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Seagrass losses since mid-20th century fuelled CO_2 emissions from soil carbon stocks

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Abstract

Seagrass meadows store globally significant organic carbon (C_{org}) stocks which, if disturbed, can lead to CO_2 emissions, contributing to climate change. Eutrophication and thermal stress continue to be a major cause of seagrass decline worldwide, but the associated CO_2 emissions remain poorly understood. This study presents comprehensive estimates of seagrass soil C_{org} erosion following eutrophication-driven seagrass loss in Cockburn Sound (23 km^2 between 1960s and 1990s) and identifies the main drivers. We estimate that shallow seagrass meadows (<5 m depth) had significantly higher C_{org} stocks in 50 cm thick soils (4.5 ± 0.7 kg C_{org}/m^2) than previously vegetated counterparts (0.5 ± 0.1 kg C_{org}/m^2). In deeper areas (>5 m), however, soil C_{org} stocks in seagrass and bare but previously vegetated areas were not significantly different (2.6 ± 0.3 and 3.0 ± 0.6 kg C_{org}/m^2, respectively). The soil C_{org} sequestration capacity prevailed in shallow and deep vegetated areas (55 ± 11 and 21 ± 7 g C_{org} m^{-2} $year^{-1}$, respectively), but was lost in bare areas. We identified that seagrass canopy loss alone does not necessarily drive changes in soil C_{org} but, when combined with high hydrodynamic energy, significant erosion occurred. Our estimates point at ~0.20 m/s as the critical shear velocity threshold causing soil C_{org} erosion. We estimate, from field studies and satellite imagery, that soil C_{org} erosion (within the top 50 cm) following seagrass loss likely resulted in cumulative emissions of 0.06–0.14 Tg CO_{2-eq} over the last 40 years in Cockburn Sound. We estimated that indirect impacts (i.e. eutrophication, thermal stress and light stress) causing the loss of ~161,150 ha of seagrasses in Australia, likely resulted in the release of 11–21 Tg CO_{2-eq} since the 1950s, increasing cumulative CO_2 emissions from land-use change in Australia by 1.1%–2.3% per annum. The patterns described serve as a baseline to estimate potential CO_2 emissions following disturbance of seagrass meadows.

KEYWORDS

Blue Carbon, carbon sinks, climate change, conservation, erosion, eutrophication, seagrass meadows

1 | INTRODUCTION

Historically, the pattern of human colonization and settlement globally has relied on the availability of sheltered coastal waters. Unfortunately, as these coastal waters have developed into harbours and anchorages there has been degradation of associated marine ecosystems and the associated loss of the services they provide (Halpern et al., 2008). Global loss of the area covered by seagrasses between 1990 and the early 2000s have been estimated at up to 7% year^{-1} (Short & Wyllie-Echeverria, 1996; Waycott et al., 2009). Anthropogenic activities play a key role in the loss of seagrass due to the impact of coastal development on seagrass ecosystems, including eutrophication and habitat loss due to dredging, anchoring and coastal infrastructure (Orth et al., 2006; Ralph, Tomasko, Moore, Seddon, & Macinnis-Ng, 2006).

Amongst the numerous important ecological services that seagrass meadows provide (Costanza et al., 1997), their capacity to sequester CO_2 has generated considerable interest for its potential role in mitigating climate change (Duarte, Losada, Hendriks, Mazarrasa, & Marba, 2013; Fourqurean et al., 2012; Lavery, Mateo, Serrano, & Rozaimi, 2013). The organic carbon (C_{org}) sequestered

and stored by the oceans and coastal ecosystems, mainly by seagrasses, mangroves and tidal marshes has been termed 'blue carbon' (BC; Nellemann et al., 2009). Seagrasses have been estimated to sequester CO_2 in their soils at rates up to two orders of magnitude faster than in soils from most terrestrial forest ecosystems (Mcleod et al., 2011) and account for 23%–78% of the 43–394 Tg C_{org}/year estimated to be buried by coastal vegetated ecosystems (i.e. seagrasses, tidal marshes and mangroves) each year (Duarte, 2017). BC strategies build on the opportunity to avoid greenhouse gas emissions and to enhance C_{org} sequestration through the conservation, restoration or creation of these ecosystems (Herr, Pidgeon, & Laffoley, 2012). Since C_{org} stores in seagrass soils are preserved over millennia, the conservation of seagrasses constitutes a relevant strategy to avoid CO_2 emissions resulting from seagrass loss (Mcleod et al., 2011).

Human and natural disturbances can result in direct or indirect impacts on seagrass soil C_{org} stocks, with different likelihood of CO_2 emissions (Lovelock, Atwood, et al., 2017). Direct impacts (e.g. dredging, moorings, storms and coastal infrastructure) can physically remove seagrasses and soils, exposing soil C_{org} to oxic
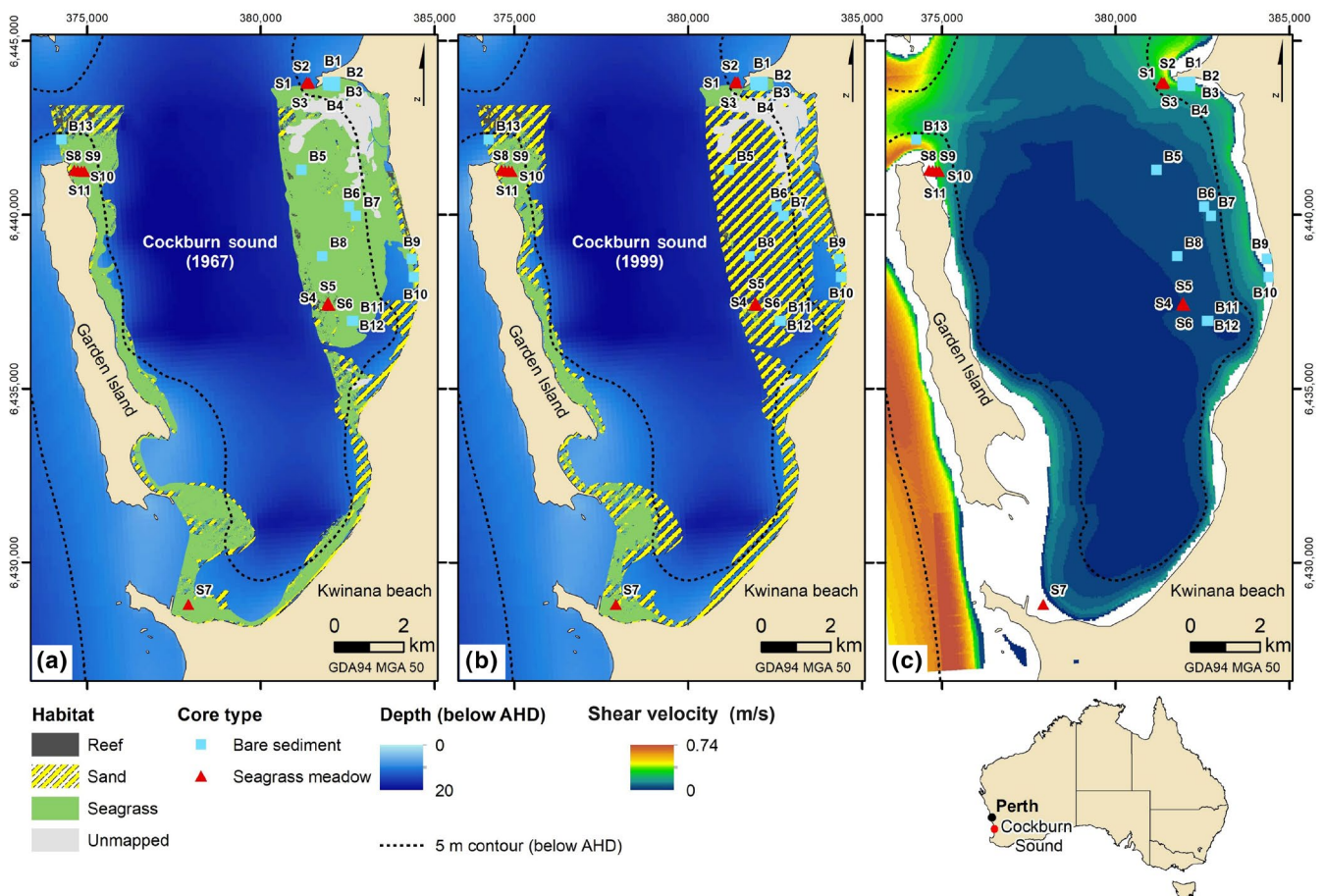

FIGURE 1 Seagrass meadow loss, shear velocity and sampling locations within Cockburn Sound, Western Australia. Changes in seagrass extent based on mapping performed in (a) 1967 and (b) 1999 (modified from Kendrick et al., 2000, 2002). Four habitat types are discerned in the maps: Seagrass (green); sand (stripped yellow); reef (dark grey); unmapped (light grey). Red triangles indicate the location of the cores sampled in persistent seagrass meadows. Light blue squares indicate the sampling areas of cores from bare but previously vegetated areas. (c) Shear velocity (m/s) in shallow (<5 m) and deep areas (>5 m). The 5 m water depth contour is indicated with a dashed line

conditions, favouring remineralization of organic matter (Lovelock, Atwood, et al., 2017; Macreadie et al., 2015; Pendleton et al., 2012; Serrano, Ruhon, et al., 2016). Indirect impacts (e.g. eutrophication, dock shading and heatwave-induced die-off) can result, initially, in the loss of the seagrass canopy, exposing soil C_{org} stocks to hydrodynamic forces and erosion, which ultimately may result in more rapid remineralization of soil C_{org} in oxic conditions (Arias-Ortiz, Serrano, et al., 2018; Marbà et al., 2015; Trevathan-Tackett et al., 2018). However, potential CO_2 emissions linked to the loss of global seagrass extent, such as the 60% loss of global extent since 1950s linked to eutrophication (30,000–110,000 km^2; Pendleton et al., 2012; Short & Wyllie-Echeverria, 1996; Waycott et al., 2009), remain unknown.

Understanding the effects of disturbances such as eutrophication on seagrass soil C_{org} stocks and sequestration rates are critical for the development of BC strategies because they account for a large proportion of global seagrass loss. Indeed, uncertainties around the loss and fate of C_{org} following disturbance of vegetated coastal ecosystems are hindering the implementation of seagrass-based BC strategies (Kelleway et al., 2017; Macreadie et al., 2019).

Here we examine the effects of seagrass loss from eutrophication on soil C_{org} stocks and accumulation rates by comparing persistent seagrass meadows with bare but previously vegetated areas in Cockburn Sound (Western Australia; Figure 1). Cockburn Sound experienced a large loss of seagrass meadows (79%–84% decline in extent equivalent to 23 km^2) between the 1960s and 1990s (Cambridge & McComb, 1984; Kendrick, Hegge, Wyllie, Davidson, & Lord, 2000; Kendrick et al., 2002) due to eutrophication following urban, port and industrial development (Cambridge, Chiffings, Brittan, Moore, & McComb, 1986). We assessed how environmental factors such as water depth, hydrodynamic energy, soil accumulation rates and soil grain size relate to changes in soil C_{org} storage following seagrass loss. Finally, we scaled up the estimates derived from the Cockburn Sound system to provide an estimate of potential CO_2 emissions resulting from indirect disturbances (i.e. eutrophication, thermal stress and light stress) resulting in seagrass canopy loss in Australia since the mid-20th century.

2 | MATERIALS AND METHODS

2.1 | Study site, coring and biogeochemical analysis

Cockburn Sound is an enclosed coastal basin of around 124 km^2 with a maximum depth of 22 m, located 25 km south of Perth, Western Australia (Figure 1). Ten seagrass species can be found in Cockburn Sound, but species of the genus *Posidonia* are dominant (Cambridge & McComb, 1984). Cockburn Sound has experienced significant disturbances (i.e. eutrophication, dredging, moorings and coastal development) following industrial development of the area since the 1950s (Cambridge et al., 1986), leading to the loss of ~80% (23 km^2) of seagrass cover between 1967 and 1999 (Figure 1a,b; Kendrick et al., 2000, 2002). Seagrass loss was most severe in the early 1970s

due to nitrogen enrichment, and increased attenuation of light to seagrasses through increased phytoplankton blooms and growth of epiphytic macroalgae (Silberstein, Chiffings, & McComb, 1986). The loss of seagrass resulted in extensive bare areas around Cockburn Sound, the extent of which has been documented from aerial photographs and mapping between 1967 and 1999 (Kendrick et al., 2000, 2002).

To assess the impacts of seagrass loss on soil C_{org}, 24 cores (11 cores in persistent *Posidonia* spp. meadows and 13 cores in bare but previously vegetated areas; Figure 1) were sampled using PVC pipes (60 mm inner diameter, 80 cm long) that were carefully hammered into the soil in 2014. The locations of the collected cores were based on the historical evidence of seagrass habitat loss from 1972 to 1999 (Kendrick et al., 2000, 2002). The cores were collected in water depths ranging from 1 to 10 m. The length of the corer inserted into the soils and the length of soil recovered were recorded to correct the core lengths for compression effects (Glew, Smol, & Last, 2001). All variables studied here are referenced to the corrected, uncompressed depths.

The cores were cut lengthwise, and soils inside the cores were cut into 1 cm thick slices. Each slice was weighed before and after oven drying at 60°C until constant weight (dry weight) to determine dry bulk density. Alternate slices were separated in two subsamples by quartering. One subsample was ground and analysed for C_{org} content and stable carbon isotope composition ($\delta^{13}C$), while the other subsample was used for soil grain-size analysis. The C_{org} content and the $\delta^{13}C$ signatures were measured by acidifying 1 g of ground sample with hydrochloric acid (4% HCl) to remove inorganic carbon (Schlacher & Connolly, 2014), then centrifuging (3,400 rpm, 5 min) and removing the supernatant with acid residues using a pipette, before washing with Milli-Q water, centrifuging and again removing the supernatant using a pipette. The residual samples were re-dried and weighed, and then encapsulated in tin capsules for C_{org} and $\delta^{13}C$ analyses using a Micro Cube elemental analyser (Elementar Analysensysteme GmbH) interfaced to a PDZ Europa 20–20 isotope ratio mass spectrometer (Sercon Ltd.) at University of California, Davis Facilities. Percentage C_{org} was calculated for the preacidified milled samples. Grain-size distribution was determined using a Coulter LS230 laser-diffraction particle analyser after digesting the organic matter with 10% H_2O_2. The soil particles were classified following a scale adapted from Brown and McLachlan (1990): mud (<0.063 mm), very fine sand (>0.063 <0.125 mm), fine sand (>0.125 <0.25 mm), medium sand (>0.25 <0.5 mm) and coarse sand (>0.5 <1 mm).

A total of 14 cores (eight seagrass cores and six from bare but previously vegetated areas) were analysed for ^{210}Pb in the fine soil fraction (<0.125 mm). The concentrations of ^{210}Pb were determined by alpha spectrometry through the analysis of ^{210}Po after the addition of ^{209}Po as an internal tracer, followed by an acid digestion using an analytical microwave (Sanchez-Cabeza, Masqué, & Ani-Ragolta, 1998). Excess ^{210}Pb ($^{210}Pb_{xs}$) concentrations were determined by subtracting ^{226}Ra concentrations to total ^{210}Pb in each of the profiles. $^{210}Pb_{xs}$ inventories were the result of the integration of $^{210}Pb_{xs}$ concentrations

with cumulative mass (g/cm^2). The concentrations of ^{226}Ra were determined using liquid scintillation counting (Wallac 1220 Quantulus) following Masqué, Sanchez-Cabeza, Bruach, Palacios, and Canals (2002).

2.2 | Numerical procedures

To allow direct comparisons among vegetated and bare but previously vegetated areas, the standing C$_{org}$ stocks per unit area were standardized to a soil thickness of 50 cm (cumulative stocks; kg C$_{org}$/m^2), which involved extrapolating linearly integrated values of cumulative C$_{org}$ stocks with depth in 13 of the 24 cores sampled (i.e. from 40 to 50 cm; R^2 = .99, p < .001; Figure S1).

Soil accumulation rates were estimated using the Constant Flux:Constant Sedimentation model (CF:CS), which assumes a constant flux of ^{210}Pb$_{xs}$ and a constant mass accumulation rate (MAR) with time (Krishnaswamy, Lal, Martin, & Meybeck, 1971). Contemporary C$_{org}$ accumulation rates (CAR) were estimated as the product of the fraction of %C$_{org}$ accumulated over a period t (t = 40 and 100 years) by the mean MAR estimated using the CF:CS model (Equation 1).

=Ct·

$$CAR = C_t \cdot MAR \tag{1}$$

For the cores that were not ^{210}Pb dated, it was assumed that they had the mean accumulation rate of the nearest dated core within each treatment (seagrass and bare).

Seagrass meadow losses in Cockburn Sound between 1967 and 1999 were estimated from the seagrass mapping presented in Kendrick et al. (2000, 2002) and a seamless digital elevation/bathymetric model (DEM). A DEM was elaborated using ArcGIS 10.5 by incorporating multiple elevation datasets, similar to Leon, Phinn, Hamylton, and Saunders (2013). Gridded multibeam bathymetric data collected by Geoscience Australia (50 m resolution) were combined with Shuttle Radar Topography Mission topographic data (250 m resolution; Farr & Kobrick, 2000). Data were filtered using a low-pass filter with a 100 m radius circular window to smooth values and remove remaining outliers. Finally, gridded data were converted to points and interpolated using the natural neighbour algorithm into a 150 m grid projected to UTM49S, WGS84 coordinate system (Figure 1c).

The process-based wave model to obtain the shear velocity consisted of eight grids (five transition grids ranging from 600 to 75 m resolution and three grids covering seagrass meadows of 25 m resolution; Table S1; Figure S2). The wave climate was estimated following the procedure tested by Callaghan, Leon, and Saunders (2015) in which Simulating Waves Nearshore (Booij, Ris, & Holthuijsen, 1999) program was used to simulate wave generation, propagation and dissipation using historical ocean wave, tide and wind measurements covering November 2001 through to January 2017. We assumed that the wave climate remained stable since the 1950s to present, based on previous research showing that wave

height increases along the coastline Western Australia over the last 30 years (0.15 m) were very small compared to natural wave height variability (1–2 m; Bosserelle, Pattiaratchi, & Haigh, 2012). Tidal information was available for 2016 from Bunbury station (Department of Transport, WA) and was repeated for the remaining years. Wind information was available for 3 hourly synoptic wind speed and direction data at Garden Island, Western Australia. These predictions were then ranked, and percentiles extracted for wave height, energy density, flux, surface, shear velocities (i.e. near-bed velocity amplitude of horizontal wave motion) and for velocity divided by square root period, a proxy for maximum velocity in a random wave train (Callaghan et al., 2015).

The data were normally distributed, and Pearson correlation tests were used to evaluate the relationships between soil C$_{org}$ content and mud content in seagrass and bare cores (Figure S3). Generalized linear models were used to test for significant effects of the fixed factors, that is, Treatment (bare and seagrass areas), Water depth (shallow and deep) and Core depth (24 depths along 50 cm thick soil cores), as well as the interaction of Treatment and Water depth on the response variables (dry bulk density, C$_{org}$ content, mud content [<0.063 mm], δ^{13}C, shear velocity and C$_{org}$ stocks). These variables were square-root transformed prior to analyses to obtain homogeneous variances (Table S2). A Change-Point Analyser model (W. Taylor V.2.3; bootstrap test) was used to determine thresholds in the relationship between shear velocity and soil C$_{org}$ stocks in bare but previously vegetated areas. Model asumptions were not tested due to insufficient data to perform testing of assumptions.

The proportion of the autochthonous (seagrass) and allochthonous (seston + macroalgae and terrestrial) C$_{org}$ present in the soils was estimated through Stable Isotope Mixing Models in R using simmr and rjags packages (Parnell, 2016; Parnell et al., 2013). This model allows the incorporation of the uncertainty linked to the use of a single isotope (i.e. δ^{13}C) by fitting a Bayesian model 'simmr_mcmc' (Parnell et al., 2013). The Bayesian model works by repeatedly producing probable values of the proportionate contribution of source material (i.e. seagrass, seston + macroalgae and terrestrial) through a Markov chain Monte Carlo, by initial burn-in iterations (1,000) discarded and subsequent iterations (10,000) stored for use in the posterior distribution and analyses of the data (Parnell, Inger, Bearhop, & Jackson, 2010; Parnell et al., 2013). A one-isotope, three-sources mixing model was built using δ^{13}C literature values of potential organic matter sources from the Perth region, and grouped into (a) terrestrial (–26.1 ± 4.6‰; Loneragan, Bunn, & Kellaway, 1997); (b) seston plus macroalgae (–18.6 ± 1.8‰; Belicka et al., 2012; Crawley, Hyndes, Vanderklift, Revill, & Nichols, 2009); and (c) shallow seagrasses (–10.85 ± 1.34‰) or deep seagrass (–11.8 ± 2.1‰) sources (Collier, Lavery, Ralph, & Masini, 2008; Serrano, Ricart, et al., 2016). The δ^{13}C values for the terrestrial and seston plus macroalgae sources were assumed to be constant in shallow and deep areas, while the seagrass δ^{13}C values used for the cores from shallow areas were ^{13}C-enriched compared to the deeper areas (Collier et al., 2008).

Differences in soil C_{org} stocks (kg/m^2), %C_{org} and δ^{13}C along soil depth between vegetated and bare but previously vegetated areas within shallow (sampled between 1 and 5 m water depth) and deep (from 6 to 10 m) habitats were assessed using a t test ($p < .05$ between the top 30–50 cm in shallow areas and $p < .05$ within the top 8 cm in deep areas). Estimates of change in soil C_{org} stocks following seagrass canopy loss were calculated based on the difference between average C_{org} stocks in shallow seagrass and shallow bare but previously vegetated areas, and between average C_{org} stocks in deep seagrass and deep bare but previously vegetated areas. Lower estimates were based on the difference between top 50 cm thick soil in seagrass soils and bare but previously vegetated areas, while upper estimates accounted for potential changes in topography and were calculated based on the difference between top 50 cm thick soils in seagrass and top 20 cm thick in bare (upper estimates for shallow sites), and between the top 50 cm thick soils in seagrass and top 42 cm thick in bare for deep sites (upper estimates in deep sites).

The upper and lower estimates of soil C_{org} stock loss per hectare at shallow and deep meadows were multiplied by the total seagrass extent loss in shallow (9 km^2) and deep areas (14 km^2) respectively. We modelled the potential $CO_{2\text{-eq}}$ emissions from the portion of soil C_{org} lost using a modified Equation (2; Lovelock, Fourqurean, & Morris, 2017).

$$C_{org\,(t)} = \alpha \times C_{org\,(0)} \times e^{-k_1 \times t} \qquad (2)$$

where α is the portion of C_{org} exposed to oxic conditions, $C_{org\,(0)}$ is the difference between the C_{org} stocks in seagrass areas and bare but previously vegetated areas, k is the decomposition rate under oxic conditions (0.0005/day; Lovelock, Fourqurean, et al., 2017) and t is time.

In our model, we assumed that between 50% and 100% of the soil C_{org} eroded was exposed to oxic conditions ($\alpha = 0.5$ and 1). The upper estimate (100%) relies in the assumption that all soil C_{org} eroded remained exposed to oxic conditions, while the lower estimate relies on the assumption that a portion of the soil C_{org} eroded (50%) ended up being buried in anoxic conditions elsewhere. The cumulative potential $CO_{2\text{-eq}}$ emissions were assessed for four periods based on estimates of seagrass extent loss between 1972 and 2014 ($t = 42$ years; 1,568 ha), 1982 and 2014 ($t = 32$ years; 599 ha), 1995 and 2014 ($t = 19$ years; 61 ha) and 1999 and 2014 ($t = 15$ years; 28 ha; Kendrick et al., 2000, 2002). Estimates of potential $CO_{2\text{-eq}}$ emissions following seagrass canopy loss due to indirect disturbances (i.e. eutrophication, thermal stress and light stress) in Australia were based on the assumptions that (a) the average C_{org} stock within the top 50 cm of seagrass soils was 56 Mg C_{org}/ha (Lavery et al., 2013); (b) 83%–85% of soil C_{org} stock has been eroded since disturbance (average loss estimated in this study, which is similar to the 78% previously reported following eutrophication-induced seagrass loss; Marbà et al., 2015) and equivalent to 46–48 Mg C_{org}/ha; (c) 50%–100% of the soil C_{org} eroded has been exposed to oxic conditions decaying at 0.0005/day (Lovelock, Fourqurean, et al., 2017) over 64 years (i.e. from 1950 to 2014); and (d) that 75% of the 161,150 ha of seagrass loss due to indirect impacts in Australia (Statton et al., 2018; Strydom et al., 2020) have been exposed to shear velocity >0.2 m/s resulting in soil C_{org} erosion.

3 | RESULTS

The MARs and soil accumulation rates over the last 40 and 100 years were estimated for six out of the 14 cores dated. MARs and soil accumulation rates could not be estimated for the other eight cores due to the lack of $^{210}Pb_{xs}$ due to erosion or lack of deposition in three bare cores (B10, B12, B13) and one seagrass core (S1), and the intense soil mixing in three bare cores (B5, B7, B11) and one seagrass core (S5; Figure S4). Soil mixing may lead to the overestimation of soil accumulation rates, hence where mixing is present (i.e. in cores S4, S8, S9, S10), rates should be considered as upper limits.

The dry bulk density was significantly lower in seagrass soils (mean ± SE; 0.95 ± 0.04 g/cm^3) than in bare but previously vegetated soils (1.17 ± 0.04 g/cm^3) at Cockburn Sound ($p < .001$; Tables S2 and S3). The t test results showed that soil C_{org} stocks in shallow seagrass and bare sites were significantly different in the upper 50 cm of the cores ($p < .05$), but %C_{org} and δ^{13}C were significantly different within the top ~30 cm soils ($p < .05$; Figure 2). At deep areas, significant downcore differences in soil C_{org} stocks, %C_{org} and δ^{13}C between seagrass and bare sites were only found within the top 8 cm ($p < .05$). Based on these results, we assumed that erosion affected the upper 30 and 8 cm of seagrass soils following canopy loss to calculate upper estimates of soil C_{org} losses in shallow and deep areas respectively.

The soil C_{org} content within the top 50 cm was up to threefold higher in seagrass soils (1.08 ± 0.07% C_{org}) than in bare but previously vegetated soils (0.32 ± 0.03% C_{org}; $p < .001$). The seagrass soil C_{org} stocks in 50 cm thick deposits in Cockburn Sound ranged from 1.8 to 5.8 kg C_{org}/m^2 (3.6 ± 0.5 kg C_{org}/m^2), with contemporary seagrass soil CARs of 38 ± 10 g C_{org} m^{-2} year^{-1} (over the last 40 years) and 23 ± 6 g C_{org} m^{-2} year^{-1} (over the last 100 years). The soil C_{org} stocks in 50 cm thick deposits in bare but previously vegetated areas ranged from 0.4 to 5.1 kg C_{org}/m^2 (1.7 ± 0.4 kg C_{org}/m^2); however, it was not possible to estimate CARs due to lack of $^{210}Pb_{xs}$ or mixing. The soil C_{org} stocks were not significantly different between seagrass soils and bare but previously vegetated soils ($p = .52$; Table S2). The seagrass soils were δ^{13}C-enriched (−12.8 ± 0.2‰) compared to bare but previously vegetated soils (−16.5 ± 0.2‰; $p < .001$). By applying a one-isotope three-source (i.e. seagrass, seston + macroalgae and terrestrial) mixing model, we estimated that seagrass detritus contributed 70 ± 3% to the C_{org} pool in seagrass soils but only 40 ± 5% in bare but previously vegetated areas. Mud content was similar in seagrass and bare cores (4.3 ± 0.4% and 6.2 ± 0.6% respectively; $p = .25$; Tables S2 and S3).

Shallow seagrass soils, closer to the upper limit of distribution (at 1–5 m depth), had significantly higher C_{org} content (1.3 ± 0.2% C_{org}) than seagrass soils closer to the deep limits of distribution (at 6–10 m depth; 0.8 ± 0.1% C_{org}; $p < .001$; Figure 2). Shallow bare but previously vegetated soils had significantly lower C_{org} content (0.12 ± 0.01% C_{org}) than deeper counterparts (0.54 ± 0.06% C_{org}; $p < .001$; Figure 2; Tables S2 and S3). The soil C_{org} stocks were up to ninefold higher in shallow seagrass soils (4.5 ± 0.7 kg C_{org}/m^2) compared to shallow bare but previously vegetated soils (0.5 ± 0.1 kg C_{org}/m^2; $p < .001$; Table 1). The CARs in shallow seagrass were estimated at
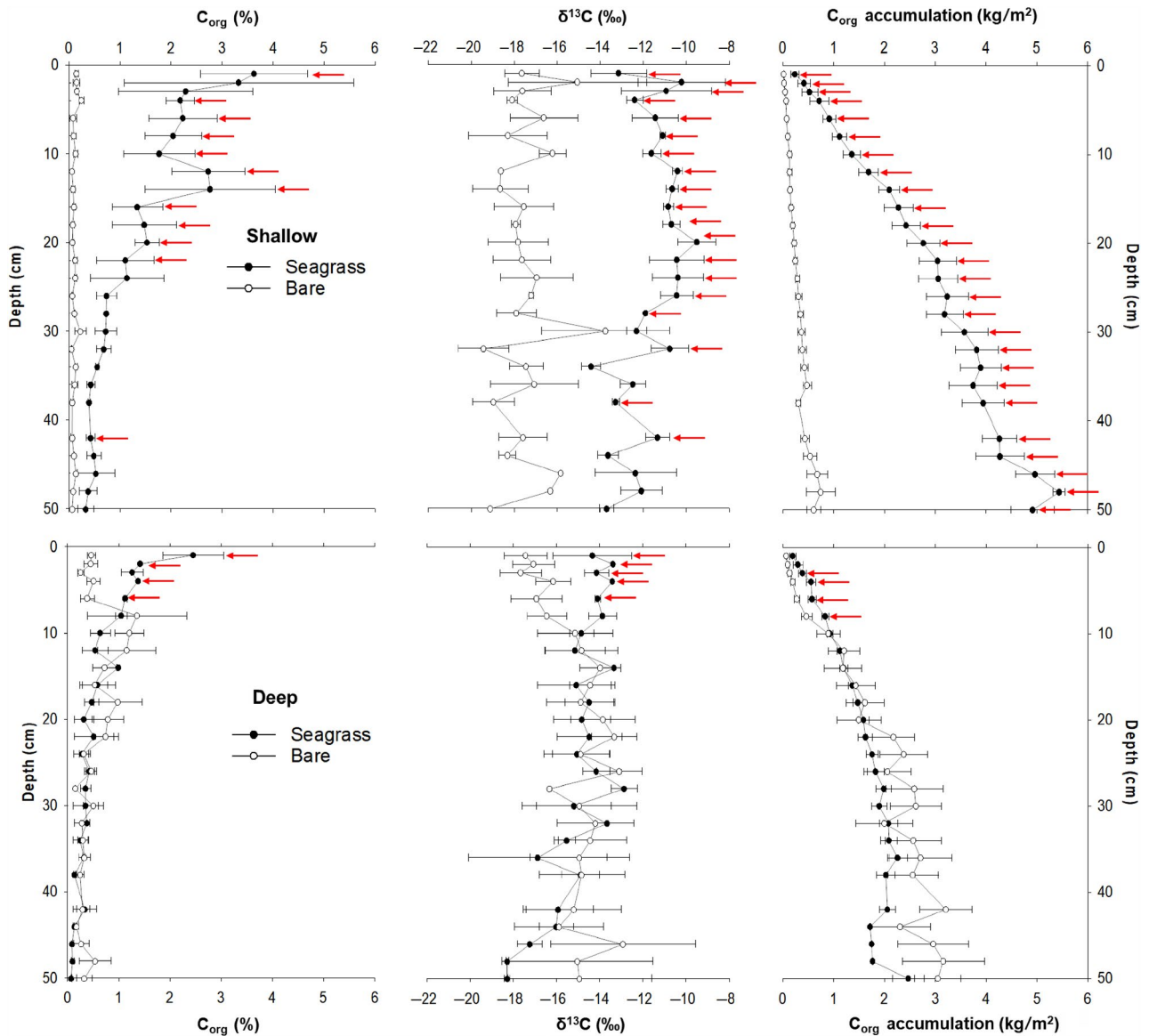
FIGURE 2 Trends in biogeochemical characteristics along soil depth in shallow and deep seagrass and bare but previously vegetated areas. C_{org} content (%), $\delta^{13}C$ (‰) and C_{org} accumulation (kg/m²) from seagrass (11 cores) and bare cores (13 cores) sampled in shallow (1–5 m; 13 cores) and deep (6–10 m depth; 11 cores) areas. Significant differences ($p < .05$; t test) between seagrass and bare areas for each depth are indicated with red arrows and conform the basis to evaluate the potential soil thickness eroded in bare but previously vegetated areas. Average ± standard error (SE)

TABLE 1 Inventories of organic carbon stocks (kg C_{org}/m²), short-term (last 100 years) soil accumulation rates (SAR) and mass accumulation rates (MAR), short-term (40 and 100 years) organic carbon (C_{org}) accumulation rates in shallow (1–5 m depth) and deep (6–10 m depth) seagrass soils at Cockburn Sound. Average ± standard error (SE). It was not possible to estimate SAR and/or MAR in bare but previously vegetated soils

| | | | | | C_{org} accumulation rates (g C_{org} m⁻² year⁻¹) | |
Depth	Treatment	Stocks (kg C_{org}/m²)	MAR (g cm⁻² year⁻¹)	SAR (cm/year)	Short term (last 40 years)	Short term (last 100 years)
Shallow	Seagrass	4.5 ± 0.7	0.19 ± 0.02	0.28 ± 0.05	55 ± 11	30 ± 10
	Bare	0.5 ± 0.1	—	—	—	—
Deep	Seagrass	2.6 ± 0.3	0.16 ± 0.06	0.18 ± 0.05	21 ± 7	16 ± 51
	Bare	3.0 ± 0.6	—	—	—	—

55 ± 11 g C_{org} m^{-2} year^{-1} and 30 ± 10 g C_{org} m^{-2} year^{-1} over 40 and 100 years respectively. However, CARs could not be estimated for neither shallow or deep bare areas because these sites experienced erosion, lack of deposition and/or soil mixing following seagrass canopy loss, which together with the relatively low content of mud within bare soils suggests that resuspension can lead to erosional processes after seagrass canopy loss occurred, in particular at the shallow sites. In deep areas, the C_{org} stocks in 50 cm thick soils were similar in both vegetated and bare areas (2.6 ± 0.2 and 3.0 ± 0.6 kg C_{org}/m^2 respectively; $p < .05$; Table 1). The $^{210}Pb_{xs}$ inventories in soils from shallow seagrass (426 ± 176 Bq/m^2) were similar to the $^{210}Pb_{xs}$ inventories in deep seagrass and bare but previously vegetated areas (440 ± 154 and 683 ± 262 Bq/m^2 respectively; $p < .05$), but one order of magnitude higher than in shallow bare soils (10 ± 10 Bq/m^2; Figure 3a).

The $\delta^{13}C$ signatures of soil organic matter in shallow seagrasses (-11.7 ± 0.2‰) were enriched in $\delta^{13}C$ compared to those in shallow bare but previously vegetated areas (-17.2 ± 1.6‰), deep seagrass areas (-16.0 ± 1.0‰) and deep bare areas (-15.6 ± 0.8‰; Table S3). The isotope mixing models applied indicated that seagrass detritus contributed 76%–83% to the soil C_{org} pool in shallow seagrasses,
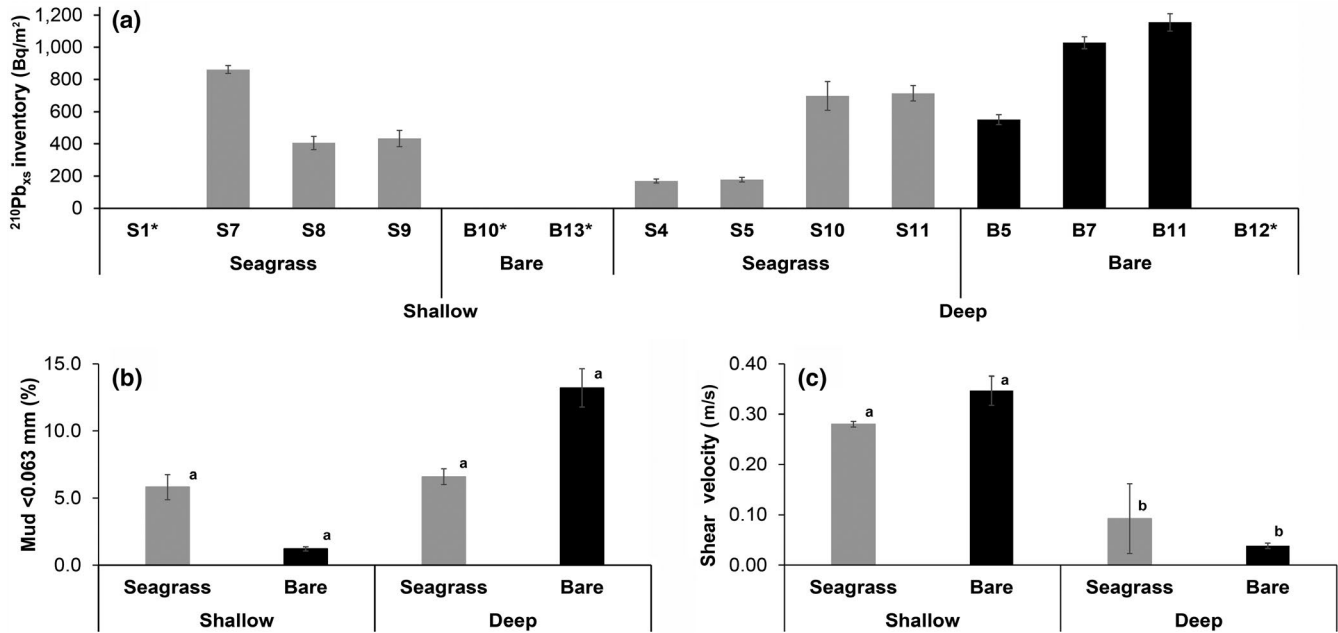

FIGURE 3 Differences in (a) ^{210}Pb excess inventories (Bq/m^2) (b) mud content <0.063 mm (%) and (c) shear velocity (m/s) between seagrass and bare but previously vegetated areas in shallow and deep areas. Significant pairwise differences ($p < .05$) are indicated with letters (a, b) based on the results of Tukey HSD posthoc test. *The excess ^{210}Pb inventories were negligible
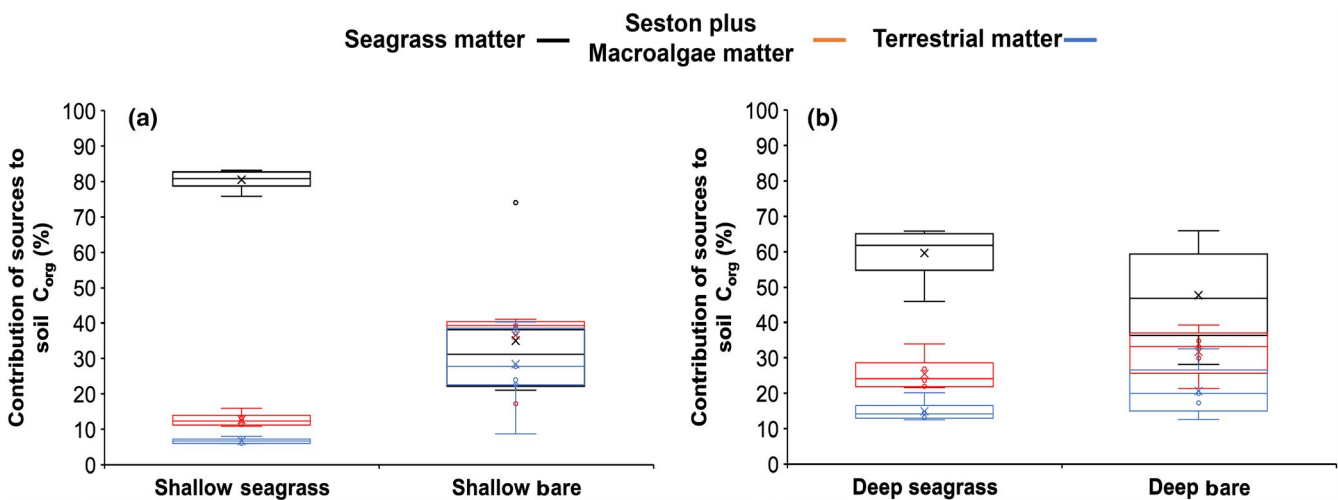

FIGURE 4 Box plots of the mixing models to determine the contribution of sources to soil C_{org} in (a) shallow and (b) deep areas within seagrass and bare but previously vegetated areas at Cockburn Sound. The contribution (%) of autochthonous source (seagrass matter, black) and allochthonous sources seston plus macroalgae matter (red) and terrestrial matter (blue). Boxes indicate interquartile range, while the whiskers extend to the most extreme data point and the individual points indicate outliers

but lower in deep seagrasses (46%–66%), deep bare but previously vegetated areas (28%–66%) and in shallow bare but previously vegetated areas (21%–74%; Figure 4). Seston plus macroalgae contributed around 17%–41% and 21%–39% to the soil C_{org} pool in shallow and deep bare but previously vegetated areas respectively. The contribution of terrestrial detritus ranged between 6%–20% and 9%–40% among seagrass and bare areas across water depths respectively. Shallow seagrass soils had up to fivefold higher mud content <0.063 mm (5.8 ± 0.9%) compared to shallow bare soils (1.2 ± 0.2%; Figure 3b). In contrast, mud content was significantly higher in deep bare soils (13.2 ± 1.4%) than in deep seagrass soils (6.6 ± 0.6%; $p < .001$). We found a lack of correlation between mud and soil C_{org} contents ($R^2 = .2$; $p > .05$; Figure S3). The wave model developed for Cockburn Sound showed that shallow areas <5 m experience up to tenfold higher shear velocity (0.31 ± 0.02 m/s) than deeper areas (0.03 ± 0.01 m/s; $p < .001$; Figure 3c).

4 | DISCUSSION

4.1 | Trends in C_{org} stocks, accumulation rates and sources in seagrass meadows

The seagrass soil C_{org} content at Cockburn Sound (ranging from 0.40% to 1.98% C_{org}) was lower than global estimates (2.5 ± 0.1% C_{org}; Fourqurean et al., 2012) but similar to Australian seagrass meadows (range 0.1%–2.1% C_{org}; Lavery et al., 2013; Macreadie, Allen, Kelaher, Ralph, & Skilbeck, 2012; Samper-Villarreal, Lovelock, Saunders, Roelfsema, & Mumby, 2016). The seagrass soil C_{org} stocks and CARs at Cockburn Sound (1.8–5.8 kg C_{org}/m^2 and 23–38 g C_{org} m^{-2} year^{-1}) are within the range of Australian seagrasses (0.5–9.7 kg C_{org}/m^2 and 16–46 g C_{org} m^{-2} year^{-1}; Arias-Ortiz, Serrano, et al., 2018; Lavery et al., 2013; Marbà et al., 2015; Serrano, Ruhon, et al., 2016), and support previous findings showing five to eightfold higher CARs in seagrass compared to terrestrial forest ecosystems (4.6 ± 1.2 g C_{org} m^{-2} year^{-1}; Mcleod et al., 2011).

The contribution of seagrass detritus to the soil C_{org} pool in seagrass areas (60%–81%) was higher than global estimates (50%; Kennedy et al., 2010), indicating a low supply rate of alternative sources of C_{org} in Cockburn Sound, which has no direct riverine discharges supplying terrestrial material (Loveless, Oldham, & Hancock, 2008), very little hard rocky substrate to support macroalgae growth and generally low phytoplankton production, excluding the period of eutrophication that resulted in increased macroalgal and phytoplankton biomass (Chiffings & McComb, 1981). Differences in soil C_{org} content can also be influenced by differences in soil mud (<0.063 mm) content (Serrano, Ricart, et al., 2016). However, the lack of correlation between mud and soil C_{org} content supports the hypothesis of low terrigenous inputs in Cockburn Sound.

The higher soil C_{org} storage capacity of shallow seagrasses (between 1 and 5 m depth) compared to meadows closer to the deep limits of distribution (at 6–10 m depth) was likely related to the higher productivity, cover and density of shallower meadows (Serrano,

Lavery, Rozaimi, & Mateo, 2014; Serrano, Ricart, et al., 2016). The higher Sediment Accumulation Rates and contribution of seagrass detritus to the soil C_{org} in shallower seagrass meadows compared to deep meadows supports this hypothesis.

4.2 | Drivers of soil C_{org} erosion following seagrass loss

From the 1960s, seagrass meadows in Cockburn Sound experienced continuous losses driven by eutrophication (Cambridge et al., 1986), with 79%–84% (~23 km^2) losses between 1967 and 1999 in its distribution range between 1 and 10 m water depth (Figure 1; Kendrick et al., 2000, 2002). About 40% (9 km^2) of the losses occurred in shallow areas (1–5 m), while the remaining 60% (~14 km^2) occurred in deep areas. The ecosystem shifts from seagrass meadows to bare sediments resulted in a decline of soil C_{org} stocks in shallow areas estimated between 4.0 ± 0.7 kg C_{org}/m^2 (lower estimates comparing stocks in 50 cm thick soils) and 4.3 ± 0.6 kg C_{org}/m^2 (upper estimates accounting for potential soil erosion), which is equivalent to 88%–95% C_{org} stock loss after ~40 years. However, soil C_{org} stock change in deep areas ranged from −0.4 to 0.02 kg C_{org}/m^2, equivalent to −15 to 1% C_{org} stock gain and loss, respectively after ~40 years. Seagrass loss also entailed the loss of C_{org} sequestration capacity in both shallow and deep areas. These point to significant differences in soil C_{org} erosion following seagrass canopy loss among deep and shallow habitats, which can be related to differences in the interactions among hydrodynamic energy, mud content, the recalcitrance and amount of soil C_{org} stocks and water depth (Lovelock, Atwood, et al., 2017). In particular, the relationship between soil C_{org} stock in bare areas and shear velocity showed an upper threshold to erosion of soil C_{org} of 0.20 m/s (threshold ranging from 0.03 to 0.25 m/s; Figure 5) in Cockburn Sound. The lack of soil C_{org} data from areas with 0.15–0.24 m/s shear velocities precluded constraining the threshold. Therefore, the upper threshold estimated
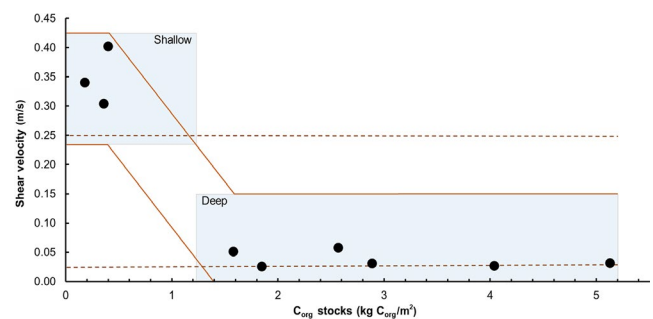

FIGURE 5 Shift in C_{org} stocks (kg C_{org}/m^2) in bare but previously vegetated areas driven by differences in shear velocity (m/s) among study areas. The coloured areas represent the regions expected to contain all the values based on a Change-Point Analyzer model (W. Taylor V.2.3). The red dashed lines indicate the upper and lower limits (range between 0.03 and 0.25 m/s). The upper threshold (>0.20 m/s) was identified as a limit resulting in soil C_{org} erosion at Cockburn Sound, which occurred at shallow (<5 m) areas but not at deep (>5 m) areas

in our study (0.20 m/s) is conservative, and indeed, is in strong agreement with previous estimates pointing at ~0.20 m/s as the critical shear velocity thresholds causing sediment resuspension in bare areas (Dahl et al., 2018). The shear velocity in Cockburn Sound is driven mainly by wave action modulated by water depth, but this may not be the case elsewhere. Further research should explore the susceptibility of seagrass soil C_{org} erosion prior to the deterioration of the meadows, based on shield stress that accounts for the soil dry bulk density and grain-size characteristics on sediment resuspension, to inform conservation efforts aimed at protecting BC sinks.

The comparison of biogeochemical soil characteristics among seagrass and bare cores at shallow and deep areas also supports the hypothesis of soil C_{org} erosion following seagrass canopy loss. Shallow seagrass soils had up to fivefold higher mud content and up to 40-fold higher $^{210}Pb_{xs}$ inventories compared to shallow bare soils (Figure 3). In contrast, mud contents and ^{210}Pb inventories were similar between deep seagrass and deep bare soils, suggesting that the loss of soil C_{org} predominantly occurred in shallow areas and was linked to hydrodynamic forces causing soil resuspension and erosion. The erosion of mud particles, which is associated with high C_{org} and ^{210}Pb concentrations (Arias-Ortiz, Masqué, et al., 2018), has been identified as the main process leading to soil C_{org} loss. In contrast, the relatively low shear velocity in deep areas supports a stable depositional environment even after seagrass canopy loss, with extant rhizome and root debris present underneath the soil surface.

In shallow areas, the loss of seagrass resulted in a reduction of seagrass-C_{org} and an increase in seston plus macroalgae-C_{org} (Figure 4), despite the relatively high amounts of degradation-resistant organic compounds in seagrass matter (e.g. lignin and cellulose) compared to seston and algal detritus (Burdige, 2007; Laursen, Mayer, & Townsend, 1996), which are more prone to remineralization during early diagenesis (Macko, Engel, & Parker, 2011). Selective preservation of recalcitrant compounds (i.e. lignin), which are enriched in $\delta^{13}C$ (Lehmann, Bernasconi, Barbieri, & McKenzie, 2002), could also explain the decrease in $\delta^{13}C$ values of soil C_{org} in bare areas. Together, these findings suggest that relative high shear velocity in shallow areas led to the resuspension and erosion of soil C_{org} stocks, including below-ground seagrass biomass, following seagrass canopy loss, enhanced by the resuspension of C_{org}-rich fine sediments (i.e. sandification; Van Katwijk, Bos, Hermus, & Suykerbuyk, 2010) and the remineralization of more labile sources of soil C_{org} (Figure 6). Therefore, the risk of soil C_{org} loss and CO_2 emissions following seagrass disturbance varies among habitats, a finding that has implications for conservation and restoration strategies aiming to mitigate climate change.

4.3 | Carbon dioxide emissions following seagrass loss

Eutrophication-driven seagrass loss at Cockburn Sound resulted in the erosion of 92% of the C_{org} stock within the top 50 cm of soil over the last 40 years, in habitats with shear velocity >0.20 m/s.

The cumulative soil C_{org} losses in the upper 50 cm of soil across the 9 km^2 of shallow seagrass meadows lost between 1967 and 1999 at Cockburn Sound were estimated at 35,000–38,200 Mg C_{org}. The 88%–95% soil C_{org} erosion estimated in our study is comparable, albeit slightly higher than the 78% loss reported for an estuarine *Posidonia* meadow in a more sheltered bay, due to eutrophication over a similar period (Marbà et al., 2015) and the estimates of soil C_{org} loss following direct physical disturbance such as boat moorings (75%; Serrano, Ruhon, et al., 2016) and seismic testing (73%; Macreadie et al., 2015). In addition, the decay rate of seagrass soil C_{org} under oxic conditions has been estimated at 0.0005/day, which converts in ~70%–80% loss of soil C_{org} over ~40 years when the eroded C_{org} becomes exposed to oxic conditions after disturbance (Lovelock, Fourqurean, et al., 2017). Therefore, both empirical case studies and models support similar rates of soil C_{org} loss following seagrass disturbance.

The fate of the eroded soil C_{org} remains unknown, but assuming that 50%–100% of the soil C_{org} lost from bare but previously vegetated soils was exposed to an oxic environment since 1972, we can estimate a cumulative emission of 0.06–0.14 Tg CO_{2-eq} over the last 42 years at Cockburn Sound. Within Australia, seagrass losses linked to indirect disturbances could have resulted in cumulative emissions of 11–21 Tg CO_{2-eq}. These emissions (averaging 0.16–0.33 Tg CO_{2-eq}/year since the 1950s) would have increased emissions from land-use change in Australia (14.4 Tg CO_2 annually at 2000s rates; Haverd et al., 2013) by 1.1%–2.3% per annum. These first order estimates need to be regarded as lower limits, because the extent of seagrass lost due to indirect impacts in Australia reported by Statton et al. (2018) is likely an underestimate, soil C_{org} disturbance can reach deeper than 50 cm depth (Pendleton et al., 2012; this study) and the emissions from living plant biomass were not accounted for.

Nevertheless, these estimates are extrapolations from one case study only and therefore, they should be interpreted with caution. Seagrasses occupy a small portion of the world's surface (0.1%), but its loss can result in disproportionally large CO_2 emissions compared to disturbing green carbon ecosystems (Mcleod et al., 2011). Coastal eutrophication accounted for 60% of loss of seagrass extent since 1950s worldwide, equivalent to 30,000–110,000 km^2 (Pendleton et al., 2012; Waycott et al., 2009), and further studies are required to estimate the magnitude and fate of soil C_{org} losses from disturbance of seagrass ecosystems to understand their implications in the carbon cycle at global scales (Macreadie et al., 2019).

4.4 | Conservation strategies for climate change mitigation

Here we add to existing knowledge of the processes that impact on C_{org} sequestration and greenhouse gas emissions (Marbà et al., 2015) by demonstrating that seagrass canopy loss poses a significant risk of CO_2 emissions. Avoiding seagrass canopy losses should, therefore, be an important component of BC strategies. Seagrass conservation and restoration provide opportunities for enhancing CO_2 sequestration
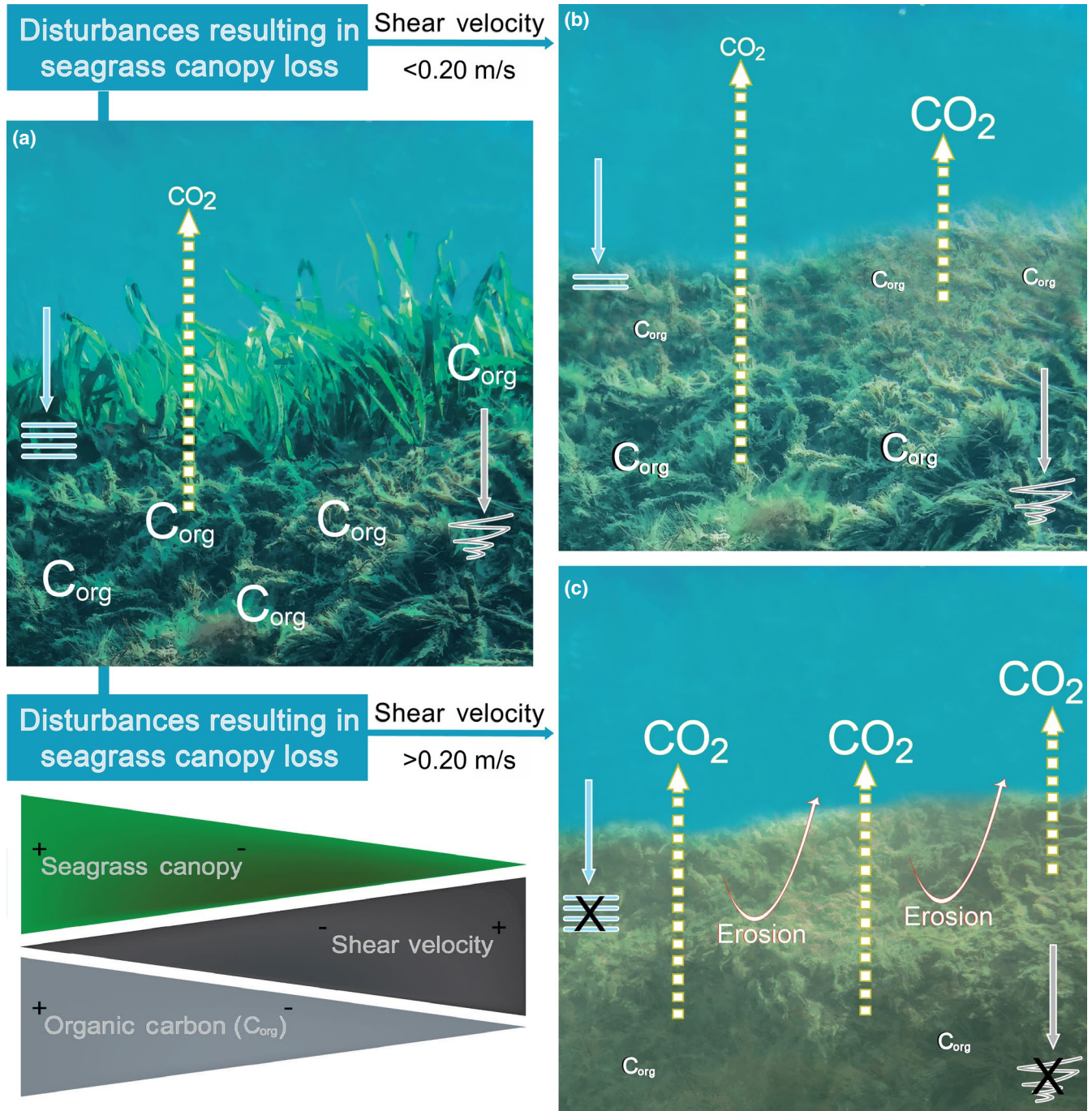
FIGURE 6 Conceptual diagram of the changes in soil organic carbon (C_{org}) following seagrass canopy loss. (a) Seagrass meadows in healthy condition. (b) Bare but previously vegetated soils affected by shear velocity <0.20 m/s. (c) Bare but previously vegetated soils affected by shear velocity >0.20 m/s. Bare soils exposed to shear velocities <0.20 m/s experienced lower erosion and loss of soil C_{org} stocks compared to areas exposed to shear velocities >0.20 m/s. Blue symbols indicate soil C_{org} accumulation, grey symbols show C_{org} stocks and yellow symbols indicate CO_2 emissions

and/or avoid CO_2 emissions, in addition to maintaining or enhancing additional ecosystem services. The potential of seagrass conservation for climate change mitigation relies on the preservation of their millenary soil C_{org} stocks. Disturbance of seagrass ecosystems can result in the exposure of a portion of the soil C_{org} to oxic conditions and decaying at a fast rate (estimated at 0.0005/day; Lovelock, Fourqurean, et al., 2017), which can result in the remineralization of 88%–95% of

the soil C_{org} stock within a decade. Since major historic losses of seagrass extent worldwide occurred more than two decades ago, restoration of these areas may have little benefit in terms of avoided CO_2 emissions, although would contribute to CO_2 sequestration in addition to recovering several additional ecosystem services such as fisheries, biodiversity and coastal protection (Orth et al., 2006). The results obtained here demonstrate that the loss of seagrass over 40 years has

resulted in more significant loss of seagrass soil C_{org} stocks in areas where bare soils are exposed to shear velocity >0.20 m/s (e.g. shallow areas at Cockburn Sound), suggesting that these areas may be more appropriate for the focus of seagrass conservation efforts aimed to avoid CO_2 emissions, where C_{org} stocks are higher and at risk of erosion. This finding reinforces the need to develop baseline data and estimates of C_{org} sequestration in seagrass ecosystems that follow the tiers 2 and 3 from IPCC (Kelleway et al., 2017) for application in greenhouse gas crediting projects rather than relying on global averaged emission factors.

AUTHOR CONTRIBUTION

C.S. and O.S. designed the study, performed the experiment, analysed the data and drafted the first version of the manuscript. J.L. and D.C derived the hydrodynamic models and A.A.-O. and P.M. derived the dating models. All authors contributed to the writing and editing of the manuscript.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Edith Cowan University Research portal, http://doi.org/10.25958/5ed5bab3b80bc.

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SUPPORTING INFORMATION

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

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