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**Arjunwadkar, Chaitanya, Tebbett, Sterling B., Bellwood, David, Bourne, David G., and Smith, Hillary A. (2022) *Algal turf structure and composition vary with particulate loads on coral reefs*. *Marine Pollution Bulletin*, 181 .**

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<https://doi.org/10.1016/j.marpolbul.2022.113903>

1           **Algal turf structure and composition vary with particulate loads on coral reefs**

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30 **ABSTRACT**

31 Algal turfs trap and retain particulates, however, little is known about the relationship  
32 between particulate accumulation and taxonomic composition of algal turfs. We  
33 investigated how particulate mass related to algal turf structure (length and density) and  
34 community composition (taxonomic and functional) on two disparate reefs. Particulate  
35 mass was positively related to algal turf length. By contrast, the relationship between  
36 particulate mass and turf density was more complex and followed a negative parabolic  
37 shape; density increased with particulate mass before stabilising and then declining.  
38 Community analyses showed taxonomic, but not functional group compositions differed  
39 significantly between reefs and with increasing particulate mass. Our results suggest high  
40 loads of particulates accumulated in algal turfs are related to a longer, lower density turf  
41 structure, typified by filamentous forms such as *Cladophora*. Changes in algal turf structure  
42 and composition could have a variety of bottom-up influences on coral reef ecosystems.

43 1. Introduction

44 Globally, aquatic ecosystems are being reconfigured by stressors derived from human  
45 actions, often resulting in the loss of complex habitat-forming organisms and the spread of  
46 smaller, low-lying organisms (Filbee-Dexter and Wernberg, 2018; Vercelloni et al., 2020;  
47 Pessarrodona et al., 2021). Coral reefs represent a particularly clear example of this  
48 phenomenon as the progressive degradation of these ecosystems has led to marked  
49 changes in their composition and biological diversity (Hughes et al., 2018; Bruno et al., 2019;  
50 Vercelloni et al., 2020). Indeed, it is now projected that coral reefs in the Anthropocene will  
51 be characterised by reduced coral cover, flattened topography, and in many cases an  
52 increased coverage of diminutive algal communities (Alvarez-Filip et al., 2009; Bellwood et  
53 al., 2019a; Jouffray et al., 2019). These algal communities, otherwise termed ‘algal turfs’, are  
54 comprised of a multi-taxon assemblage of short (< 2 cm), morphologically diverse algae and  
55 cyanobacteria (Connell et al., 2014; Lopez et al., 2017; Tebbett and Bellwood, 2019). Such  
56 algal turfs are already the most abundant benthic cover on many coral reefs (Smith et al.,  
57 2016; Emslie et al., 2019; Jouffray et al., 2019), with this coverage poised to increase further  
58 alongside future declines in live coral cover (Holbrook et al., 2016; Kennedy et al., 2020;  
59 Koester et al., 2020).

60 While increased algal turf cover is often associated with reef degradation, turfs play an  
61 essential role in various coral reef processes, and changes in their structure can modify  
62 these processes. For example, algal turfs are often the key contributors to benthic  
63 productivity (Hatcher, 1988; Klumpp and McKinnon, 1992), supporting core trophic  
64 pathways including energy transfer up the food chain through herbivorous fishes (Russ,  
65 2003; Kelly et al., 2017; Tebbett et al., 2018). However, increasing evidence suggests the  
66 length of algal turfs is pivotal to both their role on coral reefs and how other reef organisms  
67 interact with them (Arnold et al., 2010; Ford et al., 2018; Steneck et al., 2018). For example,  
68 longer algal turfs are associated with reduced coral settlement rates (Arnold et al., 2010;  
69 Ford et al., 2018), a decreased capacity to deliver nutritional resources to fishes (Tebbett

70 and Bellwood, 2020), and an increased capacity to compete with other benthic organisms  
71 (Steneck, 1997; Ford et al., 2018).

72 Compared to the length of algal turfs, other structural features of the turf community (e.g.,  
73 the density of thalli) have received far less attention (reviewed in Connell et al., 2014).  
74 Despite the terms 'sparse' and 'dense' being used frequently to characterise algal turfs (e.g.,  
75 Rogers and Salesky, 1981; Bruggemann et al., 1994; Clements et al., 2017), turfs are still  
76 often defined by their length rather than their cover/how densely packed they are in  
77 benthic space (e.g., Bruggemann et al., 1994; Wakwella et al., 2020). Most studies to date  
78 have quantified 'turf cover' in relation to other benthic organisms (e.g., Smith et al., 2010;  
79 Rasher et al., 2012), while quantification of the relative abundance of filaments or thalli to  
80 specifically compare the nature of turfs has been exceedingly limited (but see Tebbett et al.,  
81 2017a). Given the importance of algal turf length in modifying processes such as coral  
82 recruitment and benthic competition, enhancing our understanding of other structural  
83 properties of algal turf communities is warranted.

84 Despite advances in our understanding of how the length of algal turfs relates to reef  
85 processes, our knowledge on algal turf taxonomic and functional composition has also  
86 lagged. Our understanding, in this respect, is largely limited to the knowledge that algal turf  
87 composition can be modified by herbivory (Wanders, 1976; Sammarco, 1983; Scott and  
88 Russ, 1987) as well as nutrients (McClanahan et al., 2007), and is highly variable across  
89 multiple spatial (Bruggemann et al., 1994; Scott and Russ, 1987; Harris et al., 2015) and  
90 temporal scales (Diaz-Pulido and McCook, 2002; Fricke et al., 2011; Loke et al., 2016).  
91 Studies have previously highlighted that community composition is critical to understanding  
92 how assemblages of various types of organisms function on coral reefs (Tout et al., 2014;  
93 Bellwood et al., 2019b; McWilliam et al., 2020). Therefore, enhancing our knowledge of  
94 algal turf community composition, as well as how other factors beyond herbivory and  
95 nutrients relate to it, is a particularly important research endeavour.

96 One factor that may be strongly related to algal turf community composition on coral reefs  
97 is particulate/sediment load. Algal turfs readily trap and accumulate particulates due to the  
98 development of a diffusive boundary layer that enhances deposition and accumulation  
99 (Carpenter and Williams, 1993). This capacity for particulate trapping and retention  
100 increases with increasing algal turf length (Rasher et al., 2012; Latrille et al., 2019).  
101 Furthermore, when particulates become trapped within algal turfs, they can release the  
102 algal community from grazing pressure by changing fish feeding behaviour (Tebbett et al.,  
103 2017b; Fong et al., 2018; Ng et al., 2021). As a result, it is now recognised that algal turf  
104 condition can transition (in a continuous manner) from 'short productive algal turfs' (SPATs)  
105 to 'long sediment-laden algal turfs' (LSATs) as accumulated particulates/sediments increase  
106 (Goatley et al., 2016; Tebbett and Bellwood, 2020). Such transitions may compromise the  
107 capacity of reefs to recover following disturbances due to decreased coral settlement  
108 (Speare et al., 2019; Evans et al., 2020). In addition, these transitions may result in less  
109 productive ecosystems with a reduced capacity to deliver essential ecosystem services such  
110 as fishable biomass production (Tebbett et al., 2021). Evidence from temperate systems  
111 suggests increased particulate accumulation may shape the community composition of

112 temperate algal turfs (Airoidi and Virgilio, 1998; Gorgula and Connell, 2004). However, it  
113 remains to be determined if sediments are related to changes in the composition of algal  
114 turfs on tropical coral reefs. This comes at a time when increased sediment inputs and  
115 declining water quality represent major stressors to coral reefs, with the potential that  
116 these stressors may increase further with ongoing coastal development and land clearing  
117 (Bainbridge et al., 2018; Suarez-Castro et al., 2021). Therefore, understanding how  
118 particulate accumulation relates to algal turf structure and composition on coral reefs is  
119 becoming increasingly important.

120 Our understanding of how and why algal turf structure and community composition varies is  
121 far from comprehensive. The small, highly diverse nature of these algal communities, along  
122 with limited taxonomic resolution, has potentially stymied growth of this research topic.  
123 However, as algal turfs are a core benthic component on many coral reefs, a more  
124 comprehensive understanding of their structure and composition is critical. Therefore, our  
125 aim with this study was to examine how the structure and composition of algal turf  
126 communities on coral reefs varies in relation to accumulated particulate loads. Specifically,  
127 this study explores how algal turf length, density, taxonomic diversity, taxonomic  
128 composition, and functional group composition relate to accumulated particulate loads on  
129 two markedly different coral reefs on the Great Barrier Reef (GBR). As the environmental  
130 context varies considerably between these two reef systems, this study will provide broad  
131 insights into the generality of relationships between particulates/sediment and algal turf  
132 structure and composition on coral reefs.

## 133 2. Materials and methods

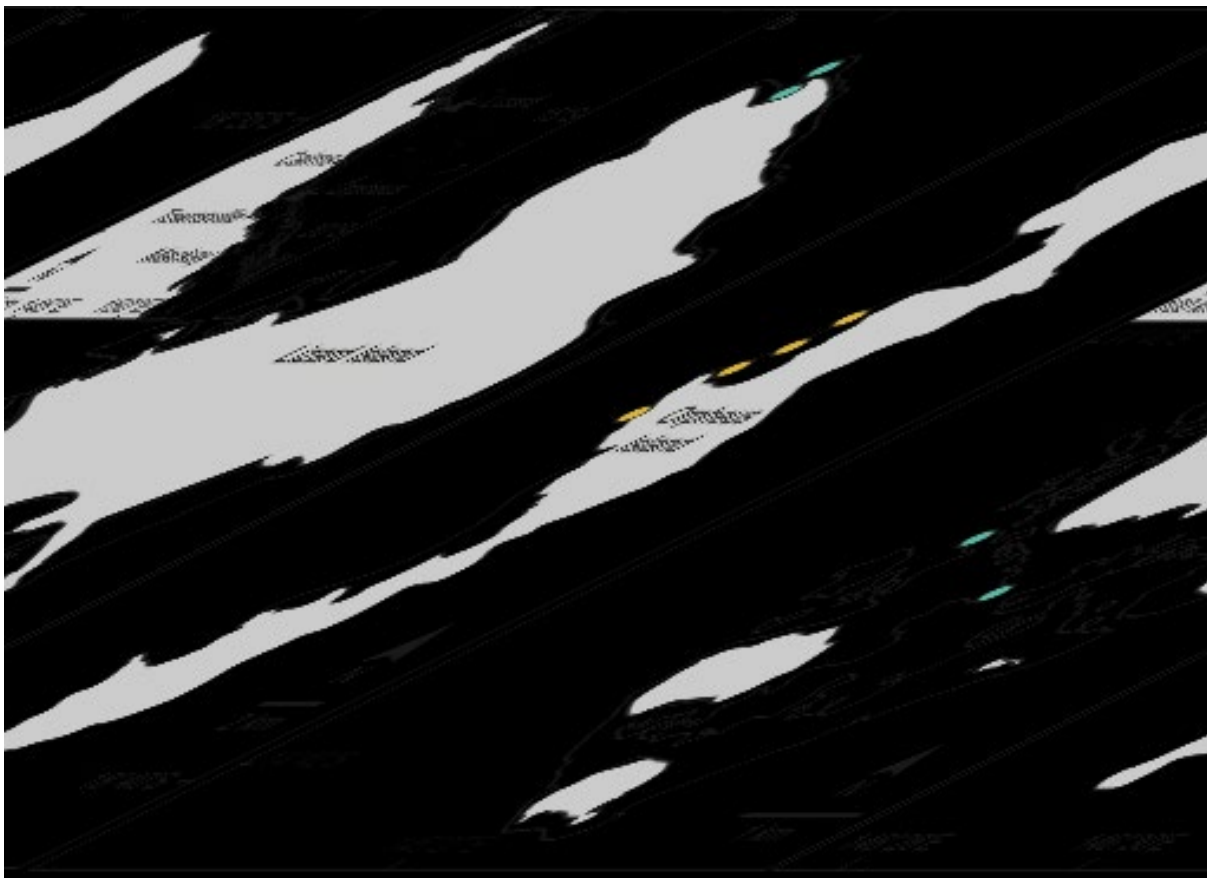
### 134 2.1. Study sites and field sampling

135 Field sampling was conducted in December 2019 at Orpheus Island in the Central Great  
136 Barrier Reef (GBR), and February 2020 at Lizard Island in the Northern GBR (Fig. 1). Orpheus  
137 Island is located on the inner-shelf of the GBR approximately 15 km from the mainland,  
138 while Lizard Island is located on the mid-shelf, approximately 30 km from the mainland. As  
139 the influence of terrestrial sediment inputs and sediment dynamics in general (Fabricius et  
140 al., 2014; Tebbett et al., 2017c), as well as other key environmental gradients, such as  
141 hydrodynamic exposure (Lambrechts et al., 2008; Gallop et al., 2014) and herbivory (Russ,  
142 1984; Cheal et al., 2012), vary markedly across the continental shelf, these two islands  
143 provide contrasting insights into how sediment dynamics may relate to the physical  
144 structure and community composition of algal turfs. We collected samples from four sites at  
145 each island, with all sites experiencing low wave exposure since they are located in  
146 protected leeward, back reef or lagoonal areas at each island (Fig. 1). Samples were  
147 collected from the reef crest/reef edge habitat, approximately 1–4 m below chart datum.  
148 We selected this as it represents a critical habitat in terms of reef productivity and herbivory  
149 dynamics (Bellwood et al., 2018).

150 At each site, 14–15 flat (i.e.,  $\sim <15^\circ$  from horizontal) areas of consolidated reef matrix  
151 covered in algal turfs were selected for sampling to represent the full breadth of algal turf  
152 conditions (i.e., the continuous spectrum from short productive algal turfs, SPATs, to long

153 sediment-laden algal turfs, LSATs; following Tebbett and Bellwood, 2020) present at each  
154 site. We sampled a total of 118 locations (Orpheus Island, n = 58; Lizard Island, n = 60).  
155 Selected sampling locations were outside the territories of damselfishes, and free of large  
156 sediment- retaining pits, macroalgae and encrusting organisms. Upon selection, we  
157 delineated each sampling location using a 58 cm<sup>2</sup> PVC ring and four samples/measurements  
158 were collected: (1) particulates, (2) turf density, (3) turf length, and (4) the algal community.

159 Firstly, (1) we collected all particulate material within the sampling ring using a submersible  
160 electronic vacuum sampler (modified after Purcell, 1996). (2) After particulate sampling, we  
161 photographed the algal turfs using a Nikon Coolpix AW130 digital camera for density  
162 estimates (described below). (3) Ten haphazardly selected algal turf filaments were then  
163 measured using the depth probe of vernier calipers (following Tebbett and Bellwood, 2019),  
164 with these ten measurements averaged per sampling ring to yield the average length of the  
165 sampled turf community. (4) We then collected the algal turf community by fitting a steel  
166 tube to the intake hose of the vacuum sampler and scraping the substratum to a depth of ~1  
167 mm. The dislodged algal and carbonate material was collected in a 220 μm mesh filter fitted  
168 between the tube and the electronic pump. Following sampling, the filter was removed  
169 from the vacuum, placed in an individual zip-lock plastic bag, and placed on ice post-dive.  
170 Once on land, we transferred the material from the filters to 10–25 mL plastic falcon tubes  
171 and snap froze them in liquid nitrogen (when possible), before storing them at – 80 °C until  
172 further processing.



174 **Fig. 1.** (a) Locations of Orpheus Island and Lizard Island relative to the mainland. (b) Map of  
175 Lizard Island, and (c) Orpheus Island with coloured dots showing sampling locations (note  
176 the dots are not to scale).

## 177 2.2. Particulate sample processing

178 Particulate samples were individually transferred into 9 L settling containers with 15 mL of 4  
179 % buffered formaldehyde to fix the organic material. The samples were left for a minimum  
180 of 3 h before decanting the water to allow particulate material > 10 µm to settle (Purcell,  
181 1996). All samples were transferred to 120 mL sample jars and wet sieved through a 2 mm  
182 stainless steel mesh so only material < 2 mm was retained (sands, silts, and clays; ISO 14688-  
183 1:2017). Note this process did not exclude a substantial fraction of sediments as material > 2  
184 mm is limited in algal turfs (see Purcell, 2000). Each sample was rinsed with fresh water  
185 three times to remove salts, leaving at least a 3 h settling period between rinses. Each  
186 sample was then vigorously shaken and allowed to settle for 24 h. Once settled, we  
187 measured the depth of particulates in the 120 mL sample jars (all jars were completely flat-  
188 bottomed). Depth was recorded (to the nearest 0.01 mm) at three haphazard locations  
189 around the outside of the jar using digital calipers to yield a mean particulate depth for each  
190 sample (Supplementary Fig. 1). Mean depth measurements were standardised by the field  
191 sampling area to give the relative depth of particulates on the reef benthos. Finally, we  
192 dried the samples at 60 °C and weighed them to 0.0001 g to obtain total accumulated  
193 particulate mass.

## 194 2.3. Quantification of algal turf structure: length and density

195 Algal turf density for the sampled areas was estimated from photographs (see Section 2.2)  
196 using the software photoQuad (Trygonis and Sini, 2012). A circular quadrat was manually  
197 drawn around the delineated 58 cm<sup>2</sup> circular sampled area using the Freehand function.  
198 Forty points were placed within the quadrat using the Uniform function to quantify how  
199 densely or sparsely algal turfs were packed in space (density) (Supplementary Fig. 2). The  
200 presence or absence of turf algae under each point was subsequently recorded. Density is  
201 generally calculated as number of individuals per unit area, however, given the diminutive  
202 structure of turf algae, estimation of density by counting individual turf thalli is difficult  
203 (reviewed in Connell et al., 2014). Therefore, algal turf density was estimated as percent  
204 cover  $((N/40) * 100$ , where N is the number of points under which turf algae occurred).

205 In sampled areas with high numbers of turf algae recorded under points, it was taken to  
206 imply that turf algae thalli were more densely packed in these sample areas. It should be  
207 noted that this measurement could be taken to represent algal turf cover, however, we  
208 have used the term 'density' here to maintain terminology that has been applied to turfs  
209 previously (i.e., sparse versus dense turfs) in relation to how densely packed turf thalli are  
210 (Connell et al., 2014). In addition, we have applied this term to ensure our measurements  
211 are not confused for 'turf cover' at a larger scale. Such confusion may arise as quantifying  
212 the cover of benthic organisms (e.g., coral cover, algae cover) at this broader scale  
213 represents one of the most common measurements on coral reefs. Algal turf length was  
214 measured by divers underwater (see Section 2.1).

#### 215 2.4. Community composition of algal turfs

216 Frozen algal turf samples ( $n = 20$  haphazardly selected samples for both Lizard and Orpheus  
217 Island) were thawed, and turf algae spread haphazardly over a petri dish with a  $15 \times 15$  grid  
218 (box width =  $\sim 0.9$  cm) taped underneath (Supplementary Fig. 3). Twenty-five grid squares  
219 were randomly selected and turf taxa within each were observed under a Nikon SMZ745  
220 photomicroscope and photographed using the software Capture V2.2. Turf algae taxa were  
221 identified to the lowest taxonomic level possible (generally genus) following Price and Scott  
222 (1992), Huisman (2019), and AlgaeBase.org, an online global algal database (Guiry and  
223 Guiry, 2020). Identified genera were then classified into functional groups following Harris  
224 et al. (2015). For those taxa that did not appear in Harris et al. (2015), classification into  
225 functional groups followed thalli descriptions from AlgaeBase.org (Guiry and Guiry, 2020)  
226 and Steneck and Dethier (1994). Relative abundance of turf taxa in each sample was  
227 calculated as the percentage of grid squares from which each taxon was recorded (i.e.,  
228 presence/absence in each of the 25 grid squares). We repeated this step for functional  
229 groups.

#### 230 2.5. Statistical analyses

231 Generalized linear mixed-effects models (GLMMs) were used to examine the relationships  
232 between particulate mass and (a) particulate depth, (b) algal turf length and (c) algal turf  
233 density. Particulate mass, rather than particulate depth, was used as the explanatory  
234 variable as this is the most common unit of measure used to quantify algal turf particulates,  
235 and, therefore, ensures our study can be placed within the context of most past ecological  
236 research within this field (reviewed in Tebbett and Bellwood, 2019). For the turf density and  
237 particulate depth models, the relationship between log particulate mass appeared to be  
238 non-linear and, in these cases, a second-order polynomial term was included for particulate  
239 mass. In all cases, a full model was initially fitted to include the interaction between the  
240 fixed effects of particulate mass and island identity. We selected the most parsimonious  
241 model based on the corrected Akaike Information Criterion (AICc; Supplementary Table 2).  
242 The turf density model was based on a Beta distribution with a logit link due to the  
243 proportional nature of the data. The particulate depth and turf length models were both  
244 based on Gamma distributions with a log link due to the continuous, positive nature of the  
245 data. All models incorporated sampling location (i.e., the four sites at each island) as a  
246 random effect to account for any lack of spatial independence. Model fit and assumptions  
247 were evaluated using residual plots, which were satisfactory in all cases.

248 Three indices of algal turf diversity (taxonomic richness (S), Shannon diversity ( $H'$ ), and  
249 species evenness (E)) were calculated for the algal turf communities at both islands. GLMMs  
250 modelled the relationships between particulate mass and S,  $H'$ , and E, respectively.  
251 Taxonomic richness was modelled using a Poisson distribution (log link), diversity was  
252 modelled using a Gamma distribution (log link), and evenness was modelled using a Beta  
253 distribution (logit link). Models were initially fit with the interaction between the fixed  
254 effects of particulate mass, turf density, and island identity, with sampling location as a  
255 random effect. Model selection through AICc indicated that all three metrics were best  
256 modelled using particulate mass alone (i.e., not island or turf density), and all three models



257 incorporated the random effect of sampling location (i.e., four sites at each island;  
258 Supplementary Table 2). Model diagnostics (e.g., dispersion, deviation, zero inflation) were  
259 validated prior to model investigations, as above.

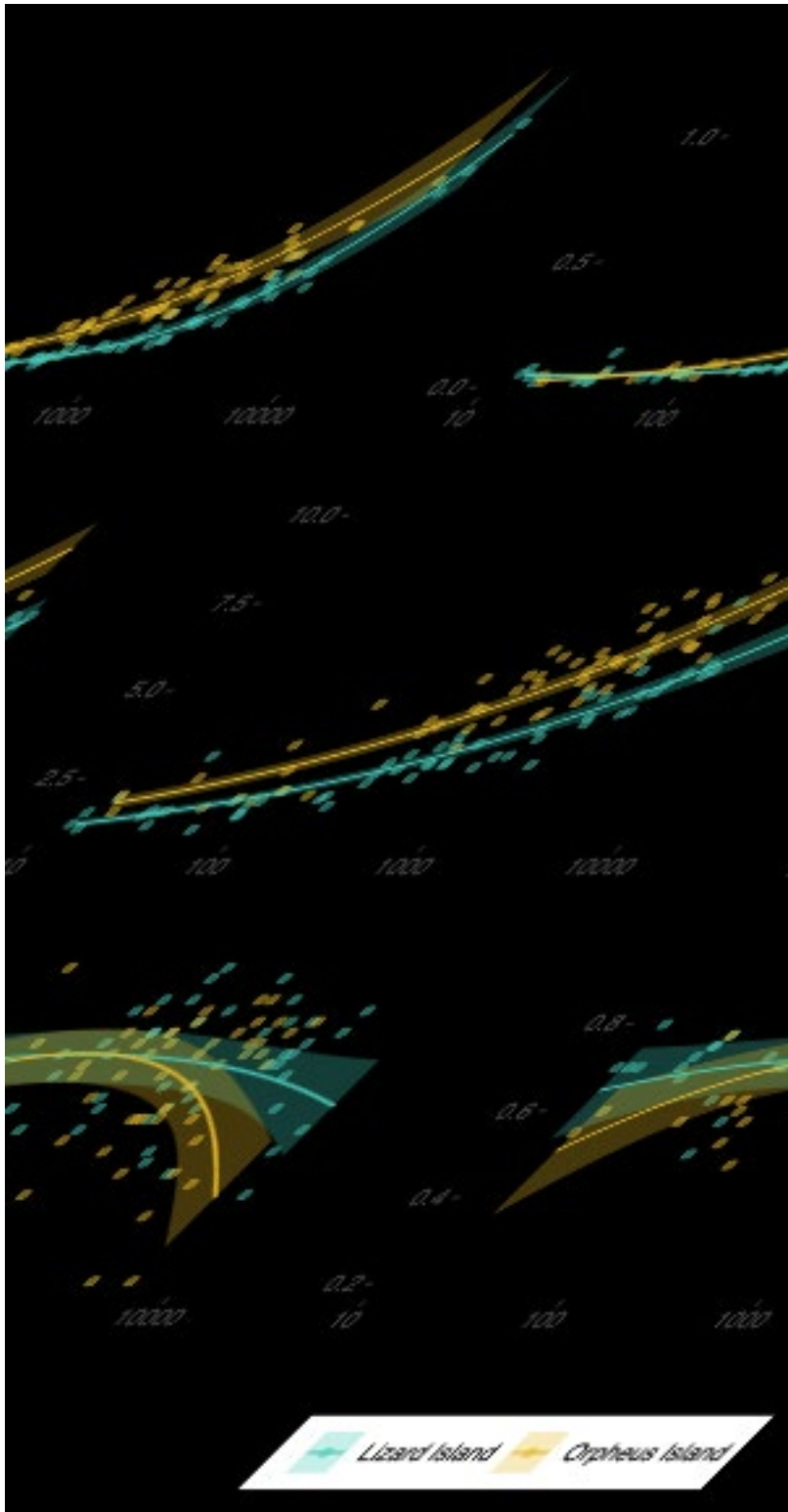
260 Turf taxonomic composition was examined using a Bray-Curtis dissimilarity matrix based on  
261 Wisconsin double-standardised abundance data. A redundancy analysis (RDA), constrained  
262 by the factors of island, scaled turf density, and scaled particulate mass was then performed  
263 on this matrix. Analysis of variance (ANOVA) was used to determine which factors had a  
264 significant association with the RDA axes, after which these factors were fitted to the  
265 ordination space using envfit (Oksanen et al., 2020). Following tests to ensure homogeneity  
266 of multivariate dispersion between groups, a permutational analysis of variance  
267 (PERMANOVA) with 999 permutations was used to test for differences in community  
268 composition between islands and with increasing particulate mass. PERMANOVAs were fit  
269 similarly to the GLMMS, whereby a full model was fitted incorporating the interaction of  
270 Island, particulate mass, and turf density, and the most parsimonious model was selected  
271 using AICc using custom code for PERMANOVAs (kdyson, 2021). The same processes were  
272 repeated for functional groups; however, the RDA was unconstrained because none of the  
273 factors were found to have significant effects using PERMANOVA. All analyses were  
274 performed using the statistical software R (R Core Team, 2021) with the packages vegan  
275 (Oksanen et al., 2020), glmmTMB (Brooks et al., 2017), DHARMA (Hartig, 2021), MuMIn  
276 (Barton, 2020), emmeans (Lenth, 2021) and ggplot2 (Wickham, 2016).

### 277 **3. Results**

#### 278 *3.1. Relationships between particulates and algal turf structure*

279 There were strong relationships between particulate depth, turf algal length, and turf algal  
280 density with particulate mass for both Lizard and Orpheus Island (Fig. 2A, B, & C).  
281 Specifically, the strong, positive change in sediment depth with increasing particulate mass  
282 was best described with a second order polynomial (GLMM,  $z = 8.8$ ,  $p < 0.05$ ;  $R^2 = 0.93$ ),  
283 however the curve was significantly steeper for Orpheus Island compared to Lizard Island ( $z$   
284  $= -4.7$ ,  $p < 0.05$ ; Fig. 2A). Similarly, a significant positive increase in turf length was  
285 documented with increasing particulate mass ( $z = 22.9$ ,  $p < 0.05$ ; Fig. 2B). While there was  
286 no interactive effect of Island, turf length was, on average, significantly longer at Orpheus  
287 Island compared to Lizard Island across the same particulate loads ( $z = 7.7$ ,  $p < 0.05$ ). The  
288 relationship between turf density and particulate mass followed a negative parabola shape  
289 (Fig. 2C). Specifically, turf density increased initially with particulate mass until  $\sim 100 \text{ g m}^{-2}$ ,  
290 where it plateaued at a density of approximately 70 % until a particulate mass of  $\sim 660 \text{ g m}^{-2}$   
291 (Fig. 2C). Beyond a particulate mass of  $\sim 660 \text{ g m}^{-2}$  the density of turf algal filaments  
292 declined. However, the nature of this relationship differed significantly ( $z = -2.3$ ,  $p < 0.05$ ;  
293 Fig. 2C) between Orpheus Island, where the relationship between particulate mass and turf  
294 density was more apparent, and Lizard Island, where a comparatively flatter relationship  
295 was documented.

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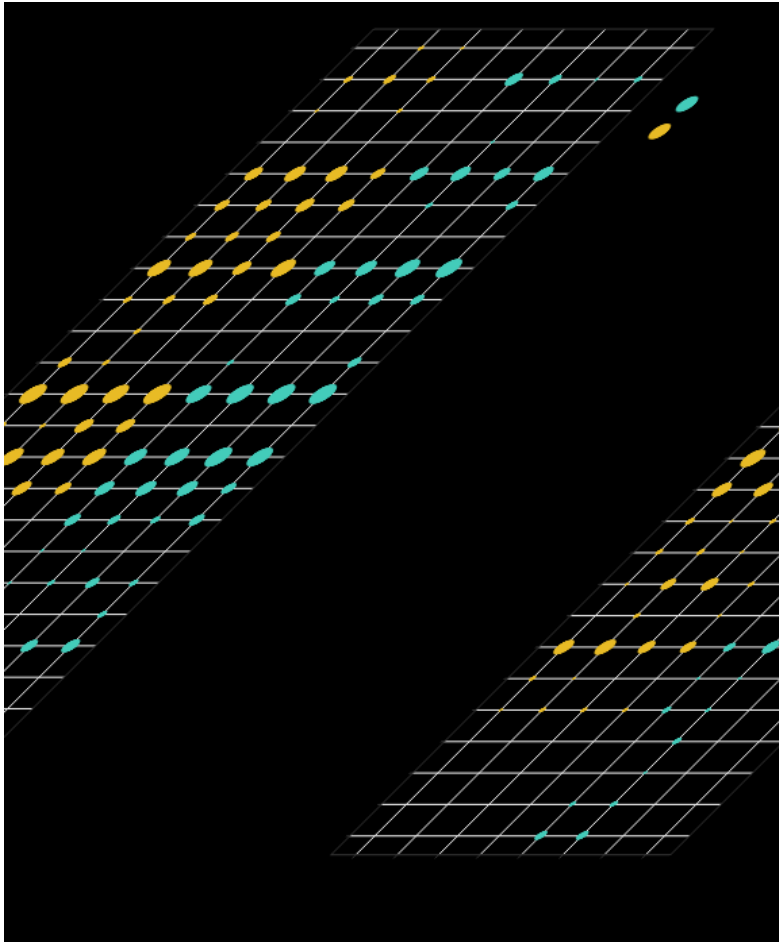
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298 **Fig. 2.** Relationship between (A) sediment depth, (B) turf length, and (C) turf density and  
 299 particulate mass at Lizard Island (cyan) and Orpheus Island (yellow) on the Great Barrier  
 300 Reef, Australia. The coloured lines indicate the mean predicted model fit and the shaded  
 301 areas show 95 % confidence intervals, while the coloured dots are the raw data points. An  
 302  $R^2$  value is not provided for turf density (C) as there is no reliable calculation of  $R^2$  for Beta  
 303 distributed data.

### 304 3.2. Community composition of algal turfs

305 We identified a total of 26 taxa (including four taxa that were not identifiable to genus or  
306 other levels) from 10 orders and four algal phyla across all samples (Supplementary Table 1).  
307 From Lizard Island, 21 taxa were identified, with the phylum Rhodophyta (red algae) being  
308 the most represented and accounting for 10 of the 17 (~55 %) genera we could identify. The  
309 algal turf assemblage at Orpheus Island also included 21 taxa. The phylum Rhodophyta was  
310 also the most represented at Orpheus Island, accounting for 12 of the 21 (~57 %) identified  
311 taxa. Rhodophyta abundance across both the islands was driven by the order Ceramiales,  
312 which represented seven of the 21 taxa at Lizard Island and seven of the 21 taxa at Orpheus  
313 Island.

314 The most frequently recorded taxa were cyanobacteria and the red algae *Polysiphonia*, both  
315 of which were observed in 100 % of samples, regardless of island (Fig. 3, Supplementary  
316 Table 1). At Lizard Island, the second most frequently recorded taxon was *Gelidiella* which  
317 was present in 95 % of the samples, followed by *Cladophora* (75 %) and *Ceramium* (75 %). At  
318 Orpheus Island, *Gelidiella* was recorded from 95 % of the samples, followed by  
319 *Chondria/Laurencia* (85 %), *Ceramium* (75 %), and *Derbesia* (75 %). A total of 12 and 11 taxa  
320 were observed from only 25 % or fewer of the Lizard Island and Orpheus Island samples,  
321 respectively (Fig. 3, Supplementary Table 1). From Lizard Island, seven taxa were rarely  
322 recorded including *Griffithsia* and *Parvocaulis* (observed in two samples), and *Martensia*,  
323 and *Caulerpa* (observed in one sample; Fig. 3, Supplementary Table 1). Two unidentified  
324 taxa were recorded in only one sample. Orpheus Island samples also contained rare taxa;  
325 *Dictyota*, *Caulerpa*, and *Halimeda* were observed in only two samples, while *Hypnea* was  
326 recorded from only one sample. Five of the 21 taxa recorded from Lizard Island were unique  
327 to this island, with *Martensia*, and four unidentified taxa recorded only from this location  
328 (Supplementary Table 1). Five of the 21 taxa recorded from Orpheus Island were unique to  
329 the location, including *Hypnea*, *Coelothrix*, *Taenioma*, *Dictyota*, and *Halimeda* (Fig. 3,  
330 Supplementary Table 1). samples), and *Martensia*, and *Caulerpa* (observed in one sample;  
331 Fig. 3, Supplementary Table 1). Two unidentified taxa were recorded in only one sample.  
332 Orpheus Island samples also contained rare taxa; *Dictyota*, *Caulerpa*, and *Halimeda* were  
333 observed in only two samples, while *Hypnea* was recorded from only one sample. Five of  
334 the 21 taxa recorded from Lizard Island were unique to this island, with *Martensia*, and four  
335 unidentified taxa recorded only from this location (Supplementary Table 1). Five of the 21  
336 taxa recorded from Orpheus Island were unique to the location, including *Hypnea*,  
337 *Coelothrix*, *Taenioma*, *Dictyota*, and *Halimeda* (Fig. 3, Supplementary Table 1).



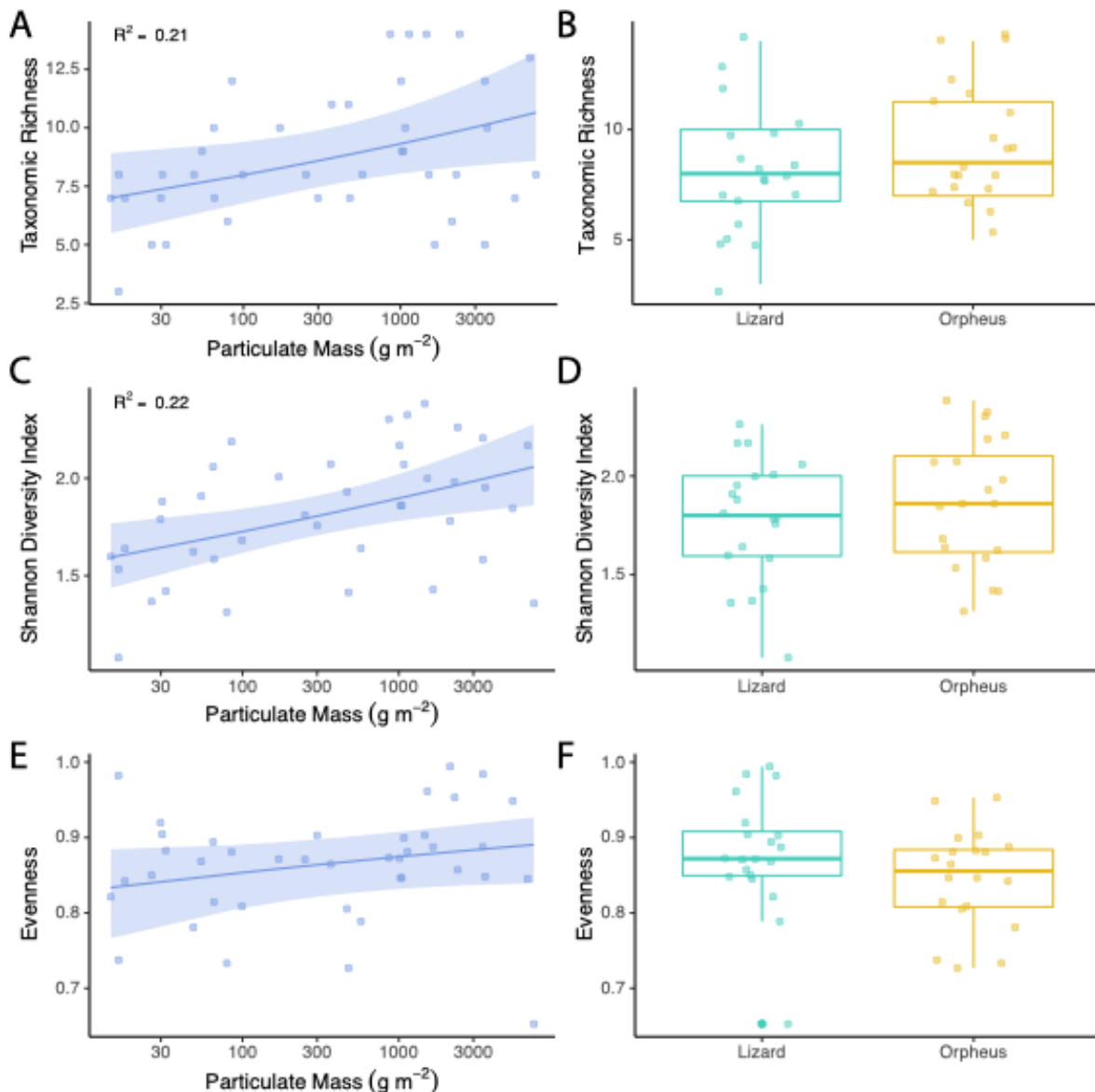
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339 **Fig. 3.** Turf algae community composition (functional groups and genera) in collected  
 340 samples ( $n = 5$ ) from each of the four sites at both Lizard Island (cyan) and Orpheus Island  
 341 (yellow). Point size represents mean relative abundance across the five samples per site.

342 Six functional groups were represented in both Orpheus and Lizard Island samples  
 343 (Supplementary Fig. 4), namely cyanobacterial filaments (CBF), corticated terete (CRT),  
 344 complex foliose (CFL), simple uniseriate filaments (hereafter referred to as filamentous)  
 345 (FIL), siphonous (SIP), and articulated coralline (ART; Fig. 3, Supplementary Table 1). The  
 346 siphonous group was the most represented (eight taxa), followed by the corticated terete  
 347 group (six taxa) in the Lizard Island samples (Fig. 3, Supplementary Fig. 4). In contrast, the  
 348 corticated terete functional group was most represented in Orpheus Island samples (nine  
 349 taxa), followed by the siphonous and filamentous groups (four taxa each; Fig. 3,  
 350 Supplementary Fig. 4).

351 The AICc suggested that any differences between islands in terms of algal turf taxonomic  
 352 richness ( $S$ ), Shannon diversity index ( $H'$ ), or evenness ( $E$ ) was negligible (Fig. 4B, D, F), and  
 353 therefore Island identity was not included in the GLMM. Particulate mass did have a  
 354 significant positive relationship with both taxonomic richness ( $z = 2.3$ ,  $p < 0.05$ ; Fig. 4A) and  
 355 Shannon diversity index ( $z = 3.02$ ,  $p < 0.05$ ; Fig. 4C), but not on evenness (Fig. 4E).

356



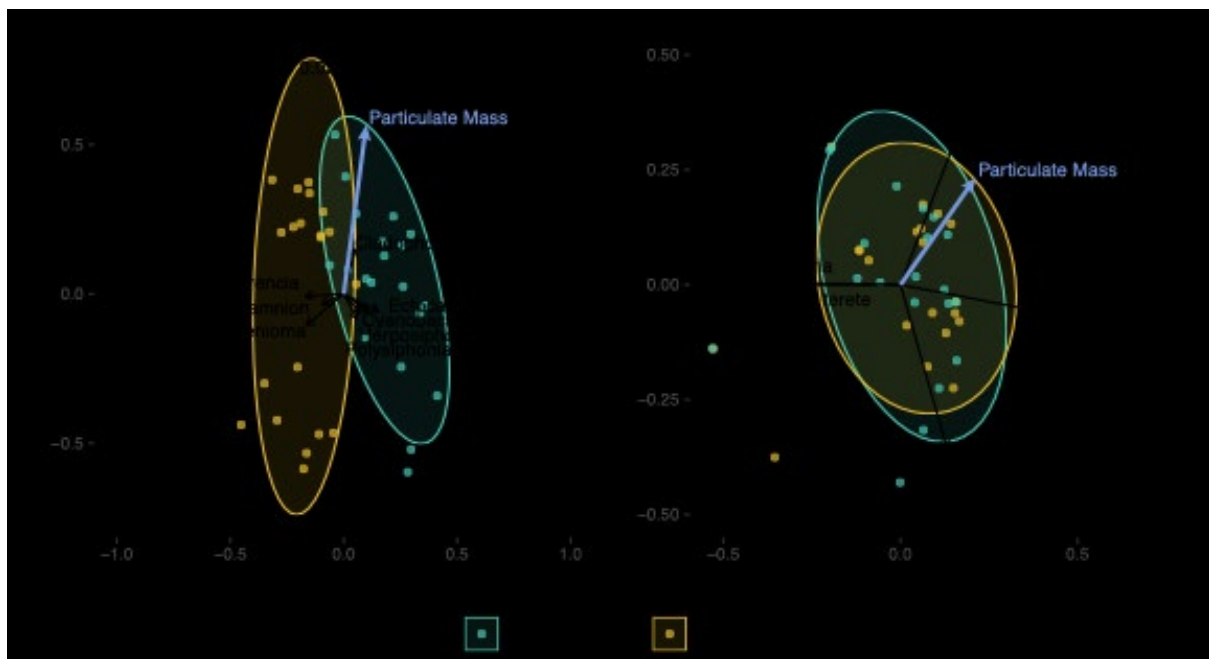
357  
 358 **Fig. 4.** Relationship between particulate mass and (A) taxonomic richness [ $S$ ], (C) Shannon  
 359 diversity index [ $H'$ ], and (E) evenness [ $E$ ]; the line denotes the predicted model fit, the  
 360 shaded area denotes the 95 % confidence interval, and points denote the raw data. Boxplots  
 361 illustrating (B) taxonomic richness, (D) Shannon diversity index, and (F) evenness in Lizard  
 362 Island (cyan) and Orpheus Island (yellow) samples. Median values and interquartile ranges  
 363 are indicated in the boxplots and points are raw data.

364

365 The taxonomic composition of algal turfs varied significantly between islands ( $F = 4.6$ ,  $df = 1$ ,  
 366  $p < 0.05$ ), as well as with increasing particulate mass ( $F = 2.4$ ,  $df = 1$ ,  $p < 0.05$ ; Fig. 5A).  
 367 Indeed, there was little overlap between data clouds from each island (Fig. 5A), with this  
 368 divergence being predominantly driven by higher abundance of *Chondria/Laurencia* and  
 369 *Taenioma* in Orpheus Island samples and higher abundance of *Ectocarpus* in Lizard Island  
 370 samples. The RDA plot suggested that the only genus correlated with increasing particulate  
 371 mass was *Cladophora* (Fig. 5A). In contrast to taxonomy, the functional group composition

372 of algal turfs did not differ significantly between islands ( $F = 0.10$ ,  $df = 1$ ,  $p > 0.05$ ) nor with  
373 increasing particulate mass ( $F = 1.7$ ,  $df = 1$ ,  $p > 0.05$ ; Fig. 5B). The RDA plot visualised the  
374 similarities in functional group composition, with data clouds for the two islands completely  
375 overlapping (Fig. 5B). Despite the lack of significant effect of particulate mass on turf  
376 functional group composition, the loading vector for particulate mass was positively  
377 correlated with the filamentous turf functional group (Fig. 5B). In contrast, the articulated  
378 functional group appeared to be negatively correlated with increasing particulate mass (Fig.  
379 5B).

380



381  
382 **Fig. 5.** Redundancy Analysis (RDA) plot showing the multivariate variation in terms of (A) turf  
383 algae genera, and (B) turf algae functional groups and particulate mass between Lizard  
384 Island (cyan) and Orpheus Island (yellow) sites. Vectors indicate the direction and strength  
385 of each variable. Shaded ellipses represent the 95 % confidence intervals of the centroids.

386

#### 387 4. Discussion

388 Algal turfs represent a major space holder on many coral reefs (Smith et al., 2016; Emslie et  
389 al., 2019; Jouffray et al., 2019), yet they are still largely viewed as a single functional group  
390 (reviewed in Connell et al., 2014). Recent studies have recognised that the structure (length)  
391 of algal turfs differs fundamentally based on the quantities of particulates accumulated in  
392 their canopies (Goatley et al., 2016; Tebbett and Bellwood, 2020). Our study supports this  
393 by highlighting the strong positive relationship between algal turf length and accumulated  
394 particulate load. However, we also highlight that another key physical trait of algal turf  
395 communities, their density, is also related to accumulated particulate mass, though the  
396 nature of this relationship appears to be more complex. Beyond the structure of turfs, our  
397 study also extends prior findings based on temperate marine systems (Stewart, 1983; Airoidi

398 et al., 1995) to coral reefs by revealing that the community composition of algal turfs is  
399 related to accumulated particulate mass. Clearly, strong relationships between accumulated  
400 particulate mass and algal turf structure/ composition are widespread in marine systems.

401

#### 402 4.1. Relationships between particulates and algal turf structure

403 The structure (length and density) of algal turfs and the quantity of accumulated  
404 particulates were strongly related to each other. The strong positive relationship between  
405 algal turf length and particulate mass observed here has also been widely documented in  
406 previous studies (Purcell and Bellwood, 2001; Fong et al., 2018; Pessarrodona et al., 2022),  
407 highlighting the ubiquity of this relationship. However, the relatively simple nature of this  
408 relationship may be underpinned by complex feedback in which it is difficult to determine  
409 the directionality. This is because increasing particulate mass suppresses herbivory allowing  
410 algal turfs to grow longer (Bellwood and Fulton, 2008; Goatley and Bellwood, 2013; Fong et  
411 al., 2018), and/or increasing particulate mass may reduce the availability of light to algae,  
412 which in turn could exhibit high rates of vertical growth to reach light (discussed in more  
413 detail below). Simultaneously, longer algal turfs also trap more particulates (Rasher et al.,  
414 2012; Latrille et al., 2019; McAndrews et al., 2019). As such, a positive feedback loop exists  
415 whereby an increase in accumulated particulates can suppress herbivory, allowing turfs to  
416 grow longer, thereby trapping and retaining more particulates. Nevertheless, regardless of  
417 the directionality, the relationship between turf length and particulate mass appears to be a  
418 simple positive correlation.

419 Unlike the simple relationship between turf length and particulate mass, the relationship  
420 between turf density and particulate mass was more complex, following a negative  
421 parabolic shape. Importantly, this shape was hypothesised to exist by Steneck (1997) based  
422 on the relationships between algal turfs, particulates, and herbivory. Specifically, the  
423 reduction in grazing pressure by increased particulate mass appears to have a beneficial  
424 influence on turf density as density increases as a result of being released from top-down  
425 herbivore control. However, this beneficial influence appears to fade as particulates  
426 continue to accumulate. Indeed, as particulate mass increases further, it appears to have a  
427 progressively more detrimental effect on algal turf density. Such detrimental effects of  
428 particulates on algal turf density may result from the development of unfavourable anoxic  
429 conditions in the basal layers of the particulates. For example, Clausen et al. (2014)  
430 demonstrated that when particulates accumulated to a depth of 4 mm, algal turf growth  
431 was suppressed, and this was associated with the accumulation of hydrogen sulphide in the  
432 basal layers of sediment. Therefore, depending on the context, particulates could shape  
433 algal turf communities via both positive and negative effects.

434 The formation of anoxic conditions is likely to differ between locations depending on the  
435 nature of the particulates and associated microbiota (Weber et al., 2012). The differences in  
436 the relationship between turf density and particulate mass at Lizard compared to Orpheus  
437 Island could therefore be explained by differences in particulates. In this respect, the  
438 relationship between particulate depth and particulate mass at the two islands is

439 informative (Fig. 2A), being closely related ( $R^2 = 0.93$ ) at the two island study sites, and,  
440 therefore, represent co-linear metrics influencing patterns in the algal turf structure and  
441 composition. However, the relative magnitude (slope) of this tight relationship between the  
442 two islands is crucial because it suggests Orpheus Island particulates had a greater depth  
443 than Lizard Island particulates, at the equivalent particulate mass. This difference suggests  
444 that the properties of the particulates differed between the two islands, with particulates at  
445 Orpheus Island probably containing a higher proportion of very fine material due to the  
446 proximity to land and inputs of fine terrestrial derived siliceous sediments and associated  
447 organic flocs (Fabricius et al., 2014; Goatley et al., 2016; Gordon et al., 2016). As the  
448 development of anoxic conditions is dependent on the depth of sediments (Clausing et al.,  
449 2014), this, therefore, suggests the particulates at Orpheus Island have a greater propensity  
450 to form hypoxic or anoxic layers across an equivalent range of particulate masses. As such, if  
451 anoxic conditions form more easily at Orpheus Island, this could explain the stronger  
452 detrimental effects of particulates on turf density at this location.

453 These strong relationships between accumulated particulates and the structure of algal turfs  
454 have several key ecological ramifications for herbivorous fishes. For example, as particulates  
455 appear to negatively affect turf density at high levels, this could decrease the potential of  
456 algal turf communities to deliver nutritional resources to herbivorous fishes. Indeed, a  
457 previous experiment demonstrated that particulate addition drove declines in algal turf  
458 nutritional resource yields to herbivorous fishes (Tebbett et al., 2018). Decreases in turf  
459 density could be one of the mechanisms underpinning this previous result. Likewise,  
460 previous studies highlighted that, unlike strong turf length versus particulate mass  
461 relationships, turf biomass versus particulate mass relationships are far weaker (Purcell and  
462 Bellwood, 2001; Tebbett and Bellwood, 2020), and again this could be due to turf density  
463 decreasing at high particulate loads. Importantly, as algal turfs represent a highly productive  
464 nutritional resource that may fuel herbivorous fish communities on reefs (Hatcher, 1988;  
465 Russ and St. John, 1988; Rasher et al., 2012), any reductions in the productivity or standing  
466 stock of this resource may have bottom-up effects on herbivorous food chains, potentially  
467 constraining the population sizes of herbivorous fishes that a given reef ecosystem can  
468 support (Tebbett et al., 2021). As a positive feedback loop appears to exist between  
469 particulate accumulation, algal turf structure and herbivorous fishes, alteration to any one  
470 of these factors could lead to marked changes in algal turf communities. Although as algal  
471 turfs exist on a continuous spectrum from SPATs to LSATs it is difficult to pinpoint thresholds  
472 of particulate mass where major changes in turf state could occur (refer to Tebbett and  
473 Bellwood, 2020 for a more detailed discussion on potential threshold levels). This makes  
474 identifying changes in turf condition in the field difficult without detailed examination.  
475 Nevertheless, given the interrelationship between algal turfs, sediments and herbivorous  
476 fishes on reefs (Duran et al., 2019; Akita et al., 2022; Pessarrodona et al., 2022) such  
477 changes may bring about alterations that reverberate up through reef food chains.

478 In addition to herbivory, the accumulation of particulates and the associated changes in the  
479 structure of algal turfs has implications for the recruitment and survival of corals. When  
480 settling on the benthos, coral larvae can interact closely with algal turfs (Arnold et al., 2010;  
481 Speare et al., 2019). If algal turfs are relatively sparse with low-levels of accumulated



482 particulates, previous research suggests coral settlement rates are comparable to bare  
483 substrata (Birrell et al., 2005) or crustose coralline algae-covered substrata (Diaz-Pulido et  
484 al., 2010). By contrast, longer, denser algal turfs with high particulate loads have been  
485 shown to reduce coral settlement rates (Birrell et al., 2005; Arnold et al., 2010; Speare et al.,  
486 2019; Wakwella et al., 2020). Moreover, even if corals do successfully settle to sediment-  
487 laden algal turfs, these turfs can be competitively dominant when interacting with corals,  
488 therefore reducing coral fitness and subsequent survival (Gowan et al., 2014; Liao et al.,  
489 2019). Successful settlement and survival of juvenile corals can underpin recovery rates of  
490 coral cover following disturbances (Evans et al., 2020; Tebbett et al., 2022), therefore, long  
491 sediment-laden algal turfs could compromise the resilience of coral reef systems.

#### 492 4.2. Community composition of algal turfs

493 The majority of the 26 algal/cyanobacteria taxa identified in our study have previously been  
494 reported from the Great Barrier Reef (Borowitzka et al., 1978; Scott and Russ, 1987; Diaz-  
495 Pulido and McCook, 2002; Stuercke and McDermid, 2004), and are common in other Indo-  
496 Pacific regions (Hixon and Brostoff, 1996; Harris et al., 2015). Interestingly, cyanobacteria  
497 and *Polysiphonia* were ubiquitous, being observed in all samples, and the prevalence of  
498 these taxa is also consistent with algal turf studies from other, markedly different locations  
499 (Airoldi et al., 1995; Fricke et al., 2011). The prevalence of cyanobacteria in algal turf  
500 communities may be due to their strong competitive ability (Fricke et al., 2011), while  
501 *Polysiphonia* may be abundant as they have a strong capacity for vegetative propagation  
502 (Airoldi et al., 1995). The ubiquity of cyanobacteria in turf communities may also provide a  
503 line of evidence which supports the hypothesis that parrotfishes target cyanobacteria as  
504 their primary nutritional resource (as proposed by Clements et al., 2017). This is because  
505 cyanobacteria represent a readily available resource in algal turfs with a high nitrogen  
506 content (Fricke et al., 2011). However, as cyanobacteria is widespread, the question arises  
507 as to whether parrotfishes selectively target cyanobacteria or whether they are the only  
508 group that feeds on the entire turf community (EAM). As such, parrotfishes may not target  
509 cyanobacteria; they may just be able to exploit it, particularly if cyanobacteria are deeper in  
510 the EAM.

511 Despite the ubiquity of some algal taxa in the turf communities, we also found marked  
512 differences in community composition between the two islands. Indeed, the inner-shelf turf  
513 communities at Orpheus Island were largely typified by *Taenioma*, *Spermothamnion*, and  
514 *Chondria/Laurencia*, while those at Lizard Island were typified by *Ectocarpus*. Notably, this  
515 conclusion supports that of Scott and Russ (1987), who revealed algal turf community  
516 composition was most variable between inner- shelf versus mid-/outer-shelf reefs on the  
517 GBR. Furthermore, while Harris et al. (2015) noted the greatest variance in algal turf  
518 taxonomic composition occurred at small spatial scales (i.e., centimetres), they did find  
519 taxonomic composition varied significantly at all spatial scales (from centimetres to  
520 kilometres). This variance at large spatial scales could relate to hydrodynamic processes  
521 which underpin the transport of propagules and subsequent recruitment dynamics (as  
522 previously suggested by Harris et al., 2015) or an indirect effect via the amount of sediment  
523 and relative herbivory rates. However, the relative importance of these processes in

524 structuring algal turf taxonomic composition across broad spatial scales is currently unclear  
525 as the reproductive output and dispersal of algae in algal turf communities on coral reefs  
526 remains largely unexplored. Addressing this knowledge gap in future studies may help  
527 resolve the mechanisms underpinning differences in algal turf taxonomic composition  
528 across broad spatial scales.

529 Notwithstanding the marked differences in taxonomic composition between islands, the  
530 lack of any clear differences in taxonomic richness, taxonomic diversity, or taxonomic  
531 evenness at this scale was unexpected. This could be a result of the relatively coarse  
532 taxonomic resolution used (i.e. genus-level), which reduces the power of diversity indices to  
533 detect differences, especially when compared to species level identification (Wu, 1982).  
534 However, visually differentiating species of algae within turfs at high taxonomic resolution  
535 remains difficult (reviewed in Connell et al., 2014). The application of reliable molecular  
536 techniques and utilisation of operational taxonomic units or amplicon sequence variants  
537 could provide a way to quantify taxonomic diversity at a finer resolution and help overcome  
538 this complexity (see Casey et al., 2019; Gaither et al., 2021), thus representing an  
539 interesting, albeit challenging, avenue for future research.

540 In addition to patterns between islands, our study revealed relationships between  
541 particulate mass and algal turf composition. Notably, high particulate mass was negatively  
542 or neutrally correlated with the occurrence of all taxa except *Cladophora*, which was  
543 positively correlated with higher particulate mass. The mechanism underpinning this  
544 observation could relate to the traits of *Cladophora* and specifically its grouping within the  
545 filamentous functional group. Although it should be noted that the other three filamentous  
546 algal taxa in this study did not appear to be strongly correlated with particulate mass in the  
547 multivariate analysis (Fig. 5A). This is likely due to the lower abundance in these taxa relative  
548 to *Cladophora* (Fig. 3) and their high variation in abundance (especially *Ectocarpus* and  
549 *Spermothamnion*) in samples between islands, rather than with particulate loads (Figs. 3,  
550 5A). Nevertheless, evidence from temperate systems also suggests the filamentous  
551 functional group of algae can tolerate high particulate loads (Airoldi, 1998; Connell, 2005)  
552 and this was also supported by our ordination plot in our study (Fig. 5B), which suggested  
553 only filamentous algae were correlated with high particulate mass (albeit not statistically  
554 significantly). This relationship between particulate mass and filamentous *Cladophora* could  
555 be related to a) growth form or b) nutrient uptake, both of which are considered below.

556 The correlation between high accumulated particulate mass and the filamentous functional  
557 group generally, and the *Cladophora*, specifically, could come down to a high capacity for  
558 growth via apical/vertical extension (Kraft, 2007). Algae are photosynthetic organisms,  
559 requiring access to suitable levels of light (Carpenter, 1985; Klumpp and McKinnon, 1992)  
560 and therefore vertical extension may ensure at least the apical component of filamentous  
561 turfs can reach the light and persist even when particulate loads are high. *Cladophora* and  
562 *Griffithsia* (part of the filamentous functional group) are characterised by an elongated,  
563 unbranched morphology under low light conditions (Waaland and Cleland, 1972) which  
564 provides a mechanism for this apical/vertical growth (Kraft, 2007). By contrast, algal taxa  
565 that rely to a greater extent on horizontal growth via thallus creeping, may be unable to

566 persist in conditions of high particulate accumulation. For example, the taxa *Taenioma* and  
567 *Herposiphonia* (part of the corticated terete functional group) rely on thallus  
568 creeping/lateral growth (Price and Scott, 1992) and both were negatively related to  
569 particulate mass (Fig. 5A). Indeed, if we consider how particulate accumulation relates to  
570 the structure of turfs (i.e., a strong positive relationship with length (Fig. 2B; Purcell, 2000;  
571 Fong et al., 2018; Tebbett and Bellwood, 2020); a negative parabolic relationship with  
572 density (Fig. 2C), and a very weak relationship with biomass (Purcell and Bellwood, 2001;  
573 Tebbett and Bellwood, 2020)), this evidence all points to vertical extension being favoured  
574 as particulates progressively accumulate.

575 In addition to growth form, it is possible taxa such as *Cladophora* possess traits which allow  
576 them to readily capitalise on increased nutrient supplies (which may be associated with  
577 particulates (Fabricius et al., 2014)). Indeed, various species within this genus have been  
578 shown to rapidly assimilate nitrogen in experimental studies (Lapointe and O'Connell, 1989;  
579 Peckol et al., 1994; Smith et al., 2005), and the genus is known to be favoured in eutrophic  
580 conditions (Lapointe and O'Connell, 1989; Dodds and Gudder, 1992; Smith et al., 2005;  
581 McClanahan et al., 2007). The association of *Cladophora* with higher particulate mass in this  
582 study suggests increased sediments may deliver higher nutrient concentrations, with the  
583 capability of *Cladophora* to uptake these nutrients favouring its growth (Lapointe and  
584 O'Connell, 1989; Peckol et al., 1994; Smith et al., 2005). Nevertheless, regardless of the  
585 exact mechanism, particulate mass is related to various metrics of algal turf community  
586 composition at both islands, suggesting it may be a universal environmental gradient  
587 operating across large spatial scales. This conclusion is supported by prior studies which  
588 have demonstrated that particulate mass is also related to algal turf community  
589 composition in temperate rocky reef marine systems (Stewart, 1983; Airoidi et al., 1995).

590 Unfortunately, despite the strong relationship between particulate mass and composition,  
591 the directionality of this relationship is, once again, hard to pinpoint (i.e., does algal  
592 composition influence particulate accumulation or vice versa). However, some insights may  
593 be gleaned by considering the findings of prior experimental work. Specifically, the addition  
594 of particulates can directly drive changes in the physical structure and productivity of algal  
595 turfs (Goatley and Bellwood, 2013; Clausing et al., 2014; Tebbett et al., 2018). In addition,  
596 herbivory has been experimentally demonstrated to drive changes in algal turf community  
597 composition (Wanders, 1976; Sammarco, 1983; Scott and Russ, 1987), and, as outlined  
598 above, we know herbivory can also be directly mediated by the quantity of particulates  
599 bound within algal turfs (Tebbett et al., 2017b). Given this prior knowledge, it can be  
600 concluded that increases in accumulated particulates would likely structure algal turf  
601 community composition both directly and indirectly via their relationship with herbivory.

602 Variation in algal turf taxonomic composition may have several ecological implications.  
603 Specifically, different algae have varying productivity levels (Rogers and Salesky, 1981;  
604 Bruno et al., 2006;), palatability or accessibility to herbivorous fishes (Wylie and Paul, 1988;  
605 Clements, 2015), and can affect the settlement of coral larvae (Birrell et al., 2008; Diaz-  
606 Pulido et al., 2010). As such, the rates of these processes (i.e., primary productivity,  
607 herbivory, and coral settlement) could be dependent, at least to some extent, on the

608 taxonomic composition of algal turfs. However, as the direct links between specific algal turf  
609 compositions and these processes remains unclear, our capacity to make inferences beyond  
610 this is currently limited. Quantifying these links in future studies is important considering  
611 stressors such as sediment mobilisation from dredging activities (Pollock et al., 2014; Fisher  
612 et al., 2018; Evans et al., 2020) and increased terrestrial derived sediment inputs from land-  
613 clearing (Cortes and Risk, 1985; Bainbridge et al., 2018; Wenger et al., 2020), could lead to  
614 higher accumulated particulate loads in algal turfs and associated changes in algal turf  
615 composition.

616

### 617 4.3. Conclusions

618 Overall, we found both the structure and community composition of algal turfs was closely  
619 related to accumulated particulate loads. This extends the findings of several previous  
620 studies (e.g., Purcell, 2000; Clausing et al., 2014; Gordon et al., 2016; Tebbett and Bellwood,  
621 2020) by showing that not only is algal turf length related to particulates on coral reefs, but  
622 density and community composition are also related. As such, this adds to the burgeoning  
623 body of literature which has highlighted how variation in algal turf particulate loads may  
624 play a critical role as a key environmental gradient in coral reef ecosystems (McAndrews et  
625 al., 2019; Speare et al., 2019; Tebbett et al., 2021). Unfortunately, human activities are now  
626 mobilising and releasing particulates/ sediments in the vicinity of coral reefs in greater  
627 quantities than ever before (Erftemeijer et al., 2012; Bainbridge et al., 2018; Suarez-Castro  
628 et al., 2021). Given the remarkable propensity for algal turfs to trap and retain this  
629 particulate material, the effects of particulates on algal turfs as well as on coral reef  
630 ecosystems more generally, may become increasingly prevalent. These effects may be  
631 particularly notable when combined with other stressors, such as global climate change,  
632 which are reducing coral cover on reefs and facilitating the expansion of algal turf cover  
633 (Gilmour et al., 2013; Kennedy et al., 2020; Koester et al., 2020). By continuing to enhance  
634 our knowledge of the interrelationship between algal turfs and particulates, we can better  
635 understand and manage the future reef systems in which high coral cover is becoming an  
636 increasingly rare condition.

637

### 638 **CRedit authorship contribution statement**

639 Chaitanya V. Arjunwadkar: Writing – original draft, Investigation, Methodology. Sterling B.  
640 Tebbett: Methodology, Formal analysis, Writing – review & editing. David R. Bellwood:  
641 Funding acquisition, Writing – review & editing. David G. Bourne: Supervision, Writing –  
642 review & editing. Hillary A. Smith: Supervision, Formal analysis, Visualization, Writing –  
643 review & editing.

### 644 **Declaration of competing interest**

645 The authors declare that they have no known competing financial interests or personal  
646 relationships that could have appeared to influence the work reported in this paper.

647 **Acknowledgements**

648 We thank: C.H.R. Goatley, M. Mihalitsis, the Orpheus Island Research Station staff and the  
649 Lizard Island Research Station staff for field support; two anonymous reviewers for insightful  
650 comments; and the Australian Research Council (DRB: CE140100020 and FL190100062), and  
651 the Orpheus Island Research Station Morris Family Trust (SBT) for financial support. DGB  
652 and HAS are supported by a partnership with Earthwatch Institute and Mitsubishi  
653 Corporation, and HAS is additionally supported by an Australian Government Research  
654 Training Program Scholarship.

655

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