Inshore, turbid coral reefs from northwest Borneo exhibiting low diversity, but high cover show evidence of resilience to various environmental stressors (#31951)

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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 input 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 *Pachyseries* 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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ABSTRACT

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 kms. 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 *Pachyseries* showing partial

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INTRODUCTION

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

Despite elevated resilience to naturally turbid conditions, many inshore turbid reefs face threats from local pressures, largely related to declining water quality and increased sediment input. In South East (SE) Asia, 95% of reefs are threatened from local threats (Burke et al., 2011) and are, therefore, regarded as the most endangered reefs globally. Since the 1980's these reefs have suffered an average [illegible] loss in coral cover with hard coral cover declining from 45% to 22% in 200[illegible] (Bruno et al. (2007). Most reefs in SE Asia are located in close proximity to countries with rapidly emerging economies and fast population growth (Wilkinson, 2006; Burke et al., 2011; Heery et al., 2018). They are further characterised by poorly developed environmental policies, inadequate regulation, lack of enforcement, a shortage of institutional and technical capacity, insufficient community support and involvement, and conflicts and tensions between stakeholders (Fidelman et al., 2012). The synergistic effects of these factors has led to poor water quality on many inshore reefs via pollution and sediment input derived by rapid land development, and over-fishing activities (McManus, 1997; Wilkinson, 2006). As a consequence, sedimentation rates are high (>10 mg cm^2 day^{-1}) with SE Asian coastal systems experiencing the highest siltation loads globally (Kamp-Nielsen et al., 2002; Syvitski et al., 2005).

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

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

MATERIALS & METHODS

Study sites

The study was conducted on three reefs (Eve's Garden, Anemone Garden and Siwa Reef) in the MSCRNP (Fig. 1). These sites were of a comparable depth (5-15 m) and size (<0.11 km^2), and had 10-50% coral cover (Elcee Instumentation Sdn Bhd, 2002). Eve's Garden (EG) is a shallow inshore reef close to shore (7.3 km) with a coral community dominated by platy and massive corals such as *Pachyseris* sp. and *Porites* sp. (Ferner, 2013). Anemone's Garden (AG) is further offshore (11.7 km) and consists of a considerable density of anemone colonies, with platy forms of *Acropora sp*. and exceptionally large massive *Porites sp*. and *Diploastrea sp.* colonies (1-5 m length). Siwa Reef (SW) situated further to the south is the most biologically diverse of the studied reefs consisting of encrusting and massive coral forms (Ferner, 2013). These reefs lie on an inshore to offshore transect from the Baram (sediment influx 2.4 x 1010 kg.year-1; Nagarajan et al., 2015) and Miri River mouths, located to the north of EG (10 km from Miri river and 30 km from Baram river).

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

Physical data collection

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

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

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

Biological data collection

In water data collection

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

To assess seasonal fluctuations in coral reef health, signs of compromised health (disease, bleaching, bioerosion, pigmentation, mucus production, scars) were recorded in September 2016 and May 2017. The belt transect methodology was used, covering a wider area along the transect line via a zig-zag pattern (40 m^2 for each 20 m transect). Coral colonies within each belt transect were identified to genus level and classified as either healthy or affected by an impaired health sign (Beeden et al., 2008). Bleaching was further subdivided into whole, partial, focal and non-focal bleaching. To determine if bleached corals recover or die, a total of 14 coral colonies from EG and SW in both sampling seasons that showed signs of bleaching were tagged and photographed (4 *Diploastrea*, 6 *Pachyseris*, 4 *Porites*). The percentage of bleached tissue was assessed from scaled photographs using CPCe software (1=normal, 2=pale, 3=0-20%, 4=20-50%, 5=50-80% and 6=80+% bleached).

Symbiont density and chlorophyll a analysis

In May 2017, fragments of three coral species (*Montipora sp., Pachyseris sp.* and *Acropora sp.*) were collected from EG, AG and SW for chlorophyll *a* and symbiont density analysis. Fragments (5-10 cm for branching corals and ~10 x 10 cm for foliose corals) were collected using cutters and placed in ziplock bags. Samples were placed on ice during transportation back to the laboratory where they were stored at -80^{o}C until further analysis. Symbiont density and chlorophyll *a* content were quantified following the removal of coral tissue from the skeleton. The protocol for extracting tissue was adapted from Ben-Haim et al. (2003) (Supplementary material).

Statistical analysis

Univariate statistical analysis was conducted in R Studio Desktop version 1.1.383. Prior to analysis, normal distribution and homogeneity of variances were checked using the Shapiro Wilk test and the Levene's test, respectively. To assess if there were significant differences in benthic cover (hard coral, soft coral, algae) and diversity among sites a one way analysis of variance (ANOVA, n= 6, α= 0.05) was used followed by a Tukey HSD post-hoc test (Bonferroni method), if necessary. Significant differences in the prevalence of compromised health signs (bleaching, bioerosion, mucus production, pigmentation and scars) among sites and between seasons were identified for both total hard coral cover and for the most abundant coral species (*Porites, Pachyseris, Montipora, Diploastrea, Acropora*) using a Full Factorial ANOVA (FF ANOVA, n= 6, α= 0.05) and a Tukey HSD post- hoc test. If required, a log10 transformation was carried out for datasets to meet homogeneity of variance. To recognize differences in physiology (chlorophyll *a* content and zooxanthellae density) between the three coral species sampled (*Acropora* n=17, *Pachyseris* n=13, *Montipora* n=15) and across sites, a non-parametric Kruskal Wallis test was performed. Furthermore, to evaluate cell health differences between the three genera and among reefs, the percentage of cells from each grade were compared using the Kruskal-Wallis test. Differences in sediment accumulation rates among reefs (Kruskal-Wallis) and particle size characteristics (median, fine/course fraction) among reefs and between the trapped sediments and the benthic sediments were also tested (FF ANOVA, n=18).

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

RESULTS

Physical parameters

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

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

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

Benthic cover

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

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

Coral reef health

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

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

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

Drivers of benthic cover and health

Environmental variables (depth, sediment accumulation rate, distances from shore/river mouth, concentration of silt/fine/coarse particles, median particle size) explained 62.5% of the variation in benthic composition among reefs. Key drivers ($p<0.05$) were distances from river mouth (30.3%) and shore (1%), median particle size (16.4%), and sediment accumulation rate (2.3%; Table 4). Variability among sites was higher than within, with sedimentation rate and particle size a key driver of benthos at EG and AG, and distance of river and shore more closely associated with SW (Fig. 11a).

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

DISCUSSION

The three reef sites in the MSCRNP are characterised by healthy coral cover yet low coral diversity. Average live coral cover among the three reefs was 30%, ranging from 22% at EG to 39% at Siwa Reef. This is lower than reefs to the north in Sabah, where several papers report live coral cover from 23 to 75% (Pilcher and Cabanban, 2000; Chou and Tun, 2002; Lee, 2007; Praveena et al., 2012; Waheed et al., 2016), but greater than the average coral cover for the wider Pacific region, estimated at 22% in 2003 (Bruno and Selig, 2007). Previous assessment of coral cover in 2000 on the Miri reefs range from 28% (Pilcher and Cabanban, 2000) to 22-58% (Elcee Instumentation Sdn Bhd, 2002). Although the higher coral cover reported by the latter study is most likely an artefact of the methodology used (ex-situ Acoustic Ground Discrimination System). Regardless, our data would suggest that coral cover has been relatively stable over the last couple of decades. Despite high hard coral cover at levels comparable to both turbid and clear water reefs (Roy and Smith, 1971; Loya, 1976; Larcombe et al., 2001; Wesseling et al., 2001; Palmer et al., 2010; Goodkin et al., 2011), diversity was comparatively low (14 to 25 genera per reef) for the Coral Triangle region. Turak and Devantier (2010) reported 291 coral species on reefs near Brunei (~80 km from Miri), and Teh and Cabanban (2007) reported 120 species within 71 hard coral genera for Banggi Island in Sabah. A comprehensive biodiversity assessment of all 30 reefs with the MSCRNP in 2000 reported 66 genera (203 coral species; Elcee Instumentation Sdn Bhd, 2002). We only observed a third of the number of coral genera, which may suggest a decline in biodiversity over the last 17 years. However, this report also found that coral diversity was highly variable among reefs, with an average of 9 coral genera per transect. It is likely that reefs not surveyed in this study found further to the south as well as in deeper (15-35 m) offshore waters include several coral species not observed at our shallow nearshore sites, which are heavily influenced by terrestrial sedimentation from both natural and anthropogenic processes.

Low diversity at the surveyed sites is likely the result of poor water quality in the nearshore shallow coastal zone. Inshore reefs in Miri lie within the 7 to 15 m depth range as such there is a lack of reef structure within the 1-5 m depth range that is often characterised by a distinct set of coral species (Morgan et al., 2016; DeVantier and Turak, 2017). This may in part explain lower coral diversity than on reefs to the north in Brunei and Sabah. However, these inshore reefs are also characterised by high levels of terrigenous sediments, which can also reduce coral diversity (Rogers, 1990; Fabricius, 2005; Anthony, 2006). High sediment loads from rivers are typically correlated with high nutrient loads that can lead to increase in reef algal biomass (De'ath et al., 2012). Algal cover on all three reefs was high (>50%) and will most likely be competing with corals for space on the reef. Some coral taxa will be less resilient to both sediments and algal competition resulting in lower coral diversity (Fabricius et al., 2005; De'ath and Fabricius, 2010). In Indonesia, Edinger et al. (1998), recorded lowest coral diversity on reefs with algae cover reaching 40%. Reduced diversity was also attributed to land pollution as well as destructive and over-fishing practices that destroy the reef structure and reduce fish biomass thereby removing the top-down control on algal growth (Hughes, 1994; Rogers and Miller, 2006; De'ath and Fabricius, 2010). In Miri, overfishing as well as poor land management practices have been a long-term concern for the regional government (Elcee Instumentation Sdn Bhd, 2002) but there are limited funds to actively protect the reefs (Teh and Teh, 2014). Low diversity does not necessarily suggest worse reef condition. Typically, low diversity in nature results in lower resilience (Raymundo et al., 2005) and community stability (Bellwood et al., 2004). Yet there is growing evidence to suggest that a few but tolerant species can maintain reef resilience to local and global impacts, and implies that the diversity-resilience links need further investigation (Bellwood et al., 2004; Fabricius et al., 2005; Nystrom et al., 2008)

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

The inshore to offshore gradient in hard coral cover, diversity and composition is the result of spatial differences in sediment related parameters. Over 62% of the variation in benthic cover at our three reef sites is explained by differences in depth, sediment accumulation rates and distance from sediment sources as well as sediment particle size characteristics. Consequently, we saw a significant increase in both coral cover and diversity with increasing distance from the river mouths. Similar observations have been reported from Indonesia and Puerto Rico, where hard coral cover nearly halved towards shore (Loya, 1976; Edinger et al., 2000), and in Hong Kong, where inshore coral cover was 20% lower than offshore (Goodkin et al., 2011). Reduced coral cover may occur due to low larval recruitment as a consequence of limited hard substrate following sediment settling (Birrell et al., 2005; Fabricius, 2005; Dikou and van Woesik, 2006), or colony mortality caused by anoxic conditions that occur under sediment layers (Rogers, 1983; Riegl and Branch, 1995; Wesseling et al., 2001). The sediment particle size and source (marine versus terrestrial) are considered to be equally if not more important than sediment volume in assessing the impacts of sediments on coral health. Recent studies show that as the percentage of terrestrial sediments with higher organic content increases, there are greater declines in coral cover (Bégin et al., 2016; Fourney and Figueiredo, 2017). Although we did not measure organic content here, it is likely sediments were transported onto the reef given that the trapped sediments had a different sediment signature (significantly finer) from the benthic sediments. Terrestrial sediments reaching reefs at distance of >10 km from the river mouth are typically composed of clay and finer silt particles (Bainbridge et al., 2012), which would suggest that the trapped sediments were of terrestrial origin. As such, these data confirm that sediments, most likely from the Baram and Miri rivers, have influenced coral cover particularly on reefs closest to the river mouths. The reefs, however, maybe in a temporally stable state given low dead coral cover and the limited decline in coral cover over the last two decades.

The prevalence of impaired health signs was low (10-20%), but dominated by bioerosion and pigmentation with no signs of coral disease (with one exception). These health indicators are commonly related to high sediment and nutrient influx. High levels of bioerosion in particular has been linked to land based pollution whereby lower light, due to high turbidity, reduces coral density (Risk and Sammarco, 1991; Lough and Barnes, 1992) weakening the coral and increasing susceptibility to bioeroders (e.g. molluscs, worms etc.; Prouty et al., 2017). Furthermore, high nutrient levels can lead to an increase in the abundance of bioeroding organisms (Hallock and Schlager, 1986; Prouty et al., 2017). Bioerosion levels were significantly greater following the wet season when the impact of sediments on the Miri reefs were elevated as indicated by declines in light and higher suspended sediment loads. Conversely, pigmentation rates were higher following the dry season. Pigmentation is an indicator of immune function in response to a stressor (Willis et al., 2004; Palmer et al., 2009). These stressors have been related to settling sediments (Pollock et al., 2014) or lesions from abrasion or scars (Willis et al., 2004), or for the case of Miri reefs could be due to the elevated SSTs recorded in the region in 2016 leading to the documented bleaching event. Spatially, pigmentation rates were significantly lower at Siwa, which may suggest that corals at the least sediment impacted site were also less stressed than at AG and EG. Sediments can also promote diseases in corals (Voss and Richardson, 2006; Haapkyla et al., 2011; Pollock et al., 2014). Diseases such as Black Band Disease and White Plaque have been widely observed in the Indo-Pacific (Harvell et al., 2007; Beeden et al., 2008), but disease occurrence is generally low (~8% of current global records) in SEA reefs compared to the Caribbean (Green and Bruckner, 2000). Suggested explanations for this include poor reporting of marine life in such countries and relatively high coral diversity that might aid in diminishing a quick spread of a disease (Raymundo et al., 2005). At Miri, the more likely explanation of low to no coral diseases are more resilient individual corals and coral species, and potentially limited connectivity with nearby coral populations, although this remains speculative until further work is conducted.

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

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

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

CONCLUSIONS

In conclusion, the MSCRNP reefs are characterized by relatively high coral cover, low prevalence of impaired health and are composed of a few but tolerant coral taxa. Low dead coral cover and almost no decline in coral cover over the last two decades indicates these reefs are stable despite elevated sediment inputs and regular exposure to thermal stress events. There are, however, potential risks from proposed coastal and in-land developments given we found that sediment related parameters have resulted in an on- to offshore gradient in coral cover, diversity and health. Furthermore, high bioerosion and algae cover indirectly suggests high nutrient influx, most likely from the Baram River. The high prevalence of bioerosion observed in *Porites* colonies is a concern given that this coral is a key reef framework builder, and declines in *Porites* health will reduce coral reef complexity and habitat availability for other invertebrate and fish species. Currently, there is no baseline data on spatial and temporal changes in river outputs and sediment plume dynamics within the MSCRNP, which is crucial in evaluating future threats to these reefs. Local management agencies will need to address this knowledge gap if they plan to develop strategies that address the potential impacts of changing land use on MSCRNP. The reefs current health state and elevated stress tolerance does, however give hope that these reefs could be resilient to future climate change but only if local water quality does not deteriorate.

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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)

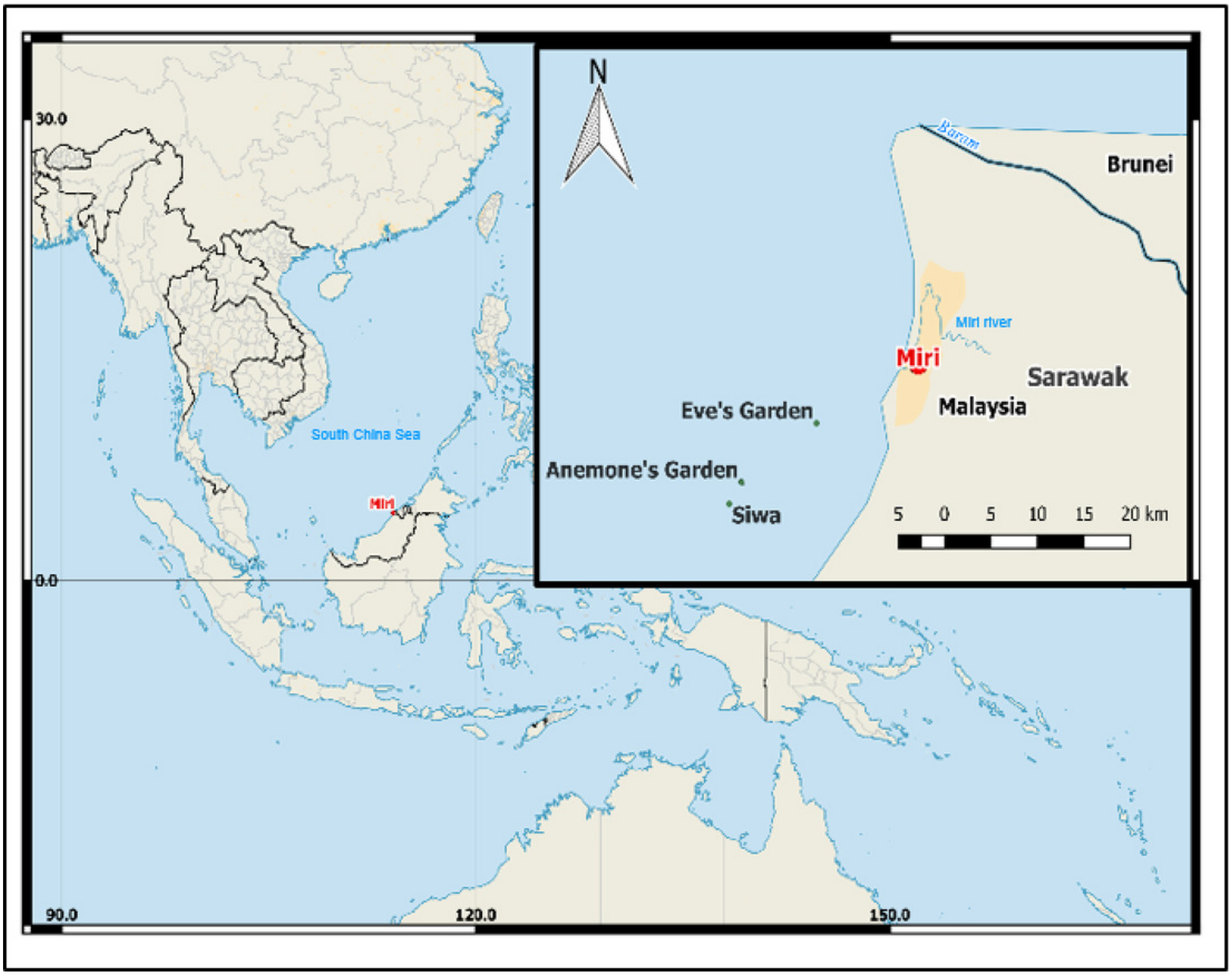
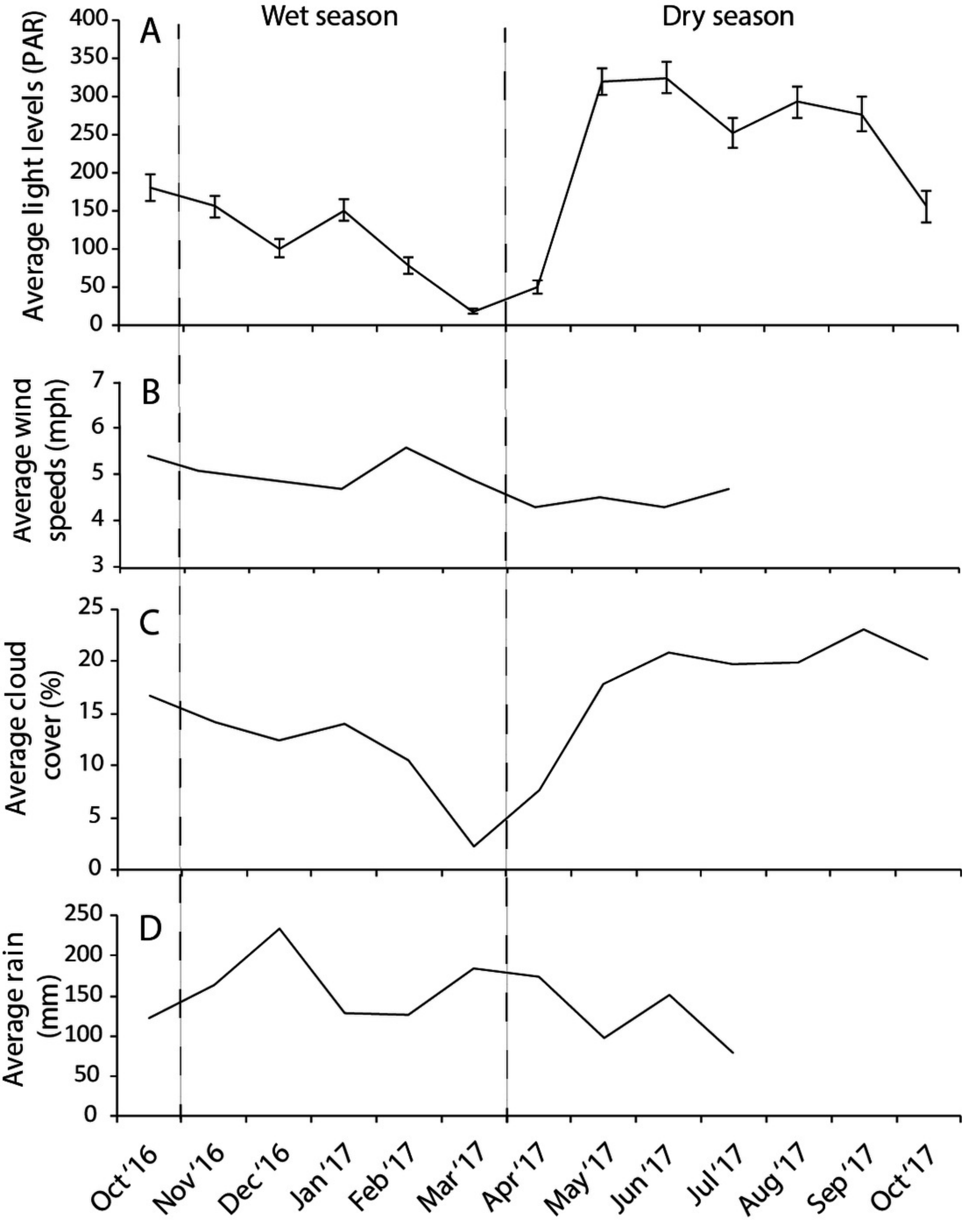


Figure 2

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 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.*


Wet season
Dry season
A
Average light levels (PAR)
400
350
300
250
200
150
100
50
0
B
Average wind speeds (mph)
7
6
5
4
3
C
Average cloud cover (%)
25
20
15
10
5
0
D
Average rain (mm)
250
200
150
100
50
0
Oct '16
Nov '16
Dec '16
Jan '17
Feb '17
Mar '17
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May '17
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Aug '17
Sep '17
Oct '17

Figure 3

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

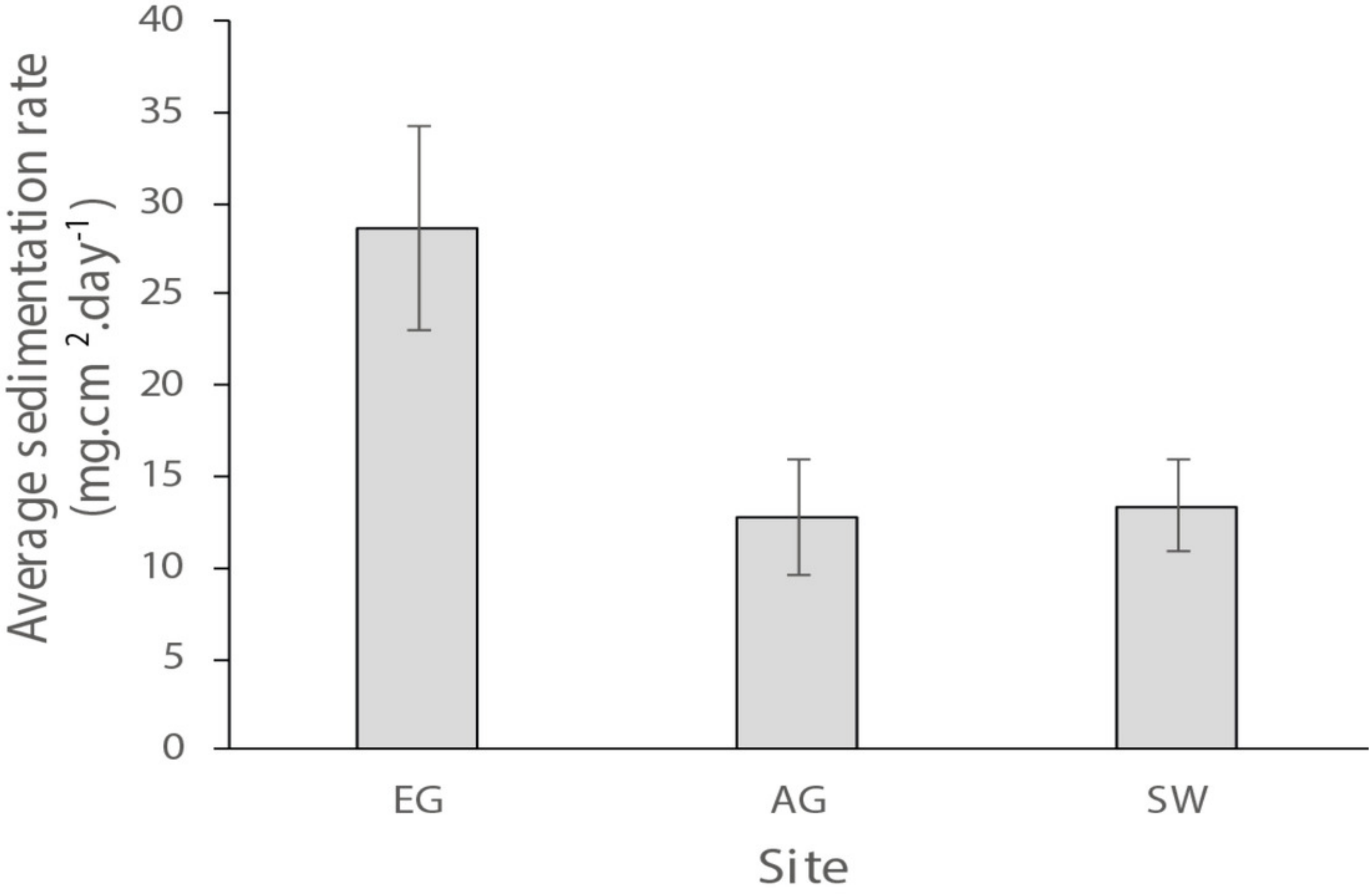

Figure 4

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

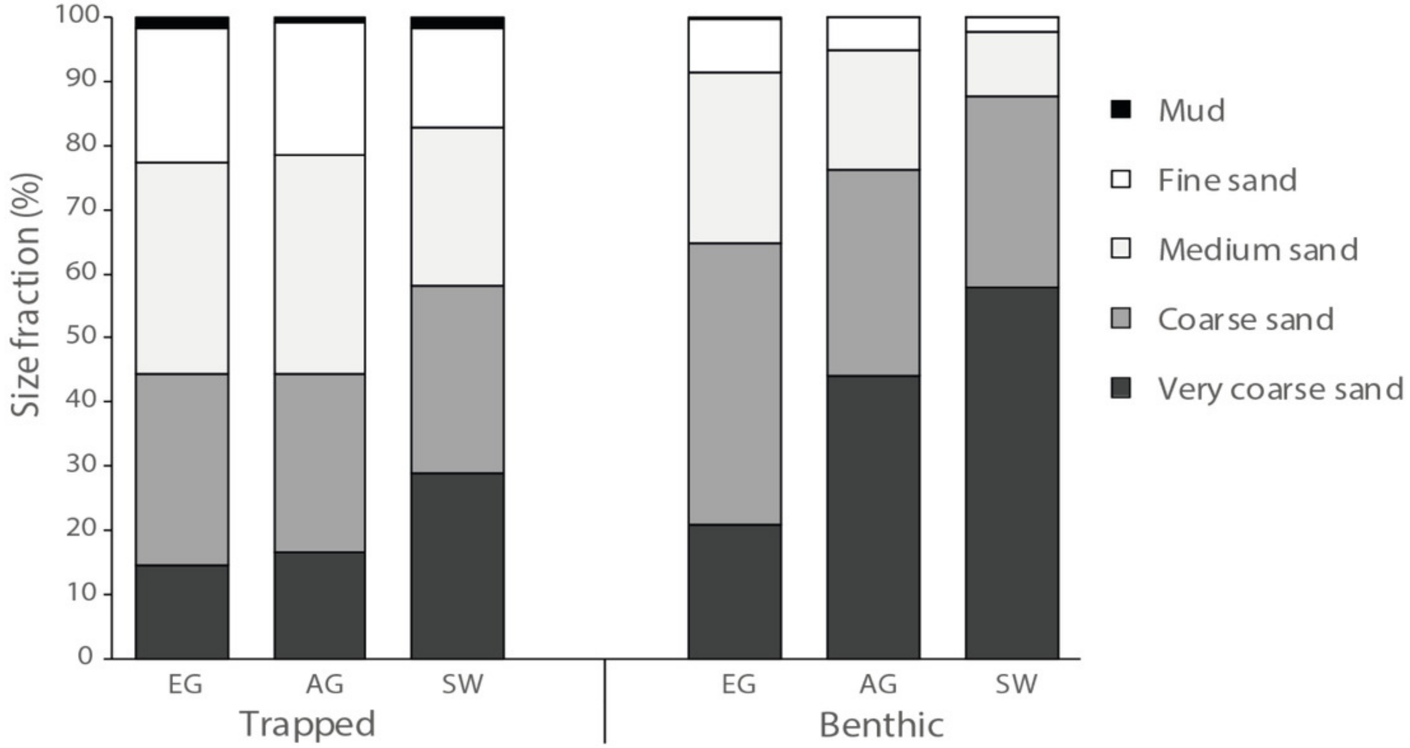

Figure 5

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

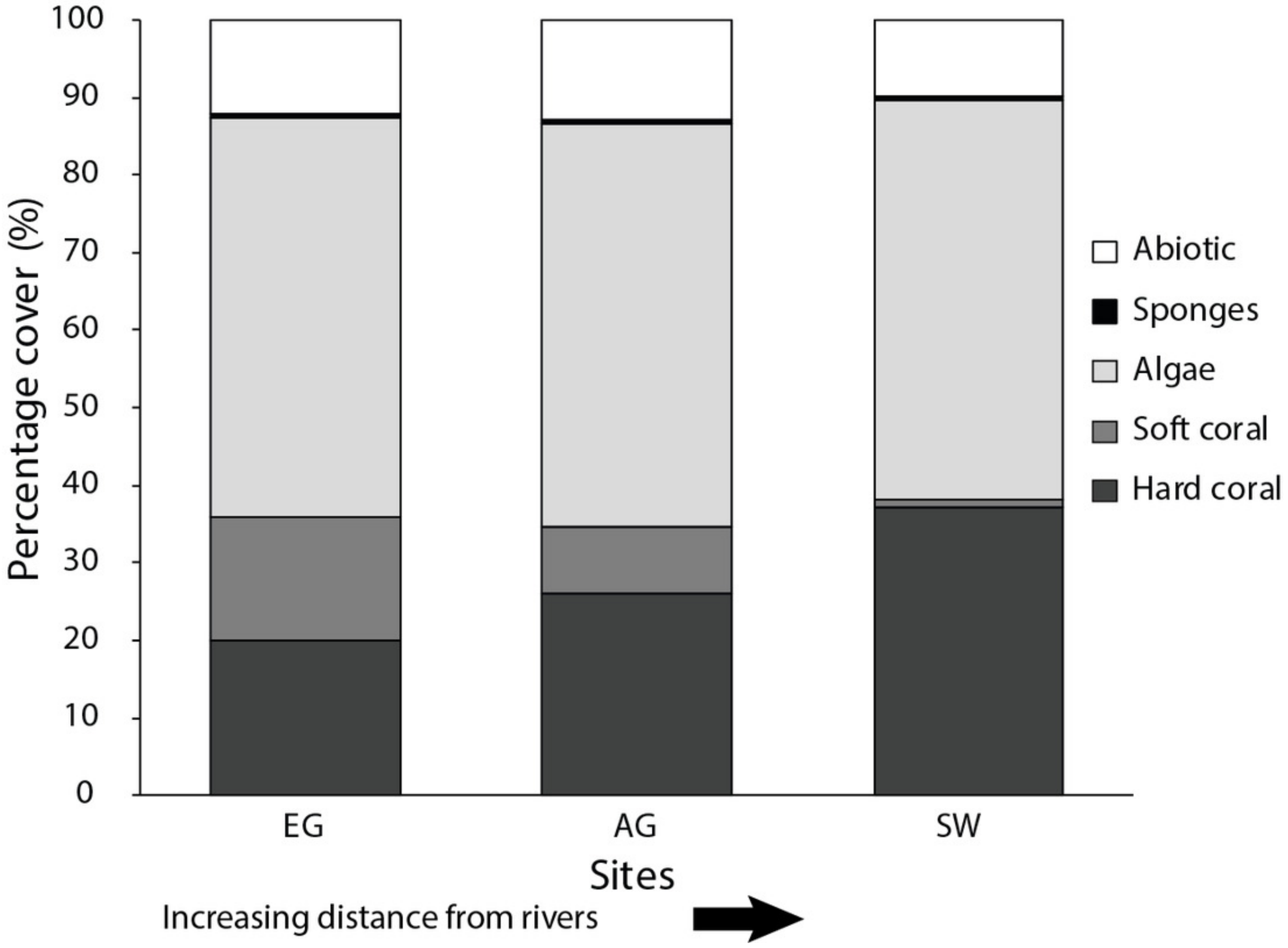

Figure 6

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

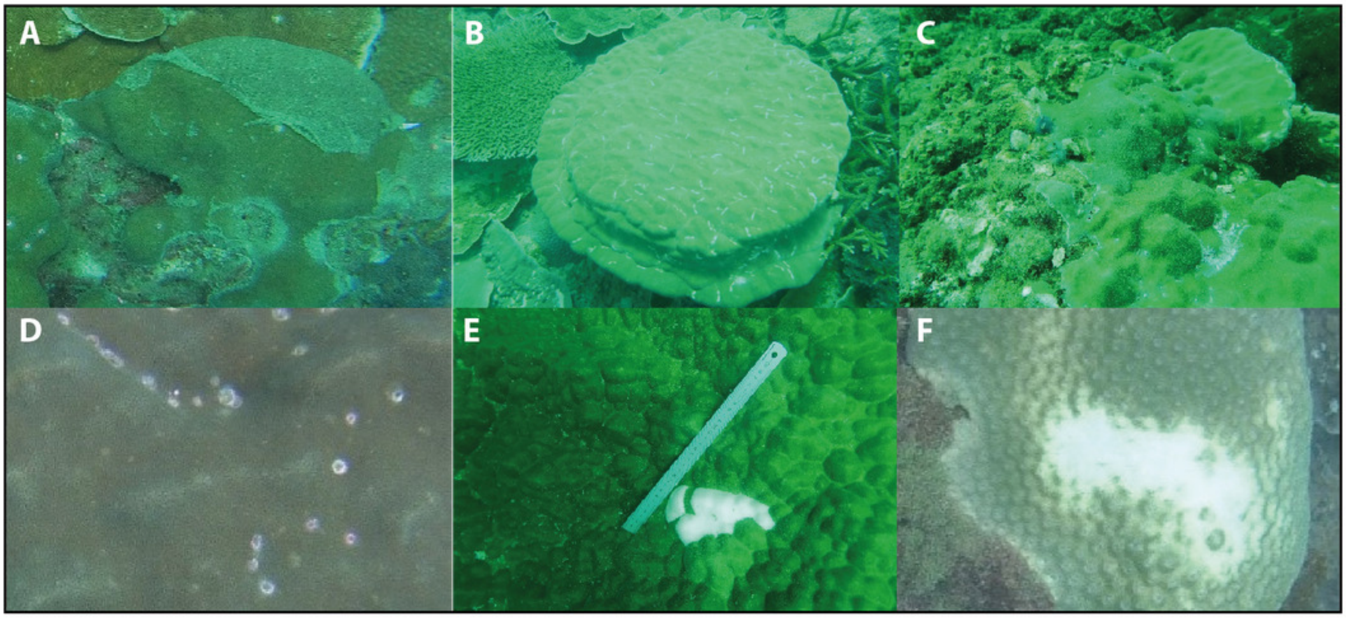

Figure 7

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.

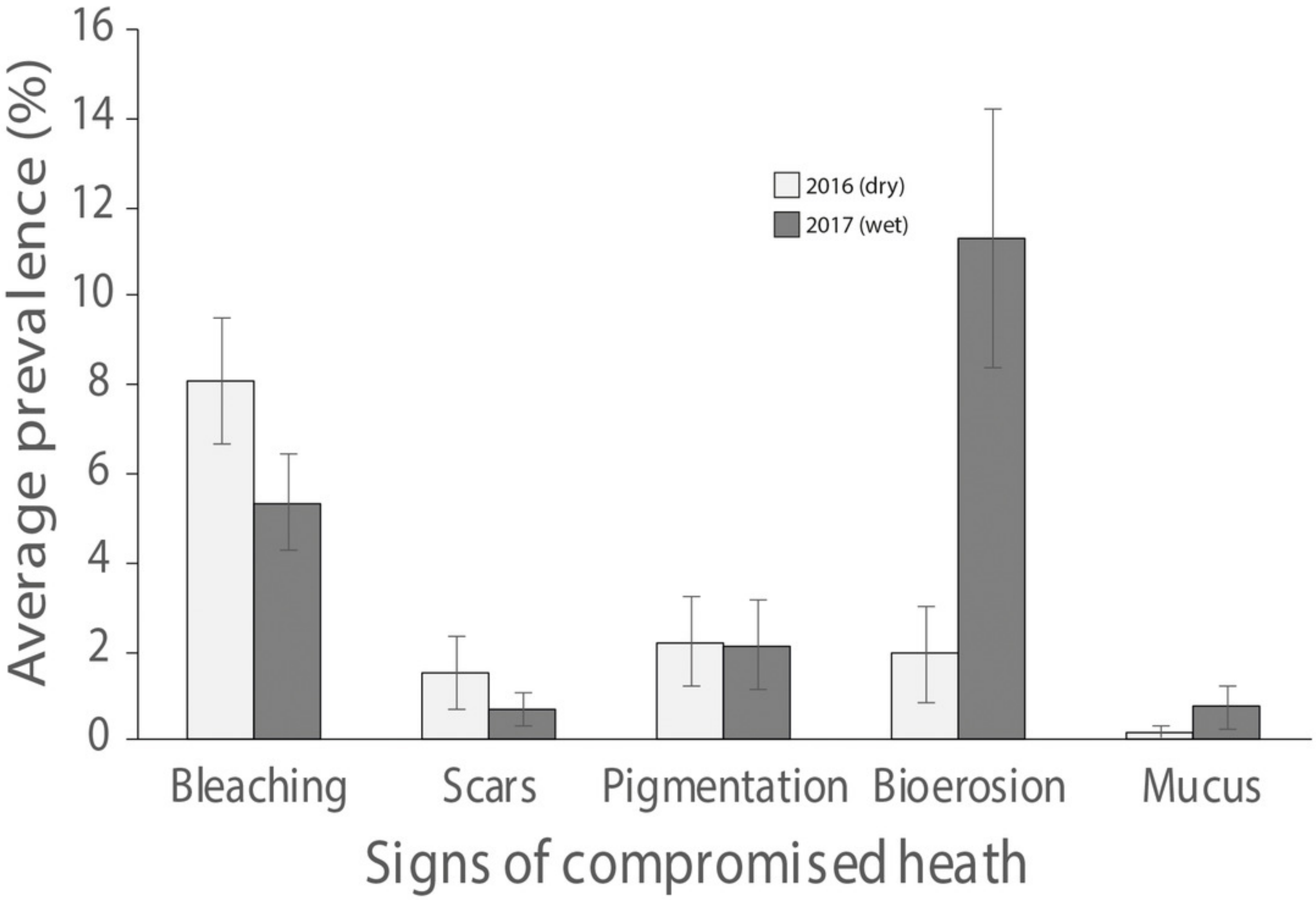

Figure 8

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

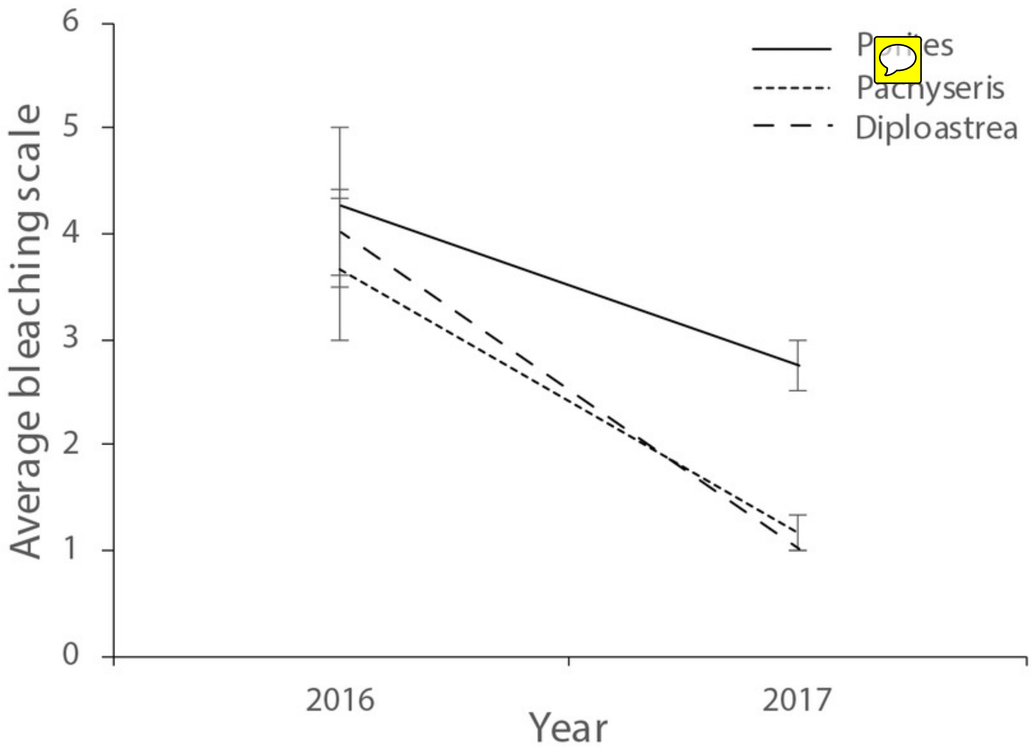

Figure 9

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).

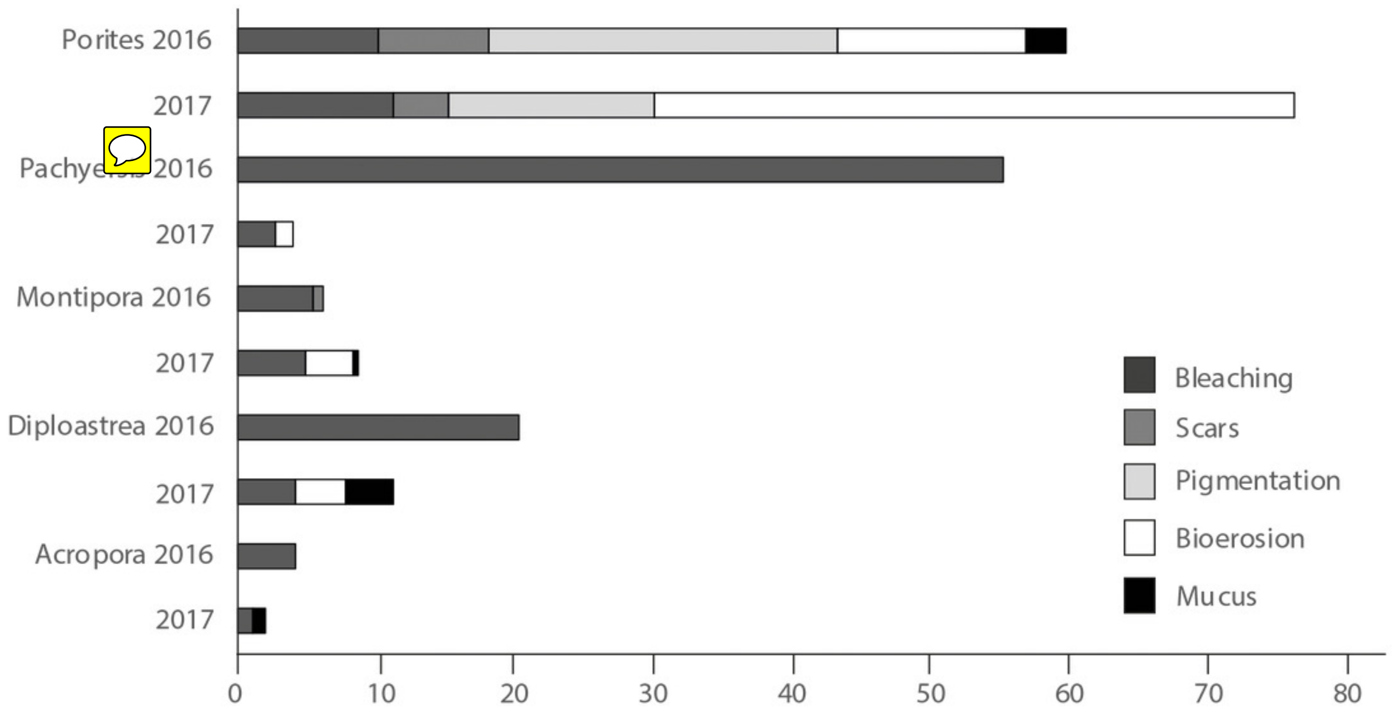

Figure 10

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.

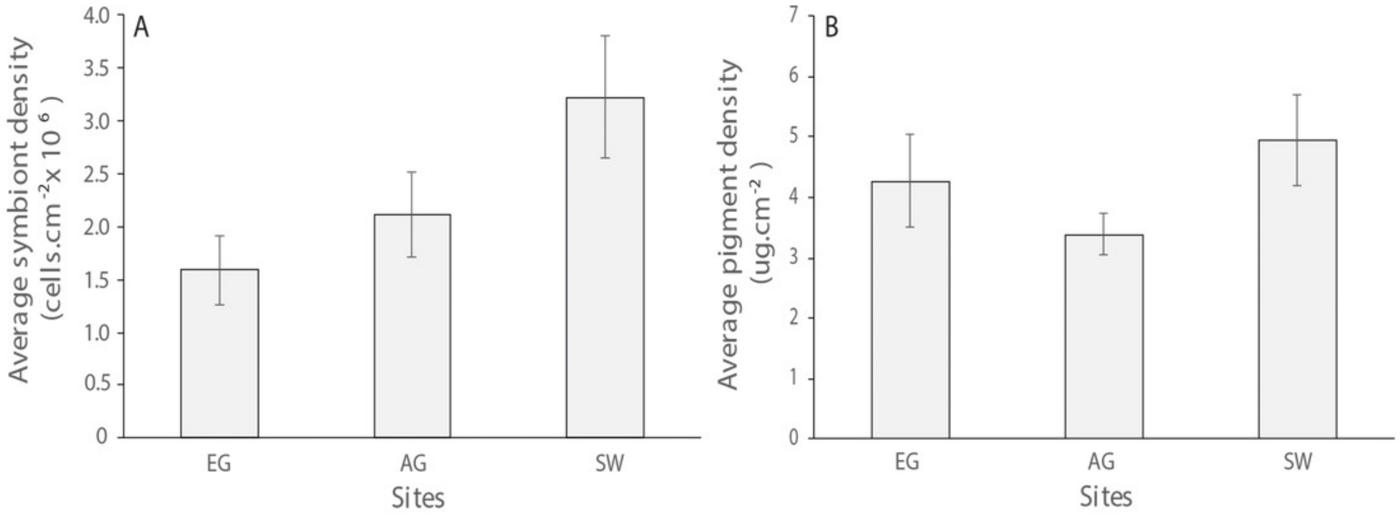

Figure 11

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

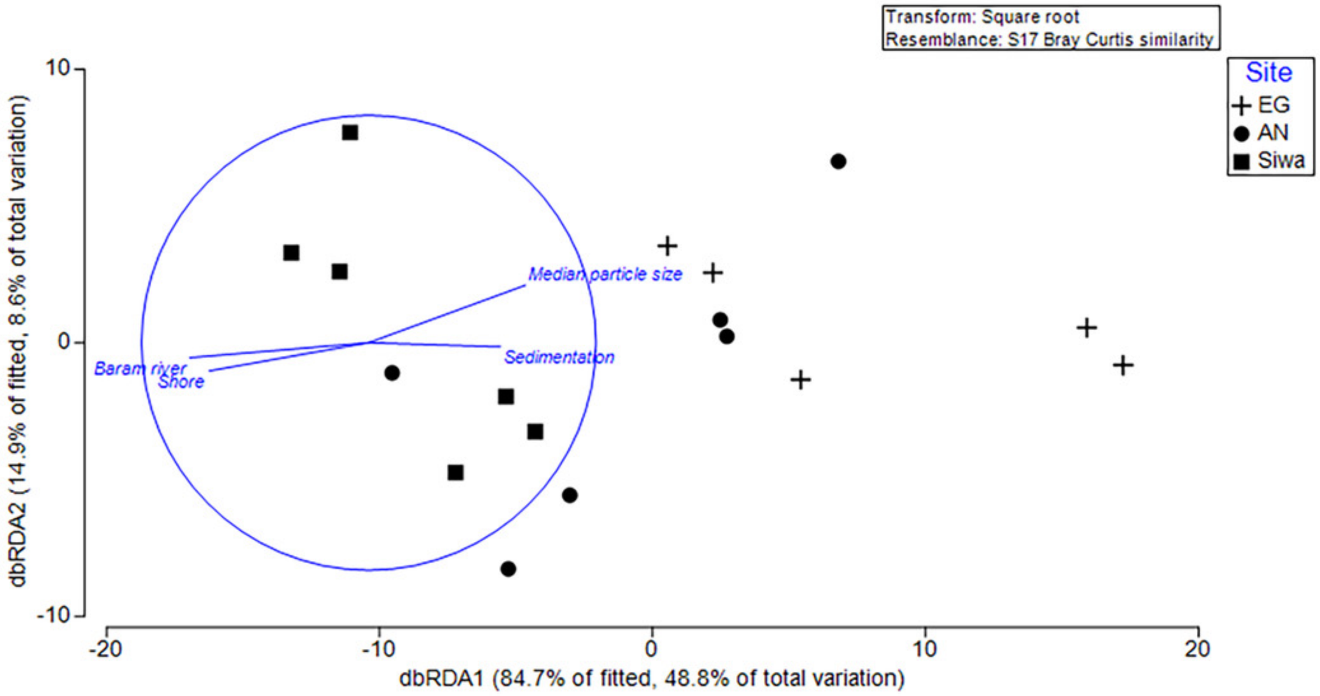

Figure 12

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.

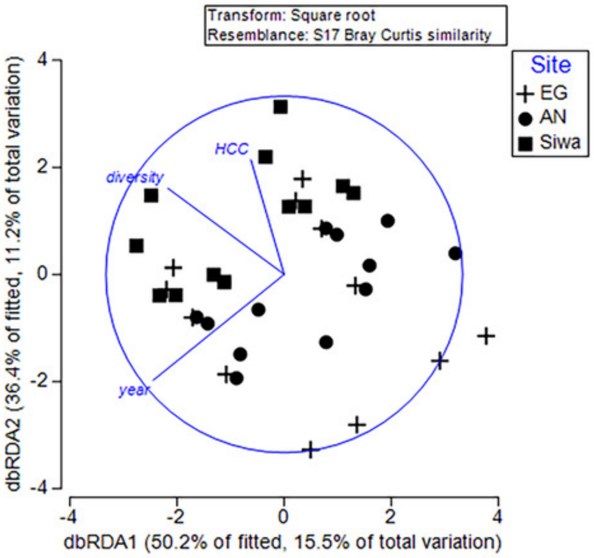

Table 1(on next page)

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	***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	

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
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

Table 4(on next page)

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

Explanatory variable	**p value**	**Pseudo-F**	**R^2**
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

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

Explanatory variable	**p value**	**Pseudo-F**	**R^2**
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**	**R^2**
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