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REPORT

Relationship of internal macrobioeroder densities in living massive *Porites* to turbidity and chlorophyll on the Australian Great Barrier Reef

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Abstract This study investigates the relationship between the density of internal macrobioeroders in living massive *Porites* and nutrient status. The study was conducted along turbidity and chlorophyll gradients towards river mouths on 12 reefs in four regions of the inshore Great Barrier Reef. Mean internal macrobioeroder densities doubled from 2 to 8 m depth, and at the 8 m sites, densities increased 4- to 7-fold towards the river mouths in all regions. Densities also increased 1.6-fold for each additional 1 NTU turbidity and 650-fold per 1 μg L^{-1} additional chlorophyll *a*. The study shows that the density of macrobioeroder boreholes in living massive *Porites* is a simple bioindicator measure for changing turbidity and chlorophyll concentrations on the Great Barrier Reef for sites from which direct water quality measurements are unavailable.

Keywords Internal macrobioeroder · Live massive *Porites* · Bioindicator · Eutrophication · Inshore Great Barrier Reef

Introduction

Bioerosion is a major destructive process affecting the balance between reef accretion and erosion. Bioerosion derives from the action of both micro- and macroorganisms that externally or internally erode live and dead reef substrata (Kiene and Hutchings 1994; Risk et al. 1995). While external bioerosion is caused by the grazing of mobile echinoids and fishes, internal bioerosion results from the action of benthic macro- and microorganisms living within substrata (Hutchings 1986; Sammarco 1996). The four main internal macrobioeroder groups are sponges, molluscs, polychaetes and sipunculans. They all find shelter from predation by either actively boring into or chemically eroding the calcium carbonate skeletons of live corals and dead reef substrata, or by becoming passively enclosed as the living coral grows around them (Bromley 1970, 1994; Scoffin and Bradshaw 2000).

A majority of internal macrobioeroders filter-feed on nano- and picoplankton, and a few obtain a positive carbon balance in oligotrophic waters (Birkeland 1997). Any increase in food availability due to human activities (e.g., sewage, agricultural runoff, mining) should increase their densities (Risk and MacGeachy 1978; Pastorok and Bilyard 1985). Indeed, the relationship between varying nutrient availability or terrestrial runoff and internal macrobioerosion has been widely studied, with a review of the literature yielding >20 studies investigating this relationship over the last 2–3 decades alone (Table 1). These studies were conducted using living *Porites*, coral rubble or experimental blocks cut from *Porites* skeletons as substrata. Many of these studies showed that total internal macrobioeroder density increases as nutrient availability increases (e.g., Sammarco and Risk 1990; Holmes 1997, 2000; Kiene 1997; Holmes et al. 2000; Kleemann 2001; Tribollet and Golubic 2005; Fonseca et al. 2006; Cooper et al. 2008; Table 1). However, a number of other studies showed different patterns (Zubia and Peyrot-Clausade 2001; Tribollet et al. 2002) or questioned the existence of such

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Table 1 Findings of some of the main studies investigating the relationships between internal macrobioeroder densities and water quality, eutrophication or terrestrial runoff

Substratum type & duration of exposure	Macrobioeroder group	Location and number of sites	Finding	Source
Porites lobata (collection of living colonies)	Total density	200 km cross-shelf transect, central Great Barrier Reef (GBR, 5 reefs, 3 sites per reef)	Total per cent bioerosion was dominated by internal macrobioeroders, rates decreasing from 11% inshore to 1.3% offshore	Sammarco and Risk (1990)
	Bivalves, sponges, polychaetes, sipunculans		Bivalve and sponges abundances increase from inshore to offshore reefs, whereas polychaete and sipunculan abundances do not significantly differ	
Porites lobata (collection of living colonies)	Total density	Java (6 sites) and Ambon (4 sites)	Bioerosion rates positively correlated with eutrophication in Java but not in Ambon	Holmes et al. (2000)
(collection of branching coral rubble)			Bioerosion rates positively related to eutrophication in both regions, indicating suitability as measure of water quality changes	
Porites lobata (collection of living colonies)	Total density	Caño Island (1 site) and Golfo Dulce (2 sites), Pacific side of Costa Rica	Diversity and total density of macrobioeroders higher at the most polluted sites affected by high loads of terrestrial runoff due to deforestation than at the least polluted sites	Fonseca et al. (2006)
	Bivalves, sipunculans		Bivalve density increases and sipunculan density decreases with eutrophication	
Massive *Porites* (in situ, living colonies)	Total density	Coastal reef (1 site) and mid-shelf reefs (2 sites), central GBR	Density of macrobioeroders higher inshore than mid-shelf; low temporal variation within a two-year observation period	Cooper et al. (2008)
Living corals (mostly *Porites* and *Montipora* sp.)	Bivalve *Pedum spondyloideum*	Bay of Safaga, Egypt (14 sites) and Hurghada (15–20 sites)	Higher survival rates and denser population at highest nutrient concentrations	Kleemann (2001)
Montastrea cavernosa (in situ, living colonies)	*Cliona delitrix*	The Grand Cayman (2 reefs)	5-fold increase of *C. delitrix* biomass on sites affected by runoff of untreated faecal sewage	Rose and Risk (1985)
Reef substrata	*Cliona inconstans*	La Saline reef, Reunion Island (3 zones)	60 to 80% of the substratum is covered by *Cliona inconstans* in an area strongly affected by submarine groundwater discharge rich in nutrients	Cuet et al. (1988)
Rubble (*Porites porites*)	Clionid sponges	Barbados fringing reefs, West Indies (7 reefs, 3 sites per reef)	Clionid abundance in the most eutrophic zones (41%) was twice as high as that in the least eutrophic zones (24%)	Holmes (2000) and Holmes (1997)
Collection of dead branches *(Acropora formosa)*	Polychaetes and sipunculans	La Saline fringing reef, Réunion Island (2 sites)	No variation in the total number between both sites, but changes in community structure: abundances of *Polydora* sp. and *Dodecaceria* spp. highest at the most polluted site, while that of Sabellidae highest at least polluted sites	Zubia and Peyrot-Clausade (2001)
Experimental blocks *(Porites lutea)*—3-years exposure	Polychaetes, sipunculans, vermetid gastropods	One tree Island, GBR (12 lagoon patch reef, 3 sites per reef)	Enrichment with dissolved inorganic nitrogen and phosphorus had no effect on bioerosion rates within microatolls	Kiene (1997)
Experimental blocks (*Porites lobata*)—one-year exposure	Total density	La Saline fringing reef, Reunion Island (3 sites)	Lowest macrobioerosion rate and macrobioeroder density in sites with highest nutrient concentration due to submarine groundwater discharge	Chazottes et al. (2002)

Table 1 continued

Substratum type & duration of exposure	Macrobioeroder group	Location and number of sites	Finding	Source
Experimental blocks (*Porites lutea*)—2 and 5 years of exposure	Total density	High Islands (3 sites) vs. atolls (4 sites), French Polynesia	More boring individuals at high island sites (eutrophic sites) than at atoll sites (oligotrophic sites)	Hutchings and Peyrot-Clausade (2002)
	Polychaetes, sipunculans		Deposit feeding sipunculans tended to be dominant at the high island sites (eutrophic) while suspension feeding polychaetes were dominant at the atoll site (oligotrophic)	
Experimental blocks (*Porites lutea*)—5 years of exposure	Sponges	High Islands (3 sites) vs. atolls (4 sites), French Polynesia	Sponge bioerosion appeared at all sites except for one eutrophic site. Highest sponge bioerosion rate at an oligotrophic site	Pari et al. (2002)
Experimental blocks (*Porites* sp.)—one-year exposure	Total density	200 km cross-shelf transect, Northern GBR (2 inshore, 1 mid-shelf, 2 offshore, 1 Coral Sea site)	Low rate of macrobioerosion and no significant difference across shelf	Tribollet et al. (2002)
Experimental blocks (massive *Porites*)—2, 3 and 4 years of exposure	Total density	200 km cross-shelf transect, Northern GBR (2 inshore, 1 mid-shelf, 2 offshore, 1 Coral Sea site)	Higher rates of internal macrobioerosion at two inshore and one offshore site than at the remaining three reefs Macrobioeroders were the dominant agents of erosion at inshore sites	Osorno et al. (2005) and Tribollet and Golubic (2005)
	Polychaetes, sipunculans		Polychaete and sipunculan abundance did not significantly vary across the shelf after 2 and 4 years of exposure	
			Suspension feeding polychaetes were more abundant offshore while deposit feeding polychaetes were more abundant inshore	
	Bivalves		Bivalve abundance higher inshore than mid-shelf and offshore after 2 years exposure, and higher inshore and mid-shelf than offshore after 4 years exposure	
	Sponges		Sponge abundance was higher inshore and at one mid-shelf reef than offshore after 4 years exposure	
Experimental blocks (*Porites*)—4 years of exposure	Polychaetes	289 km cross-shelf transect, northern GBR (2 inshore, 1 mid-shelf, 2 offshore, 1 Coral Sea site)	*Arabella*, *Lysidice* and *Eunice* spp. did not vary between sites	Hutchings et al. (2005)
			Polydora spp. had lower abundance at the inshore and one offshore than the other sites	
			Dodecaceria spp. had higher abundance inshore sites and to a lesser extent at one of the mid-shelf site	
			The sabellid *Hypsicomus* was found in very low abundance at the inshore and one of the mid-shelf sites compared to the other sites	
Acropora formosa: collection from dead portions of the base of live colonies	Total density	110 km cross-shelf transect, central GBR (2 inshore, 3 mid-shelf, 1 offshore)	Low level of total internal macrobioerosion on the outer shelf compared to the inshore and mid-shelf reefs.	Risk et al. (1995)
All living coral colonies infested by coral associates (macrobioeroders and coral predators organisms)	Gastropods bivalves polychaetes crustaceans	South-eastern coast of Sulawesi, Indonesia (4 sites with increasing anthropogenic damage)	Lithophagid bivalve densities and number of infested colonies were highest in the most impacted and one of the intermediate sites	Scaps and Denis (2008)

relationships (Pari et al. 2002; Hutchings et al. 2005; Tribollet and Golubic 2005). Most studies that did not find such relationships were conducted on experimental blocks of dead coral substrata with less than 3 years of exposure, rather than in old rubble or live coral (Table 1). Although young dead substrata are colonised by macrobioeroders, 3 years appears an insufficient time for complete succession towards abundant sponge and bivalve establishment (Kiene and Hutchings 1994; Chazottes et al. 1995). After initial colonisation by microbioeroders (cyanobacteria, other bacteria, algae and fungi; Tribollet et al. 2002; Carreiro-Silva et al. 2005), polychaetes start appearing on experimental blocks after ~2 months of exposure. Such polychaetes are short-lived, leaving behind burrows for larvae of other organisms to settle (Hutchings et al. 1992). After ~6 months, sipunculans colonise microfractures left by polychaetes. Sponges and bivalves are typically not yet present on blocks after 2 years of exposure but start to appear after 3 years, in sufficient numbers to accelerate the internal macrobioerosion process (Davies and Hutchings 1983; Peyrot-Clausade et al. 1992; Chazottes et al. 1995; Pari et al. 2002).

The literature shows that responses to varying nutrient availability not only vary as a function of substratum age, but also vary between live coral and old dead substrata, and across individual macrobioeroder taxa (Table 1). In boring sponges and bivalves, which are both filter feeders, abundances were found to increase with eutrophication in most studies (e.g., Rose and Risk 1985; Cuet et al. 1988; Siegrist et al. 1991; Schroeter et al. 1993; Holmes 1997, 2000; Kleemann 2001; Osorno et al. 2005; Tribollet and Golubic 2005; Fonseca et al. 2006). Amongst the polychaetes, the patterns were more complex. Osorno et al. (2005) reported deposit feeders such as *Dodecaceria* spp. to be dominant at eutrophic sites, possibly due to abundant epilithic algae trapping sediment-associated nutrients. In contrast, suspension feeding polychaetes, such as *Polydora* spp., dominated at oligotrophic sites, where endolithic algae proliferated while epilithic algae were sparse (Le Bris et al. 1998). However Zubia and Peyrot-Clausade (2001) found that in old dead *Acropora* branches, both *Polydora* spp. (suspension feeders) and *Dodecaceria* spp. (deposit feeders) were more abundant at the most polluted sites, whereas Sabellidae (suspension feeders) thrived at the least polluted sites. Finally, results for sipunculans were also varied, with Hutchings and Peyrot-Clausade (2002) reporting highest abundances at the most eutrophic sites, Fonseca et al. (2006) reporting highest abundances at the least polluted sites, and other studies reporting that species composition, but not the total abundance, of sipunculids varied with eutrophication (Sammarco and Risk 1990; Zubia and Peyrot-Clausade 2001; Osorno et al. 2005). In summary, the existing literature suggests that in living corals and old substrata, filter feeding bivalves and sponges tended to have higher densities in nutrient-rich than in oligotrophic waters, while polychaetes and sipunculans often do not vary in their density, but do vary in community composition (Table 1).

A number of studies have proposed or shown that the rate of internal macrobioerosion may serve as a bioindicator of changes in water quality (Risk and MacGeachy 1978; Edinger et al. 2000; Holmes et al. 2000; Risk et al. 2001, Cooper et al. 2008, 2009). For this purpose, different methods have been used to estimate internal macrobioerosion. Methods involved either the deployment of experimental units, the collection of living corals, or the collection of coral rubble for later determination of bioerosion in the laboratory (Edinger et al. 2000; Holmes et al. 2000; Hutchings and Peyrot-Clausade 2002; Tribollet and Golubic 2005). These three methods have the advantage that they provide data on total internal bioerosion rates. Holmes et al. (2000) demonstrated that bioerosion rates in randomly collected coral rubble in the field showed a strong positive correlation with two eutrophication gradients (Java and Ambon), while bioerosion in collected live massive corals was positively related with only one eutrophication gradient (Java), suggesting that macrobioerosion in coral rubble was more sensitive to varying nutrient availability than that in live corals. However the method of collecting coral rubble is limited by the unknown age of the rubble: branching corals are often killed during mass mortality events from bleaching, floods or crown-of-thorns outbreaks, and the slow succession of bioeroders makes it difficult to compare amongst sites with different disturbance histories. Similarly, the method of collecting living corals is limited by the number of replicates that can be collected without causing unacceptable damage to the reef. The method of using deployed experimental units is unsuitable because of incomplete succession (Table 1). A proposed alternative method is the in situ count of macrobioeroder apertures on living colonies of massive *Porites* (Risk et al. 2001; Cooper et al. 2008; Scaps and Vianney 2008). Cooper et al. (2008) estimated internal macrobioeroder density by counting macrobioeroder apertures on the surface of live massive *Porites* and showed that macrobioeroder density was consistently higher on a coastal reef than on two mid-shelf reefs over a two-year study. Although contributing only a proportion of the total bioerosion that occurs on coral reefs (Sammarco and Risk 1990), the number of externally visible macrobioeroder orifices may serve as a simple proxy to estimate total macrobioerosion rates of living massive *Porites* with which they appear correlated (Edinger et al. 2000; Holmes et al. 2000). Massive *Porites* are relatively slow-growing, with ~1.4 cm yr^{-1} mean linear extension on the GBR (De'ath et al. 2009). As a result, living massive *Porites*

provide standardised surfaces that integrate exposure over prolonged periods of time. Massive *Porites* are also reliably identified and often abundant even in moderately polluted conditions. Furthermore, the method is rapid, cheap and non-destructive, therefore fulfilling the requirement for an effective early warning indicator of changing water quality (Risk et al. 2001; Cooper et al. 2009). This technique is used in the present study to quantify the variation in the total number of externally visible macrobioeroders on living massive *Porites* in response to changing water quality in four inshore regions of the Great Barrier Reef (GBR) and to test whether this method could be used as an indicator of water quality.

Methods

This study was conducted on four regions of the inshore GBR (Fig. 1): Keppels (23°14′S; 150°52′E–23°09′S; 151°04′E), Whitsundays (20°22′S; 148°53′E–20°06′S; 148°39′E), Burdekin (19°08′S; 146°50′E–18°37′S; 146°29′E) and Wet Tropics (17°56′S; 146°09′E–16°56′S; 145°59′E). In each region, three reefs located at increasing distance from a river mouth ('near', 'mid' and 'far' stations) but at similar distance (<20 km) from the coast were surveyed. Two replicate sites were sampled at the leeward sides of each reef, and at each site, samples were taken at two depths (shallow: 1–3 m and deep: 7–9 m below lowest astronomical tide). Ten colonies were investigated along each transect (359 colonies in total). Only one massive *Porites* was found at one deep site of the 'mid' station (Pandora Reef) in the Burdekin region, this site was omitted from the analyses.

On the living surface of each colony, the density of internal macrobioeroders, as estimated by counts of external borehole openings, was quantified within a 149 × 149 mm stainless steel frame. Total densities of externally visible macrobioeroders were counted rather than that of individual macrobioeroder taxa, as the visual differentiation between the small bore holes of young bioeroders is not practical in the field (Fig. 2). Typically, the counts were calculated in triplicates, but in small colonies, two quadrats were used or the entire colony surface was counted. The surface area of the colony was determined by measuring the diameter of the colony and the length perpendicular to it. Massive *Porites* were considered as half spheres, and their surface area calculated as $2r^2\pi$. Internal macrobioeroder densities of living massive *Porites* were standardised to the surface area of the quadrat or the colony surface area. Turbidity and chlorophyll *a* values from each of the 12 studied reefs were obtained from the

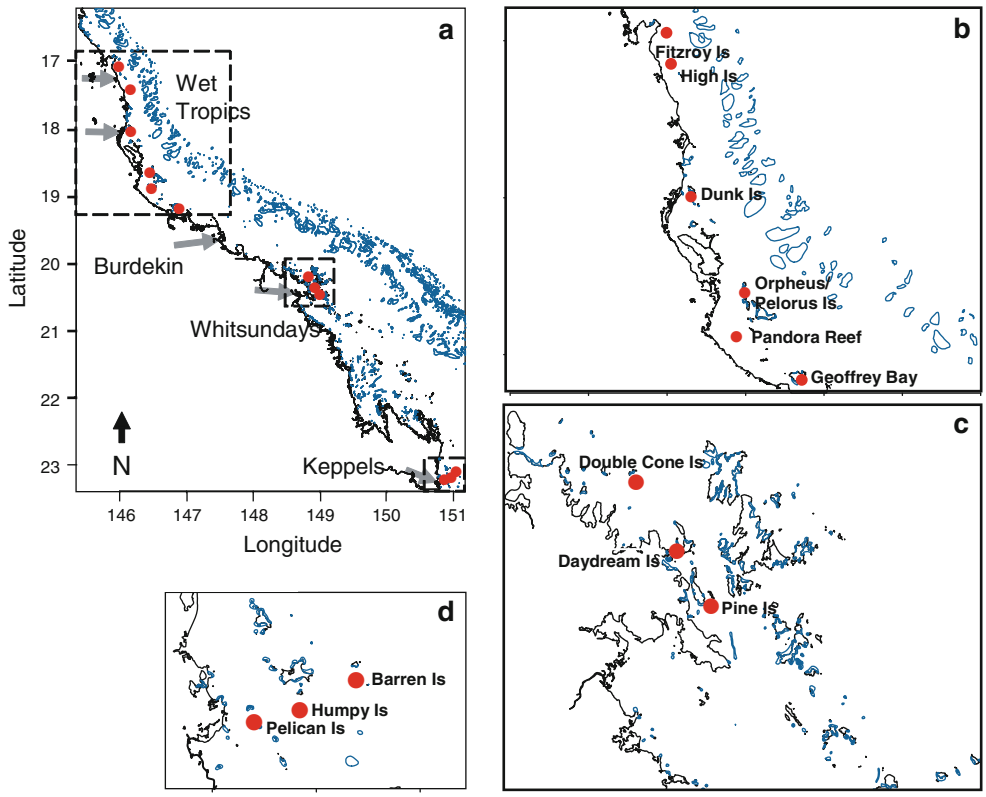

Fig. 1 Location of the four study regions across the Great Barrier Reef **a**, and details of the Wet Tropics and Burdekin Regions **b**, the Whitsundays Region **c** and Keppels Region **d**. The blue arrows indicate the locations of the river mouths

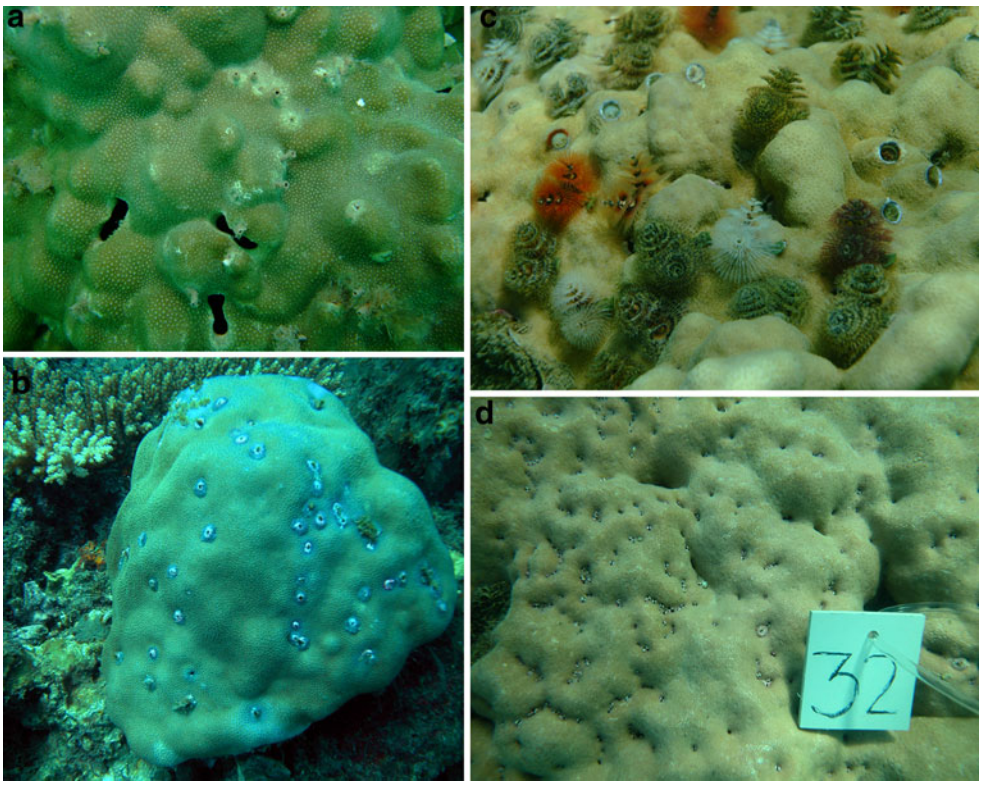

Fig. 2 Some examples of the diverse range of externally visible macrobioeroder orifices on living massive *Porites* of the inshore Great Barrier Reef

AIMS inshore marine water quality monitoring programme (Schaffelke et al. 2009). Turbidity is a key determinant of light availability and particle loads, while chlorophyll *a* is a proxy for primary production in the water column providing an estimate of nutrient availability (van Woesik et al. 1999). At one site of each reef, a logger (FLNTU Eco Combination Meter) was deployed at 5-m depth. Mean levels of turbidity (Nephelometric turbidity unit, NTU) and chlorophyll *a* (μg L^{-1}) were derived from the continuous 10-min records over 12 months.

For the statistical analyses, the variation in long-term mean turbidity and chlorophyll *a* was compared between the four GBR inshore regions and the three stations (near, mid and far distance from the river) within each region using separate sequential two-way ANOVAs. Turbidity and chlorophyll were highly correlated, and their effects were therefore analysed separately. The spatial variation in internal macrobioeroder densities of living massive *Porites* (log2-transformed) across regions, depths and stations was assessed with a three-way ANOVA. The slopes of the relationship of their densities (log2-transformed) to turbidity or chlorophyll were also investigated with a non-sequential generalised linear mixed effects model, with region and depth as additional factors. Since interactions were weak, the results were presented based on partial dependence plots, firstly displaying the relationship to turbidity while accounting for the average joint effect of depth and region, and in a separate analysis to chlorophyll, depth and region. All analyses were done using the statistical software R (R Development Core Team 2010).

Results

Mean long-term turbidity varied >13-fold between reefs (0.37–5.05 NTU). Levels were similar across regions ($F_{(3,6)} = 0.84$, $p = 0.52$) but varied with distance from the river mouths ($F_{(2,6)} = 6.87$, $p = 0.028$; Fig. 3). In all regions, turbidity was highest at the near stations, lower at the mid stations, and in all regions except in the Wet Tropics, lowest at the far stations. Mean long-term chlorophyll concentrations varied >2-fold between reefs (0.32–0.72 μg L^{-1}) and also differed between regions ($F_{(3,6)} = 7.89$, $p = 0.017$; Fig. 3). Chlorophyll *a* declined strongly away from the river in the Keppels region, but varied non-systematically with distance from the river mouths in the other regions ($F_{(2,6)} = 3.23$, $p = 0.11$).

At the 12 inshore reefs of the GBR, densities of internal macrobioeroders living in massive *Porites* significantly differed between regions, depths and with distance from the river (Fig. 4; Table 2). Site averaged densities ranged from >3,200 bioeroders m^{-2} colony surface area

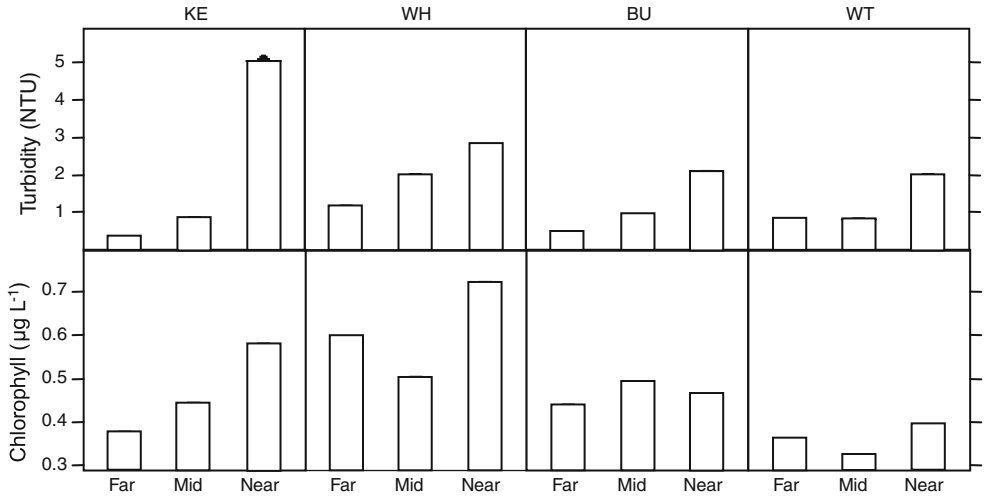

Fig. 3 Mean water column turbidity (NTU) and chlorophyll *a* (µg L^{-1}) at each station (near, mid, far from the river mouth) from the 4 regions of the Great Barrier Reef. KE Keppels, WH Whitsundays, BU Burdekin and WT Wet tropics. Data provided by the Reef Plan Marine Monitoring Program

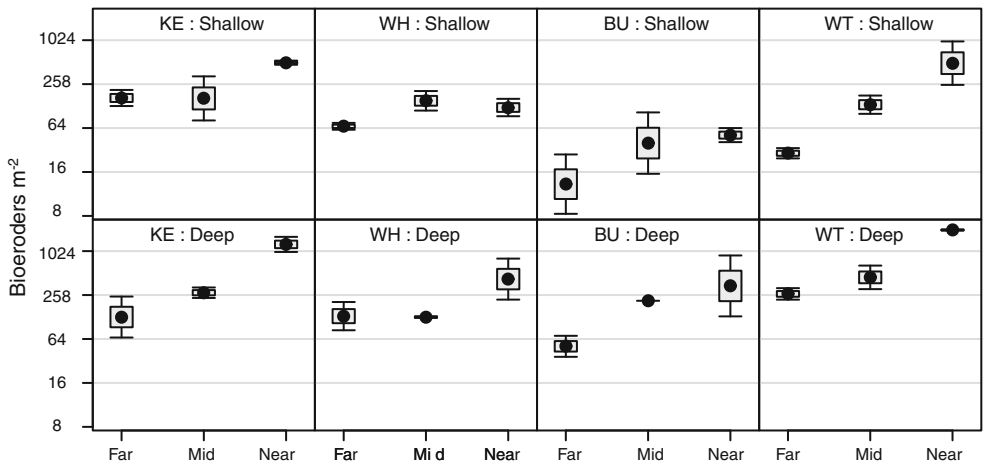

Fig. 4 Site-averaged densities of macrobioeroders (number m^{-2} of externally visible orifices on living colony surface on massive *Porites*; backtransformed data) at the shallow and deep sites at each of the far, mid and near stations in each of the four inshore regions. Points indicate mean values, boxes show ranges ($N = 2$ sites)

Table 2 Results of three-way anovas on the variation of total macrobioeroder density (m^{-2}) between the 4 Great Barrier Reef inshore regions, the 3 stations (near, mid and far distance from the river) within each region, and the 2 depth zones

	df	MS	*F*	*P*
Region	3	11.626	13.077	<0.0001
Depth	1	25.006	28.127	<0.0001
Region/Station	8	5.899	6.635	<0.0001
Region * Depth	3	3.129	3.519	0.026
Residuals	31	0.889		

(backtransformed data (BD)) at the deep sites of the Wet Tropics region, to <60 m^{-2} at the shallow sites of the Burdekin region, $a > 50$-fold difference. Overall, mean densities were ~ 2.2 times higher at deep sites than at shallow sites. At the deep sites of all regions, site averaged densities markedly decreased from near to far stations. Densities were >7 times higher at the deep near station than at the deep far stations both in the Keppels (884 vs 121 bioeroders m^{-2} (BD)) and in the Wet Tropics (3,059 vs 347). In the two other regions, densities declined ~ 4-fold away from the river mouth (Whitsundays: 1,041 vs 232, Burdekin: 700 vs 170 bioeroders m^{-2} BD). At the shallow sites, densities also differed between near, mid and far stations, but differences were less pronounced.

The partial dependence plots showed that internal macrobioeroder densities strongly increased with increasing turbidity and chlorophyll *a*, while also increasing with depth and varying across regions (Fig. 5; Table 3). The

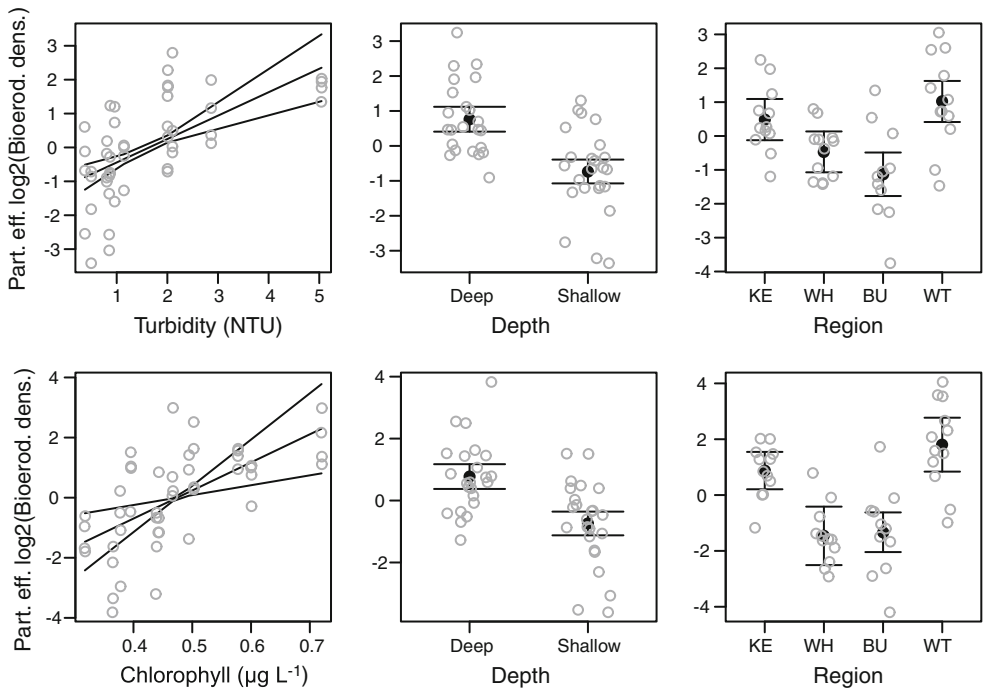

Fig. 5 Variation in bioeroders densities (log2-transformed) in response to changing turbidity (NTU) or chlorophyll (μg L^{-1}), across the 2 depth categories (deep and shallow) and the 4 Great Barrier Reef inshore regions. The plots show outputs of partial dependence model estimates of means and 95% CI, white points are residuals

Table 3 Results of linear model analyses on the variation in bioeroders densities (log2-transformed) in response to changing turbidity (NTU; a) and chlorophyll *a* (μg L^{-1}; b). Slopes are outputs of partial effects models, also accounting for the 2 depth categories (deep and shallow) and the differences between the 4 Great Barrier Reef inshore regions

	Estimate	*SE*	*t*	*P*
(a)				
(Intercept)	7.484	0.491	15.239	<0.0001
Turbidity: slope	0.691	0.145	4.773	<0.0001
Depth difference				
Shallow to deep	−1.496	0.348	−4.296	<0.001
Region difference				
WH to KE	0.953	0.487	1.957	0.057
BU to KE	−1.614	0.514	−3.139	0.003
WT to KE	0.535	0.503	1.063	0.294
(b)				
(Intercept)	4.586	1.474	3.111	0.003
Chl *a*: Slope	9.348	3.027	3.088	0.004
Depth difference				
Shallow to deep	−1.51	0.391	−3.873	<0.001
Region difference				
WH to KE	−2.338	0.695	−3.366	0.002
BU to KE	−2.2081	0.559	−3.947	<0.001
WT to KE	0.9286	0.635	1.462	0.151

analyses showed a significant linear relationship with turbidity ($t = 4.18$, $P < 0.0001$), with a 1.6-fold ($SE = 1.1$) increase in bioeroders m^{-2} with every 1 NTU increase, or a 9-fold increase along the observed turbidity gradient spanning from 0.37 to 5.05 NTU on the 12 reefs (Table 3). Similarly, the relationship with chlorophyll *a* was linear ($t = 3.30$, $P < 0.002$), with a slope indicating a 650-fold ($SE = 8.2$) increase in bioeroders m^{-2} for a 1 μg L^{-1} increase in chlorophyll *a*, or a 14-fold increase along the observed chlorophyll *a* gradient spanning from 0.32 to 0.72 μg L^{-1}. Both sets of analyses also showed that mean densities were >2 times higher at the deep compared with the shallow sites, and 2 times higher in the Wet Tropics region than in the other regions, even after having accounted for differences in chlorophyll *a* or turbidity and depth.

Discussion

This study showed that the density of externally visible internal macrobioeroders living on massive *Porites* increased with increasing turbidity and chlorophyll *a* and declined with distance from the river mouths, but also differed between the two depths and four regions of the GBR. Densities increased 9-fold and 14-fold along the

turbidity and chlorophyll *a* gradients respectively, providing strong evidence that internal macrobioeroder densities in living *Porites* strongly increase in response to water column turbidity and chlorophyll *a*. This confirms that the simple in situ assessment method provides similar results to those reported in previous studies based on either the collection of living *Porites* or coral rubble (Edinger et al. 2000, Holmes et al. 2000; Table 1).

Most internal macrobioeroders in living *Porites* are filter feeders, the density of which is known to increase in response to nutrient enrichment (Smith et al. 1981). Inshore reefs have naturally higher sediment and nutrient levels than mid-shelf and offshore reefs, which is reflected in a higher rate of internal macrobioeroder densities inshore compared with offshore (Sammarco and Risk 1990; Edinger et al. 2000). The present data show that concentrations of suspended particulate matter are also higher on inshore reefs near river mouths compared to inshore reefs away from the rivers, with the gradients likely intensified because of the four- to ten-fold increase in river nutrient and sediment loads compared with pre-colonisation times due to agricultural development (McKergow et al. 2005). The density of filter feeders such as *Lithophaga* spp., a dominant group of internal macrobioeroders on upper surfaces of living massive *Porites* on inshore reefs of the GBR (Sammarco and Risk 1990), appears therefore nutrient limited, and this limitation is released near rivers due to the terrestrial runoff of nutrients and sediments.

This study showed that internal macrobioeroder density on living massive *Porites* was twice as high at 7–9 m depth then at 1–3 m depth. The reasons for this strong and consistent depth effect are unknown, but may possibly be related to faster tissue and skeletal growth of living *Porites* in well-illuminated shallow water, and hence greater ability to repair small tissue lesions. At deeper depth, sediment deposition is higher due to attenuated wave energy, potentially increasing the number of tissue lesions. Perry (1998) demonstrated that bioerosion rates in dead coral substrata also increased from 5 to 30 m depth, and suggested that this increase might be due to a depth-dependent decline in calcification rates and skeletal densities (Bosscher 1993). However, other studies did not find any correlation between depth and internal macrobioerosion intensity (Cantera et al. 2003; Londoño-Cruz et al. 2003).

Although strongly related to turbidity, chlorophyll *a* and depth, internal macrobioeroder densities in massive *Porites* are also affected by a number of other biotic and abiotic factors (Hutchings et al. 1992; Perry 1998; Londoño-Cruz et al. 2003). For instance, sedimentation may affect the abundance of some bioeroders by blanketing the habitat available for settlement (Londoño-Cruz et al. 2003), and strong water currents are also related to high abundances of some filter feeders such as lithophagids (Cantera et al. 2003; Londoño-Cruz et al. 2003). For macrobioeroders recruiting as pelagic larvae, local currents might influence their recruitment (Osorno et al. 2005), and the presence of conspecifics might be a cue to settlement. The settlement and metamorphosis of larvae of some polychaetes is induced by the contact with conspecifics contributing to the patchy distribution of the adult population (Jensen and Morse 1984). Larvae of lithophagids can delay metamorphosis for up to 4 months to select the best place to settle (Jensen and Morse 1984). These processes contribute to patchiness and unaccounted variability of internal macrobioeroder densities at all scales ranging from colonies to regions.

The strong link between total internal macrobioeroder density and the nutrient status of reefs demonstrated in this study confirms previous suggestions that this parameter could be used as a bioindicator of water quality (Edinger et al. 2000; Holmes et al. 2000; Risk et al. 2001; Cooper et al. 2008, 2009). Cooper et al. (2009) defined five criteria to rank the suitability of a bioindicator to detect change in water quality on coral reefs: specificity, monotonicity, invariance, practicability and relevance. The density of internal macrobioeroders has high specificity and responds monotonically to change in water quality. Our study demonstrated monotonicity along four separate regional gradients. Cooper et al. (2008) showed that macrobioeroder density, quantified as the density of macrobioeroder apertures on live massive *Porites,* was quite stable over time, suggesting that seasonal and other temporal variations in macrobioeroder density are low, and that macrobioeroders best indicate chronic change rather than episodic exposure to changes in water quality. Although between-colony variability is high, estimates will improve through a better understanding of relevant covariates such as depth, and a collection of baseline data will allow optimising region-specific sampling intensity. Without the requirement of collection and follow-up laboratory analyses, the count of total macrobioeroder density on living *Porites* is a particularly practical (i.e., quick, cost-effective and non-destructive) method, and the measure is ecologically relevant (Cooper et al. 2009). In conclusion, our study confirms that the in situ assessment of internal macrobioeroder densities on living *Porites* is suitable as a bioindicator to assess exposure to changing water quality on the many reefs from which long-term water quality data are unavailable.

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