

Interpreting Long-Term Patterns of Seagrasses Abundance: How Seagrass Variability Is Dependent on Genus and Estuary Type

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Abstract

Seagrass habitats are recognised as providing essential ecosystem services and being indicators of estuarine health, and are under increasing threat globally. This study examined the spatial and temporal variability of four dominant seagrass genera (*Posidonia, Zostera, Halophila* and *Ruppia*) among five geomorphic estuary types and four levels of estuarine maturity in New South Wales (NSW), Australia, over a 40-year period. While there was a decline in total seagrass area across NSW over the last 40 years, this was mostly attributed to *Ruppia*, the genus with the greatest temporal variability. The composition of seagrasses differed among estuary types and with the maturity of Barrier estuaries. *Posidonia* was found to be the least temporally variable genus over the last 40 years. The greatest overall annual rate of decline was 1.85% year⁻¹ for *Ruppia* which is considerably less than the global estimated rate of 5% year⁻¹ over the same time period. Average annual rates of decline were greater over the last 18 years than the last 40 years, but only for the most transient genera and only in some estuary types. Recent declines in *Posidonia* were greater than those over the last 40 years in two of the most heavily urbanised estuaries. No relationships were found between catchment disturbances, measured as land use or population density, and seagrass change or temporal variability at the estuary scale. Our results highlight the importance of distinguishing among seagrass genera when interpreting changes over time and considering factors such as estuary type, which is effectively a surrogate for environmental conditions.

Keywords Seagrass · *Posidonia* · *Zostera* · *Halophila* · *Ruppia* · Mapping · Change detection · Temporal analysis · Southeast Australia, NSW, Australia

Introduction

Estuaries are among some of the most important aquatic ecosystems on earth and are also some of the most vulnerable and threatened environments (Dafforn et al. 2012; Hallett et al. 2016; Lotze et al. 2006; Worm et al. 2006). As transition zones, estuaries lie between terrestrial freshwater flows and oceanic waters, creating some of the most biologically productive areas on earth (Kennish 2002). Extensive coastal development, primarily in close proximity to estuaries, has

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Greg J. West gregory.west@dpi.nsw.gov.au significantly impacted coastal habitats, with many, including seagrasses, declining globally (Orth et al. 2006; Short et al. 2011; Waycott et al. 2009).

Seagrasses are recognised as providing essential habitat and refuge for many commercial and recreational species (Bell and Pollard 1989; de la Torre-Castro and Rönnbäck 2004). Seagrass meadows also provide crucial ecosystem functions including sediment stabilisation, wave attenuation, shoreline protection, nutrient cycling, improving water quality, water clarity and carbon sequestration (Costanza et al. 1997; Duarte 2002; Macreadie et al. 2014; Walker and McComb 1992).

Seagrass growth and distribution is dependent on available light, with most species generally requiring greater than 11% surface irradiance, salinity greater than 5% and sandy to muddy substrates (Duarte 2002). As such, seagrasses are limited to the shallow and intertidal regions of coasts and estuaries and are often in close proximity to humans. For

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example, in Australia, it is estimated that 85% of Australians live within 50 km of the coast (Clark and Johnston 2017), and in the most populous state, New South Wales (NSW), 80% of people are concentrated within the coastal catchments that feed the estuaries where seagrasses are found. This high population density can lead to either indirect or direct pressures on seagrasses. Indirect pressures include reductions in salinity and increases in turbidity and nutrients, many of which are due to land-based disturbances such as clearing of natural vegetation, agriculture, mining, industrial development, urbanisation and pollution (Foster et al. 2017; Kilminster et al. 2015). Direct physical pressures often result in the complete removal of seagrasses and include boat moorings (Glasby and West 2018; Hastings et al. 1995; Walker et al. 1989), anchoring (La Manna et al. 2015; Milazzo et al. 2004), boat propellers (Bell et al. 2002), dredging (Larkum and West 1990), harvesting and trampling (Butler and Jernakoff 1999). In many cases, indirect and direct pressures may interact, making it difficult to identify the underlying drivers of impacts (Fonseca et al. 2013).

Seagrass meadows are naturally dynamic with some species showing high levels of natural variability in growth and extent over seasons (Guidetti et al. 2002; Duarte et al. 2006) or years (Duarte et al. 2006; Lyons et al. 2013). As such, Kilminster et al. (2015) proposed that there are two primary forms of seagrass meadow, enduring and transitory. Enduring meadows are composed primarily of persistent genera, such as Posidonia, which, in comparison to other seagrass species, have a relatively long life (Kilminster et al. 2015), slow growth (Marbà and Duarte 1998) and low seasonal variability (Guidetti et al. 2002). In some cases, however, enduring meadows can include species of Zostera (Campbell and Miller 2002; Kerr and Strother 1990) and Halophila (Hillman et al. 1995), which have a relatively shorter life (Kilminster et al. 2015) and can show high seasonal above and below ground variability in biomass, but nevertheless create meadows that persist over longer periods of time. In contrast, transitory meadows show much greater short-term temporal variability in above and below ground biomass, and extent. Transitory meadows typically include more opportunistic species such as species of Zostera, Halophila and Ruppia (Congdon and McComb 1979; Kerr and Strother 1990; Yaakub et al. 2014) and as such often occur where physical conditions are highly variable (Kilminster et al. 2015).

Physical conditions can vary according to the geomorphic type and maturity of estuaries (Roy et al. 2001; Ferguson et al. 2018). In NSW, there are five broad estuarine types according to decreasing marine influence: ocean embayments, drowned river valleys, barrier estuaries, intermittent estuaries and freshwater-dominated estuaries (Roy et al. 2001). These can be further sub-divided according to relative maturity: youthful, intermediate, semi-mature and

mature, based on the level of sediment infilling (Roy et al. 2001). Intermittent coastal lagoons and freshwater estuaries are believed to be the most sensitive to land-derived human influences, primarily as a result of their limited tidal flushing, small volume and variable water levels (Boyd et al. 1992; Haines et al. 2006). The gentle sloping shores and associated wide photic zones of Barrier estuaries are thought to result in increased seagrass abundance in these estuaries relative to the steep-sided drowned river valleys that have stronger currents and higher turbidity (Roy et al. 2001). However, one test of this hypothesis found no difference between these two estuary types when comparing total area of all seagrasses across NSW estuaries (Saintilan 2004). It has also been proposed that seagrass area reduces as estuaries mature and that this is due to reduced water area. increased turbidity and reduction of overall depth (Roy et al. 2001), and indeed, there was some support for this prediction for barrier estuaries (Saintilan 2004).

Effective management of seagrasses requires a good understanding of species' distributions and changes over time (Leriche et al. 2004). There are numerous species of seagrasses in NSW with the dominant ones being Posidonia australis Hook.f., Zostera muelleri subsp. capricorni (Ascherson) S. W. L. Jacobs and multiple species of Halophila (Wilson 2011). There are also several species of Ruppia, and two species of Halodule (H. tridentata, H. uninervis), the latter being known from just a few locations. All seagrasses in NSW are protected under the NSW Fisheries Management Act (1994), but P. australis is also listed as endangered in six NSW estuaries-Lake Macquarie, Brisbane Water, Pittwater, Sydney Harbour, Botany Bay and Port Hacking (Fig. 1). P. australis is also classified as a threatened ecological community under national legislation in the aforementioned six estuaries, in addition to Wallis Lake, Port Stephens and the Hawkesbury River (Fig. 1).

Various methods have been developed to map and monitor the distribution and extent of seagrass. The earliest methods relied on field-based surveys and transect to produce maps (e.g. King 1986; Wood 1959). Increasingly, remote sensing has been used to a provide cost-effective and systematic methodology for mapping large areas, and numerous imaging systems have been employed including satellite-based platforms (e.g. Landsat, Quickbird) and airborne multispectral and hyperspectral devices (Phinn et al. 2008; Roelfsema et al. 2013; Valle et al. 2015). However, aerial photography has been most widely used to capture seagrass extent, change over time, and physical impacts in estuaries that are not excessively turbid (Glasby and West 2018; Kendrick et al. 2000; Walker et al. 1989; Williams and Meehan 2004). Aerial photography has the advantage of providing greater control over image resolution, time of acquisition and optimal capture conditions including sun angle, wind, water clarity and tides (Dobson et al. 1995).





Air photo-based mapping has been the primary methodology applied in NSW with several mapping programs being completed during the last 40 years. The first of these was completed in the 1980s and relied on the visual interpretation of non-georeferenced large format aerial images to map 133 estuaries. From 2000 to 2009, 143 estuaries were surveyed using Geographic Information Systems (GIS) and ortho-rectified large format imagery including more recent imagery sourced through advanced digital airborne systems. Most recently (2012–present), there has been a shift in the mapping techniques, from visual interpretation to Object-Based Image Analysis (OBIA). This method utilises highresolution digital aerial imagery and multi-scale image segmentation to extract features based on colour and texture (Lathrop et al. 2006). The net result has been significant advancements in mapping technologies and techniques over time which has led to improvements in mapping scale and accuracy.

In this study, we combine 40 years of data to examine temporal trends of the main seagrass genera among estuaries in NSW and investigate the potential drivers of change. These data are however derived using a variety of mapping methods and at different scales, which can cause issues with interpreting temporal patterns (Leriche et al. 2004; Meehan et al. 2005). As such, a first step of this study was to generate digitised versions of the earliest maps so that the same GIS method could be used for area estimates for each time of mapping thereby minimised differences in methodology. The remaining differences in scale and resolution of mapping among times mean that comparisons herein have been made with caution. We tested the following three hypotheses:

- 1. The proportions of seagrass genera (*Posidonia*, *Zostera*, *Halophila*, *Ruppia*) are related to estuary type and estuary maturity.
- 2. Temporal change and variability of seagrass extent differs among genera and estuary type.
- 3. Long-term seagrass temporal variability is related to abiotic estuarine variables (e.g. water area, depth) and catchment variables, including types of land use and human population.

Methods

Seagrass Mapping

Seagrass mapping was divided into four time periods. The first comprehensive mapping of 133 NSW estuaries (hereafter Time 1) was carried out approximately between 1980 and 1984 by West et al. (1985). Although the maps indicated different seagrass genera, there were no reported areas for individual genera, only total combined seagrass. Data were captured utilising a method known as the camera lucida technique at a fixed scale of 1:25,000, with areas of mapped polygons calculated using a dot grid method. The original field notes indicate that most of the mapping was field-validated and that the final maps were edited to reflect a combination of the original photo interpretation and field information. The camera lucida and dot grid methods have been shown to be far less accurate for estimating seagrass areas than are new GIS techniques (Meehan et al. 2005); hence, the first step of the current study was to digitise the time 1 maps. This involved the imaging of the original maps in sections using a high-resolution DSLR. Each map section was corrected for lens distortion and merged to create a high-resolution mosaic image of the original map. These maps were imported into ArcGIS and georeferenced to NSW topographic 1:25,000 map sheets. Habitat polygons were initially captured using pixel-based classification techniques to extract the habitat polygon boundaries. The derived polygons were then refined using a combination of buffering, smoothing and manual on-screen digitising. This final process corrected any poorly defined or incorrect boundaries, overlaps or gaps and captured any missing features. Digitising and editing were carried out at a scale of 1:5000. Attributes were then validated against the original maps, field notes and dot grid area calculations. The polygons were then validated for topological correctness and attributes updated to be consistent with the more contemporary GIS mapping methodologies.

The second comprehensive mapping of seagrasses (hereafter time 2), which surveyed 143 estuaries, occurred from 1999–2006 and used GIS-based mapping protocols. These methods involved the adoption of a digital GIS approach in which individual seagrass patches were manually digitised at a scale of 1:1500 using the best available ortho-rectified scanned or digital aerial imagery with the smallest feature captured being approximately 4 m². Initial presumptive maps were then field validated using differential GPS, towed underwater video and side-scan sonar. Field updates were applied to improve the initial mapping. The final polygons were classified into sub-classes based on the seagrasses present, with individual polygons representing either a single genus or multiple genera if they were present, an example is shown in Online Resource 1.

A further 52 estuaries were remapped a third time (hereafter time 3), using a combination of the GIS method and, after 2012, a refined mapping technique building on the previous digital mapping methods but shifting from onscreen digitising to Object-Based Image Analysis (OBIA) techniques. This method utilises Trimble eCognitionTM to generate the initial polygon boundaries based on segmenting highresolution ortho-rectified image into smaller image objects based on colour, texture and shape. Seagrass polygons were classified according to the dominant genera present (Table 1) using onscreen manual classification techniques. Another 11 estuaries were remapped a fourth time (time 4) using the refined OBIA method. The initial polygon line work and classification for both times 3 and 4 were validated in the field using the same field techniques as for time 2.

Area estimates for each seagrass genus were calculated by summing individually mapped seagrass polygons in each estuary for each time based on the genus combinations presented in Table 1. For polygons comprised of only one genus, the seagrass area for that genus was calculated as 100% of the mapped area. For polygons with mixed habitats, where two or more genera were present, the area per genus was reported as 100% of the total mapped polygon area. One estuary, Batemans Bay, had areas of seagrass that were not surveyed or mapped in the 1980s but were mapped in subsequent times and considered to have been present in

 Table 1
 Habitat hierarchy and attributes used in the mapping of NSW estuarine macrophytes

Dominant genus	Habitat				
Posidonia	Posidonia				
	Posidonia/Zostera				
	Posidonia/Zostera/Halophila				
	Posidonia/Halophila				
	Posidonia/Halophila/Ruppia				
	Posidonia/Ruppia				
Zostera	Zostera				
	Zostera/Halophila				
	Zostera/Halophila/Ruppia				
	Zostera/Ruppia				
Halophila	Halophila				
	Halophila/Ruppia				
Ruppia	Ruppia				

the 1980s. The area of seagrass used in this analysis for this estuary is only for the areas that were consistent through time. The latest maps of for all estuaries are available on the NSW Fisheries Spatial Data Portal (NSW DPI 2021a) and the entire historic dataset can be viewed on the NSW Estuarine Habitat Dashboard (NSW DPI 2021b).

Abiotic Data

Estuarine catchment statistics including catchment area, estuarine water area and average water depth were sourced from Roper et al. (2011). Catchment land use statistics were sourced from the NSW SEED data portal (NSW DPIE 2019). Land use is classified into 5 main classes: class 1, conservation and natural environments; class 2, production from relatively natural environments; class 3, production from dryland agriculture and plantations; class 4, production from irrigated agriculture and plantations; and class 5, intensive uses. In this study, classes 1 and 2 are considered natural or near natural vegetation and will be considered undisturbed, and classes 3, 4 and 5 include land use types ranging from agriculture through urban, industrial and mining and will be classed as disturbed.

Human population data were sourced from the 2016 Australian Census at the finest resolution for the state (Australian Bureau of Statistics 2016 Census). Non-populated regions consisting of State Forest, National Parks or reserves were removed from the estuarine catchment areas. Total resident population was then calculated for the remaining populated portion of the catchments, and data were also standardised by dividing total catchment area. The population in NSW since time 1 grew linearly from 5.5 to 7.7 million in 2016 (ABS 2016).

Analyses

Because the mapping used in this analysis was not replicated within years or standardised at particular times of year (e.g. seasons), any short-term variability in the extent of transient seagrass meadows could confound the interpretation of longer term patterns (see "Discussion" section). For this reason, analyses for transient species focussed on temporal changes among estuary types or with estuary maturity. Temporal changes for individual estuaries were examined only for the more persistent *Posidonia* meadows, which also have a higher conservation status.

Long-term annual rates of change (% increase or decrease) were calculated for each estuary and for each seagrass genus by dividing the difference between time 1 and the latest mapped time by the number of intervening years (~40 years depending on the estuary). For estuaries that had been mapped more than two times, we also calculated more recent rates of change over the last ~18 years by comparing the latest mapped time (time 3 or 4 depending on the estuary) with the previous mapped time.

Statistical analyses comparing seagrass genera over time and comparing estuary types were performed using PRIMER 7 + PERMANOVA. Comparisons of seagrass areas among different types and ages (maturity) of estuaries were done using a two factor ANOSIM with a Bray Curtis similarity matrix of seagrass area data (double square root transformed to highlight differences in proportions among estuaries). Separate analyses were done for each time of mapping and for each seagrass genus to ensure data were independent. SIMPER was used to investigate which seagrass genera were responsible for significant differences among estuaries. Temporal variability of seagrass extent across all times of mapping was estimated as coefficient of variation (CV) and compared using a three factor PERMANOVA with the factors seagrass genus (fixed), estuary type (fixed) and estuary maturity (fixed). Estuaries were used as replicates. The same PERMANOVA design was used to test for differences in the rates of (a) increase or (b) decrease in seagrass per year. This was done for two separate time periods, namely the long-term (40 years) period from time 1 to the latest mapped time and the most recent ~ 18-year period by comparing the latest two mapped times for estuaries mapped more than two times and was also compared formally between the two time periods for each seagrass genus. Finally, relationships between seagrass temporal variability (CV) and normalised abiotic estuarine variables (e.g. water area, depth) and catchment variables were examined using the RELATE routine to test for Spearman rank correlations between biotic and abiotic data matrices.

Results

Digital Conversion of Historic Data

Of the 133 estuaries surveyed in time 1, 110 contained mapped seagrass. The total area of seagrass across NSW for time 1 was estimated to be 178 km² using the new digital version, which is some 25.5 km² greater than the original values calculated with the dot grid method (West et al. 1985). The new GIS-derived seagrass areas were greater than the original dot grid estimates in 95 estuaries (or 86%), a comparison of the maps and area calculations is presented in Online Resource 2. When averaged across all estuaries, the original dot grid method underestimated the actual mapped polygon area by 14%, with underestimates in some estuaries being considerably greater than this, especially Little Lake (84%), Moonee Creek (83%), Boambee Creek (83%) and Merrica River (100%); the latter value due to the polygons originally mapped being too small for the dot grid method to capture. In 15 estuaries, the dot grid method overestimated the area of seagrass, with the greatest overestimate in Kioloa Lagoon (155%), followed by Arrawarra Creek (45%) and Spring Creek (35%). A comparison of the overestimated polygon versus underestimated polygon areas across all estuaries showed that the underestimated polygons were slightly larger than the overestimated polygons $(0.081 \text{ km}^2 \text{ compared to } 0.052 \text{ km}^2)$; however, there was no significant difference between these values ($F_{1,7069} = 2.88$, P > 0.05).

Seagrass Changes in NSW

Seagrass was found in 121 of the 143 estuaries surveyed for all combined times (Table 2). *Posidonia* occurred in 17 estuaries spanning three estuary types: ocean embayments, drowned river valleys and barrier estuaries. *Zostera* is the most widespread seagrass, occurring in 105 estuaries with representation in all five estuary types. *Halophila* occurs in 54 estuaries and in all types, except for 'freshwater' estuaries (primarily brackish barrier lakes), while *Ruppia* occurs in 46 estuaries but is not present in any of the ocean embayments (Table 2). Seagrass was not found in 22 estuaries, 18 of which were classified as intermittent estuaries, one freshwater estuary (Saltwater Creek), one ocean embayment (the highly industrialised Port Kembla), one drowned river valley (the heavily disturbed Cooks River, a tributary of Botany Bay) and one barrier estuary (Jerusalem Creek, the entrance of which is known to close intermittently).

Averaged across all NSW estuaries, two genera declined in area over the entire 40-year period with the greatest decline in area (41.2 km²) attributed to *Ruppia*, a highly opportunistic genus. The total area of the more persistent *Posidonia* declined by 0.003 km^2 (30 ha) across the state. Both Zostera and Halophila showed an increase of 2.59 km² and 5.4 km², respectively, over the same time period. Over the last 40 years, the maximum rate of decline was 1.85% year⁻¹ for *Ruppia*, with a negligible annual rate of decline for Posidonia (0.0003% year⁻¹). On average, Zostera had an annual rate of increase of 0.05% year⁻¹ with Halophila showing the greatest overall increase of 0.69% year⁻¹ over the last 40 years. As discussed below, these long-term patterns of change for transient species may not be particularly meaningful due to considerable interannual variability in extent.

While there was an overall decline in extent of *Posidonia* across the state over the last 40 years, it is more meaningful to examine estuary-scale patterns, with overall increases in six estuaries and decreases in 10 with one estuary, Bermagui River, showing a continuous decline (Table 3). Of the estuaries with 4 times of mapping, three of the most urbanised (Lake Macquarie, Pittwater and Botany Bay) had declines in *Posidonia* for three time periods (Table 3). Two estuaries (Port Stephens and Port Hacking) showed an increasing trend for *Posidonia* area for all time periods. In another five estuaries, the long-term decline in *Posidonia*

 Table 2
 Seagrass presence in NSW estuaries for all estuary types and levels of estuarine maturity for all times combined, with seagrass presence representing the presence of any of the four dominant genera

Estuary type	Number of estuaries with seagrass present					Seagrass genus			
	Bay ¹	Youthful	Intermediate	Semi-mature	Mature	Posidonia	Zostera	Halophila	Ruppia
Ocean embayment	4					4	4	3	
Drowned River Valley		3	2	3		5	8	6	1
Barrier Estuary		7	9	7	26	8	48	28	11
Intermittent		4	15	27	12		43	17	33
Freshwater ²		1		1			2		1
Total	4	15	26	38	38	17	105	54	46

¹Bays are not described in Roy et al. (2001) as having a level of maturity

²Defined as brackish barrier lakes or back swamps (Roy et al. 2001)

Table 3 Rates of change (per year) for Posidonia for each estuary for each mapped time period. Declines are highlighted in bold

Estuary	Estuary type	Years mapped for each time			ne	Annual rate of change (%)				
		T1	T2	T3	T4	Overall rate	T1—T2 rate	T2—T3 rate	T3—T4 rate	
Wallis Lake ²	BE	1985	2002	2017		-0.7%	-2.2%	2.9%	NA	
Port Stephens ²	DRV	1985	2004	2017		2.2%	1.2%	3.2%	NA	
Lake Macquarie ^{1,2}	BE	1985	2001	2009	2012	-0.6%	-1.3%	1.5%	-0.3%	
Brisbane Water ^{1,2}	BE	1985	2000	2005	2020	-0.9%	-2.9%	2.1%	2.5%	
Hawkesbury River ²	DRV			2005		NA	NA	NA	NA	
Pittwater ^{1,2}	DRV	1985	2000	2005	2019	-0.2%	-0.5%	-0.4%	0.3%	
Port Jackson ^{1,2}	DRV	1985	2003	2018		-0.4%	0.3%	-1.2%	NA	
Botany Bay ^{1,2}	OE	1985	1999	2008	2019	-0.5%	-0.1%	1.7%	-2.5%	
Port Hacking ^{1,2}	DRV	1985	2002	2008		1.6%	0.1%	7.3%	NA	
Jervis Bay	OE	1985	2004	2020		-0.3%	-1.2%	1.4%	NA	
St Georges Basin	BE	1985	2004			4.7%	4.7%	NA	NA	
Batemans Bay	OE	1985	2005	2012		19.5%	39.6%	-4.8%	NA	
Wagonga Inlet	BE	1985	2002	2019		-0.7%	-2.4%	3.5%	NA	
Bermagui River	BE	1985	2002	2020		-0.8%	-0.6%	-1.2%	NA	
Merimbula Lake	BE	1985	2004			0.8%	0.8%	NA	NA	
Pambula Lake	BE	1985	2004			9.3%	9.3%	NA	NA	
Twofold Bay	OE	1985	2004			-3.4%	-3.4%	NA	NA	

T1, T2, T3 and T4 are the time periods that estuaries were mapped

Overall change is calculated by comparing the earliest and latest times of mapping

NA = comparison not available as only one time of mapping, or no mapping for a particular time period

BE barrier estuary, DRV drowned river valley, OE ocean embayment

¹Posidonia listed as an endangered population

²Posidonia listed as a threatened ecological community

area was reversed for the latest mapped period (Table 3). Batemans Bay (the estuary with the least *Posidonia* at time 1) shows the greatest apparent long-term trend of increase in *Posidonia*, but this was reversed to a decline for the latest mapping period. Twofold Bay (the estuary with the smallest amount of *Posidonia* averaged over all times) showed the greatest overall rate of loss of 3.4% year⁻¹. One estuary, the Hawkesbury River, has only had the areal extent of *Posidonia* was first noted in the Hawkesbury in 1999 (Williams and Watford 1999), the relatively small extent was not mapped until 2005.

Associations Among Seagrass Areas, Estuary Type and Maturity

Multivariate comparisons of areas of seagrass meadows (dominated by *Posidonia*, *Zostera*, *Halophila* or *Ruppia*) were similar for times 1 and 2 and the latest mapped time. Areas of the four seagrass genera differed significantly among estuary types for time 1 (ANOSIM: R = 0.161, P < 0.005), time 2 (R = 0.163, P < 0.005) and the latest time of mapping (R = 0.193, P < 0.005). Pairwise comparisons

and SIMPER analyses demonstrated that this difference was due primarily to barrier estuaries being significantly different from other estuary types as they contained large proportions of all genera (Fig. 2). *Posidonia* was absent from intermittent and freshwater estuaries, while *Ruppia* represented a large proportion of seagrasses in these two estuary types (Fig. 2).



Fig. 2 Average seagrass area (km²) represented as forth root transformed data of the latest mapped extent for all four dominant seagrass genera; Posidonia, Zostera, Halophila and Ruppia, for each type of estuary

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Fig. 3 Average area (km²) represented as forth root transformed data of the latest extent of seagrass for the four dominant genera: Posidonia, Zostera, Halophila and Ruppia, for estuarine geomorphic age

Areas of the four seagrass genera differed significantly according to estuary maturity at time 1 (R = 0.147, P < 0.005), time 2 (R = 0.099, P < 0.01) and the latest time of mapping (R = 0.113, P < 0.005). Pairwise comparisons showed that this difference was due to the relative seagrass areas in the most mature estuaries being significantly less than in the three other estuary age classes (Fig. 3). The most obvious driver of this pattern was the absence of Posidonia in the most mature estuaries, but areas of the other three genera were also significantly less in mature estuaries compared to the other age classes (Fig. 3). Notably, the most mature estuaries consisted only of intermittent estuaries (none of which contained *Posidonia*) and barrier estuaries (many of which did contain *Posidonia*). Thus, the result of interest here is that Posidonia did not occur in mature barrier estuaries, despite barrier estuaries having the most extensive overall seagrass coverage. There were no significant correlations between abiotic variables (estuary volume, area, perimeter, depth, or catchment disturbance measures) and the latest mapped areas of seagrass when considering all genera ($\rho = 0.001$, P = 0.48), or only the more transient Zos*tera*, *Halophila* and *Ruppia* ($\rho = -0.052$, P = 0.83).

Temporal Trends

Temporal variability (measured as %CV) of mapped seagrass areas differed significantly among genera (pseudo $F_{3,203} = 6.65$, P = 0.002), with the most persistent genus (*Posidonia*) being the least variable and *Zostera* showing less temporal variability than *Ruppia* and *Halophila* (Fig. 4). Patterns of temporal variability among seagrass genera were generally similar in most estuary types. In ocean embayments, however, temporal variability was similar for all genera, while in intermittent and freshwater estuaries, variability of *Zostera* over time was as great as that of *Ruppia* (Fig. 5).



Fig. 4 Variation in area $(\pm SE)$ for each genus averaged across all estuary types and times. The number of estuaries used to estimate variability for each genus shown in parentheses

Variability in *Posidonia* area over time did not differ significantly among the three estuary types in which it was found (pseudo $F_{2, 13} = 1,84$, P = 0.199), although there was a trend for *Posidonia* variability to be less in drowned river valleys than ocean embayments or barrier estuaries (Fig. 5). *Zostera* variability differed among estuary types (pseudo $F_{4,99} = 3.87$, P = 0.004), being significantly less in barrier estuaries than in intermittent estuaries (Fig. 5). Variability in areas of *Halophila* and *Ruppia* did not differ among the four estuary types in which these genera were found (Fig. 5, P > 0.50 for both).

Estuary maturity was somewhat related to temporal variability of seagrasses, but patterns depended on seagrass genus and estuary type (pseudo $F_{8, 176}=2.15$, P=0.035). Temporal variability of *Posidonia* and *Zostera* did not differ with estuary maturity in barrier estuaries or drowned river valleys. For Intermittent estuaries, *Zostera* temporal variability was greater in mature and semi-mature estuaries than in intermediate or youthful estuaries (although there were only two of the latter). For barrier river type estuaries, the variability of *Halophila* was significantly less in estuaries of an intermediate maturity than in youthful, semi-mature or mature estuaries. There were no other interpretable patterns related to estuary maturity.

Long-term rates of decline of seagrass (over ~40 years) differed significantly among seagrass genera (pseudo $F_{3,101} = 4.96$, P = 0.002) and estuary type (pseudo $F_{4,101} = 34.95$, P = 0.003), with no significant interaction between these two factors (pseudo $F_{6, 101} = 0.76$, P = 0.605). Annual rates of loss for *Ruppia* and *Halophila* were greater than for *Zostera* and *Posidonia* (P = Z < H = R; Fig. 6). Pairwise tests did not unequivocally identify how the rates differed among estuary types, but it was clear that the overall rate of loss was greatest in intermittent estuaries and considerably less in ocean embayments and freshwater estuaries (Fig. 6). Recent rates of decline of seagrass (over the last ~18 years) showed the same significant patterns among genera **Fig. 5** Variation in area (\pm SE) for the dominant seagrass genera for each geomorphic estuary type across all times of mapping. OE, ocean embayment; DRV, drowned river valley; BE, barrier estuary; Int, intermittent; and FW, freshwater. Number of estuaries used to estimate variability for each estuary type for each genus shown in parentheses



(pseudo $F_{3,50} = 6.48$, P = 0.001) and estuary types (pseudo $F_{4,50} = 4.35$, P = 0.005) as the long-term rates (Fig. 6).

Notably, mean annual rates of decline in seagrass extent were significantly greater over the more recent time period than over the long-term period (genus × time period: pseudo $F_{3, 156} = 6.12$, P = 0.001) for the more transient *Zostera*, *Ruppia* and *Halophila* but not for *Posidonia* (despite a similar trend for the latter; Fig. 6).

Rates of increase of seagrass were extremely variable among estuaries and genera, with increases well over 100% for *Zostera*, *Halophila* and *Ruppia* in some estuaries for each of the long-term and recent time periods. No significant differences in rates of increase were detected among estuary types or genera for either the long-term or most recent time period.

Associations Between Seagrass Change and Abiotic Variables

Given the significant differences in temporal variability among seagrass genera described above, associations between abiotic variables and temporal variability were analysed separately for each genus. There were, however, no significant multivariate associations between estuarine characteristics or catchment disturbance variables and seagrass variability for *Posidonia* ($\rho = -0.058$, P = 0.65), *Zostera* ($\rho = 0.037$, P = 0.12), *Halophila* ($\rho = 0.051$, P = 0.22) or *Ruppia* ($\rho = 0.027$, P = 0.34). Although associations were not significant when considering all abiotic variables in a multivariate analysis, there was one notable significant univariate correlation between *Zostera* variability and average estuary depth (r = -0.24, P < 0.01). That is, variability in *Zostera* area decreased with increasing estuary depth (Fig. 7).

There were no apparent relationships between annual rates of change in seagrass extent for either *Posidonia* or *Zostera* relative to catchment-related variables (catchment size, estuary area, perimeter), human population or catchment disturbance. These relationships were non-significant for either the long-term rates (*Posidonia* $\rho = -0.33$, P=0.982; *Zostera* $\rho = -0.088$, P=0.912) or more recent rates of change (*Posidonia* $\rho = -0.23$, P=0.853; *Zostera* $\rho = 0.06$, P=0.225).

-35% (4) -30% Annual rate of decline -25% -20% (11) (1) -15% (3) (6) -10% (4)(3) Not present (19) - (9) present Not present Not present Not present (4) (7) (18) (8) (1)-5% (28)(2) (23) (3) (3) (3) (1)(5) (1) þ 0% R Ρ Н Ρ Ζ Н R P Ζ Н R Ρ Ζ Н R Ζ н R Drowned River Valley Ocean embayment Barrier Estuary Intermittent Freshwater □ Overal annual rate of decline Latest annual rate of decline

Fig. 6 Long-term (~40 years) and recent (~last 18 years) annual rates of decline for all four seagrass genera for each estuary type. P, Posidonia; Z, Zostera; H, Halophila; R, Ruppia. Number of estuaries used to estimate rate of decline for each genus shown in parentheses



Fig. 7 Relationship between the temporal variability in Zostera area and average estuary depth for the five estuary types; ocean embayment (triangle), drowned river valley (square), barrier estuary (circle), intermittent (X) and freshwater (cross)

Discussion

The findings of this study lead to a better understanding of the trends of seagrass in NSW in numerous ways. First, digital estimates for seagrass areas have been obtained for the original maps of all NSW estuaries, which are directly comparable to more recent area estimates. Although there has been an overall decline in the amount of seagrass in NSW since the 1980s, most of this is attributed to the transient genus Ruppia. There were, however, some notable losses of Posidonia and Zostera in particular estuaries. Second, the composition of seagrasses differs among estuary types and with the maturity of barrier estuaries and was unrelated to estuarine characteristics including volume, area, perimeter or depth. Posidonia is most abundant in ocean embayments and not present in intermittent estuaries or mature barrier estuaries. Zostera dominates barrier and freshwater estuaries, while intermittent estuaries are characterised by more ephemeral Ruppia and Halophila. Third, Posidonia is the least temporally variable genus, followed by Zostera, Halophila and Ruppia. The variability of Zostera, in particular, is related to the type of estuary in which it occurs. The temporal variability of seagrasses differs among estuary types, and for Zostera, this variability is related to depth and is greatest in the shallow intermittent and freshwater estuaries. Fourth, there was no relationship found between total seagrass change and temporal variability at the estuary scale and catchment disturbances measured as land use or population density.

Digital Conversion of the Historic Data

The newly derived digital area of the original West et al. (1985) seagrass maps for all NSW estuaries was 178 km², which is 25 km² greater than the originally reported value. This discrepancy arose primarily due to the dot grid method

used to calculate the original area being unable to accurately estimate the area of the smallest polygons, which were the majority of those mapped. In isolation, this result suggests that previous reporting of changes in seagrass area in NSW that relied on these original reported areas will have underestimated any changes in seagrass areas. Importantly, however, there is another source of error in the original mapped estimates related to the method of drawing habitat boundaries (i.e. generating polygons) using the camera lucida technique (Meehan et al. 2005). Specifically, these hand-drawn polygons generally overestimate the actual habitat extent when compared to digitally created habitat boundaries derived from the same original aerial photos (Meehan et al. 2005). This overestimate of boundaries is not surprising given the limitations of technology at the time; the original fixed mapped scale 1:25 000 was coarser than now, meaning it was far more difficult to capture small or fragmented habitats often leading to the area for these features being over represented (West et al. 1989).

Improving the accuracy of the originally mapped features would make change estimates more accurate (Cuttriss et al. 2013; Leriche et al. 2004), but this is unlikely to ever be done at a state-wide scale given the enormity of the task. This means that it will be difficult to accurately estimate the true changes in seagrass area that may have occurred since time 1 (1985). For this reason, we suggest using only the more recent data (e.g. over the last ~18 years) as these will provide the most accurate estimates of actual change in seagrass area, and indeed, it is these changes that would be the most practical to respond to from a managerial perspective. If changes since 1985 do need to be interpreted, our new digital area estimates for time 1 should result in relatively conservative conclusions regarding impacts to seagrass extent (i.e. resulting in a type II error when testing hypotheses about anthropogenic impacts). Specifically, real decreases should be accurately identified as such, slight increases might be mistakenly interpreted as showing stable patterns and true stability is likely to be incorrectly interpreted as a decline in seagrass area. Therefore, we may conclude there was a loss of seagrass when there was in fact none, which is consistent with the precautionary principle (Kriebel et al. 2001).

Seagrass Temporal Variability in Different Estuary Types

Based on latest estimates, the overall seagrass area has declined by 14% across NSW since the mapping in the 1980s, which equates to a decline of 0.4% year⁻¹ over 40 years since 1980. This rate is substantially less than the global rate of seagrass decline, estimated as 5% year⁻¹ since 1980, or 7% year⁻¹ since the 1990s (Waycott et al. 2009). Importantly, however, the decline described here was

attributed primarily to the transient genus Ruppia, which tends to dominate intermittent and freshwater estuaries, and which is the most temporally variable genus in NSW. Species in this genus have short life spans with high turnovers (Fonseca et al. 2008; Mannino et al. 2015) and as such are well suited to living in estuaries that can have extremely variable environmental conditions (Robinson et al. 1982, Pollard et al. 1994). Apparent long-term changes in areas of this genus, particularly in intermittent and freshwater estuaries, are likely a reflection of natural shorter-term fluctuations in abundance, which this study did not estimate. The major drivers contributing to the distribution and abundance of Ruppia are salinity (the genus is tolerant of a wide range of salinities), temperature and light (Brock 1982; Yaakub et al. 2014; Ferguson et al. 2018). For those estuaries that showed declines in seagrass, rates of decline over the last ~ 18 years were greater than over the last 40 years. But importantly, this occurred only for Zostera, Ruppia and Halophila and only in intermittent and barrier estuaries. The result for intermittent estuaries likely reflects the natural variability of these genera in these estuary types, which again highlights the importance of reporting changes in seagrass by genus and, where appropriate, estuary type, which is effectively a surrogate for environmental conditions (Fergusson et al. 2018; Scanes et al. 2020). The increased rate of decline of Zostera in barrier estuaries over the last 18 years relative to the last 40 years warrants further investigation.

Our results support the predictions of Roy et al. (2001) regarding seagrasses in different estuary types and, to some extent, declining seagrass area in relation to increasing estuary maturity. Specifically, barrier estuaries contained the largest amounts of seagrass, and this was consistent for all genera. Although our results showed a general trend for the total amount of seagrass to decline from youthful to mature estuaries, it was only the most mature estuaries that were significantly different from the other age classes. The areas of each seagrass genus were least in the most mature estuaries, but the most notable result was the absence of Posido*nia* in mature estuaries. Given that only barrier estuaries and intermittent estuaries have been classified as mature, and Posidonia does not occur in Intermittent estuaries (of any maturity), then the relationship between estuary age and Posidonia area was specifically due to Posidonia being absent from mature barrier estuaries (discussed below). This latter result highlights the importance of interpreting patterns per genus rather than generalising across all seagrasses.

Notably, we also found that in intermittent and freshwater estuaries, the temporal variability of *Zostera* was similar to that of *Halophila* and *Ruppia*, whereas *Zostera* variability was considerably less in estuaries that have greater oceanic influence. As a result of their geography and geomorphology, intermittent and freshwater estuaries have highly variable salinity, water clarity and temperature ranges (Haines et al. 2006; Roper et al. 2011; Roy et al. 2001) and high levels of dissolved inorganic nitrogen and ammonia (Fergusson et al. 2018). The fact that Zostera is found in all types of estuaries reflects its relatively high tolerance to a wide variety of environmental conditions (Collier et al. 2014; Maxwell et al. 2014). However, Zostera can show significant seasonal and temporal variability particularly in its extent and biomass (Kerr and Strother 1990; McKenzie 1994) and can rapidly recover after disturbances related to changes in water quality (Plus et al. 2003), provided that propagules are available (Scanes et al. 2020). We suggest that the pattern we identified for the temporal variability of Zostera to increase with decreasing average estuary depth is due to the influence of freshwater inputs and levels of turbidity in shallow estuaries being greater than in deeper estuaries. Increasing water depth is typically related to reduced physical harshness (Duarte et al. 2006), and increased turbidity is known to reduce seagrass abundance (Short and Wyllie-Echeverria 1996). The tolerance of Zostera to low salinities is complex, apparently related to the frequency of exposure to lower salinity and possibly the rate at which salinity is reduced. If salinity is reduced gradually over 4 days, Zostera muelleri can tolerate 3 ppt for many weeks (Collier et al. 2014). However, repeated short-term (3-4 days) exposure to < 8 ppt (with periods of normal salinity in between) can kill the same species (Glasby unpubl. data). Effects of reduced salinities can also take > 1 month to manifest (Glasby unpubl. data), further complicating attempts to relate salinity reductions in estuaries with short-term reductions in seagrass. Importantly, freshwater inputs may affect a range of factors other than salinity, particularly levels of dissolved organic nitrogen which may also affect seagrass abundance (Fergusson et al. 2018).

These results point to the importance of catchment inputs versus oceanic influences on the variability of these seagrasses. The consequence of these large fluctuations in seagrass areas (up to 100%) in intermittent and freshwater estuaries is that tests for anthropogenic impacts on the areal extent of seagrasses will require intensive temporal sampling (Underwood 1991), ideally correlated with water quality measurements. Specifically, long-term patterns within specific estuaries need to be interpreted relative to shorter-term fluctuations; otherwise, erroneous conclusions could be drawn about the temporal patterns (Underwood 1991, 1994; O'Brien et al. 2018). Indeed, changes in the area of Halophila and Ruppia will be equally difficult to interpret in estuaries of other types without considerably more temporal replication than used here. Consistent declines in seagrass area over multiple years in particular estuaries may however indicate ongoing impacts. The small natural temporal variability of Posidonia area in all estuary types in NSW means we can have confidence that these rates of change are not confounded with shorter-term fluctuations in area.

As reported by others, Posidonia occurs in three of the five estuary types, namely ocean embayments, drowned river valleys and barrier estuaries, but not in other estuary types where water quality is affected greatly by catchment inputs (Roy et al. 2001; West 2010). Posidonia was the least temporally variable genus in NSW, which is expected for a "persistent" seagrass compared to the more opportunistic genera (Guidetti et al. 2002; Kilminster et al. 2015). Although the temporal variability of *Posidonia* did not differ significantly among estuary types, there was a trend for variability to be least in drowned river valleys, i.e. the estuary type with the most consistent salinity and temperature regime and greatest tidal flushing (Yassini & Jones, 1995; Roy et al. 2001). The composition of seagrasses was also found to differ significantly in the most mature estuaries when compared to less mature estuaries, and this was mainly due to the lack of Posidonia in the former. Mature barrier estuaries differ in their degree of infilling and can have a pronounced salinity gradient from the entrance to their upper reach (Roy et al. 2001). Thus, the effects of reduced salinity and/or increased turbidity in much of the estuary, together with the comparatively small area of marine tidal delta near the entrance, likely limit the potential for Posidonia to survive in mature barrier estuaries.

Losses of Posidonia in the early to mid-twentieth century were one of the major reasons for listing the seagrass as endangered in NSW. It has been estimated that between 1942 and 1984, 58% of the Posidonia was lost from Botany Bay in Sydney (Larkum and West 1990). In a recent study, Evans et al. (2018) used similar methods to those herein to identify changes in seagrass meadows dominated by Posidonia at specific sites in five Sydney estuaries and reported declines at most sites, ranging from of 2-40%. This led to the conclusion that in Port Jackson (Sydney Harbour), Posidonia declined at an average rate of 10% year⁻¹ between 2009 and 2014 (Evans et al. 2018). Our results indicate a much slower rate of Posidonia decline across the entire Port Jackson estuary $(1.2\% \text{ year}^{-1} \text{ from } 2003-2018)$. There is no doubt that Posidonia is being lost at high rates from some sites due to specific disturbances (e.g. boat moorings; Glasby and West 2018); however, the present study highlights that these patterns may not be representative of the entire estuary. Future studies should identify where these hotspots of decline are occurring in order to direct management actions.

In six of 17 estuaries, mapped *Posidonia* area increased over ~40 years since the 1980s, and in seven estuaries, *Posidonia* extent increased over the most recent time period (the last ~ 18 years). Estuary-scale declines in *Posidonia* extent since the 1980s were documented in ten estuaries, with six estuaries showing declines over the most recent time period and one estuary showing continuous decline over all time periods (Table 3). Although across all estuaries there was no significant increase in the rate of decline of *Posidonia* over the last 18 years compared to the last 40 years, there were clear trends for this in all estuary types (Fig. 6). In the two most heavily urbanised estuaries (Port Jackson and Botany Bay), the rate of decline of Posidonia was greatest in the most recent time period. The patterns of recent decline for Posidonia in Lake Macquarie, Port Jackson and Botany Bay match the average temporal trends described from smaller scale sampling by Evans et al. (2018), despite very different estimates of rates of decline. Interestingly, Port Stephens and Port Hacking show increasing rates of gain of Posidonia since 2004 and 2002, respectively, but Port Hacking has not been mapped since 2008. The global rate of seagrass decline since the 1990s has been estimated as 7% year⁻¹ (Waycott et al. 2009). Over a similar time period, the greatest rate of decline of *P. australis* in NSW was 4.8% year⁻¹ for P. australis in Batemans Bay, while in all other estuaries, areas of *P. australis* either declined at rates of < 4% year⁻¹ or increased at rates of 2–7.3% year⁻¹. Batemans Bay shows the greatest overall rate of increase of 39.6% year⁻¹ and Twofold Bay shows the greatest overall decline of *Posidonia* $(3.4\% \text{ year}^{-1})$. Interestingly, these estuaries have the smallest amounts of mapped Posidonia and are possibly most susceptible to historic mapping inaccuracies which may constitute a larger proportion of the total mapped area. Regardless, both estuaries warrant further investigation with the latest mapping techniques to test whether declines in Posidonia have been continuing over recent years. Bermagui River was the only estuary to show a continuous decline in Posidonia for all mapped times. The overall rate of decline for this estuary is relatively small $(0.8\% \text{ year}^{-1})$, but there is an increasing trend in the rate of decline from 0.6% year⁻¹ between times 1 and 2 to 1.2% year⁻¹ for the latest times (Table 3). While these rates of decline are relatively small, the continuous and potentially increasing rate of decline in this estuary is concerning and warrants further investigation.

Estuary-Scale Anthropogenic Impacts on Seagrasses

Land use classification and level of urbanisation were used as proxies for anthropogenic impacts across 119 of the estuaries compared in this study. The comparison of seagrass genus, estuary type and estuary maturity found no relationship between these variables and seagrass variability or total change in area over time, matching recent results for presence vs absence of seagrasses in NSW estuaries (Scanes et al. in press). Identifying the causes of seagrass degradation is often difficult due to many factors operating at the same time, or because physical variables and seagrass areas are not measured concomitantly (Ralph et al. 2007; Walker and McComb 1992). Furthermore, these pulse disturbances (sensu Bender et al. 1984) may not have immediate effects on seagrasses, and there would more likely be a lag in any effects (O'Brien et al. 2018). So, given the temporal scales of this study, the lack of association between trends in seagrass area and measures of catchment disturbance is perhaps not surprising. Unless catchment inputs are constant and affect the entire estuary homogeneously (or at least affect most of the estuary), then it is perhaps unlikely that we could have detected changes in seagrass areas associated with catchment pressures. Changes in rainfall will affect salinity, nutrient and contaminant inputs, but these will occur over temporal scales much shorter than sampled herein. Moreover, catchment inputs may only affect seagrasses in the upper reaches of estuaries, particularly in tide-dominated estuaries, or disturbances may not lead to declines in areal extent. Declines in seagrass density or condition could not be detected by the current study, meaning that ecologically important impacts could be missed (e.g. Campbell and Miller 2002; Maxwell et al. 2017). These declines in overall health could in turn lead to declines in ecosystem function and productivity which, if left unchecked, can lead to complete loss of seagrass (Connell et al. 2017; Unsworth et al. 2014). As such, the lack of association between anthropogenic disturbances and seagrass areas in this study should not be taken as strong evidence for a lack of human impacts from catchment disturbances. It is likely that this study would have been capable only of detecting estuary-scale impacts from disturbances that operated over long time periods, for example reduction in nutrient inputs over many years due to a drought (Hirst et al. 2016).

Early detection of any human-induced impacts to seagrasses is paramount for adequate management (Kennish 2002). However, the high temporal variability of some seagrass genera, particularly in certain estuary types, makes detection of anthropogenic impacts difficult. The frequency of mapping needs to relate to the temporal scales of the natural variability of the seagrass species (Calleja et al. 2017), which can differ among estuary types. Although there is little doubt that large areas of seagrass have been lost from numerous estuaries throughout the globe, the significant temporal variability in areas for the majority of seagrasses in NSW described here suggests that caution is needed when averaging results among genera and estuary types. These results add further weight to the argument that the management of seagrasses should be species-specific (Kendrick et al. 2008) due to inherent differences in temporal and spatial dynamics and differing abilities to recovery from disturbances (Kilminster et al. 2015).

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References

- Australian Bureau of Statistics. 2016. Census GeoPackages https:// datapacks.censusdata.abs.gov.au/geopackages/ [Verified September 2019].
- Bell, J.D., and D.A. Pollard. 1989. Ecology of fish assemblages and fisheries associated with seagrasses. In Seagrass ecosystems - an Australian Perspective, ed. A.W.D. Larkum, A.J. McComb, and S.A. Shepherd, 565–609. Amsterdam: Elsevier.
- Bell, S.S., M.O. Hall, S. Soffian, and K. Madley. 2002. Assessing the impact of boat propeller scars on fish and shrimp utilizing seagrass beds. *Ecological Applications* 12: 206–217.
- Bender, E.A., T.J. Case, and M.E. Gilpin. 1984. Perturbation experiments in community ecology: Theory and practice. *Ecology* 65: 1–13.
- Boyd, R., R. Dalrymple, and B.A. Zaitlin. 1992. Classification of clastic coastal depositional environments. *Sedimentary Geology* 80: 139–150.
- 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.
- Butler, A., and P. Jernakoff. 1999. *Seagrass in Australia: Strategic review and development of an R & D plan.* Collingwood, Vic: CSIRO.
- Calleja, F., C. Galvan, A. Silio-Calzada, J.A. Juanes, and B. Ondiviela. 2017. Long-term analysis of Zostera noltei: A retrospective approach for understanding seagrasses' dynamics. *Marine Environmental Research* 130: 93–105.
- Collier, C.J., C. Villacorta-Rath, K. van Dijk, M. Takahashi, and M. Waycott. 2014. Seagrass proliferation precedes mortality during hypo-salinity events: a stress-induced morphometric response. *PLOS One* 9: e94014.
- Campbell, S.J., and C.J. Miller. 2002. Shoot and abundance characteristics of the seagrass *Heterozostera tasmanica* in Westernport estuary (south-eastern Australia). *Aquatic Botany* 73: 33–46.
- Clark, G.F., and E.L. Johnston. 2017. Australia state of the environment 2016: coasts, independent report to the Australian Government Minister for Environment and Energy, Australian Government Department of the Environment and Energy, Canberra.
- Congdon, R.A., and A.J. McComb. 1979. Productivity of Ruppia: Seasonal changes and dependence on light in an Australian estuary. *Aquatic Botany* 6: 121–132.
- Connell, S.D., M. Fernandes, O.W. Burnell, Z.A. Doubleday, K.J. Griffin, A.D. Irving, J.Y.S. Leung, S. Owen, B.D. Russell, and L.J. Falkenberg. 2017. Testing for thresholds of ecosystem collapse in seagrass meadows. *Conservation Biology* 31: 1196–1201.
- Costanza, R., R. d'Arge, R. de Groot, S. Farber, M. Grasso, B. Hannon, K. Limburg, S. Naeem, R.V. O'Neill, J. Paruelo, R.G. Raskin, P. Sutton, and M. van den Belt. 1997. The value of the world's ecosystem services and natural capital. *Nature* 387: 253–260.
- Cuttriss, A.K., J.B. Prince, and J.G. Castley. 2013. Seagrass communities in southern Moreton Bay, Australia: Coverage and fragmentation trends between 1987 and 2005. *Aquatic Botany* 108: 41–47.
- Dafforn, K.A., S.L. Simpson, B.P. Kelaher, G.F. Clark, V. Komyakova, C.K.C. Wong, and E.L. Johnston. 2012. The challenge of choosing

environmental indicators of anthropogenic impacts in estuaries. *Environmental Pollution* 163: 207–217.

- de la Torre-Castro, M., and P. Rönnbäck. 2004. Links between humans and seagrasses—an example from tropical East Africa. Ocean & Coastal Management 47: 361–387.
- Dobson, J.E., E.A. Bright, R.L. Ferguson, D.W. Field, L.L. Wood, K.D. Haddad, H. Iredale, J.R. Jensen, V. Klemas, R.J. Orth, and J.P. Thomas. 1995. NOAA Coastal Change Analysis Program (C-CAP): Guidance for regional implementation. NOAA Tech. Rep. NMFS 123: 92.
- Duarte, C.M. 2002. The future of seagrass meadows. *Environmental Conservation* 29: 192–206.
- Duarte, C.M., J.W. Fourqurean, D. Krause-Jensen, and B. Olesen. 2006. Dynamics of seagrass stability and change. In *Seagrasses: Biology, ecology and conservation*, ed. A.W.D. Larkum, R.J. Orth, and C.M. Duarte, 271–294. Dordrecht: Springer.
- Evans, S.M., K.J. Griffin, R.A.J. Blick, A.G.B. Poore, and A. Vergés. 2018. Seagrass on the brink: Decline of threatened seagrass *Posidonia australis* continues following protection. *PLOS One* 13: e0190370.
- Ferguson, A.J.P., P.R. Scanes, J.D. Potts, M.P. Adams, and K.R. O'Brien. 2018. Seagrasses in the south-east Australian region distribution, metabolism, and morphology in response to hydrodynamic, substrate, and water quality stressors. In Seagrasses of Australia: Structure, Ecology and Conservation, ed. A. Larkum, G. Kendrick, and P. Ralph, 419–444. Cham, Switzerland: Springer.
- Fisheries Management Act. 1994. Available at https://legislation.nsw. gov.au/#/view/act/1994/38/historical2016-11-25/full [Accessed 12th Nov 2021].
- Fonseca, M.S., W.J. Kenworthy, E. Griffith, M.O. Hall, M. Finkbeiner, and S.S. Bell. 2008. Factors influencing landscape pattern of the seagrass Halophila decipiens in an oceanic setting. *Estuarine*, *Coastal and Shelf Science* 76: 163–174.
- Fonseca, V.F., R.P. Vasconcelos, R. Gamito, S. Pasquaud, C.I. Gonçalves, J.L. Costa, M.J. Costa, and H.N. Cabral. 2013. Fish communitybased measures of estuarine ecological quality and pressure–impact relationships. *Estuarine, Coastal and Shelf Science* 134: 128–137.
- Foster, N.R., D.G. Fotheringham, D.J. Brock, and M. Waycott. 2017. A resourceful and adaptable method to obtain data on the status of seagrass meadows. *Aquatic Botany* 141: 17–21.
- Glasby, T.M., and G. West. 2018. Dragging the chain: Quantifying continued losses of seagrasses from boat moorings. *Aquatic Con*servation: Marine and Freshwater Ecosystems 28: 383–394.
- Guidetti, P., M. Lorenti, M.C. Buia, and L. Mazzella. 2002. Temporal dynamics and biomass partitioning in three Adriatic seagrass species: *Posidonia oceanica*, *Cymodocea nodosa*, *Zostera marina*. *Marine Ecology* 23: 51–67.
- Haines, P.E., R.B. Tomlinson, and B.G. Thom. 2006. Morphometric assessment of intermittently open/closed coastal lagoons in New South Wales, Australia. *Estuarine, Coastal and Shelf Science* 67: 321–332.
- Hallett, C.S., F. Valesini, and M. Elliott. 2016. A review of Australian approaches for monitoring, assessing and reporting estuarine condition: I. International context and evaluation criteria. *Environmental Science & Policy* 66: 260–269.
- Hastings, K., P. Hesp, and G.A. Kendrick. 1995. Seagrass loss associated with boat moorings at Rottnest Island, Western Australia. Ocean & Coastal Management 26: 225–246.
- Hillman, K., A.J. McComb, and D.I. Walker. 1995. The distribution, biomass and primary production of the seagrass *Halophila ovalis* in the Swan/Canning Estuary, Western Australia. *Aquatic Botany* 51: 1–54.
- Hirst, A.J., A.R. Longmore, D. Ball, P.L.M. Cook, and G.P. Jenkins. 2016. Linking nitrogen sources utilised by seagrass in a temperate marine embayment to patterns of seagrass change during drought. *Marine Ecology Progress Series* 549: 79–88.

- Kendrick, G.A., B.J. Hegge, A. Wyllie, A. Davidson, and D.A. Lord. 2000. Changes in seagrass cover on Success and Parmelia Banks, Western Australia between 1965 and 1995. *Estuarine, Coastal and Shelf Science* 50: 341–353.
- Kendrick, G.A., K.W. Holmes, and K.P. Van Niel. 2008. Multi-scale spatial patterns of three seagrass species with different growth dynamics. *Ecography* 31: 191–200.
- Kennish, M.J. 2002. Environmental threats and environmental future of estuaries. *Environmental Conservation* 29: 78–107.
- Kerr, E.A., and S. Strother. 1990. Seasonal changes in standing crop of Zostera muelleri in south-eastern Australia. *Aquatic Botany* 38: 369–376.
- Kilminster, K., K. McMahon, M. Waycott, G.A. Kendrick, P. Scanes, L. McKenzie, K.R. O'Brien, M. Lyons, A. Ferguson, P. Maxwell, T. Glasby, and J. Udy. 2015. Unravelling complexity in seagrass systems for management: Australia as a microcosm. *Science of the Total Environment* 534: 97–109.
- King, R.J. 1986. Aquatic angiosperms in coastal saline lagoons of New South Wales. I. The Vegetation of Lake Macquarie. *Proceedings* of the Linnean Society of New South Wales 109: 13.
- Kriebel, D., J. Tickner, P. Epstein, J. Lemons, R. Levins, E.L. Loechler, M. Quinn, R. Rudel, T. Schettler, and M. Stoto. 2001. The precautionary principle in environmental science. *Environmental Health Perspectives* 109: 871–876.
- La Manna, G., Y. Donno, G. Sarà, and G. Ceccherelli. 2015. The detrimental consequences for seagrass of ineffective marine park management related to boat anchoring. *Marine Pollution Bulletin* 90: 160–166.
- Larkum, A.W.D., and R.J. West. 1990. Long-term changes of seagrass meadows in Botany Bay, Australia. Aquatic Botany 37: 55–70.
- Lathrop, R.G., P. Montesano, and S. Haag. 2006. A multi-scale segmentation approach to mapping seagrass habitats using airborne digital camera imagery. *Photogrammetric Engineering & Remote Sensing* 72: 665–675.
- Leriche, A., C.-F. Boudouresque, G. Bernard, P. Bonhomme, and J. Denis. 2004. A one-century suite of seagrass bed maps: Can we trust ancient maps? *Estuarine, Coastal and Shelf Science* 59: 353–362.
- Lotze, H.K., H.S. Lenihan, B.J. Bourque, R.H. Bradbury, R.G. Cooke, M.C. Kay, S.M. Kidwell, M.X. Kirby, C.H. Peterson, and J.B.C. Jackson. 2006. Depletion, degradation, and recovery potential of estuaries and coastal seas. *Science* 312: 1806–1809.
- Lyons, M.B., C.M. Roelfsema, and S.R. Phinn. 2013. Towards understanding temporal and spatial dynamics of seagrass landscapes using time-series remote sensing. *Estuarine, Coastal and Shelf Science* 120: 42–53.
- Macreadie, P.I., P.H. York, C.D.H. Sherman, M.J. Keough, D.J. Ross, A.M. Ricart, and T.M. Smith. 2014. No detectable impact of small-scale disturbances on 'blue carbon' within seagrass beds. *Marine Biology* 161: 2939–2944.
- Mannino, A.M., M. Menéndez, B. Obrador, A. Sfriso, and L. Triest. 2015. The genus Ruppia L. (Ruppiaceae) in the Mediterranean region: An overview. *Aquatic Botany* 124: 1–91.
- Marbà, N., and C. Duarte. 1998. Rhizome elongation and seagrass clonal growth. *Marine Ecology Progress Series* 174: 269–280.
- Maxwell, P.S., K.A. Pitt, D.D. Burfeind, A.D. Olds, R.C. Babcock, and R.M. Connolly. 2014. Phenotypic plasticity promotes persistence following severe events: Physiological and morphological responses of seagrass to flooding. *Journal of Ecology* 102: 54–64.
- Maxwell, P.S., J.S. Eklöf, M.M. van Katwijk, K.R. O'Brien, M. de la Torre-Castro, C. Boström, T.J. Bouma, D. Krause-Jensen, R.K.F. Unsworth, B.I. van Tussenbroek, and T. van der Heide. 2017. The fundamental role of ecological feedback mechanisms for the adaptive management of seagrass ecosystems – a review. *Biological Reviews* 92: 1521–2153.

- McKenzie, L.J. 1994. Seasonal changes in biomass and shoot characteristics of a Zostera capricorni Aschers dominant meadow in Cairns Harbour, northern Queensland. Marine and Freshwater Research 45: 1337–1352.
- Meehan, A.J., R.J. Williams, and F.A. Watford. 2005. Detecting trends in seagrass abundance using aerial photograph interpretation: Problems arising with the evolution of mapping methods. *Estu*aries 28: 462–472.
- Milazzo, M., F. Badalamenti, G. Ceccherelli, and R. Chemello. 2004. Boat anchoring on Posidonia oceanica beds in a marine protected area (Italy, western Mediterranean): Effect of anchor types in different anchoring stages. *Journal of Experimental Marine Biology and Ecology* 299: 51–62.
- NSW Department of Planning, Industry and Environment. 2019. NSW Landuse 2017. https://datasets.seed.nsw.gov.au/dataset/nsw-landu se-2017 [Verified September 2019].
- NSW Department of Primary Industries. 2021a. Fisheries Spatial Data Portal, https://webmap.industry.nsw.gov.au/Html5Viewer/index. html?viewer=Fisheries_Data_Portal [Verified July 2021].
- NSW Department of Primary Industries. 2021b. NSW Estuarine Habitat Dashboard, https://nsw-dpi.shinyapps.io/NSW_Estuarine_Habitat/ [Verified July 2021].
- O'Brien, K.R., M. Waycott, P. Maxwell, G.A. Kendrick, J.W. Udy, A.J.P. Ferguson, K. Kilminster, P. Scanes, L.J. McKenzie, K. McMahon, M.P. Adams, J. Samper-Villarreal, C. Collier, M. Lyons, P.J. Mumby, L. Radke, M.J.A. Christianen, and W.C. Dennison. 2018. Seagrass ecosystem trajectory depends on the relative timescales of resistance, recovery and disturbance. *Marine Pollution Bulletin* 134: 166–176.
- Orth, R.J., T.J.B. Carruthers, W.C. Dennison, C.M. Duarte, J.W. Fourqurean, K.L. Heck, A.R. Hughes, G.A. Kendrick, W.J. Kenworthy, S. Olyarnik, F.T. Short, M. Waycott, and S.L. Williams. 2006. A Global Crisis for Seagrass Ecosystems. *Bio-Science* 56: 987–996.
- Phinn, S., C. Roelfsema, A. Dekker, V. Brando, and J. Anstee. 2008. Mapping seagrass species, cover and biomass in shallow waters: An assessment of satellite multi-spectral and airborne hyper-spectral imaging systems in Moreton Bay (Australia). *Remote Sensing of Environment* 112: 3413–3425.
- Plus, M., J.-M. Deslous-Paoli, and F. Dagault. 2003. Seagrass (*Zostera marina* L.) bed recolonisation after anoxia-induced full mortality. *Aquatic Botany* 77: 121–134.
- Pollard, D.A. 1994. A comparison of fish assemblages and fisheries in intermittently open and permanently open coastal lagoons on the south coast of New South Wales, South-Eastern Australia. *Estuaries* 17: 631–646.
- Ralph, P.J., M.J. Durako, S. Enríquez, C.J. Collier, and M.A. Doblin. 2007. Impact of light limitation on seagrasses. *Journal of Experimental Marine Biology and Ecology* 350: 176–193.
- Robinson, K.I.M., P.J. Gibbs, J.B. Barclay, and J.L. May. 1982. Estuarine flora and fauna of Smiths Lake, New South Wales. *Proceedings of the Linnean Society of New South Wales* 107: 19–34.
- Roelfsema, C., E.M. Kovacs, M.I. Saunders, S. Phinn, M. Lyons, and P. Maxwell. 2013. Challenges of remote sensing for quantifying changes in large complex seagrass environments. *Estuarine*, *Coastal and Shelf Science* 133: 161–171.
- Roper, T., B. Creese, P. Scanes, K. Stephens, R. Williams, J. Dela-Cruz, G. Coade, B. Coates, and M. Fraser. 2011. Assessing the condition of estuaries and coastal lake ecosystems in NSW, Monitoring, evaluation and reporting program, Technical report series, Office of Environment and Heritage, Sydney.
- Roy, P.S., R.J. Williams, A.R. Jones, I. Yassini, P.J. Gibbs, B. Coates, R.J. West, P.R. Scanes, J.P. Hudson, and S. Nichol. 2001. Structure and function of south-east Australian estuaries. *Estuarine*, *Coastal and Shelf Science* 53: 351–384.

- Saintilan, N. 2004. Relationships between estuarine geomorphology, wetland extent and fish landings in New South Wales estuaries. *Estuarine, Coastal and Shelf Science* 61: 591–601.
- Scanes P. R., A. Ferguson, and J. Potts. 2020. Catastrophic events and estuarine connectivity influence presence of aquatic macrophytes and trophic status of intermittently-open coastal lagoons in eastern Australia. *Estuarine Coastal and Shelf Science* 238: 106732.
- Short, F.T., and S. Wyllie-Echeverria. 1996. Natural and human-induced disturbance of seagrasses. *Environmental Conservation* 23: 17–27.
- Short, F.T., B. Polidoro, S.R. Livingstone, K.E. Carpenter, S. Bandeira, J.S. Bujang, H.P. Calumpong, T.J.B. Carruthers, R.G. Coles, W.C. Dennison, P.L.A. Erftemeijer, M.D. Fortes, A.S. Freeman, T.G. Jagtap, A.H.M. Kamal, G.A. Kendrick, W. Judson Kenworthy, Y.A. La Nafie, I.M. Nasution, R.J. Orth, A. Prathep, J.C. Sanciangco, and Tussenbroek, B.v., Vergara, S.G., Waycott, M., & Zieman, J.C. 2011. Extinction risk assessment of the world's seagrass species. *Biological Conservation* 144: 1961–1971.
- Underwood, A.J. 1991. Beyond BACI: Experimental designs for detecting human environmental impacts on temporal variations in natural populations. *Australian Journal of Marine and Freshwater Research* 42: 569–587.
- Underwood, A.J. 1994. On beyond BACI: Sampling designs that might reliably detect environmental disturbances. *Ecological Applications* 4: 3–15.
- Unsworth, R.K.F., M. van Keulen, and R.G. Coles. 2014. Seagrass meadows in a globally changing environment. *Marine Pollution Bulletin* 83: 383–386.
- Valle, M., V. Palà, V. Lafon, A. Dehouck, J.M. Garmendia, Á. Borja, and G. Chust. 2015. Mapping estuarine habitats using airborne hyperspectral imagery, with special focus on seagrass meadows. *Estuarine, Coastal and Shelf Science* 164: 433–442.
- Walker, D.I., R.J. Lukatelich, G. Bastyan, and A.J. McComb. 1989. Effect of boat moorings on seagrass beds near Perth, Western Australia. *Aquatic Botany* 36: 69–77.
- Walker, D.I., and A.J. McComb. 1992. Seagrass degradation in Australian coastal waters. *Marine Pollution Bulletin* 25: 191–195.
- Waycott, M., C.M. Duarte, T.J.B. Carruthers, R.J. Orth, W.C. Dennison, S. Olyarnik, A. Calladine, J.W. Fourqurean, K.L. Heck, A.R. Hughes, G.A. Kendrick, W.J. Kenworthy, F.T. Short, and S.L. Williams. 2009. Accelerating loss of seagrasses across the globe threatens coastal ecosystems. *Proceedings of the National Academy of Sciences* 106: 12377–12381.
- West, R.J., C.A. Thorogood, T.R. Walford, and R.J. Williams. 1985. An estuarine inventory for New South Wales, Australia. Fisheries Bulletin 2. Department of Agriculture. *New South Wales* 140.
- West, R.J., A.W.D. Larkum, and R.J. King. 1989. Regional studies seagrasses of south eastern Australia. In *Biology of seagrasses:* A treatise on the biology of seagrasses with specific reference to the Australian region, ed. A.W.D. Larkum, A.J. McComb, and S.A. Shepherd, 230–260. Amsterdam, The Netherlands: Elsevier.
- West, R.J. 2010. The seagrasses of New South Wales estuaries and embayments. *Wetlands Australia* 3: 11.
- Williams, R.J., and A.J. Meehan. 2004. Focusing management needs at the sub-catchment level via assessments of change in the cover of estuarine vegetation, Port Hacking, NSW, Australia. Wetlands Ecology and Management 12: 499–518.
- Williams, R.J., and F.A. Watford. 1999. Distribution of seagrass, mangrove and saltmarsh in the Cowan Creek Catchment Management Area. Contract report to SHURE and the Cowan Creek Catchment Management Committee 27.
- Wilson, A. 2011. Flora of Australia: Volume 39 Alismatales to Arales. ABRS/CSIRO Publishing, Melbourne. 301.
- Wood, E. 1959. Some aspects of the ecology of Lake Macquarie, N.S.W., with regard to an alleged depletion of fish. VI. Plant

Communities and their Significance. *Marine and Freshwater Research* 10: 322–340.

- Worm, B., E.B. Barbier, N. Beaumont, J.E. Duffy, C. Folke, B.S. Halpern, J.B.C. Jackson, H.K. Lotze, F. Micheli, S.R. Palumbi, E. Sala, K.A. Selkoe, J.J. Stachowicz, and R. Watson. 2006. Impacts of biodiversity loss on ocean ecosystem services. *Science* 314: 787–790.
- Yaakub, S.M., E. Chen, T.J. Bouma, P.L.A. Erftemeijer, and P.A. Todd. 2014. Chronic light reduction reduces overall resilience to

additional shading stress in the seagrass Halophila ovalis. *Marine Pollution Bulletin* 83: 467–474.

Yassini, I., and B.G. Jones. 1995. Foraminiferida and Ostracoda from estuarine and shelf environments on the southeastern coast of Australia. Australia: University of Wollongong Press.

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