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RESEARCH ARTICLE

Inorganic nutrient availability affects organic matter fluxes and metabolic activity in the soft coral genus *Xenia*

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SUMMARY

The release of organic matter (OM) by scleractinian corals represents a key physiological process that importantly contributes to coral reef ecosystem functioning, and is affected by inorganic nutrient availability. Although OM fluxes have been studied for several dominant reef taxa, no information is available for soft corals, one of the major benthic groups in tropical reef environments. Thus, this study investigates OM fluxes along with other key physiological parameters (i.e. photosynthesis, respiration and chlorophyll *a* tissue content) in the common soft coral genus *Xenia* after a 4-week exposure period to elevated ammonium (N; 20.0 μmol l^{-1}), phosphate (P; 2.0 μmol l^{-1}) and combined inorganic nutrient enrichment treatment (N+P). Corals maintained without nutrient enrichment served as non-treated controls and revealed constant uptake rates for particulate organic carbon (POC) (–0.315±0.161 mg POC m^{-2} coral surface area h^{-1}), particulate nitrogen (PN) (–0.053±0.018 mg PN m^{-2} h^{-1}) and dissolved organic carbon (DOC) (–4.8±2.1 mg DOC m^{-2} h^{-1}). Although DOC uptake significantly increased in the N treatment, POC flux was not affected. The P treatment significantly enhanced PN release as well as photosynthesis and respiration rates, suggesting that autotrophic carbon acquisition of zooxanthellae endosymbionts influences OM fluxes by the coral host. Our physiological findings confirm the significant effect of inorganic nutrient availability on OM fluxes and key metabolic processes for the soft coral *Xenia*, and provide the first clues on OM cycles initiated by soft corals in reef environments exposed to ambient and elevated inorganic nutrient concentrations.

Key words: organic carbon, nitrogen, release, uptake, photosynthesis, respiration, phosphate, ammonium, enrichment.

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INTRODUCTION

Tropical coral reefs principally occur in oligotrophic waters with dissolved inorganic nutrient concentrations close to the limits of analytical detection. However, over the last few decades, elevated inorganic nutrient concentrations, mainly attributable to anthropogenic activities, have been reported from various coral reef environments worldwide (Bell, 1991; Dubinsky and Stambler, 1996; Lapointe and Clark, 1992; Tomascik and Sander, 1987). Elevated inorganic nutrient concentrations can seriously impact coral reef ecosystems by reducing calcification rates, reproductive success and recruitment of corals, while concomitantly promoting the growth of reef-associated benthic macroalgae (Dubinsky et al., 1990; Koop et al., 2001). This may subsequently result in a substantial loss of coral cover and ensuing benthic community phase shifts, i.e. from scleractinian coral dominance to dominance by other invertebrates (i.e. soft corals, sponges, hydrozoans and ascidians) or benthic macroalgae (Dubinsky and Stambler, 1996; Fleury et al., 2000; Hawker and Connell, 1989). Besides enhancing the growth of benthic macroalgae, elevated inorganic nutrient concentrations may also fuel coral endosymbiotic microalgae (i.e. zooxanthellae), thereby potentially influencing the symbiotic interaction (Dubinsky and Stambler, 1996). Previous studies on scleractinian coral taxa have revealed that under oligotrophic conditions zooxanthellae are nutrient limited and contribute importantly to the coral's nutrition by translocating up to 97% of all photosynthetically fixed carbon to their host (e.g. Muscatine et al., 1984). Elevated ambient inorganic nutrient concentrations enable zooxanthellae to retain significantly more fixed carbon for their own metabolism, and consequently less of it is eventually translocated (Dubinsky and Jokiel, 1994). This reduced transfer of energy-rich photosynthates creates an insufficient diurnal energy supply in the host (Leletkin, 2000), and may consequently affect organic matter (OM) exudation, as up to 40% of carbon fixed by photosynthesis is being released into surrounding reef waters, most of it presumably as coral mucus (Crossland et al., 1980).

Exudation of mucus fulfils important functions for corals as well as the entire reef ecosystem. Mucus secretion onto the epidermal tissue surface by mucus gland cells (i.e. mucocytes) forms a protective surface mucus layer, which supports heterotrophic ciliary feeding ability, protects the coral against desiccation (Krupp, 1984), sedimentation (Riegl and Branch, 1995) and pathogens (Ritchie, 2006), as well as physical and ultraviolet-radiation-related damage (reviewed in Brown and Bythell, 2005; Drollet et al., 1993), and enhances coral resistance to changes in temperature and salinity (Marcus and Thorhaug, 1982). The protective surface mucus layer of scleractinian corals is continuously replaced, and thus large amounts of particulate (POM) and dissolved organic matter (DOM) are released into the water column (Ferrier-Pagès et al., 1998; Naumann et al., 2010; Wild et al., 2008). There, coral-derived OM importantly sustains reef ecosystem functioning by acting as an efficient particle trap and energy carrier in biogeochemical element cycles (Naumann et al., 2009; Wild et al., 2004).

Despite our current knowledge on elevated inorganic nutrient concentrations in coral reef environments, to date only two recent studies (Naumann et al., 2010; Tanaka et al., 2010) have described their effect on OM release rates by scleractinian corals. Interestingly, both of these studies have observed reduced POM and DOM release in response to elevated inorganic nutrient concentrations. Besides effects on specific key physiological processes, such as coral-derived OM release, elevated inorganic nutrient concentrations may affect overall biogeochemical OM cycles in coral reefs as a result of bottom-up effects on benthic community structure. Beyond coral–algae phase shifts, rising inorganic nutrient concentrations possess the potential to cause alternative states in coral reefs, such as a substantial increase in soft coral abundance (reviewed in Norström et al., 2009). Although OM fluxes by scleractinian corals have recently been well described (Naumann et al., 2010; Naumann et al., 2011; Wild et al., 2004; Wild et al., 2008), our general understanding of biogeochemical OM cycles initiated by reef-associated soft coral taxa is still very limited, and no information exists regarding a potential influence by elevated inorganic nutrient concentrations.

Therefore, this laboratory study quantifies OM fluxes by the common soft coral genus *Xenia* following a 4-week exposure period to control (non-enriched) and enriched inorganic nutrient concentrations. A series of post-exposure incubation experiments conducted in non-nutrient-enriched seawater investigates variations in net fluxes of particulate organic carbon (POC), particulate nitrogen (PN) and dissolved organic carbon (DOC). These measurements are complemented by quantitative assessments of *Xenia* key physiological parameters [photosynthesis, respiration and chlorophyll *a* (chl *a*) tissue content], likewise determined after exposure to control (non-enriched) and enriched inorganic nutrient conditions.

MATERIALS AND METHODS

Collection and maintenance of corals

The colony-forming soft coral *Xenia* is an abundant genus that is common in various Indo-Pacific reef ecosystems (Benayahu and Loya, 1977; Dinesen, 1983; Fishelson, 1970; Mergner and Schuhmacher, 1981; Tursch and Tursch, 1982). *Xenia* colonies were collected in 5 to 10 m water depth from a northern Red Sea reef near the city of Aqaba (Jordan) and subsequently maintained under constant conditions in a closed aquarium system for approximately 3 years before the experiments described herein. The respective *Xenia* colonies appeared creamy coloured with monomorphic, pinnulled, pulsating and non-retractile tentacles. According to Reinicke (Reinicke, 1997), we assume that *Xenia* specimens used in the present study belong to the species *Xenia umbellata* Lamarck 1816, which is described as a common pulsating *Xenia* species from the Red Sea. However, because of uncertainty in accurate species identification, we refer to the genus *Xenia* throughout this manuscript.

Experimental design

Experiments were carried out in the laboratory under controlled conditions. A total of 24 healthy *Xenia* colonies, each attached to a small piece of rock, were collected from the maintenance reef aquarium. For better handling, *Xenia* colonies were fixed with their attached rock onto ceramic tiles (4.6×4.6 cm) using conventional coral glue. A 200 l aquarium was used as an experimental tank, inside which the corals were acclimatized to the respective experimental water temperature and light intensity (i.e. 25.3±0.3°C and 57.2±0.6 μmol photons m^{-2} s^{-1}; mean ± s.e.m.) 2 weeks prior to experimentation. The light intensity used for experimentation was adjusted to light levels measured with data loggers (Onset HOBO Pendant UA-002-64; spectral detection range: 150–1200 nm; temperature accuracy: ±0.53°C; Bourne, MA, USA) in the Gulf of Aqaba, Northern Red Sea (Dahab, Egypt, 13 March 2010) at ~5 m water depth, where many *Xenia* colonies were observed in their natural environment. A full-spectrum metal halide lamp (Oceanlight 150+, AB Aqua Medic, Bissendorf, Germany) provided constant irradiance over a daily 12 h photoperiod. Water temperature and light intensity were continuously recorded with data loggers. Light intensity (lx) readings were converted to photosynthetically active radiation (PAR; μmol quanta m^{-2} s^{-1}, wavelength 400–700 nm) using the following approximation: 1 μmol quanta m^{-2} s^{-1}=51.2 lx (Valiela, 1984).

The experiment described in the following was carried out over a period of 4 weeks. A total of 18 *Xenia* colonies (25–96 polyps per colony) were randomly assigned to one of three nutrient treatments, while six colonies served as non-nutrient-treated controls. The aquarium water used for nutrient treatments was either enriched with ammonium (N; 20.0 μmol l^{-1} NH_4^+), phosphate (P; 2.0 μmol l^{-1} PO_4^{3-}) or both inorganic nutrients (N+P; 20.0 μmol l^{-1} NH_4^+ and 2.0 μmol l^{-1} PO_4^{3-}). The respective elevated inorganic nutrient concentrations were chosen for good comparability to previous manipulative studies (Bucher and Harrison, 2000; Godinot et al., 2011). Non-treated corals were held in local aquarium water without ammonium and/or phosphate addition. Inorganic nutrient concentrations in the aquarium water were monitored once per week using a Genesys 10 UV spectro-photometer with photometric ammonium and phosphate test kits (Spectroquant, Merck, Darmstadt, Germany). Results remained below method detection limits (concentrations: <0.8 μmol l^{-1} NH_4^+ and <0.1 μmol l^{-1} PO_4^{3-}) for the duration of the experiment, and thus are regarded to be within the range of *in situ* concentrations reported for the northern Gulf of Aqaba (Rasheed et al., 2002). During the experimentation period of 4 weeks, each coral colony was maintained individually in a 1 l glass beaker filled with 800 ml nutrient-enriched (treatment corals) or local aquarium water (non-treated corals) to avoid pseudoreplication within each treatment. The particular seawater solutions used for nutrient-enriched treatments were prepared separately in 12 l buckets and distributed from there, ensuring equal nutrient concentrations in all replicate glass beakers. To this end, concentrated ammonium chloride (8 mmol l^{-1} NH_4Cl) and sodium phosphate (0.8 mmol l^{-1} NaH_2PO_4) stock solutions were prepared weekly and stored refrigerated (4°C). Treatment seawater media of the desired final concentrations were subsequently prepared in the 12 l buckets from aquarium water and the respective stock solutions. The treatment or non-treatment media in all glass beakers were renewed daily in the morning. For the remainder of the day, all 24 beakers were placed in the aquarium with their rims 5 cm above the water surface. The position of each beaker was randomly changed every day to ensure comparable temperature and light conditions for each coral replicate over the entire 4-week exposure period.

Quantification of OM fluxes

To quantify OM fluxes by *Xenia* corals maintained for 4 weeks under nutrient-treated (N, P and N+P) and non-treated conditions, laboratory experiments were carried out following the established beaker incubation technique (Herndl and Velimirov, 1986). Incubation media for all individual beaker incubations of nutrient-treated and non-treated *Xenia* colonies were prepared from one large volume of non-nutrient-enriched aquarium seawater to ensure comparable incubation conditions among treatments. These

concerned, in particular, inorganic nutrient and OM concentrations, as well as planktonic microbial activity of the incubation medium. After coral-attached rocks and tiles had been carefully cleaned of algal turf, each colony was placed individually into a pre-cleaned glass beaker (500 ml) after a very short air exposure (<2 s). Beakers only filled with aquarium seawater (without coral) served as seawater controls (N=5). After 20 min, all beakers were carefully submerged into the large volume of the experimental tank, resulting in the complete renewal of the beaker volume, which was meant to avoid elevated initial OM concentrations possibly caused by initial coral air exposure. Thereafter, all beakers were positioned in the experimental tank with their rims 5–10 cm above the water surface to ensure equal water temperature and light conditions, as during the 4-week nutrient exposure period. All beakers were covered with transparent cellophane foil to avoid the input of airborne particles, leaving two small side openings for air exchange. The incubation media were not stirred during the relatively short-term incubation period (5–6 h) in order to rule out the potential effect of water flow on the structural composition of *Xenia*-derived organic carbon and to allow for an adequate comparison to previous studies using the same beaker incubation technique (Haas et al., 2010; Herndl and Velimirov, 1986; Naumann et al., 2010; Wild et al., 2005).

Incubations were terminated after 5–6 h by carefully removing the corals from the beakers using clean tweezers. Immediately after incubations (≤5 min), water subsamples were drawn from the homogenized incubation medium. For DOC, 10 ml subsamples were drawn from each beaker using clean syringes and passed through sterile polyethersulfone membrane filters (0.2 µm pore-sized, pre-washed with 6 ml sample; VWR International, Darmstadt, Germany). The filtrate was collected in pre-combusted (450°C, 6 h) glass vials, which were kept frozen at –20°C pending analysis. Leakage of DOC from polyethersulfone filter membranes (Khan and Subramania-Pillai, 2007) was found to be insignificant, as quantified by repeated analyses of different lots of original filters following the described sampling protocol. For analysis, DOC samples were defrosted, acidified to a pH <2 by adding 50 µl of 2 mol l^{-1} HCl, and purged with O_2 for 2 min to remove dissolved inorganic carbon. Subsequently, DOC concentrations were determined by high-temperature catalytic oxidation using a DIMA-TOC 100 total organic carbon analyzer (Dimatec Analysentechnik, Essen, Germany) with potassium hydrogen phthalate as elemental standard. After DOC sampling, O_2 concentrations in all incubation media were determined using an optode sensor (HQ 10, accuracy ± 0.05%; HACH LANGE, Düsseldorf, Germany) to confirm oxic conditions during incubation experiments. The remaining incubation medium (350–450 ml) was vacuum filtered through pre-combusted (450°C, 6 h) GF/F filters (25 mm diameter; Whatman, Maidstone, UK) in order to quantify POC and PN contents. The filters were immediately dried for at least 48 h at 40°C and kept dry until further analysis. As the presence of particulate inorganic carbon could not be ruled out by test measurements of the incubation water, samples were not treated with HCl prior to analysis. For POM analysis, dried filters were wrapped in silver foil and measured using a Thermo NA 2500 elemental analyzer (standard deviation <3%, ThermoFisher Scientific, Passau, Germany) with atropine and cyclohexanone-2,4-dinitrophenylhydrazone as elemental standards.

After incubation, the number of polyps of each colony was counted and the mean surface area of a *Xenia* polyp was determined by geometric measurements on 100 completely protruded polyps randomly distributed over all 24 colonies. The diameter (2r, where r is the radius) and the length of a tentacle foot [height (h)] were measured using a ruler (±0.1 cm accuracy). Thus the surface area of a *Xenia* polyp was mathematically handled as a two-sided circle ($2\pi r^2$) on top of a cylindrical tentacle foot ($2\pi rh$). The mean surface area of a polyp was subsequently multiplied by the number of polyps to generate the total surface area of each incubated *Xenia* colony. POC:PN ratios were calculated from molar contents of POC and PN of the respective coral and seawater control incubation media. As all incubations were carried out in non-nutrient-enriched aquarium seawater, mean POC, PN and DOC concentrations measured in seawater control incubations were subtracted from the concentrations measured in *Xenia*-incubated water. The results were related to the volume of the incubation medium and subsequently normalized by incubation time and colony surface area in order to calculate net OM flux rates (mg m^{-2} h^{-1}).

Physiological measurements

Following the OM incubation procedure, each coral was placed individually in a gas-tight 500 ml glass chamber completely filled with non-nutrient-enriched aquarium seawater and incubated for 2–3 h at experimental temperature and light conditions. An initial incubation was carried out in the light for net photosynthesis (P_{net}) determination, while a subsequent dark incubation without previous dark acclimatization of corals was conducted to measure dark respiration (R). Higher R rates of light- compared with dark-adapted corals (Anthony and Hoegh-Guldberg, 2003; Porter et al., 1984) provide a better approximation for gross photosynthesis (P_{gross}) calculation. Photosynthesis may show a lag response during the first minutes of dark incubation, but O_2 evolution can be regarded as negligible, if seen in the context of 2–3 h incubation time. O_2 concentrations were measured at the beginning and end of each incubation period using an O_2 optode sensor (HQ 10, ±0.05% accuracy, HACH LANGE). To calculate P_{net} and R rates, O_2 end concentrations were subtracted from start concentrations and the results were normalized by incubation duration. Parallel to the above incubations, five seawater controls (without corals) were incubated to measure planktonic background metabolism. As all incubations were carried out in non-nutrient-enriched seawater, P_{net} and R rates obtained from seawater control incubations could finally be subtracted from the rates obtained from coral incubations. These rates were related to incubation volume and normalized to coral surface area. P_{gross} rates were calculated according to $P_{gross}=P_{net}+R$. As light R rates during active photosynthesis may be significantly higher than dark R rates (Fabricius and Klumpp, 1995), the presented P_{gross} rates are conservative estimates based on dark respiration rates.

After incubation, three polyps from each colony were cut off using clean scissors. The tissue material was washed four times with pure water to remove all salt before the samples were freeze-dried (Lyovac GT2/GT2-E, SRK Systemtechnik, Riedstadt-Goddelau, Germany) for dry mass measurement. For pigment extraction, 10 ml of 90% acetone was added and samples were stored in the dark for 24 h pending analysis. Total pigment contents of chl *a* and phaeophytin were measured by fluorimetry (TD-700, GAT-Gamma Analysentechnik, Bremerhaven, Germany) according to Holm-Hansen et al. (Holm-Hansen et al., 1965). After an initial measurement, 24 µl of HCl were added to the extract to convert chl *a* to phaeophytin followed by a measurement 2 min after. This procedure yielded the phaeophytin-free chl *a* content, which was finally normalized by *Xenia* tissue dry mass.

Data analysis

All statistical analyses were carried out using the Statistica software package (StatSoft, Hamburg, Germany). Prior to analyses, outlier values within the individual treatments were identified using

Dean–Dixon tests and data were tested for homogeneity of variance and normality using Levene and Shapiro–Wilk tests. If preconditions for parametric analysis were fulfilled, one-way ANOVAs were performed followed by Tukey's *post hoc* tests for between-group comparisons. If data did not meet parametric assumptions, non-parametric Kruskal–Wallis tests were used. The individual differences among the four groups were evaluated using Kruskal–Wallis multiple-comparison *Z*-tests with Bonferroni adjustment for multiple comparisons. All statistical tests were evaluated at an alpha level of 0.05.

RESULTS

OM fluxes

Table 1 provides an overview on DOC, POC and PN concentrations as well as POC:PN ratios in the incubation media measured at the end of all coral and seawater control incubations in non-nutrient-enriched aquarium seawater (means ± s.e.m.). Normalized flux rates (Fig. 1, means ± s.e.m.) calculated after subtraction of seawater control values revealed an uptake of DOC ($–4.8±2.1\,mg\,DOC\,m^{-2}\,h^{-1}$) and POM ($–0.315±0.161\,mg\,POC\,m^{-2}\,h^{-1}$, $–0.053±0.018\,mg\,PN\,m^{-2}\,h^{-1}$) by non-treated corals maintained for 4 weeks under non-nutrient-enriched conditions.

Exposure to elevated inorganic nutrient concentrations over 4 weeks significantly affected DOC fluxes by *Xenia* (Kruskal–Wallis test, H=8.28, d.f.=3, P=0.041; Fig. 1A). DOC fluxes of nutrient-treated corals were not significantly different from those of non-treated corals (Kruskal–Wallis multiple comparison, P>0.05), whereas differences between the nutrient treatments were evident. Analysis revealed significantly higher DOC uptake rates of N-treated ($–7.9±0.5\,mg\,DOC\,m^{-2}\,h^{-1}$; Kruskal–Wallis multiple comparison, P=0.042) compared with P-treated corals ($–2.6±0.9\,mg\,DOC\,m^{-2}\,h^{-1}$). DOC uptake of N+P-treated corals ($–7.4±1.2\,mg\,DOC\,m^{-2}\,h^{-1}$) also increased compared to P-treated corals, albeit this was not statistically significant (Kruskal–Wallis multiple comparison, P>0.05).

Inorganic nutrient exposure also affected POM fluxes as well as POC:PN ratios in the incubation water. After subtraction of seawater controls, significant differences in POM fluxes became evident for PN (Kruskal–Wallis test, H=10.01, d.f.=3, P=0.019), whereas no differences were found for flux rates of POC (Kruskal–Wallis test, H=3.12, d.f.=3, P=0.37; Fig. 1B,C). This revealed significantly enhanced PN release rates (Kruskal–Wallis multiple comparison, P=0.015) by P-treated corals ($0.052±0.023\,mg\,PN\,m^{-2}\,h^{-1}$) compared with non-treated corals ($–0.053±0.018\,mg\,PN\,m^{-2}\,h^{-1}$). In contrast, N ($–0.023±0.015\,mg\,PN\,m^{-2}\,h^{-1}$) and N+P ($0.002±0.004\,mg\,PN\,m^{-2}\,h^{-1}$) treatments exhibited no effect on PN fluxes (Kruskal–Wallis multiple comparison, P>0.05). The POC:PN ratio in the incubation water showed significant differences between the treatments (one-way ANOVA, F=13.95, d.f.=3, P<0.001; Table 1), with significantly reduced ratios in the incubation water of P-treated corals (7.3±0.4) compared with N-treated (9.2±0.3; *post hoc* Tukey's test, P=0.003), N+P-treated (8.8±0.4; *post hoc* Tukey's test, P=0.016) and non-treated corals (10.0±0.2; *post hoc* Tukey's test, P<0.001).

Physiological measurements

Chl *a* tissue content of non-treated *Xenia* colonies averaged $0.11±0.01\,\mu g\,chl\,a\,mg^{-1}$ tissue dry mass and was significantly affected after 4 weeks exposure to elevated inorganic nutrient concentrations (one-way ANOVA, F=19.77, d.f.=3, P<0.001). Compared with non-treated corals, P-treated ($0.22±0.02\,\mu g\,mg^{-1}$) and N+P-treated corals ($0.25±0.02\,\mu g\,mg^{-1}$) showed significantly higher chl *a* tissue content (*post hoc* Tukey's test, P<0.001), whereas the N treatment ($0.14±0.01\,\mu g\,mg^{-1}$) revealed no effect (Fig. 2). Comparison between the treatments showed significantly higher chl *a* content of P-treated (*post hoc* Tukey's test, P=0.003) and N+P-treated corals (*post hoc* Tukey's test, P<0.001) compared with N-treated corals.

Rates of P_{gross} averaged $21.6±2.2\,mg\,O_2\,m^{-2}\,h^{-1}$, and R rates were $9.3±0.5\,mg\,O_2\,m^{-2}\,h^{-1}$ for non-treated *Xenia* (Fig. 3). Exposure to elevated inorganic nutrient concentrations significantly affected *Xenia* P_{gross} (one-way ANOVA, F=8.84, d.f.=3, P<0.001) and R rates (one-way ANOVA, F=5.44, d.f.=3, P=0.007). Compared with non-treated corals, P-treated *Xenia* showed significantly higher P_{gross} ($40.8±3.6\,mg\,O_2\,m^{-2}\,h^{-1}$; *post hoc* Tukey's test, P=0.005) and R rates ($14.3±0.8\,mg\,O_2\,m^{-2}\,h^{-1}$; *post hoc* Tukey's test, P=0.033), whereas no significant change was observed for N-treated (P_{gross}: $17.6±2.9\,mg\,O_2\,m^{-2}\,h^{-1}$, R: $8.1±0.8\,mg\,O_2\,m^{-2}\,h^{-1}$) or N+P-treated corals (P_{gross}: $31.0±4.6\,mg\,O_2\,m^{-2}\,h^{-1}$, R: $12.0±2.0\,mg\,O_2\,m^{-2}\,h^{-1}$; *post hoc* Tukey's test, P>0.05). Among nutrient treatments, P_{gross} (*post hoc* Tukey's test, P<0.001) and R rates (*post hoc* Tukey's test, P=0.008) were significantly higher for P-treated than N-treated corals.

The P_{gross}/R ratio (Fig. 3) of non-treated corals (2.3±0.2) was nearly identical to that of N-treated corals (2.2±0.2). Although the P_{gross}/R ratio of P-treated (2.8±0.1) and N+P-treated corals (2.6±0.2) increased compared with non-treated corals, these differences were not statistically significant (Kruskal–Wallis test, H=3.78, d.f.=3, P=0.29).

DISCUSSION

Our results of laboratory-based incubation experiments involving specimens of the common soft coral *Xenia* provide the first information on OM flux rates by reef-associated soft corals, one of the key benthic groups in tropical coral reef environments. In addition to presenting flux rates of soft-coral-derived OM species (POC, PN and DOC) determined under non-nutrient-enriched control conditions, we show evidence for the significant effect of mid-term exposure (4 weeks) to enriched inorganic nutrient (ammonium and phosphate) concentrations complemented by integrated measurements of key physiological parameters (P_{gross}, R and chl *a* tissue content). These physiological findings confirm the significant effect of inorganic nutrient availability on OM fluxes and key metabolic processes for the soft coral *Xenia*, and provide

Table 1. Dissolved (DOC) and particulate (POC) organic carbon and particulate nitrogen (PN) concentrations as well as POC:PN ratios in *Xenia* incubation water and seawater controls measured at the end of beaker incubation experiments

Treatment	DOC ($\mu mol\,l^{-1}$)	POC ($\mu mol\,l^{-1}$)	PN ($\mu mol\,l^{-1}$)	POC:PN
P	277±15	20±2	2.82±0.29	7.3±0.4
N	241±6	18±1	1.98±0.13	9.2±0.3
N+P	234±7	19±1	2.17±0.04	8.8±0.4
Non-treated	272±23	17±2	1.69±0.18	10.0±0.2
Seawater control	319±36	20±2	2.16±0.21	9.3±0.2

Values are given as means ± s.e.m. of N=5–6 replicates.
P, phosphate addition; N, ammonium addition; N+P, combined ammonium and phosphate addition; non-treated, no inorganic nutrient addition.

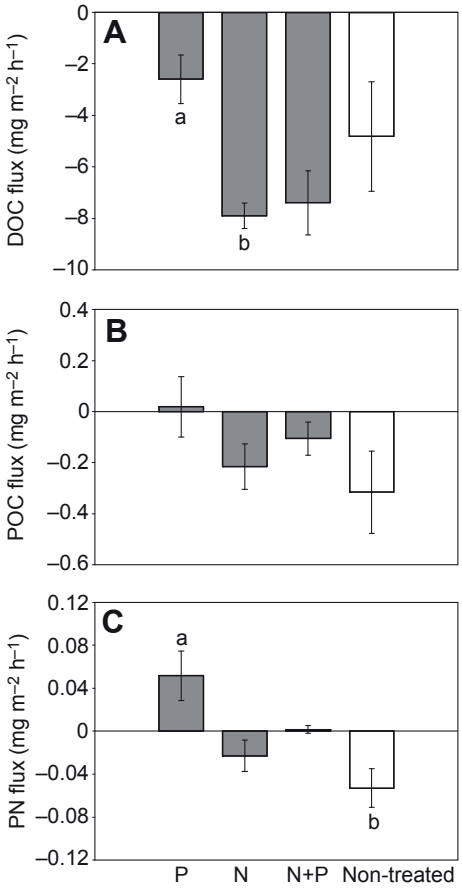

Fig. 1. (A) Dissolved (DOC) and (B) particulate organic carbon (POC) and (C) particulate nitrogen (PN) fluxes of nutrient-treated and non-treated *Xenia* corals. Values are given as means ± s.e.m. of *N*=5–6 replicates after seawater control correction (positive values indicate net release and negative values indicate net uptake). P, phosphate addition; N, ammonium addition; N+P, combined ammonium and phosphate addition; non-treated, no inorganic nutrient addition. Columns marked with 'a' are significantly different from columns marked with 'b' (one-way ANOVA, *post hoc* Tukey's test and Kruskal–Wallis multiple-comparison *Z*-test with Bonferroni adjustment, $P<0.05$).

the first insights into the contribution of soft corals to OM budgets within reef environments exposed to ambient and elevated inorganic nutrient concentrations.

OM fluxes under non-enriched inorganic nutrient conditions

Recent studies have advanced our understanding of OM release and uptake processes performed by scleractinian corals in tropical reef environments (Houlbrèque and Ferrier-Pagès, 2009; Naumann et al., 2010; Wild et al., 2004). However, these processes are still unexplored for reef-dwelling soft corals, including the common taxon *Xenia*. Corals of this genus possess a high abundance of mucocytes and harbor POM in their gastrovascular cavities, which indicates their physiological ability to both release and uptake POM from the surrounding seawater (Al-Sofyani and Niaz, 2007; Fabricius and Dommisse, 2000; Lewis, 1982). However, our findings revealed net POM uptake for *Xenia* colonies exposed to non-nutrient-enriched conditions. This stands in contrast to previously investigated benthic reef taxa (scleractinian corals, fire corals, reef algae and jellyfish) from the northern Red Sea showing net POM release under ambient inorganic nutrient concentrations

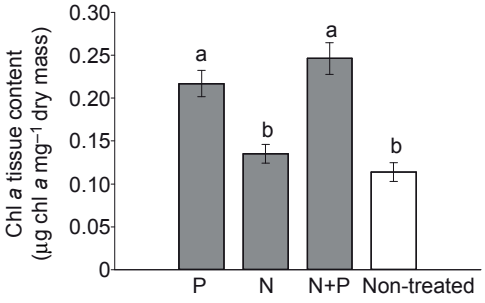

Fig. 2. Chlorophyll *a* (chl *a*) tissue content of nutrient-treated and non-treated *Xenia* corals. Values are given as means ± s.e.m. of *N*=6 replicates after seawater control correction. P, phosphate addition; N, ammonium addition; N+P, combined ammonium and phosphate addition; non-treated, no inorganic nutrient addition. Columns marked with 'a' are significantly different from columns marked with 'b' (one-way ANOVA, *post hoc* Tukey's test, $P<0.05$).

(Table 2). Coral-derived POM release fulfils important ecological functions *via* efficient particle trapping and by the concomitant recycling of energy and essential nutrients within the reef ecosystem (Wild et al., 2004; Wild et al., 2011). We therefore conclude that the soft coral *Xenia* may not contribute to ecosystem engineering *via* POM release as found for the majority of scleractinian corals.

Similar to POM fluxes, *Xenia* showed net DOC uptake under non-nutrient-enriched conditions. Uptake of DOC represents a common feeding mode in cnidarians and is known from numerous scleractinian taxa (Ferrier, 1991; Ferrier-Pagès et al., 1998; Naumann et al., 2010). Heterotrophic DOM uptake has been shown to contribute significantly to the daily metabolic demand of the zooxanthellate soft coral *Heteroxenia fuscescens* (Schlichter, 1982), and likely also represents an important carbon source for *Xenia*. In the present study, DOC uptake rates by *Xenia* (-4.8 ± 2.1 mg DOC m^{-2} h^{-1}) were in the range described for the scleractinian coral genera *Fungia* (-14.2 ± 5.5 mg DOC m^{-2} h^{-1}) and *Stylophora* (-14.1 ± 12.8 mg DOC m^{-2} h^{-1}), and for the jellyfish *Cassiopea* sp. (-1.2 ± 4.4 mg DOC m^{-2} h^{-1}) occurring in the northern Red Sea (Naumann et al., 2010; Niggl et al., 2010). Nevertheless, the majority of scleractinian corals as well as other benthic reef taxa investigated by previous studies net released DOC (Haas et al., 2010; Naumann et al., 2010; Niggl et al., 2010) (Table 2).

The observed differences in net OM fluxes between *Xenia* and several previously investigated scleractinian coral species may result from specific differences regarding each respective coral's nutrition. Soft corals are described to rely more on heterotrophic feeding due to their lower photosynthetic productivity compared with scleractinian corals. This has been demonstrated by lower P_{gross}/R ratios in soft corals (1.0–1.3) compared with scleractinian corals (2–4) (Fabricius and Klumpp, 1995; Mergner and Svoboda, 1977). In the present study, the P_{gross}/R ratio of non-treated *Xenia* corals (2.3±0.2) was higher than that previously described for soft corals (e.g. *Xenia* spp., *Efflatounaria* sp. and *Sarcophyton* spp.), but still in the lower range compared with scleractinian corals (e.g. *Pocillopora damicornis* and *Fungia scutaria*). Therefore, our findings indicate that *Xenia* may indeed be more dependent on heterotrophic carbon acquisition *via* OM uptake from the surrounding seawater compared with scleractinian coral taxa.

Enrichment effects on DOC fluxes

This study is the first to investigate the effect of single and combined elevated inorganic nutrient concentrations on DOC fluxes by corals

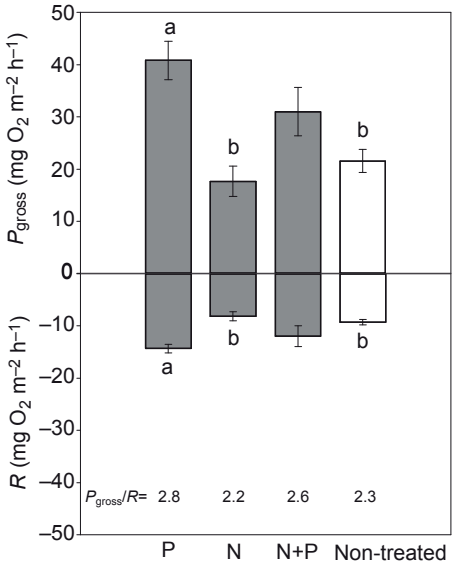

Fig. 3. Gross photosynthesis (P_{gross}) and respiration (R) rates of nutrient-treated and non-treated *Xenia* corals. Values are given as means ± s.e.m. of N=6 replicates after seawater control correction. P, phosphate addition; N, ammonium addition; N+P, combined ammonium and phosphate addition; non-treated, no inorganic nutrient addition. Columns marked with 'a' are significantly different from columns marked with 'b' (one-way ANOVA, *post hoc* Tukey's test, P<0.05). P_{gross}/R ratios are given for each of the specific treatments.

under controlled laboratory conditions. Only one previous study has looked at the effect of a combined addition of nitrate and phosphate (10 μmol l^{-1} NO_3^- and 0.5 μmol l^{-1} PO_4^{3-}) on DOM fluxes by the scleractinian coral *Montipora digitata* (Tanaka et al., 2010). Our results indicate increased DOC uptake in N-treated compared with P-treated *Xenia* corals after the 4-week exposure period. This increase may be attributed to the coral's metabolic activity, as P_{gross} rates in N-treated corals were significantly lower than those of P-treated corals. Lower P_{gross} rates in the N treatment may indicate that less carbon was available for translocation from zooxanthellae to the soft coral host (Ferrier-Pagès et al., 2000). Compared with the P treatment, N+P-treated corals showed no changes in P_{gross} rates or DOC fluxes, while non-treated corals exhibited reduced P_{gross} rates, without differences in DOC fluxes. Thus, we conclude that besides reduced P_{gross} rates in the N treatment, elevated ammonium concentrations were mainly responsible for stimulating DOC uptake. Under low ambient inorganic nutrient concentrations, zooxanthellae metabolism and growth are limited with respect to nitrogen, and carbon is photosynthetically fixed in excess. This surplus in carbon is translocated to the host together with small amounts of nitrogen (Muscatine et al., 1984; Stimson and Kinzie, 1991; Tanaka et al., 2006). At elevated inorganic nitrogen levels in ambient seawater, zooxanthellae are enabled to retain more carbon for their own metabolism and growth, and consequently less of it is being translocated to their host (Dubinsky and Jokiel, 1994). The coral may balance this carbon deficiency by increased heterotrophic DOC uptake from the surrounding seawater, as likely observed here. Tanaka et al. (Tanaka et al., 2010) found no change in DOC release rates normalized by surface area of *M. digitata* after exposure to elevated nitrate and phosphate concentrations, but DOC release decreased if related to chl *a* tissue content. Likewise, DON flux direction in the study of Tanaka et al. (Tanaka et al., 2010) changed from release (0.40±0.16 nmol DON cm^{-2} h^{-1}) to uptake (–0.32±0.17 nmol DON cm^{-2} h^{-1}). Like the mentioned change in DON flux direction, our findings of increased DOC uptake may result from the same physiological mechanism involving reduced carbon and nitrogen translocation from zooxanthellae to the host under excess inorganic nutrient supply. Ferrier-Pagès et al. (Ferrier-Pagès et al., 1998) demonstrated higher DOC release rates for fed than for starved specimens of *Galaxea fascicularis* and described DOM fluxes of corals as an indicator of their trophic status. In the present study, ammonium addition may have caused a nutritional status comparable to starvation due to reduced carbon supply *via* the zooxanthellae. Therefore, our findings suggest that *Xenia* most likely balances a resulting carbon deficiency by increasing DOC uptake.

Enrichment effects on POM fluxes

POM fluxes by *Xenia* corals were not affected in N and N+P treatments, but were mainly influenced by exposure to elevated phosphate concentrations. Under these conditions, PN release significantly increased compared with non-treated corals, and consequently caused decreased POC:PN ratios in the incubation water. Previous studies have shown that corals respond to change in environmental parameters, such as light intensity and temperature, by increasing rates of POM release to the surrounding seawater and/or by expelling their zooxanthellae endosymbionts (Brown, 1997; Brown and Bythell, 2005; Crossland et al., 1980). However, POM release by corals in response to variability in inorganic nutrient concentrations has only been described by one previous study. Naumann et al. (Naumann et al., 2010) found decreased POC and PN release rates in several scleractinian coral genera in response to seasonally increased nitrate concentrations (seasonal range: 0.14–0.83 μmol l^{-1} NO_3^-), whereas seasonal variability in concentrations of ammonium (0.21–0.31 μmol l^{-1} NH_4^+) and phosphate (0.03–0.07 μmol l^{-1} PO_4^{3-}) showed no effect. This is in contrast to our findings, but the results are hardly comparable, as *in situ* concentrations of ammonium and phosphate are obviously significantly lower in Red Sea reef waters than concentrations used for enrichment here (20.0 μmol l^{-1} NH_4^+ and 2.0 μmol l^{-1} PO_4^{3-}).

Table 2. Dissolved (DOC) and particulate (POC) organic carbon and particulate nitrogen (PN) fluxes for various classes of benthic reef organisms in comparison with non-nutrient-treated *Xenia* soft corals

Study site	Organism	DOC (mg m^{-2} h^{-1})	POC (mg m^{-2} h^{-1})	PN (mg m^{-2} h^{-1})	Method	Reference
Red Sea	Scleractinian coral	–20.7±21.2	2.8±0.3	0.29±0.03	Beaker	Naumann et al., 2010
Red Sea	Reef algae	14.5±2.3	5.1±0.5	0.35±0.03	Beaker	Haas et al., 2010
Red Sea	Fire coral	9.2±12.8	0.3±0.1	0.04±0.01	Beaker	Naumann et al., 2010
Red Sea	Jellyfish	–1.2±4.4	21.0±9.0	2.3±1.1	Beaker	Niggl et al., 2010
Laboratory	Soft coral (*Xenia*)	–4.8±2.1	–0.3±0.2	–0.05±0.02	Beaker	Present study

Rates are given as means ± s.e.m. for five scleractinian coral genera (*Acropora*, *Fungia*, *Goniastrea*, *Pocillopora* and *Stylophora*), nine benthic reef algae genera (i.e. *Caulerpa*, *Peyssonnelia* and turf algae), one hydrozoan genus (*Millepora*) and one scyphozoan genus (*Cassiopea*). Positive values indicate net release and negative values indicate net uptake.

We suggest that increased PN release within the P treatment may be strongly related to the observed physiological changes in the coral–zooxanthellae symbiosis, as P-treated corals revealed significantly higher P_{gross} rates and higher P_{gross}/R ratios than non-treated corals. Our calculated P_{gross} rates represent conservative estimates among all treatments, thus allowing an accurate treatment comparison of the physiological response to variable inorganic nutrient concentrations. Changes in P_{gross} rates and P_{gross}/R ratios can serve as indicators of the amount of photosynthates potentially available for translocation from zooxanthellae to the host (Ferrier-Pagès et al., 2000). Endosymbiotic zooxanthellae are the primary site for inorganic nutrient (e.g. ammonium and phosphate) assimilation from the surrounding seawater (Godinot et al., 2011; Grover et al., 2002) and play an important role in processes controlling the amount and composition of coral-derived OM release (Brown and Bythell, 2005). As up to 40% of net photosynthetically fixed carbon is released as mucus POC or DOC, increased photosynthesis in corals may consequently enhance POM release, as observed in the present study. Tanaka et al. (Tanaka et al., 2006) demonstrated that the carbon to nitrogen ratio of translocated photosynthetic products from zooxanthellae to the host decreases in response to elevated ambient inorganic nutrient concentrations. This may simultaneously affect the composition of OM released by the coral and is in line with our findings, which show significantly enhanced PN release and reduced POC:PN ratios in incubation media of P-treated corals. In contrast, P_{gross} rates in N- and N+P-treated corals remained unaffected, likely explaining why POM release by these specimens showed no detectable increase compared with non-treated corals.

Our data strongly indicate that the corals during experimentation were more limited by the availability of inorganic phosphate than by ammonium. Previously, it has been demonstrated that elevated ambient ammonium as well as phosphate concentrations may trigger a significant increase in photosynthesis, chl *a* tissue content and zooxanthellae abundance in several scleractinian species (Bucher and Harrison, 2000; reviewed by Davy et al., 2012; Dubinsky et al., 1990; Ferrier-Pagès et al., 2000; Godinot et al., 2011). Elevated P_{gross} rates by P-treated *Xenia* corals are most likely caused by increased chl *a* tissue content. If we assume a higher algae density in P-treated corals as a result of increased photosynthesis and chl *a* tissue content, *Xenia* may react to an overpopulation of zooxanthellae by expelling these cells into the surrounding water. Expulsion of algae from cnidarian hosts has been described as one primary regulator process for symbiont population density, as observed, among other anthozoans, in the soft coral *Xenia macrospiculata* (Baghdasarian and Muscatine, 2000; Hoegh-Guldberg et al., 1987; Stimson and Kinzie, 1991). As zooxanthellae generally posses a lower carbon to nitrogen ratio (5.9) than free-living phytoplankton organisms (6.6) (Belda et al., 1993), zooxanthellae expulsion may provide another explanation for the observed increase in PN release and the reduced POC:PN ratio found in the incubation water of P-treated corals.

Ecological implications

Our findings demonstrate that the soft coral *Xenia* shows no OM net release under oligotrophic conditions, while supplementary enrichment of inorganic nutrient concentrations only results in comparably minor to insignificant POM release rates. This is in contrast to the majority of previously investigated scleractinian coral, algae and jellyfish taxa releasing comparably high amounts of POM and/or DOM. In oligotrophic coral reef environments, usually dominated by scleractinian corals, the role of *Xenia* in biogeochemical OM cycles may thus generally represent a net sink for OM.

These findings are of special interest, as soft corals represent dominant taxa within the benthic community of many reefs, as well as major space competitors for scleractinian corals because of their ability to quickly colonize vacant reef substrate. Moreover, soft coral dominance over OM-releasing scleractinian coral taxa, as a consequence of local disturbances, has been documented from various global reef locations (Fox et al., 2003; reviewed in Norström et al., 2009; Tilot et al., 2008). Norström et al. (Norström et al., 2009) suggested that such shifts in benthic reef community composition, which coincide with a substantial decrease of scleractinian coral cover and loss of their important role as reef ecosystem engineers, are frequently associated with changes in the dynamics of bottom-up factors (e.g. inorganic nutrient enrichment). Taking this into account, our current findings strongly indicate that the important contribution of coral-derived OM release to biogeochemical element cycles may be greatly reduced under eutrophic conditions in reef ecosystems dominated by *Xenia* or other soft coral taxa, consequently causing a decline in coral ecosystem engineering with concomitant implications for overall ecosystem functioning (Wild et al., 2011).

Besides OM release, the three-dimensional reef framework built by scleractinian corals provides habitat for a highly associated biodiversity (Wild et al., 2011), while its biological and physical erosion generates calcareous reef sands acting as important biocatalytical filter systems, enhancing nutrient- and OM-recycling processes supported by an abundant heterotrophic microbial community (Wild et al., 2004; Wild et al., 2006). As soft corals only marginally contribute to calcareous reef accretion (Jeng et al., 2011), they are not a substitute for the scleractinian ecosystem engineering capacities, which consequently may not be sustained in soft-coral-dominated reef communities, likely resulting in ecosystem degradation. Nevertheless, *in situ* studies in scleractinian- and soft-coral-dominated reef ecosystems are required to increase our understanding of these dynamic processes and provide important insights into the potential changes of reef ecosystem functioning after phase shifts from scleractinian to soft coral dominance.

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