Master of Science
Course ***ISATEC***

Nutrient interactions between sponges and corals

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Presented to the University of Bremen, Faculty for Biology & Chemistry

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Bremen, August 2012

Universität Bremen

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AWI
Alfred-Wegener-Institut
für Polar- und Meeresforschung
in der Helmholtz-Gemeinschaft

Abstract

Corals are able to conserve and recycle inorganic nutrients in a generally nutrient poor environment due to their photosynthesizing symbionts. However it has been demonstrated that sponges are the main producers of nitrogenous nutrients in coral reefs contributing to a greater extent to the nutrient recycling than corals. The present study examined if sponges support corals in terms of nutrient supply. The study further investigated if sponges have an influence on the "well-being" of corals by releasing additional nutrients.

Corals and sponges were incubated separately and together in either artificial seawater or artificial seawater enriched with cyanobacteria and nutrients (ammonium and nitrate). Changes in dissolved inorganic nutrients, in total dissolved nitrogen and dissolved organic nitrogen as well as in dissolved and total organic carbon were measured and compared between the different treatments. Furthermore, particulate matter on filters of the water samples was analysed for its carbon and nitrogen contents and ratios. According to the carbon and nitrogen measurements, sponges ingested cyanobacteria while the carbon and nitrogen ratios of the corals are not indicative of a consumption of cyanobaceria. An accumulation of nitrate was detected when sponges alone were incubated in water enriched with cyanobacteria and nutrients. This accumulation was not found in incubations of corals alone. When both organisms were incubated together a slight elevation in nitrate and nitrite concentrations occurred. Besides, the maximum electron transport rate of the coral symbionts was significantly higher in the presence of a sponge. These results indicate that sponges are able to convert the added cyanobacteria to nutrients and that corals may directly benefit from the additional nutrients released by the sponges.

Key words: sponge-coral interaction, nutrient recycling, nitrogen

Acknowledgements

I would like to give special thanks to my first supervisor **Prof. Dr. Claudio Richter** for making all this possible and for his constant ideas and advice on this study.

I am grateful to my second supervisor **Prof. Dr. Christian Wild** for his willingness to support my work.

Moreover, I wanted to thank **Dr. Somkiat Khokiattiwong** and the whole **Thai team** (especially Jaa, Nueng, Eak, Ip and Lok) for their incredible help and the special time in Thailand. You were all so great!

A very special thank you goes to **Dr. Gertraud Schmidt** for all the great advices, feedbacks and help throughout the whole time. It would not have been possible without you. Thank you so much!

Besides, I want to thank **Dr. Thorsten Dittmar** and **Matthias Friebe** for making it possible to analyse all my DOC, TOC, POC, DON and TdN samples and the really nice working atmosphere.

A special word of thanks goes to **Cesar** and **Laura** for sharing this wonderful time in Thailand, for their help and driving :D. A special thank you goes to Cesar for introducing us into the Thai culture and the input, big help and assistance during my lab work.

I am also thankful to **Matthias Birkicht** for helping me to analyse my nutrient samples.

I would further like to express my thanks to the DAAD for their financial support.

Last but not least, I want to thank my family and amazing friends (especially Svenja, Eva, Sybille, Nicky and Cora) for supporting me, believing in me and always encouraging me. A special word of thanks goes to all the Polarstern people ☺. I am so happy that I got to know you all!

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1 Introduction

The understanding of nutrient and organic matter cycling in the face of climate change and increasing eutrophication is essential for the prediction of coral reef health. Most of the research done in this field focused on corals themselves though it is crucial to investigate the roles and functions of other organisms on the reef as well as their interactions with corals.

1.1 Nitrogen in Coral reefs

Coral reefs are one of the most productive ecosystems despite of low inputs of nutrients in reef waters (Odum and Odum 1955). This high production can be maintained due to the high retention efficiency of the material entering the system (Yahel et al. 1998; Pile et al. 1997) and the tight recycling of inorganic nutrients within the reef (Van Duyl and Gast 2001).
Nitrogen is one element of special interest since it represents a limiting nutrient in coral reefs (Badgley, Lipschultz, and Sebens 2006). Inorganic nutrients exist in reef waters in relatively low concentrations. Nitrogen concentrations range from 0.3 to 1 µmol/l for nitrate and from 0 to 0.4 µmol/l for ammonium (Bythell 1990; D'elia and Wiebe; Furnas 1991). Corals have the ability to efficiently take up ammonium and nitrate (Grover et al. 2002), but only the endosymbiotic algae can reduce nitrate to ammonium (Crossland and Barnes 1977; Miller and Yellowlees 1989). Thus scleractinian corals are able to conserve and recycle nitrogenous nutrients due to the support of their algal symbionts (Cook 1983). Corals that are well supplied with nutrients will maintain higher photosynthetic efficiencies and an increased maximum rate of photosynthesis. Besides they will have higher zooxanthellae densities, higher mitotic indices and higher chlorophyll a concentrations per algal cells (Titlyanov et al. 2001; Houlbrèque et al. 2003; Borell and Bischof 2008).
Moreover, the symbionts supply the corals with photosynthetically fixed carbon but the photosynthates are deficient in phosphate and nitrogen which therefore have to be acquired through heterotrophic feeding (Ferrier-Pagès et al. 2011). There are three different forms of heterotrophic feeding of corals. First, the ingestion of either suspended detrital particulate organic matter (POM), POM trapped in sediment (Mills and Sebens 2004), or in form of mucus (Wild et al. 2004a); second, the uptake of dissolved organic matter, such as carbohydrates, urea and dissolved free amino acids, via active transport (Grover et al. 2006;

Grover et al. 2008) and third and most important the capture of live organic matter (LOM). Corals are able to capture particles through tentacle grabbing, nematocyst discharges or via mucus adhesion (Muscatine 1973). Zooplankton is a major food source of corals and they are capable of feeding on 20-80% of the oncoming zooplankton (Glynn 1973). However zooplankton comprises the smallest part of biomass within the planktonic community (Ducklow 1990; see also figure 1).

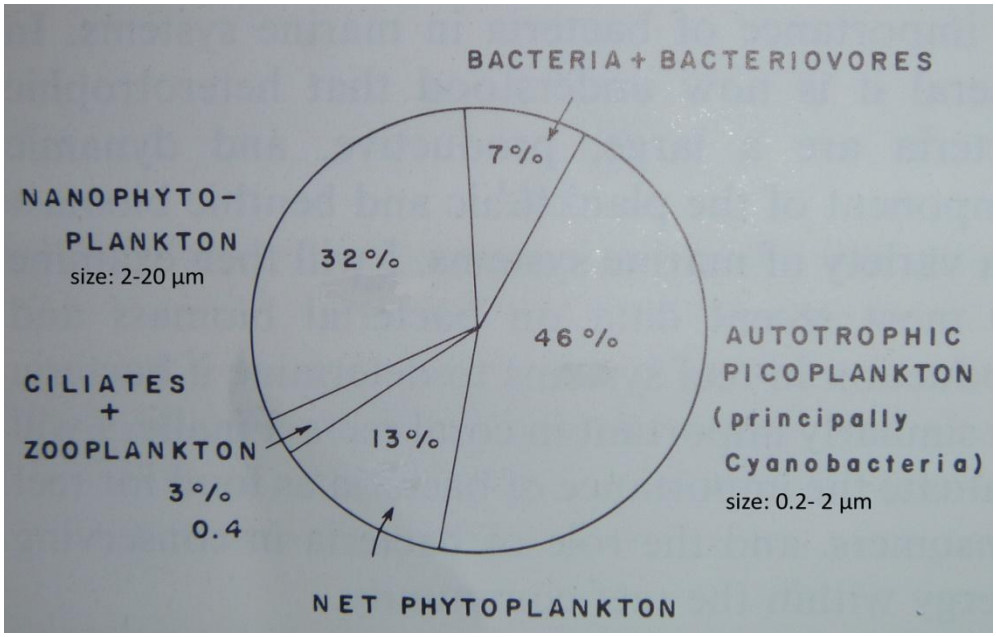

Fig. 1: The graph modified from Ducklow (1990) shows the carbon biomass composition within the planktonic community of coral reefs.

In coral reef ecosystems, picophytoplankton accounts for 80% of total chlorophyll a and phytoplankton biomass as well as 70% of the total primary production (Li and Harrison 2001; Marañón et al. 2001) with cyanobacteria as one of the most important groups. The chroococcoid cyanobacteria *Synechococcus* is hereby the most important organism, contributing to 90% of the picoplankton biomass (Charpy 2005). It is known that filter-feeders subsist on this minute particulate food (Richter et al. 2001) but it was long disregarded as a possible food source for other benthic reef taxa, such as corals, due to its small size and the absence of specific capture mechanisms. The first evidence that corals are also able to feed on picoplankton came from a study of Fabricius et al. (1995) which showed that the diet of four soft corals in the Red Sea is mainly composed of phytoplankton. They

were able to detect picoplankton cells in the gastrovascular cavities of the soft coral polyps though the capture mechanisms were not completely understood.

A growing number of studies (Ayukai 1995; Houlbreque et al. 2004; Wild et al. 2004a; Naumann et al. 2009) revealed that even scleractinian corals are able to feed on picoplankton. Naumann et al. (2009) demonstrated that picoplankton could be removed by corals by using their mucus floats as a trap. They could detect a significant difference in *Synechococcus* enrichment of mucus aggregates compared to the surrounding sea water. Besides, it is assumed that these mucus aggregates can be captured as well and consumed by other benthic reef taxa.

1.2 Importance of other reef organisms

Particle feeding by the benthic community is considered to have great effects on bentho-pelagic processes (Yahel et al. 1998; Pile et al. 1997; Ribes et al. 2005).

Especially sponges are important functional and structural members in the coral reef system, exceeding corals species even in terms of biomass in certain areas (M. C. Diaz and Rutzler 2001). They belong to the most efficient optimal foragers on account of the low energetic costs of their filter-feeding activities. Riisgaard and Larsen (1995) reported that their pumping in relation to the respiratory output accounts for solely 0.8%.

Moreover, they are known to act as key grazers in many marine and freshwater environments (Pile et al. 1997; Richter et al. 2001; Ribes et al. 2005) due to their ability to filter large volumes of water (up to 100.000 times their own volume per day; Weisz 2006). Additionally, they are able to feed on a wide spectrum of prey including phyto- and nanoplankton, dissolved organic matter and bacteria (Reiswig 1971; Yahel et al. 2003). Ribes et al. (2005) detected that the removal of particles <2µm is directly related to the cover of ascidians and sponges and not to the growth of corals. Furthermore, it could be demonstrated that plankton- depleted water layers developed over the benthos of the lake Baikal (Pile et al. 1997) or over coral reefs due to filter-feeding activities by sponges (Yahel et al. 1998; Richter et al. 2001).

Furthermore, they may have symbiotic associations with phototrophic (Wilkinson 1983), methanotrophic (Vacelet et al. 1995) and chemosynthetic microorganisms (M. Diaz and Ward 1997; Hoffmann et al. 2005) which enables them to gain energy from additional

sources. It is even reported that they have the ability to distinguish between symbiotic and food bacteria (Wilkinson, Garrone, and Vacelet 1984) and that they ingest food selectively after capturing (Yahel, Eerkes-Medrano, and Leys 2006). They may not actively pick out their food cells but it is hypothesized that some cells could resist the degradation and pass through the food vacuoles intact (Van Donk et al. 1997).

1.3 Role of sponges in nitrogen cycling on coral reefs

Several studies demonstrated that sponges are the first animals that release considerable amounts of ammonia, nitrate and nitrite and contribute in this way to a far greater extent to the recycling of nitrogen within coral reefs than corals (Corredor et al. 1988; M. Diaz and Ward 1997; Jiménez and Ribes 2007; Melissa W. Southwell, Popp, and Martens 2008). Nitrification in sponges is the result of combined activities of aerobic sponge cells, heterotrophic bacteria and cyanobacteria (Corredor et al. 1988; M. Diaz and Ward 1997; Melissa W. Southwell, Popp, and Martens 2008). The organic matter filtered by sponges is metabolized by sponge cells and bacteria to amino nitrogen which is later on assimilated and released as ammonium. This ammonium in turn is oxidized to nitrate by nitrifying bacteria (M. Diaz and Ward 1997).

In fact, their nitrification rates (up to 12±2.2 mmol N* m^{-2}*d^{-1}, Corredor et al. 1988; Diaz and Ward 1997) exceed by far those calculated for coral reef sediments (1.68 mmol N* m^{-2}* d^{-1}, Capone et al. 1992) and temperate continental shelf sediments (2.1mmol N* m^{-2}* d^{-1}, Hopkinson, Giblin, and Tucker 2001).

The multifold ways of food- procurement of both sponges as well as corals and the fact that the abundance of sponge species in coral reefs is further increasing while that of corals declines (Hoegh-Guldberg 1999; Wilkinson and others 2000; Szmant 2002; Alcolado et al. 1994; Zea et al. 1994) imposes to study their interactions in terms of nutrient supply more closely.

Possible reasons for the shift in species composition might be that sponges can cope better with higher sediment exposure and are able to thrive in slightly eutrophicated areas (Alcolado et al. 1994; Zea et al. 1994). On account of this it might be expected that the role of sponges and their interactions with corals in coral reef systems may become considerably more important under present days´ increasing anthropogenic disturbances.

1.4 Research question, hypotheses and objectives

Based on the facts mentioned above, the question arises if sponges and corals are competing for food sources or if sponges might help corals in terms of food supply. To answer this question, the following study consisted of three different incubation experiments. Initially solely corals, subsequently only sponges and finally both sponges and corals were incubated together.

The study was based on the hypothesis that sponges influence the dissolved inorganic nutrients (DIN: NH_4,NO_x) speciation in the water column and thereby regenerate large quantities of nitrogen for the reef. In order to test this hypothesis the contribution of *Cacospongia sp.* to the nitrogen cycling was quantified by measuring the changes in dissolved inorganic nutrients, changes in dissolved and total organic nitrogen (DON/TON), changes in dissolved and total organic carbon (DOC/TOC) and changes in the C/N ratio of the cyanobacterial cells. On the basis of the relation of carbon and nitrogen content on the filters it can be determined if grazing on cyanobacterial cells occurred.

Besides, it was investigated if *Cacospongia sp.* was capable of nitrification due to detecting an accumulation of nitrate during the incubations.

Moreover, the study aimed to demonstrate that sponges influence the “well-being” of corals by introducing them to a food source they would not be able to exploit to a greater extent by themselves. In order to examine this hypothesis, it has been tested if corals use the waste material released by the filter feeding activity of sponges. This was accomplished by comparing the nutrient uptake and the change in DOC/TOC, DON/TON and changes in C/N ratio of cyanobacterial cells of corals alone and in the presence of a sponge. Besides, the coral tissue was analysed as well. Furthermore, the photosynthetic efficiency and the maximum rate of photosynthesis were measured and compared before and after the incubations of the corals alone and the corals together with sponges by pulse amplitude modulated (PAM) fluorometry.

2 Materials and Methods

2.1 Study site

The present study was conducted at the Phuket Marine Biological Center (PMBC), Thailand (latitude: 7°48`1.09”N, longitude: 98°24`32.37”E). The PMBC is located at the southern end of Phuket Island on the promontory Laem Panwa at the Andaman Sea coast.

Sponges for experiments were collected from the bay of the Radisson Plaza Resort (latitude: 7°48`37.14”N, longitude: 98°24`11.35”E) situated in the vicinity of the PMBC (Fig. 2). The reef represents a typical fringing reef with a distinct zonation (wide reef flat, narrow reef edge and reef slope) and a lagoon. The lagoon is composed of a sea-grass bed, followed by a sandy reef edge with coral patches and finally the reef slope. The bay is subjected to a semi-diurnal tide (maximum tidal range: 2.8-3m during spring tides) which causes the reef flat, reef edge and parts of the reef slope to be completely exposed to the air during low tide.
High loads of sediment can be found in the bay which causes increased water turbidity.
Sponges of the genus *Cacospongia sp.* of various size classes grow within the coral patches in the reef edge and in the reef slope. They are often situated in the immediate vicinity of corals of the family *Faviidae*.

The Island of Ko Racha (latitude: 7°35`51.51”N, longitude: 98°21`58.47”E) is situated approximately 18 km south from the peninsula of Phuket. The reef in front of the Ban Raya Resort on the eastern side of the island holds certain spots in depths of 4 to 8m which are densely covered by fungiid corals (Fig. 5). All *Fungia* spp. polyps used in this study were collected from these densely covered locations.

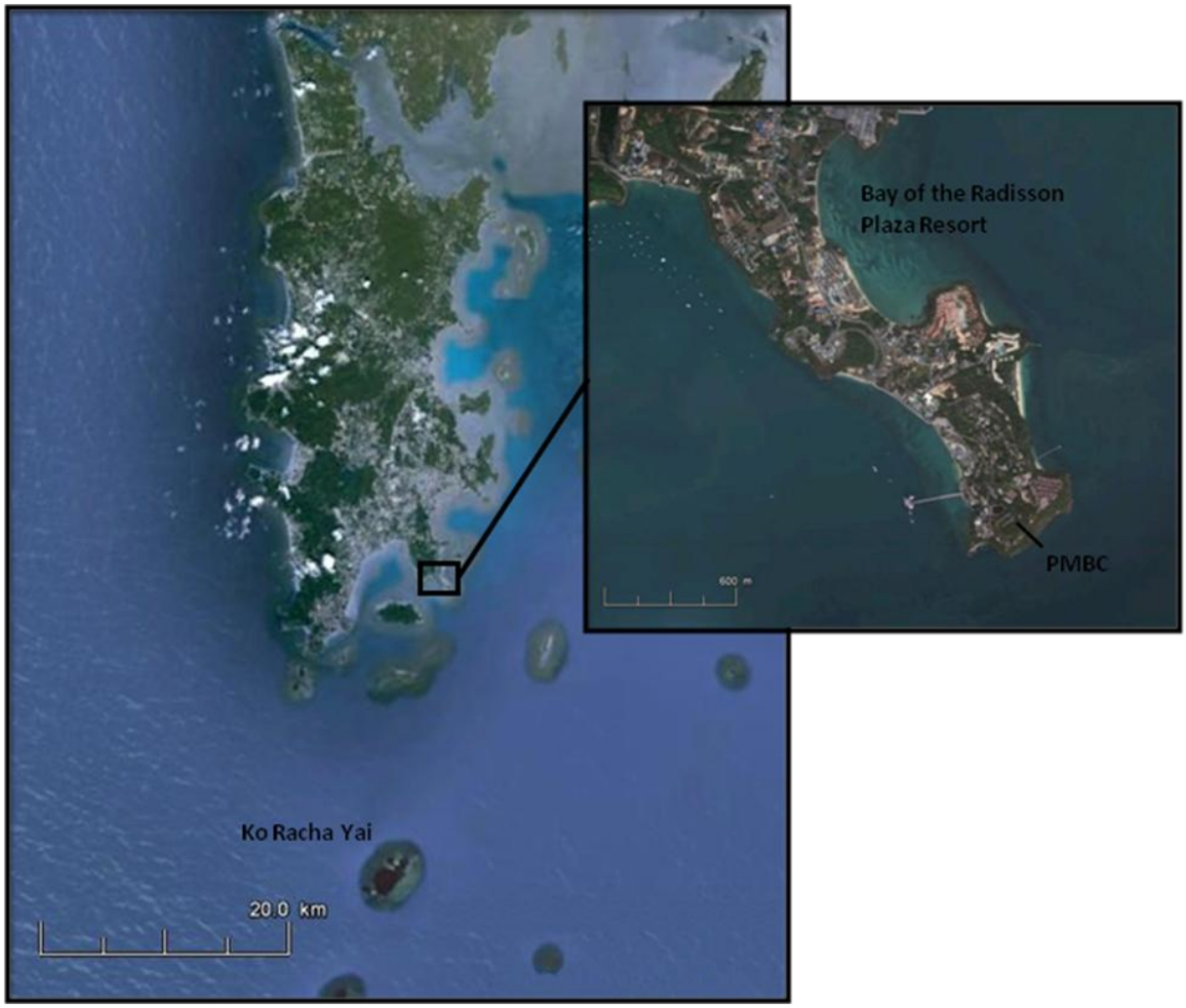

Fig. 2: On the left side: Overview of the island of Phuket and the position of Ko Racha. On the right side: close-up of Laem Panwa illustrating the location of the Phuket Marine Biological Center (PMBC) and the bay of the Radisson Plaza Resort (Google Earth 2012).

2.2 Sampling of sponges and corals

Sponges of the species *Cacospongia sp.* were collected from the bay in front of the Radisson Plaza Resort. At low tide, the bay is completely exposed so the sponges could be spotted easily by walking around. Sampling took place at low tide when the sponges were still covered with water. Two equal pieces were cut out from each sponge individual (n = 20) and attached to acrylic plates (6x6 cm) with plastic cable ties (Fig. 3a).

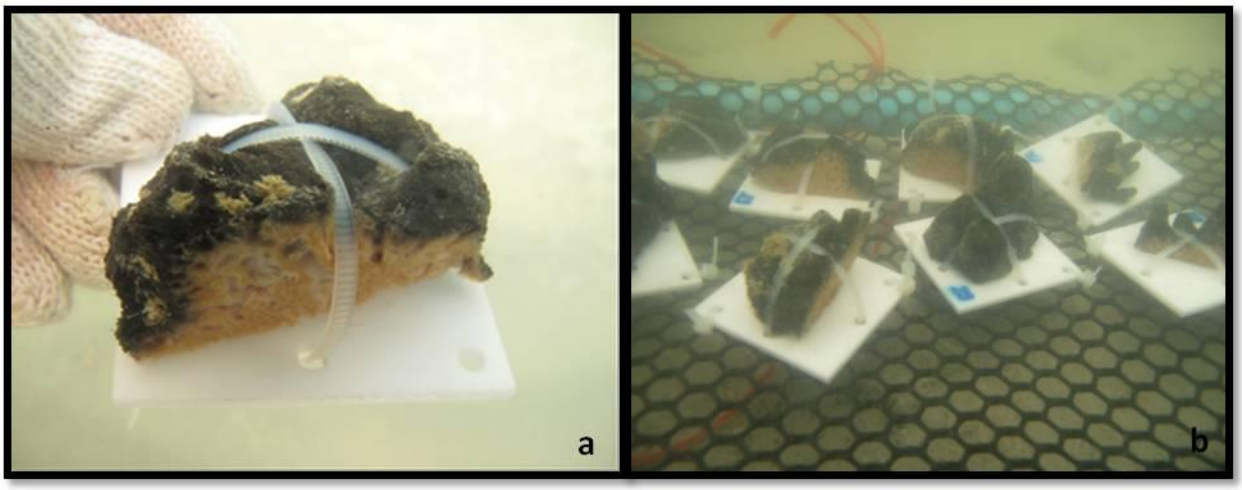

Fig. 3a and b: Sponges have been attached to acrylic plates with cable ties (a) and fixed subsequently to PVC racks (b).

The sponge pieces were at no time exposed to the air. The plates were fixed to PVC racks on the reef by snorkeling and left there for at least 5 weeks in order for the sponges to recover from the handling stress and to develop new tissue (Fig. 3b).
Healed sponges for experiments were collected after 5 to 8 weeks and taken to the aquaria facilities at the Phuket Marine Biological Center (PMBC).

Hard coral polyps of the genus *Fungia* were collected by SCUBA from the reef of the Ban Raya Resort at depths of 4- to 8 m (Fig. 4). After their removal, they were stored in water filled boxes until the arrival at the PMBC, where they were transferred into the rearing aquaria. The advantages of conducting experiments with this coral species are that every organism represents one solitary, free living polyp. Fungiids are among the largest known hard coral polyps (Hoeksema et al. 1989). Hence, they can be sampled without any

mechanical damage to the surrounding reef. Furthermore, the corals can be used as a whole and no fragments have to be broken off which influences the nitrogen uptake (Muscatine and D'elia 1978).

The diameter of all polyps was measured and digital photos for species identification were taken with a Panasonic Lumix DMC-FT10 digital camera. Species identification was conducted based on the book "Corals of the World" (Vernon 2000). The identification revealed that 4 species within the corals were used for the experiments: *Fungia repanda* (12x), *Fungia fungites* (10x), *Fungia cocinna* (1x) and *Fungia granulosa* (1x).

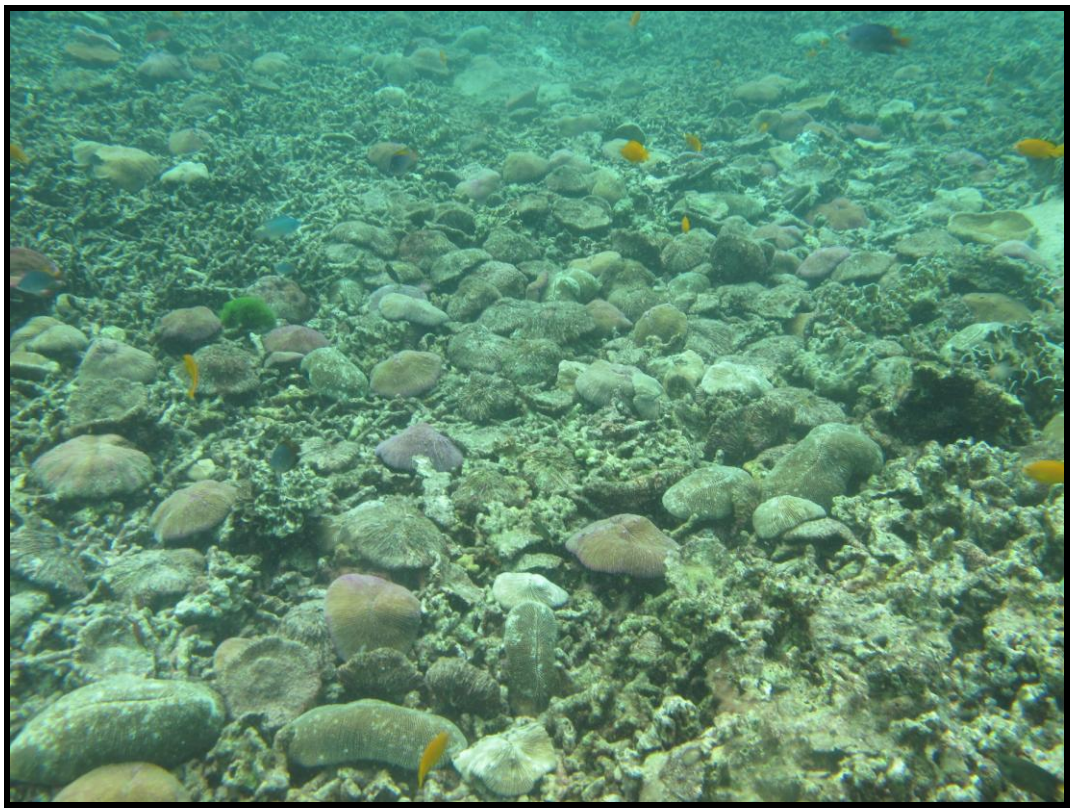

Fig. 4: Reef at the east side of Racha Island densely covered by fungiid species (depth: 5m).

2.3 Culturing conditions of sponges and corals

The sponges and corals were maintained in a flow-through system at the facilities of the PMBC. Water was pumped from the bay next to the institute and filtered before arriving to a 100 l tank. In this tank the running seawater was constantly supplied with oxygen by air bubbling. From there, the different basins with the organisms were provided with a continuous water supply by passive flow (gravity controlled).

The flow-through system consisted out of 6 basins (48x33x19 cm), 4 or 5 of them contained individuals of fungiids and 1 or 2 the sponges (Fig. 5). The corals received a constant water flow at a rate of 29.65 ± 4.77 l h^{-1} and the sponges of 103.47 ± 9.84 l h^{-1}.

Fig. 5: The flow- through system with corals and sponges.

A 12 h day and night cycle was reproduced with metal halide lamps (5000W). Irradiance levels in PAR (photosynthetically active radiation; µmol quanty m^{-2} s^{-1}) were controlled regularly with a pulse amplitude modulated (PAM) fluorometer (diving PAM, Walz GmbH, Effeltrich, Germany). Values fluctuated between 51 and 91 µmol m^{-2} s^{-1} for the corals and

72 – 112 µmol m^{-2} s^{-1} for the sponges. The temperature in the different basins was monitored every 3 minutes by TidbiT v2 temperature loggers (Onset Computer). The mean temperature in the basins was 28.78 °C ± 0.89 with single peaks exceeding 30 °C due to sporadic irregularities in the flow-through system. Oxygen levels were monitored as well on a regular basis by using a YSi ProODO sensor (eco Tech Umwelt-Meßsysteme GmbH, Bonn, Germany) for dissolved oxygen and ranged between 189.76 and 217.92 µmol l^{-1}.

Corals were fed once a week with *Artemia* nauplii until 3 days before the experiments started since feeding interacts with nitrogen uptake (Muller-Parker et al. 1988; Grover et al. 2002).

2.4 Cultivation of cyanobacteria

Picoplanktonic chroococcoid cyanobacteria of the genus *Synechococcus* were selected for the experiments. Specific clonal strains were ordered from Roscoff Culture Collection (RCC, France) and cultivated in nitrate-enriched liquid ASN III/2 (artificial seawater nutrients; table A. 1) medium which had been adjusted to the local seawater salinity values prevailing in Thailand (salinity ≈ 33 ‰). The main components of the ASN III/2 medium were added separately to a basis of deionized water until a solution was obtained and stocked up to 1 l. The trace metal solution, a further additive, was prepared separately. Vials for maintaining cyanobacteria and media composition were autoclaved at 121 °C for 30 min. All media components were autoclaved at 120 °C for 20 min (Drath 2008).

Final composition was carried out under a flame hood after cooling to 21 °C. Cultivation took place in Erlenmeyer flasks at ambient temperature and light intensity of approximately 60 µmol m^{-2} s^{-1} (12 and 12 h light and dark cycle). The addition of 50 – 100 ml of fresh media took place twice a week.

From the *Synechococcus* strains brought to Phuket RS 9909 (RCC 2383), RS 9916 (RCC 555) from the Red Sea and OLI031FJ (RCC 44) from the Pacific Ocean were selected due to their good growth performance under the local laboratory conditions.

2.5 Experimental design

After at least 1 week of acclimatization to the aquarium system for the corals and 5 days for the sponges they were used for the experiments. Solely sponges with healthy appearance (i.e. no visible wounds or decay, open oscules, regeneration of cut tissue) were selected for the incubation experiments. All vials, chambers, aquaria, syringes and filters in contact with the artificial seawater were pre-washed twice with 0,4 M hydrochloric acid and once with deionized water.

The selected organisms were incubated for 5 h in 3 identical glass aquaria (45x30x45 cm) filled to a water volume of 40 l with artificial seawater (Fig. 6 a). Small plastic chambers (25x15x20 cm) were placed inside these glass aquaria. One side of these plastic aquaria consisted of a perforated plate and had a flow pump (Turbelle® nanosteam® 6025 or 6055, Tunze Aquarientechnik GmbH, Penzberg, Germany) installed on its opposite side (Fig. 6 b).

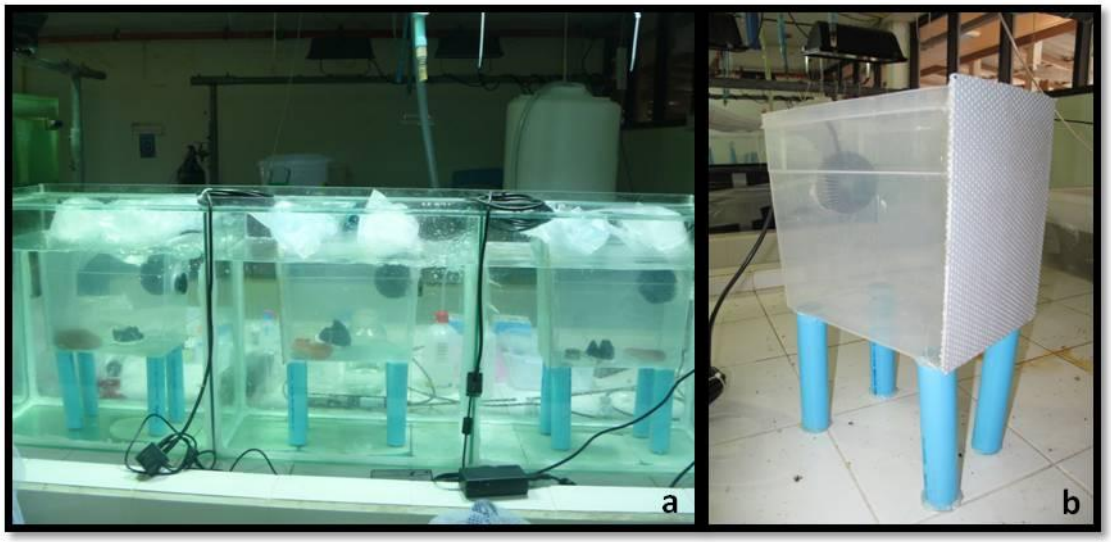

Fig. 6a and b: The 3 glass aquaria with the plastic chambers and experimental organisms (a). One of the plastic chambers in detail (b) with the flow pump on one side and the perforated plate on the opposite.

Within the plastic aquaria a laminar flow was maintained over the sponges and corals inside. Care was taken that the water level did not exceed the plastic aquaria since this would have caused a disturbance of the laminar flow. Accordingly, the plastic aquaria were placed on 4 stakes in order to keep the water level in the glass aquaria below the edge of the plastic aquaria.

Tab. 1: The experimental set-up of the incubations.

	Sponges	Corals	Sponges + Corals
NH_4 + NO_3 and Cyanobacteria	6	6	6+6
Control	6	6	6+6

The whole experiment was divided into 3 experimental runs. In the first two runs corals and sponges were incubated separately with either artificial seawater or artificial seawater enriched with cyanobacteria and nutrients (ammonium NH_4 and nitrate NO_3). In the third run, both, sponges and corals, were incubated together. Experiments for all species were conducted in the end of January and beginning of February 2012 in each case between 9:30 am and 07:00 pm.

The artificial seawater was always prepared in the evening before the start of the experiments in a 200 l container using drinking water (S.P.A Drinking Water CO., LTD). Red Sea Salt was added until the desired salinity of 32 - 34 ‰ was reached (Yanagi et al. 2001; Buranapratheprat et al. 2002). The nutrient solutions were prepared in the morning of the experimental day. On that account, 0,102 g $NaNO_3$ and 0,064 g NH_4Cl were dissolved in a small amount of drinking water to reach a final concentration of 30 µmol NH_4^+ and 30 µmol NO_3^- in the experimental chambers, respectively. These unnaturally high concentrations were chosen to observe the potential for nitrogen uptake in sponges and corals.

Before the organisms were placed in the experimental set-up, they were transferred in a separate basin which was filled and flushed with artificial seawater in order to ensure that the artificial seawater did not get contaminated. Additionally, the corals were dark adapted before and after the experiments for 30 minutes and rapid photosynthetic versus irradiance curves were measured by pulse amplitude modulated (diving PAM) fluorometry.

Before corals and sponges were placed in the aquaria water samples were taken to check for a potential contamination of the artificial seawater or the glass aquaria.

Corals and sponges were left for 1 hour in the experimental set up before the start of the incubation in order to allow them to acclimate to the new flow regime and to recover from the relocation stress. Incubations were only started when the oscules of the sponges were open and the fungiids showed their tentacles extracted since retracted tentacles and closed oscules are an indicator for stress and disturbance (Reiswig 1971; Reiswig 1974; Southwell 2007; Ginsberg 2008).

Subsequently, the experiments were started immediately or after spiking the system with a nitrate and ammonium solution to achieve the desired concentration of 30 µmol l^{-1} and 100 ml of cyanobacterial cells. Zero time samples for nutrients and cyanobacteria were taken in order to determine the initial concentrations. Uptake rates were calculated from the change in nitrate, ammonium and cyanobacterial cell concentration following the 1 h acclimation period.

The parameters measured over time were temperature, dissolved oxygen, dissolved organic carbon (DOC), total organic carbon (TOC), concentration of cyanobacteria and dissolved inorganic nutrients. Water samples (150 ml) were collected in plastic syringes and filtered immediately through Whatman^{TM} GF/F glass fiber filters (25 mm diameter, 0.7 µm pore-size). The samples were taken from the water column and from the oscules of the sponges if sponges and corals were incubated together. The velocity of sample taking was 2 ml 4 s^{-1}. Concentrations of cyanobacteria were quantified at time 0, 15, 30, 60 and 300 minutes. All other parameters were analyzed at time 0, 30, 60, 300 and 500 minutes. Temperature was recorded every 3 minutes using TidbiT v2 temperature loggers. Care was taken to ensure that the temperature never exceeded 30°C. For this reason frozen water bottles were wrapped in hydrochloric acid rinsed zip blocks and put into the glass aquaria. The light intensity varied between 52 and 109 µmol m^{-2} s^{-1}.

At the end of each incubation run, photographs were taken of each specimen and the surface area of the corals and the dryweight of the sponges were determined for later normalizing the uptake and/or release rates to surface area or dryweight. For this purpose, the sponges were dried at 60 °C for at least 48 h until their weight remained constant (Trussell et al. 2006; Weisz et al. 2008). The surface area of corals was measured based on the diameter of the nearly circular shaped *Fungia* corals (Naumann 2005) and the coral tissue analysis took place at the AWI in Bremerhaven. The surface area of sponges was

calculated by means of height, length and width assuming a rectangular geometry since this geometrical shape describes the form of the sponges the best (Weisz et al. 2008).

2.6 Nutrient analyses

Water samples for nutrient analysis were collected in acid-rinsed 60ml PP (polypropylene) bottles and kept frozen at -20°C until further analyses. The nutrient analyses were performed at the PMBC by manual methods and at the Leibniz Center for Tropical Marine Ecology (ZMT, Bremen, Germany) with a San^{++} Continuous Flow Analyzer (CFA; SKALAR, Breda, The Netherlands). The adding of reagents and heating, in the case of ammonium measurements, were performed in a closed tubing system between inlet and photometer (NO_x) or fluorometer (NH_4). The sample stream of the continuous flow analysis was segmented into subsamples by injecting air. Before entering the detection cell, the air bubbles were guided into the waste outlet via a de- bubble- device. The peaks and the resultant concentrations were detected with the Skalar software Version 2.0. The methodology of analyzing, nitrate, nitrite was according to (Grasshoff et al. 1983) and the one for ammonium according to Aminot et al. (2001). MOOS-2 (Cape Breton Island, NS, Canada; http://www.nrc-cnrc.gc.ca/obj/inms-ienm/doc/crm-mrc/eng/MOOS-2_e.pdf) was used as a certified reference material in order to verify the precision and accuracy of the measurements.

For all measurements standards were prepared by the volumetric dilution of a stock solution containing 1000 mg l^{-1} nitrate, nitrite or ammonium, respectively.

2.6.1 Determination of Nitrite (NO_2^{2-})

An aliquot of 10 ml water sample was taken for the nitrite analysis. The determination of Nitrite is based on the reaction of the nitrite ion with an aromatic amine (sulfanilamide hydrochloride) resulting in the formation of a diazonium

compound. This diazonium compound subsequently couples with a second aromatic amine (N-(1-naphthyl)- ethylendiamine) producing an azo dye with a deep red colour. The nitrite concentration was be quantified via a Perkin Elmer Lambda 25 spectrophotometer with a 1000 µl semi-micro cell quartz cuvette (Hellma 108-QS Quartz SUPRASIL) at a wavelength of 540 nm (Rand et al. 1976).

2.6.2 Determination of Nitrate (NO_3^-)

The methodology for analyzing nitrate was modified from the nitrate-nitrite reduction method of Rand et al. (1976). Ammonium chloride solution was added as a buffer to 50 ml of the water sample. Thereupon the water sample had to run through a cadmium micro reductor column. This column consisted of a glass tube containing pre-sieved 63 micron grained-size copper-coated cadmium granules. A peristaltic pump was connected to the reductor column which moved the water sample over the cadmium granules. The granules were used to reduce nitrate to nitrite. The first 35 ml were used for cleaning the column and discarded.

The concentration of inorganic nitrate was quantified by applying the methodology for the nitrite analysis.

2.6.3 Determination of Ammonium (NH_4^+)

For the determination of ammonium an aliquot of 20 ml water sample was required. The analysis of ammonium was based on its reaction with alkaline phenol and hypochlorite under alkaline conditions resulting in the formation of indophenol blue. Trisodium citrate solution was added as a buffer before the addition of hypochlorite. The blue colour was further intensified through the addition of sodium nitroprusside.

The blue indophenol complexes were formed as a final product after an incubation period overnight, of at least 6 h but not exceeding 30 h, stored in a light protected box at an ambient temperature of 25 °C.

The amount of ammonium was measured with a Perkin Elmer Lambda 25 spectrophotometer with 1000 µl semi-micro cell quartz cuvette (Hellma 108-QS Quartz SUPRASIL) at a wavelength of 630 nm (Rand et al. 1976).

2.7 Analysis of dissolved organic carbon (DOC), total organic carbon (TOC) and total dissolved nitrogen (TDN)

Water samples were taken directly out of the incubation chambers with an acid- washed polycarbonate syringe. Aliquots of each 10 ml were collected in pre-combusted (5 h, 550 °C) glass vials. TOC samples were directly transferred into the glass vials whereas samples for DOC were first filtered through a 0.7 µm pore-sized pre-combusted Whatman^{TM} GF/F glass fiber filter (4 h, 450 °C). Subsequently, samples were acidified to pH 2 with HCl (10 M) and straightaway closed with screw caps which had been sterilized for 7 d in an acidic solution (pH = 2). Afterwards, samples were immediately frozen and stored at -20 °C.

Samples were defrosted and stored at 4°C prior to analysis at the Max Planck Research Group for Marine Geochemisty (Oldenburg, Germany) with a Shimadzu TOC-V_{CPH} analyzer. L-Arginin served as standard for both DOC and TDN measurements (Dittmar, instructions and pers. communication). In addition to the standard a deep seawater reference material from the Consensus Reference Material Project (CRM http://yyy.rsmas.miami.edu/groups/biogeochem/CRM.html) was employed in order to determine the precision and accuracy of the measurements. The DOC/TOC and TDN concentrations of the consensus material were 41-44 µmol DOC/TOC and 31-33 µmol TDN, respectively.

2.8 Carbon and nitrogen ratio analysis

The changes in carbon and nitrogen content were calculated by the Elemetaranalyzer Euro EA 3000 (HEKAtech GmbH, Wegberg). Once the water samples (V = 100 ml) had been taken and filtered, the GF/F filters were frozen and stored at -20 °C until further analysis. Filters were dried for 24 h at 40 °C. Afterwards they were wrapped in tin capsules (10x10 mm; IVA Analysentechnik e.K., Meerbusch) and their nitrogen and carbon content was determined with the Callidus^{TM} Software (EuroVector SpA, Milan). Acetanilid was used as a standard for the measurements in order to verify the accuracy of the analyzer.

2.9 Coral tissue analysis

A standardized sized piece with a mean of 1.72 cm^2 ± 0.16 was taken from each individual coral polyp in order to examine the health status. The coral piece was either immediately frozen at -20 °C or frozen in liquid nitrogen. All coral pieces were transported to the AWI in Bremerhaven after the end of the experiments. There, the tissue of each fragment was removed with an air-brush with filtered seawater and homogenized with an ultra turrax. The volume of the resulting stock solution of the tissue-seawater-slurry was recorded.

2.9.1 Chlorophyll content

A 5 ml subsample of the homogenized stock solution was filtered on a GF/F filter (25 mm diameter) and the filter frozen at -20 °C until further analysis.

The frozen filters were transferred into falcon tubes and covered with 5 ml Acetone (90 %). The chlorophyll was extracted from the filters by incubating them at 4 °C for 4 h following an ultrasonic bath for 15 min. Subsequently, the falcon tubes were centrifuged and 1 ml of the supernatant was transferred into a cuvette. The chlorophyll content was measured with a Spectrophotometer UV-1800 SHIMADZU at a wavelength of 750, 665, 664, 647, 630, 510 and 480 nm. The amount of chlorophyll *a* per coral surface was calculated after Lorenzen (1967).

2.9.2 Zooxanthellae density

An aliquot of at least 10 ml of the stock solution was taken and the number of zooxanthellae was counted under a microscope with a Fuchs- Rosenthal- counting slide. One haemocytometer consists of 2 counting chambers with 16 square sub-grids each. For each tissue sample 6 replicas were counted with 1 replicate comprising the counts of 5 out of the 16 square sub grids.

The zooxanthellae density per cm^2 of coral surface area could then be quantified following a correction for volume of the used stock solution and surface area.

2.9.3 Protein analysis

In order to determine the protein concentration in the animal tissue, parts of the skeleton and symbionts tissue had first to be separated from the animal fraction. Therefore, an aliquot of 1 ml of the stock solution was centrifuged in an Eppendorf cup for 8 min at 3500 rpm. The supernatant (animal fraction) was frozen immediately at -20 °C.

The protein content was quantified with a standard protein assay (BioRad) and with a Spectrophotometer UV-1800 SHIMADZU at a wavelength of 750 nm. Following this, the obtained values had to be corrected for the volume of the used stock solution and surface area.

2.10 Pulse amplitude modulated (PAM) fluorometry

The photophysiological response of the coral symbionts, the zooxanthellae, was assessed by pulse amplitude modulated fluorometry (Diving- PAM, Walz GmbH; Effeltrich, Germany). Prior to each experiment the corals were dark adapted for 30 minutes. Subsequently, rapid light curves (photosynthesis vs. irradiance PI curves) were conducted applying increasing light intensities at 10s intervals, each of which was finished with a saturation pulse. The PI curves were measured with the fiberoptics of the PAM fluorometer at a 1 cm distance to the coral surface. The maximum quantum yield of photosystem II was determined before the actinic light rose.

The relative electron transport rate (rETR) was calculated for each replicate in order to obtain the maximum electron transport rate and the photosynthetic efficiency. For this purpose, the effective quantum yield (ΔF/Fm`) had to be multiplied with the light irradiance to calculate the rETR. The PI curves were obtained by plotting the rETR against the different light irradiances. The maximal electron transport rate (ETR_{max}) and the photosynthetic efficiency (slope α) were calculated from the light curves following the model of Jassby and Platt (1976).

2.11 Statistical analysis

Measurements over time were analyzed using a repeated measures analysis of variance (ANOVA). Significant differences were compared pairwise with the Duncan´s Method. Students t- tests were applied in order to test if single sample points varied from zero or to examine if parameters in the water entering and exiting the oscules of the sponges differed significantly from each other. If the assumptions of a normal distribution and homogeneity of variances were not fulfilled a Mann- Whitney Rank Sum test was performed.

All parameters of the coral tissue and the photophysiological responses of corals in the different experiments were compared and tested for significance with a one way ANOVA. When there were marked variations they were compared pairwise with the Duncan´s Method. If the assumptions of a normal distribution and homogeneity of variances were not fulfilled a Kruskal- Wallis one way ANOVA was conducted.

The statistical analyses were performed by using Sigmaplot 12.0.

3 Results

3.1 Nutrient analyses

The accumulation or decline of ammonium and nitrate during the incubations is shown separately for each dissolved inorganic nitrogen (DIN) species and treatment (Fig. 7- 12). An increase of DIN was interpreted as an excretion by the organisms whereas a decline was interpreted as consumption.

3.1.1 Corals

The incubations with corals in artificial seawater exhibited no changes in the concentrations of ammonium and nitrate over time, neither between the single samplings nor to zero (= control; Appendix; repeated measures ANOVA and Mann- Whitney Rank Sum Test, table A. 2 and 3; Fig. 7a and b).

During the incubations with corals in seawater enriched with cyanobacteria and nutrients (= treatment) strong fluctuations in the ammonium concentrations were measured, yet no statistical differences were detectable due to the highly variable concentrations in the replicate measurements (repeated measures ANOVA and Mann- Whitney Rank Sum Test, table A. 2 and 4; Fig. 7c). The nitrate concentrations decreased inconsiderably without showing significant changes between the single samplings in time or to zero (repeated measures ANOVA and Mann- Whitney Rank Sum Test, table A. 2 and 4; Fig. 7d).

No nitrite at all could be measured in any of the experiments.

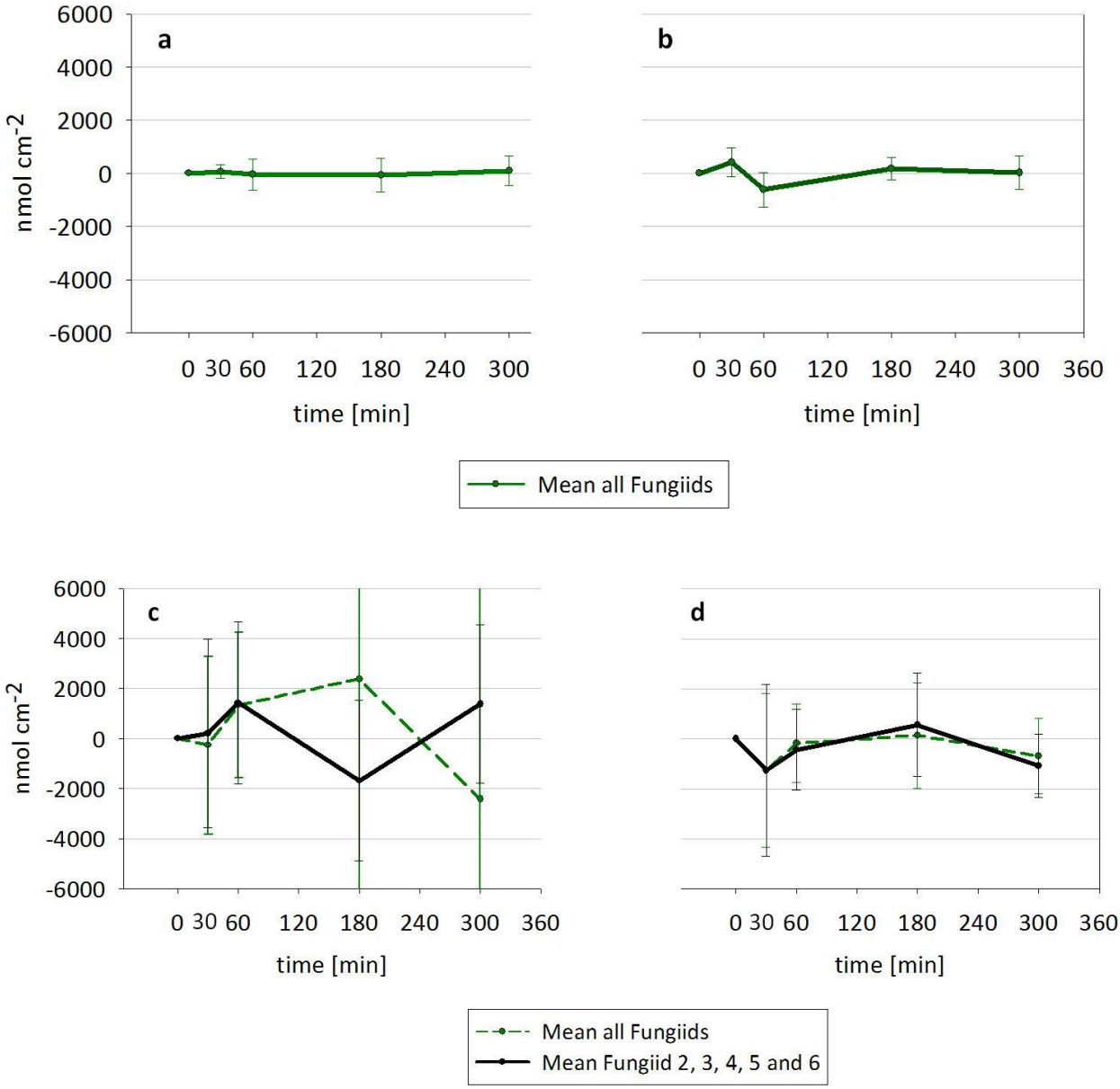

Fig. 7 a-d: Time-series of ammonium concentrations [nmol cm^{-2}] in coral incubations with artificial seawater (= control, means ±SD, n=6, a) and in coral incubations with artificial seawater enriched with cyanobacteria and nutrients (=treatment, means ± SD, n=5, c). Time-series of nitrate concentrations [nmol cm^{-2}] in coral control incubations (means ±SD, n=6, c) and in coral treatment incubations (means ± SD, n=5, d). Given is the net change in nutrient concentrations relative to the previous sampling interval per surface area of coral. Colours of the graphs indicate if they outline a selection of replicates (black) or if all replicates are displayed (green). The fungiid no.1 was excluded in the statistical analysis since it displayed unusually high values for ammonium (see appendix, Fig. A 1).

3.1.2 Sponges

Sponges incubated in artificial seawater (= control) revealed no variation in nitrate concentrations with constant values throughout the experiments (Appendix; repeated measures ANOVA; table A. 5; Mann- Whitney Rank Sum Test, table 2; Fig. 8a). Besides, there was no difference in the concentration of ammonium between the single samplings (Appendix; repeated measures ANOVA; table A. 5), but the values for ammonium declined between 60 minutes and 180 minutes of the experiment compared to zero (p= 0.002). Nevertheless, the concentration at 300 minutes did not differ to zero (Mann- Whitney Rank Sum Test, table 2; Fig. 8b)

The most conspicuous changes in DIN concentrations were shown by sponges incubated in artificial seawater enriched with nutrients and cyanobacteria (= treatment). Ammonium concentrations fluctuated strongly in time during the experiment. The ammonium concentrations dropped distinctly in the first 30 minutes and again in the time between 60 and 180 minutes (Students t-test, p= 0.012 and p= 0.003; table 3; repeated measures ANOVA; table 4; Fig. 8c). The lowest values ranged from -29.79 µmol $g(dw)^{-1}$ (first 30 minutes) down to -41.61 µmol $g(dw)^{-1}$ (between 60 and 180 minutes).

The nitrate concentrations remained constant at zero during the first 180 minutes of incubation. After 180 minutes the nitrate values rose until the end of the experiment with up to 69.58 µmol $g(dw)^{-1}$ (Students t-test; p=0.007; table 3; Fig. 8d).

Nitrite remained at submicromolar levels during both experiments (control: 0.00 to 0.09 and treatment: 0.02 to 0.10 µmol l^{-1}).

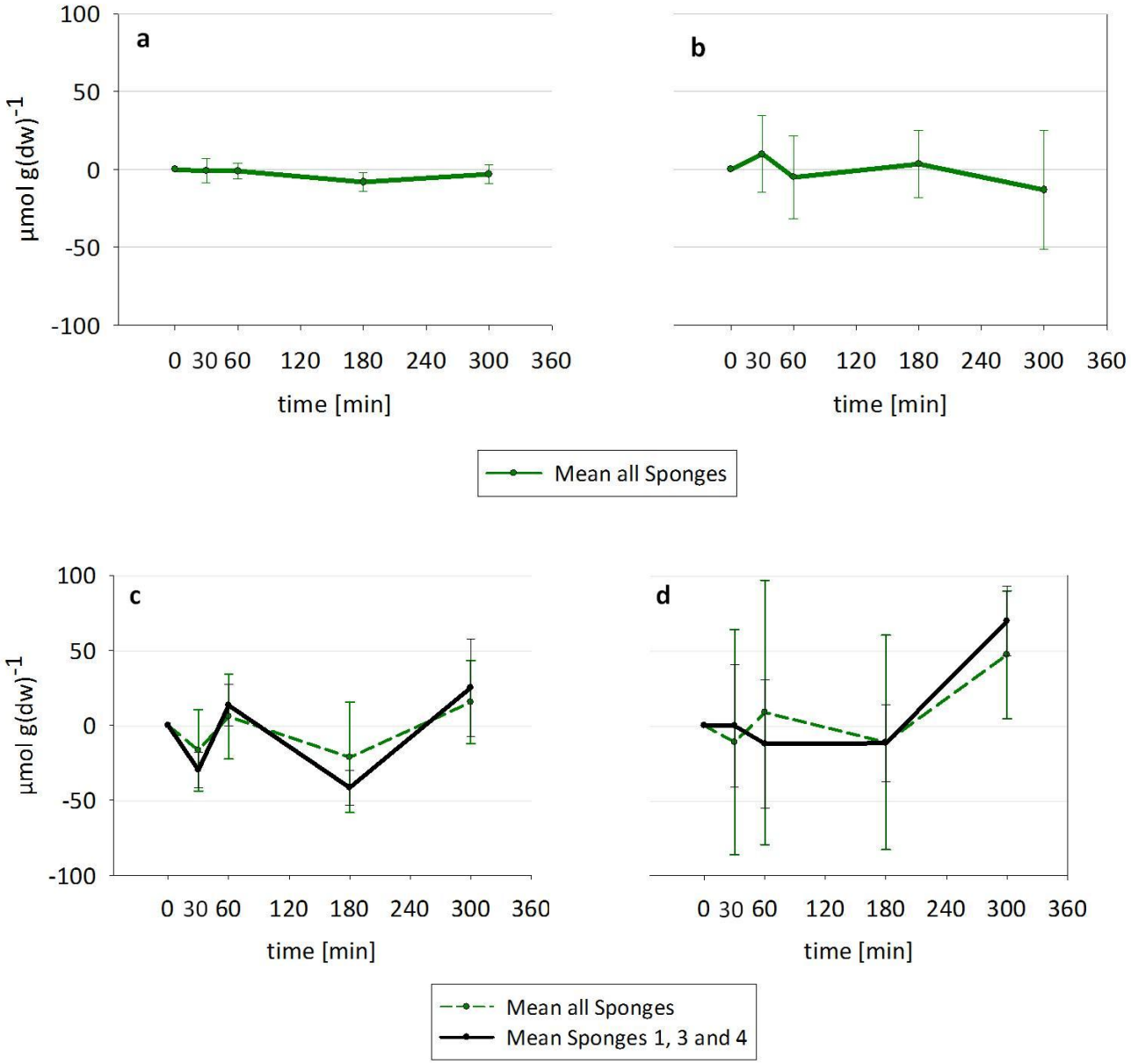

Fig. 8 a- d: Time-series of ammonium concentrations [µmol g(dw)$^{-1}$] in sponge incubations with artificial seawater (= control, means ±SD, n=6, a) and in sponge incubations with artificial seawater enriched with cyanobacteria and nutrients (=treatment, means ± SD, n=3, c). Time- series of nitrate concentrations in sponge control incubations (means ±SD, n=6, b) and in sponge treatment incubations (means ± SD, n=3, d). Given is the net change in nutrient concentrations relative to the previous sampling interval per dry weight of sponge. Colours of the graphs indicate if they outline a selection of replicates (black) or if all replicates are displayed (green). Three replicates were excluded for the statistical analysis in the treatment group. Sponge 2 was excluded since it showed a completely different pattern in its pumping activity than the other sponges. Sponge 5 was not considered because it did not pump during the course of the experiment. Sponge 6 was as well not included since it stopped its pumping activities after 180 minutes of incubation (see appendix, Fig. A. 2).

Tab. 2: Pair wise Mann- Whitney Rank Sum Test of dissolved inorganic nutrient (DIN) changes versus zero in incubations with sponges in artificial seawater (control group) over time. Comparison of single measurements in time with zero: Levels of significance: *p<0.05 and **p<0.01. Replicates per treatment (N=6) and total number of measurements in time (n=4).

Time [min]	NH_4^+	NO_3^-
30	1.000	0.065
60	0.394	0.394
180	0.002**	1.000
300	0.065	1.000

Tab. 3: Pair wise Students t-test of dissolved inorganic nutrient (DIN) changes versus zero in incubation with sponges in artificial seawater enriched with cyanobacteria and nutrients (treatment group) over time. Comparison of single measurements in time with with zero: Levels of significance: *p<0.05 and **p<0.01. Replicates per treatment (N=3) and total number of measurements in time (n=4).

Time [min]	NH_4^+	NO_3^-
30	0.012*	0.995
60	0.172	0.648
180	0.003**	0.469
300	0.250	0.007**

Tab. 4: One way repeated measures ANOVA to test for differences in ammonium concentrations in incubation with sponges in artificial seawater enriched with cyanobacteria and nutrients (treatment group) over time. The Duncan´s Method was applied for the pair wise multiple comparison procedure (for details see Appendix table A. 6). Levels of significance: *p<0.05 and **p<0.01. Replicates per treatment (N=3) and total number of measurements in time (n=4).

Parameter	Df	SS	F	p
NH_4^+	11	12464.339	6,386	0.027*

3.1.3 Corals and Sponges

Corals and sponges incubated together in artificial seawater (=control) showed no changes in DIN in all samplings over time (Appendix; repeated measures ANOVA, table A. 7). However, there were increases in ammonium, nitrate and nitrite concentrations at single points in time. The ones of ammonium rose from 60 minutes on, the ones of nitrate ascended until 60 minutes of the experiment and the nitrite values showed an elevation until the end of the experiment (p= 0.029; Mann- Whitney Rank Sum Test; table 5; Fig. 9a and b and 10a). Nevertheless, there were no differences in water entering and exiting the oscules (Appendix; Mann- Whitney Rank Sum Test and Students t-test; table A. 8; Fig. 11a and b and 12a).

When sponges and corals were incubated in artificial seawater enriched with cyanobacteria and nutrients (=treatment) there were no changes in the nutrient concentrations except at two time intervals in the first 30 minutes and between 60 and 180 minutes during which the ammonium values declined (p= 0.029; Mann- Whitney Rank Sum Test; table 6; Fig. 9c and d and 10b). There were no differences between water entering and exiting the oscules (Fig. 11c and d and 12b). It seemed that the ammonium values in water released by sponges was higher than the ambient water at 30 minutes of the experiments but this changes failed to be statistically significant (Appendix; Mann- Whitney Rank Sum Test and Students t-test; table A. 9).

Tab. 5: Pair wise Mann- Whitney Rank Sum Test of dissolved inorganic nutrient (DIN) changes versus zero in the sponges and coral control group (=artificial seawater) over time. Comparison of single measurements in time to zero. Replicates per treatment (N=4) total number of measurements in time (n=4).

Time [min]	NH_4^+	NO_3^-	NO_2^{2-}
30	0.343	0.343	1.000
60	1.000	0.029*	0.343
180	0.029*	0.343	0.343
300	1.000	0,343	0.029*

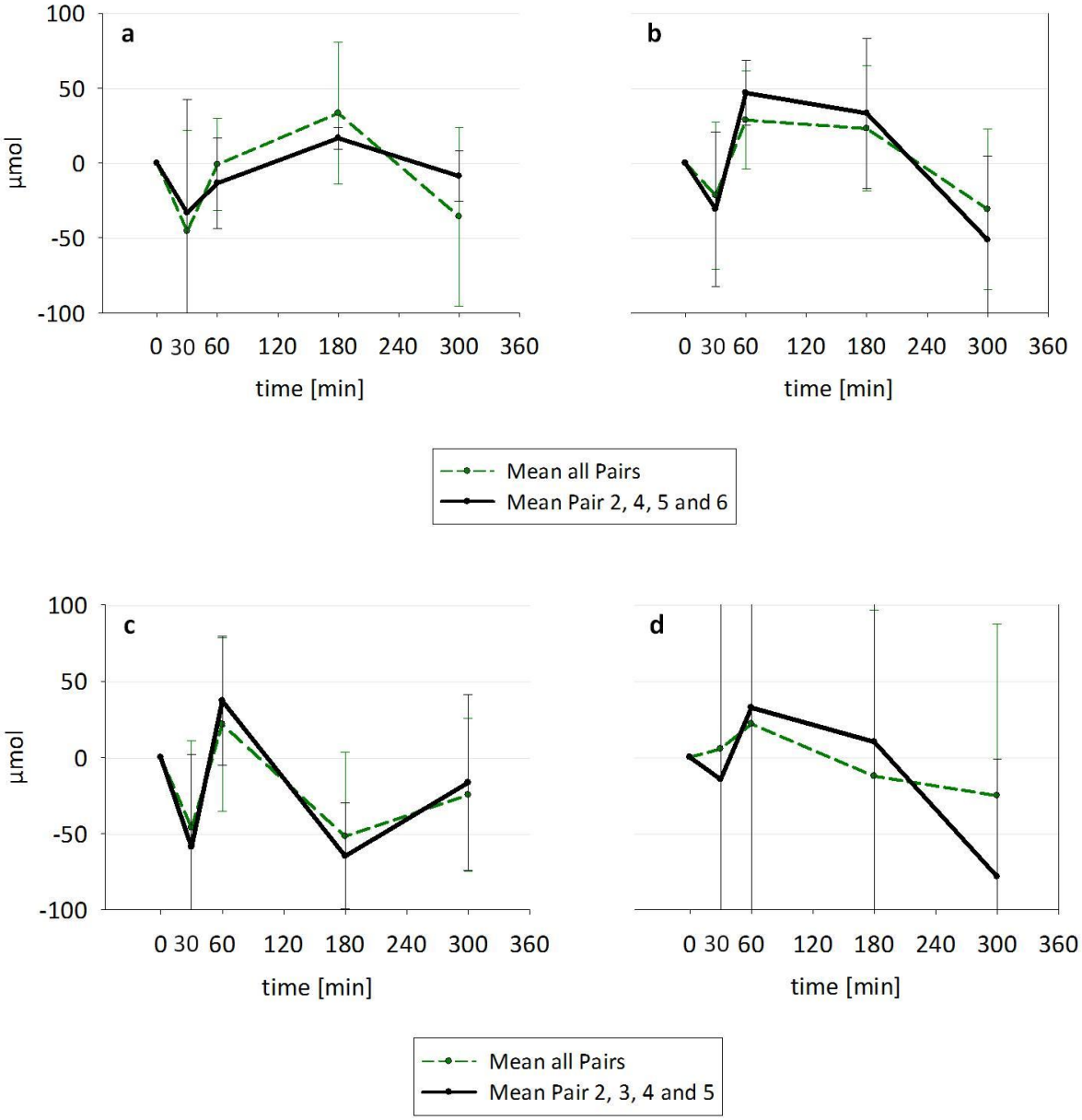

Fig. 9a- d: Time-series of ammonium concentrations [µmol] in coral and sponge incubations with artificial seawater (= control, means ±SD, n=6, a) and in coral and sponge incubations with artificial seawater enriched with cyanobacteria and nutrients (=treatment, means ± SD, n= 4, c). Time- series of nitrate concentrations in coral and sponge incubations (control, means ±SD, n=6, b) and in coral and sponge treatment incubations (means ± SD, n=4, d). Given is the net change in nutrient concentrations relative to the concentration measured previous sampling interval. Colours of the graphs indicate if they outline a selection of replicates (black) or if all replicates are displayed (green). Two replicates were excluded for the statistical analysis in the treatment group since they showed a completely different pattern than all the other pairs of corals and sponges (see appendix, Fig. A. 3 and 4).

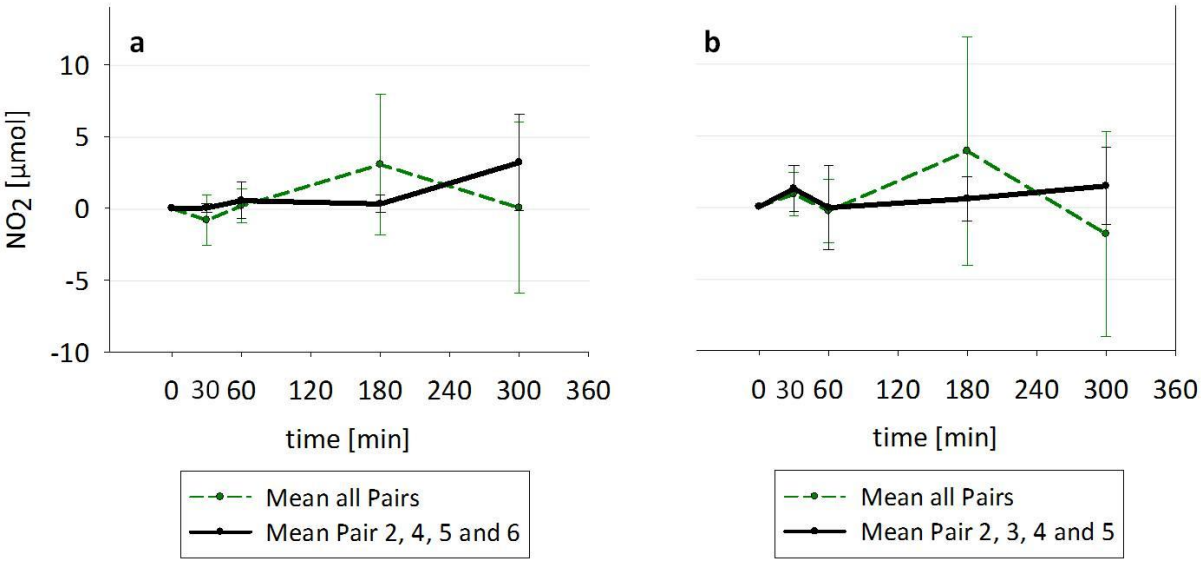

Fig. 10a- d: Time- series of nitrite concentrations [µmol] in coral and sponge incubations with artificial seawater (= control, means ±SD, n=4, a) and in coral and sponge incubations with artificial seawater enriched with cyanobacteria and nutrients (=treatment means ±SD, n=4, a). Given is the net change in nutrient concentrations relative to the concentration measured at the previous sampling interval. Colours of the graphs indicate if they outline a selection of replicates (black) or if all replicates are displayed (green). Two replicates were excluded for the statistical analysis in the treatment group since they showed a completely different pattern than the all other corals and sponges (see appendix, Fig. A. 2).

Tab. 6: Pair wise Mann- Whitney Rank Sum Test of dissolved inorganic nutrient (DIN) changes versus zero in the sponges and coral treatment group (=artificial seawater enriched with cyanobacteria and nutrients) over time. Comparison of single measurements in time to zero. Replicates per treatment (N=4) and total number of measurements in time (n=4).

Time [min]	NH_4^+	NO_3^-	NO_2^{2-}
30	0.029*	1.000	0.629
60	0.343	1.000	0.629
180	0.029*	1.000	0.498
300	0.343	0.343	1.000

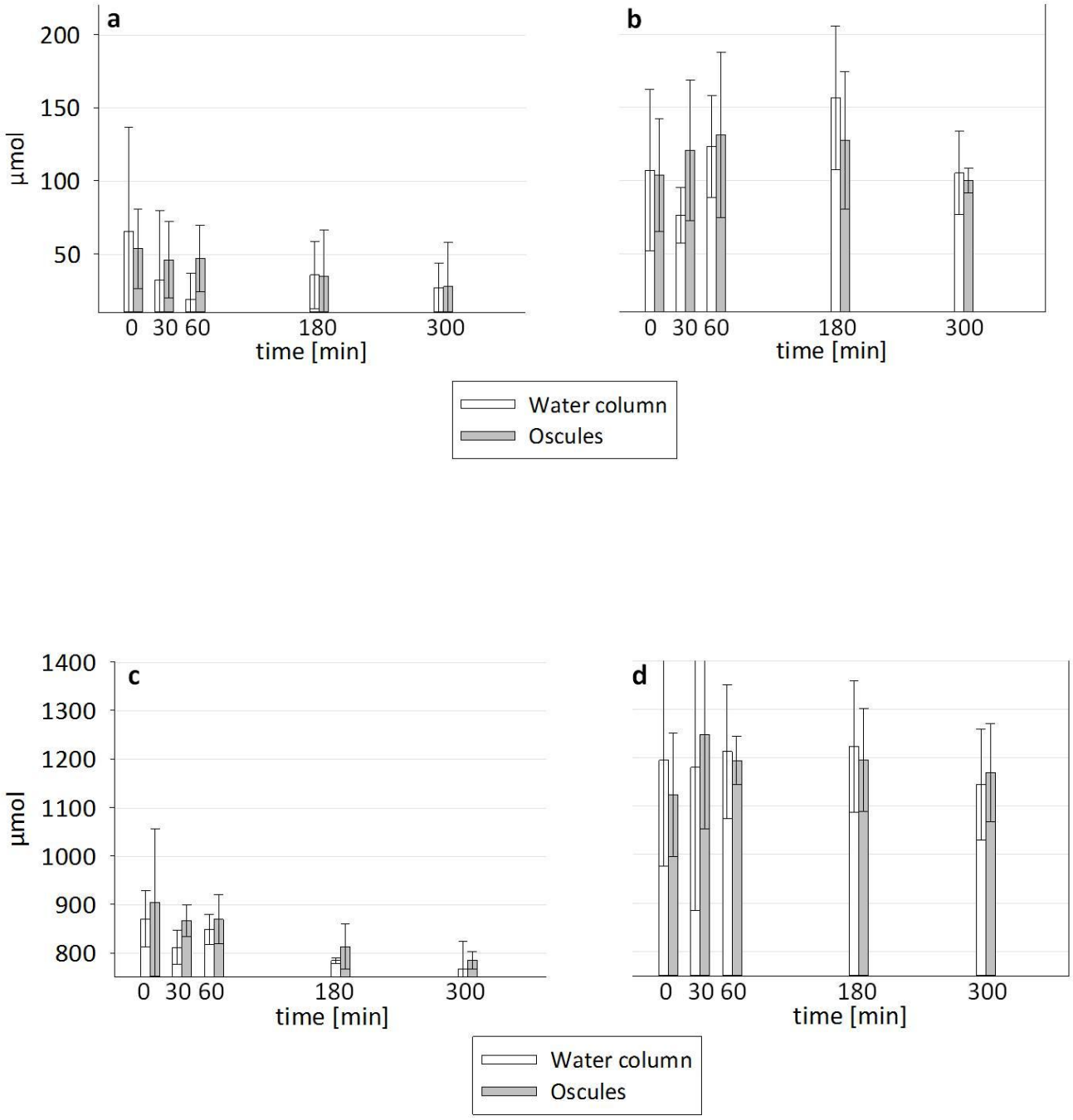

Fig. 11: Comparison of ammonium [µmol] in the water column (white bars) and exiting the oscules (grey bars) of corals and sponges in the control group (artificial seawater, means ±SD, n=4, a) and in artificial seawater enriched with cyanobacteria and nutrients (treatment, means ±SD, n=4, c). Comparison of the nitrate concentrations [µmol] of the corals and sponges in the control group (means ±SD, n=4, b) and in the treatment group (means ±SD, n=4, d).

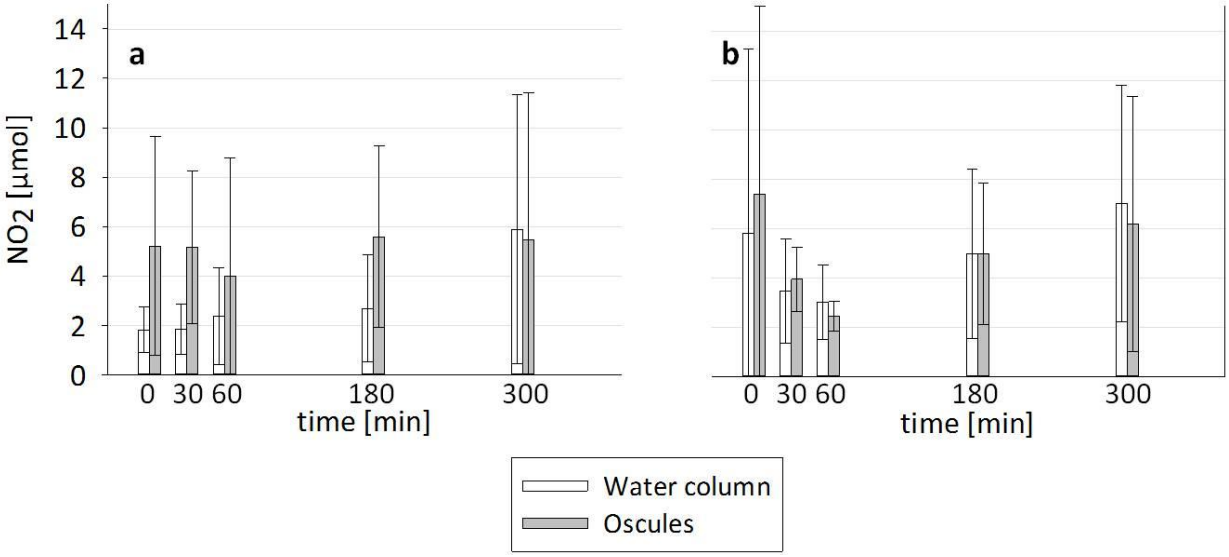

Fig. 12: Comparison of nitrite concentrations [µmol] in the water column (white bars) and exiting the oscules (grey bars) of the sponges in the control group (artificial seawater, means ±SD, n=4, a) and of sponges in artificial seawater enriched with cyanobacteria and nutrients (=treatment, means ±SD, n=4, a).

3.2 Dissolved and total organic carbon (DOC/TOC)

3.2.1 Corals

Neither dissolved (DOC) nor total (TOC) or particulate organic carbon (POC) changed in the water column of corals incubated in solely artificial seawater (Appendix; Mann- Whitney Rank Sum Test; table A. 10, 11 and 12; Fig. 13a).

In coral incubations enriched with cyanobacteria and nutrients POC and TOC concentrations seemed to decline but these changes failed to be statistically significant (Appendix; Mann-Whitney Rank Sum Test; table A. 11 and 12; Fig. 13b). The concentration of DOC did as well not vary over time (Appendix; Mann- Whitney Rank Sum Test; table A. 10; Fig. 13b).

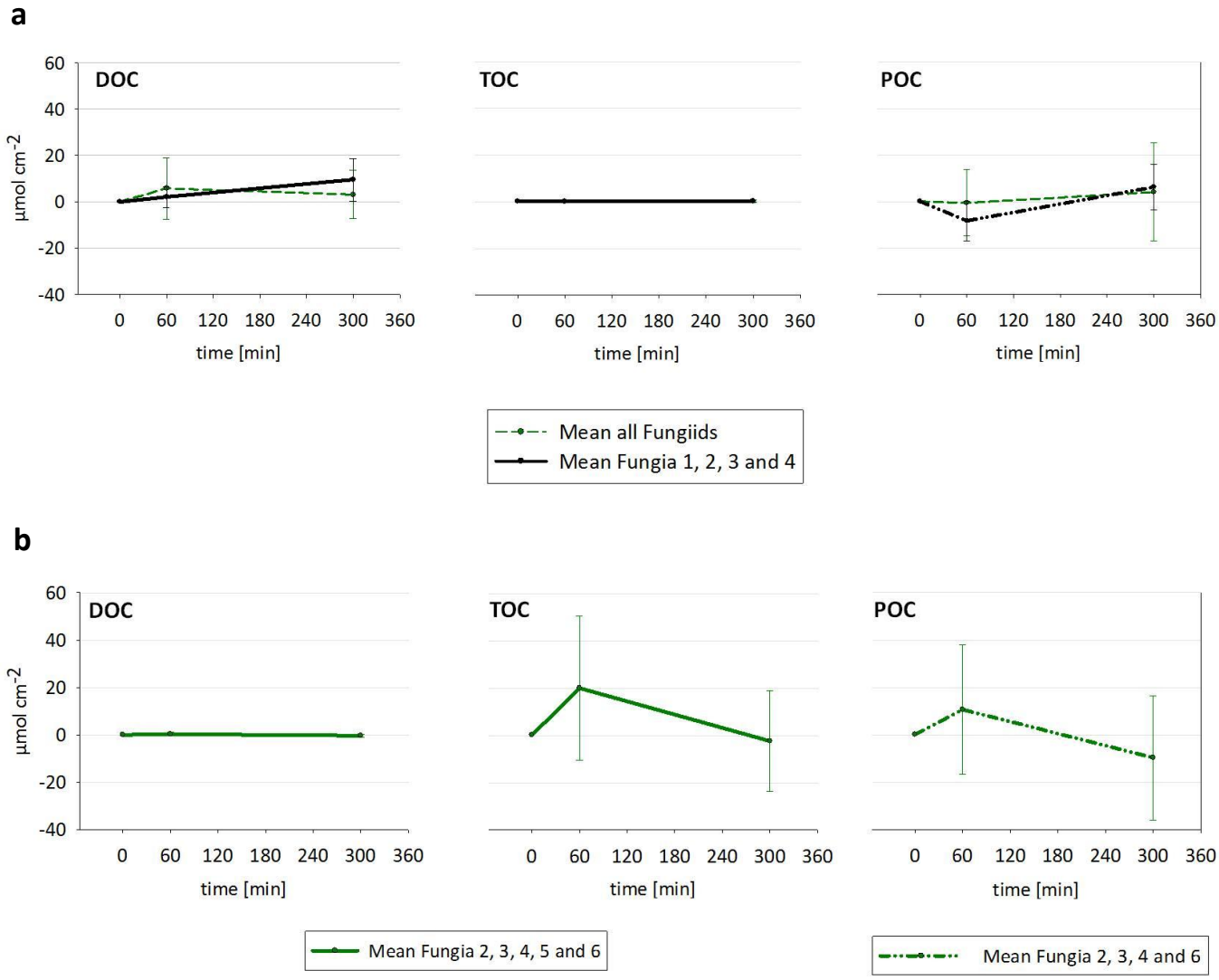

Fig. 13: Time- series of the concentration of dissolved (DOC), total (TOC) and particulate organic carbon (POC) [µmol cm $^{-2}$] during the 300 minutes incubation of corals in artificial seawater (=control, a) and artificial seawater enriched with cyanobacteria and nutrients (=treatment, b). Given is the net change in carbon concentrations relative to the previously measured concentration per surface area of coral. Colours of the graph indicate a selection of replicates (black, n=4) or all replicates displayed (green, n=6). Changes in DOC, TOC and POC are illustrated as mean±SD. Changes in POC displayed as a dashed and dotted line since POC concentrations were calculated based on the obtained DOC and TOC values (POC= TOC- DOC). The fungiids no.1, 5 and 6 were excluded from statistical analysis since the samples got contaminated during the handling procedure.

3.2.2 Sponges

Sponges incubated in artificial seawater did neither produce nor release DOC, TOC and POC (Appendix; Mann- Whitney Rank Sum Test; table A. 10, 11 and 12; Fig. 14a).

Sponges in the treatment group (artificial seawater enriched with cyanobacteria and nutrients) exhibited a considerable elevation in DOC values from 180 minutes of the experiment on (Appendix; Mann- Whitney Rank Sum Test; $p=0.029$; table A. 10; Fig. 14b). Although POC seemed to decrease during the first 60 minutes of incubation these changes failed to be statistically significant as well as the ones for TOC (Appendix; Mann- Whitney Rank Sum Test; table A. 11 and 12; Fig. 14b).

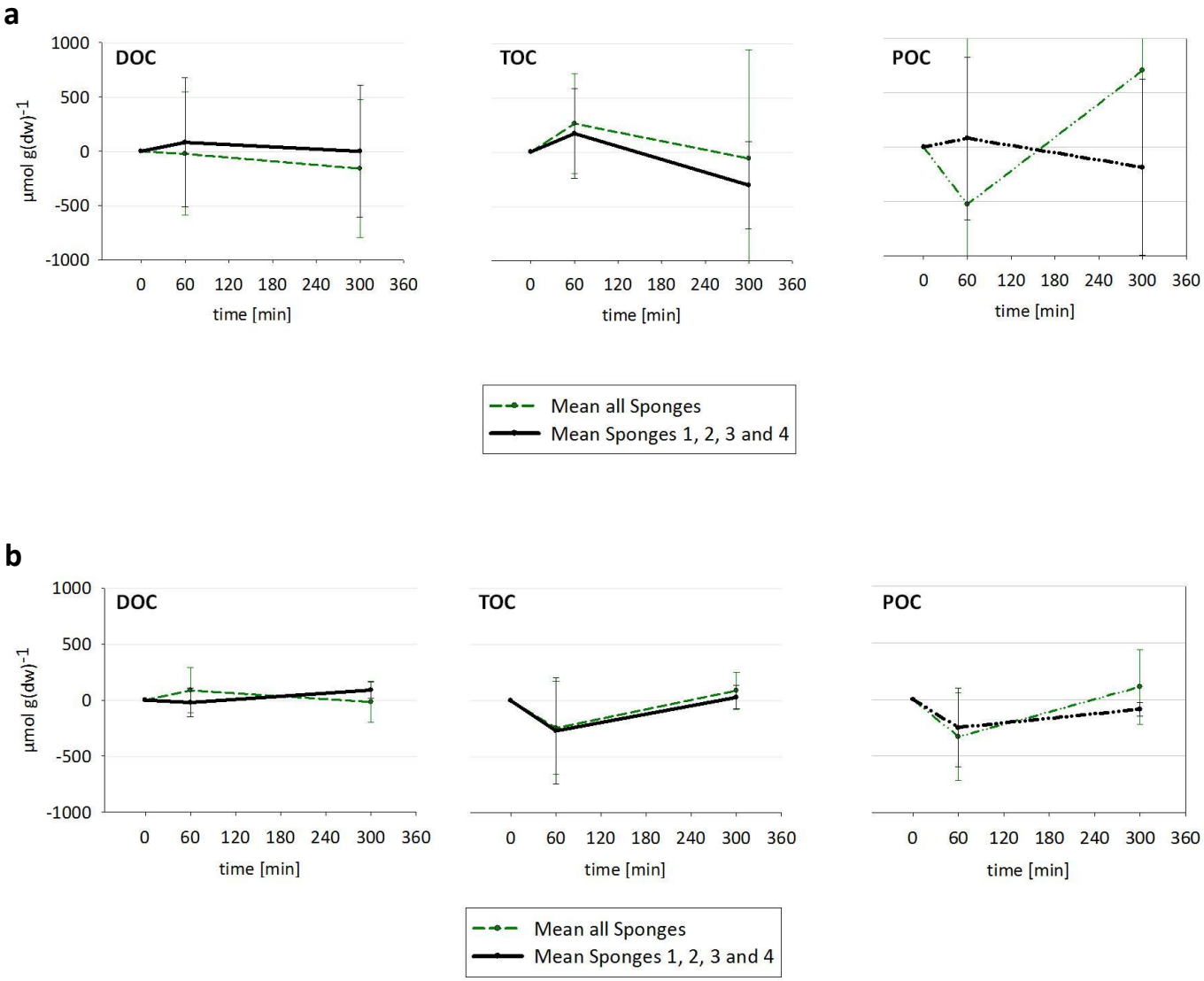

Fig. 14: Time- series of the concentration of dissolved (DOC), total (TOC) and particulate organic carbon (POC) [µmol g(dw)$^{-1}$] during the 300 minutes incubation of sponges in artificial seawater (=control, a) and artificial seawater enriched with cyanobacteria and nutrients (=treatment, b). Given is the net change in carbon concentrations relative to the previously measured concentration per dry weight of sponge. Colours of the graph indicate a selection of replicates (black, n=4) or all replicates displayed (green, n=6). Changes in DOC, TOC and POC are illustrated as mean±SD. Changes in POC displayed as a dashed and dotted line since POC concentrations were calculated based on the obtained DOC and TOC values (POC= TOC- DOC). The sponges no.5 and 6 in the treatment group did not pump continuously or at all and were therefore excluded from the statistical analysis. The sample of sponge no. 6 got contaminated and the sponge no.5 showed unusually high values in the control group (see Appendix, Fig. A. 5).

3.2.3 Corals and Sponges

Neither an increase nor a decline in DOC, TOC and POC in the water column could be detected in incubations with sponges and corals together in artificial seawater (Appendix; Mann- Whitney Rank Sum Test; table A. 10, 11 and 12; Fig. 15a). A difference in water entering and exiting the oscules of the sponges could be as well not observed (Students t-test and Mann- Whitney Rank Sum Test; table A. 13; Fig. 16a).

There were as well no changes in the DOC, TOC and POC concentrations in the incubations of sponges with corals treated with artificial seawater enriched with nutrients and cyanobacteria (Appendix; Mann- Whitney Rank Sum Test; table A. 10, 11 and 12; Fig. 15b). Although the differences in concentrations in the water column were not statistically significant, there was less DOC released by sponges compared to the present concentration in the ambient water in the first 60 minutes of the incubation ($p=0.026$; Mann- Whitney Rank Sum Test; table A. 13; Fig. 16b). Moreover, water exiting the oscules of the sponges at the end of the incubation contained less POC and TOC than water entering them ($p= 0.003$ and $p= 0.002$; Students t-test and Mann- Whitney Rank Sum Test; table A. 13; Fig.16b).

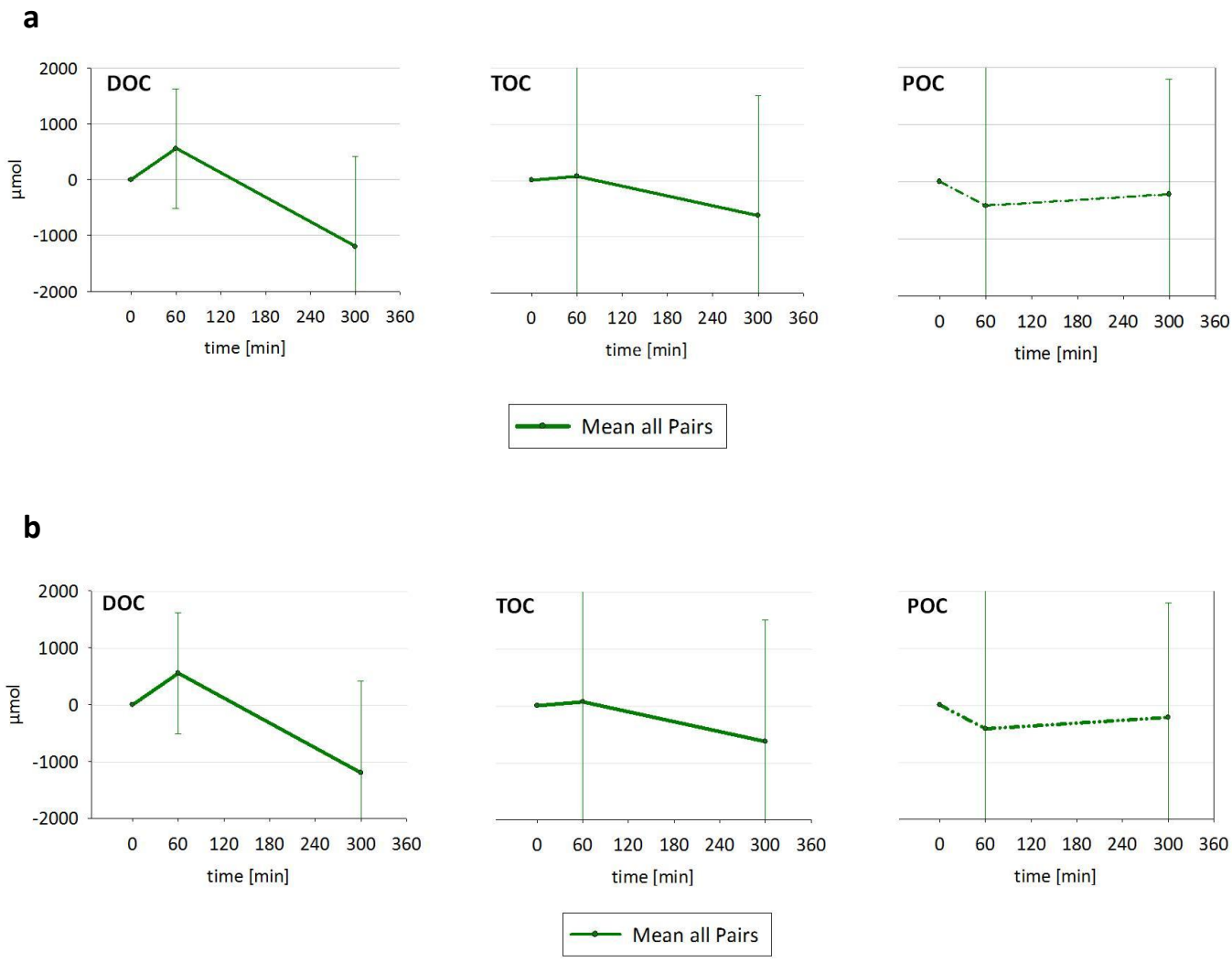

Fig. 15: Time- series of the concentration of dissolved (DOC), total (TOC) and particulate organic carbon (POC) [µmol] during the 300 minutes incubation of corals and sponges in artificial seawater (=control, a) and artificial seawater enriched with cyanobacteria and nutrients (=treatment, b). Given is the net change in carbon concentrations relative to the previously measured concentration. Changes in DOC, TOC and POC are illustrated as mean±SD. Changes in POC displayed as a dashed and dotted line since POC concentrations were calculated based on the obtained DOC and TOC values (POC= TOC- DOC).

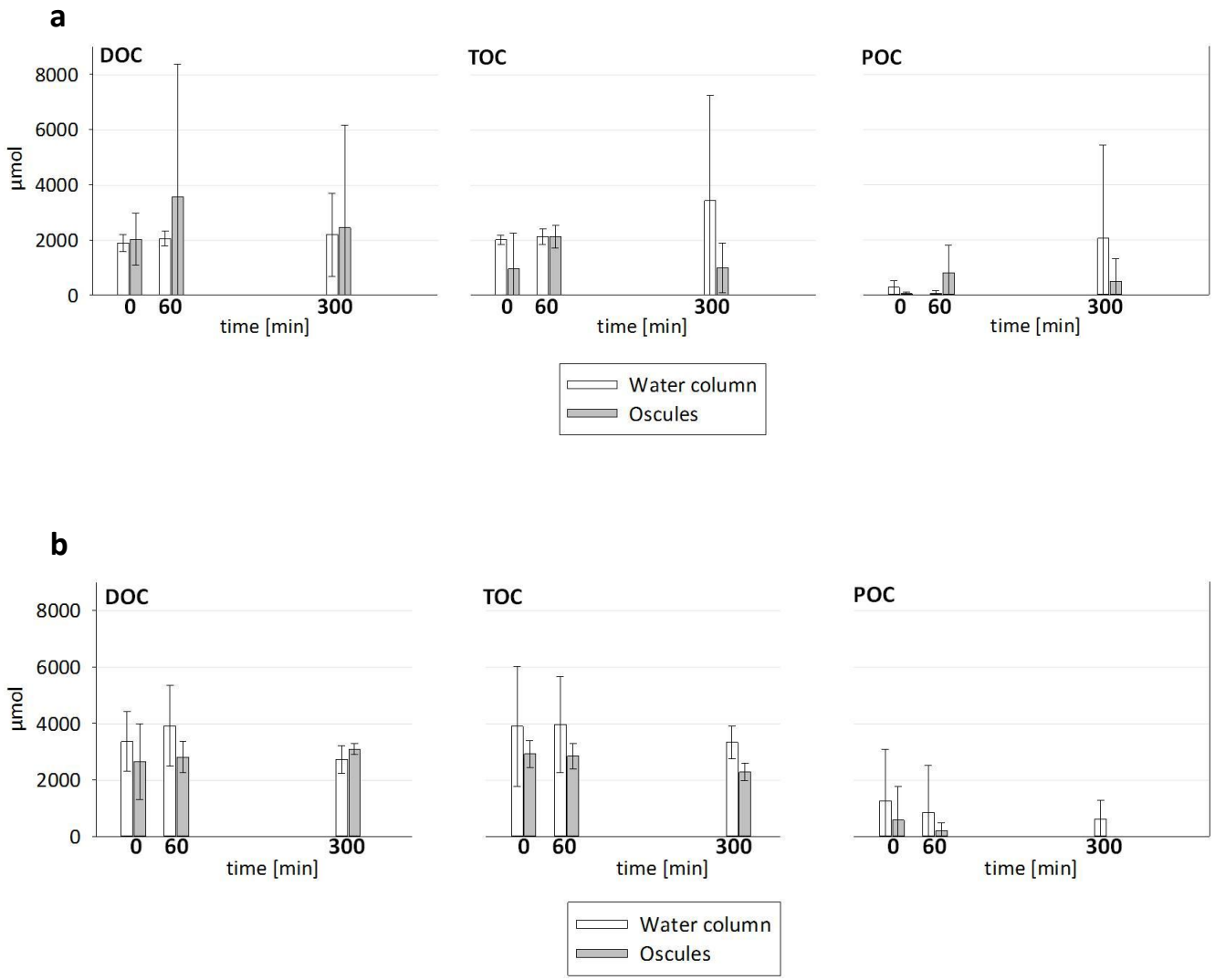

Fig. 16: Comparison of dissolved (DOC), total (TOC) and particulate organic carbon (POC) µmol] in the water column (white bars) and exiting the oscules (grey bars) of corals and sponges in the control group (artificial seawater, means ±SD, n=6, a) and in artificial seawater enriched with cyanobacteria and nutrients (treatment, means ±SD, n=6, b).

3.3 Dissolved organic and total dissolved nitrogen (DON/TdN)

3.3.1 Corals

There were no changes in dissolved organic nitrogen (DON) in the water column of corals incubated solely in artificial seawater (Appendix; Students t- test and Mann- Whitney Rank Sum Test; table A. 15; Fig. 17a). However, the measured concentrations of total dissolved nitrogen (TdN) decreased in the first 60 minutes of incubation (Appendix; Mann- Whitney Rank Sum Test; table A. 14).

In experiments with corals and artificial seawater enriched with cyanobacteria and nutrients, neither variations in the concentration of DON nor TdN were measured (Appendix; Mann-Whitney Rank Sum Test; table A. 14 and 15; Fig. 17b).

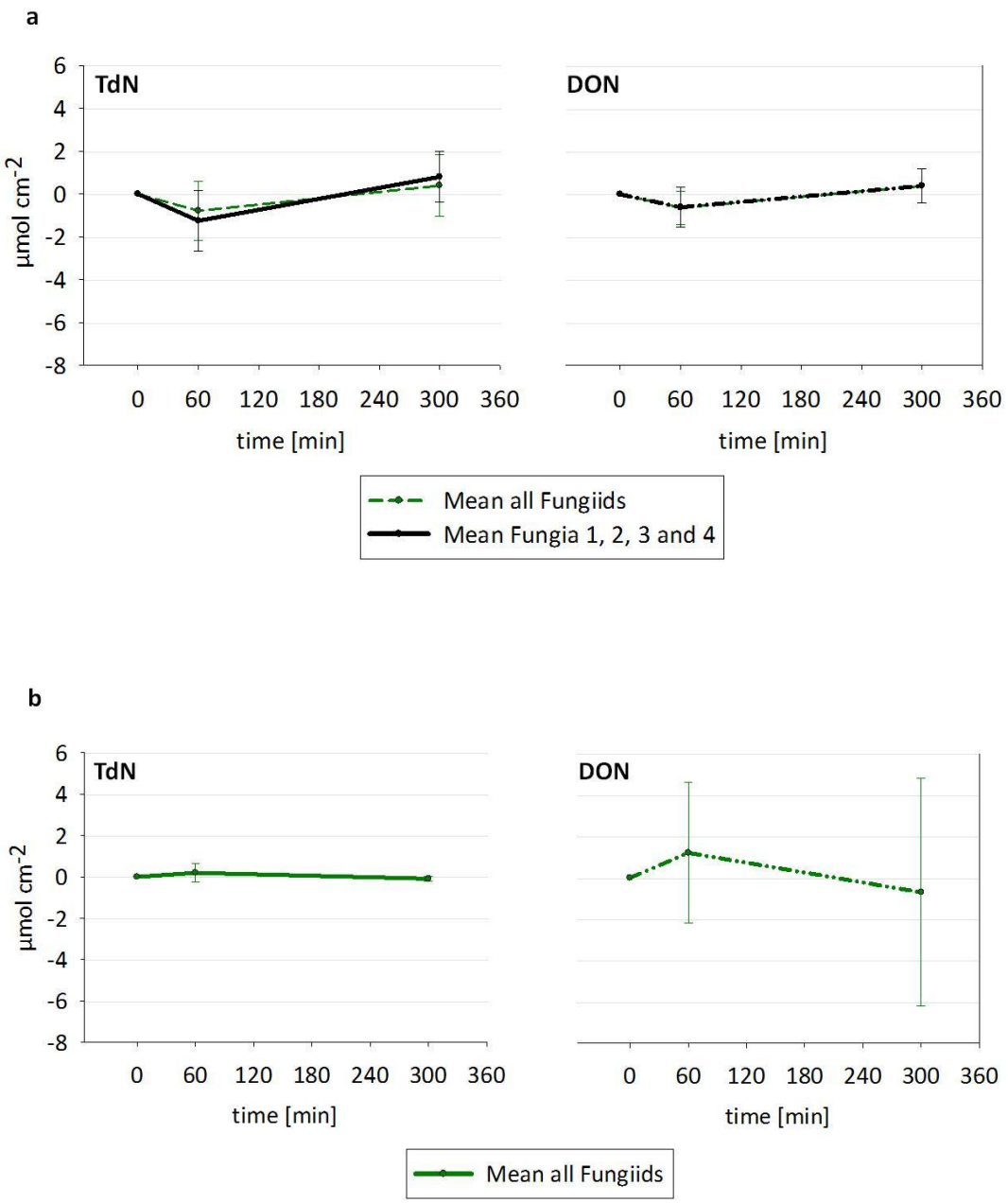

Fig. 17: Time- series of the concentration of dissolved (DON) and total dissolved nitrogen (TdN) [µmol cm^{-2}] during the 300 minutes incubation of corals in artificial seawater (=control, a) and in artificial seawater enriched with cyanobacteria and nutrients (=treatment; b). Given is the net change in nitrogen concentrations relative to the concentration of the previous sampling interval per surface area of coral. Colours of the graph indicate a selection of replicates (black, n=4) or all replicates displayed (green, n=6). Changes in DON and TdN are illustrated as mean±SD. Changes in DON are displayed as a dashed and dotted line since DON concentrations were calculated based on the obtained DIN and TdN values (DON= TdN- DIN). The fungiids no.5 and 6 were excluded from statistical analysis since the samples got contaminated during the handling procedure.

3.3.2 Sponges

There were no changes in DON and TdN in the water column of sponges incubated solely in artificial seawater (Appendix; Mann- Whitney Rank Sum Test; table A. 14 and 15; Fig. 18a).

In sponge incubations enriched with cyanobacteria and nutrients there were no variations in the concentration of DON but in the first 60 minutes of the experiment the total dissolved nitrogen (TdN) declined (Appendix; Students t- test; table A. 14 and 15; Fig. 18b). It seemed that the TdN rose between 60 minutes and 300 minutes of the incubation time though this change failed to be statistically significant.

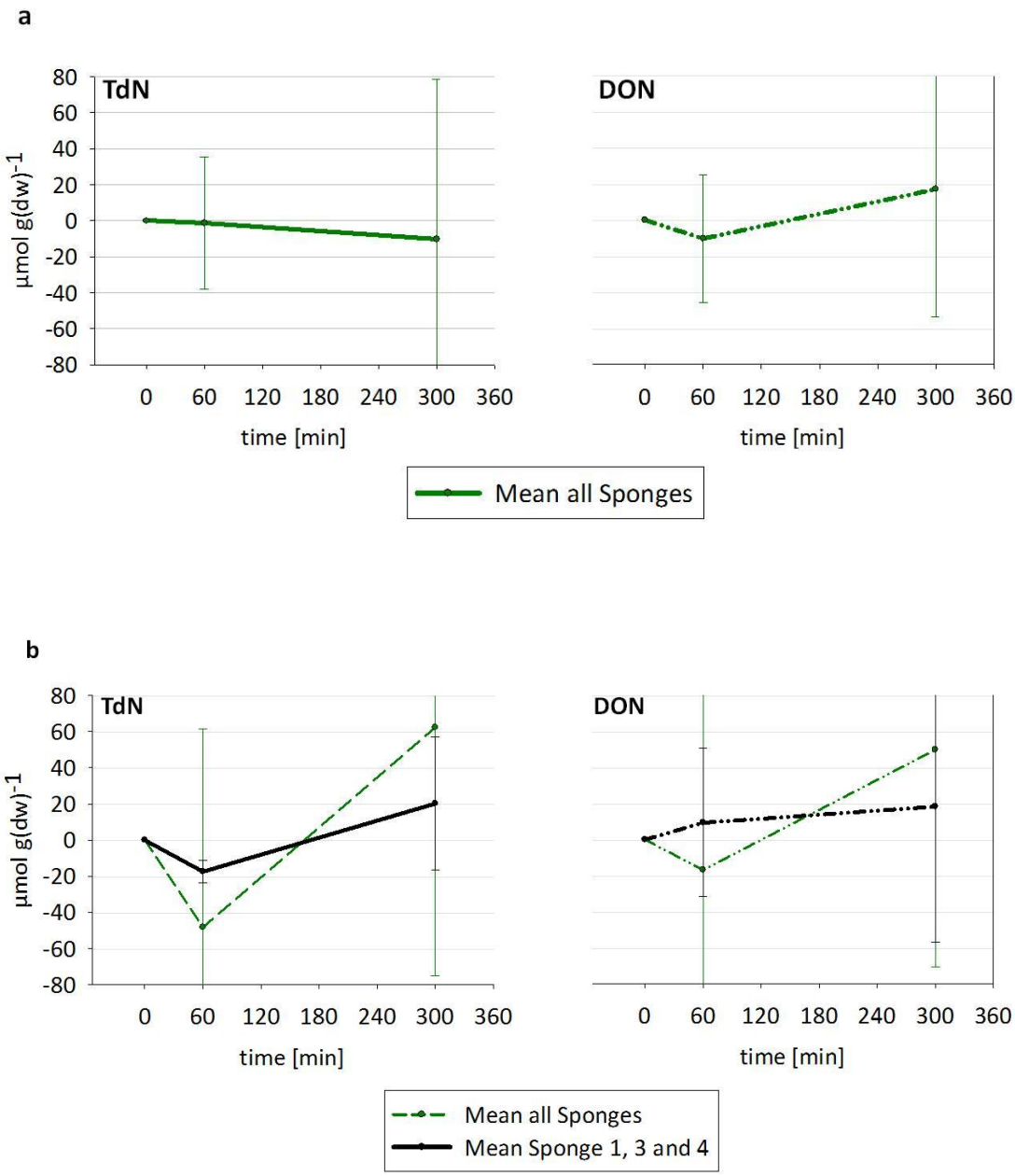

Fig. 18: Time- series of the concentration of dissolved (DON) and total dissolved nitrogen (TdN) [µmol g(dw)$^{-1}$] during the 300 minutes incubation of sponges in artificial seawater (=control, a) and in artificial seawater enriched with cyanobacteria and nutrients (treatment; b). Given is the net change in nitrogen concentrations relative to the concentration of the previous sampling interval per dry weight of sponge. Colours of the graph indicate a selection of replicates (black, n=3) or all replicates displayed (green, n=6). Changes in DON and TdN are illustrated as mean±SD. Changes in DON are displayed as a dashed and dotted line since DON concentrations were calculated based on the obtained DIN and TdN values (DON= TdN- DIN). The sponges no.2, 5 and 6 were excluded from statistical analysis since the sponges did not pump, stopped or displayed an unusual pattern in their pumping.

3.3.3 Corals and Sponges

There were no changes in DON in the water column of experiments with corals and sponges in artificial seawater (Appendix; Mann- Whitney Rank Sum Test; table A. 15; Fig. 19a), but the concentration of TdN dropped in the first 60 minutes of the incubation time (Appendix; Students t- test; Mann- Whitney Rank Sum Test; table A. 14; Fig. 19a).

In sponge incubations enriched with cyanobacteria and nutrients there was a reduction in both, DON and TdN, in the first 60 minutes of incubation (Appendix; Students t- test; Mann-Whitney Rank Sum Test; table A. 14 and 15; Fig. 19b).

There was no difference in the water entering and exiting the oscules of the sponges in both experiments (Appendix; Students t- test; Mann- Whitney Rank Sum Test; table A. 16; Fig. 20a and b).

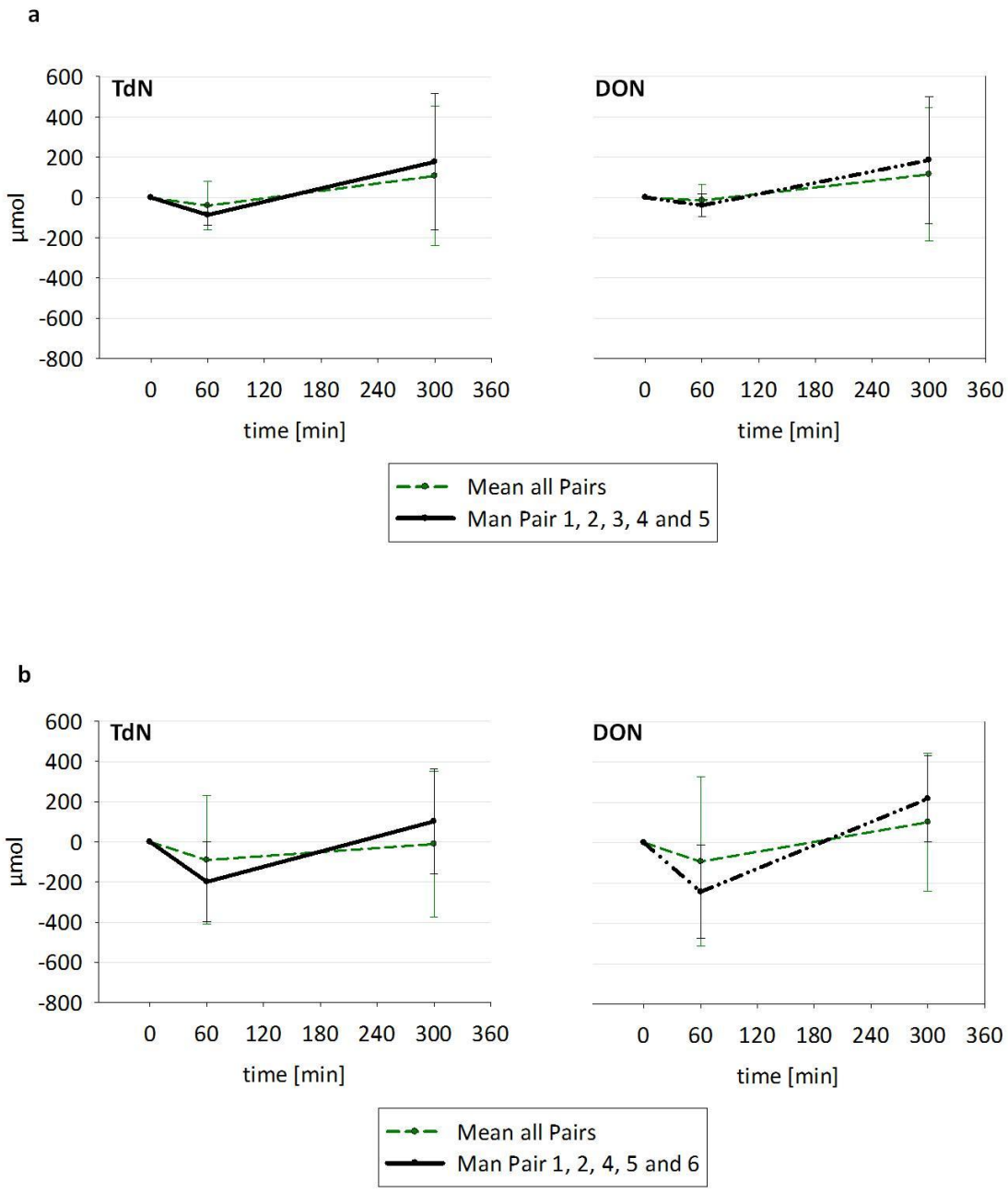

Fig. 19: Time- series of the concentration of dissolved (DON) and total dissolved nitrogen (TdN) [µmol] during the 300 minutes incubation of corals and sponges in artificial seawater (=control, a) and in artificial seawater enriched with cyanobacteria and nutrients (treatment; b). Given is the net change in nitrogen concentrations relative to the concentration of the previous sampling interval in µmol. Colours of the graph indicate a selection of replicates (black, n=5) or all replicates displayed (green, n=6). Changes in DON and TdN are illustrated as mean±SD. Changes in DON are displayed as a dashed and dotted line since DON concentrations were calculated based on the obtained DIN and TdN values (DON= TdN- DIN). The pairs no. 6 and 3 were excluded from statistical analysis since they displayed an unusual pattern (see Appendix; Fig. A. 6 and 7).

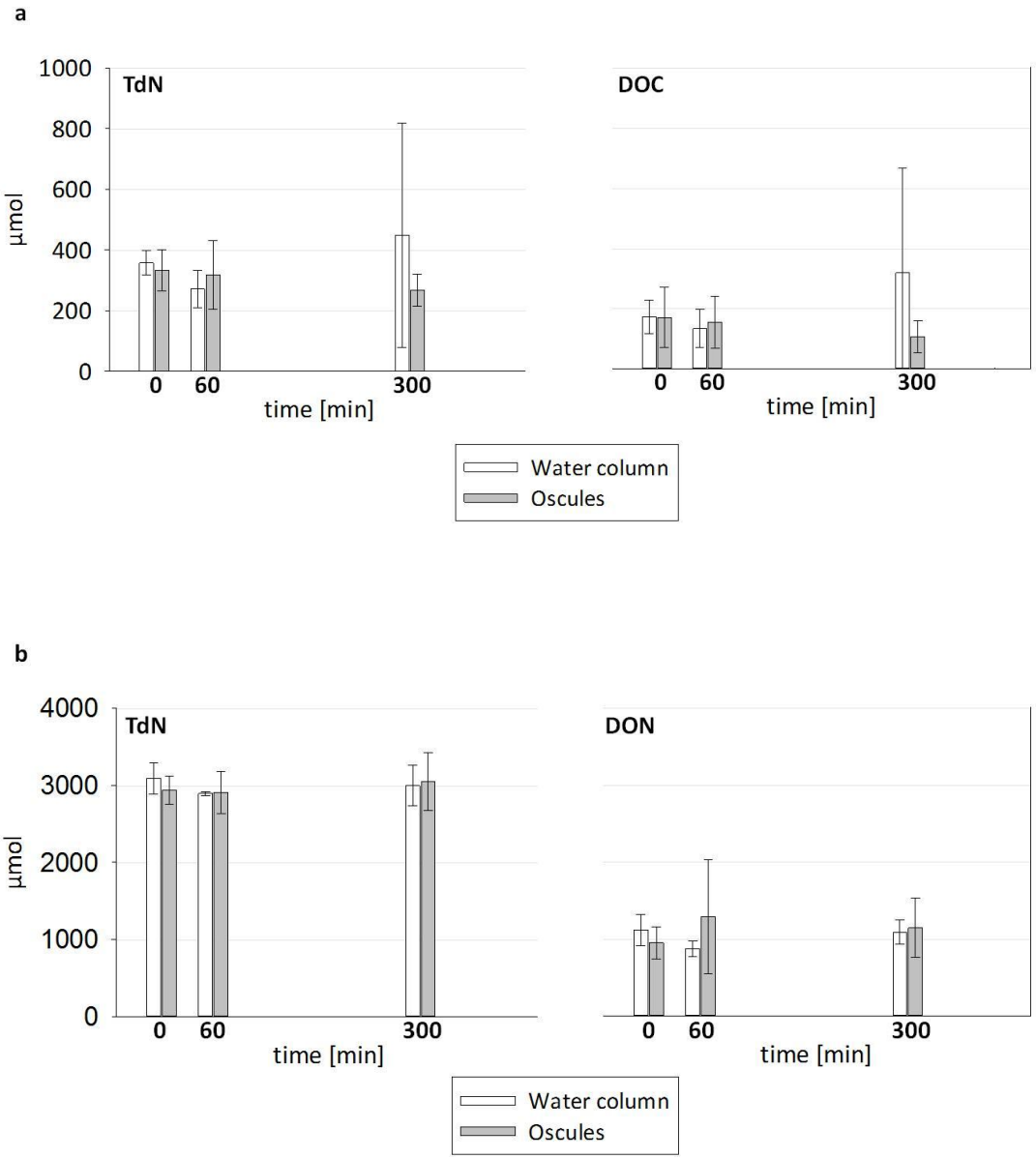

Fig. 20: Comparison of dissolved and total organic nitrogen (mean DON/ TdN) in µmol in the water column (white bars) and exiting the oscules (grey bars) of corals and sponges in the control group (artificial seawater, n=6; Fig. a) and in the treatment group (artificial seawater enriched with nutrients and cyanobacteria, n=5; Fig. b). The error bars represent the standard deviation.

3.4 Carbon/ nitrogen content

3.4.1 Corals

The carbon and nitrogen content on the filters of corals incubated in artificial seawater (=control) and in artificial seawater enriched with nutrients and cyanobacteria (= treatment) did not change during the 180 minutes of the experiment (Appendix; Students t- test; table A. 17; Fig. 21a and b). However, the carbon/nitrogen (C/N) ratio of the control group declined between the start of the incubation and 180 minutes (p=0.015; Mann- Whitney Rank Sum test; Appendix; table A. 17). The C/N ratio of treatment group showed no differences between 0 and 180 minutes (table 7; Appendix; Students t- test; table A. 17).

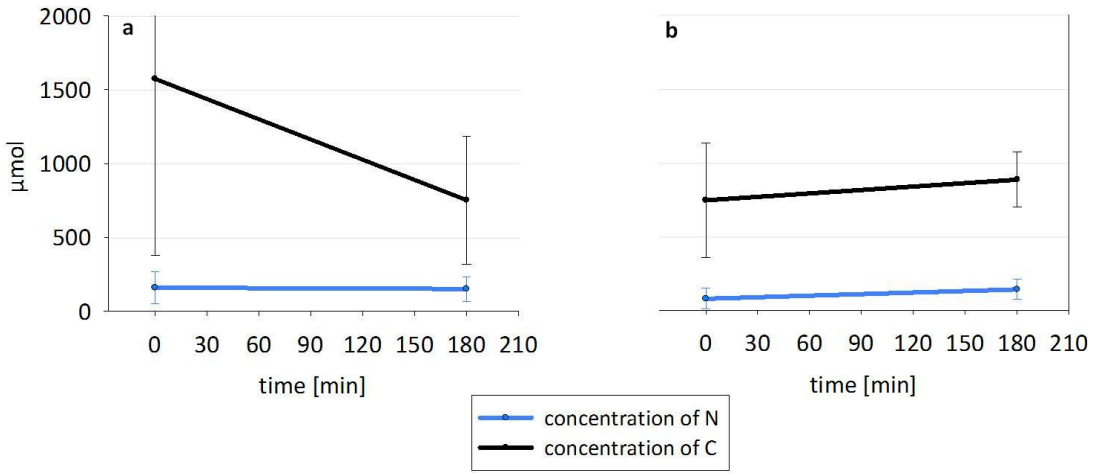

Fig. 21: The carbon and nitrogen content (mean ± SD) on GF/F filters of corals incubated in artificial seawater (a, n=6) and in artificial seawater enriched with cyanobacteria and nutrients (b, n=6) during 180 minutes of the experiment**.**

Tab. 7: C/N ratios (mean ± SD) of corals incubated in artificial seawater (control, n=6) and in artificial seawater enriched with cyanobacteria and nutrients (treatment, n=6) at the start of the experiment and after 180 minutes.

Kind of incubation	0 minutes	180 minutes
Control	12.35 (± 6.26)	4.17 (± 2.02)
Treatment	11.29 (± 7.84)	8.97 (± 7.44)

3.4.2 Sponges

The carbon and nitrogen content on the filters as well as the C/N ratios of sponges in experiments with artificial seawater (= control) did not vary during the 180 minutes of the incubations (repeated measures ANOVA; table 9; Fig. 22a). Though, sponges incubated in artificial seawater enriched with nutrients and cyanobacteria (= treatment) exhibited a distinct decline in both, carbon and nitrogen content between 0, 30 and 180 minutes ($p= 0.048$ and $p= 0.008$; repeated measures ANOVA; table 9; Fig. 22b). Moreover, there was a marked increase in the C/N ratio after 180 minutes of incubation compared to the ones at 0 and 30 minutes (repeated measures ANOVA; table 9).

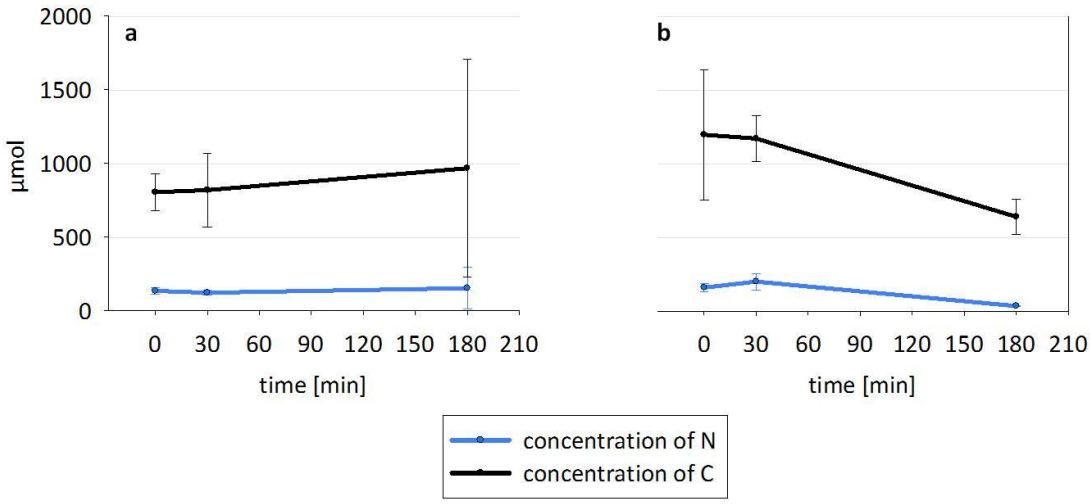

Fig. 22: The carbon and nitrogen content (mean ± SD) on GF/F filters of sponges incubated in artificial seawater (a, n=4) and in artificial seawater enriched with cyanobacteria and nutrients (b, n=3) during 180 minutes of the experiment.

Tab. 8: C/N ratios (mean ± SD) of sponges incubated in artificial seawater (control, n=6) and in artificial seawater enriched with cyanobacteria and nutrients (treatment, n=6) at the start of the experiment and after 180 minutes.

Kind of incubation	0 minutes	30 minutes	180 minutes
Control	5.99 (± 0.66)	6.62 (± 1.26)	7.88 (± 3.39)
Treatment	7.52 (± 1.83)	6.29 (± 1.91)	19.46 (± 5.12)

Tab. 9: One way repeated measures ANOVA to test for differences in carbon and nitrogen concentrations and ratios in incubations with sponges in artificial seawater (control group, n=4) and in artificial seawater enriched with cyanobacteria and nutrients (treatment group, , n=3) during 180 minutes. The Duncan´s Method (Appendix; table A. 18- 20**)** was applied for the pair wise multiple comparison procedure. Levels of significance: *p<0.05 and **p<0.01.

Kind of incubation	Parameter	Df	SS	F	p
Control	Carbon	11	1203.880	0.130	0.880
	Nitrogen	11	40.330	0.138	0.874
	C/N	11	61.302	0.537	0.610
Treatment	Carbon	8	663.974	7.150	0.048*
	Nitrogen	8	32.941	21.056	0.008**
	C/N	8	417.102	20.610	0.008**

3.4.3 Corals and Sponges

The carbon and nitrogen content on the filters and also the C/N ratios of corals and sponges in the experiments with artificial seawater (= control) did not change during 180 minutes (Appendix; Students t-test; table A. 21; Fig. 23a). However, the values for carbon and nitrogen in the incubations with seawater enriched with nutrients and cyanobacteria (= treatment) displayed a considerable elevation between 0 and 180 minutes (p= 0.029; Mann- Whitney Rank Sum Test; table 11; Fig. 23b). A difference in the C/N ratios during the experiment could not be detected (Students t-test; table 11).

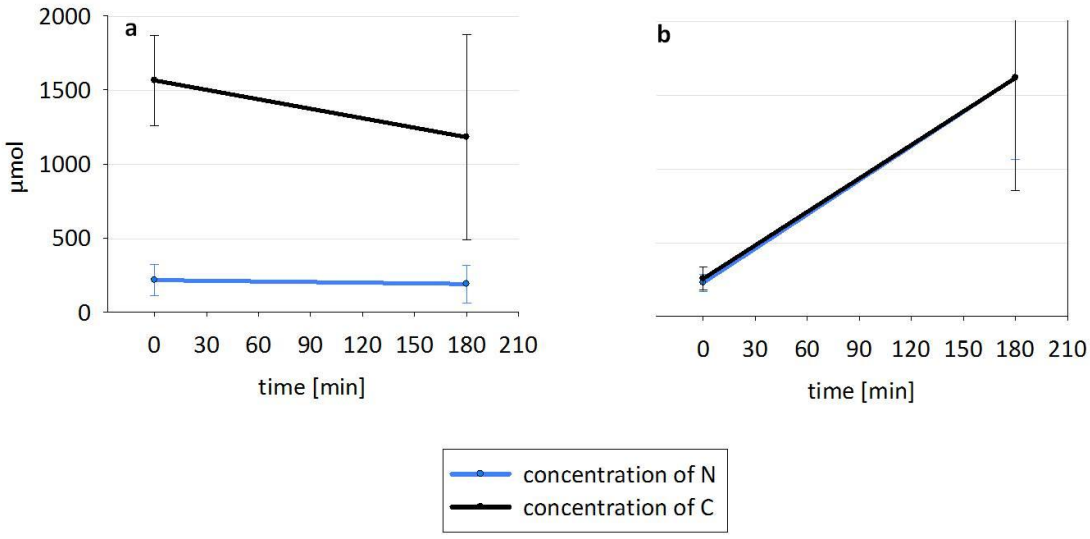

Fig. 23: The carbon and nitrogen content (mean ± SD) on GF/F filters of sponges incubated in artificial seawater (a, n=6) and in artificial seawater enriched with cyanobacteria and nutrients (b, n=4) during 180 minutes of the experiment. Two samples got contaminated during the analysis procedure.

Tab. 10: C/N ratios (mean ± SD) of corals and sponges incubated in artificial seawater (control, n=6) and in artificial seawater enriched with cyanobacteria and nutrients (treatment, n=4) at the start of the experiment at 30 minutes and after 180 minutes in the water column and exiting the oscules.

	Water column		**Oscules**	
Kind of incubation	**0 minutes**	**180 minutes**	**0 minutes**	**180 minutes**
Control	8.59 (± 3.59)	5.64 (± 3.06)	5.48 (± 1.29)	5.26 (± 0.88)
Treatment	7.02 (± 0.62)	6.17 (± 0.81)	5.31 (± 1.15)	5.33 (± 1.65)

Tab. 11: Students t-test to examine differences in carbon and nitrogen concentrations and ratios in incubations with corals and sponges in artificial seawater (control group, n=6) and in artificial seawater enriched with cyanobacteria and nutrients (treatment group, n=4) during 180 minutes. Levels of significance: *p<0.05 and **p<0.01.

Parameter	**P**	**T**	**T**	**n**
N	0.029*	-	10.000	4
C	0.029*	-	10.000	4
C/N	0.196	1.455	-	4

There were no variations in both, the control and treatment groups, between water entering and exiting the oscules (Appendix; Students t-test and Mann- Whitney Rank Sum Test; table 22; Fig. 24a and b). The only detectable difference was a decline in the C/N ratio of water exiting the oscules in the treatment group at the start of the experiment compared to the ambient water (Appendix; Students t-test; table 22).

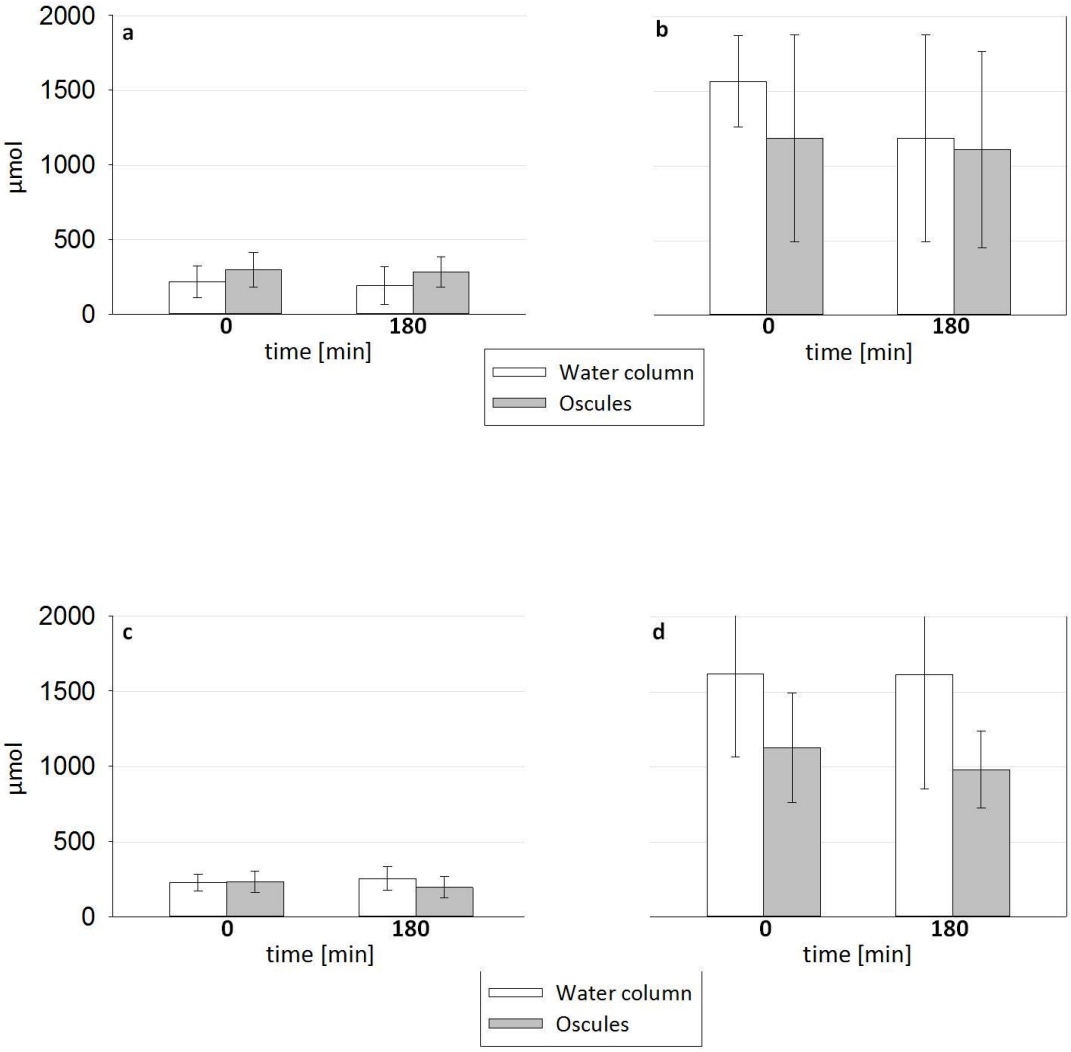

Fig. 24: Comparison of nitrogen (a, c) and carbon (b, d) content (mean ± SD) [µmol] in the water column (white bars) and exiting the oscules (grey bars) of the sponges in the control group (artificial seawater, n=6; a and b) and in the treatment group (artificial seawater enriched with nutrients and cyanobacteria, n=4; c and d). The error bars represent the standard deviation.
Pairs no.5 and 6 were excluded in the statistical analysis and graphical illustration since their filters got contaminated during the analysis.

Tab. 12: C/N ratios (mean ± SD) of corals and sponges incubated in artificial seawater (control, n=6) and in artificial seawater enriched with cyanobacteria and nutrients (treatment, n=4) at the start of the experiment at 30 minutes and after 180 minutes in the water column and exiting the oscules.

	Water column		**Oscules**	
Kind of incubation	**0 minutes**	**180 minutes**	**0 minutes**	**180 minutes**
Control	8.59 (± 3.59)	5.64 (± 3.06)	5.48 (± 1.29)	5.26 (± 0.88)
Treatment	7.02 (± 0.62)	6.17 (± 0.81)	5.31 (± 1.15)	5.33 (± 1.65)

3.5 Tissue analysis

The results of the tissue analysis of all fungiids after the incubations are summarized in table 13. No significant differences were found in all examined parameters between the different experiments (Appendix; one way ANOVA and Kruskal- Wallis one way ANOVA; table A. 23).

Tab. 13: Mean values (± SD) of protein and chlorophyll a (chla) content, zooxanthellae density and mitotic index of corals of the genus *Fungia* (n=6) in the control (= artificial seawater) and treatment (artificial seawater enriched with cyanobacteria and nutrients) group.

Organism	Kind of incubation	Protein content [mg cm^{-2}]	chl*a* [µg cm^{-2}]	Zooxanthellae density [10^5 cm^{-2}]	Mitotic Index [%]
Fungia	Control	3.78 (± 1.97)	2.15 (± 0.88)	1.48 (± 0.54)	0.36 (± 0.30)
	Treatment	4.61 (± 2.59)	2.32 (± 1.71)	0.99 (± 0.31)	0.35 (± 0.31)
Fungia + Sponge	Control	4.28 (± 2.33)	4.13 (± 2.16)	1.61 (± 0.89)	0.43 (± 0.19)
	Treatment	4.73 (± 2.18)	3.45 (± 1.98)	1.16 (± 0.60)	0.27 (± 0.30)

3.6 Photophysiological responses

It appeared that the photosynthetic efficiency of corals with no additional nutrient and cyanobacteria supply (= control) declined during the incubations, though it failed to be statistically significant. There were even no changes in the photosynthetic performance of the corals either caused by supplementary nutrients and cyanobacterias (= treatment) or by the presence of a sponge (Appendix; Kruskal- Wallis One Way ANOVA; table A. 24). The photosynthetic efficiency at the end of any of the four incubations did not differ from the one at the beginning (Appendix; Students t-test or Mann- Whitney Rank Sum Test; table A. 25).

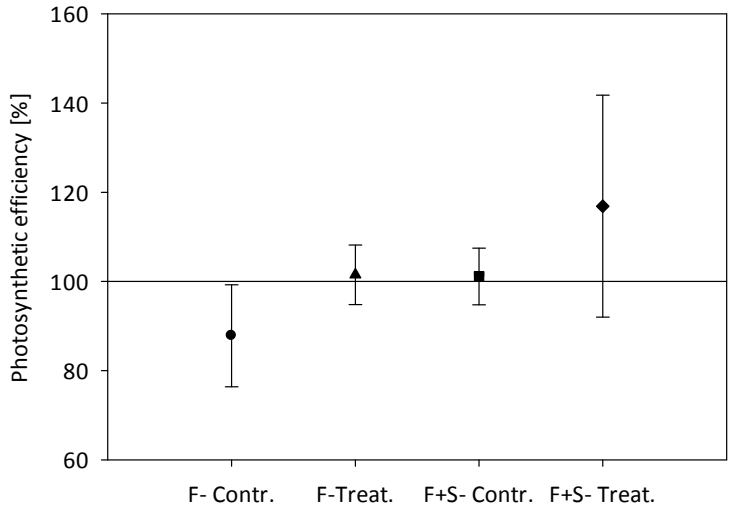

Fig. 25: Mean values of the photosynthetic efficiencies [%] at the end of the different incubations. Start mean values calculated as 100% (solid line). Error bars represent standard deviation. Control: incubations in artificial seawater (ASW). Treatment: incubations in ASW with cyanobacteria and nutrients. Replicates for each measurement: Start (n=6), Fungiids Control (F-Contr.: n=6) Fungiids Treatment (F-Treat.: n=5), Fungiids and Sponges Control (F+S-Contr.: n=4),Fungiids and Sponges Treatment (F+S-Treat.: n=3).

The maximum photosynthetic rate of corals incubated alone in the control group did decline compared to the beginning (p= 0,002) whereas the one of corals when nutrients and cyanobacteria were added remained unchanged (Mann- Whitney Rank Sum Test; table 14). Besides, the presence of a sponge in either the control or treatment group resulted in an increased photosynthetic rate of corals in comparison to the start of the experiments (Whitney Rank Sum Test; p= 0,002 and p= 0,024; table 14; Fig. 25).

The presence of a sponge, the addition of nutrients and cyanobacteria as well as both combined produced a considerable elevation of the photosynthetic rate of corals compared to corals incubated solely in artificial seawater (p=0,003; Kruskal Wallis One Way ANOVA; table 15).

However, the presence of a sponge in the treatment group (artificial seawater enriched with nutrients and cyanobacteria) did not have an effect on the photosynthetic rate of corals (Appendix; Kruskal Wallis One Way ANOVA; table A. 24).

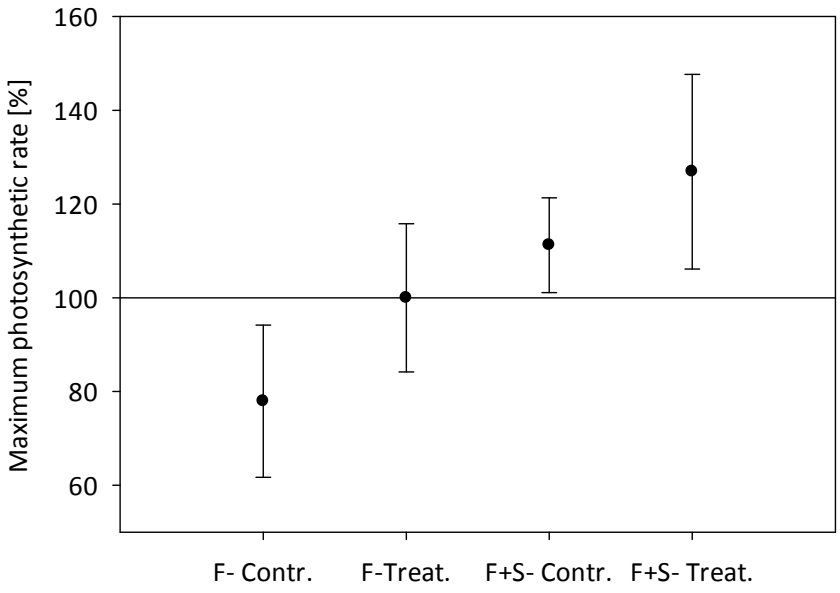

Fig. 26: Mean values of the maximum photosynthetic rates [%] at the end of the different incubations. Start mean values calculated as 100% (solid line). Error bars represent standard deviation. Control: incubations in artificial seawater (ASW). Treatment: incubations in ASW with cyanobacteria and nutrients. Replicates for each measurement: Start (n=6), Fungiids Control (F-Contr.: n=6), Fungiids Treatment (F-Treat.: n=5), Fungiids and SpongesControl (F+S-Contr.: n=4),Fungiids and Sponges Treatment (F+S-Treat.: n=3).

Tab. 14: Pair wise Mann- Whitney Rank Sum Test to test for difference between start (100%) and end values [%] in the maximum photosynthetic rate of different experiments. n: replicates per treatment; levels of significance: *p<0.05 and **p<0.01.

Experiment	P	N
Fungiids- Control	0.002**	6
Fungiids- Treatment	0.662	5
Fungiids + Sponges- Control	0.010*	4
Fungiids + Sponges- Treatment	0.024*	3

Tab. 15: Kruskal- Wallis one way ANOVA to test for differences in the maximum photosynthetic rate of corals between the different incubations and treatments. FC: Fungiids in the control group (artificial seawater); FT: Fungiids in the treatment group (artificial seawater enriched with nutrients and cyanobacteria); FSC: Fungiids together with sponges in the control group and FST: Fungiids together with sponges in the treatment group.The Holm- Sidak method was applied for the pairwise multiple comparison procedure (for details see Appendix table A. 26). Levels of significance: *p<0.05 and **p<0.01.

SS	F	p	Df
9089.418	8.459	0.001**	23

4 Discussion

4.1 Nutrients

4.1.1 Corals

The corals incubated in artificial seawater (= control) exhibited no changes in ammonium and nitrate concentrations. This result was expected since the corals had nothing to feed on. Small negligible variations are likely caused by strong excretion of mucus induced by stress during the transfer process from the maintaining aquaria into the experimental chamber (personal observation).

Corals incubated in artificial seawater enriched with cyanobacteria and nutrients (= treatment) showed as well no differences in ammonium and nitrate concentrations in the 300 minutes of the experiment. Overall, the nitrate concentrations had a tendency to decline whereas the ones of ammonium tended to increase until the end of the incubations while displaying opposing patterns in their fluctuations during the time course of the experiment. However, the fluctuations failed to be statistically significant because of the high variability in the feeding response of the corals.

It is known that corals of the genus *Fungia* have the ability to take up nitrate with rates up to 5.6 nmol cm^{-2} h^{-1} (Webb and Wiebe 1978) as well as ammonium (Burris 1983). For ammonium there were no uptake rates given, but different corals are reported to ingest 1 to 20 nmol cm^{-2} h^{-1} ammonium (Atkinson et al. 1994).

The extremely high variations of nitrate and ammonium values in this study are presumably induced by the pronounced excretion of mucus (personal observation). Moreover, corals are known to both consume and produce nitrate (Wafar et al. 1990) and ammonium (Lipschultz and Cook 2002). That the fungiids alternately released and took up both nutrients during the incubation might be as well the case and could be an explanation for the strong fluctuations. The ingestion of ammonium and nitrate is dependent on a variety of factors such as their concentration in the water column, the water flow and the time of day (Burris 1983; Grover et al. 2003; Badgley et al. 2006). The consumption of nitrate is additionally subjected to the exposure of ammonium and light levels (Wilkerson and Trench 1985; Grover et al. 2003; Badgley et al. 2006).

It was observed for *Diploria strigosa*, *Stylophora pistillata*, *Pocillopora damicornis*, *Seriatopora hystrix* and *Fungia fungites* that uptake rates increased with an elevation of the nutrient concentrations in seawater. The uptake rates varied between 1.4 and 8.0 N ng h^{-1} cm^{-2} (0.3 µmol and 3µmol NO_3^- enrichment; Burris 1983; Grover et al. 2003). Moreover, the consumption of ammonium was 20 times lower at 0.2 compared to 1 or 5 µmol NH_4^+ enrichment. Besides, there were no differences in the uptake rates between 1 or 5 µmol NH_4^+ enrichment. Thus, the incorporation of nitrogen in corals is assumed to be saturated at a concentration of 1 µmol ammonium (Burris 1983). For *Diploria strigosa* a saturation concentration of approximately 3 µmol NO_3^- was detected (Badgley et al. 2006). The uptake rates in this study should not be negatively influenced since in the treatment groups the incubation water was spiked with 33.37 (± 5.17) µmol NH_4^+ l^{-1} and 32.79 (± 4.22) µmol NO_3^- l^{-1}.

Low water flow causes the creation of a boundary layer due to the fact that any incorporation of a dissolved substance provokes a localized depletion in the water surrounding the coral. An increased water flow ensures that this boundary layer gets thinner or breaks down completely and delivers greater amounts of DIN to the coral surface enabling an increased ingestion of DIN (Thomas and Atkinson 1997; Patterson 1992). The uptake of ammonium for instance differs by two times during a 10- fold change in water flow (Atkinson et al. 1994). However, the flow rate plays solely a decisive role at low concentrations but it was spotted that at higher concentrations of 6 µmol NO_3^- kinetic limitation was crucially for ingestion of nitrate (Badgley et al. 2006). The water velocity of 3.27 to 6.08 cm s^{-1} in this study was sufficient to prevent a diffusional limitation since flow rates on some reefs in Bermuda were usually less than 7 cm s^{-1} (Badgley et al. 2006). Nevertheless, the experimental chamber in the present study produced a laminar flow while it is proven that oscillatory flow as a result of wave action and currents leads to twofold to threefold higher rates of mass transfer than laminar flow (Atkinson et al. 2001; Hearn et al. 2001). However, it could be assumed that the adequate flow rates combined with spiking such high concentrations of ammonium and nitrate rather facilitated the nutrient uptake.

Some corals demonstrated a distinct diurnal cycle with the highest uptake rates in the late afternoon and the lowest in the early morning (Bythell 1990). This fact is unlikely to explain the strong fluctuations in nutrient excretion and consumption in the only 5 hour incubation time in this study.

More importantly, it is observed that ammonium can inhibit the ingestion of nitrate (Wilkerson et al. 1985; Badgley et al. 2006). No inhibition of nitrate occurred when *Diploria strigosa* was exposed to 0.5 µmol ammonium. Though after a 48 h exposure to ammonium levels the nitrate uptake was completely inhibited (Badgley et al. 2006). Other studies (Wilkerson et al. 1986; Grover et al. 2003) found that the nitrate uptake was dependent on the ammonium concentration, but it was rather a preferential consumption of ammonium than a repression of the ingestion of nitrate. Moreover, in the presence of ammonium the nitrate consumption was demonstrated to be dependent on the light levels with higher ingestion under high light (Grover et al. 2003).

In contrast, Bythell (1990) even observed a simultaneous uptake of nitrate and ammonium with the net rates of nitrate uptake twofold higher than the ones for ammonium. An explanation for these results could be that ammonium is involved in an internal recycling and therefore nitrate represents the major external source of nitrogen and that there is a variable direction of ammonium flux at low concentrations (Bythell 1990). Besides, it is shown that if there is an inhibition caused by ammonium it cannot be generalized especially when organisms are nitrogen- starved (Dortch 1990).

In this study it could be possible that there occurred an inhibition of nitrate uptake due to the exceptionally high ammonium concentrations. A simultaneous ingestion of both nutrients seems not conceivable considering the opposing patterns of both nutrients over the time course of the experiment in the treatment group.

4.1.2 Sponges

Sponges in solely artificial seawater (= control) did not show any variation in dissolved inorganic nutrients (DIN) except of a decrease in ammonium concentrations of 7.14 µmol g(dw)$^{-1}$ between 60 and 180 minutes. This decline can be interpreted as a consumption of the sponge. An elevation in nitrate concentrations could not be detected.
The findings that there were no major changes in DIN concentrations are consistent with the idea that microbial communities associated with the sponge tissue are responsible for DIN transformations and not other processes taking place in artificial seawater during the time of the incubation (Diaz and Ward 1997).
In the treatment group (=artificial seawater enriched with cyanobacteria and nutrients) the sponges displayed a net accumulation of nitrate in the incubation water, presumably as a result of nitrate production from the sponges. The significant excretion of nitrate indicates microbially- mediated nitrification (Corredor et al. 1988; Diaz and Ward 1997; Jiménez and Ribes 2007) since most animals typically release ammonium or amino- rich compounds (Baldwin 1970; Barnes 1974). Besides, bacteria and archaea ammonia oxidizers are the only organisms capable of oxidizing ammonium to nitrate (Ward 2000). In this study, the bacterial composition of sponges was not investigated, thus their presence can only be suspected.
The nitrate production rates had a maximum of up to 69.58 µmol g(dw)$^{-1}$. Moreover, ammonium an expected nitrogenous waste product of the sponge metabolism did not accumulate in the incubation water. Ammonium was rather consumed than released by the sponge, *Cacospongia spec.*. During two time intervals of the experiment, in the first 30 minutes and between 60 and 180 minutes, an intake of ammonium occurred. These findings are coherent with the results of other studies (Diaz and Ward 1997; Jiménez and Ribes 2007). In the experiments of Diaz and Ward (1997) the sponge *Chondrilla nucula* either consumed ammonium or produced negligible amounts of ammonium and in incubations of Jiménez and Ribes (2007) the sponges *Chondrosi reniformis* and *Aplysina aerophoba* ingested as well ammonium. All three sponges exhibited increments in nitrate concentrations. On that account it is assumed that *Cacospongia spec.* like the other sponges is equipped with an efficient coupling between ammonium production and subsequent ammonium and nitrite oxidation. In that way a net increase in nitrate can take place without a comparable accumulation of ammonium in the water column.

The maximum nitrate production rates of other sponges ranged from 0.77 µmol g(dw)$^{-1}$ h^{-1} (*A. aerophoba*, Jiménez and Ribes 2007) to 2.65 µmol g(dw)$^{-1}$ h^{-1} (*C. nucula*, Diaz and Ward 1997). The maximum nitrate production rate of 69.58 µmol g(dw)$^{-1}$ obtained in this study is considerably higher than in the other studies. Nevertheless, similar rates of DIN fluxes were measured in *Aplysina lacunosa*, *Aplysina cauliformis* and *Smenospongia aurea* with rates ranging from 4 to 7 µmol h^{-1} cm^{-2} (Southwell 2007) compared to 5.43 µmol cm^{-2} between 180 and 300 minutes of incubation in this study. The surface area of sponges is calculated by means of height, width and length assuming a cuboid geometry. However, this could represent an oversimplification probably resulting in a lack of accuracy in the calculated surface areas.

Earlier studies (Fisher et al. 1982; Corredor et al. 1988; Capone et al. 1992; Morell and Corredor 1993) reported all distinctly lower nitrification rates. The volume effect is a likely explanation for the lower rates of DIN production previously observed. It is caused by a drop in oxygen concentrations and/ or nutrients due to high filtration rates of tropical sponges (Reiswig 1971; Weisz 2006). Corredor et al. (1988) used 2.25l chambers and Diaz and Ward (1997) used on the one hand 3l chambers and on the other hand 20l chambers for incubations of the same sponge species and found considerably lower values in nitrate release in the smaller chambers. Moreover, the accumulation of ammonium in the incubation chambers could have artificially increased the nitrification rates since in the ocean ammonium would be lost via diffusion (Olson 1981). In the present study ammonium was even added supplementary to a final concentration of 30 µmol l^{-1}. Furthermore, the bacterial composition dominating the internal of the sponge mesohyl could vary and result in different nitrification rates (Santavy et al. 1990; Diaz and Ward 1997).

In similar experiments (Diaz and Ward 1997; Jiménez and Ribes 2007; Southwell 2007) the nitrate production took place linearly. However, in this study the values for nitrate remained unchanged followed by a marked release between 180 and 300 minutes in all sponges. A possible reason could be differences in the pumping patterns of the sponges. Sponges are known to exhibit patterns in their pumping rates and even slow down their pumping rates periodically dependent on a variety of factors, such as temperature, reorganization and cleaning of canals or physical disturbances (Reiswig 1971; Weisz 2006). These variations could be already observed between the single individuals in the incubations. Sponge 5 did not pump at all probably due to its greater susceptibility to physical disturbances during the

transfer process into the experimental chamber. Sponge 2 exhibited an exceptional pumping activity and sponge 6 ceased to pump after 180 minutes of incubation (Appendix; Fig. A. 2). A likely explanation could be that the sponges had to recover from the stress caused by the transfer process from the maintaining aquaria to the experimental one.

4.1.3 Corals and Sponges

When sponges and corals were incubated together in artificial seawater (= control) there was an increase in nitrate concentrations after 60 minutes, an elevation of ammonium concentrations after 180 minutes and a rise in nitrite concentrations from 180 minutes until the end of the incubation. However, there were no significant differences found between the water column and water exiting the oscules of the sponges. Nevertheless, it can be assumed that the nitrite production is the result of the sponge metabolism since there were no changes in nitrite detected in the coral incubations and sponges capable of nitrification often produce small amounts of nitrite as well (Diaz and Ward 1997; Jiménez and Ribes 2007). Moreover, the sponges seemed to be stressed by the sampling of water exiting their oscules with a syringe. Therefore, they started to close their oscules partially (personal observation). This could have as well lead to anoxic conditions inside the sponge tissue since sponges are known to have the ability to control their ventilation behaviour thereby providing an adequate habitat for both aerobic and anaerobic microbial communities (Reiswig 1971; Vogel 1977; Pile et al. 1997; Hoffmann et al. 2009). Sponges with a massive growth form, such as *Cacospongia sp.* in this study, are reported to become anoxic within 15 minutes after ceasing of their pumping activity (Hoffmann et al. 2008). Oxygen deficiencies could develop when the pumping activity is reduced by for instance closing partially their oscules (Gatti et al. 2002; Hoffmann et al. 2007). These oxygen deficiencies could have fueled anaerobic microbial processes like denitrification, the reduction of nitrate (NO_3^-) to nitrogen (N_2) in which nitrite (NO_2^{2-}) would be an intermediate product. However, no changes in nitrogen concentrations were measured in order to prove this assumption. It would seem likely since there was a change in the behavior of the sponges (partially closing their oscules) and it is demonstrated that both processes (nitrification and denitrification) can occur simultaneously in the same sponge individual (Hoffmann et al. 2009). Another explanation of the high nitrite concentrations could be that nitrite oxidizers in the sponge could not cope so well as ammonia oxidizers with the stress caused by sample taking. As a result, solely partial nitrification might have taken place.

Again the corals excreted a lot of mucus due to the transfer stress which could be a possible source of dissolved organic carbon (DOC) for the sponges. A possible reason why the nitrate concentration after 60 minutes of incubation did not differ from zero could be that the

corals took up the nitrate produced by the sponges. Then again the high nitrate concentration in the first 60 minutes of incubation could be caused as well by the strong secretion of coral mucus.

When sponges and corals received additionally nutrients and cyanobacteria (=treatment) the patterns in nutrient release/ consumption were similar. The nitrate concentrations rose as well in the first 60 minutes and the nitrite concentrations increased also between 180 and 300 minutes of the incubation; however these increases failed to be statistically significant. The ammonium concentrations showed two markedly declines, one between 0 and 30 minutes and the other between 60 and 180 minutes. It is striking that both declines in ammonium concentrations are accompanied by a subsequent rise once in the nitrate and once in the nitrite concentrations even if those elevations were not statistically significant. This would then indicate that the sponges nitrified or partially nitrified. Again it could be possible that higher nitrate concentrations after 60 minutes of incubation were not detected since the corals could have taken up nitrate released by the nitrification activity of the sponges.

4.2 Dissolved, total and particulate organic carbon (DOC/ TOC/ POC) and dissolved and total dissolved nitrogen (DON/ TdN)

4.2.1 Corals

Corals incubated solely in artificial seawater (= control) displayed no variations in dissolved, particulate and total organic carbon (DOC, POC, and TOC) or dissolved organic nitrogen (DON). Only the total dissolved nitrogen (TdN) concentrations declined in the first 60 minutes of the experiment. Since there was no simultaneous decrease in DON concentrations a concomitant reduction in the dissolved inorganic nitrogen (DIN) species would be expected. The values for nitrate exhibited a decline but it failed to be statistically significant.

However, a rise in POC and a decrease in DOC, DON and TdN was expected since it is known that corals are able to release large amounts of POC and DOC and particulate organic nitrogen (PON) and DON in the form of coral mucus (Crossland 1987; Ferrier-Pages et al. 1998). Besides, especially corals of the genus *Fungia* are reported to have a strong mucus production (Wild et al. 2005). In all corals an excretion of mucus in form of gel- like threads could be observed during their 1 hour acclimation period. However, corals of the genus *Fungia* are reported to even show a net uptake of DOC with rates of

-14.2 ± 5.5 mg DOC m^{-2} h^{-1} (Naumann et al. 2010). Nevertheless, neither an uptake nor a release of DOC was measured in the experiments.

Further, it was demonstrated that the excretion of dissolved organic matter (DOM) is dependent on the feeding history of the corals with release rates 2 to 3 times elevated in fed corals. Moreover, it was shown that fed corals released more DOC than unfed corals but did not differ in the release rates of DON (Ferrier- Pages et al. 1998). The same results were obtained by Naumann et al. (2010) who found that the released particulate organic matter (POM) was dominated by POC and consisted solely of a small amount of particulate nitrogen (PN). Therefore it could be concluded that the zooxanthellae are nitrogen limited and heterotrophic food intake provides the corals with nitrogen while carbon obtained through heterotrophic feeding is subsequently excreted (Muscatine et al. 1989; Z. Dubinsky and Jokiel 1994; Ferrier-Pages et al. 1998). The corals used in the present study were fed once

per week with *Artemia nauplii* which should have encouraged the excretion of DON, PN and especially DOC and POC. A reason why there occurred no elevation in DON, DOC, POC and PON could be (a) that the volume of the incubation chamber was too large to determine the smaller changes in DON and PON and (b) that there was indeed an excretion of mucus, but that it was ingested again by the corals before significant changes could be detected. Coral associated bacteria (epibiotic or intracellular) are responsible for an uptake of DOC and differences in the ingestion of DOC is the result of variations in bacterial communities inhabiting the coral or of the dominance by a certain bacterial group (Ferrier-Pages et al. 1998; Rohwer et al. 2002). In an experiment of Ferrier- Pages et al. (1998) the DOM concentrations declined after 2 hours of their release by corals. A consumption of free living bacteria could be excluded since they were present in only small concentrations in the incubations and in experiments performed with the addition of antibiotics the release of DOM was not followed by a subsequent uptake (Ferrier- Pages et al. 1998). The coral associated bacteria are able to quickly take up the released mucus and use it for their own growth requirements. In this way they can provide the coral with other essential nutrients or serve as a food source for the corals (Schlichter 1982; Sorokin 1993).

When corals were incubated in artificial seawater enriched with nutrients and cyanobacteria no changes in DON, TdN, DOC, POC or TOC could be observed. According to expectations an elevation in TdN and POC and a decline in DON, DOC should have occurred since Fungiids are known to consume DOC (Naumann et al. 2010). Moreover, an increase of nitrate concentrations should have resulted in a decrease of POC and PN release (Naumann et al. 2010). The zooxanthellae of corals are primarily responsible for the uptake of nitrate (Grover et al. 2003) and if their growth is encouraged by an abundant nitrate supply they reduce the transfer of photosynthates to the coral host. This in turn results in a decreased release of mucus (POC and PN) which consists of up to 40 % of the photosynthetically fixed carbon and in *Fungia sp.* even of up to 98 % (Crossland 1987; Ikeda et al. 1995; Marubini and Davies 1996).

However, their released mucus is known to stimulate bacterial growth (POM; (Moriarty 1979; Moriarty et al. 1985; Marubini and Davies 1996). Especially the labile part of their exudates is metabolized quickly by autotrophic plankton (Palenik and Morel 1990). Even small amounts (0.5 to 10 % of maximum DOC concentrations) of coral exudates are sufficient to increase bacterial growth by a factor of up to 6 (Ferrier-Pages et al. 2000). Moreover,

freshly released exudates of *Fungia* polyps already contained background levels of synechococcoid cyanobacteria because they belong to the coral associated bacteria or were trapped during the time in the maintaining aquaria with normal seawater (Naumann et al. 2009). It is demonstrated that corals are able to efficiently trap POM in their mucus flocs with clearance rates for synechococcoid cells of up to 43 % within one hour of chamber rotation (Wild et al. 2004a; Naumann et al. 2009). Nevertheless, the formation of mucus aggregates loaded with cyanobacteria was not observed during the incubations.

4.2.2 Sponges

When sponges were incubated in artificial seawater (=control), there were no variations in DOC, TOC, POC, TdN or DON concentrations which corresponds to the expectations since no nutrition in form of nutrients or cyanobacteria was added. However, there the TdN concentrations seemed to decline between 60 minutes and 300 minutes of the experiment, but this changes failed to be statistically significant. This decline would be consistent with a decrease in the ammonium concentration starting from 60 minutes of the incubation.

Sponges incubated in artificial seawater enriched with nutrients and cyanobacteria (=treatment) produced DOC starting 60 minutes after the start of the experiment and consumed TdN in the first 60 minutes. No variations could be measured in the other parameters such as DON, POC or TOC.

The excretion of DOC and the uniform DON values did not meet the expectations since DON and especially DOC are known to be a major food source of sponges (Yahel et al. 2003; De Goeij et al. 2008a; de Goeij et al. 2008b). Even if sponges represent efficient filter feeders and are able to remove most of the living cells which enter their filtration system, it is demonstrated that they gain most of the carbon from the dissolved pool, 2 ± 1 µmol C l^{-1} compared to 10 ± 7 µmol C l^{-1} (Yahel et al. 2003). De Goeij et al. (2008a) examined the DOC removal rates of 3 encrusting sponges and revealed that they account for more than 90 % of the total organic carbon uptake. The first evidence of the direct incorporation of DOM by sponges presented a study (De Goeij et al., 2008b) with labeled ^{13}C-enriched diatoms which could detect ^{13}C-enrichment patterns not only in bacteria-specific but also in nonbacterial fatty acids of sponges. This fact proves that not only the microbial community, but also sponges in the reef systems are able to transform DOM to biomass and thus retain it in the system (De Goeij et al., 2008b). It was not investigated if the sponge species incubated in this study contained associated bacteria and to what extent they possibly might be involved in the nutrition of the sponge. In this study *Cacospongia sp.* released 89.00 µmol g(dw)$^{-1}$ in 300 minutes. A possible explanation why an increase in DOC concentration could be observed would be that the sponge, *Cacospongia sp.*, is not equipped with bacteria which utilize DOM either to a greater extent or not at all. This was also suggested by Ribes et al. (1999) who observed that *Dysidea avara* showed a net production of DOC (0.33 ± 0.15 mg C h^{-1} g ash free dryweight^{-1}). This sponge species has no

symbiotic bacteria (Turon et al. 1997) and thus no ability to take up DOC (Frost 1987; Ribes et al. 1999).

The decline in TdN in the first 60 minutes of the incubation fulfilled the expectations since the sponges consumed ammonium in the first 30 minutes and between 60 and 180 minutes. A further decrease in TdN values was not expected since the nitrate concentrations started to rise from 180 minutes of the incubation.

There appeared to be a reduction in POC concentrations in the first 60 minutes of the experiment but this failed to be statistically significant. Pico- and nanoplancton, such as cyanobacteria, are reported to be the major sources of POC for sponges with the highest retention efficiencies for cyanobacteria (89- 99 %; Reiswig 1971; Pile et al. 1996). They accounted for approximately 74 % of the total ingested carbon. Besides, sponges have the ability to process vast volumes of water, up to 100.000 times their own volume per day resulting in a fast depletion of POC (Weisz 2006). It is even reported that plankton depleted layers developed over reefs or in lakes (Pile et al. 1997; Yahel et al. 1998). Consequently, it was expected that *Cacospongia sp.* would as well deplete very fast the present cyanobacteria.

4.2.3 Corals and Sponges

In the experiments with corals and sponges incubated in artificial seawater (=control) there were no changes in DOC, POC, TOC, DON or TdN in the water column or between water entering and exiting the oscules.
It would have been expected that the concentrations of DON and TdN rose and the ones of POC and DOC either showed no changes or increased.
DON, DOC and POC should show increases since the corals exuded mucus consisting of dissolved and particulate organic carbon and nitrogen (Crossland 1987; Ferrier Pages et al. 1998). It is in fact demonstrated that mucus flocs are known to increase the growth of autotrophic plankton (Palenik and Morel 1990). However, the DOC uptake rates of fungiids could as well exceed the release rates (Naumann et al. 2010). Moreover, it appeared that *Cacospongia sp.* harbors no symbiotic bacteria which are able to utilize DOC and therefore should rather produce DOC (Ribes et al. 1999). Besides, due to the high filtration and retention efficiency of sponges autotrophic plankton growth by coral exudates should be inhibited (Pile et al. 1997; Weisz 2006). On that account the DOC and POC concentration should have increased or displayed no changes.
The TdN values were expected to rise since there was both no decrease in DON concentrations and an increase in dissolved inorganic nutrients (DIN).

When corals and sponges were incubated in artificial seawater enriched with cyanobacteria and nutrients (=treatment) there were no variations in DOC, POC and TOC but a decline in both DON and TdN values during the first 60 minutes of incubation. A decrease in POC concentration seemed to take place in the first 60 minutes but it failed to be statistically significant. This would correspond to the expectations since sponges would be able to rapidly deplete the present cyanobacteria (Pile et al. 1997; Weisz 2006). A rise in DOC and DON values was expected since corals exuded mucus and even whole particles (personal observation). Besides, it is suspected that *Cacospongia sp.* has not the ability to metabolize DOC but in fact produce DOC.
The decline in TdN values is consistent with both a decrease in DON and ammonium concentrations in the first 60 minutes. There was a second drop in ammonium

concentrations between 60 and 180 minutes of incubation but no further decrease in the TdN concentrations.

However, there were differences in water exiting and entering the oscules of sponges. During the first 60 minutes of the experiment *Cacospongia sp.* released considerably less DOC through its oscules. This fact is in contrast to the findings in all other incubation runs. Therefore it is assumed that this lower DOC excretion is an error of measurement as a result of the increasingly contracting oscules during the first 60 minutes of incubation. During this time the sponges had to endure 3 samplings out of their oscules which implied great stress for the animals and possible physical disturbances.

Furthermore, there were changes in both the POC and TOC values. Between 180 minutes and the end of the incubation they ingested cyanobacteria (POC) which would fulfill the expectations since cyanobacteria represent the major food source of sponges (Reiswig 1971; Pile et al. 1996). The consumption of cyanobacteria occurred not until 180 minutes of the experiment. This could have the same reason like the error of measurement for the DOC values, namely that the sponges were too stressed during the first 60 minutes of sampling and contracted their oscules which resulted in a limited pumping activity.

4.3 Carbon and nitrogen content

4.3.1 Corals

The carbon and nitrogen content of corals solely incubated in artificial seawater (=control) displayed no variations during the 180 minutes of experiment. A decline in the carbon content should have occurred since the corals excreted mucus in the beginning which is reported to contain in *Fungia* polyps up to 98 % of the photosynthetically fixed carbon (Ikeda et al. 1995). It was expected that the nitrogen concentrations rose slightly because coral mucus has a higher nitrogen content compared to other detritus in reef environments (Coles and Strathmann 1973; Hickel 1974).

The high carbon contents are as well caused by dissolved inorganic carbon (DIC) since the filters were not exposed to hydrochloric acid before the analysis. There was certainly also inorganic carbon or carbon grains on the filters because the mucus strings of the corals are solely visible if they are contaminated with carbon grains or other detritus (Wild et al. 2004b). Moreover, it was demonstrated that coral mucus results in an elevation of DIC production in incubation chambers. Increased DIC production in combination with an enhancement in respiration indicated that the sediment utilized and degraded coral mucus (Wild et al. 2004b). However, in the present study there was no sediment in the incubation chamber, but a consumption of mucus could be possible by bacteria in the water column (Moriarty et al. 1985).

When corals were incubated in artificial seawater enriched with cyanobacteria and nutrients (=treatment) both, the carbon and nitrogen content in the coral seemed to increase, but this failed to be statistically significant. An elevation of nitrogen and carbon contents was expected since the corals excreted mucus and autotrophic plankton, such as the added cyanobacteria, is known to quickly metabolize the exudates (Palenik and Morel 1990). It could be that cyanobacterial cells detected on the filter exhibited a higher nitrogen and carbon content and this was counteracted by a degradation of the mucus by other, possibly in cell size smaller bacteria. Another reason could be that the consumption of mucus occurred not as rapidly as the reproduction of cyanobacterial cells since cyanobacteria of the genus *Synechococcus* divide approximately 1 time per day in oligotrophic conditions with

increasing light intensity and rising temperatures promoting growth (Campbell and Carpenter 1986). On that account no changes could be measured.

The C/N ratios in the beginning of both incubations of 12.35 (± 6.26) and 11.29 (± 7.84) corresponded to the values of coral mucus of other studies which ranged from 5-20 for different coral species (Wild et al. 2004a; Tanaka et al. 2008; Naumann et al. 2010). The lower values at the end of both incubations indicate that bacteria could have degraded the mucus within 180 minutes of the experiment since their numbers on the mucus are reported to be up to 100 times higher than in the surrounding seawater and it is shown to be an attractive substrate for bacteria in the water column (Moriarty et al. 1985; Wild et al. 2004b). This would be consistent with a decline in the oxygen concentrations in the control group during the incubation as it is assessed that bacteria degrade coral mucus aerobically (Wild et al. 2004b). A decrease in oxygen levels could not be observed in the treatment group because of problems with the oxygen probe (Appendix; table A. 27).

The C/N ratio declined only in the control group after 180 minutes and no changes were detectable in the treatment group. Reasons could be that the corals in the control group released more mucus in the beginning and additionally that in the treatment group the cyanobacteria were still present in the water column and even utilized the mucus as food source (Palenik and Morel 1990).

4.3.2 Sponges

The carbon and nitrogen content as well as the C/N ratios on filters of sponges incubated in artificial seawater (=control) displayed no variations. This corresponds to the expectations since nothing was added to the incubation medium.

When sponges were incubated in artificial seawater enriched with nutrients and cyanobacteria (=treatment) there was a drop in both, the nitrogen and carbon content on the filters. This is consistent with the assumption that sponges ingested the cyanobacterial cells. Moreover, there was an elevation in the C/N ratio during 180 minutes of the experiment. In the beginning the value of the C/N ratio amounted to 7.52 (± 1.83) which is in accordance with ratios measured for the cyanobacteria *Synechococcus sp.* used in the present study (7.4- 7.8, Kaiser and Benner 2008). After 180 minutes the C/N ratios rose to 19.46 (± 5.12) indicating that grazing on cyanobacterial cells occurred (Bisset et al. 1999).

4.3.3 Corals and Sponges

Corals and sponges incubated together in artificial seawater (=control) showed no variations in both carbon and nitrogen content or in C/N ratios on the filters. The carbon content seemed to decline but this reduction was not statistically significant. It was also expected that the carbon concentrations decreased since the corals released solely exudates in the beginning of the incubations consisting of up to 98 % of the photosynthetically fixed carbon in *Fungia* polyps (Ikeda et al. 1995). Besides it would be anticipated that the excreted mucus is consumed by bacteria in the water column or the particulate fraction ingested by the sponge (Moriarty et al. 1985).

Contrary to expectations the carbon and especially the nitrogen content on filters increased considerably during incubations with sponges and corals in artificial seawater enriched with cyanobacteria and nutrients (=treatment). Sponges should have consumed rapidly the present cyanobacteria as it is demonstrated that they are able to process large volumes of water and have the highest retention efficiencies for cyanobacteria (Reiswig 1971; Pile et al. 1997; Weisz et al. 2006). Due to the other obtained results for dissolved inorganic nutrients (DIN), dissolved and particulate organic carbon (DOC/ POC) of incubations with sponges and corals together which were as well not coherent with the results of sponges alone it can be concluded that sponges with corals together were too stressed or limited in their pumping activity caused by differences in sample taking. When sponges were incubated alone only samples out of the water column were taken. In contrast, when sponges and corals were together in the experimental chamber, samples were taken out of the water column and additionally out of the oscules of the sponges. In doing so, the syringe could either have touched individuals during sampling or might be impacted by a too rapidly withdrawal of water resulting in contraction of the oscules due to physical disturbance (Reiswig 1971; Weisz 2006). Furthermore, there was solely a decline in C/N ratios exiting the oscules compared to the water column at the start of the experiment which was not detectable any more after 180 minutes. This could be another indication that sponges were not disturbed or constraint in their pumping activity at first, but got increasingly stressed after 3 more sample trials. The C/N ratios at the start of these incubations of 7.02 (± 0.62) are also in agreement with values of C/N ratios reported for *Synechoccoccus sp.* (7.4- 7.8, Kaiser et al. 2008). There

was no further elevation in C/N ratios in the water column which would have represented an evidence for grazing on cyanobacterial cells (Bisset et al. 1999).

4.4 Coral tissue

The zooxanthellae density, mitotic indices, the protein and chl*a* content did not vary at the end of the incubation between the different experiments. This corresponds to the expectations since detectable changes in all analyzed parameters due to elevated nutrient concentrations occurred only in long- term experiments after at least 3 weeks (Muscatine et al. 1989; Hoegh-Guldberg and Smith 1989; Marubini and Davies 1996).

The obtained protein contents of 3.78- 4.73 mg cm^{-2} are consistent with other corals (*Monastrea annularis*: 3.84- 5.19 mg cm^{-2}, *Porites porites*: 3.77- 4.96 mg cm^{-2}; Marubini and Davies 1996). However, they differed from values in a study with other fungiids which is most likely caused by the different method in protein analysis (1.65 mg cm^{-2}; Masuda et al. 1993). The chlorophyll *a* content of 2.15- 4.13 µg cm^{-2} is as well coherent with that of other fungiids (*Fungia repanda* and *Fungia echinata*: 2.4- 5.0 µg cm^{-2}; Masuda et al. 1993).

The zooxanthellae density was reduced by the power of ten compared to other studies (Szmant-Froelich and Pilson 1984; Masuda et al. 1993; Marubini and Davies 1996). A possible reason could be problems in tissue homogenizing. The tissue of fungiids is thick and after spraying with the airbrush it comes off in big clutches. In order to not destroy the proteins inside the tissue it was probably not homogenized long enough with the ultra turrax. Therefore there were often big patches of tissue slurry visible in the counting chamber. If such a patch was found during the counting process a new sample was taken from the tissue solution.

4.5 Photophysiological responses

The maximun photosynthetic rate of corals incubated in artificial seawater (=control) was lower after the experiment than before. When the artificial seawater was enriched with cyanobacteria and nutrients (=treatment) there was no decline but also no increase observable. In contrast, the maximum photosynthetic rate of corals incubated with a sponge either in the control or treatment group showed an elevation at the end of the experiment compared to the start. Moreover, all other experiments exhibited a considerably higher maximum rate of photosynthesis than the coral control group. This is consistent with other studies which revealed that rates of photosynthesis in fed corals are 2- 10 times higher than in starved ones (Taylor 1978; Summons et al. 1986; Titlyanov et al. 2001; Houlbrèque et al. 2003). Further, it would imply that adding a sponge to the coral has a similar effect than the addition of nutrients. In *Acropora cervicornis* and *Stylophora pistillata* high concentrations of ammonium (20 - 70 µmol) resulted in an increase of the photosynthetic rate of zooxanthellae, but high concentrations of nitrate had no effect (Taylor et al. 1978; Summons et al. 1986)

The photosynthetic efficiency of corals showed the same pattern as the maximum rate of photosynthesis but the differences were not statistically significant. However, in other studies more than at least two weeks were necessary to observe a difference in the maximum photosynthetic rate or in the photosynthetic efficiency (Titlyanov et al. 2001; Houlbrèque et al. 2003; Borell and Bischof 2008). It is assumed that in starved corals the ammonium assimilation in the symbiotic zooxanthellae and also the photosynthetic rates are reduced (Titlyanov et al. 2001; Fitt and Cook 2001). Besides, it was revealed that in a starved sea anemone the same amounts of photosynthates were translocated to the host regardless whether the anemone was fed or starved. The quality of the translocated photosynthates varied with higher amounts of nitrogen- rich amino acids in fed anemones (Davy and Cook 2001). This could be as well the case for corals since an elevation in protein levels could be detected in fed corals most likely attributable to an enhanced nitrogen content of translocated photosynthates (Muller-Parker et al. 1994; Titlyanov et al. 2001; Houlbrèque et al. 2003).

5 Conclusion and Outlook

Sponges seem to support corals with additional nutrients due to their ability to nitrify. The produced nitrate is most likely derived from the remineralization of cyanobacteria since shortly after their decline the observed rise in nitrate concentrations occurred. In that way sponges appear to regenerate nitrogen for the corals which is a growth limiting nutrient for zooxanthellae (Marubini et al. 1996; Badgley et al. 2006). The applied InEx method (according to Yahel et al. 2005) did not prove to be an adequate method for the sponge species investigated in this study due to its distinctly small oscules.

The investigation and identification of ammonia oxidizers in sponges could help estimate the rates of nitrification and excreted compounds (nitrate and/ or nitrite). Moreover, the use of isotopic tracers (^{15}N) and labeling of cyanobacteria could be helpful in order to gain further insight into the process of nitrification and to what extent sponges supply corals with nitrogen.

However, even if sponges appeared to support corals in terms of nutrient supply in short time incubations and in the laboratory, the high nutrient release could as well affect coral reef health negatively. The elevated nutrient concentrations could result in an enhanced growth of macroalgae (Littler and Littler 1984, Larned 1998), an increase in the virulence of coral pathogens (Bruno et al. 2003) and decrease coral fecundity (Koop et al. 2001).

Therefore long term experiments in the reef would be useful to study the multiple consequences of the increased dissolved inorganic nutrient (DIN) production of sponges on coral reef health and ecology more closely.

Appendix

Tab. A.1: The composition of ASN III/2 + Künstliches Seewassermedium, stickstoffhaltig (15‰) and the Trace Metal Mix (TMM). All components were dissolved in 1l of deionized water and the components of the TMM were dissolved before its addition in 100ml of deionized water.

Components	Composition [g or ml]
NaCl	27.5
$MgCl_2*6H_2O$	1.10
KCl	0.25
$MgSO_4*7H_2O$	1.75
$NaNO_3$	0.75
$CaCl_2*2H_2O$	0.25
Na_2CO_3	0.12
$K_2HPO_4*3H_2O$- Lsg. (4g/l)	2.50
Fe-NH_4-Citrat- Lsg. (6g/l)	0.25
TMM-Lsg.	0.50

Trace Metal Mix (TMM)

Components	Composition [g]
$NA_3Citrat*2H_2O$	0.300
$NA_2EDTA*2H_2O$	0.550
H_3BO_3	0.286
$MnCl_2*4H_2O$	0.181
$ZnSO_4*7H_2O$	0.0330
$Na_2MoO_4*2H_2O$	0.0318
$CuSO_4*5H_2O$	0.0079

Tab. A. 2: One way repeated measures ANOVA to test for differences in nitrite, nitrate and ammonium concentrations during the 5 hour incubation of corals in artificial sea water (= control, n=6) and in artificial seawater enriched with nutrients and cyanobacteria (=treatment, n=5).

Parameter	Kind of incubation	Sum of Squares (total)	F	p	Df
NO_3^-	Control	9999138.766	2.895	0.07	23
	Treatment	91298929.763	0.567	0.647	19
NH_4+	Control	5670143.866	0.123	0.945	23
	Treatment	211620902.939	0.797	0.519	19

Tab. A. 3: Pair wise Mann- Whitney Rank Sum Test of dissolved inorganic nutrient (DIN) changes versus zero in the coral control group (= artificial seawater) over time. Replicates per treatment (N=6) and total number of measurements in time (n=4).

Time [min]	NH_4^+	NO_3^-
30	0.394	0.065
60	1.000	0.065
180	0.065	0.394
300	1.000	1.000

Tab. A. 4: Pair wise Mann- Whitney Rank Sum Test of dissolved inorganic nutrient (DIN) changes versus zero in the coral treatment group (=artificial seawater enriched with cyanobacteria and nutrients) over time. Replicates per treatment (N=5) and total number of measurements in time (n=4).

Time [min]	NH_4^+	NO_3^-
30	0.690	0.690
60	0.353	0.151
180	0.274	0.557
300	0.359	0.092

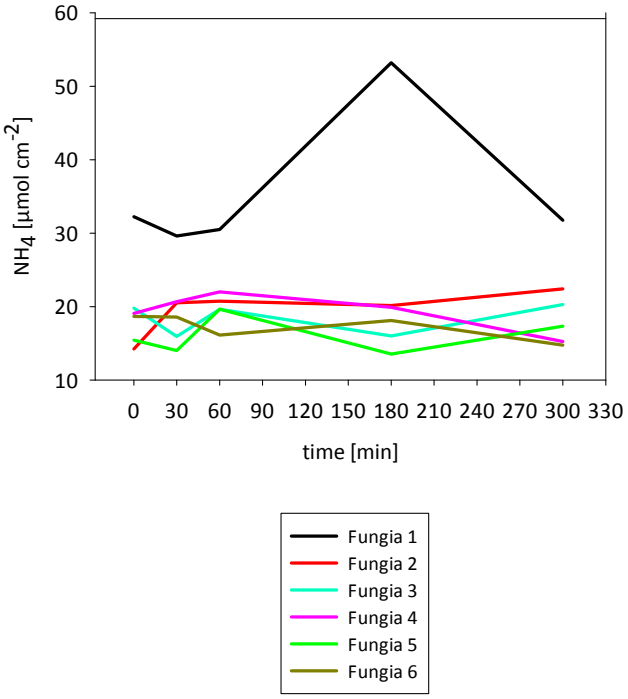

Fig. A. 1: Time-series of ammonium concentrations [µmol cm^{-2}] in coral incubations with artificial seawater enriched with cyanobacteria and nutrients (= treatment). The fungiid no. 1 was excluded in the statistical analysis since it displayed unusually high values.

Tab. A. 5: one way repeated measures ANOVA to test for differences in nitrite, nitrate and ammonium concentrations during the 5 hour incubation of sponges in artificial sea water (= control, n=6) and artificial seawater enriched with nutrients and cyanobacteria (=treatment, n=3).

Parameter	Kind of incubation	Sum of Squares (total)	F	p	Df
NO_3^-	Control	21430.278	0.670	0.620	29
	Treatment	26852.123	2.469	0.129	14
NH_4+	Control	995.474	1.364	0.292	23

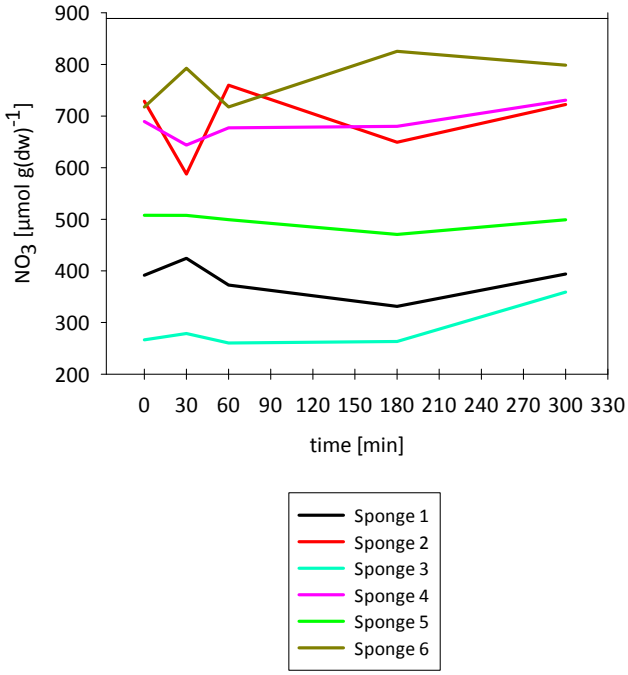

Fig. A. 2: Time-series of nitrate concentrations [µmol g(dw)$^{-1}$] in sponge incubations with artificial seawater enriched with cyanobacteria and nutrients (= treatment). Sponge 2 exhibited a completely different pattern in its pumping activity than the other sponges. Sponge 5 did not pump during the course of the experiment and sponge 6 stopped its pumping activities after 180 minutes of incubation.

Tab. A. 6: The Duncan´s Method applied for the pair wise multiple comparison procedure to test for differences in ammonium concentrations in incubation with sponges in artificial seawater enriched with cyanobacteria and nutrients (treatment group) over time. Levels of significance: *p<0.05 and **p<0.01. Replicates per treatment (N=3) and total number of measurements in time (n=4).

Comparison	Difference of Means	p
300 vs. 30 minutes	54.835	0.027*
300 vs. 60 minutes	11.727	0.542
300 vs. 180 minutes	66.659	0.013*
60 vs. 30 minutes	43.108	0.055
60 vs. 180 minutes	54.923	0.027*
30 vs. 180 minutes	11.824	0.539

Tab. A. 7: One way repeated measures ANOVA to test for differences in nitrite, nitrate and ammonium concentrations during the 300 minutes incubation of sponges and corals in artificial seawater (= control, n=4) and artificial seawater enriched with nutrients and cyanobacteria (=treatment, n=4).

Parameter	Kind of incubation	Sum of Squares (total)	F	p	Df
NO_2^{2-}	Control	66.229	3.114	0.081	15
	Treatment	55.504	0.234	0.867	13
NO_3^-	Control	53857.807	3.789	0.052	15
	Treatment	539748.061	0.174	0.911	15
NH_4+	Control	26076.326	0.906	0.475	15
	Treatment	56606.953	2.776	0.103	15

Tab. A. 8: Mann- Whitney Rank Sum Test and Students t-test to test for differences in dissolved inorganic nutrients (DIN) of corals and sponges incubated in artificial seawater (control, n=4) and in artificial seawater enriched with cyanobacteria and nutrients (treatment, n=4) at the start of the experiment at 30 minutes and after 180 minutes in the water column and exiting the oscules.

Time [min]	NO_2^{2-}	NO_3^-	NH_4^+
0	0.184	0.686	0.766
30	0.114	0.343	0.634
60	0.558	1.000	0.101
180	0.200	0.423	0.970
300	1.000	0.745	0.965

Tab. A. 9: Mann- Whitney Rank Sum Test and Students t-test to test for differences in dissolved inorganic nutrients (DIN) of corals and sponges incubated in artificial seawater enriched with cyanobacteria and nutrients (treatment, n=4) during the 300 minutes of incubation in the water column and exiting the oscules.

Time [min]	NO_2^{2-}	NO_3^-	NH_4^+
0	0.247	0.590	0.725
30	0.288	0.717	0.057
60	0.722	0.835	0.575
180	0.699	0.762	0.589
300	0.619	0.755	0.367

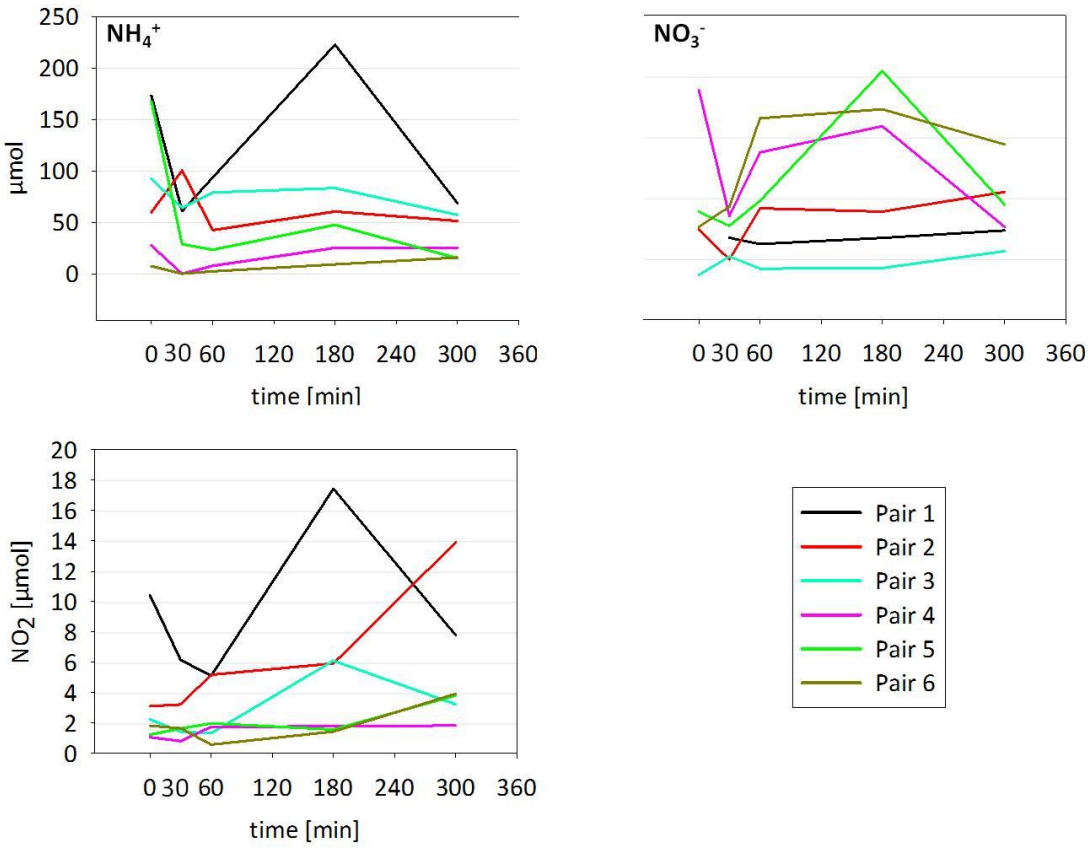

Fig. A. 3: Time-series of nitrate, ammonium and nitrite concentrations [µmol] in incubations with corals and sponges in artificial (= control).

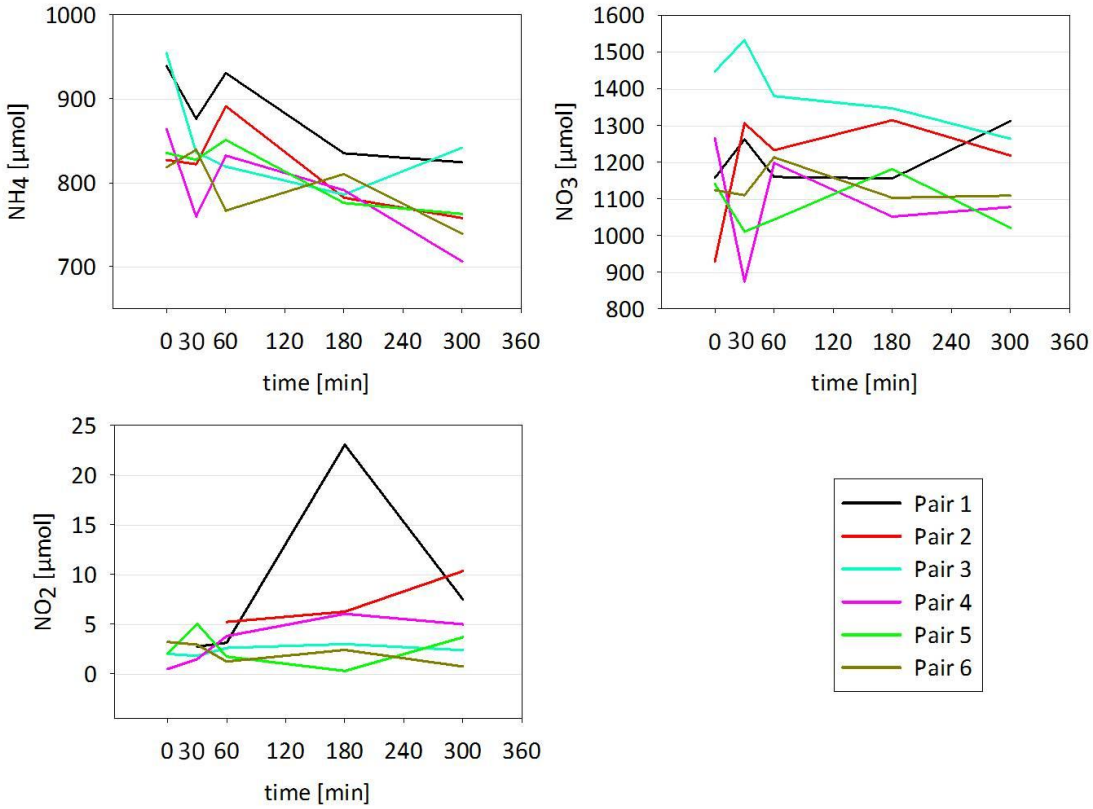

Fig. A. 4: Time-series of nitrate, ammonium and nitrite concentrations [µmol] in incubations with corals and sponges in artificial seawater (= control).

Tab. A. 10: Mann- Whitney Rank Sum Test to test for differences in dissolved organic carbon (DOC) in incubations with artificial seawater (= control) and artificial seawater enriched with cyanobacteria and nutrients (=treatment). Pair wise comparison of single measurements in time to zero. Levels of significance: *p<0.05 and **p<0.01.

Organisms	Kind of incubation	Time [min]	p	n
Fungiids	Control	60	0.343	4
		300	1.000	4
	Treatment	60	0.690	5
		300	0.218	5
Sponges	Control	60	1.000	4
		300	0.343	4
	Treatment	60	0.343	4
		300	0.029*	4
Fungiids + Sponges	Control	60	1.000	4
		300	1.000	4
	Treatment	60	0.394	6
		300	0.065	6

Tab. A. 11: Mann- Whitney Rank Sum Test to test for differences in total organic carbon (TOC) in incubations with artificial seawater (= control) and artificial seawater enriched with cyanobacteria and nutrients (=treatment). Pair wise comparison of single measurements in time to zero. Levels of significance: *p<0.05 and **p<0.01.

Organisms	Kind of incubation	Time [min]	p	n
Fungiids	Control	60	0.151	4
		300	0.151	4
	Treatment	60	0.182	5
		300	0.214	5
Sponges	Control	60	0.343	4
		300	0.343	4
	Treatment	60	0.343	4
		300	0.596	4
Fungiids + Sponges	Control	60	1.000	4
		300	1.000	4
	Treatment	60	0.394	6
		300	1.000	6

Tab. A. 12: Mann- Whitney Rank Sum Test to test for differences in particulate organic carbon (POC) in incubations with artificial seawater (= control) and artificial seawater enriched with cyanobacteria and nutrients (=treatment). Pair wise comparison of single measurements in time to zero. Levels of significance: *p<0.05 and **p<0.01.

Organisms	Kind of incubation	Time [min]	p	n
Fungiids	Control	60	0.686	4
		300	0.197	4
	Treatment	60	0.196	4
		300	0.151	4
Sponges	Control	60	1.000	4
		300	0.343	4
	Treatment	60	0.322	4
		300	0.057	4
Fungiids + Sponges	Control	60	0.342	3
		300	0.373	3
	Treatment	60	0.394	6
		300	0.394	6

Tab. A. 13: Mann- Whitney Rank Sum Test and Students t-test to test for differences in dissolved, total and particulate organic carbon (DOC/ TOC/ POC) of corals and sponges incubated in artificial seawater (= control) and in artificial seawater enriched with cyanobacteria and nutrients (= treatment) during the 300 minutes of incubation in the water column and exiting the oscules. Levels of significance: *p<0.05 and **p<0.01.

Parameter	Kind of incubation	Time [min]	P	n
DOC	Control	0	0.486	4
		60	0.460	4
		300	0.139	4
	Treatment	0	0.329	6
		60	0.026*	6
		300	0.114	6
TOC	Control	0	0.343	4
		60	0.994	4
		300	0.261	4
	Treatment	0	0.818	6
		60	0.065	6
		300	0.003*	6
POC	Control	0	0.195	3
		60	0.263	3
		300	0.480	3
	Treatment	0	0.699	6
		60	1.000	6
		300	0.002*	6

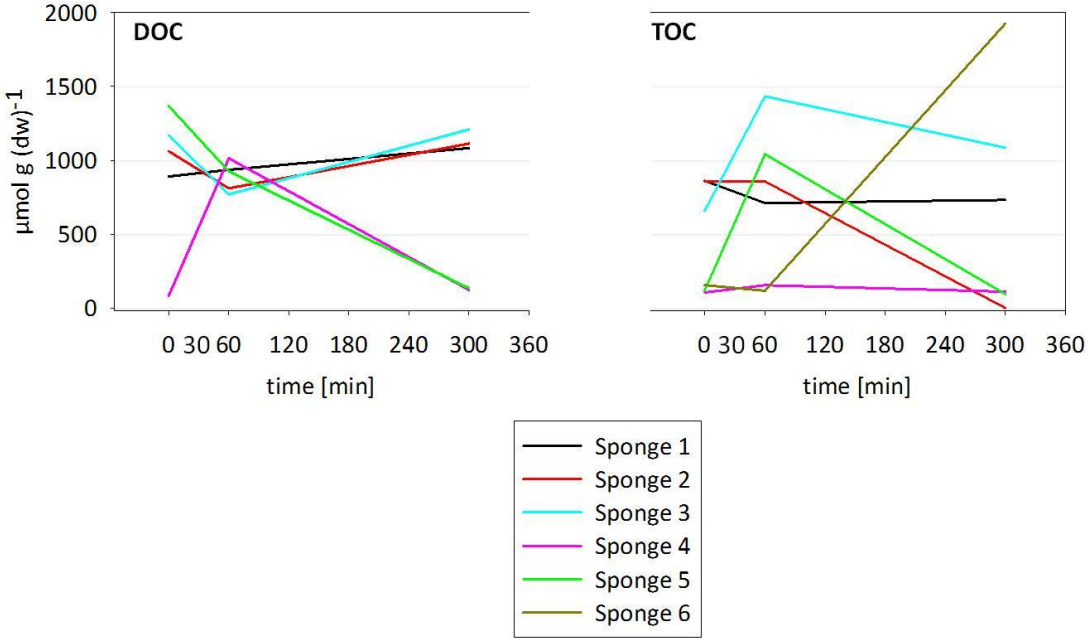

Fig. A. 5: Time- series of dissolved and total organic carbon (DOC/ TOC) of sponges incubated in artificial seawater (= control).

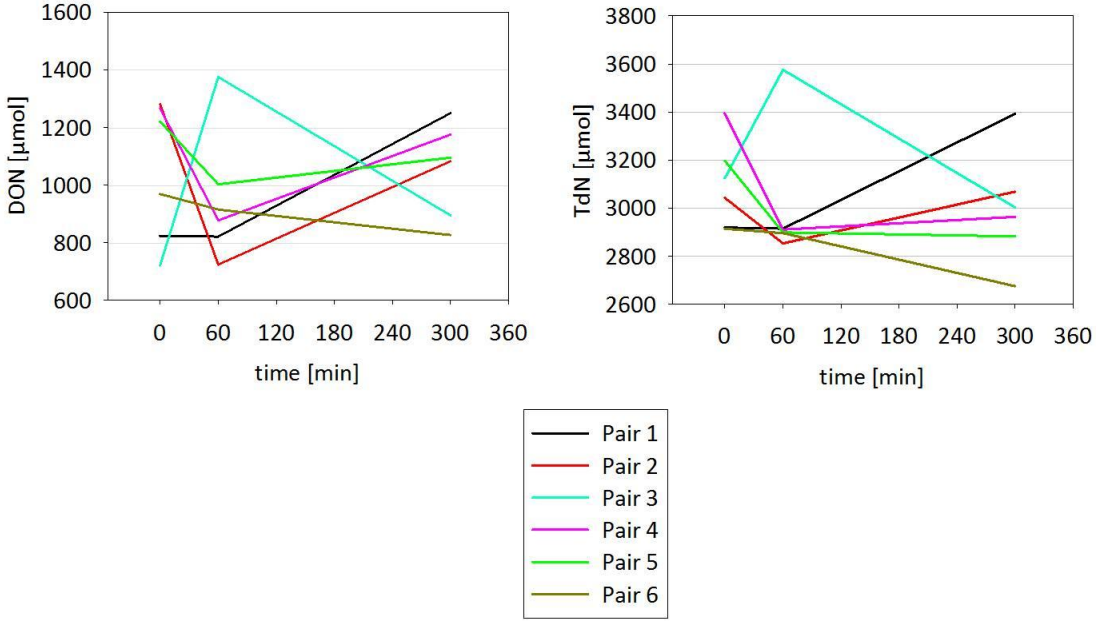

Fig. A. 6: Time- series of dissolved and total dissolved organic nitrogen (DON/ TdN) of sponges and corals incubated in artificial seawater enriched with cyanobacteria and nutrients (= treatment).

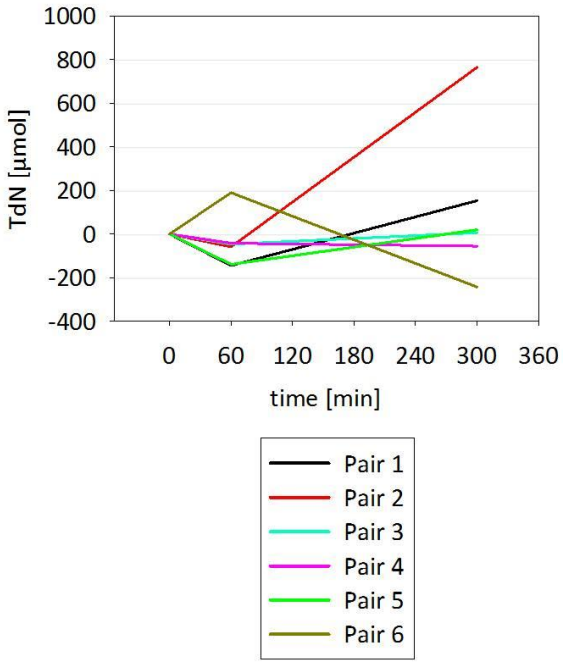

Fig. A. 7: Time- series of total dissolved organic nitrogen (TdN) of sponges and corals incubated in artificial seawater (= control).

Tab. A. 14: Mann- Whitney Rank Sum Test and Students t- test to test for differences in total dissolved nitrogen (TdN) in incubations with artificial seawater (= control) and with artificial seawater enriched with cyanobacteria and nutrients (=treatment). Pair wise comparison of single measurements in time to zero. Levels of significance: *p<0.05 and **p<0.01.

Organisms	Kind of incubation	Time [min]	p	t	T	n
Fungiids	Control	60	0.029*	-	26.000	4
		300	0.343	-	14.000	4
	Treatment	60	0.394	-	33.000	6
		300	0.394	-	33.000	6
Sponges	Control	60	1.000	-	39.000	6
		300	1.000	-	39.000	6
	Treatment	60	0.008**	-4.832	-	3
		300	0.397	-0.948	-	3
Fungiids + Sponges	Control	60	0.005**	3.782	-	5
		300	0.151	-	20.000	5
	Treatment	60	0.008**	-	40.000	5
		300	0.411	-0.868	-	5

Tab. A. 15: Mann- Whitney Rank Sum Test and Students t- test to test for differences in dissolved organic nitrogen (DON) in incubations with artificial seawater (= control) and with artificial seawater enriched with cyanobacteria and nutrients (=treatment). Pair wise comparison of single measurements in time to zero. Levels of significance: *p<0.05 and **p<0.01.

Organisms	Kind of incubation	Time [min]	p	T	T	n
Fungiids	Control	60	0.237	1.313	-	4
		300	1.000	-	18.000	4
	Treatment	60	0.699	-	36.000	6
		300	0.699	-	36.000	6
Sponges	Control	60	0.065	-	27.000	6
		300	0.394	-	33.000	6
	Treatment	60	0.714	0.394	-	3
		300	0.696	-0.421	-	3
Fungiids + Sponges	Control	60	0.151	-	20.000	5
		300	0.151	-	20.000	5
	Treatment	60	0.046*	2.360	-	5
		300	0.051	-2.295	-	5

Tab. A. 16: Mann- Whitney Rank Sum Test and Students t-test to test for differences in dissolved and total dissolved organic nitrogen (DON and TdN) of corals and sponges incubated in artificial seawater (= control) and in artificial seawater enriched with cyanobacteria and nutrients (= treatment) in the water column and exiting the oscules during the 300 minutes of incubation. Levels of significance: *p<0.05 and **p<0.01.

Organisms	Kind of incubation	Time [min]	p	T	T	n
DON	Control	0	0.963	0.0485	-	6
		60	0.673	-0.437	-	6
		300	0.095	-	36.000	6
	Treatment	0	0.236	1.282	-	5
		60	0.310	-	22.000	5
		300	0.690	-	30.000	5
TdN	Control	0	0.505	0.697	-	6
		60	0.446	-0.801	-	6
		300	0.548	-	31.000	6
	Treatment	0	0.238	1.276	-	5
		60	0.920	-0.104	-	5
		300	0.795	-0.268	-	5

Tab. A. 17: Mann- Whitney Rank Sum Test and Students t-test to test for differences in carbon and nitrogen content and ratios of corals incubated in artificial seawater (= control) and in artificial seawater enriched with cyanobacteria and nutrients (= treatment) during 180 minutes of incubation.

Kind of incubation	Parameter	p	t	T	n
Control	N	0.887	0.146	-	6
	C	1.583	0.145	-	6
	C/N	0.015	-	54.000	6
Treatment	N	0.145	-1.579	-	6
	C	0.818	-	37.000	6
	C/N	0.642	0.479	-	6

Tab. A. 18: The Duncan´s Method applied for the pair wise multiple comparison procedure to test for differences in carbon contents in incubations with sponges in artificial seawater enriched with cyanobacteria and nutrients (treatment group, n=3) during 180 minutes. Levels of significance: *p<0.05 and **p<0.01.

Comparison	Difference of Means	p
0 vs. 30 minutes	0.649	0.884
0 vs. 180 minutes	13.925	0.031*
30 vs. 180 minutes	13.276	0.033*

Tab. A. 19: The Duncan´s Method applied for the pair wise multiple comparison procedure to test for differences in nitrogen contents in incubations with sponges in artificial seawater enriched with cyanobacteria and nutrients (treatment group, n=3) during 180 minutes. Levels of significance: *p<0.05 and **p<0.01.

Comparison	Difference of Means	p
0 vs. 30 minutes	1.020	0.210
0 vs. 180 minutes	3.125	0.010*
30 vs. 180 minutes	4.145	0.004**

Tab. A. 20: The Duncan´s Method applied for the pair wise multiple comparison procedure to test for differences in carbon and nitrogen ratios in incubations with sponges in artificial seawater enriched with cyanobacteria and nutrients (treatment group, n=3) during 180 minutes. Levels of significance: *p<0.05 and **p<0.01.

Comparison	Difference of Means	P
0 vs. 30 minutes	1.231	0.616
0 vs. 180 minutes	11.937	0.006**
30 vs. 180 minutes	13.168	0.005**

Tab. A. 21: Students t-test to test for differences in carbon and nitrogen content and ratios of corals and sponges incubated in artificial seawater (= control) during 180 minutes of the experiment.

Parameter	p	t	n
N	0.713	0.379	6
C	0.243	1.240	6
C/N	0.192	1,399	6

Tab. A. 22: Mann- Whitney Rank Sum Test and Students t-test to test for differences in carbon and nitrogen contents and ratios of corals and sponges incubated in artificial seawater (= control) and in artificial seawater enriched with cyanobacteria and nutrients (= treatment) in the water column and exiting the oscules during the 180 minutes of the experiment.

Kind of incubation	Parameter	Time [min]	p	t	T	Df
Control	N	0	0.264	-1.192	-	9
		180	0.231	-1.284	-	9
	C	0	0.547	0.626	-	9
		180	0.481	-0.734	-	9
	C/N	0	0.052	-	19.000	9
		180	0.814	0.243	-	9
Treatment	N	0	0.913	-0.114	-	6
		180	0.312	1.105	-	6
	C	0	0.191	1.474	-	6
		180	0.167	1.573	-	6
	C/N	0	2.382	0.049*	-	7
		180	0.190	-	26.000	7

Tab. A. 23: One way ANOVA and Kruskal- Wallis one way ANOVA to test for differences in chlorophyll *a* (chl *a*) and protein content, zooxanthellae density and mitotic index at the end of experiments between corals incubated in artificial seawater (= control), in artificial seawater enriched with cyanobacteria and nutrients (= treatment) and corals incubated together with sponges in the treatment and control group.

Parameter	SS	F	H	p	Df
chl *a*	85.310	1.373	-	0.281	22
Protein	-	-	1.865	0.601	3
Zooxanthellae	106583254458.962	1.048	-	0.393	23
Mitotic index	6297943.793	0.789	-	0.514	23

Tab. A. 24: Kruskal- Wallis one way ANOVA to test for differences in photosynthetic efficiencies between different experiments. C: start value of all experiments; FC: Fungiids in the control group (artificial seawater); FT: Fungiids in the treatment group (artificial seawater enriched with nutrients and cyanobacteria); FSC: Fungiids together with sponges in the control group and FST: Fungiids together with sponges in the treatment group.

H	p	Df
7.875	0.096	4

Table A. 25: Pair wise Mann- Whitney Rank Sum Test or Students t-test to examine for difference between start (100%) and end values [%] in the photosynthetic efficiency. n: replicates per treatment; levels of significance: *p<0.05 and **p<0.01.

Experiment	P	n
Fungiids- Control	0.065	6
Fungiids- Treatment	0.548	5
Fungiids + Sponges- Control	0.257	4
Fungiids + Sponges- Treatment	0.548	3

Tab. A. 26: Holm- Sidak method applied for the pair wise multiple comparison procedure to test for differences in maximum rate of photosynthesis between different experiments. FC: Fungiids in the control group (artificial seawater); FT: Fungiids in the treatment group (artificial seawater enriched with nutrients and cyanobacteria); FSC: Fungiids together with sponges in the control group and FST: Fungiids together with sponges in the treatment group. Levels of significance: *p<0.05 and **p<0.01.

Experiment	P
FC vs. FT	0.049*
FC vs. FSC	0.007**
FC vs. FST	0.001**
FT vs. FST	0.119

Tab. A. 27: Decrease in the oxygen concentration in mol l^{-1} (mean ±SD) in coral incubations with artificial seawater and artificial seawater enriched with cyanobacteria and nutrients. Four out of the twelve corals were excluded since there were problems in the handling with the oxygen probe.

Time [min]	O_2- concentration [mol l^{-1}]
0	0.209 (±0.015)
30	0.205 (± 0.012)
60	0.200 (±0.010)
180	0.194 (±0.003)
300	0.191 (±0.005)

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Declaration of Authorship

"Statement according to §6 (8) Prüfungsordnung der Universität Bremen für den Masterstudiengang "International Studies in Aquatic Tropical Ecology" (ISATEC) vom 7. Januar 2002:

Hereby I declare that I have written this Master's Thesis by my own and without any assistance from third parties. Furthermore, I confirm that no other sources and resources have been used than those indicated in the thesis itself and that all quotations are marked.

Bremen,