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NOTE

RELEASE OF PARTICULATE AND DISSOLVED ORGANIC CARBON BY THE SCLERACTINIAN CORAL *ACROPORA FORMOSA*

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ABSTRACT

Measurements of both particulate and dissolved organic carbon (POC and DOC) release by corals are important in understanding the organic carbon cycle in reef systems. In this study, branches of *Acropora formosa* (Dana, 1846) were incubated for 5 hrs and the release of POC and DOC into the ambient water was simultaneously measured. POC release rate (average ± SD) was 8.93 ± 1.67 mg C m^{-2} hr^{-1} while DOC release rate was 14.98 ± 4.26 mg C m^{-2} hr^{-1}. Consequently, the majority (ca. 63%) of organic carbon released by *A. formosa* dissolves into the seawater.

The fixed carbon translocated to the coral host from endosymbiotic zooxanthellae represents a primary source of energy for scleractinian corals (Falkowski et al., 1984; Davies, 1991; Lesser et al., 2000). However, corals exude up to half of that organic carbon provided by their zooxanthellae into the surrounding water (e.g., Crossland et al., 1980; Davies, 1984; Muscatine et al., 1984) as both particulate and dissolved forms (Crossland, 1987; Wild et al., 2004a). Particulate organic carbon (POC) released by corals in the form of mucus can trap various organic particles while suspended in the water column due to its mucoid structure (Wild et al., 2004a; Huettel et al., 2006; Naumann et al., 2009). Thus, the organic content of coral mucus increases as it settles to reef sediments to be decomposed mainly by the benthic microbial community (Wild et al., 2004a,b, 2005b). Coral mucus suspended in the water is utilized by both the coral-associated and free-living bacterial community (e.g., Ducklow and Mitchell, 1979; Herndl and Velimirov, 1986; Vacelet and Thomassin, 1991; Ferrier-Pagès et al., 1998). It is also utilized by fish (Hiatt and Strasburg, 1960; Johannes, 1967; Benson and Muscatine, 1974), soft corals (Fabricius and Dommisse, 2000), coral-associated crab (Knudsen, 1967), shrimp (Daumas and Thomassin, 1977), zooplankton (Richman et al., 1975; Gottfried and Roman, 1983), and coral-associated worm (Naumann et al., 2010a). On the other hand, dissolved organic carbon (DOC) released by corals undergoes degradation by the microbial community associated with the releasing coral (e.g., Ferrier-Pagès et al., 1998) and/or in surrounding reef waters (e.g., Ferrier-Pagès et al., 2000). Thus, it is important to examine the release of both POC and DOC by corals to better understand the subsequent carbon pathways in the reef system (Tanaka et al., 2008).

To date, organic matter release by corals has been reported in several coral species for both the particulate (Richman et al., 1975; Herndl and Velimirov, 1986; Means and Sigleo, 1986; Wild et al., 2005a; Tanaka et al., 2008; Wild et al., 2008; Nakajima et al., 2009; Naumann et al., 2010b) and dissolved fraction (Marshall, 1969; Crossland et al., 1980; Crossland, 1987; Sorokin, 1995; Ferrier-Pagès et al., 1998; Ferrier-Pagès et al., 2000; Tanaka et al., 2006, 2008; Wild et al., 2008; Nakajima et al., 2009; Tanaka

et al., 2009a,b; Naumann et al., 2010b), but relatively few data are available on concurrent measurements of both particulate and dissolved organic matter release by corals (Crossland, 1987; Tanaka et al., 2008; Wild et al., 2008; Nakajima et al., 2009; Naumann et al., 2010b). To quantify the input of organic matter released by corals to organic matter cycles in reef systems accurately, it is crucial to measure POC and DOC release by various coral species. The scleractinian coral, *Acropora formosa* (Dana, 1846), is widely distributed in the Indo-Pacific region and is very common and frequently dominant in lagoons and fringing reefs (Veron, 1993). Here, we report the release of POC and DOC by *A. formosa* to contribute to the current limited data on organic matter release by corals.

Methods

Study Site.—This study was carried out on 7 May 2008 on the fringing reefs of the Marine Park at Tioman Island (2°50′00″N, 104°10′00″E), located 32 km off the east coast of Peninsular Malaysia. The live coral coverage of the sampling site was 16% with 16% of dead corals and 68% of other bottom substrate (e.g., sand and rock). *Acropora formosa* was the dominant coral at the sampling site, which accounted for ca. 40% of live corals (A. Nakayama, Soka University, unpubl. data).

Coral Collection.—The water depth of the coral collection site was 1.8 m. Collection of *A. formosa* was carried out by two divers, who looked for branches with 8–10 cm length of live tip and a lower dead section. Before collecting the corals, the tip of the live coral branch was loosely tied with a piece of fishing line (diameter, ca. 0.5 mm), carefully avoiding contact with the rest of the live branch. To avoid mechanical damage when a live branch was broken off, the dead section < 1 cm below the live section was broken off using a chisel and hammer. The tied fishing line was held by one of the divers before breaking the corals to prevent the branch from falling. In total, nine branches were collected and each immediately transferred into 2-L glass bottles (ca. 25 cm height with 10 cm mouth diameter). Each branch was hung in the middle of the bottle by securing the fishing line to the bottle cover upon sealing. The nine bottles, each containing one coral branch, were brought back to the field laboratory within 10 min.

Organic Carbon Release Quantification.—We measured organic carbon release by the corals using a method similar to that described by Herndl and Velimirov (1986) and Wild et al. (2005a, 2008); i.e., we incubated glass bottles containing both seawater and corals for experimental runs and bottles containing only seawater as control for a certain period of time. The release rate of organic matter was obtained by subtracting the control value from the experimental value. Before the start of incubation, the seawater in the nine glass bottles was replaced with filtered seawater pre-filtered through a 0.22-μm pore size membrane filter (Omnipore, PTFE, Millipore) at ambient seawater temperature of the coral collection site (29.5 °C) using a siphon tube to protect the corals from aerial exposure. More specifically, the seawater in each bottle was siphoned out and reduced to 400 ml while care was taken so that the coral branch remained submerged underwater and did not come into contact with the sides of the bottle. Next, 400 ml of 0.22-μm filtered seawater was siphoned into the bottle from the bottom to reach a volume of 800 ml, after which 400 ml of the water was siphoned out once again. This procedure was repeated four times in order to exchange the initial seawater in the bottle (400 ml) with filtered seawater. In a preliminary experiment, we successfully exchanged 400 ml of dyed water with filtered seawater only by repeating this procedure three times. Thus, in the present study, we assumed that the initial seawater in the bottle was completely replaced with filtered seawater. Later, we added 1.4-L filtered seawater to the bottle to reach a final volume of 1.8 L.

The nine corals were suspended in each bottle with the fishing line and incubated during daytime for 5 hrs (1100–1600 hrs) with two control bottles (only 0.22-µm filtered seawater without coral) in an outdoor aquarium under natural sunlight. The aquarium was continuously supplied with running fresh seawater and the water temperature was controlled at 29.5 °C, the exact temperature when we collected the corals, using a water temperature regulator (Rei-Sea LX120EXA), which acted as a water bath to keep temperature constant inside the bottles. The thermometer in the temperature regulator was calibrated with a mercurial thermometer before use. The mouth of the bottle was covered with a 0.22-µm pore size membrane filter to reduce the chances of contamination from air during the incubation. The incubated medium was repeatedly hand-stirred with a glass bar every hour. The glass bar was wiped with 70% ethanol, then washed with Milli Q water (Millipore™) and dried every time before using. At the end of the incubation period, the experimental corals were removed from the bottles and the incubation medium was thoroughly homogenized before triplicate subsamples were taken from each bottle for DOC (5 ml) and total organic carbon (TOC; 5 ml) measurements, respectively. The release rates of DOC and TOC by the corals were obtained by subtracting the average value of two control bottles from each experimental value (Table 1). Subsamples for DOC analysis were filtered through a 0.22-µm membrane filter (Durapore PVDF, Millex, Millipore™) and the filtrate was immediately transferred into precombusted (500 °C; 4 hrs) glass ampoules which were immediately sealed and stored at –20 °C until analysis. Subsamples for TOC were also transferred into pre-combusted glass ampoules without pre-filtering and stored at –20 °C until analysis. DOC and TOC concentrations were measured by the high temperature catalytic oxidation method (HTCO) using TOC-5000 (Shimadzu) following Ogawa et al. (2003). The release rate of POC was calculated by subtracting the release rate of DOC from that of TOC. Statistical differences in the release rates of POC and DOC were determined using two-sided Mann-Whitney's U-test. A difference at $P < 0.05$ was considered significant.

Bacterial Abundance Estimation.—There is a possibility of coral-associated bacteria and/or air-contaminated bacteria consuming the DOC released by the corals and their subsequent numerical increase may contribute to the increase in POC concentrations in the incubation media (Ferrier-Pagès et al., 1998; Tanaka et al., 2008). Thus, bacterial abundance was also determined in triplicate subsamples (5 ml) at the end of the coral incubation and the increase in bacterial abundance was obtained by subtracting the average value of control bottles from each value of the experimental bottles. The samples for bacterial abundance determination were fixed with buffered formalin to a final concentration of 2%. Bacterial abundance was determined using the protocol of Shibata et al. (2006).

Coral Surface Determination.—The surface area of the incubated coral specimens was measured following Nakajima et al. (2009). The coral specimens were wrapped in aluminum foil and the surface area of the opened foil was derived from pictures taken with a digital camera with a scale for calibration. The foil area was estimated by tracing the foil outline on digital photographs using Scandium software (Olympus) to calculate coral surface area.

Results and Discussion

The average release rate (± SD) of POC, DOC, and TOC per unit surface area by *A. formosa* was 12.29 (± 2.27), 17.86 (± 5.14), and 30.15 (± 5.86) mg C m^{-2} hr^{-1}, respectively (Table 1). However, the above values may include some measurement error. Firstly, we incubated 8–10 cm length, live coral branches with ca. 1 cm length dead section and algal overgrowth on the dead section may influence the incubation results as algae is reported to release a significant amount of organic matter (Khailov and Burlakova, 1969; Wild et al., 2009; Haas et al., 2010). Because turf algae was the major algae growing on our dead branches, we estimated POC and DOC released

Table 1. Release rates (mg C m^{-2} coral surface hr^{-1}) of total, dissolved, and particulate organic carbon (TOC, DOC, and POC) by *Acropora formosa*. Release of DOC and TOC by the corals was obtained by subtracting the average value of two parallel control incubations from the results of the coral incubation. Values in parentheses are means of the two control values. POC release is given as TOC minus DOC releases. Average values for experiments are given with standard error of triplicate measurements. Average values for TOC, DOC, and POC releases are given with standard deviation.

Experimental bottle number	Surface area of the experimental coral (cm^2)	TOC (mg C L^{-1})	DOC (mg C L^{-1})	TOC release (mg C m^{-2} coral surface hr^{-1})	DOC release (mg C m^{-2} coral surface hr^{-1})	POC release (mg C m^{-2} coral surface hr^{-1})
1	39.55	1.77 ± 0.04	1.58 ± 0.01	44.83	32.74	12.09
2	33.75	1.45 ± 0.04	1.29 ± 0.04	18.44	7.11	11.32
3	87.85	1.76 ± 0.03	1.55 ± 0.06	19.72	13.45	6.26
4	46.65	1.49 ± 0.05	1.34 ± 0.01	16.76	8.64	8.12
5	87.85	1.64 ± 0.03	1.48 ± 0.01	14.94	10.56	4.38
6	19.77	1.46 ± 0.03	1.26 ± 0.08	33.77	6.92	26.86
7	19.40	1.59 ± 0.04	1.48 ± 0.01	59.17	46.52	12.65
8	19.42	1.55 ± 0.02	1.40 ± 0.01	51.13	32.68	18.44
9	45.49	1.44 ± 0.03	1.25 ± 0.07	12.65	2.14	10.51
Mean				30.15 ± 5.86	17.86 ± 5.14	12.29 ± 2.27
Control 1		1.29 ± 0.00	1.25 ± 0.02			
Control 2		1.26 ± 0.02	1.20 ± 0.02			
		(1.28)	(1.22)			

by the algae from a previous study on POC and DOC release by turf algae on dead corals (i.e., 1.34 and 1.46 mg C m^{-2} hr^{-1}, respectively; see table 1 in Wild et al., 2009). Accordingly, the corrected POC and DOC release by *A. formosa* would be 11.60 (± 2.17) and 17.11 (± 4.87) mg C m^{-2} hr^{-1}, respectively.

Another problem in our method may include the effect of light intensity on the organic matter release by the corals. We conducted the coral incubation in an aquarium under sunlight (the corals were incubated in glass bottles ca. 10 cm below the surface of the medium), thus the light environment was different from in situ conditions (the coral collection site was 1.8 m water depth). In fact, underwater light environment changes with depth at a few centimeters as light absorption and scattering occurs (Kirk, 1994). Previous studies revealed that organic matter release by corals decreases with decreasing ambient light intensity due to the decrease in photosynthetic activity of the zooxanthellae (Crossland, 1987; Naumann et al., 2010b). The opposite may be true in our results as organic matter release may have been somewhat overestimated due to increased light intensity compared with the in situ environment. The values in our results could be comparable to that present in extremely low tides situations at our study site, because the light environment may have been similar to that in situ at extremely low tides when the tops of coral colonies reach close to 10 cm of the seawater surface (R. Nakajima, Soka University, pers. obs.). However, the corals are submerged deeper underwater in mean tide conditions and experience lower light availability. We can estimate the release rates in mean tide conditions using underwater light data and previously reported regressions for light attenuation and organic matter release by corals. Naumann et al. (2010b) recently reported the relationship between light attenuation and release rate in POC and DOC by *Acropora* and *Fungia* corals in Aqaba, Jordan, and found positive linear relation in POC release and quadratic polynomial function relation in DOC release to in situ light availability. Although light data were not directly measured in the

present study, these data were obtained from the Malaysian Meteorological Department. The average surface light intensity (± SD) was 1048.41 ± 261.67 μmol photons m^{-2} s^{-1} during the 5-hr incubation period. The underwater light intensity at 0.1 m and 1.8 m water depths can be estimated using the attenuation coefficient (K_d) measured at the study site (0.194 m^{-1}, Kuwahara et al., 2010) and was 1028.27 and 739.39 μmol photons m^{-2} s^{-1}, which corresponded to 98.1% and 70.5% of the surface irradiance, respectively. We assigned the two light % data into the reported regressions for POC and DOC release for *Acropora* coral (see fig. 3 in Naumann et al., 2010b), in which their *x* axes were converted to percent surface irradiance using the attenuation coefficient measured at their study site (Stambler, 2005). Assuming the algal corrected POC and DOC release by *A. formosa* were those at 0.1 m water depth, the POC and DOC release by *A. formosa* at 1.8 m water depth would be 8.93 (± 1.67) and 14.98 (± 4.26) mg C m^{-2} hr^{-1}, respectively, by proportional relation. Although we tied a fishing line over the living coral tissue during the experiment, it was loosely tied and no visible damage was observed after incubation, thus we considered that the effect of the fishing line was not significant in our experiment.

The increase in bacterial abundance in the nine experimental bottles after the 5-hr incubation was in the range between 19,223 and 150,052 cells ml^{-1} (mean ± SD: 64,659 ± 54,426 cells ml^{-1}). The bacterial increase resulted in an average 1.6% overestimation in POC concentration and 4.7% underestimation in DOC concentration in the incubation media, assuming the carbon content of a single bacterial cell as 30 fg (Fukuda et al., 1998) and the bacterial growth efficiency at 20% (del Giorgio and Cole, 2000). However, both the over- and underestimation could be negligible considering the bias of 4.1% for the detection accuracy of our TOC analyzer (average calibration slope ± SD = 601.5 ± 24.4 area μM^{-1} C, n = 55). Thus, the microbial growth during incubations had no significant effect on the measured release rates and insignificant effect on organic carbon dynamics.

It is difficult to strictly compare the values for POC and DOC release by *A. formosa* with those in other coral species because of differences in applied methodologies and estimation of release rate (e.g., differences in light condition and stirring; Table 2). Still, if comparisons are to be made, they are as follows: POC and DOC release by *A. formosa* were in the range of the previously reported values in several corals (Table 2). POC release of *A. formosa* was lower than that of *Acropora millepora* (Ehrenberg, 1834) (Wild et al., 2005b) and *Acropora nobilis* (Dana, 1846) (Nakajima et al., 2009), but higher than those of other corals; *Cladocora cespitosa* (Linnaeus, 1767) (Herndl and Velimirov, 1986), *Acropora variabilis* (Klunzinger, 1879) and *Stylophora pistillata* (Esper, 1797) (Crossland, 1987), *Acropora aspera* (Dana, 1846) (Wild et al., 2005a), *Acropora pulchra* (Brook, 1981) and *Porites cylindrica* (Dana, 1846) (Tanaka et al., 2008), *Lophelia pertusa* (Linnaeus, 1758) (an azooxanthellate cold water coral, Wild et al., 2008), and *Acropora* spp., *Fungia* spp., *Stylophora* spp., *Goniastrea* spp., *Pocillopora* spp., and *Millepora* spp. (Naumann et al., 2010b). However, this is only true for measurements conducted under submerged conditions. Wild et al. (2005a) found a higher POC release of 117 mg C m^{-2} hr^{-1} for *A. millepora* under natural tidal air-exposure.

DOC release rate for *A. formosa* was lower than *S. pistillata* (Crossland, 1987), *L. pertusa* (Wild et al., 2008), *A. nobilis* (Nakajima et al., 2009), *Acropora* spp., and *Goniastrea* spp. (Naumann et al., 2010b), but higher than *A. variabilis* (Crossland, 1987), *A. pulchra* (Tanaka et al., 2008, 2009b), *P. cylindrica* (Tanaka et al., 2008),

Table 2. Summary of release rate of particulate and dissolved organic carbon (POC and DOC) by several corals under submerged conditions [GBR: Great Barrier Reef, NM: not measured]. Release rates for *Acropora formosa* are given with standard error.

Study site	Taxa	POC release (mg m^{-2} coral surface hr^{-1})	DOC release (mg m^{-2} coral surface hr^{-1})	Incubation method (Volume of incubation medium, L)	Incubation time (hr)	Lighting	Stirring	Source
Off Piran, Slovenia	*Cladocora cespitosa*	5.9	NM	Bottle (<1)	3–4	Fluorescent lamp	No stirring	Herndl and Velimirov, 1986
Bight of Piran	*Acropora variabilis*	4.2	11.7	Flow-through chamber	3	In situ	Flow-through	Crossland, 1987
Bight of Piran	*Stylophora pistillata*	3.3	17.2	Flow-through chamber	3	In situ	Flow-through	Crossland, 1987
Heron Reef, GBR	*Acropora millepora*	10	NM	Beaker (0.5–2)	4–6	Shading sunlight	No stirring	Wild et al., 2005b
Heron Reef, GBR	*Acropora aspera*	7	NM	Beaker (0.5–2)	4–6	Shading sunlight	No stirring	Wild et al., 2005b
Ishigaki Island, Japan	*Acropora pulchra*	3.7	1.9	Bottle (8)	96	Direct sunlight	Continuous	Tanaka et al., 2008
Ishigaki Island, Japan	*Porites cylindrical*	3	1.7	Bottle (8)	96	Direct sunlight	Continuous	Tanaka et al., 2008
Bergen, Norway	*Lophelia pertusa*	1.4	47	Beaker (0.7–0.8)	4	Dark	No stirring	Wild et al., 2008
Bidong Island, Malaysia	*Acropora nobilis*	12.2	26.5	Plastic bag (2–8)	24	In situ	No stirring	Nakajima et al., 2009
Ishigaki Island, Japan	*A. pulchra*	NM	4.4	Bottle (0.7)	5	Halogen lamp	Continuous	Tanaka et al., 2009b
Aqaba, Jordan	*Acropora* spp.	1.8	30.7	Beaker (0.8–1)	6	Shading sunlight	No stirring	Naumann et al., 2010b
Aqaba, Jordan	*Fungia* spp.	1.3	−14.2	Beaker (0.8–1)	6	Shading sunlight	No stirring	Naumann et al., 2010b
Aqaba, Jordan	*Stylophora* spp.	6.5	−14.1	Beaker (0.8–1)	6	Shading sunlight	No stirring	Naumann et al., 2010b
Aqaba, Jordan	*Goniastrea* spp.	1.4	22	Beaker (0.8–1)	6	Shading sunlight	No stirring	Naumann et al., 2010b
Aqaba, Jordan	*Pocillopora* spp.	3.3	−263.4	Beaker (0.8–1)	6	Shading sunlight	No stirring	Naumann et al., 2010b
Aqaba, Jordan	*Millepora* spp.	0.3	9.2	Beaker (0.8–1)	6	Shading sunlight	No stirring	Naumann et al., 2010b
Tioman Island, Malaysia	*Acropora formosa*	8.93 ± 1.67	14.98 ± 4.26	Bottle (1.8)	5	Direct sunlight	Every hour	Present study

and *Millepora* spp. (Naumann et al., 2010b; Table 2). As for *Fungia* spp., *Stylophora* spp., and *Pocillopora* spp., Naumann et al. (2010b) found a negative DOC net release, probably because of DOC uptake by coral-associated bacteria and/or by the coral itself (coral-zooxanthellae). Wild et al. (2005a) did not measure DOC release by *A. millepora* and *A. aspera*, but they observed that a major part (56%–80%) of mucus produced by the corals immediately dissolves into the ambient water (Wild et al., 2004a). If this estimate is applied to the POC production by *A. millepora* and *A. aspera* (10 and 7 mg C m^{-2} hr^{-1}, respectively; Wild et al., 2005a), their DOC release would be 12.7–40 mg C m^{-2} hr^{-1} and 8.9–28 mg C m^{-2} hr^{-1}, respectively, which are comparable to the DOC release of *A. formosa*.

In the present study, POC and DOC release by *A. formosa* varied considerably depending on the experimental bottles (Table 1), with no statistically significant difference between POC and DOC release by the corals ($P = 0.5457$). Thus, we could not identify which fraction contributed relatively more. However, on average, 62.6% of the released organic carbon by *A. formosa* consisted of DOC and the remaining 37.4% was POC. Consequently, approximately 63% of the organic carbon released by *A. formosa* dissolves into the seawater. Relatively high DOC release compared to POC has been reported previously: 74% DOC by *A. variabilis* and 84% DOC by *S. pistillata* (Crossland, 1987), 70% DOC by *A. nobilis* (Nakajima et al., 2009), 97% DOC by cold-water coral *L. pertusa* (Wild et al., 2008), 94% DOC by *Acopora* and *Goniastrea* corals, and 97% DOC by *Millepora* corals (Naumann et al., 2010b). However, Tanaka et al. (2008) observed higher POC than DOC release by *A. pulchra* and *P. cylindrica* (66% and 63% POC, respectively) at Ishigaki Island, Japan. Small differences in the methods may cause significant differences in coral-derived organic matter release. For example, Tanaka et al. (2008) applied continuous stirring during coral incubation while Wild et al. (2008), Nakajima et al. (2009), and Naumann et al. (2010b) applied no stirring (Table 2). However, Crossland et al. (1987) carried out coral incubation using a flow-through chamber where the water in the chamber was continuously replaced by in situ filtered seawater and still found higher DOC than POC release. Another methodological difference would be the timing of DOC and POC sample collection, as Crossland (1987), Wild et al. (2008), Nakajima et al. (2009), and Naumann et al. (2010b) took samples for DOC and POC measurements simultaneously, while Tanaka et al. (2008) collected DOC and POC samples at different points in time. This may influence the results of the proportion of DOC and POC release. With the exception of Tanaka et al. (2008), it could be generally accepted that corals release more DOC than POC into the water. Additional studies on organic matter (both POC and DOC) release by various coral species in different coral reefs are needed to improve our understanding of the organic carbon cycle in the coral reef ecosystem.

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Literature Cited

Benson, A. A. and L. Muscatine. 1974. Wax in coral mucus: energy transfer from corals to reef fish. Limnol. Oceanogr. 19: 810–814.

Crossland, C. J. 1987. In situ release of mucus and DOC-lipid from the corals *Acropora variabilis* and *Stylophora pistillata* in different light regimes. Coral Reefs 6: 35–42.

_____, D. J. Barnes, and M. A. Borowitzka. 1980. Diurnal lipid and mucus production in the staghorn coral *Acropora acuminata*. Mar. Biol. 60: 81–90.

Daumas, R. and B. A. Thomassin. 1977. Protein fractions in coral and zoantharian mucus: possible evolution in coral reef environments. Proc. 3rd Int. Coral reef Symp. 1: 517–523.

Davies, P. S. 1984. The role of zooxanthellae in the nutritional energy requirements of *Pocillopora eydouxi*. Coral Reefs 2: 181–186.

_____. 1991. Effect of daylight variations on the energy budgets of shallow-water corals. Mar. Biol. 108: 1432–1793.

del Giorgio, P. A. and J. J. Cole. 2000. Bacterial energetics and efficiency. Pages 289–325 *in* D. L. Kirchman, ed. Microbil Ecology of the Ocean. Wiley-Liss, New York.

Ducklow, H. W. and R. Mitchell. 1979. Bacterial populations and adaptations in the mucus layers on living corals. Limnol. Oceanogr. 24: 715–725.

Fabricius, K. E. and M. Dommisse. 2000. Depletion of suspended particulate matter over coastal reef communities dominated by zooxanthellate soft corals. Mar. Ecol. Prog. Ser. 196: 157–167.

Falkowski, P. G., Z. Dubinsky, L. Muscatine, and J. W. Porter. 1984. Light and the bioenergetics of a symbiotic coral. BioScience 34: 705–709.

Ferrier-Pagès, C., N. Leclercq, J. Jaubert, and S. P. Pelegrí. 2000. Enhancement of pico- and nanoplankton growth by coral exudates. Aquat. Microb. Ecol. 21: 203–209.

_____, J.-P. Gattuso, G. Cauwet, J. Jaubert, and D. Allemnd. 1998. Release of dissolved organic carbon and nitrogen by the zooxanthellate coral *Galaxea fascicularis*. Mar. Ecol. Prog. Ser. 172: 265–274.

Fukuda, R., H. Ogawa, T. Nagata, and I. Koike. 1998. Direct determination of carbon and nitrogen contents of natural bacterial assemblages in marine environment. Appl. Environ. Microbiol. 64: 3352–3358.

Gottfried, M. and M. R. Roman. 1983. Ingestion and incorporation of coral-mucus detritus by reef zooplankton. Mar. Biol. 72: 211–221.

Haas, A. F., M. S. Naumann, U. Struck, C. Mayr, M. el-Zibdah, and C. Wild. 2010. Organic matter release by coral reef associated benthic algae in the Northern Red Sea. J. Exp. Mar. Biol. Ecol. 389: 53–60.

Herndl, G. J. and B. Velimirov. 1986. Microheterotrophic utilization of mucus released by the Mediterranean coral *Cladocora cespitosa*. Mar. Biol. 90: 363–369.

Hiatt, R. W. and D. W. Strasburg. 1960. Ecological relationships of the fish fauna on coral reefs of the Marshall Islands. Ecol. Monogr. 30: 65–127.

Huettel, M., C. Wild, and S. Gonelli. 2006. Mucus trap in coral reefs: formation and temporal evolution of particle aggregates caused by coral mucus. Mar. Ecol. Prog. Ser. 307: 69–84.

Johannes, R. E. 1967. Ecology of organic aggregates in the vicinity of a coral reef. Limnol. Oceanogr. 18: 189–195.

Khailov, K. M. and Z. P. Burlakov. 1969. Release of dissolved organic matter by marine seaweeds and distribution of their total organic production to inshore communities. Limnol. Oceanogr. 14: 521–527.

Kirk, J. T. O. 1994. Light and photosynthesis in aquatic ecosystems, 2nd ed. Cambridge University Press, Cambridge. 509 p.

Knudsen, J. W. 1967. *Trapezia* and *Tetralia* (Decapoda, Brachyura, Zanthidae) as obligate ectoparasites of pocilloporid and acroporid corals. Pacific Sci. 21: 51–57.

Kuwahara, V. S., R. Nakajiam, B. H. R. Othman, M. R. M. Kushairi, and T. Toda. 2010. Spatial variability of UVR attenuation and bio-optical factors in shallow coral-reef waters of Malaysia. Coral Reefs 29: 693–704. doi:10.1007/s00338-010-0618.1.

Lesser, M. P., C. Mazel, D. Phinney, and C. S. Yentsch. 2000. Light absorption and utilization by colonies of the congeneric hermatypic corals *Montastraea faveolota* and *Montastaea cavernosa*. Limnol. Oceanogr. 45: 76–86.

Marshall, N. 1969. Notes on mucus and zooxanthellae discharged from reef corals. Proc. 1st Int. Coral Reef Symp. 59–65.

Means, J. C. and A. Sigleo. 1986. Contribution of coral reef mucus to the colloidal organic pool in the vicinity of Discovery Bay, Jamaica, W.I. Bull. Mar. Sci. 39: 110–118.

Muscatine, L., P. G. Falkowski, J. W. Porter, and Z. Dubinsky. 1984. Fate of photosynthetically fixed carbon in light- and shade-adapted colonies of the symbiotic coral *Stylophora pistillata*. P. Roy. Soc. Lond. B. Bio. 222: 181–202.

Nakajima, R., T. Yoshida, B. A. R. Azman, K. Zaleha, B. H. R. Othman, and T. Toda. 2009. In situ release of coral mucus by *Acropora* and its influence on the heterotrophic bacteria. Aquat. Ecol. 43: 815–823.

Naumann, M. S., C. Mayr, U. Struck and C. Wild. 2010a. Coral mucus stable isotope composition and labeling –experimental evidence for mucus uptake by epizoic acoelomorph worms. Mar. Biol. doi:10.1007/s00227-010-1516-3.

_____, C. Richter, M. el-Zibdah and C. Wild. 2009. Coral mucus as an efficient trap for picoplanktonic cyanobacteria –implications for pelagic-benthic coupling in the reef ecosystem. Mar. Ecol. Prog. Ser. 385: 65–76.

_____, A. Haas, U. Struck, C. Mayr, M. el-Zibdah and C. Wild. 2010b. Organic matter release by dominant hermatypic corals of the Northern Red Sea. Coral Reefs 29: 649–659.

Ogawa, H., T. Usui, and I. Koike. 2003. Distribution of dissolved organic carbon in the East China Sea. Deep-Sea Res. Pt. II 50: 353–366.

Richman, S., Y. Loya, and L. B. Slodokin. 1975. The rate of mucus production by corals and its assimilation by the coral reef copepod *Acartia negligens*. Limnol. Oceanogr. 20: 918–923.

Shibata, A., Y. Goto, H. Saito, T. Kikuchi, T. Toda, and S. Taguchi. 2006. Comparison of SYBR Green I and SYBR Gold stains for enumerating bacteria and viruses by epifluorescence microscopy. Aquat. Microb. Ecol. 43: 223–231.

Sorokin, Y. I. 1995. Coral reef ecology. Springer, Berlin Heidelberg New York, 465 p.

Stambler, N. 2005. Bio-optical properties of the northern Red Sea and the Gulf of Eilat (Aqaba) during winter 1999. J. Sea Res. 54: 186–203.

Tanaka, Y., T. Miyajima, and H. Ogawa. 2009a. Bacterial degradability of dissolved organic carbon in coral mucus. Proc. 11th Coral Reef Symp. 945–949.

_____, _____, I. Koike, T. Hayashibara, and H. Ogawa. 2008. Production of dissolved and particulate organic matter by the reef-building corals *Porites cylindrica* and *Acropora pulchra*. Bull. Mar. Sci. 82: 237–245.

_____, _____, Y. Umezawa, T. Hayashibara, H. Ogawa, and I. Koike. 2009b. Net release of dissolved organic matter by the scleractinian coral *Acropora pulchra*. J. Exp. Mar. Biol. Ecol. 37: 101–106.

_____, _____, _____, H. Fukuda, I. Koike, H. Ogawa, and T. Hayashibara. 2006. Effect of nitrate enrichment on release of dissolved organic carbon and nitrogen from zooxanthellate coral, *Acropora pulchra* and *Porites cylindirca*. Proc. 10th Int. Coral Reef Symp. 925–931.

Vacelet, E. and B. A. Thomassin. 1991. Microbial utilization of coral mucus in long term *in situ* incubation over a coral reef. Hydrobiologia 211: 19–32.

Veron, J. E. N. 1993. Corals of Australia and the Indo-Pacific. University of Hawaii Press, Honolulu. 644 p.

Wild, C., H. Woyt, and M. Huettel. 2005a. Influence of coral mucus on nutrient fluxes in carbonate sands. Mar. Ecol. Prog. Ser. 287: 87–98.

_____, A. Haas, M. Naumann, C. Mayr, and M. el-Zibdah. 2009. Comparative investigation of organic matter release by corals and benthic reef algae-implications for pelagic and benthic microbial metabolism. Proc. 11th Int. Coral Reef Symp. 1319–1323.

_____, M. Huettel, A. Klueter, S. G. Kremb, M. Rasheed, and B. B. Jørgenssen. 2004a. Coral mucus functions as an energy carrier and particle trap in the reef ecosystem. Nature 428: 66–70.

_____, M. Rasheed, U. Werner, U. Franke, R. Johnstone, and M. Huettel. 2004b. Degradation and mineralization of coral mucus in reef environments. Mar. Ecol. Prog. Ser. 267: 159–171.

_____, C. Mayr, L. Wehrmann, S. Schöttner, M. Naumann, F. Hoffmann, and H. T. Rapp. 2008. Organic matter release by cold water corals and its implication for fauna-microbe interaction. Mar. Ecol. Prog. Ser. 372: 67–75.

_____, M. Rasheed, C. Jantzen, P. Cook, U. Struck, M. Huettel, and A. Boetius. 2005b. Benthic metabolism and degradation of natural particulate organic matter in carbonate and silicate reef sands of the northern Red Sea. Mar. Ecol. Prog. Ser. 298: 69–78.

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