

Changes in algal, coral and fish assemblages along water quality gradients on the inshore Great Barrier Reef

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Abstract

Macroalgae, hard corals, octocorals, and fish were surveyed on 10 to 13 inshore coral reefs of the Great Barrier Reef, along a water quality gradient in two regions with contrasting agricultural land use. A water quality index was calculated for each reef based on available data of particulate and dissolved nutrients, chlorophyll and suspended solids. Strong gradients in ecological attributes occurred along the water quality gradient. Macroalgae of the divisions Rhodophyta and Chlorophyta increased with increasing nutrients, while Phaeophyta remained similar. Octocoral richness and abundances of many hard coral and octocoral taxa decreased, and none of the hundreds of species increased. At reefs in higher nutrient environments, hard coral and octocoral assemblages were composed of subsets of the many species found in lower nutrient environments, whereas fish and macroalgal assemblages consisted of contrasting suites of species. The study identifies species groups that are likely to increase or decrease in abundance with changing water quality.

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Keywords: Nutrient enrichment; Sedimentation; Coral reef; Macroalgae; Hard coral; Octocoral; Fish; Biodiversity

1. Introduction

Evidence that nutrient enrichment, increased siltation and excess turbidity can lead to the local degradation of coral reefs is unequivocal (Smith, 1981; Hunter and Evans, 1995; Grigg, 1995; Stimson and Larned, 2000; Stimson et al., 2001; Loya et al., 2004; review in Fabricius, in press). Field studies suggest that areas downstream of well-defined point sources are characterized by (a) low or locally reduced coral biodiversity, (b) low (or failed) coral recruitment, (c) high rates of partial mortality, (d) reduced skeletal density, (e) reduced depth

distribution, (f) high rates of bioerosion, and (g) a transition of hard coral dominated communities to communities dominated by non-reef building organisms, especially turfing and fleshy macroalgae (Montaggioni et al., 1993; West and Van Woesik, 2001, review by Schaffelke et al., in press), and filter feeders (Smith, 1981; Birkeland, 1988).

While pollution effects on coral reefs at local scales are well understood, links at regional scales between increasing sediment and nutrient loads in rivers, and the degradation of coral reefs, have been more difficult to demonstrate (Fabricius and De'ath, 2004). This is due to a lack of historic data and the confounding effects of other disturbances such as bleaching, cyclones, fishing pressure and outbreaks of the coral eating crown-of-thorns starfish (*Acanthaster planci*), and is further complicated by the naturally high variability in monsoonal

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river flood events. Organism responses are poorly understood, as each of the numerous inshore species has its own tolerance limit at every life stage, and interactions between the organisms add to the complexity. Though considerable knowledge has been gained from single-species exposure experiments in the laboratory, it is difficult to extrapolate from such laboratory studies to field settings and ecosystem responses. Taxonomically detailed field survey data of major assemblages along environmental gradients should therefore provide valuable information about ecosystem responses to changing water quality.

In the Great Barrier Reef (GBR), two coastal regions, including about 200 coral reefs, have been classified at high risk of exposure to terrestrial runoff (Devlin et al., 2003). Exposure risk was estimated based on distance and direction of the reef from each river (quantifying the probability that a plume reaches the reef), and data on river pollution. The two areas classified as high risk (Fig. 1) were: the inner southern reefs of the Whitsunday Islands group (central GBR, 20° 0'–20° 30' S), and the Wet Tropics in the northern section of the GBR (Northern GBR, 15° 40'–17° 50' S).

In the Whitsunday Islands, ecological changes have been documented on seven reefs along a gradient of increasing concentrations of water and sediment parameters (especially suspended particulate matter, turbidity, silicate, and total organic matter in sediments) towards reefs located near the Proserpine and O'Connell Rivers

(van Woesik et al., 1999). Towards the river mouth, macroalgal cover increased from 0% to 74%, octocoral cover decreased from 19% to 1%, hard coral richness decreased from 15 to 5 species per transect, and the maximum depth of reef development was reduced from 12 to 4 m. Furthermore, hard coral communities changed from those dominated by *Acropora* and massive *Porites* 80 km away from the river, to reefs dominated by Favidae, encrusting *Montipora*, encrusting *Porites* and *Turbinaria* spp. at the reefs more exposed to terrigenous influences. A mismatch between Holocene reef accretion rates and present-day reef growth at the reefs most exposed to terrigenous influences was used as evidence of recent change in response to anthropogenic activities in the river catchments.

Inshore reefs of the Wet Tropics (16–18° S), the largest region considered at risk at exposure to terrestrial runoff, have declined in coral cover since the early 1990s, apparently due to failure to recover from a series of disturbances (Ayling and Ayling, 2002; unpublished AIMS Long-Term Monitoring data). Comparatively few ecological and water quality data are available from the Far Northern GBR, the only inshore region where risk of exposure to terrestrial runoff is considered minimal (Fig. 1). However, water column chlorophyll *a* concentrations, monitored in the GBR since 1992 as proxy measure for nutrient concentrations, show that chlorophyll levels are twice as high on the inner 20 km along the Wet Tropics Coast that receives river floods from

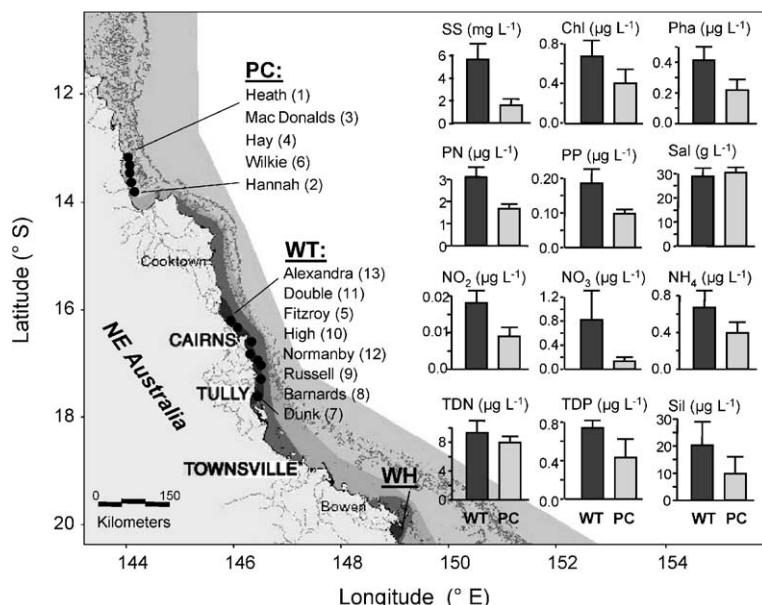


Fig. 1. Map of the Great Barrier Reef, indicating study regions (PC = Princess Charlotte Bay, WT = Wet Tropics, WH = Whitsunday Islands), study reefs (black dots) and relative risk of exposure to river flood plumes (Devlin et al., 2003): shading indicates (from darkest to lightest): 'high risk', 'moderate risk', 'low risk', and 'minimal concern' of reef being affected by terrestrial runoff. 'Risk' level is estimated using functions of distance and angle (as measure of probability that a plume reaches the reef) of each river in relation to the target reef, and the level of pollution of each river. Numbers in brackets indicated the rank order of each reef based on its water quality index (WQI; values increasing from the cleanest to least clean water; Fig. 2). The bar graphs indicate mean regional concentrations ± 1 SE of water quality variables around the study reefs (abbreviations are listed in Section 2), recorded during up to nine visits between 2000 and 2002.

agriculturally used catchments, as in the Far Northern region (14° S) where land use is minimal (Brodie et al., 1997; Devlin et al., 2003). Across the continental shelf, chlorophyll increases steeply towards the coast in the Wet Tropics but not in the Far North (Fabricius and De'ath, 2004), indicating that nutrient availability is higher in the former region.

In this study we present field survey data on the biodiversity of algae, hard corals, octocorals and fish on naturally turbid inshore coral reefs that vary in their level of exposure to water-borne sediment, nutrient and chlorophyll concentrations, and in the degree of agricultural modification in the adjacent catchments from where flood plumes originate. We investigate the relationships between water quality and a number of ecological attributes, and discuss the evidence for water quality effects on coral reef communities on these inshore reefs.

2. Methods

2.1. Study sites

The study focussed on five to eight (dependent on the organism) inshore reefs in the Wet Tropics (WT) between Tully and Port Douglas, and five reefs in the Claremont Isles, north of the Princess Charlotte Bay region (PC; Fig. 1). Surveys were conducted on both the windward and leeward sides of the reefs at several depth zones. The eight reefs surveyed in the Wet Tropics were (from south to north) Dunk, Barnards, Russell, Normanby, High, Fitzroy, Double and Alexandra, and the five reefs north of Princess Charlotte Bay were Hannah, Wilkie, Hay, McDonalds and Heath (Fig. 1). All five PC reefs were surveyed for all four groups, whereas of the eight WT reefs, Alexandra Reef was only surveyed for octocorals, Dunk and Double Island were not surveyed for fish and the Barnard Islands were not surveyed for hard corals.

All study reefs are located <20 km from north to south oriented coastlines at <20 m bathymetry. Reefs in WT have been identified as having the highest risk of exposure to agricultural runoff (Devlin et al., 2003), since they experience river plumes every few years from wet tropical catchments with intensive agriculture (Johnstone, Russell-Mulgrave, Tully River), and plumes from the large, dry tropical Burdekin River on a decadal basis. Reefs in PC are exposed to runoff from the dry tropical Normanby and Stewart Rivers, whose catchments are only slightly modified, being dominated by low density cattle grazing, and having received little or no fertilizers and pesticides. Data on the disturbance history from both regions are sparse. In the last two decades some of the WT reefs experienced an outbreak of *Acanthaster planci* (early 1990s), two tropical cyclones (1986 and 1990), and bleaching-related coral mortality

(1998), whereas the reefs in PC have probably not experienced *A. planci* outbreaks, but have been impacted by four tropical cyclones in the last two decades, and bleaching mortality in 2002 (after the surveys reported here were completed).

2.2. Field data

2.2.1. Water quality data

Concentrations of 12 water quality variables (particulate nitrogen and phosphorus (PN, PP), nitrate, nitrite, ammonium, total dissolved nitrogen and phosphorus (TDN, TDP), silicate (Sil), chlorophyll (Chl), phaeopigments (Phae), salinity (Sal) and suspended solids (SS)) were determined by taking surface water samples at each reef during each of nine ship trips to both regions between December 2000 and April 2002. For logistic reasons, our water sampling was limited to nine visits (Alexandra Reef only 5 times), but the regional differences we found were consistent with data from a monthly water column chlorophyll *a* monitoring program that commenced in 1992 (Brodie et al., 1997), which shows that inshore chlorophyll concentrations are twice as high in the central section of the GBR including WT, compared to the remote Far Northern section including PC (Fabricius and De'ath, 2004). Furthermore, in the central GBR but not in the Far North, chlorophyll concentrations increase steeply towards the coast, indicating that more nutrients are available inshore in the former area (Brodie et al., unpublished data).

For dissolved nitrogen, phosphorus and silicate, six 10 ml subsamples were filtered through sterile polycarbonate filters with $0.2 \mu\text{m}$ pore size, and the particle-free water frozen at -18°C for later analysis. For particulate nutrients, chlorophyll and phaeopigments, duplicate subsamples (250 ml, and 100 ml respectively) were filtered onto pre-combusted 25 mm Whatman GF/F filters ($0.2 \mu\text{m}$ nominal pore size) at low vacuum (8 kPa). Filters were then wrapped into pre-combusted aluminium foil, and frozen until further analysis. Dry weight of suspended solids was determined from duplicate 1000 ml water samples filtered through pre-weighed 45 mm polycarbonate filters with $0.4 \mu\text{m}$ pore size. Surface salinity was determined from a 500 ml water sample stored in airtight bottles at room temperature. In the laboratory, the samples were analysed following standard procedures (Furnas and Mitchell, 1996).

2.2.2. Abundances and biodiversity

Four groups of taxa were surveyed using rapid ecological assessments based on standardized scuba-swims by experts: macroalgae, here defined as fleshy macroalgae, excluding crustose coralline and fine filamentous forms (McCook et al., 2000), hard corals (Devantier et al., 1998), octocorals (Fabricius and De'ath, 2001),

and fish (Williams, 1982). Abundances of the three benthic groups were rated on a 6-point scale as 0 = ‘absent’, 1 = ‘rare’, 2 = ‘uncommon’, 3 = ‘common’, 4 = ‘abundant’, and 5 = ‘dominant’. Abundances of some of the fish species were estimated on a log (base 5) scale (Williams, 1982), whereas less abundant fish species such as *Lethrinus* spp., *Lutjanus* spp., *Plectropomus* spp., *Chætodon* spp., and some pomacanthids, plectorhynchids and *Choerodon* spp., were fully enumerated.

Macroalgae surveys were conducted at three depths (slope: 18–3 m, crest: 3–1 m, and the reef flat) in early summer, late summer, and winter, in total covering 12 reefs with 218 surveys. Macroalgae were identified to genus level, except for *Rhipilia* and *Avrainvillea*, and *Galaxaura* and *Tricleocarpa*, which were aggregated. Relative abundances of Rhodophyta (red algae), Chlorophyta (green algae) and Phaeophyta (brown algae, now also called Heterokontophyta) were estimated as the sum of ratings of individual genera within these three major groups of fleshy macroalgae. Hard corals (Scleractinia) were identified to species level, and were surveyed at 2 depths (deep: 18–8 m, and shallow: 6–1 m) on 10 reefs, in a total of 48 surveys. Octocorals (Octocorallia: zooxanthellate and azooxanthellate alcyonarian soft corals and sea fans) were identified to genus level and were surveyed at 5 depths (18–13 m, 13–8 m, 8–3 m, 3–1 m, and reef flat) on 13 reefs, in a total of 147 surveys (each survey covering about 200–300 m²). Cover of the main benthos groups (hard and octocorals, turf and coralline algae, macroalgae, sand and rubble, sponges etc) were also estimated during the octocoral surveys for each depth zone. Fish were surveyed between 12 m and the reef crest on 10 reefs, in a total of 34 surveys. Fish species were identified to species or species groups.

2.3. Statistical analyses

To facilitate comparison between taxonomic groups, all analyses were carried out on reef-level data (means over all survey periods, locations and depths per reef). Principal components analysis of log-transformed water quality concentrations (averaged over all visits) was used to characterize the study reefs and the relationships between the water quality variables. Concentrations of all variables except salinity were highly and positively correlated. Therefore, a water quality index (WQI) was calculated, as follows: (1) all water quality variables (except salinity) were standardized to mean zero and standard deviation one (*z*-scores), and (2) the standardized values were summed over the 12 variables for each reef. Thus, a reef with a high WQI will typically have high concentrations of most of the variables that form the index, and a reef with low values has lower concentrations. Water with a high WQI value would typically appear murkier while one with a low WQI is clearer.

Species abundances were fourth-root transformed (except hard corals) and reef-averaged over depths and sites. Redundancy analyses (RDA, Rao, 1964; Jongman et al., 1995) were used to relate differences in the assemblages to regional and water quality effects. Permutation tests (ter Braak, 1992) were used to assess the statistical significance of the relationships.

Log-linear regression models were used to determine the regional and gradient effects on benthic cover, abundances and richness. Analyses followed the methods of Fabricius and De’ath (2004). These models were chosen because variation increased with the mean, and the implicit log transformation helped linearise the gradient effects. The models included regional effects to account for differences that may be unrelated to the water quality gradients. For each response, five models were fitted: (i) different slopes (gradient effects) within each region and different intercepts (region effects), (ii) same slope for both regions, but different intercepts (iii) single gradient common to both regions, (iv) no gradient effect but regional effects, and (v) no gradient or regional effects. The number of reefs investigated was small (10–13), and preliminary analyses indicated relatively weak associations between the responses and explanatory variables. Model averaging (Raftery, 1995; Raftery, 1988) of models based on the Bayesian Information Criterion (BIC) (Schwarz, 1978) was used for all analyses of abundances and richness (Fabricius and De’ath, 2004).

Based on BIC, we calculated the probability of each model (i) to (v), and the probability of a regional effect, defined as $P(\text{iv})/(P(\text{iv}) + P(\text{v}))$, for all taxa seen on at least 25% of reefs. Probabilities were classified as strong to moderate ($P > 0.8$) or weak ($0.8 > P > 0.5$). Where differences existed, the direction of this difference was determined (WT > PC, or WT < PC), to calculate the percentage of taxa that had higher or lower abundances in WT. Finally, taxa that increased or decreased in abundance along the water quality gradient were identified. Only taxa that were encountered on at least 50% of the reefs were included in this assessment. For each of these taxa, the probability of the presence of a gradient effect was calculated as the sum of the probabilities of the models (i), (ii) and (iii). Probabilities were again classified as strong to moderate or weak for positive and negative relationships with water quality. All data analyses used S-Plus Statistical Sciences (Statistical Sciences, 1999).

3. Results

3.1. Water quality

Concentrations of many of the water quality variables differed between the Wet Tropics (WT) and Princess Charlotte Bay (PC) regions (Fig. 1). Mean suspended

solids, chlorophyll, particulate nitrogen, particulate phosphorus and nitrate were higher in WT than in PC during the visits. Nitrate was particularly high in the WT, and negatively related to salinity. Water around most of the WT reefs had higher nutrient, sediment and chlorophyll concentrations than around PC reefs. While mean concentrations around the PC reefs were fairly homogeneous, water quality around the WT reefs varied more widely. Overall, the water quality index (WQI) was strongly associated with reefs of the WT, however Fitzroy Island and the Barnard Reefs in WT had a WQI that was similar to that of Wilkie Reef in PC (Fig. 2). Some WT reefs (Alexandra Reef and Double Island) were strongly associated with particulate matter (suspended solids, particulate nitrogen and phosphorus, chlorophyll and phaeopigments). Two other WT reefs (Normanby and High Islands) were strongly associated with high concentrations of dissolved nutri-

ents (nitrate, total dissolved nitrogen and phosphorus, and silicate) and reduced salinity.

3.2. Assemblages

3.2.1. Regional differences

Regional differences in cover, abundances and richness of some of the assemblages were pronounced (Table 1, Figs. 3 and 4). WT reefs were predominantly covered in algae and had low hard coral and octocoral cover. In WT, total algal cover was almost twice as high as PC, mostly due to differences in turfing algae, whereas cover of macroalgae and coralline algae were similar. Hard coral cover was less than a third, and octocoral cover was about half as high as in PC, whereas the cover of dead standing corals was 4.5 times higher in WT than in PC. Abundances of fish in WT were about a third of those in PC.

The taxonomic richness of some of the inshore reefs was high (Table 1). A total of 88 genera of fleshy macroalgae, 318 species of hard corals, 56 genera of octocorals, and 148 species of fish were distinguished in the surveys. Hard coral richness was twice as high in PC compared with WT reefs (Fig. 4): 44 species per site in WT (68–152 species per reef), compared with 89 species per site in PC (157–215 species per reef). Octocoral richness was also 30% lower in WT than PC (10 vs. 15 genera per site, 25 vs. 35 genera per reef). Richness of hard corals was highest on Hannah Reef, where the surveys yielded a total of 215 species, whereas the highest octocoral richness was found at Hay Reef (42 genera per reef). In contrast, the mean richness of macroalgal genera was 30% higher in WT than PC, whereas the richness of fish species was similar in both regions (Table 1).

A comparison of the types of taxa that contrasted in abundances provided insight into the nature of the regional differences. Among the macroalgae, abundances of Rhodophyta and Chlorophyta were 50% and 70% higher, respectively, in WT than PC (Table 1, Fig. 5). In contrast, abundances and richness of Phaeophyta were similar in both regions. Overall, nine genera had a moderate to high probability for occurring at higher abundances in WT compared with PC, of which six belonged to the division Rhodophyta, three were Chlorophyta, while none of the Phaeophyta was represented (Table 2). Only three taxa occurred at reduced abundances in WT compared to PC (one of each of the three main divisions; Table 2).

For the hard corals, ninety species representing most of the major families and genera were more abundant in PC than in WT (Table 2, Fig. 6). The families Fungiidae, Faviidae and Pectiniidae, and the common genera *Acropora*, *Montipora*, *Alveopora* and *Goniopora* were all more abundant in PC than WT, whereas abundances of the genera *Porites*, *Turbinaria* and *Galaxea* showed no difference. In contrast to the 90 species that were

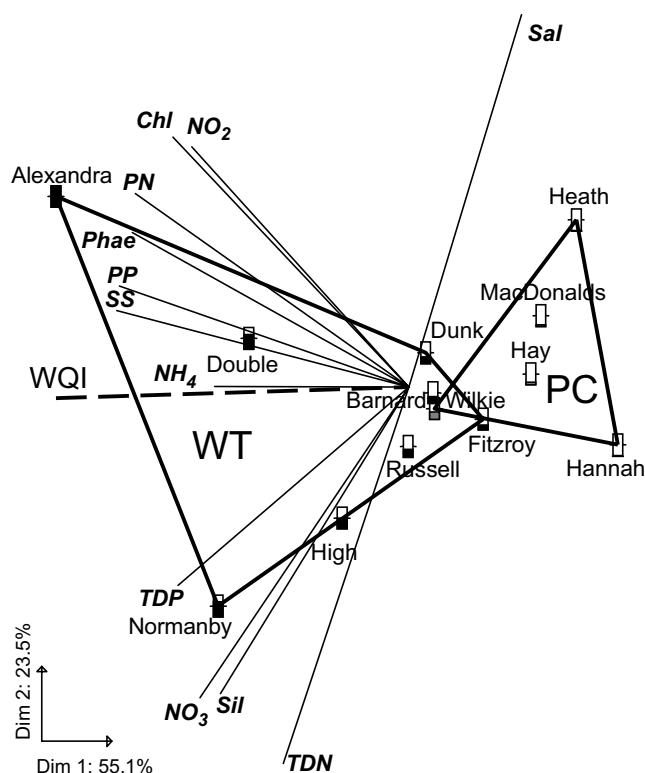


Fig. 2. Water quality around inshore reefs in PC and WT, displayed by a principal components analysis biplot. The water quality vectors point towards the location with highest concentrations (abbreviations are listed in Section 2). The vector of the water quality index (WQI, dashed line) is strongly associated with reefs of the WT. The WT and PC reefs are represented by black and grey thermometer symbols, respectively, with the fill of each symbol representing the water quality index of each reef. Concentrations of all particulate matter (suspended solids, particulate phosphorus and nitrogen, chlorophyll and phaeopigments) were highest at Alexandra Reef and lowest at Hannah Reef, whereas concentrations of silicate and lowest salinity were highest at Normanby Reef and High Island.

Table 1

Regional comparison of ecological reef attributes around inshore reefs of the Wet Tropics (WT) and Princess Charlotte Bay (PC) (Fig. 3)

Attribute	PC ± SE	WT ± SE	Ratio WT/PC
WQI	−6.94 ± 0.8	4.3 ± 2.7	−0.63
Turf algae % cover	23.6 ± 1.9	50.7 ± 8.1	2.15
Coralline algae % cover	3.2 ± 0.2	3.7 ± 1.3	1.15
Macroalgae % cover	12.7 ± 1.7	13.3 ± 5.4	1.05
Rhodophyta ($\Sigma_{\text{rel.abund.}}$)	10.0 ± 0.6	14.6 ± 1.4	1.46
Chlorophyta ($\Sigma_{\text{rel.abund.}}$)	4.0 ± 0.1	6.7 ± 0.8	1.70
Phaeophyta ($\Sigma_{\text{rel.abund.}}$)	7.9 ± 0.3	7.7 ± 2.0	0.97
Hard coral % cover	28.7 ± 0.6	8.2 ± 2.9	0.28
Octocoral % cover	7.9 ± 0.6	4.04 ± 0.7	0.51
Rubble % cover	15.1 ± 2.3	22.5 ± 4.9	1.49
Sand % cover	23.5 ± 1.8	19.1 ± 4.6	0.81
Fish abundance reef ^{−1}	38710 ± 4310	13330 ± 5660	0.34
Macroalgae richness	9.0 ± 0.2	12.04 ± 1.4	1.33
Rhodophyta	3.8 ± 0.2	5.79 ± 0.6	1.51
Chlorophyta	2.1 ± 0.1	3.21 ± 0.3	1.50
Phaeophyta	2.7 ± 0.1	2.75 ± 0.6	1.01
Hard coral richness	89.3 ± 2.6	43.60 ± 5.0	0.49
Octocoral richness	15.2 ± 0.6	9.96 ± 0.9	0.65
Zooxanthellate	8.2 ± 0.3	6.47 ± 0.8	0.79
Azooxanthellate	7.0 ± 0.6	3.49 ± 0.5	0.50
Fish richness	51.6 ± 2.2	48.54 ± 6.7	0.94

The table lists means and standard errors for each region, together with the ratio for WT/PC. Relative abundances of macroalgae are estimated as the mean sum of the relative abundance of each genus encountered per site, fish abundance is the mean sum of all fish encountered per site. Richness represents the mean number of taxa per site (genera for macroalgae and octocorals, species for hard corals and fish).

more abundant in PC, only six species (the common *Pocillopora verrucosa* and *Porites rus*, and four uncommon to rare species) were more abundant in WT than PC.

For the octocorals, 11 genera belonging to the major families Nephtheidae and Xeniidae, and four gorgonian genera were significantly more abundant in PC than in WT, whereas the two low encrusting or stolon-forming genera *Clavularia* and *Briareum* had higher representation in WT but were missing or rare in PC (Table 2).

Finally, 25 species of fish were likely to occur at higher abundance in PC than in WT. These included ten species susceptible to fishing pressure, three coral-dependent species (*Chaetodon aureofasciatus*, *C. lineolatus*, *C. plebeius*), and two grazing herbivores. In contrast, 13 fish species had a high to moderate probability of occurring at higher abundance in WT than in PC. These included no coral-dependent species, only one species susceptible to fishing pressure and six grazing herbivores (Table 2).

The percentages of algal, coral and fish taxa that significantly differed in abundances between regions are summarized in Fig. 6. Among the macroalgae that strongly differed in abundance between the regions,

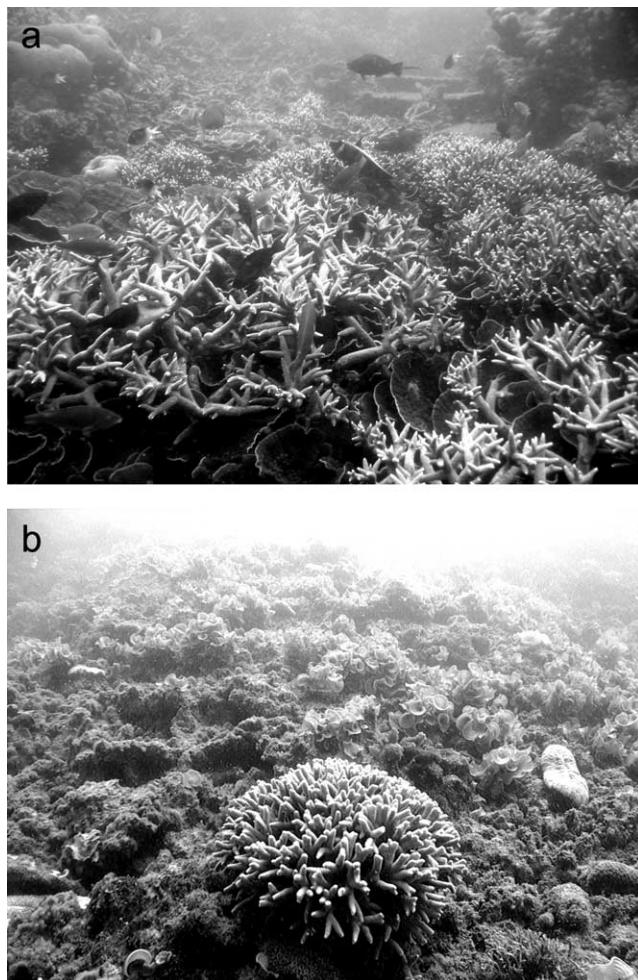


Fig. 3. Examples of aspect of inshore reef assemblages in Princess Charlotte Bay (a) and the Wet Tropics (b).

75% occurred predominantly in WT, whereas most of the hard coral and octocoral species were predominantly found in PC. In fish, the percentage of taxa that occurred predominantly in PC was 63%, while 37% appeared predominantly in WT.

In summary, the two regions differed in abundances and species composition of all four assemblages. Macroalgae and fish assemblages were composed of different suites of species in the two regions. In the hard corals and octocorals, most species were associated with PC reefs, and only a few species were well-represented at WT reefs; WT hard coral and octocoral assemblages were therefore composed not of a different suite of species, but of a subset of those species encountered in PC, and species that did grow in WT occurred in reduced numbers.

3.2.2. Gradients within regions

To investigate more specifically the role of water quality in shaping the reef communities, we related

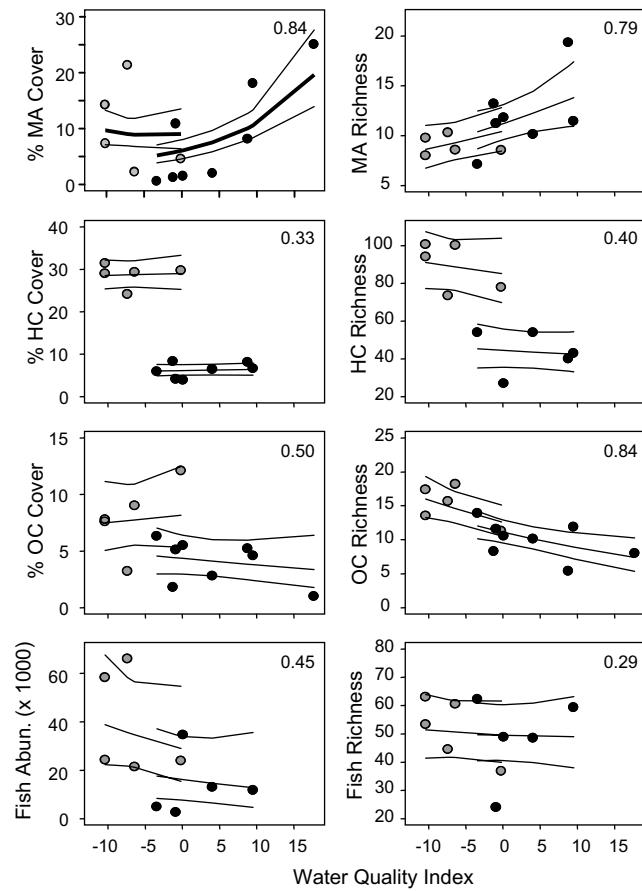


Fig. 4. Cover, relative abundances and richness of fleshy macroalgae (MA), hard corals (HC), octocorals (OC) and fish from reefs in the two study regions, plotted against water quality (WQI). Black and grey points indicate WT and PC reefs, respectively. High WQI values represent high nutrient concentrations and low values represent relatively clean water. Solid lines are linear regression fits. The value in each panel indicates the probability for a gradient effect.

cover or abundances and richness of the four groups to the water quality index (WQI) scores of individual reefs. For macroalgae, total cover was highly variable, but cover tended to increase from a mean of 5% to 18% within WT with increasing WQI—i.e., increasing concentrations of particulate and dissolved nutrients, suspended solids and chlorophyll (Fig. 4). Macroalgal richness increased from 8 to 13 genera per site. Both abundances and the generic richness of Rhodophyta, and abundances of Chlorophyta strongly increased with increasing WQI (Fig. 5). Abundances and richness of Phaeophyta, and richness of Chlorophyta, were unrelated to WQI. Hard coral cover and richness and octocoral cover, all of which varied strongly between the regions, were unrelated to WQI (Fig. 4). In contrast, four hard coral families (Agariciidae, Mussidae, Pocilloporidae and Faviidae) were strongly negatively related to water quality (Fig. 6). Similarly, octocoral richness was strongly negatively related to WQI. Within WT,

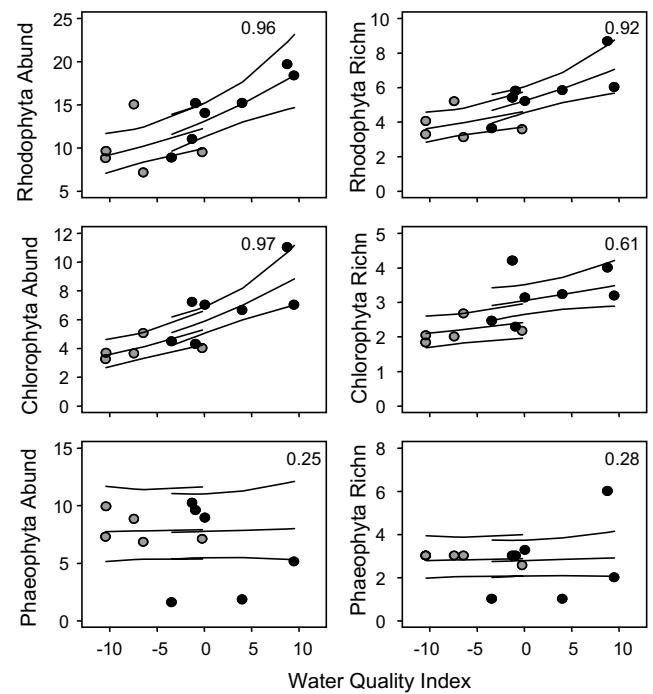


Fig. 5. Cover, relative abundances and richness of the three main divisions of macroalgae, namely Phaeophyta, Chlorophyta, and Rhodophyta, from reefs in two regions, plotted against water quality (WQI). Black and grey points indicate WT and PC reefs, respectively. High WQI values represent high nutrient concentrations and low values represent relatively clean water. Solid lines are linear regression fits. The value in each panel indicates the probability for a gradient effect.

octocoral richness decreased by almost 50% from 12 genera per site (36 genera per reef) on the reef with the lowest WQI (best water quality) to 7 genera per site (19 genera per reef) on the reefs with highest WQI, whereas 13–16 genera per site (28–42 genera per reef) were recorded in PC. For fish, richness was similar but total relative abundances differed between regions (higher in PC than WT); however there was almost equally strong evidence that total abundances declined along the water quality gradient towards reefs with higher nutrient and sediment loads.

The percentages of algal, coral and fish taxa with positive or negative relationships to WQI are summarized in Table 2 and Fig. 7(b). The probabilities for gradients in abundances were weaker than probabilities for regional differences, due to the limited water quality data and small number of reefs. Nevertheless, in the macroalgae, 83% of the genera included in the analyses tended to increase in abundance with increasing WQI, compared with 17% that tended to decrease. Two to three of the macroalga species were strongly and positively related to WQI: these were the Rhodophyte *Laurencia*, the chlorophyte *Neomeris*, and to a slightly lesser extent *Asparagopsis*; all three taxa increased 5- to 6-fold along the water quality gradient. In contrast, none of the hard

Table 2
List of species that differ in abundance between regions (a), and change in abundances along the water quality gradient (b)

Algal genera	Hard coral species	Octocoral genera	Fished fish species	Herbivorous fish species	Other fish species
(a) Regional differences: PC > WT					
<i>Tolytiocladia</i> (R)*	<i>Acropora nobilis</i> *	<i>Klyxum</i>	<i>Plectropomus leopardus</i>	<i>Naso annulatus</i>	<i>Acanthurus blochi</i>
<i>Boodlea</i> (C)	<i>Montipora hoffmeisteri</i> *	<i>Nephthea</i> *	<i>Cromileptes altivelis</i> *	<i>Zebrasoma veliferum</i> *	<i>Caesio cuning</i> *
<i>Hydroclathrus</i> (P)	<i>Palauastrea ramosa</i> *	<i>Stereonephthya</i> *	<i>Lethrinus laticaudus</i> *		<i>Pterocaesio marri</i>
	<i>Galaxea astreata</i> *	<i>Scleronephthya</i>	<i>Lethrinus nebulosus</i> *		<i>Scarus altipinnis</i>
	<i>Merulina scabrida</i> *	<i>Lemnalia</i>	<i>Lutjanus carponotatus</i> *		<i>Hippocampus longiceps</i>
	<i>Pectinia alcicornis</i> *	<i>Xenia</i>	<i>Choerodon schoenlini</i> *		<i>Chaetodon aureofasciatus</i>
	<i>Hydnophora rigida</i> *	<i>Cespitularia</i> *	<i>Chelinus fasciatus</i> *		<i>Chaetodon lineolatus</i> *
	<i>Echinopora horrida</i> *	<i>Annella</i> *	<i>Cheilinus undulatus</i> *		<i>Chaetodon plebeius</i> *
	<i>Echinopora pacificus</i> *	<i>Iciligorgia</i>	<i>Plectorhyncus chrysotaenia</i> *		<i>Acanthochromis polyacanthus</i> *
	<i>Lobophyllia dentatus</i> *	<i>Alertigorgia</i> *	<i>Plectorhyncus lineatus</i> *		<i>Abudefduf sexfasciatus</i> *
	<i>Oulophyllia bennettae</i> *	<i>Menella</i> *			<i>Pomacentrus nagasakiensis</i>
	etc (total of 90 spp)				<i>Pomacanthus sexstriatus</i>
WT > PC					
<i>Asparagopsis</i> (R)*	<i>Porites rus</i>	<i>Clavularia</i>	<i>Choerodon graphicus</i> *	<i>Acanthurus triostegus</i> *	<i>Gomphosus varius</i>
<i>Galaxaura-Trichleocarpa</i> (R)*	<i>Montipora turtlensis</i> *	<i>Briareum</i>		<i>Naso tuberosus</i> *	<i>Thalassoma jansenii</i> *
<i>Actinotrichia</i> (R)*	<i>Pocillopora verrucosa</i>			<i>Naso unicornus</i>	<i>Chaetodon citrinellus</i> *
<i>Portieria</i> (R)	<i>Pocillopora eydouxi</i> *			<i>Scarus rubroviolaceus</i> *	<i>Chaetodon lunula</i>
<i>Titanophora</i> (R)	<i>Echinopora gemmacea</i> *			<i>Siganus corallinus</i>	<i>Abudefduf vaigiensis</i> *
<i>Liagora Yamadaella</i> (R)*	<i>Sympyllia radians</i> *			<i>Kyphosus</i> sp.*	<i>Stegastes apicalis</i> *
<i>Dictyosphaeria</i> (C)*				<i>Acanthurus triostegus</i> *	
<i>Neomeris</i> (C)					
<i>Chlorodesmis</i> (C)*					
(b) Gradients: decrease with WQI					
<i>Jania</i> (R)	<i>Acropora selago</i>	<i>Klyxum</i> *	<i>Lethrinus lentjan</i> *		<i>Scarus schlegeli</i>
	<i>Astreopora gracilis</i> *	<i>Scleronephthya</i>	<i>Lutjanus carponotatus</i>		<i>Chaetodon rafflesii</i>
	<i>Astreopora myriophthalma</i>	<i>Astrogorgia</i>	<i>Lutjanus lemniscatus</i> *		<i>Pomacentrus nagasakiensis</i> *
	<i>Pectinia alcicornis</i> *	<i>Menella</i>	<i>Lutjanus sebae</i>		
	<i>Pavona explanulata</i>				
	<i>Ctenactis echinata</i>				
	<i>Goniastrea australensis</i> *				
	<i>Goniastrea pectinata</i>				
	<i>Favia matthai</i>				
	<i>Favites halicora</i>				
	<i>Favites russelli</i> *				
	<i>Montastrea magnistellata</i>				
	<i>Diploastrea heliopora</i>				
	<i>Herpolitha weberi</i>				
	<i>Turbinaria peltata</i> *				
Increase with WQI					
<i>Laurencia</i> (R)*		<i>Briareum</i>		<i>Stegastes apicalis</i> *	<i>Scarus ghobban</i> *
<i>Asparagopsis</i> (R)					<i>Chromis atripectoralis</i>
<i>Neomeris</i> (C)*					<i>Neopomacentrus azyron</i> *
<i>Halimeda</i> (C)					

Species with high probabilities (>0.95) are marked by an asterisk, all others are $P > 0.8$. In the algae, letters behind the genus name indicate the division they belong to (R = Rhodophyta, C = Chlorophyta, P = Phaeophyta).

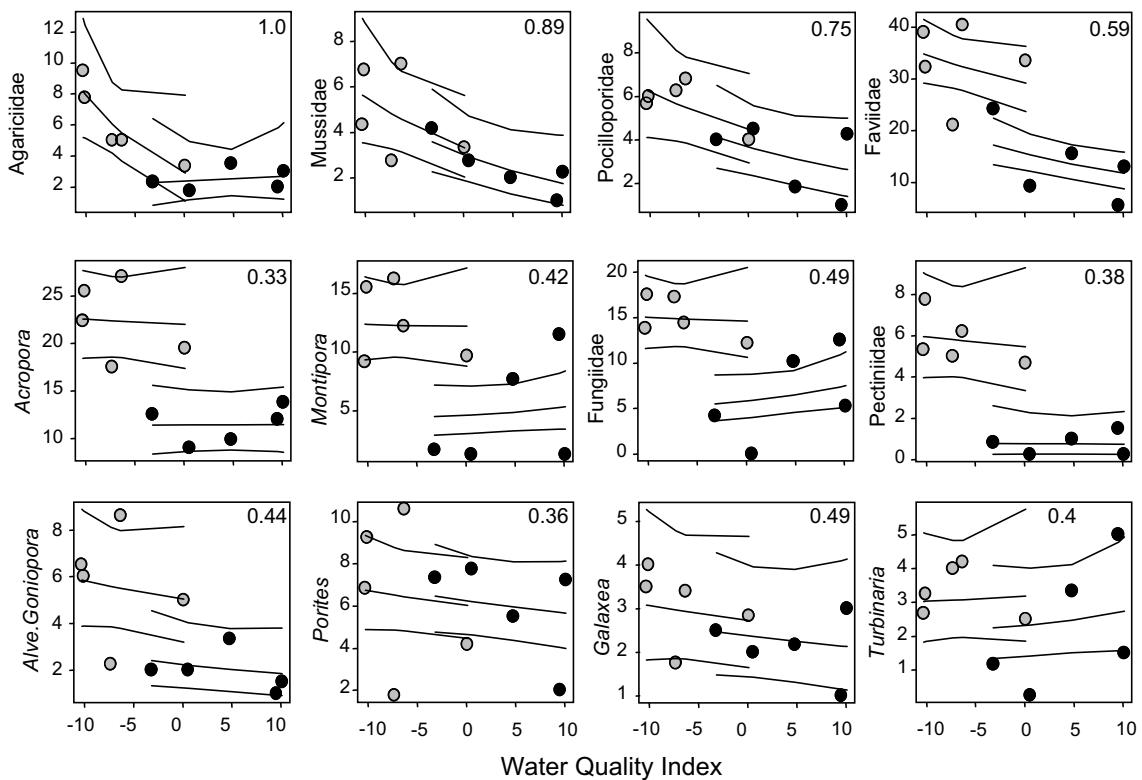


Fig. 6. Changes in relative abundances between regions and along the WQI of the 12 main families and genera of hard corals. High WQI values represent high nutrient concentrations and low values represent relatively clean water. Black and grey points indicate WT and PC reefs, respectively. Solid lines are linear regression fits. The value in each panel indicates the probability for a gradient effect.

corals and octocorals had a high probability of increasing with increasing WQI. Instead, 13% of hard corals and 25% of octocorals showed a strong to moderate negative relationship with WQI, i.e., their abundances decreased with increasing nutrients, and overall the percentage of hard and octocoral taxa that tended to decrease with WQI was 60% and 85%, respectively. For the fish, three of the species included in the analyses increased and three decreased with WQI. Permutation tests on the abundances of all taxa in each of the four assemblages indicated that the assemblage structure of octocorals were strongly related to water quality and more weakly related to regions (Table 3). In contrast, for the assemblages of macroalgae, hard corals and fish, regional differences were stronger than the water quality effects.

In summary, while the water quality gradient was short and based on only limited water quality data and few reefs, the aggregated data showed clear increases in Rhodophyta and Chlorophyta along the water quality gradient, a clear decline in octocoral richness, and in the hard coral families Agariciidae, Mussidae, Pocilloporidae and Faviidae. In octocorals, gradient effects were stronger than regional differences, whereas for the other three assemblages, regional differences dominated the patterns in the assemblages.

4. Discussion

4.1. The inshore Great Barrier Reef: water quality and geography

Turbid inshore coral reefs of the Great Barrier Reef (GBR) can support highly diverse assemblages of hard corals, octocorals, algae and fish, and high coral cover. On the 10 inshore reefs surveyed, a total of 318 species of hard corals were recorded, representing 80% of the 400 hard coral species known to occur on the GBR (Veron, 2000). Similarly, 13 inshore surveys yielded 80% of the 70 documented GBR octocoral genera (Fabricius and Alderslade, 2001), and 85% of the 103 fleshy macroalgae from the GBR (McCook et al., 2000). Likewise, 70% of all GBR hard coral species have previously been recorded on inshore reefs of the Whitsunday Islands (Devantier et al., 1998). Our study therefore added evidence to the suggestion that turbid shallow inshore reefs can represent highly diverse coral reef habitats. The inshore reefs of Princess Charlotte Bay that have remained relatively undisturbed by terrestrial runoff and other anthropogenic influences were particularly rich, both in ecological and aesthetic terms. Other inshore reefs closer to human influences appear depauperate in comparison, but it has been unclear whether

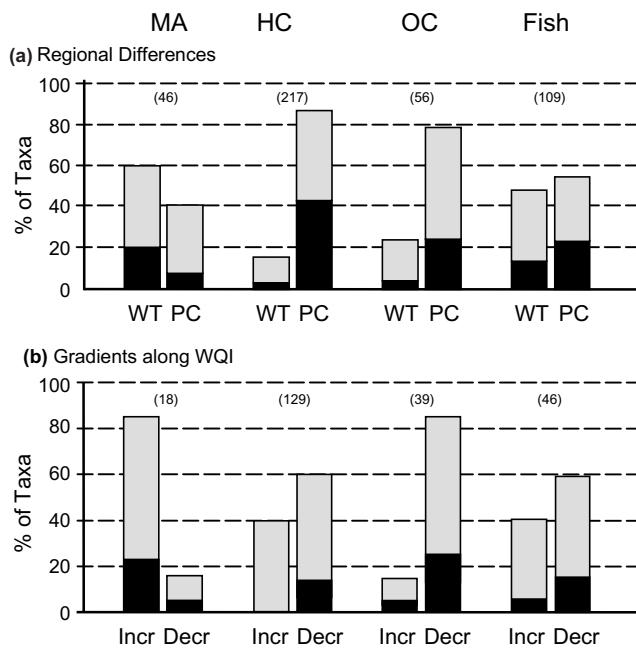


Fig. 7. Percentage of fleshy macroalgae (MA), hard coral (HC), octocoral (OC) and fish taxa that differ in abundances between the regions (a), and that in both regions consistently positively or negatively related to the WQI gradient, hence increase or decrease in abundance with increasing nutrients (b). Analyses only included taxa that were found at least at 25% (a) and 50% (b) of reefs; taxa that followed the WQI gradient but in which the direction of change was inconsistent in the two regions were also excluded. Numbers of taxa included in the analyses are given in brackets. Probabilities are AIC probabilities for the existence of gradients in abundances along the water quality gradient; black bars indicate high to moderate probability for an association ($P > 0.8$), grey = weak ($P \leq 0.8$).

these differences have always existed, and to what extent they may have been related to nutrient enrichment and increased siltation from agricultural runoff.

Table 3

Redundancy analysis for the effects of regions (WT and PC) and water quality (WQI) on assemblages of MA = fleshy macroalgae, HC = hard corals, OC = octocorals, and fish. Sequential sums of squares were summed over the responses of each species or genus in each group to give analysis of variance tables. The pseudo-F (pF) statistic was bootstrapped and bias adjusted. Perm-P is the P -value of the permutation test used to assess the significance of the effect. For octocorals, there was a strong water quality effect and a weak region effect, whereas for the other three groups, regional differences were stronger than the water quality effect

		DF	SS	%SS	pF	Perm-P
MA	Region	1	14.7	18.9	2.3	0.001
	WQI	1	4.8	6.2	0.7	0.785
	Residuals	9	58.1	74.9		
HC	Region	1	110.0	31.0	3.6	0.003
	WQI	1	29.0	8.2	0.9	0.603
	Residuals	7	216.0	60.8		
OC	WQI	1	17.0	23.2	3.4	0.005
	Region	1	6.3	8.6	1.3	0.155
	Residuals	10	50.0	68.3		
Fish	Region	1	27.9	33.6	4.0	0.005
	WQI	1	5.9	7.1	0.8	0.653
	Residuals	7	49.1	59.2		

Our water quality data indicated that mean concentrations of particulate and dissolved nutrients were generally higher on WT reefs than in PC. The existence of such regional differences is supported by 2-fold differences in long-term chlorophyll *a* values recorded monthly since 1992 in both regions (Brodie et al., 1997; Fabricius and De'ath, 2004). Water column chlorophyll concentration is widely used as a proxy for nutrient status in shallow waters. In the central GBR but not in the Far North, chlorophyll concentrations increase steeply towards the coast, indicating that the differences can not be explained just by latitude or by cross-shelf patterns, but that more nutrients are available in WT inshore compared with WT offshore and PC inshore and offshore (Brodie et al., unpublished data). New nutrients in inshore waters are predominantly derived from river plumes (Furnas, 2003). Nutrient and sediment discharges by river floods from agriculturally used catchments in the central GBR (including WT) have increased 5 to 10-fold since European settlement, whereas concentrations have remained relatively similar in the Far North (including Princess Charlotte Bay) where agriculture is minimal (McCulloch et al., 2003; Furnas, 2003). However, since historic water quality data from the GBR are sparse, it is impossible to determine whether or not chlorophyll levels in this region have increased in response to past and present land use practices.

The shallowness and width of the northeast Australian continental shelf of the GBR plays an important role in the retention of imported material. It distinguishes the GBR system from many other Indo-Pacific coral reefs surrounded by deeper water. The median depth of the GBR seafloor is 35 m (range: intertidal to 90 m), and the shelf-width ranges from 50 km in the north to over 300 km in the south. The inshore seafloor is particularly

shallow (intertidal to 20 m depth), and much of the fine sediment is therefore easily resuspended by swell. While river plumes are short-lived, biological uptake by phytoplankton and bacteria converts dissolved inorganic nutrients into particulate organic matter, the repeated resuspension of which contributes to turbidity and reduces the lower depth limit for seagrass and corals (Short et al., 1995; Longstaff and Dennison, 1999; Anthony and Fabricius, 2000; Yentsch et al., 2002). A large proportion of the particulate material may remain in the inshore system for prolonged periods of times (probably years to decades), undergoing cycles of deposition and resuspension while it is slowly transported northwards, prior to final deposition in a sheltered area (Larcombe et al., 1995), or offshore transport such as observed in the Cairns region (Wolanski et al., 2003a). The main issues dominating the water quality of inshore areas are therefore organic enrichment and the loss of light rather than the short-lived dissolved inorganic nutrients. One of the problems in assessing future effects of terrestrial runoff is the unknown capacity of the system to absorb inputs of phosphates and organic materials to the GBR lagoon.

4.2. Macroalgae

Total cover of macroalgae, abundance and richness of Rhodophyta, and abundance of Chlorophyta increased along the water quality gradient from lowest to highest nutrient and particle concentrations. The doubling in relative abundances in both groups was due to small increases in a large number of genera, rather than a take-over of one or few genera. The response in Rhodophyta and Chlorophyta and the absence of a response in the Phaeophyta is intriguing. While hard coral cover was strongly negatively related to turf algal cover, it was unrelated to macroalgal cover and abundance of Rhodophytes and Chlorophytes. While algal abundances may have been enhanced by coral disturbance (McCook et al., 2001; Diaz-Pulido and McCook, 2004), the data did not suggest that the coral decline lead to a release in fleshy macroalgae at a whole-reef scale. The pattern may instead represent a direct response of Rhodophytes and Chlorophytes to water quality, or to other unspecified habitat characteristics along the water quality gradient. Non-calcifying chlorophytes, such as *Enteromorpha* (Lotze and Schramm, 2000) and *Dictyosphaeria* (Smith, 1981) were identified in previous studies of severe eutrophication as potential indicators for nutrient enrichment, and various studies have proposed the use of Rhodophytes as indicators of eutrophication (Lapointe, 1987; Horrocks et al., 1995). The Rhodophyte *Asparagopsis taxiformis*, one of the taxa strongly correlated with the water quality gradient, is commonly found in disturbed sites, from eutrophic inshore reefs (Diaz-Pulido and McCook,

2002) to pristine offshore sites (Hatcher, 1984). The lack of response in the phaeophytes is consistent with previous results showing that *Sargassum* thrives and is nutrient-replete on offshore reefs (McCook, 1996), but the interpretation of these patterns is complex. For example, the growth of *Sargassum* is enhanced by small additions and depressed at slightly higher additions of dissolved inorganic nutrients, but growth is also enhanced by the adhesion of particulate matter to the leaf surfaces in controlled laboratory studies (Schaffelke and Klumpp, 1998; Schaffelke, 1999). Similarly, slow-release fertilizer application suppressed brown frondose macroalgae in a field study in the Caribbean, while enhancing the green filamentous macroalgae *Enteromorpha prolifera* and other green turf algae and having no effect on red algae (McClanahan et al., 2002).

Net growth rates in macroalgae can be limited by one or a combination of factors, including nutrients, herbivory, light, flow and wave action, and limitations can depend on species, habitat types and region. In particular, herbivory is known to obscure the responses of algae to nutrients and sediments (McCook, 2001; Miller et al., 1999; McCook et al., 2001; Jompa and McCook, 2002; Smith et al., 2001). However, in our study, macroalgal abundance increased with increasing nutrients within the WT reefs, despite the relatively high abundance of herbivores on the WT reefs. This suggests that growth rates of some algae outstripped consumption by herbivores, perhaps due to nutrient enhanced growth or reduced fish grazing as a result of increased sediment trapping by the algae.

4.3. Hard corals

For hard corals, richness was only half as high in WT as in PC. This was due to low abundances in the sensitive taxa *Acropora* and *Montipora*, some of the Pocilloporidae, and some of the more persistent Pectiniidae and Fungiidae. In contrast, differences were weaker in the genera *Porites*, *Galaxea* and *Turbinaria*, which are known to be among the most persistent and sediment- and nutrient-tolerant coral genera (Done, 1982; Stafford-Smith and Ormond, 1992; Birkeland, 2000; Philipp and Fabricius, 2003). Coral cover has declined due to bleaching, *A. planci* and a cyclone on Russell and Normanby Reefs in WT since 1990 (Ayling and Ayling, 2002), and these hard coral specific disturbances will have strongly contributed to the low abundances of the more sensitive taxa in WT. On these reefs, coral cover did not recover but either remained level or continued to decline in the years when no obvious disturbances were recorded. A similar ~1% per year decline in coral cover from an average of 22% in 1986 to ~8% in 2002 was recorded on eight WT inshore reefs in the WT region (AIMS Long-term Monitoring Program, unpublished manta tow data), three of which

were part of our investigation (Barnard, Normanby, and Fitzroy Reef). These two data sets indicate that storms, bleaching and *A. planci* were the direct causes for the observed decline in coral cover, explaining the low abundances of genera such as *Montipora* and *Acropora*. However, our data of a number of species gradually decreasing along the water quality gradient suggest that water quality conditions may have added to the effects of other disturbances and latitude.

Along the water quality gradient, decreases were observed in the moderately resilient, long-lived and relatively bleaching-insensitive families Mussidae, Agariciidae and Faviidae, and the pioneer family Pocilloporidae. In contrast, no changes along the water quality gradient were recorded in the most sensitive genera and families (as these taxa were largely missing in WT), and in the toughest genera and families. A latitudinal decline in hard coral richness is well established, but the 50% difference in richness between the regions cannot be entirely explained by latitude: hard coral richness decreases by only 25% along the whole length of the GBR, and richness of inshore reefs increases both south and north of WT (Devantier et al., unpublished data). Many of the species that were found in higher abundances in PC than in WT in this study, also occur in the Whitsunday Islands at the cleaner sites but not at sites with high chlorophyll levels closer to the river mouth (e.g., *Hydnophora rigida*, *Palauastrea ramosa*, *Acropora nobilis*, *Echinopora horrida*, and many others; van Woesik et al., 1999; Devantier et al., 1998). The low abundances or absence of many of these taxa in WT is therefore not due to latitudinal effects and only partly due to the specific disturbance history of the WT, but likely to be at least partly related to water quality conditions. It is important to note that the assemblages on our study reefs did not undergo species replacement from low to high nutrient conditions. Instead, reefs in the most nutrient-rich environments supported a subset of species of the least nutrient-enriched environments, with about 50% of species missing and no additional species entering the assemblage.

Early life stages of hard corals are particularly sensitive to changes in water quality, and coral settlement and juvenile survival are inhibited by sedimentation especially when sediments are organically enriched (Babcock and Smith, 2002; Fabricius et al., 2003). Hard coral recruitment rates are 3 times higher on PC than WT inshore reefs, for unknown reasons (Fabricius, unpublished data). It is possible that the main effect of organic enrichment on hard coral assemblages is impairment of recruitment. Thus, while the present-day WT inshore hard coral assemblages reflect a history of repeated disturbances, water quality may affect hard coral assemblages by slowing their recovery rates, or by increasing their vulnerability to disturbances. In the absence of further severe disturbances, these reefs may

eventually return to being occupied by highly diverse hard coral assemblages.

4.4. Octocorals

Octocoral richness declined by 60% along the water quality gradient. Octocoral richness declines with latitude by ~30% along the length of the GBR (Fabricius and De'ath, 2001). Hence as with hard corals, latitude alone is insufficient to explain the difference between the two regions. Soft coral abundance has been found to be significantly negatively correlated with turbidity, suspended particulate matter, silicate and total organic sediment contents (van Woesik et al., 1999). Furthermore, richness of zooxanthellate octocorals has been found to decline along a gradient of increasing chlorophyll across the continental shelf off the Wet Tropics (Fabricius and De'ath, 2004), and declines by one genus for each meter of visibility lost in otherwise comparable GBR habitats (Fabricius and De'ath, 2001). An investigation of the types of taxa missing in WT further confirms that water quality affects octocoral richness. The two taxa found in higher abundances in WT than PC (*Briareum* and *Clavularia*) generally occur in highest abundances in turbid waters throughout the GBR, whereas genera within the families Neptheidae and Xeniidae (that had higher representation in PC than in WT) are generally found in moderately clear water (Dinesen, 1983; Fabricius and Alderslade, 2001). Evidence is therefore increasing that octocorals respond more strongly and more specifically to water quality than do hard corals.

4.5. Fish

For fish, total relative abundances were 3 times higher in PC than WT, however there was also evidence that total abundances declined with decreasing water quality. Importantly, fish assemblages were composed of different suites of species in the two regions. This contrasted with the hard corals and octocorals in which WT assemblages were composed of subsets of PC species rather than different suites of species. The most striking differences in the fish assemblages were the greater abundance of species vulnerable to fishing in PC and the greater abundances of grazing herbivores in WT. The greater fishing pressure in WT compared to PC (Mapstone et al., 2004; Williams, 2002), and the observation that any fished species in WT were generally at or below the minimum legal size for capture (in contrast to their large sizes in PC) strongly indicates that the difference in species vulnerable to fishing between the regions is a result of relative fishing pressures. The second major difference was the greater abundance of the common grazing herbivores in WT, with six species that comprised the majority of grazers being more abundant in the more

turbid waters of WT than PC. Only two common grazing species were more abundant in PC than WT. The roles of modified habitat complexity and altered food availability for coral- and algae-feeding guilds deserve more attention. The finding of increased herbivore abundances in WT is intriguing as there is no evidence that herbivore abundances are food regulated, and it also contrasts with the conclusion of Wolanski et al. (2003b), that the abundance of herbivorous fish in the GBR is predicted by water clarity.

Overall, the species richness of fish on the WT and PC inshore reefs were similar, and intermediate between that of another well-studied inshore reef of the central GBR south of WT (Pandora Reef) and three mid-shelf reefs of the Central GBR off Townsville (Williams, 1982). Acanthurids and labrids were notably richer on the WT reefs than PC but, surprisingly, the largely coral-dependent butterflyfishes (Chaetodontidae) were equally rich (but some were less abundant) in the WT and PC, despite differences in coral cover. Among the WT reefs, fish diversity was particularly low on South Barnard Island, which was characterized by a rocky substratum and low dead or live coral cover. The relatively high diversity of fish on other WT reefs may be related to the close proximity to the diverse communities on adjacent mid-shelf reefs that may serve as a source of recruits (similar mid-shelf reefs in the region to the north of PC have relatively low diversity; Williams, unpublished data).

4.6. Assessing ecological responses in inshore reef communities

Our study showed that detailed surveys at relatively fine taxonomic resolution, when cautiously interpreted in the context of available biophysical environmental data and biological knowledge of key species, can provide important information on the health and status of inshore coral reefs. A cross-comparison of the results indicates that of the four taxonomic groups investigated, octocorals were the assemblage most strongly related to water quality. Octocoral abundances are particularly tightly linked to physical environmental conditions (Fabricius and De'ath, 1997; Karlson et al., 1996), possibly because no major predator exists for octocorals (*A. planci* do not eat octocorals; De'ath and Moran, 1998), whereas abundances of the other three groups are partly controlled by predation: most macroalgae are affected by fish grazing, hard corals by *A. planci*, and some of the larger fish by human fishing pressure. Our data also show strong responses in a number of Rhodophytes and Chlorophytes to water quality, which deserves closer investigation. Among the hard corals, water quality effects were most noticeable in the families Mussidae, Agariciidae and Faviidae, which are moderately resilient, long-lived, relatively bleaching-insensitive and not

among the most preferred food for *A. planci*. In contrast, the most sensitive genera and families were largely missing in WT, and the toughest genera and families did not change in abundance along the water quality gradient. Changes in abundances of moderately sensitive groups such as the Mussidae, Agariciidae and Faviidae, are therefore most suitable as indicators for environmental stress. For fish, there appeared to be a relationship between total abundances and water quality, and some of the species decreased whereas others increased in abundance with water quality.

Causes for differences in assemblages are naturally difficult to determine definitively in ecological studies, especially if historic data are sparse. A framework based on epidemiological criteria can help synthesize and weigh available evidence to assess the likelihood of a causal association (Fabricius and De'ath, 2004). In our study, both the regional differences in water quality and assemblages, and the existence of ecological gradients along the water quality gradients, added evidence that many of the responses were related to the differences in water quality. The changes along the water quality gradient that were consistent in direction with other studies (decreasing corals and increasing algae), the monotonic responses, and the large and ecologically relevant effect sizes, all added evidence that the inshore reef assemblages are strongly shaped by present-day water quality conditions. The implementation of management plans to halt or reverse a decline in water quality, through improved upstream land-use practices and waste water treatment, is vital to ensure the long-term health of inshore reefs of the GBR (The State of Queensland and Commonwealth of Australia, 2003).

Acknowledgment

We are very grateful to Michelle Skuza, Margaret Wright and Jane WuWon for carrying out the water quality analyses. Many thanks to Lyndon Devantier, Jon Brodie and two reviewers for helpful comments to the manuscript, and to Howard Choat for advice on diets of scarids and acanthurids. Thanks also to a number of volunteers and the crew of the RV 'The Lady Batten' for invaluable support with the fieldwork. The study was funded by the Cooperative Research Centre for the Great Barrier Reef World Heritage Area (CRC Reef), and the Australian Institute of Marine Science (AIMS).

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