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River discharge reduces reef coral diversity in Palau

Yimnang Golbuu^{a,b,*}, Robert van Woesik^c, Robert H. Richmond^d, Peter Harrison^b, Katharina E. Fabricius^e^a Palau International Coral Reef Center, 1 M-Dock Road, P.O. Box 7086, Koror 96940, Palau^b Coral Reef Research Center, Southern Cross University, P.O. Box 157, Lismore, NSW 2480, Australia^c Department of Biological Sciences, Florida Institute of Technology, 150 West University Boulevard, Melbourne, FL 32901-6975, USA^d Kewalo Marine Laboratory, University of Hawaii at Manoa, 41 Ahui Street, Honolulu, HI 96813, USA^e Australian Institute of Marine Science, PMB No. 3, Townsville MC, Qld 4810, Australia

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ABSTRACT

Coral community structure is often governed by a suite of processes that are becoming increasingly influenced by land-use changes and related terrestrial discharges. We studied sites along a watershed gradient to examine both the physical environment and the associated biological communities. Transplanted corals showed no differences in growth rates and mortality along the watershed gradient. However, coral cover, coral richness, and coral colony density increased with increasing distance from the mouth of the bay. There was a negative relationship between coral cover and mean suspended solids concentration. Negative relationships were also found between terrigenous sedimentation rates and the richness of adult and juvenile corals. These results have major implications not only for Pacific islands but for all countries with reef systems downstream of rivers. Land development very often leads to increases in river runoff and suspended solids concentrations that reduce coral cover and coral diversity on adjacent reefs.

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1. Introduction

One of the major issues facing coral reefs worldwide is the increase in sedimentation that stems from poor land-use practices (Bryant et al., 1998; Wolanski et al., 2003a). In Palau, and in many other small Pacific islands, erosion and sedimentation are major problems because of land-use change, steep topography, highly erodible young volcanic soils, and high rainfall. Several studies have demonstrated the negative effects of sedimentation on coral reefs adjacent to small, tropical Pacific Ocean islands (Golbuu et al., 2003, 2008; Wolanski et al., 2003b; Victor et al., 2006; Fabricius et al., 2007; Richmond et al., 2007). Sediments adversely affect reefs in several ways; they cause reductions in coral cover, coral richness, coral colony abundance, and coral recruitment (reviewed by Fabricius (2005)). Yet, measuring terrestrial discharge at the mouth of rivers gives little insight on reef processes because sediment flux differs with local tidal regimes, different levels of wave exposure, and local bathymetry (Golbuu, 2010; Golbuu et al., 2011). These hydrodynamic differences influence sediment dispersal patterns and change the receiving water characteristics,

which in turn influences reef composition (Rogers, 1990; van Woesik et al., 1999; Fabricius, 2005).

Although the composition of coral communities reflects the interactions among complex chemical, physical, and biological attributes of a particular site, it is often difficult to assess the relative contribution of each specific attribute. Three approaches are most often used. The first approach selects sites at the end points of a known environmental gradient (sometimes also including mid-gradient sites), and examines differences between those sites (Randall and Birkeland, 1978; Acevedo and Morelock, 1988; van Katwijk et al., 1993; McClanahan and Obura, 1997). The second approach selects sites along a known environmental gradient, and examines differences in coral-reef communities at numerous sites along that gradient (Tomascik and Sander, 1987; van Woesik et al., 1999; Fabricius et al., 2005; Dikou and van Woesik, 2006; Fabricius and McCorry, 2006; Cooper et al., 2007; Golbuu et al., 2008). Taking this second approach requires considerable preliminary field work to identify the gradient in the first place. Also, such field studies often infer processes, but rarely measure them (Tomascik and Sander, 1987; van Woesik et al., 1999; Dikou and van Woesik, 2006).

The third approach involves coral transplantation. Davies (1990) measured the growth rate of *Porites porites* and *Montastrea annularis* along a gradient of increased nutrients. *Pocillopora damicornis* transplants were used to assess the impact of a sewer outfall on growth, mortality, and fecundity (McKenna et al., 2001). Bucher

* Corresponding author at: Palau International Coral Reef Center, 1 M-Dock Road, P.O. Box 7086, Koror 96940, Palau. Fax: +680 488 6950.

E-mail addresses: ygolbuu@picrc.org (Y. Golbuu), rvw@fit.edu (R. van Woesik), richmond@hawaii.edu (R.H. Richmond), pharriso@scu.edu.au (P. Harrison), k.fabricius@aims.gov.au (K.E. Fabricius).

and Harrison (2002) used *Acropora longicyathus* colonies at One Tree Island, Great Barrier Reef, to assess the impact of increased nutrients on linear extension rates and buoyant weight. In Hawaii, 3–4 cm *Pocillopora damicornis* branches were used to determine the influence of differing levels of sedimentation on coral growth (Piniak and Brown, 2008). Such manipulative studies are rigorous and comparative, but miss the early post-settlement stages, when corals are most vulnerable (van Woessik et al., 1999). Therefore, in this study we combine the second and third approaches. We measured the physical environmental conditions along a gradient moving away from the mouth of Ngermeduu Bay in Palau. The environmental variables included sedimentation, salinity, suspended solids, and temperature. We used coral transplant manipulations to determine the relationship between the physical environmental and coral growth and mortality rates. This study aimed to assess the effects of watershed discharge on coral com-

munity structure by examining relationships between the environmental variables and the biological parameters.

2. Methods

2.1. Study area

The study area was located in Palau, adjacent to the Ngermeduu watershed, Babeldaob's largest watershed (86.3 km²) (Fig. 1). The watershed contains several farms and unpaved roads. Three rivers flow through the Ngermeduu watershed, draining into Ngermeduu Bay; the watershed's sediment yield is the second highest in Palau, approximated at 216 ton km⁻² yr⁻¹ (Golbuu, 2010; Golbuu et al., 2011). Five similar coral reef sites were selected along a perceived discharge gradient (Fig. 1); Site 1 was located near the mouth of the bay, whereas Site 5 was farthest away.

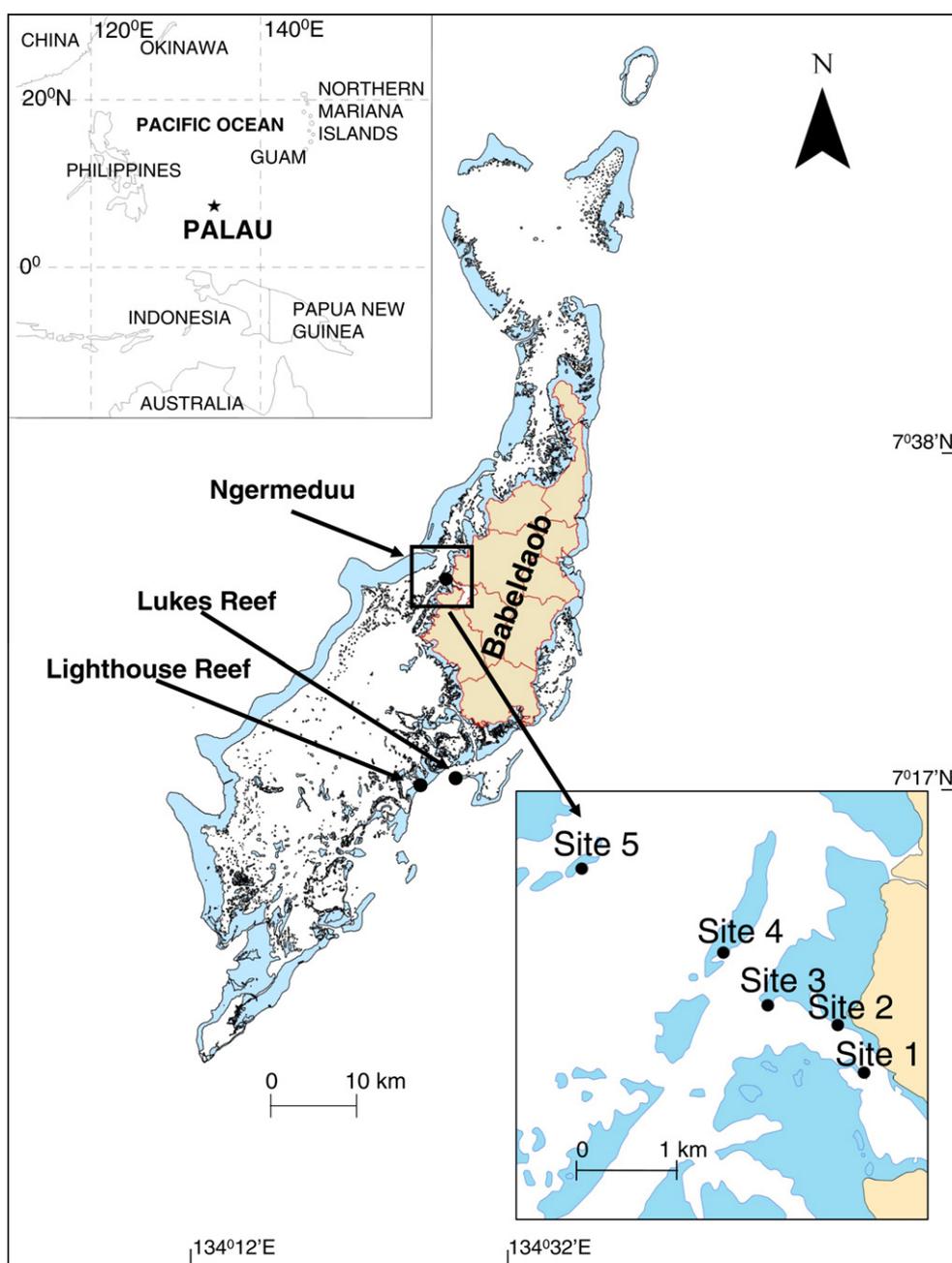


Fig. 1. Study location; an aerial photograph of Babeldaob showing Ngermeduu study area and a close-up view of the study sites.

2.2. Physical parameters

Rainfall data were collected using a HOBO Weather Station Rain Gauge from August to November 2007. Oceanographic moorings were deployed at 3 m at all five sites (Fig. 1). Self-logging CTD-cum nephelometers (YSI model 6920) were used to measure suspended solids concentrations (SSC), temperature, and salinity. Data were logged every 10 min. Logger wipers cleaned the turbidity sensors every 10 min. The loggers were deployed at all five sites from 9 to 22 August 2007. They were retrieved to download the data, serviced, and redeployed at Sites 1, 3 and 5 from 23 August to 11 September 2007, and 14 September to 9 October 2007. Collection of data for Sites 2 and 4 were discontinued after 22 August 2007. At each site, six bottom-mounted-sediment traps (5.1 cm diameter, 61 cm height), were deployed during the coral transplant period. Accumulated sediments were measured every month, for 3 months (7 August to 11 September 2007; 14 September to 15 October 2007; 17 October to 27 November 2007). Collected sediments were dried and weighed to the nearest 0.1 mg using an analytical semi-micro balance (A&D™ GR-120) to obtain total sedimentation rates ($\text{mg dry weight cm}^{-2} \text{d}^{-1}$), and re-weighed after treatment with 10% hydrochloric acid to determine the carbonate fraction. The sediments were re-weighed after burning at 600 °C for 2 h to remove organic matter. The remaining weight was used to estimate the amount of terrestrial (i.e., inorganic, non-carbonate) sediments.

2.3. Benthic surveys

Benthic cover, adult coral richness (generic), and overall community composition, including corals, were recorded using video transects in October 2007. At each site, five 20 m transects were haphazardly placed on the reef at 3 m. The substratum was recorded with an underwater video camera about 60–70 cm above the benthos, at a speed of about 2 min per 20 m transect. In the laboratory, 40 non-overlapping frames were sampled for each 20 m transect, and within each frame (image) we identified the benthos using five fixed sampling points on the computer screen. Coral richness (genera) and community composition were assessed from the same images that were used for the benthic surveys. Community composition included estimates of the abundance of all hard and soft coral genera, ascidians, carbonate substrata, *Halimeda* spp., *Lobophora* sp., other macroalgae, *Millepora* spp., mud, rubble, sand, sponge, and turf algae. The richness measurement from videos did not include corals less than 5 cm in diameter. The diameter and genus of all juvenile corals, between 0.5 and 5 cm, were recorded using visual surveys along 0.3 m either side of the first 10 m of each transect ($n = 5$). This provided an area of 3 m², in which the density of juvenile corals was calculated. In the results, density was then divided by 3 to give density per m².

2.4. Coral transplants

Six colonies of *Acropora digitifera* were collected from Lukes Reef and six colonies of *Porites cylindrica* were collected from Lighthouse Reef on 1 August 2007 (Fig. 1). From these 12 colonies, nubbins of three size classes (1, 2, and 4 cm) were created by breaking off branch tips. Each nubbin was weighed using the buoyant weight method (Ohaus™ Adventure Pro electronic balance) to the nearest 0.1 g. The bases of the nubbins were placed in tubes, which were inserted into holes drilled into cinder blocks. Each cinder block had three *P. cylindrica* and three *A. digitifera* nubbins of either 1, 2, or 4 cm size attached. To avoid pseudoreplication, the average, or mean growth and mean mortality was calculated for each cinder block and was used as the primary sampling unit. Nine blocks with nubbins of the three different sizes were placed in each

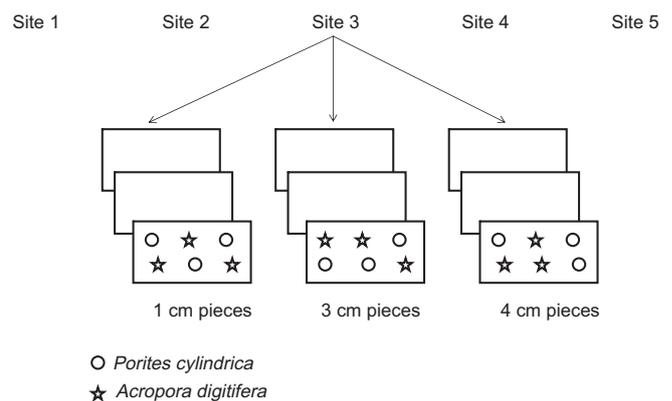


Fig. 2. Schematic of experimental design for the transplantation study (note that the primary sampling unit was a block, therefore the growth rates were averaged across each rectangular block and used as the primary data).

of the five sites ($n = 45$) (Fig. 2). The blocks were transplanted to the five sites adjacent to Ngermeduu Bay on 6 August 2007. Every month from September to November (11 September 2007, 16 October 2007, 28 November 2007), the nubbins were brought to the laboratory and weighed, mortality was recorded, and the nubbins were then returned to the field. The nubbins remained in the field for 5 months; at the end of the 5th month (16 January 2008), only mortality was assessed, no growth data was collected. Forty-one of the nubbins fell off the blocks during the experiment and were categorized for data analysis as missing.

3. Data analysis

3.1. Multivariate gradient analyses

To examine potential differences in overall community structure (which included hard and soft corals, sponges, sand, rubble, turf and macroalgae), non-metric Multi-Dimensional Scaling (nMDS) analysis was conducted using PRIMER v6.1 (Clarke et al., 2005). The data matrix consisted of mean benthic cover of the major benthic categories. For coral communities, the data matrix consisted of mean coral cover of each coral genera, at each site. The samples were comprised of survey data from each transect, at each site. A Bray-Curtis Similarity matrix was created from the square root transformed data matrix prior to conducting the nMDS analysis. A permutation-based hypothesis testing analysis of similarities (ANOSIM in PRIMER 6.1) was used to conduct pair-wise comparisons between locations (Clarke and Gorley, 2001; Clarke and Warwick, 2001). Subsequent SIMPER analyses were conducted to examine which coral genera contributed most to the group differences.

3.2. Statistical analyses

Prior to statistical analysis, the raw data were tested for violations to the assumptions of normality and homogeneity of variance; normality was assessed using the normal probability plot procedure and the Shapiro–Wilks test. Homogeneity of variances was tested using Levene's test, and where appropriate, transformations were applied to the data. To compare total coral cover, coral richness, juvenile coral density and juvenile coral richness across the five sites, one-way Analysis of Variance (ANOVA) tests were performed using site as a fixed factor. To compare growth rates of the transplanted *A. digitifera* and *P. cylindrica* nubbins, two-way ANOVAs were conducted using site and initial size of nubbins as fixed factors. These analyses were conducted using the software Statistica®.

Table 1
Physical and biological characteristics of the five study sites.

	Site 1	Site 2	Site 3	Site 4	Site 5
Distance to river mouth (m)	2519	2953	3515	4046	5327
Salinity (ppt) mean \pm SE	32.0 \pm 0.008	33.8 \pm 0.02	33.6 \pm 0.002	33.5 \pm 0.01	33.4 \pm 0.004
Salinity minimum (ppt)	25.4	29.3	32.1	30.3	29.8
Temperature ($^{\circ}$ C) mean \pm SE	29.6 \pm 0.008	29.0 \pm 0.008	29.6 \pm 0.002	29.0 \pm 0.009	29.7 \pm 0.003
Temperature minimum, maximum ($^{\circ}$ C)	28.0, 31.0	28.0, 29.9	28.8, 30.4	27.7, 30.1	27.9, 30.6
Suspended solids concentration (SSC) (mg L^{-1}) mean \pm SE	7.4 \pm 0.05	1.0 \pm 0.02	3.1 \pm 0.05	0.9 \pm 0.03	1.5 \pm 0.01
SSC maximum (mg L^{-1})	218.9	9.1	152.4	8.0	27.7
Sedimentation (terrestrial) mean ($\text{mg cm}^{-2} \text{d}^{-1}$) mean \pm SE	9.3 \pm 0.7	1.6 \pm 0.2	0.6 \pm 0.1	0.2 \pm 0.1	0.1 \pm 0.01
Sedimentation (organic) mean ($\text{mg cm}^{-2} \text{d}^{-1}$) mean \pm SE	4.4 \pm 0.4	0.7 \pm 0.1	0.3 \pm 0.05	0.1 \pm 0.02	0.05 \pm 0.005
Sedimentation (carbonate) mean ($\text{mg cm}^{-2} \text{d}^{-1}$) mean \pm SE	3.7 \pm 0.3	1.0 \pm 0.1	0.8 \pm 0.2	0.6 \pm 0.07	1.5 \pm 0.1
Sedimentation (total) mean ($\text{mg cm}^{-2} \text{d}^{-1}$) mean \pm SE	17.5 \pm 1.2	3.3 \pm 0.4	1.7 \pm 0.3	0.9 \pm 0.1	1.6 \pm 0.1
Coral cover (%)	5.40 \pm 2.22	6.40 \pm 2.32	21.80 \pm 4.99	38.30 \pm 4.15	22.30 \pm 3.28
Adult coral diversity (no. taxa) mean \pm SE	1.16 \pm 0.40	3.20 \pm 0.97	5.20 \pm 0.20	9.20 \pm 1.16	8.00 \pm 0.71
Juvenile coral density (no. m^{-2}) mean \pm SE	0.13 \pm 0.08	0.67 \pm 0.30	1.40 \pm 0.29	7.33 \pm 1.31	8.07 \pm 1.32
Juvenile coral richness (no. spp.) mean \pm SE	0.40 \pm 0.24	1.40 \pm 0.60	2.80 \pm 0.66	5.40 \pm 0.81	6.20 \pm 0.73

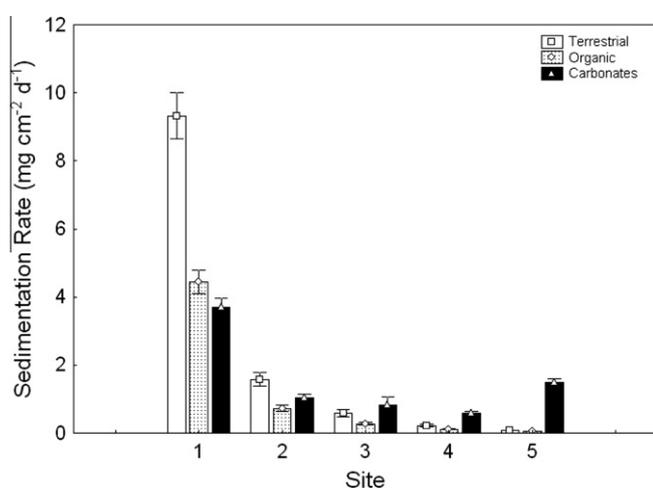


Fig. 3. Sedimentation rate (mean \pm SE) at the five study sites, including terrestrial, organic and carbonate sediments.

Simple regression analyses were conducted to determine relationships between distance from the mouth of the bay and (i) coral cover, (ii) coral richness, (iii) density of juvenile corals, and (iv) generic richness of juvenile corals. Linear models were also used to assess the relationships between the two dependent variables mortality and growth rates of transplants, and the distance from the mouth of the bay, colony size, and coral species. Multiple backward, stepwise regression analyses were performed to assess the relationships of different physical parameters with the biological parameters, which included coral cover, adult coral richness, juvenile coral density, and juvenile coral richness. Independent variables (mean salinity, minimum salinity, mean SSC, maximum SSC and terrestrial sedimentation) were tested and removed from the regression equation one-step at a time to obtain the best fit regression. All analyses were conducted using the software Statistica®.

4. Results

4.1. Physical parameters

The daily mean rainfall for the 4-month study period was 10.3 mm d^{-1} , which was similar to rainfall data collected from 2005 to 2007 that showed a daily mean of 10 mm d^{-1} (Golbuu et al., 2011). Mean salinity was similar at all sites, although there was a clear pattern of increasing minimum salinity from Site 1 to Site 5 (Table 1). At all sites, the temperature was similar throughout the study, ranging from 28 to $30 \text{ }^{\circ}\text{C}$. The mean suspended solids

concentration (SSC) decreased from Site 1 towards Site 5, with the decrease in maximum SSC even more pronounced (Table 1). Similarly, terrestrial sedimentation rates decreased substantially from the mouth of the bay out to Site 5 (Fig. 3; Table 1). Total sedimentation rate, and the organic component of the sediments, showed a sharp gradient of decreasing sedimentation from Site 1 to Site 5 (Table 1).

4.2. Benthic surveys

Coral cover had a significant, positive relationship with distance from the mouth of the bay ($R^2 = 0.29$, $p < 0.05$, Fig. 4a) with mean coral cover increasing by $7 \pm 2\%$ for every km away from the river. Mean coral cover was also negatively related to mean SSC (Table 2a), declining by 2.6% with every mg L^{-1} of SSC increase. Adult coral richness clearly increased away from the mouth of the bay towards Sites 4 and 5 (Fig. 4b; $R^2 = 0.55$, $p < 0.001$). The number of coral taxa per transect increased by 2.5 ± 0.3 with every km away from the mouth of the bay. Adult coral richness was best explained by terrestrial sedimentation, decreasing by 0.53 taxa with every addition of $1 \text{ mg cm}^{-2} \text{d}^{-1}$ of sediment (Table 2b).

There was a significant positive relationship between the mean density of juvenile corals and distance from the mouth of the bay (Fig. 4c; $R^2 = 0.66$, $p < 0.001$), with density increasing by 3.2 ± 0.27 juvenile corals m^{-2} for every km from the mouth of the bay. Terrestrial sedimentation was negatively related to the density of juvenile corals, with a decrease of 0.49 juvenile corals m^{-2} for every increase in $1 \text{ mg cm}^{-2} \text{d}^{-1}$ of sediment (Table 2c). Juvenile generic richness increased with distance away from the mouth of the bay by 2.2 ± 0.2 additional genera per transect for every km. The generic richness of juvenile corals was also negatively related with terrestrial sedimentation, with a decrease of 0.41 genera transect $^{-1}$ with every $1 \text{ mg cm}^{-2} \text{d}^{-1}$ increase in sedimentation (Table 2d).

Benthic communities clearly differed among the five sites (ANOSIM Global $R = 0.768$, $p = 0.001$; Fig. 5a). Comparisons between sites revealed that all five sites had clearly different benthic communities. Site 1 was distinct and was primarily a mud-covered substrata. Site 2 was mainly rubble, turf algae, and macroalgae (*Lobophora* sp.). Site 3 was mainly rubble, turf algae, and carbonate, while Site 4 was mainly rubble, *Seriatopora* sp., and carbonate. Sites 4 and 5 had some overlapping benthic communities, but overall the sites differed from each other (ANOSIM $R = 0.578$, $p = 0.032$). Site 5 was mainly, rubble, carbonate, and ascidians.

Coral communities had overlapping but clearly different assemblages (ANOSIM Global $R = 0.509$, $p = 0.001$; Fig. 5b). SIMPER analyses revealed that the coral communities at Sites 1 and 2 were defined primarily by *Porites*, which contributed 43% to transect

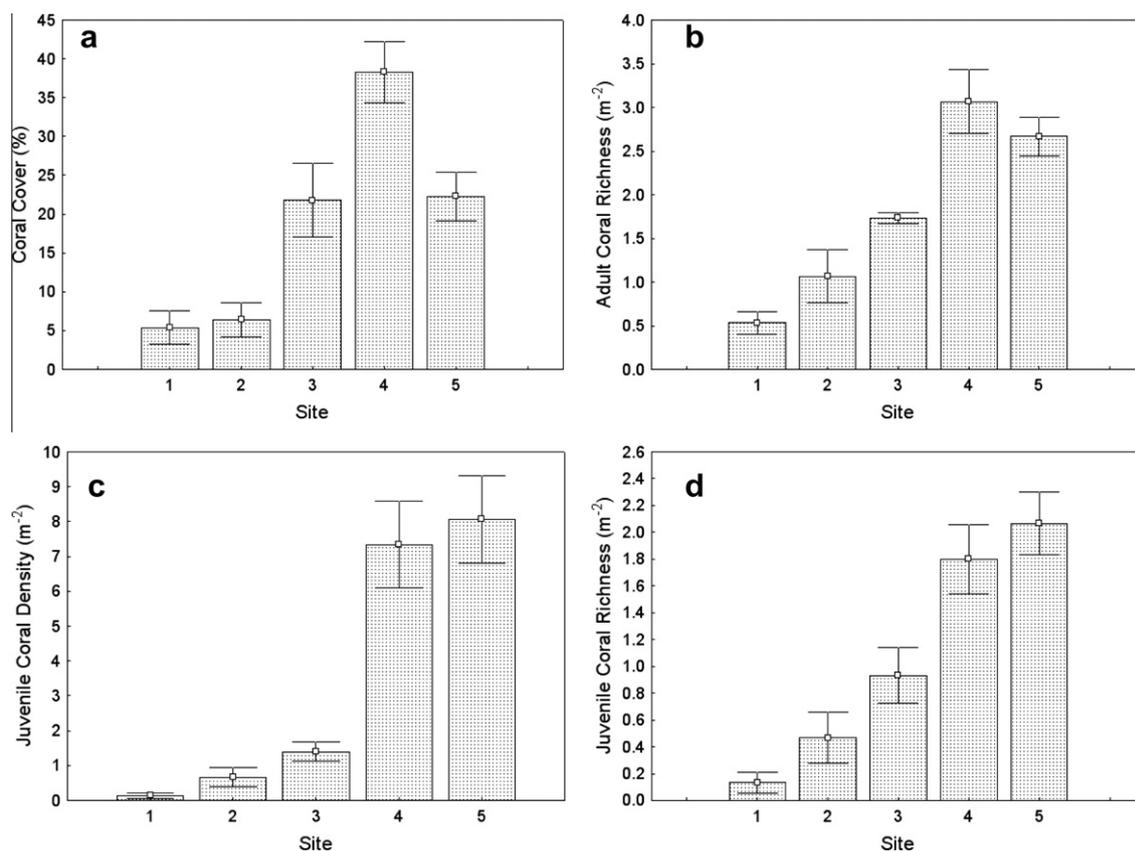


Fig. 4. (a) Coral cover (%), (b) adult coral richness (m⁻²), (c) juvenile coral density (m⁻²) and (d) juvenile coral richness (mean ± SE) (m⁻²) at the five study sites.

Table 2
Multiple regression analysis results that compared the relationship between reef community parameters and mean salinity, minimum salinity, mean suspended solids concentration (SSC), maximum SSC and terrestrial sedimentation. Of the 5 variables that were included in the model, only those with significant values ($p < 0.05$; $F \geq 11$) are shown, the others were excluded by backward elimination.

		Multiple R ²	F	p-level	Slope ± SE
(a) Coral cover	SSC (mean)	0.34	22.1	<0.001	-2.6 ± 0.6
(b) Adult coral richness	Sedimentation (terrestrial)	0.54	51.2	<0.001	-0.53 ± 0.07
(c) Density of juvenile corals	Sedimentation (terrestrial)	0.33	21.2	<0.001	-0.49 ± 0.11
(d) Richness of juvenile corals	Sedimentation (terrestrial)	0.47	38.4	<0.001	-0.41 ± 0.07

similarities, at Site 1, and 37% to similarities at Site 2. *Acropora* defined similarities at Site 3, contributing to 31% of the similarities. *Seriatopora* contributed to 36% of the similarities at Site 4, whereas *Montipora* contributed to 43% of the similarities at Site 5.

4.3. Coral transplants

After 5 months in the transplant sites, survival of *P. cylindrica* transplants was significantly higher than that of *A. digitifera* transplants (11% compared with 4%; Kruskal–Wallis ANOVA, $p = 0.02$); but results showed neither site nor size differences in survival rates. At the end of 115 d in the transplant sites, both *Acropora* and *Porites* transplants had increased in weight, but there was no significant difference in growth rates among the five sites (Fig. 6). Growth rates of *A. digitifera* nubbins increased significantly with an increase in nubbins sizes (ANOVA, $p < 0.001$), while *P. cylindrica* displayed no size-related difference in growth rates.

5. Discussion

The composition of the benthic communities clearly depended on how close they were to the mouth of Ngermeduu Bay. The sites

closest to the mouth of the bay were mainly mud covered, supporting no *Acropora* colonies. Suspended solids concentrations and sedimentation rates were highest near the mouth of the bay, whereas salinity was consistently low. There were clear increases in coral cover and coral richness moving away from the mouth of the bay. These results are similar to those from previous studies that have reported low coral cover and low coral diversity in areas near rivers exposed to high turbidity (van Woesik et al., 1999; Edinger et al., 2000; West and van Woesik, 2001; Fabricius et al., 2005; Dikou and van Woesik, 2006; Fabricius and McCorry, 2006; Golbuu et al., 2008), and for areas exposed to eutrophication and sedimentation (Tomascik and Sander, 1987; Edinger et al., 2000).

Differential sedimentation, particularly terrigenous sedimentation, seemed to strongly govern juvenile coral density and composition. Our results are similar to the study by Dikou and van Woesik (2006) in Singapore, and the numerous larval settlement experiments that have shown strong responses to differential sedimentation rates (Hodgson, 1990; Gilmour, 1999; Birrell et al., 2005). However, the present results differ from a study in the inner Great Barrier Reef (GBR) (van Woesik et al., 1999) that showed no relationship between sedimentation and recruitment, and no relationship with sedimentation and coral-community composition.

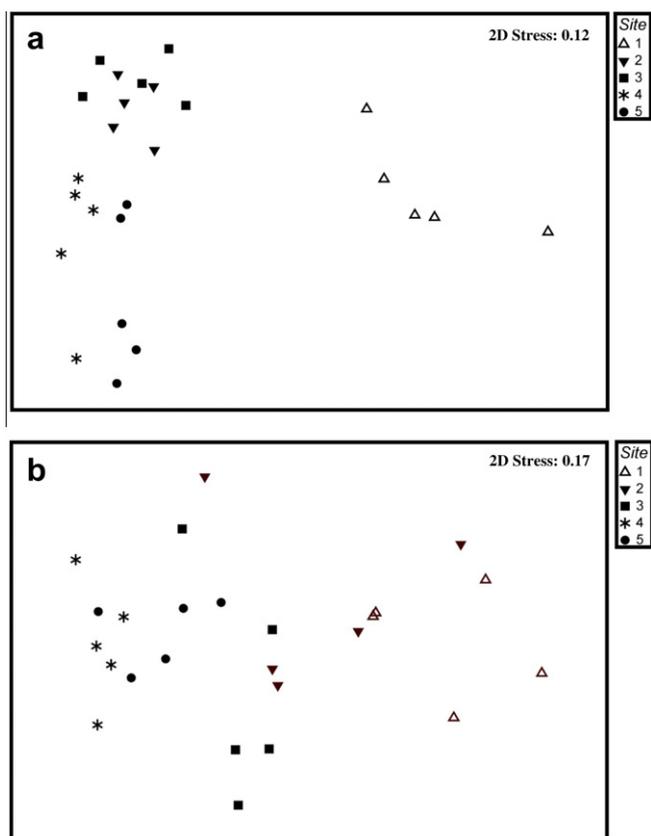


Fig. 5. Non-metric multidimensional scaling plot of (a) benthic and (b) coral communities at the five study sites. The data matrix consisted of mean benthic cover for the major benthic categories (a) and mean coral cover for each coral genus at each site (b). The samples were surveyed data from each transect, at each site. Individual points represent a transect at each site.

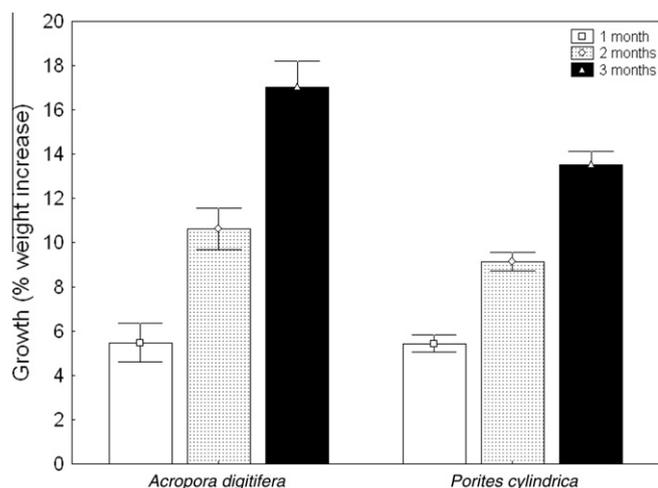


Fig. 6. Growth rates of *Acropora digitifera* and *Porites cylindrica* transplants (means across the five study sites).

We note that the inner GBR reefs, in the vicinity of the Whitsunday Islands are constantly subjected to ~4 m semi-diurnal tidal fluctuations. These large tides cause consistently high water-flow rates, preventing sedimentation except in extremely sheltered bays (van Woessik et al., 1999). Indeed, Maxwell (1968) pointed out that the benthic environment between islands and reefs within the Whitsunday region were devoid of fine-grained sediment because

of the consistently high water-flow rates. Therefore, extrapolating the results of the present study to other reef regions requires some caution, because although land-use change increases terrestrial sediment discharge, the effects of sedimentation varies greatly between sites and is primarily dependent on differences in local hydrodynamics (Golbuu et al., 2011).

We showed that the growth rates of *A. digitifera* and *P. cylindrica* were not significantly different among sites, although the large *Acropora* nubbins grew faster than the small nubbins. In contrast, *P. cylindrica* displayed no size-related difference in growth rates. Previous studies examining coral growth rates exposed to various forms of pollution have given contrasting results. For example, Tomascik and Sander (1985) found that linear extension rate of *M. annularis* increased initially with increased suspended particulate matter (SPM), but decreased when SPM exceeded a critical threshold – showing a unimodal response. *A. longicyathus* increased their linear extension rates when exposed to elevated concentrations of phosphate, while exposure to elevated ammonium concentrations resulted in an increase in buoyant weight (Bucher and Harrison, 2002). Growth rates of *Porites lobata*, measured as linear extension, were not different between unpolluted and eutrophic sites (Edinger et al., 2000). Similarly, De'ath et al. (2009) found no significant difference in growth rates of 328 colonies of massive *Porites* between inshore and offshore reefs along the Great Barrier Reef. In the Caribbean, Davies (1990) found no increase in growth rates of *P. porites* with increasing nutrients, but found significant reductions in growth rates of *M. annularis* under the same conditions. Most recently in Hawaii, Piniak and Brown (2008) reported that growth of *Pocillopora damicornis* did not decrease with an increasing sediment load. Such contrasting results are not surprising given that different coral species respond to different physical stimuli. Therefore, simply using linear extension of corals as an indicator of land-use change is problematic because some corals may respond positively whereas other species may respond negatively.

Acropora transplants showed higher mortality rates than *Porites* transplants, although we detected no differences in mortality according to colony size or location. Similarly, van Woessik et al. (1999) showed no differences in recruitment rates near and far from a river, but clear differences between juvenile and adult communities near the river mouth and at a distance. The authors suggested that high post-settlement mortality near the river was primarily responsible for the differences in coral-community composition. The present study may give insight into a size-escape effect. Although the smallest transplanted *Acropora* colonies were only 1 cm, this size may have given the colonies enough vertical extension to escape the rain of sediment. A one centimeter *Acropora* colony is at least 12 months old. Differences in larval settlement rates could further contribute to the observed differences in the distribution of *Acropora*. The discrepancy between site-independent transplant survival rates across sites and the rarity of *Acropora* near the river mouth suggests that the first year of life is the most vulnerable period for *Acropora* colonies. It is this early period when the selective pressures of the physical environment are most likely the highest (van Woessik et al., 1999). Settlement studies looking at newly metamorphosed spat are needed to explore this critical life-history stage.

Although Palau experienced a massive bleaching event in 1998 (Golbuu et al., 2007), that thermal stress event did not however change the conclusion of the present study. Certainly, thermal stress and subsequent bleaching differentially influences *Acropora* over *Porites* (Loya et al., 2001), and nearshore reefs in Palau were somewhat protected from thermal stress because of reduced irradiance through high turbidity (Golbuu et al., 2007). Since low irradiance can effectively reduce photoinhibition and bleaching, then such a thermal event would show a high survival of *Acropora*

nearshore. However, we saw the opposite – *Acropora* increased away from shore, along the discharge gradient. Therefore, the differences in coral community structure at our study sites cannot be attributed to the bleaching event of 1998, but rather the patterns we recorded were most likely attributed to the differential effects of watershed discharge.

In the present study, there were significant relationships between terrestrial sedimentation and (i) adult coral richness, (ii) juvenile coral density, and (iii) coral richness. Mean coral cover was not significantly related to terrestrial sedimentation rates, but showed a strong relationship with mean suspended solids concentrations. Similarly, a recent, large scale examination of the Great Barrier Reef, found that hard-coral richness had negative relationships with both turbidity and chlorophyll concentrations (De'ath and Fabricius, 2010). These results agree in part with a previous study, at a smaller scale, showing a strong, negative relationship with chlorophyll a concentrations and both coral cover and coral species richness (van Woesik et al., 1999). Yet, as reported above, the Whitsunday Island study did not find such relationships with turbidity. The differences between the studies may be simply a matter of scale, since the Whitsunday study was at a scale that was an order of magnitude smaller than the De'ath and Fabricius (2010) Great Barrier Reef study, while the present study was at a scale that was an order of magnitude smaller than the Whitsunday study. Indeed, other studies have found relationships between coral composition, percentage coral cover, and light extinction (Fabricius et al., 2005; Dikou and van Woesik, 2006; Fabricius and McCorry, 2006).

Our study found that absence of *Acropora* species was a good indicator of river discharge effects. Notably, massive and branching *Porites* survive high sedimentation and turbidity, and these colonies often form large monospecific stands. Yet, for this study, we found a significant relationship between coral cover and distance away from the mouth of Ngermeduu Bay and a negative relationship with suspended solids concentration. While this study showed that mean coral cover could be used as a proxy for stress, caused by fluvial discharge linked to land-use change, coral cover was not as powerful an indicator as coral diversity in explaining the observed trend in the data. Low coral diversity was a better indicator of terrestrial-discharge stress, and the lack of *Acropora* species was particularly indicative. Together, these results show that sedimentation and turbidity exert strong influences on near-shore coral-reef communities, reducing their diversity. The results have important implications for reefs in Palau and all reef systems downstream of rivers. Land development very often leads to increases in river runoff and suspended solids concentrations that reduce coral cover and coral diversity on adjacent reefs. These increases in terrestrial discharge need to be controlled and mitigation procedures put in place, to ensure that these nearshore reefs continue to support diverse and productive systems as they have for the past millennia.

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