Borneo coral reefs subject to high sediment loads show evidence of resilience to various environmental stressors

Nicola Browne [1, 2], Christina Braoun [3], Jennifer McIlwain [Corresp., 1, 2], Ramasamy Nagarajan [4], Jens Zinke [1, 2, 3, 5, 6, 7]

1 Molecular and Life Sciences, Curtin University, Perth, WA, Australia

2 Curtin Sarawak Research Institute, Curtin University, Miri, Sarawak, Malaysia

3 Department of Biology, Chemistry and Pharmacy, Freie Universität, Berlin, Germany

4 Department of Applied Geology, Curtin University, Miri, Sarawak, Malaysia

5 School of Geography, Geology and Environment, University of Leicester, Leicester, United Kingdom

6 Australian Institute of Marine Science, Townsville, WA, Australia

7 Institute for Geosciences, Section Paleontology, Freie Universität, Berlin, Germany

Corresponding Author: Jennifer McIlwain
Email address: jennifer.mcilwain@curtin.edu.au

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 and health 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 at distances <10 kms. As well as distance to shore, we included other environmental variables like reef depth and sediment trap accumulation that explained 62.5% of variation in benthic composition among sites. Miri's reefs showed little 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%). Tagged colonies of *Diploastrea* and *Pachyseris* suffering partial bleaching in 2016 had fully (90-100%) recovered the following year. There were, however, seasonal differences in bioerosion rates, which increased five-fold after the 2017 wet season. Differences in measures of coral physiology, like that of symbiont density and chlorophyll *a* for *Montipora*, *Pachyseris* and *Acropora,* were not detected among sites. We concluded that Miri's reefs may be in a temporally stable state given

minimal recently dead coral and a limited decline in coral cover over the last two decades. 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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6 Zinke[1,2,3,5,6,7]

8 [1] Molecular and Life Sciences, Curtin University, Perth, WA, Australia
9 [2] Curtin Sarawak Research Institute, Curtin University, Malaysia
10 [3] Department of Biology, Chemistry and Pharmacy, Freie Universität, Berlin, Germany
11 [4] Department of Applied Geology, Curtin University, Malaysia
12 [5] School of Geography, Geology and the Environment, University of Leicester, Leicester, United
13 Kingdom
14 [6] Australian Institute of Marine Science, Townsville, Australia
15 [7] Institute for Geosciences, Section Paleontology, Freie Universität, Berlin, Germany
16 Corresponding Author:
17 Jennifer McIlwain[1]
18 5 Rue du Gouverneur Guyon, Noumea, 98800, New Caledonia
19 Email address: jennifer.mcilwain@curtin.edu.au

ABSTRACT

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23 environmental policies and a lack of enforcement has led to poor water quality and compromised
24 coral health from increased sediment and pollution. Those inshore turbid coral reefs, subject to
25 significant sediment inputs, may also inherit some resilience to the effects of thermal stress and
26 coral bleaching. We studied the inshore turbid reefs near Miri, in northwest Borneo through a
27 comprehensive assessment of coral cover and health in addition to quantifying sediment-related
28 parameters. Although Miri Reefs had comparatively low coral species diversity, dominated by
29 massive and encrusting forms of *Diploastrea*, *Porites*, *Montipora*, *Favites*, *Dipsastrea* and
30 *Pachyseris*, they were characterised by a healthy cover ranging from 22-39%. We found a
31 strong inshore to offshore gradient in hard coral cover, diversity and community composition as
32 a direct result of spatial differences in sediment at distances <10 kms. As well as distance to
33 shore, we included other environmental variables like reef depth, sediment trap accumulation and
34 particle size that explained 62.5% of variation in benthic composition among sites. Miri's reefs
35 showed little evidence of coral disease and relatively low prevalence of compromised health
36 signs including bleaching (6.7%), bioerosion (6.6%), pigmentation (2.2%), scars (1.1%) and
37 mucus production (0.5%). Tagged colonies of *Diploastrea* and *Pachyseris* suffering partial
38 bleaching in 2016 had fully (90-100%) recovered the following year. There were, however,
39 seasonal differences in bioerosion rates, which increased five-fold after the 2017 wet season.
40 Differences in measures of coral physiology, like that of symbiont density and chlorophyll *a* for
41 *Montipora*, *Pachyseris* and *Acropora*, were not detected among sites. We concluded that Miri's
42 reefs may be in a temporally stable state given minimal recently dead coral and a limited decline
43 in coral cover over the last two decades. This study provides further evidence that turbid coral

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

INTRODUCTION

48 Turbid reefs are commonly regarded as marginal reefs living near their environmental limits

49 (Kleypas et al., 1999; Guinotte et al., 2003; Perry and Larcombe, 2003; Palmer et al., 2010;

50 Goodkin et al., 2011). As such, these reefs are traditionally perceived to be in a reduced health

51 status (Kleypas, 1996; Kleypas et al., 1999) and more sensitive to rising sea surface temperatures

52 (SST; Nugues and Roberts, 2003; Crabbe and Smith, 2005; Fabricius, 2005; Woolridge, 2008).

53 Yet there is growing evidence that turbid reefs may actually be more resilient to future climate

54 change effects (Goodkin et al., 2011; Morgan et al., 2017) and serve as refugia for surviving

55 corals (Cacciapaglia and van Woesik, 2015; 2016; Morgan et al., 2016). This has been

56 demonstrated on turbid reefs with high coral cover and diversity yet experience significant

57 sediment and nutrient inputs, low bleaching, and rapid recovery rates from bleaching and

58 cyclonic events (Larcombe et al., 2001; Browne et al., 2010; Richards et al., 2015; Morgan et al.,

59 2016). Studying the level of resilience and survival of turbid reefs in different environmental

60 settings will provide clearer insights into the future of reefs subject to climate change (Guinotte

61 et al., 2003; Hennige et al., 2010; Richards et al., 2015).

62

63 Despite elevated resilience to naturally turbid conditions, many inshore turbid reefs face threats

64 from local pressures, largely related to declining water quality and increased sediment input. In

65 South East (SE) Asia, 95% of reefs are threatened from local sources and, therefore, are,

66 regarded as the most endangered reefs globally (Burke et al., 2011). From the 1980's to early

67 2000's these reefs have suffered an average 2% loss in coral cover per year with hard coral cover

68 declining from 45% to 22% in 2003 (Bruno and Selig, 2007). Most SE Asian reefs are located in

69 close proximity to countries with rapidly emerging economies and fast population growth

70 (Wilkinson, 2006; Burke et al., 2011; Heery et al., 2018). They are further characterised by

71 poorly developed environmental policies, inadequate regulation, lack of enforcement, a shortage

72 of institutional and technical capacity, insufficient community support and involvement, and

73 conflicts and tensions between stakeholders (Fidelman et al., 2012). The synergistic effects of

74 these factors has led to poor water quality on many inshore reefs via pollution and sediment input

75 derived by rapid land development, and over-fishing activities (McManus, 1997; Wilkinson,

76   2006). As a consequence, sedimentation rates are high (>10 mg cm^2 day^{-1}; Rogers 1990) with SE

77   Asian coastal systems experiencing the highest siltation loads globally (Kamp-Nielsen et al.,

78   2002; Syvitski et al., 2005).

79

80   Nearshore coral reefs along the north central section of Sarawak, on the island of Borneo, are

81   highly diverse with an estimated 518 fish species (Shabdin, 2014) and 203 hard coral species

82   from 66 genera (Elcee Instumentation, 2002). Sarawak is a deforestation hotspot with only 3% of

83   its forest cover intact (Bryan et al., 2013). Ongoing deforestation and poor land use practices are

84   a growing threat for these biological diverse reefs that also support local fisheries and an

85   expanding dive tourism industry (Elcee Instumentation, 2002). As such, in 2007 a marine park

86   (the Miri-Sibuti Coral Reef National Park; MSCRNP) that covered 11,020 km^2 was established

87   to promote and protect 30 coral reefs adjacent to Miri, the second largest town in Sarawak. In

88   2001, a broad assessment of coral reef health within the park indicated that live coral cover was

89   approximately 35-50% and dead coral cover was 0.5% (Elcee Instumentation, 2002). Subsequent

90   Reef Check surveys in 2010 and 2014 concluded these same reefs were experiencing multiple

91   stressors, but were in 'fair' condition (~40% HCC; Reef Check, 2010;2014). However, despite

92   these claims there is limited quantitative data on coral health and biodiversity (Shabdin, 2014),

93   and more importantly no comprehensive assessment of environmental drivers of reef health. For

94   example, the Baram River (10 km north of the reef complex), is known to discharge 2.4 x 10^{10}

95   kg yr^{-1} of sediments into the coastal zone (Straub and Mohrig, 2009), such that sediment and

96   nutrient influx are considered to be the greatest threat to these poorly studied reefs (Pilcher and

97   Cabanban, 2000; Ferner, 2013; Shabdin, 2014). Without thoroughly quantifying sediment

98   impacts on corals, no conclusions can be made on coral tolerance levels, the drivers of

99   community composition and future resilience to both local and global pressures. Given the

100   Baram River delta is in a destructive phase due to rising sea level (Lambiase et al., 2002),

101   together with the increased frequency and intensity of rainfall events and plans for future

102   modification of both the river and adjacent land development (Nagarajan et al., 2015), it is likely

103   that threats from sediments will only increase.

104

105   The reefs within the MSCRNP provide a valuable opportunity to address several knowledge gaps

106   on turbid coral reef health and their potential resilience to local and global threats. The last

107 comprehensive assessment of coral cover on Miri's reefs was in 2001, with no assessments of

108 coral taxa health and disease for any Sarawak reefs recorded to date. In particular, coral disease

109 studies are rarely undertaken on SE Asian reefs largely due to a lack of resources and expertise

110 (Green and Bruckner, 2000; Raymundo et al., 2005; Heintz et al., 2015). The lack of quantitative

111 data on the health and stability (as defined by resistance, resilience and maintenance of key

112 functional groups) of these reefs coupled with ongoing unsustainable land use practices in

113 Sarawak, raises concerns over their long-term viability. This is of particular concern as Sarawak

114 reefs currently provide an estimated revenue of 6 million AUD per year in tourism and 13.5

115 million AUD from fisheries (Elcee Instumentation, 2002). We argue there is an urgent need for a

116 comprehensive assessment of coral cover and health measured alongside key environmental and

117 sediment-related parameters. The key objectives of this study therefore are to: 1) quantify

118 benthic cover, coral cover and health, 2) compare the prevalence of impaired health in the

119 dominant coral species, 3) identify key parameters related to sediment delivery that influence

120 benthic cover and health along an inshore to offshore gradient, and 4) assess how resilient these

121 inshore reefs are to future changes in sediment supply. These data will improve our

122 understanding of turbid coral reefs composition and potential resilience to both local and global

123 stressors, and promote current management strategies that aim to protect inshore turbid reefs

124 from future changes to land use.

125

126 ## MATERIALS & METHODS

127 **Study sites**

128 The study was conducted on three low profile submerged patch reefs (Eve's Garden, Anemone

129 Garden and Siwa Reef) in the MSCRNP (Fig. 1). These sites were of a comparable depth (5-15

130 m) and size (<0.11 km^2). Eve's Garden (EG) is a shallow inshore reef close to shore (7.3 km)

131 with a coral community dominated by platy and massive corals such as *Pachyseris* sp. and

132 *Porites* sp. (Ferner, 2013). Anemone Garden (AG) is further offshore (11.7 km) and consists of a

133 considerable density of anemone colonies, with platy forms of *Acropora* sp. and exceptionally

134 large massive *Porites* sp. and *Diploastrea* sp. colonies (1-5 m length). Siwa Reef (SW) situated

135 further to the south is the most biologically diverse of the studied reefs consisting of encrusting

136 and massive coral forms (Ferner, 2013). These reefs lie on an inshore to offshore transect from

137   the Baram (sediment influx 2.4 x 1010 kg.year^{-1}; Nagarajan et al., 2015) and Miri River mouths,

138   located to the north of EG (10 km from Miri River and 30 km from Baram River).

139

140   Physical (temperature, light, turbidity and sediment trap accumulation) and biological (benthic

141   cover, coral health) data were collected at the end of the dry season (15th September to 20th

142   October 2016) and during the wet season (11th May to 3rd June 2017). At each of the three reefs,

143   six replicate line transects (20 m), separated by 20 m intervals to ensure independence were run

144   across the reef surface (EG = 8-12 m; AG =10-14 m; SW= 8-14 m). These reefs are not

145   characterized by typical windward and leeward reef edges, but are low profile patch reefs where

146   the majority of the reef sits in one relatively flat plane, sloping gently on all sides to the sea floor.

147   As such, all transects were laid out along the same axis across the flat section of each reef.

148

149   **Physical data collection**

150   Seasonal changes in light (measured with Photosynthetic Irradiance Recording System by

151   Odyssey, New Zealand) and temperature (measured with HOBO Pro V2 loggers, Australia) were

152   recorded every 10 minutes from September 2016 for 9 months (temperature at EG and AG) and

153   12 months (light at EG). To capture changes in suspended sediment loads over a tidal cycle,

154   turbidity loggers were deployed (in a horizontal position) for two weeks at the end of the 2016

155   dry season (September; EG and SW) and end of the 2017 wet season (May; EG; AQUA logger

156   210/310TY, Aquatech, UK). Data on cloud cover, rainfall and wind speed over the period from

157   October 2016 to October 2017 was retrieved from the online database World Wide Weather

158   (2017).

159

160   To assess small-scale spatial variation in sediment trap accumulation, four sediment traps per

161   three transects (8 traps in total per reef) were deployed at each reef in September 2016 to collect

162   sediments during the NE monsoon. Each trap consisted of 3 cylindrical PVC plastic containers

163   (diameter of 7.6 cm) attached to a metal rod positioned 30 cm above the substrate (Storlazzi et

164   al., 2011). The traps remained *in-situ* until May 2017. To determine if trapped sediments were

165   from local resuspension or transported on to the reef, 500 g of benthic sediment at the base of

166   each trap was sampled. The content of each container was emptied into a labelled plastic bag

167 and stored at -20°C until further analysis at the Curtin University Malaysia Laboratory facilities

168 (Laboratory SK2 204)~~, Malaysia~~.

169

170 Sediment samples were analysed for weight and particle size characteristics. Frozen samples

171 were thawed and allowed to settle overnight. Water remaining on the surface was filtered (0.45

172 μm filter paper) to capture the fine suspended sediments. The sediments (washed, settled and

173 filtered) were oven-dried at 60 °C for 2-3 weeks and weighed to the nearest 0.001 g.

174 Sedimentation accumulation rate (g cm^2 day^{-1}) was calculated as the weight of sediment trapped

175 (g) divided by the number of days the trap was deployed and the surface area of the trap (cm^2).

176 For the grain size analysis, the settled dry sediments were manually homogenized and weighed

177 before sieving. The sediments were homogenized using a pestle and mortar given the sediments

178 were mostly sand and loosely aggregated. Sediments were separated into 5 class fractions (>1

179 mm, 500 to <1000 μm, 250 to <500 μm, 125 to <250 μm and 63 to 125 μm) by placing the sieve

180 stack on a mechanical shaker for 20 minutes. Each of the 5 sediment fractions were weighed to

181 the nearest 0.001 g.

182

183 **Biological data collection**

184 *In water data collection*

185 The benthic cover and coral diversity (to genus level) were assessed in September 2016 using the

186 photographic transect method (Bégin et al., 2013). Photographs were taken using a Canon

187 Powershot G7 mark II digital camera at a fixed height of 0.75 m above the transect line every 1

188 m along the transect (n = 21). Photographs (1 m^2) were analysed in Coral Point Count (CPCe)

189 with a uniform grid of 25 points to calculate benthic cover for each of 7 categories (hard coral,

190 soft coral, recently dead coral, turf algae, macroalgae, sponge, abiotic substance) (CPCe; Kohler

191 and Gill, 2006). The hard coral category was further subdivided into 38 genera common to the

192 Indo-Pacific region according to Kelley (2009).

193

194 To assess seasonal fluctuations in coral reef health, signs of compromised health (disease,

195 bleaching, bioerosion, pigmentation, mucus production, scars) were recorded in September 2016

196 and May 2017. The belt transect methodology was used, covering a wider area along the transect

197 line via a zig-zag pattern (40 m^2 for each 20 m transect). Coral colonies within each belt transect

198   were identified to genus level and classified as either healthy or affected by an impaired health

199   sign (Beeden et al., 2008). Signs of bioerosion included the presence of organisms such as

200   Christmas tree worms, boring bivalves and sponges, and bleaching was further subdivided into

201   whole, partial, focal and non-focal bleaching (as defined in Beeden et al., 2008). To determine if

202   bleached corals recovered or died, a total of 14 coral colonies from EG and SW in both sampling

203   seasons that showed signs of bleaching were tagged and photographed (4 *Diploastrea* sp., 6

204   *Pachyseris* sp., 4 *Porites* sp.). The percentage of bleached tissue was assessed from scaled

205   photographs using CPCe software (1=normal, 2=pale, 3=0-20%, 4=20-50%, 5=50-80% and

206   6=80+% bleached). While this is a low sample size, the data is included to provide further

207   insight into the recovery potential of corals on these reefs. Field work was approved by the

208   Sarawak Forestry Commission (#61JHS/NCCD/600-7/2/107).

209

210   ***Symbiont density and chlorophyll a analysis***

211   In May 2017, fragments of three coral genera (*Montipora* sp.*, Pachyseris* sp. and *Acropora* sp.)

212   were collected from EG, AG and SW for chlorophyll *a* and symbiont density analysis. Higher

213   chlorophyll *a* and symbiont densities are typically recorded on turbid reefs (Browne et al., 2015)

214   as this increases the coral's ability to photosynthesis under low light levels as they acclimate to

215   suspended sediments (Hennige et al., 2010). Fragments (5-10 cm for branching corals and ~10 x

216   10 cm for foliose corals) were collected using cutters and placed in plastic bags. Samples were

217   placed on ice during transportation back to the laboratory where they were stored at -80 ºC until

218   further analysis. Symbiont density and chlorophyll *a* content were quantified following the

219   removal of coral tissue from the skeleton. The protocol for extracting tissue was adapted from

220   Ben-Haim et al. (2003) (Supplementary material).

221

222   **Statistical analysis**

223   Univariate statistical analysis was conducted in R Studio Desktop version 1.1.383. Prior to

224   analysis, normal distribution and homogeneity of variances were checked using the Shapiro Wilk

225   test and the Levene's test, respectively. To assess if there were significant differences in benthic

226   cover (hard coral, soft coral, algae) and diversity among sites a one way analysis of variance

227   (ANOVA, n= 6, α= 0.05) was used followed by a Tukey HSD post-hoc test (Bonferroni

228   method), if necessary. Significant differences in the prevalence of compromised health signs

229 (bleaching, bioerosion, mucus production, pigmentation and scars) among sites and between

230 seasons were identified for both total hard coral cover and for the most abundant coral genera

231 (*Porites, Pachyseris, Montipora, Diploastrea, Acropora*) using a Full Factorial ANOVA (FF

232 ANOVA, n= 6, α= 0.05) and a Tukey HSD post- hoc test. If required, a log10 transformation

233 was carried out for datasets to meet homogeneity of variance. However, as the bleaching

234 recovery was assessed using a scale, these data were tested using a Wilcoxon test to determine if

235 there had been a significant recovery in tagged coral colonies between years. To determine

236 differences in physiology (chlorophyll *a* content and zooxanthellae density) between the three

237 coral genera sampled (*Acropora* n=17, *Pachyseris* n=13, *Montipora* n=15) and across sites, a

238 non-parametric Kruskal Wallis test was performed. Furthermore, to evaluate cell health

239 differences between the three genera and among reefs, the percentage of cells from each grade

240 were compared using the Kruskal –Wallis test. Differences in sediment trap accumulation rates

241 was tested among reefs (Kruskal – Wallis). In addition particle size characteristics (median,

242 fine/coarse fraction) among reefs, and between the trapped sediments and the benthic sediments

243 were also tested (FF ANOVA, n=18).

244

245 Permutational multivariate analysis was conducted in PRIMER-7 version 7.0.13. A Distance-

246 based Linear Model (DISTLM) was used to determine how much of the variation in community

247 assemblage (hard coral cover=HCC, soft coral cover=SCC, algae, recently dead coral

248 cover=DCC, H' index, number of coral genera) among transects and reefs was driven by depth,

249 distance from the two nearby river mouths, distance from shore and differences in sediment trap

250 accumulation rates and particle size characteristics. Depth was included in the analysis as depth

251 is known to influence sediment dynamics (Wolanski et al., 2005) as well as declines in light

252 associated with suspended sediments (Falkowski et al., 1990). A distance- based resemblance

253 matrix was created for the biological data set using Bray - Curtis similarity values following a

254 square-root transformation and for the environmental data using Euclidean distances and

255 normalised values. A DISTLM, using the BEST fit model with the Akaike's Information

256 Criterion (AIC) and 9,999 permutations was performed using the resemblance matrices. The

257 multivariate scale relationship between the predictor (environmental) and response variables

258 (biological) was presented on a plot with a distance- based redundancy analysis (dbRDA;

259 Legendre and Anderson, 1999). To investigate whether environmental factors contributed to

260   differences in health status among sites again a DISTLM model was used followed by dbRDA

261   plotting as above. Predictor variables included substrate structure (hard coral cover (HCC),

262   diversity) and physical conditions (depth, sediment trap accumulation rate, particle size

263   characteristics, distance from both river mouths and distance from shore). Hard coral cover

264   (HCC) and diversity were used since higher HCC can contribute to a greater probability of

265   impaired coral health (Bruno and Selig, 2007). In contrast, reefs that are more diverse can lower

266   susceptibility as it reduces the quick spread of a disease (Raymundo et al., 2005; Aeby et al.,

267   2011). As sediment data were obtained at the end of the wet season (May 2017), these were used

268   to explain the 2017 health data. For the 2016 coral health data, which had no associated sediment

269   data, only sampling year, HCC and coral diversity together with distance from shore and rivers

270   were used as explanatory variables.

271

272

273   **RESULTS**

274   *Physical parameters*

275   The dry season was characterized by less variable, warmer SST's (mean monthly range = 30.0 to

276   30.7 °C; sup Fig. 2), greater in-water light penetration (mean monthly range at EG = 156 to 320

277   μmol photons m^{-2} s^{-1}) and reduced rainfall (mean monthly rainfall range = 78 to 166 mm) and

278   cloud cover (Fig. 2). In contrast, the wet season was cooler (mean monthly range = 28.0 to 30.1

279   °C) with higher rainfall (mean monthly range 126 to 234 mm) and reduced light levels on the

280   reef (mean monthly range at EG = 19 to 150 μmol photons m^{-2} s^{-1}). Wind speeds were also

281   slightly elevated during the wet season months (Fig. 2d). Mean sediment trap accumulation rates

282   following the wet season ranged from 13 to 28 mg cm^{-2} day^{-1}, with a rate almost three times

283   higher at EG compared to AG and SW (H_2 = 10.3, p<0.005; Fig. 3). Site differences in potential

284   sediment load were also observed during the dry season with higher and more variable turbidity

285   recorded at the nearshore EG reef (mean monthly range = <1 to 24 FTU) than at SW (mean

286   monthly range = 1-7 FTU) located 10 km further south from the large Baram River mouth (sup

287   Fig. 3).

288

289   All three reefs were dominated by sand (>98%), with the median particle size of benthic

290   sediments significantly increasing (F_2=13.6, p<0.005) with distance from the mouths of the

291   Baram and Miri Rivers (Fig. 4). Benthic sediments at SW comprised 58% of very coarse sand,

292   nearly three times that of EG (20%) (F_3=24.9, p<0.001; PH: SW>EG, AG; sup Fig. 4) and a

293   significantly smaller proportion of medium/fine sands (F_2=17.2, p=<0.001; PH: SW>AG>EG).

294   In contrast there was little difference in the median particle size from the sediment traps among

295   sites (F_2=2.25, p=0.133), although particle sizes of the benthic sediment were significantly

296   greater compared to the trapped sediments (F_1=60.93, p<0.001).

297

298   ***Benthic cover***

299   Hard coral cover increased with distance from the major sediment source (Baram River) and

300   varied significantly among sites (F_2=5.3, p=0.01; PH: SW>EG). SW had the highest HCC

301   (39.3%) and EG almost half the HCC (21.9%; Fig. 5). Soft corals also varied significantly but

302   declined with increasing distance from the major sediment source (H_2 = 8.6, p=0.01; MWPH:

303   EG>AG, SW) with EG having nearly 15-fold higher cover than SW. Turf algae dominated the

304   algal community and contributed to 52-57% of all reefs' benthos . However, there was no

305   significant difference in turf algal cover among reefs (F_2=0.103, p>0.05). Dead coral cover was

306   consistently low among sites (4.25%).

307

308   In total 28 genera were recorded (Table 1). Coral diversity was considerably different among

309   sites (F_2=4.6, p=0.03; PH: SW>EG) with SW the highest richness and 25 genera (H'=1.93), and

310   EG and AG 16 and 14 genera, respectively (H' ~1.4). The surveyed sites were composed of

311   similar communities, with the most dominant genera including *Diploastrea* sp., *Porites* sp.,

312   *Montipora* sp., *Favites* sp., *Dipsastrea* sp. and *Pachyseris* sp. (Table 1). All other species

313   comprised a small fraction of the community (<2% cover). Most notable differences in the

314   composition were with the high cover of *Diploastrea* sp. at AG and EG, *Galaxea* sp. at EG, and

315   *Acropora* and *Montipora* sp. at SW.

316

317   ***Coral reef health***

318   Of the compromised health signs recorded at each reef, the five most commonly observed were

319   mucus production (0.5 ± 0.3%), pigmentation (2.2 ± 0.7%), bioerosion (6.6 ± 2%), bleaching

320   (6.7 ± 0.9%) and scars (1.1 ± 0.4%; Fig. 6). No diseases *per se* were observed except at EG

321   where one colony of massive *Porites* sp. had ulcerative white spots. Despite a clear decline in

322   prevalence along an inshore to offshore gradient following the dry season in 2016 (Fig. 7), total

323   prevalence of compromised health (sum of the five commonly observed signs) was not

324   statistically significant among sites and seasons (p>0.05; Table 2). The prevalence of mucus

325   production by corals at Eves Garden (5%), however, was nearly five times that of other reefs

326   (F_2=3.6; p<0.05; EG<AG, SW), and SW recorded the lowest levels of pigmentation prevalence

327   (Fig 7b; Table 2; F_2=5.3; p<0.05; AG>SW). In contrast, bioerosion was comparatively similar

328   among sites within each season, but increased five-fold from $2.7 \pm 0.6\%$ to $10 \pm 1.3\%$ following

329   the 2017 wet season (Table 1; F=20.2; p<0.001; 2017>2016). During both seasons, overall

330   bleaching prevalence was ≤10% with partially bleached the most common form and whole

331   bleaching the least observed (sup Fig. 5). Bleaching prevalence declined from $8.1 \pm 1.4\%$

332   following the dry season to 5.4 ± 1.1 % after the wet season. Although this decline was not

333   statistically significant (F=3.3; p=0.08), the recovery of bleached corals that had been tagged the

334   year before was significant (p=0.002). The average bleaching scale dropped from 3.9 ± 0.4 to 1.6

335   ± 0.2 (Fig. 8) with all *Diploastrea* sp. and *Pachyseris* sp. colonies recovered by 90-100% in

336   2017.

337

338   Patterns of compromised health differed among five representative coral genera (*Acropora* sp.*,*

339   *Montipora* sp.*, Pachyseris* sp.*, Diploastrea* sp. and *Porites* sp.). *Acropora* sp. displayed the least

340   signs of stress in both seasons (<3.5%). *Porites* sp. were the most compromised (2016 = 50.8 $\pm$

341   6%; 2017 = 72 $\pm$ 5%; Fig. 9) and the only coral genera with a significant increase in stress

342   symptoms (p=0.004), because of a 40% increase in bioerosion after the wet season (F_1=10.17;

343   p<0.001; Table 3). *Montipora* sp. and *Diploastrea* sp. also suffered from an increase in

344   bioerosion between sampling seasons, although this as not statistically significant (p>0.05; Table

345   3). Despite a slight increase in the number of bleached *Porites* sp. corals, bleaching occurrence

346   for the other four corals declined, most notably for *Pachyseris* sp. (55% to 3%; F_1=9.03;

347   p=0.008). Furthermore, the most abundant genera *Porites* sp. was the only coral to show

348   elevated signs of pigmentation (>10%) although this health sign was less prevalent at SW, the

349   most offshore site (F2=5.3; p=0.01; Table 3).

350

351   For the three coral genera, *Montipora* sp., *Pachyseris* sp. and *Acropora* sp., there was no

352   difference in symbiont density (H = 4.0397, df=2, p>0.05) and chlorophyll *a* among sites (H =

353   2.3769, p>0.05) although SW scored the highest of both measures ($3.2*10^6 \pm 5.5$ cells/cm^2; 4.94

354 $\pm$ 0.75 µg.cm^2; Fig. 10a,b). Symbiont density differed among the three coral genera (chi-square =

355 23.1, df=2, p<0.001; MWPH: AC>MT,PH) with *Acropora* sp. scoring four and five times higher

356 symbiont densities (sup Fig. 6). Over 50% of the symbionts observed where healthy (stage 1;

357 sup Fig. 7a) with slightly more healthy cells observed at SW (H=1.7, p>0.05) and marginally

358 more degraded cells (stage 5) observed at AG (H=3.4, p>0.05). Among genera, *Acropora* had a

359 greater number of healthy cells (69 $\pm$3.9%) than both *Montipora* (49.4$\pm$5) and *Pachyseris* (52.6 $\pm$

360 4.8; H= 14.4, p<0.001; sup Fig. 7b).

361

362 ***Drivers of benthic cover and health***

363 Environmental variables (depth, sediment trap accumulation rate, distances from shore/river

364 mouth, concentration of silt/fine/coarse particles, median particle size) explained 62.5% of the

365 variation in benthic composition among reefs. Key drivers (p<0.05) were distances from river

366 mouth (30.3%) and shore (1%), median particle size (16.4%), and sediment trap accumulation

367 rate (2.3%; Table 4). Variability among sites was higher than within, with sediment trap

368 accumulation rate and particle size a key driver of benthos at EG and AG, and distance of river

369 and shore more closely associated with SW (Fig. 11).

370

371 To determine key drivers of coral health, two DistLM models were run. The first model

372 included health data from both sampling seasons, with six explanatory variables (season, HCC,

373 diversity, distance from river mouth and shore, and depth). The second model included health

374 data and sediment related variables following the wet season and sediment trap contents

375 (sediment trap accumulation rate, concentration of silt/fine/coarse sediments, median particle

376 size). For the first model, year, HCC and diversity significantly explained <31% of the variation

377 in coral health among transects and sites (Table 5). Sites within a sampling season were

378 separated along a HCC and diversity gradient (Fig. 12), with transects at SW typically

379 characterised by higher HCC and diversity but lower prevalence of scars, pigmentation and

380 bleaching (sup Fig. 8). Furthermore, repeat transects were separated between seasons, with those

381 completed in 2017 recording higher bioerosion, but lower bleaching and pigmentation (sup Fig.

382 7), supporting our previous results. Of the sediment drivers, the BEST model included both silt

383 and the coarse sediments, which explained 18% of the variations in coral health in 2017. Higher

384 sediment trap accumulation rates, although not statistically significant (p=0.06; Table 5),

385   explained 7% of the variation in health, and were most often associated with higher prevalence

386   of pigmentation, bioerosion and bleaching (sup Fig. 9).

387

388   **DISCUSSION**

389   The three reef sites in the MSCRNP are characterised by healthy coral cover yet low coral

390   diversity. Average live coral cover among the three reefs was 30%, ranging from 22% at EG to

391   39% at Siwa Reef. This is lower than reefs to the north in Sabah, with reports of live coral cover

392   from 23 to 75% (Pilcher and Cabanban, 2000; Chou and Tun, 2002; Lee, 2007; Praveena et al.,

393   2012; Waheed et al., 2016), but greater than the average coral cover for the wider Pacific region,

394   estimated at 22% in 2003 (Bruno and Selig, 2007). Previous assessment of coral cover in 2000

395   on the Miri reefs range from 28% (Pilcher and Cabanban, 2000) to 22-58% (Elcee

396   Instumentation, 2002). Although the higher coral cover reported by the latter study is most likely

397   an artefact of the methodology used (ex-situ Acoustic Ground Discrimination System), which

398   can result in the misidentification and, therefore, quantification of live coral cover. Regardless,

399   our data suggest that coral cover at Miri's reefs has been relatively stable over the last two

400   decades. Miri's coral cover is comparable to both turbid and clear water reefs (Roy and Smith,

401   1971; Loya, 1976; Larcombe et al., 2001; Wesseling et al., 2001; Palmer et al., 2010; Goodkin et

402   al., 2011), yet diversity was comparatively low (14 to 25 genera per reef) for the Coral Triangle

403   region. Turak and Devantier (2010) reported 391 coral species (~70 genera) on reefs near Brunei

404   (~80 km from Miri), and Teh and Cabanban (2007) reported 120 species within 71 hard coral

405   genera for Banggi Island in Sabah. A comprehensive biodiversity assessment of all 30 reefs with

406   the MSCRNP in 2000 reported 66 genera (203 coral species; Elcee Instumentation, 2002). We

407   only observed a third of the number of coral genera (n=28), which is expected given we surveyed

408   only 10% (n=3) of the reefs surveyed in 2002. However, this report also found that coral

409   diversity was highly variable among reefs, with an average of nine coral genera per transect. It is

410   likely that MSCRNP reefs found further to the south and in deeper (15-35 m) offshore waters but

411   outside the scope of this study (characterized by different environmental conditions) include

412   several coral species not observed at our shallow nearshore sites, which are influenced by

413   terrestrial sedimentation from both natural and anthropogenic processes.

414

415   Low diversity at the surveyed sites is likely the result of poor water quality in the nearshore

416   shallow coastal zone. The inshore reefs of Miri are found in a narrow depth range between 7 and

417   15 m, hence there is a complete lack of reef structure in 1-5 m depth range. These very shallow

418   depths, however, are often characterised by a distinct set of coral species (Morgan et al., 2016;

419   DeVantier and Turak, 2017) which in part may explain lower coral diversity than on reefs to the

420   north in Brunei and Sabah that have reached sea level. But these inshore reefs are also

421   characterised by high levels of terrigenous sediments, which can also reduce coral diversity

422   (Rogers, 1990; Fabricius, 2005). High sediment input from rivers are typically correlated with

423   high nutrient loads that can lead to increase in reef algal biomass (De'ath et al., 2012). Algal

424   cover on all three reefs was high (>50%) compared to reefs in northern Borneo (0 to 29%;

425   Waheed et al., 2015), and will most likely be competing with corals for reef space. Some coral

426   taxa will be less resilient to both sediments and algal competition resulting in lower coral

427   diversity (Fabricius et al., 2005; De'ath and Fabricius, 2010). In Indonesia, Edinger et al. (1998),

428   recorded lowest coral diversity on reefs with algae cover reaching 46%. Reduced diversity was

429   also attributed to land pollution as well as destructive and over-fishing practices that destroy the

430   reef structure and reduce fish biomass thereby removing the top-down control on algal growth by

431   herbivore browsers (Hughes, 1994; Rogers and Miller, 2006; De'ath and Fabricius, 2010). In

432   Miri, overfishing and poor land management practices have been a long-term concern for the

433   regional government (Elcee Instumentation, 2002) but there are limited funds to actively protect

434   the reefs (Teh and Teh, 2014) and collect data on these impacts.

435

436   Low coral diversity does not necessarily suggest a degraded reef condition. Typically, low

437   diversity in nature results in lower resilience (Raymundo et al., 2005) and community stability

438   (Bellwood et al., 2004). Yet there is growing evidence to suggest that a few but tolerant species

439   can maintain reef resilience to local and global impacts, and implies that the diversity-resilience

440   links need further investigation (Bellwood et al., 2004; Fabricius et al., 2005; Nystrom et al.,

441   2008). A recent study on relatively undisturbed and well protected reefs in the Philippines that

442   looked to identify site specific benchmarks for coral diversity, measured high coral cover (>30%)

443   at the majority of sites, but lower generic diversity (10 to 25 coral genera per 75 m by 25 m area;

444   Licuanan et al., 2017). This highlights that high diversity is not necessarily a key benchmark for

445   a healthy reef system. As well as assessing the number of coral species on a reef, it is important

446   to determine if and how coral community structure has changed over time. Significant shifts in

447   coral composition can affect the reef's ecological function such as framework building, habitat

448   complexity and food source diversity (Aronson et al., 2004; Pratchett, 2005; Graham et al.,

449   2006). At six reef sites on the Great Barrier Reef coral communities shifted over 12 years

450   towards a high abundance of *Porites* spp. and soft corals; a community assemblage that is less

451   likely to re-establish to the pre-disturbance coral assemblage (Johns et al., 2014). Inshore reefs

452   in Miri are similarly dominated by massive corals including *Porites* sp. and *Diploastrea* sp., with

453   some (e.g. EG) also characterized by high soft coral cover (>10%). While we have no long-term

454   data sets to evaluate change in both diversity and composition, Miri's reefs may have

455   experienced a community shift due to reduction in water quality. Yet our tendency as coral reef

456   ecologists to focus on coral cover, composition and diversity, has resulted in a misconception as

457   to what constitutes an overall healthy reef (Vroom, 2011). Some reefs may naturally be

458   dominated by non-coral organisms, such as calcifying algae that are equally important for reef

459   accretion and stability but possibly less resilient to climate change. Thus our perception of the

460   reefs current state and its future trajectory are likely inaccurate and need adjusting to go beyond

461   diversity assessments.

462

463   The MSCRNP reef community can best be described as representative of turbid reefs in the

464   Indo-Pacific. The dominant coral species include several genera (*Acropora*, *Montipora*, *Porites*,

465   *Pachyseris*, *Faviidae* and *Galaxea* spp.) that have been observed on nearshore reefs in Singapore

466   (Chou, 1988; Dikou and van Woesik, 2006), the Great Barrier Reef (GBR) (Ayling and Ayling,

467   1991; Larcombe et al., 2001; Browne et al., 2010; Morgan et al., 2016), Thailand (Tudhope and

468   Scoffin, 1994), Hong Kong (Goodkin et al., 2011) and Sabah (Pilcher and Cabanban, 2000).

469   These corals are considered to be more resilient to sediment influx either through: 1) enhanced

470   photo-acclamatory abilities required during periods of low light (e.g. *Stylophora*; Dubinsky et al.,

471   1984; Browne et al., 2014), 2) active sediment removal processes by the coral polyp (e.g.

472   *Goniastrea*; Rogers, 1990; Erftemeijer et al., 2012), 3) enhanced mucus production to remove

473   settled sediments (e.g. *Porites*; Bessell-Browne et al., 2017) or, 4) morphological advantages that

474   result in greater degree of vertical growth thereby reducing tissue mortality from sediment burial

475   (e.g. *Acropora* and *Montipora*; Erftemeijer et al., 2012). There were also distinct differences in

476   the community assemblages particularly between SW Reef and EG. Siwa Reef had a mixed

477 assemblage of branching, foliose and massive corals, whereas EG was dominated by massive

478 corals, such as *Porites* sp. and *Diploastrea* sp. These coral community differences suggest there

479 are significant differences in environmental drivers (including sediments) over a comparatively

480 small spatial scale (10 km's).

481

482 The inshore to offshore gradient in hard coral cover and diversity, and differences in coral

483 composition is heavily influenced by the spatial differences in sediment related parameters. Over

484 62% of the variation in benthic cover at our three reef sites is explained by differences in depth,

485 sediment trap accumulation rates and distance from sediment sources as well as sediment particle

486 size characteristics. Consequently, we saw a significant increase in both coral cover and diversity

487 with increasing distance from the river mouths. Similar observations have been reported from

488 Indonesia and Puerto Rico, where hard coral cover nearly halved towards shore (Loya, 1976;

489 Edinger et al., 2000), and in Hong Kong, where inshore coral cover was 20% lower than offshore

490 (Goodkin et al., 2011). Reduced coral cover occurs because of low larval recruitment as a

491 consequence of limited hard substrate following sediment settling (Birrell et al., 2005; Fabricius,

492 2005; Dikou and van Woesik, 2006), or colony mortality caused by anoxic conditions that occur

493 under sediment layers (Rogers, 1983; Riegl and Branch, 1995; Wesseling et al., 2001). The

494 sediment particle size and source (marine versus terrestrial) are considered equally important to

495 sediment volume in assessing the impacts of sediments on coral health (Weber et al., 2006).

496 Recent studies show that as the percentage of terrestrial sediments increases, there are greater

497 declines in coral cover either through direct contact of sediments on corals (Bégin et al., 2016) or

498 following the reduction of coral recruitment (Fourney and Figueiredo, 2017). The significantly

499 lower hard coral cover and diversity at EG than at SW could be driven in part by a higher

500 percentage of terrestrial sediments from the Baram and Miri Rivers. Although we did not assess

501 sediment origin, sediment trap accumulation rates at EG were over double that at AG and SW,

502 which may be due to the reefs closer proximity to the two river mouths. However, it could also

503 be the result of increased sediment resuspension in shallow water or a combination of these

504 factors. Sediment traps do not provide a comprehensive assessment of sediment dynamics on

505 reefs, and given that our traps were out for 7 months, we recognize that our monthly sediment

506 trap accumulation rates can only be compared among our study sites and not to other studies.

507 Regardless, it is likely that river flow and sediments are influencing reef health, but these reefs

508   appear to be in a temporally stable state given low recently dead coral cover (4.35%) and the

509   limited decline in coral cover over the last two decades.

510

511   The prevalence of impaired health signs was dominated by bioerosion and pigmentation with no

512   signs of coral disease (with one exception). These health indicators are typically related to high

513   sediment and nutrient influx. High levels of bioerosion in particular has been linked to land

514   based pollution whereby lower light, from high turbidity, reduces $CaCO_3$ density (Risk and

515   Sammarco, 1991; Lough and Barnes, 1992) weakening the coral skeleton and increasing

516   susceptibility to bioeroders (e.g. molluscs, worms etc.; Prouty et al., 2017). Furthermore, even

517   modest increases in nutrient levels can lead to an increase in the abundance of bioeroding

518   organisms shifting a reef community from one of net production to net erosion (Hallock and

519   Schlager, 1986; Hallock, 1988; Prouty et al., 2017). Bioerosion levels were significantly greater

520   following the wet season when the impact of sediments on the Miri reefs were elevated as

521   indicated by declines in light and higher suspended sediment loads. Conversely, pigmentation

522   rates were higher following the dry season. Pigmentation is an indicator of immune function in

523   response to a stressor (Willis et al., 2004; Palmer et al., 2009). These stressors have been related

524   to settling sediments (Pollock et al., 2014) or lesions from abrasion or scars (Willis et al., 2004),

525   or for the case of Miri reefs elevated SST's recorded in the region in 2016 leading to the

526   moderate bleaching event as observed by the diving operators and fisherman. Spatially,

527   pigmentation rates were significantly lower at SW, which may suggest that corals at the least

528   sediment impacted site were also less stressed than at AG and EG. Sediments can also promote

529   diseases in corals (Voss and Richardson, 2006; Haapkyla et al., 2011; Pollock et al., 2014) with

530   Black Band Disease and White Plaque widely observed in the Indo-Pacific (Harvell et al., 2007;

531   Beeden et al., 2008), although generally low (~8% of current global records) in SE Asian reefs

532   compared to the Caribbean (Green and Bruckner, 2000). Suggested explanations for this include

533   poor reporting of coral diseases and relatively high coral diversity that might aid in diminishing a

534   quick spread of a disease (Raymundo et al., 2005). At Miri, the more likely explanation of low to

535   no coral diseases are more resilient individual corals and coral species, and potentially limited

536   connectivity with nearby coral populations, although this remains speculative until further work

537   is carried out.

538

539   Hard coral cover and diversity also explained a significant portion of the variation in coral

540   health. Miri reefs with a higher frequency of impaired health at sites recorded less coral cover

541   and diversity. In a recent study by Miller et al. (2015) reefs in Sabah, had four common coral

542   diseases at varying frequencies (<0.1 to 0.6 per affected colonies in an m^2) and signs of tissue

543   necrosis and pigmentation responses. They found a positive correlation between disease

544   frequency and coral cover, which suggested that host density was a key driver of disease

545   prevalence and compromised health. This relationship is due to reduced distances between

546   colonies, and greater shading and competition by fast growing species as coral cover increases

547   (Bruno and Selig, 2007). In Miri, we see the reverse trend suggesting that factors other than host

548   density are driving coral health, most likely changing sediment loads and finer sediment particles

549   not present in Sabah. However other variables often associated with sediment such as nutrient

550   levels and pollution such as heavy metal loads are also worth investigating.

551

552   Variable species composition among sites would also partly explain the spatial variation in coral

553   health. Different coral taxa have different susceptibilities to bioerosion, bleaching, disease and

554   compromised health (Raymundo et al., 2005; Couch et al., 2014; Heintz et al., 2015). In Miri

555   signs of pigmentation and bioerosion were most prominent on massive *Porites* sp. colonies.

556   *Porites* sp., although typically considered a hardier coral taxa (Raymundo et al., 2005) tolerant of

557   turbid waters, often have the most lesions, highest tissue loss and pigmentation response

558   (Tribollet et al., 2011; Pollock et al., 2014; Heintz et al., 2015) as well as being a target for

559   disease (Raymundo et al., 2005). The level of bleaching observed in *Porites* at Miri was

560   comparable to other abundant coral genera, but recovery potential after 9 months was lower,

561   possibly due to other stress symptoms. Bleaching was the most common sign of impaired health

562   among coral taxa, most commonly observed in *Pachyseris*, *Porites*, *Montipora*, *Dipsastrea* and

563   *Acropora* spp. (in declining order). A comprehensive study by Marshall and Baird (2000) of 40

564   coral taxa on the GBR found the same coral taxa were highly (>50% bleached or dead) or

565   severely (>15% dead) susceptible to thermal stress. In contrast, the other five most abundant

566   corals at the Miri reefs (*Diploastrea, Favites, Galaxea, Echinopora, Merulina* spp.) are

567   considered to be less sensitive to rising SST's (Marshall and Baird, 2000; Guest et al., 2016).

568   However, bleaching susceptibility does vary considerably according to the thermal history of a

569   region. For example, *Acropora* sp. is susceptible to bleaching on some reefs (Marshall and Baird,

570   2000; Pratchett et al., 2013; Hoogenboom et al., 2017), but was less susceptible on other reefs

571   (e.g. Singapore following the 2010 bleaching event: Guest et al., 2012). Only ~5% of *Acropora*

572   sp. colonies in Miri showed signs of thermal stress, which suggests moderate thermal tolerance

573   to high SST's. High levels of algal density in coral tissue are linked to higher thermal stress

574   resistance (Glynn, 1993; Stimson et al., 2002) due to the symbionts providing a greater

575   concentration of mycosporine-like amino acids that protect corals from UV radiation (Xu et al.,

576   2017). Symbiont densities measured at Miri were high (mean = $2.4* 10^6$ cells per cm^2) but

577   comparable to corals on other turbid reefs like those from Singapore (e.g. 0.5 to $3*10^6$ cells per

578   cm^2; (Browne et al., 2015). However, it was *Acropora* sp. that had significantly higher symbiont

579   density than the more frequently bleached *Montipora* sp. and *Pachyseris* sp. Our results suggest

580   that resilience to stress for these corals is a complex, but synergistic relationship between level

581   and frequency of environmental stressors, community composition and a coral's adaptability to

582   increased SST.

583

584   In 2016, a severe coral bleaching event occurred throughout the Indo-Pacific region. The

585   impacts of this event were thoroughly assessed on the GBR, where over 90% of reefs bleached

586   resulting in the loss of 29% of shallow water coral cover (Great Barrier Reef Marine Park

587   Authority, 2016). In January to March 2016, SST along the northern shore of Borneo were in the

588   highest 10% of global records since 1990 (Great Barrier Reef Marine Park Authority, 2016). SST

589   reported by NOAA for Brunei peaked in May to June 2016 at 31°C (the bleaching threshold

590   temperature; Fig. 12). During this time there was 1 to 2.5 Degree Heating Weeks (DHW) and

591   mid-level bleaching warnings. SST remained at ~30°C until January 2017 (National Oceanic &

592   Atmospheric Administration, 2018), which agree with our in-water assessment of SST during

593   September 2016 to early 2017 (sup Fig. 2). This suggests that while corals at Miri were subject

594   to elevated SST's for 5 or more months our surveys revealed low bleaching rates (~10% of

595   colonies bleached), and high recovery rates (as suggested by the tagged corals; >90%). This

596   suggests these nearshore turbid water reefs are resilient to high SST's supporting the growing

597   body of evidence that turbid reefs bleach less severely and frequently than their clear-water

598   counterparts (Marshall and Baird, 2000; Heintz et al., 2015; Morgan et al., 2017). Low

599   bleaching and high recovery rates of Miri reefs is possibly due to nearshore coral assemblages

600   more frequent exposure to higher temperatures than their offshore deeper conspecifics, resulting

601   in the development of adaptive mechanisms (Marshall and Baird, 2000; Guinotte et al., 2003;

602   Guest et al., 2016; Morgan et al., 2017). It may also be due to lower UV light penetration that

603   can exacerbate temperature stress (Courtial et al., 2017), or potentially from higher heterotrophy,

604   which increases the supply of essential metals to the symbionts thus sustaining them through

605   elevated temperatures (Ferrier-Pagès et al., 2018). This study further suggests that while turbid

606   reefs are more potentially more resilient to elevated SST, the mechanism/s responsible for this

607   resilience remain unclear.

608

CONCLUSIONS

610   In conclusion, the MSCRNP reefs are characterized by relatively high coral cover, low

611   prevalence of impaired health and are composed of a few but tolerant coral taxa. Low recently

612   dead coral cover and almost no decline in coral cover over the last two decades indicates these

613   reefs are stable despite elevated sediment inputs and regular exposure to thermal stress events.

614   There are, however, potential risks from proposed coastal and in-land developments given we

615   found that sediment related parameters have resulted in an on- to offshore gradient in coral

616   cover, diversity and health. Furthermore, high bioerosion and algae cover indirectly suggests

617   high nutrient influx, most likely from the Baram River. The high prevalence of bioerosion

618   observed in *Porites* sp. colonies is a concern given that this coral is a key reef framework

619   builder, and any notable declines in *Porites* sp. health will reduce coral reef complexity and

620   habitat availability for other invertebrate and fish species. Currently, there is no baseline data on

621   spatial and temporal changes in river outputs and sediment plume dynamics within the

622   MSCRNP, which is crucial in evaluating future threats to these reefs. Local management

623   agencies will need to address this knowledge gap if they plan to develop strategies that address

624   the potential impacts of changing land use on MSCRNP. The reefs current health state and

625   elevated stress tolerance does, however give hope that these reefs could be resilient to future

626   climate change but only if local water quality does not deteriorate.

627

628

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636

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Figure 1

Map of south China Sea with enlarged map of study area, showing locations of the three reefs, Miri city and the closest rivers.

(Image credit Hedwig Krawczyk modified from Natural Earth - Free vector and raster map data).

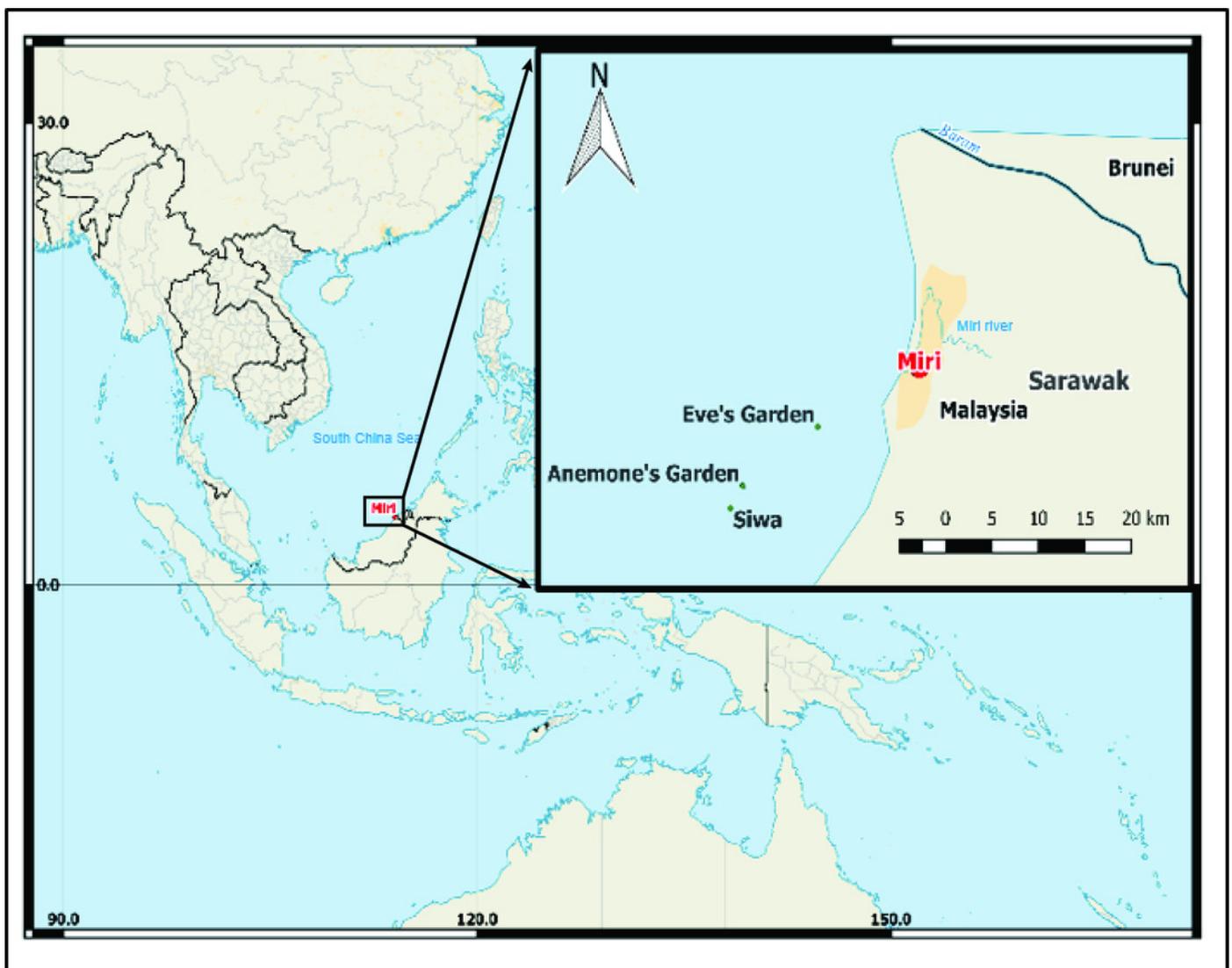



Figure 2

Average monthly data for A. light, B. wind speeds, C. cloud cover, and D. rain fall.

Light data was collected at EG as part of this study whereas wind, cloud and cover data was taken from the worldwideweatheronline.com website (error bars = SE).

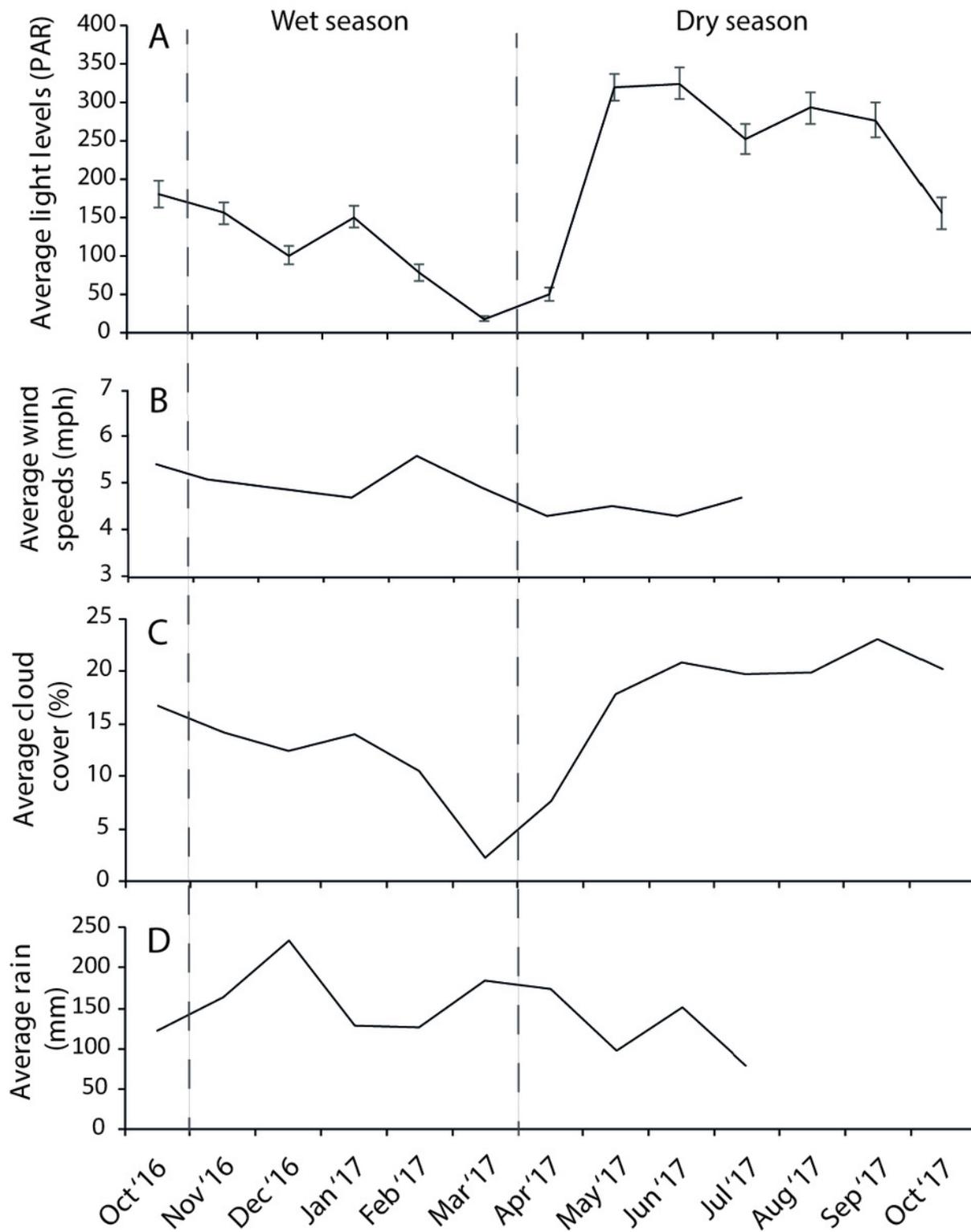



Figure 3

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

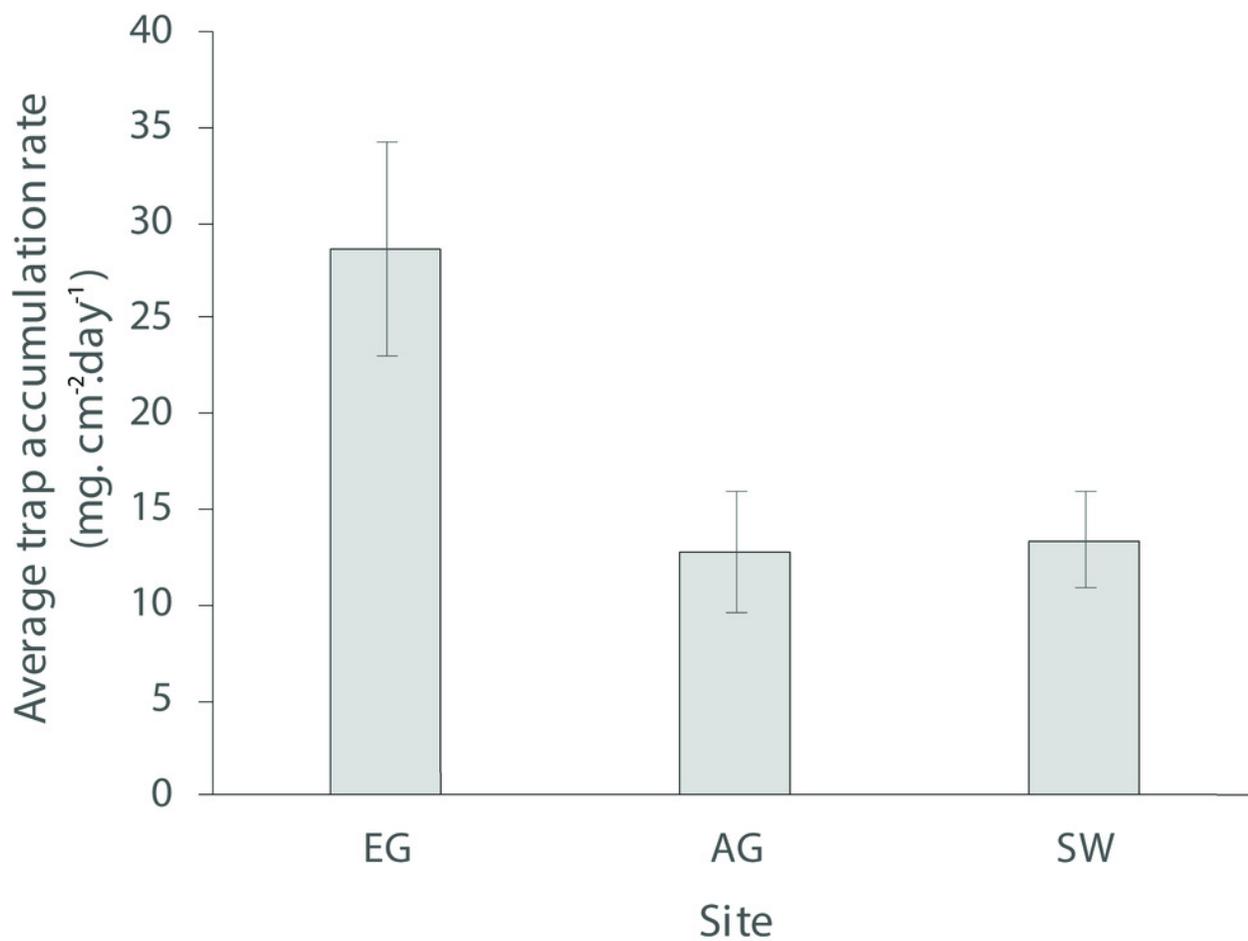



Figure 4

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

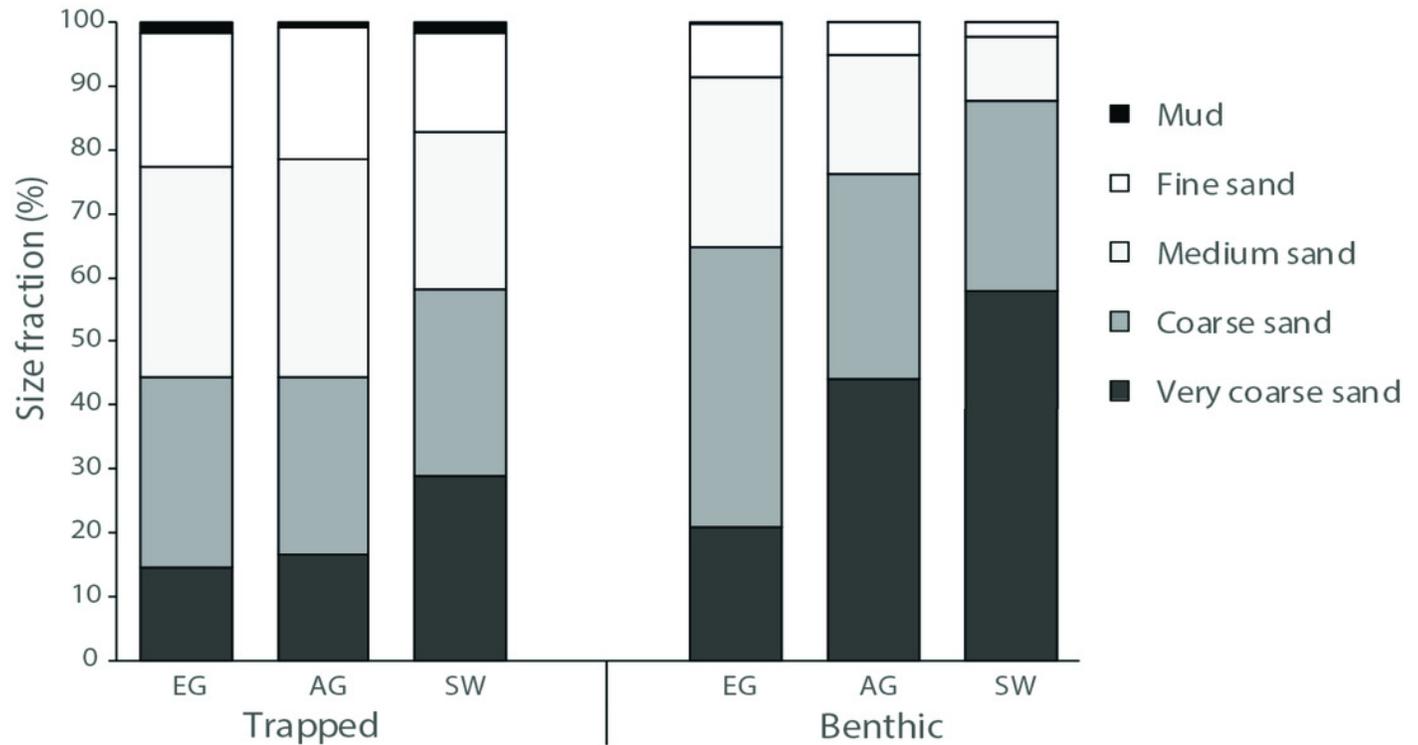



Figure 5

Average percentage benthic cover at EG, AG and SW. Sites are organised from inshore to offshore (error bars = SE).

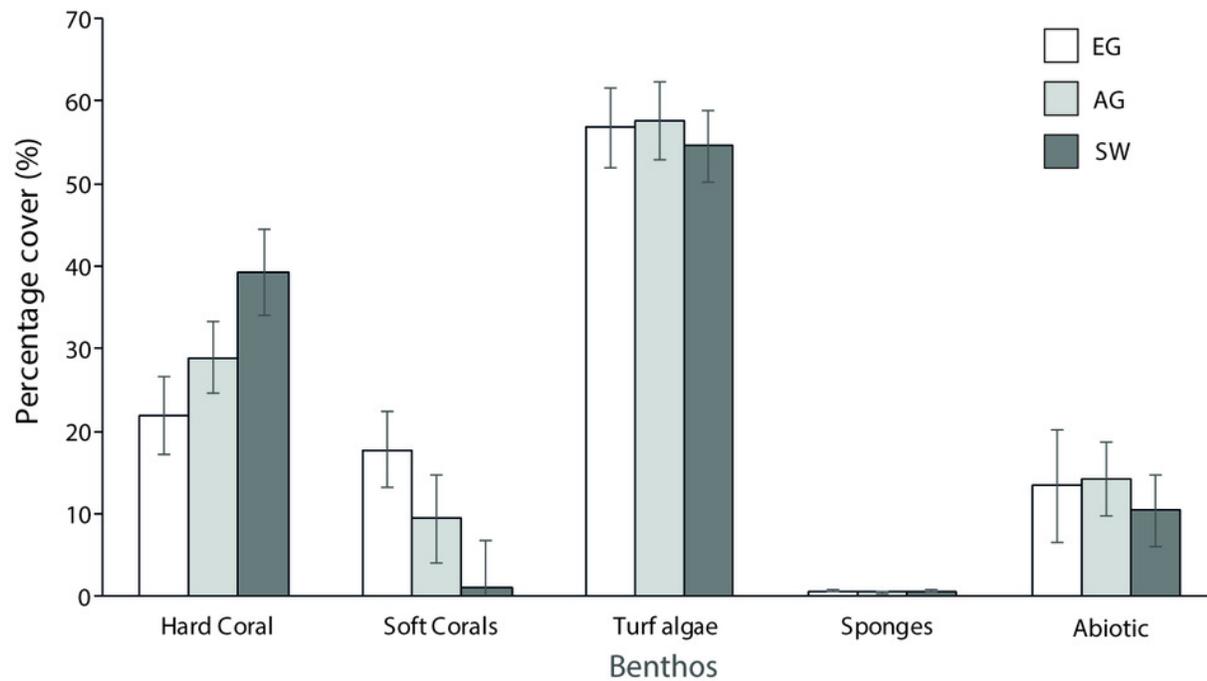



Figure 6

Signs of impaired health

A. Mucus, B. Feeding scars, C. Christmas tree worms and bivalves, D. pigmentation response in *Porites* sp. E. Non-focal bleaching, and F. Partial bleaching.

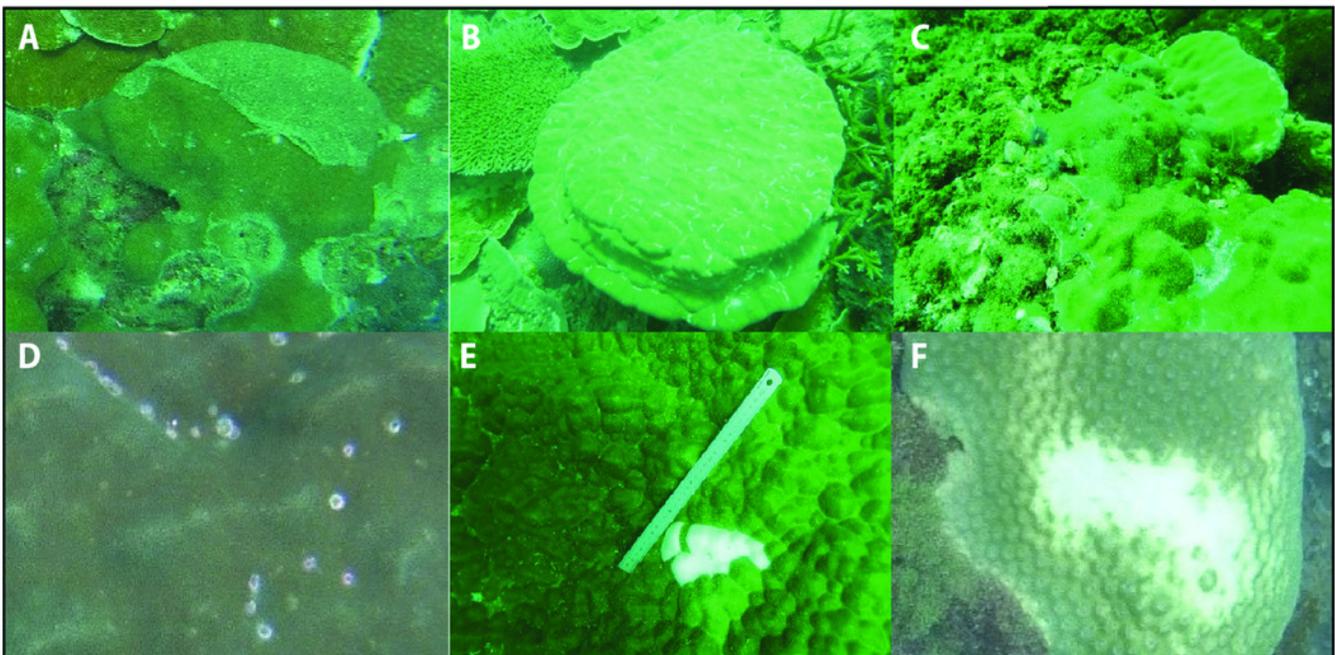



Figure 7

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 (error bars = SE).

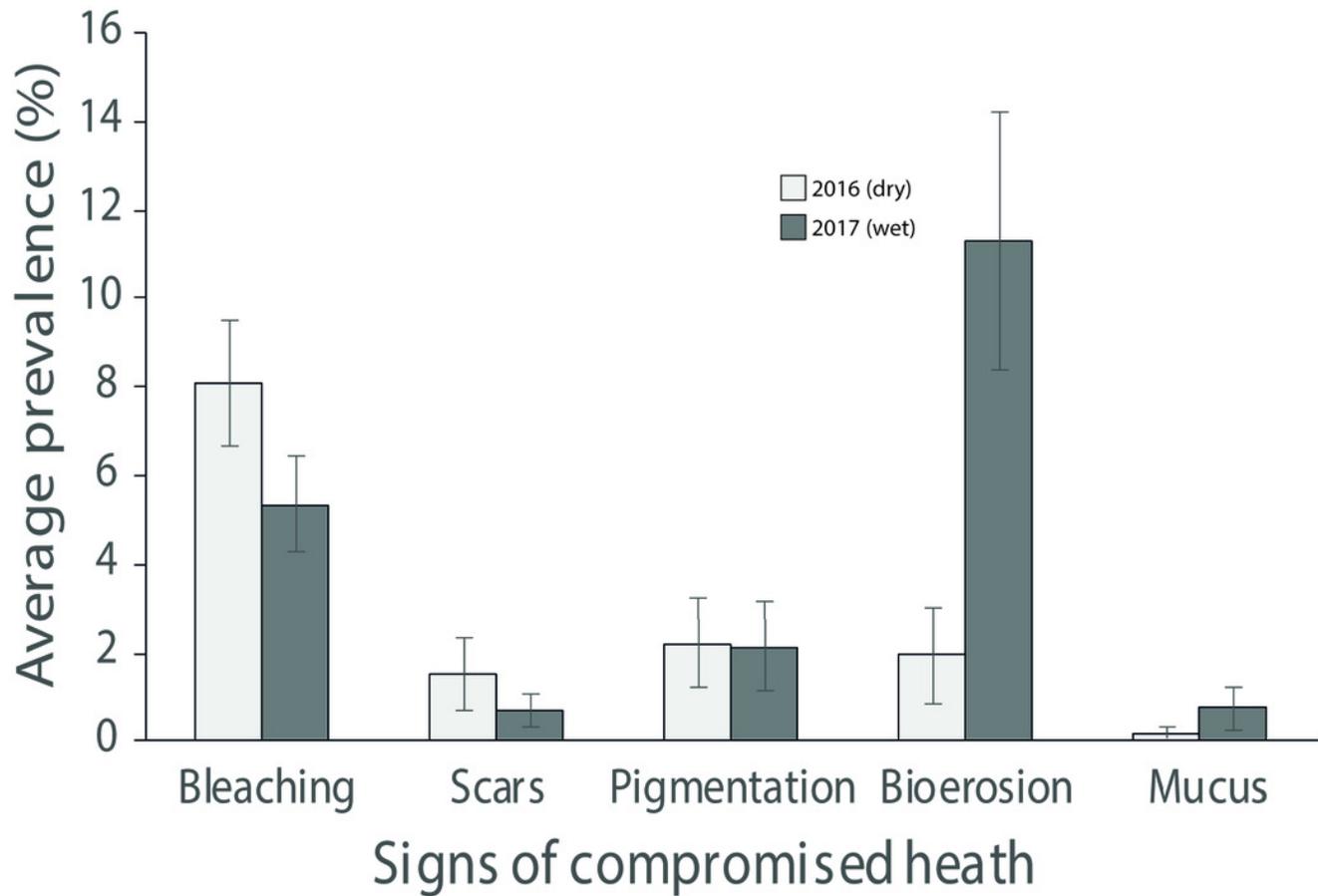



Figure 8

Average bleaching scale for the three coral genus across the three survey sites (EG, AG, SW) that were tagged in September 2016 following the warm dry season and cooler wet season (error bars = SE).

(1=normal, 2=pale, 3=0-20% bleached, 3=21-50% bleached, 4=51-80% bleached, 5=81-100% bleached)

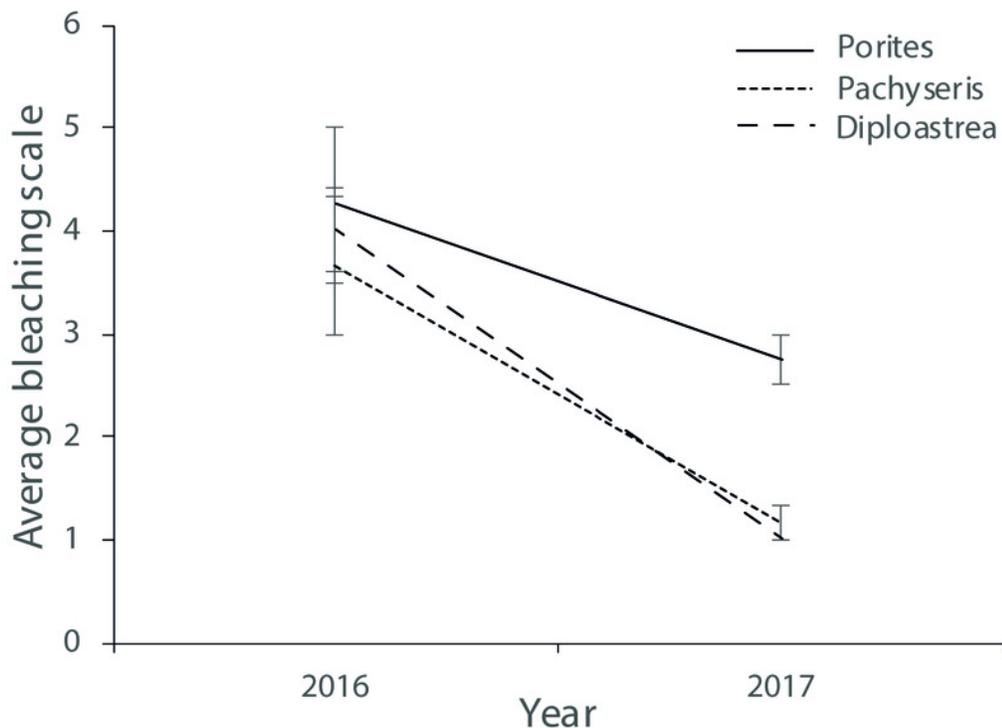



Figure 9

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).

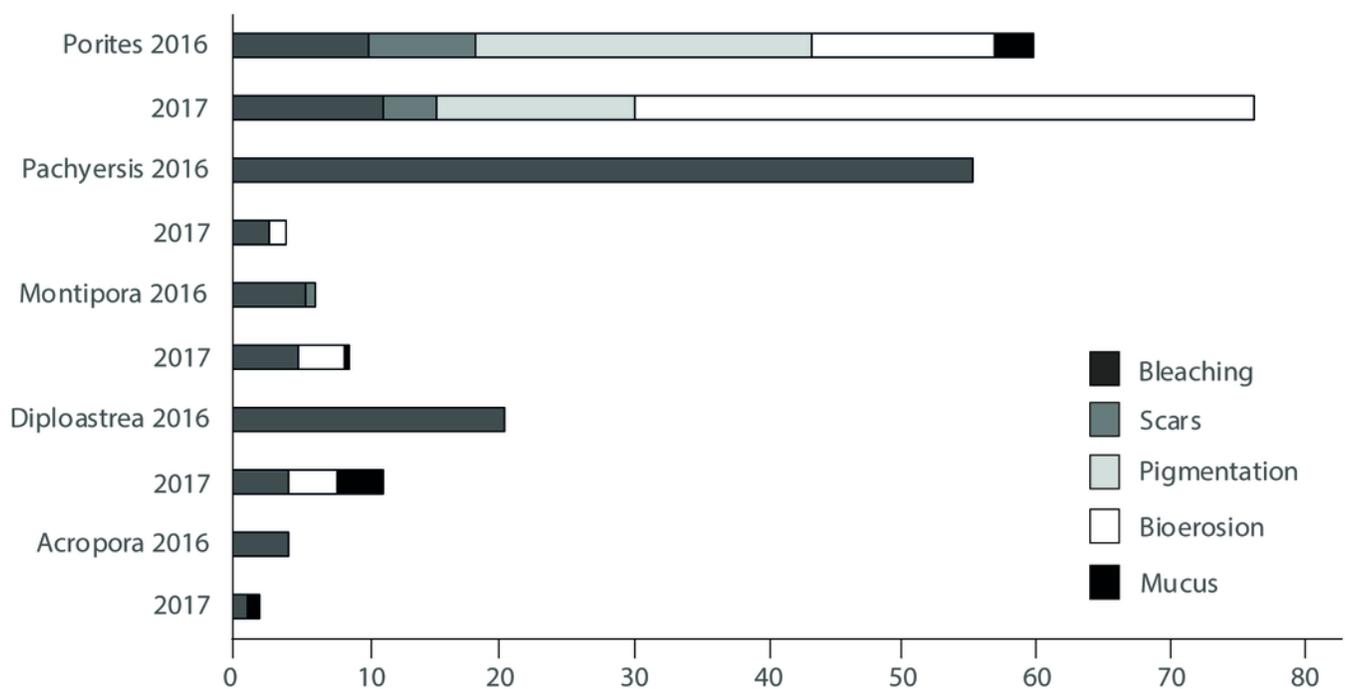



Figure 10

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 (error bars = SE).

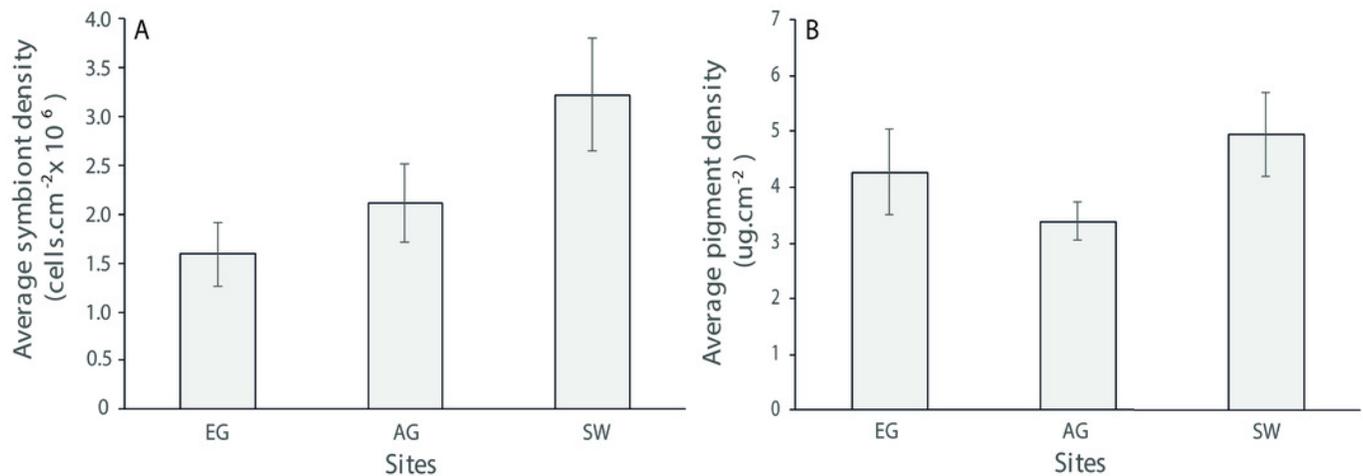



Figure 11

Distance-based redundancy analysis (dbRDA) plot with an AIC criterion selection illustrating the significant environmental factors (p<0.05) that influence community composition at EG, AG and SW.

The length and direction of the vectors represent the strength of the correlation (circle denotes a correlation of 1) and direction (+/-) of the relationship with transects (points plotted) at each site.

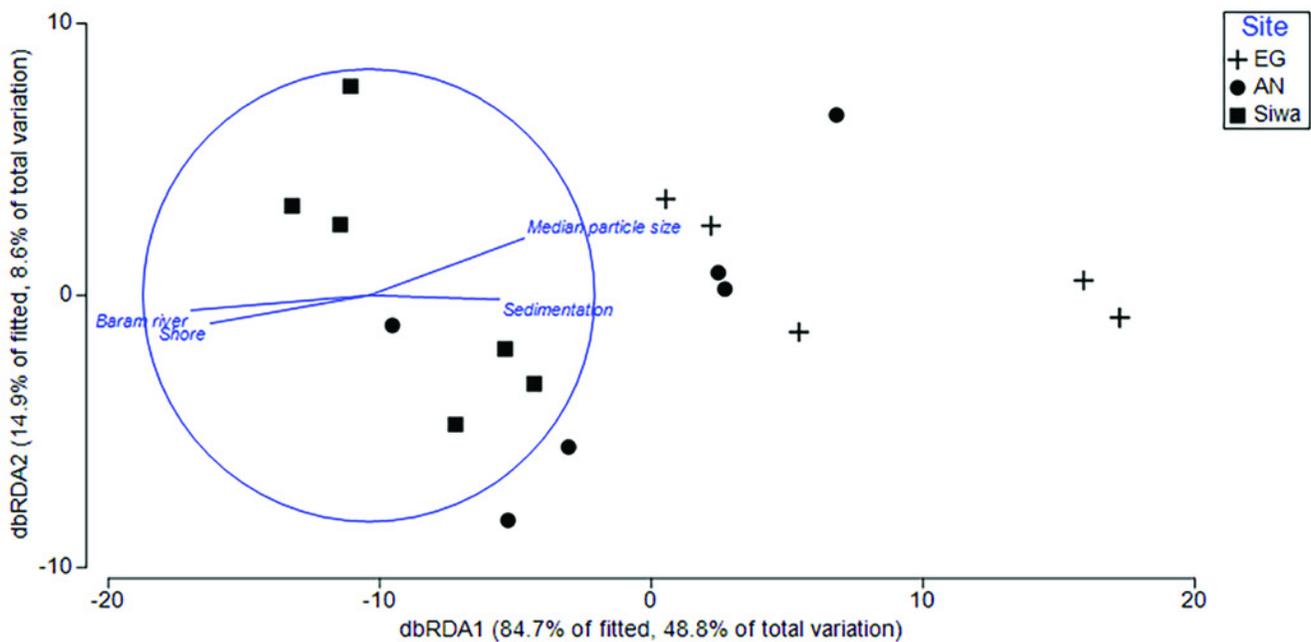
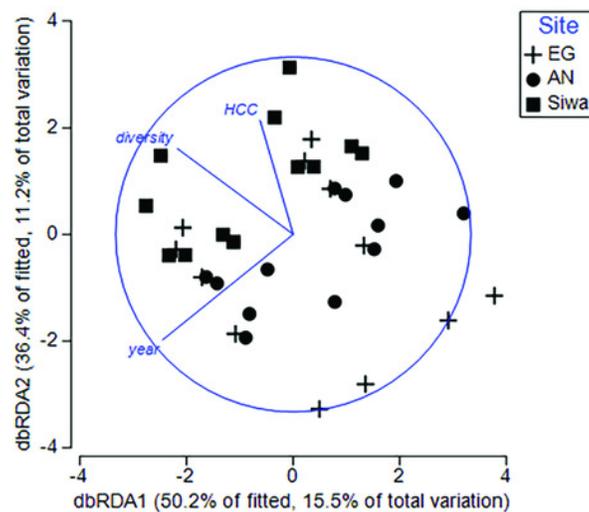



Figure 12

Distance-based redundancy analysis (dbRDA) plot with an AIC criterion selection illustrating the that influence coral health at at EG, AG and SW.

Significant explanatory variables (p<0.05; HCC = hard coral cover, diversity = coral diversity, year = Sept 2016 and May 2017). The length and direction of the vectors represent the strength and direction (+/-) of the relationship with transects (points plotted) at each site. (Image credit: Amitay Moody).

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

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	*0.040*	EG<AG,SW
	Season	1	0.15	0.700	
	Site*Season	2	7.20	*0.003*	
Bioerosion	Site	2	0.87	0.430	
	Season	1	20.20	*<0.001*	2017>2016
	Site*Season	2	3.80	0.040	
Pimentation	Site	2	5.30	*0.010*	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	

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 and season and the interaction.

If impaired health result is missing then it was not observed for that coral genus. Sites; EG = Eves Garden, AG = Anenomes Garden, SW = Siwa: Seasons; 2016, 2017.

Species	Health sign	Factor	df	F value	p value	Post hoc
Porites	Total	Site	2	1.71	0.202	
		Year	1	10.17	*0.004*	2017>2016
		Site*year	2	4.00	*0.031*	
	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	*0.034*	EG>SW
		Year	1	2.64	0.104	
		Site*year				
	Bioerosion	Site	2	1.61	0.219	
		Year	1	21.79	*<0.001*	2017>2016
		Site*year	2	6.29	*0.006*	
	Pimentation	Site	2	8.79	*0.001*	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	
Pachyseris	Total	Site	2	0.30	0.744	
		Year	1	9.02	*0.008*	2016>2017
		Site*year	2	0.14	0.869	
	Bleaching	Site	2	0.37	0.699	
		Year	1	9.69	*0.006*	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	
Montipora	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	
Diploastrea	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
Acropora	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

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

Explanatory variable	p value	Pseudo-F	R²
Depth	0.094	2.3	0.010
Dist. Baram River	*0.002*	7.0	0.303
Dist. Shore	*0.007*	5.1	0.008
Sedimentation rate	*0.025*	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	*0.010*	5.0	0.164

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 of a DistLM that includes data from the sediment traps among reefs in 2017 only.

Explanatory variable	p value	Pseudo-F	R²
Year	*0.003*	5.0	0.128
HCC	*0.042*	2.8	0.052
Diversity	*0.003*	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

Sediment variable	p value	Pseudo-F	R²
Sedimentation rate	0.059	2.4	0.070
Course sediments	*0.031*	2.9	0.152
Fine sediments	*0.031*	2.9	0.030
Silt	0.067	2.3	0.110
Median particle size	0.083	2.2	0.024