Sediment generation by *Halimeda* on atoll interior coral reefs of the southern Maldives: A census-based approach for estimating carbonate production by calcareous green algae

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**Abstract**

Methods for quantifying rates and size fractions of carbonate sand production on reefs remain limited, despite the urgent need for such data to support assessments of reef island and tropical beach-dominated shoreline resilience. Here we present a census-based approach that supports estimates of sediment generation by the calcareous green alga *Halimeda* spp., which is an often conspicuous reef and lagoon substrate coloniser. Based on data from Kandahalagala (South Huvadhoo atoll, southern Maldives), we present carbonate sediment production data for the two dominant *Halimeda* spp. (*Halimeda macrophyrsa* and *Halimeda micronesica*) that occur on the reef flat and reef slope habitats. Whilst total mean production rates by *Halimeda* spp. are similar in both habitats (reef flat average, 67.49 g CaCO$_3$ m$^{-2}$ yr$^{-1}$; reef slope, 70.89 g), individual species contributions differ markedly. *H. micronesica* dominates on the reef flat (annual mean 41.91 g CaCO$_3$ m$^{-2}$ yr$^{-1}$, compared to 25.08 g by *H. macrophyrsa*), whilst production is dominated by *H. macrophyrsa* on the reef slope (*H. macrophyrsa* 40.49 g, *H. micronesica* 29.01 g CaCO$_3$ m$^{-2}$ yr$^{-1}$). In terms of sediment generation we show that these species also contribute very differently to the sediment reservoir. Whilst the sedimentary breakdown products from *H. micronesica* are somewhat bimodal (~17% is in the medium to very coarse sand fraction, and ~76% in the silt and clay fraction), almost all (~90%) of the segments produced by *H. macrophyrsa* rapidly degrade to silt and clay sized sediment. Based on our census data this suggests that *Halimeda* spp. will contribute only between 7 and 9 g m$^{-2}$ yr$^{-1}$ of sand grade sediment on the reef flat and shallow slope habitats, but ~55–60 g m$^{-2}$ yr$^{-1}$ of mud grade sediment. Scaled to the total area of combined reef habitat around Kandahalagala (~130,583 m$^2$) this equates to *Halimeda* spp. producing ~2192 kg of sand-grade sediment, but ~15,181 kg of mud-grade sediment per year. However, sediment compositional data suggests that *Halimeda* sp. are actually a very minor constituent of reef and islands sediments, especially in the fine sediment fractions. This 1) suggests that much of the predominantly finer-grained sediment generated by *Halimeda* has little actual relevance to the later stages of reef island development, and 2) highlights the potential for marked discrepancies in terms of sediment generating reef species abundance and resultent sediment generation rates, especially in terms of the types and sizes of sediment that are appropriate to supply adjacent beaches and islands.

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**1. Introduction**

There is major on-going debate about the resilience of low-lying coral reef islands and of carbonate-dominated tropical beaches to climate and sea-level change (e.g., Wetzel et al., 2012; McLean and Kench, 2015), with an acknowledgement that carbonate sediment supply (as dictated by the ecology of the adjacent corals reefs) has a key role to play in this respect (Perry et al., 2011). However, our ability to relate reef species abundance data to measures of sediment generation, and to quantify the sediment grain size fractions that result (and the durability of these constituents), remains limited. One visually conspicuous coloniser of both coral reef framework and lagoonal sands is the calcifying green algae *Halimeda* spp. which, when present in high densities, has the potential to produce carbonate at very high rates e.g., reportedly in excess of 2 kg CaCO$_3$ m$^{-2}$ yr$^{-1}$ (Drew, 1983; Freile and Hillis, 1997). The body (thallus) of *Halimeda* spp. plants comprises a number of calcified segments which progressively calcify through time. This process results initially from the precipitation of needle-shaped aragonite inside the segments, many of which can rapidly alter to anhedral equant aragonite nanograins in living specimens, although post-mortem, the plant segments are released into the surrounding sediment reservoir, initially contributing individual plates to the coarse sand to gravel grade size fractions (i.e., the 1–4 mm fraction), but with a proportion then disaggregating into mud-grade (<63 μm) carbonate sediment as needles and nanograins are liberated (Folk and Robles, 1964; Neumann and Land, 1975; Ford and...
Kench, 2012). As a result, Halimeda spp. can contribute to a wide range of sediment size fractions across reef sedimentary systems (Hewins and Perry, 2006), and some of this sediment may also form extensive bioherms (Rees et al., 2007), or be appropriate to contribute to the development of adjacent reef-associated landforms (e.g., beaches, reef islands; see Kench et al., 2005; Morgan and Kench, 2016).

However, at least 44 species of Halimeda have been described across tropical reef-building regions (Guiry, 2016). These exhibit a diverse range of growth morphologies, which differ in terms of segment sizes (Hillis-Colinvaux, 1980), and occupy a wide variety of habitats that range across sediment-dominated lagoons to deep fore-reef slopes and walls. For example, some species form small, compact bushes that grow semi-cryptically on hard substrates producing either small (~5–10 mm diameter) segments (e.g., Halimeda microcnorica, or larger (to ~20 mm) segments e.g. Halimeda tuna. Other species form tall (up to 10–15 cm), erect plants that have larger segments (up to 10 mm diameter) and holdfasts enabling a sand-dwelling mode of life (e.g. Halimeda incrassata, Halimeda monile), whilst others form elongate, hanging plants on the surfaces of walls and caves, some with very small segments (to ~5 mm diameter) (e.g. Halimeda goreauii), others with segments exceeding 30 mm in diameter (e.g. Halimeda gigas). Although not well quantified there also appears to be considerable inter-species variability in terms of plant growth and turnover rates (Muller and Clavijo, 1989) and in terms of the degree of segment calcification (Hillis-Colinvaux, 1980; Freile and Hillis, 1997).

Based on the above observations it is thus reasonable to hypothesise that both overall carbonate production rates, and the types (and size fractions) of sedimentary carbonate produced by different Halimeda spp. may vary significantly, which has evident implications for estimating reef carbonate budgets and understanding carbonate sediment supply. However, such inter-species variability remains poorly constrained. For example, data on Halimeda production rates derive, largely for field logistical reasons, overwhelmingly from studies of the common sand-dwelling species H. incrassata (e.g., Wefer, 1980; Muller, 1988; Payri, 1988; Freile, 2004), with data from other species that occupy very different habitats being either sparse or entirely absent. Even more poorly constrained is our knowledge of the sedimentary breakdown products of different habitats being either sparse or entirely absent. Even more poorly constrained is our knowledge of the sedimentary breakdown products of different habitats being either sparse or entirely absent. Even more poorly constrained is our knowledge of the sedimentary breakdown products of different habitats being either sparse or entirely absent.

2. Study area and methodology

Field data and samples of H. macrophysa and H. micronesica (determined from initial field investigations to be the two major shallow water species of Halimeda at this site) were collected from the reefs around Kandahalagala Island (Fig. 1A; N 00°13’33.3"; E073°12’45.1") in both January and September 2016, although the sites close proximity to the equator results in only small seasonal variations in mean sea surface temperatures (SST): mean max SST 30.1 °C, mean annual SST 29.2 °C, mean min SST 28.7 °C. Both H. macrophysa and H. micronesica are semi-cryptic, hard substrate dwelling species with small holdfasts, but differ markedly in terms of segment size. H. macrophysa form compact and erect plants, typically to about 10 cm in height, that arise from a small, single holdfast. These holdfasts are usually located within crevices in the framework or between coral rubble (Fig. 1D), with the plants growing to extend just above the framework surface, or may grow more openly under semi-protected rocky overhangs. Plant segments are up to 15 mm high and 25 mm wide, and are lightly calcified relative to some other species (average CaCO3 content of segments 62.9 ± 10.7%). H. micronesica also form compact plants up to ~10 cm tall and again grow semi-cryptically within crevices, between coral rubble, or under semi-protected areas of reef framework (Fig. 1B). Branching is often dense, but the plants comprise much smaller segments (typically about 5 mm high and 6–7 mm wide), and these are more heavily calcified (average CaCO3 content of segments 87.9 ± 4.2%) than in H. macrophysa.

In order to assess the potential of using non-destructive censused-based approaches to estimate rates of carbonate production (g CaCO3 m−2 yr−1) by species of Halimeda (in this case for H. macrophysa and H. micronesica) we developed an approach based on the in situ collection of readily measurable plant dimensions so as to quantify plant volumetric space (cm3). For each species we then established an empirical relationship between plant volume and the number of segments, and which can then be combined with data on average segment carbonate content (g CaCO3), species turnover rate (crops per year) and site specific plant densities (number of plants m−2) to yield a measure of carbonate production (g CaCO3 m−2 yr−1) (see also Muller and Clavijo, 1989; Freile, 2004).

To first establish the volumetric space occupied of individual plants we collected specimens of each Halimeda species across the full size range observed within the study area (n = 90 specimens of H. macrophysa, n = 65 specimens of H. micronesica). For each plant we measured its maximum height and its maximum and minimum widths. The growth morphology and resultant volumetric space occupied by these (and many other) Halimeda species can be defined most simply by the volume (V) of an inverted elliptical cone, which can be determined as:

\[ V = \frac{1}{3} \pi a b h \]  

(1)

Where, \( a \) = the radius of the minor axis (i.e., of the minimum plant width), \( b \) = the radius of the major axis (i.e., of the maximum plant width), and \( h \) = the height of the plant.

We then counted the total number of segments in each collected plant to establish a relationship between plant volume and the number of segments. To determine the average carbonate content (g CaCO3) per plant segment we collected replicate branches of similar lengths from 25 individual plants of each species. Average number of segments per branch was 7.4 for H. macrophysa and 83.4 for H. micronesica, the difference reflecting the very different segment sizes associated with each species. Samples were then washed in distilled water to remove any surficial filamentous algal overgrowth and any calcareous encrusters (specifically benthic foraminifera) were removed with a scalp. Samples were then oven dried (40 °C), weighed, subject to treatment with 2 M HCl until no further reaction with the carbonate was visible, rinsed in distilled water, re-dried and then re-weighed to determine carbonate loss, which was then averaged as a function of the number of segments per branch. To determine an annual turnover rate for each species we measured the number of new segments produced by each species over time, based on the widely used Alizarin Red staining method (see
Multer, 1988; Freile and Hillis, 1997; Vroom et al., 2003 for methodological descriptions). Staining experiments (n = 30 specimens per species) were conducted in September 2016 and rates are reported as an average for each species.

To determine the sediment size-fractions to which the two species of Halimeda under investigation contribute post-mortem, we followed the same experimental approach to that used by Neumann and Land (1975) in a study of Caribbean green algal breakdown. We collected nine fully calcified specimens of each species and placed these in elongate (25 cm × 10 cm × 6 cm) lidded plastic vessels containing a 50:50 solution of distilled water and 5% commercial bleach. Total dry weight of each plant pre-treatment ranged between ~9 and 12 g. The experimental vessels were then placed on a see-saw rocker plate (Stuart Model SSL4) set to operate at a tilt rate of 28 oscillations/min, which was determined as sufficient to enable slow, gentle continuous agitation of the samples. Each experiment was left to run for 3, 12 and 21 days. Samples were then wet sieved through a sieve stack (sieve sizes of 4 mm, 2 mm, 1 mm, 500 μm, 200 μm, 125 μm, 63 μm, and 31 μm to conform to the standard grain size divisions under the Udden-Wentworth scheme). Each retained fraction was then filtered, dried and weighed to determine the proportion of sediment in each size fraction.

To determine the abundance of the two Halimeda sp. on the reefs around Kadahalagala we undertook quadrat based surveys across both the reef flats and along the upper sections of the reef slope (1–3 m depth) along the southern side of the island (Fig. 1C). Surveys were conducted in both January and September 2016. In each zone we counted the numbers of each species of Halimeda present in 50 replicate 0.5 × 0.5 m quadrats, and measured the a, b, h dimensions of each plant to determine plant volume (as above). These data were then integrated with: 1) the size:volume relationship established for each species to estimate the total number of segments in each plant; 2) the measured average segment carbonate content for each species; and 3) the plant turnover rate calculated for each species (5.7 crops per year for H. macrophysa and 9.7 crops per year for H. micronesica). Following the approach of Freile (2004) we then used these metrics to make a conservative estimate of carbonate production (g CaCO₃ m⁻² yr⁻¹) (conservative because the segment and plant size calculations represent the population at a single point in time, and thus capture plants in different stages of maturity), based on the following equation:

\[ G \text{ (g CaCO}_3\text{ m}^{-2}\text{ yr}^{-1}) = d \times c \times s \times w \]  

(2)
Where, $d =$ thalli density (no. plant/m$^2$), $c =$ number of crops per year, $s =$ average number of segments/plant, $w =$ weight per segment (g CaCO$_3$).

To determine the sedimentary significance of *Halimeda* in the reef sediments around Kandahalagala Island and in the island itself, we collected replicate ($n = 3$) surficial sediment samples to determine both the relative abundance of *Halimeda* within the sediments, and the size fractions to which it contributes. Samples were recovered from each major reef zone (lagoon, reef flat and fore-reef slope), from the flanks of the island (island moat) and from along the island top margin. Samples of the $>63$ µm fractions from each sample were prepared as thin-sections and analysed by counting 300 grains under a polarising microscope. Samples of the 63, 31 and $<31$ µm fractions were prepared as separate mounts for Scanning Electron Microscopy (SEM) analysis, and then point counted (200 points per sample). Compositional data from each were recorded and integrated with grain size data to give a weighted % abundance for each size fraction in each sampled habitat.

### 3. Results

#### 3.1. *Halimeda* spp. abundance and calculated plant volume: plant segment relationships

*Halimeda* spp. are visually very abundant on the reef environments around Kandahalagala, with two species dominating within the reef flat and upper reef slope (1–3 m depth) habitats, *H. macrophysa* and *H. micronesica*. However, the density of each species varied between habitats. On the reef flat, *H. micronesica* (mean: January 19.28 plants m$^{-2}$; September 23.20 plants m$^{-2}$) was significantly more abundant in both January ($t(49) = 14.0140, p < 0.0001$) and September ($t(49) = 15.2541, p < 0.0001$) than *H. macrophysa* (mean: January 11.12 plants m$^{-2}$; September 10.40 plants m$^{-2}$) (Table 1). In contrast, on the reef slope (1–3 m depth) *H. macrophysa* (means: January 20.88 plant m$^{-2}$; September 23.31 plants m$^{-2}$) was significantly more abundant in both January ($t(49) = 13.7501, p < 0.0001$) and September ($t(49) = 17.7148, p < 0.0001$) than *H. micronesica* (means: January 16.24 plants m$^{-2}$ September 21.71 plants m$^{-2}$) (Table 1). However, small-scale heterogeneity in this plant probably reflects local scale variations in reef substrate structure and complexity, given that both species exhibit a preference for semi-cryptic habitats and most commonly grow from crevices in the framework or from between branched coral rubble (Fig. 1D). We also note that within both habitats these species of *Halimeda* are present across a wide range of sizes, ranging up to about 165 cm high and 120 cm wide in specimens of *H. macrophysa*, and around 120 cm high and 115 cm wide in *H. micronesica*. Furthermore, our analysis of measured plant volumes and associated total segment counts indicate that there is a strong positive correlation between these variables in both species (Fig. 2). This observation provides confidence in the use of readily measurable size parameters (height and widths of plants) as a basis for estimating segment counts for individual plants, and which can thus be used in estimates of *Halimeda* spp. carbonate production (see Eq. (2)). We note that there is an approximate one order of magnitude difference in segment numbers for a given volume of plant in *H. micronesica* compared to *H. macrophysa* (Fig. 2).

#### 3.2. *Halimeda* spp. carbonate production rates and sediment size fraction contributions

To estimate rates of carbonate production (g CaCO$_3$ m$^{-2}$ yr$^{-1}$) by the two species of *Halimeda* we combined data on the number of segments per plant (as a function of plant volume – see above), with measured segment carbonate content data (g CaCO$_3$) (see Table 1), calculated rates of species turnover (Table 1), and counts of the number of plants m$^{-2}$ (as described above). Total rates of carbonate production by the two *Halimeda* spp. did not differ significantly between the two habitats in either field sampling period: January reef flat mean 70.58 ± 74.90 g CaCO$_3$ m$^{-2}$ yr$^{-1}$; January reef slope mean 71.71 ± 57.09 g CaCO$_3$ m$^{-2}$ yr$^{-1}$ ($t(98) = 0.0937, p = 0.9256$); September reef flat mean 64.39 ± 32.77 g CaCO$_3$ m$^{-2}$ yr$^{-1}$; September reef slope mean 70.07 ± 35.42 g CaCO$_3$ m$^{-2}$ yr$^{-1}$ ($t(98) = 0.6343, p = 0.5280$) (Fig. 3). However, individual species contributions to these totals differ markedly between habitats. *H. micronesica* produces significantly more carbonate on the reef flat in both January (mean 43.74 ± 36.97 g CaCO$_3$ m$^{-2}$ yr$^{-1}$) and September (mean 40.09 ± 30.91) compared to *H. macrophysa* (January 26.83 ± 49.38; September 23.33 ± 26.75 g CaCO$_3$ m$^{-2}$ yr$^{-1}$) ($t(49) = 4.0425, p = 0.0002$; Sept $t(49) = 12.4123, p = 0.0001$). In contrast, on the reef slope, *H. macrophysa* produced significantly more carbonate than *H. micronesica* in the September sample period (*H. macrophysa* 41.95 ± 33.89, *H. micronesica* 25.35 ± 22.56, t (49) = 7.4916, p = 0.0001), although this difference was not quite significant in the January sampling period (*H. macrophysa* 29.03 ± 32.05, *H. micronesica* 32.67 ± 48.94, t (49) = 2.0022, p = 0.0505). These inter-site variations broadly reflect observed differences in plant densities across the two habitats.

Plant breakdown experiments indicate that, from the perspective of sediment generation, these two species of *Halimeda* are likely to contribute very differently, post-mortem, to the sediment reservoir (Fig. 4). In the very early stages of segment disarticulation (Fig. 4B – 3 days) the grain size distribution of *H. micronesica* is strongly bimodal, reflecting early release of the intact small segments. However, over time these segments disaggregate into mud-grade carbonate (Fig. 4B – Days 12 and 21) such that whilst the end of experiment breakdown products from *H. micronesica* remain somewhat bimodal (~17% of sediment is in the medium to very coarse sand fraction) a significant proportion (about 76%) is in the silt and clay i.e., <63 µm, fraction. In contrast, and whilst some of the larger segments released by *H. macrophysa* remain after 3 days of agitation, most of the larger segments released by

### Table 1

<table>
<thead>
<tr>
<th>Species</th>
<th>Reef flat (0–1 m depth)</th>
<th>Reef slope (1–3 m depth)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Plant density (no. m$^{-2}$)</td>
<td>January 2016</td>
<td>September 2016</td>
</tr>
<tr>
<td><em>H. macrophysa</em></td>
<td>11.12 ± 2.57</td>
<td>10.40 ± 2.32</td>
</tr>
<tr>
<td><em>H. micronesica</em></td>
<td>19.28 ± 3.31</td>
<td>23.20 ± 3.23</td>
</tr>
<tr>
<td>Segment CaCO$_3$ content (mg)</td>
<td>(21,960, 4,266)</td>
<td>(21,960, 4,266)</td>
</tr>
<tr>
<td>Crops per year</td>
<td>5.7</td>
<td>9.7</td>
</tr>
<tr>
<td>Carbonate production (g CaCO$_3$ m$^{-2}$ yr$^{-1}$)</td>
<td>26.83 ± 29.38</td>
<td>23.33 ± 26.75</td>
</tr>
<tr>
<td>Total carbonate production (g CaCO$_3$ m$^{-2}$ yr$^{-1}$)</td>
<td>28.63 ± 32.98</td>
<td>24.33 ± 30.51</td>
</tr>
</tbody>
</table>

Metrics on plant densities, segment carbonate content and calculated rates of carbonate production (± 1 standard deviation) in reef flat and slope environments around Kandahalagala, and total rates of carbonate production per habitat (bold). Figures in parentheses show maximum and minimum values.
this species very rapidly disaggregate, such that a very high proportion of the resultant sedimentary material exists in the silt and clay sized fractions (>70% after 12 days, and >90% after 21 days; Fig. 4, B). Based on this knowledge and in combination with the plant density data above, this suggests that *Halimeda* spp. currently produce only around 9.1 g m\(^{-2}\) yr\(^{-1}\) of sand grade sediment on the reef flat, and about 7.7 g on the reef slope, but between 55 and 60 g m\(^{-2}\) yr\(^{-1}\) of mud grade sediment in both environments (Fig. 4, C, D). We note that no large segments comparable to those produced by the species *H. macrophysa* were preserved following the experiment run, but that some relatively unbroken or partially fragmented segments of *H. micronesica* were preserved. It is the segments from this latter species which thus appear to have the greatest potential to persist into the longer term sedimentary record at this site.

### 4. Discussion

*Halimeda* spp. are abundant and conspicuous on the reef flat and shallow (1–3 m depth) reef slope habitats around Kandahalagala, with average total plant densities measuring ~32 and 39 plants m\(^{-2}\) in the two habitats respectively across both the January and September sampling periods. Measured rates of carbonate production, based on census, plant segment abundance, measured turnover rates and segment carbonate content data, suggest these plants are likely to be meaningful contributors to the general reef sediment reservoir, with both *H. macrophysa* contributing more carbonate than *H. micronesica* on the reef slope, but *H. micronesica* contributing about twice as much as *H. macrophysa* on the reef flat. However, the resultant sediment contributions from these species are actually likely to be very variable. Whilst *H. micronesica* plants appear to breakdown into size fraction proportions that are broadly comparable to those reported for the erect, sand dweller *H. incrassata* (Neumann and Land, 1975), our experiments suggest that *H. macrophysa* plants degrade post-mortem almost entirely to mud size sediment (i.e., <63 μm). If scaled to the total area of combined reef flat and shallow fore-reef slope habitat around Kandahalagala (~130,583 m\(^2\)) this thus equates to *Halimeda* spp. producing ~2192 kg of sand-grade sediment, but around 7 times as much mud-grade carbonate (~15,181 kg) per year. Given the strong likelihood that much of this mud-grade sediment may be flushed from the reefs, or may be unsuitable for contributing to island building (which contains <1 wt% mud sized sediment – see below), this raises some key issues about the assumed inherent sedimentary linkages that exist between the ecology of those reefs that are proximal to reef islands and carbonate dominated beaches, and sediment supply (Perry et al., 2011). Indeed, it may well be that some very abundant reef taxa do not, because of their post-mortem breakdown pathways, actually represent important producers of the types and sizes of sediment needed to sustain reef landform building, even when numerically abundant on the adjacent reefs. Data on which taxa are most important in this respect are sparse. However, it is clear that the assumed breakdown of *Halimeda* spp. into (at least in part) gravel and coarse sand grade sediment that may be most

**Fig. 2.** Relationships between measured plant volumes (cm\(^3\)) and number of segments in (A) *Halimeda macrophysa*, and (B) *Halimeda micronesica*.

**Fig. 3.** Carbonate production rates by *Halimeda* spp. at Kandahalagala. Box (median and 50% quantile) and whisker (95% quantile) plots showing calculated rates of annual carbonate production (g CaCO\(_3\) m\(^{-2}\) yr\(^{-1}\)) for both *Halimeda macrophysa* and *Halimeda micronesica* within reef flat and reef slope habitats in both January and September 2016, and total rates of carbonate production for each habitat.
appropriate for incorporation into beaches and islands (e.g., about 75% of the production in the classic study of Neumann and Land, 1975), may be an inappropriate assumption for many other Halimeda spp. Indeed, the longer-term preservation of these larger segments may, for some species, only be realistic in the most sheltered environments e.g., where segments settle out within protected framework cavities. Thus for Halimeda, at least, both plant abundance and species are likely to be key influences on sediment generation.

Based on the census and experimental data from Kandahalagala we thus hypothesise that despite their visual abundance on the surrounding reefs that Halimeda spp. is not a major overall contributor to the island sediments. Indeed we predict that whilst the most robust, small segments derived from H. micronesica may contribute to a proportion of the sand-grade material present across both the reef and into the lagoon and island itself at this site, that larger segments derived from H. macrophysa are unlikely to be present except perhaps most proximal to their sites of growth (and, for example, we note these are clearly visible in the sediments on the reef slope sites). Furthermore, we would expect that whilst some of the large amount of Halimeda sourced mud-grade carbonate may be an important constituent of the lagoon infilling in these sites, a significant proportion of this fine sedimentary material may also be exported off-reef.

These suggestions are strongly supported by sedimentary data collected from across the reef to island system around Kandahalagala (Fig. 5). Halimeda constitutes no >5–10% of the total sediment across the reef, lagoon and island moat habitats, and is especially sparse (<5%) within the island sediments themselves, this despite the fact that Halimeda sp. are visually and numerically abundant across the main reef areas. This contrasts with observations from lagoonal and back-reef settings in Florida where Halimeda abundance in the sediments was more closely correlated with areas of highest measured productivity (Bosence, 1989; Bosence et al., 1985). This may reflect differences in either the preservation potential of the Halimeda segments being produced by the different species involved in Florida, or reduced transport/winnowing potential in the lower energy lagoonal settings in Florida. We also note that the contribution of Halimeda to the finest sediment size fractions around Kandahalagala is very small (<1–2%), this being an especially significant observation given that the measured breakdown products from both species are predominantly in the silt and clay size fractions. Indeed, it is evident in the textural data that fine-grained sediments i.e., the <63 μm size fractions, are overall very minor elements (<5%) of the sediment reservoir around Kandahalagala, with the exception of the lagoon habitat where muds constitute about 25 wt% of the sediment. These findings thus point to a major disconnect between the ecological abundance of specific reef sediment producing species, and their resultant sedimentary significance.

A further key outcome of this study is that it demonstrates the potential to utilise non-destructive census based approaches to estimate plant
segment numbers, which can then be utilised alongside plant density data, and species appropriate measures of segment carbonate content and annual turnover rates to estimate annual carbonate production rates. This has the distinct advantage of not requiring the harvesting of plants, and is conceptually comparable to the methodologies that have been widely utilised to assess seagrass epiphyte carbonate production (e.g., Patriquin, 1972; Nelson and Ginsburg, 1976; Perry and Beavington-Penney, 2005). However, two issues arise as a result of our current capabilities in this respect. The first relates to the applicability of the approach to other species of Halimeda (and indeed other green algal species) which may differ markedly in growth form and habitat preference. The second relates to the consistency of the resultant carbonate production rate data to that generated in other studies based on plant harvesting and biomass data (e.g., Payri, 1988; Garrigue, 1991).

In terms of the first point, the presented relationships probably have some general level suitability to apply to similar hard substrate dwelling (lithophitic) taxa with similar life modes and segment sizes. However, it would clearly be preferable for additional species specific datasets to be collected. To this end we have thus far undertaken a similar analysis based on a collection of Halimeda cylindracea plants, a sand-dwelling taxa with a larger holdfast comparable to H. incrassata, collected from around Lizard Island on the Great Barrier Reef. The resultant plant volume: segment size plots (Fig. 6A) show a similarly strong positive relationship to that identified for H. macrophysa and H. micronesica, suggesting that there is clear potential to extend this approach to other species. Furthermore, resultant plant breakdown experiments on this species (Fig. 6B) also show the importance of understanding species specific breakdown patterns in terms of predicting potential sedimentary contributions. Our data show that H. cylindracea plants degrade into proportional size fractions more similar to those identified in the classic Neumann and Land (1975) study of H. incrassata breakdown, with ~45% in the gravel and sand size fraction, and 55% in the mud size fractions, proportional contributions that differ from both H. macrophysa and H. micronesica.

In terms of consistency of the resultant carbonate production rate data to that generated in studies with other methodologies, this is rather harder to directly compare because there is no previously published production rate data for either H. macrophysa or H. micronesica. Our data for H. micronesica suggest that on the reef flat average plant densities of 21 m\(^{-2}\) produce ~42 g CaCO\(_3\) m\(^{-2}\) yr\(^{-1}\) (an average of ~2.0 g plant yr\(^{-1}\)) and for H. macrophysa ~11 plants m\(^{-2}\) produce 25.1 g CaCO\(_3\) (i.e., ~2.3 g plant yr\(^{-1}\)). We note that these rates are not inconsistent with those derived from equivalent plant densities in other studies, albeit for other Halimeda spp. For example the following production rates have been reported for the erect, sand-dweller H. incrassata (which, of the species we examined, is most similar to H. micronesica in terms of segment size): 2.0 to 3.1 g plant yr\(^{-1}\) (Multer, 1988) and 2.3 g plant yr\(^{-1}\) (Freile and Hillis, 1997); and for

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**Fig. 5.** Sediment textural properties and relative compositional data for different sediment size fractions within the five distinct cross reef to island habitats around Kandahalagala. n = 3 samples per site.

**Fig. 6.** (A) Relationship between measured plant volume (cm\(^3\)) and number of segments in Halimeda cylindracea; (B) wt% contributions to different grain size fractions following experimental breakdown (21 days) of Halimeda cylindracea. Samples collected from Lizard Island, Great Barrier Reef, Australia in February 2016.
the compact reef substrate coloniser *H. opuntia* 0.6 g plant yr\(^{-1}\) (Neumann and Land, 1975). Higher rates of ~6.0 g plant yr\(^{-1}\) were reported for the large segmented sand dweller *H. macrolobata* by Mayakun et al. (2014). Comparisons to other carbonate production rate studies are harder as these use an alternative metric based on harvesting of plants to determine dry weight per unit area rather than plant densities.

5. Conclusions

Concerns about the maintenance of adequate sediment supply to reef islands and beaches suggest an urgent need for reproducible and transferable census-based methodologies, which can be integrated with experimental data on the sedimentary breakdown products from different reef calcifying species, to quantify both the amounts and types (grain sizes) of carbonate sand produced annually. Here we show the potential to apply such approaches to the often visually abundant substrate experimental data on the sedimentary breakdown products from different erable census-based methodologies, which can be integrated with ex-rate studies are harder as these use an alternative metric based on har-

Mayakun et al. (2014). Comparisons to other carbonate production reported for the large segmented sand dweller


Perry, C.T., Beavington-Penney, S.J., 2005. Epiphytic calcium carbonate production and fa-

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