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Budget of coral-derived organic carbon in a fringing coral reef of the Gulf of Aqaba, Red Sea

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ABSTRACT

The continuous release of organic C-rich material by reef-building corals can contribute substantially to biogeochemical processes and concomitant rapid nutrient recycling in coral reef ecosystems. However, our current understanding of these processes is limited to platform reefs exhibiting a high degree of ecosystem closure compared to the globally most common fringing reef type. This study carried out in the northern Gulf of Aqaba (Red Sea) presents the first quantitative budget for coral-derived organic carbon (COC) in a fringing reef and highlights the importance of local hydrodynamics. Diel reef-wide COC release amounted to 1.1 ± 0.2 kmol total organic carbon (TOC) representing 1–3% of gross benthic primary production. Most COC (73%) was released as particulate organic C (POC), the bulk of which (34–63%) rapidly settled as mucus string aggregates accounting for approximately 28% of total POC sedimentation. Sedimentation of mucus strings, but also dilution of suspended and dissolved COC in reef waters retained 82% of diel COC release in the fringing reef, providing a potentially important organic source for a COC-based food web. Pelagic COC degradation represented 0.1–1.6% of pelagic microbial respiration recycling 32% of diel retained COC. Benthic COC degradation contributed substantially (29–47%) to reef-wide microbial respiration in reef sands, including 20–38% by mucus string POC, and consumed approximately 52% of all retained COC. These findings point out the importance of COC as a C carrier for different reef types. COC may further represent a source of organic carbon for faunal communities colonising reef framework cavities complementing the efficient retention and recycling of COC within fringing reef environments.

1. Introduction

Warm water coral reef ecosystems thriving in oligotrophic marine environments are nevertheless characterised by high rates of primary productivity, which is principally attributed to efficient utilization, recycling and conservation of the sparsely available nutritious organic material suspended or dissolved in reef waters (Muscatine and Porter, 1977; Richter et al., 2001; Wild et al., 2004a). Scleractinian corals are usually dominant taxa in warm water coral reef ecosystems and can contribute importantly to the organic matter pool in reef waters by continuously releasing particulate (POM) and dissolved (DOM) organic matter, e.g. as mucus (Crossland, 1987; Naumann et al., 2010a; Wild et al., 2004a). Coral mucus is a transparent organic exopolymer principally composed of C-rich components (carbohydrates, glycoproteins and lipids), which is synthesised and exuded by ectodermal cells as a protective mucoid layer covering the coral's tissue surface (Krupp, 1985; Marshall and Wright, 1993; Meikle et al., 1987; Ritchie, 2006; Schuhmacher, 1977; Wild et al., 2010b). The process of ectodermal mucus secretion is accompanied by the immediate dissolution of a significant mucus fraction and a successive ablation of particulate mucus components from the coral surface, consequently resulting in the entry of this material into the DOM and POM pools of reef waters (Wild et al., 2004a). Coral mucus can be released in such quantities that it dominates the suspended matter in reef-surrounding water (Johannes, 1967), where it significantly influences the growth and metabolism of pelagic microbial communities (Ferrier-Pagès et al., 2000; Wild et al., 2004a, 2008). Acting as a particle trap in the water column and on the coral surface, particulate coral mucus importantly supports benthic–pelagic coupling processes by rapid sedimentation of highly enriched aggregates forming mucus strings entering

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rapid sedimentation (Huettel et al., 2006; Mayer and Wild, 2010; Naumann et al., 2009a; Wild et al., 2004a, 2005b). This particle trapping contributes significantly to the retention of limiting nutrients, such as nitrogen and phosphorus in the reef ecosystem (Wild et al., 2004a), while it qualifies enriched coral mucus aggregates as a food source for various reef-dwelling organisms (Benson and Muscatine, 1974; Coffroth, 1984; Gottfried and Roman, 1983). The greater sum of these nutrient cycling and regeneration processes highlights organic matter release as one of the major ecosystem engineering functions performed by hermatypic (reef-building) corals dwelling in shallow (Wild et al., 2011) and deep reef ecosystems (Naumann et al., 2011; Wild et al., 2008).

While several studies have investigated general reef organic C metabolism with emphasis on ecosystem primary productivity and organic matter cycling (e.g. Charpy and Charpy-Roubaud, 1991; Gordon, 1971; Hata et al., 2002; Odum and Odum, 1955), only few studies (Huettel et al., 2006; Wild et al., 2004a,b) have focussed on the contribution and related function of organic C contained in coral mucus for organic C dynamics in reef ecosystems. These earlier studies describe the important role of coral mucus in nutrient cycling within the platform reef system of Heron Island (Australia) pointing out the role of this coral-derived organic C (COC) in nutrient conservation and regeneration via the efficient trapping of suspended particles and initiation of element cycles. Further, these studies provide evidence for the important contribution of COC to bulk sedimentary and pelagic decomposition processes highlighting it as a substantial source of degradable C in coral reef environments.

However, our current understanding of the contribution and related function of COC in ecosystem organic C metabolism is still limited to platform reef systems. These platform reefs are considered relatively closed systems compared to other reef types by exhibiting increased water residence times, nutrient recycling and internal fluxes accompanied by decreasing levels of boundary fluxes, external connectedness and material export processes (Hatcher, 1997). Consequently, the actual contribution and role of COC in hydrodynamically more open and complex, but globally more common reef ecosystems types, such as fringing reefs, is still unknown. In addition, previous COC budget studies have exclusively focussed on POM release by only few coral species (Wild et al., 2004a, 2005a) possibly misjudging the actual contribution of particulate (POC) and dissolved organic carbon (DOC) released by the usually diverse coral community using extrapolation approaches. Recently, also other dominant benthic reef taxa, in particular macroalgae, have been shown to release substantial amounts of organic C into reef-surrounding waters (Haas et al., 2010a,b). The present study focuses on the investigation of a COC budget to firstly quantify the acting processes in a reef ecosystem dominated and engineered by scleractinian corals.

In consideration of and comparison to the above mentioned findings for platform reef systems, the present study was conducted in a typical fringing reef of the Northern Red Sea principally aiming (1) to assess the contribution of COC to ecosystem organic C metabolism, and (2) to investigate the possible functions and fate of COC in trophic pathways of fringing coral reefs.

2. Methods

2.1. Study site

This study was carried out in a fringing reef of the Northern Red Sea (Gulf of Aqaba) during 4 seasonal expeditions (November/December 2006 (fall), August/September 2007 (summer), February/March 2008 (winter) and May 2008 (spring)) to the Marine Science Station (MSS) Aqaba, Jordan (location: 29° 27′ N, 34° 58′ E). According to earlier investigations regarding morphology and zonation, this fringing reef can be partitioned in a reef flat divided into back reef (depth: 0.0–1.8 m), reef crest (0.5–1.0 m) and reef slope (1–6 m) joined by a fore reef facing the open sea (Mergner and Schuhmacher, 1974). The fore reef consists of an upper (4–8 m water depth), middle (8–20 m) and lower (20–40 m) part distinguished by morphological features and species composition. The fringing reef system extends approximately 1.1 km along its reef crest bordering the coastline in a half-ellipsoid shape (Fig. 1). Investigations carried out by the present study focussed on the reef area framed by the coast line and the middle fore reef (depth range: 0–20 m; hereinafter called: reef-wide).

2.2. Ecosystem assessment

2.2.1. Reef bathymetry

A high-resolution multi-spectral satellite image (Quickbird, DigitalGlobe), recorded on 18th March 2009, was analysed to create a digital bathymetric profile of the study site (Green et al., 2000; Heege et al., 2007; Lafon et al., 2002; Vanderstraete et al., 2003). The satellite image provided four discrete non-overlapping spectral bands and 11-bit collected information depth. Image resolution was 2.4 m at a spectral range from 450 to 900 nm. The image data were corrected for atmospheric, air–water interface and water column effects using the physical based Modular Inversion & Processing System (Heege and Fischer, 2004; Kiselev and Bulgarelli, 2004). The resulting digital bathymetric map (Fig. 1) was used to calculate the overall 2D (planar) reef surface area (i.e. a = ca. 0.19 km^2) in successive depth ranges (0–1, 1–5, 5–10 and 10–20 m), the reef-wide water column volume (i.e. 1.1×10^6 m^3) as well as the average length (905 m), width (205 m) and water depth (6.1 m) of the study site using a geographic information system (ArcGIS 9.3 software, ESRI).

2.2.2. Hydrodynamics

The current regime within the study site, dominated by long shore currents in northern direction (Manasrah et al., 2006, 2010), was recorded throughout the entire study period (November 2006 to May 2008) by continuous measurements (10 min intervals) using an acoustic Doppler current profiler (Workhorse 300 kHz, RD Instruments) moored centrally at 34 m water depth (location: 29° 27′ 17.45″ N, 34° 58′ 12.72″ E) in the lower fore-reef area (Fig. 1). Comprehensive records of horizontal and vertical current components in 17 water column layers allowed for the calculation of seasonal horizontal current velocities (average ± SD of all seasons: cross shore = 2.9 ± 1.0, long shore = 5.8 ± 1.9 cm s^{-1}). These were used together with the average length, width and depth data of the study site (see above) to approximate seasonal residence times of the water column by its flow rate:

$$\varphi = \left((\varphi_x)^2 + (\varphi_y)^2 \right)^{0.5},$$

where φ is the flow rate (m^3 h^{-1}) of the water column and

$$\varphi_x = u \text{ x } A_x \text{ and } \varphi_y = v \text{ x } A_y,$$

where φ_x and φ_y are the respective cross and long shore horizontal flow rate components (m^3 s^{-1}) across the corresponding vertical interface areas (A_x and A_y) (m^2), products of mean study site length and depth (for A_x) and width and depth (for A_y), and u and v are seasonal average cross and long shore current velocities (m h^{-1}). Variability in resulting seasonal water column residence times (ca. 3%) was considered negligible for the study site. Consequently, a calculated annual average flow rate φ (i.e. $0.57 \pm 0.02 \times 10^6$ m^3 h^{-1}, mean ± SD) and the total water column volume (see 2.2.1) were used to derive the annual mean water column residence time within the study site (2.02 ± 0.07 h) as:

$$T = V/\varphi,$$

where T is annual mean residence time (h), V is water column volume (m^3) and φ is annual average flow rate (m^3 h^{-1}).

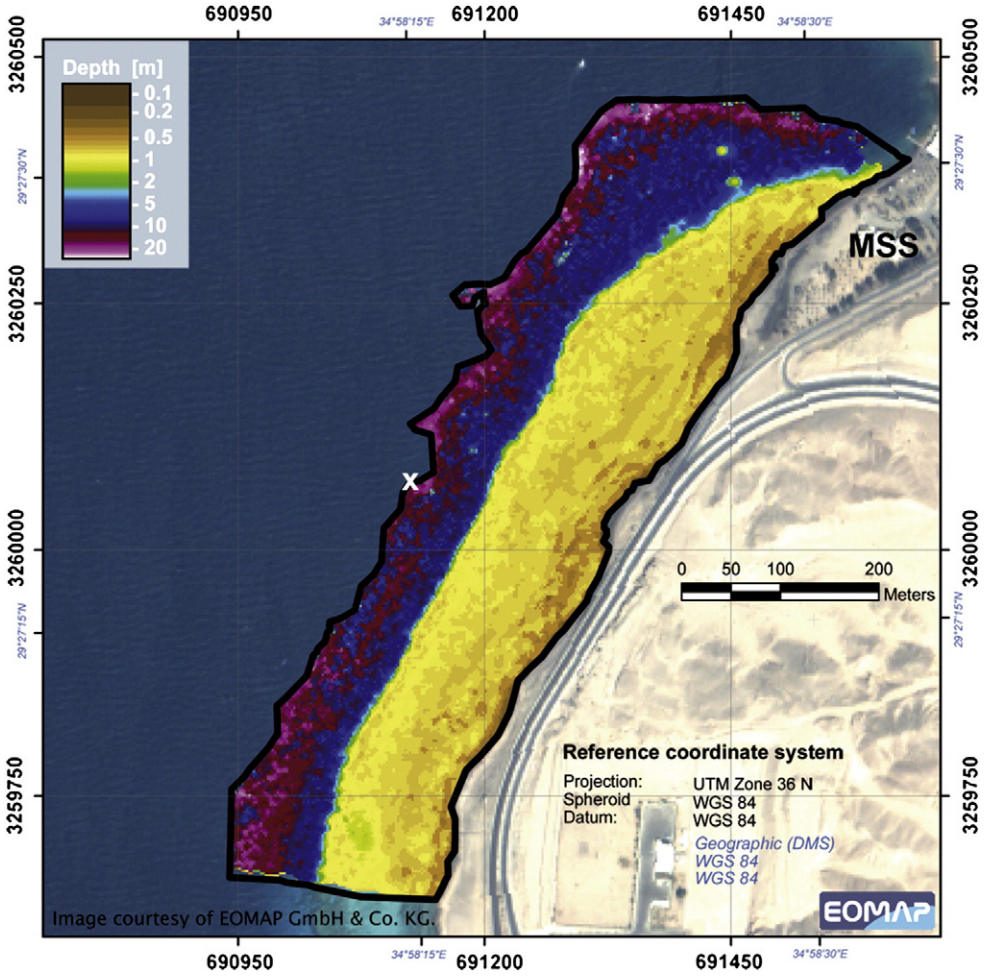

Fig. 1. Bathymetric map of the study site derived from multi-spectral satellite image analysis. White x indicates mooring location of the acoustic Doppler current profiler in the sloping fore-reef area. MSS = Marine Science Station Aqaba, Jordan.

2.2.3. Benthic cover

To assess the benthic reef assemblage by substrate types and to identify the dominant hermatypic coral genera in the study site, line-point intercept (LIP) surveys (total: $n = 44$), as described by Naumann et al. (2010a), were carried out at 0.5, 1.0, 5.0, 10.0 and 20.0 m water depth during the seasonal expeditions. Analysis of LPI data yielded the percentage coverage by main substrate types including the live coral cover and the contribution of dominant hermatypic coral genera (i.e. anthozoans: *Acropora*, *Fungia*, *Goniastrea*, *Pocillopora* and *Stylophora*, and the hydrozoan *Millepora*) (Table 1). The respective areal cover by each particular substrate type contributing to the reef framework derived from percentages of the reef-wide 2D area (a) was used to calculate an overall 2D reef area estimate excluding sand areas (total reef framework area: 1.21 km^2). The 2D area covered by sand was added to the total 3D area of the reef framework subsequently calculated using a specific 2D/3D approximation factor (6.6). This approximation factor had been derived from comparisons of surface area values measured from an array of corals of various genera and growth forms using either advanced geometric techniques or planar projection photography (Naumann et al., 2009b).

2.2.4. Seawater bulk organic C content

To investigate bulk organic C concentrations in the reef-overlying water column, seawater samples (3000–5000 ml; $n = 4$) were collected from the fore-reef area in 10 m water depth using pre-rinsed (HCl 10% and sampling seawater) opaque sampling containers on three dates during each of the seasonal expeditions. To ensure comparability of results between and within seasonal seawater samplings, identical sampling containers were used and special care was taken to guarantee an immediate short transfer from sampling location to the laboratory. This transport was accomplished without major agitation of the sampling containers to minimize disintegration of POC contents. Directly after arrival of the containers in the laboratory, samples for DOC analysis were prepared (as described by Wild et al., 2010a). Briefly, subsamples (10 ml) from each sampling container were processed by filtration through sterile polyethersulfone (PES) membrane filters (0.2 µm pore size, VWR International, cat. no. 28145–501) to remove POC contents. The first 4 ml of the resulting filtrate were discarded and the following

Table 1
Benthic coverage by reef substrates types within the study site (seasonal range of 3 successive years, 2006–2008). Water depth range: 0–20 m; LCC = live coral coverage.

Substrate	Benthic coverage (%)
Live coral coverage	37–43
Dominant genera ($n = 6$)	38–49 (of LCC)
Non-dominant genera ($n \approx 62$)	51–62 (of LCC)
Macro-algae	19–22
Bare coral rock	7–11
Sand	26–31
Other	3–7

6 ml were collected as DOC sample in pre-combusted (450 °C, 4 h) brown glass ampoules, which were instantly sealed and kept frozen at −20 °C until analysis. Potential leakage of DOC from PES filter membranes (Khan and Subramania-Pillai, 2007) was found insignificant, as quantified by repeated analyses of different lots of original filters following the described sampling protocol. DOC concentrations were determined by high temperature catalytic oxidation using a Rosemount Dohrmann DC-190 total organic carbon (TOC) analyser. A certified TOC standard (ULTRA Scientific, cat. no. IQC-106-5) was used for instrument calibration and quality control. Analytical precision was <3% of the certified value. Subsamples (1000 ml) for POC analysis were vacuum filtered (100 mmHg) onto pre-combusted (450 °C; 4 h) GF/F filters (Whatman, 25 mm diameter), subsequently dried for at least 48 h at 40 °C and analysed for POC content using a Thermo NA 2500 elemental analyser typically showing standard deviations <3% (elemental standards: atropine, cyclohexanone-2,4-dinitrophenylhydrazone; Thermo Quest). As the presence of detectable amounts of particulate inorganic carbon could be ruled out by test measurements conducted during all seasons, samples were not treated with HCl prior to analysis.

2.2.5. Pelagic metabolism

Two subsamples from each seawater sampling container were used to determine microbial respiration (R) in reef-overlying waters. The initial dissolved O_2 concentration was measured in the first subsample using an optical dissolved O_2 sensor (Hach Lange HQ10, accuracy ± 0.05%). The second subsample was filled into a 60 ml gas-proof Winkler glass bottle by ensuring a doubled volume overflow and the complete removal of air bubbles from within the bottle. This Winkler bottle was incubated in a laboratory-based water bath at in-situ temperature (seasonal range: 21–29 °C) in the dark for 16–24 h. Oxygen concentration was subsequently measured at the end of the incubation period as described above and the difference was used to calculate R rates. These rates were subsequently converted to C equivalents assuming that 1 mol organic C was consumed by 1 mol O_2 under aerobic conditions (Atkinson and Mavituna, 1983).

2.2.6. Benthic metabolism in reef sands

Benthic gross primary production (P) and R in calcareous reef sands was assessed during 2 expeditions (fall and summer) by measuring O_2 dynamics in seawater enclosed by stirred benthic chambers as described by Wild et al. (2005b, 2009a). Briefly, between 1 and 4 stirred benthic chambers were used during each seasonal deployment carried out at a referenced lagoon site in 2.5 m water depth. Transparent (P measurements) and opaque (R measurements) acrylic chambers were inserted into calcareous reef sands to a sediment depth of about 12 cm. The volume inside the chambers was ca. 5.7 l and incubations lasted for 5–8 h. At pre-set time intervals (30–120 min), water samples (60 ml) were collected ($n = 1$ per chamber) through sampling ports for subsequent analyses of O_2 concentrations. Simultaneous opening of sampling ports on opposite sides of the chambers enabled the extraction of water samples without inducing suction of sediment pore waters. The introduction of O_2 by the 60 ml (ca. 1% chamber volume) of fresh seawater on each sampling occasion was regarded as negligible. Fixation of water samples took place within 15 min after collection. O_2 concentrations were measured by Winkler titration within 1 h after fixation. P and R rates in calcareous reef sands were determined by linear regression of O_2 concentrations over time (at least 4 data points per chamber) and finally related to the volume and sediment surface enclosed by the chambers. All normalized O_2 flux rates were in the following converted to C equivalents as described above for of pelagic metabolism rates.

2.2.7. Sedimentation of bulk particulate organic carbon

To determine the amount of bulk POC settling to the seafloor, sediment traps were deployed in triplicates at 1, 5, 10 and 20 m water depth during each of the seasonal expeditions. Traps were designed and used as described by Wild et al. (2009a). All traps (total: $n = 48$) were placed on reef sands with their opening at a height of 15 cm above the seafloor. Traps were deployed for 48 h, after which the collected contents were prepared for POC analysis by filtering the particulate material onto pre-combusted (450 °C, 4 h) GF/F filters. Samples were subsequently dried for 48 h at 40 °C and exposed to a fuming HCl (1 N) atmosphere for 24 h to remove particulate inorganic C contents, before they were analysed using an elemental analyser, as described above. Trap POC contents were finally related to the trapping area (i.e. trap opening in m^2) and time of deployment to generate bulk POC sedimentation rates.

2.3. Organic C net fluxes by hermatypic corals

Quantification of organic C net fluxes (release or uptake) by the 6 dominant hermatypic coral genera was carried out according to the established laboratory beaker incubation technique (Herndl and Velimirov, 1986; Wild et al., 2005a) following the modified procedure described by Naumann et al. (2010a). Briefly, fragments from 5 different coral colonies of each of the dominant coral genera or 5 individual *Fungia* polyps were collected from 5 m water depth using SCUBA during each seasonal expedition. Further, 5 specimens of each of the genera *Acropora* and *Fungia* were sampled from each of 3 additional water depths (1, 10 and 20 m) during spring and winter expeditions, respectively. Corals from each genus and all depths were incubated individually ($n = 5$) in 1000 ml glass beakers filled with fresh seawater, in parallel with seawater controls ($n = 5$), for 6 h during daylight (10:00–16:00). Two additional night time incubations (20:00–02:00) of *Acropora* and *Fungia* corals (each $n = 5$) originating from 5 m water depth were conducted to assess organic C fluxes during the night. To rule out the influence of water currents on the structural composition of coral-derived organic C (i.e. POC disintegration and/or formation) released during incubation and to allow comparisons with previous studies employing the beaker incubation technique (Herndl and Velimirov, 1986; Wild et al., 2005a) beaker contents were not stirred during the relatively short incubation period. In-situ conditions (light availability and temperature) comparable to the original water depth of the incubated corals were ensured during incubations inside a water bath by comparative measurements using data loggers (Onset HOBO Pendant UA-002-64) and application of variable layers of black plastic gauze. The water bath containing the incubation beakers was covered with transparent cellophane foil to avoid the input of airborne particles, leaving 2 small side openings for air exchange. Following incubation, corals were removed from the beakers using clean tweezers, and water samples for POC and DOC analysis were prepared and processed, as described above for seawater samplings, to quantify POC and DOC net fluxes by concentration differences in coral beakers relative to controls. Following DOC sampling, dissolved O_2 concentration was determined in all incubation beakers using an O_2 optode (Hach Lange, HQ 10) to ensure that oxic conditions (>85% O_2 saturation) prevailed in coral incubations and controls during all conducted experiments. The seawater volume filtered for POC measurements ranged from 770 to 900 ml for all coral incubations (depending on coral volume) and was 900 ml for the controls. Quantification of the skeleton surface area of all incubated corals was carried out applying advanced geometric techniques involving individual measurements of particular morphological sections of the coral skeletons and subsequent computation using specific approximation factors. Those factors were derived from comparison with techniques employing 3D reconstruction by computer tomography (Naumann et al., 2009b). POC and DOC net flux rates per coral surface area and incubation time were calculated by subtraction of control beaker contents from those measured in the incubation water of the beakers containing corals. The resulting net POC and DOC concentrations of coral incubations were subsequently normalised using the measured coral specific skeleton surface area and incubation time to generate POC and DOC net flux rates.

2.4. Degradation of coral-derived organic C

2.4.1. Pelagic turnover

Microbial degradation rates of COC in reef waters were measured using dark incubation of seawater subsamples (ca. 140 ml) taken from each individual beaker at the end of all conducted coral beaker incubations, as described by Wild et al. (2009b, 2010a). For every subsample, 2 gas-proof Winkler glass bottles (volume: 60 ml) were filled. The initial O_2 concentration in one of the bottles was measured using Winkler titration or an optical dissolved O_2 sensor (Hach Lange HQ10, accuracy ± 0.05%). The second bottle was incubated for at least 16 h in the dark at in-situ temperature, after which O_2 concentration of the enclosed water was determined as described above. O_2 consumption in the incubation water was calculated by subtracting final from initial concentration. Pelagic microbial turnover of COC (% h^{-1}) was calculated using the respective measured initial TOC (i.e. POC + DOC) content and the rate in O_2 consumption over time in COC containing bottles relative to controls assuming equimolar aerobic oxidation of the organic C added (Atkinson and Mavituna, 1983).

2.4.2. Benthic turnover in reef sands

Microbial COC degradation in calcareous reef sands was studied in situ using 4 opaque stirred benthic chambers (see above), as described by Wild et al. (2009b). Briefly, experiments were carried out at a sandy reef site (water depth: 2.5 m), described by Wild et al. (2005b). At the beginning of 2 independent experiments, COC released by *Acropora* or *Fungia* corals during beaker incubations (58 and 39 μmol TOC, respectively) was added in-situ to half of the opaque chambers via a sampling port using syringes, while the remaining chambers served as controls for bulk organic C turnover in reef sands. All in all, a total of 4 benthic COC turnover runs ($n = 2$ for *Acropora* and *Fungia* respectively) were conducted. The duration of the individual chamber experiments ranged between 5 and 8 h. Water samples (60 ml) were taken from each chamber, as described above for measurements of bulk benthic metabolism, at least after every 2 h. O_2 concentrations in the chamber water were measured by Winkler titration. Benthic microbial turnover rates of the added COC (% h^{-1}) were calculated, as described above for pelagic microbial degradation, after subtraction of control chambers O_2 consumption rates.

2.5. Calculations

2.5.1. Coral-derived organic carbon net flux

Differences in POC and DOC net flux rates measured as a result of variable light availability during daytime at variable water depth, as well as variations between day and night time found for *Acropora* and *Fungia* corals (Naumann et al., 2010a), were used to generate approximation factors. These were applied to approximate POC and DOC net flux rates for the remaining investigated coral genera for day and night time conditions at 1, 10 and 20 m water depth during all seasons:

$$F_{\text{genus}} = E_{\text{genus}} \times AF_{\text{Depth/Light}},$$

where F_{genus} is POC or DOC net flux of one particular coral genus at a specific depth at day or night time (mmol C m^{-2} day^{-1}), E_{genus} is the POC or DOC net flux measured for the respective coral genus at standard conditions (5 m water depth during day time) (mmol C m^{-2} day^{-1}), and $AF_{\text{Depth/Light}}$ is the mean approximation factor derived from parallel comparisons of POC and DOC release rates at standard conditions to release rates at variable depth and during night time by the genera *Acropora* and *Fungia*.

Diel POC, DOC and TOC net flux rates (F_{diel}) were calculated for each water depth and dominant genus as the mean of day and night time rates. For non-dominant genera average POC and DOC net flux rates derived from all dominant genera were applied. Seasonal reef-wide fluxes were calculated individually and depth-specific for all taxa from their POC, DOC and TOC net fluxes (F_{diel}) and respective 3D reef area coverage, which was derived from the 2D areal cover at each particular water depth and growth form-specific approximation factors (Naumann et al., 2009b):

$$F_{\text{coral}} = F_{\text{diel}} \times A \times AF_{\text{3D/2D}},$$

where F_{coral} is the reef-wide flux of POC, DOC or TOC by a particular coral genus at a specific water depth (mol C day^{-1}), F_{diel} is the genus-specific diel POC, DOC or TOC flux rate (mmol C m^{-2} day^{-1}), A is the planar surface area covered by a particular genus at a given depth (m^2), and $AF_{\text{3D/2D}}$ is a coral growth form-specific approximation factor (i.e. branching: 9.04; massive: 2.82; disk-like: 4.59). For the non-dominant genera, the percentage contribution by different coral growth forms to the planar reef coverage was considered.

Results for each coral genus at all depths were summed on a seasonal basis and all seasonal values were averaged to yield mean annual reef-wide net fluxes generated by the entire hermatypic coral community S for POC, DOC and TOC. These fluxes were subsequently recalculated using the reef framework 3D/2D approximation factor (i.e. 6.6; Naumann et al., 2009b) to relate them to the planar reef surface area and finally normalised by the reef-wide planar area (a) to generate m of POC, DOC and TOC, as net fluxes m^{-2} reef area day^{-1}:

$$m_{(\text{n})} = S_{(\text{n})} / AF_{\text{reef}} / a,$$

where m is COC release (mmol C m^{-2} reef area h^{-1}) and S annual reef-wide COC flux of n (POC, DOC or TOC), AF_{reef} is the reef framework 3D/2D approximation factor, and a is the reef-wide planar surface area (m^2).

2.5.2. Mucus string sedimentation

Over the course of the present study, Mayer and Wild (2010) conducted in-situ surveys and samplings focussing on the formation, particle trapping and sedimentation of coral mucus string aggregates during 2 of the seasonal expeditions (fall and summer). Their findings add essentially to the present COC budget calculations by providing quantitative information on the contribution of particulate COC to mucus string aggregates, particulate COC release and bulk POC sedimentation. Mayer and Wild (2010) describe a frequent (95% of all coral mucus aggregates) and short-range (<120 cm distance to producing coral colony) sedimentation of particulate COC in the form of mucus strings aggregates. In the following, we apply findings by Mayer and Wild (2010) to estimate the contribution of these mucus strings to reef-wide coral-derived POC net flux and bulk POC sedimentation. Mean mucus string volume (≈0.9 cm^3) and POC concentration (2.4 mmol C l^{-1}) of freshly released gel-like mucus were applied to quantify the particulate COC content of individual mucus strings. In the following, mucus string POC content was used to estimate diel mucus string POC release assuming a conservative mucus string production of 9 strings h^{-1} by 27% of hermatypic coral colonies (Mayer and Wild, 2010):

$$MS_{(\text{n})} = Y \times D \times B \times (N \times 0.27),$$

where MS is the amount of particulate COC (kmol C day^{-1}) released as mucus strings by all coral colonies within a specific water depth range n (0–1, 1–5, 5–10, 10–20 m), Y is the mean volume of a mucus string (l), D is the POC content of mucus POC (kmol C l^{-1}), N is the number of coral colonies within a given depth range, B is the production rate of mucus strings per coral colony (h^{-1}), and 0.27 is the percentage factor of colonies showing visible production of mucus strings (Mayer and Wild, 2010). The depth range specific total number of colonies was derived from mean abundances m^{-2} planar reef area (i.e. 12–29; Luna, unpublished data) and area estimates for planar reef framework coverage derived from our LPI surveys.

Depth range specific results were summed to gain the diel reef-wide mucus string POC production (MS_{reef}), of which a major fraction (95%) was expected to immediately enter short-range sedimentation, thus becoming unavailable for potential COC export from the study site. The percentage share of MS_{reef} in diel particulate COC release ($S_{(POC)}$) was subsequently quantified, as well as its diel sedimentation rate MS_{sed} (mmol C m^{-2} day^{-1}) normalised by the reef-wide planar area.

2.5.3. Contribution of coral-derived organic C to biogeochemical processes

Organic carbon concentrations (POC, DOC and TOC) in reef waters attributable to COC release were determined by taking into account the continuous COC release and replacement by oceanic waters derived from current profiling:

$$c_{(n)} = m_{(n)} \times a/\varphi,$$

where c is COC concentration (μmol l^{-1}) and m is COC release (μmol C m^{-2} reef area h^{-1}) of n (POC, DOC or TOC), a is the reef-wide planar surface area (m^2), and φ is annual average water column flow rate ($l\,h^{-1}$) accounting for total water column volume (see 2.2.1). Mucus string POC release entering short-range sedimentation before suspension in reef waters was subtracted from m prior to calculation.

The differentiation of diel COC release into one fraction retained in reef waters ($COC_{retained}$) and another fraction readily exported to oceanic waters ($COC_{exported}$) was quantified by relating $c_{(TOC)}$ to the undiluted concentration of diel COC release into a theoretically closed system of identical water volume, but without flow and exchange by oceanic water ($c_{(undiluted)}$).

$$COC_{retained} = c_{(TOC)}/c_{(undiluted)} \times 100,$$

where $COC_{retained}$ is the fraction of COC release (%) retained within reef waters of the study site, $c_{(TOC)}$ is the actual concentration of COC in waters of the study site (μmol l^{-1}), and $c_{(undiluted)}$ is the undiluted concentration of COC in a theoretically closed reef system. $COC_{exported}$ (%) was subsequently derived from subtraction of $COC_{retained}$ (%) from 100%.

The contribution of the retained COC species to bulk pelagic organic C pools was obtained from the relation of calculated $c_{(POC)}$, $c_{(DOC)}$ and $c_{(TOC)}$ to the measured concentrations of the respective bulk organic C components (Table 2). The relative share of pelagic COC degradation in diel pelagic R was calculated by applying COC turnover rates to $c_{(TOC)}$ and relating the results to the mean of measured bulk pelagic R rates (Table 2).

Benthic COC turnover rates derived from chamber experiments were used to estimate diel reef-wide COC degradation as well as the contribution of bulk COC (including MS_{reef}) to benthic R in reef sands. The contribution of mucus string POC short-range sedimentation (95% of MS_{reef}) to reef-wide bulk POC sedimentation was derived from relation of values after normalisation to planar reef area (Table 2). Bulk POC sedimentation rates were corrected for POC degradation occurring during the 48 h trap deployment period applying pelagic organic C turnover rates (see 3.2). Supply of respiratory organic C demand in reef sands by sedimentary mucus string POC was further estimated by relating MS_{sed} to bulk R rates in the reef sediments (Table 2).

3. Results

3.1. Organic C net flux by hermatypic corals

Genus-specific COC (POC, DOC and TOC) net flux rates normalised to coral surface area (F_{diel}) of dominant and non-dominant hermatypic corals are presented in Table 3, together with diel estimates for the respective reef-wide fluxes quoted for single genera and the entire hermatypic coral community ($S_{(n)}$). Reef-wide, $S_{(POC)}$ as well as $S_{(DOC)}$ were net positive and showed a substantial release into surrounding waters. Average release amounted to 0.8 ± 0.2 and 0.29 ± 0.09 kmol C day^{-1}, for POC and DOC respectively, consequently adding up to a reef-wide diel TOC release ($S_{(TOC)}$) of 1.1 ± 0.2 kmol C (annual mean ± SD). The major fraction (73%) of COC was released in the form of POC (Fig. 2). Genus-specific F_{diel} rates for POC and DOC and variable areal coverage were reflected in the contribution of specific coral genera to $S_{(TOC)}$ (Table 3). In TOC terms, *Acropora* and *Stylophora* were identified as the main COC contributing genera by releasing 19 and 4-fold higher amounts, respectively, than the sum of all other measured genera. Non-dominant corals were responsible for approximately 30–46% of $S_{(TOC)}$ reflecting their 51–62% area share of live coral coverage (Table 1). Related to projected reef area, net release by the hermatypic coral community (m) amounted to 3.8 ± 1.1 mmol POC, 1.0 ± 0.5 mmol DOC or 4.8 ± 0.9 mmol TOC m^{-2} reef day^{-1} (annual mean ± SD). MS_{sed} was quantified as 1.8 ± 0.8 mmol POC m^{-2} reef day^{-1} (Table 2), which accounted for 34–63% of $S_{(POC)}$.

3.2. Contribution of coral-derived organic C to reef biogeochemical processes

Short water residence times of 2.02 ± 0.07 h resulted in a measurable $COC_{exported}$ flux to oceanic waters. On average, 18% of $S_{(TOC)}$ (0.2 ± 0.1 kmol TOC day^{-1}) was exported, while $COC_{retained}$ accounted for 0.9 ± 0.2 kmol TOC day^{-1} accessible to fringing reef metabolism (Table 3). Suspended and dissolved COC released into reef waters contributed only marginally (up to 0.5% POC) to the particular pelagic organic carbon pools (Table 2), while rapid MS_{sed} accounted for 12–65% (mean: 28%) of bulk POC sedimentation (Fig. 2). Benthic microbial COC degradation contributed substantially (by 29–47%) to reef-wide benthic R measured in reef sands (Table 2), where COC turnover (23.7 ± 4.8% h^{-1}) amounted to 39–65% (mean: 52% or 0.5 kmol C day^{-1}) of $COC_{retained}$, including a substantial 25–34% (mean: 28% or 0.2 kmol C day^{-1}) contribution by MS_{sed}, which supplied 17–32% of bulk organic C demand in reef sands. Pelagic microbial COC turnover was variable (0.2–6% h^{-1}, mean: 2.3 ± 1.7% h^{-1}), but substantially increased compared to bulk rates in reef waters (0.1–0.7% h^{-1}), where it accounted for 0.1–1.6% of pelagic R. This contribution was further representative of ca. 32% (0.3 kmol C day^{-1}) of $S_{(TOC)}$ (Fig. 2).

Table 2
Pelagic organic C pools, pelagic and benthic organic C reef metabolism and contribution by COC. Mean values are presented ± SD. P = primary production, R = microbial respiration, COC = coral-derived organic carbon, POC = particulate organic carbon, DOC = dissolved organic carbon, TOC = total organic carbon.

	Pelagic				Benthic		
	POC	DOC	TOC	R	P (reef sands)	R (reef sands)	POC sedimentation
	(μmol C l^{-1})			(μmol C l^{-1} day^{-1})	(mmol C m^{-2} day^{-1})		
	7–12	65–96	72–108	1–5	15–30	15–27	2–12
Mean	9 ± 3	80 ± 16	89 ± 18	3 ± 1	19 ± 4	19 ± 6	5 ± 3
COC contribution	0.02 ± 0.01	0.01 ± 0.01	0.03 ± 0.02	0.02 ± 0.02		7.3 ± 1.8	1.8 ± 0.8

Table 3
Diel net flux rates of coral-derived organic carbon species (POC, DOC and TOC) for the dominant and non-dominant hermatypic coral genera occurring within the study site. Area normalised data (F_{diel}) are presented as per square meter coral surface area. Retained POC and TOC fractions include mucus string POC. Values are given as mean ± SD. POC = particulate organic carbon, DOC = dissolved organic carbon, TOC = total organic carbon, $S_{(n)}$ = sum of reef-wide annual mean COC release (mol C day^{-1}) of n (POC, DOC or TOC) ± seasonal SD.

	POC		DOC		TOC	
Coral	F_{diel} (mmol m^{-2} day^{-1})	(mol day^{-1} reef-wide)	F_{diel} (mmol m^{-2} day^{-1})	(mol day^{-1} reef-wide)	F_{diel} (mmol m^{-2} day^{-1})	(mol day^{-1} reef-wide)
Dominant						
Acropora	11.0 ± 8.8	328.7 ± 183.7	5.6 ± 7.9	219.1 ± 59.2	16.6 ± 15.0	547.8 ± 224.2
Fungia	3.1 ± 1.4	0.9 ± 0.5	0.9 ± 1.8	0.5 ± 0.7	4.0 ± 2.1	1.4 ± 1.1
Goniastrea	5.8 ± 3.7	4.6 ± 2.2	4.8 ± 6.1	4.7 ± 4.2	10.6 ± 8.5	9.3 ± 6.4
Millepora	0.3 ± 0.3	5.0 ± 2.2	0.6 ± 0.5	9.8 ± 4.3	0.9 ± 0.8	14.9 ± 6.5
Pocillopora	13.9 ± 8.1	3.1 ± 1.6	2.4 ± 4.8	0.5 ± 0.6	16.4 ± 10.1	3.6 ± 1.0
Stylophora	26.8 ± 14.6	129.1 ± 38.4	−1.2 ± 4.9	−13.4 ± 38.8	25.6 ± 16.1	115.6 ± 26.2
Non-dominant	10.2 ± 5.9	316.9 ± 43.7	2.2 ± 3.8	69.9 ± 38.3	12.3 ± 8.3	386.8 ± 53.9
Mean/$S_{(n)}$	10.2 ± 8.8	788.2 ± 150.8	2.2 ± 2.4	291.1 ± 82.8	12.3 ± 8.3	1,079.4 ± 222.5
Retained		697.1 ± 130.9		189.4 ± 33.9		886.6 ± 164.8
Exported		90.1 ± 130.9		101.4 ± 33.9		191.4 ± 164.8

4. Discussion

4.1. Budget of coral-derived organic C in a fringing reef ecosystem

This study represents the first quantitative assessment of reef-wide COC release and its contribution to biogeochemical processes in a hydrodynamically open fringing reef system. The presented COC budget is based on a comprehensive data set of COC net flux rates recorded in unprecedented spatiotemporal resolution, differentiation of organic carbon species (POC and DOC) and coverage of dominant hermatypic genera. In addition to the quantification of COC net fluxes, results from COC degradation experiments, seasonal assessments of bulk pelagic and benthic reef metabolism and concomitant measurements of reef hydrodynamics and bathymetry allow for new insights regarding the function and fate of COC in fringing reefs. The budget presented here outlines biogeochemical element cycles of COC in a northern Red Sea fringing reef assessed under stable environmental conditions. All 4 seasonal expeditions were conducted under the expected natural regional climatic conditions (temperature, light intensity and current regime), while likewise no significant impacts on reef community health and composition (no bleaching event or other diseases, no *Acanthaster planci* or other pest outbreaks, no major benthic community phase-shift) were evident. The budget described could thus serve as a baseline against Red Sea fringing reefs

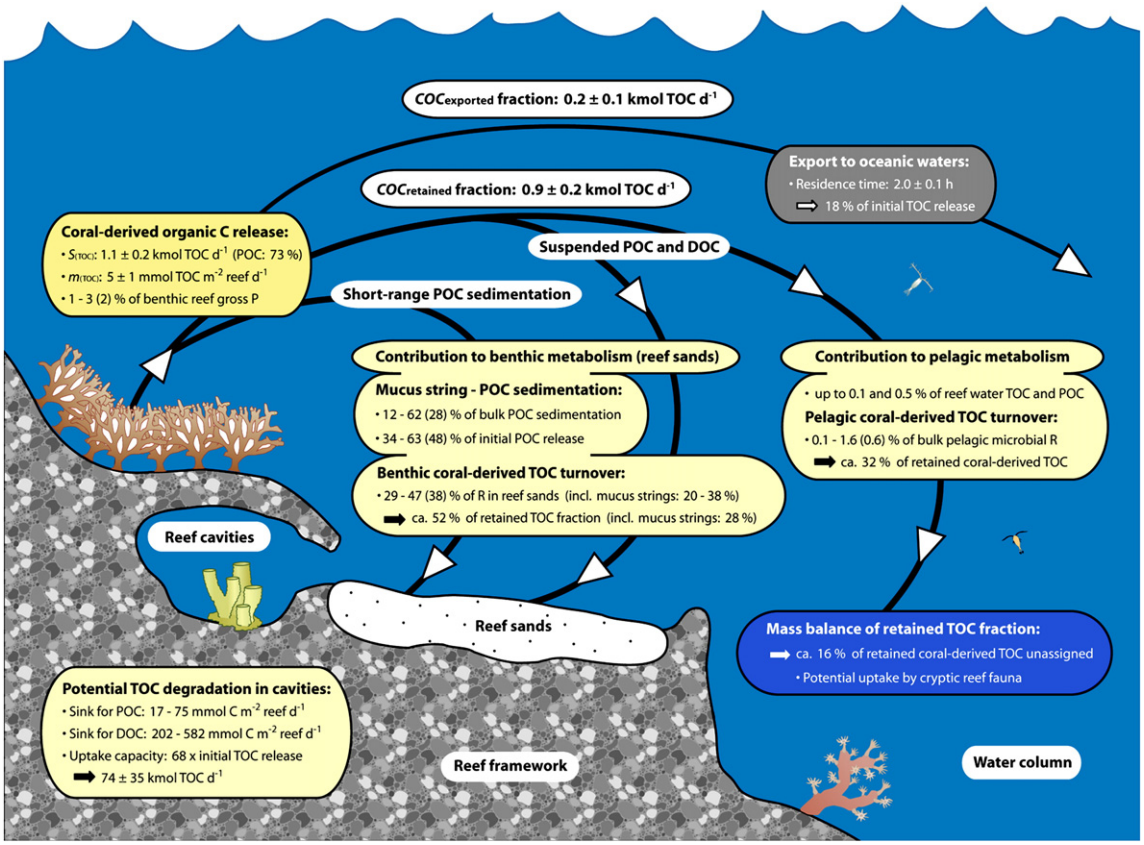

Fig. 2. Budget of coral-derived organic C in a typical fringing reef ecosystem. Presented is a simplified schematic cross-section of a Red Sea fringing reef disregarding the reef-wide contribution of living scleractinian corals and dead coral skeleton to the reef framework, as well as the actual encrusting morphology of reef cavity-dwelling sponges depicted here schematically as erect barrels. Mean values are given in parenthesis. P = primary production, R = microbial respiration, POC = particulate organic carbon, DOC = dissolved organic carbon, TOC = total organic carbon, $S_{(TOC)}$ = reef-wide diel TOC release, $m_{(TOC)}$ = coral-derived TOC release per square meter planar reef area day^{-1}, $COC_{retained}$ = fraction of coral-derived organic carbon retained within the study site, $COC_{exported}$ = fraction of coral-derived organic carbon exported from the study site.

under environmental stress, local impacts and/or significant shifts in benthic reef community composition.

Although our study represents the most comprehensive data set available on this topic to date, the significance of its findings may be limited by a number of factors influencing some of the main variables of the budget calculations. The overarching reason for all possibly limiting factors mentioned in the following is clearly of logistical origin induced by local technical constraints and issues regarding long-distance sample transport capacity. We were successful in quantifying for the first time COC net fluxes of all dominant scleractinian coral genera together representing up to 49% of live coral coverage in a Red Sea fringing reef. However, our quantification data set eventually covers only 6 out of ca. 68 genera occurring in the study site. As our focus was predominantly on the spatiotemporal resolution of COC net fluxes, a limitation to the dominant coral genera was a consequential logistical margin. Logistical constraints also limited the seasonal measurements of benthic metabolism in reef sands using the bulky in-situ chamber setup, which thus were only conducted during 2 expeditions (i.e. seasons). Further, we cannot be certain if our continuous water current measurements, conducted on a single central reef location only, can be representative of the reef-wide flow regime including possible local influences by 3D structures within the reef framework and small scale differences in flow maybe impacting COC net fluxes and/or the proportions of retained and exported COC. Nevertheless, the complete coverage and high temporal resolution of our current profile data set may potentially be able to account for these spatial limitations by providing more large-scale, although comprehensive, seasonal and annual mean water flow rates within the study site. Finally, our sampling approach to monitor reef water POC and DOC pools and ecosystem metabolism is likewise spatially limited to repeated seasonal samplings at identical locations within the study site. Here again, our data set is characterized by a high temporal resolution, but as well by low spatial coverage as a result of logistical constraints. As concluded for the water current profile data set, the high temporal resolution of our seasonal background monitoring approach may eventually be able to account for possible spatial variability.

Our findings reveal that the diel reef-wide COC release by hermatypic corals (1.1 ± 0.2 kmol C) can account for 1–3% of gross benthic *P* (Fig. 2) regarding accepted rates (200–500 mmol C m^{-2} planar reef day^{-1}) reviewed by Hatcher (1990). This is very close to results obtained by Johannes (1967), who estimated a 2% export of particulate coral-derived material from gross benthic *P* at Eniwetok Atoll, even if the DOC fraction neglected by the former study is added a posteriori. In terms of coral-derived POC release, our findings (3.8 ± 1.1 mmol POC m^{-2} reef day^{-1}) are very similar to rates measured by Wild et al. (2004a) for the more closed platform reef system at Heron Island (3.9 mmol POC m^{-2} reef day^{-1}). However, the majority of COC release (73%) measured by the present study is composed of POC (2.7-times of DOC net flux) contrasting with the results by Wild et al. (2004a), who found a 56–80% contribution of DOC to COC release. This may be explained by the fact, that the former study quantified POC/DOC fractionation of COC by separately conducted dissolution measurements using gel-like coral mucus, unlike our direct DOC net flux determinations. On average, COC turnover contributed 0.6% to bulk pelagic *R*, which is in the lower range of findings by Wild et al. (2004a) for the lagoon waters of Heron Island (0.1–2.5%), and representative of approximately 32% of diel retained COC release. These similarities in quantitative COC release, share of COC from reef-wide benthic *P* and contribution to pelagic *R* (i.e. microbial respiration) may indicate similarities in biogeochemical element cycles across different hard coral-dominated reef ecosystem types likely effecting growth and bacterioplankton community structure via COC release (Nelson et al., 2011; Wild et al., 2011).

For Heron Island lagoon sediments, Wild et al. (2004a) measured an input of 1.3–2.4% to benthic respiration via degradation of coral-derived POC. The noticeable higher contribution by benthic COC (i.e. TOC) turnover found here (mean: 38%) is responsible for a major degradation (52%) of retained COC. This underscores previous findings of rapid COC degradation in calcareous reef sands (Wild et al., 2005a,b), which is largely attributable to the turnover of particulate COC (28% of retained COC) supplied by the process of short-range mucus string sedimentation described by Wild et al. (2005b) and Mayer and Wild (2010). These authors identified a short-linked nutrient cycle in the study site characterised by predominant (95% of all coral mucus aggregates) and short-range (<120 cm distance to producing coral colony) sedimentation of highly POC-enriched (340–2000 x) mucus strings onto reef sediments, importantly fuelling sedimentary POC turnover. Our findings indicate that this process may involve up to 63% of the initial particulate COC release (Fig. 2), which confirms the results obtained from observations by the previous studies. The important contribution of this short-linked nutrient cycle is likewise reflected by its relatively high (mean: 28%) share of bulk POC sedimentation within the study site, where POC input by mucus string POC to reef-wide sedimentation was previously quantified ranging from 5 to 67% (Mayer and Wild, 2010). This particulate COC input can provide 17–32% (mean: 22%) of sedimentary organic C demand, while subsequent degradation of mucus string POC on average represents more than half (26%) of the bulk COC contribution (38%) to bulk *R* in reef sands. Benthic consumption of mucus string POC thus accounts for approximately 50% of retained COC turnover in sandy reef sediments. These findings emphasise the importance of COC (in particular particulate COC) as an energy and nutrient source in fringing reef ecosystems, which is further complemented by its significant contribution to regenerative short-linked element cycling and nutrient retention via particle trapping (Mayer and Wild, 2010; Wild et al., 2004a).

The quantified flux of diel COC release to oceanic waters (ca. 18%) characterises coral-dominated fringing reef ecosystems as net exporters of organic C derived from coral *P*. In addition to the pelagic food web surrounding fringing reefs, this exported energy may as well influence organic C metabolism in and support connectivity with adjacent ecosystem, such as seagrass beds or other reefs, by continuous fertilisation with rapidly degradable organic compounds (Ogden, 1988). Despite this continuous export, the major fraction of COC retained in reef waters contributes notably to fringing reef organic C metabolism (Fig. 2). This is remarkable, as the described processes suggest a similar (i.e. pelagic compartment) or in parts larger (i.e. benthic compartment) metabolic contribution by COC for an open fringing reef systems in comparison the hydrodynamically less open platform reefs (Hatcher, 1997; Wild et al., 2004a). Rapid turnover and metabolic contribution of COC to a high flow-through ecosystem may be explained by efficient degradation via highly specialised pelagic microbial communities able of utilising available organic carbon sources in timescales of relatively short residence times (Nelson et al., 2011). The efficient turnover within the benthic reef compartment may likewise be attributable to a dense and specialised heterotrophic microbial community (Wild et al., 2006) continuously supplied with particulate COC. Consequently, pelagic and benthic metabolism may act in union achieving a significant retention of released COC in hydrodynamically open fringing reef systems. Nevertheless, the fate of a considerable proportion (about 16%) of diel retained COC release still remains to be balanced by other processes prevailing within the study site (Fig. 2), which are discussed in the following.

4.2. The reef framework as potential sink for coral-derived organic C

Besides the reef-overlying water column and sandy reef sediments, coral reefs harbour a diverse community of organisms highly specialized in the capture and consumption of POC and DOC compounds (Anthony and Fabricius, 2000; Fabricius et al., 1995; Ferrier-Pagès et al., 2000; Houlbrèque et al., 2004; Palardy et al., 2008). The bioactive

surface area of the reef framework is composed of the outer exposed reef surface and an area made up of a complex system of cavities within the framework (Richter et al., 2001). Scleractinian corals, while dominantly dwelling on the outer exposed reef surface, are also able to take up POC (Anthony, 1999) and DOC (Ferrier-Pagès et al., 1998; Tremblay et al., 2012) to cover their metabolic demands. However, as organic C release calculations carried out here are based on POC and DOC net flux rates by corals measured in closed incubation systems; this potential uptake of organic C has already been considered. Other groups of benthic filter feeders thriving on the outer exposed reef surface (e.g. sponges and gorgonians) or coral-associated fauna (like acoelomorph worms) may contribute to the consumption of COC in fringing reef ecosystems (Coffroth, 1984; Naumann et al., 2010b; Yahel et al., 2003). However, their low areal coverage (maximum: 3–7%, Table 1) and scattered occurrence (Barneah et al., 2007) suggest only a minor contribution by these taxa to reef-wide COC uptake. Other authors have reported on the ingestion and incorporation of mucus aggregates by reef zooplankton (Benson and Muscatine, 1974; Richman et al., 1975) and fish (Gottfried and Roman, 1983), which represent processes likely to occur in the study site. Unfortunately however, a lack of quantitative data impedes reef ecosystem-wide projection of these trophic pathways and thus any evaluation for COC cycling.

More information is available on the inner cavity surface of the reef framework, which is densely populated by a diverse community of suspension feeding fauna including cavity-dwelling sponges (Richter and Wunsch, 1999; Wunsch et al., 2002), covering up to 60% of cavity surfaces (Richter et al., 2001). These cryptic communities remove substantial amounts of suspended and dissolved organic material (75 mmol POC and up to 582 mmol DOC m^{-2} cavity area day^{-1}), thus qualifying reef framework cavities as major sinks for organic C, which are constantly flushed by free-stream waters (De Goeij and van Duyl, 2007; De Goeij et al., 2008a,b; Richter and Wunsch, 1999; Richter et al., 2001). Applying the factor of 6.375 derived from comparison of the projected 2D reef area to measured 3D cavity surface area in the study site (Richter et al., 2001), cavity surfaces represent at least 71% of the estimated 3D outer reef surface area. Further taking into account TOC removal rates measured by De Goeij and van Duyl (2007) in Indo-Pacific reef cavities (90 ± 45 mmol TOC m^{-2} cavity area day^{-1}) exhibiting a comparable sponge coverage compared to the study site (De Goeij, personal communication), calculations arrive at a 74 kmol day^{-1} TOC uptake by the reef-wide cryptic faunal community (Fig. 2). This substantial uptake is many times above the unassigned fraction (16%) of diel retained COC, but also equal to 68-fold of diel initial COC release. These values clearly demonstrate the capacity of cavity-dwelling faunal communities for the efficient TOC uptake from reef waters and suggest framework cavities as a potential sink in the cycling of COC in fringing reef systems, e.g. for a substantial input of particulate COC aggregates (including mucus strings) highly enriched (3 orders of magnitude) in organic C content by efficient particle trapping initiated on the coral surface mucus layer (Mayer and Wild, 2010). A minor fraction (up to 6%) of coral-derived TOC release is suggested to enter the pelagic refractory organic carbon pool (Tanaka et al., 2011). However, no information exists on the refusal of refractory organic compounds by cavity communities (De Goeij, personal communication), but new evidence is emerging for the efficient depletion of the predominantly refractory organic carbon pool in seawater flushing fringing reefs (Nelson et al., 2011; Suzuki et al., 2000). These findings may render biodegradability of COC irrelevant to its uptake in reef framework cavities.

Thus, COC may contribute substantially to the organic carbon supply of cavity communities (De Goeij and van Duyl, 2007) resulting in the retention and important recycling of this material within fringing reef biogeochemical cycles. In fact, findings by a recent study point to COC as an important food component (up to 66% of diet) for cavity sponges in Caribbean fringing reefs (van Duyl et al., 2011). However, whether this finding may directly be transferable to Indo-Pacific reef systems remains to be investigated. In-situ tracer studies applying stable isotope labelling of COC (Naumann et al., 2010b) are currently underway to elucidate the actual contribution of Indo-Pacific cryptic reef fauna to COC degradation and potentially other reef trophodynamics describing the fate and functions of this, and other organic materials released by dominant taxa (e.g. macroalgae or scyphozoans; Haas et al., 2010a,b, 2011; Niggl et al., 2010) in fringing reef environments.

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