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REPORT

Coral community responses to declining water quality: Whitsunday Islands, Great Barrier Reef, Australia

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Abstract A five-year period (2002–2006) of below-median rainfall followed by a six-year period (2007–2012) of above-median rainfall and seasonal flooding allowed a natural experiment into the effects of runoff on the water quality and subsequent coral community responses in the Whitsunday Islands, Great Barrier Reef (Australia). Satellite-derived water quality estimates of total suspended solids (TSS) and chlorophyll-*a* (Chl) concentration showed marked seasonal variability that was exaggerated during years with high river discharge. During above-median rainfall years, Chl was aseasonally high for a period of 3 months during the wet season (February–April), while TSS was elevated for four months, extending into the dry season (March–June). Coinciding with these extremes in water quality was a reduction in the abundance and shift in the community composition, of juvenile corals. The incidence of coral disease was at a maximum during the transition from years of below-median to years of above-median river discharge. In contrast to juvenile corals, the cover of larger corals remained stable, although the composition of communities varied along environmental gradients. In combination, these results suggest opportunistic recruitment of corals during periods of relatively low environmental stress with selection for more tolerant species occurring during periods of environmental extremes.

Keywords Coral community · River runoff · Coral juveniles · Coral disease · Satellite remote sensing

Introduction

It has long been recognised that key environmental parameters controlling the local distribution of coral species include their exposure to sediment (e.g., Darwin 1851) and the availability of light (Dana 1853). Following these early observations has been a large body of literature serving to further identify physical and chemical environmental conditions that are stressful to corals (see reviews by Fabricius 2005, 2011; Erftemeijer et al. 2012). The repeated conclusion has been that eutrophication, a term taken here to encompass nutrient enrichment, increased sedimentation and the introduction of toxins related to human activities, similar to Tomascik and Sanders (1987) in reference to coral reefs, has resulted in coral community degradation (Fabricius 2005).

The term eutrophication remains particularly pertinent to corals as it explicitly acknowledges that stress to colonies is a result of the interactions between many environmental parameters. For example, if one considers the increased supply of sediments, local hydrodynamics will determine the balance between the accumulation or resuspension and removal of settling material (Storlazzi et al. 2004). The depth of the water will influence the exposure to wave-driven resuspension (Wolanski et al. 2005), but also light attenuation as a result of turbidity. Grainsize will influence the effectiveness of corals' self-

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cleaning mechanisms (Stafford-Smith 1993). In combination, the availability of nutrients will enhance microbial activity both within the water column and sediment, altering the composition of settling material (Bainbridge et al. 2012), further influencing the energetic cost of self-cleaning, limiting survival of coral recruits (Fabricius et al. 2003) and promoting coral disease (Weber et al. 2006, 2012).

Physiological differences between species govern the ability to maintain a positive energy balance along environmental gradients (Anthony and Connolly 2004), e.g., the efficiency of sediment shedding (Rogers 1983; Stafford-Smith 1993) and the ability to utilise a range of energy sources (Anthony and Fabricius 2000). Such physiological differences likely explain observed changes in species composition of coral communities along environmental gradients such as light availability, exposure to sedimentation and water movement (Loya 1976; Rogers 1979; Sheppard 1982; Kleypas et al. 1999). Within species, this 'niche' may be broad as physiological (Falkowski et al. 1990; Anthony and Fabricius 2000; Hennige et al. 2008) and morphological (Todd 2008) plasticity allows individual corals to acclimate to local environmental conditions. As a result, coral communities within a particular location will be both adapted but also acclimated to those conditions, meaning that species-specific tolerances will vary as a function of a coral's environmental setting (as discussed by Erftemeijer et al. 2012). The susceptibility to eutrophication also varies among life-history stages with egg production, fertilisation, settlement and postsettlement survival all sensitive to substantially lower levels of sediment and/or nutrient exposure than adult colonies (Fabricius 2005, 2011).

Degradation of coral reef communities in response to acute increases in sediment supply, such as those caused by dredging, is well documented (Erftemeijer et al. 2012), as are those resulting from severe eutrophication in association with local nutrient discharges (e.g., Walker and Ormond 1982; Pastorok and Bilyard 1985; Loya 2004). Responses of coral communities attributed to chronic degradation of environmental conditions have largely been inferred from observed differences in community attributes such as species composition, coral cover, colony size distributions, incidence of disease, or abundance of space competitors along environmental gradients (e.g., Tomascik and Sanders 1987; Sutherland et al. 2004; Fabricius et al. 2005, 2012; Dikou and van Woesik 2006; Kline et al. 2006; De'ath and Fabricius 2010; Golbuu et al. 2011). In most cases, environmental condition was assumed to have deteriorated; however, such changes were rarely demonstrated. At the scale of regions (10's of km), evidence for the degradation of coral communities as a consequence of chronic eutrophication has remained difficult to demonstrate (Fabricius 2005).

Coral reefs in the inshore area of the Great Barrier Reef, Australia (GBR), are situated in naturally turbid waters, as fine terrigenoclastic sediment is continuously resuspended by prevailing south-easterly winds and tidal currents (Larcombe et al. 1995, 2001; Wolanski et al. 2005; Orpin and Ridd 2012). In addition, suspended solids, nutrients, pesticide residues and other contaminants are delivered by catchment runoff during seasonal flooding of adjacent rivers (Devlin and Brodie 2005; Devlin and Schaffelke 2009; Brodie et al. 2010) and reach the inshore reefs (McCulloch et al. 2003; Jupiter et al. 2008; Kennedy et al. 2012; Bainbridge et al. 2012; Devlin et al. 2012). Since European colonisation, the loads of sediment, total nitrogen and total phosphorus transported to the coastal GBR as runoff are estimated to have increased by factors of 5.5, 5.7 and 8.9, respectively (Kroon et al. 2012). These additional pollutant fluxes accumulate in the inshore environment contributing to the turbidity and nutrient stocks for periods of months to years (Luick et al. 2007; Wolanski et al. 2008; Lambrechts et al. 2010; Andutta et al. 2011; Brodie et al. 2012; Fabricius et al. 2013), and have been implicated in the decline of inshore coral communities (Brodie et al. 2012).

Despite clear evidence for differences in coral reef communities that correspond to environmental conditions within the turbid inshore zone of the GBR (van Woesik et al. 1999; Fabricius et al. 2005, 2012; DeVantier et al. 2006; Cooper et al. 2007; De'ath and Fabricius 2010; Browne et al. 2010, 2012; Uthicke et al. 2010), it remains difficult to directly demonstrate that coral communities have changed as a response to increased pollutant fluxes. The lack of baseline data against which current coral communities and water quality can be compared has been problematic. At a small number of locations, palaeoecological data allow comparisons between historical and present-day coral communities. Roff et al. (2013) describe the loss of staghorn *Acropora* species that persisted for hundreds of years—a change they interpret as resulting from increased sediment and nutrient fluxes as a result of agricultural development on adjacent catchments. In contrast, in very turbid waters Perry et al. (2008, 2009) demonstrate the continued persistence of a low diversity community, albeit limited to very shallow water. The discrepancy between these studies may suggest species-specific susceptibilities to changed conditions, or differing degrees of change in conditions between sites.

In this study, we took advantage of a coral community monitoring dataset that captured the transition between two climatically distinct periods; a five-year period of below-median river discharge (2002–2006), followed by six year of above-median river discharge (2007–2012). The availability of remotely sensed estimates of total suspended solids (TSS) and chlorophyll-*a* (Chl) concentrations over

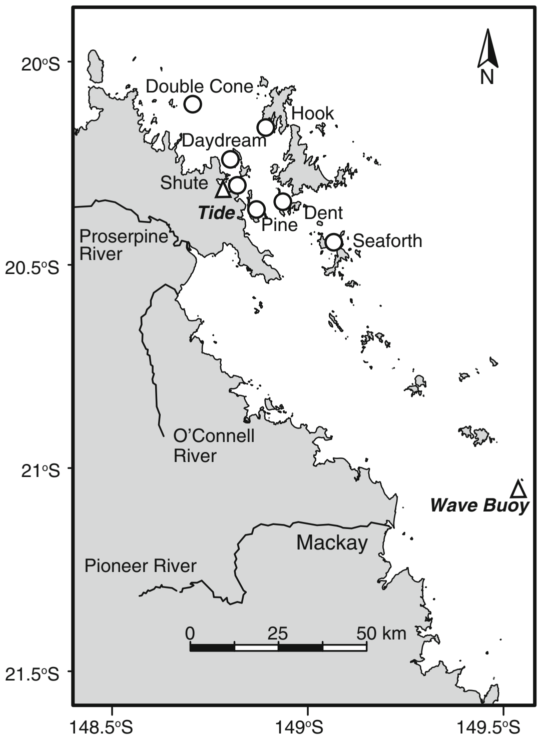

Fig. 1 Map of study area. Location of coral (*circles*) and environmental (*triangles*) monitoring locations

this period allowed us to investigate whether increased river runoff resulted in measurable differences in environmental conditions at the regional scale and, if so, how coral communities responded to these changes. We consider the marked increase in river discharge and any observed change in remotely sensed water quality as proxies for increased fluxes of sediments, nutrients and other contaminants from the adjacent catchments. We then focus on coral community dynamics as a way of understanding the responses of coral communities to eutrophication of the inshore GBR. The dataset was explicitly selected because confounding acute disturbances such as severe storms, coral bleaching, or outbreaks of the coral-eating crown-of-thorns seastar were largely absent. Over the period of monitoring, the only acute disturbance was Tropical Cyclone Ului in 2009, which caused substantial physical damage to corals at only one of the seven study reefs.

Methods

Coral community data

Coral community data were collected at seven reefs in the Whitsunday Islands, located within the turbid inner-shelf of the central GBR. Sites were selected at locations at which fringing reefs had developed and were spaced along a gradient of increasing distance from the mouths of regionally significant rivers (Fig. 1). At each location, two sites were selected along contiguous sections of reef slope and separated by at least 250 m. Within each of these sites, five 20-m-long transects were deployed along depth contours at both 2 and 5 m below lowest astronomic tide (LAT). Transects were permanently marked with steel markers at the mid points and each end. Compass bearings were recorded at each point of inflection to ensure accurate relocation between surveys.

Of the seven reefs, Daydream, Double Cone and Pine were sampled once a year from 2005 to 2012. The remaining four reefs were sampled in 2005 and 2006 and then only every other year: Hook and Shute in 2007, 2009 and 2011, and Dent and Seaforth in 2008, 2010 and 2012 (Fig. 1). Sampling was conducted opportunistically during periods of calm weather and occurred in May (2006, 2011), June (2007, 2008, 2010), July (2005) and was split between May and July in 2009 and 2012. Only the disease data were used from 2005 surveys, as slight inconsistencies in methodology between the first survey in 2005 and subsequent surveys precluded the use of cover and juvenile coral estimates. The cover of major benthic groups for each transect was estimated using the photo point-intercept method developed by the Australian Institute of Marine Science (AIMS) for monitoring of coral reef communities (Jonker et al. 2008). In brief, digital images capturing a nominal 0.1 m^2 of substrate were taken at 50-cm intervals, and the benthos falling below five evenly spaced points identified. Only the estimates of hard coral cover were included in this analysis, with corals consistently identified to genus.

The abundance of juvenile corals (<10 cm in diameter) was counted within 34-cm-wide (dive slate width) transects co-located with the point-intercept transects. Annual sampling was conducted at least five months after the major summer spawning period on the GBR, and most juveniles surviving settlement and early postsettlement mortality were expected to have attained a size available to observation. Care was taken to exclude colonies considered to have resulted from the partial mortality or fragmentation of larger colonies. Possible inconsistencies in taxonomic differentiation of very small corals necessitated the pooling of some genera into the following four groups: *Favia*, *Montastrea*, and *Barabattoia; Favities* and *Goniastrea*; *Lobophyllia*, *Symphyllia*, and *Scolymia; Echinophyllia* and *Oxypora.* In each case, these groups combine genera from the same family and species with similar traits; for species in these groups included in Darling et al. (2012), all were classified as stress tolerant. For convenience, when these taxonomic groups are referred to in following sections, only the most abundant genus within each group is named.

Instances of coral mortality were recorded within a 2-m-wide belt along each transect following the 'scuba search method' developed by AIMS (Miller 2003). For each colony suffering recent or partial mortality, the cause of mortality was classified as either: 'white syndrome' where ongoing mortality and tissue necrosis or discoloration at the tissue/skeleton interface was observed, 'brown band' or 'skeletal eroding band' where ciliates were observed, 'atramentous necrosis' where tissue was being decomposed by sulphur-reducing bacteria (Jones et al. 2004), 'sedimentation' where tissue beneath sediment deposits was in a state of decomposition, or 'unknown' where no obvious cause could be determined or entire colonies were recently dead. In practice, there was a continuum between colonies classified as either 'atramentous necrosis' or 'sedimentation', and these were grouped prior to analysis and hereafter referred to as 'sediment damage'.

Environmental data

Chl and TSS estimates were extracted from daily MODIS-Aqua satellite observations from a square of nine, 1-km^2 pixels located in optically deep waters as closely adjacent to coral sampling locations as possible. The average values of Chl and TSS estimated from these nine pixels constituted daily estimates over the period 2002–2012 for each reef.

Chl and TSS concentrations were derived using a regionally adapted physics-based ocean colour algorithm (Brando et al. 2012; Schroeder et al. 2007, 2012). This was necessary because of the significant contribution of terrestrial dissolved and particulate organic matter in the water column, resulting in the frequent failure of MODIS standard ocean colour algorithms (Qin et al. 2007). Recent validation results across the entire GBR using ground observations collected within ±3 h to the satellite measurements showed that for individual points, the error for the retrieval of Chl and TSS from the regionally adapted algorithm was ±90 and 70 %, respectively, compared to errors exceeding 240 % for MODIS standard Chl and TSS products.

Algorithm performance could not be evaluated in a similar fashion for our study region due to an insufficient number of coincident in-situ and satellite observations. However, for TSS, we had access to two additional datasets that allowed us to evaluate the magnitude of MODIS-derived TSS to that observed at the reef sites. At three of the study reefs (Daydream, Double Cone and Pine; Fig. 1), WETLabs Eco FLNTUSB turbidity sensors were deployed at the 5-m-deep coral sites from 2007 onward and recorded turbidity (in nephelometric turbidity units, NTU) at 10-min intervals. At these same reefs, water samples were collected close to the sensors and from the surface, mid water and near-bottom of the water column within 250 m of the reef at approximately 4-month intervals, again from 2007 onward, from which $\mathrm{TSS_f}$ (total suspended solids, filtered) data were derived. The MODIS-derived TSS estimates were then evaluated by substitution of terms between model 2 regressions (Legendre and Legendre 1998) of MODIS TSS with NTU and $\mathrm{TSS_f}$ with NTU.

To relate variability in TSS to river discharge, TSS estimates were first standardised for the influence of wave and tidal conditions at the time of sampling. Tidal range estimates were the difference between the daily maximum and minimum in observed sea level values from tide gauge data supplied by the Queensland Department of Transport and Main Roads (Fig. 1). Mean wave height for each day and the three days preceding observations of TSS were calculated from wave-buoy recordings provided by the Queensland Department of Environment and Heritage Protection (Fig. 1).

Daily discharge volumes of the Proserpine, O'Connell and Pioneer rivers were obtained from the Queensland Department of Natural Resources and Mines. These three rivers enter the ocean to the south of the study area (Fig. 1), with plumes merging to become indistinguishable from each other at the study locations (Brodie et al. 2012; Schroeder et al. 2012). As a point of reference, long-term median discharges were estimated from records from 1967 to 2000 (Proserpine River), 1971–2000 (O'Connell River) and 1979–2000 (Pioneer River).

The proportion of reef sediments with grainsizes <63 µm was estimated from five 1-cm-deep sediment cores collected from available surface deposits along each 5-m-deep coral site at the time of coral surveys. The grainsize distributions of the samples were estimated by MALVERN laser analysis of the portion of samples that passed through a 1-mm sieve.

Data analysis

Chl and TSS data were explored graphically to identify the duration of influences attributable to river discharge. The relationships between observed Chl and TSS over these identified periods and the discharge of local rivers were assessed with generalised additive mixed models (GAMM; Wood 2006). The mean concentrations of Chl and TSS for each reef and each year were modelled against the cumulative discharge from the beginning of the water year (1 October) to the end of April for Chl, and to the end of June for TSS. To account for the inherent auto-correlation of means from the same locations, a random-effect term 'reef' was included. As turbidity is strongly influenced by resuspension, the TSS estimates included in the GAMM were first standardised for the predictable influence of resuspension by separately fitting generalised additive models (GAM; Wood 2006) including terms for 'tidal range', 'average wave height' and 'average wave height over the preceding 3 days to the TSS observations for each reef.

The influence of environmental conditions on variation in the coral community attributes: density of juvenile corals, coral cover and disease incidence was investigated with linear models. For each community attribute, reef-level means were modelled against the three environmental variables: mean Chl, mean TSS and mean proportion of fine sediment. Model selection based on Akaike's information criterion values was used to identify any environmental variable contributing to the variation in the coral community attributes between reefs.

Differences in univariate community attributes between depths were assessed with linear mixed-effects models (LME; Pinheiro et al. 2013) applied to data averaged to reef and depth. Models included a random-effect term for reef to account for auto-correlation between communities at the same reef.

Changes in coral community attributes over the study period were investigated using separate GAMMs, applied to each attribute and depth. For coral cover and juvenile coral densities, these GAMMs included a term for year and random term for reef. No additional terms for environmental variables were included as both coral cover and juvenile density are the result of processes operating over several years. For coral disease, separate models including terms for annual estimates of Chl, TSS or the proportion of sediments with grainsizes less than 63 μm were assessed. For these analyses, Chl was averaged over the months of February–April while TSS was averaged over the months of March–May. This period was one month shorter than the period when TSS was identified to be influenced by runoff (March–June) and was used because in several years the disease surveys were completed in May. For each reef and depth combination, disease incidence was scaled to a distribution with a mean = 0 and a standard deviation = 1 to account for differences in disease susceptibility because of compositional differences between communities.

Analyses of multivariate genus-level juvenile and coral cover data were based on Bray–Curtis dissimilarities between square-root-transformed observations (Bray and Curtis 1957). The unconstrained structure in communities was visualised in bi-plots of reef and genus scores against the first two axis of principal coordinates analyses (PCoA; Legendre and Legendre 1998). The influence of depth, Chl, TSS and sediment grainsize composition was analysed with permutational MANOVA models (Anderson 2001), fitted separately for each combination of environmental variable and community type. For these analyses, community data and environmental variables were averaged over years to avoid any issues of auto-correlation between observations from the same reefs. As the focus was on consistent changes in community composition rather than abundance, as investigated by univariate analyses, data were standardised by dividing the transformed genus-level abundances by the sum of the transformed abundances for that reef. When permutational MANOVA tests indicated the significant influence of an environmental parameter, canonical analyses of principal coordinates (CAP; Anderson and Willis 2003) were used to identify genera corresponding to those environmental conditions. Change in community composition through time was analysed by permutational MANOVA including a term for year and with permutations limited to occur within reefs. Genera demonstrating correlations with time were identified on the basis of their scores against the canonical axis of a partial CAP, which first removed spatial variability in community composition attributed to different reefs (Oksanen et al. 2013).

Results

Influence of river discharge on water quality

The combined long-term median annual discharge of the O'Connell, Proserpine and Pioneer Rivers was 518 GL. From 2002 to 2006, discharge was consistently below this median, while from 2007 to 2012 discharge was well above the median (Fig. 2). It was on the basis of this difference that we categorised the pre-2007 years as 'Dry' and 2007 to 2012 as 'Wet'.

Remotely sensed TSS and Chl concentrations, while variable, were seasonally high during and following the summer wet season (Fig. 3). Over the months February to April, the mean wet period Chl concentration was 0.53 μg l^{-1} and 31 % higher than during the dry period. Over the months March to June, the wet period TSS was 1.47 mg l^{-1} and 51 % higher than during the dry period. Simultaneous solving of model 2 regressions: $\log(TSS) = -0.026 + 1.0628*\log(NTU)$ with $R^2 = 0.54$, and $\log(TSS_f) = 0.27 + 1.1.216*\log(NTU)$ with $R^2 = 0.76$, demonstrated that TSS_f sampled close to the reef was higher than TSS estimated from MODIS in open water. Wet period TSS_f was estimated at 2.17 mg l^{-1} with 95 % confidence intervals of 1.75 to 2.62 mg l^{-1}.

Both TSS and Chl concentrations showed a significant relationship with river discharge (Fig. 4a, b). The relationship between TSS and discharge levelled out at the extremely high discharge values observed during 2011 (Fig. 4a). It is important to note that TSS was standardised prior to analysis to remove any predictable influence of

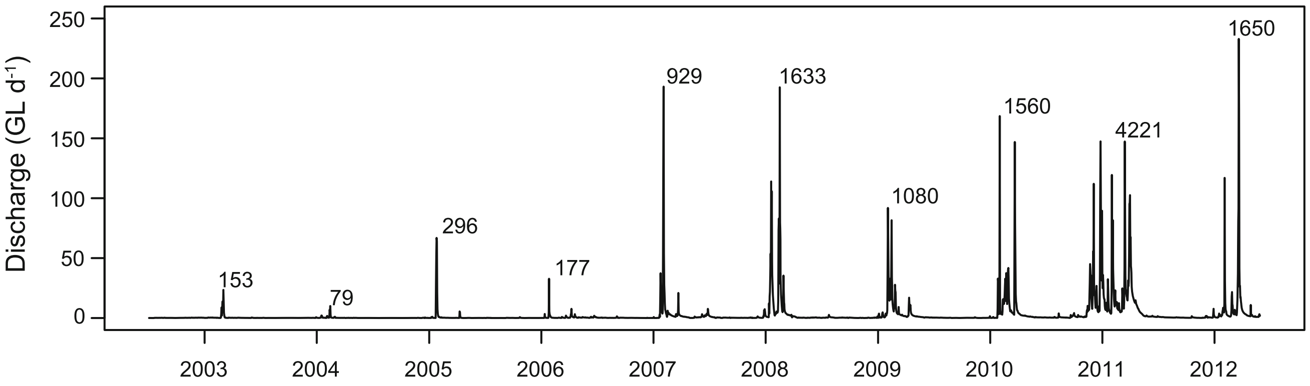

Fig. 2 Combined daily discharge of the O'Connell, Pioneer and Proserpine Rivers. *Numbers* indicate the total annual discharge (GL) based on water years (1 October–31 September)

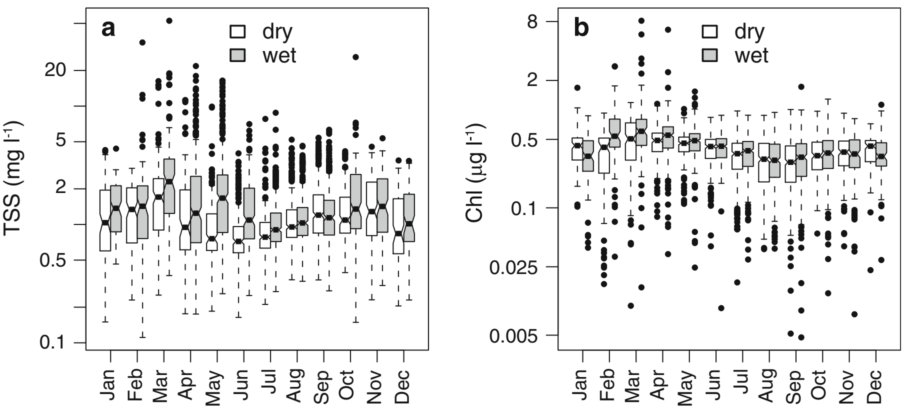

Fig. 3 Seasonal trends in MODIS-Aqua satellite observations for **a** total suspended solids (TSS) and **b** chlorophyll-*a* (Chl). For each calendar month, unfilled boxes include data from the dry period (2002–2006) and *filled boxes* the wet period (2007–2012). *Boxes* include the median and second and third quartiles of the data; *whiskers* extend to twice the interquartile range

wave height or tidal range that, in combination, explained between 21 and 32 % of the variation in TSS observed at the seven study reefs.

Variation in environmental conditions between reefs

The environmental conditions at the study reefs were characterised by the two water quality parameters (TSS and Chl) and by the grainsize of sediments. TSS and Chl were significantly different between reefs; however, these differences were relatively small compared to the temporal variability within the reefs (Fig. 5a, b). For TSS, contrasting means for each reef against Daydream indicated higher levels at Pine ($p < 0.001$) and lower levels at Hook ($p < 0.001$), Double Cone ($p < 0.001$) and Seaforth ($p = 0.011$). For Chl, Double Cone ($p = 0.005$), Hook ($p < 0.001$) and Seaforth ($p = 0.025$) had lower mean concentrations than Daydream. These differences in mean conditions between reefs only accounted for 7 % (TSS) and 3 % (Chl) of the overall variability observed. In contrast, between-reef differences in the proportion of sediment with a grainsize <63 µm accounted for 72 % of the variability in that dataset. Double Cone ($p = 0.006$), Hook ($p = 0.001$) and Seaforth ($p = 0.005$) had a lower proportion of sediment with grainsize <63 µm than Daydream; the grainsize distributions at the remaining reefs did not differ from Daydream (Fig. 5c).

Separate linear models relating the reef-level mean for each of the three environmental variables to the coral community attributes of mean coral cover and mean juvenile density at each of the 2 and 5 m depths revealed no relationships ($p > 0.1$ for all 12 models).

Variation in coral reef community attributes

Over the period of our study, the density of juvenile corals declined (Fig. 6a, b). In contrast, there was no consistent trend in coral cover (Fig. 6c, d). At 2 m depth, there was a rapid increase in coral cover at Double Cone and Shute between 2010 and 2012. These increases largely reflect changes in the cover of *Acropora* that accounted for 80 % of the increase in cover from 33 to 46 % at Double Cone and 74 % of the increase in cover from 35 to 43 % at Shute. In contrast, the decline in cover at both depths at Daydream was almost entirely due to reductions in cover of branching *Acropora* species as a result of damage incurred

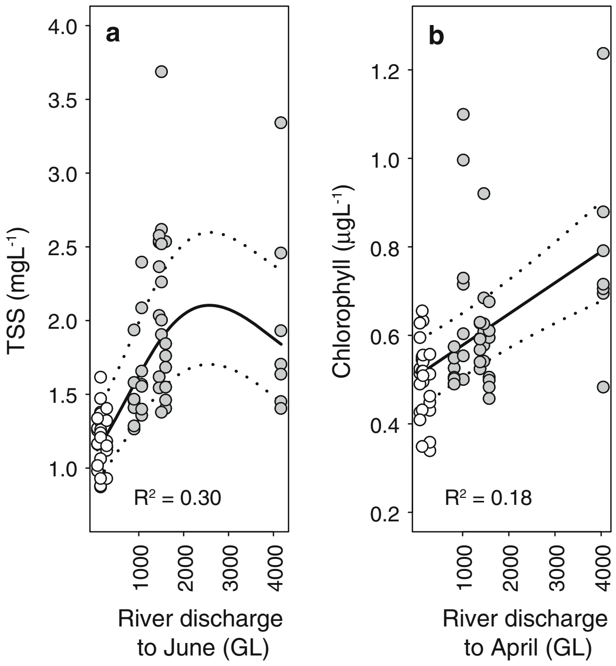

Fig. 4 Water quality relationships with river discharge, **a** total suspended solids (TSS) in the months March–June, **b** chlorophyll-*a* (Chl) in the months February–April. River discharge is the cumulative flow since October of the previous year to, **a** June, **b** April. *Open circles* include data from the dry period (2002–2006) and *filled circles* the wet period (2007–2012). TSS was standardised for the influence of waves and tidal range. Estimated trends derived from generalised additive mixed model analysis are indicated by *bold lines*, bounded by the 95 % confidence intervals of those trends (*dotted lines*)

during the passage of Tropical Cyclone Ului in early 2009. At all other sites, only minimal changes in cover were observed.

Variation in coral disease

The incidence of disease varied among reefs (Table 1); ‘white syndrome’ at 5 m depth was positively correlated with the proportions of fine-grained sediments ($p = 0.001$, $R^2 = 0.88$) while ‘unknown scarring’ was more prevalent on reefs with high proportions of fine-grained sediments at both 2 m ($p = 0.017$, $R^2 = 0.65$) and 5 m ($p = 0.038$, $R^2 = 0.53$) depths. The distributions of ‘white syndrome’ and ‘unknown scarring’ show broad similarities, and as there is potential inconsistency in the differentiation between these classifications, we have combined the response of these for presentation (Fig. 7a). The relationship between both ‘white syndrome’ and ‘unknown scaring’ with fine sediments was primarily driven by high incidences at the two reefs with highest cover of branching growth forms of the genus *Acropora:* 5 m depths at Daydream (mean *Acropora* cover 25.4 %) and Dent (mean *Acropora* cover 12.3 %). The combined category ‘sediment damage’ at 5 m depth was positively associated with TSS concentration ($p = 0.018$; Fig. 7b). This relationship was strongly influenced by the highest disease incidence at the most turbid site, Pine Island, where corals are mostly of massive or laminar growth form and accumulation of sediment onto living corals was observed over a wide range of genera.

The highest incidence of disease was observed in 2007 and 2008 (Fig. 8a), reflecting the high incidence of ‘white syndrome’, ‘brown band disease’, ‘unknown scaring’ and ‘skeletal eroding band’ variously among reefs (Fig. 8b–e). Overall, incidence of disease was higher in 2007 than in either 2005 ($p = 0.009$), 2006 ($p = 0.018$) or 2009 ($p = 0.02$). This maximum was coincident with the

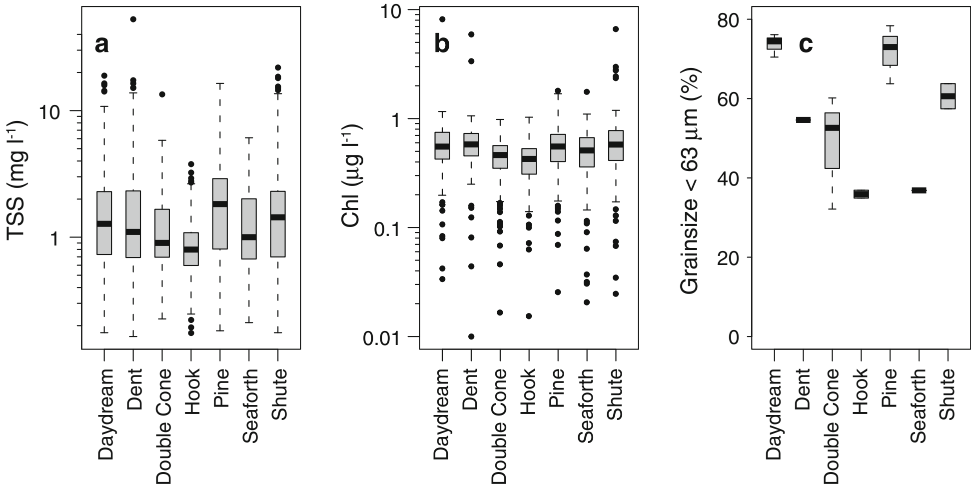

Fig. 5 Environmental variables at study reefs, **a** total suspended solids (TSS; March–June), **b** chlorophyll-*a* (Chl; February–April) and **c** proportion of sediments with grainsizes <63 µm. *Boxes* represent the median and second and third quartiles of all observations of TSS and Chl from 2003 to 2012 and from 2007 to 2012 for Grainsize; *whiskers* extend to twice the interquartile range of the data

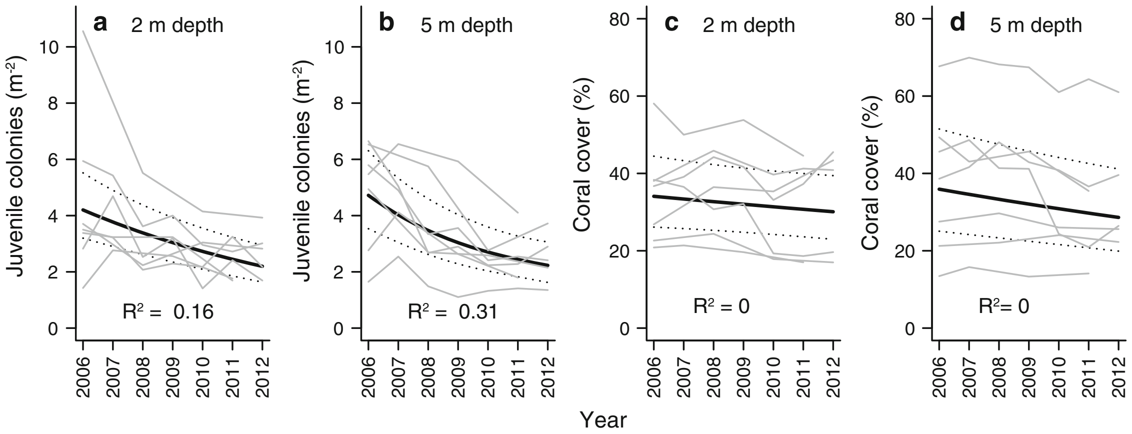

Fig. 6 Temporal changes in coral communities: **a** juvenile density at 2 m, **b** juvenile density at 5 m, **c** coral cover at 2 m, and **d** coral cover at 5 m. Estimated trends derived from generalised additive mixed model analysis are indicated by *bold lines*, bounded by the 95 % confidence intervals of those trends (*dotted lines*). *Grey lines* represent observations for individual reefs

Table 1 Incidence of coral disease

Reef	Depth (m)	Brown band	Skeletal eroding band	Sediment damage	Unknown scarring	White syndrome
Daydream	2	4.4	0.1	0.5	19.8	4.1
	5	2.5	0.5	3.2	22.5	23.2
Dent	2	2.4	1.6	0.2	15.6	7
	5	4.2	1	1.8	15.8	9.6
Double cone	2	0.5	0.5	1	11.2	3.1
	5	0.1	1.6	1.8	12.4	2
Hook	2	0.6	1.2	0.4	5.4	0.8
	5	0	0	1.4	2.4	0.8
Pine	2	0.2	0.1	7.9	13.1	4.9
	5	0.5	0.2	14.2	9.9	6
Seaforth	2	0	0	0	4.6	0.4
	5	0	0	0.2	5.6	0.8
Shute	2	0.2	0.6	1.8	7	2
	5	0.4	0	4.8	8.6	2.4

Values are the number of colonies observed within 400 m^2 belts (sum of the ten 40 m^2 transects at each depth) averaged over all observations between 2005 and 2012

transition from the Dry to the Wet climactic period. Subsequent observations indicated no further increase in disease despite higher river discharges in subsequent years (Fig. 2). Relationships between disease incidence and changes in environmental conditions were only observed between the 'sediment damage' categorisation and both total discharge (at 5 m $p = 0.002$, $R^2 = 0.18$; at 2 m $p = 0.002$, $R^2 = 0.15$) and mean TSS (at 5 m $p < 0.001$, $R^2 = 0.19$; at 2 m $p = 0.01$, $R^2 = 0.1$).

Responses of coral community composition to changes in water quality

The composition of coral communities differed both between reefs and between depths within reefs (Fig. 9). Constrained analyses found no strong relationship between juvenile community composition and environmental conditions (Tables 2, 3). Rather, the spread of observations from each reef–depth combination in the unconstrained analysis demonstrates the variability in the composition of juvenile assemblages through time (Fig. 9a; Table 2). The genera identified as declining most consistently over the period of the study (Table 3) were largely aligned with the first principal coordinate, demonstrating that changes in composition of communities over the period of the study were more consistent than, or aligned with, any unresolved environmental variable structuring these assemblages (Fig. 9b). The second principal coordinate aligns with those genera showing the most consistent variation with depth (Fig. 9b; Table 3).

In contrast to the juvenile communities, the composition of coral cover at each reef was less temporally variable

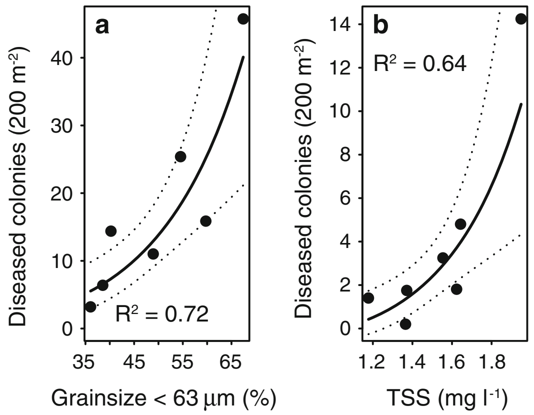

Fig. 7 Variation in disease incidence attributable to environmental conditions of **a** sediments with grainsizes <63 µm on the combined incidence of 'white syndrome' and 'unknown scarring' at 5 m depth and of **b** total suspended solids (TSS) on the combined incidence of 'sediment damage' at 5 m depth

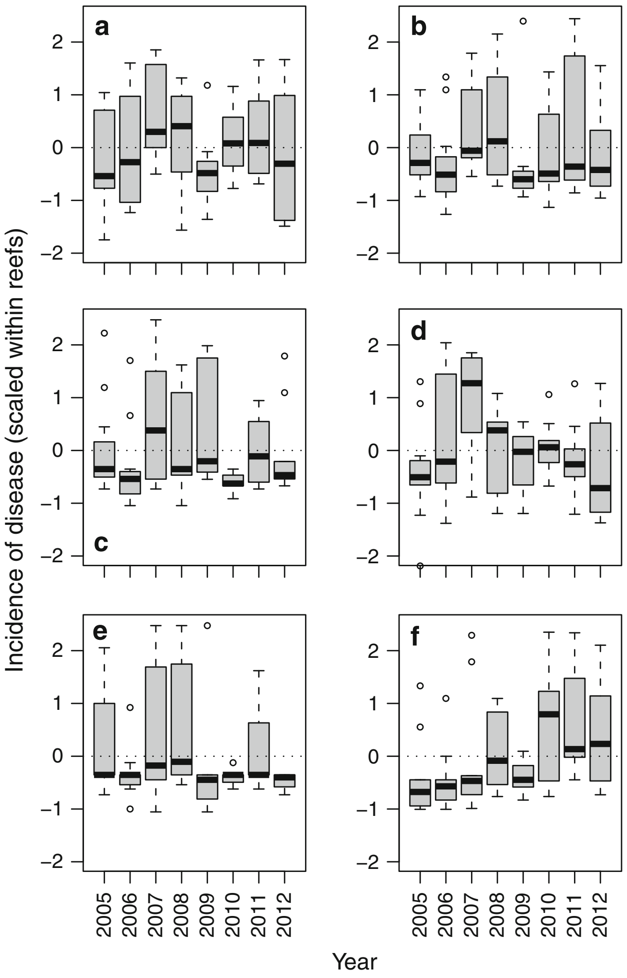

Fig. 8 Relative incidence of coral disease categories over time: **a** sum of all categories, **b** 'white syndrome', **c** 'brown band disease', **d** 'unknown scarring', **e** 'skeletal eroding band', and **f** 'sediment damage'. Disease incidence is scaled to a mean of zero and standard deviation of one within each reef

(Fig. 9c; Table 2). *Acropora* was the only genus to show a consistent decline over the period of the study, and this was more pronounced at 5 m than at 2 m depths (Table 3). The first principal component strongly aligned with the cover of *Acropora* and *Goniopora*, the genera that most influenced the observed difference in composition between depths (Table 3). The composition of coral cover also varied in response to differences in TSS concentration (5 m only) and the proportion of fine-grained sediments in reefal substrata (Table 2). In contrast to *Acropora* and *Goniopora,* the remaining genera showing relationships to TSS and the sediment composition (*Galaxea*, *Pavona*, *Pectinia* and *Porites*; Table 3) were aligned with the second principal component of the unconstrained ordination (Fig. 9d).

Discussion

The change between a period of below-median discharge to a period of above-median discharge and flooding of local rivers resulted in higher Chl and TSS concentrations and concomitant coral community responses. Our observations were consistent with the general concept that variable selection pressure along environmental gradients influences the composition of coral communities. However, the variability in response among reefs reiterates some of the issues that limit a clear demonstration of coral community responses to chronic eutrophication at regional scales.

Short time series of turbidity document the strong influence of wave-driven resuspension on turbidity in coastal waters of the GBR (Larcombe et al. 1995), leading to ongoing debate as to the magnitude of influence that any additional flux of materials from rivers could have on the conditions experienced by corals (Orpin and Ridd 2012). For the Whitsunday Region, the decade-long MODIS-Aqua time series demonstrated that Chl and TSS concentrations in waters surrounding inshore coral reefs were influenced by river discharge. The prolonged (months) elevation of TSS supports emerging evidence that flood-derived fine sediments are retained within the inshore GBR (Lambrechts et al. 2010; Fabricius et al. 2013), as shown elsewhere (Draut et al. 2009), and add to turbidity as a result of repeated resuspension until being winnowed away by wave and tidal activity (Storlazzi et al. 2009). The demonstrated relationship between discharge of local rivers and Chl reiterates the relationship between runoff and the availability of nutrients in coastal waters (Furnas et al. 2005, 2011; Wooldridge et al. 2006).

The exposure of corals to stressful conditions associated with a higher concentration of TSS varies as a result of

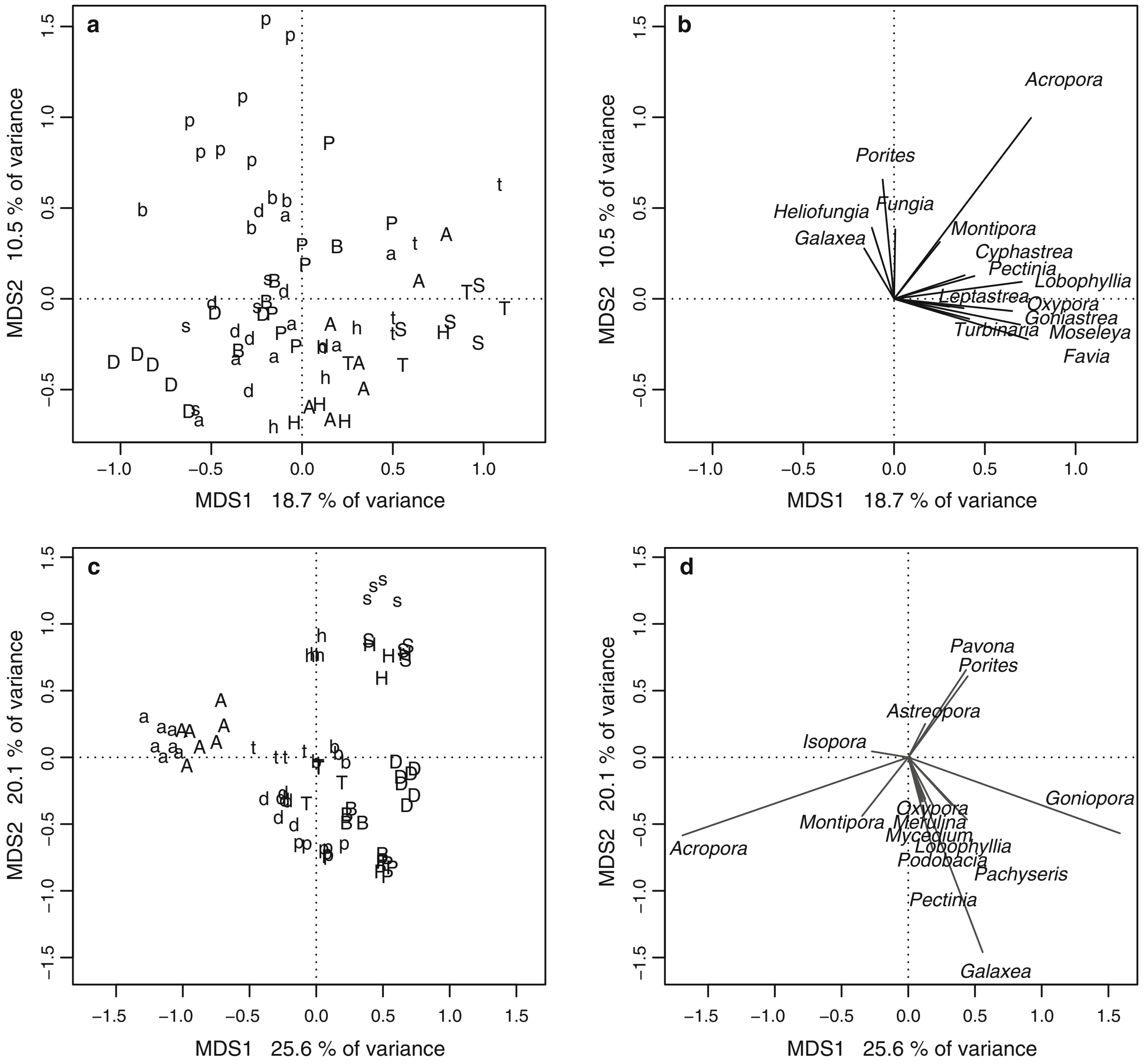

Fig. 9 Unconstrained principal coordinates biplots of coral communities for: juveniles (**a**, **b**) and cover (**c**, **d**). For clarity, site scores and genus vectors are presented in *separate panels*. *Letters* in site-level ordinations (**a**, **c**) differentiate the seven study reefs (A: Daydream, B: Dent, D: Double Cone, H: Hook, P: Pine, S: Seaforth and T: Shute), *upper case* indicate 5 m depth communities, and *lower case* 2 m depth communities. Of the 53 genera of juvenile corals and 49 genera for which cover estimates were analysed, only those with absolute scores of 0.2 or greater against either the first or second principal coordinates are presented (**b**, **d**)

interactions between local hydrodynamics and depth as determinants of rates of sedimentation and light attenuation (Wolanski et al. 2005; Storlazzi et al. 2009), but also the susceptibility of the corals present (Rogers 1983; Erftemeijer et al. 2012). While teasing apart such fine-scale processes was beyond the scope of our data, in general it could reasonably be assumed that observed increases in TSS would have resulted in both an increased sediment flux and reduction in light at the substrate level. Light attenuates in water exponentially as a function of the light attenuation coefficient of the water and depth in metres, with the type and concentration of suspended matter influencing the light attenuation coefficient of turbid waters (Van Duin et al. 2001). For three of the reefs monitored in this study, Cooper et al. (2007) estimate attenuation coefficients, the mean of which was 0.2055. Using this attenuation coefficient at mid-tide (LAT +1.5 m), our 2-m sites would receive 49 % of surface irradiation and our 5-m sites 26 %, demonstrating the potential stress associated with reduced light availability over even this small depth range.

Table 2 Results of permutational MANOVA of the responses of coral community attributes to depth, water quality and time

Depth	*F* (model)	*R*-square	*P*(>*F*)
Juveniles	1.681	0.123	0.02
Cover	1.056	0.081	0.029
Chlorophyll *F* *R*-square *P*(>F)			
Juveniles (2 m)	1.206	0.194	0.218
Juveniles (5 m)	0.960	0.161	0.534
Cover (2 m)	0.991	0.165	0.444
Cover (5 m)	1.616	0.244	0.115
TSS *F* *R*-square *P*(>*F*)			
Juveniles (2 m)	1.037	0.215	0.125
Juveniles (5 m)	0.745	0.130	0.771
Cover (2 m)	1.334	0.211	0.215
Cover (5 m)	1.898	0.275	0.033
Fine sediment *F* *R*-square *P*(>*F*)			
Juveniles (2 m)	1.039	0.172	0.398
Juveniles (5 m)	1.055	0.174	0.403
Cover (2 m)	2.438	0.328	0.02
Cover (5 m)	2.183	0.304	0.009
Time *F* *R*-square *P*(>*F*)			
Juveniles (2 m)	1.703	0.046	0.001
Juveniles (5 m)	3.810	0.098	0.001
Cover (2 m)	0.523	0.015	0.052
Cover (5 m)	0.461	0.013	0.047

Each row represents a separate analysis of log-transformed genus-level observations of mean coral cover or juvenile density over the years 2006–2012 from each reef and depth sampled. Depth was a categorical variable differentiating communities at 2 and 5 m below lowest astronomical tide. The other environmental variables were averaged over all available data from each reef

The partial contribution of TSS to the attenuation coefficient is variable within the literature; however, the value of 0.067*TSS reported by Devlin et al. (2008) is within the bounds of those reported elsewhere (e.g., Van Duin et al. 2001). Using this partial contribution of TSS to adjust the attenuation coefficient implies a further reduction of surface light to ∼20 % at our 5-m sites as result of the proportional increase in TSS we observed. This level of surface light attenuation is approaching the limit for reef development of 6–8 % reported by Cooper et al. (2007), and the lower limit for corals in general in the range of 2–8 % reported by Titlyanov and Latypov (1991). In combination, the observed increases in Chl and TSS demonstrate the increased exposure of these reefs to catchment-derived contaminants, including the likelihood for exposure to other contaminants such as pesticides that, while not measured here, have been shown to correlate to runoff within the GBR (Kennedy et al. 2012).

The influence of the ‘first flush’ of the rivers in this region was evident in our coral disease records with disease incidence at a maximum in 2007, following the first drought-breaking rains after a period of dry years. The timing of maximum disease incidence demonstrates the selective pressures associated with environmental extremes, with susceptible colonies that had persisted during conditions of lower Chl and TSS concentrations dying as water quality declined. This conclusion is supported by reports of increased disease prevalence in response to stress associated with floods, increased nutrient availability and sedimentation (Bruno et al. 2003; Haapkyla et al. 2011, 2013; Lesser et al. 2007; Weber et al. 2006, 2012; Vega Thurber et al. 2014).

The absence of a continued increase in coral disease at higher river discharges was consistent with our observations of a levelling of the relationship between TSS and discharge. Rivers’ TSS loads may be decoupled from discharge volume as a result of the timing of peak flows within individual wet seasons or within longer-term climatic cycles that alter the availability of erodible and mobile sediment within the catchments (e.g., Kuhnert et al. 2012). The peak discharge occurred in 2011 after four -years of above-median flows, which is likely to have flushed out available sediments that had accumulated during the preceding dry period as well as resulting in higher vegetation cover in the catchments, thus reducing the availability of sediments to erosional processes. A further consideration is that susceptible colonies had died on first exposure to sufficiently stressful conditions, resulting in the remaining community being less susceptible to subsequent exposure to similar conditions. Our estimates of disease incidence were potentially confounded by the slight seasonal differences in the timing of surveys. The three years 2005, 2009 and 2012 for which sampling was undertaken in July returned the lowest overall precedence of disease, a result consistent with lower winter prevalence of ‘ulcerative white spots’ and ‘white syndrome’ (Haapkyla et al. 2010) and of ‘atramentous necrosis’ (Jones et al. 2004), though contrasting with a higher incidence of ‘brown band disease’ in winter (Haapkyla et al. 2010). However, we also observed a similarly low incidence of disease during the earliest sampling of May 2006, detracting from seasonal confounding as an explanation of our observed patterns of disease incidence.

The reduction in density and change in assemblage composition of juvenile corals over the study period was consistent with the well-documented sensitivity of early life-history stages of corals to eutrophication (Fabricius 2005, 2011; Erftemeijer et al. 2012). That the responses of the juvenile communities were more pronounced at 5 m than at 2 m depth was consistent with the expected compounding of reduced light availability and increased deposition of sediments with increasing depths (Wolanski et al. 2005; Cooper et al. 2007). This was particularly

Table 3 Results of canonical analysis of principal coordinates

Genus	Depth		TSS	Fine sediment		Time			
	Juveniles	Cover	Cover 5 m	Cover 2 m	Cover 5 m	Juveniles 2 m	Juveniles 5 m	Cover 2 m	Cover 5 m
Acropora	−0.18	−0.35	0.17	0.54	0.48	−0.33	−0.52	−0.17	−0.30
Cyphastrea						−0.18	−0.17		
Echinopora									
Favia						−0.15			
Fungia	−0.22								
Galaxea			0.20	0.22					
Goniastrea						−0.22	−0.20		
Goniopora		0.32	−0.27		−0.32		−0.22		
Leptastrea							−0.20		
Lobophyllia						−0.18	−0.28		
Montipora	−0.17								
Moseleya	0.15								
Mycedium									
Oxypora									
Pachyseris									
Pavona			−0.20	−0.27	−0.17				
Pectinia			0.24		0.17		−0.31		
Pocillopora						0.18			
Podobacia							−0.18		
Porites	−0.22		−0.29	−0.29	−0.18		−0.15		
Turbinaria									
% Variance explained	37.6	29.2	27.5	32.3	30.4	10.3	17.3	4.2	4.9

Coral genera for which juvenile density or cover corresponded to the constraining canonical axis for each analysis are presented along with their weightings on the canonical axis. Only community and environmental variable combinations for which the permutational MANOVA indicated significant effects of environmental variable, *p* values <0.05 (Table 2), are represented. Only genera with weightings $>\pm 0.15$ are included. The sign of the weightings indicates either a positive or negative relationship with the constraining variable

pertinent as our study reefs were located in sheltered locations prone to the accumulation of fine sediments at 5 m depth: a point demonstrated by high proportions of clay and silt-sized fractions in sediments. Indeed, although unquantified, it was the observation of increased accumulation of fine sediments from 2007 that prompted this study. Such conditions have been shown to be particularly detrimental to the settlement of coral larvae, which require suitable stable substratum (Babcock and Mundy 1996; Birrell et al. 2005) as well as chemical settlement cues associated with specific benthic bio-films on that substratum (Negri et al. 2001; Webster et al. 2004; Tebben et al. 2011).

Comparing the responses between juvenile and adult communities provides insight into the processes governing coral community composition and dynamics in the study area. For both juvenile and coral cover assemblages, the composition of communities varied between the 2 and 5 m depths, demonstrating the selective pressure of light availability and exposure to sedimentation. There were, however, few genera that showed consistent preference for the 2 or 5 m depths; *Acropora* was the only genus consistently having both higher numbers of juveniles and higher cover at 2 m compared with 5 m depth. *Acropora* was also the only genus to show declines over the study period in both juvenile abundance and cover at both depths. These clear indications of a preference for lower exposure to eutrophication were at odds with the positive relationship of *Acropora* cover at 5 m depth with TSS and at both depths with the proportion of fine grainsizes in sediments. The *Acropora* community on these reefs was dominated by branching species (predominantly *A. muricata* and *A. micropthalma*) that form thickets on sheltered reef crests. These thickets appear to tumble down the reef slope as they grow, which might explain their presence where juvenile densities were low. In contrast to the predominance of branching *Acropora* species in cover, the majority of juvenile *Acropora* observed were species that develop corymbose growth forms and from our observations within the turbid waters of the GBR, as a group, suffer high incidence of disease and appear to be transient in the communities studied here.

Interpreting the observed relationships between cover of individual genera and environmental conditions was confounded by the highly variable composition of communities between reefs, the limited number of study reefs and differences in environmental conditions suggesting variable exposure to environmental stressors. The majority of genera we identified as varying along environmental gradients could be categorised as having high cover at only one or two reefs compared to low to very low cover elsewhere. A combination of more locations, spread across longer environmental gradients, would improve confidence in assigning distributions of individual genera to environmental parameters.

The changes in the taxonomic composition of communities through time were more informative. Within the juvenile community, 11 genera declined at one or both 2 and 5 m depths compared to just one genus, *Pocillopora,* which increased in abundance at 2 m depths. *Pocillopora* is particularly susceptible to coral bleaching (Marshall and Baird 2000). Reefs in this region were moderately bleached by high temperatures in 2002, and it is possible that the low initial numbers of juvenile *Pocillopora* were related to the loss of local broodstock during this event. The consistency of decline among other genera implies a limitation to recruitment. In contrast, with the exception of a decline in *Acropora*, the composition of cover remained remarkably stable, implying that the majority of colonies present were tolerant of the environmental conditions over the period of high river discharge. This is unsurprising given the large size of many corals, which indicates their tolerance to past fluctuations in environmental conditions.

Our study demonstrates that selective pressures manifest during environmental extremes and vary along depth-gradients and between the life-history stages of corals. Despite this generalisation, exposure to stressful conditions resulting from increased runoff will vary in response to unique combinations of site-specific hydrodynamics, historical disturbance regimes (Harmelin-Vivien 1994), proximity to rivers and the runoff characteristics of those rivers. High rates of sedimentation are generally detrimental to corals (Fabricius 2005, 2011; Erftemeijer et al. 2012). However, these high rates of sedimentation require a combination of supply in the form of high concentrations of suspended particles, measurable as high turbidity, coupled with a low energy hydrodynamic setting that allows these particles to settle and accumulate (Wolanski et al. 2005). While such conditions were typical of the reefs included in this study, even here, shallow water coral communities were less affected by the altered conditions than communities in deeper water. From a regional perspective that recognises individual reefs as supporting small populations of coral taxa belonging to regionally connected meta-populations, it is important that generalisations relating to the effects of runoff be made at the appropriate scale. Studies focused only on reefs in relatively shallow areas exposed to frequent wave energy may overestimate the resilience of communities, while studies in areas predisposed to high rates of sedimentation, such as those at our deeper sites, may underestimate resilience. We suggest that the careful interpretation of community dynamics in the context of detailed environmental data is necessary to tease apart the influence of environmental degradation from naturally varying environmental condition. Further, our data suggest that the primary response to runoff in this region was the result of the short-term (months) exceedance of ambient environmental conditions as a result of pollutants delivered as runoff during high flow conditions. That community selection appeared to occur during extreme conditions, while entirely logical, is a key point demonstrated by our work. The implication is that observations during periods of relatively benign conditions will almost certainly document community dynamics divorced from selective processes.

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