Vol. 411: 61–71, 2010
doi: 10.3354/meps08653

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published July 29

OPEN ACCESS

Organic matter release by Red Sea coral reef organisms — potential effects on microbial activity and *in situ* O_2 availability

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ABSTRACT: This study presents a comprehensive dataset (223 reef organisms that were separately incubated during 44 independent experiments during 4 seasonal expeditions) of dissolved and particulate organic matter (DOM and POM) release by dominant benthic organisms from the Northern Red Sea. Reef organisms studied were scleractinian and fire corals, the upside-down jellyfish and reef-associated algae. Subsequently, the effect of this organic matter (OM) release on microbial activity was determined. These studies were complemented by high resolution, *in situ* O_2 concentration measurements within reef environments that were dominated by corals or algae. Dissolved organic carbon (DOC) release was 14.5 ± 2.3 mg m^{-2} surface area h^{-1} for all 9 investigated reef algae, which was significantly higher than DOC release by scleractinian corals during all seasons except winter. POM release (particulate organic carbon and nitrogen, POC and PON, respectively) was observed for all investigated reef organisms. Benthic reef algae released 5.1 ± 0.5 mg POC m^{-2} h^{-1} and 0.35 ± 0.03 mg PON m^{-2} h^{-1}, which are significantly higher than POM release rates by scleractinian corals in spring and autumn. Algae-derived OM, presumably the DOC fraction, stimulated microbial activity in the adjacent water more significantly than OM released by the investigated scleractinian and fire corals. Consequently, the daily mean and minimum *in situ* O_2 concentrations in the water directly above the reef (≤10 cm) were significantly higher in coral dominated than in algae dominated sites, confirming the *in situ* relevance of results of previous laboratory studies. Findings also suggest that benthic reef algae decrease O_2 availability in waters close to reef environments via the release of labile OM and its subsequent fast microbial degradation.

KEY WORDS: Red Sea · Coral reefs · Benthic organisms · Organic matter release · Coral–algae–microbe interaction · *In situ* O_2 availability

INTRODUCTION

Quantitative data on organic matter release by common benthic coral reef organisms other than corals are rare. Recent research showed that scleractinian corals, through the release of both dissolved and particulate organic matter (DOM and POM), can affect biogeochemical cycles and establish fauna–microbe interactions in warm- (Wild et al. 2005a) and cold-water (Wild et al. 2008, Wild et al. 2009a) coral-reef ecosystems. Ducklow & Mitchell (1979) demonstrated that other reef cnidarians, at least under manipulative stress conditions, release organic matter (OM) into their surroundings. However, OM release rates by these organisms under undisturbed conditions are undetermined.

Smith et al. (2006) indicated that coral reef-associated benthic algae might affect processes such as microbial activity in their surroundings via a hypothetical release of OM. This could reduce O_2 availability in coral reef environments and may, thus, have severe consequences for coral metabolism and ecosystem functioning. In coral reefs, hypoxia (i.e. dissolved O_2 concentrations that are below saturation) is a common phenomenon (Nilsson & Östlund-Nilsson 2004). During the night when no O_2 is produced by coral zooxanthellae, severe hypoxic conditions (down to 0.7 mg O_2 l^{-1}) can occur between the

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branches of coral colonies (Shashar et al. 1993, Kühl et al. 1995). Although corals may overcome periods of low O_2 concentrations by extending their tentacles or decreasing their respiration (Shashar et al. 1993), severe hypoxia or anoxia can cause widespread coral mortality (Simpson et al. 1993). A recent study also described the occurrence of hypoxia in interactions between corals and some turf or fleshy macroalgae in coral reef ecosystems (Barott et al. 2009).

In this context, it is surprising that only few data are available on O_2 availability in coral reef ecosystems. Low O_2 concentrations caused by the decomposition of organic materials may constitute a significant stress factor for corals (Johannes 1975), and the release of labile OM by reef organisms may stimulate microbial activity that could result in such O_2 deficiency (Simpson et al. 1993).

This study, therefore, presents comparative quantitative data of OM release by dominant benthic coral reef organisms that were investigated during 4 seasonal expeditions to a typical fringing reef in the northern Red Sea. These studies were supplemented by investigations on (1) the effects of this release on the planktonic microbial activity measured as O_2 consumption in the adjacent water, and (2) the potential implication for *in situ* O_2 availability within benthic communities dominated by different reef organisms.

MATERIALS AND METHODS

Transect surveys. The study was conducted during 4 seasonal expeditions (autumn: Nov/Dec 2006, summer: Aug/Sep 2007, winter: Feb/Mar 2008, spring: May 2008) to a fringing reef close to the Marine Science Station (MSS), Aqaba, Jordan (29° 27′ N, 34° 58′ E). The target dominant benthic organisms were identified at the beginning of the first expedition using the line point intercept (LPI) transect survey technique modified from Loya (1978) and Nadon & Stirling (2006). At water depths of 0.5, 1.0, 5.0, 10.0 and 20.0 m, duplicate 50 m transect surveys at 0.5 m point intervals were carried out parallel to the reef crest at a northern and a southern reef location using SCUBA. LPI transect data were analysed to derive the percent coverage of the dominant benthic organisms in the study area. In total, 44 transect surveys were carried out during the 4 seasonal expeditions.

Collection of specimens. Collection of all specimens took place in the MSS fringing reef at water depths of 5 to 10 m using SCUBA. All specimens were collected in replicates (at least 5) for each subsequent incubation experiment.

During the field trips, replicate fragments (6 to 10 cm coral branch length) were broken off *in situ* from colonies of the dominant hard coral genera *Acropora*, *Pocillopora*, *Stylophora* and the calcifying hydroid fire coral genus *Millepora*. In addition, similarly sized colonies and individual polyps of the scleractinian coral genera *Goniastrea* and *Fungia*, respectively, were collected. All coral specimens except *Fungia* polyps were fixed onto ceramic tiles (4 × 4 cm) using small amounts of coral glue (Reef Construct, Aqua Medic); this was done on-site to reduce mechanical stress during experimental handling. Corals were allowed to heal in a flow-through aquarium with water that was directly pumped from the field at *in situ* water temperatures (21 to 29°C depending on season; monitored using Onset HOBO temperature loggers) and light intensity for 7 to 14 d prior to the incubation experiments. Maintenance was therefore very close to natural conditions, thus, minimizing disturbance to the corals. Consequently, all corals looked healthy (no pigment change or tissue loss, polyps often extended) and no visible differences from corals in the field could be detected.

Benthic jellyfish of the genus *Cassiopea* (5 to 8 cm in diameter) were collected by carefully lifting them from the seafloor and transferring them into seawater-filled plastic bags (polyethylene zip locked, ~500 ml volume). Subsequently, *Cassiopea* specimens were transferred to two 40 l flow-through tanks supplied with *in situ* seawater at exchange rates of ~1.5 l min^{-1} and *in situ* water temperatures for at least 2 d prior to the incubation experiments.

Additionally, small pieces (6 to 14 cm lengths) of the 3 most dominant types of benthic algae were collected *in situ* during each of the seasonal expeditions: the green algae *Caulerpa* sp., the red algae *Peyssonnelia* sp. and typical filamentous turf algae consortia growing on dead coral skeletons. The seasonally occurring algal genera *Ulva*, *Enteromorpha* (all green), *Lobophora*, *Sargassum*, *Hydroclathrus* (all brown) and *Liagora* (red) were only collected during winter or spring expeditions. All algae were placed in a flow-through aquarium for at least 12 h for cleaning and healing purposes, prior to the experiments.

Quantification of OM release. OM release by all collected reef organisms was carried out as described by Herndl & Velimirov (1986). Animals and algae were separately transferred into 1000 ml glass beakers (previously rinsed with acetone followed by a thorough seawater rinse) that were filled with 800 to 1000 ml of untreated, freshly pumped seawater from the field. Identical beakers filled with seawater served as controls. Beakers were kept in a flow-through aquarium during the day at *in situ* temperatures. Nylon gauze was clamped above the beakers to simulate light intensities at 5 m water depth as verified by light loggers (Onset Pendant). After a 6 h incubation, organisms were removed from the beakers and subsamples were

taken from the incubation water for determination of the following parameters.

Dissolved organic carbon: Approximately 10 ml of the incubation water collected from both control and treatment beakers at the end of incubations were filtered through 0.2 µm sterile syringe filters (polyethersulfone [PES] membrane, VWR International). DOC leakage from PES filter membranes as noted by Khan & Subramania-Pillai (2007) was insignificant, as assured by repeated analyses of different lots of untreated filters according to the following sampling procedure: the first 4 ml of the filtrate were discarded and the remaining 6 ml were collected in pre-combusted brown glass bottles or ampoules, which were instantly frozen at −20°C and kept frozen until analysis. Potential contamination of samples was also prevented by using powder-free gloves during all manual handlings.

DOC concentrations were determined by high temperature catalytic oxidation (HTCO) using a total organic carbon (TOC) analyser (Rosemount Dohrmann DC-190) (e.g. Sharp et al. 1993). A certified TOC standard (ULTRA Scientific) was used for instrument calibration (10-point) and as a regular quality control after every 4th sample. Analytical precision was <3% of the certified value.

After defrosting, each sample was treated by adding 100 µl of 20% phosphoric acid and purged for 5 min using pure O_2 to remove dissolved inorganic carbon. The DOC concentration of each sample was measured using 5 single injections of 100 µl sample volumes. An outlier test of the resulting DOC concentrations was conducted, and the remaining values were averaged.

Particulate organic carbon and nitrogen: Between 400 and 800 ml of the incubation water were filtered on pre-combusted GF/F (Whatman, 25 mm diameter), which were then dried for at least 48 h at 40°C and kept dry until analysis. During this sampling, inclusion of larger, visible particles such as faecal pellets (in the case of jellyfish) or tissue fragments (in the case of algae) was avoided. Particulate organic carbon (POC) and nitrogen (PON) concentration measurements and respective stable isotope analyses were performed with an elemental analyzer (Carlo Erba NC 2500). Elemental concentrations were calculated from certified elemental standards (atropine, cyclohexanone-2,4-dinitrophenylhydra-zone; Thermo Quest) and typically showed SDs that were <3%.

For the calculation of OM release rates (DOC as well as POC and PON), values from control beakers were subtracted from those measured in the incubation water of the beakers containing the organisms, followed by normalisation to individual organism surface area, incubation time and incubation water volume. Respective surface areas were measured as a reference parameter using geometric approximation for all corals and turf algae growing on dead coral fragments (see Naumann et al. 2009a for detailed methodology) or the image analysis software ImageJ to analyze digital photographs of the other organisms.

Effects on planktonic microbial O_2 consumption. Approximately 140 ml of the incubation water collected from each beaker at the end of the incubation experiments were used to fill two 60 ml glass bottles. O_2 concentration was measured immediately in one of the bottles, and after incubation of the enclosed water for at least 16 h in the dark at *in situ* temperature in the second bottle. O_2 concentration was measured using the modified Winkler titration technique described by Carpenter (1965) during the autumn expedition or a sensor (Hach HQ 10) during the spring, summer and winter expeditions. The sensor was calibrated using Winkler titration. O_2 consumption by microbes (including Bacteria, Archaea, small Protozoa) in the incubation water was determined by subtracting the final O_2 concentration from that at the start of the incubation. Final O_2 concentration values were always >10% lower than initial values, rendering differences clearly detectable with both methodologies used. Resulting values were then related to the surface area of the incubated organism.

Supplementary *in situ* studies. The effect of differences in benthic reef community composition on *in situ* O_2 availability in the overlying water column was investigated during both spring and winter expeditions by deploying dissolved O_2 loggers (Eureka Midge). During 3 (spring) or 6 (winter) occasions, 2 loggers were simultaneously deployed for 24 h at water depths of 4 to 7 m within different small (<5 m^2) reef sections dominated by scleractinian corals (coral cover: 20 to 95%, algal cover: 0 to 10%) or benthic reef algae (algal cover: 35 to 100%, coral cover: 0 to 15%). O_2 concentration and water temperatures were measured and logged every 5 min over the entire deployment period (288 data points for each deployment). Water currents were measured in triplicates during each deployment via tracking of natural suspended particles along known distances using a ruler and a watch.

Data analysis. Differences in mean DOC and POM concentrations in the incubation waters between the controls and the treatments (see Table 1) were investigated using paired *t*-tests. Where the requirements for paired *t*-tests were not met, Wilcoxon signed rank tests were used.

Net OM release (DOC, POC, PON) by the investigated reef organisms and subsequent effects on microbial O_2 consumption rates were calculated by subtracting mean control values of the respective parameters from those of each treatment. Statistical

analyses for these data were carried out using Mann-Whitney *U*-tests, as homogeneity of variances was proven (Levene test), but the data were not normally distributed (Kolmogorov-Smirnov test).

For comparison of data obtained from simultaneously deployed *in situ* O_2 loggers, paired *t*-tests were used. These data showed homogeneity of variances and were normally distributed.

RESULTS

Fig. 1 gives an overview of the benthic coverage by the different groups of investigated organisms in the MSS fringing reef. Among the study organisms, hard corals exhibited the highest benthic coverage followed by reef algae, fire corals and jellyfish. Seasonal algae only appeared during the winter and spring expeditions and could account for up to 26% of the seafloor area of the investigated coral reef. Water currents reversed or changed direction regularly and exhibited velocities of 3.2 to 7.1 cm s^{-1} during all logger deployments, with identical current velocities at the scleractinian coral dominated and the reef algae dominated sites during each deployment.

Comparative OM release

In total, 223 separate incubations of the different coral reef organisms were conducted in 44 independent experiments using identical methodologies during the 4 different expeditions. Detailed information about the temporal, spatial and species-specific resolution of these investigations are presented in the studies of Naumann et al. (2010) for scleractinian and fire corals, Haas et al. (2010) for benthic reef algae, and Niggl et al. (2010b) for jellyfish.

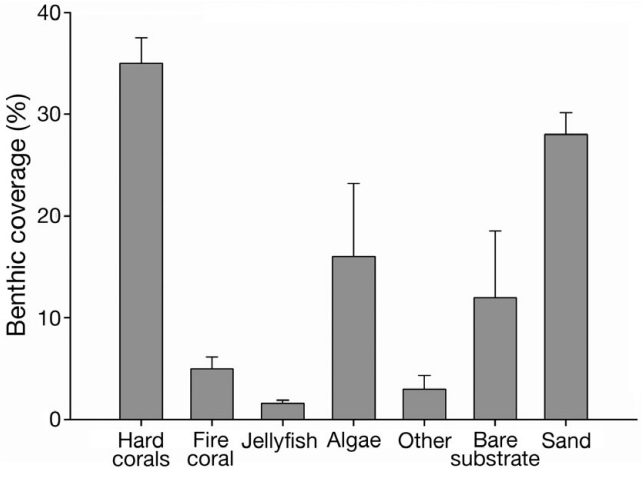

Fig. 1. Benthic coverage (mean + SD) by the different reef organisms and substrates at the Marine Science Station fringing reef as determined by Line Point Intercept surveys. 'Other' = other organisms

Table 1 shows the OM concentrations in all water samples from the incubation experiments. The difference in DOC concentrations between control and organism incubations was clearly above the analytical precision (<3%) for all experiments. OM release rates were calculated by subtracting OM concentrations of the control beakers from those measured in the incubation water of the beakers containing the organisms. Whereas POC concentrations in the beakers were consistent over all 4 seasons, DOC concentrations were up to one order of magnitude elevated in autumn (Table 1). However, there is no justification to remove DOC values for autumn from the dataset since identical methodologies were used throughout all seasonal samplings, contamination of samples was avoided, and similar values have been reported in the water column at the study area during autumn (Wild et al. 2009b).

DOC concentrations in waters of scleractinian coral incubations (3698 ± 984 µg l^{-1}) during all the 4 seasons (n = 17) were not significantly different ($p < 0.05$) from those of controls (5167 ± 1775 µg l^{-1}). In contrast, POC concentrations in waters with coral incubation (293 ± 35 µg l^{-1}) were significantly ($p < 0.001$) higher when compared to the controls (134 ± 12 µg l^{-1}), clearly indicating POC release. DOC concentrations (n = 22) in waters with algal incubation (6974 ± 2181 µg l^{-1}) were significantly ($p < 0.001$) higher compared to the controls (5026 ± 1638 µg l^{-1}). POC concentrations (n = 18) were also significantly ($p < 0.001$) higher in waters with algal incubation (566 ± 83 µg l^{-1}) when compared to the controls (129 ± 15 µg l^{-1}). This emphasizes the feasibility of net OM release measurement with the applied methodology.

Fig. 2 summarizes the mean net OM release by the different groups of reef organisms during the 4 seasons as related to the surface area of the incubated organism. Average net DOC release for all 9 reef algae species during all seasons was 14.5 ± 2.3 mg m^{-2} h^{-1}, with turf algae releasing the highest DOC (33.6 ± 6.9 mg m^{-2} h^{-1}). While scleractinian corals (–20.7 ± 21.2 mg m^{-2} h^{-1}) and jellyfish (–1.2 ± 4.4 mg m^{-2} h^{-1}) rather took up DOC, fire corals exhibited a net DOC release of 9.2 ± 12.8 mg m^{-2} h^{-1}. Benthic algae released significantly more DOC compared to the scleractinian corals during all 4 seasons except in winter and significantly more DOC than jellyfish in spring (Fig. 2a).

POC and PON release was observed for all investigated reef organisms (Fig. 2b,c). The jellyfish *Cassiopea* released about one order of magnitude more POM compared to all other organisms. Benthic reef algae on average released 5.1 ± 0.5 mg POC m^{-2} h^{-1} and 0.35 ± 0.03 mg PON m^{-2} h^{-1}, thereby exhibiting significantly

Table 1. DOC and POC (dissolved and particulate organic carbon) concentrations (µg l^{-1}) in the incubation waters of the various organisms and the respective controls during the 4 seasonal samplings. Values are mean ± SE, with numbers of replicates in parentheses; na = not assessed

Season	Date	Organism	Control		Treatment	
			DOC	POC	DOC	POC
Spring 2008	May 17	*Acropora*	1501 ± 18 (2)	85 ± 3 (5)	1385 (1)	164 ± 26 (5)
	12	*Fungia*	1615 ± 86 (3)	95 ± 8 (5)	1328 ± 66 (4)	184 ± 25 (5)
	16	*Stylophora*	1778 ± 696 (2)	93 ± 6 (5)	1357 ± 121 (3)	402 ± 68 (4)
	10	*Liagora*	1292 ± 175 (3)	na	1710 ± 87 (5)	na
	11	*Hydroclathrus*	1435 ± 97 (4)	na	1834 ± 114 (4)	na
	12	*Caulerpa*	1495 ± 33 (2)	136 ± 36 (5)	2326 ± 211 (5)	255 ± 62 (5)
	16	*Peyssonnelia*	1080 (1)	133 ± 46 (5)	1316 ± 82 (4)	449 ± 104 (5)
	17	Turf algae	1499 ± 18 (2)	84 ± 4 (5)	3096 ± 257 (4)	504 ± 102 (5)
	10	*Cassiopea*	1399 ± 163 (4)	117 ± 4 (5)	1533 ± 132 (6)	578 ± 59 (6)
	11	*Cassiopea*	1507 ± 103 (5)	102 ± 4 (5)	1752 ± 89 (5)	1058 ± 220 (6)
	20	*Cassiopea*	1670 ± 137 (4)	89 ± 6 (3)	1425 ± 206 (5)	384 ± 46 (6)
Summer 2007	Aug 26	*Acropora*	1512 ± 185 (4)	104 ± 8 (3)	1832 ± 107 (5)	398 ± 127 (5)
	23	*Fungia*	2042 ± 515 (2)	115 ± 5 (3)	1646 ± 125 (5)	346 ± 98 (5)
	Sep 04	*Goniastrea*	1715 ± 232 (3)	86 ± 1 (4)	2207 ± 124 (4)	178 ± 21 (5)
	Aug 29	*Pocillopora*	1888 ± 100 (4)	107 ± 5 (5)	1651 (1)	286 ± 48 (5)
	Sep 02	*Stylophora*	1617 ± 72 (3)	75 ± 4 (5)	1522 ± 224 (2)	258 ± 28 (5)
	07	*Millepora*	2938 (1)	72 ± 8 (3)	1469 (1)	87 ± 4 (5)
	Aug 20	Turf algae	2424 ± 496 (3)	na	2991 ± 226 (3)	na
	23	Turf algae	2177 ± 328 (3)	109 ± 7 (4)	2182 ± 42 (2)	688 ± 74 (5)
	26	*Caulerpa*	1510 ± 185 (4)	96 ± 8 (4)	3331 ± 423 (4)	500 ± 85 (4)
	29	Turf algae	1918 ± 184 (4)	170 ± 60 (5)	2727 ± 380 (4)	695 ± 82 (4)
	Sep 02	*Peyssonnelia*	1579 ± 55 (3)	80 ± 5 (4)	3057 ± 1055 (4)	424 ± 89 (4)
Autumn 2006	Nov 25	*Acropora*	6446 ± 372 (3)	244 ± 14 (2)	14213 ± 7377 (4)	240 ± 37 (5)
	19	*Fungia*	7129 ± 1263 (2)	169 ± 1 (3)	2545 ± 426 (5)	361 ± 115 (5)
	20	*Goniastrea*	11252 ± 8541 (3)	201 ± 16 (2)	10774 ± 3983 (5)	267 ± 12 (5)
	22	*Pocillopora*	28329 ± 1236 (3)	140 ± 1 (3)	5997 ± 1429 (4)	476 ± 70 (5)
	23	*Stylophora*	16103 ± 1960 (3)	204 ± 18 (2)	10192 ± 1176 (3)	693 ± 65 (5)
	Dec 01	*Millepora*	1963 ± 151 (3)	244 ± 19 (3)	2796 ± 537 (5)	285 ± 16 (5)
	Nov 15	*Caulerpa*	5887 ± 987 (3)	164 ± 22 (3)	10930 ± 3566 (5)	1306 ± 283 (3)
	21	*Peyssonnelia*	25294 ± 3725 (3)	245 ± 148 (3)	31626 ± 2684 (5)	1100 ± 155 (5)
	26	Turf algae	23517 ± 3594 (3)	93 ± 8 (3)	31748 ± 2837 (4)	684 ± 130 (5)
	28	Turf algae	19885 ± 2129 (3)	95 ± 6 (3)	29732 ± 4502 (5)	1420 ± 220 (4)
	Dec 02	*Caulerpa*	11574 ± 3848 (2)	280 ± 183 (3)	13084 ± 2435 (5)	699 ± 113 (4)
Winter 2008	Feb 28	*Acropora*	1140 ± 67 (5)	71 ± 10 (3)	1535 ± 78 (5)	137 ± 26 (3)
	17	*Fungia*	1299 ± 45 (3)	140 ± 10 (4)	1743 ± 150 (4)	191 ± 9 (5)
	24	*Goniastrea*	1279 ± 80 (4)	118 ± 53 (4)	1529 ± 108 (4)	170 ± 34 (5)
	Mar 01	*Stylophora*	1194 ± 36 (5)	136 ± 9 (3)	1416 ± 84 (5)	229 ± 77 (4)
	Feb 17	*Enteromorpha*	1250 ± 54 (3)	123 ± 19 (4)	1969 ± 128 (5)	264 ± 95 (4)
	24	Turf algae	1283 ± 63 (4)	230 ± 119 (4)	1815 ± 273 (3)	458 ± 196 (4)
	28	*Ulva*	1139 ± 67 (4)	61 ± 12 (3)	1717 ± 271 (5)	112 ± 11 (4)
	29	*Peyssonnelia*	1201 ± 65 (3)	45 ± 7 (4)	1443 ± 119 (4)	307 ± 43 (3)
	Mar 01	*Caulerpa*	1192 ± 43 (5)	126 ± 11 (3)	1935 ± 108 (5)	174 ± 26 (3)
	06	*Lobophora*	974 ± 117 (3)	93 ± 12 (2)	1485 ± 70 (5)	313 ± 60 (4)
	06	*Sargassum*	974 ± 117 (3)	93 ± 12 (2)	1368 ± 76 (5)	405 ± 53 (2)

higher POC release rates than scleractinian corals in spring and autumn and significantly higher PON release rates in autumn. Fire coral POC (0.34 ± 0.14 mg m^{-2} h^{-1}) and PON (0.04 ± 0.01 mg m^{-2} h^{-1}) release was always significantly lower when compared to benthic reef algae and scleractinian corals (POC: 2.8 ± 0.3 mg m^{-2} h^{-1}; PON: 0.29 ± 0.03 mg m^{-2} h^{-1} for scleractinian corals).

Effects on microbial activity and *in situ* O_2 availability

Induction of microbial activity (Fig. 2d), which was measured as O_2 consumption, was highest for *Cassiopea*-derived OM (15.2 ± 1.6 mg O_2 l^{-1} h^{-1} normalized m^{-2} of surface area), significantly exceeding those of scleractinian corals and benthic algae. Corrected planktonic microbial O_2 consumption was 3.7 ± 0.2 mg

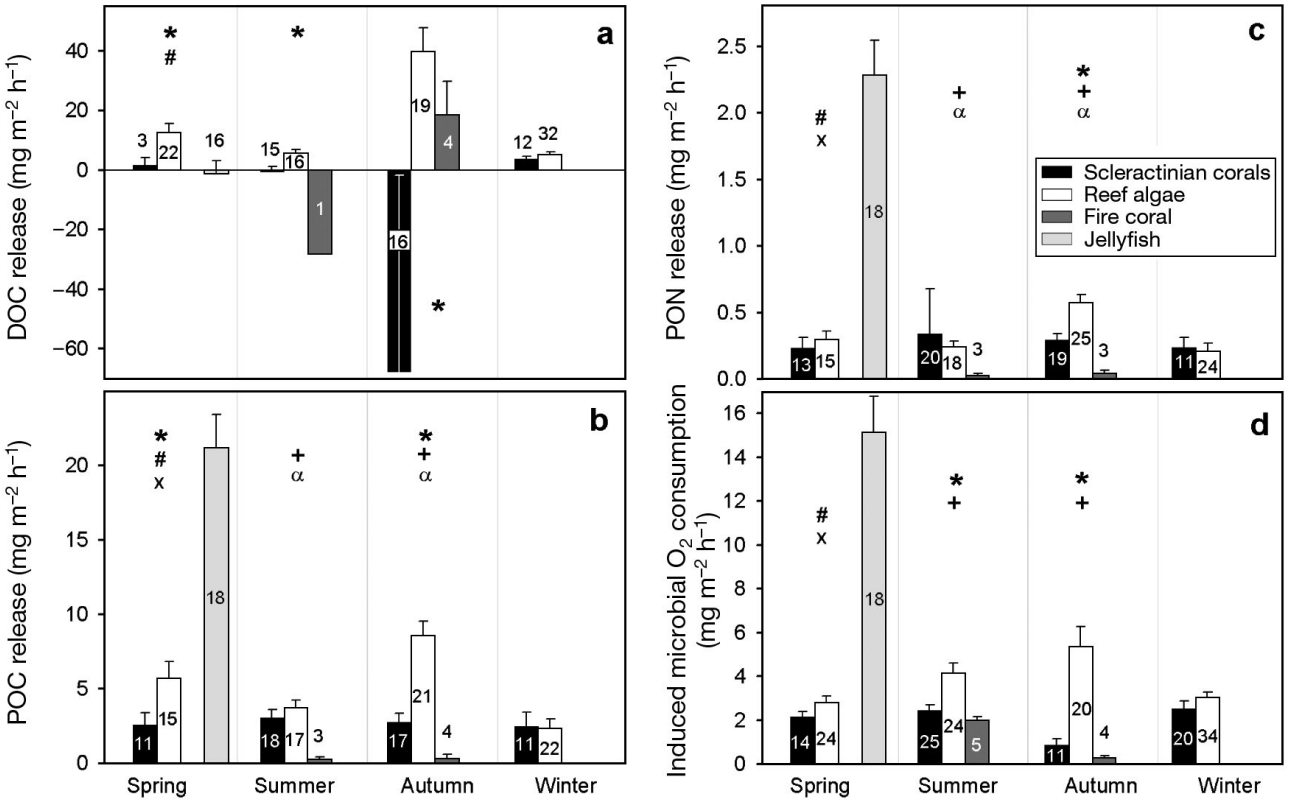

Fig. 2. Comparative organic matter (a) DOC, (b) POC, and (c) PON release by the investigated coral reef organisms and its effects on microbial O_2 consumption (d) during the 4 seasonal expeditions. Values for microbial activity in (d) are normalized to 1 l of incubation water. Values are mean + SE, numbers within or above columns: replication. Symbols above columns indicate statistically significant differences ($p < 0.05$) between scleractinian corals and reef algae (*), fire coral (α), or jellyfish (x), as well as between reef algae and fire coral (+), or jellyfish (#)

O_2 l^{-1} h^{-1} for algal incubations, and 2.2 ± 0.2 and 1.2 ± 0.3 mg O_2 l^{-1} h^{-1} for scleractinian and fire coral incubations respectively. Stimulation of microbial activity by reef algae-derived OM significantly exceeded those by scleractinian and fire coral-derived OM in summer and autumn.

Algae dominated sites showed strong diurnal variation in O_2 concentrations ranging from 5.1 to 9.3 mg l^{-1} in spring and 5.1 to 10.3 mg l^{-1} in winter, with lowest values being observed after dusk and before dawn, and highest values around midday (Fig. 3). In contrast, O_2 values at coral dominated sites ranged from 6.6 to 8.5 mg l^{-1} in spring and 7.0 to 9.5 mg l^{-1} in winter.

During all 9 parallel deployments of O_2 loggers at coral or algae dominated reef sites, daily mean O_2 concentrations in the water directly above the reef were significantly higher (2-sided, paired *t*-tests; $p < 0.05$) at the scleractinian coral dominated compared to the benthic reef algae dominated sites. Diurnal variations in O_2 concentrations at algae dominated sites were significantly higher than at coral dominated sites and displayed strong positive correlation with benthic algal cover (Pearson product moment correlation, $r = 0.90$, $p = 0.001$).

DISCUSSION

OM release by different groups of reef organisms

Net OM release by coral reef organisms has been investigated in the 1970s (Richman et al. 1975, Ducklow & Mitchell 1979). However, in contrast to these earlier studies, which either focused on a single group of organisms (Richman et al. 1975) or investigated OM release under manipulative stress conditions (Ducklow & Mitchell 1979), the present study delivers a comprehensive dataset on net OM release by the dominant benthic reef organisms in the Northern Red Sea under 'low stress' conditions.

Results of the present study showed that all investigated benthic reef organisms released POM (POC and PON) into their surroundings in significant quantities.

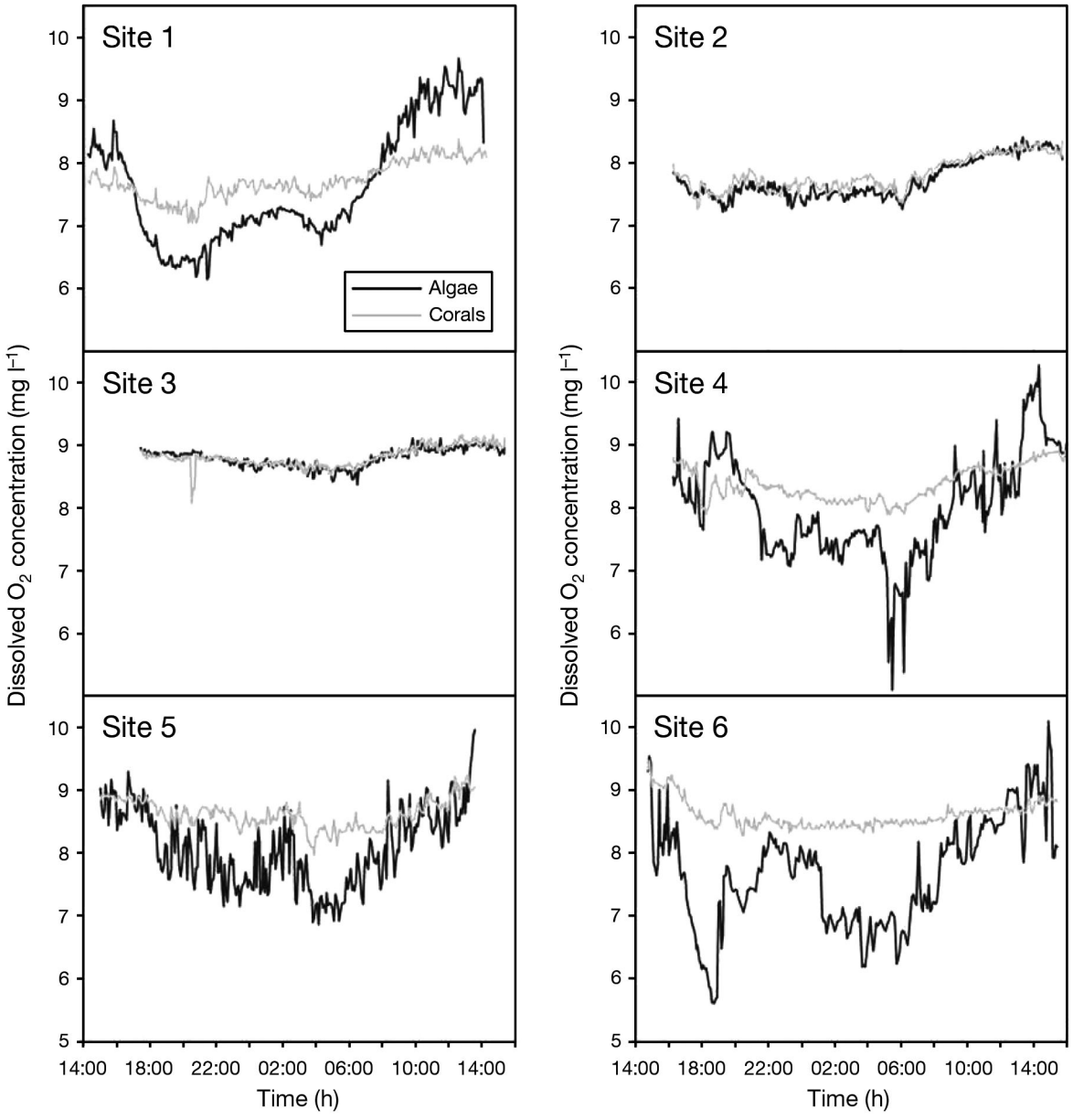

Fig. 3. Diurnal *in situ* dissolved O_2 concentrations in the water column directly above (<10 cm) reef sites with benthic communities that are dominated by scleractinian corals or reef algae as measured with O_2 loggers (Midge). Water temperatures were 21.5 to 21.8°C during winter and 22.3 to 22.7°C during spring measurements

For corals, this release can account for up to half of the carbon assimilated by their zooxanthellae (Crossland et al. 1980, Davies 1984, Muscatine et al. 1984). Coral-derived POM release rates were similar to those described elsewhere (Crossland 1987, Wild et al. 2005b), while hydrozoan, scyphozoan and macroalgal POM release rates were quantified here for the first time. As release of OM has been attributed to surplus carbon fixation during intense photosynthesis (Fogg 1983, Davies 1984), similarities in POM release between algae and corals may be explained by similar photosynthetic overproduction as well as concurrent limited nutrient availability since very low nitrate (0.12 to 0.90 µM) and phosphate (0.03 to 0.07 µM) concentrations were observed at the study site during the 4 expeditions (Wild et al. 2009b).

Net DOM release by corals has been demonstrated by Ferrier-Pages et al. (1998). In the present study, however, net release of DOC was only observed for 3 of the investigated coral genera. This finding is most likely due to the variety of feeding mechanisms of zooxanthellate corals and jellyfish. Besides using

photosynthetic products from zooxanthellae (Muscatine 1990), corals are able to change to other feeding modes, such as the capture of zooplankton by polyps and the uptake of dissolved organic compounds from the surrounding seawater (Sorokin 1973, Ferrier 1991, Muller-Parker & D'Elia 1996). This DOM uptake may have exceeded release for most of the investigated corals. The same explanation likely applies to the jellyfish *Cassiopea* sp. In contrast, all algal species, particularly turf algae, released DOC, which is in agreement with previous studies (Khailov & Burlakova 1969, Brylinsky 1977). In contrast to zooxanthellate corals and jellyfish, benthic algae are strictly photoautotrophic in terms of their energy and carbon requirement (Tuchman 1996); thus, reabsorption of DOM is unlikely, but may still occur.

The exceedingly high OM release rates found for turf algae can potentially be attributed to an underestimation of surface areas due to the exclusion of fine filaments. As larger proportions of structural tissue are needed for more complex morphologies, Littler & Littler (1984) suggested a higher performance of primary production in algae with filamentous morphology. This also creates an increased surface area, thereby providing a large interface with the surrounding that may lead to a faster exchange of metabolic products with the ambient environment. Another reason may be the N fixing ability of turf algae associated cyanobacteria (Williams & Carpenter 1998), which can affect net OM production by overcoming N limitation (Smith 1982).

Effects on microbial activity and potential implications for *in situ* O_2 availability

The comparably high DOC release by benthic reef algae in combination with the observed high stimulation of planktonic microbial activity confirms previously postulated statements (Kline et al. 2006, Smith et al. 2006, Dinsdale et al. 2008), suggesting that DOM released by benthic algae may stimulate planktonic microbial O_2 consumption. High microbial respiration of the biologically labile algae-derived OM may reduce O_2 availability in the surrounding seawater (Nguyen et al. 2005). The results of several laboratory studies suggest that this O_2 deficiency can lead to damage or death of scleractinian corals (Mitchell & Chet 1975, Kuntz et al. 2005, Kline et al. 2006, Smith et al. 2006). The mesocosm study of Haas et al. (2009) in this context also indicated that DOC addition might negatively influence corals in interaction with algae via decreased water O_2 concentrations.

The present study supplements these laboratory studies by demonstrating that there could be similar effects *in situ* via a strong influence of benthic algae on O_2 availability in the reef, likely via the release of labile DOM. Various factors can influence the occurrence of hypoxia around corals *in situ*. The morphology of coral colonies can promote hypoxic conditions by creating a region of weak water exchange between the inner branches (Chamberlain & Graus 1975), and hypoxia on corals has also been found along natural interactions between corals and algae *in situ* (Barott et al. 2009). In contrast, the mutualistic relationship between branching corals and sleep-swimming fish helps to aerate the colony, thus preventing hypoxia (Goldshmid et al. 2004).

There are few studies using O_2 sensors to investigate water O_2 concentrations in coral reefs (Barnes 1983, Barnes & Devereux 1984). To our knowledge, the present study is the first comparison of adjacent sites with different benthic communities, revealing significantly lower water O_2 concentrations at algae dominated sites compared to adjacent coral dominated sites.

In the present study, the O_2 sensors did not measure a particular parcel of water since water from coral dominated sites likely exchanged with water from the algae dominated sites and vice versa because of alternating tidal currents. In addition, the pronounced reef topography and high sedimentary permeability at the study site (Wild et al. 2005a, Wild et al. 2009b) likely facilitated advective water exchange (Huettel & Gust 1992, Ziebis et al. 1996), which counteracted the establishment of O_2 gradients as described by Shashar et al. (1993). Nevertheless, significant differences in O_2 concentration between neighbouring sites were observed during all comparative logger deployments, which indicate *in situ* establishment of spatially limited O_2 gradients despite such counteracting factors as described in detail by Niggl et al. (2010a). Another reason may be that benthic algae grow preferentially in areas where high advective upwelling of nutrient rich and O_2 depleted pore water takes place. However, the laboratory findings of Smith et al. (2006) under exclusion of sediments and advection emphasized that there are indeed negative effects of benthic reef algae on O_2 concentrations; hence, the above mentioned explanation seems to be unlikely. Therefore, the recorded O_2 concentrations are obviously controlled by the benthic community composition of the respective site.

Physical factors such as water flow, or topographic characteristics as well as biological factors such as respiration and photosynthetic activity may influence water O_2 concentrations *in situ* (Kraines et al. 1996). The deployed O_2 loggers in the present study were placed at comparable sites in close proximity to each other where differences in topography and flow speeds between the algae and coral locations are unlikely to occur. In addition, higher respiration by benthic algae is also unlikely to explain the findings of the

present study since coral respiration is usually higher than benthic reef algal respiration (C. Jantzen unpubl. data). Lower O_2 concentrations at algae dominated sites may therefore be most likely due to strong stimulation of microbial activity by algae-derived OM. At algae dominated sites, O_2 concentrations in the dark dropped well below 100% saturation (~7 mg l^{-1}), but not at coral dominated sites (Fig. 3) or in the water column (Wild et al. unpubl. data). This may indicate that algae dominated sites are O_2 sinks in the coral reef. However, upstream–downstream measurements are required in order to confirm this assumption.

Ecological implications

All investigated groups of organisms can obviously control reef processes, in particular interaction with microbes via OM release. However, corals likely contribute differently to reef functioning than benthic algae. The OM released by corals stimulates microbial activity generally less than algae-derived OM. Further, corals mainly release POM in the form of coral mucus (Crossland 1987), which is a transparent exopolymer (Krupp 1985, Meikle et al. 1987) that is able to trap particles, thereby fulfilling an important role as an energy carrier and nutrient trap in coral reef ecosystems (Wild et al. 2004a, Huettel et al. 2006, Naumann et al. 2009b). In contrast, algae release OM that is predominantly in dissolved form, and the particulate fraction of algae-derived organic material mainly consists of detritus and dead algal cells (Duarte & Cebrian 1996, Mannino & Harvey 2000). This is unlikely to substitute for the important role of coral mucus as particle traps as already hypothesized by Wild et al. (2009c). Apart from lacking the function of particle trapping, algae-derived OM potentially supports a different microbial community. Coral-derived OM can be degraded to some extent by microbes on the coral surface, but this material is mainly (>90%) degraded by the microbial community associated with the reef sands after detachment (Wild et al. 2004b). In contrast, algae-derived OM is likely utilized predominantly by the planktonic microbial community in the surrounding water column. This assumption is further supported by the *in situ* O_2 logger measurements that showed significantly lower water O_2 concentrations at algae dominated compared to coral dominated reef areas.

Thus, this study supports assumptions of negative consequences of OM release on O_2 availability in reefs subjected to a phase shift from coral to algae dominated ecosystems, owing to labile OM released by benthic algae (Kuntz et al. 2005, Kline et al. 2006, Smith et al. 2006). It further indicates that these 2 key groups of primary producers may contribute differently to coral reef ecosystem functioning, owing to the differential rates and locations of microbial utilization of their released OM.

Acknowledgements. We thank the staff of the Marine Science Station, Aqaba, Jordan for welcoming us and for logistical support, particularly M. Rasheed, M. Khalaf and M. el-Zibdah. C. Jantzen and F. Mayer (CORE, Munich, Germany) are acknowledged for their assistance during the sample collection and experiments. We also thank the contributing editor P. Edmunds and 3 anonymous reviewers for their help in improving the manuscript. This work was funded by German Research Foundation (DFG) grant Wi 2677/2-1 to C.W.

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Editorial responsibility: Peter Edmunds, Northridge, California, USA

Submitted: November 25, 2009; Accepted: May 5, 2010
Proofs received from author(s): July 9, 2010