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Rapid recycling of coral mass-spawning products in permeable reef sediments

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ABSTRACT: During the annual synchronous release of gametes by corals, a large amount of energy-rich organic material is released to the reef environment. In November 2001, we studied a minor spawning event at Heron Island in the Great Barrier Reef (GBR), Australia. Laboratory experiments showed that egg release by the staghorn coral *Acropora millepora* amounted to 19 ± 15 g dry mass (mean ± SE, n = 8) per m^2 coral surface. Carbon content reached 60.1 ± 4.0% and nitrogen content 3.6 ± 0.4% of the egg dry mass. During this minor spawning period, *Acropora* corals from the reef crest released 7 g C and 0.4 g N as eggs m^{-2} reef. *In situ* experiments (n = 11) using stirred benthic chamber measurements revealed that the sedimentary O_2 consumption (SOC) of the lagoon sediments increased sharply immediately after the coral spawning. Extreme SOC rates of 230 mmol O_2 m^{-2} d^{-1} were reached 2 d after the event, exceeding the pre-spawning rate by a factor of 2.5. This maximum was followed by a steep decrease in SOC rates that gradually levelled off and reached pre-spawning values 11 d after the event. The immediate and strong response of SOC shows that the coral spawning event provides a strong food impulse to the benthic food chain. Our results demonstrate high decomposition efficiency of permeable carbonate reef sands and underline the role of these sediments as a biocatalytical recycling system in the oligotrophic reef environment.

KEY WORDS: Corals · Mass spawning · Permeable sediments · Sedimentary oxygen consumption · SOC · Coral reefs · Recycling

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INTRODUCTION

In 1981, a spectacular phenomenon was discovered by scientists in the Central Great Barrier Reef (GBR), Australia: the synchronous mass release of gametes by many species of coral (Harrison et al. 1984). This event was termed coral spawning, and occurs only on a few predictable nights each year, in the GBR typically during the week following each full moon from October to December (Harrison 1993). Besides the lunar phase, other factors such as temperature change, salinity, current velocity, tidal amplitudes (Oliver et al. 1989, Hayashibara et al. 1993) and even chemical messengers (Atkinson & Atkinson 1992) are suggested as possible triggers for the coral spawning event. Corals can possibly benefit from the mass release of gametes, because of an enhanced fertilisation success and fast predator satiation (Hughes et al. 2000).

Simultaneous multi-species coral spawning has also been observed in other regions, including Singapore (Guest et al. 2002), Japan (Van Woesik 1995) and the Gulf of Mexico (Gittings et al. 1992, Hagman et al. 1998), but not in the Red Sea (Shlesinger & Loya 1985) nor the Caribbean (Szmant 1986). Synchronous release of sexual products is also known for a variety of planktonic and other benthic marine invertebrates including polychaetes (Itano & Buckley 1988), hydrozoan fire corals (Soong & Cho 1998) and gorgonians (Lasker et al. 1996). It was also observed that green algae on coral reefs show a mass spawning behaviour (Clifton 1997).

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Research in the GBR revealed that at least 140 coral species participate in the mass-spawning event (Babcock et al. 1986, Oliver et al. 1989) that occurs throughout the whole GBR region (Oliver et al. 1989). A broadcast spawning (buoyant gamete release) with external fertilisation is typical for the GBR corals (Harriott 1992). During the very brief spawning period, a large amount of organic matter is released into the reef ecosystem as so-called egg–sperm bundles. The bundles float to the sea surface, because their high lipid content makes them positively buoyant (Arai et al. 1993). Subsequently, the buoyant egg–sperm bundles break apart, releasing eggs and sperm into the surrounding water (Coll et al. 1994). Visible surface aggregations (coral spawn slicks) can form from the coral eggs and embryos as a consequence of local hydrodynamic features such as fronts between water parcels, and wakes and eddies behind a reef (Oliver & Willis 1987, Willis & Oliver 1990). Coral eggs and slicks are transported to other reefs by wind and currents (Wolanski et al. 1989, Sammarco et al. 1991) or stay within the same reef due to self-seeding patterns (Andrews et al. 1989, Wolanski et al. 1989).

It is very likely that parts of the released gametic material reach the reef sediments after a short pelagic period, since there is an intense coupling between water column and sediments in these shallow-water environments. Wolanski et al. (1989) found that coral eggs were partly trapped in the lagoon of the studied reef. At Ningaloo Reef, Western Australia, Simpson et al. (1993) observed that large amounts of coral spawn were trapped in a bay and formed extensive slicks on the sediment surface.

In this study we investigated the response of the lagoon sediments to a coral spawning event in order to assess the contribution of the coral sands to the decomposition of the organic material released by the corals. For these investigations, benthic chambers were deployed in the lagoon of the Heron Island Reef, Australia, and the sedimentary O_2 consumption (SOC) was measured before, during and after the coral spawning event in November 2001.

MATERIALS AND METHODS

Study site. All sample collections and experiments were done in November 2001 at Heron Island, a platform-reef system with a total area of 26.4 km^2, located in the Southern GBR (23° 27′ S, 151° 55′ E), Australia (Fig. 1). Egg release was quantified in the laboratory facilities of the Heron Island Research Station (HIRS). The benthic chamber experiments took place in Shark Bay, a shallow-water environment (max. water depth 2.5 m) situated on the southeastern edge of the island.

Sediment characteristics. We took sediment cores (n = 7) in Shark Bay and measured a permeability of $1.2 \pm 0.34 \times 10^{-10}$ m^2 (mean ± SD) using a constant-head permeameter as described by Klute & Dirksen (1986). Sediment porosity was 44.3 ± 1.9% wt/wt (n = 9) calculated from weight loss of wet sediment after drying at 60°C for 24 h. Particulate organic carbon (POC) and nitrogen (PON) contents were measured using a CHNO-rapid elemental analyser (Heraeus) with sulphanilamide as a calibration standard. The samples were pre-treated with 6 N HCl until gas development ceased, and then washed twice with distilled water and dried at 60°C. Measurements showed values of 0.24% for POC and 0.042% for PON. The median grain size of Shark Bay sands was 838 µm, characterising the sediment as dominated by coarse sands.

Egg-release quantification. On 4 November 2001, dominant *Acropora* species of the Heron Island reef flat were examined for signs of spawning readiness by inspecting the cross-sections of coral branches. Only a few species, *A. millepora*, *A. digitata* and *A. pulchra*, showed pinkish-reddish septal contents, indicating the production of gametes. The other tested species *A. aspera*, *A. nobilis* and *A. formosa* did not show any recognisable maturation of eggs. Between 2 and 3 colonies (size approx. 40 × 40 × 30 cm) from each of the 3 species with visible gametes were collected and

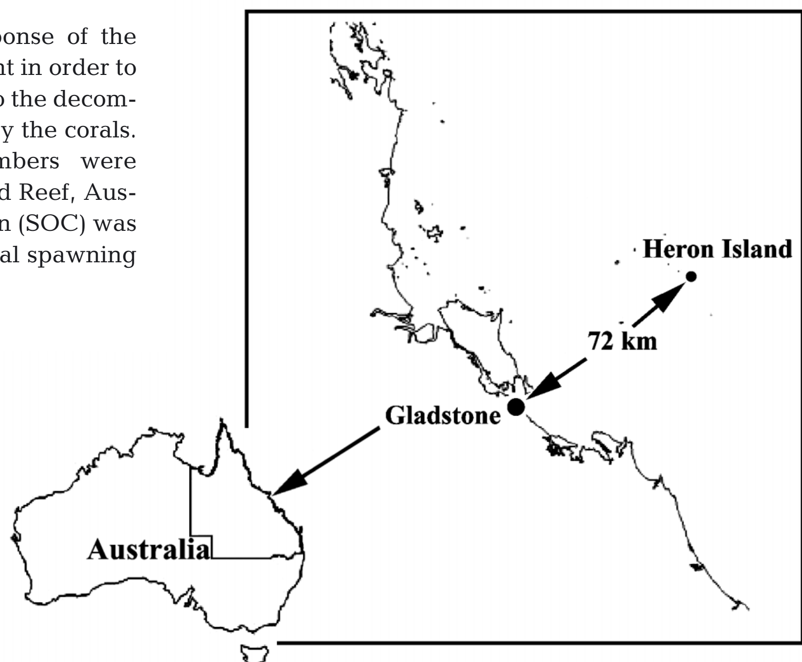

Fig. 1. Location of Heron Island on Australian Great Barrier Reef

transferred to aerated flow-through tanks at HIRS without exposure to air. One of the *A. millepora* colonies was split into 8 similar-sized fragments, which were left in a separate aquarium for 3 d to recover.

Every day at sunset, starting on 7 November 2001, these fragments were transferred to 500 ml glass beakers filled with unfiltered fresh seawater and kept in complete darkness. These beakers were examined for gamete release every 30 min until 22:00 h using a torch covered with a red transparent film. Spawning of all 8 *Acropora millepora* fragments occurred on 9 November at 21.00 h, lasting for about 45 min (Fig. 2a). Egg–sperm bundles (Fig. 2d) floating to the water surface of each beaker were filtered through gauze (50 µm) to separate eggs and sperm. The eggs then were filtered on pre-weighed Whatman #1 filters and dried for 48 h at 40°C. Egg dry weights were related to the surface area of the parental *A. millepora* fragments. These surface areas were assessed by the wax method described by Stimson & Kinzie (1991).

Carbon and nitrogen measurements in coral eggs. Freshly released and filtered eggs (sperms were removed) from *Acropora millepora*, *A. digitata* and *A. pulchra* were also dried for 48 h at 40°C. Dried eggs were subsequently frozen at –20°C until further analysis. Total organic carbon (TOC) and nitrogen (TON) were measured using an element analyser (Fisons NA1500) with sulphanilamide as the calibration standard.

Determination of sedimentary O_2 consumption (SOC). In total, 11 *in situ* chamber experiments were carried out before, during and after the November coral spawning event. All experiments were done in Shark Bay, always starting 2 h after low tide (water height approximately 0.5 m) and ending between 2 and 7 h later. Cylindrical stirred benthic chambers, as described in Huettel & Gust (1992), were used. Plastic lids covered the chambers and were fixed by 4 stainless steel clips. Each lid contained a sampling port with syringe holder for water samples and another port to replace the sampled water. A horizontally rotating disk (20 rpm) agitated the water in the chamber and generated a pressure gradient at the sediment surface of 1.1 Pa between the centre and the chamber wall. Pressure gradients in this order of magnitude develop when sediment topography and boundary flows found at the study site interact (Huettel & Gust 1992, Glud et al. 1995), and can induce advective transport of water and solutes into permeable sediments. With the chambers used, we were therefore able to generate hydrodynamic conditions very similar to field conditions.

For each experiment, 3 of the benthic chambers were used, with the exception of the first 2 experiments, which used only 1 chamber each because of technical problems. The chambers were inserted gently into the sediment to a depth of about 10 cm, and thus contained a water column of approximately 22 cm height. The lids then were fitted to the chambers and fixed by clips.

All chambers were protected from light by wrapping them with black PVC foil and secured with weight belts to prevent movement by wind and waves. Recording of light intensity and temperature under the PVC foil and in the surrounding seawater at least every 2 min, using Onset™ HOBO and Tidbit dataloggers, showed that no light intrusion and heating took place in the chambers during the *in situ* incubations. In-situ water temperature was between 22 and 29°C in all chamber experiments.

The oxygen concentration in the chamber water was measured at regular intervals using the Winkler titration method (Winkler 1888). SOC was calculated from linear regression of the O_2 concentration decrease in the chambers.

Respiration measurements in the water column. In order to quantify the O_2 consumption of the water column and to relate it to the results of the chamber experiments, surface water from Shark Bay was collected on 17 November, filled in nine 30 ml Winkler bottles and incubated under dark conditions and at *in situ* temperature (26–29°C). The O_2 concentrations were measured in a time series using the Winkler titration method, and O_2 consumption rates were derived from linear regression of O_2 concentrations over time.

RESULTS

In situ and laboratory observations during the spawning period

The coral spawning event in November 2001 at Heron Island was not very pronounced. Only a few coral species collected from the Heron Island Reef showed morphological signs of spawning preparation. The release of egg–sperm bundles (Fig. 2c) by corals was directly observed in the laboratory aquarium, but not in the field, although the water temperature on the reef flat (range 22–29°C) was identical with the aquarium temperature (range 22–25°C). Spawning of the corals in the laboratory occurred between 20:30 and 22:00 h on 3 consecutive nights (9–11 November). This was later than the predicted week after full moon (1 November). The spawning event was obviously small, since the typical odour or beach slicks of coral spawning products were not detectable on the mornings during the spawning period. Nevertheless, divers observed slicks of spawning material at the water surface in the lagoon near Shark Bay during high tide on 10 November.

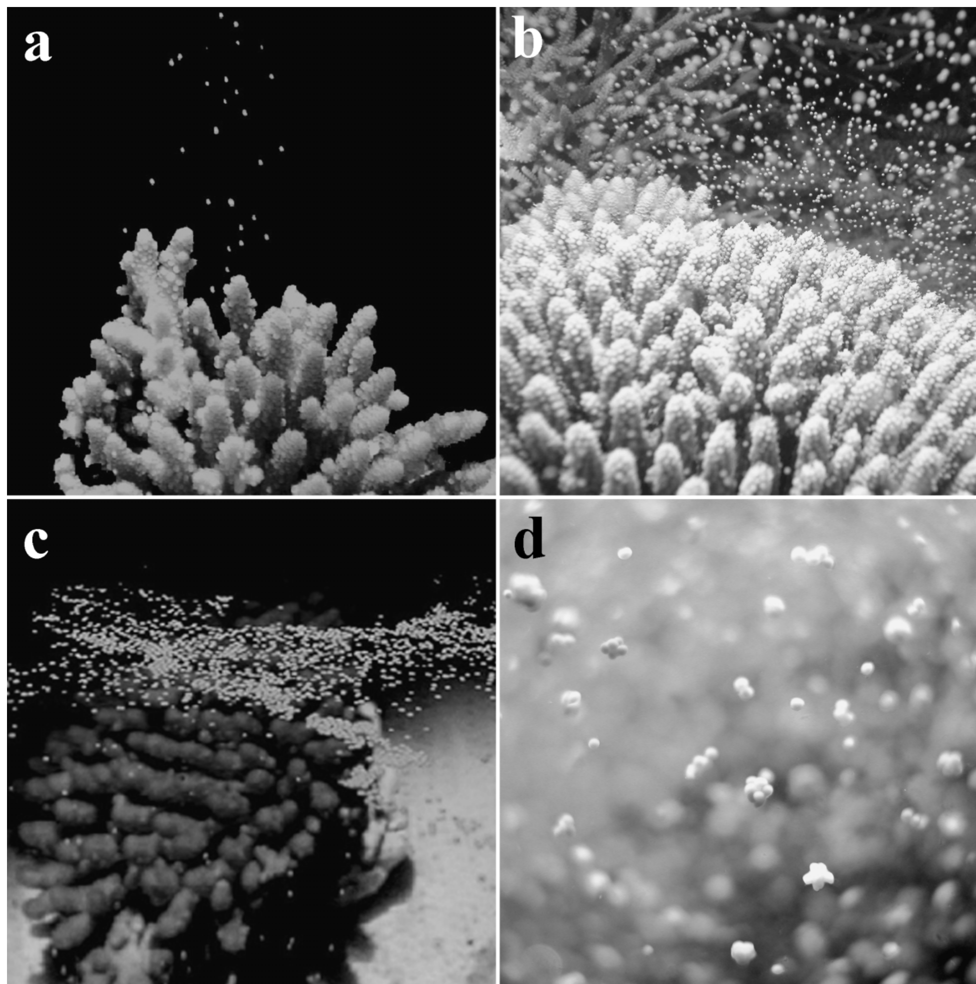

Fig. 2. *Acropora* spp. (a) Colony of *Acropora millepora* in aquarium releasing gametes during November spawning 2001; (b) hard corals of genus *Acropora* on Heron Island reef crest during main spawning event in November 2002; (c) egg–sperm bundle forms slick on water surface; (d) detail of egg–sperm bundles released by corals of genus *Acropora*

The corals in the aquarium showed a species-specific behaviour with *Acropora millepora* spawning on 9 November (8 fragments, 2 larger colonies) and 11 November (1 larger colony), and *A. digitifera* and *A. pulchra* spawning on 10 November (2 larger colonies each). A species-specific spawning behaviour was also observed by Hagman et al. (1998) for corals in the Gulf of Mexico.

Released egg–sperm bundles of 2 different colonies of *Acropora pulchra* (total vol. = 1 ml) incubated in aerated 1 l glass beakers showed that the sperm and eggs separated within 30 min. Sperm was then suspended in the water, whereas intact eggs floated at the water surface. The beakers were examined 5 times a day, the dead material was removed, and 10 % of the water volume was replaced with fresh seawater. Within 48 h, 50 % of the eggs lost their coloration, died and sank to the beaker bottom. Pigmented eggs were still floating at the water surface after 48 h, but subsequently gradually lost their positive buoyancy and changed to oval-shaped moving planula larvae. The latter were observed for the first time after 5 d incubation.

Carbon and nitrogen in coral eggs

Coral eggs released during the spawning event had a high carbon content of 57–66 % (dry mass), whereas nitrogen accounted only for 3–4 % of the egg dry mass (Table 1). Thus, the C:N ratio showed values of 16–21. There were no species-specific differences in C and N content.

Egg release by *Acropora* spp.

The measurements revealed a release of 19 ± 15 g egg dry mass m^{-2} coral surface (n = 8) by *Acropora*

Table 1. *Acropora* spp. Carbon and nitrogen contents (mean ± SD) of eggs released by 3 species in relation to egg dry mass (dm). n: no. of replicates

Species	n	C (mg g^{-1} dm)	N (mg g^{-1} dm)	C:N ratio
A. digitifera	6	572 ± 59	38 ± 9	16 ± 4
A. pulchra	3	659 ± 43	32 ± 9	21 ± 4
A. millepora	6	601 ± 43	36 ± 4	17 ± 2

millepora during the November spawning event. This corresponds to at least 11.6 and 0.7 g C and N, respectively, released as eggs m^{-2} coral surface.

In situ chamber experiments

Despite the relatively small volume of gametes released during the spawning event, the benthic response to the organic matter input was immediate and strong. The average pre-spawning SOC of 94 ± 2 mmol m^{-2} d^{-1} (mean ± SE, n = 4) increased by a factor of 2.5 to a maximum of 230 mmol m^{-2} d^{-1} on the second day after the spawning event (Fig. 3).

The decrease in the O_2 consumption rate was nearly as steep as the increase; however, significantly (α = 0.025, 1-sided *U*-test: Wilcoxon, Mann-Whitney) higher SOC rates compared to pre-spawning values (5–8 November, n = 5) could still be measured 9 d after the spawning (Fig. 3).

SOC 11 d after the start of the spawning event was not significantly different from measured pre-spawning values (α > 0.2, 2-sided *U*-test: Wilcoxon, Mann–Whitney). SOC rates measured 11 d after the spawning event ranged from 93 to 95 mmol m^{-2} d^{-1}. These values are at the upper limit of SOC values derived from *in situ* chamber incubations during the previous (52–80 mmol m^{-2} d^{-1}, n = 3) and following (49–92, n = 6) Australian summer at Heron Island outside the spawning period (Wild et al. 2004a,b).

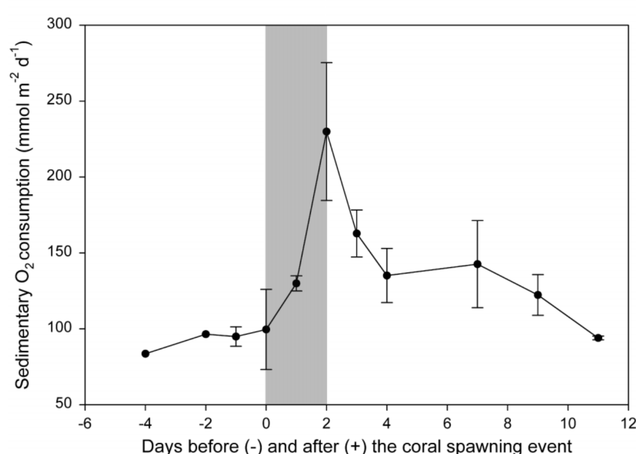

Fig. 3. Sedimentary O_2 consumption (SOC) measured in 11 chamber experiments before, during and after coral *Acropora* spp. spawning period. Error bars = ±SD. Number of replicate chambers = 1 for first 2 experiments and 3 for remaining experiments. Point zero on abscissa indicates day on which spawning was first observed, grey area indicates all days on which spawning occurred

O_2 consumption in the water column

On 17 November, when SOC rates were still increasing, we measured an O_2 consumption rate for Shark Bay waters of 15.4 µmol l^{-1} d^{-1}, i.e. not higher than the values (between 5 and 41 µmol l^{-1} d^{-1}) measured by C. Wild et al. (unpubl. data) in Shark Bay waters in January 2002. Using the water O_2 consumption rate measured on 17 November to calculate the water O_2 consumption in the benthic chambers (max. 7 l), this corresponds to a rate of 3.9 mmol m^{-2} d^{-1}, i.e. about 3% of the O_2 consumption rates of the previous (16 November: 142.6 mmol m^{-2} d^{-1}) and following (18 November: 122.3 mmol m^{-2} d^{-1}) days. This means that >95% of the O_2 consumption in the chambers was due to sedimentary metabolism and only a minor fraction to water column respiration.

DISCUSSION

In 2001, coral spawning at Heron Island was split into a minor November spawning event and a major December spawning event (S. Dove & S. Ward pers. comm.). In 2002, this scenario was reversed, with a major spawning event in November and a smaller one in December (R. Tollrian pers. comm.). Fig. 2b shows a major spawning event on the Heron Island reef crest in November 2002.

In 2001, we were able to study the smaller event and showed that even a relatively small coral spawning can increase the SOC significantly for more than 1 wk. In order to explain the measured temporal link between the coral spawning event and the enhanced SOC rates, we must first assume that a fraction of the spawning products reached the sediment soon after release from the corals. This can occur through direct sedimentation of eggs, which is supported by our incubation experiments, where we observed that within 48 h 50% of the eggs lost their pigments, died and sank to the ground. Oliver & Willis (1987) also observed that coral spawn slicks appearing on the days after coral spawning consisted to over 99% of dead eggs and breakdown products. Bacteria possibly degrade the low-density components (e.g. lipids) of this material, leading to loss

of buoyancy and sedimentation of the dead spawning products.

A second source of organic matter may be the introduction of diluted sperm into the sediment. Sperm cells are not positively buoyant, and become diluted upon release from the egg–sperm bundles.

Additionally, spawning products can also reach the sediment via food-chain transfer processes. Many different coral reef organisms, e.g. fishes and zooplankton (Westneat & Resing 1988, Baird et al. 2001, Pratchett et al. 2001) feed intensely on the spawning products and process them into faecal pellets. Faecal pellets are generally known to increase the sedimentary flux of organic material (Turner 2002).

All these factors lead to an increased sedimentation of organic matter derived from the spawning event. Regardless of how the spawning products reached the reef sediments, in these permeable reef sands advective processes play an important role in the rapid and efficient degradation of organic matter (Rasheed et al. 2004, Wild et al. 2004).

Release of organic C and N during coral spawning event

Corals of the genus *Acropora* cover 15.7% of the Heron Island rim, which includes the reef crest and slope (A. Klueter unpubl. data). From a satellite picture we calculated that the Heron Island rim covers a total area of about 6.9 km^2. Hard corals of the genus *Acropora* therefore exclusively cover approximately 1.1 km^2 of the Heron Island reef rim. Because of the 3-dimensional structure of the corals, this *Acropora*-covered rim-surface area corresponds to an actual coral-surface area 3.8-fold larger (approx. 4.2 km^2). Our results show that 11.6 g C and 0.7 g N were released m^{-2} coral surface by the staghorn coral *A. millepora* as eggs during the coral spawning event in 2001. Extrapolated to the reef-rim area and assuming that the other *Acropora* species release roughly the same amount of eggs, this would account for a release of 7.1 g C and 0.4 g N m^{-2}. Our data further suggest that all hard corals from Heron Island may release roughly 310 t C and 18 t N as eggs during spawning; the simultaneous release of sperm is not included in this estimate.

Effect of coral spawning on SOC

With values exceeding 200 mmol m^{-2} d^{-1}, the SOC in the coarse carbonate sands of Heron Island after the spawning event reached rates exceeding those measured in most coastal sediments (Table 2). Higher SOC rates are measured only in microbially highly active sediments, e.g. those beneath cages of a salmon farm (Nickell et al. 2003). Diffusive oxygen uptake rates of the seafloor range usually between 10 and 30 mmol m^{-2} d^{-1}, with maximum rates of approximately 94 mmol m^{-2} d^{-1} (Jørgensen 2001).

Ehrenhauß & Huettel (2004) simulated the sedimentation of a phytoplankton bloom by adding dead diatoms (amount of added material comparable to the amount of material reaching the sediment after a spring algal bloom) to benthic chambers identical to those used in this study. The SOC in very fine to coarse sands from the German North Sea increased afterwards by a factor of 2.0–3.3, similar to the maximum increase observed in this study. This indicates that the coral spawning event may have a similar effect on SOC as sedimentation during an algal bloom. The measured SOC rates in the silicate sediments (63–1000 µm grain size) used by Ehrenhauß & Huettel (2004) were between 1.2 and 6.7 mmol m^{-2} d (without algae addition) and 6.7–11.0 mmol m^{-2} d^{-1} (after algae addition), indicating that much more organic matter can be mineralised in the carbonate sands from Heron Island with a similar grain size (838 µm).

SOC was enhanced compared to the pre-spawning level (94 ± 2 mmol m^{-2} d^{-1}) for 9 d after the spawning

Table 2. Sedimentary O_2 consumption (SOC) measured in different marine shelf sediments with benthic chamber incubations

Location	SOC	Sediment	Source
Douro River Estuary (Portugal)	<96	Silicates	Magalhaes et al. (2002)
Salmon farm, Loch Creran (Scotland)	9–468	Silicates	Nickell et al. (2003)
North and Baltic Sea	42–170	Silicates	Forster et al. (1999)
Balearic Islands (Spain)	195	Silicates	Lopez et al. (1995)
Bay of Cadiz (Spain)	138	Silicates	Forja et al. (1994)
Shellfish farm, Carteau Bay (France)	<105	Silicates	Barranguet et al. (1994)
Bay of Cadiz (Spain)	99–189	Silicates	Gomezparra & Forja (1993)
South Atlantic Bight	35	Silicates	Marinelli et al. (1998)
New Caledonia	11–54	Carbonates	Grenz et al. (2003)
New Caledonia	18	Carbonates	Boucher et al. (1994)
Heron Island	84–230	Carbonates	This study

event (see Fig. 3). Integration of the additional SOC due to the spawning event (measurements were interpolated for days on which no measurements were made) results in 490 mmol O_2 m^{-2}. If it is assumed that 1 mol of O_2 oxidises 1 mol of reduced carbon (in this case coral eggs), then 41 mg of C was oxidised m^{-2} Heron Island reef flat area during the 9 d period. This is equivalent to 800 kg C for the entire reef flat area of 19.5 km^2. We calculated a possible egg production of 66 t C for *Acropora* spp. and 310 t C for all hard corals of the Heron Reef (see preceding subsection). As such, between 0.2% (spawning of all hard corals) and 1.6% (only *Acropora* spp. spawned) of the egg dry mass could have produced the observed increase in the SOC rate.

These numbers may be even smaller, since we could not include the organic matter derived from coral sperm in this calculation. The sedimentary community can rapidly degrade sperm, which is diluted and transported into the permeable sediments via advection. However, it cannot be concluded that only a very small fraction of all coral eggs is degraded in the reef system. The shallow location where the chamber measurements were carried out is exposed to tidal currents and waves. Thus, sedimentation of low-density material such as spawning products in this area is impeded and therefore relatively small. Much higher sedimentation of spawning products can be expected in deeper or calm parts of the lagoon, as supported by reports of Wolanski et al. (1989) and Simpson et al. (1993).

The fast SOC response of the Heron Island sediments hints at a rapid input of organic matter to the sediments. The effect of the spawning event, however, is not restricted to additional C and N being released to the reef. Atkinson & Atkinson (1992) reported that during a coral spawning event the total phosphate concentrations in the water column increased 600-fold. High P concentrations in the water column can stimulate the growth of bacteria in the water column and in the sediment of oligotrophic reef systems (Kuffner & Paul 2001). This may also have contributed to the high SOC rates observed in this study.

Even a small coral spawning event, such as that we studied, supplies enough organic material and nutrients to maintain sedimentary metabolism above the initial level for at least 1 wk. A more pronounced spawning (such as the November spawning event in 2002: Fig. 2b) or split-spawning could cause an increased SOC level over an even longer period of time.

Our findings show that coral spawning events may play a periodical but important role in the nutrition of benthic (microbial) reef communities. The result of this study hint at an important trophic link between the corals and the sedimentary community, especially during the spawning period, in addition to the proposed trophic link via spawning products between corals and reef fishes (Pratchett et al. 2001).

The trapping of spawning products in the reef lagoon and the rapid processing of the products by reef organisms reduces the loss of organic matter from the reef, and therefore represents a recycling process that retains and accumulates nutrients in the oligotrophic reef system.

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