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3   **Census estimates of algal and epiphytic carbonate production highlight tropical seagrass**

4   **meadows as sediment production hotspots**

5

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15   **Abstract**

16   Tropical shelf, platform and reef-lagoon systems are dominated by calcium carbonate ($CaCO_3$)

17   sediments. However, data on habitat-specific $CaCO_3$ sediment production rates by different sediment

18   producing taxa are sparse, limiting understanding of where and in what form $CaCO_3$ sediment is

19   produced, and how overall sediment budgets are influenced by habitat type and scale. Using novel

20   census methodologies, based primarily on measures of plant biovolumes and carbonate content, we

21   assessed habitat-scale production by two ubiquitous biogenic $CaCO_3$ sediment producers, calcareous

22   green algae and seagrass epiphytes, across southern Eleuthera Bank, Bahamas (area ~140 km^2). Data

23   from species-specific plant disaggregation experiments and from X-ray diffraction (XRD) analysis of

24   calcified plants also allowed us to resolve questions about the size fractions and mineralogies of the

25   carbonates produced. Production rates varied significantly among habitats (range: 1.8–237.3 g $CaCO_3$

26   m^{-2} yr^{-1}), collectively totalling ~0.98 M kg annually across the study area. Outputs comprise similar

27   amounts of aragonite and high Mg-calcite, with ~54% of the $CaCO_3$ produced being contributed as

28   mud-grade (<63 μm) sediment. Our analysis also reveals that habitat type and extent - especially of

29   medium and high density seagrass beds - strongly influence the amounts and types of carbonate

30   sediment generated. Dense seagrass beds were identified as the dominant per unit area production

31   sites, contributing ~17% of total $CaCO_3$ despite covering only 0.5% of the study area. These findings

32   have direct relevance for quantifying present-day sediment budgets and for predicting changes in

33   sediment generation at the system scale in responses to modified habitat extent and productivity.

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35

36   **Keywords**

37   Carbonate budgets, carbonate sediments, calcareous algae, *Halimeda*, seagrass, biovolumes

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40   **Introduction**

41   Calcium carbonate ($CaCO_3$) dominated tropical and sub-tropical coral reef, lagoon, and shallow shelf

42   and platform systems cover an area estimated at >11 M km^2 (Milliman and Droxler, 1996; Green et

43   al., 2000). These environments are not only focal points of marine $CaCO_3$ accumulation, but they also

44   provide sediments to sustain tropical shorelines and islands (Perry et al., 2015) and export material to

45   adjacent deeper-water deposits (Berelson et al., 2007). In both shallow and deep-water settings

46   significant $CaCO_3$ dissolution also occurs (Walters et al., 1993; Berelson et al., 2007; Brock et al.,

47   2006; Eyre et al., 2018), and thus the production, accumulation and cycling of shallow marine $CaCO_3$

48   sediment is a critical element of the marine inorganic carbon cycle. A defining characteristic of these

49   shallow carbonate systems is that a high proportion of the accumulating sediment derives from *in-situ*

50   biogenic sources. Direct contributions can derive post-mortem from fauna such as molluscs and

51   foraminifera (Bosence, 1989), and from flora such as the calcareous green algae, which disaggregate

52   to release carbonate after death (Lowenstam, 1955). Many seagrass species also contribute $CaCO_3$ to

53   the sediment reservoir from the post-mortem release of calcareous epiphytes that colonise the seagrass

54   blades (Corlett and Jones, 2007) and potentially from directly facilitated carbonate secretions

55   (Enriquez and Schubert, 2014). Significant quantities of sediment can also be generated indirectly by

56   the grazing activities of species of parrotfish and urchins, which excrete carbonate particles after

57   ingestion (Bellwood, 1996), and recent work has shown that all bony marine fish (teleosts) excrete

58   fine grained carbonates with a diverse range of morphologies and mineralogies (Perry et al., 2011;

59   Salter et al., 2012; Salter et al., 2018). In addition, several locally important, non-skeletally-derived,

60   sources of fine-grained carbonate have been identified. These nclude the generation of carbonate mud

61   via "whiting" events (Robbins et al., 1997), and the precipitation of carbonate within oolitic sands

62   (Newell et al., 1960). Complex cycles of carbonate precipitation and dissolution may also occur

63   within permeable reef and platform sediments (Eyre et al., 2018) and may thus also influence net

64   carbonate production rates (Brock et al., 2006).

65

66   Whilst very high localised rates of gross $CaCO_3$ sediment production have been reported from some

67   sources (e.g., up to 1.4 kg $CaCO_3$ m^{-2} yr^{-1} for *Halimeda* and 2.8 kg $CaCO_3$ m^{-2} yr^{-1} for seagrass

68   epiphytes; Patriquin, 1972; Payri, 1988), such rates - being a function of species abundance and

69   productivity - are inherently highly variable. Thus habitat heterogeneity and associated variations in

70   plant/species density and productivity will exert a major influence on the rates and types (and

71   consequently the mineralogies and size fractions) of sediment generated, such that assumptions about

72   the predominant role of one producer over another in driving $CaCO_3$ sediment production are too

73   simplistic. Such variation is a non-trivial issue because the type of sediment generated influences

74   sediment preservation and accumulation due to differential susceptibility to post-depositional

75   taphonomic processes, dissolution and transport (Braithwaite, 1973; Walters and Morse, 1984; Perry,

76   1996; 1998; 2000; Ford and Kench, 2012; Eyre et al., 2018). However, whilst a number of studies

77   have estimated sediment production rates for individual species, including foraminifera (Doo et al.,

78   2012), calcareous green algae (*Halimeda*; Multer, 1988), and epiphytes on seagrass (Nelsen and

79   Ginsburg, 1986), and which add detail to wider system scale estimates of net community-scale

80   carbonate production based on up-scaling of mesocosm and hydrochemical studies (e.g., see Atkinson

81   and Grigg, 1984; Brock et al., 2006; Courtney et al., 2016), there have been few attempts to use

82   detailed in-situ census data to quantify sediment production at the habitat-scale (but see Bosence et

83   al., 1985; Perry et al., 2017). Furthermore, and to our knowledge, there have been no attempts to date

84   to quantify rates, grain sizes and mineralogies of $CaCO_3$ sediment being generated in different habitats

85   across carbonate systems. These gaps in knowledge are significant not only because environments

86   dominated by $CaCO_3$ sediments are spatially extensive across the tropics and sub-tropics, but also

87   because: i) the assumption that different habitats produce and preserve distinct sedimentary signatures

88   represents the fundamental basis for interpreting palaeoenvironmental facies (Flugel, 2004); and ii)

89   an understanding of variation in production at system scales can support an applied understanding of

90   sediment supply to proximal beaches and shorelines.

91

92   Here we report a methodology designed to underpin habitat-scale estimates of $CaCO_3$ sediment

93   production that resolve for sediment grain size and mineralogy. This method is based on empirical

94   data collected for epiphytic communities of the bladed seagrass *Thalassia testudinum*, as well as for

95   seven species of calcareous green algae: *Halimeda incrassata*, *Pencillus capitatus*, *Penicillus*

96   *dumetosus*, *Rhipocephalus phoenix*, *Udotea flabellum*, *Udotea cyathiformis* and *Acetabularia*

97   *calyculus*. These species are ubiquitous across the Caribbean, with closely related species also

98   common across most tropical and sub-tropical shallow marine carbonate systems globally. We then

99   applied this methodology across a range of shallow-water habitats within the southern area of

100   Eleuthera Bank, The Bahamas to determine rates of sediment production (g $CaCO_3$ m^{-2} yr^{-1})

101   associated with calcareous green algae and seagrass epiphytes within each habitat. For most green

102   algal species production estimates were based on a non-destructive census method adapted from

103   methods previously used to estimate sponge and gorgonian biovolumes (Santavy et al., 2013), and as

104   previously tested on *Halimeda* species in the central Indian Ocean (Perry et al., 2016). Alongside

105   these approaches, we used established methodologies (Nelsen and Ginsburg, 1986) to assess epiphytic

106   carbonate production associated with the seagrass *T. testudinum*. The sediment size-fractions to which

107   the different species contribute post-mortem were determined from plant (or for *T. testudinum*

108   from epiphyte) disaggregation experiments following the methods used by Neumann and Land (1975)

109   and Perry et al. (2016). X-ray diffraction (XRD) was used to quantify carbonate mineralogies

110   produced by each species, which are described as the proportions of aragonite, high Mg-calcite

111   (HMC; >4% mol% $MgCO_3$) and low Mg-calcite (LMC; 0-4 mol% $MgCO_3$). In combination with

112   measures of $CaCO_3$ production by each algal type or from epiphytes per habitat and measures of the

113   extent of the habitats, the total amounts of gravel, sand and mud grade $CaCO_3$ and the volumes of

114   different mineralogical sediment fractions could be estimated for the various contributors.

115

116   **MATERIAL AND METHODS**

117   **Study site and habitats**

118   Sampling and surveying were undertaken at sites across the shallow water environments within the

119   southern section of Eleuthera Bank, Eleuthera Island, The Bahamas (24°50' N, 76°20' W; Fig. 1). The

120   total extent of this survey area is 140.5 km^2. Eleuthera Bank, located in the lee of the island, is up to

121   ~8 m deep along the seaward margin that borders the deep-water Exuma Sound, but it is mostly <3-4

122   m deep and influenced by strong diurnal tidal currents that reach up to 0.5 m s^{-1} (Dravis, 1979;

123   Harborne et al., 2017). The platform itself comprises a range of sub-tidal and intertidal habitats, and

124   whilst there is inevitably some gradation between habitat boundaries, the following major habitat

125   types were delineated: mangrove fringed tidal creeks and embayments; hardgrounds sparsely

126   colonised by green algae, sponges and corals; large expanses of patchily bioturbated sands colonised

127   by sparse green algae and seagrass (a mix of *T. testudinum* and, less commonly, *Syringodium*

128   *filiforme*); and beds of *T. testudinum* seagrass. Seagrass beds were further differentiated based on

129   average blade densities: sparse (mean <200 blades/m^2); medium (mean 200-600 blades/m^2), and dense

130   (mean >600 blades/m^2). Numerous patch reefs also occur throughout the bay, but they occur as

131   discrete build-ups surrounded by sands and/or seagrass beds and were not included in our censuses.

132   Along the northern section of the survey area, numerous, tidally-emergent shoals of oolitic sand

133   occur. These shoals are largely devoid of algae and seagrass and thus although they are an important

134   areas of non-biogenic $CaCO_3$ precipitation (Newell et al., 1960), no survey work was undertaken on

135   these. The innermost areas of Eleuthera Bank (known as Rock Sound; Fig. 1) are characterised by

136   fine-grained, heavily bioturbated sediments which are also essentially devoid of seagrass and algae,

137   and no detailed surveys were undertaken in this area.

138

139   The area of each habitat was determined using a habitat map derived from QuickBird ortho-ready

140   imagery, extensive ground-truthing, and standard remote sensing analytical techniques (Green et al.,

141   2000). Land and deepwater areas were masked before pixels of marine habitat were assigned to

142   habitat classes using unsupervised classification based on ground-truthing information, and any

143   apparent errors were corrected with contextual decision rules. Some habitats (particularly 'sands and

144   sparse algae' and 'sparse seagrass beds') could not be distinguished reliably from the imagery, despite

145   being distinguishable in situ. Therefore, they were generally mapped as a combined habitat, but

146   examination of ground-truthing data indicated that ~50% of ground-truthing points in this combined

147   habitat could be assigned to either class. Consequently, areal extents were calculated for each specific

148   habitat type as 50% of the area of the combined habitat. Narrow inter-tidal mangrove habitats can be

149   difficult to map accurately using spectral signals, so here they were delineated by eye from the

150   imagery. Resultant measured areas of each of these habitats were: mangrove fringed creeks and

151   embayments 0.07 km^2; hardgrounds 11.26 km^2; sands and sparse algae 78.94 km^2; sparse seagrass

152   beds 43.73 km^2; medium seagrass beds 1.45 km^2; dense seagrass beds 0.70 km^2; patch reefs 0.12 km^2;

153   oolitic sand shoals 1.69 km^2; and bioturbated muds 2.54 km^2. Our resultant sediment production

154   calculations necessarily assume that the extent of these habitats is relatively fixed over the annual

155   timescale in question, but acknowledge that over multi-annual to decadal timescales habitat extent

156   may vary slightly with resultant impacts on sediment production rates.

157

158   **Calculating algal and seagrass epiphyte CaCO$_3$ production**

159   To estimate rates of carbonate production (g CaCO$_3$ m^{-2} yr^{-1}) by six of the seven calcareous green

160   algal species present (the species *A. calyculus* was treated differently as described below) we first

161   established an empirical relationship between plant volume (cm^3) and average plant carbonate content

162   (g CaCO$_3$) based on collections of replicate specimens of *H. incrassata* (n = 142), *P. capitatus* (n =

163   57), *P. dumetosus* (n = 84), *R. phoenix* (n = 92), *U. flabellum* (n = 74) and *U. cyathiformis* (n = 58)

164   across the full size range observed within the study area. This approach allows plant biovolumes to be

165   calculated from measures taken in the field, and it is comparable to approaches recently used to

166   quantify biovolumes of corals (Naumann et al., 2009), and surface areas of sponges and gorgonians

167   (Santavy et al., 2013). For both species of *Penicillus* (*P. dumetosus* and *P. capitatus*) and for *U.*

168   *cyathiformis* the growth morphology and resultant volumetric space was defined by the sum of the

169   volume (V) of an inverted elliptical cone (for the head) and a cylinder (for the stem) (Fig. 2A), and

170   which can be determined as:

171    $V = (\frac{1}{3} \Pi a\ b\ h) + (\Pi\ r^2\ s)$ (1)

172   Where, a = the radius of the minor axis (i.e., of the minimum head width), b = the radius of the major

173   axis (i.e., of the maximum head width), h = the height of the head, s = height of the stem, and r = the

174   radius of the stem.

175

176   For *U. flabellum*, plant volumetric space was defined by the sum of the volume of a triangular prism

177   (for the head) and a cylinder for the stem (Fig. 2D), and which can be determined as:

178    $V = (((h\ x\ d1) * 0.5) * d2) + (\Pi\ r^2\ s)$ (2)

179   Where, h = the height of the head, s = height of the stem, d1 = the maximum width of the plant head,

180   d2 = is fixed at 0.5 mm to represent the thickness of the head, and r = the radius of the stem.

181

182   For *R. phoenix*, plant volume was defined as the sum of the volume of an ellipsoid (head) and cylinder

183   (stem) (Fig. 2B), and which can be determined as:

184    $V = \Pi/6 (*d1 *d2* h) + (\Pi\ r^2\ s)$ (3)

185   Where, h = the height of the head, s = height of the stem, d1 = the maximum width of the plant head,

186   and d2 = the minimum width of the plant head.

187

188   For *H. incrassata*, which comprises multiple calcified segments, we defined growth morphology and

189   resultant volumetric space by the volume of an inverted elliptical cone (Fig. 2C), which can be

190   determined as:

191    $V = \frac{1}{3} \Pi a\ b\ h$ (4)

192   Where, a = the radius of the minor axis (i.e., of the minimum plant width), b = the radius of the major

193   axis (i.e., of the maximum plant width), and h = the height of the plant.

194

195   To determine the relationship between volume and carbonate content (g $CaCO_3$/plant), we used two

196   different approaches depending on species. For specimens of *P. capitatus*, *P. dumetosus*, *R. phoenix*,

197   *U. flabellum* and *U. cyathiformis* we equated the total weight of carbonate (g) in each specimen to the

198   weight lost after treatment in acid. All plants were first soaked in two separate distilled water

199   treatments to remove salts and checked for epiphytic encrustations (which were removed with a

200   scalpel). Plants were then oven dried (40°C for 24 hours), weighed, treated in 2M HCl until no further

201   carbonate reaction was visible, and left in the solution for a further two hours. The solution was then

202   decanted, and the remnant organic fibres transferred to pre-weighed filters and rinsed with distilled

203   water to remove any remaining salts. Filtered samples were then re-dried (40°C for 24 hours),

204   reweighed, and carbonate content determined as the net weight loss. For *H. incrassata,* we used a

205   different approach based on that proposed by Perry et al. (2016). For this species, we counted the total

206   number of segments in each plant to establish a relationship between plant volumetric space and the

207   number of segments. To then determine the average carbonate content (g $CaCO_3$) per plant segment,

208   we collected replicate branches (n= 25) that comprised multiple (n = 15-20) segments of varying

209   size/age so as to determine an average content for whole plants. Samples were cleaned, washed and

210   acid treated as described above to determine carbonate content, which was then averaged as a function

211   of the number of segments per branch. Average segment carbonate content was (mean ± SD) 0.0016 ±

212   0.0009 g. Resultant volume: carbonate content relationships are shown in Fig. 3, and these were used

213   to determine plant carbonate content from plant dimensions measured in-situ in our surveys (see

214   below).

215

216   The very small size of the other calcifying algal species common in some habitats on Eleuthera Bank,

217   *A. calyculus*, makes *in-situ* dimensional measurements for this species problematic, so we instead

218   determined an average carbonate content per plant. Based on a similar acid digest procedure to that

219   described above, we determined the average weight of carbonate per plant to be (mean ± SD) 0.0135

220   ± 0.0095 g (n = 60). *T. testudinum* contributes to carbonate sediment production indirectly through the

221   post-mortem release of lightly calcified epiphytes that colonise the seagrass blades (coralline algae,

222   foraminifera, serpulids; Corlett and Jones, 2007). Plant and blade density are important controls on

223   production rates (Nelsen and Ginsburg, 1986; Perry and Beavington-Penney, 2005) and we thus

224   sampled individual blades from habitats with different average blade densities (sparse, medium, dense

225 – see above) to determine the average weight of epiphytic carbonate per blade. This was determined

226 using the weight loss after acidification method (as above) and as previously used to estimate seagrass

227 epiphyte production (Nelsen and Ginsburg, 1986; Bosence, 1989) based on analysis of replicate (n =

228 20) mature blade samples (defined as blades with distinct browning of the tips; Nelsen and Ginsburg,

229 1986). In order to determine natural weight loss of blades during acid treatment, 10 unencrusted

230 seagrass blades were collected from each habitat and treated in the same way as the encrusted blades.

231 Epiphytic calcium carbonate per blade was then determined as follows:

232 Epibiont calcium carbonate/blade (g $CaCO_3$) = A – (B + (A * C))   (5)

233 where; A = weight of the encrusted dry blades, B = weight of the acid treated blades, C = proportion

234 of weight loss from unencrusted blades treated with acid.

235

236 On this basis, average carbonate content/blade was determined as (mean ± SD) 0.018 ± 0.005 g

237 (sparse seagrass beds), 0.023 ± 0.010 g (medium seagrass beds), and 0.053 ± 0.034 g (dense seagrass

238 beds).

239

240 To determine growth rates for each green algal species, we measured the increase in plant biomass (g

241 dry weight) and, for *H. incrassata*, we measured the number of new segments produced by each

242 species over time with the widely used Alizarin Red staining method (Multer, 1988; Friele and Hillis,

243 1997; Vroom et al., 2003). Staining experiments (*H. incrassata* n = 157, *P. capitatus* n = 25, *P.*

244 *dumetosus* n = 73, *R. phoenix* n = 24, *U. flabellum* n = 28 and *U. cyathiformis* n = 36) were conducted

245 in both winter (November) 2016 and summer (June) 2017 to factor as far as possible for any seasonal

246 variability. The variable sample sizes reflect the different plant densities in the areas of study. Plant

247 staining was undertaken by enclosing an area of seafloor under a clear plastic container (28 litre

248 internal volume) fitted with a sealable plastic pipe into which Alizarin Red stain (10 ml per treatment)

249 could be injected with a large volume syringe (Freile, 2004). Staining experiments were undertaken in

250 a range of shallow (2-4 m depth) habitats in the vicinity of, and just offshore from, Cape Eleuthera

251 Institute. Each box was weighted down and the edges buried in the sediment to a depth of several cm

252 to ensure minimal leakage of stain. Each box was re-checked after ~6 hours and additional stain added

253   as necessary. Boxes were removed after ~18 hours, the edges of each plot marked with stakes and

254   plants were left undisturbed for periods of 10-12 days after which selective harvesting (of target

255   species and sizes) was undertaken.

256

257   Post-harvesting, each plant was individually bagged and returned to the laboratory. Plants were rinsed

258   in sequential distilled water washes to remove salts, and then left to soak in a dilute commercial

259   bleach solution to remove plant chlorophyll. This allows the clear delineation of areas of older

260   (stained) and new growth (see Supplementary Figure S1. Areas of new growth where trimmed with a

261   scalpel, the new and old portions were dried and weighed, and growth rate was determined as the ratio

262   of new to old material as a function of growing period (after Multer, 1988). For *H. incrassata*, growth

263   rates were determined in the same way but were based on the number of new versus old segments.

264   Turnover rates were then calculated as function of the total time taken for plants to renew their

265   standing stock and scaled to an annual rate based on the methods of Multer (1988), Friele and Hillis

266   (1997) and Vroom et al. (2003). Turnover rates were not calcuated for *A. calyculus* or *T. testudinum* in

267   this study. In the absence of published data for *A. calyculus*, we used a turnover rate (7.7 crops/year)

268   based on the average for all other green algal species measured in this study. For *T. testudinum* we

269   used the average turnover rate (5.9 crops per year) for this species from published studies conducted

270   in the Caribbean (Patriquin, 1972; Nelsen and Ginsburg, 1986; Frankovich and Zieman, 1995).

271

272   **Determining calcareous algal and seagrass densities**

273   To determine the density and size of calcareous algal species and the density of seagrass in each

274   habitat type colonised by algae and/or seagrass across Eleuthera Bank, surveys were conducted in

275   winter (November) 2016. Water temperatures are relatively low at this time of year (mean 25 to 27°C;

276   Salter et al. 2012), and plant turnover rates a little lower compared to the summer (see below). Thus

277   the data generated are considered to provide a conservative estimate of annual carbonate production

278   rates. Within each habitat, two separate survey areas were established, and data were collected using

279   0.5 x 0.5 m quadrats laid in a checkerboard arrangement along multiple (n = 16) 10 m transects.

280   Identities and relevant dimensions needed to calculate volumes (height, widths, etc. for heads, stems

281   and other relevant sections of plants; Fig. 2) were recorded for each plant present. Additional

282   plant/seagrass blade density data (but not size measurements) were made from the same survey areas

283   in summer (June) 2017 to compare plant/seagrass blade densities between warmer and cooler periods

284   of the year.

285

286   To then estimate total carbonate sediment production (CaCO$_3$ production (g) /plant/yr) by each green

287   algal species and by seagrass epiphytes (using data from the Nov 2016 surveys) the following

288   calculations were made. For each *H. incrassata* the volume: segment content relationship (Fig. 3) was

289   used to estimate the total number of segments in each plant from the in-field measured plant

290   dimensions, and then multiplied by the average CaCO$_3$ content of each segment (0.0016g - see above)

291   and the average plant turnover (crops per year) rate. For specimens of *P. capitatus*, *P. dumetosus*, *R.*

292   *phoenix*, *U. flabellum* and *U. cyathiformis*, the volume: carbonate content relationships (Fig. 3) were

293   used to estimate plant carbonate content from dimensions measured in the field, and again multiplied

294   by the average plant turnover (crops per year) rate for each species. The same approach was used for

295   *A. calyculus* except that the volume : carbonate content relationship approach was substituted for an

296   average weight carbonate per plant. To determine a rate of epiphytic carbonate production from *T.*

297   *testudinum* the total number of blades per quadrat were counted and multiplied by the average weight

298   of epiphytic carbonate per blade (as determined for sparse, medium or dense seagrass beds – see

299   above) and the average plant turnover (crops per year) rate (following the method of Nelsen &

300   Ginsburg, 1986). A total estimated carbonate production rate (g CaCO$_3$ m^{-2} yr^{-1}) by each species per

301   transect (n = 16 per habitat) was then calculated, and from this a habitat mean rate ($\pm$ SD) per species

302   determined (Supplementary Table S1). An overall habitat mean production rate was then calculated as

303   the sum of production from all species, with overall error terms (σ) calculated as:

304    $\sigma = \sqrt{\delta a^2 + \delta b^2 + \delta c^2 \ldots + \delta z^2}$ (6)

305   Where a, b, c etc = species or transect level production rates

306

307   These data were then used to calculate total habitat scale production as a function of habitat extent,

308   and from this a total platform-scale production estimate (kg per habitat/year), with an error term

309 calculated using Eq 6 above. Mean results are reported as means ± standard deviation throughout the

310 manuscript.

311

312

313

314 **Determining calcareous algal and epiphyte breakdown products**

315 To determine the sediment size-fractions to which the different green algal species contribute post-

316 mortem, we followed the same experimental approach to that used by Neumann and Land (1975) in a

317 study of Caribbean green algal breakdown, and as recently used by Perry et al. (2016). We collected

318 nine mature and fully calcified specimens of each algal species and placed three specimens in each of

319 three elongate (25 cm x 10 cm x 6 cm) lidded plastic vessels containing a 50:50 solution of distilled

320 water and 5% commercial bleach. The experimental vessels were then placed on a see-saw rocker

321 plate (Stuart Model SSL4) set to operate at a tilt rate of 28 oscillations/min, which was determined as

322 sufficient to enable slow, gentle continuous sample agitation. Each experiment was left to run for 21

323 days. Samples were then wet sieved through a sieve stack (sieve sizes of 4 mm, 2 mm, 1 mm, 500 µm,

324 250 µm, 125 µm, 63 µm, and 31 µm to conform to the standard grain size divisions under the Udden-

325 Wentworth scheme). Each retained fraction was filtered, dried and weighed to determine size fraction

326 contributions (Supplementary Table S2). Past studies have assumed that all epiphytic carbonate

327 derived from *T. testudinum* blades is either released as, or rapidly disaggregates post-release to, mud-

328 grade (<63µm) carbonate (Land, 1970; Nelsen and Ginsburg, 1986). Whilst this may seem a

329 reasonable assumption given the lightly calcified coralline algal crusts and small sizes of serpulid

330 worm cases and encrusting foraminifera that colonize seagrass blades (Corlett and Jones, 2007), we

331 tested this by carefully scraping the epiphytic carbonate from rinsed and dried blades of *T. testudinum*

332 (n = 20) to generate one bulk sample that was then analysed using the same sieving protocol as above.

333

334 **Determining algal and epiphyte carbonate mineralogies**

335 Bulk carbonate mineralogies for each algal species, seagrass epiphytes, and surface sediments from

336 each habitat were determined using XRD (Bruker D8 Advance). Dry samples were ground to a

337 powder in an agate mortar and mixed with a powdered quartz standard before being mounted on glass

338 slides. Diffraction patterns were obtained using Cu Kα radiation (1.5418 nm) generated at 40 kV and

339 40 mA, initially employing coarse scan parameters (step size 0.04 °2Θ; step time 0.4 s; scan interval

340 16–60 °2Θ) to confirm that aragonite, low-Mg calcite, and high-Mg calcite were the only

341 mineralogies present. Subsequent high resolution scans (step size 0.02 °2Θ; step time 1.0 s; scan

342 interval 23–32 °2Θ) were performed to facilitate estimation of: i) the $MgCO_3$ content(s) of calcite,

343 based on the position(s) of the calcite d_{104} peak(s) (after Goldsmith et al., 1961); ii) the relative

344 abundances (wt%) of calcite and aragonite, based on the integrals of calcite d_{104} and aragonite d_{111} and

345 d_{021} peaks (after Davies and Hooper, 1963); and iii) the relative abundances (wt%) of component

346 calcite phases (with different $MgCO_3$ contents) assuming that the ratio of the integrals of their

347 respective d_{104} peak integrals is approximately equal to the ratio of their abundances (Sepulcre et al.,

348 2009). To determine these parameters, a peak-fitting procedure was performed using PeakFit software

349 (v4.12) to decompose overlapping peaks (which occur when multiple calcite phases with differing

350 $MgCO_3$ contents are present) and fit a computer-generated line profile to the observed data. Resulting

351 peak positions were corrected for goniometer misalignment and/or specimen-dependant errors by

352 reference to known fixed peak positions of the internal quartz standard. Although this approach is

353 widely used to estimate $MgCO_3$ contents, we qualify our results with the caveat that for biogenic

354 carbonates this approach can carry significant uncertainties ($\geq\pm$ 5 mol% $MgCO_3$; Bischoff et al.,

355 1983). Consequently, calcites with estimated $MgCO_3$ contents in the range 0-9 mol% can only

356 tentatively be categorised as either HMC or LMC, although in terms of categorising HMC (which are

357 the dominant form) these carbonates have measured ranges from 13-15 mol% and should not be

358 misclassified. The applicability of the aragonite:calcite calibration curve was tested for known

359 mixtures of biogenic aragonite and high-Mg calcite (at ratios of 1:0, 3:1, 1:1, 1:2, and 0:1) and found

360 to be accurate to within ±3%.

361

362 **Results**

363 Census data collected across southern Eleuthera Bank indicate that algal densities were generally low

364 in most habitats in both seasons (Fig. 4). Total mean plant densities (excluding *Thalassia* seagrass)

365 were lowest in the sand/sparse algal habitat (Nov 1.9 ± 0.6 plants/m^2; June 7.1 ± 1.8 plants/m^2) and

366 the fringing mangrove habitat (Nov 3.3 ± 1.4 plants/m^2; June 4.7 ± 2.1 plants/m^2). Highest mean

367 densities were measured in the medium density seagrass beds (Nov 15.3 ± 4.4 plants/m^2; June $13.2 \pm$

368 3.7 plants/m^2). At the individual species/genera level *H. incrassata* was most abundant in the

369 hardground (Nov 7.3 ± 9.3, June 9.4 ± 12.4 plants/m^2), medium density seagrass (Nov 10.7 ± 10.7,

370 June 9.2 ± 13.4 plants/m^2) and dense seagrass (Nov 4.6 ± 6.4, June 10.2 ± 6.7 plants/m^2 respectively)

371 habitats. *Penicillus* spp. are generally sparsely distributed (all sites/both seasons ≤ 3 plants/m^2), the

372 exception being *P. dumetosus* which is present in the fringing mangrove habitats at densities

373 averaging ~5 plants/m^2. *Udotea* spp. are present in all habitats, but in very low densities (≤ 2

374 plants/m^2).

375

376 Seagrass blade density varied considerably even within habitat classes, but in the 'sparse' seagrass

377 beds densities (blades/m^2) averaged 66.5 ± 33.5 (Nov) and 81.4 ± 46.5 (June), in the 'medium'

378 seagrass beds 400.5 ± 144.0 (Nov) and 479.2 ± 95.4 (June), and in the 'dense' seagrass beds $715.1 \pm$

379 171.8 (Nov) and 816.3 ± 199.5 (June). Algal and seagrass census data thus suggest slightly higher

380 average plant densities in summer (June) compared to winter (November) months (Fig. 4), but these

381 differences were not significant in any habitat (t-test: fringing mangrove $t = 0.9278$, $P = 0.3961$; bare

382 sands $t = 1.6072$, $P=0.1689$; sparse seagrass $t = 1.1949$, $P=0.2772$; medium seagrass $t = 0.9777$, $P =$

383 0.3660; dense seagrass $t = 1.0426$, $P = 0.3373$). The only exception is the hardground habitat where

384 significantly higher densities of *A. calyculus* were calculated in June compared to November

385 ($p<0.0001$).

386

387 Turnover (crops per year) rates for each algal species were measured in both sampling seasons, and

388 indicate slightly higher summer as opposed to winter rates (Table 2). However, differences between

389 the two seasons were not statistically significant ($p > 0.5$). The exception is *P. dumetosus*, with higher

390 summer versus winter turnover rates ($t = 2.1130$, $p<0.05$). Turnover rate data (using an annual

391 average crops per year rate for each species) were then integrated with plant size/carbonate content

392 conversion data and habitat-specific plant density data to estimate annual rates of carbonate

393   production (g CaCO$_3$ m^{-2} y^{-1}) by each species per unit area of habitat. In terms of the plant size/density

394   metrics, we deliberately used only data from our winter surveys to ensure that our calculated rates of

395   production remain conservative, and thus resultant rates can be considered to represent minimum

396   annual carbonate production rates by algal and seagrass epiphytes.

397

398   These data were then used to explore the question of how much carbonate is produced by

399   algae/seagrass epiphytes in each habitat. Rates are highly variable among habitats as a function of

400   both algal species presence and density, and of seagrass presence and density. Lowest production

401   rates were calculated in the bare sand/sparse algal habitat (1.89 ± 2.06 g CaCO$_3$ m^{-2} yr^{-1}) and the

402   fringing mangrove habitat (6.73 ± 5.22 g CaCO$_3$ m^{-2} yr^{-1}) (Fig. 5A), whilst higher rates were

403   calculated in the medium (68.29 ± 15.74 g CaCO$_3$ m^{-2} yr^{-1}) and dense seagrass beds (238.26 ± 55.84 g

404   CaCO$_3$ m^{-2} yr^{-1}) (Fig. 5A; Table 3). Much higher production rates thus occur from seagrass epiphyte

405   production in areas of dense seagrass development, suggesting that dense seagrass beds represent

406   important "hotspots" of carbonate sediment production. Furthermore, and even with relatively high

407   densities of algae in seagrass habitats (Fig. 4), per unit area epiphyte production estimates

408   significantly outweigh those associated with calcareous green algae (Table 3). We also note that even

409   in habitats where green algae are the dominant sources of carbonate sediment, per unit area rates of

410   production are low relative to those reported in other settings (Multer, 1988; Freile, 2004) because

411   algal densities themselves are low across much of the study area.

412

413   To then estimate total rates of generation of carbonate sediment, we up-scaled the habitat production

414   rates as a function of measured habitat area. On this basis, total estimated sediment production is ~

415   980 (± 261) x 10^3 kg/yr. This is equivalent to an average of only ~6.9 g CaCO$_3$ m^{-2} yr^{-1} when factoring

416   for the spatial extent of habitats and including both the plant/algal colonised and uncolonised habitats

417   in the study area. There are, however, marked inter-habitat variations evident that reflect both habitat

418   spatial extent and between-habitat production rate variability. The single largest contribution to this

419   total derives from the sparse seagrass habitat (~428 x 10^3 kg/yr; Fig. 5B) which covers a large area

420   (~31%) of the Bank. A significant, but much smaller total contribution (~166 x 10^3 kg/yr) is

421   associated with the dense seagrass bed habitat, which despite having very much higher per unit area

422   production rates covers a very small proportion of the area (< 1%). The smallest contributions (478

423   kg/yr) derive from the fringing mangrove habitats, reflecting both their small spatial extent and the

424   low calculated per unit area production rates (Fig. 5B).

425

426   Arising from these data, is the additional question of how much sediment in different size fractions is

427   generated as a function of algal/seagrass abundance and overall across the study area. This question is

428   important because of the differential transport (Braithwaite, 1973; Ford and Kench, 2012) and

429   preservation (Perry, 2000) pathways that sediments of different size fractions and types follow. Our

430   algal/epiphyte breakdown experiments clearly show there are marked differences in the size fractions

431   of sediment generated by each species, and that not all material produced is mud-grade carbonate.

432   Much of the inter-species variability probably relates to the differential breakdown of stem versus

433   head sections of green algal species as discussed by Neumann and Land (1975), but some common

434   patterns emerge. Firstly, *H. incrassata* generates sedimentary material with a distinct bi-modal grain

435   size distribution. Thus, whilst many segments disaggregate to mud-grade carbonate, some

436   (presumably those that are more heavily calcified) remain as intact plates that contribute to the coarse

437   sand to gravel grade size fractions (Fig. 6A). In contrast, *P. capitatus*, both *Udotea* species, and *R.*

438   *phoenix* disaggregate to produce predominantly (>60 wt%) mud-size sediment, with especially large

439   proportions of <32 µm sediment being produced by *P. capitatus* and the *Udotea* species (Fig. 6A).

440   Furthermore, *P. dumetosus* disaggregates to produce more biomodally distributed sediment, albeit

441   skewed towards the finer size fractions (Fig. 6A). The fine and lightly calcified *A. calyculus* plants

442   also disaggregate to predominantly mud-grade carbonate (Fig. 6A), whilst seagrass epiphytes produce

443   sediment that is a mix of medium-fine sands (~ 40 wt%) and mud-grade carbonate (~ 50 wt %) (Fig.

444   6A).

445

446   Using these data, along with the habitat specific production rates, we make first-order estimates of the

447   sediment grain size distributions generated post-mortem by calcareous green algae and seagrass

448   epiphytes, both by habitat and overall for this area of platform. The highest proportions of sediment

449 produced are in the mud/silt size class (Fig. 6B), exceeding 50 wt% of sediment generated in most

450 habitats. However, it is pertinent to note the high proportions of fine sand grade sediment generated in

451 the seagrass (~35%) and fringing mangrove (~40%) habitats, and the high relative proportions (~32%)

452 of gravel grade sediment generated in the hardground habitat (Fig. 6B). Resultant estimates of total

453 sediment production (kg/yr) within each sediment size class across the study area are as follows:

454 gravel 82 x 10^3 kg/yr (8.4% of total); medium/coarse sand 91 x 10^3 kg/yr (9.4%); fine sand 280 x 10^3

455 kg/yr (28.5%); mud/silt 527 x 10^3 kg/yr (53.6%), with the overwhelmingly largest contribution being

456 from the spatially extensive sparse seagrass and algal meadow habitats (Fig. 6C).

457

458 The above data clearly show that different algal species and seagrass epiphytes contribute to different

459 sediment grain size fractions (Fig. 6A). XRD analysis also shows that these species precipitate

460 different proportions of $CaCO_3$ mineralogies: aragonite, high Mg-calcite (HMC) and low Mg-calcite

461 (LMC). All of the calcareous green algal species precipitate predominantly aragonite (range: ~93 to

462 99 weight %), with small amounts of HMC (1-5 weight %), and trace amounts of LMC (mostly <1%)

463 (Table 4), consistent with data reported from other Caribbean settings (Gischler and Zingeler, 2016).

464 In contrast, calcareous epiphytes on *T. testudinum* blades comprise ~80 wt% HMC, and ~18 wt%

465 aragonite, again consistent with compositions reported in other studies (Bosence et al., 1985). Based

466 on these data and our calculated production rates by each species in each habitat, we estimate that

467 ~51% of total algal/epiphytic carbonate produced across the entire study area is aragonite, ~48% is

468 HMC, and ~1% is LMC (Table 5). However, clear differences among habitats reflect the dominant

469 contribution by epiphytic carbonates in dense seagrass meadows. Thus, whilst most carbonate

470 produced in the mangrove, hardground, and sparse algal habitats is aragonite, HMC dominates

471 production in the seagrass beds (Table 5). Furthermore, and although the dense seagrass beds occupy

472 a small proportion of the study area (<1%), the very much higher production rates per unit area in this

473 habitat, significantly increases estimated total HMC production. What these results clearly show is

474 that habitat type and extent, and especially the extent of dense seagrass beds, strongly influences the

475 amounts and phases of carbonate sediment being generated across tropical and sub-tropical carbonate

476 platform and shelf settings

477

Discussion

479 The methodology presented here is designed to support census-based estimates of carbonate sediment

480 production by a range of calcareous green algae and by seagrass epiphytes in a way that can be

481 applied relatively rapidly across habitats typical of Caribbean platforms and ultimately integrated with

482 other assessments of $CaCO_3$ production rates (e.g., from fish) to quantify total rates of $CaCO_3$

483 sediment generation. Importantly, the approach supports estimates of the grain-size fractions and

484 mineralogy of sediments being produced, which can critically influence subsequent post-deposition

485 sediment transport and diagenetic pathways. Calcareous green algae and seagrass epiphytes have

486 particular relevance to such assessments because they are ubiquitous substrate colonisers across

487 tropical and sub-tropical reef, shelf and platform systems, and they are widely regarded as major

488 benthic carbonate sediment producers. Specifically, the approach integrates both long established

489 methods of quantifying rates of production by seagrass epiphytes (e.g., Nelsen and Ginsburg, 1986;

490 Perry and Beavington-Penney, 2005) with the recently tested use of volume and $CaCO_3$ content for

491 quantifying production rates by the calcareous green algae *Halimeda* (Perry et al., 2016), and the

492 results can then be combined with local (or published) metrics on algal/seagrassturnover rates to

493 estimate $CaCO_3$ production as a function of species abundance in different habitats. Similar

494 applications of geometric shape have been used in the past to estimate biovolumes and surface areas

495 of phytoplankton (Vadrucci et al., 2013), and to assess aspects of sponge (Santavy et al., 2013) and

496 coral (Naumann et al., 2009) ecology because the data can be collected rapidly and non-invasively.

497 Our analysis shows such approaches also have good potential for estimating production of $CaCO_3$

498 sediment by plants.

499

500 Resultant data using these new approaches and scaled for seagrass/algal abundance and habitat extent

501 suggest that a conservative estimate of carbonate sediment production by calcareous green algae and

502 from seagrass epiphytes over the study area is ~0.98 M kg $CaCO_3$ yr^{-1}. Additionally, data on the

503 breakdown of plants suggest that >55% of this carbonate is released post-mortem as carbonate mud

504 (<63μm fraction) and a further ~28% as fine-grained sand. However, whilst these amounts seem

505   large, they actually equate to an average production rate of only ~7 g $CaCO_3$ m^{-2} yr^{-1}. This result

506   reflects the fact that whilst some small areas of the platform have high seagrass/algal densities and

507   result in high per unit area production estimates (~238g $CaCO_3$ m^{-2} yr^{-1}), very large areas of the

508   platform are sparsely colonised by algae and/or seagrass (<10 plants/m^2), and some areas are entirely

509   devoid of algal/seagrass producers. In terms of understanding platform-scale sediment production,

510   there is thus a clear need to account for such marked spatial variations in the abundance of benthic

511   species that produce carbonate and the habitats they define. In particular, the presence or absence of

512   extensive and dense *Thalassia* spp. meadows is likely to strongly influence rates of production, grain

513   sizes and the proportions of different carbonate phases. These observations emphasise the need to

514   understand habitat specific sources of sediment to more fully appreciate variations in both inter- and

515   intra-shelf/platform sediment budget variations and, in the context of seagrass beds, further extend the

516   idea that these ecosystem contribute critical ecosystem services (Orth et al., 2006; Mazarrasa et al.,

517   2015).

518

519   Several previous studies have reported high sediment production rates from both epiphytes (Patriquin,

520   1972) and algal meadows (Multer, 1988), but often from systems with very high plant densities over

521   large spatial areas. Eleuthera Bank is generally more sparsely colonised by seagrass than lagoonal and

522   back-reef settings in other areas of the Bahamas and, indeed, the Caribbean. This difference may arise

523   from the strong currents generated during ebb- and flood tides, but the key point is that it is

524   inappropriate to assume that specific species always dominate production at the higher end of the rates

525   previously reported in the literature. Indeed, if dense seagrass beds were absent from the present study

526   area, the average rate of $CaCO_3$ sediment production per unit area would fall even further (by ~50%).

527   This issue is interesting because of questions around the expansion or loss of coastal seagrass habitat

528   under anthropogenic and environmental pressures (Waycott et al., 2009). For example, local nutrient

529   enrichment from coastal urbanisation has been reported to drive rapid expansion of seagrass extent

530   (Udy et al., 1999), and this would have the potential to drive significant local increases in sediment

531   production if epiphyte densities remain similar, although any such increases in epiphyte production

532   may potentially be offset by nutrification-enhanced microbial $CaCO_3$ sediment dissolution

533   (Andersson, 2015), and as reported for back-reef seagrass beds in Florida (Brock et al., 2006).

534   Conversely, deliberate removal of seagrass beds for reclamation or visual/tourist amenity reasons

535   (Daby, 2003) would significantly reduce sediment production budgets. Changes in seagrass extent

536   also may occur due to other environmental pressures, such as sea-level rise, and whilst modelling

537   studies show divergent responses of seagrass extent under sea-level rise scenarios (Albert et al.,

538   2017), the potential to change sediment generation rates markedly is clear.

539

540   An obvious question arising from the above data, however, relates to how realistic our production rate

541   estimates are, and we make the following observations. In terms of production rates by seagrass

542   epiphytes, we note that our estimates are in line with those from other studies using comparable

543   approaches. For example, our estimates of epiphyte production per unit area average 96 g $CaCO_3$ m^{-2}

544   yr^{-1} and with average blade densities of 389 m^{-2}. These rates are consistent with those calculated in

545   Florida Bay (Nelsen and Ginsburg, 1986), where production rates averaged 118 g m^{-2} yr^{-1}, a little

546   above our rates, but from sites with higher average blade densities (670 m^2). Relationships between

547   blade density and rates of $CaCO_3$ production are overall a little higher at our sites but this difference

548   arises from thehigher average weight of epiphytic carbonate per blade in our study (0.034g v 0.026 g

549     $CaCO_3$ /blade in Florida), and the increase in epiphytic carbonate with increased density of blades.

550   We are thus confident that our epiphyte production rates are broadly consistent with those calculated

551   using similar approaches elsewhere in the region.

552

553   In terms of calcareous algal production rates, direct like-for-like comparisons with past studies are

554   hard due to methodological differences. In the present study, total rates of calcareous green algal

555   production range from 1.4 g in the bare sand/sparse algal habitat to 12.4 g and 10.7 g $CaCO_3$ m^{-2} yr^{-1}

556   in, respectively, the medium and dense seagrass habitats (Table 2), and 12.2 g $CaCO_3$ m^{-2} yr^{-1} in the

557   hardground habitat,. While the studies available for comparison from the Caribbean inherently have

558   different habitat configurations,algal densities, and used different or partially different methodologies,

559   we note that average production rates from comparable depositional settings suggest our methodology

560   delivers estimates consistent with these earlier studies. For example, data from lagoon settings

561   (dominated by seagrass beds) in Florida Bay (Bach, 1979) calculated average calcareous green algal

562   production rates (based on two different methodologies) of 10.3 g $CaCO_3$ m^{-2} yr^{-1}. Plant density data

563   are not given but production rates were highest by *Halimeda* spp. (6.7 g), and with *P. capitatus*, *R.*

564   *phoenix* and *U. flabellum* contributing 1.8 g, 1.6 g and 0.3 g $CaCO_3$ m^{-2} yr^{-1} respectively. These rates

565   are very similar to the average rates we calculate for total green algal production in comparable

566   (medium and dense) *Thalassia* seagrass habitats.

567

568   Several other studies do report both production rates and algal densities, and although average annual

569   production rates by *Halimeda* spp. are significantly higher in these studies, these results are derived

570   from sites with much higher average plant densities. Freile (2004), for example, report production by

571   *H. incrassata* from sheltered (seagrass-dominated) lagoon habitats in San Salvador of 141.7 g $CaCO_3$

572   m^{-2} yr^{-1}, with average plant densities of 28 m^{-2}, whilst Multer (1988) reports production/plant density

573   averages for three sites in Antigua of 36 plants m^{-2} (114.3 g $CaCO_3$ m^{-2} yr^{-1}), 30 plants m^{-2} (62.1 g

574     $CaCO_3$ m^{-2} yr^{-1}), and 26 plants m^{-2} (60.7 g $CaCO_3$ m^{-2} yr^{-1}). When differences in plant densities are

575   taken into account, these rates are not dissimilar to those we present. Very detailed data have also

576   been presented from shallow seagrass-dominated lagoon sites in Abaco, Bahamas across a range of

577   the same green algal species considered here (Neumann & Land 1975). Although between-site

578   differences in plant sizes cannot be taken into account, we note that average measures of plant $CaCO_3$

579   content (g/plant) are similar to those we report: *P. capitatus* (this study 0.36 g v 0.27g/plant), *P.*

580   *dumetosus* (this study 0.42 g v 0.40 g/plant), *R. phoenix* (this study 0.30 g v 0.41 g/plant), and *U.*

581   *flabellum* (this study 0.11 g v 0.23 g/plant). On the basis of these comparisons, and despite differences

582   between sites in terms of additional confounding factors (wave energy, local environmental

583   parameters), we are confident that the rates generated by combining the census-based approach with

584   species specific geometric volume to carbonate content relationships provides a valid approach for

585   estimating rates of algal and epiphyte-derived $CaCO_3$ production.

586

587   Equally relevant here is the observation that variations in species presence and abundance will result

588   in both variable rates of production of $CaCO_3$ sediment between sites and marked differences in the

589   carbonate phases (aragonite, HMC, LMC) produced. Whilst such differences at the wider shelf and

590   platform scale have previously been discussed (Matthews, 1966; Husseini and Matthews, 1972) data

591   on habitat-specific production of sediment mineralogies are sparse. Here, we have shown that sites

592   where green algae are the dominant elements of the benthic community (fringing mangroves,

593   hardground and bare sand/sparse algal habitats) are predicted to produce predominantly aragonite-rich

594   sediment. In contrast, in seagrass-dominated habitats, and as seagrass densities increase, so the

595   proportion of HMC produced increases, such that aragonite is a secondary component of the sediment

596   production in these habitats. On this basis, one might thus expect clear, habitat-specific, patterns to

597   emerge in terms of sediment mineralogical compositions.

598

599   However, over the habitat scales we have studied, our data indicates markedly uniform sediment

600   mineralogical compositions, with the proportion of aragonite to HMC in the sediment accumulating

601   across most of the habitats being in the range of 2:1 (Fig. 7). Exceptions are the inner muddy

602   bioturbated embayment of Rock Sound and the dense seagrass beds where the ratio of aragonite to

603   HMC is much higher. In essence, this result means that the sediments accumulating beneath the

604   seagrass beds contain a much higher proportion of aragonite than would be expected from

605   calculations of production by green algae and seagrass, whilst surrounding habitats dominated by

606   calcareous green algae have higher proportions of HMC. In combination, these results suggest that

607   dilution or homogenization of sediments is occurring, and three particularly significant contributing

608   factors can be identified; 1. sedimentary inputs from other sources; 2. post-depositional

609   recrystallization and dissolution; and 3. the effects of physical sediment working and transport. These

610   factors are relevant to understanding not only the relative importance of calcareous green algae and

611   seagrass epiphytes in budgets for production of carbonate sediment, but also may explain why algae

612   and seagrass epiphytes may play relatively small roles in rates of sediment generation across larger

613   areas of some depositional systems, despite being visually obvious.

614

615   In terms of additional sediment inputs, a number of potential contributing sources can be identified.

616   These include fine-grained carbonates derived from "whitings" (suspended lime muds) (Shinn et al.,

617   1989, Robbins et al., 1997), with Shinn et al. (1989) estimating that whitings on the Great Bahama

618   Bank generated ~8 g $CaCO_3$ m^{-2} yr^{-1}, and comprise ~85% aragonite and ~12% HMC sediment. We

619   note that such rates are around the mean for algal carbonate production across our sites, so such inputs

620   could well represent an important additional input of aragonite-rich sediment. Additional benthic

621   biogenic sediment also derives from the post-mortem abrasion and breakdown of molluscan shells and

622   from foraminifera, with the shells of bivalves comprising species-specific layers of either aragonite, or

623   both aragonite and calcite (Chave 1962), and foraminifera typically comprising LMC or HMC

624   (Chave 1962). Recent work also points to locally significant amounts of fine grained $CaCO_3$ being

625   produced intestinally by fish. These carbonates are mostly <10 µm in size, are dominated (~60%) by

626   HMC carbonate phases, with estimates of production in the Bahamas being locally as high as 16.7 g

627    $CaCO_3$ m^{-2} yr^{-1} (but averaging <1 g when habitats devoid of high fish biomass are included) (Salter et

628   al., 2017). Significant amounts of fine-grained and aragonite-rich sediment reportedly can be

629   precipitated directly by *Thalassia* seagrass inside their blades (Enriquez and Schubert, 2014) and, if

630   applicable to seagrass beds in Eleuthera, such processes could help explain the evident disparity

631   between the HMC-dominated epiphyte production and the dominance of aragonite in the seagrass bed

632   sediments. Most importantly however, in terms of understanding system scale rates and types of

633   carbonate sediment production, these observations clearly show that whilst calcareous algae and

634   epiphytes can contribute large amounts of sediment locally, other sources of carbonate can be equally,

635   or more important, both across the more sparsely colonised areas of such shelf and platform systems

636   and even potentially within the seagrass beds whereepiphyte production dominates. Thus, a picture of

637   highly divergent inter-habitat sediment production regimes emerges.

638

639   Equally important in terms of the mineralogical composition of the accumulating sediments will be

640   the effects of post-depositional sediment diagenesis and reworking. Reid et al. (1992) showed that

641   widespread post-deposition abrasion, bioerosion, and micritization of skeletal grains can result in

642   primary skeletal forms and mineralogies being rapidly altered, whilst rapid recrystallization of

643   aragonite in calcareous algae to HMC has also been documented (Macintyre and Reid, 1995).

644   Furthermore, it has been shown that net sediment dissolution can occur in some sediment-dominated

645   platform systems (Andersson, 2015; Eyre et al., 2018) and, if this results in the preferential loss of

646   specific carbonate phases, it could further explain some of the sediment homogenization we observe.

647   Equally, important in systems like Eleuthera, which experience strong ebb- and flood-tide currents

648   (Dravis, 1979; Salter et al., 2014), will be the entrainment and reworking of sediments, moving

649   material both on- and off-platform. This transport may well be a major factor influencing sediment

650   accumulation across Eleuthera Bank given the clear homogeneity we observe in sediment mineralogy.

651   The abundance of aragonite in the sediment in the denser seagrass beds (which mainly produce HMC-

652   rich carbonates) and the predominance of fine-grained aragonite rich sediments in Rock Sound itself,

653   which is essentially devoid of algal carbonates, are suggestive of these transport processes being

654   important.

655

656   **Conclusions**

657   Methodologies to support estimates of shallow tropical marine sediment production are limited, and

658   this major knowledge gap is important for reasons that include the supply of sediment to shorelines

659   and islands. Here, we present a methodology designed to support estimates of the rates, grain sizes

660   and mineralogies of carbonate sediment generated by several species of calcareous green algae and by

661   seagrass epiphytes that are ubiquitous substrate colonisers across many tropical and sub-tropical

662   marine systems. This method is based on the use of readily measurable dimensions of plants, thus

663   allowing habitat-scale estimates of sediment production by each species that can then be integrated

664   with estimates of production from other sources (see Perry et al., 2015) to quantify total carbonate

665   sediment budgets for different habitats and systems. The specific findings of this study point to major

666   inter-habitat differences in rates and types of algal and seagrass epiphyte-derived sediment

667   production, with large areas of the study area actually having very low per unit area production rates

668   (<10 g $CaCO_3$ m^{-2} yr^{-1}). In contrast, spatially restricted dense seagrass beds produce carbonate at high

669   rates (>230 g $CaCO_3$ m^{-2} yr^{-1}). This observation, of a disproportionately important role of seagrass

670   beds in sediment generation, has direct relevance to emerging ideas about rates of habitat loss or

671   change. Seagrass beds specifically are, for example, threatened by direct removal/dredging, but may

672   also experience expansion under nutrient enrichment. Methodologies, such as those presented here,

673   have the potential to contribute to our understanding of the impacts of such changes because seagrass

674   and algal meadows commonly co-exist and represent important benthic carbonate sediment producers

675   in such systems.

676

677   **AUTHOR CONTRIBUTIONS**

678   Project funding was secured by CP. Field work was carried out by CP, MS, KM and AH. Data

679   analysis was undertaken by CP and MS. The manuscript was prepared by CP, MS, KM and AH. All

680   authors gave their final approval for publication.

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691   **References**
692
693   Albert, S., Saunders, M.I., Roelfsema, C.M., Leon, J.X., Johnstone, E., Mackenzie, J.R., Hoegh-Guldberg, O., Grinham,
694   A.R., Phinn, S.R., Duke, N.C., Mumby, P.J., Kovacs, E., and Woodroffe, C.D. (2017). Winners and losers as
695   mangrove, coral and seagrass ecosystems respond to sea-level rise in Solomon Islands. *Environmental Research*
696   *Letters* 12.
697   Andersson, A. (2015). A fundamental paradigm for coral reef carbonate sediment dissolution. *Frontiers in Marine Science*
698   2,52.
699   Atkinson, M.J., and Grigg, R.W. (1984). Model of a coral reef ecosystem. *Coral Reefs* 3, 13-22.
700   Bach, S. (1979). Standing crop, growth and production of calcareous Siphonales (Chlorophyta) in a south Florida lagoon.
701   *Bulletin of Marine Science* 29, 191-201.
702   Bellwood, D. (1996). Production and reworking of sediment by parrotfishes (family Scaridae) on the Great Barrier Reef,
703   Australia. *Marine Biology* 125, 795-800.
704   Berelson, W.M., Balch, W.M., Najjar, R., Feely, R.A., Sabine, C., and Lee, K. (2007). Relating estimates of CaCO3
705   production, export, and dissolution in the water column to measurements of CaCO3 rain into sediment traps and
706   dissolution on the sea floor: A revised global carbonate budget *Global Biogeochemical Cycles* 21.
707   Bischoff, W., Bishop, F., and Mackenzie, F. (1983). Biogenically produced magnesian calcite: inhomogeneities in chemical
708   and physical properties; comparison with synthetic phases. *American Mineralogist* 68, 1183-1188.
709   Bosence, D. (1989). Biogenic carbonate production in Florida Bay. *Bulletin of Marine Science* 44, 419-433.
710   Bosence, D., Rowlands, R., and MI, Q. (1985). Carbonate budget Florida mud mound. *Sedimentology* 32, 317-343.

711   Braithwaite, C. (1973). Settling behaviour related to sieve analysis of skeletal sands. *Sedimentology* 20**,** 251-262.

712   Brock, J., Yates, K., Halley, R., Kuffner, I., Wright, C., and Hatcher, B. (2006). Northern Florida reef tract benthic metabolism
713   scaled by remote sensing. *Marine Ecology Progress Series* 312**,** 123-139.

714   Corlett, H., and Jones, B. (2007). Epiphyte communities on Thalassia testudinum from Grand Cayman, British West Indies:
715   Their composition, structure, and contribution to lagoonal sediments. *Sedimentary Geology* 194**,** 245-262.

716   Courtney, T.A., Andersson, A.J., Bates, N.R., Collins, A., Cyronak, T., De Putron, S.J., Eyre, B.D., Garley, R., Hochberg,
717   E.J., Johnson, R., Musielewicz, S., Noyes, T.J., Sabine, C.L., Sutton, A.J., Toncin, J., and Tribollet, A. (2016).
718   Comparing Chemistry and Census-Based Estimates of Net Ecosystem Calcification on a Rim Reef in Bermuda.
719   *Frontiers in Marine Science* 3.

720   Daby, D. (2003). Effects of seagrass bed removal for tourism purposes in a Mauritian bay. *Environmental Pollution* 125**,** 313-
721   324.

722   Davies, T., and Hooper, P. (1963). The determination of the calcite:aragonite ratio in mollusc shells by X-ray diffraction.
723   *Mineralogical Magazine* 33**,** 608-612.

724   Doo, S., Hamylton, S., and Bryne, M. (2012). Reef-Scale Assessment of Intertidal Large Benthic Foraminifera Populations
725   on One Tree Island, Great Barrier Reef and Their Future Carbonate Production Potential in a Warming Ocean.
726   *Zoological Studies* 51**,** 1298-1307.

727   Dravis, J. (1979). Rapid and widespread generation of recent oolitic hardgrounds on a high energy Bahamian platform,
728   Eleuthera Bank, Bahamas. *Journal of Sedimentary Petrology* 49**,** 195-208.

729   Enriquez, S., and Schubert, N. (2014). Direct contribution of the seagrass Thalassia testudinum to lime mud production. *Nat
730   Commun* 5**,** 3835.

731   Eyre, B., Cyronak, T., Drupp, P., Heinen, E., De Carlo, T., Sachs, J., and Andersson, A. (2018). Coral reefs will transition to
732   net dissolving before end of century. *Science* 359**,** 908-911.

733   Flugel, E. (2004). *Microfacies of Carbonate Rocks.* Berlin-Heidelberg: Springer-Verlag.

734   Ford, M.R., and Kench, P.S. (2012). The durability of bioclastic sediments and implications for coral reef deposit formation.
735   *Sedimentology* 59**,** 830-842.

736   Frankovich, T., and Zieman, J. (1995). A comparison of methods for the accurate measurement of epiphytic carbonate.
737   *Coastal and Estuarine Research* 18**,** 279-284.

738   Freile, D. (2004). Carbonate productivity rates of *Halimeda* in two different locations, San Salvador Islad, Bahamas. *11th
739   Symposium of the Geology of the Bahamas and other regions***,** 95-106.

740   Friele, D., and Hillis, L. (1997). Carbonate productivity by *Halimeda incrassata* in a land proximal lagoon, Pico Feo, San
741   Blas, Panama. *Proceedings of 8th International Coral Reef Symposium* 1**,** 767-772.

742   Gischler, E., and Zingeler, D. (2016). The origin of carbonate mud in isolated carbonate platforms of Belize, Central
743   America. *International Journal of Earth Sciences* 91**,** 1054-1070.

744   Goldsmith, J., Graf, D., and Hc, H. (1961). Lattice constants of the calcium-magnesium carbonates. *American Mineralogist*
745   46**,** 453-457.

746   Green, E.P., Mumby, P.J., Edwards, A.J., and Clark, C.D. (2000). *Remote sensing handbook for tropical coastal
747   management.* UNESCO, Paris.

748   Harborne, A.R., Selwyn, J.D., Lawson, J.M., and Gallo, M. (2017). Environmental drivers of diurnal visits by transient
749   predatory fishes to Caribbean patch reefs. *Journal of Fish Biology* 90**,** 265-282.

750   Husseini, S., and Matthews, R. (1972). Distribution of high-magnesium calcite in lime muds of the Great Bahama Bank:
751   diagenetic implications. *Journal of Sedimentary Petrology* 42**,** 179-182.

752   Land, L. (1970). Carbonate mud: production by epibiont growth on *Thalassia testudinum*. *Journal of Sedimentary Petrology*
753   40**,** 1361-1363.

754   Lowenstam, H. (1955). Aragonite needles secreted by algae and some sedimentary implications. *Journal of Sedimentary
755   Petrology* 25**,** 270-272.

756   Macintyre, I.G., and Reid, R.P. (1995). Crystal alteration in a living calcareous alga (*Halimeda*): implications for studies in
757   skeletal diagensis. *Journal of Sedimentary Research A* 65**,** 143-153.

758   Matthews, R. (1966). Genesis of recent lime mud in southern British Honduras. *Journal of Sedimentary Petrology* 36**,** 428-
759   454.

760   Mazarrasa, I., Marbà, N., Lovelock, C.E., Serrano, O., Lavery, P.S., Fourqurean, J.W., Kennedy, H., Mateo, M.A., Krause-
761   Jensen, D., Steven, A.D.L., and Duarte, C.M. (2015). Seagrass meadows as a globally significant carbonate
762   reservoir. *Biogeosciences Discussions* 12**,** 4107-4138.

763   Milliman, J., and Droxler, A. (1996). Neritic and pelagic carbonate sedimentation in the marine environment: ignorance is not
764   bliss. *Geol Rundsch* 85**,** 496–504.

765   Multer, G. (1988). Growth rate, ultrastructure and sediment contribution of Halimeda incrassata and Halimeda monile,
766   Nonsuch and Falmouth Bays, Antigua, W.I. *Coral Reefs* 6**,** 179-186.

767   Naumann, M.S., Niggl, W., Laforsch, C., Glaser, C., and Wild, C. (2009). Coral surface area quantification–evaluation of
768   established techniques by comparison with computer tomography. *Coral Reefs* 28**,** 109-117.

769   Nelsen, J., and Ginsburg, R.N. (1986). Calcium carbonate production by epibionts on *Thalassia* in Florida Bay. *Journal of
770   Sedimentary Petrology* 56**,** 622-628.

771   Neumann, A., and Land, L. (1975). Lime mud deposition and calcareous algae in the Bight of Abaco, Bahamas: a budget.
772   *Journal of Sedimentary Petrology* 45**,** 763-786.

773   Newell, N.D., Purdy, E.G., and Imbrie, J. (1960). Bahamian Oolitic Sand. *The Journal of Geology* 68, 481-497.

774   Orth, R., Carruthers, T., Dennison, W., Duarte, C., Fourqurean, J., Heck, K., Hughes, A., Kendrick, G., Kenworthy, W.,
775   Olyarnik, S., Short, F., Waycott, M., and Williams, S. (2006). A global crisis for seagrass ecosystems. . *BioScience*
776   56**,** 987-996.

777   Patriquin, D. (1972). Carbonate mud production by epibionts on *Thalassia*: an estimate based on leaf growth rate data.
778   *Journal of Sedimentary Petrology* 42**,** 687-689.

779   Payri, C. (1988). *Halimeda* contribution to organic and inorganic production in a Tahitian reef system. *Coral Reefs* 6**,** 251-
780   262.

781   Perry, C. (1998). Grain susceptibility to the effects of microboring: implications for the preservation of skeletal carbonate.
782   *Sedimentology* 45**,** 39-51.

783   Perry, C. (2000). Factors controlling sediment preservation on a north Jamaican fringing reef: a process-based approach to
784   microfacies analysis. *Journal of Sedimentary Research* 70**,** 633-648.

785   Perry, C.T., and Beavington-Penney, S.J. (2005). Epiphytic calcium carbonate production and facies development within
786   sub-tropical seagrass beds, Inhaca Island, Mozambique. *Sedimentary Geology* 174**,** 161-176.

787   Perry, C.T., Kench, P.S., O'Leary, M.J., Morgan, K.M., and Januchowski-Hartley, F. (2015). Linking reef ecology to island
788   building: Parrotfish identified as major producers of island-building sediment in the Maldives. *Geology* 43**,** 503-
789   506.

790   Perry, C.T., Morgan, K.M., and Salter, M.A. (2016). Sediment generation by Halimeda on atoll interior coral reefs of the
791   southern Maldives: A census-based approach for estimating carbonate production by calcareous green algae.
792   *Sedimentary Geology* 346**,** 17-24.

793   Perry, C.T., Morgan, K.M., and Yarlett, R.T. (2017). Reef Habitat Type and Spatial Extent as Interacting Controls on
794   Platform-Scale Carbonate Budgets. *Frontiers in Marine Science* 4**,** 185.

795   Perry, C.T., Salter, M.A., Harborne, A.R., Crowley, S.F., Jelks, H.L., and Wilson, R.W. (2011). Fish as major carbonate mud
796   producers and missing components of the tropical carbonate factory. *Proc Natl Acad Sci U S A* 108, 3865-3869.

797   Reid, R., Macintyre, I.G., and Post, J. (1992). Micritized skeletal grains in northern Belize lagoon: a major source of Mg-
798   calcite mud. *Journal of Sedimentary Petrology* 62**,** 145-156.

799   Robbins, L., Tao, Y., and Evans, C. (1997). Temporal and spatial distribution of whitings on Great Bahama Bank and a new
800   lime mud budget. *Geology* 25**,** 947-950.

801   Salter, M.A., Harborne, A.R., Perry, C.T., and Wilson, R.W. (2017). Phase heterogeneity in carbonate production by marine
802   fish influences their roles in sediment generation and the inorganic carbon cycle. *Sci Rep* 7**,** 765.

803   Salter, M.A., Perry, C.T., Stuart-Smith, R.D., Edgar, G.J., Wilson, R.W., and Harborne, A.R. (2018). Reef fish carbonate
804   production assessments highlight regional variation in sedimentary significance. *Geology*.

805   Salter, M.A., Perry, C.T., and Wilson, R.W. (2012). Production of mud-grade carbonates by marine fish: Crystalline products
806   and their sedimentary significance. *Sedimentology* 59**,** 2172-2198.

807   Salter, M.A., Perry, C.T., and Wilson, R.W. (2014). Size fraction analysis of fish-derived carbonates in shallow sub-tropical
808   marine environments and a potentially unrecognised origin for peloidal carbonates. *Sedimentary Geology* 314**,** 17-
809   30.

810   Santavy, D.L., Courtney, L.A., Fisher, W.S., Quarles, R.L., and Jordan, S.J. (2013). Estimating surface area of sponges and
811   gorgonians as indicators of habitat availability on Caribbean coral reefs. *Hydrobiologia* 707**,** 1-16.

812   Sepulcre, S., Durand, N., and Bard, E. (2009). Mineralogical determination of reef and periplatform carbonates: calibration
813   and implications for paleoceanography and radiochronology. *Global and Planetary Change* 66**,** 1-9.

814   Shinn, E., Steinen, R., Lidz, B., and Swart, P. (1989). Whitings: a sedimentological dilema. *Journal of Sedimentary Petrology*
815   59**,** 147-161.

816   Udy, J., Dennison, W., Long, W., and Mckenzie, L. (1999). Responses of seagrass to nutrients in the Great Barrier Reef,
817   Australia. *Marine Ecology Progress Series* 185**,** 257-271.

818   Vadrucci, M.R., Mazziotti, C., and Fiocca, A. (2013). Cell biovolume and surface area in phytoplankton of Mediterranean
819   transitional water ecosystems: methodological aspects. *Transitional Waters Bulletin* 7**,** 100-123.

820   Vroom, P., Smith, C., Coyer, J., Walters, L., Hunter, C., Beach, K., and Smith, J. (2003). Field biology of Halimeda tuna
821   (Bryopsidales, Chlorophyta) across a depth gradient: comparative growth, survivorship, recruitment, and
822   reproduction. *Hydrobiologia* 501**,** 149-166.

823   Walters, L., Bischoff, S., Patterson, W., and Lyons, T. (1993). Dissolution and recrystallization in modern shelf carbonates:
824   evidence from pore water and solid phase chemistry. *Philos Trans R Soc Lond A* 344**,** 27-36.

825   Walters, L., and Morse, J. (1984). Reactive surface area of skeletal carbonates during dissolution: effect of grain size.
826   *Journal of Sedimentary Petrology* 54**,** 1081-1090.

827   Waycott, M.D., Cm, Carruthers, T., Orth, R., Dennison, W., Olyarnik, S., Calladine, A., Fourqurean, J., Heck, J.K., Hughes,
828   A., Kendricki, G., Kenworthy, W., Short, F., and Williams, S. (2009). Accelerating loss of seagrasses across the
829   globe threatens coastal ecosystems. *PNAS* 106, 12377–12381.

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Figure captions

Fig. 1. A) Regional location of Eleuthera in the Bahamas; and B) Map showing the distribution of

habitat types across the southern area of Eleuthera Bank.

Fig. 2. Schematic showing axes and dimensions used to estimate the volumetric space occupied by

species of a) *Udotea cyathiformis*, *Penicillus capitatus* and *Penicillus dumetosus*; B) *Rhipocephalus*

phoenix; C) *Halimeda incrassata*; and D) *Udotea flabellum*.

Fig. 3. Relationships between plant volumetric space (cm^3) and plant carbonate content (g CaCO$_3$) for

A) *Halimeda incrassata*; B) *Penicillus capitatus*; C) *Pencillus dumetosus*; D) *Udotea cyathiformis*; E)

Udotea flabellum; and E) *Rhipocephalus phoenix*.

Fig. 4. Mean (± SD) calcareous green algal and seagrass blades density for A) winter (November)

2016, and B) summer (June) 2017 for each of the six habitat types examined.

Fig. 5 A) Average carbonate sediment production (g CaCO$_3$ m^{-2} yr^{-1} ± SD) by habitat; and B) Total

sediment production (kg yr^{-1}) by habitat type.

Fig. 6. A) Post-disaggregation contributions to different sediment grain size classes (± SD) by

different species of calcareous green algae and seagrass epiphytes; B) Proportional contributions (±

SD) of green algae and seagrass epiphytes to different sediment size fraction classes by habitat; C)

Total estimated amounts of CaCO$_3$ sediment (± SD) by size fraction grouping produced in each

habitat type.

Fig. 7. Ternary plot showing the measured proportions of aragonite : high Mg-calcite (HMC) : low

Mg-calcite (LMC) in calcareous green algae (all species) and seagrass epiphytes against the

mineralogies of sediments from each of the major habitat types across Eleuthera Bank.

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862 Supplementary Figure S1. Images showing the new growth above Alizarin Red stain line in A)

863 *Halimeda incrassata*; B) *Penicilllus dumetosus*; and C) *Udotea flabellum*. All after 10 days of post-

864 staining growth.

865

866 Supplementary Table S1. Transect level estimates of carbonate production by each green algal species

867 and by seagrass epiphytes.

868 Supplementary Table S2. Relative % contributions to different sediment grain size fractions by each

869 algal species and by seagrass epiphytes following breakdown experiments. n = 3 per species (except

870 for *Thalassia* epiphytes which was based on a single bulk sample).

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878 **Tables**

Habitat	Mean weight %			Mean Mol% MgCO$_3$	
	% Arag	% LMC	% HMC	LMC	HMC
Bare sands	61.2 ± 2.7	2.9 ± 0.3	35.9 ± 2.6	1.9 ±1.2	15.0 ± 0.3
Hardgrounds	67.1 ± 7.7	3.0 ± 1.0	29.9 ± 8.6	1.9 ± 0.4	14.7 ± 0.1
Fringe mangroves	61.5 ± 0.3	3.9 ± 0.4	34.6 ± 0.7	1.3 ± 0.2	14.7 ± 0.4
Sparse seagrass	63.0 ± 13.4	3.6 ± 1.8	33.3 ± 14.4	2.0 ± 0.9	14.8 ± 0.2
Medium seagrass	76.2 ± 4.1	1.7 ± 0.5	22.1 ± 4.0	1.9 ± 1.0	14.7 ± 0.4
Dense seagrass	70.9 ± 9.7	3.4 ± 1.1	25.7 ± 1.9	1.6 ± 0.2	14.0 ± 0.7
Inner bay muds	81.6 ± 5.4	2.5 ± 1.0	15.9 ± 4.9	1.0 ± 0.2	13.8 ± 0.3

879

880 Table 1. Sediment mineralogies (± SD) from each habitat based on XRD analysis of bulk sediment samples.

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Species	Sample period	Crops/yr	No. samples
Halimeda incrassata	Nov 2016	8.7 ± 4.4	85

	June 2017	9.2 ± 4.1	72
	MEAN	**9.0 ± 4.3**	
Penicillus capitatus	Nov 2016	7.6 ± 3.2	8
	June 2017	7.7 ± 3.1	7
	MEAN	**7.6 ± 3.1**	
Penicillus dumetosus	Nov 2016	6.5 ± 3.6	29
	June 2017	8.9 ± 5.7	44
	MEAN	**7.9 ± 5.1**	
Udotea cyathiformis	Nov 2016	7.3 ± 3.5	12
	June 2017	7.5 ± 4.0	24
	MEAN	**7.4 ± 3.8**	
Udotea flabellum	Nov 2016	7.8 ± 7.1	10
	June 2017	8.4 ± 3.9	8
	MEAN	**8.1 ± 5.8**	
Rhipocephalus phoenix	Nov 2016	6.0 ± 3.7	12
	June 2017	7.1 ± 5.3	12
	MEAN	**6.5 ± 4.5**	

882

883 Table 2. Calculated annual turnover rates (± SD) for each green algal species for both winter (November) 2016 and summer
884 (June) 2017.

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	Habitats and associated production rates (g CaCO$_3$ m^{-2} yr^{-1})					
Species	Fringe mangrove	Hardground	Bare sands/ sparse algae	Sparse seagrass	Medium seagrass	Dense seagrass
H. incrassata	0.204 ± 0.749	6.629 ± 7.269	0.194 ± 0.424	0.699 ± 0.888	3.704 ± 2.713	3.256 ± 2.825
P. capitatus	0.273 ± 0.748	0.015 ± 0.061	0.969 ± 1.882	0.454 ± 0.587	1.665 ± 2.035	2.236 ± 8.697
P. dumetosus	4.212 ± 5.104	0.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000	0.565 ± 1.990	0.750 ± 2.640
U. cyathiformis	0.000 ± 0.000	2.696 ± 4.113	0.000 ± 0.000	0.032 ± 0.129	1.334 ± 2.645	1.392 ± 3.375
U. flabellum	0.000 ± 0.000	1.076 ± 1.108	0.157 ± 0.351	0.392 ± 0.391	1.580 ± 1.827	1.279 ± 1.034
R. phoenix	0.000 ± 0.000	1.529 ± 1.339	0.126 ± 0.408	1.835 ± 2.726	3.322 ± 2.381	1.499 ± 3.947
A. calyculus	1.847 ± 3.579	0.222 ± 0.362	0.000 ± 0.000	0.000 ± 0.000	0.249 ± 0.432	0.000 ± 0.000
T. testudinum epiphytes	0.198 ± 0.355	0.006 ± 0.025	0.449 ± 0.482	6.387 ± 2.735	55.879 ± 14.706	227.847 ± 54.769
TOTAL	**6.733 ± 5.225**	**12.172 ± 8.531**	**1.895 ± 2.060**	**9.799 ± 4.026**	**68.298 ± 15.739**	**238.259 ± 55.842**
% from green algal	97.1	99.9	76.3	34.8	18.18	4.37

887

888 Table 3 – Mean (± SD) rates of carbonate production (g CaCO$_3$ m^{-2} yr^{-1}) by calcareous green algae and seagrass epiphytes
889 within each habitat across Eleuthera Bank, and total resultant production rates (mean ± SD) for each habitat type.

Species (all bulk plant samples)	mean weight % aragonite*	mean weight % high-Mg calcite*	mean weight % low-Mg calcite*	High-Mg calcite MgCO$_3$ (mol%)	Low-Mg calcite MgCO$_3$ (mol%)
Acetabularia calyculus	94.9 ± 0.7	5.1 ± 0.7	0.0	13.9 ± 0.8	-
Halimeda incrassata	98.7 ± 0.4	1.2 ± 0.2	0.1 ± 0.2	13.7 ± 0.2	0.6
Penicillus capitatus	98.7 ± 0.7	1.3 ± 0.7	0.0	13.2 ± 0.4	-
Penicillus dumetosus	97.6 ± 0.3	2.2 ± 0.0	0.2 ± 0.3	13.4 ± 0.2	0.8
Udotea flabellum	96.7 ± 1.2	2.7 ± 1.4	0.6 ± 0.6	13.3 ± 0.5	0.4 ± 0.6
Udotea cyathiformis	92.8 ± 5.4	5.4 ± 4.3	1.9 ± 1.4	13.7 ± 0.3	1.4 ± 0.8
Rhipocephalus phoenix	94.4	4.5	1.2	13.7	1.2
Thalassia testudinum epiphytes	18.0	80.1	1.9	13.6	0.5

890 *mean weight % values are based on the calibration of Davies and Hooper (1962)

891 Table 4. CaCO$_3$ mineralogies (± SD) of each species of calcareous green algae and of seagrass epiphytes measured in this
892 study, and associated mol % MgCO$_3$ composition of high-Mg calcite and Low-Mg calcite. Note that only a single sample of
893 *R. phoenix* and one bulk *T. testudinum* sample were analysed (and hence no SD given), and that only one of the samples
894 from each of *H. incrassata* and *P.dumetosus* specimens contained any LMC (so again no SD given for those values).

Habitat	CaCO$_3$ production (kg/habitat/yr)	Proportion of carbonate phases produced			Total production by carbonate phase (kg/yr)		
		Aragonite	HMC	LMC	Aragonite	HMC	LMC
Fringe mangrove	478	0.95	0.05	0.00	452	25	1
Hardground	137,034	0.96	0.03	0.01	131,598	4,301	1,135
Bare sand/sparse algae	149,197	0.78	0.21	0.01	116,972	31,308	917
Sparse s/grass	428,117	0.44	0.55	0.02	187,706	233,799	6,611
Med seagrass	99,021	0.31	0.67	0.02	30,718	66,608	1,694
Dense s/grass	166,775	0.21	0.77	0.02	35,329	128,348	3,099
Bioturbated muds[1]	0	-	-	-	0	0	0
Patch reefs[2]	0	-	-	-	0	0	0
Oolite shoals[1]	0	-	-	-	0	0	0
TOTAL (kg)	980,621			**Total (kg)**	**502,775**	**464,389**	**13,457**
				%	**51.27**	**47.36**	**1.37**

[1] Algae and seagrass essentially absent in this habitat and no surveys conducted after initial assessments

[2] Not surveyed as mainly coral dominated

Table 5. Total proportions and amounts of aragonite, High-Mg calcite and Low-Mg calcite generated in each habitat as a function of measured mineralogies (Table 4) and plant production calculations.