



Coral sand O₂ uptake and pelagic–benthic coupling in a subtropical fringing reef, Aqaba, Red Sea

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ABSTRACT: Calcareous sands are major sites for recycling of organic matter in coral reef ecosystems. O₂ uptake and pelagic–benthic coupling were studied in coral sands using benthic chambers and sediment traps during several seasonal expeditions between May 2004 and May 2008 along a fringing reef on the Jordanian Red Sea coast. A total of 12 independent dark chamber experiments were conducted at 2.5 to 16.5 m water depth on the highly permeable calcareous reef sands covering the seafloor at the reef and back-reef lagoon. Sedimentary O₂ uptake ranged from 20 to 39 mmol m⁻² d⁻¹ and was positively correlated with water depth in the lagoon, but not in the reef, where O₂ uptake was significantly lower. Comparison of sedimentary O₂ uptake rates recorded at the same locations revealed little temporal and seasonal variation, and no significant responses to changes in environmental factors in the water column, such as temperature and concentrations of organic or inorganic nutrients. These results suggest that efficient recycling in the pelagic food web of the nutrient-deprived coral reef limits the supply of degradable organic matter to the reef sediments. Increase of sedimentary O₂ uptake with water depth in the lagoon sands may therefore be a function of lateral transport of labile organic particles produced by reef organisms (e.g. benthic algae and corals) rather than sedimentation of water column production.

KEY WORDS: Coral reefs · Calcareous sands · O₂ flux · Spatial and temporal changes · Seasonality · Pelagic–benthic coupling · Red Sea · Advection chambers

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INTRODUCTION

Coral reefs are characterized by high turnover rates and efficient recycling of energy and essential nutrients (Crossland & Barnes 1983, Hatcher 1988, 1997, Richter & Wunsch 1999, Wild et al. 2004a). The reef sediments, in particular the permeable calcareous sands with their high abundances of phototrophic and heterotrophic microbes (Wild et al. 2006), contribute significantly to primary production, carbon mineralization and nutrient cycling of reef ecosystems (Johnstone et al. 1990, Clavier & Garrigue 1999, Wild et al. 2004b,c, 2005). Sedimentary production and decom-

position processes control O₂ flux across the sediment–water interface, and investigations by Werner et al. (2006) suggest that O₂ is the dominant electron acceptor over sulphate in permeable coral reef sands. Sedimentary O₂ uptake not only reflects the aerobic degradation of organic matter, but also the microbial and chemical reoxidation of reduced electron acceptors derived from anaerobic organic matter decay (Canfield et al. 1993), which also plays an important role in coral reef sediments (Skyring & Chambers 1976, Skyring 1985, Werner et al. 2006). Thus, O₂ uptake is the parameter ultimately integrating sedimentary organic matter mineralization processes, and the

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spatial and temporal changes in sediment–water O₂ flux contain key information on the functioning of calcareous sands as sites for the recycling of carbon and nutrients in the coral reef ecosystem.

Despite increasing interest in carbon and nutrient cycling in coral reefs associated with the worldwide deterioration in reef ecosystems (Hoegh-Guldberg et al. 2007, Hughes et al. 2007), studies targeting the spatial and temporal variability of O₂ flux in reef sands are rare, and most measurements are from nonrecurring investigations exclusively focusing on one or a few shallow reef locations (Boucher et al. 1994, 1998, Rasheed et al. 2004, Reimers et al. 2004, Wild et al. 2005). To our knowledge, only Clavier & Garrigue (1999) have studied sedimentary O₂ uptake in the lagoon of a barrier reef in New Caledonia on both temporal and spatial scales; they found pronounced differences between seasons, locations and sediments with different mineralogy. All investigations of sedimentary O₂ uptake in coral fringing reefs, the world's most common tropical reef type, have been conducted at shallow locations (maximum water depth ca. 5 m), although large sections of reef lagoons are deeper (Riddle et al. 1990, Hansen et al. 1992, Kayanne et al. 1995, Chabanet et al. 1997) and may function as traps for organic material as reduced wave and current impact allows settlement of fine particles. Deeper sandy areas in the reef, therefore, may account for a large fraction of organic matter recycling. The relatively high permeability of coral sands permits water flow through the pore space of the upper sediment layers (Wild et al. 2004b,c), thereby waves and bottom flow can affect spatial and temporal O₂ distribution in the seabed (Booij et al. 1991, Ziebis et al. 1996, Falter & Sansone 2000). As the intensity of wave-generated orbital water motion and wind-driven currents decreases with depth, it is expected that the hydrodynamic effects are less pronounced in the deeper areas of the reef lagoon, leading to reduced sediment flushing and higher concentrations of reduced compounds in the sediment. The deeper lagoon sites thus may accumulate more organic matter, but may also be characterized by a slower recycling rate due to reduced sediment–water solute exchange. Seasonal changes in waves, currents and organic matter deposition as well as benthos activities may cause spatial and temporal variability in sediment–water exchange processes affecting sedimentary organic carbon decomposition and thereby O₂ flux. The few nonrecurring measurements from shallow reef locations reported in the literature do not reveal the spatial and temporal dynamics of O₂ flux in coral reef sands or the contribution of deeper sand sites to the recycling in the reef. This lack of data impedes an assessment of the role of permeable sands for the cycling of matter in the reef and led to the initiation of the present study.

The main objectives were to: (1) assess magnitude and temporal variability of sedimentary O₂ flux in fringing reef sands in order to elucidate their function in the cycling of carbon in the reef, and (2) investigate the O₂ uptake of sandy sediments located at a deeper site in the lagoon. Working hypotheses were as follows: (1) sedimentary O₂ uptake shows temporal and spatial variation caused mainly by changes in organic matter supply and water column conditions (e.g. temperature, nutrient concentrations), and (2) sandy reef sediments in deeper waters can accumulate more organic matter and thus have a higher O₂ uptake. These working hypotheses were evaluated with a temporal series of *in situ* benthic chamber and sediment trap deployments in a Red Sea subtropical fringing reef over a total period of >3 yr.

MATERIALS AND METHODS

Study site. The present study was conducted at a fringing reef located near the Marine Science Station (MSS) in Aqaba, Jordan (29° 27' N, 34° 58' E). During 3 field expeditions (May–June 2004, Nov.–Dec. 2006, Aug. 2007), 12 independent *in situ* experiments with stirred benthic chambers were carried out at different water depths on calcareous sediment locations in the lagoon and reef as summarized in Table 1; 3 stations at 2.5, 5.5 and 9.5 m water depth were established in the lagoon sand area (lagoon sands) and 2 stations at 7.0 and 16.5 m depth in the reef area on small sand patches between the coral colonies (reef sands; Fig. 1). Mean grain size at the long-term monitoring station at 2.5 m water depth was 559 µm, and organic content was 0.36% (Rasheed et al. 2003a). Sediment permeability at this station was $11.6 \pm 1.1 \times 10^{-11} \text{ m}^2$ (Wild et al. 2005). Water temperatures at the study site ranged from 20°C in February to 28°C in August. Due to strong

Table 1. Summary of all stirred benthic chamber deployments on calcareous sands in the lagoon (L) and coral reef (R) areas at the study site

Expedition	Date (dd.mm)	Area	Depth (m)	No. of chambers
Spring 2004	27.05	L	2.5	4
	31.05	L	2.5	2
	04.06	L	2.5	1
	05.06	L	2.5	1
	14.06	L	2.5	2
Autumn 2006	22.11	L	9.5	2
	26.11	L	2.5	3
	29.11	L	5.5	4
	02.12	R	16.5	3
	04.12	R	7.0	2
	06.12	L	9.5	3
Summer 2007	21.08	L	2.5	2

evaporation, salinity is relatively high (40.3 to 40.8) year-round (Manasrah et al. 2006). Water currents are relatively weak and typically do not exceed 25 cm s⁻¹ at the surface and 5 cm s⁻¹ at the bottom (Manasrah et al. 2006). Due to these calm conditions, suspended particles can settle out of the water column resulting in low turbidity and deep light penetration promoting coral growth.

In situ measurement of sedimentary O₂ uptake. For each experiment, between 1 and 4 stirred benthic chambers identical to those described by Huettel & Gust (1992) and Wild et al. (2004b,c, 2005) were used to measure sedimentary O₂ uptake. The opaque cylindrical chambers were 30 cm in height with an inner diameter of 19 cm and excluded all light from the enclosed water and sediment (benthic primary production rate was not addressed in the present study). A plastic lid containing a sampling port for water extraction and a second port permitting replacement of the sampled water volume covered each chamber. The water inside the chambers was circulated by a horizontally rotating disk 17 cm in diameter. The disk, driven by a 12 V DC motor, rotated about 8 cm above the sediment at a computer-controlled speed. For the deeper deployments, chambers were used with motors in pressure-proof titanium housings as described in Cook et al. (2007). In order to reproduce the advective pore water exchange that affects interfacial solute exchange in permeable sediments (Huettel et al. 1996, 2003), the flux chamber mimicked the lateral pressure gradients generated by the interaction of boundary layer currents with sea bed topography. The stirring in the chambers was set to produce a radial pressure gra-

dient that corresponds in magnitude to the pressure gradients produced by the interaction of boundary currents and sediment topography at the study sites. Water currents ranged from 5 to 15 cm s⁻¹ at ~10 cm above the bottom, as inferred from the movement of buoyant particles carried by the bottom flows. Topographical structures of the sandy bottom did not exceed 5 cm in height. For such settings, flume measurements have shown that lateral pressure gradients at the sediment–water interface range from 0.01 to 0.1 Pa cm⁻¹ (Huettel & Gust 1992). For our flux measurements, the chamber stirring was adjusted to 20 rpm producing a radial pressure gradient of 0.07 Pa cm⁻¹ at the sediment–water interface, which can be considered a conservative setting for the study site. Details of the functioning of these chambers are given in Huettel & Gust (1992).

The duration of the individual chamber experiments ranged between 5 and 8 h. Prior to each experiment, chambers were gently inserted into the loose calcareous sands to a depth of about 12 cm marked by a ring of tape on the chamber wall, and thus included a water column of approximately 18 cm height and 5.7 l volume. Chambers were generally operated using SCUBA. Special care was taken to remove any air bubbles enclosed in the chambers. Chambers for parallel measurements and the assessment of spatial variability of flux were placed within an area of approximately 3 × 3 m.

Water samples (60 ml) were extracted from the chambers using plastic syringes at preset time intervals (30 to 120 min) for later analyses of O₂ concentrations. Samples were fixed within 15 min after collection and measured using Winkler titration within 1 h after fixation. Sedimentary O₂ uptake was evaluated by linear regression of O₂ concentrations over time (at least 4 data points for each chamber) and related to the enclosed water volume and sediment surface.

Water column parameters. Water temperature was measured in direct vicinity to the chambers during the experiments using HOBO temperature loggers. Water samples were collected parallel to the benthic chamber experiments (see below) at 9 m water depth (1 m above the reef) in replicates of n = 4 in clean 5 l plastic containers using SCUBA. Water samples were then processed within 30 min or kept at 4°C for <12 h before processing. Subsamples were taken from the containers after homogenization through agitation. Salinity as measured with a hand refractometer was always between 41 and 42.

For measurement of dissolved organic carbon (DOC) concentrations, ca. 10 ml of the sample solutions were filtered through 0.2 μm sterile syringe filters (polyethersulfone membrane, VWR International). The first 4 ml of the filtrate were discarded and the following 6 ml were collected in new, precombusted glass am-

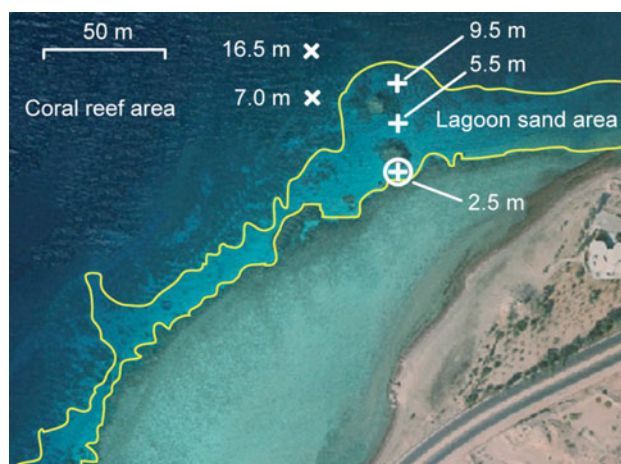


Fig. 1. Aerial photograph of the study area off Aqaba with the locations of the chamber measurements on reef sands (x) and lagoon sands (+). The long-term monitoring station is indicated by ⊕. The yellow line delineates the back-reef lagoon. The white building at right is the MSS (see 'Materials and methods—study site'). Photograph courtesy of R. Mobiedeen, ASEZA GIS Unit, Aqaba, Jordan

poules, which were instantly frozen at -20°C and kept frozen until analysis by high-temperature catalytic oxidation (HTCO) using a Rosemount Dohrmann DC-190 total organic carbon (TOC) analyzer. Non-purgable organic carbon (actual DOC) was measured by sample acidification with orthophosphoric acid to $\text{pH} < 2$ and sparging with oxygen. Specific concentrations of potassium hydrogen phthalate were measured as elemental standards ($\text{SD} < 3\%$).

Subsamples from each container were used in order to determine the microbial oxygen consumption rate. For this purpose the initial dissolved oxygen concentration of each subsample was measured using an optical dissolved oxygen sensor (HACH LANGE HQ10, accuracy $\pm 0.05\%$ of the effective range). The subsamples were then incubated in 60 ml Winkler glass bottles in the dark at *in situ* temperatures for 16 to 24 h. Oxygen concentrations at the end of the period were measured again as described and the difference was used to calculate microbial oxygen consumption rates.

Subsamples for particulate organic carbon (POC) and particulate nitrogen (PN) were obtained by filtering 500 ml (fall 2006) or 1000 ml (summer 2007, winter 2008, spring 2008) seawater from each container onto precombusted GF/F filters (Whatman, diameter: 25 mm, nominal particle retention: $0.7\ \mu\text{m}$). The filters were stored in Eppendorf cups and dried for at least 48 h at 40°C and kept dry until further analysis. POC and PN contents on the filters were measured using a THERMO™ NC 2500 elemental analyser. Peptone, atropine and cyclohexanone-2,4-dinitrophenylhydrazine were used as standards, and SD of replicate measurements were $< 3\%$.

Subsamples for chlorophyll *a* (chl *a*) analysis were obtained identical to POC and PN subsamples but stored frozen at -20°C and lightproof until further analysis. Chl *a* was extracted from the filters by immersion in 90% acetone for 24 h in the dark at 4°C and measured by fluorometric analysis as described in Rathbun et al. (1997) using a TD-700 laboratory fluorometer.

Inorganic nutrient concentrations (nitrate and phosphate) were measured monthly and provided by Drs. M. Al-Zibdah and M. Y. Rasheed, MSS Aqaba.

Particulate organic matter (POM) reaching the seafloor. In order to determine amount and composition of POM reaching the seafloor, custom-made sediment traps were used. Traps were deployed in triplicate, spaced approximately 10 m apart from each other, at 1, 5, 10 and 20 m depth during each of the field expeditions in December 2006 (autumn), August 2007 (summer), February 2008 (winter) and May 2008 (spring). The 5 m depth traps were deployed on the lagoon sands using SCUBA, while at the remaining depths, all traps were placed on the reef sands. Each

trap consisted of a plastic funnel (12 cm diameter) attached to a 600 ml plastic sampling container weighted with a 1 kg piece of lead mounted underneath. Each sampling container was partly buried in the loose sand, and the funnel was fixed at a height of 7.5 cm above the seafloor. Traps were deployed for 48 h. After the collection period, all material that settled onto the funnel was carefully washed *in situ* using SCUBA into the container, using a 60 ml syringe. Subsequently, the funnel was detached from the sampling container, which was simultaneously closed with a lid and transported to the laboratory. The water with suspended material contained in the trap was decanted into a clean 1000 ml container. Organic particles remaining in the trapped sediment were extracted by resuspending the sediment 3 times with seawater and decanting the water with suspended organic matter after the heavier carbonate grains had settled. In total, 48 trap contents were sampled and analyzed. The collected contents of the traps were either processed immediately or kept at 4°C for < 12 h before processing. Aliquots of the trapped material were prepared for the analysis of POM (POC + PN) content by filtering the particulate material onto precombusted GF/F filters (Whatman, $0.7\ \mu\text{m}$ nominal pore size), which were subsequently dried for 48 h at 40°C . Filter samples for POC analysis were exposed to a fuming HCl atmosphere for 24 h before measuring, to remove remaining small carbonate grains. All data were related to the trapping area as determined by the funnel diameter.

Subsamples for chl *a* analysis in the trapped material were obtained identically to POC and PN subsamples, but stored frozen at -20°C and lightproof until further analysis. Chl *a* was extracted from the filters by immersion in 90% acetone for 24 h in the dark at 4°C and measured by fluorometric analysis as described above.

RESULTS

Fig. 2 shows the O_2 concentration over the time course of 4 independent benthic chamber experiments on lagoon and reef sands at different water depths. O_2 concentration decreased linearly ($r^2 > 0.95$) in all 29 chamber deployments during the 12 independent chamber experiments.

Temporal variability of sedimentary O_2 uptake

Over the observation period of > 3 yr, O_2 uptake of the calcareous sands at the reference station at 2.5 m water depth ranged from $19\ \text{mmol m}^{-2}\ \text{d}^{-1}$ in June 2004

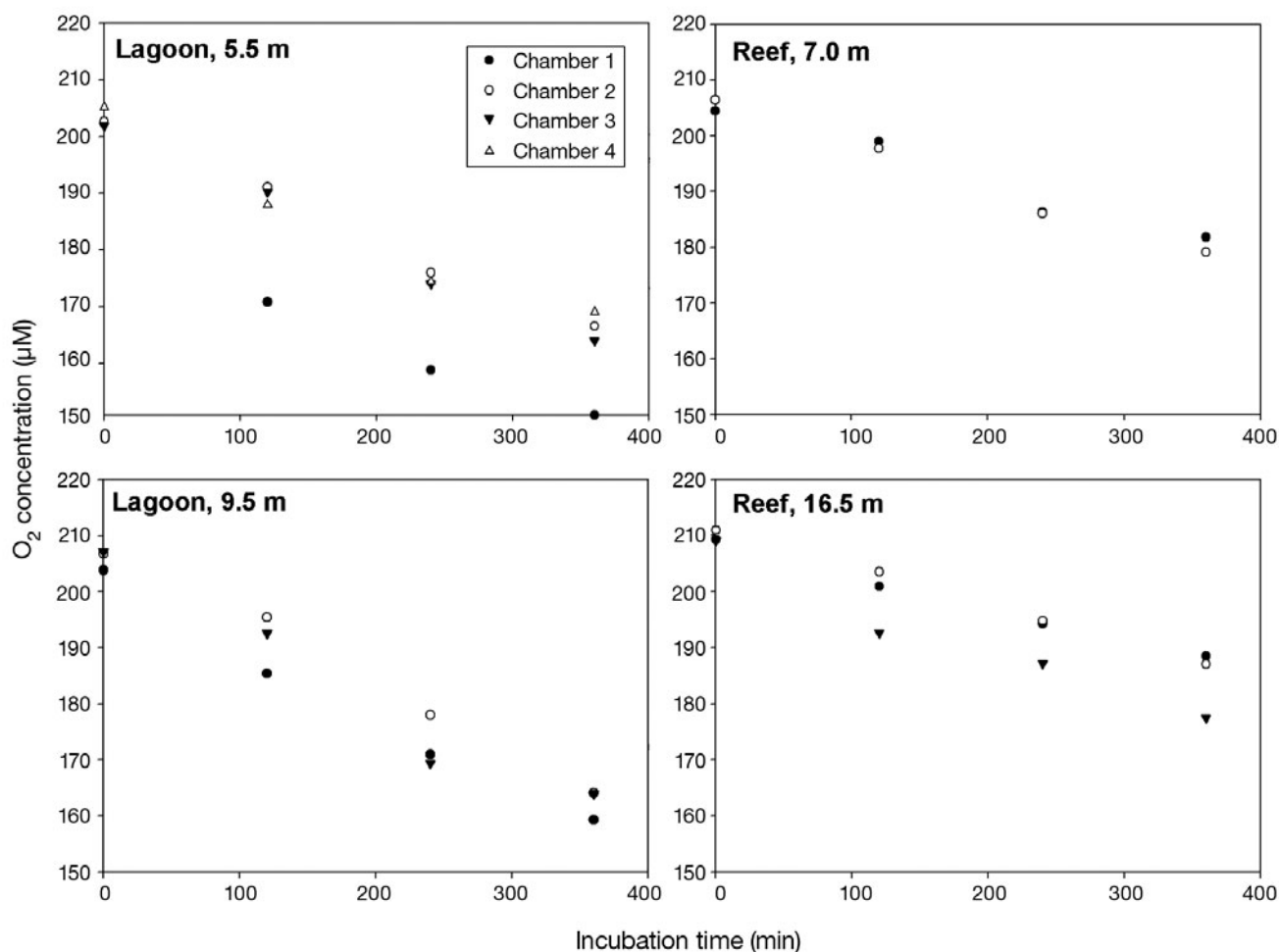


Fig. 2. O₂ concentration development during 4 independent benthic chamber experiments on lagoon and reef sands at different water depths

to 27 mmol m⁻² d⁻¹ in November 2006 (Fig. 3). The temporal variability of O₂ uptake ranged from 15 to 25 mmol m⁻² d⁻¹ (n = 10) in spring 2004, and 26 to 28 mmol m⁻² d⁻¹ (n = 3) in autumn 2006. These temporal differences in sedimentary O₂ uptake were not statistically significant (Mann-Whitney-Wilcoxon *U*-test, *p* > 0.05). Sedimentary O₂ uptake showed no correlation with water temperature, which ranged from 23 to 27°C (Fig. 3). Inorganic nutrient and chl *a* concentrations (Tables 2 & 3) were low from May to October, and high from November to April. The differences in chl *a* concentration in the water column in winter and spring, compared to summer and autumn, were significant (1-way ANOVA, *p* < 0.001).

Depth variability of reef sand O₂ uptake

In the lagoon, sedimentary O₂ uptake of the calcareous sands was positively correlated with water depth

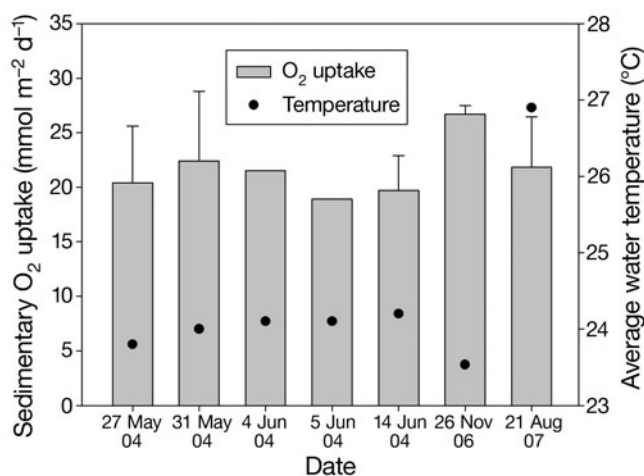


Fig. 3. Temporal changes in sedimentary O₂ uptake measured with benthic chambers (mean + SD) and mean water temperatures at the long-term monitoring station at a water depth of 2.5 m. These chamber measurements were carried out from spring 2004 to summer 2007

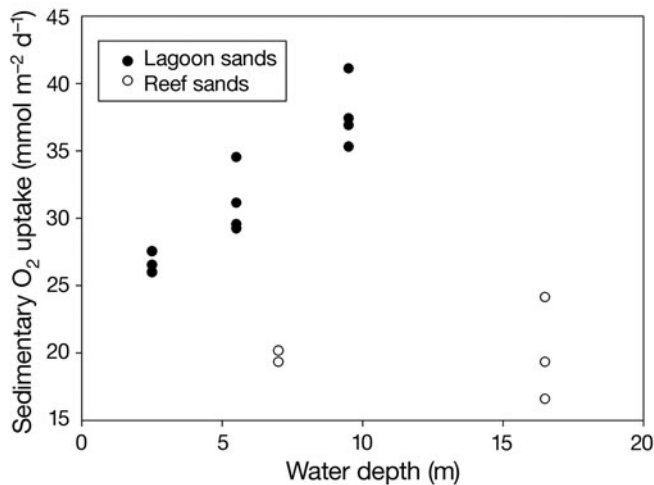


Fig. 4. Sedimentary O₂ uptake at lagoon and reef sands versus water depth as measured with benthic chambers. All chamber measurements for these investigations were carried out during the autumn expedition in November–December 2006

($R^2 = 0.85$, ANOVA of linear regression $p < 0.001$), with maximum values of almost 40 mmol m⁻² d⁻¹ at 9.0 m water depth (Fig. 4). In contrast, O₂ uptake at the reef sand patches located between coral colonies down to 16.5 m did not reveal such a trend with water depth (Fig. 4). In these reef sand patches, O₂ uptake was similar (around 20 mmol m⁻² d⁻¹) to those rates measured at the reference station at 2.5 m water depth (Fig. 3).

Organic matter sedimentation

POC and PN supply to the reef sediments, as measured seasonally by the sediment traps, did not show a positive correlation with water depth (Fig. 5). Statistical analysis revealed significantly higher annual POC supply to the reef sediments only at 10 m water depth compared to 5 m (paired *t*-test, $p = 0.029$), but the amount of sedimented material decreased again at 20 m. According to our trap samples, there were no significant temporal differences in POC and PN supply to the reef sediments, but the highest POC sedimentation rates were observed in summer (86 ± 40 mg POC m⁻² d⁻¹) and the lowest in winter (39 ± 13 mg POC m⁻² d⁻¹), whereas average PN sedimentation was highest in spring (7.3 ± 3.3 mg PN m⁻² d⁻¹) and lowest in winter (4.5 ± 1.5 mg PN m⁻² d⁻¹). Likewise, chl *a* contents in sediment traps were highly variable and thus displayed no significant temporal differences (Fig. 6).

Table 2. Water column temperature and inorganic nutrient concentrations measured parallel to the benthic chamber deployments

	Temperature (°C)	Nitrate (μM)	Phosphate (μM)
Autumn 2006	22.8–24.6	0.27–0.34	0.04–0.05
Summer 2007	26.4–28.7	0.12–0.17	0.03–0.03
Winter 2008	20.6–21.5	0.76–0.90	0.06–0.07
Spring 2008	22.0–25.7	0.37	0.04

DISCUSSION

Temporal changes in sedimentary O₂ uptake and organic matter supply

Wild et al. (2005), by using transparent and opaque benthic chambers, revealed that gross primary production in the calcareous sands at the study site ranged between 15 and 23 mmol O₂ released m⁻² d⁻¹ and sedimentary O₂ uptake accounted for 13 to 25 mmol O₂ consumed m⁻² d⁻¹, which characterizes these sands as largely independent of allochthonous carbon input. Sedimentary O₂ uptake at the long-term monitoring station at 2.5 m water depth (19 to 27 mmol m⁻² d⁻¹) was lower than rates described for other coral reef sand areas in similar water depths and investigated with identical methodology, e.g. Heron Island, Australia, with O₂ uptake ranging from 49 to 93 mmol m⁻² d⁻¹ (Rasheed et al. 2004, Wild et al. 2004a,b, Glud et al. 2008). This was very likely caused by higher nutrient availability due to abundant vegetation and a dense bird colony at Heron Island, whereas no such land-derived influence occurred at the present study site in the northern Red Sea.

Sedimentary O₂ uptake at the shallow long-term monitoring site changed less than 10 mmol m⁻² d⁻¹ between our different measurements over the 3 yr study period. This was unexpected as inorganic nutrient and chl *a* concentrations in the water column site showed temporal variations. These observations agree

Table 3. Water column organic matter concentrations and microbial O₂ consumption measured parallel to the benthic chamber deployments. POC: particulate organic carbon; PN: particulate nitrogen; DOC: dissolved organic carbon; nm: no measurement

	POC (mg l ⁻¹)	PN (mg l ⁻¹)	DOC (mg l ⁻¹)	Chl <i>a</i> (μg l ⁻¹)	O ₂ consumption (μM d ⁻¹)
Autumn 2006	0.08–0.17	0.01–0.02	5.6–11.2	0.15–0.47	4.7–24.1
Summer 2007	nm	nm	0.8–1.1	0.15–0.28	3.7–9.5
Winter 2008	0.05–0.15	0.01–0.01	0.7–2.9	0.29–1.01	2.5–6.1
Spring 2008	0.08–0.31	0.01–0.04	1.0–1.6	0.27–0.40	8.0–21.6

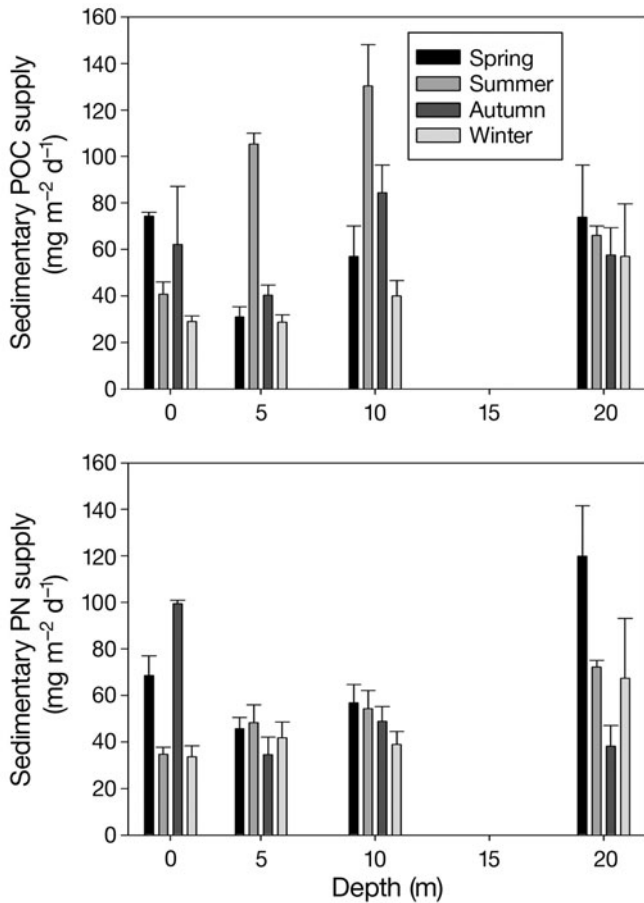


Fig. 5. Particulate organic carbon (POC) and particulate nitrogen (PN) supply to reef sediments over time measured with sediment traps (mean + SD). All traps were deployed in the reef, except traps at 5 m water depth, which were deployed in the lagoon

with those of Rasheed et al. (2002, 2003b). Measurements conducted during the present study also revealed higher DOC water concentrations during the chamber deployments in autumn 2006, compared to those in summer 2007 (Table 3). Higher planktonic microbial activity measured as O₂ consumption in autumn and spring, compared to winter and summer (Table 3), indicate temporal differences between degradability of suspended organic matter.

While the water column processes thus went through an annual cycle with low nutrient and organic carbon availability in summer and higher availability in winter (Table 3), the benthic processes did not follow this trend. This decoupling of sedimentary from water column processes may be explained by a relatively constant supply of organic matter to the sediments at the long-term monitoring station, as demonstrated by the sediment trap data, despite the production changes in the water column. The relatively large fluctuations of the C:N ratios in the trap material reflect the contribu-

tion of pieces of refractory detritus material (e.g. pieces of macrophytes and seagrass) settling into the traps. The highest POM concentrations in the water column in autumn and spring (Table 3) did not result in higher amounts of POC and PN in the sediment traps. A pulse of organic matter to the sediment results in a response in sedimentary O₂ uptake that may last for a relatively long period; for example Wild et al. (2004c) and Glud et al. (2008) observed that the sudden organic matter supply to coral reef sands in the Great Barrier Reef caused by a coral mass spawning event increased O₂ uptake over several weeks. In the present study, such an increase was not detectable, neither in autumn nor in spring after the usual phytoplankton blooms. Another reason for the observed low variability in O₂ flux may be that the reef sediments have some buffer capacity for organic matter (i.e. sediments can rapidly pick up organic matter that is then degraded over a longer time period), despite their function as biocatalytical filter systems (Wild et al. 2004a,c, 2008). This is supported by Eyre et al. (2008), who demonstrated the buffer function of reef sediments for phosphorus. After a sedimentation event, organic matter may be adsorbed by the relatively large surface area of the porous carbonate grains (Wild et al. 2006), loading the porous matrix with degradable material like a sponge soaking up water. Although the degradation rates may be high due to the advective flushing of the permeable bed (Precht & Huettel 2004, Cook et al. 2007), this loading process can dampen oscillations in the O₂ consumption rates between periods of increased organic matter input to the sediment.

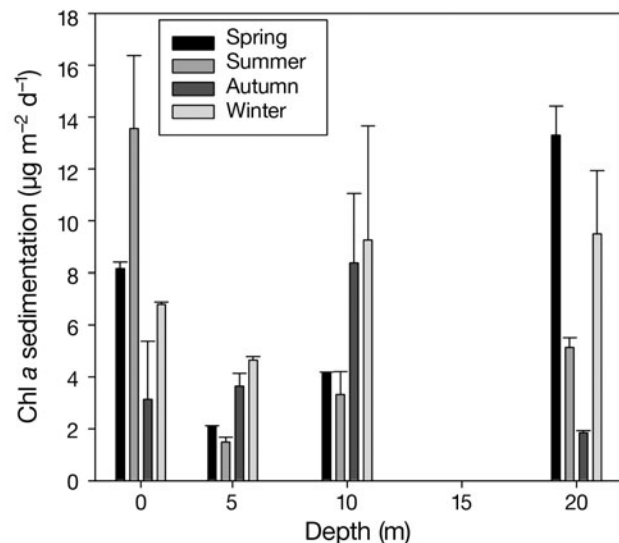


Fig. 6. Chlorophyll *a* sedimentation over time measured with sediment traps (mean + SD). All traps were deployed in the reef, except traps at 5 m water depth, which were deployed in the lagoon

Sedimentary O₂ uptake and organic matter supply at different depths

While temporal changes in O₂ flux were relatively small, larger increases in O₂ flux were observed with increasing water depths in the lagoon sands. This positive correlation may have been caused by: (1) the higher water column at the deeper sites, producing more particulate organic matter that could settle to the bottom than the shorter water column at the shallow site; (2) lateral transport processes providing more organic matter to the deeper sites; and (3) reduced sediment resuspension at the deeper sites, permitting accumulation of low-density organic particles and reduced substances (e.g. sulphide) in the sediment. In the clear oligotrophic waters where coral reefs grow, high light intensities can penetrate deeply, permitting photosynthesis at water depths of 60 m or more (Vooren 1981, Jarrett et al. 2005). Pelagic primary production here takes place throughout the water column above the reef. In the clear tropical waters, phytoplankton accumulations can form in deep water layers, where light levels are still sufficient for photosynthesis and nutrients are more concentrated than in the water near the surface (McManus & Dawson 1994, Gattuso et al. 2006). In such environments, the amount of POC integrated over the entire water column above the reef can thus increase with water depth. Where reef-forming corals grow, steep slopes can form as the reef framework, cemented by coralline algae and sponges, has more structural strength than, for example, sandy or muddy deposits. Consequently, particles that settle on the steep surfaces of the reef are easily entrained and then accumulate in the troughs and crevices of the reef framework or rush down the slopes of the reef. Our sediment traps accumulated materials settling from the water column and also materials that had been resuspended. A clear distinction of the 2 sources is difficult in the wave-swept reef environment, because a large fraction of the suspended particle load in the water originates from resuspension. The important observation here is that the trapped material did not reflect the temporal production changes in the water column. As the intensity of the hydrodynamic forces caused by surface waves and wind-driven currents decrease with depth, the deeper zones of the reef are calmer, permitting deposition of low-density materials including organic particles. Accumulation of fine particles and organic detritus in the sand decreases the permeability of the sediments in the deeper sections of the reef. Higher organic content and less hydrodynamic flushing of the sediments can lead to oxygen depletion, which leads to the build-up of sulphides resulting from microbial sulphate reduction activities.

Nevertheless, the trend of increasing sedimentary O₂ uptake with increasing depth was not observed in the reef sand patches embedded between living coral colonies. One reason may be that around these small sand patches, in contrast to the large lagoon sand areas, benthic suspension feeders, in particular hermatypic corals, occur at high abundances, covering 29 to 67% of the seafloor (M. Naumann et al. unpubl. data). The intense feeding on POM by corals has been demonstrated by Anthony (1999), but other coral reef organisms such as gastropods (Kappner et al. 2000), bivalves (Monismith et al. 1990), sponges (Richter & Wunsch 1999), ascidians (Petersen 2007), and polychaetes (Jordana et al. 2000) also filter particles from the water column, thereby reducing organic matter flux to the reef sand patches. As the digestion of the trapped materials by these animals is often incomplete (Coffroth 1984, Kappner et al. 2000, Ribak et al. 2005), the sedimentary microbial community can benefit from the nearby high macrofauna abundance through a continuous lateral supply of organic matter (e.g. in the form of fecal pellets and coral mucus), which may support the low but relatively constant sedimentary O₂ uptake rates measured at these sites.

In conclusion, the observed lack of temporal benthic O₂ uptake changes in the Aqaba reef sands reflects efficient functioning and recycling in the oligotrophic reef ecosystem. Large variations in sedimentary O₂ uptake would require large variations in the organic matter input. This could only be caused by production of organic matter that is not consumed in the water column or by benthic reef organisms, and therefore settles to the sediments. In an organic matter-limited ecosystem such as this reef, any primary production likely is effectively recycled in the food web of the water column and reef framework (Richter et al. 2001), with the detrital food web being of lower importance, as labile detrital matter cannot accumulate due to the efficient recycling. The observed sedimentary O₂ uptake increase with depth at the lagoon sands therefore is a function of the lateral supply of fresh organic particles produced by the adjacent reef organisms that actively filter particles from the water column. Coral mucus may play a major role in this process, because it often dominates suspended organic matter in coral reefs (Johannes 1967, Marshall 1968), and at the study location a majority of this material reaches the lagoon sands in very close vicinity to the reef (Wild et al. 2005, F. W. Mayer et al. unpubl. data).

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