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## A marine heatwave 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 CO<sub>2</sub> 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 biomass<sup>1</sup>. Their organic carbon (C) sink capacity is  
68 estimated to be 0.08-0.22 Pg C yr<sup>-1</sup> globally<sup>2</sup>, accounting for an offset of 0.6 - 2% of global  
69 anthropogenic CO<sub>2</sub> emissions (49 Pg CO<sub>2</sub>eq yr<sup>-1</sup>)<sup>3</sup>. However, blue carbon ecosystems are in  
70 decline worldwide<sup>2</sup>, raising concern about a potential re-emission of their C stocks to the  
71 atmosphere as CO<sub>2</sub>. CO<sub>2</sub> emissions from loss of blue carbon ecosystems are estimated at  
72 0.15 - 1.02 Pg CO<sub>2</sub> yr<sup>-1</sup>, which is equivalent to 3 - 19% of those from terrestrial land-use  
73 change<sup>4</sup>.

74 Seagrasses are marine flowering plants that consist of 72 species growing across a  
75 wide range of habitats<sup>5</sup>. Global estimates of C storage in the top meter of seagrass  
76 sediments range from 4.2 to 8.4 Pg C<sup>6</sup>, 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<sup>7,8</sup>. Since the beginning of the twentieth century, seagrass meadows worldwide  
80 have declined at a median rate of 0.9% yr<sup>-1</sup> mostly due to human impacts such as coastal  
81 development or water quality degradation<sup>9</sup>. 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 Sea<sup>10</sup> and *Amphibolis*  
85 *antarctica* in Western Australia<sup>11-13</sup>). Seagrass losses and the subsequent erosion and  
86 remineralization of their sediment C stocks are likely to continue or intensify under  
87 climate change<sup>9</sup>, especially in regions where seagrasses live close to their thermal  
88 tolerance limits<sup>14</sup>.

89 Shark Bay (Western Australia) (Fig.1) contains one of the largest (4,300 km<sup>2</sup>) and  
90 most diverse assemblage of seagrasses worldwide<sup>15</sup>, 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 growth<sup>16</sup>. 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*<sup>12,13</sup>, 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 averages<sup>17</sup>. 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 Australia<sup>18</sup>, 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 CO<sub>2</sub> emissions. Based on data from 49 sampled sites<sup>19</sup>, satellite imagery and a published  
107 model of soil C loss following disturbance<sup>20</sup>, 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 CO<sub>2</sub> 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 ± SE (2.00 ± 0.06%) values for the top meter similar to  
117 global estimates (median: 1.8% C; mean ± SE: 2.5 ± 0.1% C)<sup>6</sup>, 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:  $-25.1\text{‰}^{22}$ ; 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  $^{13}\text{C}$ -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 globally<sup>23</sup>.  
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 compounds<sup>24</sup> compared to seston and algal detritus<sup>25</sup>, which are characterized by faster  
136 decomposition rates<sup>26</sup>. 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 Sea<sup>27</sup>.

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  $161 \text{ Mg C ha}^{-1}$  ( $Q_1$  and  $Q_3$ , respectively) (Fig. 3a). While this is in agreement with reported



146 median seagrass sediment C stock at a global scale ( $140 \text{ Mg C ha}^{-1}$ )<sup>6</sup>, 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 ( $122 \text{ Mg C ha}^{-1}$ ) and tidal marshes ( $160 \text{ Mg C}$   
150  $\text{ha}^{-1}$ ), while the C stocks in Shark Bay's hotspots compare with those of mangroves and  
151 boreal forests ( $255 \text{ Mg C ha}^{-1}$  and  $296 \text{ Mg C ha}^{-1}$ , respectively)<sup>6,28</sup>. 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 ( $4.2 - 8.4 \text{ Pg C}$ )<sup>6</sup>.

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 Bay<sup>16</sup>. Seismic profiles  
159 combined with <sup>14</sup>C dating indicate that the seagrass banks here contain a continuous 4,000  
160 yr record of sediment and C accumulation<sup>16</sup>. 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<sup>16,29</sup> 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  $650 \text{ Mg C ha}^{-1}$  towards the south of the Wooramel Bank and Faure Sill, and decreased to  
167  $110 \text{ Mg C ha}^{-1}$  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  $\text{km}^2$ ), 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 meter<sup>6</sup> and  $1027 \pm 314 \text{ Mg C}$

172 ha<sup>-1</sup> over the last 4,000 yr BP<sup>27</sup>), 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<sup>-2</sup> yr<sup>-1</sup>, with a median of 11.3 g C m<sup>-2</sup> yr<sup>-1</sup> (mean ±  
178 SE: 12 ± 2 C m<sup>-2</sup> yr<sup>-1</sup>), while short-term accumulation rates (last 100 years) were estimated  
179 at 15 to 123 g C m<sup>-2</sup> yr<sup>-1</sup>, with a median of 30 g C m<sup>-2</sup> yr<sup>-1</sup> (mean ± SE: 46 ± 13 g C m<sup>-2</sup> yr<sup>-1</sup>)  
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 Mediterranean<sup>30</sup>, *P. australis* in Australia<sup>31,32</sup> and *Thalassia*  
182 *testudinum* in Florida Bay<sup>33</sup> (26 – 122 g C m<sup>-2</sup> yr<sup>-1</sup>). 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<sup>-2</sup> yr<sup>-1</sup>)<sup>1</sup> and equal short-term C accumulation in  
185 Australian tidal marshes (55 ± 2 g C m<sup>-2</sup> yr<sup>-1</sup>)<sup>34</sup>.

186 The 4,300 km<sup>2</sup> of seagrass meadows in Shark Bay contemporarily account for a  
187 sequestration of 200 ± 55 Gg C yr<sup>-1</sup> (range 65 – 527 Gg C yr<sup>-1</sup>), which represents 9% of the  
188 C sequestered by Australia's vegetated coastal ecosystems (occupying an area of 110,000  
189 km<sup>2</sup>)<sup>7,34,35</sup>. 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 **CO<sub>2</sub> 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 2010/11<sup>17</sup>. 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 erosion<sup>13</sup>, providing favorable conditions to CO<sub>2</sub>  
206 emissions<sup>36</sup>.

207         Losses of C and associated CO<sub>2</sub> emissions following degradation of seagrass  
208 ecosystems have been documented previously<sup>20</sup>. Yet, no studies have evaluated the risk of  
209 CO<sub>2</sub> emissions associated with seagrass loss due to thermal stress impacts. Carbon  
210 remineralization to CO<sub>2</sub> 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 stored<sup>36</sup>. Vegetation loss also increases the potential for  
213 sediment erosion and sediment resuspension in the water column<sup>37</sup>, increasing the oxygen  
214 exposure of previously buried sediment organic matter<sup>38</sup>, leading to 2 to 4 times higher  
215 remineralization of sediment C under oxic than anoxic conditions<sup>20</sup>. Carbon in the upper  
216 meter of sediments has been considered the most susceptible to remineralization when  
217 seagrass meadows are lost<sup>4,6</sup>. However, Lovelock *et al.*<sup>20</sup> 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<sup>-1</sup><sup>20</sup>), we estimate that between 4 to 22  
223 Mg C ha<sup>-1</sup> (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 CO<sub>2</sub>-e ha<sup>-1</sup>, and

226 assuming no seagrass recovery, it could result in cumulative C losses of 10 to 52 Mg C ha<sup>-1</sup>  
227 or 38–190 Mg CO<sub>2</sub>-e ha<sup>-1</sup> (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<sup>-1</sup>, and at 52 ± 14 Gg C yr<sup>-1</sup> over the ~1,100km<sup>2</sup> 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 CO<sub>2</sub>  
235 emissions from sediment C stocks ranging from 2 to 9 Tg CO<sub>2</sub> during the following three  
236 years after the event. This can be compared to the 14.4 Tg CO<sub>2</sub> estimated to be released  
237 annually from land-use change in Australia<sup>39</sup>, 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 CO<sub>2</sub> 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)<sup>40,41</sup> or not occur over contemporary time  
243 scales<sup>13</sup>. If damaged seagrass meadows recover, the estimates of CO<sub>2</sub> emissions after 40  
244 years might be lower than reported here. In addition, CO<sub>2</sub> emissions from organic carbon  
245 remineralization may be partially offset by the net dissolution of the underlying carbonate  
246 sediments<sup>42</sup>. 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 respiration<sup>43</sup>. 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 CO<sub>2</sub> 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 eutrophication<sup>44</sup>, but less-suited to managing global threats such as heat  
269 waves, due to the spatial scale and magnitude of these impacts<sup>45</sup>.

270 In the face of global threats, management can aim to maintain or enhance the  
271 resilience of seagrasses<sup>46</sup>. 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 rhizomes<sup>41</sup>. These  
274 characteristics provide the species with high levels of resistance to disturbance<sup>11,12</sup>.  
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 emissions<sup>36</sup>, 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<sup>47,48</sup>. Long-term actions should include management to maintain top-  
286 down controls so that herbivory is maintained at natural levels<sup>49</sup>. More contentious  
287 actions could aim to repopulate areas with more resilient seagrass genotypes sourced  
288 from outside the impacted sites<sup>50</sup>. 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 CO<sub>2</sub>  
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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326 Australia.

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 km<sup>2</sup> of seagrass sediments. The integrated  
353 sediment C stock within the 2,000 km<sup>2</sup> 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.

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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  $^{210}\text{Pb}$ ,  $^{14}\text{C}$  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 <sup>-1</sup> )		C accumulation (g C m <sup>-2</sup> yr <sup>-1</sup> )		Sediment C stocks 4,000 cal yr BP (Mg C ha <sup>-1</sup> )
	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)	
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
<b>Mean ± SE</b>	<b>2.5 ± 0.3</b>	<b>0.77 ± 0.11</b>	<b>46 ± 13</b>	<b>12 ± 2</b>	<b>439 ± 124</b>

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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.**  $\alpha$  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 <sup>2</sup> )	Extrapolated values for the entire Bay (13,000km <sup>2</sup> )
Baseline seagrass area (km <sup>2</sup> )	2689	4300
Dense	1925	3096
Sparse	765	1204
C stock top meter (Tg C)	34 ± 14	55 ± 22
Seagrass area loss (km <sup>2</sup> )	581	929
Shift to sparse seagrass (km <sup>2</sup> )	118	190
Total damaged seagrass area (km <sup>2</sup> )	699	1125
3 yr net C loss from 1 m sediment stock (Tg C)		
$\alpha$ 0.10	0.30 ± 0.05	0.49 ± 0.08
$\alpha$ 0.25	0.76 ± 0.10	1.23 ± 0.15
$\alpha$ 0.50	1.52 ± 0.17	2.45 ± 0.27
40 yr net C loss from 1 m sediment stock (Tg C)*		
$\alpha$ 0.10	0.72 ± 0.27	1.16 ± 0.53
$\alpha$ 0.25	1.81 ± 0.35	2.91 ± 0.62
$\alpha$ 0.50	3.61 ± 0.50	5.81 ± 0.80
3yr net CO <sub>2</sub> emissions (Tg CO <sub>2</sub> )	1.1 - 5.6	1.8 - 9.0
40 yr potential CO <sub>2</sub> emissions (Tg CO <sub>2</sub> )*	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  $^{210}\text{Pb}$ ,  $^{14}\text{C}$  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<sup>7,16,52</sup>. From Bufarale and Collins  
546 (2015), we took core FDW2 (here W4) dated by  $^{14}\text{C}$  and we analyzed grain size, %C and  
547  $\delta^{13}\text{C}$  to include it in the dataset. From Fourqurean *et al.*<sup>52</sup> we included the C data from the 8  
548 long sediment cores (here W5 – W8 and FS15 – FS18) and from Lavery *et al.*<sup>7</sup> we included  
549 C and  $\delta^{13}\text{C}$  data of twelve 27 cm-long cores (here P1 and P2) in this study<sup>19</sup>. Compression  
550 of seagrass sediments during coring was corrected by distributing the spatial discordances  
551 proportionally between the expected and the observed sediment column layers<sup>53</sup> 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<sup>7,16</sup>. 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 m<sup>16</sup>.

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<sup>54,55</sup>. The sediment  $\delta^{13}\text{C}$  signature is expressed as  $\delta$  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  $\pm 0.1\text{‰}$  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 program<sup>56</sup>, 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)<sup>57</sup>. 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 environments<sup>58</sup>.

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  $^{210}\text{Pb}$  concentrations to determine recent  
595 (ca. 100 years) sediment accumulation rates.  $^{210}\text{Pb}$  was determined through the analysis of  
596  $^{210}\text{Po}$  by alpha spectrometry after addition of  $^{209}\text{Po}$  as an internal tracer and digestion in  
597 acid media using an analytical microwave<sup>59</sup>. The concentrations of excess  $^{210}\text{Pb}$  used to  
598 obtain the age models were determined as the difference between total  $^{210}\text{Pb}$  and  $^{226}\text{Ra}$   
599 (supported  $^{210}\text{Pb}$ ). Concentrations of  $^{226}\text{Ra}$  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.*<sup>60</sup>. 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 present<sup>61</sup>. 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  $^{210}\text{Pb}$  were also radiocarbon-dated at the Direct AMS-Radiocarbon Business Unit,  
607 Accium Biosciences, USA, following standard procedures<sup>62</sup>. The conventional radiocarbon  
608 ages reported by the laboratory were converted into calendar dates (cal yr BP) using the  
609 Bacon software (Marine13 curve)<sup>63</sup> and applying a marine reservoir correction (i.e.  
610 subtracting Delta R value of  $85 \pm 30$  for the East Indian Ocean, Western Australia)<sup>64</sup>.  
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  $^{210}\text{Pb}$  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 <sup>14</sup>C-dated bottom sediments was 1,117± 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 deposits<sup>16</sup>.  
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<sup>-1</sup>) 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<sup>-1</sup>, with a  
629 mean value of  $116 \pm 13$  Mg C ha<sup>-1</sup> and median 109 Mg C ha<sup>-1</sup>. 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<sup>-1</sup>, 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 ( $103 \pm 11$  Mg C ha<sup>-1</sup>  
634 and 73 Mg C ha<sup>-1</sup>, 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<sup>2</sup> encompassing the South Wooramel Bank, Faure Sill  
637 and Peron Peninsula seagrass banks<sup>65,66</sup>. 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 <sup>14</sup>C data were available and the length sampled embraced ≥

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 estimates<sup>27</sup> 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/](http://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 km<sup>2</sup> 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 CO<sub>2</sub> 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<sub>(0)</sub> is the measured C stock in the top meter, α is the fraction of the C stock  
680 exposed to oxic conditions and k<sub>1</sub> is the decomposition rate of seagrass sediment C (0.183  
681 yr<sup>-1</sup>)<sup>20</sup> 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<sup>-1</sup>) 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 CO<sub>2</sub> 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 CO<sub>2</sub>  
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 km<sup>2</sup>).

#### 695 **Data availability**

696 Seagrass sediment data on dry bulk density (DBD), C, δ<sup>13</sup>C, <sup>210</sup>Pb concentrations and <sup>14</sup>C  
697 raw ages that support the findings of this study have been deposited in Edith Cowan

698 University Research portal with the identifier doi:

699 <https://dx.doi.org/10.4225/75/5a1640e851af1>.

700

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