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A marine heat wave drives massive losses from the world's largest seagrass carbon stocks

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Abstract

Seagrass ecosystems contain globally significant organic carbon (C) stocks. However, climate change and increasing frequency of extreme events threaten their preservation. Shark Bay, Western Australia, has the largest C stock reported for a seagrass ecosystem, containing up to 1.3% of the total C stored within the top meter of seagrass sediments worldwide. Based on field studies and satellite imagery, we estimate that 36% of Shark Bay's seagrass meadows were damaged following a marine heat wave in 2010/11. Assuming that 10 to 50% of the seagrass sediment C stock was exposed to oxic conditions after disturbance, between 2 and 9 Tg CO_2 could have been released to the atmosphere during the following three years, increasing emissions from land-use change in Australia by 4 - 21% per annum. With heat waves predicted to increase with further climate warming, conservation of seagrass ecosystems is essential to avoid adverse feedbacks on the climate system.

Vegetated coastal ecosystems, including seagrass meadows, mangroves and tidal marshes, are collectively termed "blue carbon" ecosystems storing globally-relevant carbon stocks in their sediments and biomass[1]. Their organic carbon (C) sink capacity is estimated to be 0.08-0.22 Pg C yr^{-1} globally[2], accounting for an offset of 0.6 - 2% of global anthropogenic CO_2 emissions (49 Pg CO_2eq yr^{-1})[3]. However, blue carbon ecosystems are in decline worldwide[2], raising concern about a potential re-emission of their C stocks to the atmosphere as CO_2. CO_2 emissions from loss of blue carbon ecosystems are estimated at 0.15 - 1.02 Pg CO_2 yr^{-1}, which is equivalent to 3 – 19% of those from terrestrial land-use change[4].

Seagrasses are marine flowering plants that consist of 72 species growing across a wide range of habitats[5]. Global estimates of C storage in the top meter of seagrass sediments range from 4.2 to 8.4 Pg C[6], although large spatial variability exists related to differences in biological (e.g., meadow productivity and density), chemical (e.g., recalcitrance of C) and physical (e.g., hydrodynamics and bathymetry) settings in which they occur[7,8]. Since the beginning of the twentieth century, seagrass meadows worldwide have declined at a median rate of 0.9% yr^{-1} mostly due to human impacts such as coastal development or water quality degradation[9]. Climate change impacts, such as ocean warming and extreme events (e.g., ENSO), are exacerbating this trend. Marine heat waves have led to losses of foundation seagrass species that form organic-rich sediment deposits beneath their canopies (e.g. *Posidonia oceanica* in the Mediterranean Sea[10] and *Amphibolis antarctica* in Western Australia[11–13]). Seagrass losses and the subsequent erosion and remineralization of their sediment C stocks are likely to continue or intensify under climate change[9], especially in regions where seagrasses live close to their thermal tolerance limits[14].

Shark Bay (Western Australia) (Fig.1) contains one of the largest (4,300 km^2) and most diverse assemblage of seagrasses worldwide[15], occupying between 0.7 and 2.4% of the world seagrass area. Up to 12 seagrass species are found in Shark Bay, storing C in their sediments and shaping its geomorphology. The two most notable seagrass banks, the Wooramel Bank and the Faure Sill, are the result of ~8,000 yr of continuous seagrass growth[16]. Despite seagrasses having thrived over millennia in Shark Bay, unprecedented widespread losses occurred in the austral summer of 2010/2011 in both the above- and below-ground biomass of the dominant seagrass *A. antarctica* and to a minor extent *P.* australis[12,13], the two species forming large continuous beds. For more than 2 months, a marine heat wave elevated water temperatures 2-4°C above long-term averages[17]. The event was associated with unusually strong La Niña conditions during the summer months that caused an increased transfer of tropical warm waters down the coast of Western Australia. With increased rates of seawater-warming in the South-East Indian Ocean and in the continental shelf of Western Australia[18], Shark Bay's seagrass meadows are at risk from further ocean warming and acute temperature extremes due to their location at the northern edge of their geographical distribution. This trends could potentially accelerate the loss of one of the largest remaining seagrass ecosystems on earth, and result in large CO_2 emissions. Based on data from 49 sampled sites[19], satellite imagery and a published model of soil C loss following disturbance[20], we quantify the sediment C stocks and accumulation rates in Shark Bay's seagrasses and estimate the total seagrass area lost after the marine heat wave. We then provide a comprehensive assessment of the potential impact of seagrass losses on sediment C stocks and associated CO_2 emissions in the short- (3 years) and long-term (40 years) related to changes from anoxic to oxic conditions of previously vegetated sediments.

Sediment C content and sources

The C content of seagrass sediments in Shark Bay varied widely (0.01 - 9.00%), with the median (1.5%) and mean ± SE (2.00 ± 0.06%) values for the top meter similar to global estimates (median: 1.8% C; mean ± SE: 2.5 ± 0.1% C)[6], though spatial variability was observed (Fig. 2). C content increased eastwards towards Shark Bay's main coastline, inversely to dry bulk density (DBD) (ρ = -0.69; $P \leq 0.001$) (Supplementary Fig. S1 and Table S1). Seagrass sediments had an average δ^{13}C-value of −13.3 ± 0.1‰ (±SE) throughout the entire Bay and thickness of the sampled sediment deposits. The δ^{13}C signatures of potential C sources (seagrasses: -9.4 ± 1.3‰[21]; terrestrial-derived C from the Wooramel River:-25.1‰[22]; seston, i.e., suspended organic matter in the water column: -19.3 ± 2.5‰[22] and macroalgae: -18.1 ± 1.8‰[21]) indicated that seagrasses were the main sources of sediment C as allochthonous matter (i.e. terrestrial inputs, seston or macroalgae) could not account for the ^{13}C-enriched C pools stored in seagrass sediments (Supplementary, Table S2). Using a three source mixing model and literature values for putative sources, the average contribution of seagrass to the entire depth of the sediment C stocks was estimated to be ~65% (Supplementary, Fig. S2), higher than the ~50% estimate of seagrass contribution to surface sediments in seagrass ecosystems globally[23]. The predominantly autochthonous nature of sediment C pools in Shark Bay seagrass meadows and the weak correlation between sediment C and sediment physical properties such as grain size (Supplementary, Table S1) reinforces their significance for carbon sequestration. Seagrass detritus contains relatively high amounts of degradation-resistant compounds[24] compared to seston and algal detritus[25], which are characterized by faster decomposition rates[26]. The relatively high contribution of seagrass matter throughout the 2-3 m thick sediment deposits at Shark Bay is likely related to the low land-derived C inputs and the stability and high productivity of these meadows, which promotes the accumulation of thick organic-rich sediments, comparable to those found in *P. oceanica* meadows in the Mediterranean Sea[27].

Seagrass C storage hotspot

The C stocks per unit area in the top meter of seagrass sediments in Shark Bay averaged 128 ± 7 Mg C ha^{-1} (±SE), with 50% of the stocks having values between 92 and 161 Mg C ha^{-1} (Q_1 and Q_3, respectively) (Fig. 3a). While this is in agreement with reported median seagrass sediment C stock at a global scale (140 Mg C ha^{-1})[6], the southeastern half of Shark Bay (i.e., South Wooramel Bank and Faure Sill) constitutes a hotspot of C storage (245 ± 6 Mg C ha^{-1}). Average sediment C stocks in 1 m-thick deposits in Shark Bay are similar to those in temperate-tropical forests (122 Mg C ha^{-1}) and tidal marshes (160 Mg C ha^{-1}), while the C stocks in Shark Bay's hotspots compare with those of mangroves and boreal forests (255 Mg C ha^{-1} and 296 Mg C ha^{-1}, respectively)[6,28]. Assuming that the C stocks in the surveyed area are representative of the entire seagrass extent (4,300 km^2), we estimated that seagrass sediments at Shark Bay contained a total of 55 ± 3 Tg C in the top 1 meter, which is equivalent to 0.65 - 1.3% of the total C stored in seagrass sediments worldwide (4.2 - 8.4 Pg C)[6].

These estimates are limited to the upper meter of seagrass sediment C stocks (as are the global estimates) and, therefore, are likely underestimates of full C inventories since seagrass C deposits reach several meters in thickness in Shark Bay[16]. Seismic profiles combined with ^{14}C dating indicate that the seagrass banks here contain a continuous 4,000 yr record of sediment and C accumulation[16]. This corresponds to an average sediment thickness of 3.1 ± 0.4 m, as indicated by long-term sediment accumulation rates estimated in this study (mean ± SE: 0.77 ± 0.11 mm yr^{-1}; Table 1), in agreement with vertical accretion rates of ~1 mm yr^{-1} published by others[16,29] and supported by the dominant seagrass $\delta^{13}C$ signature of sediment C along the cores. Based on those, the C stocks accumulated over the last 4,000 cal yr BP averaged 334 ± 34 Mg C ha^{-1}. Stocks were as high as 650 Mg C ha^{-1} towards the south of the Wooramel Bank and Faure Sill, and decreased to 110 Mg C ha^{-1} towards the northwest (Fig. 3b). Assuming that the average millenary C deposits studied here are representative throughout the entire seagrass extent (4,300 km^2), the seagrass sediments in Shark Bay would have accumulated a total of 144 ± 14 Tg C over the last 4,000 yr. While Mediterranean *P. oceanica* meadows have the highest sediment C stocks per unit area (372 ± 38 Mg C ha^{-1} in the top meter[6] and 1027 ± 314 Mg C ha^{-1} over the last 4,000 yr BP[27]), the vast extent of Shark Bay's meadows makes their sediments the world's largest seagrass C stocks yet reported for a seagrass ecosystem.

C sequestration in seagrass sediments

Long term (over 1,000 years) C accumulation rates in Shark Bay seagrass meadows ranged from 2.5 to 32.1 g C m^{-2} yr^{-1}, with a median of 11.3 g C m^{-2} yr^{-1} (mean ± SE: 12 ± 2 C m^{-2} yr^{-1}), while short-term accumulation rates (last 100 years) were estimated at 15 to 123 g C m^{-2} yr^{-1}, with a median of 30 g C m^{-2} yr^{-1} (mean ± SE: 46 ± 13 g C m^{-2} yr^{-1}) (Table 1). These estimates are in the range of modern (i.e. last 100 yr) C accumulation rates of *P. oceanica* in the Mediterranean[30], *P. australis* in Australia[31,32] and *Thalassia testudinum* in Florida Bay[33] (26 – 122 g C m^{-2} yr^{-1}). Both the long- and short-term C accumulation rates estimated here exceed those of terrestrial forest soils by 3- to 10- fold (average rates in forest soils: 4.6 ± 1 g C m^{-2} yr^{-1})[1] and equal short-term C accumulation in Australian tidal marshes (55 ± 2 g C m^{-2} yr^{-1})[34].

The 4,300 km^2 of seagrass meadows in Shark Bay contemporarily account for a sequestration of 200 ± 55 Gg C yr^{-1} (range 65 – 527 Gg C yr^{-1}), which represents 9% of the C sequestered by Australia's vegetated coastal ecosystems (occupying an area of 110,000 km^2)[7,34,35]. This comparison highlights the disproportionate C sequestration capacity of Shark Bay seagrasses, contributing significantly to the C sequestration by seagrasses, mangroves and tidal marshes in Australia.

CO_2 emissions after seagrass loss

Seagrass meadows in Shark Bay experienced extensive declines driven by the marine heat wave that impacted the coast of Western Australia in the austral summer 2010/11[17]. Mapping inside the Marine Park (68% of Shark Bay's area) in 2014 revealed a net reduction of approximately 22% in seagrass habitat from the 2002 baseline (Fig.4). The net loss of seagrass extent was accompanied by a dramatic shift in seagrass cover from dense to sparse across large areas of the Bay, with dense seagrass areas declining from 72% in 2002 to 46% in 2014 (Table 2). Most losses occurred across the northern half of the western gulf, and at the northern part of the Wooramel Bank. After the event, water clarity decreased progressively and significantly due to the loss of sediment stabilization. In addition, widespread phytoplankton and bacterial blooms were observed in both gulfs of Shark Bay as a result of increased nutrient inputs to the water column from degraded seagrass biomass and sediment erosion[13], providing favorable conditions to CO_2 emissions[36].

Losses of C and associated CO_2 emissions following degradation of seagrass ecosystems have been documented previously[20]. Yet, no studies have evaluated the risk of CO_2 emissions associated with seagrass loss due to thermal stress impacts. Carbon remineralization to CO_2 is accelerated after disturbance through the decomposition of dead biomass and from the alteration of the physical and/or biogeochemical environment in which the sediment C was stored[36]. Vegetation loss also increases the potential for sediment erosion and sediment resuspension in the water column[37], increasing the oxygen exposure of previously buried sediment organic matter[38], leading to 2 to 4 times higher remineralization of sediment C under oxic than anoxic conditions[20]. Carbon in the upper meter of sediments has been considered the most susceptible to remineralization when seagrass meadows are lost[4,6]. However, Lovelock *et al.*[20] recently suggested that the proportions of the C stock that may be exposed to oxic conditions after disturbance in seagrass ecosystems could be lower than previously assumed, likely due to their permanently submerged condition and lower levels of exposure to air. Assuming that between 10 to 50% of the seagrass sediment C stock is exposed to an oxic environment after disturbance (experiencing a decay of 0.183 yr^{-1} [20]), we estimate that between 4 to 22 Mg C ha^{-1} (4 - 20% of the C stock in the upper meter of sediments) might have been lost in Shark Bay from previously vegetated sediments during the first 3 years after the marine heat wave. This may have resulted in the net emission of 16–80 Mg CO_2-e ha^{-1}, and assuming no seagrass recovery, it could result in cumulative C losses of 10 to 52 Mg C ha^{-1} or 38–190 Mg CO_2-e ha^{-1} (10-50% of the C stock in the upper meter of sediments) 40 years after the event. In addition to accelerated sediment C loss, the reduced seagrass standing stock (i.e. biomass) would in turn lead to a lower capacity of Shark Bay's seagrasses to sequester C. The reduction in the modern C sequestration is estimated at 0.46 ± 0.13 Mg C ha yr^{-1}, and at 52 ± 14 Gg C yr^{-1} over the ~1,100km^2 damaged area.

Excluding potential emissions from remineralization of seagrass biomass and extrapolating estimates per unit area to the total damaged seagrass area, we estimate that the widespread loss of seagrasses in Shark Bay in 2010/11 may have resulted in CO_2 emissions from sediment C stocks ranging from 2 to 9 Tg CO_2 during the following three years after the event. This can be compared to the 14.4 Tg CO_2 estimated to be released annually from land-use change in Australia[39], which did not account for emissions associated with seagrass losses, hence would have increased the national land-use change estimate by 4% to 21% per annum. Cumulative emissions due to seagrass die-off could range between 4 to 21 Tg CO_2 after 40 years assuming no seagrass recovery during this period, a reasonable assumption given that the recovery of *A. antarctica* and *P. australis* has been shown to take decades (>20 yr)[40,41] or not occur over contemporary time scales[13]. If damaged seagrass meadows recover, the estimates of CO_2 emissions after 40 years might be lower than reported here. In addition, CO_2 emissions from organic carbon remineralization may be partially offset by the net dissolution of the underlying carbonate sediments[42]. On the other hand, decomposition rates of C may be enhanced in persistent vegetated and degraded areas due to increased seawater temperature that influences respiration[43]. However, the potential and magnitude of such effects is unclear, and therefore, were not considered in this study.

Building resilience for climate change mitigation

Conservation of seagrass meadows and their millenary sediment C deposits is an efficient strategy to mitigate climate change, through the preservation of seagrass C sequestration capacity but especially through avoiding CO_2 emissions from sediments following habitat degradation, which greatly surpass the annual sequestration capacity by undisturbed seagrass meadows. With increasing frequency of extreme events, there is a necessity to advance our understanding of how seagrass ecosystems, especially those living close to their thermal tolerance limit, will respond to global change threats, both direct and through interactive effects with local pressures. Local threats in Shark Bay include seagrass loss associated with turbidity and nutrient inputs from flooding of poorly-managed pastoral leases, release of gypsum from a salt mine, changes in the trophic dynamics of the system through overfishing or targeted fishing, and more local damage to seagrasses from vessel propellers and anchors associated with growth in tourism. Current management at Shark Bay includes the declaration of special zones for seagrass protection, promoting public awareness of the significance of seagrass, and providing information on responsible boating (Shark Bay Marine Reserves Management Plan 1996-2006: https://www.sharkbay.org). These practices are well-suited to localized stressors, such as eutrophication[44], but less-suited to managing global threats such as heat waves, due to the spatial scale and magnitude of these impacts[45].

In the face of global threats, management can aim to maintain or enhance the resilience of seagrasses[46]. The heat wave-associated seagrass die-off in 2010/11 mostly affected *A. antarctica* followed by *P. australis*, which are persistent seagrasses with slow growth rates but capable to build large stores of carbohydrates in their rhizomes[41]. These characteristics provide the species with high levels of resistance to disturbance[11,12]. However, once lost, their capacity to recover is limited and slow, and largely depends on the immigration of seeds or seedlings. Therefore, conservation actions to preserve these seagrass meadows, thereby maintaining their C sequestration capacity and avoiding greenhouse gas emissions[36], should primarily aim to avoid the loss of vegetative material and prevent local pressures exacerbating those of global change to enhance their resilience. Actions following acute disturbance could include the removal of seagrass detritus after die-off to reduce detritus loading, lessening the threat of acute eutrophication; and the restoration of impacted areas using seed-based restoration approaches such as the movement of seeds and viviparous seedlings to impacted sites or the provision of anchoring points in close proximity to donor seagrass meadows to enhance recovery[47,48]. Long-term actions should include management to maintain top-down controls so that herbivory is maintained at natural levels[49]. More contentious actions could aim to repopulate areas with more resilient seagrass genotypes sourced from outside the impacted sites[50]. The wide range of salinity and temperature in the Bay, together with the uneven loss of meadows following the event in 2010/11, may indicate differences in adaptation and resilience among meadows across the Bay. This offers the possibility of identifying heatwave-resistant genotypes and using these to supplement the genetic diversity and resilience of existing meadows. Genotypic mapping could also allow identifying the meadows at greatest risk of heat waves where management actions may be focused.

Our results show that seagrass meadows from Shark Bay support the largest seagrass C stocks worldwide, that while making a large contribution to C sequestration by vegetated coastal ecosystems, their loss may disproportionally add to Australian CO_2 emissions. With increasing frequency and intensity of extreme climate events, the permanence of these C stores might be compromised, further stressing the importance of reducing green-house gas emissions, and implementing management actions to enhance and preserve natural carbon sinks.

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Author contributions

O.S., P.L., G.A.K. and C.M.D. designed the study. A.A.O., O.S., M.R, A.E. and N.M., carried out field and/or lab measurements. U.M. derived geostatistical models and A.A.O. and P.M. dating models. K.M. and M.R. mapped seagrass area. J.W.F. and M.A.M. contributed data. A.A.O. analyzed the data and drafted the first version of the manuscript. All authors contributed to the writing and editing of the manuscript.

Competing financial interests:

The author(s) declare no competing financial interests.

Figure Legends

Figure 1. Shark Bay World Heritage Site with spatial distribution of seagrass. The two most notable seagrass banks are the Faure Sill (FS) and Wooramel (WB) seagrass banks. The dashed region represents Shark Bay's Marine Park and locations of individual sites within the study region are represented as solid dots (seagrass spatial distribution source: ref. 51).

Figure 2. Spatial distribution of organic carbon in seagrass sediments of Shark Bay. Measured (**a**) organic carbon content (%C) and (**b**) $\delta^{13}C$ (‰) isotopic signature of C along

the entire thickness of the sampled sediments. Average $\delta^{13}C$ values for the main seagrass banks: Wooramel Bank: -13.83 ± 0.02‰; Faure Sill: -13.0 ± 0.1‰; Peron: -13.4 ± 0.1‰.

Figure 3. Spatial distribution of organic carbon stocks in seagrass sediments of Shark Bay. (a) Top meter C stocks; **(b)** C stocks accumulated over the last 4,000 cal yr BP. Area with C storage estimates covers 2,000 km^2 of seagrass sediments. The integrated sediment C stock within the 2,000 km^2 of surveyed seagrass area was estimated at 24 Tg C in the top meter and 64 Tg C over the last 4,000 cal yr BP.

Figure 4. Seagrass extent change within Shark Bay's Marine Park before (2002) and after (2014) the marine heat wave in 2010/11. Black = dense (> 40%) seagrass cover; grey = sparse (< 40%) seagrass cover; red = seagrass loss; dark blue = seagrass gain; light grey = sand; white = no data; gold = marine park boundary.

Tables

Table 1. Short- and long-term sedimentation, organic carbon (C) accumulation rates and sediment C stocks accumulated over the last 4,000 yr BP. Sedimentation and C accumulation rates were estimated by ^{210}Pb, ^{14}C dating of sediments and the depth-weighted average of C concentrations (short-term normalized to 100 yr depth, and long-term to 1,000 cal yr BP depth). Uncertainties represent SE of the regression and the result of error propagation for sedimentation rates, and C accumulation rates and stocks, respectively.

Core ID	Sedimentation rates (mm yr^{-1})		C accumulation (g C m^{-2} yr^{-1})		Sediment C stocks 4,000 cal yr BP
	Short-term (last 100 yr)	Long-term (last 1,000 - 6,000 cal yr BP)	Short-term (last 100 yr)	Long-term (last 1,000 cal yr BP)	(Mg C ha^{-1})
W3	2.3 ± 0.9	0.58 ± 0.08	77 ± 41	14.1 ± 2.6	369 ± 51
W4		1.08 ± 0.33		32.1 ± 13.9	1338 ± 390
FS7	2.3 ± 0.3	1.48 ± 0.06	29 ± 5	12.9 ± 0.7	
FS9	1.7 ± 0.1	0.74 ± 0.03	27 ± 3	8.5 ± 0.4	304 ± 12
FS11	3.1 ± 0.2		123 ± 14		
FS13	2.6 ± 0.2	0.69 ± 0.02	25 ± 3	8.7 ± 0.3	528 ± 14
FS14	4.5 ± 0.5	1.31 ± 0.07	45 ± 7	15.2 ± 1.2	
P5		0.43 ± 0.05		6.7 ± 0.3	242 ± 6
P7		0.66 ± 0.02		11.3 ± 0.3	310 ± 6
P8		0.39 ± 0.02		2.5 ± 0.1	99 ± 2
P10	1.8 ± 0.7	0.39 ± 0.01	15 ± 9	6.4 ± 0.3	167 ± 4
P12	1.6 ± 0.2	0.74 ± 0.03	31 ± 7	16.8 ± 1.1	594 ± 27
Mean ± SE	**2.5 ± 0.3**	**0.77 ± 0.11**	**46 ± 13**	**12 ± 2**	**439 ± 124**

Table 2. Effects of the marine heat wave event to seagrass area and organic carbon (C) stocks under degraded seagrass meadows. *α* is the fraction of sediment C stock within the top meter exposed to oxic conditions. Biomass C loss is not included in the calculations as much of the primary production might likely be buried or exported, rather than remineralized *in situ*.

	Marine Park area (8,900 km^2)	Extrapolated values for the entire Bay (13,000km^2)
Baseline seagrass area (km^2)	2689	4300
Dense	1925	3096
Sparse	765	1204
C stock top meter (Tg C)	34 ± 14	55 ± 22
Seagrass area loss (km^2)	581	929
Shift to sparse seagrass (km^2)	118	190
Total damaged seagrass area (km^2)	699	1125
3 yr net C loss from 1 m sediment stock (Tg C)		
α 0.10	0.30 ± 0.05	0.49 ± 0.08
α 0.25	0.76 ± 0.10	1.23 ± 0.15
α 0.50	1.52 ± 0.17	2.45 ± 0.27
40 yr net C loss from 1 m sediment stock (Tg C)*		
α 0.10	0.72 ± 0.27	1.16 ± 0.53
α 0.25	1.81 ± 0.35	2.91 ± 0.62
α 0.50	3.61 ± 0.50	5.81 ± 0.80
3yr net CO_2 emissions (Tg CO_2)	1.1 - 5.6	1.8 - 9.0
40 yr potential CO_2 emissions (Tg CO_2)*	2.6 - 13.2	4.3 - 21.3

*Loss and emission after 40 years of disturbance assuming no seagrass recovery.

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Methods

Seagrass sediments were sampled using PVC cores (100 - 300 cm long, 6.5 cm internal diameter) that were hammered into the substrate at 0.5 to 4 m water depth. In the laboratory, the PVC corers were cut lengthwise, and the sediments inside the corers were sliced at 1 or 3 cm-thick intervals. Analysis of ^{210}Pb, ^{14}C and grain size were conducted in cores cut at 1 cm resolution (11 cores), while dry bulk density (DBD), %C, $\delta^{13}C$ were measured in all cores (28 cores) in alternate slices every 3 cm (upper 50 cm), and every 6 cm (below 50 cm). We combined our data with previously published studies in Shark Bay involving coring in seagrass sediments[7,16,52]. From Bufarale and Collins (2015), we took core FDW2 (here W4) dated by ^{14}C and we analyzed grain size, %C and $\delta^{13}C$ to include it in the dataset. From Fourqurean *et al.*[52] we included the C data from the 8 long sediment cores (here W5 – W8 and FS15 – FS18) and from Lavery *et al.*[7] we included C and $\delta^{13}C$ data of twelve 27 cm-long cores (here P1 and P2) in this study[19]. Compression of seagrass sediments during coring was corrected by distributing the spatial discordances proportionally between the expected and the observed sediment column layers[53] and was accounted for in the calculations of C stocks standardized to 1 m depth and 4,000 cal yr BP. Average compression was 20% and was applied to published data where compression existed but was not measured during sampling[7,16]. Published and unpublished cores from this study comprised 49 locations covering a range of 3 seagrass genera forming monospecific and mixed meadows, 34 contained data deeper than 1 meter with 23 sites extending down to 2-3 meters (Supplementary, Table S3). None of the cores penetrated the entire thickness of seagrass-accumulated sediment estimated to range from 4 to 6 m[16].

The C content of sediments was measured in pre-acidified (with 1 M HCl) samples. One gram of ground sample was acidified to remove inorganic carbon after weighing, centrifuged (3,400 revolutions per minute, for 5 min), and the supernatant with acid residues was carefully removed by pipette, avoiding resuspension. The sample was then washed with Milli-Q water, centrifuged and the supernatant removed. The residual samples were then re-dried at 60ºC and encapsulated in tin capsules for C and $\delta^{13}C$ analyses using an Elemental Analyzer - Isotope Ratio Mass Spectrometer (Hilo Analytical Laboratory) at the University of Hawaii. C content (%C) was calculated for the bulk (pre-acidified) samples using the formula ($C_{bulk} = C_{acidified} \cdot \frac{mass\ acidified}{mass\ pre-acidified}$). The method used to remove inorganic carbon prior to C analyses may lead to the loss of part of the organic C (soluble fraction), thereby potentially leading to an underestimation of sediment C content[54,55]. The sediment $\delta^{13}C$ signature is expressed as δ values in parts per thousand relative to the Vienna Pee Dee Belemnite. Replicate assays and standards indicated measurement errors of ±0.04% and ±0.1‰ for C content and $\delta^{13}C$, respectively. The relative contribution of seagrass, macroalgae and seston (that includes living and non living matter in the water column) and terrestrial matter to seagrass top meter sediment carbon pools was computed applying a three-component isotope-mixing model as described by Phillips and Gregg (2003) and calculated by means of the IsoSource Visual Basic program[56], using a 1% increment and 0.1‰ tolerance. We used literature values for putative C sources and macroalgae and seston were combined as a single C source since their published $\delta^{13}C$ endmembers were not significantly different (Supplementary, Table S2).

Sediment grain-size was measured with a Mastersizer 2000 laser diffraction particle analyzer following digestion of bulk samples with 10% hydrogen peroxide at the Centre for Advanced Studies of Blanes. The d_{50} (i.e. the median particle diameter) was used as a proxy for the particle size distribution. Sediments were classified as sand (0.063 - 1 mm), silt (0.004 - 0.063 mm) and clay (< 0.004 mm), and the mud fraction was calculated as the sum of the fractions of silt and clay (< 0.063 mm) (size scale: Wentworth, 1922)[57]. Sand:mud ratio was used as a proxy for depositional conditions and hydrodynamic energy, where higher sand content could be associated with higher energy environments[58].

Spearman correlation tests were used to assess significant relationships between C concentrations and environmental (i.e. DBD, d50, %sand, %mud and sand:mud ratio) and biological (i.e. %C and $\delta^{13}C$) variables measured in seagrass sediment cores as none of the variables followed a normal distribution (Supplementary, Table S1).

Eleven sediment cores were analyzed for ^{210}Pb concentrations to determine recent (ca. 100 years) sediment accumulation rates. ^{210}Pb was determined through the analysis of ^{210}Po by alpha spectrometry after addition of ^{209}Po as an internal tracer and digestion in acid media using an analytical microwave[59]. The concentrations of excess ^{210}Pb used to obtain the age models were determined as the difference between total ^{210}Pb and ^{226}Ra (supported ^{210}Pb). Concentrations of ^{226}Ra were determined for selected samples along each core by low-background liquid scintillation counting method (Wallac 1220 Quantulus) adapted from Masqué *et al.*[60]. Mean sediment accumulation rates over the last 100 years could be estimated for eight out of the eleven sediment cores dated using the CF:CS model below the surface mixed layer when present[61]. Mixing was common from 0 to 4 cm in half of the dated sediment cores, hence average modern accumulation rates should be considered as upper limits. Two to five samples of shells per core from the cores dated by ^{210}Pb were also radiocarbon-dated at the Direct AMS-Radiocarbon Business Unit, Accium Biosciences, USA, following standard procedures[62]. The conventional radiocarbon ages reported by the laboratory were converted into calendar dates (cal yr BP) using the Bacon software (Marine13 curve)[63] and applying a marine reservoir correction (i.e. subtracting Delta R value of 85 ± 30 for the East Indian Ocean, Western Australia)[64]. Average short-term C accumulation rates were estimated by multiplying sediment accumulation rates (g cm^{-2} yr^{-1}) by the fraction of C accumulated to 100 yr depth determined by ^{210}Pb dating. Bacon model output was used to estimate average long-term sediment accumulation rates (g cm^{-2} yr^{-1}) during the last 1,000 yr BP. Long-term C accumulation rates were determined following the same method as for short-term accumulation rates, but the fraction of C was normalized to 1,000 cal yr BP, as the minimum age of the ^{14}C-dated bottom sediments was 1,117± 61 cal yr BP (Supplementary, Table S4).

C stocks at the 49 locations were estimated for 1 m sediment thickness and for a period of accumulation of 4,000 years, similar to the time of formation of the C deposits[16]. We standardized the estimates of sediment C stocks to one meter thick deposits since this allows comparisons with estimates of global stocks. Where necessary (i.e. in 15 cores), we inferred C stocks below the limits of the reported data to 1 m, extrapolating linearly integrated values of C content (cumulative C stock Mg C ha^{-1}) with depth. C content was reported to at least 27 cm in 12 cores out of these 15, while the other 3 cores had C data down to 55 - 83 cm. Correlation between extrapolated C stocks from 27 cm to 1 m and measured C stocks in sediment cores ≥ 1 m was $\rho = 0.82$ $P < 0.001$ (Supplementary, Fig. S3a). Sediment C stocks in the ≥ 1 meter cores ranged from 23 to 322 Mg C ha^{-1}, with a mean value of 116 ± 13 Mg C ha^{-1} and median 109 Mg C ha^{-1}. Extrapolating data on cumulative C stocks from cores of at least 27 cm depth at a further 15 sites to 1 m, we estimated C storage at those sites to range between 26 and 313 Mg C ha^{-1}, similar to sites with full inventories. Combining the estimates extrapolated from shallow cores with full core inventories, the resulting mean and median sediment C storage (103 ± 11 Mg C ha^{-1} and 73 Mg C ha^{-1}, respectively)(Supplementary, Fig. S4) were not significantly different ($P > 0.05$) from those for full core inventories. We applied ordinary kriging to estimate the top 1 meter C stocks across 2,000 km^2 encompassing the South Wooramel Bank, Faure Sill and Peron Peninsula seagrass banks[65,66]. We used a maximum of the 16 nearest neighbours within a search circle of radius 25 km. Ordinary kriging inherently declusters the input data and produces smoothed estimates, so that the extremely high or low values found within seagrass meadows of the Bay do not disproportionately influence the global mean.

We estimated seagrass sediment C stocks accumulated over the last 4,000 years in 1 to 3 m long cores where ^{14}C data were available and the length sampled embraced ≥

2,000 yr of sediment and C accumulation (i.e. in 8 cores). The correlation between extrapolated and measured C stocks was r = 0.90 ($P < 0.05$) (Supplementary, Fig. S3b). Bay-wide estimates of sediment C stocks accumulated over 4,000 cal yr BP were estimated by combining extrapolated and full 4,000 cal yr BP core inventories, and applying collocated cokriging with top meter C stocks as the secondary variable. Correlation between top meter and 4,000 yr BP carbon stocks was 0.6 ($P < 0.01$) and the percentage of noise specific to the background was set to 20%. Spatial variability of C stocks was mapped after applying Ordinary Kriging (OK) to top meter C stocks and collocated co-kriging to millenary C stock (4,000 cal yr BP).

Data on seagrass sediment C stocks accumulated during the last 4,000 yr in *P. oceanica* were extracted or extrapolated from published estimates[27] of sediment cores with a sampled depth of at least 2,000 yr, as this is the same method we used to estimate long-term C_{org} stocks at Shark Bay.

The extent of seagrass meadows in Shark Bay before and after the extreme climatic event was determined by the Western Australian Department of Biodiversity, Conservation and Attractions as part of a broader long-term seagrass monitoring program. Seagrass extent was derived using a supervised classification of imagery captured by Landsat–5 Thematic Mapper (TM) in 2002 and Landsat–8 Operational Land Imager (OLI) in 2014 (United States Geological Survey (glovis.usgs.gov/)). The spatial resolution of these images is 30 m. The 2002 and 2014 classifications used a combination of historical ground-truthing, long-term monitoring data and expert knowledge for training sites and validation. The imagery was classified into three distinct classes; ‘dense seagrass’ (> 40% cover); ‘sparse seagrass’ (< 40% cover) and ‘other’ which included all remaining habitat types. The Shark Bay Marine Park (SBMP) covers approximately 8,900 km^2 of seafloor. The seagrass mapping presented here covers approximately 78% of SBMP. The entire extent was not mapped due to poor image quality caused by depth and water clarity and the lack of data in some areas.

Net seagrass area losses and shifts in seagrass cover from dense to sparse were considered as damaged areas, where the seagrass sediment organic matter is more exposed oxygen due to erosion and sediment resuspension, hence is more susceptible to being rapidly remineralized. We modelled the potential CO_2 emissions associated with this disturbance and subsequent remineralization of sediment C stocks using equation 1 based on varying proportions of sediment C being exposed to oxic conditions following disturbance:

$$C(t) = \alpha \cdot C_{(0)} \cdot e^{-k_1 \cdot t} \tag{1}$$

where $C_{(0)}$ is the measured C stock in the top meter, α is the fraction of the C stock exposed to oxic conditions and k_1 is the decomposition rate of seagrass sediment C (0.183 yr^{-1})[20] in oxic sediment conditions.

This required a number of assumption which were: (1) the C stock over the top meter (Mg C ha^{-1}) of sampled seagrass meadows was representative of the C stock contained in sediments within the damaged seagrass area prior to the heat-wave; (2) the fraction of the sediment C in disturbed seagrass meadows exposed to oxic environments was in the range of 0.1 to 0.5; (3) the potential contribution of seagrass biomass remineralization to CO_2 emissions was not accounted for due to the lack of knowledge about the export and fate of plant biomass following meadows loss; and (4) there will be no recovery of seagrass in the long-term (i.e., 40 yr). With the exception of the last assumption, these were conservative, in an effort to avoid over-estimation of potential CO_2 emissions. We assessed the loss of C to the atmosphere after 3 years post disturbance (in 2014) and also assessed potential releases over a 40-year time frame consistent of tier 1 and 2 methods of IPCC (2006) for organic soils. The C stock loss per hectare 3 years and 40 years post disturbance was multiplied by the damaged seagrass area (1,125 km^2).

Data availability

Seagrass sediment data on dry bulk density (DBD), C, $\delta^{13}C$, ^{210}Pb concentrations and ^{14}C raw ages that support the findings of this study have been deposited in Edith Cowan

University Research portal with the identifier doi: https://dx.doi.org/10.4225/75/5a1640e851af1.

References related to Methods

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