasses: Stationary volumetric elastic modulus and osmotic pressure of the leaf cells of *Halophila ovalis*, *Zostera capricorni* and *Posidonia australis*. *Plant Physiology*, 69, 957–965. <https://doi.org/10.1104/pp.69.4.957>
- Walker, B., Holling, C. S., Carpenter, S. R., & Kinzig, A. (2004). Resilience, adaptability and transformability in social–ecological systems. *Ecology and Society*, 9, 5.
- Watson, R., Adler, J., Booth, S., Christensen, V., Kaschner, K., Kitchingman, A., Lai, S., Palomares, M. L. D., Valdez, F., Zeller, D., & Pauly, D. (2004). Welcome to www.seaaroundus.org: Launching our 'product' on the web. *Sea around Us Newsletter*, March/April, (22), 1–8.
- Webster, C. L., McMahon, K. M., Lavery, P. S., Strydom, S., Sánchez Alarcón, M., Kilminster, K. L., Bennet, K., & McNamara, S. (2021). Journal of Ecology 2021: Global rainfall seagrass resilience Swan River. Edith Cowan University. Research Online - Institutional Repository. <https://doi.org/10.25958/49p6-na70>
- Wells, S. R., Wing, L. C., Smith, A. M., & Smith, I. W. G. (2019). Historical changes in bivalve growth rates indicate ecological consequences of human occupation in estuaries. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 29, 1452–1465. <https://doi.org/10.1002/aqc.3039>
- Wetz, M. S., & Yoskowitz, D. W. (2013). An 'extreme' future for estuaries? Effects of extreme climatic events on estuarine water quality and ecology. *Marine Pollution Bulletin*, 69, 7–18. <https://doi.org/10.1016/j.marpolbul.2013.01.020>
- Wernberg, T. (2020). Marine heatwave drives collapse of kelp forests in Western Australia. In J. G. Canadell, & R. B. Jackson (Eds.), *Ecosystem collapse and climate change*. Ecological Studies. Springer-Nature.
- Whitfield, A. K. (2017). The role of seagrass meadows, mangrove forests, salt marshes and reed beds as nursery areas and food sources for fishes in estuaries. *Review in Fish Biology and Fisheries*, 27, 75–110. <https://doi.org/10.1007/s11160-016-9454-x>
- Wolf, K. K. E., Hoppe, C. J. M., & Rost, B. (2018). Resilience by diversity: Large intraspecific differences in climate change responses of an Arctic diatom. *Limnology and Oceanography*, 63, 397–411. <https://doi.org/10.1002/lno.10639>
- Wong, V. N. L., Johnston, S. G., Bush, R. T., Sullivan, L. A., Clay, C., Burton, E. D., & Slavich, P. G. (2010). Spatial and temporal changes in estuarine water quality during a post-flood hypoxic event. *Estuarine, Coastal and Shelf Science*, 87, 73–82. <https://doi.org/10.1016/j.ecss.2009.12.015>
- Wood, G., Marzinelli, E. M., Coleman, M. A., Campbell, A. H., Santini, N. S., Kajlich, L., Verdura, J., Wodak, J., Steinberg, P. D., & Vergés, A. (2019). Restoring subtidal marine macrophytes in the Anthropocene: Trajectories and future-proofing. *Marine & Freshwater Research*, 70, 936–951. <https://doi.org/10.1071/MF18226>
- York, P. H., Smith, T. M., Coles, R. G., McKenna, S. A., Connolly, R. M., Irving, A. D., Jackson, E. L., McMahon, K., Runcie, J. W., Sherman, C. D. H., Sullivan, B. K., Trevathan-Tackett, S. M., Brodersen, K. E., Carter, A. B., Ewers, C. J., Lavery, P. S., Roelfsema, C. M., Sinclair, E. A., Strydom, S., ... Whitehead, S. (2017). Identifying knowledge gaps in seagrass research and management: An Australian perspective. *Marine Environment Research*, 127, 163–172. <https://doi.org/10.1016/j.marenvres.2016.06.006>
- Zhou, B., Gu, L., Ding, Y., Shao, L., Wu, Z., Yang, X., Li, C., Li, Z., Wang, X., Cao, Y., Zeng, B., Yu, M., Wang, M., Wang, S., Sun, H., Duan, A., An, Y., Wang, X. U., & Kong, W. (2011). The great 2008 Chinese ice storm its socioeconomic–ecological impact and sustainability lessons learned. *Bulletin of the American Meteorological Society*, 92, 47–60. <https://doi.org/10.1175/2010BAMS2857.1>
- Zuur, A. F., Ieno, E. N., & Smith, G. M. (2007). Analyzing ecological data, methods. <https://doi.org/10.1016/B978-0-12-387667-6.00013-0>

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Webster CL, Kilminster KL, Sánchez Alarcón M, et al. Population-specific resilience of *Halophila ovalis* seagrass habitat to unseasonal rainfall, an extreme climate event in estuaries. *J Ecol*. 2021;00:1–20. <https://doi.org/10.1111/1365-2745.13648>