

Linking reef ecology to island building: Parrotfish identified as major producers of island-building sediment in the Maldives

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ABSTRACT

Reef islands are unique landforms composed entirely of sediment produced on the surrounding coral reefs. Despite the fundamental importance of these ecological-sedimentary links for island development and future maintenance, reef island sediment production regimes remain poorly quantified. Using census and sedimentary data from Vakkaru island (Maldives), a sand-dominated atoll interior island, we quantify the major sediment-generating habitats, the abundance of sediment producers in these habitats, and the rates and size fractions of sediment generated by different taxa. The estimated annual sediment production is 685,000 kg (or 370 m³), ~75% of which is produced on the narrow outer reef flat, despite composing only 21% of the total platform area. Approximately 65% of the platform acts solely as a sediment sink. Census data identify parrotfish as the major sediment producers, generating >85% of the 5.7 kg m⁻² of new sand-grade sediment produced on the outer reef flat each year. *Halimeda* (macroalgae) produce a further 10%, most as gravel-grade material. Comparisons between production estimates and sedimentary data indicate that reef ecology and island sedimentology are tightly linked; reef flat and lagoon sediments are dominated by coral and *Halimeda*, although fine- to medium-grained coral sand is the dominant (~59%) island constituent. The generation of sediment suitable for maintaining this reef island is thus critically dependent on a narrow zone of high-productivity reef, but most especially on the maintenance of healthy parrotfish populations that can convert reef framework to sand-grade sediment.

INTRODUCTION

Coral reef islands are considered among the most vulnerable landforms to climate change, and future sea-level rise is considered to be a specific threat (Woodroffe, 2008; Nurse et al., 2014). This is, in part, a function of their low elevations, which rarely exceed 3 m above mean sea level, as well as their often poorly consolidated sediment-dominated structures. However, future island vulnerability is a complex and arguably island-specific issue and will be influenced by various interacting factors that include the rate of reef growth, the rate of sea-level rise, reef evolutionary stage and thus accommodation space, island geomorphology, and the contemporary relationship between islands and their surrounding process and sedimentary regimes (Perry et al., 2011). All coral reef islands are inherently dependent on their surrounding reef habitats, not only because they provide the foundations for island development (Perry et al., 2013), but also because they are the primary production sites for the sediments necessary to sustain island building, growth, and maintenance.

Marked interregional and intraregional variations are known to occur in terms of reef island sediment constituents, with benthic foraminifera dominating in some settings, and coral and *Halimeda* (macroalgae) in others (Perry et al., 2011), and it is acknowledged that sediment production regimes can change as the reef systems around islands evolve (Kench et al., 2005), or the surrounding reef flats mature (Yamano et al., 2000). Generally, however, and with the exception of a few studies from eastern Australia (Yamano et al., 2000; Hart and Kench, 2007; Dawson et al., 2014), there is a lack of understanding of how islands and their surrounding sediment production zones interact. Here we combine field census

and sedimentary data to quantify the dominant sediment-generating species and processes within the reef-lagoon habitats around Vakkaru island (Maldives), and make preliminary estimates of the amounts of sediment generated by these species, both overall and in relation to different sediment size fractions. Collectively, these data are used to identify those ecological and sedimentary processes most critical for contemporary island sediment supply.

FIELD SETTING AND METHOD

The Maldives Archipelago comprises a double chain of 22 atolls (Fig. 1A) containing ~1200 reef islands. Our study focused on Vakkaru, an atoll interior reef (0.46 km² in area) in Northern Maalhosmadulu Atoll (Raa Atoll) (Fig. 1B). Vakkaru island is 0.19 km² in area and occupies 42% of the platform (Fig. 1C); surficial island sediments are composed of fine- to medium-grained sands, and coral (59%) and *Halimeda* (25%) are the dominant constituents (Fig. 2). The subtidal portion of the platform comprises three ecogeomorphic zones: (1) an outer reef flat, covering an area of 0.1 km² (21.9% of the platform), and varying in width from ~25 m along the northern and southern margins to ~150 m in the northeast; (2) an inner reef flat, 0.06 km² in area (13.7% of the platform); and (3) a platform interior lagoon and sand moat (0.11 km² in area, or 22.1% of the platform) that extends seaward from the toe of the beach to the inner reef flat, and varies in width from ~5 m along the northern margin to ~175 m in the southwest (Fig. 1C). The atoll has a microtidal regime (range ~1.2 m) and thus the depths of these subtidal zones vary subtly through the tide cycle. Field census techniques, using an adapted version of the ReefBudget methodology (Perry et al., 2012), were used to quantify benthic commu-

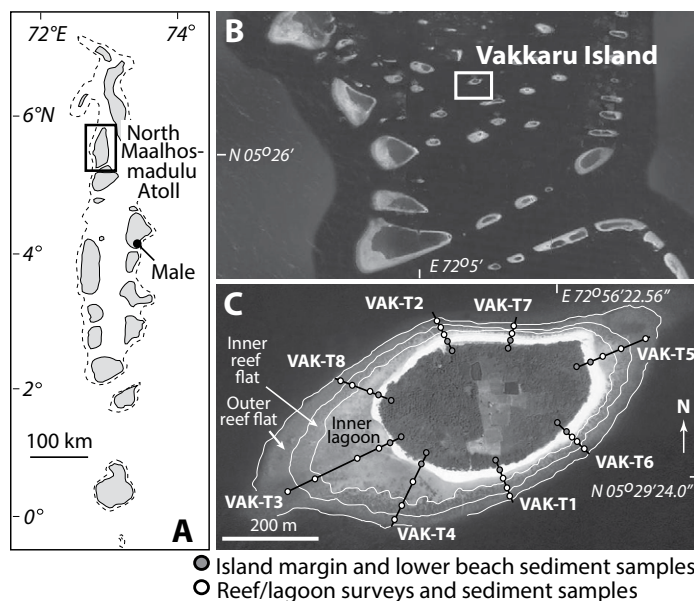


Figure 1. A: Location of Northern Maalhosmadulu Atoll (Maldives). B: Location of Vakkaru island (Maldives). C: Vakkaru island, showing geocological zones, study transects, and reef and island survey and sediment sampling stations.

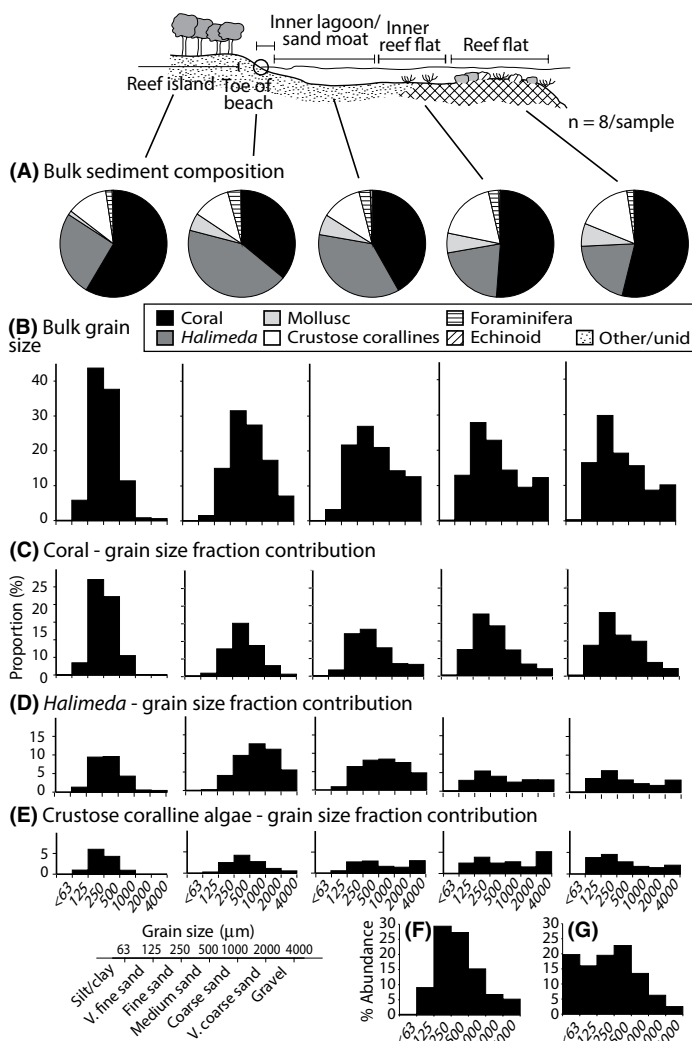


Figure 2. Bulk sediment composition (A) and grain size characteristics (B) of Vakkaru reef (Maldives) and reef island sediments (v.—very). C–E: Contributions of corals, *Halimeda*, and coralline algae to individual grain size fractions. Note that molluscs, foraminifera, and echinoids contribute <2% at all sites and are not plotted. F: Average coral size fraction distributions from the inner and outer reef flats at Vakkaru. G: Average grain size distributions of sediment from the intestines of parrotfish (after Hoey and Bellwood, 2008).

nity composition, reef surface complexity (rugosity), and the abundance of sediment-producing biota in each zone. Published data on species-level carbonate production rates were used to estimate rates of new carbonate sediment generation by each species in each zone, and published data on sediment size fractions produced by each species and process were used to estimate contributions to different size fractions. Thin section analysis was used to quantify reef and island sediment composition and to determine the contributions of different constituents within different sediment size classes (see the GSA Data Repository¹ for our methods).

ABUNDANCE OF SEDIMENT-PRODUCING BIOTA

The subtidal zones around Vakkaru vary markedly in benthic substrate composition and sediment-generating species abundance. The outer

reef flat is dominated by reef framework and coral rubble (there is very little sediment; Table DR1 in the Data Repository), with live coral cover (mainly *Acropora* sp., *Montipora* sp., *Pocillopora* sp., and *Porites* sp.) averaging $25.7\% \pm 9.6\%$, and coralline algal cover of $12.7\% \pm 5.9\%$. This zone has a rugosity value averaging 2.3, creating complex habitat space for reef-dwelling biota. This is reflected in the high (relative) abundance of the calcareous green algae *Halimeda* (mean of 90.4 thalli/m²), gastropods (infaunal and epifaunal bivalves were rare), and especially parrotfish (mainly the excavator species *Chlorurus sordidus* and *Chlorurus strongylocephalus*, and the scraper species *Scarus niger*, *Scarus frenatus*, and *Scarus rubroviolaceus*), with average densities of 0.02 fish/m² (Tables DR2 and DR3). In contrast, the inner reef flat has a less continuous reef framework, comprising *Acropora* sp. thickets and *Porites* bommies (i.e., coral outcrops that may be partially exposed at low tide) with sandy substrate between. Average live coral cover ($19.7\% \pm 8.0\%$) and substrate rugosity (mean 1.7) are lower than on the outer reef, sediment cover (30.2%) is higher (Table DR1), and sediment-producing biota (coralline algae, *Halimeda*, molluscs, and parrotfish) are less abundant (Tables DR2 and DR3). Other known producers of skeletal carbonates, such as benthic foraminifera and echinoids, are rare across the entire platform. The platform interior lagoon and sand moat is dominated (94.8%) by wave-rippled sands; there is no live coral, parrotfish were not recorded, and there are no sediment-producing biota.

SEDIMENT GENERATION RATES

Estimated rates of new sand-grade sediment production (G, where G = kg CaCO₃ m² yr⁻¹) (Table 1; Tables DR2–DR5) are 5.71 G on the outer reef flat, 1.90 G on the inner reef flat, and 0.00 G in the inner lagoon and sand moat. This equates to ~685,000 kg (or ~370 m³) of new sediment production each year, the overwhelming majority (86.3% and 81.6% on the outer and inner reef flats, respectively) being produced by parrotfish (mostly by excavating species; Table 1; Table DR3). Only parrotfish, *Halimeda*, and endolithic sponges produce at a rate >0.1 G (Table 1). Rates of sediment production by foraminifera, bivalves, gastropods, and that resulting from urchin erosion are negligible (collectively <5%). Using published data on the relative proportions of sediment of different size fractions generated by these producers, combined with our sediment generation measures (Tables DR2–DR5), estimates can be made of the amount of sediment (of different types) produced within different size fractions (Table 2; Table DR6). On the outer reef flat, a high proportion (40.6%) of new sediment is in the 125–500 μm (fine to medium sand) range, and is mostly coral, and a further 22% is in the <63 μm (silt) range (Table 2). Similar size fraction ranges are generated in the inner reef flat (Table 2), and in both zones most can be attributed to excavating parrotfish. Endolithic sponges contribute as much as 5% of the <63 μm sedi-

TABLE 1. TOTAL NEW SEDIMENT GENERATION AND PROPORTION CONTRIBUTIONS

	Outer reef flat		Inner reef flat	
	Sediment production rate (G)	Percent of new sediment production	New sediment production rate (G)	Percent of new sediment production
Scraper parrotfish	0.08	1.40	0.07	3.68
Excavator parrotfish	4.85	84.94	1.48	77.89
Halimeda	0.5	8.76	0.18	9.47
Endolithic sponges	0.2	3.50	0.10	5.26
Other (forams, molluscs, urchins)	0.08	1.40	0.07	3.68
Total new sediment	5.71		1.90	

Note: G is new sand-grade sediment production (G = kg CaCO₃ m² yr⁻¹). For rate calculations, see Tables DR2–DR4 (see text footnote 1).

¹GSA Data Repository item 2015181, methods and Tables DR1–DR6, is available online at www.geosociety.org/pubs/ft2015.htm, or on request from editing@geosociety.org or Documents Secretary, GSA, P.O. Box 9140, Boulder, CO 80301, USA.

TABLE 2. PROPORTIONAL CONTRIBUTIONS MADE BY DIFFERENT SEDIMENT PRODUCERS TO THE SIZE CLASSES OF NEWLY GENERATED SEDIMENT AT VAKKARU, MALDIVES

	Outer reef flat							Inner reef flat						
	Grain size classes							Grain size classes						
	Silt	Vfs	Fs	Ms	Cs	Vcs	Gr	Silt	Vfs	Fs	Ms	Cs	Vcs	Gr
Scraper parrotfish	0.4	0.3	0.3	0.3	0.1	0.0	0.0	1.0	0.8	0.8	0.7	0.4	0.1	0.0
Excavator parrotfish	18.1	12.9	19.0	21.1	11.2	3.4	0.4	17.1	12.2	17.9	19.9	10.6	3.3	0.4
<i>Halimeda</i>							8.9							9.9
Endolithic sponges	3.4	0.0						5.2	0.0					
Total (%)	21.8	13.3	19.2	21.4	11.3	3.5	9.3	23.3	13.0	18.7	20.7	11.0	3.3	10.3

Note: See Table DR5 (urchins by species and size data, and estimated rates of substrate erosion or sediment generation; see text footnote 1). Lagoon and/or sand moat were excluded as no sediment generation occurs. Silt is <63 μm; Vfs—very fine sand, 63–125 μm; Fs—fine sand, 125–250 μm; Ms—medium sand, 250–500 μm; Cs—coarse sand, 500–1000 μm; Vcs—very coarse sand, 1–2 mm; Gr—gravel, 2–4 mm.

ment, and *Halimeda* produce ~10% of the gravel-grade (2–4 mm) sediment (Table 2).

REEF TO REEF ISLAND SEDIMENTOLOGY

Reef and reef island sediments at Vakkaru are dominated by coral and *Halimeda* (Fig. 2). However, there are subtle but important variations in constituent abundance, grain size distributions, and the contributions of different sediment constituents to grain size fractions. Sediments from the outer and inner reef flats are compositionally similar and comprise poorly sorted, medium- to coarse-grained (1.0–1.7 ϕ) sands. Coral is the major constituent (53% and 51%, respectively, of outer and inner reef flat sediments) and occurs within all grain size fractions, but is especially abundant in the very fine to coarse sand fractions (Fig. 2C). *Halimeda* contribute preferentially to the fine to medium sand fractions, but also contribute, in the form of intact plates, to the larger (gravel grade and larger) fractions (Fig. 2D). Silt and clay-grade sediment is present in minor quantities (<2%; Fig. 2). Sediments from the inner lagoon and sand moat and island beach are also compositionally similar (Fig. 2), but comprise lower amounts of coral (41.7%) and higher proportions of *Halimeda* (35.9%) compared to the reef flat, and are increasingly well-sorted nearshore. Corals contribute mainly to the fine to coarse sand fractions, but *Halimeda* are more important constituents of very coarse to gravel-grade fractions (often as intact plates). Surficial sediments from the island are distinctive, comprising moderately to moderately well sorted, medium- to fine-grained (0.8–0.6 ϕ) sands, and are dominated by coral (58.5%; Fig. 2), *Halimeda* being an important secondary constituent. A notable difference from the subtidal sediments is the paucity of coarser grained particles. Benthic foraminifera and echinoids do not collectively compose more than 4% of the sediment in any reef or island zone.

DISCUSSION: REEF TO REEF ISLAND SEDIMENT LINKS

Using ecological census and sedimentary data we explore the links between reef ecology and contemporary sediment production regimes within the Vakkaru reef island system. We identify the outer reef flat as the main site of active sediment generation (5.71 G generated annually), despite this zone composing only 20% of the reef platform. Only 1.90 G of new sediment is generated in the inner reef flat, and there appears to be no new sediment generated within the platform interior and sand moat, which is a site of sediment storage. Sedimentary data show that coral and *Halimeda* are the main reef flat sediment constituents and contribute across a wide range of size fractions, but that corals contribute mainly to the fine to coarse sand fractions, and *Halimeda* more significantly to very coarse sand and gravel fractions (Fig. 2). These same constituents dominate in the inner platform lagoon; *Halimeda* contribute preferentially to the coarser grain size fractions, and often occur as intact plates. Given the susceptibility of *Halimeda* to rapid abrasion-driven disintegration (Ford and Kench, 2012), the occurrence of these plates in the lagoon and sand moat (where no *Halimeda* grow) suggests that rapid transport across the

reef flats must occur. This suggestion is consistent with process models that show that transport vectors are mainly toward the central areas of such small platforms (Mandlier and Kench, 2012), and local sediment transport studies that show that rapid sediment fluxes occur across these platforms, especially around the period of seasonal monsoon wind shifts (Morgan and Kench, 2014). However sediment data from the island indicate that a smaller proportion of this *Halimeda* actually contributes to the island, and that most does so within the fine to medium sand fraction. Large intact plates are rare. We speculate that following rapid transport to the swash zone, *Halimeda* plates are partially disaggregated, leaving a smaller proportion of fractured plates that can be episodically supplied to the island. Coral, in contrast, is abundant both in the reef flat and inner platform lagoon sediments, and is a major (~60%) island constituent. This must partly reflect high rates of coral sediment supply, but also its high durability relative to other grains types (Ford and Kench, 2012).

However, while coral cover is high around Vakkaru, there is clearly a necessary step required to convert coral framework to sand-grade sediment. Coral can be denuded to sand in various ways: (1) through abrasion of rubble, (2) as a by-product of endolithic bioerosion by endolithic sponges, or (3) as an excretory byproduct of urchin or parrotfish bioerosion. Our data (Table DR4) clearly identify parrotfish as the major producers of sand-grade sediment at this site. Furthermore, we can exclude most other potential sources of coral sediment on the basis of grain size at the point of generation or ecological rarity criteria. Branched coral rubble, for example,

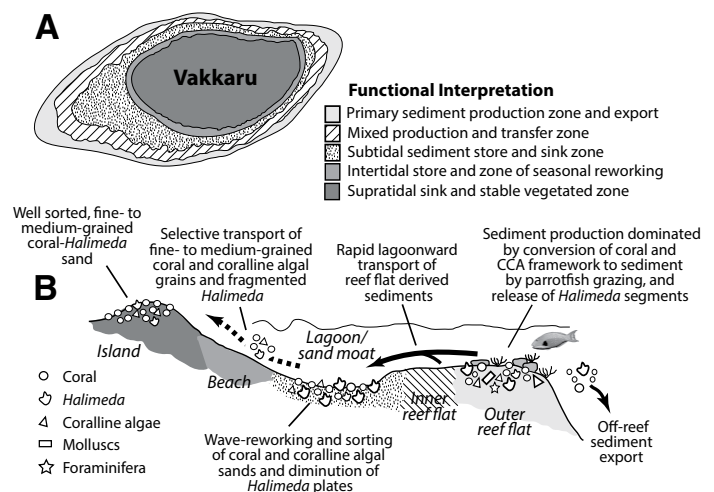


Figure 3. A: Delineation of functional zones around Vakkaru (Maldives) based on their geocological and sedimentary characteristics. B: Schematic summarizing the major sedimentary processes and sediment generation rates within the main geocological zones around Vakkaru. CCA—crustose coralline algae.

is very durable (Ford and Kench, 2012), and while coral rubble is relatively common on the outer reef flat, it is not a major island constituent at this site. Endolithic sponge bioerosion can also be excluded, as surveys showed that endolithic sponges are numerically rare and because they produce sediment that is predominantly silt-sized (<63 µm) (Fütterer 1974) and which is not abundant at this site. Grazing urchins also produce mainly silts and very fine sands (Hunter, 1977), but are not abundant on these reefs.

Consequently, parrotfish, which produce sediment as an excretory byproduct of grazing (Bellwood, 1996), are the only viable source of sand-grade coral. Parrotfish are known to produce sediment spanning exactly the same size fraction ranges in which coral is most abundant at Vakkaru, as evident from the parrotfish particle size distribution data of Hoey and Bellwood (2008) (Figs. 2F and 2G). The one noticeable difference is the lack of silt-grade coral in the Vakkaru sediment, but as reported by Bellwood (1996), this is probably a function of selective fine sediment loss as a result of hydrodynamic sorting. Therefore, it is clear that while parrotfish represent the major source for coral sediment generated at this site, not all of this sediment will be available for island construction. A proportion can realistically be assumed to be lost offshore (e.g., Morgan and Kench, 2014), while selective removal of the very finest size fractions of parrotfish-derived coral sediment is also likely to be flushed offshore.

CONCLUSIONS

At Vakkaru the ecology and ecological processes operating on the outer reef flat are tightly coupled to the composition of surficial island sediments, with sediment production dominated by parrotfish grazing of coral and by *Halimeda*. Despite a close correlation between the ecology of the reefs and the composition of these sediments, the paucity of sediment stored on the outer reef suggests that rapid onshore and offshore sediment transport occurs (Fig. 3). On the platform, the inner platform lagoon and sand moat act as a store and sink for sediment, but wave reworking in the swash zones appears to rapidly denude *Halimeda* plates, which are then relatively underrepresented in the near-surface island sediment record (Fig. 3). In contrast, more durable coral sand is a dominant island constituent. Census data show that a very high proportion of this coral sand is produced by parrotfish on the reef flat. The maintenance of the healthy parrotfish populations that characterize these Maldives reefs (and that are high in regional terms; Graham and McClanahan, 2013) is thus critical to sustaining contemporary sediment generation regimes, and appears necessary for island building and maintenance at this site. While the need to protect parrotfish populations is commonly based on the need to sustain benthic ecological interactions, this study demonstrates their further critical beneficial role as producers of carbonate sediment and thus as key biogeoenvironmental species that can sustain local landform maintenance.

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