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

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

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38 **Abstract**

39 Seagrass ecosystems contain globally significant organic carbon (C) stocks. However,
40 climate change and increasing frequency of extreme events threaten their preservation.
41 Shark Bay, Western Australia, has the largest C stock reported for a seagrass ecosystem,
42 containing up to 1.3% of the total C stored within the top meter of seagrass sediments
43 worldwide. Based on field studies and satellite imagery, we estimate that 36% of Shark
44 Bay's seagrass meadows were damaged following a marine heat wave in 2010/11.
45 Assuming that 10 to 50% of the seagrass sediment C stock was exposed to oxic conditions
46 after disturbance, between 2 and 9 Tg CO₂ could have been released to the atmosphere
47 during the following three years, increasing emissions from land-use change in Australia
48 by 4 - 21% per annum. With heat waves predicted to increase with further climate
49 warming, conservation of seagrass ecosystems is essential to avoid adverse feedbacks on
50 the climate system.

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65 Vegetated coastal ecosystems, including seagrass meadows, mangroves and tidal
66 marshes, are collectively termed “blue carbon” ecosystems storing globally-relevant
67 carbon stocks in their sediments and biomass¹. Their organic carbon (C) sink capacity is
68 estimated to be 0.08-0.22 Pg C yr⁻¹ globally², accounting for an offset of 0.6 - 2% of global
69 anthropogenic CO₂ emissions (49 Pg CO₂eq yr⁻¹)³. However, blue carbon ecosystems are in
70 decline worldwide², raising concern about a potential re-emission of their C stocks to the
71 atmosphere as CO₂. CO₂ emissions from loss of blue carbon ecosystems are estimated at
72 0.15 - 1.02 Pg CO₂ yr⁻¹, which is equivalent to 3 – 19% of those from terrestrial land-use
73 change⁴.

74 Seagrasses are marine flowering plants that consist of 72 species growing across a
75 wide range of habitats⁵. Global estimates of C storage in the top meter of seagrass
76 sediments range from 4.2 to 8.4 Pg C⁶, although large spatial variability exists related to
77 differences in biological (e.g., meadow productivity and density), chemical (e.g.,
78 recalcitrance of C) and physical (e.g., hydrodynamics and bathymetry) settings in which
79 they occur^{7,8}. Since the beginning of the twentieth century, seagrass meadows worldwide
80 have declined at a median rate of 0.9% yr⁻¹ mostly due to human impacts such as coastal
81 development or water quality degradation⁹. Climate change impacts, such as ocean
82 warming and extreme events (e.g., ENSO), are exacerbating this trend. Marine heat waves
83 have led to losses of foundation seagrass species that form organic-rich sediment deposits
84 beneath their canopies (e.g. *Posidonia oceanica* in the Mediterranean Sea¹⁰ and *Amphibolis*
85 *antarctica* in Western Australia¹¹⁻¹³). Seagrass losses and the subsequent erosion and
86 remineralization of their sediment C stocks are likely to continue or intensify under
87 climate change⁹, especially in regions where seagrasses live close to their thermal
88 tolerance limits¹⁴.

89 Shark Bay (Western Australia) (Fig.1) contains one of the largest (4,300 km²) and
90 most diverse assemblage of seagrasses worldwide¹⁵, occupying between 0.7 and 2.4% of
91 the world seagrass area. Up to 12 seagrass species are found in Shark Bay, storing C in

92 their sediments and shaping its geomorphology. The two most notable seagrass banks, the
93 Wooramel Bank and the Faure Sill, are the result of ~8,000 yr of continuous seagrass
94 growth¹⁶. Despite seagrasses having thrived over millennia in Shark Bay, unprecedented
95 widespread losses occurred in the austral summer of 2010/2011 in both the above- and
96 below-ground biomass of the dominant seagrass *A. antarctica* and to a minor extent *P.*
97 *australis*^{12,13}, the two species forming large continuous beds. For more than 2 months, a
98 marine heat wave elevated water temperatures 2-4°C above long-term averages¹⁷. The
99 event was associated with unusually strong La Niña conditions during the summer months
100 that caused an increased transfer of tropical warm waters down the coast of Western
101 Australia. With increased rates of seawater-warming in the South-East Indian Ocean and
102 in the continental shelf of Western Australia¹⁸, Shark Bay's seagrass meadows are at risk
103 from further ocean warming and acute temperature extremes due to their location at the
104 northern edge of their geographical distribution. This trends could potentially accelerate
105 the loss of one of the largest remaining seagrass ecosystems on earth, and result in large
106 CO₂ emissions. Based on data from 49 sampled sites¹⁹, satellite imagery and a published
107 model of soil C loss following disturbance²⁰, we quantify the sediment C stocks and
108 accumulation rates in Shark Bay's seagrasses and estimate the total seagrass area lost
109 after the marine heat wave. We then provide a comprehensive assessment of the potential
110 impact of seagrass losses on sediment C stocks and associated CO₂ emissions in the short-
111 (3 years) and long-term (40 years) related to changes from anoxic to oxic conditions of
112 previously vegetated sediments.

113

114 **Sediment C content and sources**

115 The C content of seagrass sediments in Shark Bay varied widely (0.01 - 9.00%),
116 with the median (1.5%) and mean \pm SE (2.00 \pm 0.06%) values for the top meter similar to
117 global estimates (median: 1.8% C; mean \pm SE: 2.5 \pm 0.1% C)⁶, though spatial variability
118 was observed (Fig. 2). C content increased eastwards towards Shark Bay's main coastline,

119 inversely to dry bulk density (DBD) ($\rho = -0.69$; $P \leq 0.001$) (Supplementary Fig. S1 and
120 Table S1). Seagrass sediments had an average $\delta^{13}\text{C}$ -value of $-13.3 \pm 0.1\text{‰}$ ($\pm\text{SE}$)
121 throughout the entire Bay and thickness of the sampled sediment deposits. The $\delta^{13}\text{C}$
122 signatures of potential C sources (seagrasses: $-9.4 \pm 1.3\text{‰}^{21}$; terrestrial-derived C from the
123 Wooramel River: -25.1‰^{22} ; seston, i.e., suspended organic matter in the water column: $-$
124 $19.3 \pm 2.5\text{‰}^{22}$ and macroalgae: $-18.1 \pm 1.8\text{‰}^{21}$) indicated that seagrasses were the main
125 sources of sediment C as allochthonous matter (i.e. terrestrial inputs, seston or
126 macroalgae) could not account for the ^{13}C -enriched C pools stored in seagrass sediments
127 (Supplementary, Table S2). Using a three source mixing model and literature values for
128 putative sources, the average contribution of seagrass to the entire depth of the sediment
129 C stocks was estimated to be $\sim 65\%$ (Supplementary, Fig. S2), higher than the $\sim 50\%$
130 estimate of seagrass contribution to surface sediments in seagrass ecosystems globally²³.
131 The predominantly autochthonous nature of sediment C pools in Shark Bay seagrass
132 meadows and the weak correlation between sediment C and sediment physical properties
133 such as grain size (Supplementary, Table S1) reinforces their significance for carbon
134 sequestration. Seagrass detritus contains relatively high amounts of degradation-resistant
135 compounds²⁴ compared to seston and algal detritus²⁵, which are characterized by faster
136 decomposition rates²⁶. The relatively high contribution of seagrass matter throughout the
137 2-3 m thick sediment deposits at Shark Bay is likely related to the low land-derived C
138 inputs and the stability and high productivity of these meadows, which promotes the
139 accumulation of thick organic-rich sediments, comparable to those found in *P. oceanica*
140 meadows in the Mediterranean Sea²⁷.

141

142 **Seagrass C storage hotspot**

143 The C stocks per unit area in the top meter of seagrass sediments in Shark Bay
144 averaged $128 \pm 7 \text{ Mg C ha}^{-1}$ ($\pm\text{SE}$), with 50% of the stocks having values between 92 and
145 161 Mg C ha^{-1} (Q_1 and Q_3 , respectively) (Fig. 3a). While this is in agreement with reported

146 median seagrass sediment C stock at a global scale (140 Mg C ha^{-1})⁶, the southeastern half
147 of Shark Bay (i.e., South Wooramel Bank and Faure Sill) constitutes a hotspot of C storage
148 ($245 \pm 6 \text{ Mg C ha}^{-1}$). Average sediment C stocks in 1 m-thick deposits in Shark Bay are
149 similar to those in temperate-tropical forests (122 Mg C ha^{-1}) and tidal marshes (160 Mg C
150 ha^{-1}), while the C stocks in Shark Bay's hotspots compare with those of mangroves and
151 boreal forests (255 Mg C ha^{-1} and 296 Mg C ha^{-1} , respectively)^{6,28}. Assuming that the C
152 stocks in the surveyed area are representative of the entire seagrass extent ($4,300 \text{ km}^2$),
153 we estimated that seagrass sediments at Shark Bay contained a total of $55 \pm 3 \text{ Tg C}$ in the
154 top 1 meter, which is equivalent to 0.65 - 1.3% of the total C stored in seagrass sediments
155 worldwide ($4.2 - 8.4 \text{ Pg C}$)⁶.

156 These estimates are limited to the upper meter of seagrass sediment C stocks (as
157 are the global estimates) and, therefore, are likely underestimates of full C inventories
158 since seagrass C deposits reach several meters in thickness in Shark Bay¹⁶. Seismic profiles
159 combined with ¹⁴C dating indicate that the seagrass banks here contain a continuous 4,000
160 yr record of sediment and C accumulation¹⁶. This corresponds to an average sediment
161 thickness of $3.1 \pm 0.4 \text{ m}$, as indicated by long-term sediment accumulation rates estimated
162 in this study (mean \pm SE: $0.77 \pm 0.11 \text{ mm yr}^{-1}$; Table 1), in agreement with vertical
163 accretion rates of $\sim 1 \text{ mm yr}^{-1}$ published by others^{16,29} and supported by the dominant
164 seagrass $\delta^{13}\text{C}$ signature of sediment C along the cores. Based on those, the C stocks
165 accumulated over the last 4,000 cal yr BP averaged $334 \pm 34 \text{ Mg C ha}^{-1}$. Stocks were as high
166 as 650 Mg C ha^{-1} towards the south of the Wooramel Bank and Faure Sill, and decreased to
167 110 Mg C ha^{-1} towards the northwest (Fig. 3b). Assuming that the average millenary C
168 deposits studied here are representative throughout the entire seagrass extent ($4,300$
169 km^2), the seagrass sediments in Shark Bay would have accumulated a total of $144 \pm 14 \text{ Tg}$
170 C over the last 4,000 yr. While Mediterranean *P. oceanica* meadows have the highest
171 sediment C stocks per unit area ($372 \pm 38 \text{ Mg C ha}^{-1}$ in the top meter⁶ and $1027 \pm 314 \text{ Mg C}$

172 ha⁻¹ over the last 4,000 yr BP²⁷), the vast extent of Shark Bay's meadows makes their
173 sediments the world's largest seagrass C stocks yet reported for a seagrass ecosystem.

174

175 **C sequestration in seagrass sediments**

176 Long term (over 1,000 years) C accumulation rates in Shark Bay seagrass
177 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 ±
178 SE: 12 ± 2 C m⁻² yr⁻¹), while short-term accumulation rates (last 100 years) were estimated
179 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)
180 (Table 1). These estimates are in the range of modern (i.e. last 100 yr) C accumulation
181 rates of *P. oceanica* in the Mediterranean³⁰, *P. australis* in Australia^{31,32} and *Thalassia*
182 *testudinum* in Florida Bay³³ (26 – 122 g C m⁻² yr⁻¹). Both the long- and short-term C
183 accumulation rates estimated here exceed those of terrestrial forest soils by 3- to 10- fold
184 (average rates in forest soils: 4.6 ± 1 g C m⁻² yr⁻¹)¹ and equal short-term C accumulation in
185 Australian tidal marshes (55 ± 2 g C m⁻² yr⁻¹)³⁴.

186 The 4,300 km² of seagrass meadows in Shark Bay contemporarily account for a
187 sequestration of 200 ± 55 Gg C yr⁻¹ (range 65 – 527 Gg C yr⁻¹), which represents 9% of the
188 C sequestered by Australia's vegetated coastal ecosystems (occupying an area of 110,000
189 km²)^{7,34,35}. This comparison highlights the disproportionate C sequestration capacity of
190 Shark Bay seagrasses, contributing significantly to the C sequestration by seagrasses,
191 mangroves and tidal marshes in Australia.

192

193 **CO₂ emissions after seagrass loss**

194 Seagrass meadows in Shark Bay experienced extensive declines driven by the
195 marine heat wave that impacted the coast of Western Australia in the austral summer
196 2010/11¹⁷. Mapping inside the Marine Park (68% of Shark Bay's area) in 2014 revealed a
197 net reduction of approximately 22% in seagrass habitat from the 2002 baseline (Fig.4).
198 The net loss of seagrass extent was accompanied by a dramatic shift in seagrass cover

199 from dense to sparse across large areas of the Bay, with dense seagrass areas declining
200 from 72% in 2002 to 46% in 2014 (Table 2). Most losses occurred across the northern half
201 of the western gulf, and at the northern part of the Wooramel Bank. After the event, water
202 clarity decreased progressively and significantly due to the loss of sediment stabilization.
203 In addition, widespread phytoplankton and bacterial blooms were observed in both gulfs
204 of Shark Bay as a result of increased nutrient inputs to the water column from degraded
205 seagrass biomass and sediment erosion¹³, providing favorable conditions to CO₂
206 emissions³⁶.

207 Losses of C and associated CO₂ emissions following degradation of seagrass
208 ecosystems have been documented previously²⁰. Yet, no studies have evaluated the risk of
209 CO₂ emissions associated with seagrass loss due to thermal stress impacts. Carbon
210 remineralization to CO₂ is accelerated after disturbance through the decomposition of
211 dead biomass and from the alteration of the physical and/or biogeochemical environment
212 in which the sediment C was stored³⁶. Vegetation loss also increases the potential for
213 sediment erosion and sediment resuspension in the water column³⁷, increasing the oxygen
214 exposure of previously buried sediment organic matter³⁸, leading to 2 to 4 times higher
215 remineralization of sediment C under oxic than anoxic conditions²⁰. Carbon in the upper
216 meter of sediments has been considered the most susceptible to remineralization when
217 seagrass meadows are lost^{4,6}. However, Lovelock *et al.*²⁰ recently suggested that the
218 proportions of the C stock that may be exposed to oxic conditions after disturbance in
219 seagrass ecosystems could be lower than previously assumed, likely due to their
220 permanently submerged condition and lower levels of exposure to air. Assuming that
221 between 10 to 50% of the seagrass sediment C stock is exposed to an oxic environment
222 after disturbance (experiencing a decay of 0.183 yr⁻¹²⁰), we estimate that between 4 to 22
223 Mg C ha⁻¹ (4 - 20% of the C stock in the upper meter of sediments) might have been lost in
224 Shark Bay from previously vegetated sediments during the first 3 years after the marine
225 heat wave. This may have resulted in the net emission of 16–80 Mg CO₂-e ha⁻¹, and

226 assuming no seagrass recovery, it could result in cumulative C losses of 10 to 52 Mg C ha⁻¹
227 or 38–190 Mg CO₂-e ha⁻¹ (10-50% of the C stock in the upper meter of sediments) 40 years
228 after the event. In addition to accelerated sediment C loss, the reduced seagrass standing
229 stock (i.e. biomass) would in turn lead to a lower capacity of Shark Bay's seagrasses to
230 sequester C. The reduction in the modern C sequestration is estimated at 0.46 ± 0.13 Mg C
231 ha yr⁻¹, and at 52 ± 14 Gg C yr⁻¹ over the ~1,100km² damaged area.

232 Excluding potential emissions from remineralization of seagrass biomass and
233 extrapolating estimates per unit area to the total damaged seagrass area, we estimate that
234 the widespread loss of seagrasses in Shark Bay in 2010/11 may have resulted in CO₂
235 emissions from sediment C stocks ranging from 2 to 9 Tg CO₂ during the following three
236 years after the event. This can be compared to the 14.4 Tg CO₂ estimated to be released
237 annually from land-use change in Australia³⁹, which did not account for emissions
238 associated with seagrass losses, hence would have increased the national land-use change
239 estimate by 4% to 21% per annum. Cumulative emissions due to seagrass die-off could
240 range between 4 to 21 Tg CO₂ after 40 years assuming no seagrass recovery during this
241 period, a reasonable assumption given that the recovery of *A. antarctica* and *P. australis*
242 has been shown to take decades (>20 yr)^{40,41} or not occur over contemporary time
243 scales¹³. If damaged seagrass meadows recover, the estimates of CO₂ emissions after 40
244 years might be lower than reported here. In addition, CO₂ emissions from organic carbon
245 remineralization may be partially offset by the net dissolution of the underlying carbonate
246 sediments⁴². On the other hand, decomposition rates of C may be enhanced in persistent
247 vegetated and degraded areas due to increased seawater temperature that influences
248 respiration⁴³. However, the potential and magnitude of such effects is unclear, and
249 therefore, were not considered in this study.

250

251 **Building resilience for climate change mitigation**

252 Conservation of seagrass meadows and their millenary sediment C deposits is an

253 efficient strategy to mitigate climate change, through the preservation of seagrass C
254 sequestration capacity but especially through avoiding CO₂ emissions from sediments
255 following habitat degradation, which greatly surpass the annual sequestration capacity by
256 undisturbed seagrass meadows. With increasing frequency of extreme events, there is a
257 necessity to advance our understanding of how seagrass ecosystems, especially those
258 living close to their thermal tolerance limit, will respond to global change threats, both
259 direct and through interactive effects with local pressures. Local threats in Shark Bay
260 include seagrass loss associated with turbidity and nutrient inputs from flooding
261 of poorly-managed pastoral leases, release of gypsum from a salt mine, changes in the
262 trophic dynamics of the system through overfishing or targeted fishing, and more local
263 damage to seagrasses from vessel propellers and anchors associated with growth in
264 tourism. Current management at Shark Bay includes the declaration of special zones for
265 seagrass protection, promoting public awareness of the significance of seagrass, and
266 providing information on responsible boating (Shark Bay Marine Reserves Management
267 Plan 1996-2006: <https://www.sharkbay.org>). These practices are well-suited to localized
268 stressors, such as eutrophication⁴⁴, but less-suited to managing global threats such as heat
269 waves, due to the spatial scale and magnitude of these impacts⁴⁵.

270 In the face of global threats, management can aim to maintain or enhance the
271 resilience of seagrasses⁴⁶. The heat wave-associated seagrass die-off in 2010/11 mostly
272 affected *A. antarctica* followed by *P. australis*, which are persistent seagrasses with slow
273 growth rates but capable to build large stores of carbohydrates in their rhizomes⁴¹. These
274 characteristics provide the species with high levels of resistance to disturbance^{11,12}.
275 However, once lost, their capacity to recover is limited and slow, and largely depends on
276 the immigration of seeds or seedlings. Therefore, conservation actions to preserve these
277 seagrass meadows, thereby maintaining their C sequestration capacity and avoiding
278 greenhouse gas emissions³⁶, should primarily aim to avoid the loss of vegetative material
279 and prevent local pressures exacerbating those of global change to enhance their

280 resilience. Actions following acute disturbance could include the removal of seagrass
281 detritus after die-off to reduce detritus loading, lessening the threat of acute
282 eutrophication; and the restoration of impacted areas using seed-based restoration
283 approaches such as the movement of seeds and viviparous seedlings to impacted sites or
284 the provision of anchoring points in close proximity to donor seagrass meadows to
285 enhance recovery^{47,48}. Long-term actions should include management to maintain top-
286 down controls so that herbivory is maintained at natural levels⁴⁹. More contentious
287 actions could aim to repopulate areas with more resilient seagrass genotypes sourced
288 from outside the impacted sites⁵⁰. The wide range of salinity and temperature in the Bay,
289 together with the uneven loss of meadows following the event in 2010/11, may indicate
290 differences in adaptation and resilience among meadows across the Bay. This offers the
291 possibility of identifying heatwave-resistant genotypes and using these to supplement the
292 genetic diversity and resilience of existing meadows. Genotypic mapping could also allow
293 identifying the meadows at greatest risk of heat waves where management actions may be
294 focused.

295 Our results show that seagrass meadows from Shark Bay support the largest
296 seagrass C stocks worldwide, that while making a large contribution to C sequestration by
297 vegetated coastal ecosystems, their loss may disproportionately add to Australian CO₂
298 emissions. With increasing frequency and intensity of extreme climate events, the
299 permanence of these C stores might be compromised, further stressing the importance of
300 reducing green-house gas emissions, and implementing management actions to enhance
301 and preserve natural carbon sinks.

302

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306

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327

328 **Author contributions**

329 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
330 field and/or lab measurements. U.M. derived geostatistical models and A.A.O. and P.M.
331 dating models. K.M. and M.R. mapped seagrass area. J.W.F. and M.A.M. contributed data.
332 A.A.O. analyzed the data and drafted the first version of the manuscript. All authors
333 contributed to the writing and editing of the manuscript.

334

335 **Competing financial interests:**

336 The author(s) declare no competing financial interests.

337

338 **Figure Legends**

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

344

345 **Figure 2. Spatial distribution of organic carbon in seagrass sediments of Shark Bay.**

346 Measured (a) organic carbon content (%C) and (b) $\delta^{13}\text{C}$ (‰) isotopic signature of C along

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

349

350 **Figure 3. Spatial distribution of organic carbon stocks in seagrass sediments of**
351 **Shark Bay. (a) Top meter C stocks; (b) C stocks accumulated over the last 4,000 cal yr BP.**
352 Area with C storage estimates covers 2,000 km² of seagrass sediments. The integrated
353 sediment C stock within the 2,000 km² of surveyed seagrass area was estimated at 24 Tg C
354 in the top meter and 64 Tg C over the last 4,000 cal yr BP.

355

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

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370 **Tables**

371 **Table 1. Short- and long-term sedimentation, organic carbon (C) accumulation rates**
 372 **and sediment C stocks accumulated over the last 4,000 yr BP.** Sedimentation and C
 373 accumulation rates were estimated by ^{210}Pb , ^{14}C dating of sediments and the depth-
 374 weighted average of C concentrations (short-term normalized to 100 yr depth, and long-
 375 term to 1,000 cal yr BP depth). Uncertainties represent SE of the regression and the result
 376 of error propagation for sedimentation rates, and C accumulation rates and stocks,
 377 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

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385 **Table 2. Effects of the marine heat wave event to seagrass area and organic carbon**
 386 **(C) stocks under degraded seagrass meadows.** α is the fraction of sediment C stock
 387 within the top meter exposed to oxic conditions. Biomass C loss is not included in the
 388 calculations as much of the primary production might likely be buried or exported, rather
 389 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

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

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537 **Methods**

538 Seagrass sediments were sampled using PVC cores (100 - 300 cm long, 6.5 cm
539 internal diameter) that were hammered into the substrate at 0.5 to 4 m water depth. In
540 the laboratory, the PVC corers were cut lengthwise, and the sediments inside the corers
541 were sliced at 1 or 3 cm-thick intervals. Analysis of ^{210}Pb , ^{14}C and grain size were
542 conducted in cores cut at 1 cm resolution (11 cores), while dry bulk density (DBD), %C,
543 $\delta^{13}\text{C}$ were measured in all cores (28 cores) in alternate slices every 3 cm (upper 50 cm),
544 and every 6 cm (below 50 cm). We combined our data with previously published studies
545 in Shark Bay involving coring in seagrass sediments^{7,16,52}. From Bufarale and Collins
546 (2015), we took core FDW2 (here W4) dated by ^{14}C and we analyzed grain size, %C and
547 $\delta^{13}\text{C}$ to include it in the dataset. From Fourqurean *et al.*⁵² we included the C data from the 8
548 long sediment cores (here W5 – W8 and FS15 – FS18) and from Lavery *et al.*⁷ we included
549 C and $\delta^{13}\text{C}$ data of twelve 27 cm-long cores (here P1 and P2) in this study¹⁹. Compression
550 of seagrass sediments during coring was corrected by distributing the spatial discordances
551 proportionally between the expected and the observed sediment column layers⁵³ and was
552 accounted for in the calculations of C stocks standardized to 1 m depth and 4,000 cal yr BP.
553 Average compression was 20% and was applied to published data where compression
554 existed but was not measured during sampling^{7,16}. Published and unpublished cores from
555 this study comprised 49 locations covering a range of 3 seagrass genera forming
556 monospecific and mixed meadows, 34 contained data deeper than 1 meter with 23 sites
557 extending down to 2-3 meters (Supplementary, Table S3). None of the cores penetrated
558 the entire thickness of seagrass-accumulated sediment estimated to range from 4 to 6 m¹⁶.

559 The C content of sediments was measured in pre-acidified (with 1 M HCl) samples.
560 One gram of ground sample was acidified to remove inorganic carbon after weighing,
561 centrifuged (3,400 revolutions per minute, for 5 min), and the supernatant with acid
562 residues was carefully removed by pipette, avoiding resuspension. The sample was then

563 washed with Milli-Q water, centrifuged and the supernatant removed. The residual
564 samples were then re-dried at 60°C and encapsulated in tin capsules for C and $\delta^{13}\text{C}$
565 analyses using an Elemental Analyzer - Isotope Ratio Mass Spectrometer (Hilo Analytical
566 Laboratory) at the University of Hawaii. C content (%C) was calculated for the bulk (pre-
567 acidified) samples using the formula ($C_{\text{bulk}} = C_{\text{acidified}} \cdot \frac{\text{mass acidified}}{\text{mass pre-acidified}}$). The method
568 used to remove inorganic carbon prior to C analyses may lead to the loss of part of the
569 organic C (soluble fraction), thereby potentially leading to an underestimation of sediment
570 C content^{54,55}. The sediment $\delta^{13}\text{C}$ signature is expressed as δ values in parts per thousand
571 relative to the Vienna Pee Dee Belemnite. Replicate assays and standards indicated
572 measurement errors of $\pm 0.04\%$ and $\pm 0.1\%$ for C content and $\delta^{13}\text{C}$, respectively. The
573 relative contribution of seagrass, macroalgae and seston (that includes living and non
574 living matter in the water column) and terrestrial matter to seagrass top meter sediment
575 carbon pools was computed applying a three-component isotope-mixing model as
576 described by Phillips and Gregg (2003) and calculated by means of the IsoSource Visual
577 Basic program⁵⁶, using a 1% increment and 0.1‰ tolerance. We used literature values for
578 putative C sources and macroalgae and seston were combined as a single C source since
579 their published $\delta^{13}\text{C}$ endmembers were not significantly different (Supplementary, Table
580 S2).

581 Sediment grain-size was measured with a Mastersizer 2000 laser diffraction
582 particle analyzer following digestion of bulk samples with 10% hydrogen peroxide at the
583 Centre for Advanced Studies of Blanes. The d_{50} (i.e. the median particle diameter) was
584 used as a proxy for the particle size distribution. Sediments were classified as sand (0.063
585 - 1 mm), silt (0.004 - 0.063 mm) and clay (< 0.004 mm), and the mud fraction was
586 calculated as the sum of the fractions of silt and clay (< 0.063 mm) (size scale: Wentworth,
587 1922)⁵⁷. Sand:mud ratio was used as a proxy for depositional conditions and
588 hydrodynamic energy, where higher sand content could be associated with higher energy
589 environments⁵⁸.

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

594 Eleven sediment cores were analyzed for ^{210}Pb concentrations to determine recent
595 (ca. 100 years) sediment accumulation rates. ^{210}Pb was determined through the analysis of
596 ^{210}Po by alpha spectrometry after addition of ^{209}Po as an internal tracer and digestion in
597 acid media using an analytical microwave⁵⁹. The concentrations of excess ^{210}Pb used to
598 obtain the age models were determined as the difference between total ^{210}Pb and ^{226}Ra
599 (supported ^{210}Pb). Concentrations of ^{226}Ra were determined for selected samples along
600 each core by low-background liquid scintillation counting method (Wallac 1220
601 Quantulus) adapted from Masqué *et al.*⁶⁰. Mean sediment accumulation rates over the last
602 100 years could be estimated for eight out of the eleven sediment cores dated using the
603 CF:CS model below the surface mixed layer when present⁶¹. Mixing was common from 0 to
604 4 cm in half of the dated sediment cores, hence average modern accumulation rates should
605 be considered as upper limits. Two to five samples of shells per core from the cores dated
606 by ^{210}Pb were also radiocarbon-dated at the Direct AMS-Radiocarbon Business Unit,
607 Accium Biosciences, USA, following standard procedures⁶². The conventional radiocarbon
608 ages reported by the laboratory were converted into calendar dates (cal yr BP) using the
609 Bacon software (Marine13 curve)⁶³ and applying a marine reservoir correction (i.e.
610 subtracting Delta R value of 85 ± 30 for the East Indian Ocean, Western Australia)⁶⁴.
611 Average short-term C accumulation rates were estimated by multiplying sediment
612 accumulation rates ($\text{g cm}^{-2} \text{ yr}^{-1}$) by the fraction of C accumulated to 100 yr depth
613 determined by ^{210}Pb dating. Bacon model output was used to estimate average long-term
614 sediment accumulation rates ($\text{g cm}^{-2} \text{ yr}^{-1}$) during the last 1,000 yr BP. Long-term C
615 accumulation rates were determined following the same method as for short-term
616 accumulation rates, but the fraction of C was normalized to 1,000 cal yr BP, as the

617 minimum age of the ^{14}C -dated bottom sediments was $1,117 \pm 61$ cal yr BP (Supplementary,
618 Table S4).

619 C stocks at the 49 locations were estimated for 1 m sediment thickness and for a
620 period of accumulation of 4,000 years, similar to the time of formation of the C deposits¹⁶.
621 We standardized the estimates of sediment C stocks to one meter thick deposits since this
622 allows comparisons with estimates of global stocks. Where necessary (i.e. in 15 cores), we
623 inferred C stocks below the limits of the reported data to 1 m, extrapolating linearly
624 integrated values of C content (cumulative C stock Mg C ha^{-1}) with depth. C content was
625 reported to at least 27 cm in 12 cores out of these 15, while the other 3 cores had C data
626 down to 55 - 83 cm. Correlation between extrapolated C stocks from 27 cm to 1 m and
627 measured C stocks in sediment cores ≥ 1 m was $\rho = 0.82$ $P < 0.001$ (Supplementary, Fig.
628 S3a). Sediment C stocks in the ≥ 1 meter cores ranged from 23 to 322 Mg C ha^{-1} , with a
629 mean value of 116 ± 13 Mg C ha^{-1} and median 109 Mg C ha^{-1} . Extrapolating data on
630 cumulative C stocks from cores of at least 27 cm depth at a further 15 sites to 1 m, we
631 estimated C storage at those sites to range between 26 and 313 Mg C ha^{-1} , similar to sites
632 with full inventories. Combining the estimates extrapolated from shallow cores with full
633 core inventories, the resulting mean and median sediment C storage (103 ± 11 Mg C ha^{-1}
634 and 73 Mg C ha^{-1} , respectively)(Supplementary, Fig. S4) were not significantly different (P
635 > 0.05) from those for full core inventories. We applied ordinary kriging to estimate the
636 top 1 meter C stocks across 2,000 km^2 encompassing the South Wooramel Bank, Faure Sill
637 and Peron Peninsula seagrass banks^{65,66}. We used a maximum of the 16 nearest
638 neighbours within a search circle of radius 25 km. Ordinary kriging inherently declusters
639 the input data and produces smoothed estimates, so that the extremely high or low values
640 found within seagrass meadows of the Bay do not disproportionately influence the global
641 mean.

642 We estimated seagrass sediment C stocks accumulated over the last 4,000 years in
643 1 to 3 m long cores where ^{14}C data were available and the length sampled embraced \geq

644 2,000 yr of sediment and C accumulation (i.e. in 8 cores). The correlation between
645 extrapolated and measured C stocks was $r = 0.90$ ($P < 0.05$) (Supplementary, Fig. S3b).
646 Bay-wide estimates of sediment C stocks accumulated over 4,000 cal yr BP were estimated
647 by combining extrapolated and full 4,000 cal yr BP core inventories, and applying
648 collocated cokriging with top meter C stocks as the secondary variable. Correlation
649 between top meter and 4,000 yr BP carbon stocks was 0.6 ($P < 0.01$) and the percentage of
650 noise specific to the background was set to 20%. Spatial variability of C stocks was
651 mapped after applying Ordinary Kriging (OK) to top meter C stocks and collocated co-
652 kriging to millenary C stock (4,000 cal yr BP).

653 Data on seagrass sediment C stocks accumulated during the last 4,000 yr in *P.*
654 *oceanica* were extracted or extrapolated from published estimates²⁷ of sediment cores
655 with a sampled depth of at least 2,000 yr, as this is the same method we used to estimate
656 long-term C_{org} stocks at Shark Bay.

657 The extent of seagrass meadows in Shark Bay before and after the extreme climatic
658 event was determined by the Western Australian Department of Biodiversity,
659 Conservation and Attractions as part of a broader long-term seagrass monitoring program.
660 Seagrass extent was derived using a supervised classification of imagery captured by
661 Landsat-5 Thematic Mapper (TM) in 2002 and Landsat-8 Operational Land Imager (OLI)
662 in 2014 (United States Geological Survey (glovis.usgs.gov/)). The spatial resolution of
663 these images is 30 m. The 2002 and 2014 classifications used a combination of historical
664 ground-truthing, long-term monitoring data and expert knowledge for training sites and
665 validation. The imagery was classified into three distinct classes; 'dense seagrass' (> 40%
666 cover); 'sparse seagrass' (< 40% cover) and 'other' which included all remaining habitat
667 types. The Shark Bay Marine Park (SBMP) covers approximately 8,900 km² of seafloor.
668 The seagrass mapping presented here covers approximately 78% of SBMP. The entire
669 extent was not mapped due to poor image quality caused by depth and water clarity and
670 the lack of data in some areas.

671 Net seagrass area losses and shifts in seagrass cover from dense to sparse were
672 considered as damaged areas, where the seagrass sediment organic matter is more
673 exposed oxygen due to erosion and sediment resuspension, hence is more susceptible to
674 being rapidly remineralized. We modelled the potential CO₂ emissions associated with this
675 disturbance and subsequent remineralization of sediment C stocks using equation 1 based
676 on varying proportions of sediment C being exposed to oxic conditions following
677 disturbance:

$$678 \quad C(t) = \alpha \cdot C_{(0)} \cdot e^{-k_1 \cdot t} \quad (1)$$

679 where C₍₀₎ is the measured C stock in the top meter, α is the fraction of the C stock
680 exposed to oxic conditions and k_1 is the decomposition rate of seagrass sediment C (0.183
681 yr⁻¹)²⁰ in oxic sediment conditions.

682 This required a number of assumption which were: (1) the C stock over the top
683 meter (Mg C ha⁻¹) of sampled seagrass meadows was representative of the C stock
684 contained in sediments within the damaged seagrass area prior to the heat-wave; (2) the
685 fraction of the sediment C in disturbed seagrass meadows exposed to oxic environments
686 was in the range of 0.1 to 0.5; (3) the potential contribution of seagrass biomass
687 remineralization to CO₂ emissions was not accounted for due to the lack of knowledge
688 about the export and fate of plant biomass following meadows loss; and (4) there will be
689 no recovery of seagrass in the long-term (i.e., 40 yr). With the exception of the last
690 assumption, these were conservative, in an effort to avoid over-estimation of potential CO₂
691 emissions. We assessed the loss of C to the atmosphere after 3 years post disturbance (in
692 2014) and also assessed potential releases over a 40-year time frame consistent of tier 1
693 and 2 methods of IPCC (2006) for organic soils. The C stock loss per hectare 3 years and 40
694 years post disturbance was multiplied by the damaged seagrass area (1,125 km²).

695 **Data availability**

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

698 University Research portal with the identifier doi:

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700

701 **References related to Methods**

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