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Changes in coral reef community structure along a sediment gradient in Fouha Bay, Guam

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ABSTRACT

High sedimentation rates have well-documented, deleterious impacts on coral reefs. However, few previous studies have attempted to quantitatively describe a coral reef community across a large continuous sediment gradient. In this study distinct benthic assemblages in Fouha Bay, Guam, were identified using a Moving Window Analysis conducted along a two-order of magnitude sediment gradient, with transition boundaries that were generally consistent with sediment thresholds identified in the literature. Coral richness dropped exponentially with increasing sedimentation rate. Richness was nearly three times greater in assemblages with sedimentation rates <10 mg cm^{-2} d^{-1} compared to assemblages experiencing rates between 10 and 50 mg cm^{-2} d^{-1}, and nearly 30 times greater than assemblages experiencing rates between 50 and 100 mg cm^{-2} d^{-1}. No corals were found in assemblages

with sedimentation rates >110 mg cm^{-2} d^{-1}. Reducing sedimentation in this area could result in a shift of more diverse and abundant coral assemblages toward the head of the bay.

KEYWORDS: coral reef, Guam, sediment, Moving Window Analysis, restoration, gradient, algae

INTRODUCTION

Coral reefs form biologically diverse ecosystems that provide important ecological functions and services to humans (Woodhead et al. 2019) and other organisms. They create habitat that supports diverse assemblages of plants and animals (Graham and Nash 2013, Fisher et al. 2015), including economically- and culturally-important fisheries (Golden et al. 2016, Grafeld et al. 2016); provide nearshore protection against storm waves (Ferrario et al. 2014, Beck et al. 2018), reduce coastal erosion; generate revenue through tourism-related activities (Spalding et al. 2017); and possess intrinsic and cultural value (Cinner et al. 2014, Grafeld et al. 2016).

Human activity has contributed to the widespread degradation of coral reefs (Wilkinson 2008, Jackson et al. 2014), primarily through centuries of resource over-extraction and the introduction of land-based pollutants, the latter mainly the result of poor land use practices that allow runoff of terrestrial sediments and other contaminants to reach nearshore reefs (Acevedo et al. 1988, Rogers 1990, Rongo 2004, Fabricius 2005, De'ath and Fabricius 2010). In recent decades, anthropogenic climate change has further stressed coral reefs across the globe, including remote reefs exposed to few or no local-scale stressors (Hughes et al. 2003, 2018; Heron et al. 2016a, 2016b).

Corals show species-specific (Erftemeijer et al. 2012, Cziesielski et al. 2018) and genotypic (Tisthammer et al. 2021) tolerances to stressors, thus the coral assemblage at a site likely represents the biological response to the physical, chemical and biological processes at that site integrated over time (van Woesik 2002). Assuming regional hydrodynamic processes and recruitment are similar, the differences in coral assemblages at adjacent sites are likely the result of the long-term effect of each site's local environmental condition on individual corals via selection of colonies that are tolerant to the local conditions, and removing those that are not (van Woesik 2002, Hughes et al. 2017, Ellis et al. 2019).

High islands in the Pacific, such as Guam, experience large, often intense, rain events; generally have highly erosive clay soils; and a history of watershed alterations that have significantly increased erosion rates and sediment loadings onto nearshore reefs (Minton 2005, Burdick et al. 2008, Shelton and Richmond 2016). In the absence of human activities, natural levels of suspended sediments on reefs are usually less than 5 mg l^{-1} and rarely exceed 40 mg l^{-1} (Larcombe et al. 1995; Kleypas 1996), but on reefs adjacent to degraded watersheds suspended sediments can reach 1,000 mg l^{-1} during periods of heavy rain (Wolanski et al. 2003, Rongo 2004).

Sediment directly settling onto coral colonies at high or chronic levels may directly kill them or exact an energetic cost by forcing sediment shedding (Fabricius 2005). Sediment covering the bottom impairs coral settlement and recruitment (Richmond 1997, Gilmour 1999, Fabricius and Wolanski 2000) and inhibits herbivory (Bellwood and Fulton 2008, Goatley and Bellwood 2012), although these interactions may be non-linear (Wakwella et al. 2020). Nutrients and other pollutants associated with sediment particles can stimulate algal and microbial growth (Erftemeijer et al. 2012, Weber et al. 2012), potentially shifting the competitive balance on the reef and contributing to a shift in assemblage structure (Hughes 1994). Silt and clay particles can remain suspended (or be re-suspended) and block sunlight from driving photosynthesis in symbiotic zooxanthellae (Fabricius et al. 2003, Erftemeijer et al. 2012, Jones et al. 2016, Bessell-Brown et al. 2017). These conditions contribute to decreased reef resiliency and threaten the persistence of coral reefs in the face of a changing climate.

While the direct impacts of sedimentation on coral reefs have been extensively studied (see reviews in Rogers 1990; Gilmour 1999; McCook 2001, Erftemeijer et al. 2012), little has been done to correlate sedimentation rates with changes in benthic community structure other than to propose sediment thresholds associated with categorical impact levels (e.g., low, moderate, severe). Notable exceptions include West and van Woesik (2001), who documented coral assemblage changes along a sediment gradient in Okinawa and correlated them with sedimentation rates, and Rongo (2004), who conducted a similar study in Fouha Bay, Guam, upon which this study builds.

Sediment gradients produced by river discharge affect coral assemblages over decadal time periods. Distinct coral assemblages are often observed, and may have either gradual or distinct delineations, based on the abruptness of the sediment decay rate (West and van Woesik 2001). A steep decay rate can result in significant decreases in sedimentation over relatively small spatial scales and can magnify the presence of sediment thresholds resulting in distinct and identifiable assemblage transition boundaries. Using a Moving Window Analysis (MWA) both West and van Woesik (2001) and Rongo (2004) identified and described several distinct coral assemblages along riverine sediment gradients on Pacific coral reefs. Assuming sediment is the primary ecological driver on these reefs, the sedimentation rate at each assemblage transition boundary represents a threshold rate likely responsible for the change in the coral assemblage. Conceivably, any change in the amount of sediment discharged from the river would shift the spatial location of the transition boundary, causing the adjacent benthic assemblages to "migrate" through space.

This study expands on the work of Rongo (2004) in Fouha Bay by increasing the taxonomic breadth from coral to all benthic organisms, and by examining benthic assemblage change at two depths. Furthermore, it attempts to identify indicator taxa in each assemblage along the sediment gradient, with the goal of understanding ecological changes that could occur if sedimentation rates were reduced through improved management of terrestrial runoff.

METHODS

Study Location

Fouha Bay (Fig. 1), on the southwest shore of Guam, is a small, well-mixed, funnel-shaped bay approximately 400 meters (m) long. The bay possesses a well-developed coral reef bisected by a channel that runs from the mouth of the La Sa Fua River to the mouth of the bay. The channel depth varies from <1 m on the reef flat to 11 m at the bay's mouth. The La Sua Fua River drains into the eastern end of the Bay but has minimal flow (0.1 m^{-3} sec^{-1}) under non-storm conditions, which creates a small surface plume (0.5 m thick) with a minimum salinity of ~34 parts per thousand (ppt) (Wolanski et al. 2003). Under storm conditions this plume can thicken to 1.5 m (but generally is around 1 m thick) with a minimum salinity of 22 ppt near the river mouth, but well-mixed to near ocean salinity by the time it reaches the mouth of the bay.

Improper erosion control during road construction adjacent to the bay in the 1980s allowed sediment to run into the bay, burying and killing many corals (Richmond 1993), and likely shifting the coral reef community into a different state. Prior to road construction, 155 coral species in 46 genera were reported from Fouha Bay (Randall and Birkeland 1978). Two decades after road construction, Wolanski et al. (2003) and Rongo (2004) observed 102 and 92 species, respectively.

The La Sa Fua River drains a watershed in which erosion rates range from 480 to 1,200 tons of soil km^{-2} yr^{-1} (Schemann et al. 2002). These high erosion rates are the result of grazing by introduced deer; mass wasting associated with unstable streambanks; and vegetation burning by hunters, which exposes steeply-sloped, highly erodible lateritic soils; and the presence of paved and unpaved roads that expose soil and accelerate sheet flow (Rongo 2004). The average annual rainfall in the La Sa Fua watershed is about 2.5 m yr^{-1} with distinct wet and dry seasons. During the wet season, rainfall is frequent and often intense, contributing to sediment pulses and suspended sediment loads that exceed 1,000 mg l^{-1} (Wolanski et al. 2003). Rongo (2004) measured average daily sedimentation rates in excess of 200 mg cm^{-2} d^{-1} near the river mouth. The sedimentation rate decreased exponentially with distance from shore, with most sediment deposited within ~160 m of the river mouth (Rongo 2004). The sediment accumulates within Fouha Bay during calm periods, but can be flushed out during episodic southern swell events (Wolanski et al. 2003).

Benthic Surveys

Between April and August 2014, benthic communities were assessed along four transects extending from near the river mouth to the seaward end of Fouha Bay, with two transects each on the north and south sides of the bay (Fig. 1). Transects were placed at 1 m and 6 m depth (hereafter, shallow and deep, respectively), and varied in total length from 150–450 m. Transects were surveyed starting at the head of the bay and working seaward; the only exception being the north deep (ND) transect, which was surveyed in reverse due to poor weather conditions and time limitations. For these same reasons, surveys along the ND transect were stopped after 150 m, resulting in a line that was less than half the length of the others, with a landward position significantly farther offshore than the other three transects. As a result, data obtained along this transect was not analyzed, but are provided in the supplemental information.

At five-meter intervals along each transect, surveyors assessed the benthic community within a 1-m^2 quadrat strung in a grid with 25 intersections. Data in each quadrat were collected using two survey methods, including a point intercept (PI) survey and a coral colony count/size survey (CCS). For the PI survey, the benthic organism beneath each intersecting point of the grid was identified to the lowest possible taxonomic level. If no benthic organism occurred beneath the intersection, the substrate type (e.g., sand, silt, rubble, etc.) was identified. Percent cover was calculated by dividing the total number of points found for each taxon by the total number of points in the quadrat (25) yielding a minimum percent cover resolution of 4%. For the CCS survey, all corals whose geometric center fell within the quadrat (Zvuloni et al. 2008) were identified to the lowest possible taxonomic level and measured to the nearest centimeter along two axes: (a) the longest dimension (=length), and (b) at the coral's widest point, perpendicular to the longest dimension (=width). Planar surface area (PSA) of all coral colonies was estimated assuming the colonies were ovals, an approach that likely biases estimates towards higher values, with the magnitude of bias positively correlated with length and width measures. A plot of average colony length (generated using longest axis measurements) showed no relationship with position on the transect line (except for a short stretch at around the 200 m mark on both shallow transects), suggesting that computational biases are constant along the length of the transect and are unlikely to affect the analysis.

Surveys of the ND transect were interrupted for several months during an extended period of high surf that made field conditions hazardous for divers. During this time, a mass bleaching event affected many of Guam's reefs, including those in Fouha Bay. All other transects were completed prior the 2014 bleaching event. Analyses of data collected at 48 sites around Guam during a coral bleaching event in 2013 found acroporids and pocilloporids were particularly susceptible to thermal and irradiative stress (Reynolds 2016, Raymundo et al. 2019). Surveyors observed numerous *Pocillopora* skeletons that exhibited a similar state of erosion along the north shallow (NS) transect, an area of Fouha Bay where living colonies were known to have occurred prior to 2013, strongly suggesting that the mortality of all or most of these colonies was the result of the 2013 bleaching event. To assess the potential effects of these bleaching-related mortalities on our analyses, surveyors also identified any bleached and recently dead corals along the transects. Analyses that included the *Pocillopora* skeletons as if living colonies were conducted, and produced the same results as those excluding the skeletons.

Moving Window Analysis

A Moving Window Analysis (MWA) is a scaling technique adapted from landscape ecology to investigate spatial relationships between landscapes, and to differentiate transition boundaries within those landscapes. MWA uses a relative measure of dissimilarity between consecutive samples along an environmental gradient to identify transition boundaries. Dissimilarity indices are calculated between adjacent "windows" and plotted against the distance from a point source, in this case the start of each transect at the head of Fouha Bay. A high dissimilarity value is generated when two “windows” are sufficiently different, with the "spike" signifying a boundary between two potentially different assemblages.

For each of the four transects, two separate MWA analyses were conducted using different data (Table 1): 1) cover of coral taxa, grouped by genera, derived from the PI survey method (hereafter referred as MWA-PI), and 2) PSA of coral taxa, grouped by genera, as calculated from the CCS data (MWA-CCS).

Only coral data were used in the MWA because other studies found they yielded the best signal-to-noise ratio and clearest results (West and van Woesik 2001, Rongo 2004). Likewise, data grouped above the species level (e.g., genera, morphology) provided better MWA results than species-level data. Average coral cover (all taxa) over much of the south deep transect was <4%, resulting in 72% of the quadrats from the PI survey method having no coral identified within them. Therefore, the MWA-PI was not conducted for this transect, but the cover estimates for non-coral organisms derived from the PI method were used to describe any assemblages identified by the MWA-CCS.

Following guidance in West and van Woesik (2001), window size was varied initially to identify the number of consecutive quadrats that would maximize the signal-to-noise ratio and provide the clearest delineation of likely transition boundaries. Each analysis window was created by averaging across two adjacent quadrats (for shallow water transects) or three adjacent quadrats (for deep water transects) along the length of the transect line. For example, analysis windows along a shallow transect would include the average of quadrats one and two, two and three, etc., such that windows comprised ($\bar{x}_{1,2}$), ($\bar{x}_{2,3}$), ($\bar{x}_{3,4}$). . . . ($\bar{x}_{Rn-1,n}$).

Dissimilarity for each adjacent set of windows was calculated using the Bray-Curtis distance, D_{jk}:

$$\sum \frac{|(Y_{ij} - Y_{ik})|}{(Y_{ij} + Y_{ik})}$$

where *p* represents the genus; Y_{ij} represents the abundance of the *i*th genus in the *j*th window; and Y_{ik} represents the abundance of the *i*th genus in the *k*th window (i.e., adjacent windows). A resulting value close to 100% indicates two windows with low similarity and represents a potential transition boundary between two dissimilar assemblages.

The dissimilarity matrix did not significantly change when recently dead pocilloporid corals were included in the MWA as if still alive. Changes in the matrix were generally less than 0.001%, and none of the differences change the results of the MWA. Therefore, only the results from the analyses without the dead corals are included.

Potential transition boundaries were confirmed by conducting an Analysis of Similarities (ANOSIM) (Clark and Warwick 2001) on the identified assemblages using the coral genera data from the quadrats within each assemblage (Table 1). If the ANOSIM found no significant difference between the two assemblages, the transition boundary was determined to be "false" and the two assemblages combined into a single one and the ANOSIM analysis was re-run. The process continued until no additional "false" boundaries were identified.

All assemblages supported by ANOSIM were investigated using a Similarity-Percentages Analysis (SIMPER), which calculates the contribution of taxa to overall similarity of all quadrats within the assemblage. For this analysis, all taxa from the PI data were used to describe the complete benthic assemblage (Table 1). A species was considered representative of an assemblage if its contribution to the similarity of the quadrats comprising the assemblage divided by its standard deviation (SIM/SD ratio) was greater than 1.3 (Clark and Warwick 2001). Representative taxa are those present across all or most of the quadrats within the assemblage and thus can be considered characteristic of that assemblage. ANOSIM and SIMPER analyses were conducted using Primer-6 (PRIMER-E, Plymouth). Data are presented as mean ± standard error of the mean (SEM).

Sedimentation Rate

Transition boundaries were compared to sedimentation rates estimated from the sediment decay model developed for Fouha Bay by Rongo (2004):

$$S = A\,e^{-r\,d}$$

Where S is the average annual sedimentation rate in g cm^{-2} yr^{-1}, A is a constant derived from modeling the sedimentation rate at Rongo's sediment trap nearest to the river mouth (A=37.382 g cm^{-2} yr^{-1}), d is the distance from that sediment trap in meters, and r is a constant derived from Rongo's exponential decay in sedimentation rate derived from his Fouha Bay trap data (r=0.0145 m^{-1}). While having a good fit overall, Rongo's model underestimated sediment loads closest to shore. Rongo's sediment trap nearest the river mouth was located at approximately the 35-m mark on the shallow water transects in this study, so sedimentation estimates were calculated with 35 m as "zero" distance in Rongo's model.

Rongo developed the model from sediment trap data collected along the south side of the Fouha Bay, but for this study the results have been applied to all transects. Rongo found no significant differences in sedimentation rates (as measured by traps) between the north and south sides of the bay, but variability was high, and his data suggested higher sedimentation rates in deep compared to shallow water and along the south compared to the north side of the bay. Where applicable, this was taken into consideration when interpreting results.

While a decade old, Rongo's sedimentation data and model are the best available sedimentation rate information for Fouha Bay. Small-scale erosion control and reforestation efforts in the La Sa Fua watershed have occurred over the last decade (Shelton and Richmond 2016), but given the long time-scale associated with such restoration projects and continued wildfire activity within the watershed, these efforts, which were begun in June 2012, were unlikely to have had time to significantly reduce sediment loads onto the reef by the time of our Fouha Bay surveys. It is likely that the corals surveyed in Fouha Bay were a product of the chemical, physical, and biological conditions that existed at the time of Rongo's study, excepting the impacts of the recent coral bleaching event.

RESULTS

South Shallow (SS) Transect

The MWA-PI and MWA-CCS identified three distinct assemblages along the SS transect (Fig. 2, Table 2) with transition boundaries at 85 m and 190 m. The PI data also identified three "false" transition boundaries (330 m, 375 m, and 405–410 m) that were not supported by follow-up ANOSIM analysis.

The SS1 assemblage (0–85 m) was closest to the head of Fouha Bay and characterized by high cover of turf algae (75.4 ± 3.6% cover), the presence of the lightly-calcified macroalgae *Padina* sp. (2.7 ± 0.7%), and unconsolidated sediment (16.4 ± 4.4%). No corals occurred in this assemblage. Total taxa richness included only 11 algal taxa (Supplemental Table S.2), most of which were rare. The average daily sedimentation rate estimated from Rongo's (2004) model ranged from 49.6 to 164.2 mg cm^{-2} d^{-1}.

Offset by a sharp transition boundary with SS1, the SS2 assemblage (85–190 m) was characterized by the coral *Porites* sp. (massive) (35.2 ± 9.4%), turf algae (26.0 ± 5.0%) and the macroalgae *Tricleocarpa fragilis* (8.4 ± 1.5%). Total richness increased to 34 taxa, including 12 corals (Tabel S.1). The average daily sedimentation rate ranged from 10.8 to 49.6 mg cm^{-2} d^{-1}.

At 190 m, SS2 transitioned into the SS3 assemblage (190–445 m), which had a total of 75 taxa, including 38 coral taxa (Table S.1). Turf algae (50.2 ± 2.5%) continued to be a dominant benthic organism, but *Porites* sp. (massive) decreased in abundance and *Goniastrea retiformis* (13.9 ± 2.5%) became the dominant hard coral species. Towards the mouth of Fouha Bay, the abundance of *Millepora platyphylla* increased, suggesting increased water motion in that area. This is further supported by increases in the cover of several taxa of macroalgae generally found in moderate to rough water (e.g., *Turbinaria ornata* and *Amphiroa* cf. *fragilissima*) near the end of the SS transect. These gradual shifts in assemblage structure likely accounted for the false transition boundaries observed in the MWA-PI. The average daily sedimentation rate ranged from <1 to 10.8 mg cm^{-2} d^{-1}.

North Shallow (NS) Transect

The MWA-PI and MWA-CCS identified different transition breaks, and the interpretation was not as straightforward as with the SS transect. The MWA-CCS identified only two assemblages along the NS transect (Fig. 3), with a single sharp transition boundary at 25 m (Table 3). In contrast, the MWA-PI identified seven potential assemblages with transition boundaries at 80 m, 115 m, 330 m, 360 m, 375 m, and 410 m.

When the results from both the MWA-PI and MWA-CCS were considered, three transition boundaries were identified with a high level of confidence. A sharp transition boundary occurred 25 m, as identified by the MWA-CCS. The NS1 assemblage (0–25 m) was characterized by turf algae (42.4 ± 10.3%) and an absence of all coral. Five other algal taxa were found in NS1, including *Acanthophora spicifera* (20.8 ± 6.9%) and *Padina* sp. (2.8 ± 2.3%), which are commonly found in calm, sedimented areas (Minton pers. obs.). Much of the bottom was unconsolidated sediment (29.2 ± 18.8%), and the average daily sedimentation rate ranged from 118.5 to 164.2 mg cm^{-2} d^{-1}.

The first coral colonies appear after the transition boundary at 25 m, but the PI survey method lacked the sensitivity to detect these colonies, whereas the CCS survey method detected a few small *Leptastrea purpurea* colonies, which accounted for only 0.2 ± 0.1% cover between 25 and 80 m.

After 80 m, two additional coral species were detected, *Porites* sp. (massive) and *Pocillopora damicornis*, lending support to the 80 m transition boundary identified by the MWA-PI. The second highest dissimilarity peak in the MWA-CCS data also occurred at 80 m (DISS=70.5%), further supporting an 80 m transition boundary.

The NS2 assemblage (25–80 m) was characterized by a single coral taxon, *Leptastrea purpurea*, and high cover of turf algae (60.9 ± 4.5%). Total richness was 16 taxa, and comprised mostly algae species associated with hard bottom. The average daily sedimentation rate ranged from 53.4 to 118.5 mg cm^{-2} d^{-1}.

Beyond 80 m coral diversity was high (45 taxa), but with only 4 species accounting for approximately 80% the total coral PSA and five species accounting for nearly 70% of all coral colonies. While these species had general "zones" in which they occurred (Fig. 4), the zones were likely not sufficiently distinct to create clear transition boundaries. The MWA-PI identified five transition boundaries beyond 80 m (Fig. 3), but three were the result of quadrats with no coral (115 m, 375m, and 410 m), and likely resulted from the lack of sensitivity of the PI method, and were not meaningful transitions. Coral cover was generally <4%, which made it difficult for the PI method to detect it, so while coral was present in every quadrat from 25–450 m (as found with the CCS method), the PI survey method estimated 0% coral cover in several. Removing these transition boundaries from consideration, the MWA-PI detected three transitions: 80 m, 330 m, and 360 m, only two of which (80 m and 360 m) were supported by follow-up ANOSIM analysis (Table 3). The NS3 assemblage (80–330 m) was characterized by high taxa richness (73 total taxa including 39 coral taxa), and showed a gradual change in composition with increasing distance from the head of Fouha Bay (Fig. 4). *Porites* sp. (massive) was the dominant coral nearest the head of the bay, gradually losing dominance to *Goniastrea retiformis*. Turf algae (45.4 ± 1.9%) and crustose coralline algae (11.6 ± 1.0%) were also representative of the assemblage. The average daily sedimentation rate ranged from 1.4 to 53.4 mg cm^{-2} d^{-1}.

The NS4 assemblage (330-450 m) shared many taxa with NS3. Turf algae (57.2 ± 3.6%) and crustose coralline algae (19.7 ± 2.5%) continued to be dominant organisms, but the hydrocoral, *Millepora platyphylla* (22.8 ± 10.5%), increased in abundance, replacing *Goniastrea retiformis* as the dominant structure builder (Fig. 4). In this assemblage taxa richness decreased to 39 total taxa including 27 coral taxa. Many of the taxa present in this assemblage were characteristic of high water motion reefs (e.g., *M. platyphylla*). This assemblage occurs on the seaward edge of the north side of Fouha Bay, and was regularly exposed to high swell/surf conditions originating from the southwest. Given that sedimentation rates in NS4 would not likely be significantly less than that along the outer portion of NS3, the primary driver of the 330 m transition boundary is likely an increase in wave exposure. The average daily sedimentation rate ranged from <1 to 1.4 mg cm^{-2} d^{-1}.

South Deep (SD) Transect

Detecting transition boundaries along the SD transect proved difficult due to low coral abundance and the patchy distributions of taxa. Coral over the first 235 m of the south deep transect was relatively rare (~2% cover), and its patchy distribution created significant problems for the MWA-CCS. However, after 235 m the distribution of coral became more consistent (Fig. 5), suggesting a transition boundary.

Follow-up ANOSIM supported a transition boundary at 235 m, but the low R-statistic (R=0.078) suggests that the two assemblages were not strongly different from each other.

This transition boundary is likely associated with a change in geomorphology. From 0–235 m the transect ran along the base of the channel wall, which was nearly vertical and often undercut. This geomorphology resulted in much of the area being heavily shaded, and nearly half of the cover (46.9 ± 5.1%) comprised of organisms growing on unconsolidated bottom (primarily turf algae). After 235 m, the transect emerged from the channel onto hard substratum, and the amount of unconsolidated bottom dropped to 11.0 ± 1.8%.

The SD1 assemblage (0–235 m) was dominated by turf algae (64.7 ± 3.7%) and bare unconsolidated substratum (18.1 ± 2.7%). A total of 41 taxa, including 25 coral taxa (Table S.1), were found, but most were rare (<1% cover). Total coral cover was low (~3%) and comprised mostly small (<20 cm) colonies of *Porites* sp. (massive) (0.8 ± 0.2%). The average daily sedimentation rate ranged 1.6 to 49.6 mg cm^{-2} d^{-1}.

The SD2 assemblage (235–400 m) was characterized by turf (50.0 ± 0.9%) and several macroalgal taxa, including, *Hypnea* cf. *spinella* (11.5 ± 1.3%), crustose coralline algae (3.9 ± 0.5%), *Caulerpa* sp. (2.5 ± 0.4%), and *Halimeda* sp. (2.6 ± 0.3%). Forty-one coral taxa (60 total taxa) comprised <7% of the benthic cover, with *Porites* sp. (massive) (2.3 ± 0.7%) the most common. The average daily sedimentation rate was <1.6 mg cm^{-2} d^{-1}.

Sediment effects on coral and non-coral taxa

Non-coral taxa richness was negatively correlated with sedimentation rate (Fig. 6), but never reached zero. Even at the highest sedimentation rates, two to three algal taxa were consistently present in each quadrat. Declines in coral taxa abundance were exponential; coral richness in quadrats dropped by nearly 75% when sediment exceeded 10 mg cm^{-2} d^{-1} (26 to 7 taxa). Quadrats with sedimentation rates >50 mg cm^{-2} d^{-1} had only one coral taxa (*Leptastrea purpurea*), and no corals were found in quadrats with >110 mg cm^{-2} d^{-1} (Fig. 6). Colony density decreased above 50 mg cm^{-2} d^{-1} by approximately 50%, after remaining relatively constant at lower sedimentation rates (Fig. 7).

Assemblage structure was significantly correlated with sedimentation rate (RELATE, rho = 0.182, p = 0.001). Of the 15 coral and non-coral taxa that occurred in at least 20% of the survey quadrats, 10 taxa showed a significant exponential decline with increasing sedimentation, 3 taxa showed no relationship with sedimentation rate, and 2 taxa showed a significant positive relationship (Table 4). While all species were present in areas with the lowest sedimentation rate (<1 mg cm^{-2} d^{-1}), taxon-specific "upper threshold" sedimentation rates (i.e., the sedimentation rate above which the taxon was not observed) varied from as little as 16 mg cm^{-2} d^{-1} (*Udotea* sp.) to the maximum rate possible, 164 mg cm^{-2} d^{-1} (turf algae and *Padina* sp.).

Few coral taxa were present across a suitable range of sedimentation rates and had a sufficient sample size to assess size-frequency distributions across sedimentation rates. On shallow water transects (on which more coral was measured, compared to deeper transects), *Cyphastrea chalcidicum* and *Leptastrea purpurea* show a trend toward increased colony size in assemblages with lower sedimentation rates (Table 5). , *Goniastrea retiformis* and *Porites* sp. (massive) showed no clear trend.

DISCUSSION

The composition of a coral reef is shaped by the response of species to the physical, chemical, and biological processes at a site. On nearshore reefs in close proximity to river discharges, freshwater, sediment and other terrestrially-derived pollutants are often important stressors, and, along with wave action, shape community structure (West and van Woesik 2001). In Fouha Bay, all three play a role in shaping coral reef community structure, and, depending upon a site's location within the bay, any or all three stressors could be influencing the site's reef community. Disentangling these stressors is important to understanding the relative importance of the processes shaping, and potentially degrading, the reefs in Fouha Bay.

As a well-mixed embayment, no significant differences in the spatial distribution of nutrients and temperature have been found in Fouha Bay (Randall and Birkeland 1978, Wolanski et al. 2003, Rongo 2004). The La Sa Fua river is a point source for the release of freshwater and sediment and creates a gradient of improving water quality from the mouth of the river to the mouth of the bay. Freshwater plumes up to 1.5 m thick can have a surface salinity of 22 ppt, but the salinity rapidly increases to oceanic levels with depth because the funnel-shape of the bay allows the plume to spread laterally across the surface (Wolanski et al. 2003). Reefs in Fouha Bay >1 m deep are seldom exposed to salinities below 34 ppt. A range of coral species have shown few lasting effects of brief exposure to salinities as low as 30 ppt (Hoegh-Goldberg and Smith 1989), and even the most salinity-sensitive species (e.g., some *Acropora* species.) can tolerate brief exposures to salinities of ~22 ppt (True 2012), making sediment the primary stressor on coral reefs on the interior of Fouha Bay, and likely the primary stressor responsible for many of the transition boundaries observed in this study (Table 6).

High levels of terrestrial sediment are deleterious to corals and other marine organisms. Rogers (1990) estimated that sediment in excess of 10 mg cm^{-2} d^{-1} was sufficient to cause impacts to coral assemblages, including lower species diversity and reduced coral cover, colony growth rates and recruitment. However, many coral reefs survive, likely with sub-lethal metabolic costs, in areas with sedimentation rates above this threshold (Fabricius 2005 and references therein, Erftemeijer et al. 2012), including on Guam (Minton 2005).

Working with data from Fouha and Ylig Bays on Guam, Pastorok and Bilyard (1985) estimated the qualitative degree of sediment impact on coral assemblages. Slight to moderate impacts, including decreased abundance and growth rates, were expected to occur at sedimentation rates between 1–10 mg cm^{-2} d^{-1}. Moderate to severe impacts, such as greatly decreased abundance and growth rates, altered growth forms, and reduced recruitment were expected at sedimentation rates of 10–50 mg cm^{-2} d^{-1}. Severe impacts, including the exclusion of many species and colony death, were expected to occur with sedimentation in excess of 50 mg cm^{-2} d^{-1}.

Consistent with Pastorok and Bilyard (1985), this study found severe community level impacts at modeled sedimentation rates above ~50 mg cm^{-2} d^{-1} in Fouha Bay (Figure 8). In these severely impacted areas, only three coral taxa were observed (Table 7), of which *Leptastrea purpurea* was the most common, even though it comprised <1% of the benthic cover. The two other taxa (represented by three total colonies) were located in a quadrat adjacent to the transition boundary. Non-coral taxa richness was low (20 taxa) and was dominated by turf algae. Turf algae can increase the retention times of sediment on reefs (Purcell 2000), and alter the bottom condition, making it less conducive to settlement from coral and other reef-associated organisms (e.g., many macroalgae settle on hard, sediment free substratum). No corals were observed in quadrats with modeled sedimentation rates above 110 mg cm^{-2} d^{-1}. In this severely impacted area (Figure 8), richness was reduced to six taxa (turf algae, *Padina* sp. *Acanthophora spicifera*, *Actinotrichia* cf. *fragilis*, *Hydrolithon* sp., and cyanobacteria), all of which are sediment tolerant, but most of which were also rarely encountered. This assemblage closely matches Rongo's (2004) N1 and S1 assemblages, which occurred along transects running through the same shallow reef areas as those in this study. Even the locations of the transition boundaries are nearly identical in each study at ~70 m (Note: Rongo's transition boundary was at 40 m, but the beginning of his transect lines were offset ~35 m offshore relative to this study, producing a nearly equivalent location of ~75 m).

Moderate impacts were found on reef areas farther away from the river mouth, where modeled sedimentation rates were between 10–50 mg cm^{-2} d^{-1}. Richness of all taxa was higher than on severely impacted reefs (Table 7), but taxa richness declined precipitously over the range of sedimentation rates associated with moderate impacts (Figure 8). Coral colonies were primarily massive or encrusting growth forms in the genera *Porites* and *Leptastrea*, which tend to be more tolerant of sediment (Erftemeijer et al. 2012). The algal assemblage was also more diverse than that on severely impacted reefs and included many macroalgae common to coastal hard bottoms, including species of *Amphiroa*, *Turbinaria*, *Caulerpa*, and *Dictyota*. The dominant coral species agreed closely with Rongo (2004), who noted massive *Porites* spp., *Leptastrea purpurea*, and *Goniastrea retiformis* as dominant taxa on his transects. The transition boundary identified along the south transect identified by Rongo was approximately 50 m closer to shore than the boundary identified in this study. The transects in this study were not intended to perfectly repeat Rongo's, and the agreement between his boundary and the one identified here is surprisingly close considering the spatial heterogeneity on many reefs and that over a decade has passed between measurements. Rongo's transition boundaries on the north side of Fouha Bay were nearly identical to those determined in this study, with his N2 assemblage extending from 70–310 m, compared to 85–330 m found in this study.

Reef areas experiencing modeled sedimentation rates <10 mg cm^{-2} d^{-1} appear to be lightly impacted in Fouha Bay (Figure 8), at least relative to more heavily impacted reefs in the area. Taxa richness in these areas was high, at over 120 total taxa and 84 coral taxa (Table 7). In these lightly impacted reef areas, sediment no longer appears to be the primary ecological driver. A change in geomorphology on the south deep transect is likely the primary cause of the transition boundary between the SD1 and SD2 assemblages, and on the north shallow transect wave action is the mostly likely cause of the transition boundary between the NS3 and NS4 assemblages (Table 6). The NS4 assemblage is dominated by taxa generally associated with high water motion reef areas. Interestingly, Rongo (2004) noted a similar transition in the same location. This 10 mg cm^{-2} d^{-1} threshold is also consistent with the findings of Pastorok and Bilyard (1985) and Rogers (1990).

The agreement between the thresholds found in this study and with those theorized by Pastorok and Bilyard (1985) could be attributed to the data for both having been collected from the same study area. However, it is important to consider that the coral reef communities in Fouha Bay have changed significantly between these studies, and thus the data used to derive each set of thresholds were collected from what were essentially different coral reef assemblages. The pre-road coral assemblage in

Fouha was substantially different than that present today in species composition, abundance, and colony size. Most notable was a decrease in acroporid richness from 50 taxa in 1978 (Randall and Birkeland 1978) to 21 taxa in the present study. In contrast, 30 merulinid taxa were observed in 1978 compared to 25 in the present study. Many merulinids have been shown to be sediment tolerant and possess the ability to actively clear sediment (Riegl 1995), whereas many acroporids are sediment intolerant (Erftemeijer et al. 2012). Whether the current coral reef community in Fouha Bay represents an arrested recovery from a "sediment kill," a phase shift, or a hysteresis is not clear, but sedimentation appears to be the primary stressor affecting this ecosystem.

The close agreement of this study's findings with those of Rongo (2004) suggest that little has changed in Fouha Bay since his work over a decade prior. While some erosion control efforts have been underway for over a decade (Richmond et al. 2007, Shelton 2015), our results show there has been little apparent change in either the position of the transition boundaries or composition of the coral assemblage. Several, not mutually exclusive, reasons may account for this. Upland erosion control efforts may have not been successful in reducing sediment runoff into Fouha Bay, possibly because the erosion control methods were ineffective, or the scale and duration were insufficient for achieving a measurable reduction in delivered sediment. It may also be possible that legacy sediment is present on the landscape and continues to wash into Fouha Bay, or that legacy sediment trapped in the bay may require more time to flush. Sediment flushing in Fouha Bay is dependent on high swell events, and in particular typhoon-generated swell (Wolanski et al. 2003), but Guam has experienced no significant typhoons in the decade prior to this study. The lack of change in the benthic community since Rongo's study may also be explained by the apparently large reduction in sedimentation rate required to achieve a large, potentially measurable change. Results from Rongo's sediment decay model suggest that much of the reef area in Fouha Bay already experiences only light sediment stress, and improvements to these areas, while beneficial and potentially measurable, may be relatively small. Significant gains can be made near the head of Fouha Bay, but given the already high sedimentation rates in this area, substantial sediment declines will need to be made in order to mitigate the rapid rate of sediment deposition in the area extending approximately 160 m from the head of the bay (Rongo 2004). It may also be possible that the reefs in Fouha Bay have undergone a hysteresis (Mumby et al. 2007) to a new stable state community and may require significant reductions in sediment to achieve a shift back to a system similar to that which occurred prior to the construction of the road. This shift may also require more than sediment reduction, such as an increase in herbivory through fishery management actions or manually clearing algal turfs that currently trap sediment and inhibit coral recruitment and growth.

Finally, there may have been insufficient time since Rongo's study to achieve a measurable degree reef recovery. Corals grow slowly (Minton 2014), especially massive forms, and a decade may not be sufficient time for conditions to improve and for enough coral growth to be detectable given the inherent variability on most reefs and limitations inherent in the sampling approach.

Additionally, this study demonstrated that sufficiently sensitive survey methods should be used to assess changes in the reef assemblage. Many coral species, especially in severely impacted areas, are rare (e.g., low density or cover/planar area), and the standard point intercept method used to collect PI data in this study was not sensitive enough to consistently detect their presence, especially when the colonies were small and relatively few sampling points were used. This resulted in highly variable data that complicated the analysis and would hinder recovery assessments. Future efforts that rely upon the PIT method should consider using a higher density of points to improve sensitivity, especially when corals are few or small. The CCS method was superior at locating and quantifying coral colonies, even very rare species (<0.5% cover) because the entire area of the quadrat was systematically searched, and all colonies were quantified. Therefore, data obtained from the CCS method was more consistent and performed better in the MWA. These data have the added benefit of providing information on demographics and potentially on sublethal effects.

If sedimentation rates and loadings can be reduced in Fouha Bay, it logically follows that gains in coral and algae cover, abundance and diversity can be realized in areas within ~200 m of the head of Fouha Bay. Reductions in sedimentation rates, followed by flushing of the existing sediment load from the inner bay would improve benthic habitat and reduce sediment resuspension, potentially allowing some of the species currently present near the mouth of the bay to migrate toward the head of the bay. Even with a reduction in sediment. it is unclear whether the community currently in Fouha Bay will revert to one similar to the pre-road construction community documented by Randall and Birkeland (1978). While the likelihood of reversion to the pre-road coral reef community is uncertain, it is highly likely that coral richness, abundance, and cover could be improved in the interior of Fouha Bay through sediment reduction alone, and would likely manifest itself in an increase in the density and cover of species currently present toward the exterior of the bay.

DECLARATION OF COMPETING INTEREST

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

AUTHOR CONTRIBUTIONS

Dwayne Minton: Conceptualization, Methodology, Formal analysis, Visualization, Writing – Original Draft

David Burdick: Methodology, Investigation, Data Curation, Writing – Review & Editing

Valerie Brown: Methodology, Investigation, Data Curation, Writing – Review & Editing

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Figure and Table Captions

Figure 1. Four survey transects in Fouha Bay, Guam. The dark grey area is land, light grey area is the reef flat, medium grey area is the reef slope, and the white area is unconsolidated bottom. Transects are labeled by position (N=north and S=South) and depth (S=shallow and D=Deep).

Figure 2. Dissimilarity plots for the south shallow transect in Fouha Bay. The top figure was generated from the PI data. The bottom figure was generated from the CCS data. SS1-SS3 are assemblages identified by the MWA. In the top figure, a, b, and c represent "false" transitions boundaries. See text for a full discussion.

Figure 3. Dissimilarity plots for the north shallow transect in Fouha Bay. The top figure was generated from the PI data. The bottom figure was generated from the CCS data. NS1-NS4 are assemblages identified by the MWA. In the top figure, a, b, c, and d represent "false" transitions boundaries. In the bottom figure X is a second assemblage identified by the MWA-CCS that was further divided based on additional data. See text for a full discussion.

Figure 4. Abundance of four coral taxa along the north shallow transect. Grey vertical dotted lines are the transition boundaries between the four assemblages, NS1-NS4 (left to right), identified by the MWA.

Figure 5. Dissimilarity plot for the south deep transect in Fouha Bay, using the CCS data. SD1 and SD2 are assemblages identified by the MWA. See text for a full discussion.

Figure 6. Stacked bar graph of the maximum number of coral and non-coral taxa found in a quadrat vs. sedimentation rate in Fouha Bay. Sedimentation rates are in 5 mg cm-2 d-1 bins, where the number represents the upper limit of the bin, e.g., "5" represents a bin of 0 to 5 mg cm-2 d-1. Missing bins contained no survey quadrats and have been excluded for space reasons.

Figure 7. Average colony density of all coral species (colonies/m2) vs. sedimentation rate in Fouha Bay. See Figure 6 for description of bins. Error bars represent standard error of the mean.

Figure 8. Coral and non-coral taxa richness (number of taxa/m2) in low, moderate, severe, and very severe sediment impact areas in Fouha Bay. Arrows are sediment thresholds for coral taxa above which the taxa were no longer observed in the bay. G. ret= Goniastrea retiformis, C. cha = Cyphastrea chalcidicum, L. pur = Leptastrea purpurea.

Table 1. Statistical approaches and data used in the coral colony count/size (CCS) and point intercept (PI) approaches to identify and confirm transition boundaries and describe benthic assemblages along a sediment gradient in the Fouha Bay, Guam. See text for more discussion of analytical methods. MWA=Moving Window Analysis, ANOSIM=Analysis of Similarities, SIMPER= Similarity-Percentages Analysis, PSA=Planar Surface Area data, PIT=Point Intercept Transect data.

Table 2. Transition boundaries identified on the south shallow transect. DISS is the Bray-Curtis dissimilarity index between the two assemblages separated by the transition boundary; R is the ANOSIM test statistic and p is its significance. Sed. Rate is the sedimentation rate (mg cm-2 d-1) at the transition boundary estimated by Rongo's (2004) exponential decay model for Fouha Bay.

Table 3. Transition boundaries identified on the north shallow transect. DISS is the Bray-Curtis dissimilarity index between the two assemblages separated by the transition boundary; R is the ANOSIM test statistic and p is its significance. Sed. Rate is the sedimentation rate (mg cm-2 d-1) at the transition boundary as estimated by the Rongo's (2004) exponential decay model for Fouha Bay.

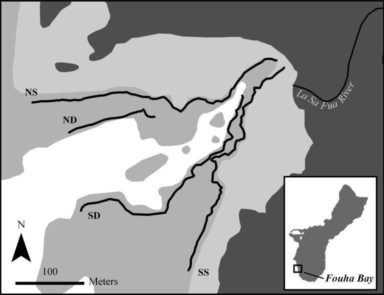
Table 4. Correlation of the abundance of 15 taxa with estimated sedimentation rate in Fouha Bay. The taxa occurred in at least 20% of all survey quadrats. Threshold is the sedimentation rate above which the taxa were not found during surveys. A threshold of 164 is the maximum estimated sedimentation near the mouth of the La Sa Fua River. Sedimentation rates were calculated from Rongo's (2004) exponential decay model for Fouha Bay.

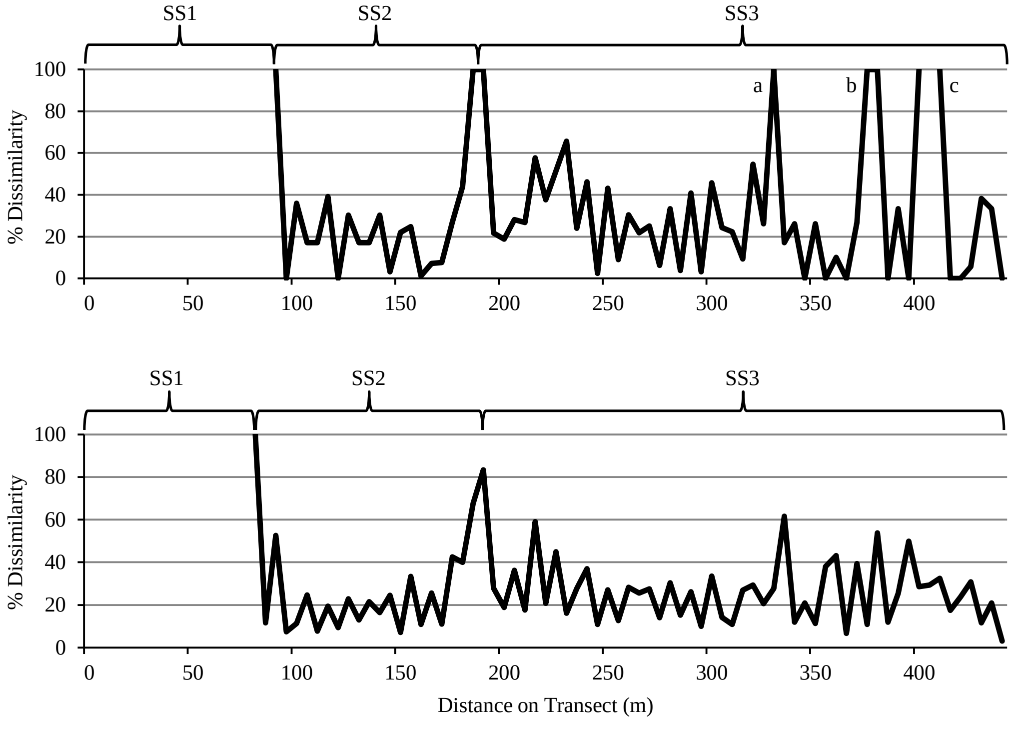
Table 5. Average coral size (cm) for four coral taxa on the north shallow and south shallow transects in Fouha Bay. The range of estimated sedimentation rates (mg cm-2 d-1) appear in parentheses below the assemblage code. Data are mean ± SEM; nc = no colonies were observed.

Table 6. The primary (x) and secondary (o) stressors most likely responsible for the benthic assemblage transition boundaries identified in Fouha Bay.

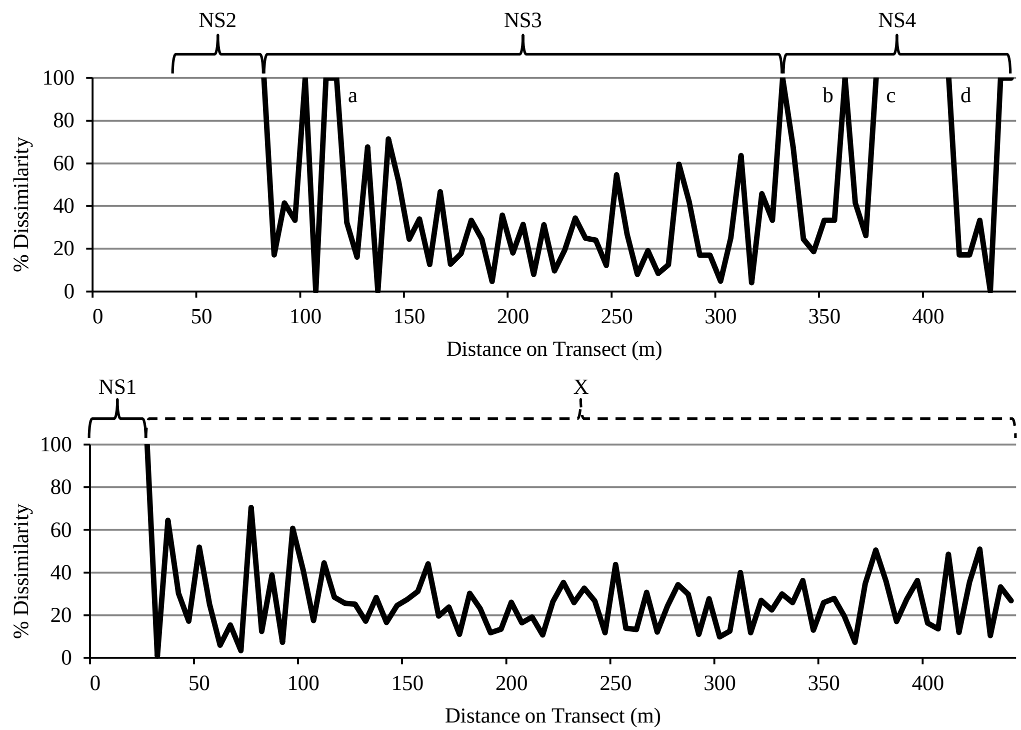
Table 6. The primary (x) and secondary (o) stressors most likely responsible for the benthic assemblage transition boundaries identified in Fouha Bay.

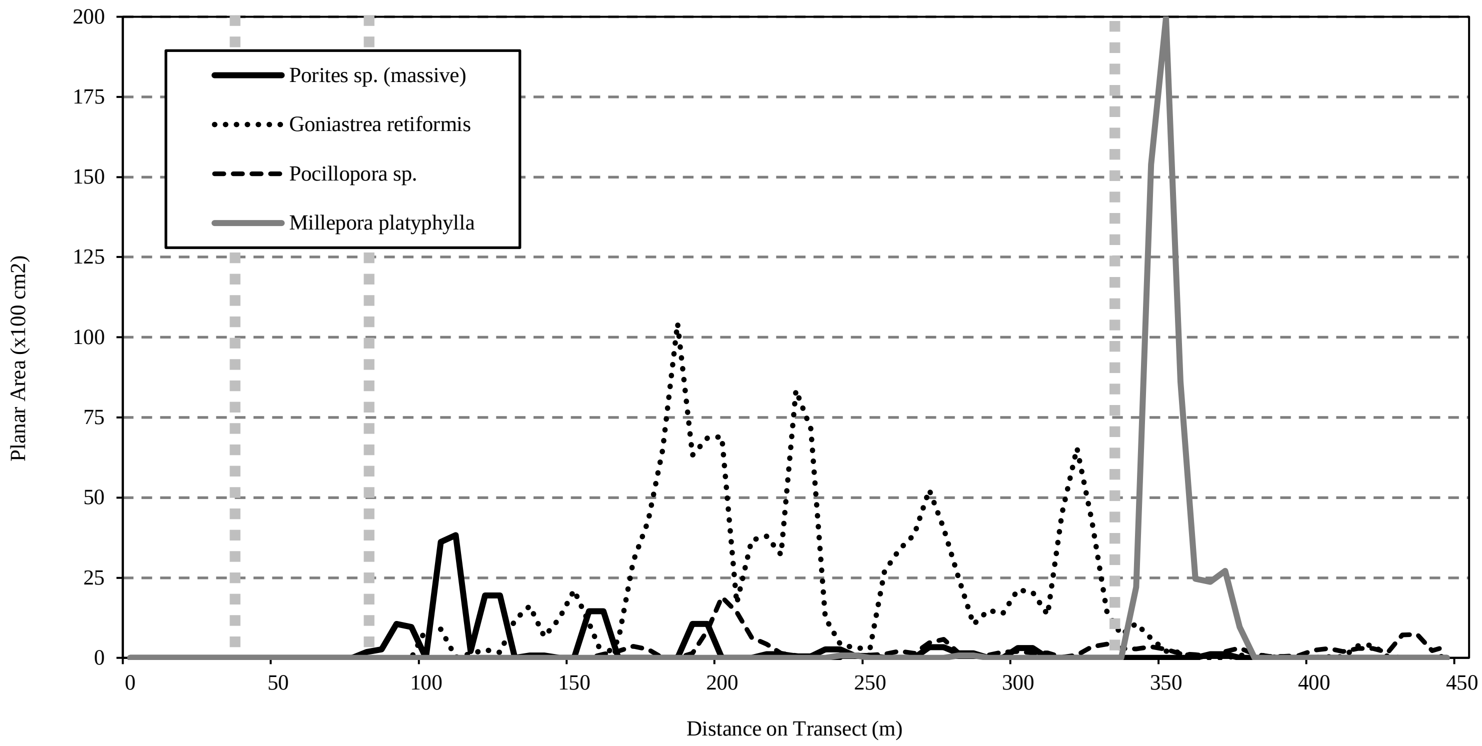
Table 7. Non-coral and coral taxa richness and indicator taxa in sediment impact zones in Fouha Bay. Data are compiled from all quadrats surveyed.


NS
ND
SD
SS
La Sa Fua River
N
100
Meters
Fouha Bay

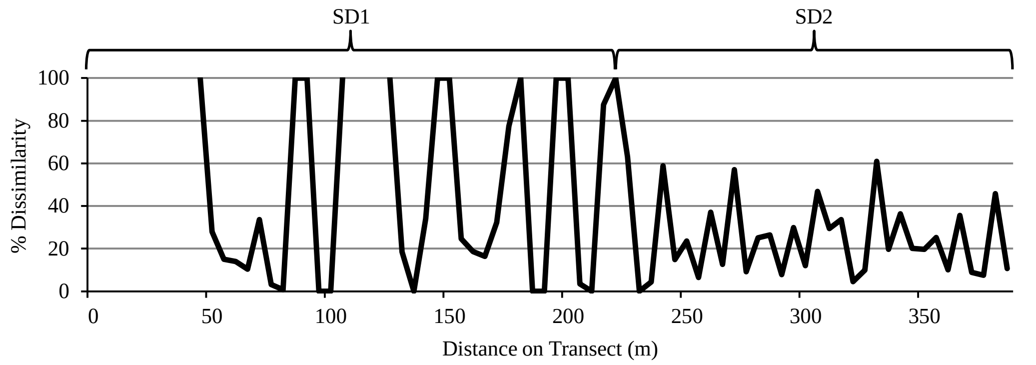


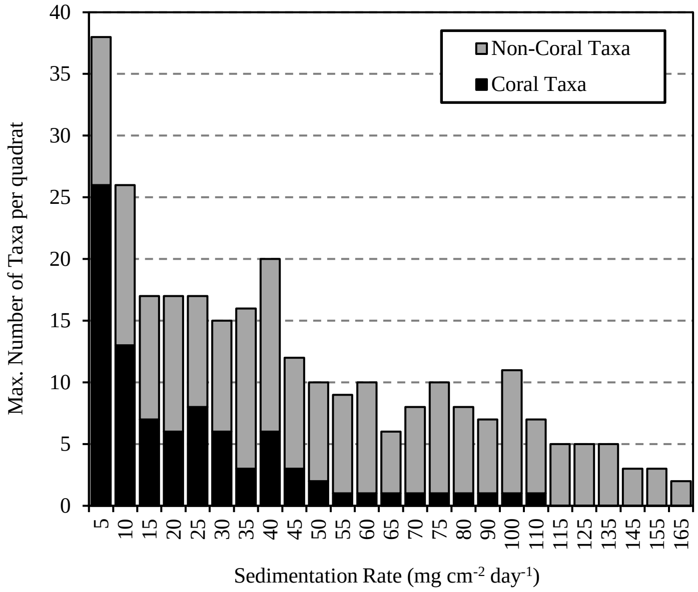
SS1
SS2
SS3
100
80
60
40
20
0
% Dissimilarity
a
b
c
0
50
100
150
200
250
300
350
400
SS1
SS2
SS3
100
80
60
40
20
0
% Dissimilarity
0
50
100
150
200
250
300
350
400
Distance on Transect (m)


NS2
NS3
NS4
a
b
c
d
% Dissimilarity
100
80
60
40
20
0
0
50
100
150
200
250
300
350
400
Distance on Transect (m)
NS1
X
% Dissimilarity
100
80
60
40
20
0
0
50
100
150
200
250
300
350
400
Distance on Transect (m)


Porites sp. (massive)
Goniastrea retiformis
Pocillopora sp.
Millepora platyphylla
Planar Area (x100 cm2)
0
25
50
75
100
125
150
175
200
0
50
100
150
200
250
300
350
400
450
Distance on Transect (m)

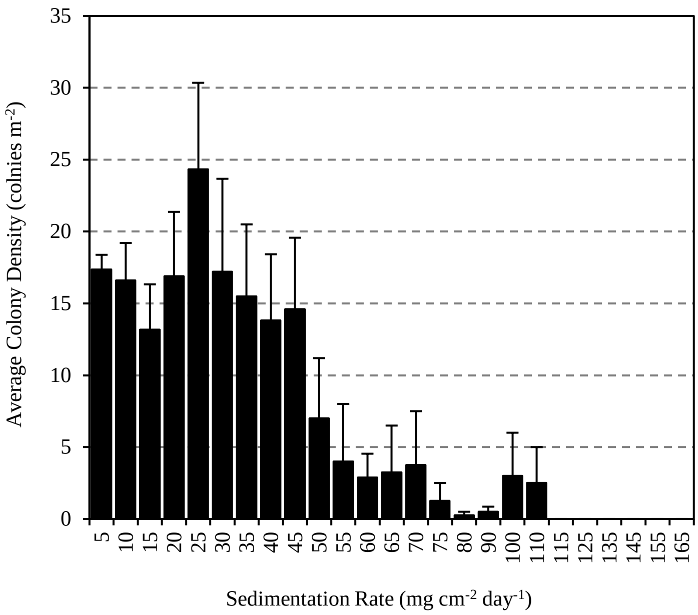
Tran Pos.	Distance	Goniastrea retiformis	Millepora platyphylla	*Pocillopora* sp.	Porites sp. (massive)
S-S-2.5	0	0	0	0	0
S-S-7.5	7.5	0	0	0	0
S-S-12.5	12.5	0	0	0	0
S-S-17.5	17.5	0	0	0	0
S-S-22.5	22.5	0	0	0	0
S-S-27.5	27.5	0	0	0	0
S-S-32.5	32.5	0	0	0	0
S-S-37.5	37.5	0	0	0	0
S-S-42.5	42.5	0	0	0	0
S-S-47.5	47.5	0	0	0	0
S-S-52.5	50	0	0	0	0
S-S-57.5	57.5	0	0	0	0
S-S-62.5	62.5	0	0	0	0
S-S-67.5	67.5	0	0	0	0
S-S-72.5	72.5	0	0	0	0
S-S-77.5	77.5	0	0	0	0
S-S-82.5	82.5	0	0	0	179.07063
S-S-87.5	87.5	0	0	0	270.17674
S-S-92.5	92.5	0	0	0	1054.003445
S-S-97.5	97.5	0	0	0	962.897335
S-S-102.5	100	896.1385475	0	0	0
S-S-107.5	107.5	896.1385475	0	0	3611.257705
S-S-112.5	112.5	21.2057325	0	0	3827.242018
S-S-117.5	117.5	131.1613825	0	0	215.9843125
S-S-122.5	122.5	256.039585	0	0	1941.895319
S-S-127.5	127.5	173.5728475	0	0	1941.895319
S-S-132.5	132.5	1185.164828	0	0	0
S-S-137.5	137.5	1619.489645	0	0	76.57625625
S-S-142.5	142.5	661.304695	0	0	76.57625625
S-S-147.5	147.5	1227.968991	0	0	0
S-S-152.5	150	2111.933878	0	0	0
S-S-157.5	157.5	1083.455851	0	0	1449.058388
S-S-162.5	162.5	0	0	113.09724	1449.058388
S-S-167.5	167.5	552.5271413	0	207.34494	0
S-S-172.5	172.5	3014.355605	0	356.9631638	0
S-S-177.5	177.5	4265.493823	0	262.7154638	0
S-S-182.5	182.5	6490.132241	0	0	0
S-S-187.5	187.5	10437.54008	0	0	0
S-S-192.5	192.5	6327.554959	0	135.4810688	1060.286625
S-S-197.5	197.5	6852.200489	0	857.2613713	1060.286625
S-S-202.5	200	6895.397351	0	1896.734963	0
S-S-207.5	207.5	1695.673203	0	1432.957739	0
S-S-212.5	212.5	3669.769819	0	627.1399038	0
S-S-217.5	217.5	3787.186745	0	431.968625	116.23883
S-S-222.5	222.5	3220.522449	0	139.4080563	116.23883
S-S-227.5	227.5	8351.131618	0	76.57625625	50.65813875
S-S-232.5	232.5	7144.368359	0	0	50.65813875
S-S-237.5	237.5	1242.498845	0	6.28318	259.181175
S-S-242.5	242.5	433.9321188	70.685775	6.28318	259.181175
S-S-247.5	247.5	300.8072425	70.685775	80.110545	64.79529375
S-S-252.5	250	289.02628	0	80.50324375	64.79529375
S-S-257.5	257.5	2699.803906	0	108.7775538	0
S-S-262.5	262.5	3380.743539	0	209.3084338	0
S-S-267.5	267.5	3845.698859	0	146.4766338	0
S-S-272.5	272.5	5248.811493	0	471.6311988	334.1866363
S-S-277.5	277.5	4038.906644	0	585.5138363	334.1866363
S-S-282.5	282.5	2497.56405	69.11498	161.0064875	141.7642488
S-S-287.5	287.5	1046.14947	69.11498	85.21562875	141.7642488
S-S-292.5	292.5	1484.008576	0	87.1791225	0
S-S-297.5	297.5	1382.692299	0	178.2852325	0
S-S-302.5	300	2121.358648	0	190.066195	302.7707363
S-S-307.5	307.5	2037.321115	0	150.0109225	302.7707363
S-S-312.5	312.5	1339.102738	0	151.5817175	0
S-S-317.5	317.5	4515.642926	0	17.278745	0
S-S-322.5	322.5	6547.466259	0	86.78642375	0
S-S-327	S-327	4274.133195	0	348.71649	0
S-S-332	S-332	1454.55617	0	429.6124325	0
S-S-337.5	337.5	717.853315	0	296.880255	0
S-S-342.5	342.5	1065.391709	2201.076494	281.9577025	0
S-S-347.5	347.5	611.039255	15395.75449	349.1091888	0
S-S-352.5	350	203.0252538	19968.73144	267.4278488	0
S-S-357.5	357.5	172.78745	8627.591538	121.7366125	0
S-S-362.5	362.5	0	2464.970054	102.101675	0
S-S-367.5	367.5	0	2369.151559	51.0508375	112.3118425
S-S-372.5	372.5	0	2717.082651	195.5639775	112.3118425
S-S-377.5	377.5	76.57625625	959.3630463	305.1269288	0
S-S-382.5	382.5	109.95565	0	109.5629513	0
S-S-387.5	387.5	33.37939375	0	41.23336875	0
S-S-392.5	392.5	0	0	47.12385	0
S-S-397.5	397.5	0	0	71.86387125	0
S-S-402.5	400	0	0	234.8338525	0
S-S-407.5	407.5	26.703515	0	291.7751713	0
S-S-412.5	412.5	26.703515	0	192.8150863	0
S-S-417.5	417.5	372.278415	0	288.6335813	0
S-S-422.5	422.5	399.3746288	0	287.8481838	0
S-S-427.5	427.5	27.09621375	0	168.8604625	0
S-S-432.5	432.5	0	0	718.6387125	0
S-S-437.5	437.5	0	0	728.84888	0
S-S-442.5	442.5	0	0	227.765275	0
S-S-447.5	447.5	56.54862	0	361.28285	0
	450				


SD1
SD2
100
80
60
40
20
0
% Dissimilarity
0
50
100
150
200
250
300
350
Distance on Transect (m)



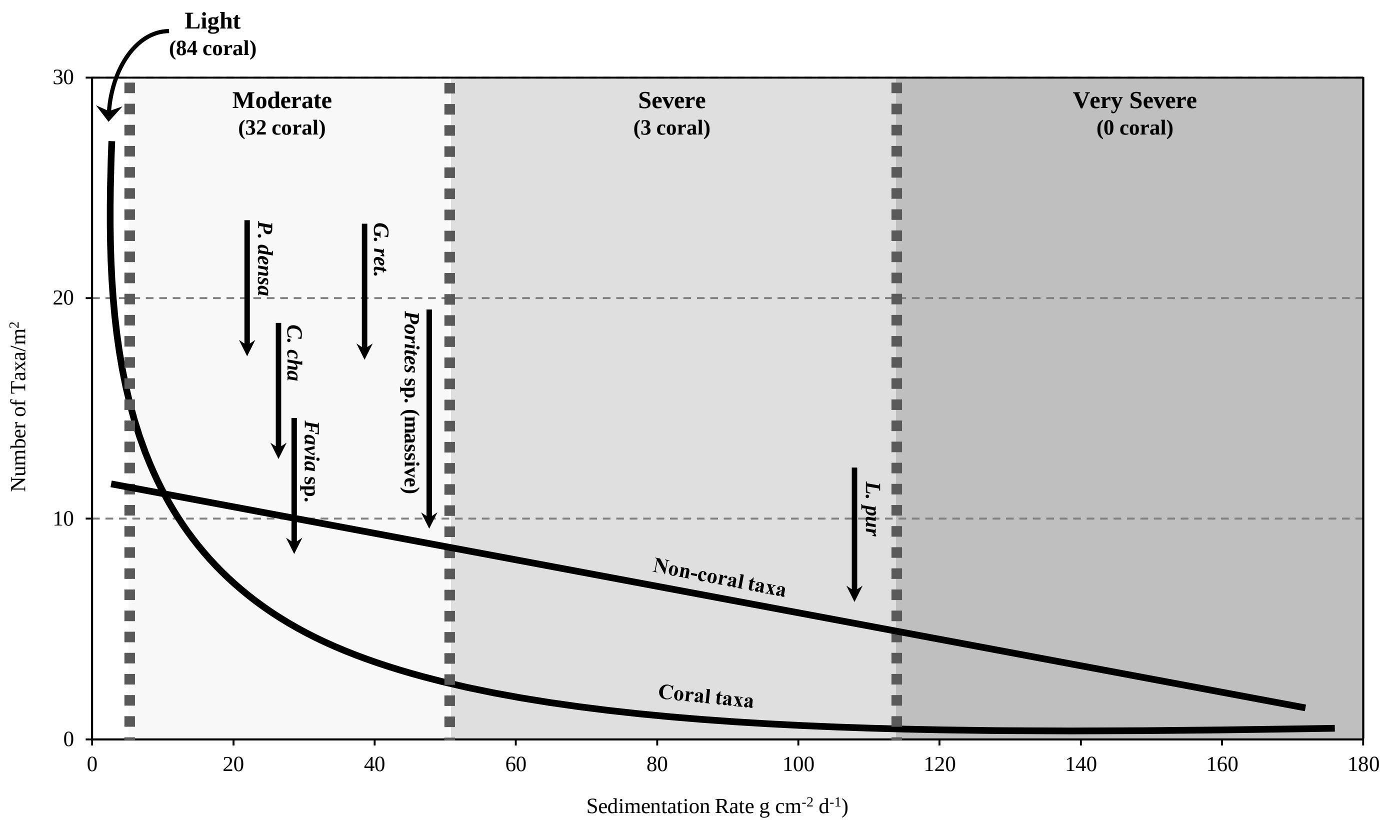
Non-Coral Taxa
Coral Taxa
Max. Number of Taxa per quadrat
Sedimentation Rate (mg cm-2 day-1)
0
5
10
15
20
25
30
35
40
5
10
15
20
25
30
35
40
45
50
55
60
65
70
75
80
90
100
110
115
125
135
145
155
165

Sediment	DIVERSITY	Coral Taxa	on-Coral Taxa
5	34	26	12
10	26	13	13
15	17	7	10
20	14	6	11
25	15	8	9
30	14	6	9
35	15	3	13
40	16	6	14
45	10	3	9
50	10	2	8
55	9	1	8
60	10	1	9
65	6	1	5
70	8	1	7
75	10	1	9
80	8	1	7
90	7	1	6
100	11	1	10
110	7	1	6
115	5	0	5
125	5	0	5
135	5	0	5
145	3	0	3
155	3	0	3
165	2	0	2



35
30
25
20
15
10
5
0
Average Colony Density (colnies m-2)
5 10 15 20 25 30 35 40 45 50 55 60 65 70 75 80 90 100 110 115 125 135 145 155 165
Sedimentation Rate (mg cm-2 day-1)

Sediment	Abundance	SEM
5	17.35	1.03
10	16.6	2.6
15	13.18	3.15
20	16.89	4.48
25	24.32	6.03
30	17.21	6.46
35	15.5	5
40	13.83	4.59
45	14.6	4.97
50	7	4.19
55	4	4
60	2.88	1.66
65	3.25	3.25
70	3.75	3.75
75	1.25	1.25
80	0.25	0.25
90	0.5	0.354
100	3	3
110	2.5	2.5
115	0	0
125	0	0
135	0	0
145	0	0
155	0	0
165	0	0



Light
(84 coral)
Moderate
(32 coral)
Severe
(3 coral)
Very Severe
(0 coral)
P. densa
G. ret.
C. cha
Porites sp. (massive)
Favia sp.
L. pur
Non-coral taxa
Coral taxa
Number of Taxa/m²
Sedimentation Rate g cm-2 d-1)
0
10
20
30
0
20
40
60
80
100
120
140
160
180

		Data Used	
Goal	**Statistical test**	**CCS-approach**	**PI-approach**
Identify transition boundaries	MWA	PSA	PIT (coral only)
Confirm transition boundaries	ANOSIM	PSA	PIT (coral only)
Identify indicator taxa	SIMPER	PIT (all)	PIT (all)

	DISS	R	p	Sed. Rate
Point Intecept				
85 m	72.1	0.74	0.001	49.6
190 m	69.7	0.521	0.001	10.8
Coral Count/Size				
85 m	100	0.905	0.001	49.6
190 m	87.2	0.455	0.001	10.8

	DISS	R	p	Sed. Rate
Point Intecept				
80 m	64.2	0.806	0.001	53.4
330 m	52.1	0.318	0.015	1.4
360 m	42.8	0.06	0.694	<1.0
Coral Count/Size				
25 m	100	0.905	0.001	118.5

Taxa	Threshold	r	p	
Turf algae	164	0.200	0.001	
Padina sp.	164	0.168	0.004	
Cyanobacteria	153	-0.119	0.044	
Turbinaria ornata	106	-0.050	0.400	ns
Halimeda sp.	106	-0.178	0.002	
Leptastrea purpurea	106	-0.173	0.003	
Trilocarpa fragilis	99	-0.031	0.598	ns
Crustose coralline algae	99	-0.324	<0.001	
Porites sp. massive	48	-0.085	0.152	ns
Amphiroa cf. *fragilissima*	39	-0.223	<0.001	
Goniastrea retiformis	39	-0.168	0.004	
Favia sp.	27	-0.182	0.002	
Cyphastrea chalcidicum	25	-0.106	0.072	ns
Porites densa	21	-0.164	0.005	
Udotea sp.	16	-0.197	0.001	

North shallow	**n**	**NS1 (118.5–170.2)**	**NS2 (53.4–118.5)**	**NS3 (1.4–53.4)**	**NS4 (<1.4)**
Cyphastrea chalcidicum	52	*nc*	*nc*	7.7 ± 1.1	*nc*
Goniastrea retiformis	387	*nc*	*nc*	21.0 ± 1.1	11.5 ± 1.2
Leptastrea purpurea	327	*nc*	2.3 ± 0.2	2.7 ± 0.1	3.1 ± 0.3
Porites sp. (massive)	116	*nc*	*nc*	20.9 ± 3.1	22.0[a]
South shallow	**n**	**SS1 (49.6–170.2)**		**SS2 (10.8–49.6)**	**SS3 (<1–10.8)**
Cyphastrea chalcidicum	21	*nc*		5.1 ± 1.2	9.2 ± 1
Goniastrea retiformis	331	*nc*		10.9 ± 2.4	13.6 ± 0.6
Leptastrea purpurea	459	*nc*		2.0 ± 0.1	3.4 ± 0.4
Porites sp. (massive)	49	*nc*		21.5 ± 3.3	21.4 ± 4.1

[a] Only one colony was in this zone.

	Freshwater	Sediment	Waves	Geomorphology
SS1–SS2	o	x		
SS2–SS3		x	o	
NS1–NS2	o	x		
NS2–NS3		x		
NS3–NS4			x	
SD1–SD2		o		x

Sediment	Fouha assemblage	Non-coral	Coral	Indicator Taxa
Light (<10 mg cm^{-2} d^{-1})	SS3, NS3 (ocean end), NS4, SD1 (ocean end), SD2	40	84	No indicator species were identified likely due to high species richness
Moderate (10–50 mg cm^{-2} d^{-1})	SS2,NS3 (land end), SD1 (land end)	34	32	*Porites* spp., *Leptastrea* spp., *Amphiroa sp.* , *Turbinaria sp.* , *Caulerpa sp.* , *Dictyota sp.*
Severe (50-110 mg cm^{-2} d^{-1})	SS1, NS2	20	3	*Leptastrea purpurea, Padina* sp. *Acanthophora spicifera* , *Actinotrichia* cf. *fragilis* , *Hydrolithon* sp., cyanobacteria
Very severe (>110 mg cm^{-2} d^{-1})	NS1	6	0	*Acanthophora spicifera* , *Padina* sp.