



Multi-scale assessments reveal changes in the distribution of the endangered seagrass *Posidonia australis* and the role of disturbances

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Abstract

Seagrasses are threatened globally by multiple anthropogenic disturbances, and management of these threats requires detailed information on where losses are occurring and why. Seagrass distribution is determined by processes operating at multiple scales, yet most assessments of change to seagrass extent are done at a single spatial scale. This study applied a multi-scale approach to quantify changes in the extent of the endangered seagrass *Posidonia australis* over the last 10–18 years using high-resolution mapping from 15 estuaries in New South Wales, Australia. Changes in *P. australis* extent and relationships with anthropogenic disturbances were examined at two spatial scales: across entire estuaries and at sub-estuary “local” scales within 50 × 50 m grids. Although increases in *P. australis* area were observed in ten estuaries, losses at local scales were prevalent in all estuaries. No disturbances correlated with seagrass change at the estuary scale; however, the greatest losses occurred in Botany Bay which is a highly modified estuary with a heavily urbanised catchment. At local scales, losses of *P. australis* were strongly associated with large areas of artificial structures and distance to the sea, and the greatest increases were observed in areas with marine reserves and no oyster aquaculture. These findings highlight the importance of quantifying changes in seagrass extent at multiple scales, as estuary-scale trends can mask localised losses if they are offset by increases in other parts of the estuary. Identifying hotspots of declines and the disturbances causing them are essential for applying focussed management actions to conserve seagrasses.

Keywords Disturbance · Endangered species · Habitat loss · Human impacts · *Posidonia* · Spatial scale

Introduction

Seagrass meadows have considerable ecological and socioeconomic importance, yet they are suffering global declines owing to multiple anthropogenic stressors, including the ongoing development and urbanisation of coastal areas (Orth et al. 2006; Waycott et al. 2009; Dunic et al. 2021). Seagrasses provide many ecosystem functions and services, such as being important habitat for a range of flora and fauna (including commercial and recreational species), stabilising sediments, attenuating wave energy, maintaining water

quality, nutrient cycling and storing carbon (Orth 1977; Lepoint et al. 2002; de Boer 2007; Gillanders 2006; Macreadie et al. 2014). However, seagrasses are susceptible to a range of anthropogenic disturbances which are linked to the loss and fragmentation of meadows (Orth et al. 2006; Waycott et al. 2009; Dunic et al. 2021; Swadling et al. 2022). Given the predicted increases in human population and development along coastlines worldwide, it is important to quantify any losses of seagrasses and better understand where and why such losses are occurring. This information is critical to help develop management strategies that promote ecologically sustainable development (Kilminster et al. 2015; Adams et al. 2016; Unsworth et al. 2019; McMahon et al. 2022).

Spatial scale is an essential consideration when identifying the mechanisms underpinning variability in species distributions, as it influences the patterns we observe, and abiotic or biotic variables also vary depending on the size of sampling unit (grain) and extent (Wiens 1989; Levin

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1992; O'Brien et al. 2018). Distributions of seagrasses, like those of other species, are influenced by environmental and anthropogenic processes operating at multiple spatial scales (Walker et al. 2006; Kendrick et al. 2008; O'Brien et al. 2018; McMahon et al. 2022). For instance, land-use changes from agricultural practises or urbanisation can cause losses at the meadow and landscape scales through increased nutrient loading and sedimentation, contaminants and poor water quality (Cambridge et al. 1986; Short and Burdick 1996; Bester 2000; Hauxwell and Valiela 2004; Orth et al. 2006; Saunders et al. 2017; Lambert et al. 2021). In comparison, physical damage associated with individual boating infrastructure or fisheries (e.g. aquaculture or trawling) generally occurs over smaller spatial scales (10s–100s m) (Fyfe and Davis 2007; Demers et al. 2013; Glasby and West 2018; Howarth et al. 2022). However, the construction and operation of infrastructure can occur across large areas and at high densities, so their combined impacts may cause substantial loss and fragmentation of seagrass meadows (Glasby and West 2018; Unsworth et al. 2019; Swadling et al. 2022). Failing to investigate species–environment relationships at the appropriate scales can lead to incomplete or misleading information on the factors impacting their distribution, which may in turn compromise management and conservation actions (Andrew and Mapstone 1987; Underwood 1993).

The long-lived seagrass genus *Posidonia* has a limited capacity to recover from anthropogenic disturbances as its species are slow growing, and recolonisation by seedlings can be infrequent (Kilminster et al. 2015; O'Brien et al. 2018). In New South Wales (NSW) Australia, *P. australis* Hook. f occurs in 17 estuaries and has suffered losses in its extent at several locations, particularly in heavily urbanised estuaries (Larkum 1976; Larkum and West 1990; West 2011; Evans et al. 2018; West and Glasby 2021). Estimates of *P. australis* decline differ depending on sampling design. For example, rates of decline in *P. australis* meadows in Port Jackson (Sydney Harbour) have been estimated to be 10% yr⁻¹ from investigations at specific sites known to be disturbed (Evans et al. 2018), whereas estimates are much lower (1.2% yr⁻¹) when comparing meadow change across the entire estuary (West and Glasby 2021). Given that changes in seagrass meadows and disturbances vary spatially, targeted local-scale studies are unlikely to provide a representative estimate of meadow change across estuaries, although they are useful for quantifying specific impacts. In contrast, studies of meadow change at the scale of estuaries (or at broader scales such as regionally or globally) can provide a more accurate estimate of the overall trajectory of seagrass extent, yet the coarse resolution means that hot-spots of decline and the drivers of loss may be overlooked. A multi-scale approach that quantifies changes in seagrass extent at both the estuary and sub-estuary scales will provide

a more comprehensive understanding of seagrass trajectories and help prioritise management actions for protecting species within and amongst estuaries. The need for spatially explicit information on changes in *P. australis* extent is further underscored by the species' endangered status in six NSW estuaries under state legislation (NSW Fisheries Management Act, 1994), plus an additional three estuaries under national legislation (Environment Protection and Biodiversity Conservation Act, 1999) due to anthropogenic threats operating at multiple scales.

In this study, we quantified changes in the extent of *P. australis* within 15 estuaries and examined whether these were related to multiple anthropogenic disturbances at 2 spatial scales: (1) across entire populations in estuaries, and (2) at sub-estuary “local” scales (i.e. in 50×50 m grids). We used the high-resolution habitat mapping from West and Glasby (2021) to quantify changes in *P. australis* extent over 10–18 years in all but two of the estuaries where the species occur in NSW, Australia. We built on this previous research using an augmented dataset (updated maps for six estuaries) and by correlating changes in *P. australis* area at local scales with key disturbances. The disturbances selected were based on previous findings (West 2011; West and Glasby 2021; Swadling et al. 2022) and availability of data at the appropriate scales, and included human population density, catchment land usage, terrestrial nutrient inputs, artificial structures, moorings and oyster aquaculture leases. We hypothesised that estuaries with highly populated, urbanised catchments and high nutrient loading would suffer greater losses in *P. australis* area, whereas meadow area in less disturbed estuaries would be relatively stable. At the sub-estuary scale, it was hypothesised that losses have occurred where there are artificial structures (jetties, marinas, pontoons and rock groynes), aquaculture leases and moorings, as these disturbances are known to affect seagrasses (Fyfe and Davis 2007; West 2011; Glasby and West 2018; Howarth et al. 2022; Swadling et al. 2022). Many of the surveyed estuaries contained marine reserves (locally known as sanctuary zones within either marine parks or aquatic reserves), where human impacts to seagrasses are minimised via regulations preventing activities that may harm or remove fauna or flora. We, therefore, included the presence of marine reserves in the analyses, predicting that the loss of *P. australis* meadows would be less in estuaries and at local sites containing reserves when compared to non-protected areas.

Materials and methods

Study area

Meadows of *Posidonia australis* were mapped in 15 estuaries across ~750 km of coastline in NSW, Australia

(32.27°–37.11° S; Fig. 1). These sites spanned the entire distribution of the species in NSW estuaries, ranging from Wallis Lake in the north to Twofold Bay in the south (Fig. 1). Surveyed estuaries experienced different levels of disturbances, with the highest rates of urbanisation and infrastructure for estuaries within the Greater Sydney Region (i.e. Brisbane Water, Pittwater, Port Jackson, Botany Bay, Port Hacking; Fig. 1). The total extent of *P. australis* across the 15 study estuaries was ~2994 ha, representing 99.6% of the total known area of the species in NSW. Only two estuaries (Cowan Creek and Batemans Bay) containing *P. australis* were excluded from the analyses due to recent mapping being unavailable, and combined these only represent a small area (< 11 ha) of the species. Cowan Creek, located in the Hawkesbury River, was the only population classified as endangered that was not included in our study (Fig. 1).

Quantifying seagrass change

Change in *P. australis* area was quantified using detailed habitat mapping from two time periods, 10–18 years apart (mean ~ 15 years difference) depending on the estuary (Table 1). Two different techniques were used to map seagrass, as outlined in West and Glasby (2021). Maps produced between 2000 and 2008 (T1; Table 1) were created using a digital GIS method where individual seagrass patches were manually captured using onscreen digitising at a scale of 1:1500. This was done using ortho-rectified scanned or digital aerial imagery with the smallest identifiable features $\geq 4 \text{ m}^2$. A refined mapping method was used for maps created after 2017 (T2; Table 2), which involved using object-based image analysis (OBIA) techniques in Trimble eCognition™ v10.2. The OBIA method

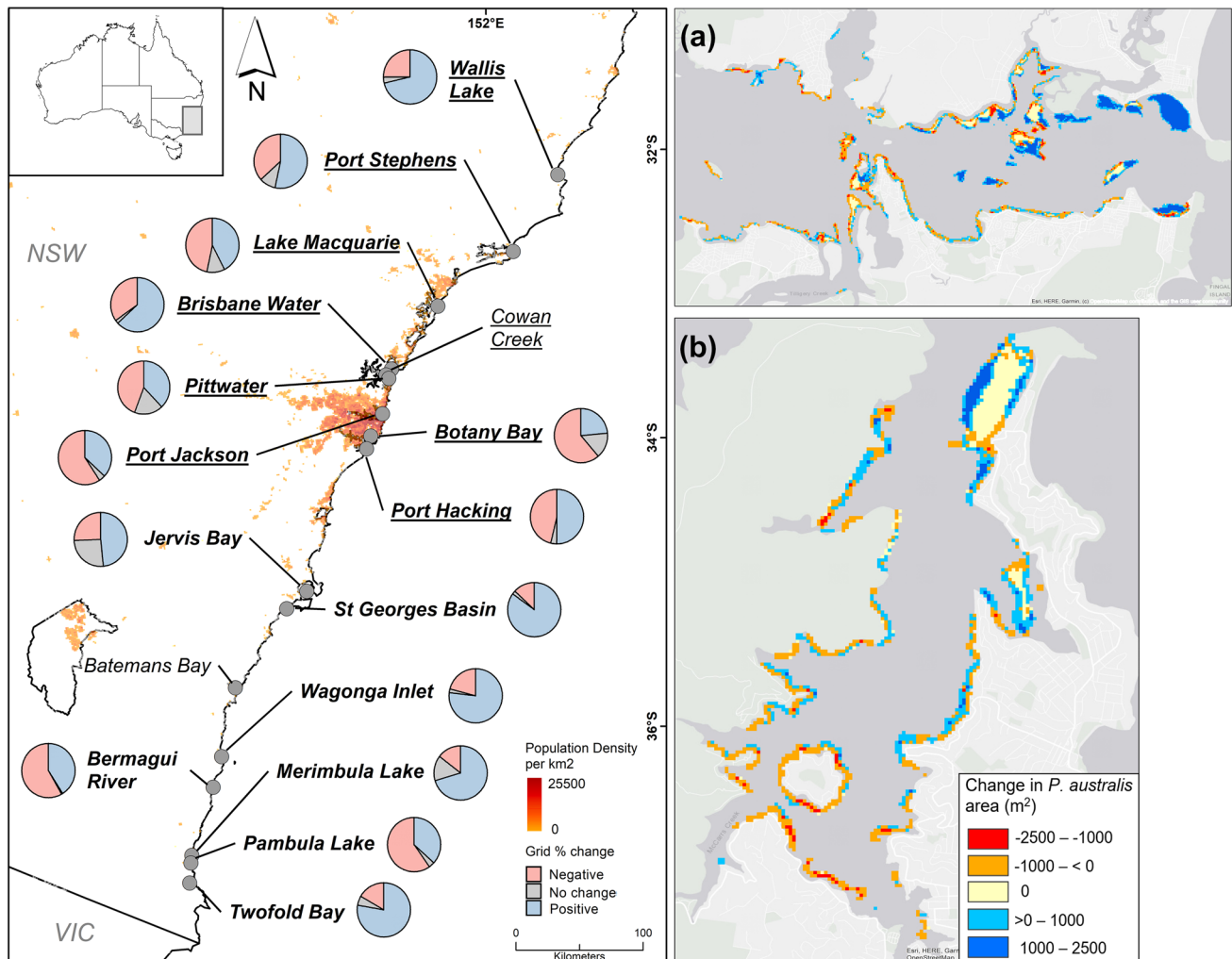


Fig. 1 Location of estuaries containing *Posidonia australis* in NSW, Australia. Estuaries in bold were included in the study and those underlined have populations listed as endangered under state or national legislation. Pie charts illustrate the proportion of 50×50 m

grids experiencing negative (red), positive (blue) or no change (grey) in *P. australis* area within estuaries between mapping times. Maps on the right show change in area for 50×50 m grids across **a** Port Stephens, and **b** Pittwater

Table 1 Details on the mapping year for each estuary, the morphology of estuaries, the area (ha) of *Posidonia australis* mapped for each time and the overall rate of change (ha yr⁻¹) observed

Estuary	Estuarine morphology	Years mapped		Years difference	<i>P. australis</i> area (ha)		Rate of change (ha yr ⁻¹)
		T1	T2		T1	T2	
Wallis Lake	BE	2002	2017	15	242.91	348.39	7.03
Port Stephens	DRV	2004	2017	13	409.7	596.27	14.35
Lake Macquarie	BE	2012	2022	10	98.24	93.68	-0.46
Brisbane Water	BE	2005	2020	15	95.87	131.35	2.37
Pittwater	DRV	2005	2019	14	139.49	146.12	0.47
Port Jackson	DRV	2003	2018	15	10.42	8.51	-0.13
Botany Bay	OE	2008	2019	11	315.12	225.8	-8.12
Port Hacking	DRV	2008	2021	13	63.35	63.59	0.02
Jervis Bay	OE	2004	2020	16	513.12	629.76	7.29
St Georges Basin	BE	2004	2020	16	140.12	403.85	16.48
Wagonga Inlet	BE	2002	2019	17	60.51	96.76	2.13
Bermagui River	BE	2002	2020	18	8.04	6.33	-0.095
Merimbula Lake	BE	2004	2022	18	115.67	175.56	3.33
Pambula Lake	BE	2004	2022	18	52.32	36.72	-0.87
Twofold Bay	OE	2004	2022	18	0.45	1.1	0.04

Estuarine geomorphologies were obtained from Roy et al. (2001) which included, *BE* barrier estuary, *DRV* drowned river valley, and *OE* ocean embayment

Table 2 Generalised additive models predicting change of *Posidonia australis* at the estuary and local scales

Response		Model	AICc	ωAICc	r ²	edf
Estuary scale	Percent change per year	Disturbed catchment (%)	86.48	0.166	0.21	2
		Population per ha	86.57	0.159	0.2	2
		Null	86.77	0.144	0	1
Local scale	Change in area per year (m ²)	Aquaculture + artificial structure area + distance to sea + marine reserve	301,835.5	0.997	0.12	19.54

All models within ± 2 AICc values are presented and the most parsimonious are in bold

segments high-resolution ortho-rectified aerial imagery into polygon objects of similar colour, texture and shape. The derived image objects are then manually classified into estuarine habitats, with seagrass meadows classified to a species level. These latter maps were more detailed and captured seagrass patches ≥ 1.5 m². Initial presumptive seagrass polygons produced by both techniques were extensively validated in the field using a range of visual methods including towed underwater videos, drones (for latest mapping), side-scan sonar and differential GPS. In all maps, *P. australis* meadows were defined as any polygons containing the species, regardless of density (which was not estimated). Although we could not determine the extent to which any differences in seagrass area were associated with the change in the mapping method, previous comparisons have shown that more detailed mapping typically results in smaller area estimates for

mapped polygons (West and Glasby 2021). Therefore, if there is any methodological bias it would likely be towards detecting reductions in area over time. Furthermore, it was assumed that the relative difference between times and methods was similar for each estuary and so unlikely to influence comparisons of change amongst estuaries. Older maps are available, but they are not as accurate as contemporary mapping and may overestimate seagrass extent (West and Glasby 2021). We, therefore, used only recent maps created over the last 10–18 years and these contemporary changes are the most practical to respond to from a managerial perspective. The latest seagrass maps from this project are available at the NSW Fisheries Spatial Data Portal (NSW DPI 2021a). The entire dataset (latest and historic mapping) plus changes in *P. australis* area over time at both estuary and local scales can be viewed on the NSW Estuarine Habitat Dashboard (NSW DPI 2021b).

Changes in *P. australis* area were quantified at two spatial scales, across entire estuaries and at the sub-estuary scale (hereafter “local scale”). At the estuary scale, the area of *P. australis* for each mapping time was calculated by summing the area of all polygons in respective estuaries (Table 1). Differences in *P. australis* area between times at the local scale were determined within 50 × 50 m grids (hereafter 50 m grids), created using the fishnet tool in ArcGIS v10.8.1 across the species distribution in NSW.

Abiotic variables

All abiotic variables used data representative of disturbances in the present day (T2), as historical data (for T1) were not available. Data on the catchment and sub-catchments for each estuary, land use and the quantity of nitrogen entering estuaries from terrestrial run-off were sourced from Roper et al. (2011) and the NSW SEED data portal (NSW DPIE 2019). Land usage was classified into the proportion of catchments with either natural or disturbed areas, with natural areas containing natural or near natural vegetation and disturbed areas being agricultural or urban areas. Terrestrial nitrogen input data were modelled values (expressed as kg/ha) for each sub-catchment in estuaries. Values for nitrogen inputs were summed for all sub-catchments bordering estuaries within tidal limits. Human population density in estuarine catchments was calculated using data from the 2021 Australian Census (Australian Bureau of Statistics 2021). Human population was included in the analyses as it can act as a surrogate for a variety of different anthropogenic stressors and has been used previously to identify impacts of humans in marine systems (Todd et al. 2019; Rees et al. 2021; Swadling et al. 2022). Human population data were calculated per hectare of catchment for each estuary.

We considered three different types of marine infrastructure in our analyses, specifically artificial structures, oyster leases and the number of boat moorings. The area of artificial structures was mapped from aerial imagery using OBIA techniques and included jetties, pontoons, marinas and rock groynes, and the total area was calculated per 50 m grid. Structures < 2 m in either length or breadth could not be reliably and efficiently mapped, meaning that structures used in oyster aquaculture were not mapped. Spatial data on currently active leases were, therefore, derived from maps of allocated leases (NSW DPI 2021a). It is also important to note that the arrangement and density of structures within a lease area can change over time. Because of these two limitations, we have only effectively considered gross changes in *P. australis* area at the scale of entire aquaculture leases, despite changes in seagrass extent being captured at much smaller scales.

Originally, at the local scale, the area of oyster leases within 50 m grids was calculated. However, these data were

highly skewed (large numbers of zeroes or total coverage (2500 m²) of a grid) so the variable was transformed to the presence or absence of leases within grids. The total number of boat moorings was summed within each 50 m grid. At the estuary scale, the area of artificial structures and oyster leases and the number of boat moorings were summed from all grids in a respective estuary. This meant that only disturbances in, or directly adjacent to (i.e. within 50 m), seagrass meadows were included for estuary-scale analyses. Marine reserves in this study were defined as sanctuary zones in either aquatic reserves or marine parks, both of which have protection measures to prevent harm to marine vegetation. Marine reserves were present in grids containing *P. australis* in five estuaries (Port Stephens, Botany Bay, Port Hacking, Jervis Bay and Wagonga Inlet), and their presence or absence was recorded for each 50 m grid. It was notable that the marine reserve in Port Hacking (Shiprock Aquatic Reserve) is focussed over a rocky reef but contains a section of an extensive *P. australis* meadow, so it was retained in the analysis.

The distance of local sites from the sea (i.e. estuary mouth) was included as a predictor variable because it can influence water quality traits that affect seagrass health such as turbidity, temperature and salinity (Ferguson et al. 2018). This is important to account for when quantifying the distribution of *P. australis*, as the species is largely restricted to marine-dominated, well-flushed locations (West et al. 1989; Roy et al. 2001). Distance to the sea was calculated at the centre point of the 50 m grids using the ‘cost distance tool’ in the spatial analyst extension in ArcGIS. This tool was used as it measured the distance between sites and the ocean without crossing land. The geomorphology of estuaries was included because it can also be a driver of water quality, hydrodynamics and sedimentology (Roy et al. 2001; Ferguson et al. 2018).

Statistical analyses

The influence of anthropogenic disturbances and location covariates (distance to the sea and estuarine geomorphology) on the change in *P. australis* area at the estuary and local scales was investigated using generalised additive models (GAMs). GAMs were selected for the analyses as they account for non-linear and non-monotonic relationships between the response and explanatory variables (Guisan et al. 2002). At the estuary scale, the response variable was the annual rate of change in *P. australis* area (% increase or decrease), calculated as the difference between times 1 and 2 divided by the number of years between mapping times (Table 1). At the local scale, the response variable was the difference in *P. australis* area (m²) between time periods, which was divided by the number of years between mapping times to standardise for the varying temporal scales in

sampling. Given that marine reserves and oyster aquaculture leases were not present in all estuaries, preliminary analyses were done to compare relationships between these variables and the change in *P. australis* area using the full dataset (containing all estuaries) and a restricted dataset (only estuaries with these variables). These analyses revealed little differences in the results and did not affect the interpretation of the relationship (Fig. S1), so the full dataset containing all 15 estuaries was used in the formal analyses.

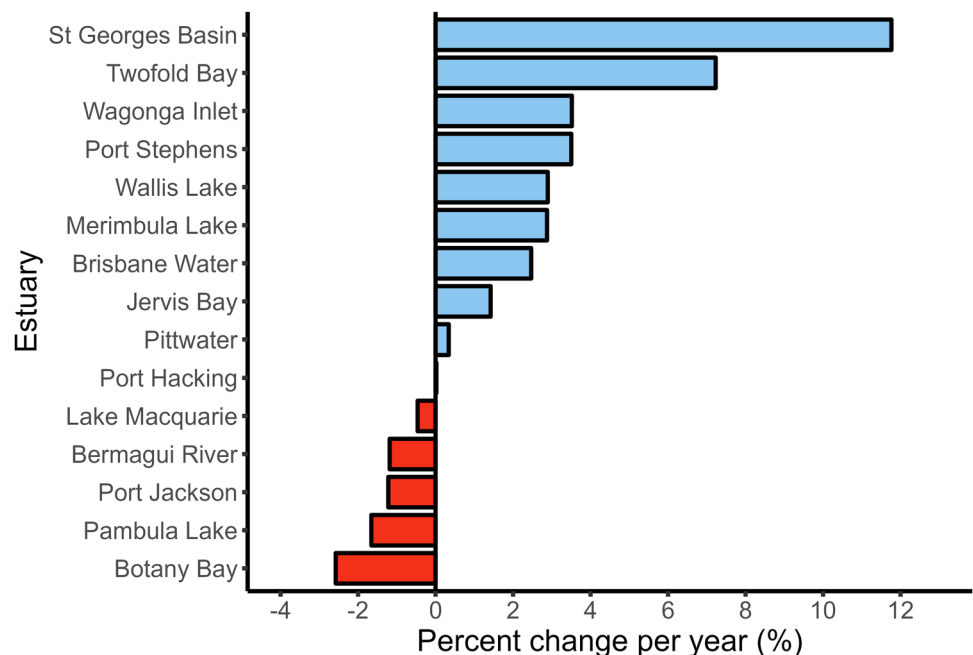
A full-subset method was used to fit GAMs of all possible combinations (Fisher et al. 2018). Models were fit with a maximum of five predictors and variables with Pearson's correlation greater than 0.4 were not permitted in the same model. The smoothing parameter was restricted to a simple spline to only allow monotonic relationships ($k=3$). Models were fit with a Gaussian distribution and for the local-scale analyses, the estuary ID and an interaction term of latitude and longitude were included as random effects. Model selection was done using the Akaike's information criterion for small sample sizes (AICc), with the best model having the lowest AICc units (Burnham and Anderson 2002). Models differing by less than two AICc units show weak evidence of support, and when multiple candidate models occurred (i.e. within 2 AICc), the most parsimonious model with the fewest predictors was selected (Burnham and Anderson 2002). Data manipulation, statistical analyses and plots were generated using the statistical computing programme 'R' (R Core Team 2022) and the packages 'dplyr' (Wickham et al. 2022), 'FSSGAM' (Fisher et al. 2018), 'mgcv' (Wood 2011) and 'ggplot2' (Wickham 2016).

Results

Across all 15 surveyed estuaries in NSW, there was an increase of 698.45 ha in *P. australis* area during the period (average ~ 15 years) between mapping times. Estuary wide increases (i.e. positive annual change) in area occurred in ten estuaries and overall declines were observed in five estuaries (Fig. 2). Port Hacking only had a minor increase (0.02%) and likely represents no change. The largest percent gains in *P. australis* area were found in St Georges Basin and Twofold Bay, which increased by 11.8% and 7.2% per year, respectively (Fig. 2). Notably, Twofold Bay had the smallest area of *P. australis* in NSW and despite the large percentage gained per year, the overall rate of increase was small (0.04 ha yr⁻¹; Table 1). The greatest percent losses detected were in the highly urbanised Botany Bay (−2.6% yr⁻¹), followed by Pambula Lake (−1.7% yr⁻¹), Port Jackson (−1.2% yr⁻¹), Bermagui River (−1.2% yr⁻¹) and Lake Macquarie (−0.5% yr⁻¹; Fig. 2). In terms of the overall area of *P. australis* lost per year, rates were generally similar amongst estuaries (> −1 ha yr⁻¹) except for Botany Bay where declines were an order of magnitude greater (−8.12 ha yr⁻¹; Table 1).

There was little evidence to suggest that change in *P. australis* area at the estuary scale was related to anthropogenic disturbances or estuarine geomorphology, with the null GAM model identified as the best model (Table 2). There were two models within ± 2 AICc of the null which contained either population density or the proportion of disturbed catchment. Interestingly, both variables had negative associations with the annual rate of change in seagrass

Fig. 2 Annual rate of change (%) in *Posidonia australis* area for surveyed estuaries calculated over 10–18 years. Estuaries with gains are represented in blue and declines are in red



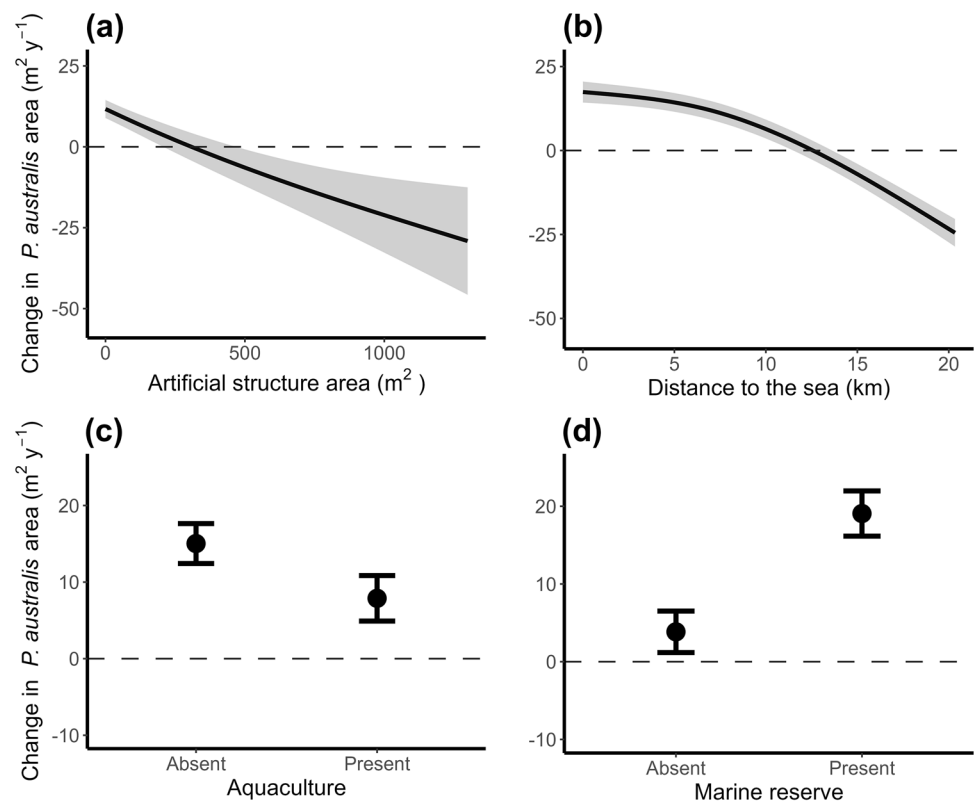
area, with losses of *P. australis* predicted in estuaries with a population density > 27 people per hectare or with > 50% of disturbed catchment (Fig. S2).

Despite many estuaries experiencing increases in *P. australis* area, localised losses were identified in all surveyed estuaries (Fig. 1). Declines in seagrass meadows within 50 m grids ranged between 13% of grids in St Georges Basin and 61.3% of grids in Botany Bay. Out of the estuaries experiencing net gains, Port Hacking and Pittwater had large percentages of grids (44–46%) with declines. Four variables were found to best predict the change of *P. australis* at the local scale, and this model explained 12% of the variation (Table 2). The number of moorings was not present in the best model. Change in *P. australis* area per year declined with artificial structure area, and seagrass losses were predicted to occur where there was $\geq 310 \text{ m}^2$ of artificial structures (i.e. pontoons, jetties or rock groynes) per 50 m grid (2500 m^2), which equates to $\geq 12.4\%$ of a grid occupied by artificial structures (Fig. 3a). A non-linear relationship was found between the distance to the sea and *P. australis* meadow change, with seagrass area most likely to be lost > 12.6 km from the sea (Fig. 3b). Upon further inspection, however, it appeared that this relationship varied with estuarine morphology (Fig. S3). Specifically, declines in *P. australis* far from the sea only occurred in drowned river valley

estuaries, and these were the only estuarine morphology to have distances > 15 km. For instance, a gradient can be observed in the Port Stephens and Pittwater estuaries which are both drowned river valleys, where gains are more common at their mouths and losses are frequent in the upper sections of the estuaries (Fig. 1a, b). In comparison, the opposite relationship was observed for the other estuarine geomorphologies (coastal embayments and barrier estuaries) where declines occurred at the estuary mouths and increases were predicted far from the sea (Fig. S3).

When analysed across all 15 estuaries, grids containing oyster aquaculture leases were associated with a 47.5% reduction in the rate of change in *P. australis* area (Fig. 3c). It was notable that whilst the overall change in area was still positive when averaged over all estuaries, constraining the analyses to only the nine estuaries containing oyster aquaculture resulted in losses of *P. australis* being apparent in some grids with leases, although, on average, small gains were still observed in the presence of aquaculture when measured at the scale of entire lease areas (mean $\pm$ SE = $1.75 \pm 3.15 \text{ m}^2 \text{ y}^{-1}$; Fig. S1a). Marine reserves were associated with increased gains in *P. australis* area (mean $\pm$ SE = $19.1 \pm 2.9 \text{ m}^2 \text{ y}^{-1}$) when compared to non-reserve areas (mean $\pm$ SE = $3.85 \pm 2.7 \text{ m}^2 \text{ y}^{-1}$; Fig. 3d).

Fig. 3 Relationships between explanatory variables in the best model, **a** artificial structure area (m^2), **b** distance to the sea (km), **c** oyster aquaculture presence, and **d** marine reserve presence and the total change in *P. australis* area per year ($\text{m}^2 \text{ y}^{-1}$) at the local scale (within $50 \times 50 \text{ m}$ grids). Fitted GAMM prediction curves (solid line) are included, and ribbons and error bars represent $\pm$ SE



Discussion

Although there are global trends of seagrass meadow loss, there are encouraging signs in some regions that declines are stabilising or have been reversed (Waycott et al. 2009; Dunic et al. 2021; Krause-Jensen et al. 2021). Changes in seagrass meadows are often estimated using studies or meta-analyses over regional, national or global scales, which provide insights into the overall trajectory of seagrass meadows (Waycott et al. 2009; Grech and Coles 2010; Dunic et al. 2021; Turschwell et al. 2021). However, it is also important to identify where seagrass losses are occurring within systems and what the specific causes are, with such assessments needed at scales relevant to potential disturbances (Duarte et al. 2006; O'Brien et al. 2018; West and Glasby 2021). Here, we used a comprehensive dataset to assess changes in the extent of the endangered seagrass *Posidonia australis* at 2 spatial scales across 15 estuaries spanning ~ 750 km of coastline. The area of *P. australis* was found to increase in 66% or 10 of the 15 estuaries surveyed over the 10–18 year period, which supports the findings of West and Glasby (2021). Whilst this result is promising and may indicate that management actions are working, investigation at smaller spatial scales (i.e. in 50 × 50 m grids) revealed localised losses are prevalent in all estuaries. Such findings demonstrate that estimates of estuary-scale change can mask smaller-scale losses if they are offset by gains in other areas. No disturbance variables were found to correlate with the change in *P. australis* area at the estuary scale (supporting West and Glasby 2021). In comparison, local losses were associated with the area of artificial structures and greatest increases were observed in marine reserves, or in areas without oyster aquaculture leases. Overall, these findings highlight the importance of applying multi-scale techniques for determining the trajectory of meadows across a system and identifying hotspots of decline. The latter is essential for applying focussed management actions and to optimise the allocation of efforts to reduce negative human impacts on seagrasses.

Although localised losses of *P. australis* were observed in all estuaries, ten estuaries experienced net gains in meadow area over the last 10–18 years. The increases in *P. australis* were somewhat surprising, as the species is classified as a persistent seagrass which forms enduring meadows with only small variation in its extent (Kilminster et al. 2015). The colonisation rate of *P. australis* is considered to be slow, and it can take decades to recover from disturbances. This notion comes largely from estimates of spreading rates for *P. australis* to be 20–80 cm yr⁻¹ in areas where disturbances have occurred (Meehan and West 2000; Paling and McComb 2000; Cambridge et al. 2002; Bastyan and Cambridge 2008). However, it has been

proposed that growth rates of seagrass rhizomes may not scale up to the growth dynamics at the patch or meadow scales (Duarte and Sand-Jensen 1995; Vidondo et al. 1997; Kendrick et al. 2005). Indeed, the results of the current study suggest that *P. australis* meadows in estuarine environments may have a greater capacity to expand than previously thought (e.g. St Georges Basin 16.48 ha yr⁻¹ and Port Stephens 14.35 ha yr⁻¹). The mechanisms (e.g. rhizome extension, seedling recruitment, fragment dispersal) underpinning the large expansion of *P. australis* meadows and the colonisation of bare sediments observed in this study remain unclear. Future studies are, therefore, warranted on understanding the factors influencing the growth dynamics of *P. australis* meadows in NSW estuaries.

In the current study, there were overall losses of *P. australis* in five estuaries, including the two most heavily urbanised estuaries (Botany Bay and Port Jackson). Although there was some evidence that losses may occur in estuaries with higher populations (> 27 people/ha) or disturbed (> 50% of non-natural land-use) catchments (Fig. S2), no disturbances were found to predict changes in *P. australis* extent at the estuary scale. This supports the findings of West and Glasby (2021), who reported no relationships between catchment disturbances and changes in the extent of multiple seagrass species in NSW estuaries. We suggest that the drivers of *P. australis* loss at estuary scales may be estuary specific or due to factors not considered in this study. For example, large movements of sediment have occurred in areas of Bermagui River and Botany Bay, which may have smothered seagrass meadows (Duarte et al. 1997). It is notable, however, that *P. australis* is more tolerant to burial than other seagrass species with 50% mortality reported when buried at a depth of 19.5 cm (Cabaço et al. 2008). Furthermore, some losses in Botany Bay were observed at the deeper edge of *P. australis* meadows and not near over-water structures or moorings, and could indicate reduced water clarity, which has previously been rated poor in Botany Bay and its main tributary (NSW OEH 2010). In comparison, declines of *P. australis* in Port Jackson and Lake Macquarie occurred in areas with high densities of moorings or artificial structures, and in Pambula Lake, losses were evident near aquaculture leases. Such observations highlight that the disturbances driving change in *P. australis* extent at the estuary scale are likely context dependent, so it may be difficult to make generalisations from studies examining change in seagrasses at broad spatial scales.

The loss of seagrass due to marine infrastructure has been commonly observed worldwide (Skinner et al. 2014; Griffiths et al. 2020; Sagerman et al. 2020; Ferretto et al. 2022; Howarth et al. 2022), and the life-history traits of *P. australis* may limit the recovery potential relative to other seagrasses (Kilminster et al. 2015). Infrastructure can cause seagrass removal through mechanical damage during construction,

scouring due to changed water flow, or vessels accessing the structures may scour seagrasses (Loflin 1995; Fyfe and Davis 2007; West 2011; Bulmer et al. 2012; Howarth et al. 2022). In addition, shading by overwater structures (e.g. jetties, pontoons and aquaculture) has been shown to reduce (or inhibit) photosynthesis, and cause localised seagrass loss or lower shoot densities (Bulthuis 1983; Fitzpatrick and Kirkman 1995; Collier et al. 2009; Eriander et al. 2017; Ferretto et al. 2022). Compared to other *Posidonia* species, *P. australis* seems more susceptible to light reductions with 90% shading halving growth rates after a month (Fitzpatrick and Kirkman 1995) or shoot densities reducing 75% after 3 months under oyster aquaculture trays (Ferretto et al. 2022). Furthermore, the recovery of *Posidonia* species can be slow or non-existent after 6 months of shading (Collier et al. 2009). Coastal defence structures such as rock groynes can alter the hydrology and sedimentation in an area which also cause losses of seagrass (Duarte 2002; Airolidi and Beck 2007). Our findings demonstrate that artificial structures are negatively impacting *P. australis* meadows in NSW estuaries. Losses associated to artificial structures were detected when structures covered > 12% of a grid (i.e. 310 m²). Given that most artificial structures had an area of ~20–70 m², we postulate that larger losses of *P. australis* occurred in grids with multiple structures (e.g. jetties). In Pittwater for instance, losses were more prevalent along sections of foreshore with large numbers of boating infrastructure such as jetties, whereas the greatest gains were observed at the mouth where there were low disturbances and no boating infrastructure (Fig. 1a). It remains unclear how many structures (e.g. jetties, pontoons or rock groynes) are required in an area to generate substantial losses and whether any thresholds for structure density exist, but this is an avenue for future research.

There was some evidence that losses of *P. australis* were more prevalent in the upper reaches of estuaries, yet this pattern was only apparent in drowned river valley estuaries (Fig. S3). The opposite trend was observed in barrier estuaries and coastal embayments. These patterns may relate to the different hydrological and sediment characteristics of these three estuary types. Drowned river valley estuaries were much longer than the other morphologies and have a large tidal range which results in well-flushed estuarine mouths and more turbid conditions in the upper reaches. It is, therefore, not surprising that declines in *P. australis* occurred upstream as these areas would be at the edges of its distributional limits within these estuaries, because the species is generally restricted to well-flushed and marine conditions (West et al. 1989; Ferguson et al. 2018). In comparison, losses at the entrances of barrier estuaries could be attributed to the presence of narrow tidal deltas that commonly form here. Shifting sands in these deltas may smother seagrasses or erode meadows (West et al. 1989; Roy et al. 2001;

Cabaço et al. 2008; West and Glasby 2021). This is likely for the many barrier estuaries (e.g. Bermagui River) with their entrances trained by break walls, which alter water flow and cause the entrance shoals to be more mobile (Ferguson et al. 2018). Finally, coastal embayments are subjected to strong wind and wave conditions (West et al. 1989) at their mouths, which may be exacerbated by dredging in Botany Bay (Larkum and West 1990), and this could result in the removal of *P. australis* via physical damage or sediments smothering meadows.

Marine reserves are being employed globally to conserve biodiversity (Spalding et al. 2008; Halpern et al. 2010; Knott et al. 2021), and seagrasses are regularly incorporated into reserve design due to their widespread degradation and ecological importance (Orth et al. 2006; Coles et al. 2015; Howard et al. 2017; Strachan et al. 2022). Whilst previous studies often report that seagrass may continue to decline despite being protected within marine reserves (Marbà et al. 2002; Frascchetti et al. 2013; Quiros et al. 2017; Tin et al. 2020), our results were consistent with *P. australis* meadows benefiting from protection afforded by reserves. The positive effects of protection are likely due to key disturbances in our study system being minimised in reserves. For example, seagrass loss in reserves has been linked to the anchoring of vessels or trampling (Milazzo et al. 2004; La Manna et al. 2015; Travaille et al. 2015). However, vessel anchoring in areas with seagrass in many NSW reserves is not permitted, and a few reserves have designated anchorages or public moorings. Furthermore, the development of artificial structures in marine reserves is restricted. Seagrass declines within reserves elsewhere have also been reported where adjacent disturbances flow into protected areas (e.g. land-use practises in watersheds; Quiros et al. 2017), but we did not identify any impacts of such disturbances at the estuary scale. Some ecological functions such as herbivory may be enhanced within marine reserves and have indirect positive impacts to seagrasses. Higher abundances of herbivores within reserves have been shown to increase grazing rates (Prado et al. 2008; Planes et al. 2011; Ferguson et al. 2016), and seagrass grazing can stimulate shoot production (Valentine et al. 1997; Gulick et al. 2021) or reduce epiphyte loading to allow greater light availability (Orth and van Montfrans 1984; Howard and Short 1986). Nevertheless, our findings suggest that marine reserves may present conservation benefits to *P. australis* populations, most likely by minimising localised negative impacts through increased regulatory mechanisms.

Traditional block and chain boat moorings are the most common type of mooring in NSW, and they are known to physically scour seagrass meadows and generate scarring (Walker et al. 1989; West 2011; Demers et al. 2013; Glasby and West 2018). The size of mooring scars in *P. australis* is reported to increase at an average rate of 6.3 m² per month,

meaning it takes about 30 months to attain an average size of 185 m² in water 2–6 m deep (Glasby and West 2018). We propose the lack of any association between mooring density and changes in the extent of *P. australis* over the last 10–18 years likely reflects the stable impact of moorings, rather than a lack of mooring effects. This is supported by many of the moorings included in this study being present in the same area for at least a decade (authors' pers. obs. from aerial imagery).

The development of estuaries will undoubtedly increase as the human population continues to grow (Bulleri and Chapman 2010; Dafforn et al. 2015), making it important for management to minimise direct and indirect negative impacts to seagrasses or introduce seagrass-friendly infrastructure designs. Our findings suggest that one way to reduce the loss of *P. australis* in NSW estuaries is to prevent more artificial structures being constructed in or directly adjacent to seagrass meadows. Although current legislation (NSW Fisheries Management Act 1994) in NSW prevents certain types of marine infrastructure being built in *P. australis* meadows, there are increasing pressures to allow more of these structures and other legislative mechanisms can allow this to occur. Endangered populations of *P. australis* should be the highest priority for protection, particularly those in the Greater Sydney Region and Lake Macquarie where declines are still occurring. Developing and implementing seagrass-friendly designs for marine infrastructure is another option for research and management to help conserve seagrasses into the future. In the construction of jetties for instance, the use of mesh decking over timber or jetty designs which are high and narrow may provide greater light penetration and reduce negative impacts to seagrass (Burdick and Short 1999; Gladstone and Courtenay 2014).

In NSW, seagrass-friendly designs are being increasingly implemented in oyster aquaculture, with a shift from the use of traditional cultivation methods (trays and longline baskets) to floating bags and baskets. When floating bags are deployed in low densities and in water no shallower than 1 m, they can have no significant impacts on *P. australis* shoot density or growth over a 6-month period, whereas trays and longline baskets negatively affect photosynthesis and cause adverse impacts (Ferretto et al. 2022). The increasing implementation of floating structures may in part explain the overall gains in seagrass predicted where aquaculture was present (notwithstanding these gains being significantly less than in areas without aquaculture), as these new structures may allow *P. australis* to recolonise deeper areas (> 1 m) previously shaded by trays or longline baskets. It is notable that most oyster aquaculture leases in this study have been operational for almost 100 years, so many negative impacts to *P. australis* meadows had likely already occurred prior to mapping. An alternative explanation for the gains in

seagrass around aquaculture may be the spatial scale of the assessment. Although changes in seagrass could be documented at small spatial scales (> 1.5 m²), it was not possible to map individual aquaculture infrastructure in the same way that other artificial structures were mapped. As such, we effectively assessed for changes in seagrass at the scale of entire oyster leases, which were almost always far larger areas than those covered by oyster infrastructure. Thus, any losses of *P. australis* under aquaculture structures would be obscured by gains of other parts of the lease where there were no structures. Future studies are required to examine changes in the cover of seagrasses around aquaculture structures at scales smaller than those used in this study.

In conclusion, this study has provided important insights into how the extent of the endangered seagrass *P. australis* is changing across NSW estuaries. Specifically, we revealed using a multi-scale assessment that although gains are evident in the species' distribution at the estuary-scale, localised losses are still prevalent throughout estuaries. This approach also allowed us to identify anthropogenic disturbances responsible for local losses such as artificial structures and there were more gains in marine reserves and in the absence of oyster aquaculture leases. More broadly, our findings highlight the need for studies quantifying patterns in seagrass distribution to move away from single-scale approaches to provide a better understanding on patterns of seagrass change. Such information is essential to inform management strategies to combat the degradation of seagrass meadows and support ecologically sustainable development as the population increases along coastlines worldwide.

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Data availability The latest seagrass maps from this project are available at the NSW Fisheries Spatial Data Portal (<https://www.dpi.nsw.gov.au/fishing/fisheries-research/spatial-data-portal>). All other datasets generated and analysed in the study are available from the corresponding author on reasonable request.

Declarations

Conflict of interest The authors declare no conflict of interest.

Ethical approval No ethics approval was required for this study.

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