

# **An extreme climatic event and experimental loss of predation risk accelerates herbivore-driven seagrass loss and tropicalization**

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1 **Abstract:** Extreme climatic events (ECEs) and predator loss co-occur widely, but it remains  
2 unclear when predator removal can influence ecosystem resilience to ECEs, and the interactive  
3 role these two may play in marine tropicalization. We performed a 16-month field experiment to  
4 determine whether experimentally simulated loss of tiger sharks (*Galeocerdo cuvier*) exacerbated  
5 seagrass loss and tropicalization driven by a marine heat wave in Shark Bay, Australia by  
6 experimentally simulating patterns of dugong (*Dugong dugon*) herbivory predicted if tiger sharks  
7 were extirpated. Grazing treatments targeted and removed tropical seagrasses, but also  
8 incidentally accelerated temperate seagrass losses. This shows herbivore behavioral changes in  
9 response to predator loss can exacerbate ECE effects and promote tropicalization- even without  
10 species range expansions- and that predation risk can generate resilience to ECEs. By implication,  
11 ongoing losses of apex predators may combine with increasingly frequent ECEs to amplify climate  
12 change impacts across diverse ecosystems and large spatial scales.

13

14 **One Sentence Summary:** Predator loss can exacerbate tropicalization driven by extreme climatic  
15 events even without range shifts of plants or herbivores, suggesting that predator loss can erode  
16 the resilience of ecosystems to such ECEs.

## 17 **Introduction**

18           One of many ways in which climate change is altering ecosystems is through widespread  
19 “tropicalization”, whereby species assemblages in a location shift to represent those in warmer,  
20 more equatorial climates (Vergés et al. 2014). Tropicalization can be driven not only by abiotic  
21 forcing brought about by climate change, but also by changes to biotic interactions such as when  
22 tropical herbivores expand their ranges into formerly temperate ecosystems and generate novel  
23 species interactions (e.g., Vergés et al. 2014, Bennett et al. 2015). These novel biotic interactions  
24 can act as “biotic multipliers of climate change” (Zarnetske et al. 2012), altering not only the  
25 likelihood of tropicalization, but also how easy or difficult it is to reverse (e.g., Bennett et al.  
26 2015).

27           Extreme climatic events (ECEs *sensu* Jentsch et al. 2007) associated with anthropogenic  
28 climate change are becoming more frequent and intense (e.g., Pachauri et al. 2014, Cai et al. 2014,  
29 2015, Oliver et al. 2018). As a result, the need to assess the ecosystem effects of ECEs has become  
30 critical. Recent work has shown that ECEs, particularly marine heat waves, can drive rapid  
31 tropicalization of marine ecosystems (e.g., Wernberg et al. 2013, Bennett et al. 2015). The  
32 response of ecosystems to ECEs will of course be dependent on the structure and connectivity of  
33 these ecosystems. It is crucial, therefore, to understand the role of multiple stressors (Mineur et  
34 al. 2014) and species interactions (Zarnetske et al. 2012) in mediating ecological responses to  
35 climate change, including ECEs.

36           Apex predators may be particularly important biotic multiplier of climate change because  
37 they interact with many species, have low functional redundancy, and are disproportionately  
38 vulnerable to exploitation (Heithaus et al. 2008, Ritchie and Johnson 2009, Zarnetske et al. 2012).  
39 Indeed, though not universal, trophic cascades induced by the loss of top predators have been

40 widely documented in terrestrial, aquatic, and marine ecosystems (e.g., Daskalov et al. 2007,  
41 Heithaus et al. 2008, Estes et al. 2011, Ripple et al. 2014) and may result from alterations in direct  
42 predation, predation risk, or their interaction (e.g., Werner and Peacor 2003, Preisser et al. 2005,  
43 Heithaus et al. 2008). Disruption of these top-down effects can alter ecosystem function and  
44 services (e.g., Schmitz 2008, Estes et al. 2011, Atwood et al. 2015). Maintenance of trophic  
45 cascades, particularly those that suppress herbivores, may therefore be critical to promoting  
46 ecosystem recovery and resilience following large climatic disturbances to primary producer  
47 communities.

48 Like climate change effects, human-driven loss of apex predators is widespread in both  
49 aquatic and terrestrial ecosystems (e.g., Ferretti et al. 2010, Estes et al. 2011, Ripple et al. 2014).  
50 Furthermore, there is growing evidence that climate change and predators interact to structure  
51 ecosystems (e.g., Kirby and Beaugrand 2009, Kratina et al. 2012), including evidence that  
52 predators can mediate the ecological impacts of climate change and climate variability (e.g.,  
53 Wilmers and Gets 2005, Wilmers et al. 2006, Sala 2006, Estes et al. 2011, Harley et al. 2011,  
54 Ripple et al. 2014). However, despite widespread co-occurrence of marine predator losses and  
55 climate related disturbances (Halpern et al. 2008), the potential for these stressors to interact  
56 remains poorly studied, particularly in the field (Crain et al. 2008). This is particularly true for  
57 ECEs, and the potential for top predator losses to alter the effects of and resilience to disturbances  
58 such as those caused by ECEs is largely unexplored. Indeed, fishing and climate change are  
59 usually viewed and modelled as separate stressors (Travers-Trolet et al. 2014), though exceptions  
60 exist (e.g., Kirby et al. 2009). If predator loss can exacerbate the ecological impacts of ECEs, apex  
61 predator conservation may be an effective strategy to impart ecological resilience to ECEs and  
62 reduce likelihood of tropicalization until the drivers of climate change can be addressed directly.

63           Seagrass ecosystems provide diverse ecosystem functions including primary and  
64 secondary production, habitat, sediment stabilization, carbon sequestration and storage (Norlund  
65 et al. 2016 and references therein). Tropical and subtropical seagrass ecosystems also often host  
66 megaherbivores such as sea turtles and sirenians that can exert considerable control over seagrass  
67 community structure (Jackson et al. 2001, Nowicki et al. 2018). Despite their importance, seagrass  
68 habitats are rapidly disappearing globally because of a variety of stressors, including ECEs (e.g.,  
69 Waycott et al. 2009, Fraser et al. 2014, Thomson et al. 2015). Seagrass habitats that contain large  
70 herbivores and have been impacted by ECEs therefore represent a valuable opportunity to  
71 determine whether and how changes to top-down control alter ecosystem responses to extreme  
72 climate events.

73           With its abundant populations of both megaherbivores and large tiger sharks, the  
74 subtropical seagrass ecosystem of Shark Bay, Western Australia has been a model system in which  
75 to study top-down control in the marine environment for more than two decades (Heithaus et al.  
76 2012). The deep understanding of species interactions in Shark Bay, combined with massive  
77 seagrass loss following the most extreme marine heat wave on Western Australian record in 2011  
78 (Fraser et al. 2014, Thomson et al. 2015, Hobday et al. 2016), offers a unique opportunity to assess  
79 whether the loss of apex predators can exacerbate the effects of an extreme climatic event (ECE)  
80 and promote tropicalization of this subtropical system.

#### 81 *Site description and background*

82           Shark Bay (25°45'S, 113°44'E) is a shallow (<15m), 13,000 km<sup>2</sup> semi-enclosed subtropical  
83 embayment approximately 800 km north of Perth, Western Australia. The bay contains 12 species  
84 of seagrasses, some with temperate and some with tropical affinities, that historically covered over  
85 4000 km<sup>2</sup> (Walker et al. 1988). This cover was overwhelmingly dominated (85% of cover) by the

86 temperate seagrass *Amphibolis antarctica*, which is at the tropical limit of its range in Shark Bay  
87 (Walker et al. 1988). *Amphibolis antarctica* is a long-lived ecosystem engineer (*sensu* Jones et al.  
88 1994) with critical and often irreplaceable ecosystem functions (Walker et al. 1988, Borowitzka et  
89 al. 2006, Burkholder et al. 2013a). The most common tropical seagrass in the bay is *Halodule*  
90 *uninervis* (Burkholder et al. 2013a), a much smaller species that does not provide the same habitat  
91 values and functions as the physically more complex and robust *A. antarctica*.

92 In the Austral summer of 2011, strong La Niña conditions strengthened the tropical  
93 Leeuwin current, increasing transport of tropical water along the Western Australia coast (Pearce  
94 and Feng 2013) and generating an extreme, category IV marine heat wave (*sensu* Hobday et al.  
95 2018) known as the “Ningaloo Niño” (Feng et al. 2013). This Extreme Climatic Event (ECE)  
96 increased water temperatures along Western Australia by 2-4° C for two months (Pearce and Fent  
97 2013, Feng et al. 2013, Hobday et al. 2016), including in Shark Bay (Nowicki et al. 2017). The  
98 ECE resulted in catastrophic (>90%) loss of temperate *Amphibolis antarctica* within the study area  
99 (Fraser et al. 2014, Thomson et al. 2015) and opened canopy and substrate to establishment and  
100 expansion of the early successional tropical seagrass *Halodule uninervis* (Nowicki et al. 2017),  
101 creating mixed species beds that had been historically rare in Shark Bay (Fig. 1).

102 In other seagrass ecosystems, such mixed species beds are vulnerable to phase shifts driven  
103 by dugong and green turtle grazing (Preen 1995, Kelkar et al. 2013). Dugongs in particular can  
104 alter seagrass community composition through destructive excavation foraging, which usually  
105 targets tropical seagrasses but can destroy less disturbance tolerant climax seagrasses incidentally  
106 (Preen 1995, Masini et al. 2001, Wirsing et al. 2007a). This form of top down control is not  
107 thought to be normally dominant in Shark Bay for two reasons: first, *A. antarctica*, which is itself  
108 not a preferred food source or target of excavation grazing (Wirsing et al. 2007a, Burkholder et al.

109 2012), establishes dense canopies that limit excavation grazer's access to tropical seagrasses. This  
110 makes it difficult for dugongs to find sufficient tropical seagrasses to excavate in full *A. antarctica*  
111 meadows (Fig. 2 a,c). Second, excavation grazing is a dangerous foraging tactic that dugongs  
112 rarely undertake in Shark Bay because of predation risk from tiger sharks (*Galeocerdo cuvier*),  
113 which are abundant and play an important role in shaping seagrass ecosystem structure and  
114 function in Shark Bay (Wirsing et al. 2007a,b,c, Heithaus et al. 2012, Burkholder et al. 2013, Fig.  
115 2 a,b). However, in Shark Bay's current state, ECE mediated loss of *A. antarctica* has made  
116 tropical seagrasses more dense, more available, and more accessible to excavators (Nowicki et al.  
117 2017), increasing the potential for excavation grazing to generate a phase shift to a seagrass  
118 community dominated by structurally simple seagrasses of tropical origin. If apex predators (in  
119 this case, tiger sharks) were extirpated and predation risk were lowered, as occurs in ecosystems  
120 globally (Ferretti et al. 2010, Estes et al. 2011, Ripple et al. 2014), then the ensuing combination  
121 could result in a phase shift towards tropicalization, typified by a low-biomass or even seagrass  
122 depauperate state (Fig. 2d), even in previously dangerous shallow seagrass habitats.

123 We used this 2011 ECE as a natural experiment to emulate changes in dugong foraging  
124 behavior consistent with tiger shark extirpation. In doing so, we sought to determine whether a  
125 combination of simulated predator loss and climatic disturbance could destabilize remaining *A.*  
126 *antarctica* beds and generate a phase shift toward tropicalization of the seagrass community.  
127 Specifically, we performed a 16 month field experiment in which divers applied risk-sensitive  
128 foraging tactics to disturbed seagrass beds at rates consistent with complete tiger shark extirpation  
129 and loss of predation risk to Shark Bay's dominant megaherbivore, the dugong (*Dugong dugon*).  
130 Our goals were to determine *a priori* (1) if emulated tiger shark (*Galeocerdo cuvier*) removal  
131 would drive habitat tropicalization by reducing *A. antarctica* cover through incidental removal

132 during dugong excavation while allowing *H. uninervis* to proliferate, and *post hoc* (2) whether  
133 such effects are dependent on the strength of initial seagrass loss.

## 134 **Methods**

### 135 *Site establishment*

136 In April-May 2013, 30 experimental plots, each measuring 3m x 3m, were placed at 2-3m  
137 depth in the interiors of two seagrass banks separated by approximately 2km. Each plot was placed  
138 in a degraded *A. antarctica* bed that was characterized by reduced *A. antarctica* cover (10-60%),  
139 prevalence of exposed, dying *A. antarctica* rhizome tissue, presence of the early successional  
140 tropical seagrass *H. uninervis*, and generally low macroalgae cover (Fig. 1, third panel). Plots  
141 were placed in a blocked design on two banks; eighteen plots were placed on a heavily impacted  
142 bank (mean initial *A. antarctica* cover =17.3%,  $s=5.2\%$ ), and twelve on a moderately impacted  
143 bank (mean initial *A. antarctica* cover =33.1%,  $s=11.3\%$ ). Each treatment level (control, moderate  
144 herbivory, intense herbivory) was equally represented within each block, and plots near each other  
145 were grouped into trios of similar initial seagrass cover before being randomly assigned a  
146 treatment. Plots were marked with a post at each corner and were generally farther than 2m from  
147 each other. The mean *H. uninervis* cover was similar on both banks (mean 46.4%  $s=21.4\%$ ,  
148 Welch's t-test:  $t_{24,2}=0.09$ ,  $p=0.93$ ). Macroalgae cover was slightly higher on the heavily impacted  
149 bank (6.8% vs 2.6%, Mann-Whitney test,  $W=118$ ,  $p=0.0015$ ) but was generally very low (mean=  
150 4.8%,  $s= 3.8\%$ ).

### 151 *Estimation of dugong foraging rates*

152 Because experimental manipulation of tiger shark predation risk is not feasible, we  
153 emulated dugong foraging impacts manually. To determine appropriate foraging rates, we used  
154 published data on predation risk-sensitive foraging by dugongs in the study area (Wirsing et al.

155 2007a,b,c) to estimate the magnitude of dugong foraging that should occur in high-risk habitats if  
156 tiger sharks were suddenly extirpated and these habitats became low-risk. Dugong foraging effort  
157 was expressed in number of seconds of foraging effort per plot per month (expressed here as  $\lambda$ ).  
158 We calculated  $\lambda$  by scaling down bank-scale estimates of foraging dugong density calculated for  
159 this system (Wirsing et al. 2007b) to the scale of individual plots. Dugong abundances and activity  
160 levels vary seasonally (Wirsing et al. 2007b), so  $\lambda$  was calculated monthly. Focal follows of  
161 dugongs in the study area suggest that trails are excavated at the rate of *ca.* 10cm of horizontal  
162 progress \*  $\text{sec}^{-1}$  (Nowicki pers. obs., Wirsing et al. 2007a), so  $\lambda$  was divided by 10 to determine  
163 the number of 1m feeding trails applied per plot for each month (rounded to nearest integer). A  
164 15 x 100 cm rebar grazing frame was used to ensure a constant area and shape of grazing  
165 treatments.

166 Dugongs can forage via two tactics: shoot cropping and rhizome excavation (Wirsing et al.  
167 2007a). Because excavation foraging is more profitable to dugongs than shoot cropping (Anderson  
168 1982, 1998, Wirsing et al. 2007a) we simulated excavation as long as dense stands of tropical  
169 seagrass were present in the plot (i.e., if at least 3 of 5 panels of grazing frame contained *H.*  
170 *uninervis*). We always targeted the densest stands of *H. uninervis* and avoided *A. antarctica* if  
171 possible. When *A. antarctica* was present, however, it was removed to mimic the incidental  
172 removal of non-target seagrasses that occurs during excavation foraging (Preen 1995).

173 Excavation trails measured 15cm W x 100 cm L x 4 cm D and were created with hand  
174 trowels to generate feeding scars consistent with dugong excavation foraging. Excavation  
175 removed all above-ground biomass, similar to actual dugong excavation trails (Preen 1995, De  
176 Iongh et al. 1995, Masini et al. 2001, Nakaoka et al. 2002). Seagrass recovery from artificial  
177 dugong excavation trails is not significantly different from natural feeding trails (De Iongh et al.

178 1995, Nakaoka and Aioi 1999), so we are confident our treatments accurately reflected natural  
179 dugong excavation. In very rare (<5%) cases where sufficient *H. uninervis* was sparse, an equal  
180 area was grazed by cropping *A. antarctica* shoots with a knife where the leaf bundle meets the  
181 stem.

### 182 *Data collection and application of grazing treatments*

183 Our experiment included three treatment levels: control, moderate herbivory, and intense  
184 herbivory. Control plots were visited to collect data but did not undergo simulated grazing to  
185 reflect the current, high-risk landscape of Shark Bay, because tiger shark abundance did not change  
186 following the ECE (Nowicki et al. 2019). The moderate herbivory treatment emulated the grazing  
187 effort that would be expected if dugong abundance remained constant but dugong habitat use  
188 shifted entirely towards shallow seagrass banks where the experiment was established. These  
189 shallow seagrass beds yield both the highest food availability and highest risk of tiger shark  
190 predation for dugongs (Wirsing et al. 2007 b). These moderate increased grazing plots received  $\lambda$   
191 grazing per visit. Intense grazing treatments were derived by increasing the moderate treatments  
192 by 50%, to act as an upper bound for potential herbivore effects and to emulate both a behavioral  
193 and numerical response of dugong populations to shark loss. Though dugong densities have  
194 declined in the study system since the seagrass die-off, multiple lines of evidence suggest that this  
195 decline was driven by short term emigration and that a return of dugong populations to pre-die-off  
196 densities is likely to occur long before recovery of *A. antarctica* is complete (Kendrick et al. 2019,  
197 Nowicki et al. 2019). Grazing treatments were applied every 30-60 days from May 2013 to August  
198 2014.

199 At 0, 7, 12, and 16 months into the experiment, we estimated cover of *A. anatarctica*, *H.*  
200 *uninervis*, and macroalgae species in each plot using a 60cm x 60cm quadrat placed 25 times in a

201 5x5 grid pattern. We then calculated mean percent cover of *A. antarctica*, *H. uninervis*, and  
202 macroalgae in each plot. Plots that were destroyed from sudden widespread seagrass defoliation  
203 or storm action were excluded from analysis from that time point forward.

#### 204 *Statistical analyses*

205 We applied mixed effects models and model selection using the glmmTMB package  
206 (Brooks et al. 2017) in RStudio version 1.2.1335 (RStudio Team 2019) to determine the influences  
207 of grazing treatment, time period, bank, and their interactions on cover estimates of *A. antarctica*,  
208 *H. uninervis*, and macroalgae. Five individual *a priori* models were run for each macrophyte group  
209 (Table 1). In each, plot ID was retained as a random effect to account for repeated measures.  
210 Percent cover data were converted to proportion data, and models were run using the beta  
211 distribution (Cribari-Neto and Zeileis, 2010). We then used multimodel inference, specifically  
212 model averaging, to evaluate whether parameters significantly contributed to model fit (Anderson  
213 2007).

#### 214 **Results**

215 Of the 30 plots established, 29 remained intact for at least 12 months and were retained in  
216 analysis; 23 remained intact until the experiment's end. Destroyed plots were compromised  
217 mostly by small-scale blowout events, and were evenly distributed between treatments (2 each in  
218 control and intense grazing treatments, 3 in moderate treatments). All plot losses occurred  
219 exclusively on the moderately impacted eastern bank.

220 Macrophyte cover declined for all species in all treatments, though the level of decline  
221 varied with treatment level. Cover of *H. uninervis* declined fastest under intense herbivory (from  
222 52.2% to 14.4% over 16 months) followed by moderate herbivory (42.4% to 23.3%), and slowest  
223 under control conditions (45.6% to 35.4%, Table S1 in supporting information, Fig. 3).

224 Interestingly, *A. antarctica* displayed the same patterns despite not being targeted by grazing;  
225 cover declined from 23.9% to 12.4% in intense grazing treatments, 24.5% to 17.3% in moderate  
226 grazing treatments, and 21.2% to 16.3% in control treatments (Table S1, Fig. 3). Macroalgae cover  
227 remained low and displayed no sensitivity to grazing treatment (Table S1, Fig. 3).

228 Generally, the suite of *a priori* models performed well as measured by cumulative Akaike  
229 weights (Table 2). Indeed, out of all possible model iterations, the *a priori* model suite for *A.*  
230 *antarctica* accounted for 95% of model weight (i.e., all other possible models only received 5% of  
231 weights when combined), whereas the *H. uninervis* and macroalgae model suites received 77%  
232 and 83% of all model weights, respectively (Table 2). Among the five *a priori* models for *H.*  
233 *uninervis*, models that included an interaction of month and treatment received high support with  
234 76.7% of total weights, indicting an herbivory treatment effect on *H. uninervis* cover over time.  
235 Similarly, most of the weight (62.9%) in the *A. antarctica* model suite went to models that included  
236 an interaction of month and treatment (Table 2). Interestingly, though only one of five models  
237 included an interaction of month, bank, and treatment (indicating that treatment effects differ by  
238 bank), this model was assigned 33.2% of the weights given to the *A. antarctica* model suite,  
239 suggesting that treatment effects on *A. antarctica* may differ by bank or initial *A. antarctica* cover.  
240 Indeed, while general seagrass recovery did not occur over the course of the experiment, *A.*  
241 *antarctica* cover remained stable in control and moderate grazing treatments on the moderately  
242 impacted eastern bank where initial cover was higher (Fig. 4).

243 Models including a treatment:month interaction on macroalgae received little support,  
244 with 5.6% of model weights (Table 2). This finding indicates that herbivory treatments contributed  
245 declines of both tropical *H. uninervis* and the temperate *A. antarctica*, even though treatments  
246 overwhelming targeted *H. uninervis* (Fig. 3,4 Tables 2, S1).

247 **Discussion**

248 Our results suggest several important points: (1) top-down control can influence non-target  
249 species as well as target species, if consumer feeding tactics are sufficiently indiscriminant; (2)  
250 predator loss can reduce ecological resilience to extreme climatic events through reducing  
251 predation risk to herbivores; (3) this effect may be mediated by the intensity of initial disturbance  
252 or quantity of plant cover remaining; and (4) in transition zones (like subtropical ecosystems),  
253 tropicalization may be driven by behavioral changes in predator and prey instead of by range  
254 expansions of producers or consumers. By implication, apex predator loss can be an important  
255 mechanism in governing the resilience of ecosystems to ECEs, and widespread co-occurrence of  
256 predator loss and climate change may provide many opportunities for these two stressors to interact  
257 to exacerbate the impact of climate extremes and to drive tropicalization.

258 *Impact to climax seagrass*

259 *A. antarctica* cover declined generally, but this decline was accelerated under herbivory  
260 treatments, despite not being targeted by these treatments (Fig. 3,4). Importantly, declines in the  
261 control and moderate herbivory treatments were driven mostly by declines in the already heavily  
262 impacted western bank (Fig. 4), suggesting that these beds are likely more vulnerable to both  
263 general collapse and top-down control, and that the strength of top-down control is likely  
264 influenced by initial post-disturbance seagrass cover. Unfortunately, we cannot unequivocally  
265 attribute this potential interaction between treatment effect and bank to initial seagrass density  
266 alone. Nonetheless, these results suggest that the vulnerability of *A. antarctica* to post-disturbance  
267 herbivory (and therefore predator loss) likely depends on the severity of initial disturbance, an  
268 important topic to explore in the future.

269 *Amphibolis antarctica* is a late successional seagrass species with recovery rates that span  
270 years to decades following large losses (Nowicki et al. 2017 and references therein). As such,  
271 mechanisms that promote or undermine post-disturbance stability are likely to be particularly  
272 important to the long-term recovery of this species. The pace of *A. antarctica* decline in our  
273 treatments (i.e., 30-50% relative losses over 16 months) implies that loss of tiger sharks and the  
274 predation risk they generate could quickly result in a phase shift toward a structurally simple  
275 tropical seagrass community. The capability for dugong excavation to generate such shifts has  
276 been demonstrated experimentally elsewhere (e.g., Preen 1995, Aragonés and Marsh 1999), where  
277 simulated excavation favored an increased relative abundance of pioneer seagrasses. Importantly,  
278 the mechanism for such decline hinges on the establishment of preferred tropical seagrasses and  
279 creation of mixed species beds that allow incidental removal of *A. antarctica* during foraging bouts  
280 targeting tropical seagrasses (Fig. 2d). As such, recovery of *A. antarctica* via seedling  
281 establishment may result in a high rate of recruitment failure if such seedlings establish in tropical  
282 or mixed seagrass beds, further inhibiting recovery in the absence of predation risk. As such  
283 tropical beds expand (Nowicki et al. 2017, Kendrick et al. 2019), the risk of such herbivore-  
284 mediated seedling establishment failure may increase.

#### 285 *Impact to pioneer seagrass and benthic macroalgae*

286 Declines in already very low algae cover (Fig. 3, 4) and contemporary benthic surveys  
287 (Nowicki et al. 2017) indicate that macroalgae do not play a dominant role in the post-disturbance  
288 macrophyte community of Shark Bay. Tropical seagrasses, however, are becoming generally more  
289 common in Shark Bay's post disturbance environment (Nowicki et al. 2017, Kendrick et al. 2019).  
290 Herbivory treatments had strong effects on *H. uninervis* cover, resulting in relative losses of 45%  
291 to 72% over 16 months, when compared to mean loss of 22.4% in control treatments. These results

292 could be interpreted to suggest that *H. uninervis* beds that drive dugong excavation may be short-  
293 lived (at which point *A. antarctica* could recover), but we think this outcome is unlikely for several  
294 reasons. *H. uninervis* is an early successional seagrass with a dormant seed bank and fast  
295 expansion rates (Larkum et al. 2006) that has expanded system-wide since 2011 (Nowicki et al.  
296 2017); in the absence of competition with *A. antarctica* or complete extirpation by herbivores, it  
297 is unlikely that *H. uninervis* will decline across the system. Instead, the decline observed in *H.*  
298 *uninervis* in control plots can be explained by patch migration (Walker et al. 2007) and the  
299 ephemeral nature of early successional seagrass beds. For example, in an herbivore enclosure  
300 experiment performed near our own, Burkholder et al. (2013b) noted high variability in *H.*  
301 *uninervis* shoot densities over 600 days. Because our plot locations were chosen non-randomly  
302 (i.e., to include high initial cover of *H. uninervis*), patch migration is more likely to result in  
303 reductions, not increases, of *H. uninervis* cover over time in our plots. Such migration may actually  
304 accelerate dugong-mediated loss of remaining sparse *A. antarctica* if *H. uninervis* migrates  
305 through damaged *A. antarctica* beds and attracts dugong excavation grazing to them. Even if  
306 grazing generates rapid losses of *H. uninervis*, such grazing may still promote a regime shift from  
307 a temperate climax seagrass community to a disturbance tolerant tropical one because tropical  
308 seagrass species can recolonize rapidly following grazing (weeks to months, Preen 1995, Nakaoka  
309 and Aioi 1999, Aragones and Marsh 1999) and because herbivores revisit sites once seagrass  
310 recolonization occurs (Bjorndal 1980, Preen 1995, de Iongh et al. 2007). We observed multiple  
311 plots in which *H. uninervis* cover increased substantially after being almost completely absent a  
312 few months earlier, indicating that similar dynamics occur in Shark Bay (see individual plot  
313 dynamics in Fig. 4). Thus, early-successional seagrass are likely to persist and continue to attract  
314 destructive excavation grazing to degraded beds of *A. antarctica*. Yet, even a complete

315 replacement of the more structurally complex *A. antarctica* with smaller, more architecturally  
316 simple tropical seagrasses likely would not result in a full recovery of ecosystem functions like  
317 sediment stabilization and habitat creation.

### 318 *Caveats*

319 By necessity, we used dugong density estimates and foraging data obtained before the  
320 marine heat wave to parameterize our treatments. Standardized surveys indicate that dugong  
321 abundances have declined by two-thirds in the study system (Nowicki et al. 2019). However, the  
322 purpose of this experiment is to evaluate whether a certain mechanism of top down control (i.e.,  
323 predation risk) should be considered as a potential source of resilience to ECEs or a potential driver  
324 of tropicalization. Several lines of evidence suggest that the fundamental mechanisms responsible  
325 for the pre-decline behaviorally-mediated trophic cascade remain, that dugong declines are likely  
326 short lived, and that the results presented here remain relevant. First, the abundance of tiger sharks,  
327 including large (>300 cm total length) tiger sharks, has not changed relative to estimates from  
328 before the ECE (Nowicki et al. 2019). Similarly, the risk-sensitive habitat use patterns of  
329 remaining dugongs also remains intact, with lower use of shallow, risky habitats when tiger sharks  
330 are abundant (Nowicki et al. 2019). As such, predation risk remains a viable mechanism to  
331 enhance post-disturbance stability of *A. antarctica* beds. Furthermore, several lines of evidence  
332 suggest that dugong declines owe to temporary emigration rather than mass mortality. Mass  
333 mortality, when it does occur, results in widespread dugong strandings (e.g., Marsh 1989, Preen  
334 and Marsh 1995, Great Barrier Reef Marine Park Authority 2014), which were neither observed  
335 nor reported in Shark Bay. Dugongs can regularly move hundreds of kilometers and often emigrate  
336 to alternative foraging locations following seagrass loss, but retain a spatial memory of productive  
337 seagrass habitat and return to disturbed habitats once tropical seagrasses recover (Preen and Marsh

338 1995, Marsh and Lawler 2001, Gales et al. 2004, Holley et al. 2006, Sheppard et al. 2006, Hodgson  
339 2007). Such recovery has been underway in Shark Bay since 2014 (Nowicki et al. 2017, Kendrick  
340 et al. 2019). Upon their return, dugongs can exert strong top down control quickly, denuding even  
341 dense seagrass beds in a matter of weeks (e.g., Preen 1995, Masini et al. 2001). Because *A.*  
342 *antarctica* will take years to decades to recover (Nowicki et al. 2017, Kendrick et al. 2019),  
343 predation risk is likely to remain a relevant driving mechanism in the recovery or tropicalization  
344 of this system.

#### 345 *Implications for tropicalization*

346 Marine tropicalization is growing worldwide and is driven by several mechanisms,  
347 including ECEs (e.g., Wernberg et al. 2013, Vergés et al. 2014). Most studies of marine  
348 tropicalization, however, have focused either partially or entirely on range expansions of primary  
349 producers or consumers, which generate novel species interactions (e.g., Vergés et al. 2014,  
350 Bennett et al. 2015, Heck et al. 2015, Hyndes et al. 2016, Zarco-Perello et al. 2017, Pecl et al.  
351 2017). This is also true among studies that focus on the role of predator-prey interactions in  
352 tropicalization (e.g., Ling et al. 2009, but see Bonaviri et al. 2017). Here, we show that climate  
353 change can promote tropicalization without range expansions of novel species. Instead, the  
354 tropicalization of Shark Bay would be amplified by a combination of loss of predation risk and  
355 differential climate vulnerability of already co-occurring foundation species (i.e., response  
356 diversity). Such conditions would be expected in areas where biome ranges overlap (e.g.,  
357 subtropical ecosystems), and where predator populations have been reduced. This mechanism of  
358 tropicalization should be explored elsewhere and incorporated into a more general framework to  
359 predict ecosystem responses to ECEs, and how predator loss may mediate those responses.

360           Whereas predator loss and climate change are both global threats to the functional integrity  
361 and resilience of ecosystems, the temporal and spatial scales at which these two stressors can be  
362 functionally addressed differ greatly. Management at local and regional levels for ecological  
363 resilience may be key to preventing catastrophic phase shifts while long-term action is taken on  
364 climate change (e.g., DeYoung et al. 2008). Conservation and restoration of top predators and the  
365 ecological resilience they can impart may be a critical (if ambitious) short-term strategy to reduce  
366 the impacts of ECEs as governments move to address climate change directly. Though it is yet  
367 unclear how widely predation risk may grant such resilience, the widespread co-occurrence of  
368 apex predator loss and climate change suggests that the potential for interactions is common.  
369 However, future work is needed to determine the ecological conditions under which predator  
370 restoration is most likely to yield measurable increases in resilience to ECEs generally. This  
371 strategy of climate resilience through predator restoration is likely to be most effective in systems  
372 with highly iteroparous herbivores (such as Shark Bay), which are likely to invest highly in anti-  
373 predator behavior (Clark 1994) and thus propagate behaviorally mediated trophic cascades  
374 (BMTCs). Indeed, such a strategy for local resilience to climate extremes may become  
375 increasingly important as megafauna restoration efforts such as those for the herbivorous green  
376 turtle (*Chelonia mydas*) continue to succeed (Heithaus et al. 2014). Without a concomitant effort  
377 to also restore the predators of these herbivores, the resilience of communities to future climate  
378 disturbances and ensuing tropicalization may be reduced. Identifying the conditions under which  
379 predator effects are most likely to yield increased resilience to ECEs and tropicalization will be  
380 critical to determining the potential effectiveness of predator restoration as a technique to increase  
381 ecological resilience and maintain ecological function in an increasingly extreme world.

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600

601 **Table 1.** Models applied to macrophyte data. Month since start (Month), bank identity (Bank),  
 602 and grazing treatment (Treat) were fixed effects. Plot ID was included as a random effect to  
 603 account for temporal autocorrelation of the repeated measures.

604

<b>Model</b>	<b>Fixed effects</b>	<b>Random effects</b>
1	Month	Plot ID
2	Month + Bank + Month:Bank	Plot ID
3	Month + Treat + Month:Treat	Plot ID
4	Month + Bank + Treat + Month:Treat + Month:Bank	Plot ID
5	Month + Bank + Treat+ Month:Treat + Month: Bank + Month:Bank:Treat	Plot ID

605

606

607 **Table 2.** Results of model construction and multi-model inference for each macrophyte group.

608 M= month, B= bank, T= treatment. An interaction of treatment and month (i.e., T:M; bold)

609 indicates an effect of treatment on percent cover. Cumulative weight of all *a priori* models is

610 included to the right, while below are combined weights of all models including that parameter

611 across the five *a priori* models (i.e., the total weight of each model divided by the cumulative

612 weight of all *a priori* models).

Species	Model parameters retained						df	log likelihood	$\Delta AICc$	weight	cumulative weight
	M	B	T	B:M	T:M	B:T:M					
Amphibolis	x	x		x			6	171.863	0	35.4%	35.4%
Amphibolis	x	x	x	x	x	x	12	178.948	0.2	31.5%	66.9%
Amphibolis	x	x	x	x	x		10	176.348	0.4	28.4%	95.3%
Amphibolis	x						4	140.929	57.4	0.0%	95.3%
Amphibolis	x		x			x	8	143.79	60.8	0.0%	95.3%
<b>Total weights</b>	100.0%	100.0%	62.9%	100.0%	<b>62.9%</b>	33.2%					
Halodule	x		x			x	8	61.586	0	44.0%	44.0%
Halodule	x						4	56.049	2	16.0%	60.0%
Halodule	x	x	x	x	x	x	12	65.014	2.93	10.1%	70.1%
Halodule	x	x	x	x	x		10	61.773	4.42	4.8%	74.9%
Halodule	x	x		x			6	56.118	6.32	1.9%	76.8%
<b>Total weights</b>	100.0%	21.9%	76.7%	21.9%	<b>76.7%</b>	13.2%					
Macroalgae	x	x		x			6	245.173	0	78.0%	78.0%
Macroalgae	x	x	x	x	x		10	246.424	7	2.4%	80.4%
Macroalgae	x	x	x	x	x	x	12	248.89	7.13	2.2%	82.6%
Macroalgae	x						4	235.629	14.6	0.1%	82.7%

Macroalgae	x		x		x	8	236.37	22.3	0.0%	82.7%
<b>Total weights</b>	100.0%	99.9%	5.6%	99.9%	<b>5.6%</b>	2.7%				

613

614

615 **Figure 1.** Representative states of the study area’s *Amphibolis antarctica* beds before and after  
616 the 2011 marine heat wave. Notice abundance of tropical early successional seagrass *Halodule*  
617 *uninervis* (small shoots) growing in between the larger shoots of *Amphibolis antarctica* (right  
618 panel, white arrow). Photo credit: J. Thomson, R. Nowicki.

619

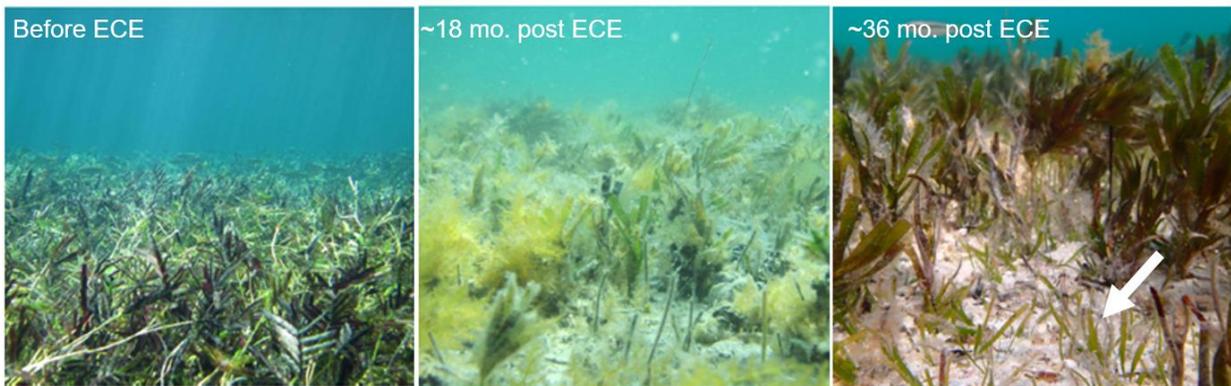
620 **Figure 2.** Conceptual diagram of the role of trophic cascades and physical feedbacks in  
621 determining the stability and structure of *A. antarctica* beds in Shark Bay. In Shark Bay’s  
622 normal, undisturbed state (a), tiger sharks regulate megaherbivores by both consumptive and  
623 non-consumptive effects (orange arrows), indirectly facilitating persistence of *A. Antarctica*  
624 (gray arrow). Dense seagrass beds generate positive physical feedbacks through physical  
625 structure and by blocking access to tropical seagrasses which inhibits excavation (gray arrows).  
626 With predator losses but without a disturbance (b), competitive dominance of *A. Antarctica*  
627 maintains its ability to generate positive physical feedbacks and inhibit excavation grazing,  
628 resulting in a probable loss of resilience but minimal direct impact on *A. Antarctica* (not tested).  
629 Following a disturbance causing *A. Antarctica* dieback (Shark Bay’s current state and control  
630 plots, c), tropical seagrasses that dugongs prefer become exposed and can proliferate to create  
631 mixed species beds, but direct predation and predation risk from tiger sharks prevent dugongs  
632 from undertaking excavation grazing and reversing positive physical feedbacks. Should a  
633 marine heat wave generate a dieoff when apex predators have been removed (experimental  
634 treatments, d), predation risk would no longer inhibit dugong excavation grazing, and the two

635 stressors may compound and generate a phase shift toward a tropical seagrass dominated or  
636 seagrass depauperate ecosystem. Photos: SBERP.

637 **Figure 3.** Effect of herbivory treatment on cover of (a) *Amphibolis antarctica*, (b) *Halodule*  
638 *uninervis*, and (c) benthic macroalgae. Initial and final cover are denoted with dark and light  
639 bars, respectively. Error bars = SE; scale of Y-axes differ.

640 **Figure 4.** Effect of herbivory treatment on cover over time for *Amphibolis antarctica*, *Halodule*  
641 *uninervis* and benthic macroalgae with individual plot dynamics visible. Notice differences  
642 between plots on heavily impacted (dark grey) and moderately impacted (light grey) banks.  
643 Scale bars differ by species.

644

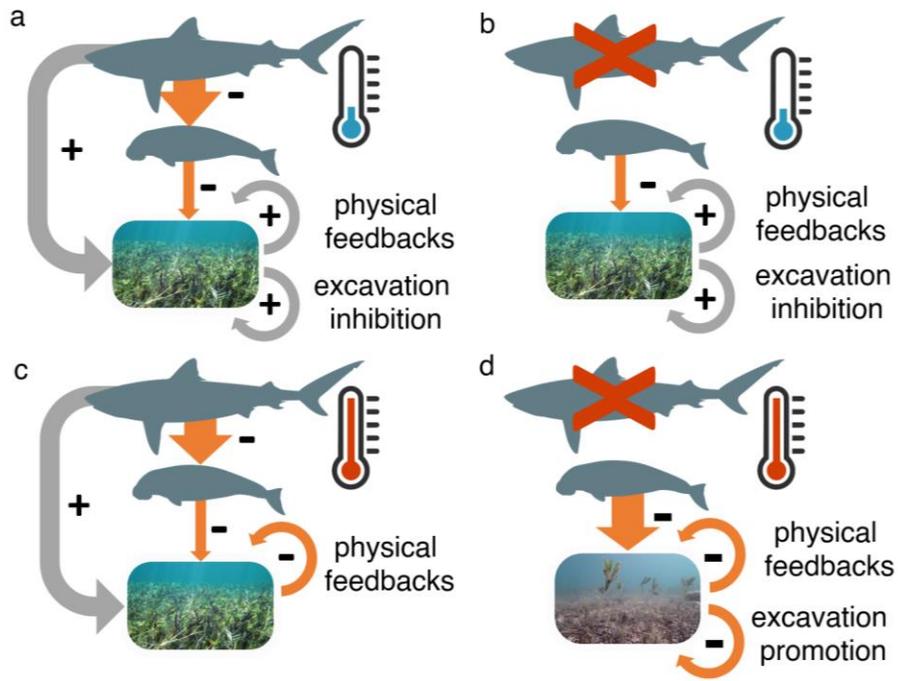


645

646 **Figure 1.**

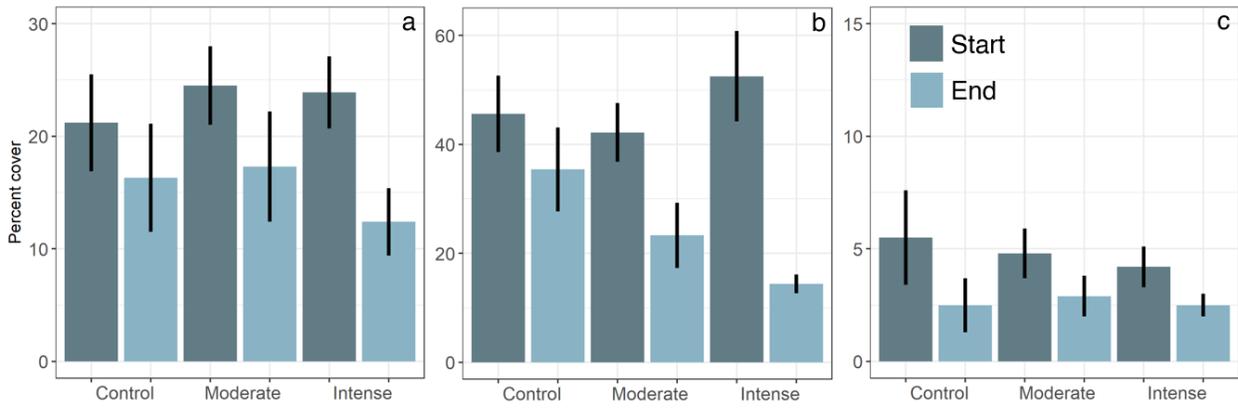
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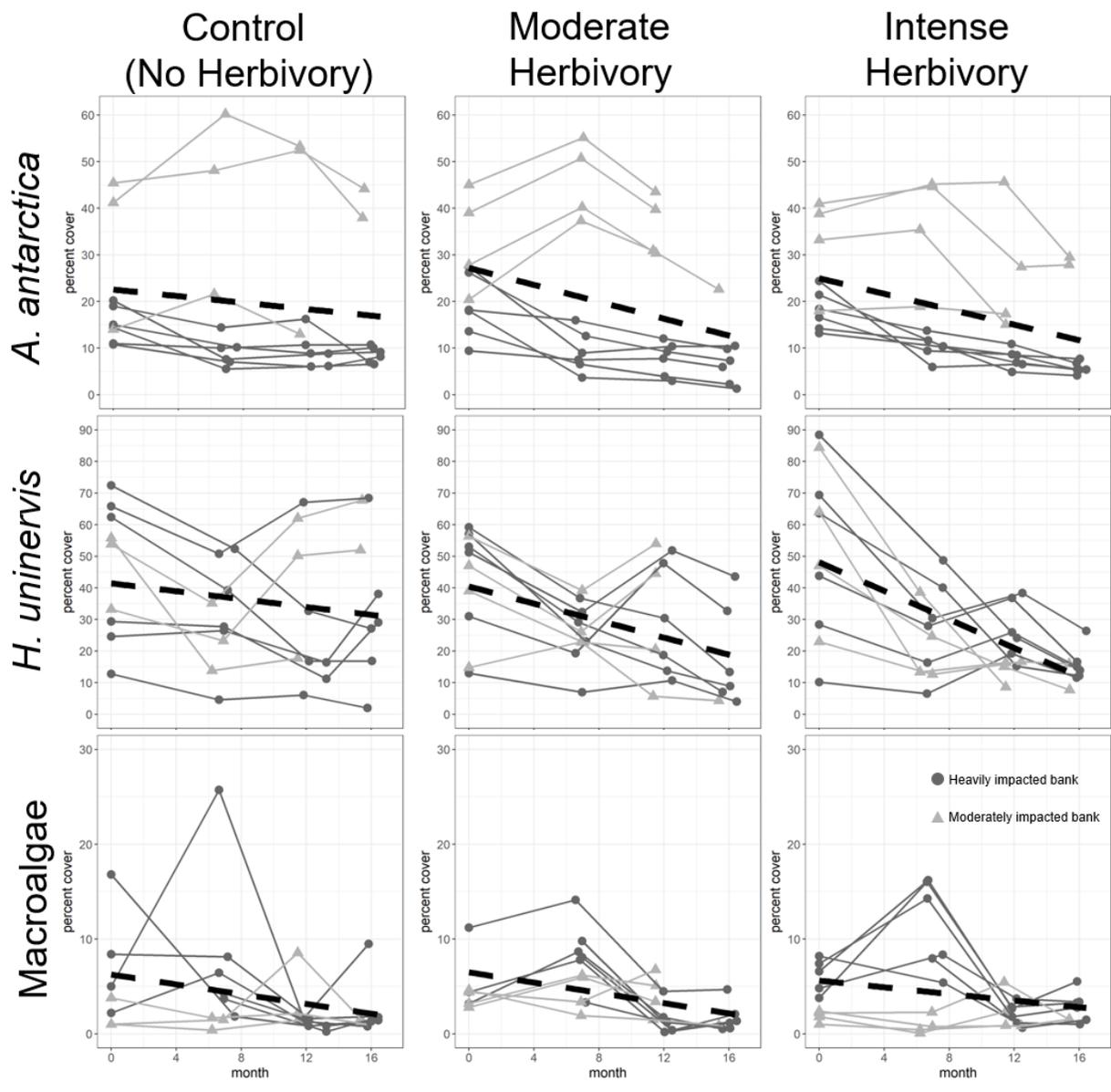
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650 **Figure 2.**



651

652 **Figure 3.**



653

654 **Figure 4.**