REPORT

Effectiveness of benthic foraminiferal and coral assemblages as water quality indicators on inshore reefs of the Great Barrier Reef, Australia

S. Uthicke · A. Thompson · B. Schaffelke

Abstract Although the debate about coral reef decline focuses on *global* disturbances (e.g., increasing temperatures and acidification), *local* stressors (nutrient runoff and overfishing) continue to affect reef health and resilience. The effectiveness of foraminiferal and hard-coral assemblages as indicators of changes in water quality was assessed on 27 inshore reefs along the Great Barrier Reef. Environmental variables (i.e., several water quality and sediment parameters) and the composition of both benthic foraminiferal and hard-coral assemblages differed significantly between four regions (Whitsunday, Burdekin, Fitzroy, and the Wet Tropics). Grain size and organic carbon and nitrogen content of sediments, and a composite water column parameter (based on turbidity and concentrations of particulate matter) explained a significant amount of variation in the data (tested by redundancy analyses) in both assemblages. Heterotrophic species of foraminifera were dominant in sediments with high organic content and in localities with low light availability, whereas symbiont-bearing mixotrophic species were dominant elsewhere. A similar suite of parameters explained 89% of the variation in the FORAM index (a Caribbean coral reef health indicator) and 61% in foraminiferal species richness. Coral richness was not related to environmental setting. Coral assemblages varied in response to environmental variables, but were strongly shaped by acute disturbances (e.g., cyclones, *Acanthaster planci* outbreaks, and bleaching), thus different coral assemblages may be found at sites with the same environmental conditions. Disturbances also affect foraminiferal assemblages, but they appeared to recover more rapidly than corals. Foraminiferal assemblages are effective bioindicators of turbidity/light regimes and organic enrichment of sediments on coral reefs.

Keywords Foraminifera · Hard coral · Water quality · Environmental indicator · Sediment quality · Redundancy analysis

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Introduction

Coral reefs are currently a focus of public and scientific debate because of their vulnerability to global disturbances such as rising sea temperatures and ocean acidification (e.g., Fabricius et al. 2007; Hoegh-Guldberg et al. 2007). In addition to climate change, regional and local anthropogenic impacts such as overfishing and eutrophication continue to affect coral reefs and are likely to interact with global stressors. Scientists and managers have realised that continued management of local disturbances is vital to provide corals and reef organisms with the maximum resilience to cope with global stressors (Bellwood et al. 2004; Marshall and Johnson 2007).

The Great Barrier Reef (GBR) lagoon receives suspended sediments and nutrients from land runoff, which has increased several-fold during the last 150 years (Neil et al. 2002; Furnas 2003; McCulloch et al. 2003); the area now exposed to runoff is about ten times larger than 100 years ago (Wooldridge et al. 2006). Coastal waters adjacent to

agricultural lands have higher concentrations of dissolved and particulate nutrients, chlorophyll *a* and suspended sediments, especially during the summer wet season, compared to coastal areas adjacent to undeveloped catchments and offshore areas (e.g., Brodie et al. 2007; Cooper et al. 2007). However, water quality parameters are highly variable in space and time which necessitates frequent measurements to adequately determine true concentration ranges. The measurement of biological indicators has significant advantages over directly measuring water quality to assess the chronic or acute effects of changes in water quality on reef health. Appropriate biological indicators can integrate the effects of acute and chronic disturbances over various time scales (Cooper and Fabricius 2007). The understanding of the consequences of high nutrients and suspended sediments for the health of inshore coral reefs is improving (Fabricius 2005; Done et al. 2007; Lirman and Fong 2007), but inferences often depend on selected indicators.

Based on changes in overall coral cover, Pandolfi et al. (2003) concluded that GBR outer shelf reefs are the most pristine reefs among reefs in 14 global geographical regions, but nonetheless about 30% are on the way towards 'ecological extinction', followed by the GBR inshore reefs (about 37%). Coral cover declined drastically on some reefs of the GBR over the last decades, similar to other Indo-Pacific reefs (Bellwood et al. 2004; Bruno and Selig 2007). However, coral cover is affected by various acute disturbances such as mass coral bleaching, tropical storms and outbreaks of the coral-eating crown-of-thorns seastar (*Acanthaster planci*), which may obscure any, perhaps more subtle, chronic water quality effects (Cooper and Fabricius 2007). Species-specific tolerances are also important; for example, differential tolerance to light attenuation has long been implicated in observed changes in coral community composition along environmental gradients (e.g., Done 1982) but not necessarily in changes in total coral cover. Various other attributes of coral-reef communities, which could be considered indicators, change along water quality gradients of increasing turbidity and availability of nutrients and organic matter towards the GBR coast. For example, macroalgal cover increases, and abundance and richness of many hard-coral and octocoral taxa decrease (van Woesik et al. 1999), maximum depth of reef development decreases (Cooper et al. 2007), and benthic microalgae show physiological adaptations to low light levels (Uthicke 2006). Coral species richness is lower on GBR reefs adjacent to land with intense agriculture (DeVantier et al. 2006), and octocorals shift from phototrophic to heterotrophic assemblages towards the coast (Fabricius and De'ath 2008).

Foraminifera are well established indicators for marine and estuarine pollution in temperate regions (Alve 1995) and have been applied as indicators for coral reef water

quality in Florida and the Caribbean using a simple index, the 'FORAM index' (Hallock 2000; Hallock et al. 2003). Shifts in the index (based on grouping foraminifera into three functional groups: symbiotic, opportunistic and 'other small') over time coincided with general reef degradation caused by land runoff (Hallock et al. 2003). The FORAM index corresponded well to a water quality gradient in the GBR, suggesting that decreased light and increased organic matter availability may cause a shift towards higher contribution of heterotrophy (Uthicke and Nobes 2008; Schueth and Frank 2008).

Here, the relationships between environmental variables (i.e., water and sediment properties) to both hard-coral and benthic foraminiferal assemblages were analysed to assess the effectiveness of either assemblage as an indicator of environmental (water and sediment) quality. We used data from a large-scale monitoring programme on inshore reefs of the GBR. Specifically, two hypotheses were tested: (1) the regional and local setting of these reefs result in different environmental conditions (e.g., different concentrations of nutrients and suspended solids in the water column, and different grain size and organic content in reef sediments); and (2) these differences in environmental setting correspond to differences in assemblage composition and diversity for coral and foraminiferal assemblages.

Materials and methods

Sampling design

The Reef Plan Marine Monitoring Program is part of a government initiative "to halt and reverse the decline in water quality entering the GBR" (Queensland Government and Commonwealth of Australia 2003) and monitors water quality and coral reef status in the inshore GBR lagoon (∼30 reefs along ∼1,000 km of coastline) since 2005. Monitoring locations were selected to represent reefs along most of the GBR coastline and can be broadly grouped into four geographical regions based on major river catchments. The four regions were the Wet Tropics (10 locations), Burdekin (6 location), Whitsunday (7 location), and Fitzroy (4 locations) regions; thus yielding a total of 27 reef locations (see Table S1 in electronic supplement). All locations are within 30 km off the coast and have a well-developed reef flat, indicating past reef accretion. At each location, sampling was conducted at two sites (separated by at least 200 m), each with five permanently marked 20-m transects (separated by 5 m) contouring the reef slope at a depth of 5 m below Lowest Astronomical Tide (LAT). Coral and foraminiferal assemblage data were collected in both 2005 and 2006 (Table S1 identifies locations which were only sampled in one year).

Hard-coral assemblages

Cover of coral genera was estimated using the point intercept technique. Digital photographs were taken at 50-cm intervals along each 20-m transect. For 32 images, the identity of the benthic organisms beneath five evenly spaced points was recorded. The taxonomic resolution varied; some coral taxa were identified to genus level, while others were identified to species. The genus *Acropora* was further divided into the growth forms bottlebrush, branching, corymbose, digitate, and tabulate. *Porites* spp. were scored as branching, submassive/encrusting, or massive growth forms. The proportion of points identified from all five transects yielded cover estimates for each taxon at each site. Cover data were averaged for each location.

Foraminiferal assemblages

Using a cut-off plastic syringe (diameter 2.8 cm), ten cores of the top 1-cm sediment layer were collected haphazardly from deposits along the five coral transects at each site. Four of these samples were pooled for sampling of foraminifera, the remaining six were pooled for the analysis of sediment-quality variables. For the estimation of foraminiferal abundances, sediments were washed with freshwater in a 63 µm sieve to remove small particles. After drying (>24 h, 60°C) and mixing, all foraminifera were collected from haphazard subsamples until a minimum of 200 specimens per site were obtained.

Only intact specimens which showed no sign of ageing and little damage were considered. Samples thus defined are a good representation of the present-day biocoenosis (Yordanova and Hohenegger 2002), although not all specimens may have been alive at the time of sampling. Foraminiferal species composition was determined in microfossil slides under a dissection microscope. Most taxa were identified to genus or species level, following Nobes and Uthicke (2008). The dry weight of the sediment and the foraminifera was determined to calculate foraminiferal densities and to estimate the per cent contribution of intact foraminifera to the total sediment. Because the main emphasis of this study was to investigate between location variation, and to allow comparison to environmental parameters, abundance data from the two sites were averaged for each location.

Sediment quality

Pooled sediment cores from each site were analysed for granulometrics and the proportional composition of organic carbon, total carbon and nitrogen. Grain size fractions were determined by dry sieving larger fractions (>1.4 mm) and MALVERN laser analysis of smaller fractions (<1.4 mm). Total carbon (carbonate carbon + organic carbon) and nitrogen were determined by combustion of dried and ground samples, on a LECO Truspec C/N Analyser. Organic carbon was measured using a Shimadzu TOC-V Analyser with a SSM-5000A Solid Sample Module after acidification of the sediment with 2 M hydrochloric acid. Inorganic (carbonate) carbon was calculated as the difference between total carbon and organic carbon values.

Water quality

Water column sampling was carried out during two wet and two dry seasons (August–September 2005, January 2006, August–October 2006 and February–April 2007) in close proximity to each survey reef. Secchi depth (a measure of water transparency, as a proxy for underwater light attenuation) was measured at each sampling location. Discrete water samples were collected from two to three depths through the water column with Niskin bottles. Salinity was measured in subsamples using a Portasal Model 8410A Salinometer. Sub-samples for total dissolved nitrogen and phosphorus (TDN, TDP) and dissolved organic carbon (DOC) were immediately filtered through a 0.45 µm filter cartridge (Sartorius MiniSart N) into acid-washed screw-cap plastic test tubes and stored at −18°C until analysis. Samples for DOC were acidified with 100 µl of AR-grade HCl and stored at 4°C until analysis. TDN and TDP were analysed after persulphate digestion (Valderrama 1981) by standard wet chemical methods for inorganic nutrients (Parsons et al. 1984) implemented on a segmented flow analyzer (Bran and Luebbe AA3). DOC concentrations were measured by high temperature combustion (680°C), using a Shimadzu TOC-5000A carbon analyser.

Sub-samples for particulate nutrients and chlorophyll *a* were collected on pre-combusted glass fibre filters (Whatman GF/F) and stored at −18°C until analyses. Particulate nitrogen (PN) was determined by high temperature combustion using an ANTEK 707/720 Nitrogen Analyser (Furnas et al. 1995). Particulate phosphorus (PP) was determined spectrophotometrically as inorganic P (PO_4, Parsons et al. 1984) after digestion in 5% potassium persulphate (Furnas et al. 1995). Particulate carbon (POC) was analysed by high temperature combustion (950°C) using a Shimadzu TOC-V carbon analyser with SSM-5000A solid sample module after acidification with concentrated phosphoric acid. Chlorophyll *a* concentrations were measured fluorometrically using a Turner Designs 10AU fluorometer after grinding the filters in 90% acetone (Parsons et al. 1984).

Sub-samples for suspended solids (SS) were collected on pre-weighed, 0.4 µm, polycarbonate filters (47 mm diameter, GE Water & Process Technologies), and SS

concentrations were determined gravimetrically from the weight difference between loaded and unloaded filters after drying overnight at 60°C. Sediment samples and water quality data were not collected from Peak Island, thus, statistical analyses comparing assemblage composition to environmental data excluded that location.

Statistical analyses

Foraminiferal counts and coral cover estimates were converted to relative abundance and cover by dividing estimates for each taxon by the total abundance or cover, respectively. Relative abundance data were fourth root transformed for all statistical analyses. Mantel tests based on Spearman Rank correlations and 10,000 permutations were used to measure relatedness of two similarity matrices (i.e., either foraminiferal or coral assemblage data from two different years, or between foraminiferal and coral data from the same set of locations). Regional differences in assemblage composition for both foraminifera and corals were tested by Analysis of Similarity (ANOSIM), and the taxa contributing most to the dissimilarity between regions were identified by Similarity percentage (SIMPER) analyses. For matrix comparisons and ANOSIM, similarity matrices were calculated using Bray Curtis similarities. Mantel tests, SIMPER, ANOSIM, and diversity calculations (S = taxa richness) for each location were conducted in Primer (Clarke and Gorley 2001). Richness of coral assemblages was calculated only for genera, not considering the different growth forms.

The influence of sediment and water quality parameters on foraminiferal and coral assemblage composition was investigated with redundancy analysis (RDA). Environmental data were z-transformed (mean = 0, SD = 1) prior to analysis to accommodate different measurement units, and data were averaged over sampling seasons and years (N = 4 water quality, N = 2 sediment quality for each reef). Fourth root transformed assemblage data were centred by row means for RDA. Exploratory correlation and principal component analyses indicated that several of the environmental parameters were highly correlated; these were combined before further analysis by averaging their z-scores, as follows. The per cent contribution of small sediments and medium-sized sediments were highly correlated; therefore sediment up to 63 μm grain size (clays and silt), those between 63 and 250 μm (very fine and fine sands), and those above 250 μm were binned. However, the latter group was omitted from statistical analyses, since the three groups were not independent (because their contribution adds up to 100%). Sediment organic carbon and nitrogen values were also combined to form a "sediment organic matter content" parameter. The water quality parameters related to water clarity (particulate organic carbon, phosphorous and nitrogen; suspended solids, chlorophyll *a*, dissolved organic carbon, Secchi depth) were pooled (Secchi depth with reversed sign) to create a combined "water column particulates" parameter. In addition, hard-coral cover was included as an environmental parameter in the foraminiferal analysis.

For the RDA, the influence of environmental parameters on the foraminiferal and coral assemblages was assessed after removing ('partialling out') the spatial effects of 'Region' which were distinct in both data sets (see "Results"). The amount of variation explained by each of the environmental variables was examined individually, and the significance of the explained variance tested with permutation tests (1,000 permutations). Only environmental variables that were at least marginally significant ($p < 0.1$) were included in the final model. Prior to RDA, a detrended correspondence analysis (DCA) was conducted with transformed assemblage data. Axis lengths for foraminiferal (Axis 1 = 1.77, 2 = 1.32) and coral data (Axis 1 = 3.15, 2 = 2.06) were within the range indicative of near monotonic response curves, thus indicating that RDA assumptions were not violated (Jongman et al. 1995).

The same environmental parameters as for the RDA (also z-transformed) were used in a multiple regression analysis to test if they could be used as predictors for the FORAM index or for foraminiferal and coral diversity (expressed as taxa richness). The FORAM index was calculated according to Hallock et al. (2003), by grouping foraminiferal taxa into symbiotic, opportunistic and 'other small' taxa. For each sample, the number of individuals of each of these groups were multiplied with a group-specific weighting factor and divided by the total number of foraminifera (Hallock et al. 2003). The resulting values for each of the three groups were added up to form the FORAM index. All environmental parameters were initially included in the model and those that did not contribute significantly to the respective model were removed from the model by backwards elimination. The latter analyses, RDA, and DCA were conducted in R (R Development Core Team 2006).

Results

Water and sediment quality

Considerable variation in several biological and environmental parameters was observed between Great Barrier Reef (GBR) inshore reefs (see Tables S1, S2 in the electronic supplement). Coral cover ranged from 5 to 71%. Organic and inorganic carbon and nitrogen content in the sediment varied three to fivefold, and the average grain size varied 33-fold between sampling locations (Electronic

Supplement Table S1). Most particulate water quality parameters and Secchi depth varied two to eightfold between locations, with the largest range observed in suspended solids concentrations (electronic supplement Table S2). Total dissolved nutrients and dissolved organic carbon varied only one to threefold, with smallest variation observed in salinity.

The first and the second axes of a Principal Component Analyses (PCA) explained 62.5% of the variation of the water and sediment quality parameters between sampling locations (Fig. 1). The percentage of clay and fine sands and the organic content (carbon and nitrogen pooled) of the sediments were negatively correlated with the inorganic carbon content; these four sediment parameters were the main contributors to the first axis. Water column particulates (the pooled parameter including several components of particulate matter, dissolved organic carbon and Secchi depth) and salinity were negatively correlated with each other and were the main contributors to the second axis. Total dissolved phosphorus and nitrogen contributed less to the first two axes of the PCA. The environmental setting of

the sampling reefs in the four 'Regions' largely overlapped, but the Whitsunday Region was different than the other regions and was associated with sediments of small grain size and high organic content.

Foraminiferal assemblages

Benthic foraminifera on the 27 inshore GBR reefs were grouped into 50 taxa. Most of these were identified to species level; however, some of the smaller-sized taxa could only be differentiated to genus level (Table 1). To facilitate later discussion, Table 1 also includes trophic status of the respective taxa, with aposymbiotic taxa presumed to be heterotrophic, and symbiont-bearing taxa mixotrophic. The symbiont type was also listed for the latter group. Total average relative abundance of foraminiferal taxa varied widely between very rare species (total average <0.1%) and common species. The most common taxa, jointly representing about 63% total relative abundance were *Calcarina mayorii* (22.4%), *Quinqueloculina* spp. (13.2%), *Amphistegina* spp. (11.5%), *Calcarina*

Fig. 1 Principal Component Analysis (PCA) biplot of the water quality and sediment data (both z-transformed) from sampling locations, pooled over 2 years. Polygons surround reefs in the same region (Wet Tropics Region: *circles*; Burdekin Region: *squares*, Whitsunday Region: *triangles*, Fitzroy Region: *diamonds*). *TDP* Total dissolved phosphorus, *TDN* Total dissolved nitrogen, *SedCN* pooled sediment organic carbon and nitrogen content, Sed <63: proportion of sediments <63 μm grain size, Sed <250: proportion of sediments between 63 and 250 μm grain size, Particulates: pooled variable including particulate organic carbon, particulate phosphorous and nitrogen, suspended solids, chlorophyll *a*, dissolved organic carbon and Secchi depth (with reversed sign, thus increasing values of this variable represent high particulate matter and low visibility), Sediment IC: sediment inorganic carbon. See electronic supplement for full names of sample locations
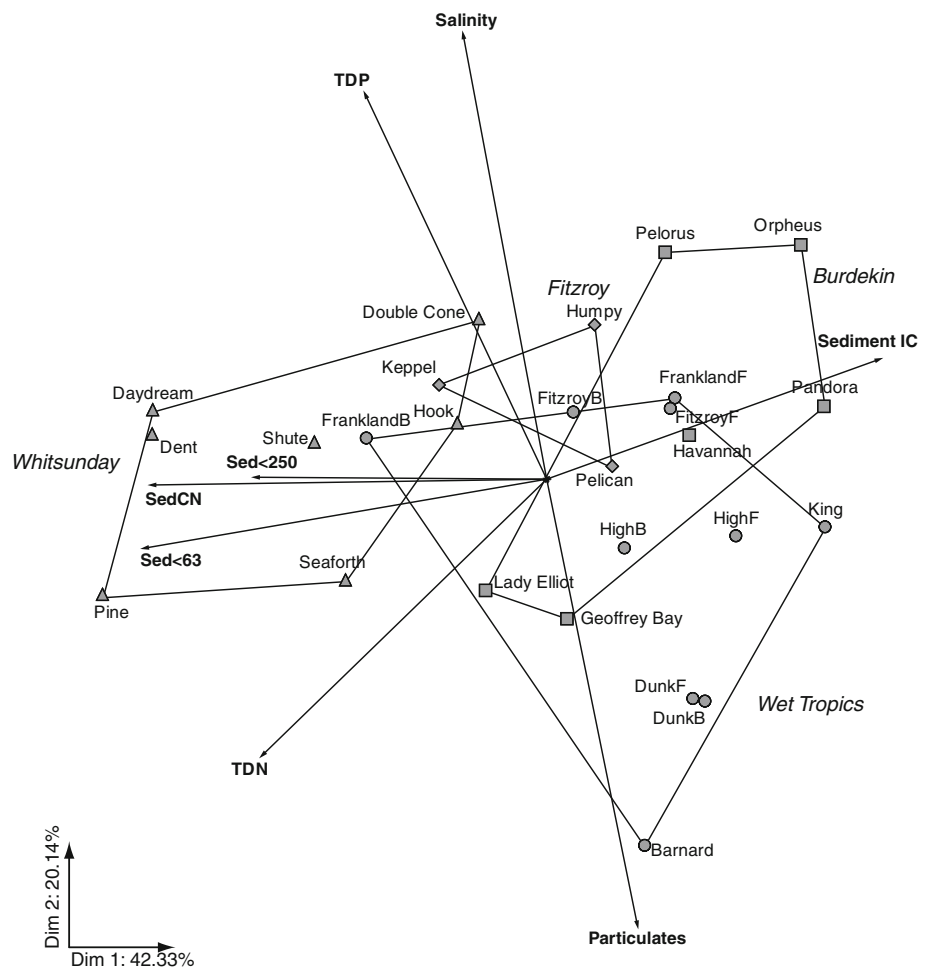
Table 1 Foraminiferal taxa and coral taxa observed

Foraminifera				Corals	
Order	Family	Species	Symbionts	Family	Taxon
Lagenida	Polymorphinidae	*Sigmoidella elegantissima*	*N*	Acroporidae	*Acropora* spp.
					Astreopora spp.
					Isopora spp.
					Montipora spp.
					Leptoseris yabei
Miliolida	Hauerinidae	*Pseudohauerina involuta*	*N*		*Pachyseris* spp.
	Miliolidae	*Discorbinella* sp.	*N**		*Pavona* spp.
		Miliolinella sp.	*N*	Astrocoeniidae	*Palauastrea ramosa*
		Planispirinella exigua	*N*	Dendrophylliidae	*Turbinaria* spp.
		Pseudomassalina sp.	*N*	Euphyllidae	*Euphyllia* spp.
		Pyrgo spp.	*N*		*Physogyra lichtensteini*
		Quinqueloculina spp.	*N*		*Plerogyra* spp.
		Triloculina spp.	*N*	Faviidae	*Caulastrea furcata*
	Nubeculariidae	*Vertebralina striata*	*N*		*Cyphastrea* spp.
	Soritidae	*Marginopora vertebralis*	Dino.		*Diploastrea heliopora*
		Sorites orbiculus	Dino.		*Echinopora* spp.
		Parasorites spp.	Greenalgae		*Favia* spp.
		Peneroplis antillarum	Red Algae		*Favites* spp.
		Peneroplis pertusus	Red Algae		*Goniastrea* spp.
		Peneroplis planatus	Red Algae		*Leptastrea* spp.
	Spiroloculinidae	*Spiroloculina angulata*	*N*		*Leptoria phrygia*
		Spiroloculina corrugate	*N*		*Montastrea* spp.
		Spiroloculina faveolata	*N*		*Moseleya latistellata*
		Spiroloculina other	*N*		*Oulophyllia* spp.
Rotaliida	Alfredinidae	*Epistomaroides polystomelloides*	*N*		*Platygyra* spp.
	Amphisteginidae	*Amphistegina radiata*	Diatom		*Plesiastrea versipora*
		Amphistegina spp.	Diatom	Fungiidae	*Ctenactis crassa*
	Bagginidae	*Cancris* sp.	*N*		*Fungia* spp.
	Calcarinidae	*Baculogypsina sphaerulata*	Diatom		*Heliofungia actiniformis*
		Calcarina hispida	Diatom		*Herpolitha limax*
		Calcarina mayorii	Diatom		*Podabacia crustacean*
		Calcarina spengleri	Diatom		*Polyphyllia talpina*
		Neorotalia calcar	Diatom		*Sandalolitha robusta*
	Cibicidae	*Cibicides*	*N**	Merulinidae	*Hydnophora* spp.
	Cymbaloporidae	*Cymbalporetta* spp.	*N*		*Merulina ampliata*
	Discorbidae	*Rosalina*	*N*		
		Rotorbis	*N*	Mussidae	*Acanthastrea* spp.
	Elphidiidae	*Elphidium* cf. *craticulatum*	Plastids*		*Lobophyllia* spp.
		Elphidium crispum	Plastids*		*Scolymia* spp.
		Elphidium reticulosum	Plastids*		*Symphyllia* spp.
	Eponididae	*Eponides* sp.	None	Oculinidae	*Galaxea* spp.
	Nummunlitidae	*Heterostegina depressa*	Diatoms	Pectiniidae	*Echinophyllia* spp.
		Operculina ammonoides	Diatoms		*Mycedium elephantotus*
	Planorbulinidae	*Planorbulina* sp.	*N*		*Oxypora* spp.
	Reussellidae	*Reussella*	*N*		*Pectinia* spp.

Table 1 continued

Foraminifera				Corals	
Order	Family	Species	Symbionts	Family	Taxon
	Rotaliidae	*Ammonia* sp.	N*	Pocilloporidae	*Pocillopora* spp.
		Pararotalia sp.	N*		*Seriatopora hystrix*
		Pararotalia venusta	N*		*Stylophora pistillata*
			N	Poritidae	*Alveopora* spp.
Textulariida	Textularidae	*Textularia* spp.	N		*Goniopora* spp.
					Porites. spp.
					Porites rus
				Siderastreidae	*Coscinaraea columna*
					Psammocora spp.
					Pseudosiderastrea tayami

Most corals were determined to genus level or species level, some genera were divided into growth forms. The type of symbiont is indicated for symbiont-bearing foraminifera. N = no symbionts, *Dino.* dinoflagellate. Species regarded as opportunistic for calculation of the FORAM index are marked with an asterisk in the "Symbionts" column

hispida (6.5%), *Amphistegina radiata* (5.0%), and *Baculogypsina sphaerulata* (4.1%).

Foraminiferal assemblages on reefs sampled in both 2005 and 2006 (24 reefs) had similar spatial patterns (Mantel test, rho = 0.761, $p < 0.001$), and data were averaged over the 2 years for all subsequent analyses.

Analysis of Similarities (ANOSIM) indicated significant differences in the foraminiferal assemblage composition between the geographical regions (Global $R = 0.381$, $p < 0.001$). Pairwise tests indicated that, with the exception of the Wet Tropics and Burdekin regions ($R = -0.041$, $p = 0.602$), all pairs of regions were significantly different from each other (all R values between 0.377 and 0.857, p in each case <0.017); this pattern is illustrated by a non-metric multi-dimensional scaling plot (NMDS, Fig. 2a).

Average within-region similarity of foraminiferal assemblages ranged from about 63 to 77% whereas between-region dissimilarities ranged from 34 to 43% [Similarity Percentage (SIMPER) analyses, Table 2]. All abundant species were also among the species contributing most to the regional differences (Table 2). Most strikingly, *C. mayori* and *B. sphaerulata* were abundant in the two northernmost regions and absent or rare in the Whitsundays and Fitzroy regions. This pattern was reversed for *Quinqueloculina* spp., which was more abundant in the latter two regions. However, several rarer foraminifera were also important to distinguish individual regions, e.g., *Discorbinella* spp. was much more dominant in the Fitzroy Region compared to the other regions, and *Cymbaloporetta* spp., *Pararotalia* sp., and *Miliolinella* sp. were found exclusively in the Whitsunday Region (Table 2).

Taxa Richness (S) for the foraminiferal assemblages varied between individual locations, ranging from 14 to 43 (Table 3). The average was distinctly higher in the
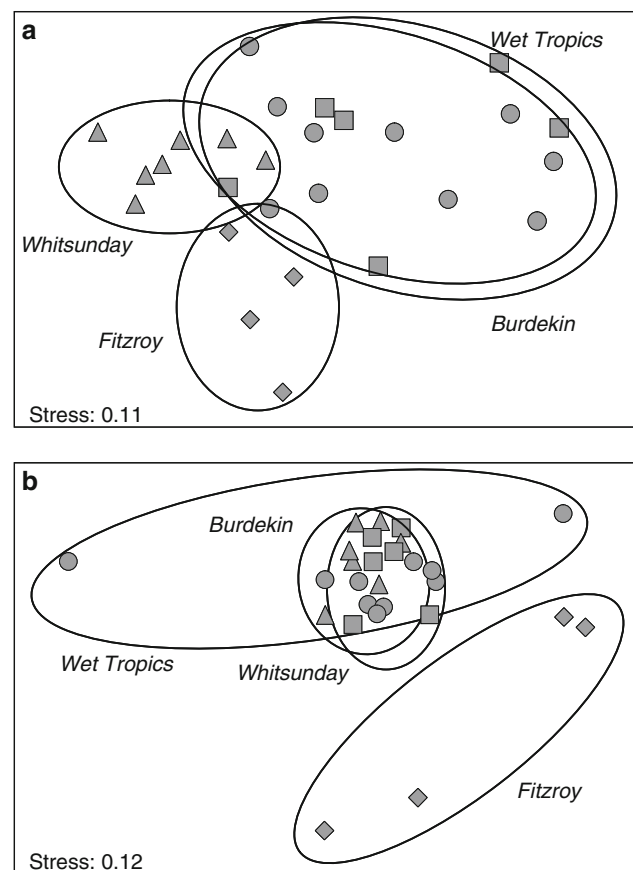
Fig. 2 Non-metric multi-dimensional scaling of foraminiferal (**a**) and hard-coral assemblages (**b**) in four inshore regions (Wet Tropics Region: *circles*; Burdekin Region: *squares*, Whitsunday Region: *triangles*, Fitzroy Region: *diamonds*) of the Great Barrier Reef. For clarity, ellipses were drawn around reefs in each region

Whitsunday Region compared to the three other regions, and the lowest taxa richness was observed in the Fitzroy Region at the southern end of the GBR.

Table 2 Similarity percentage (SIMPER) analysis of foraminiferal assemblages in four inshore regions of the Great Barrier Reef

	Wet tropics	Burdekin	Whitsunday	Fitzroy
(A) SIMPER				
Wet tropics Region	**65.39**	*34.45*	*42.80*	*40.66*
Burdekin Region	*B. sphaerulata (5.66)*	**62.94**	*41.73*	*42.45*
	Quinqueloculina spp. **(3.11)**			
	Discorbinella sp. (3.01)			
	P. planatus (2.85)			
	P. venusta (2.85)			
Whitsunday Region	*C. mayori (6.51)*	*C. mayori (6.52)*	**77.42**	*37.42*
	P. venusta (4.14)	*P. venusta (4.05)*		
	B. sphaerulata (3.43)	*C. hispida (3.82)*		
	Spiroloculina angulata (3.28)	*Spiroloculina angulata (3.77)*		
	Pararotalia sp.(3.20)			
		B. sphaerulata (3.51)		
Fitzroy Region	*C. mayori (9.98)*	*C. mayori (9.37)*	*Amphistegina.* spp. (3.79)	**70.35**
	Discorbinella sp.(6.16)	*Discorbinella* sp.(6.25)	*Miliolinella* sp. (3.77)	
	B. sphaerulata (4.48)	*C. hispida (4.96)*	*E. reticulosum (3.63)*	
	P. venusta (3.91)	*B. sphaerulata (4.25)*	*Cymbaloporetta* spp. 2 (3.41)	
	C. hispida (3.81)	*P. venusta (3.51)*	*C. hispida (3.27)*	
(B) Abundance				
B. sphaerulata	5	10	0	0
C. hispida	4	13	6	0
C. mayori	36	34	2	0
Amphistegina spp.	16	8	3	19
E. reticulosum	0	0	2	0
Spiroloculina angulata	0	0	3	1
Quinqueloculina spp.	8	9	22	17
Discorbinella sp.	0	0	3	12
P. planatus	1	0	0	0
P. venusta	1	1	10	4
Cymbaloporetta spp.2	0	0	2	0
Pararotalia sp.	0	0	2	0
Miliolinella sp.	0	0	2	0

Above diagonal (in italics): Average dissimilarity (%) between Regions; diagonal (in bold print): average within-region similarity (%); below diagonal: five taxa contributing most to between-region dissimilarity, the contribution (%) to the total dissimilarity of each taxon is given in brackets. Data were fourth root transformed. B: Average relative abundances (in %, untransformed) of the taxa listed in Table 2 (A) in each region

Hard-coral assemblages

The most abundant coral genera at the sampling locations were *Acropora* (mean relative cover: 26.8%) and *Porites* (18.0%). Other common genera included *Goniopora* (9.7%), *Montipora* (6.8%), *Turbinaria* (4.5%), and *Galaxea* (3.6%). Similar to the foraminifera, coral assemblages had congruent spatial patterns in the two observation years (Mantel test, rho = 0.880, $p < 0.001$), and data were averaged over the two survey years for following analyses.

The coral assemblages significantly differed between the four geographical regions (global ANOSIM: $G = 0.256$, $p = 0.003$). Pairwise comparisons indicated that coral assemblages in the Fitzroy Region were markedly different than the other three regions ($R > 0.58$ and, $p < 0.020$ in each case). The coral communities in the Whitsunday Region differed from those in the Wet Tropics Region ($R = 0.168$, $p = 0.047$), though neither of these regions differed from the communities on reefs in the Burdekin Region ($R = 0.063$, $p = 0.222$ for Whitsunday and $R = 0.015$, $p = 0.410$ for Wet Tropics; Fig. 2b).

Within-region similarity in coral communities was distinctly lower in the Fitzroy Region (about 37%) compared with the other three regions (52–61%, SIMPER, Table 4).

Table 3 Richness (S) for foraminiferal assemblages (taxa defined in Table 1) and coral communities (genus level) on nearshore reefs in four regions of the Great Barrier Reef

Location	Foraminifera	Corals
Wet tropics Region		
Dunk Isl. B	30	26
Dunk Isl. F	23	25
Fitzroy Isl. B	34	35
Fitzro Isl. F	15	29
Frankland Isl. B	31	8
Frankland Isl. F	27	12
High Isl. B	38	26
High Isl. F	18	28
King Rf.	14	16
North Barnard Isl.	32	22
Average (SD)	26.2 (8.3)	22.7 (8.3)
Burdekin Region		
Geoffrey Bay	33	32
Havannah Isl.	35	29
Lady Elliot Isl.	24	27
Orpheus Isl.	20	17
Pandora Rf.	14	26
Pelorus Isl.	34	26
Average (SD)	26.7 (8.7)	26.2 (5.0)
Whitsunday Region		
Daydream Isl.	33	23
Dent Isl.	40	36
Double Cone Isl.	37	33
Hook Isl.	43	27
Pine Isl.	34	34
Seaforth Isl.	35	27
Shute and Tancred Isl.	36	25
Average (SD)	36.9 (3.5)	29.3 (5.0)
Fitzroy Region		
Humpy Isl.	23	10
North Keppel Isl.	29	7
Peak Isl.	18	13
Pelican Isl.	22	25
Average (SD)	23.0 (4.5)	13.8 (7.9)

Average and standard deviation (SD) are given for each region. *B* back reef, *F* front reef

As suggested by the ANOSIM and NMDS, between-region dissimilarity in coral communities was largest between Fitzroy Region and the other three regions (Table 4). The most striking difference between coral communities in Fitzroy Region and the remaining regions was the higher representation of branching *Acropora* and *Goniastrea* and the absence of a number of genera found in the other regions (Table 4). The highest hard-coral richness was observed in the Whitsunday Region, and diversity was lowest the Fitzroy Region (Table 3).

Relationship of hard-coral and foraminiferal assemblages with water and sediment quality

The observed spatial patterns for foraminiferal and coral assemblages showed significant similarity (Mantel test, rho = 0.208, $p = 0.05$).

Redundancy analysis (RDA) was used to assess taxa–location relationships and the effects of environmental variables. A significant amount of variation in the foraminiferal distribution (Table 5) was explained by the proportion of very fine sands and fine sands (63–250 μm grain size) and clays and silts (<63 μm), sediment organic matter and inorganic carbon content and the composite water column particulate variable. Thirty-five per cent of the variation in the foraminiferal distribution was explained after partialling out effects of 'Region' (Fig. 3), and the five environmental parameters explained an additional 27.7%. Heterotrophic foraminifera were associated with high values of 'particulates' in the water and fine sediments (<63 and 63–250 μm grain size) with high sediment organic carbon and nitrogen content (Fig. 3). In contrast, symbiont-bearing species were associated with low turbidity and high inorganic carbon content in the sediment. Heterotrophic and symbiont-bearing foraminiferal species were well separated along the first two RDA axes, with only a small area of overlap (Fig. 3). Most of this overlap was due to two *Peneroplis* species, the two main taxa bearing red algal endosymbionts (see Table 1 for symbiont types of all taxa). All diatom-bearing species were clearly separated from heterotrophic taxa, whereas the dinoflagellate-bearing species contributed little to the differences in assemblage composition between reefs, possibly because of their generally low abundance in most samples.

This pattern was confirmed by multiple regression analyses, which indicated that a large amount of the variation in the FORAM index (89%) and foraminiferal taxa richness (61%) was explained by a subset of the measured environmental parameters (Table 6). The FORAM index (high values = high relative abundance of symbiont-bearing taxa) decreased with increasing proportions of sediments with small grain sizes and high organic matter content and with increasing concentrations of water column particles (and hence reduced light availability). In contrast, this index increases with increasing values of sediment inorganic carbon and increasing hard-coral cover (Table 6). Variation in foraminiferal taxa richness was also explained by environmental parameters and mainly increased with increasing proportion of sediments with small grain sizes (Table 6).

Table 4 (A) Similarity percentage (SIMPER) analysis for coral assemblage composition in four nearshore regions of the Great Barrier Reef

	Wet tropics	Burdekin	Whitsunday	Fitzroy
(A) SIMPER				
Wet tropics Region	**51.92**	*45.19*	*47.75*	*68.05*
Burdekin Region	*Porites rus* (4.24)			
	Porites Branching (3.28)	**59.45**	*40.88*	*64.99*
	Turbinaria (3.22)			
	Diploastrea (2.85)			
	Merulina (2.76)			
Whitsunday Region	*Porites rus* (4.17)	*Galaxea* (3.18)		
	Goniopora (3.34)	*Acropora* Bottlebrush (3.15)	**61.15**	*65.75*
	Acropora Branching (3.27)	*Porites* Branching (3.05)		
	Pectinia (3.20)	*Diploastrea* (3.04)		
	Porites Branching (3.02)	*Acropora* Branching (2.99)		
Fitzroy Region	*Acropora* Branching (6.21)	*Acropora* Branching (5.05)	*Goniopora* (5.06)	
	Porites rus (4.37)	*Porites* Massive (4.01)	*Acropora* Branching (5.03)	**36.8**
	Porites Massive (3.57)	*Galaxea* (3.74)	*Pectinia* (3.83)	
	Porites Branching (3.24)	*Goniopora* (3.61)	*Pachyseris* (3.42)	
	Goniastrea (3.18)	*Merulina* (3.41)	*Porites* Massive (3.14)	
(B) rel. cover				
Acropora Bottlebrush	1.1	1.1	3.1	0.05
Acropora Branching	3.1	4.8	13.9	57.5
Diploastrea	0.6	4.6	1.5	0
Galaxea	2.1	7.5	3.8	0.05
Goniastrea	2.9	2.7	0.6	9.6
Goniopora	2.8	6.4	24.8	1.4
Merulina	1.2	3.2	0.9	0
Pachyseris	1.3	4.0	2.8	0
Pectinia	0.5	2.1	4.9	0
Porites Branching	6.5	2.1	2.7	0
Porites Massive	8.1	9.9	7.1	0.2
Porites rus	16.7	0.4	0	0
Turbinaria	6.0	5.7	1.2	4.9

Above diagonal (in italics): Average dissimilarity (%) between regions; diagonal (in bold print): average within-region similarity (%); below diagonal: five taxa contributing most to between-region dissimilarity, the contribution (%) to the total dissimilarity of each taxon is given in brackets. Data were fourth root transformed for analyses. (B) Average relative cover (in %, untransformed) of the taxa listed in (A) in each region

Coral assemblage composition was also related to environmental parameters (Table 5). The proportions of sediments with small grain sizes (<63 μm and between 63–250 μm), the combined organic carbon and nitrogen content of the sediment and the composite water column parameter 'particulates' explained most of the variation in coral assemblage composition (Table 5). Twenty-five per cent of the variation in coral assemblage composition was explained after partialling out the effects of 'Region' (Fig. 4), and the environmental parameters explained an additional 27%. Several coral genera were associated with low light availability as inferred by high values of water column particulates (Fig. 4, e.g., *Hydnophora*, *Turbinaria*,

Goniastrea, and *Moseleya*). In contrast, branching and corymbose forms of *Acropora* were more common on reefs with lower values of particulates in the water column and, hence, more light availability. Some coral taxa were generally associated with sediments of small grain sizes, high organic carbon and nitrogen content (e.g., *Pachyseris*, *Porites rus* and branching *Porites*, and the unattached *Fungia* and *Ctenactis*). Another group of coral taxa (e.g., massive *Porites* and *Diploastrea*) was negatively correlated with fine sediments, but exhibited no obvious relationship with light. There was no significant relationship between the richness of coral genera and any of the environmental parameters (multiple regression analyses, Table 6).

Table 5 The amount of variance explained (%) by individual environmental parameters in a redundancy analysis of foraminiferal and coral assemblage data

Variables	Foraminifera			Corals		
	Pseudo-F	*p*	% Explained	*Pseudo*-F	*p*	% Explained
Sediment						
Grain size (0–63 μm)	2.33	**0.053**	6.46	2.02	**0.086**	6.58
Grain size (63–250 μm)	5.61	**<0.001**	13.61	5.44	**0.001**	15.46
Organic C and N	2.81	**0.029**	7.61	3.86	**0.007**	11.66
Inorganic C	2.37	**0.062**	6.55	0.82	0.44	2.84
Water column						
Particulates	2.75	**0.029**	7.49	3.1	**0.001**	9.67
TDN	1.07	0.355	3.14	0.69	0.597	2.38
TDP	1.41	0.164	4.07	0.87	0.436	3.0
Salinity	1.51	0.160	4.33	1.14	0.3	3.88
Surrounding benthos						
Hard-coral cover	0.99	0.361	2.91	–	–	–

The effect of region was partialled out for the test of each parameter. Pseudo-F and p values test the significance of each variable in permutation tests (1,000 permutations). Bold print: parameters significant at $p < 0.10$, and used in final analyses (see Figs. 3, 4). – The effect of coral cover on coral communities was not analysed

Fig. 3 Redundancy analysis (RDA) of foraminiferal relative abundances on 26 inshore reefs of the Great Barrier Reef. Only the 40% of the taxa vectors which contributed most to the assemblage differences are shown. Data were fourth root transformed and row centred. Polygons surround symbiont-bearing and aposymbiotic species, respectively. Only environmental variables (*bold lines* with *arrow heads*) explaining a significant amount of the variation (see Table 5) were included (see Fig. 1 for abbreviations)
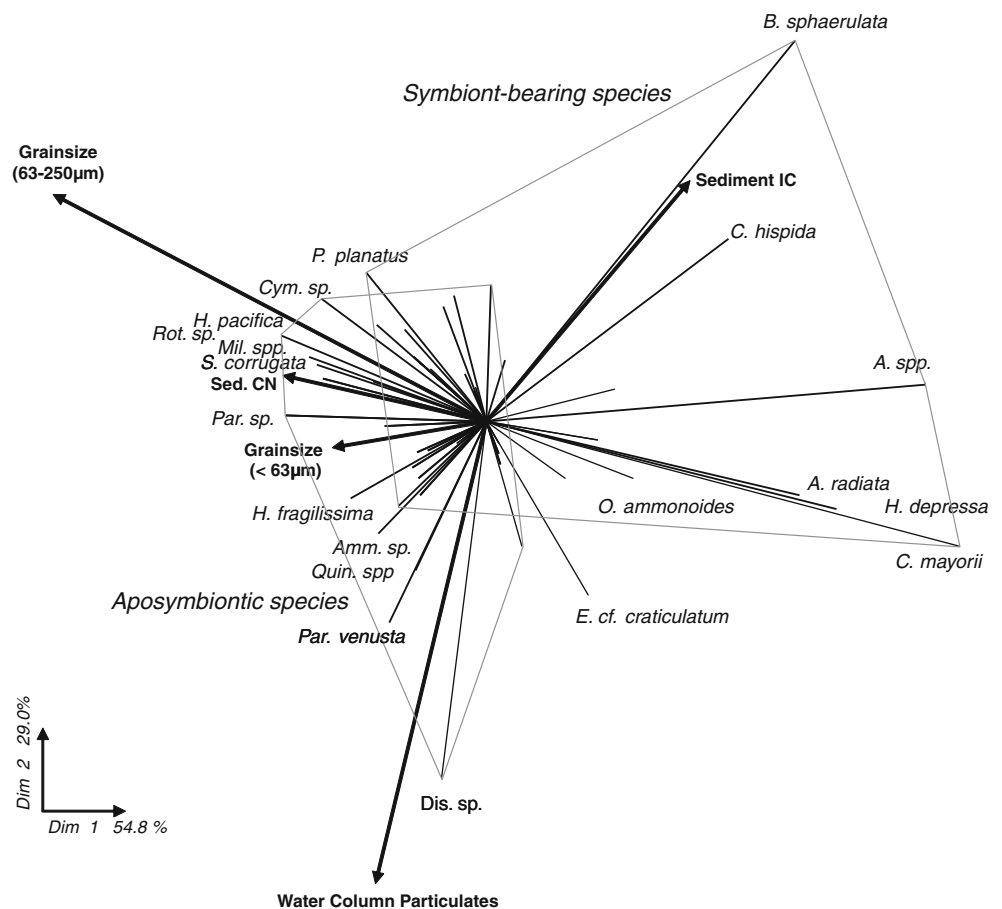
Discussion

This study investigated differences in assemblage composition of both foraminifera and hard corals on inshore reefs of the Great Barrier Reef (GBR) and their relationship with water quality and sediment characteristics. We argue below that assemblage composition of foraminifera, but not of corals, is a useful indicator of short-term (years) changes in environmental quality. Foraminifera are likely to respond faster to changes in water quality and are less susceptible to acute catastrophic disturbances. In contrast, coral data are more difficult to interpret because they are shaped by acute disturbances, and surprisingly little is known about the basic ecology of individual species.

Table 6 Multiple regression analyses for FORAM index and foraminiferal and coral genus richness

Variables	FORAM index			Foraminiferal richness			Coral richness		
	Slope	t	p	Slope	t	p	Slope	t	p
Sediment									
Grain size (0–63 μm)	Ex			4.13	2.17	**0.042**	3.45	2.05	0.052
Grain size (63–250 μm)	−0.85	−3.62	**0.001**	5.03	1.39	**0.002**	−3.29	−1.95	0.062
Organic C and N	−1.59	−4.79	**<0.001**	Ex			Ex		
Inorganic C	1.06	3.76	**0.001**	3.11	1.76	0.094	Ex		
Water column									
Particulates	−0.39	−1.48	0.154	3.38	2.01	0.057	Ex		
TDN	Ex			Ex			Ex		
TDP	Ex			2.53	1.77	0.093	Ex		
Salinity	Ex			Ex			Ex		
Surrounding benthos									
Hard-coral cover	0.94	3.90	**<0.001**	Ex			–	–	–
Intercept: total model	6.49	35.14	**<0.001**	29.00	25.82	**<0.001**	24.27	16.42	**<0.001**
R^2	0.89			0.61			0.20		
p	<0.001			<0.001			0.082		

All environmental variables were initially included in each model, and terms subsequently eliminated through stepwise backwards elimination. *Ex* term excluded by backwards elimination. Coral cover was not included in the coral richness model

Fig. 4 Redundancy analysis (RDA) of relative coral cover on 26 inshore reefs of the Great Barrier Reef. Only the 30% of the taxa vectors which contributed most to the assemblage differences are shown. Data were fourth root transformed and row centred. Only environmental variables (*bold lines* with *arrow heads*) explaining a significant amount of the variation (see Table 5) were included in this analysis (see Fig. 1 for abbreviations)
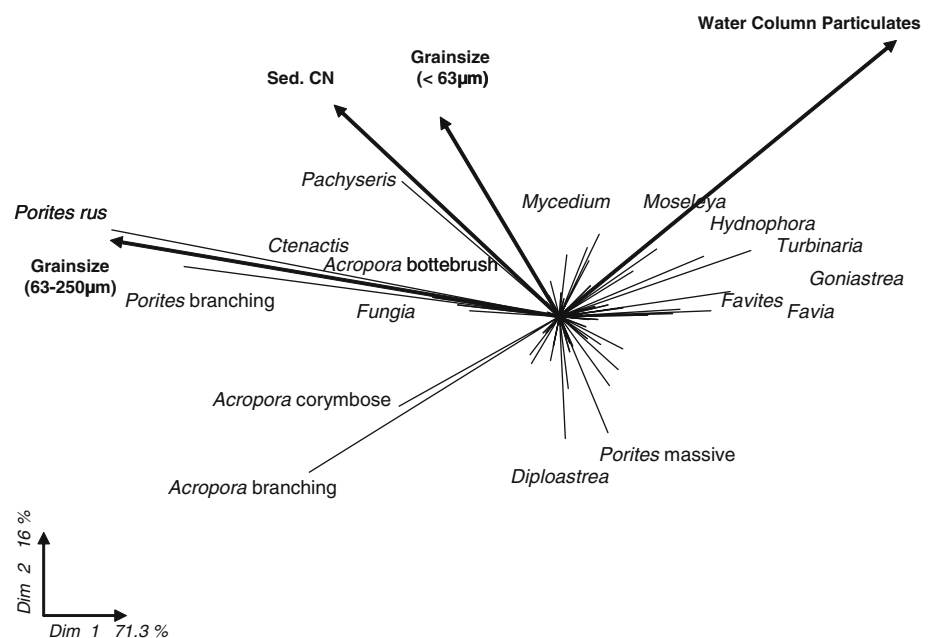
Foraminifera

Foraminiferal assemblage composition differed between study regions, confirming a previous comparison between three inshore GBR regions and midshelf reefs (Uthicke and Nobes 2008). The distribution of benthic foraminifera is influenced by a variety of factors such as water flow, depth, microhabitat and substratum type, salinity fluctuations and pollutants (e.g., Alve 1995; de Rijk 1995; Renema and Troelstra 2001; Renema 2006). In addition, food availability can be a limiting factor for heterotrophic benthic foraminifera (Jorissen 2002). In the present study, the influence of depth and microhabitat was minimised by collecting at a standard depth and focusing on sediment assemblages that integrate over several microhabitats as they represent living foraminifera on the sediment and recently dead ones from sediments and other microhabitats (Uthicke and Nobes 2008).

Most striking was the decline of the genera *Baculogypsina* and *Calcarina* from North to South. The relative abundance of these groups was 45 and 57% in the Wet Tropics and Burdekin regions, respectively, and declining to 1% (Fitzroy Region) towards the South. Other species increased towards the south (e.g., *Discorbinella* spp., *Quinqueloculina* spp.). Regions were located along a latitudinal, and hence, temperature gradient, while differences in water flow, a consequence of different tidal regimes, are also likely to be important. Winter water temperatures in the Fitzroy and Whitsunday regions are regularly below distributional limits given for *Calcarina* spp. (23°C) and *Baculogypsina sphaerulata* (21°C; Langer and Hottinger 2000), but these species have been observed on outer shelf reefs at similar latitude (Schueth and Frank 2008); suggesting that other factors such as habitat availability influence the distribution of these species.

Several environmental parameters explained variation in the foraminiferal assemblage composition after removing the effects of 'Region'. Heterotrophic and symbiont-bearing foraminiferal species separated in two distinct groups with little overlap, roughly determined by sediment grain size, nutrient content and light availability, similar to a previous study on other GBR reefs (Uthicke and Nobes 2008). In addition, high FORAM indices (Hallock et al. 2003) were associated with sediments with larger grain sizes, high inorganic carbon content, higher light availability and low amounts of particulates in the water column. Variation in foraminiferal taxa richness was mainly explained by an increase in the proportion of sediments with small grain sizes. While sediment grain size and inorganic carbon content are unlikely to be directly influenced by terrestrial runoff, the input, transformation, and retention of terrestrial nutrients, and suspended sediments can result in high organic sediment content and decreased light availability (Uthicke 2006; Cooper et al. 2007).

The combined water quality parameter 'particulates', representing light availability and organic matter load, was negatively correlated with the abundance of symbiont-bearing species such as *B. sphaerulata* and *C. hispida*. These species have been described as photophilic species, often occurring at shallow depths (Hohenegger 1994; Hohenegger et al. 1999; Lobegeier 2002). In contrast, the relative abundance of the diatom-bearing species *Amphistegina radiata*, *Heterostegina depresssa,* and *C. mayori* were independent of light availability, confirming results by Nobes et al. (2008). All three species are usually found in deeper water or shaded microhabitats, e.g., under coral rubble (Haunold et al. 1997; Hohenegger et al. 1999; Cleary and Renema 2007).

Diatom-bearing species contributed mostly to the distinction between heterotrophic and symbiont-bearing foraminifera and the respective environmental conditions they indicated. Dinoflagellate-bearing species did not contribute much to assemblage differences, possibly because of their low relative abundance in our samples. The distinction between the two trophic groups is even clearer when the two red algae-bearing species *Peneroplis planatus* and *P. pertusus* were removed (results not shown). These species were abundant on reefs characterised by sediments with small grain sizes and high organic matter and low light availability, which were generally dominated by heterotrophic species in our analyses. Little is known about the ecology of the red algae-bearing species, but they seem to occur on a variety of substrate types and depths, preferring sheltered areas (Renema 2003) and sandy substrata (Renema and Troelstra 2001; Cleary and Renema 2007). Perhaps, similar to *Elphidium* spp. which retain chloroplasts from algal food (Renema and Troelstra 2001), these species are less dependent on autotrophic production than diatom or dinoflagellate-bearing species. Fine-tuning of the FORAM index will require further studies of foraminiferal ecology, especially with regard to host–symbiont relationships.

Coral cover was positively related to the FORAM index in the inshore reefs investigated. While this could be interpreted as additional support for the validity of the FORAM index as an indicator for reef health, further work over longer time scales is required to test whether the FORAM index would also track changes in coral cover over time.

Corals

Similar to foraminiferal assemblages, coral assemblage composition varied between regions. This difference was largely because of the absence or relative rarity of a number of genera in the southernmost Fitzroy Region. Lower richness observed in the Fitzroy Region is consistent with generally declining coral richness with increasing latitude in the GBR (DeVantier et al. 2006). However, the slight differences in hard-coral assemblages among the three northern regions may be influenced by factors other than latitude, for example, the recent disturbance history and susceptibility of several coral species to acute disturbances. Disturbance alone can strongly alter coral assemblage composition (e.g., Done et al. 2007; Connell et al. 2004), and we suggest that disturbance history influences assemblage composition at regional scales and for substantial periods of time.

The communities here were surveyed about 5–9 years after major disturbance events. For example, during the 1990s, several of the Wet Tropics reefs were affected by crown-of-thorns seastar (*Acanthaster planci*) predation (Fabricius et al. 2005). Branching *Porites* (mostly *P. cylindrica*) and *P. rus* were two of the five taxa explaining

most of the variation in the data among regions and had higher abundances in the Wet Tropics. *Acanthaster planci* avoid *P. cylindrica* as prey (Pratchett 2007) and have not been observed to prey on *P. rus* in many years of targeted surveys (A. Thomson, pers. obs.). Conversely, *Acropora* and *Pectinia*, which belong to families highly susceptible to *A. planci* predation (Keesing 1990), were more common on inshore Whitsundays reefs, which did not experience *A. planci* outbreaks.

In 1998 and 2002, mass coral bleaching affected many inshore reefs (Berkelmans et al. 2004). The 1998 bleaching event resulted in mortality of susceptible species at several reefs in the Burdekin and Wet Tropics regions but not so in the Whitsunday region (Marshall and Baird 2000; Sweatman et al. 2007). In these two regions, the genera *Galaxea*, *Diploastrea* and *Turbinaria*, which have low susceptibility to bleaching remain proportionally more common than in the Whitsunday Region where bleaching, though widespread in 2002 (Berkelmans et al. 2004), has caused minimal mortality (Sweatman et al. 2007).

Independent of these regional differences due to regions and acute disturbances, hard-coral assemblage composition varied in association with sediment grain size and nutrient content and levels of the combined water quality parameter 'particulates'. Coral genera associated with fine-grained sediments included *Fungia* and *Pachyseris*, taxa that are capable of rapidly removing silt from their tissue (Stafford-Smith and Ormond 1992). *Fungia crassa* was also one of three species not affected by sedimentation in an experimental setting (Philipp and Fabricius 2003). Coral genera associated with higher turbidity included *Oxypora*, *Mycedium*, and *Turbinaria*. It appears that these species are generally sciaphillic because they prefer turbid waters (Done 1982) or are found in relatively low light settings (Titlyanov and Latypov 1991).

Part of the ability to exist in low light is due to the trophic plasticity of some corals, whereby reductions in photosynthetic energy in low light are compensated for by feeding on suspended particles (Anthony 2000), which extends the environmental niche of some corals into turbid environments (Anthony 2000; Anthony and Fabricius 2000; Anthony and Connolly 2004). The genera *Goniastrea* and *Pocillopora* were independent of turbidity/light availability in the present analyses. Energy acquisition in *Goniastrea retiformis* is highly variable, the species is found across a range of light regimes and enhanced heterotrophy in turbid environments compensates for limitation of photosynthesis by reduced light (Anthony and Fabricius 2000). Similarly, *Pocillopora damicornis* adjusts its energy acquisition mode depending on particle concentrations in the water column (Anthony 2000). Taxa in the family Pocilloporidae are regarded as pioneers, often re-growing faster than other taxa after physical disturbance

(Fabricius et al. 2005). In contrast, the genus *Porites* and corymbose and branching growth forms of *Acropora* were more abundant in low turbidity, high-light environments in the present study. *Porites cylindrica* has low photo and heterotrophic plasticity and depends more on photosynthesis for energy gain (Anthony and Fabricius 2000). There are fewer *Acropora* spp. inshore, representing a subset of the species suite on GBR offshore reefs (DeVantier et al. 2006). Done (1982) even classified GBR inshore reefs as 'non-*Acropora*' reefs, but we showed that some inshore reefs with high light availability have coral assemblages with a high relative abundance of *Acropora* spp., mostly of branching and corymbose growth forms. It is unclear whether the different coral assemblages reflect different environmental conditions, such as sedimentation and turbidity, or different disturbance histories. We suggest the observed assemblage composition at a given reef is the result of both past disturbances and the local environmental setting. Because adult coral colonies are typically less sensitive to water quality than juveniles (Fabricius 2005), existing colonies may persist in an environment in which their juveniles are unlikely to survive, or in which successful reproduction (e.g., fertilisation) is hampered through environmental conditions (Humphrey et al. 2008). Our analyses did not detect a direct relationship between environmental quality and coral generic richness. This may be due to the variable taxonomic resolution of our study (a mixture of genus, species, and growth form) compared with other studies using coral species richness (e.g., DeVantier et al. 2006). To use coral richness as an indicator of environmental change in diverse systems such as the central Indo-Pacific will require sampling of larger areas at high taxonomic resolution (e.g., through direct visual assessments and collections) to capture rare species.

Comparison between foraminiferal and coral assemblages

A similar suite of environmental parameters influenced the composition of both foraminiferal and coral assemblages. These include the proportion of fine-grained sediments, the organic carbon and nitrogen content of the sediment, and the amount of particles in the water column and associated light availability. However, the foraminiferal assemblage composition did not simply predict or track the coral assemblage composition, although a significant correlation did exist between the two assemblages.

Coral assemblages are very dynamic and constantly change due to *acute* disturbances such as cyclones, outbreaks of *A. planci*, coral bleaching and disease. Coral assemblages are also shaped by the *chronic* settings of their environment, which for example, influence coral recruitment and impede coral growth. As a result of acute and

chronic causes, very different coral communities may occur at sites with similar environmental conditions. Thus, it is likely that a mosaic of coral assemblages with different acute disturbance histories obscures the perhaps more subtle effects of environmental quality that foraminifera detect.

Some of these acute disturbances, especially temperature and light conditions leading to bleaching, might also affect foraminiferal assemblages. However, it is unlikely that effects of cyclones, for instance, are as severe. In addition, smaller size and faster turnover will allow foraminiferal assemblages to recover and reach successional endpoints more rapidly. Although ecological studies on foraminiferal succession in the Pacific Region are lacking, ecological studies of symbiont-bearing foraminifera in the Florida reef tract have shown that populations recover from bleaching-related mortality events or hurricane scouring in a matter of months to at most a year or two (Williams et al. 1997; Hallock et al. 2006, Baker et al. 2009). This is in contrast with coral communities which may need decades to fully recover colony density and diversity (Done et al. 2007; Wakeford et al. 2008). Indeed, paleontological data suggest that foraminiferal assemblages are much more persistent over time than coral assemblages (Tager et al. in press). In contrast, chronic disturbances in the environment such as nutrification can distinctly change foraminiferal assemblages and subsequently the FORAM index (Hallock et al. 2003).

We propose that foraminiferal assemblage composition, specifically the FORAM index, provides an effective bioindicator for the assessment of turbidity/light regimes and organic enrichment of sediments on coral reefs. While coral assemblage composition varied in different sediment and water quality conditions, we cannot fully interpret these changes or develop simple coral-based bioindicators for these environmental conditions, until the ecology of a wide range of coral taxa is better understood. However, future research and monitoring of coral population dynamics, especially recruitment and rate of recovery after disturbances under different environmental regimes, continues to be important, because hard-coral cover and diversity are important conservation targets. The wider application of other bioindicators, such as foraminiferal assemblage composition, which may be more sensitive and react faster to changes in water and sediment quality, will support reaching these conservation targets.

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