

1 **Algal turf sediments on coral reefs: what's known and what's next**

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25 **Abstract**

26 Algal turfs are likely to rise in prominence on coral reefs in the Anthropocene. In
27 these ecosystems the sediments bound within algal turfs will shape ecosystem functions and
28 the services humanity can obtain from reefs. However, while interest is growing in the role of
29 algal turf sediments, studies remain limited. In this review we provide an overview of our
30 knowledge to-date concerning algal turf sediments on coral reefs. Specifically, we highlight
31 what algal turf sediments are, their role in key ecosystem processes, the potential importance
32 of algal turf sediments on Anthropocene reefs, and key knowledge gaps for future research.
33 The evidence suggests that the management of algal turf sediments will be critically
34 important if we are to sustain key functions and services on highly-altered, Anthropocene
35 coral reef configurations.

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37 **Keywords:**

38 Anthropocene Coral Reefs; Epilithic Algal Matrix; Ecosystem Function; Herbivory;
39 Productivity; Sediment

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47 **1. Introduction**

48 In the wake of increasing anthropogenic disturbances, marine ecosystems have
49 changed profoundly (Hughes et al., 2017; Vergés et al., 2019; Wernberg et al., 2015). In
50 many cases these disturbances have driven a loss of canopy forming foundation organisms
51 (Airoldi and Beck, 2007; Hughes et al., 2018b; O'Brien and Scheibling, 2018; Wernberg et
52 al., 2015; Wismer et al., 2019), and a rise in the coverage of algal turfs (Feehan et al., 2019;
53 Filbee-Dexter and Wernberg, 2018; Goatley and Bellwood, 2011; Jouffray et al., 2015) (Fig.
54 1). This has been epitomised on the world's coral reefs which have now undergone three
55 global-scale coral bleaching events (Bruno et al., 2019; Hughes et al., 2018a). Indeed, the
56 effects of climate change are now interacting with a myriad of other stressors, including
57 terrestrial inputs (Bainbridge et al., 2018; Ban et al., 2014; Fabricius, 2005) and overfishing
58 (Graham et al., 2017; Jackson et al., 2001), on coral reef ecosystems. Many coral reefs now
59 exist in a coral depauperate state (Fig. 1c-f), with some punctuated by periods of apparent
60 recovery or by transitions to alternative states (Bruno et al., 2019; Gilmour et al., 2019;
61 Mellin et al., 2019; Wilson et al., 2019).

62 Following the trajectory outlined above, herein we posit that 'Anthropocene' (i.e.
63 human modified) coral reefs will be characterised by lower coral cover, lower topographic
64 complexity, and an increasing abundance of algal turfs (following Bellwood et al., 2019a, b)
65 (Fig. 1c-f). On these Anthropocene coral reefs the relative importance of ecosystem processes
66 are in a state of flux (Bellwood et al., 2019b; Hughes et al., 2017). In particular, the
67 increasing prevalence of algal turfs has brought to the fore the capacity of sediments, when
68 interacting with algal turfs, to shape reef processes such as herbivory and coral settlement
69 (Birrell et al., 2005; Duran et al., 2018; Fong et al., 2018; Goatley et al., 2016; Tebbett et al.,
70 2018a). This is because, after climate change, increasing sediment inputs/declining water
71 quality is one of the most pervasive stressors faced by coral reefs (Bainbridge et al., 2012;

72 Erftemeijer et al., 2012; Jones et al., 2019; McCulloch et al., 2003), with more than 50% of
73 the world's reefs at risk (Burke et al., 2011). Importantly, algal turfs readily trap and
74 accumulate these sediments (Gordon et al., 2016b; Tebbett et al., 2019a), and can represent
75 the major reservoir of sediments on coral reefs (the off-reef sediment apron notwithstanding)
76 (Latrille et al., 2019). As such, algal turfs represent a critical interface where sediments can
77 impact reef organisms and reef processes.

78 However, while sediment impacts on coral reefs have been the focus of a substantial
79 body of literature (reviewed in Bainbridge et al., 2018; Erftemeijer et al., 2012; Fabricius
80 2005; Jones et al., 2015; Rogers, 1990; Wenger et al., 2017), this has largely focused on
81 turbidity and water quality. By contrast, our understanding of algal turf sediments on coral
82 reefs is still in its infancy but it appears to be a burgeoning research field. To engender further
83 growth, this review will focus on providing an overview of our knowledge concerning algal
84 turf sediments on coral reefs to-date. In doing so, we will highlight what algal turf sediments
85 are, their roles in ecosystem processes, their importance on Anthropocene coral reefs, and key
86 knowledge gaps for further research.

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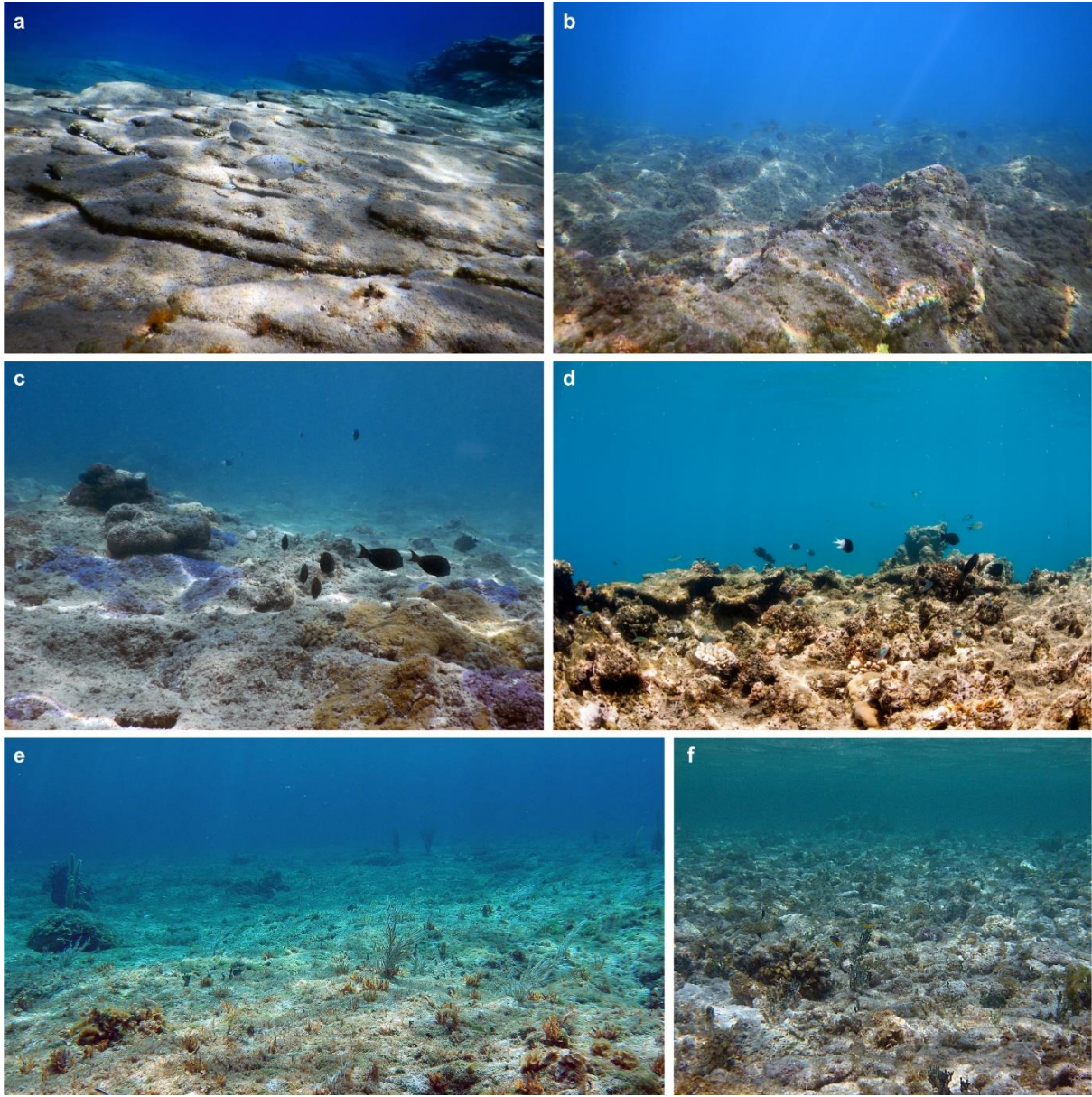
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95 **Figure 1** Low-complexity algal turf-covered a), b) subtropical rocky reefs off Crete in the
 96 Mediterranean, c), d) coral reefs around Lizard Island on the Great Barrier Reef, and e), f)
 97 coral reefs in the Caribbean off e) Little Cayman Island, and f) Carrie Bow Cay. Photographs
 98 were taken in a-d) 2018, e), 2005, and f) 2004. Photographs by a), e), f) D.R. Bellwood, b), c)
 99 S.B. Tebbett, d) V. Huertas.

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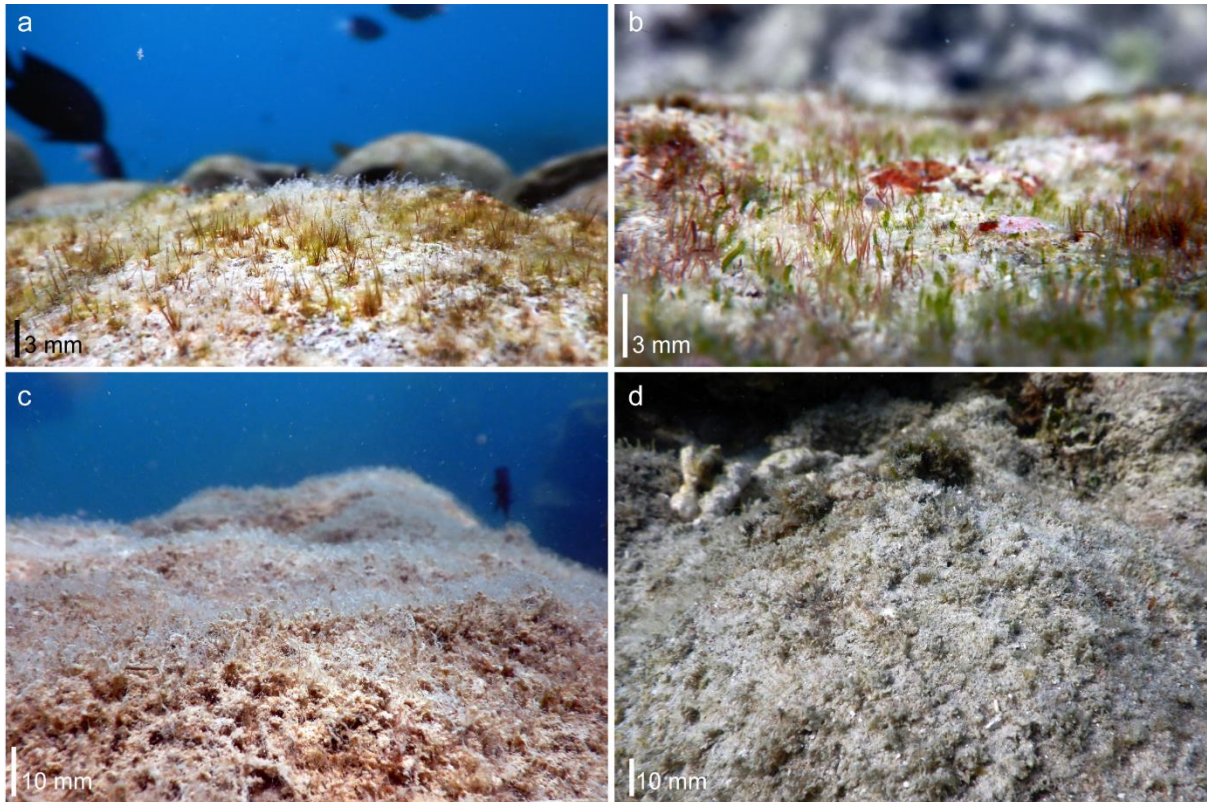
103 **2. Defining algal turf sediments**

104 *2.1. What are algal turfs?*

105 Herein, we consider algal turfs to be the short (<2 cm), multispecies assemblage of
106 generally filamentous macroscopic algae that cover the hard substratum on coral reefs (for
107 further detail see Connell et al., 2014; Fong and Paul, 2011; Steneck and Dethier, 1994). It
108 should be noted that past studies have included non-algal taxa (i.e. cyanobacteria) in their
109 definition of algal turfs (e.g. Larkum et al., 1988; Borowitzka et al., 1978), however, for
110 clarity cyanobacteria are considered separately. Algal turfs are often the most abundant
111 benthic covering on coral reefs (Arias-González et al., 2017; Jouffray et al., 2015; Smith et
112 al., 2016; Vroom et al., 2006; Wismer et al., 2009), especially following disturbances when
113 their coverage under coral canopies is revealed (Goatley and Bellwood, 2011) and early
114 successional forms readily colonise dead coral skeletons following primary colonisation by
115 cyanobacteria (which colonise within days) (Arthur et al., 2005; Diaz-Pulido and McCook,
116 2002; Houk et al., 2010). Furthermore, algal turfs are remarkably productive (Carpenter,
117 1985; Hatcher, 1988; Klumpp and McKinnon, 1992; Steneck, 1997; Wanders, 1977) and can
118 support key trophic pathways on reefs, e.g. energy flows up the food chain through
119 herbivorous fishes (Bellwood et al., 2018; Kelly et al., 2017; Russ, 2003). However, they are
120 also heterogeneous across multiple spatial (Harris et al., 2015; Scott and Russ, 1987) and
121 temporal scales (Diaz-Pulido and McCook, 2002), and have been referred to under a number
122 of different terms in the coral reef literature (see Connell et al., 2014).

123 During the 1980s-90s the term ‘epilithic algal community’ (EAC) was frequently used
124 when describing algal turfs on coral reefs, to recognise that these were far more than a
125 homogenous benthic covering and were a diverse community (e.g. Hatcher and Larkum,
126 1983; Klumpp and McKinnon, 1989; Purcell, 1996; Russ, 1987). This term morphed into the

127 ‘epilithic algal matrix’ (EAM) in the late 90s (Wilson and Bellwood, 1997) and has been used
128 frequently in the literature since (e.g. Heenan et al., 2016; McAndrews et al., 2019; Rasher et
129 al., 2013; Tebbett et al., 2017a; Wilson et al., 2003). The term EAM was coined to recognise
130 the importance of other non-algal turf constituents within the matrix including organic
131 detritus, inorganic sediments, microalgae and microbes [inc. cyanobacteria] (Wilson and
132 Bellwood, 1997). Similarly, the term ‘turf algal sediment mats’ (TAS mats) has been used in
133 reference to reefs in the Atlantic to recognise the condition of algal turfs when they become
134 laden with sediments (e.g. Lacey et al., 2013; Rodríguez-Martínez et al., 2011; Roy, 2004;
135 Shantz et al., 2015). Also in the Caribbean, the term ‘hardpan’ has been used to describe a
136 coral reef state typified by a covering of sediment-laden algal turfs (Bellwood and Fulton,
137 2008). More recently, the terms ‘short productive algal turfs’ (SPATs: ~ <5 mm and
138 relatively sediment-free algal turfs) and ‘long sediment-laden algal turfs’ (LSATs: ~ >5 mm
139 algal turfs that are laden with sediments) were coined to explicitly recognise a fundamental
140 division in the nature of algal turfs, separating those with low sediment loads from those with
141 high sediment loads (Goatley et al., 2016) (Fig. 2). The evolution of these definitions
142 highlights the increasing importance placed on sediments contained within the algal turfs.



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 144 **Figure 2** a, b) Short productive algal turfs (SPATs), note the lack of sediment (photographs
 145 R.P. Streit). c, d) Long sediment-laden algal turfs (LSATs) (S.B. Tebbett). Scale bars are
 146 approximate.

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 148 *2.2. What are algal turf sediments?*

149 Algal turf sediments are inorganic particulate material <2 mm (sands, silts and clays;
 150 ISO 14688-1:200) bound within algal turfs on coral reefs (Goatley, 2013; Tebbett et al.,
 151 2017a). However, the term ‘sediments’, when used in reference to algal turfs, has also been
 152 applied to all inorganic material in algal turfs including pieces >2 mm (e.g. Bellwood and
 153 Fulton, 2008; Goatley et al., 2012; Goatley and Bellwood, 2012; Purcell, 2000), as well as
 154 both inorganic and organic particulate material combined, especially when only sediment
 155 depth is recorded (e.g. Clausing et al., 2014; Duran et al., 2018; Eurich et al., 2018; Fong et
 156 al., 2018; Goatley and Bellwood, 2013). It should also be noted that the working definition of
 157 ‘inorganic sediments’ includes living organisms such as endolithic, microboring organisms

158 that can be contained within inorganic calcareous sediments (e.g. Perry, 1998). The organic
159 particulate component of the benthic particulate mix within the EAM is defined more broadly
160 as ‘detritus’, with a commonly used working definition of detritus being: non-living organic
161 particulate material that is also likely to contain life in the form of microbes (for a
162 comprehensive review of coral reef detritus see Wilson et al., 2003). The term ‘benthic
163 particulates’ has been applied to both the organic and inorganic components when summed
164 together, recognising this amalgamation (Tebbett et al., 2018b, 2017b). Clarity of terms and
165 distinction amongst inorganic sediments and organic components of the particulate mixture is
166 necessary to assess: a) the different effects of each component on ecosystem processes
167 (Birrell et al., 2005; Gordon et al., 2016a; Tebbett et al., 2017b), and b) how organisms can
168 utilise components. For example, the organic detrital and microbial component can represent
169 a critical nutritional resource that is specifically targeted by a wide range of fishes (Choat et
170 al., 2002; Crossman et al., 2001; Max et al., 2013; Robertson and Gaines, 1986; Wilson et al.,
171 2003).

172 Furthermore, algal turf sediments *sensu stricto* can be composed of both carbonates
173 and silicates (Gordon et al., 2016b; Latrille et al., 2019; Tebbett et al., 2018b). The carbonate
174 component is largely derived from the on-reef production of sediments via mechanisms such
175 as bioerosion (Bellwood, 1996; Hutchings, 1986; Yarlett et al., 2018) and the physical
176 breakdown of skeletal remains of calcifying organisms (Fujita et al., 2009; Scoffin, 1992). By
177 contrast, the siliceous component is largely derived from terrestrial sources (Goatley et al.,
178 2016; Gordon et al., 2016b), and can be composed of ‘new’ sediments (i.e. recently deposited
179 sediments from terrestrial runoff and river plumes) or ‘old’ sediment (i.e. settled sediments
180 that have been resuspended and transported to reefs) (Bainbridge et al., 2018; Fabricius et al.,
181 2014; Lewis et al., 2014; Orpin and Ridd, 2012; Wolanski et al., 2008). In general, the
182 different types of sediment have different characteristics including their density, association

183 with organic material, size and ability to adsorb nutrients (Bainbridge et al., 2018; Gordon et
184 al., 2016b; Lutgens and Tarbuck, 2006). With the composition and amount of sediments
185 being trapped in algal turfs depending on a range of factors including local sediment inputs
186 (Browne et al., 2013; Tebbett et al., 2018b), reef geomorphology (Hopley et al., 2007;
187 Tebbett et al., 2017a), hydrodynamics (Bodde et al., 2014; Carpenter and Williams, 1993;
188 Purcell, 2000) and the feeding activity of fishes (Goatley and Bellwood, 2010; Hoey and
189 Bellwood, 2008; Krone et al., 2011). While algal turf sediments can be disparate in terms of
190 their composition, they can all generally be defined as inorganic particulate material <2 mm
191 that reside within algal turfs.

192 *2.3. How do sediments become algal turf sediments?*

193 The diffusive boundary layer formed by the complex structure of algal turfs can slow
194 water movement and is the predominant mechanism that facilitates the deposition and
195 accumulation of sediments in algal turfs (Carpenter and Williams, 1993; Latrille et al., 2019).
196 In addition, this process is likely to be supplemented by other factors, such as the secretion of
197 mucilaginous sheaths by filamentous cyanobacteria within the EAM which can bind sand
198 particles together (Stal, 2003). As such the EAM as a whole, and algal turfs in particular,
199 appear to have a particularly remarkable propensity to accumulate and retain sediments. For
200 example, algal turf sediments can accumulate to reach ambient levels following clearing in a
201 matter of days (Tebbett et al., 2018a), and once trapped these levels can remain remarkably
202 stable over long (6 month) temporal scales (Gordon et al., 2016b). Moreover, Latrille et al.,
203 (2019) highlighted that over a week-long period, algal turfs accumulated far more sediment
204 than artificial sediment traps, which have previously been criticised for their excessive
205 trapping abilities (Storlazzi et al., 2011). Unfortunately, while we know algal turfs can readily
206 accumulate sediments and are likely to play a key role in sediment dynamics, our

207 understanding of the links between suspended sediments, sediment input rates and algal turf
208 sediment accumulation are relatively limited.

209 Recently, Latrille et al., (2019) began to place algal turf sediments into the context of
210 suspended sediments and sedimentation. Latrille et al., (2019) highlighted that lateral
211 accumulation of sediments was limited, and accumulation appeared to be driven primarily by
212 direct deposition by parrotfishes and deposition of suspended sediments (including local
213 resuspension from nearby ‘sediment-saturated’ algal turfs). Furthermore, Whinney et al.,
214 (2017) revealed that sedimentation rates were higher following turbidity peaks, however, the
215 nature of the relationship was complex and varied across temporal scales due to factors such
216 as wind speed and tidal phase. However, apart from these two studies, our understanding of
217 links between algal turf sediments, sedimentation, and suspended sediments remains limited.

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219 **3. Quantification and distribution of algal turf sediments**

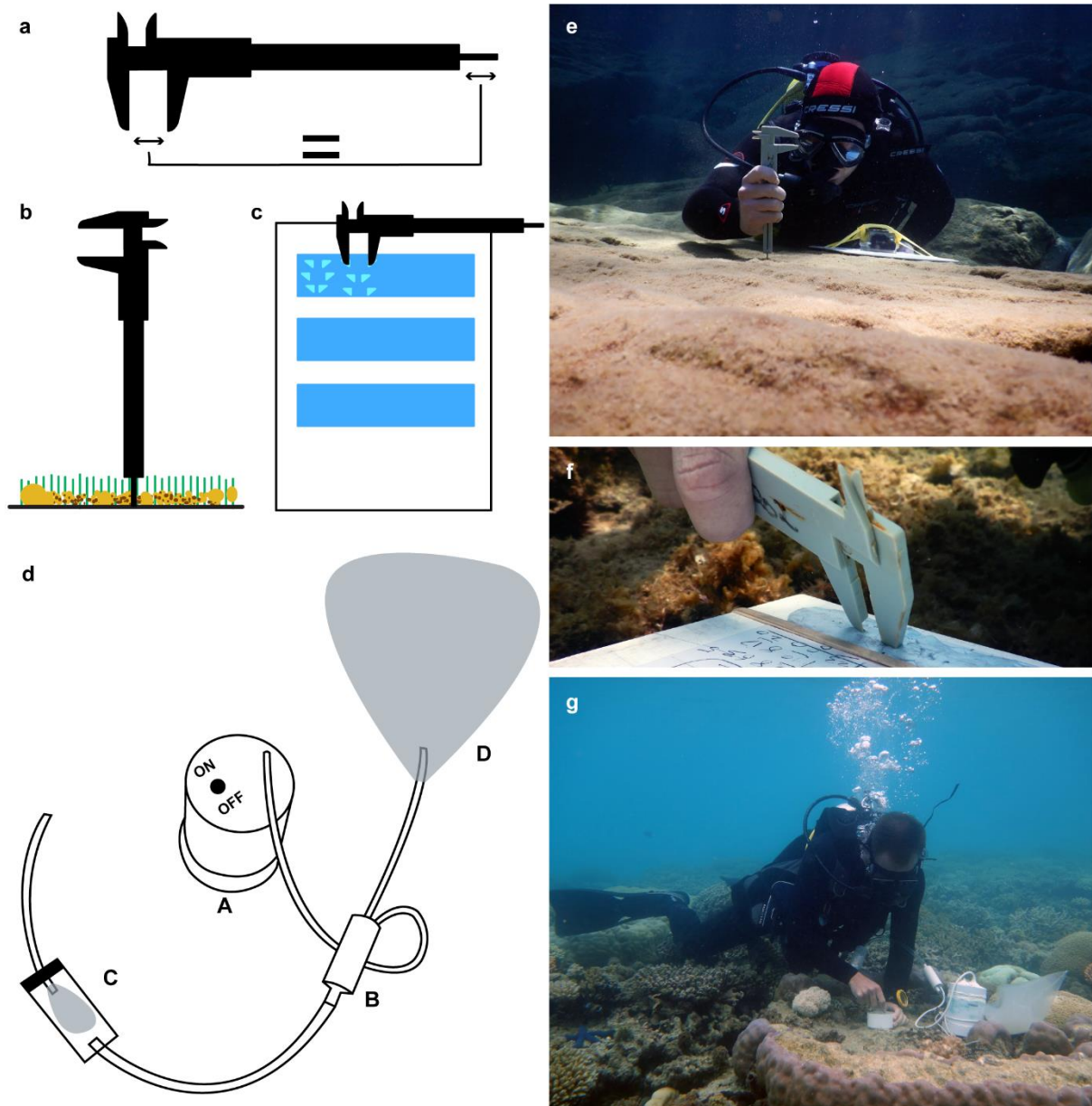
220 *3.1. How do we quantify algal turf sediment characteristics?*

221 Algal turf sediments can be quantified directly in several ways including by depth
222 (Adam et al., 2018; Clausing et al., 2014; Goatley and Bellwood, 2013), coverage (Ceccarelli
223 et al., 2005; Duran et al., 2018; Eurich et al., 2018) and mass (Gordon et al., 2016b; Purcell,
224 2000; Rasher et al., 2012; Tebbett et al., 2017a). The exact method employed depends on the
225 nature of the question being addressed and the level of detail required. As the properties of
226 algal turf sediments can differ markedly depending on their composition and size (Gordon et
227 al., 2016b; Latrille et al., 2019), the different methods vary markedly in their ability to
228 quantify different aspects. The two most frequently used methods in the literature are depth
229 measurements and underwater vacuum sampling for collection and mass analysis. Sediment

230 traps are not included as they have a limited capacity to quantify algal turf sediments (Latrille
231 et al., 2019). Each is outlined in detail below.

232 In-situ sediment depth and algal turf length measurements are non-destructive, fast
233 and inexpensive to perform. Such measurements can indicate the nature of the algal turfs and
234 the quantity of sediments they contain (i.e. SPATs vs LSATs; sensu Goatley et al., 2016), and
235 can be readily employed in experimental scenarios to monitor changes in algal turf length
236 (Fong et al., 2018; Goatley and Bellwood, 2013; Tebbett et al., 2017c). For example,
237 sediment depth and/or algal turf length can be measured using the depth probe of vernier
238 callipers, which yields the same distance as between the tips of the callipers (Fig. 3a, b, e).
239 This distance is then recorded by pressing the tips of the callipers into saltwater-resistant
240 pressure-sensitive poster adhesive (blu tack) (Fig. 3c, f), which can then be measured more
241 accurately in the laboratory using digital callipers. However, while fast and non-destructive,
242 depth measurements only provide limited information on the sediments with no detail on the
243 composition or size. Furthermore, as sediments can have different depths depending on their
244 size and density (e.g. Gordon et al., 2016b; Latrille et al., 2019), depth and mass estimates are
245 not necessarily comparable. If more detailed measures are required, depth measurements can
246 be combined with sediment collection.

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249 **Figure 3** A schematic diagram showing the tools that can be used to quantify algal turf
 250 sediments. a) The depth probe of callipers is the same as the length between the tips, b) this
 251 depth probe can be used to examine algal turf filament length and/or sediment depth, and c)
 252 these measurements can be quickly recorded underwater in ‘blu tack’ for later quantification
 253 in the lab. d) a small handheld underwater vacuum sampler is composed of: A – a waterproof
 254 housing containing the battery, controlled by a toggle switch to provide power to B – a small
 255 inline water pump. The impellor in the water pump is protected by C – a container that holds
 256 a filter (~250 μm plankton mesh) that traps coarse sediments which are retained. Finer

257 sediments pass through the filter and are retained in D – a plastic bag (~5 L). B, C and D are
258 all connected with clear vinyl tubing. e), f) S.B. Tebbett measuring algal turf length using the
259 methods described above, and g) sampling algal turf sediments using an electronic vacuum
260 sampler (photographs e), f): D.R. Bellwood, g): R.P. Streit).

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263 Small underwater vacuum samplers (Fig. 3d, g), are frequently used for collecting
264 sediments, organic detritus, and algal material from the substratum on coral reefs (e.g.
265 Crossman et al., 2001; Kelly et al., 2017; Kramer et al., 2012; Max et al., 2013; Purcell, 1996;
266 Tebbett et al., 2017a). These samplers can remove all particulate material from the algal turfs
267 for more detailed processing and scraping tools can be fitted to remove the algal turfs
268 themselves (for detailed methods see Purcell, 1996). The collected particulates can then be
269 processed to yield information including depth, mass, inorganic vs organic ratios, silicate vs
270 carbonate content, grain size distributions (using sieves or laser diffraction analysis) and
271 nitrogen fractionation (Gordon et al., 2016b; Judy et al., 2018; Latrille et al., 2019; Purcell,
272 2000; Weber et al., 2006). These indices can then be related to other properties of algal turfs
273 such as length and biomass (Purcell, 2000; Purcell and Bellwood, 2001), yielding insights
274 into local algal turf sediment dynamics (Goatley et al., 2016; Gordon et al., 2016b; Latrille et
275 al., 2019).

276 It should be noted that attempts have been made to quantify algal turf sediments
277 through more indirect methods such as sediment traps (for an overview see Storlazzi et al.,
278 2011), SedPods (for an overview see Field et al., 2013), and TurfPods (for an overview see
279 Latrille et al., 2019). However, preliminary evidence suggests that such methods provide only
280 a partial, and in some cases, unrepresentative insight into the nature of algal turf sediments

281 (for a detailed comparison of all methods see Latrille et al., 2019). Such methods are
282 designed to quantify other aspects of sediment dynamics on coral reef, rather than algal turf
283 sediments. If working on algal turf sediments, the most accurate method is probably to
284 quantify them directly.

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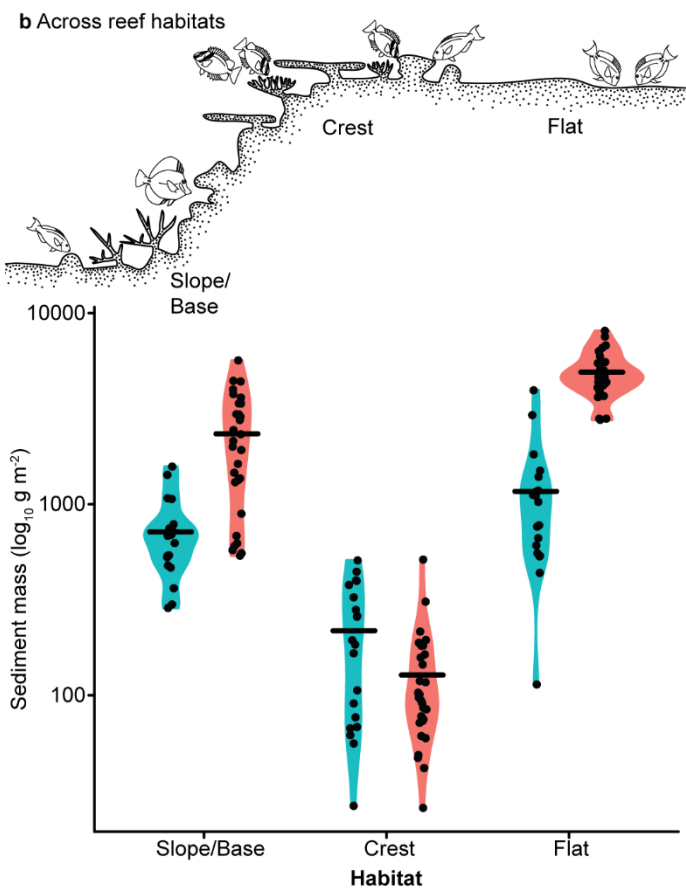
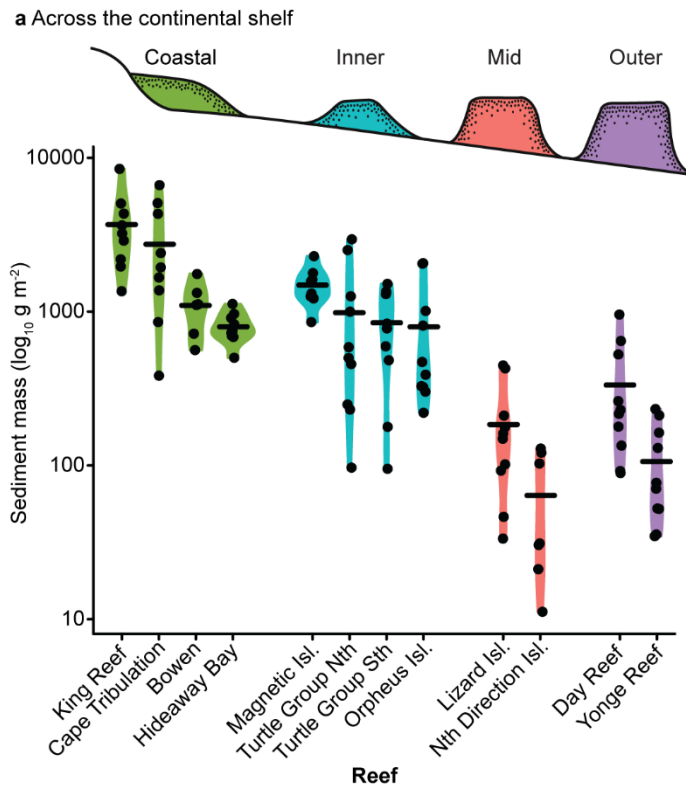
286 *3.2. Quantities and distribution of algal turf sediments*

287 Algal turfs can represent the major reservoir of sediments on coral reefs (not
288 including the off-reef sediment aprons) (Latrille et al., 2019). This is because algal turfs can
289 contain far higher sediment levels than those accumulated on corals or suspended in the water
290 column (Latrille et al., 2019). However, algal turf sediment loads can vary markedly, ranging
291 from 10s of g m^{-2} to 1000s of g m^{-2} and from <1 mm to ~ 20 mm depth (Bellwood and Fulton,
292 2008; Clausing et al., 2014; Purcell, 2000; Tebbett et al., 2018b) (Fig. 4). This variability is
293 exemplified across the continental shelf of Australia's Great Barrier Reef (GBR) with coastal
294 reef crests containing average sediment loads up to $3681.8 \pm 713.7 \text{ g m}^{-2}$, while sediment-
295 depauperate mid-shelf reef crests can maintain average loads as low as $63.8 \pm 19.4 \text{ g m}^{-2}$ (Fig.
296 4a). The composition of sediments also varies across large scales. Reefs closer to shore
297 generally have higher levels of siliceous sediments and, as expected, levels decrease with
298 distance from the coast (Gordon et al., 2016b; Tebbett et al., 2018b).

299 At smaller, within-reef scales, algal turf sediment loads vary consistently among
300 habitats (Fig. 4b). Low sediment loads occur on high-energy reef crests, while higher
301 sediment loads accumulate in lower-energy reef slope and flat habitats (Gordon et al., 2016b;
302 Purcell, 2000) (Fig. 4b). Indeed, average sediment levels over 8000 g m^{-2} have been reported
303 from the reef flat at Lizard Island, Australia (Goatley and Bellwood, 2012). In addition to the
304 amount of sediment, other metrics such as the grain size distribution (finer sediments occur in

305 lower-energy habitats) and relative detrital levels (higher proportions of detritus are found on
306 the reef crest) differ markedly among habitats (Gordon et al., 2016b; Purcell and Bellwood,
307 2001; Tebbett et al., 2017a). Within reef habitats algal turf sediment loads can also be
308 heterogenous due to fine scale factors such as fish feeding patterns (Goatley and Bellwood,
309 2010) or structural complexity (Duran et al., 2018; Tebbett et al., 2019a). Clearly algal turf
310 sediments vary at multiple spatial scales, but often in a predictable manner (i.e. regardless of
311 the reef they generally decrease with distance from shore and are lowest on high-energy reef
312 crests [Fig. 4]).

313 The predictable gradients in algal turf sediment loads may underpin other important
314 ecological gradients on coral reefs especially in organisms that associate closely with algal
315 turfs, e.g. herbivorous fishes and scleractinian corals. In the case of herbivorous fishes for
316 example, species abundance, biomass and richness are frequently correlated with water
317 quality gradients (e.g. Cheal et al., 2013; Moustaka et al., 2018). However, these correlations
318 are more likely to be explained by gradients in algal turf sediment loads, which have a
319 marked propensity to alter herbivorous fish feeding behaviour and potentially, therefore, their
320 long-term persistence (outlined in detail in section 4.3). As such, while water quality
321 gradients might be correlative, algal turf sediment gradients might offer a more plausible
322 mechanistic basis for some observed ecological gradients.



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Figure 4 Sediment loads in algal turfs at different spatial scales a) on reef crests across the continental shelf of the Great Barrier Reef, Australia, and b) across different reef habitats on

326 an inner-shelf (Orpheus Island [turquoise]) and a mid-shelf (Lizard Island [orange]) reef,
327 from the Great Barrier Reef. Note the consistent patterns of algal turf sediment loads among
328 a) different reefs in the same shelf positions, or b) habitats between different reefs. Also note
329 that the y-axis is logged in both cases. Cross-bars indicate the means. Data were sourced from
330 (Goatley et al., 2016; Gordon et al., 2016b; Purcell, 2000; Tebbett et al., 2018b, 2017a). Isl. =
331 Island.

332

333 **4. Sediment effects on coral reef organisms**

334 *4.1 Overview*

335 Intuitively, algal turf sediments appear to primarily affect coral reef taxa that closely
336 associate with the benthos, e.g. algae, nominally herbivorous fishes, and corals. Indeed, these
337 three broad taxonomic groups have been the basis of most research to-date concerning algal
338 turf sediments on coral reefs and will be the focus of this section. However, preliminary
339 results have highlighted that algal turf sediments can influence the distribution patterns,
340 and/or feeding behaviour of a suite of reef taxa including cryptofauna (Kramer et al., 2012;
341 Logan et al., 2008), invertebrate grazers (Sangil and Guzman, 2016; Tebbett et al., 2018a),
342 turtles (Goatley et al., 2012), and probably even microbes within algal turfs (Bourne et al.,
343 2016; Meirelles et al., 2018; Zaneveld et al., 2016).

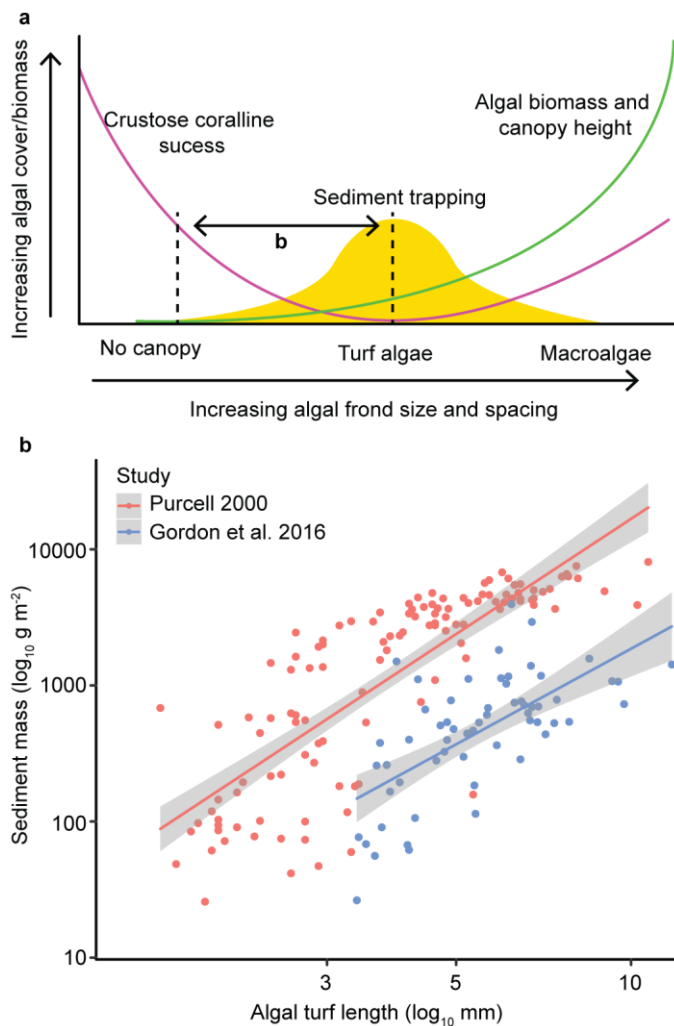
344 The primary mechanism underpinning the effects of algal turf sediments on coral reef
345 organisms appears to be the positive association between algal turfs and algal turf sediments
346 (Fig. 5). Algal turf sediments can release algal turfs from intense grazing pressure, with a
347 positive relationship occurring between algal turf length and algal turf sediment load on coral
348 reefs (Bonaldo and Bellwood, 2011; Gordon et al., 2016b; Purcell, 2000; Purcell and
349 Bellwood, 2001) (Fig. 5b). This correlation is due to either a) longer algal turfs developing

350 first and trapping more sediment (Latrille et al., 2019), or b) algal turf sediments initially
351 accumulating more sediments leading to less herbivory resulting in longer algal turfs and
352 further sediment trapping (Goatley and Bellwood, 2013; Goatley et al., 2016), or both.
353 LSATs therefore develop as a result of a positive feedback as the increase in sediments leads
354 to a decrease in herbivory, with resulting increases in algal turf length further increasing
355 sediment trapping and decreasing herbivory. It is these long sediment-laden algal turfs
356 (LSATs) that appear to have the largest effect on coral reef taxa (see below).

357

358 *4.2. How do algal turf sediments affect algae?*

359 Coral reef algae are frequently grouped together in three broad functional groups
360 (crustose coralline algae [CCA], macroalgae and algal turfs) (see Steneck and Dethier, 1994).
361 As these functional groups are united based on morphological similarities, they are affected
362 by algal turf sediments to various extents and in different ways. This was initially
363 conceptualised by Steneck (1997) who highlighted the success of algal turfs, over other algal
364 functional groups, when algal turf sediments are abundant (Fig. 5a). By contrast, CCA and
365 macroalgae are more prolific in conditions where algal turf sediments are not as high
366 (Steneck, 1997) (Fig. 5a). This functional group approach is maintained herein to highlight
367 the key effects of algal turf sediments on each group separately.



368

369 **Figure 5** a) A conceptual model (modified after Steneck, 1997) for the coexistence of three
 370 algal functional groups (crustose coralline algae, turf algae, and macroalgae) and the
 371 propensity for the assemblage to trap sediments. Note that when sediment trapping is
 372 maximised algal turfs dominate. The box delineated by dashed black vertical lines and arrows
 373 indicate the relationship described in further detail in panel b) i.e. the relationship between
 374 algal turf length and algal turf sediment mass at Orpheus Island (blue) (Gordon et al., 2016b)
 375 and Lizard Island (orange) (Purcell, 2000), on the Great Barrier Reef, Australia. The coloured
 376 lines and grey shaded areas show the predicted fit of linear models and their 95% confidence
 377 intervals.

378

379 4.2.1 *Algal turfs*

380 While algal turf length is generally positively associated with increasing algal turf
381 sediment load (Fig. 5), it is certain that a threshold exists, whereby, once too much sediment
382 is trapped, conditions can become unfavourable even for algal turfs. For example, Tebbett et
383 al. 2018a experimentally demonstrated that higher algal turf sediment loads reduced algal turf
384 biomass accrual, supported by similar results from subtropical rocky reef algal turfs (Airoidi
385 and Virgilio, 1998). One of the main factors underpinning such results may be the
386 development of unsuitable conditions in deeper layers of algal turf sediments. Indeed,
387 Clausing et al., (2014) found that at depths of 4 mm algal turf sediments can suppress the
388 growth of algal turfs through the formation of hydrogen sulphide (H₂S). This formation of
389 anoxic conditions is likely to be particularly prevalent if high loads of fine algal turf
390 sediments get trapped in habitats with limited hydrodynamic activity. Although algal turfs
391 appear to be a particularly stress-tolerant functional group of algae (Hay 1981), extreme
392 accumulation of algal turf sediments appears to influence even these resistant algae.

393 4.2.2 *Crustose coralline algae*

394 CCA play a major role in reef building through calcification and cementation of the
395 reef substratum, as well as promoting coral settlement (Adey, 1998; Harrington et al., 2004).
396 CCA are well suited to shallow, high-energy coral reef environments and are particularly
397 resistant to the grazing pressure of herbivores, unlike other algal functional forms (Steneck,
398 1983a). Indeed, for CCA to persist, it appears that high herbivory rates are crucial to control
399 the growth and expansion of algal turfs (Steneck, 1997, 1983a). However, while experimental
400 evidence assessing the impacts of algal turf sediments on CCA is limited, evidence
401 examining the influence of sediments alone suggests that CCA are likely to be highly
402 susceptible to algal turf sediment impacts (Fabricius, 2005; McClanahan, 1997; Steneck,

403 1997). For example, the cover of CCA is frequently negatively correlated with sedimentation
404 rates (Albert et al., 2008; Fabricius and De'ath, 2001; Fabricius and McCorry, 2006) and
405 burial of CCA by fine sediments has been experimentally demonstrated to decrease
406 photosynthesis and compromise survival (Fabricius, 2005; Harrington et al., 2005).
407 Therefore, under such conditions, accumulated sediments are likely to foster the competitive
408 ability of algal turfs, which can successfully compete with and overgrow CCA (Steneck,
409 1997) (Fig. 5).

410 4.2.3 Macroalgae

411 Steneck (1997) suggested that macroalgae, like CCA, are sensitive to increased
412 sediment loads. This notion was supported by Umar et al., (1998), who demonstrated that
413 increased algal turf sediment loads can significantly reduce recruitment, growth, survival and
414 vegetative regeneration in one species of tropical *Sargassum*. Unfortunately, beyond the
415 study of Umar et al., (1998) our understanding of the effects of algal turf sediments on coral
416 reef macroalgae is limited. However, these effects have been studied in far more detail in
417 subtropical and temperate rocky reef macroalgae assemblages (reviewed in Airoidi, 2003;
418 O'Brien and Scheibling, 2018). Indeed, several subtropical/temperate studies have found
419 similar results to Umar et al., (1998) in that algal turf sediments significantly impede the
420 settlement and survival of canopy forming macroalgae (e.g. Airoidi, 1998; Alestra et al.,
421 2014; Gorman and Connell, 2009; Isæus et al., 2004). The evidence gleaned to-date from
422 other systems suggests that the ability of algal turf sediments to impair the settlement abilities
423 and survival of macroalgae may be widespread. As such, coral reef systems that have
424 transitioned to LSAT-covered states may resist further transitions to macroalgae covered
425 states, as suggested in Goatley et al., (2016).

426

427

428 *4.3 How do algal turf sediments affect fishes?*

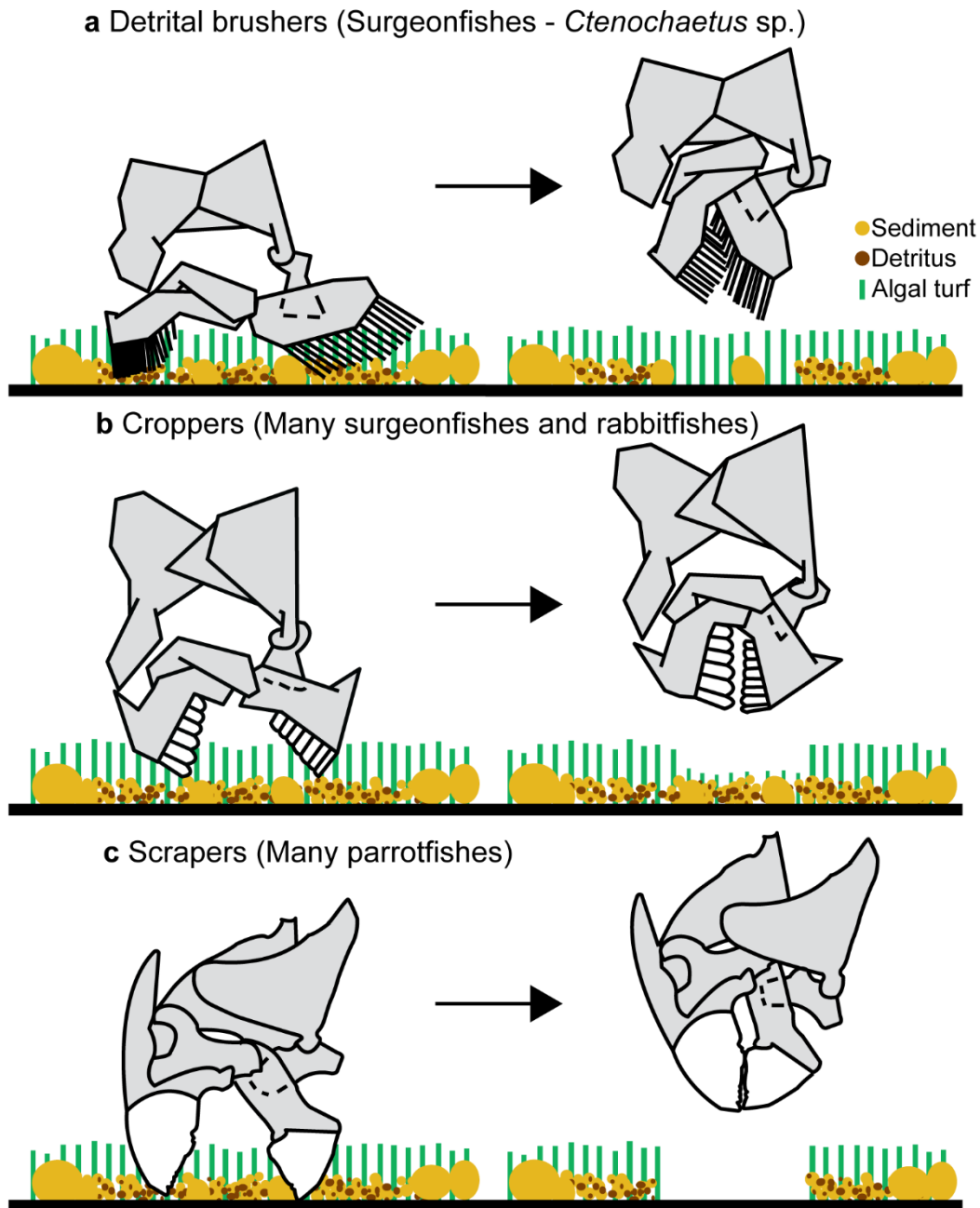
429 There are two primary mechanisms by which algal turf sediments can affect fishes: a)
430 by directly mediating feeding rates and behaviour (Bellwood and Fulton, 2008; Goatley and
431 Bellwood, 2012; Gordon et al., 2016a), and b) by reducing the quality and productivity of
432 nutritional resources in the epilithic algal matrix with the potential for bottom-up effects on
433 fish productivity (Gordon et al., 2016b; Purcell and Bellwood, 2001; Tebbett et al., 2018a).
434 These two mechanisms are discussed in more detail below.

435 *4.3.1 Feeding rates and behaviour*

436 Based on observations, Randall, (1955) suggested that surgeonfish feeding behaviour
437 was mediated by algal turf sediments, as sediments controlled how fishes removed algal
438 material and when sediments were removed by fishes they were often rejected. Initial
439 experimental studies supported these observations, as removal of algal turf sediments on
440 coral reefs led to marked increases in herbivorous fish feeding rates (Bellwood and Fulton,
441 2008; Goatley and Bellwood, 2012). Furthermore, Duran et al. (2019) highlighted that in the
442 Caribbean, surgeonfishes, especially smaller size classes, selectively fed on SPATs compared
443 to LSATs. Interestingly, these results are supported by findings from freshwater systems
444 including the African Rift Lakes and South American streams that found: a) many grazing
445 fishes avoided feeding on algae laden with sediments (Genner et al., 1999), b) feeding rates
446 increased when algal sediments were removed (Rusuwa et al., 2006) and c) size-dependent
447 selectivity for sediment-cleared grazing areas (Power, 1984). Taken together, these studies
448 highlight the pervasive nature of algal turf sediments in controlling herbivorous fish feeding
449 rates and behaviour in aquatic systems.

450 Studies on nominally herbivorous coral reef fishes have now also begun to tease apart
451 the mechanisms underpinning the interaction between fish feeding behaviour and algal turf

452 sediments. This was achieved by exploring the effects of sediment size, source, mass and
453 particulate organic content on the feeding behaviour of morphologically and functionally
454 different fishes (Gordon et al., 2016a; Tebbett et al., 2017d, 2017b). For example, the
455 ‘brushing’ surgeonfish *Ctenochaetus striatus*, must interact closely with algal turf sediments
456 when targeting detritus using its long brush-like teeth (Tebbett et al., 2018c, 2017c), and
457 appears to be highly sensitive to small increases in algal turf sediment mass (as little as 75 g
458 m⁻²) (Tebbett et al., 2017b) (Fig. 6a). By contrast, ‘croppers’ such as the surgeonfish
459 *Acanthurus nigrofuscus*, appear to be more resilient to sediment increases as they can use
460 their multidenticulate teeth to ‘crop’ off the tips of algal filaments protruding through the
461 algal turf sediment layer (Tebbett et al., 2017b) (Fig. 6b). Finally, coarser algal turf sediments
462 deter feeding by the scraping parrotfish *Scarus rivulatus* more than finer sediments (Gordon
463 et al., 2016a). This appears to be a result of their morphology, specifically their beak-like
464 teeth, which mean that scraping parrotfish must remove the entire EAM when feeding on the
465 substratum (Bellwood and Choat, 1990) (Fig. 6c). As such, scraping parrotfishes must either
466 sort and reject, or ingest the algal turf sediments within the EAM. In this case coarser
467 sediments are likely represent a less nutritional resource (fine sediments are likely to contain
468 more organic particulates) and are likely to be more energetically costly to process (Gordon
469 et al., 2016). These distinctions highlight how functionally different fishes interact with algal
470 turf sediments in markedly different ways and offer insights into the mechanisms
471 underpinning the effects of sediments on feeding behaviour. However, ultimately, in all
472 cases, algal turf sediments appear to drive increased algal turf length by either a) reducing
473 feeding rates (Goatley et al., 2016; Gordon et al., 2016a; Tebbett et al., 2017d) or b) limiting
474 feeding to the ‘above-sediment’ portion of algal filaments (Adam et al., 2018; Tebbett et al.,
475 2017b).



476

477 **Figure 6** A schematic diagram showing how three functionally distinct
 478 herbivorous/detritivorous fishes interact with algal turfs, detritus and sediment. a) the lined
 479 bristletooth surgeonfish, *Ctenochaetus striatus*, selectively feeds on detritus (particulates)
 480 removing fine organic and inorganic particulates, b) the brown surgeonfish, *Acanthurus*
 481 *nigrofuscus*, crops algal turfs above the layer of particulates and c) the surf parrotfish, *Scarus*
 482 *rivulatus*, scrapes the substratum removing the entire algal turf, sediment and detritus mixture
 483 (i.e. the complete epilithic algal matrix (EAM) including cyanobacteria, other microbes and

484 microalgae etc). These functional differences may underpin the effect of sediments on fishes.
485 *C. striatus* and *A. nigrofuscus* jaws redrawn from (Purcell and Bellwood, 1993; Tebbett et al.,
486 2017b). It should be noted that this diagram does not necessarily highlight the nutritional
487 resources targeted, or assimilated by these fishes, as biomarker data suggests there are further
488 differences between these fishes after assimilation (see Clements et al., 2017). Our diagram
489 highlights the different components of the EAM removed by fishes when feeding on coral
490 reefs.

491

492 *4.3.2 Nutritional consequences for fishes*

493 In addition to directly mediating the feeding behaviour of fishes, algal turf sediments
494 can impact the ability of nominally herbivorous fishes to extract suitable nutritional resources
495 from the EAM. Indeed, Choat (1991) suggested that sediments trapped in algal turfs could
496 reduce the nutritional return per feeding event. This is because algal turf sediments on coral
497 reefs can directly: a) reduce the productivity of the algal turfs (Tebbett et al., 2018a), b)
498 ‘water-down’ the relative level of organic material within the algal turfs (Gordon et al.,
499 2016a; Purcell and Bellwood, 2001), and/or c) lead to the formation of LSATs which are
500 likely to reduce the abundance of euendolithic cyanobacteria available for exploitation by
501 parrotfishes (Clements et al., 2017; Hutchings et al., 2005). Indeed, a recent study revealed
502 that sediment additions led to a 2000% and 3300% decrease in the potential yield of algal turf
503 biomass and nitrogen to herbivorous fishes, respectively, relative to algal turfs containing
504 ambient or reduced sediment loads (Tebbett et al., 2018a). Intuitively, such decreases in the
505 productivity/nutritional value of the algal turfs could have significant bottom-up effects on
506 the herbivorous fish community through reduced growth and/or altered distribution patterns.

507 Support for bottom-up effects of algal turf sediments on the populations of
508 herbivorous fishes can be gleaned from the freshwater literature (reviewed in Vadeboncoeur
509 and Power, 2017). For example, Munubi et al., (2018) found that sediment mass associated
510 with benthic algae/biofilms was the strongest predictor of among-site variation in the density
511 of a herbivorous cichlid in Lake Tanganyika. Furthermore, Takeuchi et al., (2010) posited
512 that a decrease in the abundance of herbivorous cichlids in Lake Tanganyika over 20 years
513 could be due to increased accumulation of sediments associated with algae/biofilms. While
514 Power, (1984) demonstrated that deposited benthic sediments imposed energetic costs on a
515 South American armoured catfish. Taken together, these studies suggest sediments deposited
516 on the benthos, particularly when associated with algae (i.e. algal turf sediments in the coral
517 reef realm), may impose bottom-up effects on the fishes that interact with these sediments. In
518 terms of coral reefs, it has been repeatedly suggested that the abundance of herbivorous and
519 detritivorous fishes is heavily influenced by bottom-up forces (e.g. Bellwood et al., 2018;
520 Clements et al., 2017; Purcell and Bellwood, 2001 Russ, 2003; Russ et al., 2015), suggesting
521 that algal turf sediments may limit nutritional resources with direct consequences for
522 herbivorous fish populations. Furthermore, as nominally herbivorous fishes can make up a
523 large proportion of artisanal fisheries catches (Edwards et al., 2014; Robinson et al., 2019;
524 Russ et al., 2015) bottom-up effects may manifest themselves as less productive fisheries
525 yields to humanity (Bellwood et al., 2018; Morais and Bellwood, 2019; Tebbett et al., 2018a).

526 *4.4 How do algal turf sediments affect corals?*

527 There are two chief mechanisms by which algal turf sediments can impact corals: a)
528 by reducing coral recruitment (Birrell et al., 2005; Speare et al., 2019) and b) by enhancing
529 the competitive abilities of algal turfs when interacting with corals (reviewed in O'Brien and
530 Scheibling 2018). Each is addressed separately below.

531 *4.4.1 Coral recruitment*

532 Coral recruitment is a critical ecosystem process on coral reefs that facilitates
533 recovery after disturbances (Elmhirst et al., 2009; Hughes et al., 2019; Ritson-Williams et al.,
534 2010). However, corals require suitable surfaces and cues to settle, especially
535 microtopographic refuges (Brandl and Bellwood, 2016; Nozawa, 2012) and crustose coralline
536 algae (Harrington et al., 2004; Ritson-Williams et al., 2010). As such, the suppression of
537 CCA development by algal turf sediments (see section 4.2.2) may suppress key cues.
538 Similarly, as the microbe community on the benthos can influence coral settlement (Sharp et
539 al., 2015), if algal turf sediments influenced the microbiome within algal turfs (Bourne et al.,
540 2016; Meirelles et al., 2018), this may also suppress coral settlement rates.

541 When it comes to direct effects of algal turf sediments most studies have focused on
542 the effects of sediments in isolation on coral recruitment. These studies have repeatedly
543 highlighted that settlement on bare surfaces (e.g. glass, tiles, settlement plates) is heavily
544 impacted by sediments (e.g. Babcock and Smith, 2000; Hodgson, 1990; Moeller et al., 2017;
545 Perez III et al., 2014; Ricardo et al., 2017; but see Traçon et al., 2013). By contrast, studies
546 that have considered the effects of algal turfs in isolation on coral settlement have found more
547 mixed results, revealing either limited changes (Diaz-Pulido et al., 2010; Speare et al., 2019)
548 or significant decreases (Arnold et al., 2010) in settlement depending on the algal community
549 (reviewed in Birrell et al., 2008). Surprisingly, studies considering both algal turfs and
550 sediments together are limited to just three (Birrell et al., 2005; Leong et al., 2018; Speare et
551 al., 2019). In these studies, algal turf sediments led to significant declines in coral settlement
552 on reefs in both the Indo-Pacific (Birrell et al., 2005; Leong et al., 2018) and the Caribbean
553 (Speare et al., 2019). Considering the paucity of studies examining the effects of algal turf
554 sediments on coral settlement, and the clear potential for profound impacts, this research
555 topic offers fertile grounds for further investigation.

556 *4.4.2 Competitive interactions*

557 Algal turf sediments also play a role in coral-algal turf competitive interactions.
558 Coral-algal turf interactions have received a substantial degree of attention on coral reefs (e.g.
559 Gowan et al., 2014; Liao et al., 2019; McCook, 2001; Nugues and Roberts, 2003; Vermeij et
560 al., 2010; Wild et al., 2014). However, the findings are far from clear and appear to be highly
561 context and taxon specific, with results ranging on a spectrum from competitive dominance
562 by corals to competitive dominance by algal turfs (reviewed in McCook et al., 2001; O'Brien
563 and Scheibling 2018). In certain contexts, algal turf sediments appear to enhance the
564 competitive abilities of algal turfs, as they foster the growth and/or increased canopy
565 height of algal turfs (Gowan et al., 2014; Liao et al., 2019) and probably alter the microbial
566 community within algal turfs (Barott and Rohwer, 2012; Brown et al., 2019; Roach et al.,
567 2017). However, in other cases sediment accumulation on corals can lead to partial mortality,
568 with subsequent expansions and development of algal turfs (Nugues and Roberts, 2003). In
569 the latter case, algal turfs are not directly competing with corals but instead are simply
570 occupying new space, and as such, algal turf sediments are not involved in this interaction.
571 Unfortunately, it can be difficult to determine whether algal turf expansion is a result of the
572 former or latter scenario (McCook et al., 2001), with other factors such as hydrodynamics
573 (Gowan et al., 2014) and nutrients (Vermeij et al., 2010) likely to influence the nature of
574 these interactions. Furthermore, studies examining competitive interactions rarely quantify
575 the amount and nature of sediments trapped in the algal turfs (but see Liao et al., 2019).
576 Without specifically investigating the nature of the algal turf sediments, our understanding of
577 their role in competitive interactions, and the mechanistic basis underpinning competition,
578 remains limited.

579

580

581 **5. Algal turf sediments on Anthropocene coral reefs**

582 *5.1. Will algal turf sediments be important on Anthropocene coral reefs?*

583 Yes. Following the global reconfiguring of coral reefs after repetitive bleaching
584 events and other disturbances, algal turf sediments are poised to play an increasingly
585 important role in structuring ecosystem processes such as coral settlement, herbivory, and
586 benthic productivity (Bellwood et al., 2019a; Bruno et al., 2019; Hughes et al., 2018a).
587 Indeed, it is becoming increasingly apparent that many, if not most, coral reefs, will simply
588 emerge as lower-complexity systems covered in algal turfs (Bellwood and Fulton, 2008;
589 Bellwood et al., 2019a; Brown et al., 2017; Jouffray et al., 2015; Smith et al., 2016). Other
590 configurations including an increased abundance of stress-tolerant coral taxa (e.g. *Porites*)
591 (Loya et al., 2001; Marshall and Baird, 2000), weedy fast-recovering coral taxa (e.g.
592 *Acropora*, *Pocillopora*) (Berumen and Pratchett, 2006; Johns et al., 2014; Torda et al., 2018),
593 other sessile invertebrates (Norström et al., 2009; Tebbett et al., 2019b), or fleshy macroalgae
594 (Graham et al., 2006; Hughes, 1994) are also possible in certain circumstances. However,
595 even in such cases, algal turfs are likely to be abundant following disturbances and during
596 regenerative phases. This is because algal turfs can be: a) ‘uncovered’ when coral canopies
597 are lost (Goatley and Bellwood, 2011), b) occupy recently dead coral skeletons rapidly
598 following primary colonisation by cyanobacteria (Arthur et al., 2005; Diaz-Pulido and
599 McCook, 2002), c) are a particularly stress-tolerant functional group of algae (Hay, 1981;
600 Steneck and Dethier, 1994) and d) even appear to benefit physiologically from future climate
601 change conditions (Bender et al., 2015; Johnson et al., 2017; Ober et al., 2016). This
602 combination of traits sets the scene for a rise in algal turf cover on Anthropocene reefs.

603 Algal turf-covered reef configurations may continue to provide key services to
604 humanity, such as fishable biomass production (Bellwood et al., 2018; Morais and Bellwood,
605 2019; Robinson et al., 2019). However, the functions provided by organisms in these

606 systems, and in-turn the services reefs provide to humanity, are heavily dependent on the
607 nature and amount of algal turf sediments (see section 4). Unfortunately, sediment-laden algal
608 turfs are likely to proliferate on algal turf-covered reefs, especially close to shore, as sediment
609 inputs are increasing from coastal development and dredging (Erftemeijer et al., 2012;
610 Wolanski et al., 2009) and increased terrestrial runoff (Bainbridge et al., 2012; McCulloch et
611 al., 2003). For example, even on the highly-regulated GBR, Hughes et al. (2015) noted that
612 “in the past 10 years, more than 25 million cubic meters of dredge spoil from ports has been
613 dumped at sea in the GBR WHA [World Heritage Area]...an amount that roughly equals the
614 total volume of sediment historically delivered from all 35 rivers draining into the GBR each
615 decade, prior to land-clearing”.

616 Algal turf sediments appear likely to underpin the functionality of many
617 Anthropocene coral reefs. Their role is likely to be further increased through the loss of
618 topographic complexity (Alvarez-Filip et al., 2009; Graham et al., 2006), which further
619 promotes sediment trapping in algal turfs (Duran et al., 2018; Tebbett et al., 2019a), as well
620 as through the overexploitation of nominally herbivorous fish communities which play a
621 central role in algal turf sediment dynamics and potentially in the maintenance of SPATs
622 (Goatley and Bellwood, 2010; Krone et al., 2011; McAndrews et al., 2019). As such, algal
623 turf sediments represent a multifaceted stressor that interacts with climate change, overfishing
624 and human development (Bellwood et al., 2018; Tebbett et al., 2018a). The study of algal turf
625 sediments therefore transcends marine/terrestrial boundaries and encompasses extensive
626 social-ecological linkages. Unfortunately, like scraping parrotfish (*sensu* Steneck, 1983b) –
627 we are still just scratching the surface when it comes to understanding algal turf sediments on
628 coral reefs.

629

630

631 *5.2 What do we need to know about algal turf sediments?*

632 Studies assessing the dynamics and ecological ramifications of algal turf sediments
633 are still in their infancy. However, work on the GBR (Goatley and Bellwood, 2012; Gordon
634 et al., 2016b; Purcell, 2000; Tebbett et al., 2018a), Pacific Islands (Clausing et al., 2014;
635 Fong et al., 2018; McAndrews et al., 2019) and Caribbean (Adam et al., 2018; Duran et al.,
636 2019; Speare et al., 2019; Steneck, 1997), suggests that this is a burgeoning research field
637 with clear opportunity for collaborations to enhance our understanding of algal turf sediments
638 across biogeographic boundaries. Furthermore, advances are being made in understanding
639 how algal turf sediments on coral reefs affect key ecosystem process (e.g. Duran et al., 2019;
640 Speare et al., 2019), are mediated by fishes (e.g. Fong et al., 2018; McAndrews et al., 2019),
641 and accumulate in algal turfs (e.g. Latrille et al., 2019; Tebbett et al., 2019a). Yet, while
642 considerable progress is being made, we still lack the answers to many basic questions.

643 In many coral reef regions we simply do not know how much sediment is in the algal
644 turfs, or how these algal turf sediments are linked to suspended sediment levels and
645 sedimentation. Furthermore, monitoring of coral reef algal turf sediment levels before, during
646 and after exceptional sedimentation events, such as dredging activities, would provide
647 valuable insights into how such events impact the deposition and accumulation of algal turf
648 sediments. Indeed, there is remarkably little long-term data on sedimentation rates and algal
649 turf sediment loads in coral reef systems. For example, examination of temporal dynamics in
650 algal turf sediments loads (>6 months) is limited to just two studies (Goatley et al., 2016;
651 Gordon et al., 2016) from a single island on the GBR. However, while it is often assumed
652 sediment loads are increasing on other reefs globally, as a result of increasing inputs (Burke
653 et al., 2011), there is little quantitative evidence to support this.

654 To achieve a comprehensive understanding of algal turf sediment dynamics this will
655 require linking research on algal turf sediments with the vast and growing literature
656 surrounding general sediment dynamics on coral reefs. For example, clear progress has been
657 made in terms of understanding ridge-to-reef sediment transport (e.g. Bainbridge et al., 2018;
658 Bartley et al., 2014; Comeros-Raynal et al., 2019; Fabricius et al., 2014), dredge plume
659 dynamics and deposition (e.g. Fisher et al., 2015; Jones et al., 2019), within reef sediment
660 transport mechanisms (e.g. Ogston et al., 2004; Orpin and Ridd, 2012; Pomeroy et al., 2017),
661 and links between turbidity and sediment deposition (e.g. Whinney et al., 2017). However,
662 apart from the study by Latrille et al., (2019) which began to place algal turf sediments into
663 this context, our understanding of the links between algal turf sediments and other sediment
664 dynamics remains exceedingly limited. Addressing these unknown links represents a critical
665 knowledge gap on ecological time scales.

666 Furthermore, on geological time scales, there has been significant progress in our
667 understanding of reef growth and development in sediment-rich habitats (e.g. Browne et al.,
668 2013; Perry et al., 2012; Roff et al., 2015; Ryan et al., 2018). This is becoming increasingly
669 topical as sea-level rise becomes an inevitability, along with the associated notion of
670 ‘drowned reefs’ (Perry et al., 2018; van Woesik et al., 2015). However, while Bellwood and
671 Fulton (2008) posited that algal turf sediments may be a key factor underpinning reef
672 drowning, algal turf sediments have received little attention within this context. As such, a
673 multidisciplinary approach linking algal turf sediments with other reef processes and
674 sediment dynamics may offer insights into the survival of coral reefs in both ecological and
675 geological time scales.

676 In terms of furthering our understanding of the direct ecological effects of algal turf
677 sediments there are several key research gaps across multiple spatial scales. For example, at
678 small spatial scales, further examination of the interaction between algal turf sediments,

679 'crevice cleaning' fishes, and coral recruitment in microtopographic refuges is particularly
680 important for understanding coral recruitment dynamics and potential recovery of reefs
681 following disturbances (Brandl and Bellwood, 2016; Ricardo et al., 2017). In conjunction
682 with this line of research, furthering our understanding of the microbiome within algal turfs is
683 necessary. As stressors such as overfishing and nutrient enrichment may affect the algal turf
684 microbiome (e.g. Meirelles et al., 2018; Zaneveld et al., 2016), with potential effects on coral
685 settlement (Bourne et al., 2016; Meirelles et al., 2018), examining the influence of algal turf
686 sediments on these microbes could offer interesting insights into coral settlement dynamics.

687 Also, at small spatial scales, there have been calls for a more nuanced understanding
688 of nutritional resources within the EAM, especially the role of cyanobacteria (Clements et al.,
689 2017). Cyanobacteria are important early colonisers of dead coral reef substrata (Diaz-Pulido
690 and McCook, 2002) and are likely to play an important role in accumulating and binding
691 algal turf sediments (Stal, 2003). However, our understanding of the relationships between
692 algal turf sediments and both epilithic and euendolithic cyanobacteria, is limited. These
693 relationships warrant further investigation, especially considering that these cyanobacteria
694 appear to be a key nutritional resource targeted by parrotfishes (Clements et al., 2017).
695 Furthermore, as algal turf communities are composed of diverse algal taxa and morphological
696 forms (Harris et al., 2015; Scott and Russ 1987), different algal turf communities are likely
697 to: a) be influenced by algal turf sediments differently and/or b) trap and retain algal turf
698 sediments at different rates. While there has been some attention paid to these factors in the
699 subtropical/temperate rocky reef literature (Airoldi et al., 1995; Stewart, 1983), our
700 understanding of the relationships between algal turf taxonomy/form/composition and algal
701 turf sediments is currently limited on coral reefs. Resolving these relationships with more
702 precision will enhance our ability to predict the effects of algal turf sediments on algal turf
703 communities, and the organisms that associate with, or use, algal turfs.

704 At larger reef-wide scales, understanding how SPATs are maintained is vital. For
705 example, a comprehensive understanding of algal turf sediment removal, transport and
706 maintenance by fishes, and the relative importance of different taxa is necessary (Bellwood,
707 1995; Goatley and Bellwood, 2010; Krone et al., 2011). At even larger regional spatial scales,
708 understanding how to maintain key services such as fisheries productivity from algal turf-
709 covered reefs is key. This is particularly important in ‘telecoupled’ (Liu et al., 2016) reef-land
710 systems, where land-use and overfishing practices are linked (see Comeros-Raynal et al.,
711 2019) which could potentially facilitate transitions to LSAT states in a synergistic nature.
712 This represents a complex socio-ecological challenge, transcending ecosystem boundaries
713 and requiring a multidisciplinary approach.

714 Clearly, there is a broad swath of questions to address in relation to algal turf
715 sediments on coral reefs. These range from basic descriptive studies to more complex,
716 multifaceted, socio-ecological investigations. Progress will require forward-looking studies
717 that identify key functional interactions in algal turf-covered coral reef systems. This
718 endeavour will help us to embrace change and address the major overarching goal of
719 managing reefs in a manner that sustains the key functions and services coral reefs provide
720 (Hughes et al., 2017).

721

722 **6. Conclusion**

723 In many cases coral reef ecosystems now exist as highly-altered configurations, and in
724 this context the importance of once-critical ecosystem functions and functional groups are
725 changing (Bellwood et al., 2019b; Hughes et al., 2017). Specifically, the importance of algal
726 turf sediments in mediating the functionality of these altered ecosystems is set to increase.
727 However, despite evidence highlighting the importance of these sediments, our understanding

728 remains limited. Herein, we have endeavoured to provide a brief overview of our knowledge
729 to-date and hope that this will act as a ‘spring-board’ to encourage further scientific
730 investigation within this field. On Anthropocene, low-coral cover reefs, there will be no
731 shortage of algal turfs and the sediments they contain.

732

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739 **Competing Interests Statement**

740 On behalf of all authors, the corresponding author states that there is no competing interests.

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