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# Inshore, turbid coral reefs from northwest Borneo exhibiting low diversity, but high cover show evidence of resilience to various environmental stressors

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For reefs in SE Asia the synergistic effects of rapid land-development, insufficient environmental policies and a lack of enforcement has led to poor water quality and compromised coral health from increased sediment and pollution. Those inshore turbid coral reefs, subject to significant sediment inputs, may also inherit some resilience to the effects of thermal stress and coral bleaching. We studied the inshore turbid reefs near Miri, in northwest Borneo, through a comprehensive assessment of coral cover, health and function in addition to quantifying sediment-related parameters. Although Miri Reefs had comparatively low coral species diversity, dominated by massive and encrusting forms of *Diploastrea*, *Porites*, *Montipora*, *Favites*, *Dipsastrea* and *Pachyseris*, they were characterised by a healthy cover ranging from 22-39%. We found a strong inshore to offshore gradient in hard coral cover, diversity and community composition as a direct result of spatial differences in sediment but over scales of <10 km. As well as distance to shore, we included other environmental variables like reef depth and sediment accumulation/size that explained 62.5% of variation in benthic composition among sites. None of the reefs showed evidence of coral disease and relatively low prevalence of compromised health signs including bleaching (6.7%), bioerosion (6.6%), pigmentation (2.2%), scars (1.1%) and mucus production (0.5%). There were, however, seasonal differences in bioerosion rates which increased five-fold after the 2017 wet season. Tagged colonies of *Diploastrea* and *Pachyseris* showing partial bleaching in 2016, had fully recovered by 90-100% the following year. Differences in measures of coral function like that of symbiont density and chlorophyll a for *Montipora*, *Pachyseris* and *Acropora* were not detected among sites. This study provides further evidence that turbid coral reefs

exposed to seasonally elevated sediment loads can exhibit relatively high coral cover and be resilient to disease and elevated sea surface temperatures.

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18

## 19 **ABSTRACT**

20 For reefs in SE Asia the synergistic effects of rapid land-development, insufficient environmental  
21 policies and a lack of enforcement has led to poor water quality and compromised coral health  
22 from increased sediment and pollution. Those inshore turbid coral reefs, subject to significant  
23 sediment inputs, may also inherit some resilience to the effects of thermal stress and coral  
24 bleaching. We studied the inshore turbid reefs near Miri, in northwest Borneo through a  
25 comprehensive assessment of coral cover, health and function in addition to quantifying sediment-  
26 related parameters. Although Miri Reefs had comparatively low coral species diversity, dominated  
27 by massive and encrusting forms of *Diploastrea*, *Porites*, *Montipora*, *Favites*, *Dipsastrea* and  
28 *Pachyseris*, they were characterised by a healthy cover ranging from 22-39%. We found a strong  
29 inshore to offshore gradient in hard coral cover, diversity and community composition as a direct  
30 result of spatial differences in sediment but over scales of <10 kms. As well as distance to shore,  
31 we included other environmental variables like reef depth and sediment accumulation/size that  
32 explained 62.5% of variation in benthic composition among sites. None of the reefs showed  
33 evidence of coral disease and relatively low prevalence of compromised health signs including  
34 bleaching (6.7%), bioerosion (6.6%), pigmentation (2.2%), scars (1.1%) and mucus production  
35 (0.5%). There were, however, seasonal differences in bioerosion rates which increased five-fold  
36 after the 2017 wet season. Tagged colonies of *Diploastrea* and *Pachyseris* showing partial

37 bleaching in 2016 had fully recovered by 90-100% the following year. Differences in measures of  
38 coral function like that of symbiont density and chlorophyll a for *Montipora*, *Pachyseris* and  
39 *Acropora* were not detected among sites. This study provides further evidence that turbid coral  
40 reefs exposed to seasonally elevated sediment loads can exhibit relatively high coral cover and be  
41 resilient to disease and elevated sea surface temperatures.

42

## 43 INTRODUCTION

44 Turbid reefs are commonly regarded as marginal reefs living near their environmental limits  
45 (Kleypas et al., 1999; Guinotte et al., 2003; Perry and Larcombe, 2003; Palmer et al., 2010;  
46 Goodkin et al., 2011). As such, these reefs are traditionally perceived to be in a reduced health  
47 status (Kleypas, 1996; Kleypas et al., 1999) and more sensitive to rising sea surface temperatures  
48 (SST; Nugues and Roberts, 2003; Crabbe and Smith, 2005; Fabricius, 2005; Woolridge, 2008).  
49 Yet there is growing evidence that these reefs may actually be more resilient to future climate  
50 change effects (Goodkin et al., 2011; Morgan et al., 2017) and serve as future refugia for corals  
51 (Cacciapaglia and van Woesik, 2015;2016; Morgan et al., 2016). This has been  
52 demonstrated on turbid reefs with high coral cover and diversity yet experience significant  
53 sediment and nutrient inputs, low bleaching, and rapid recovery rates from bleaching and  
54 cyclonic events (Larcombe et al., 2001; Browne et al., 2010; Richards et al., 2015; Morgan et al.,  
55 2016). Studying the level of resilience and survival of turbid reefs in different environmental  
56 settings will provide clearer insights into the structure of reefs subject to climate change  
57 (Guinotte et al., 2003; Hennige et al., 2010; Richards et al., 2015).

58

59 Despite elevated resilience to naturally turbid conditions, many inshore turbid reefs face threats  
60 from local pressures, largely related to declining water quality and increased sediment input. In  
61 South East (SE) Asia, 95% of reefs are threatened from local threats (Burke et al., 2011) and are,  
62 therefore, regarded as the most endangered reefs globally. Since the 1980's these reefs have  
63 suffered an average 2% loss in coral cover with hard coral cover declining from 45% to 22% in  
64 2003 (Bruno et al. (2007). Most reefs in SE Asia are located in close proximity to countries with  
65 rapidly emerging economies and fast population growth (Wilkinson, 2006; Burke et al., 2011;  
66 Heery et al., 2018). They are further characterised by poorly developed environmental policies,  
67 inadequate regulation, lack of enforcement, a shortage of institutional and technical capacity,

68 insufficient community support and involvement, and conflicts and tensions between  
69 stakeholders (Fidelman et al., 2012). The synergistic effects of these factors has led to poor  
70 water quality on many inshore reefs via pollution and sediment input derived by rapid land  
71 development, and over-fishing activities (McManus, 1997; Wilkinson, 2006). As a consequence,  
72 sedimentation rates are high ( $>10 \text{ mg cm}^2 \text{ day}^{-1}$ ) with SE Asian coastal systems experiencing the  
73 highest siltation loads globally (Kamp-Nielsen et al., 2002; Syvitski et al., 2005).

74

75 Nearshore coral reefs along the north central section of Sarawak, on the island of Borneo, are  
76 highly diverse with an estimated 518 fish species (Shabdin, 2014) and 203 hard coral species of  
77 66 genera (Elcee Instrumentation Sdn Bhd, 2002). Sarawak is a deforestation hotspot with only  
78 3% of its forest cover intact (Bryan et al., 2013). Ongoing deforestation and poor land use  
79 practices are a growing threat for these biological diverse reefs that also support local fisheries  
80 and an expanding dive tourism industry (Elcee Instrumentation Sdn Bhd, 2002). As such, in 2007  
81 a marine park (the Miri-Sibuti Coral Reef National Park; MSCRNP) that covered 11,020  $\text{km}^2$   
82 was established to promote and protect 30 coral reefs adjacent to Miri, the second largest town in  
83 Sarawak. In 2001, a broad assessment of coral reef health within the park indicated that live coral  
84 cover was approximately 35-50% and dead coral cover was 0.5% (Elcee Instrumentation Sdn  
85 Bhd, 2002). Subsequent Reef Check surveys in 2010 and 2014 concluded these same reefs were  
86 experiencing multiple stressors, but were in 'fair' condition (Reef Check, 2010;2014). However,  
87 despite these claims there is limited quantitative data on coral health and biodiversity (Shabdin,  
88 2014), and no comprehensive assessment of environmental drivers of reef health. For example,  
89 the Baram River (10 km north of the reef complex), is known to discharge  $2.4 \times 10^{10} \text{ kg yr}^{-1}$  of  
90 sediments into the coastal zone (Nagarajan et al., 2015), such that sediment and nutrient influx  
91 are considered to be the greatest threat to these poorly studied reefs (Pilcher and Cabanban,  
92 2000; Ferner, 2013; Shabdin, 2014). Without a thorough assessment of sediment impacts on  
93 corals, no conclusions can be made as to their tolerance levels, the drivers of community  
94 composition and future resilience to both local and global pressures. Given the Baram River  
95 delta is in a destructive phase due to rising sea level (Lambiase et al., 2002), rainfall events that  
96 have increased in intensity and frequency, and plans for future modification of both the river and  
97 increased land development (Nagarajan et al., 2015), it is likely that threats from sediments will  
98 only increase.

99

100 The reefs within the MSCRNP provide a valuable opportunity to address several knowledge gaps  
101 on turbid coral reef health and their resilience to local and global threats. The last comprehensive  
102 assessment of coral cover on Miri's reefs was in 2001, with no assessments of coral taxa health  
103 and disease for any Sarawak reefs recorded to date. In particular, coral disease studies are rarely  
104 undertaken on SE Asian reefs largely due to a lack of resources and expertise (Green and  
105 Bruckner, 2000; Raymundo et al., 2005; Heintz et al., 2015). The lack of quantitative data on the  
106 health and stability of these reefs coupled with ongoing unsustainable land use practices in  
107 Sarawak raises concerns over their long-term viability. This is of particular concern as Sarawak  
108 reefs, currently provide an estimated revenue of 6 million AUD per year in tourism and 13.5  
109 million AUD from fisheries (Elcee Instrumentation Sdn Bhd, 2002). We argue there is an urgent  
110 need for a comprehensive assessment of coral cover, health and function measured alongside key  
111 environmental and sediment-related parameters. The key objectives of this study therefore are  
112 to: 1) quantify benthic cover, coral cover and health, 2) compare the prevalence of impaired  
113 health in the dominant coral species, 3) identify key parameters related to sediment delivery that  
114 influence benthic cover and health along an inshore to offshore gradient, and 4) assess how  
115 resilient these inshore reefs are to future changes in sediment supply. These data will improve  
116 our understanding of why turbid coral reefs are resilient and promote current management  
117 strategies that aim to protect inshore turbid reefs from future changes to land use and highlight  
118 the value of these poorly studied reefs.

119

## 120 **MATERIALS & METHODS**

### 121 **Study sites**

122 The study was conducted on three reefs (Eve's Garden, Anemone Garden and Siwa Reef) in the  
123 MSCRNP (Fig. 1). These sites were of a comparable depth (5-15 m) and size (<0.11 km<sup>2</sup>), and  
124 had 30-50% coral cover (Elcee Instrumentation Sdn Bhd, 2002). Eve's Garden (EG) is a shallow  
125 inshore reef close to shore (7.3 km) with a coral community dominated by platy and massive  
126 corals such as *Pachyseris* sp. and *Porites* sp. (Ferner, 2013). Anemone's Garden (AG) is further  
127 offshore (11.7 km) and consists of a considerable density of anemone colonies, with platy forms  
128 of *Acropora* sp. and exceptionally large massive *Porites* sp. and *Diploastrea* sp. colonies (1-5 m  
129 length). Siwa Reef (SW) situated further to the south is the most biologically diverse of the

130 studied reefs consisting of encrusting and massive coral forms (Ferner, 2013). These reefs lie on  
131 an inshore to offshore transect from the Baram (sediment influx  $2.4 \times 10^{10}$  kg.year<sup>-1</sup>; Nagarajan  
132 et al., 2015) and Miri River mouths, located to the north of EG (10 km from Miri river and 30  
133 km from Baram river).

134

135 Physical (temperature, light, turbidity and sediment accumulation) and biological (benthic cover,  
136 coral health) data were collected at the end of the dry season (15<sup>th</sup> September to 20<sup>th</sup> October  
137 2016) and during the wet season (11<sup>th</sup> May to 3<sup>rd</sup> June 2017). At each of the three reefs, six  
138 replicate line transects (20 m), separated by 20 m intervals were run across the reef surface (EG  
139 = 8-12 m, AG = 10-14 m, SW = 8-14 m).

140

#### 141 **Physical data collection**

142 Seasonal changes in light (Odyssey, New Zealand) and temperature (HOBO, Australia) were  
143 recorded at EG every 10 minutes from September 2016 for 9 months (temperature) and 12  
144 months (light). In addition, turbidity loggers were deployed for two weeks at the end of the 2016  
145 dry season (September; EG and SW) and end of the 2017 wet season (May; EG; AQUAlogger  
146 210/310TY, Aquatech, UK) to capture changes in suspended sediment loads over a tidal cycle.  
147 Data on cloud cover, rainfall and windspeed over the period from October 2016 to October 2017  
148 was retrieved from the database [worldwideweatheronline.com](http://worldwideweatheronline.com)

149

150 To assess small-scale spatial variation in sediment accumulation, four sediment traps per three  
151 transects (8 traps in total per reef) were deployed at each reef in September 2016 to collect  
152 sediments during the NE monsoon. Each trap consisted of 3 cylindrical PVC plastic containers  
153 (diameter of 7.6 cm) attached to a metal rod 30 cm above the substrate (Storlazzi et al., 2009).  
154 The traps remained *in-situ* until May 2017. To determine if trapped sediments were from local  
155 resuspension or transported on to the reef, 500 g of benthic sediment at the base of each trap was  
156 sampled. The content of each container was emptied into a labelled ziplock bag and stored at -20  
157 °C until further analysis at the Curtin University Sarawak Laboratory facilities (Laboratory SK2  
158 204), Malaysia.

159



160 Sediment samples were analysed for weight and particle size characteristics. Frozen samples  
161 were thawed and allowed to settle overnight. Water remaining on the surface was filtered (0.45  
162 nm filter paper) to capture the fine suspended sediments. The sediments (settled and filtered)  
163 were oven-dried at 60°C for 2-3 weeks and weighed to the nearest 0.001 g. Sedimentation  
164 accumulation rate ( $\text{g cm}^2 \text{day}^{-1}$ ) was calculated as the weight trapped (g) divided by the number  
165 of days the trap was deployed and the surface area of the trap ( $\text{cm}^2$ ). For the grain size analysis,  
166 the settled dry sediments were manually homogenized and weighed before sieving to remove  
167 aggregates of particles. Sediments were separated into 5 class fractions (1 mm, 500  $\mu\text{m}$ , 250  $\mu\text{m}$ ,  
168 125  $\mu\text{m}$  and 63  $\mu\text{m}$ ) by placing the sieve stack on a mechanical shaker for 20 minutes. Each of  
169 the 5 sediment fractions were weighed to the nearest 0.001 g.

170

## 171 **Biological data collection**

### 172 *In water data collection*

173 The benthic cover and diversity (to genus level) were assessed in September 2016 using the  
174 photographic transect method (Bégin et al., 2013). Photographs were taken using a Canon  
175 Powershot G7 mark 11 digital camera at a fixed height of 0.75 m above the transect line every 1  
176 m along the transect ( $n=21$ ). Coral Point Count with a grid of 25 points was used to calculate  
177 benthic cover for each category (hard coral, soft coral, dead coral, algae on rock, algae on rubble,  
178 algae on coral, sponge, abiotic substance), (CPCe; Kohler and Gill, 2006). The hard coral  
179 category was further subdivided into 38 genera common in the Indo-Pacific region according to  
180 Kelley (2009).

181

182 To assess seasonal fluctuations in coral reef health, signs of compromised health (disease,  
183 bleaching, bioerosion, pigmentation, mucus production, scars) were recorded in September 2016  
184 and May 2017. The belt transect methodology was used, covering a wider area along the transect  
185 line via a zig-zag pattern ( $40 \text{ m}^2$  for each 20 m transect). Coral colonies within each belt transect  
186 were identified to genus level and classified as either healthy or affected by an impaired health  
187 sign (Beeden et al., 2008). Bleaching was further subdivided into whole, partial, focal and non-  
188 focal bleaching. To determine if bleached corals recover or die, a total of 14 coral colonies from  
189 EG and SW in both sampling seasons that showed signs of bleaching were tagged and  
190 photographed (4 *Diploastrea*, 6 *Pachyseris*, 4 *Porites*). The percentage of bleached tissue was

191 assessed from scaled photographs using CPCe software (1=normal, 2=pale, 3=0-20%, 4=20-  
192 50%, 5=50-80% and 6=80+% bleached).

193

#### 194 ***Symbiont density and chlorophyll a analysis***

195 In May 2017, fragments of three coral species (*Montipora sp.*, *Pachyseris sp.* and *Acropora sp.*)  
196 were collected from EG, AG and SW for chlorophyll *a* and symbiont density analysis.

197 Fragments (5-10 cm for branching corals and ~10 x 10 cm for foliose corals) were collected  
198 using cutters and placed in ziplock bags. Samples were placed on ice during transportation back  
199 to the laboratory where they were stored at -80°C until further analysis. Symbiont density and  
200 chlorophyll *a* content were quantified following the removal of coral tissue from the skeleton.  
201 The protocol for extracting tissue was adapted from Ben-Haim et al. (2003) (Supplementary  
202 material).

203

#### 204 **Statistical analysis**

205 Univariate statistical analysis was conducted in R Studio Desktop version 1.1.383. Prior to  
206 analysis, normal distribution and homogeneity of variances were checked using the Shapiro Wilk  
207 test and the Levene's test, respectively. To assess if there were significant differences in benthic  
208 cover (hard coral, soft coral, algae) and diversity among sites a one way analysis of variance  
209 (ANOVA,  $n=6$ ,  $\alpha=0.05$ ) was used followed by a Tukey HSD post-hoc test (Bonferroni  
210 method), if necessary. Significant differences in the prevalence of compromised health signs  
211 (bleaching, bioerosion, mucus production, pigmentation and scars) among sites and between  
212 seasons were identified for both total hard coral cover and for the most abundant coral species  
213 (*Porites*, *Pachyseris*, *Montipora*, *Diploastrea*, *Acropora*) using a Full Factorial ANOVA (FF  
214 ANOVA,  $n=6$ ,  $\alpha=0.05$ ) and a Tukey HSD post-hoc test. If required, a log<sub>10</sub> transformation  
215 was carried out for datasets to meet homogeneity of variance. To recognize differences in  
216 physiology (chlorophyll *a* content and zooxanthellae density) between the three coral species  
217 sampled (*Acropora*  $n=17$ , *Pachyseris*  $n=13$ , *Montipora*  $n=15$ ) and across sites, a non-parametric  
218 Kruskal Wallis test was performed. Furthermore, to evaluate cell health differences between the  
219 three genera and among reefs, the percentage of cells from each grade were compared using the  
220 Kruskal-Wallis test. Differences in sediment accumulation rates among reefs (Kruskal – Wallis)

221 and particle size characteristics (median, fine/course fraction) among reefs and between the  
222 trapped sediments and the benthic sediments were also tested (FF ANOVA, n=18).

223

224 Permutational multivariate analysis was conducted in PRIMER-7 version 7.0.13. A Distance-  
225 based Linear Model (DISTLM) was used to determine how much of the variation in community  
226 assemblage (hard coral cover=HCC, soft coral cover=SCC, algae, dead coral cover=DCC, H'  
227 index, number of coral genera) among transects and reefs was driven by distance from the two  
228 nearby river mouths, distance from shore and differences in sediment accumulation rates and  
229 particle size characteristics. A distance- based resemblance matrix was created for the biological  
230 data set using Bray- Curtis similarity values following a square-root transformation and for the  
231 environmental data using Euclidean distances and normalised values. A DISTLM, using the  
232 BEST fit model with the Akaike's Information Criterion (AIC) and 9,999 permutations was  
233 performed using the resemblance matrices. The multivariate scale relationship between the  
234 predictor (environmental) and response variables (biological) was presented on a plot with a  
235 distance- based redundancy analysis (dbRDA; Legendre and Anderson, 1999). To investigate  
236 whether environmental factors contributed to differences in health status among sites again a  
237 DISTLM model was used followed by dbRDA plotting as above. Predictor variables included  
238 substrate structure (hard coral cover (HCC), diversity) and physical conditions (depth, sediment  
239 accumulation rate, particle size characteristics, distance from both river mouths and distance  
240 from shore). HCC and diversity were used since higher HCC contributes to a greater probability  
241 of impaired coral health. Similarly more diverse reefs can lead to a greater susceptibility to  
242 disease as certain genera are more or less resilient (Mydlarz et al., 2010). As sediment data were  
243 obtained at the end of the wet season (May 2017), these were used to explain the 2017 health  
244 data. For the 2016 coral health data, which had no associated sediment data, only the substrate  
245 structure predictors were used as well as distance from shore and rivers.

246

247

## 248 **RESULTS**

### 249 *Physical parameters*

250 The dry season was characterized by less variable, warmer SSTs (mean monthly range = 30.0 to  
251 30.7°C; sup Fig. 2), greater in-water light penetration (mean monthly range at EG = 156 to 320  
252 PAR) and reduced rainfall (mean monthly rainfall range = 78 to 166 mm) and cloud cover (Fig.

253 2). In contrast, the wet season was cooler (mean monthly range = 28 to 30.1 °C) with higher  
254 rainfall (mean monthly range 126 to 234 mm) and reduced light levels on the reef (mean monthly  
255 range at EG = 19 to 150 PAR). Wind speeds were also slightly elevated during the wet season  
256 months (Fig 2d). Sediment accumulation rates following the wet season were above 10  
257 mg.cm<sup>2</sup>.day<sup>-1</sup> (a level considered a coral sedimentation threshold; Rogers, 1990) with a rate  
258 almost three times higher at EG compared to AG and SW (Chi-square = 10.3, df = 2, p<0.005;  
259 Fig 3). Site differences in potential sediment load were also observed during the dry season with  
260 higher and more variable turbidity recorded at the nearshore EG reef (mean monthly range = <1  
261 to 24 FTU) than at SW (mean monthly range = 1-7 FTU) located 10 km further south from the  
262 large Baram river mouth (sup Fig. 3).

263

264 All three reefs were dominated by sand (>98%), with the median particle size of benthic  
265 sediments significantly increasing (F=13.6, df=2, p<0.005) with distance from the mouths of the  
266 Baram and Miri rivers (Fig. 4). Benthic sediments at SW comprised 58% of very course sand,  
267 nearly three times that of EG (20%) (F=24.9, df=3, p<0.001; PH: SW>EG,AG) and a  
268 significantly smaller proportion of medium/fine sands (F=17.2, df=2, p=<0.001; PH:  
269 SW>AG>EG). In contrast there was little difference in the median particle size from the  
270 sediment traps among sites (F=2.25, df=2, p=0.133), although particle sizes of the benthic  
271 sediment were significantly greater compared to the trapped sediments (F=60.93, df=1,  
272 p<0.001).

273

#### 274 ***Benthic cover***

275 Hard coral cover increased with distance from the major sediment source (Baram River) and  
276 varied significantly among sites (F=5.3, df=2, p=0.01; PH: SW>EG). SW had the highest HCC  
277 (39.3%) and EG almost half the HCC (21.9%; Fig. 5). Soft corals also varied significantly but  
278 declined with increasing distance from the major sediment source (Chi-Square = 8.6, df=2,  
279 p=0.01; MWPH: EG>AG, SW) with EG having nearly 15-fold higher cover than SW. A large  
280 percentage (52-57%) of all reefs' benthos were occupied by algae comprised of both fleshy and  
281 filamentous types which trapped sediments (F=0.103, df=2, p>0.05)

282

283 In total 28 genera were recorded (Table 1). Coral diversity was considerably different among  
284 sites ( $F=4.6$ ,  $df=2$ ,  $p=0.03$ ; PH: SW>EG) with SW the highest richness (1.93) with 25 genera,  
285 and EG and AG 16 and 14 genera, respectively (richness  $\sim 1.4$ ). The surveyed sites were  
286 composed of similar communities, with most dominant genera including *Diploastrea sp.*, *Porites*  
287 *sp.*, *Montipora sp.*, *Favites sp.*, *Dipsastrea sp.* and *Pachyseris sp.* (Table 1). All other species  
288 comprised a small fraction of the community ( $<2\%$  cover). Most notable differences in the  
289 composition were with the high cover of *Diploastrea sp.* at AG and EG, *Galaxea sp.* at EG, and  
290 *Acropora* and *Montipora sp.* at SW.

291

### 292 ***Coral reef health***

293 Of the compromised health signs recorded at each reef, the five most commonly observed were  
294 mucus production ( $0.5 \pm 0.3\%$ ), pigmentation ( $2.2 \pm 0.7\%$ ), bioerosion ( $6.6 \pm 2\%$ ), bleaching  
295 ( $6.7 \pm 0.9\%$ ) and scars ( $1.1 \pm 0.4\%$ ; Fig. 6). No diseases *per se* were observed except for one  
296 colony of *Porites* with ulcerative white spots at EG. Despite a clear decline in prevalence along  
297 an inshore to offshore gradient following the dry season in 2016 (Fig. 7) total prevalence of  
298 compromised health (sum of the five commonly observed signs) was not statistically significant  
299 among sites and seasons ( $p>0.05$ ; Table 2). However, the prevalence of mucus production by  
300 corals at Eves Garden was nearly five times (5%) that of other reefs ( $F=3.6$ ;  $df=2$ ;  $p<0.05$ ;  
301 EG<AG, SW), and SW recorded the lowest levels of pigmentation prevalence (Fig 7b; Table 2;  
302  $F=5.3$ ;  $df=2$ ;  $p<0.05$ ; AG>SW). In contrast, bioerosion was comparatively similar among sites  
303 within each season, but increased five-fold from  $2.7 \pm 0.6\%$  to  $10 \pm 1.3\%$  following the 2017 wet  
304 season (Table 1;  $F=20.2$ ;  $p<0.001$ ; 2017>2016). During both seasons, overall bleaching  
305 prevalence remained low ( $\leq 10\%$ ) with partially bleached the most common form and whole  
306 bleaching the least observed (sup Fig. 4). Bleaching prevalence declined from  $8.1 \pm 1.4\%$   
307 following the dry season to  $5.4 \pm 1.1\%$  in the wet season. Although this decline was not  
308 statistically significant ( $F=3.3$ ;  $p=0.08$ ), the recovery of bleached corals that had been tagged the  
309 year before was significant ( $V=78$ ,  $p=0.002$ ) with the average bleaching scale dropping from  $3.9$   
310  $\pm 0.4$  to  $1.6 \pm 0.2$  (Fig. 8). All *Diploastrea* and *Pachyseris* colonies recovered by 90-100%  
311 following the wet season.

312

313 Patterns of compromised health differed among five representative coral genera (*Acropora sp.*,  
314 *Montipora sp.*, *Pachyseris sp.*, *Diploastrea sp.* and *Porites sp.*). *Acropora sp* displayed the least  
315 signs of stress in both seasons (<3.5%). *Porites sp.* were the most compromised (2016 =  $50.8 \pm$   
316  $6\%$ ; 2017 =  $72 \pm 5\%$ ; Fig. 9) and the only coral genera with a significant increase in stress  
317 symptoms ( $p=0.004$ ), as a result of an increase in bioerosion by 40% after the wet season  
318 ( $F=10.17$ ;  $df=1$ ;  $p<0.001$ ; Table 3). *Montipora* and *Diploastrea* also suffered from an increase in  
319 bioerosion between sampling seasons, although this as not statistically significant ( $p>0.05$ ; Table  
320 3). Despite a slight increase in the number of bleached *Porites* corals, bleaching occurrence for  
321 the other four corals declined, most notably for *Pachyseris* (55% to 3%;  $F=9.03$ ;  $df=1$ ;  $p=0.008$ ).  
322 Furthermore, the most abundant genera *Porites* was the only coral to show elevated signs of  
323 pigmentation (>10%) although this health sign was less prevalent at SW, the most offshore site  
324 ( $F=5.3$ ;  $df=2$ ;  $p=0.01$ ; Table 3).

325

326 For the three coral genera, *Montipora*, *Pachyseris* and *Acropora*, there was no difference in  
327 symbiont density (chi-squared = 4.0397,  $df=2$ ,  $p>0.05$ ) and chlorophyll *a* among sites (chi-  
328 squared = 2.3769,  $df=2$ ,  $p>0.05$ ) although SW scored the highest of both measures ( $3.2 \times 10^6 \pm 5.5$   
329  $\text{cells/cm}^2$ ;  $4.94 \pm 0.75 \mu\text{g.cm}^2$ ; Fig. 10a,b). Symbiont density differed among the three coral  
330 genera (chi-square = 23.1,  $df=2$ ,  $p<0.001$ ; MWPH: AC>MT,PH) with *Acropora sp.* scoring four  
331 and five times higher symbiont densities (sup Fig. 5). Over 50% of the symbionts observed  
332 were healthy (stage 1; sup Fig. 6a) with slightly more healthy cells observed at SW (chi-  
333 squared=1.7,  $df=2$ ,  $p>0.05$ ) and marginally more degraded cells (stage 5) observed at AG (chi-  
334 squared=3.4,  $df=2$ ,  $p>0.05$ ). Among genera, *Acropora* had a greater number of healthy cells ( $69$   
335  $\pm 3.9\%$ ) than both *Montipora* ( $49.4 \pm 5$ ) and *Pachyseris* ( $52.6 \pm 4.8$ ; chi-square= 14.4,  $df=2$ ,  
336  $p<0.001$ ; sup Fig. 6b).

337

### 338 ***Drivers of benthic cover and health***

339 Environmental variables (depth, sediment accumulation rate, distances from shore/river mouth,  
340 concentration of silt/fine/coarse particles, median particle size) explained 62.5% of the variation  
341 in benthic composition among reefs. Key drivers ( $p<0.05$ ) were distances from river mouth  
342 (30.3%) and shore (1%), median particle size (16.4%), and sediment accumulation rate (2.3%;  
343 Table 4). Variability among sites was higher than within, with sedimentation rate and particle

344 size a key driver of benthos at EG and AG, and distance of river and shore more closely  
345 associated with SW (Fig. 11a).

346

347 To determine key drivers of coral health, two DistLM models were run. The first model  
348 included health data from both sampling seasons, with six explanatory variables (season, HCC,  
349 diversity, distance from river mouth and shore, and depth). The second model included health  
350 data and sediment related variables following the wet season and sediment trap contents  
351 (sediment accumulation rate, concentration of silt/fine/course sediments, median particle size).  
352 For the first model, year, HCC and diversity significantly explained <31% of the variation in  
353 coral health among transects and sites (Table 5). Sites within a sampling season were separated  
354 along a HCC and diversity gradient (Fig. 11b), with transects at SW typically characterised by  
355 higher HCC and diversity but lower prevalence of scars, pigmentation and bleaching (sup Fig.  
356 7). Furthermore, repeat transects were separated between seasons, with those completed in 2017  
357 recording higher bioerosion, but lower bleaching and pigmentation (sup. Fig. 7), supporting our  
358 previous results. Of the sediment drivers, the BEST model included both silt and the course  
359 sediments, which explained 18% of the variations in coral health in 2017. Higher sediment  
360 accumulation rates, although not statistically significant ( $p=0.06$ ; Table 5) explained 7% of the  
361 variation in health, and were most often associated with higher prevalence of pigmentation,  
362 bioerosion and bleaching (sup Fig. 8).

363

## 364 **DISCUSSION**

365 The three reef sites in the MSCRNP are characterised by healthy coral cover yet low coral  
366 diversity. Average live coral cover among the three reefs was 30%, ranging from 22% at EG to  
367 39% at Siwa Reef. This is lower than reefs to the north in Sabah, where several papers report live  
368 coral cover from 23 to 75% (Pilcher and Cabanban, 2000; Chou and Tun, 2002; Lee, 2007;  
369 Praveena et al., 2012; Waheed et al., 2016), but greater than the average coral cover for the wider  
370 Pacific region, estimated at 22% in 2003 (Bruno and Selig, 2007). Previous assessment of coral  
371 cover in 2000 on the Miri reefs range from 28% (Pilcher and Cabanban, 2000) to 22-58% (Elcee  
372 Instrumentation Sdn Bhd, 2002). Although the higher coral cover reported by the latter study is  
373 most likely an artefact of the methodology used (ex-situ Acoustic Ground Discrimination  
374 System). Regardless, our data would suggest that coral cover has been relatively stable over the

375 last couple of decades. Despite high hard coral cover at levels comparable to both turbid and  
376 clear water reefs (Roy and Smith, 1971; Loya, 1976; Larcombe et al., 2001; Wesseling et al.,  
377 2001; Palmer et al., 2010; Goodkin et al., 2011), diversity was comparatively low (14 to 25  
378 genera per reef) for the Coral Triangle region. Turak and Devantier (2010) reported 391 coral  
379 species on reefs near Brunei (~80 km from Miri), and Teh and Cabanban (2007) reported 120  
380 species within 71 hard coral genera for Banggi Island in Sabah. A comprehensive biodiversity  
381 assessment of all 30 reefs with the MSCRNP in 2000 reported 66 genera (203 coral species;  
382 Elcee Instrumentation Sdn Bhd, 2002). We only observed a third of the number of coral genera,  
383 which may suggest a decline in biodiversity over the last 17 years. However, this report also  
384 found that coral diversity was highly variable among reefs, with an average of 9 coral genera per  
385 transect. It is likely that reefs not surveyed in this study found further to the south as well as in  
386 deeper (15-35 m) offshore waters include several coral species not observed at our shallow  
387 nearshore sites, which are heavily influenced by terrestrial sedimentation from both natural and  
388 anthropogenic processes.

389

390 Low diversity at the surveyed sites is likely the result of poor water quality in the nearshore  
391 shallow coastal zone. Inshore reefs in Miri lie within the 7 to 15 m depth range as such there is a  
392 lack of reef structure within the 1-5 m depth range that is often characterised by a distinct set of  
393 coral species (Morgan et al., 2016; DeVantier and Turak, 2017). This may in part explain lower  
394 coral diversity than on reefs to the north in Brunei and Sabah. However, these inshore reefs are  
395 also characterised by high levels of terrigenous sediments, which can also reduce coral diversity  
396 (Rogers, 1990; Fabricius, 2005; Anthony, 2006). High sediment loads from rivers are typically  
397 correlated with high nutrient loads that can lead to increase in reef algal biomass (De'ath et al.,  
398 2012). Algal cover on all three reefs was high (>50%) and will most likely be competing with  
399 corals for space on the reef. Some coral taxa will be less resilient to both sediments and algal  
400 competition resulting in lower coral diversity (Fabricius et al., 2005; De'ath and Fabricius, 2010).  
401 In Indonesia, Edinger et al. (1998), recorded lowest coral diversity on reefs with algae cover  
402 reaching 46%. Reduced diversity was also attributed to land pollution as well as destructive and  
403 over-fishing practices that destroy the reef structure and reduce fish biomass thereby removing  
404 the top-down control on algal growth (Hughes, 1994; Rogers and Miller, 2006; De'ath and  
405 Fabricius, 2010). In Miri, overfishing as well as poor land management practices have been a



406 long-term concern for the regional government (Elcee Instrumentation Sdn Bhd, 2002) but there  
407 are limited funds to actively protect the reefs (Teh and Teh, 2014). Low diversity does not  
408 necessarily suggest worse reef condition. Typically, low diversity in nature results in lower  
409 resilience (Raymundo et al., 2005) and community stability (Bellwood et al., 2004). Yet there is  
410 growing evidence to suggest that a few but tolerant species can maintain reef resilience to local  
411 and global impacts, and implies that the diversity-resilience links need further investigation  
412 (Bellwood et al., 2004; Fabricius et al., 2005; Nystrom et al., 2008).

413

414 The MSCRNP reef community is representative of turbid reefs in the Indo-Pacific. The dominant  
415 coral species include several genera (*Acropora*, *Montipora*, *Porites*, *Pachyseris*, *Faviidae* and  
416 *Galaxea*) that have been observed on nearshore reefs in Singapore (Chou, 1988; Dikou and van  
417 Woosik, 2006), GBR (Ayling and Ayling, 1991; Larcombe et al., 2001; Browne et al., 2010;  
418 Morgan et al., 2016), Thailand (Tudhope and Scoffin, 1994), Hong Kong (Goodkin et al., 2011)  
419 and Sabah (Pilcher and Cabanban, 2000). These corals are considered to be more resilient to  
420 sediment influx either through: 1) enhanced photo-acclamatory abilities required during periods  
421 of low light (e.g. *Stylophora*; Dubinsky et al., 1984; Browne et al., 2014), 2) active sediment  
422 removal processes by the coral polyp (e.g. *Goniastrea*; Rogers, 1990; Erftemeijer et al., 2012), 3)  
423 enhanced mucus production to remove settled sediments (e.g. *Porites*; Bessell-Browne et al.,  
424 2017) or, 4) morphological advantages that result in greater degree of vertical growth thereby  
425 reducing tissue mortality from sediment burial (e.g. *Acropora* and *Montipora*; Erftemeijer et al.,  
426 2012). There were also distinct differences in the community assemblages observed particularly  
427 between Siwa Reef and Eve's Garden. Siwa Reef was characterised by a mixed assemblage of  
428 branching, foliose and massive corals, whereas Eve's Garden was dominated by massive corals,  
429 such as *Porites* and *Diploastrea*. These coral community differences further suggest that there  
430 are significant differences in environmental drivers (including sediments) over a comparatively  
431 small spatial scale (10 km's).

432

433 The inshore to offshore gradient in hard coral cover, diversity and composition is the result of  
434 spatial differences in sediment related parameters. Over 62% of the variation in benthic cover at  
435 our three reef sites is explained by differences in depth, sediment accumulation rates and  
436 distance from sediment sources as well as sediment particle size characteristics. Consequently,

437 we saw a significant increase in both coral cover and diversity with increasing distance from the  
438 river mouths. Similar observations have been reported from Indonesia and Puerto Rico, where  
439 hard coral cover nearly halved towards shore (Loya, 1976; Edinger et al., 2000), and in Hong  
440 Kong, where inshore coral cover was 20% lower than offshore (Goodkin et al., 2011). Reduced  
441 coral cover may occur due to low larval recruitment as a consequence of limited hard substrate  
442 following sediment settling (Birrell et al., 2005; Fabricius, 2005; Dikou and van Woesik, 2006),  
443 or colony mortality caused by anoxic conditions that occur under sediment layers (Rogers, 1983;  
444 Riegl and Branch, 1995; Wesseling et al., 2001). The sediment particle size and source (marine  
445 versus terrestrial) are considered to be equally if not more important than sediment volume in  
446 assessing the impacts of sediments on coral health. Recent studies show that as the percentage of  
447 terrestrial sediments with higher organic content increases, there are greater declines in coral  
448 cover (Bégin et al., 2016; Fourny and Figueiredo, 2017). Although we did not measure organic  
449 content here, it is likely sediments were transported onto the reef given that the trapped  
450 sediments had a different sediment signature (significantly finer) from the benthic sediments.  
451 Terrestrial sediments reaching reefs at distance of >10 km from the river mouth are typically  
452 composed of clay and finer silt particles (Bainbridge et al., 2012), which would suggest that the  
453 trapped sediments were of terrestrial origin. As such, these data confirm that sediments, most  
454 likely from the Baram and Miri rivers, have influenced coral cover particularly on reefs closest to  
455 the river mouths. The reefs, however, maybe in a temporally stable state given low dead coral  
456 cover and the limited decline in coral cover over the last two decades.

457

458 The prevalence of impaired health signs was low (10-20%), but dominated by bioerosion and  
459 pigmentation with no signs of coral disease (with one exception). These health indicators are  
460 commonly related to high sediment and nutrient influx. High levels of bioerosion in particular  
461 has been linked to land based pollution whereby lower light, due to high turbidity, reduces coral  
462 density (Risk and Sammarco, 1991; Lough and Barnes, 1992) weakening the coral and  
463 increasing susceptibility to bioeroders (e.g. molluscs, worms etc.; Prouty et al., 2017).  
464 Furthermore, high nutrient levels can lead to an increase in the abundance of bioeroding  
465 organisms (Hallock and Schlager, 1986; Prouty et al., 2017). Bioerosion levels were significantly  
466 greater following the wet season when the impact of sediments on the Miri reefs were elevated as  
467 indicated by declines in light and higher suspended sediment loads. Conversely, pigmentation

468 rates were higher following the dry season. Pigmentation is an indicator of immune function in  
469 response to a stressor (Willis et al., 2004; Palmer et al., 2009). These stressors have been related  
470 to settling sediments (Pollock et al., 2014) or lesions from abrasion or scars (Willis et al., 2004),  
471 or for the case of Miri reefs could be due to the elevated SSTs recorded in the region in 2016  
472 leading to the documented bleaching event. Spatially, pigmentation rates were significantly  
473 lower at Siwa, which may suggest that corals at the least sediment impacted site were also less  
474 stressed than at AG and EG. Sediments can also promote diseases in corals (Voss and  
475 Richardson, 2006; Haapkyla et al., 2011; Pollock et al., 2014). Diseases such as Black Band  
476 Disease and White Plaque have been widely observed in the Indo-Pacific (Harvell et al., 2007;  
477 Beeden et al., 2008), but disease occurrence is generally low (~8% of current global records) in  
478 SEA reefs compared to the Caribbean (Green and Bruckner, 2000). Suggested explanations for  
479 this include poor reporting of marine life in such countries and relatively high coral diversity that  
480 might aid in diminishing a quick spread of a disease (Raymundo et al., 2005). At Miri, the more  
481 likely explanation of low to no coral diseases are more resilient individual corals and coral  
482 species, and potentially limited connectivity with nearby coral populations, although this remains  
483 speculative until further work is conducted.

484

485 Hard coral cover and diversity also explained a significant portion of the variation in coral health  
486 among reefs with a higher frequency of impaired health at sites with less coral cover and  
487 diversity. In a recent study by Miller et al., (2015) on reefs in Sabah, four common coral diseases  
488 were observed at varying frequencies (<0.1 to 0.6 per affected colonies in a m<sup>2</sup>) as well as signs  
489 of tissue necrosis and pigmentation responses. Here they found that there was a positive  
490 correlation between disease frequency and coral cover, which suggested that host density was a  
491 key driver of disease prevalence and compromised health. This relationship is due to reduced  
492 distances between colonies, and greater shading and competition by fast growing species as coral  
493 cover increases (Bruno and Selig, 2007). In Miri, we see the reverse trend suggesting that factors  
494 other than host density are driving coral health, most likely variable sediment loads and finer  
495 sediment particles.

496

497 Variable species composition among sites would also partly explain the spatial variation in coral  
498 health. Different coral taxa have variable susceptibilities to bioerosion, bleaching, disease and

499 compromised health (Raymundo et al., 2005; Couch et al., 2014; Heintz et al., 2015). In Miri  
500 signs of pigmentation and bioerosion were most prominent on *Porites* colonies. *Porites* sp.  
501 although typically considered to be a hardier coral taxa (Raymundo et al., 2005) tolerant of  
502 turbid waters, have previously been observed to have the most lesions, highest tissue loss and  
503 pigmentation response (Tribollet et al., 2011; Pollock et al., 2014; Heintz et al., 2015) as well as  
504 being a target for disease (Raymundo et al., 2005). The level of bleaching observed in *Porites* at  
505 Miri was comparable to other abundant corals, but recovery potential was lower, possibly due to  
506 other stress symptoms. Bleaching was the most common sign of impaired health among coral  
507 taxa, most commonly observed in *Pachyseris*, *Porites*, *Montipora*, *Dipsastrea* and *Acropora* (in  
508 declining order). A comprehensive study by Marshall and Baird (2000) of 40 coral taxa on the  
509 GBR found that these coral species were typically highly (>50% bleached or dead) or severely  
510 (>15% dead) susceptible to thermal stress. In contrast, the other five most abundant corals at  
511 Miri (*Diploastrea*, *Favites*, *Galaxea*, *Echinopora*, *Merulina*) are considered to be less sensitive  
512 to rising SSTs (Marshall and Baird, 2000; Guest et al., 2016). However, coral taxa bleaching  
513 susceptibility does vary considerably due to the thermal history of the region. For example,  
514 *Acropora* has been found to be susceptible to bleaching on some reefs (Marshall and Baird,  
515 2000; Pratchett et al., 2013; Hoogenboom et al., 2017), but was less susceptible on other reefs  
516 (e.g. Singapore following the 2010 bleaching event: Guest et al., 2012). Only ~5% of *Acropora*  
517 colonies in Miri showed signs of thermal stress, which would suggest some thermal tolerance to  
518 high SSTs. High levels of algal density are linked to higher thermal stress resistance (Glynn,  
519 1993; Stimson et al., 2002) due to the symbionts providing a greater concentration of  
520 mycosporine-like amino acids that protect corals from UV radiation (Xu et al., 2017). Symbiont  
521 densities measured at Miri were high (mean =  $2.4 \times 10^6$  cells per  $\text{cm}^2$ ) but comparable to corals  
522 on turbid reefs (e.g.  $0.5$  to  $3 \times 10^6$  cells per  $\text{cm}^2$  in Singapore (Browne et al., 2015). However it  
523 was *Acropora* that had significantly higher symbiont density than the more frequently bleached  
524 *Montipora* and *Pachyseris*. Our results clearly indicate that resilience to stress for these corals is  
525 a complex relationship between level and frequency of stress, community composition and their  
526 adaptability.

527

528 In 2016, a severe coral bleaching event occurred in the Indo-Pacific region. The impacts of this  
529 event were thoroughly assessed on the GBR, where over 90% of reefs bleached resulting in the

530 loss of 29% of shallow water coral cover (Great Barrier Reef Marine Park Authority, 2016). In  
531 January to March 2016, SST along the northern shore of Borneo were in the highest 10% of  
532 records since 1990 (Great Barrier Reef Marine Park Authority, 2016). SST reported by NOAA  
533 for Brunei peaked in May to June at 31°C (the bleaching threshold temperature)(Fig. 12). During  
534 this time there was 1 to 2.5 DHW and mid-level bleaching warnings. SST remained at ~30°C  
535 until January 2017. (National Oceanic & Atmospheric Administration, 2018), which agree with  
536 out in-water assessment of SST during September 2016 to early 2017 (Suppl. Fig. 2). This  
537 suggests that corals at Miri were significantly heat stressed during this time period. No in water  
538 assessment of bleaching was conducted in the MSCRNP during the peak SST, but bleaching  
539 rates were low (~10% of colonies bleached), following 5 months of elevated and sustained SST,  
540 and recovery rates were high (>90%). This suggests that these nearshore turbid water reefs are  
541 resilient to high SSTs. There is growing evidence that turbid reefs bleach less severely and  
542 frequently than their clear-water counterparts (Marshall and Baird, 2000; Heintz et al., 2015;  
543 Morgan et al., 2017). Lower bleaching rates on these reefs is possibly due nearshore coral  
544 assemblages more frequent exposure to higher temperatures than their offshore deeper  
545 conspecifics, resulting in the development of adaptive mechanisms (Marshall and Baird, 2000;  
546 Guinotte et al., 2003; Guest et al., 2016; Morgan et al., 2017). It may also be due to lower UV  
547 light penetration that can exacerbate temperature stress (Courtial et al., 2017), or potentially from  
548 higher heterotrophy, which increases the supply of essential metals to the symbionts thus  
549 sustaining them through elevated temperatures (Ferrier-Pagès et al., 2018). This study provides  
550 further evidence that turbid reefs are more resilient to elevated SST, but the mechanism/s that  
551 provide this resilience is currently unclear.

552

## 553 **CONCLUSIONS**

554 In conclusion, the MSCRNP reefs are characterized by relatively high coral cover, low  
555 prevalence of impaired health and are composed of a few but tolerant coral taxa. Low dead coral  
556 cover and almost no decline in coral cover over the last two decades indicates these reefs are  
557 stable despite elevated sediment inputs and regular exposure to thermal stress events. There are,  
558 however, potential risks from proposed coastal and in-land developments given we found that  
559 sediment related parameters have resulted in an on- to offshore gradient in coral cover, diversity  
560 and health. Furthermore, high bioerosion and algae cover indirectly suggests high nutrient influx,

561 most likely from the Baram River. The high prevalence of bioerosion observed in *Porites*  
562 colonies is a concern given that this coral is a key reef framework builder, and declines in *Porites*  
563 health will reduce coral reef complexity and habitat availability for other invertebrate and fish  
564 species. Currently, there is no baseline data on spatial and temporal changes in river outputs and  
565 sediment plume dynamics within the MSCRNP, which is crucial in evaluating future threats to  
566 these reefs. Local management agencies will need to address this knowledge gap if they plan to  
567 develop strategies that address the potential impacts of changing land use on MSCRNP. The  
568 reefs current health state and elevated stress tolerance does, however give hope that these reefs  
569 could be resilient to future climate change but only if local water quality does not deteriorate.

570

571

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580

581

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- 852

# Figure 1

Map of southern south China Sea with enlarged Map of study area, showing locations of the three reefs, Miri city and the closest rivers. (modified from Natural Earth - Free vector and raster map data)

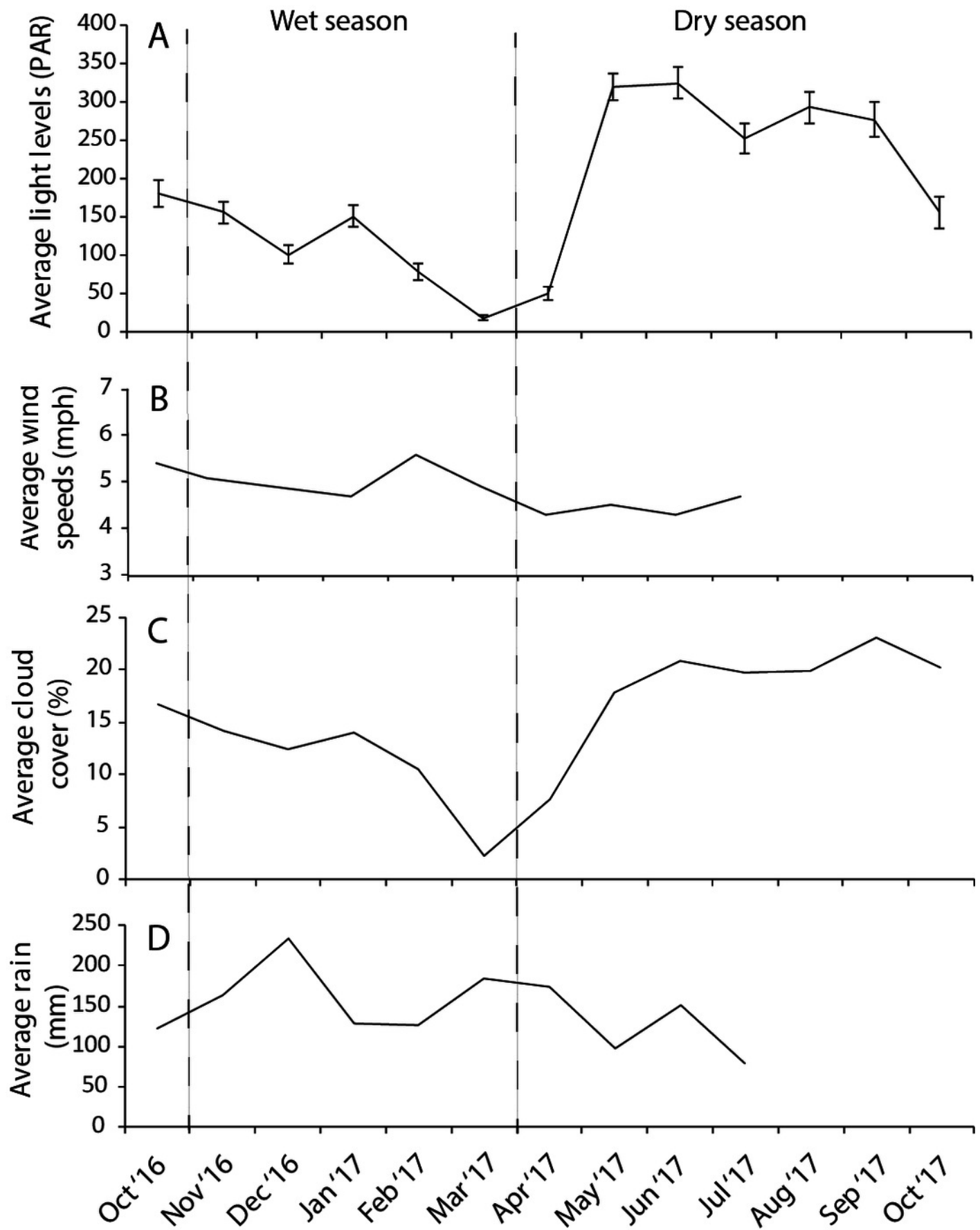


## Figure 2

Average monthly data for (A) light. (B) wind speeds. (C) cloud cover. (D) rain fall. Light data was collected as part of this study whereas wind, cloud and cover data was taken from the [worldwideweatheronline.com](http://worldwideweatheronline.com) website (error bars = SE).

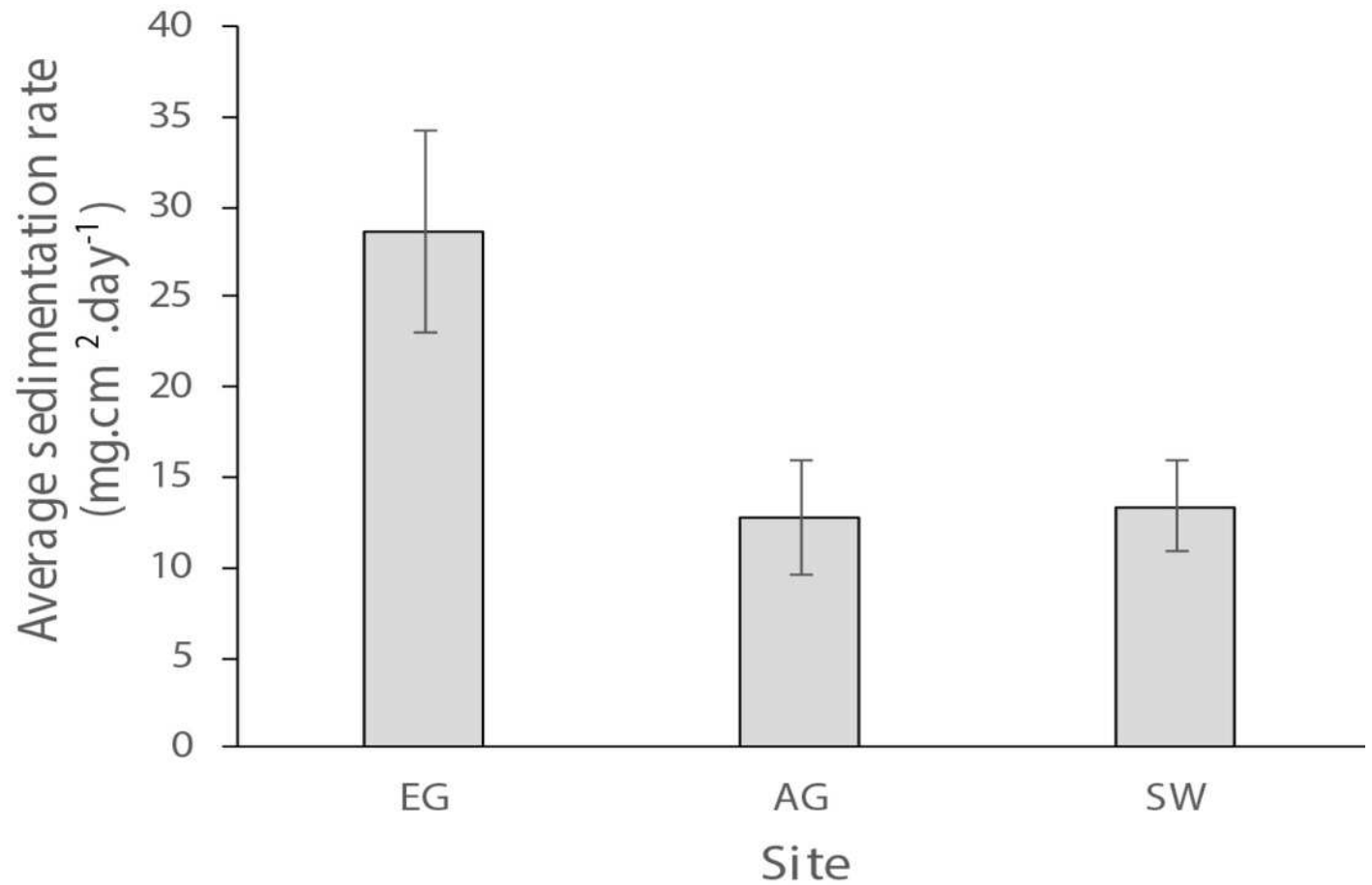
*\*Note: Auto Gamma Correction was used for the image. This only affects the reviewing manuscript. See original source image if needed for review.*





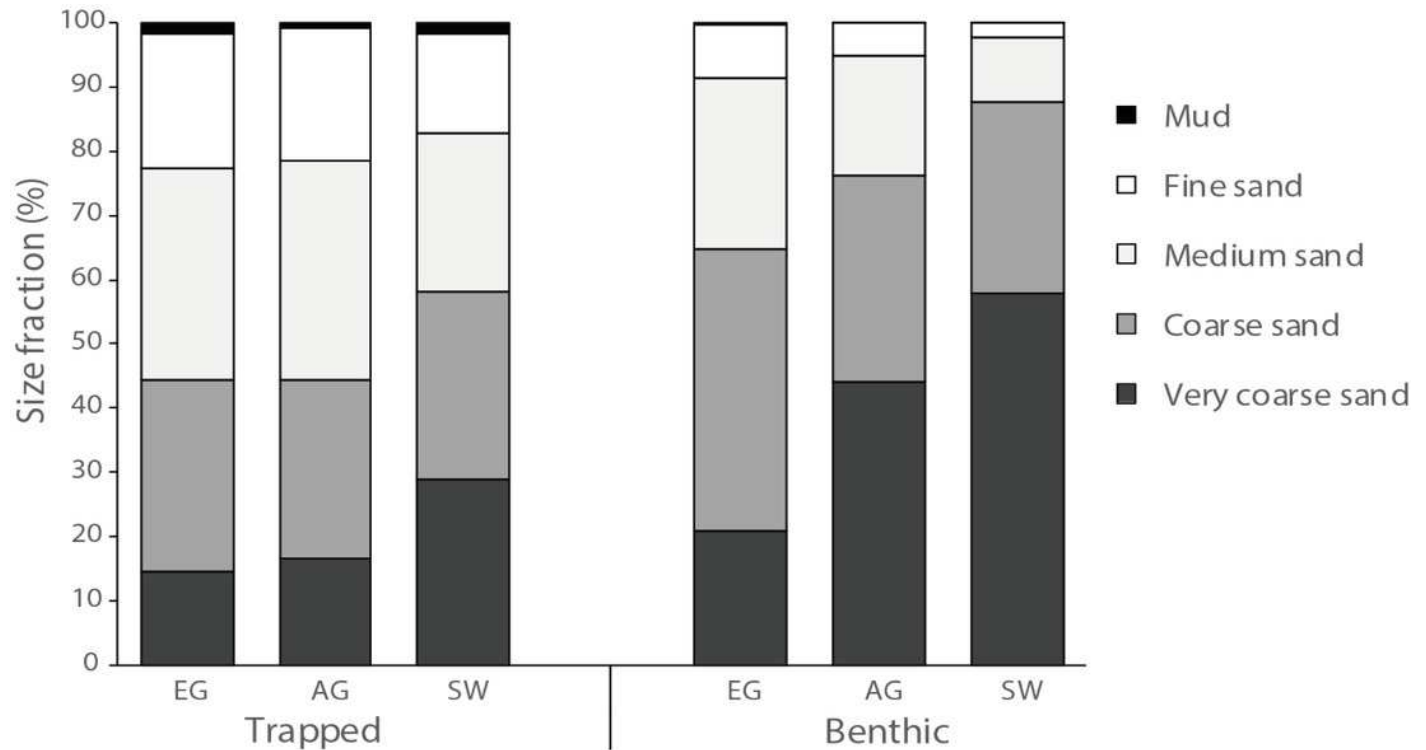
## Figure 3

Average sedimentation rates at the three surveyed sites (error bars = SE).



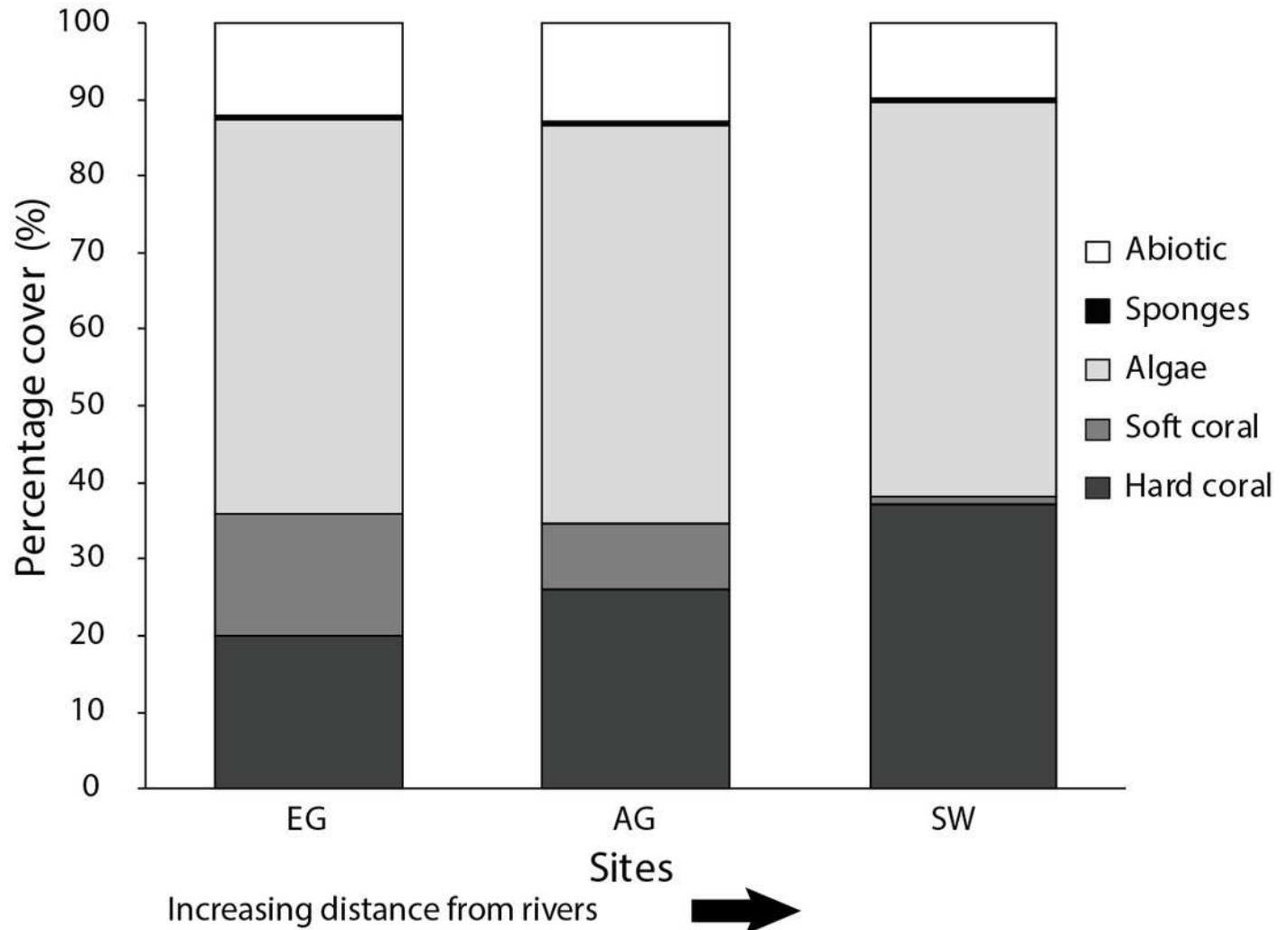
## Figure 4

Particle size data from the sediment traps and the benthos at EG, AG and SW.



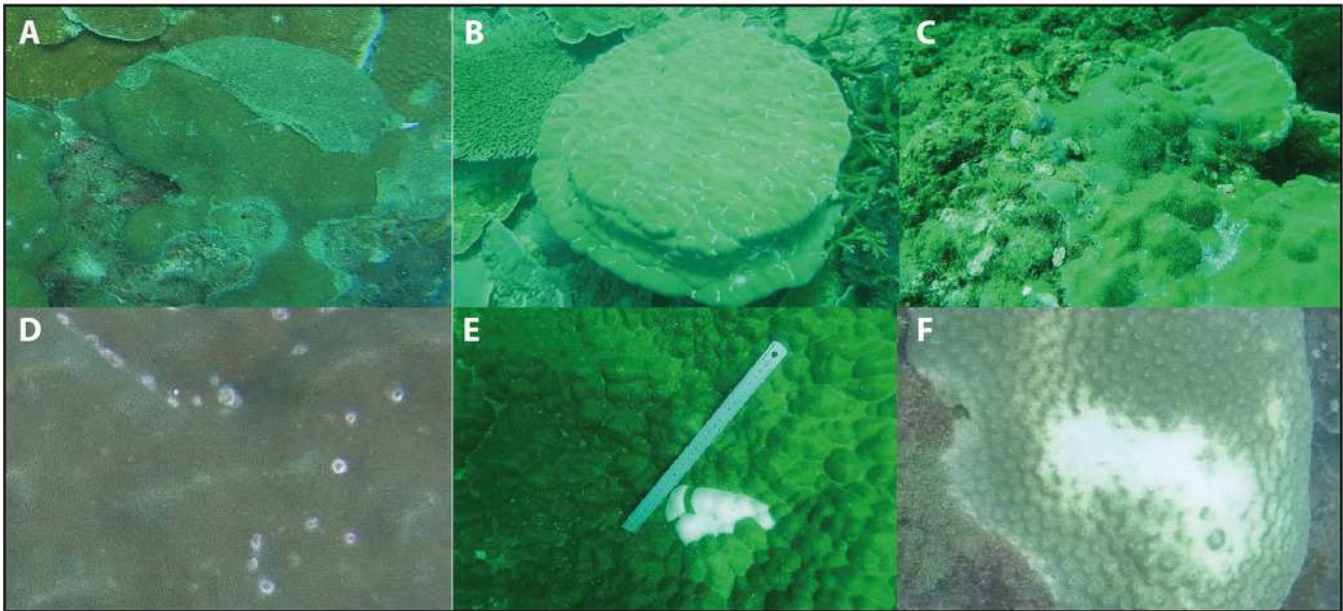
## Figure 5

Average percentage benthic cover at EG, AG and SW. Sites are organised from inshore to offshore.



## Figure 6

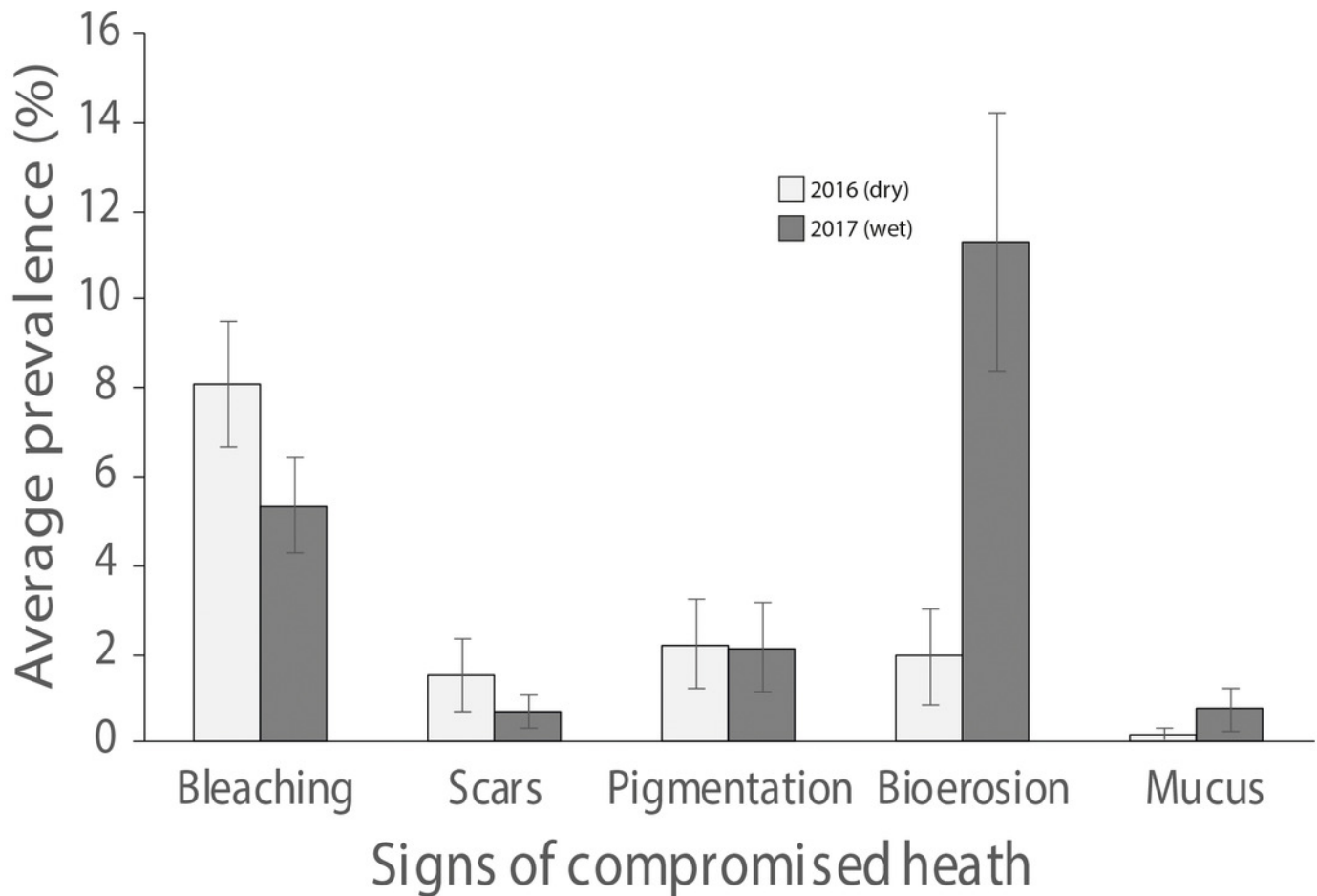
Signs of impaired health. (A) Mucus. (B) Feeding scars. (C) Christmas tree worms and bivalves. (E) Non-focal bleaching. (F) Partial bleaching.



□

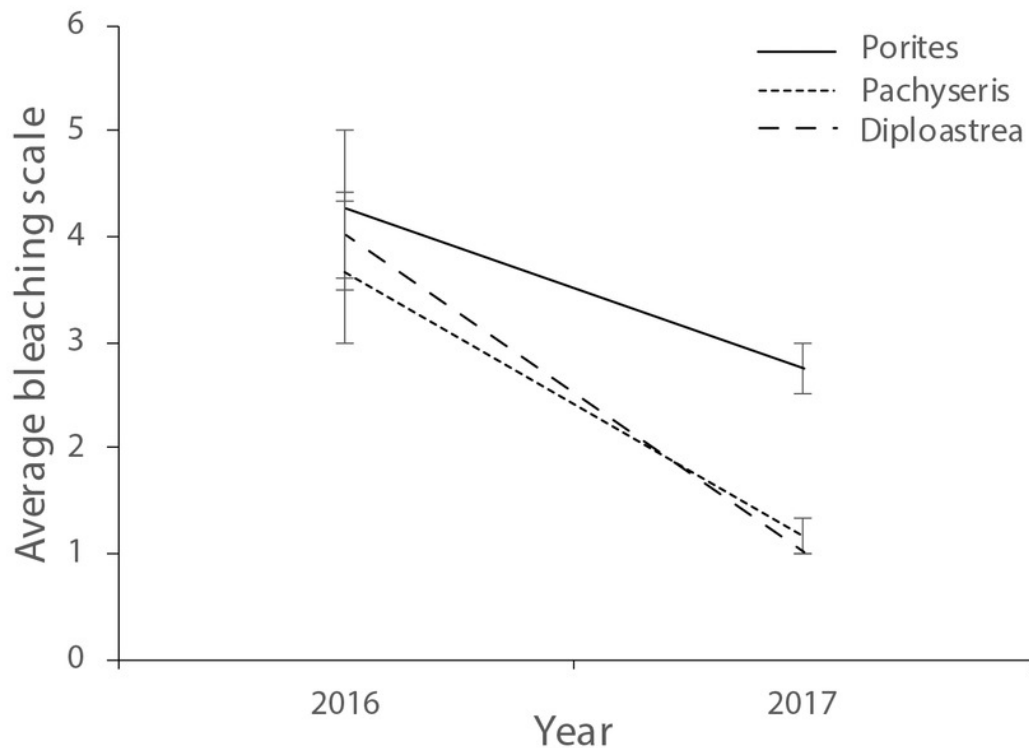
## Figure 7

Average prevalence of the dominant signs of impaired health across all three surveyed sites (EG, AG, SW) following the 2016 dry season and 2017 wet season.



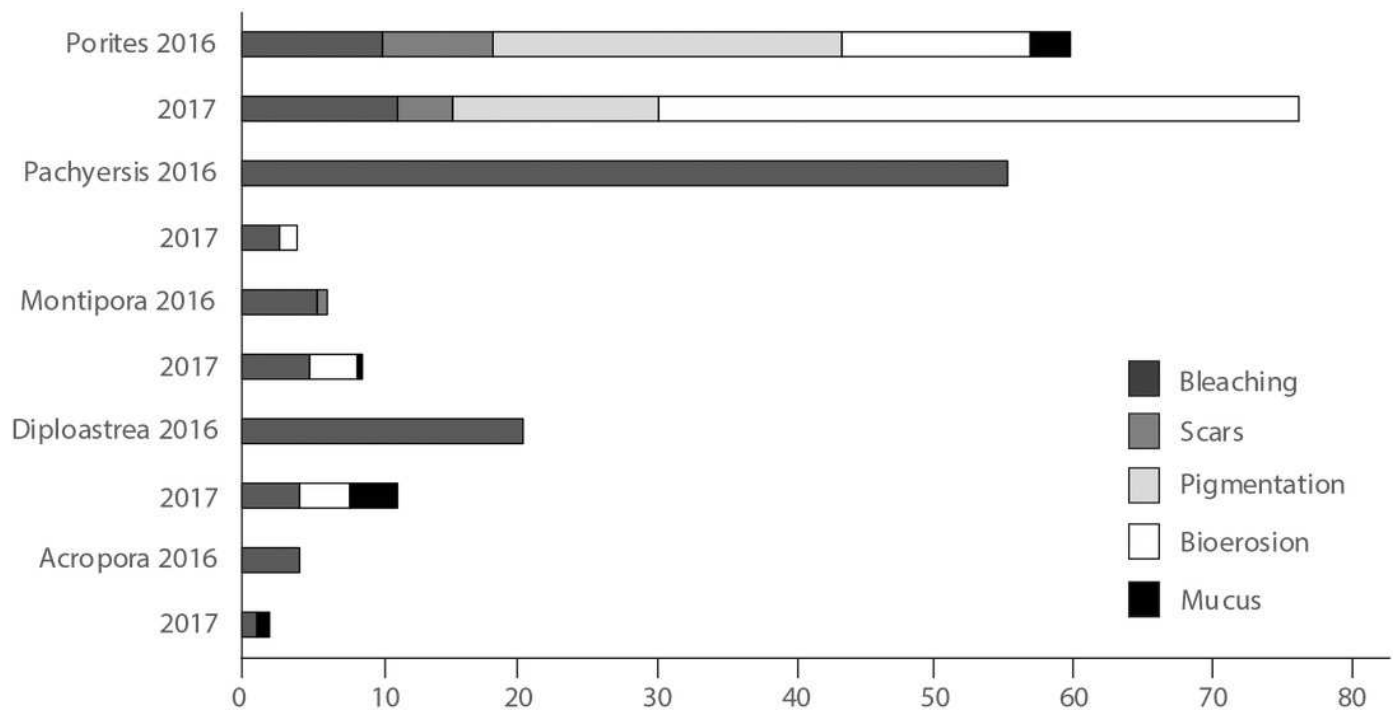
## Figure 8

Average bleaching scale (1=normal, 2=pale, 3=0-20% bleached, 3=21-50% bleached, 4=51-80% bleached, 5=81-100% bleached) for the three coral genus across the three survey sites (EG, AG, SW) that were tagged in September 2016 following on warm dry season and



## Figure 9

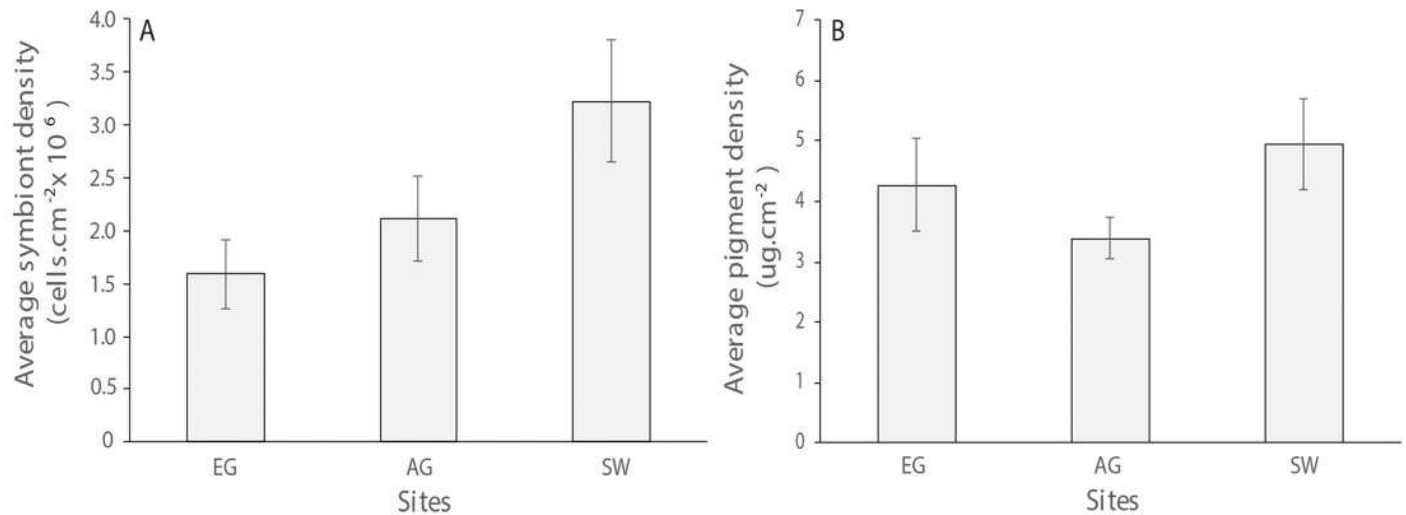
Prevalence of the most common impaired health signs following the 2016 dry season and the 2017 wet season for the five most common observed coral genus across all three sites surveyed (EG, AG < SW).





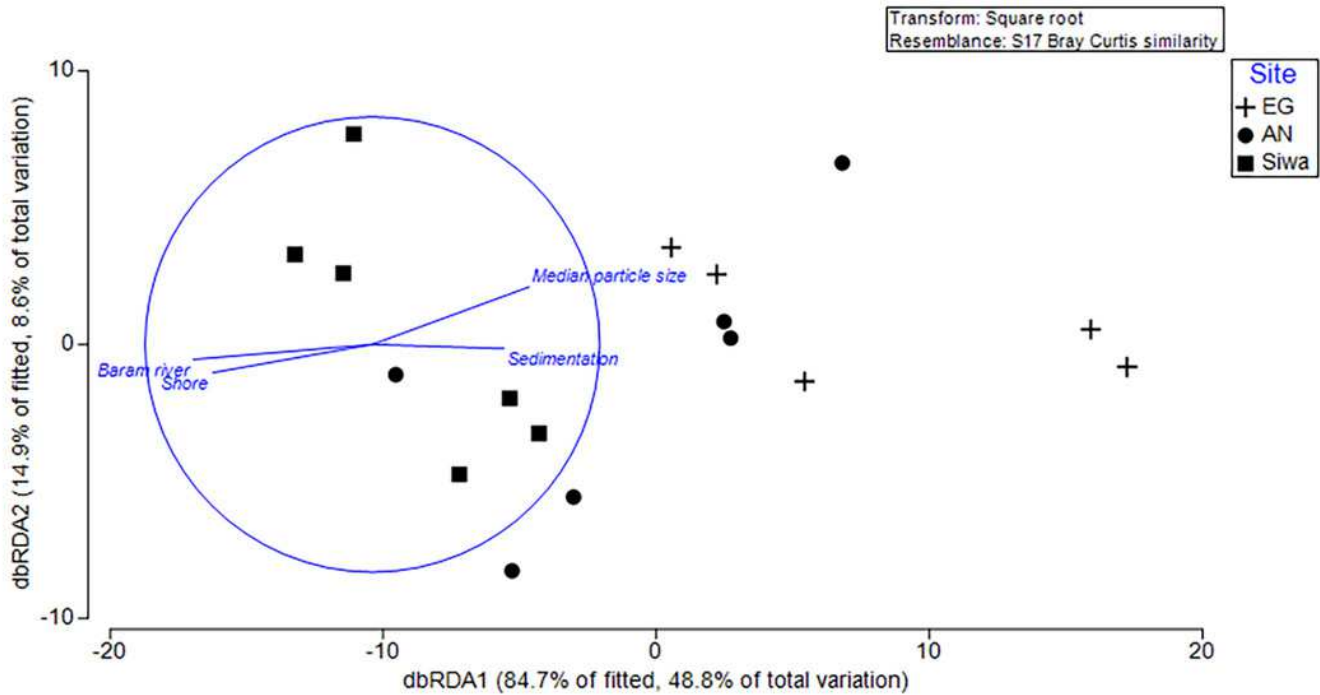
## Figure 10

Average symbiont density (A) and chlorophyll a pigment density (B) across the three coral species assessed (*Acropora*, *Monitpora* and *Pachyseris*) at EG, AG and SW.



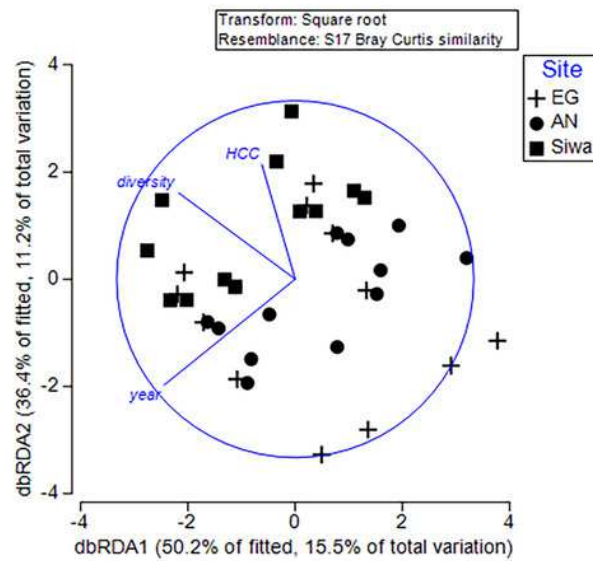
# Figure 11

DistLM output with an AIC criterion selection illustrating the significant environmental factors ( $p < 0.05$ ) that influence community composition at EG, AG and SW.



## Figure 12

DistLM output with an AIC criterion selection illustrating the significant explanatory variables ( $p < 0.05$ ; HCC = hard coral cover, diversity = coral diversity, year = Sept 2016 and May 2017) that coral health at EG, AG and SW.



**Table 1** (on next page)

Average (%) coral cover of the 28 genera observed at the three surveyed reefs illustrating the 10 most dominant coral genus.

Genus	Eve's Garden	Anemone's Garden	Siwa reef
Acropora (branching)	0.07 ± 0.07		2.60 ± 0.40
Diploastrea (massive)	14.80 ± 1.60	10.60 ± 3.70	0.40 ± 0.10
Echinopora (encrusting)		0.50 ± 0.14	1.90 ± 1.60
Dipsastrea	0.90 ± 0.30	3.44 ± 0.40	3.60 ± 2.00
Favites (massive)	1.70 ± 0.80	2.40 ± 0.86	5.10 ± 1.60
Galaxea	3.00 ± 1	0.62 ± 0.20	0.90 ± 0.30
Merulina	1.60 ± 1.5	0.10 ± 0.03	1.33 ± 0.80
Montipora (plate)	1.30 ± 100	2.09 ± 1.10	8.60 ± 3.00
Pachyseris (plate)	2.10 ± 1.10	0.50 ± 0.30	2.00 ± 1.30
Porites (massive/plate)	5.70 ± 2.80	7.30 ± 1.50	7.30 ± 2.30
Astreopora			0.90 ± 0.60
Caulastrea		0.07 ± 0.19	0.04 ± 0.04
Ctenactis (solitary)	0.07 ± 0.07	0.62 ± 0.15	0.14 ± 0.09
Echinophyllia	0.30 ± 0.30		0.06 ± 0.06
Fungia			0.10 ± 0.01
Goniastrea		0.10 ± 0.03	0.04 ± 0.04
Goniopora	0.03 ± 0.03		
Heliofungia	0.10 ± 0.10		
Leptoria	0.03 ± 0.03		0.08 ± 0.08
Leptoseris	0.17 ± 0.17		1.60 ± 1.50
Montastrea			0.04 ± 0.04
Oxypora	0.03 ± 0.03		0.17 ± 0.17
Pectinia			0.08 ± 0.08
Physogyra			0.17 ± 0.17
Platygyra (massive)	0.90 ± 0.80	1.79 ± 1.60	0.60 ± 0.40
Psammocora	0.10 ± 0.10		
Symphyllia		0.40 ± 0.20	0.69 ± 0.30
Turbinaria			0.68 ± 0.68

**Table 2** (on next page)

Statistical results from two-way ANOVA of the total impaired health and each impaired health indicator with site (EG = Eves Garden, AG = Anenomes Garden, SW = Siwa) and season (2016, 2017), and the interaction.

Health sign	Factor	df	F value	p value	Post hoc
Total impaired health	Site	2	0.25	0.780	
	Season	1	1.11	0.300	
	Site*Season	2	0.15	0.860	
Bleaching	Site	2	0.19	0.830	
	Season	1	3.30	0.080	
	Site*Season	2	0.69	0.510	
Mucus	Site	2	3.60	<b>0.040</b>	EG<AG,SW
	Season	1	0.15	0.700	
	Site*Season	2	7.20	<b>0.003</b>	
Bioerosion	Site	2	0.87	0.430	
	Season	1	20.20	<b>&lt;0.001</b>	2017>2016
	Site*Season	2	3.80	0.040	
Pimentation	Site	2	5.30	<b>0.010</b>	AG>SW
	Season	1	1.00	0.320	
	Site*Season	2	0.82	0.440	
Scars	Site	2	0.10	0.910	
	Season	1	0.33	0.570	
	Site*Season	2	2.59	0.090	

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**Table 3** (on next page)

Statistical results from two-way ANOVA of the total impaired health and each impaired health indicator for the 5 most dominant coral genera with site (EG = Eves Garden, AG = Anenomes Garden, SW = Siwa) and season (2016, 2017), and the interaction. If impa



Species	Health sign	Factor	df	F value	p value	Post hoc
<i>Porites</i>	Total	Site	2	1.71	0.202	
		Year	1	10.17	<b>0.004</b>	2017>2016
		Site*year	2	4.00	<b>0.031</b>	
	Bleaching	Site	2	0.36	0.701	
		Year	1	0.08	0.774	
		Site*year	2	1.81	0.185	
	Mucus	Site	2	6.72	<b>0.034</b>	EG>SW
		Year	1	2.64	0.104	
		Site*year				
	Bioerosion	Site	2	1.61	0.219	
		Year	1	21.79	<b>&lt;0.001</b>	2017>2016
		Site*year	2	6.29	<b>0.006</b>	
	Pimentation	Site	2	8.79	<b>0.001</b>	Eg,AG>SW
		Year	1	2.49	0.128	
		Site*year	2	2.09	0.145	
Scars	Site	2	0.46	0.637		
	Year	1	0.38	0.543		
	Site*year	2	2.25	0.126		
<i>Pachyseris</i>	Total	Site	2	0.30	0.744	
		Year	1	9.02	<b>0.008</b>	2016>2017
		Site*year	2	0.14	0.869	
	Bleaching	Site	2	0.37	0.699	
		Year	1	9.69	<b>0.006</b>	2016>2017
		Site*year	2	0.11	0.897	
	Bioerosion	Site	2	0.49	0.622	
		Year	1	1.42	0.249	
		Site*year	2	0.39	0.685	
<i>Montipora</i>	Total	Site	2	0.77	0.476	
		Year	1	1.65	0.211	
		Site*year	2	1.45	0.254	
	Bleaching	Site	2	2.06	0.149	
		Year	1	0.29	0.594	
		Site*year	2	0.73	0.494	
	Bioerosion	Site	2	0.83	0.449	
		Year	1	0.83	0.371	
		Site*year	2	0.68	0.519	
<i>Diploastrea</i>	Total	Site	2	0.66	0.527	
		Year	1	0.10	0.752	
		Site*year	2	2.54	0.104	
	Bleaching	Site	2	0.63	0.541	
		Year	1	1.69	0.209	
		Site*year	2	2.06	0.152	
	Mucus	Site	2	0.58	0.570	

		Year	1	2.75	0.113
		Site*year	2	0.71	0.502
	Bioerosion	Site	2	1.64	0.220
		Year	1	0.86	0.364
		Site*year	2	0.99	0.391
<i>Acropora</i>	Total	Site	2	1.92	0.171
		Year	1	0.22	0.644
		Site*year	2	0.14	0.872
	Bleaching	Site	2	1.27	0.300
		Year	1	1.02	0.323
		Site*year	2	0.64	0.538

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**Table 4**(on next page)

PERMANOVA results highlighting the significant drivers that explain variation in benthic community assemblage among reefs in 2017

<b>Explanatory variable</b>	<b>p value</b>	<b>Pseudo-F</b>	<b>R<sup>2</sup></b>
Depth	0.094	2.3	0.010
Dist. Baram River	<b>0.002</b>	7.0	0.303
Dist. Shore	<b>0.007</b>	5.1	0.008
Sedimentation rate	<b>0.025</b>	3.9	0.023
Course sediments	0.069	2.7	0.001
Fine sediments	0.070	2.7	0.100
Silt	0.153	1.9	0.015
Median particle size	<b>0.010</b>	5.0	0.164

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**Table 5** (on next page)

PERMANOVA results highlighting the significant drivers in coral health. The top panel are the results of a DistLM that includes substrate structure and physical conditions among reefs and across both sampling seasons, and the bottom panel are the results

<b>Explanatory variable</b>	<b>p value</b>	<b>Pseudo- F</b>	<b>R<sup>2</sup></b>
Year	<i>0.003</i>	5.0	0.128
HCC	<i>0.042</i>	2.8	0.052
Diversity	<i>0.003</i>	5.1	0.129
Dist. Baram River	0.304	1.3	0.019
Dist. Shore	0.521	0.8	0.020
Depth	0.467	0.9	0.017

<b>Sediment variable</b>	<b>p value</b>	<b>Pseudo- F</b>	<b>R<sup>2</sup></b>
Sedimentation rate	0.059	2.4	0.070
Course sediments	<i>0.031</i>	2.9	0.152
Fine sediments	<i>0.031</i>	2.9	0.030
Silt	0.067	2.3	0.110
Median particle size	0.083	2.2	0.024