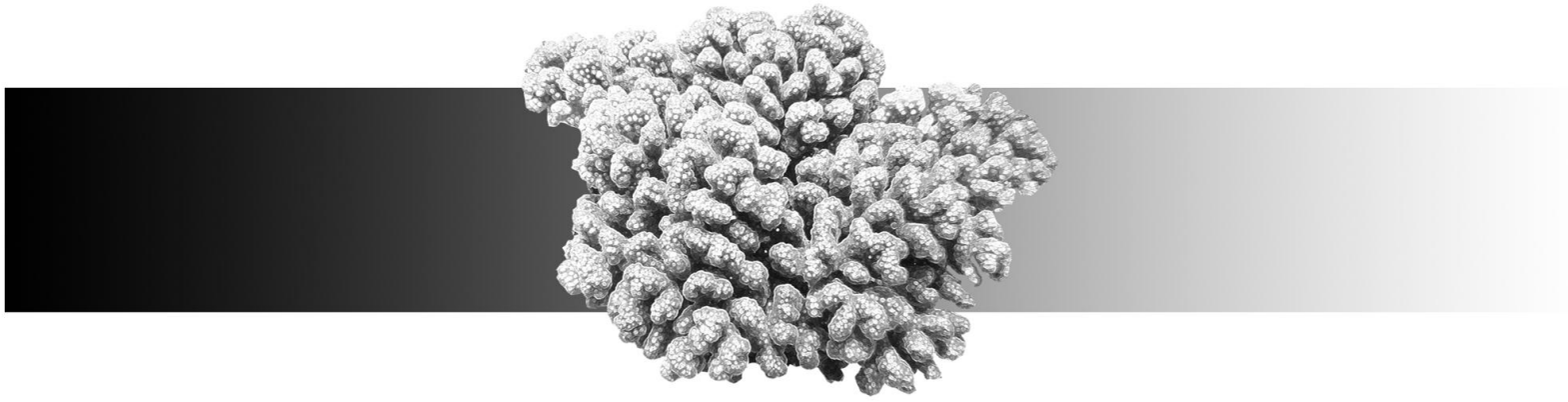
University of Kiel
in collaboration with
Helmholtz Centre for Ocean Research Kiel

CORAL RESISTANCE

Acclimatization in photophysiology and metabolic rates of the reef building coral *Pocillopora verrucosa* to human land-based pollution



MASTER THESIS

Study course "Biological Oceanography"

Kolja Beisiegel

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قطاع جدة
The Jeddah Transect

SUBPROJECT 3: NUTRIENT GRADIENTS IN THE RED SEA

A cooperation between

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Helmholtz Centre for Ocean Research Kiel

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Abstract

In times of global change, coral reefs face a multitude of anthropogenic stressors. Changing water quality is one of the major threats to these highly specialized, oligotrophic ecosystems and terrestrial runoff still presents the dominant pressure on local scale. However, little is known about the physiological resistance and actual acclimatization speed of scleractinian corals to human land-based pollution and eutrophication. In this study, metabolic rates (photosynthesis, photochemical efficiency, respiration) and tissue composition (chlorophyll a, total protein, biomass) of sewage-impacted, near-shore colonies of *Pocillopora verrucosa* were compared to non-impacted off-shore corals. Transplantation experiments between both sites revealed a significant acclimatization of colonies to new water quality within six weeks with almost no differences in metabolic performance and nutritional status compared to native corals. High concentrations of dissolved inorganic nutrients (in particular nitrate), incorporated by the symbiotic algae, caused increases in zooxanthellae growth, as reflected in enhanced areal chlorophyll a and protein. Hence, coral photosynthesis and photochemical efficiency increased in eutrophic waters. Elevated level of organic matter (live, dead or dissolved) led to an increase in polyp feeding and increased biomass as well as total protein content and stimulated zooxanthellae growth via translocation of nutrients. A high energy gain via autotrophy, in addition to good nutritional supply by heterotrophy seems to compensate lower light intensity and higher sedimentation stress. However, high zooxanthellae loaded specimens from near-shore appeared to be more susceptible to changes in water quality and displayed a slower acclimatization as well as several bleaching spots in response to oligotrophic off-shore conditions. In conclusion, trophic plasticity and the physiological acclimatization potential of *P. verrucosa* enable the coral to convert a potential stress factor into a resource, actually benefiting from nutrient supply caused by sewage inlet. These results demonstrate the ability of some coral species to acclimatize quickly and entirely, however, it remains an open question, if these corals are also able to buffer or acclimatize to global change related stressors (e.g. SST rise), or if they might even be more susceptible.

1 Introduction

1.1 Reefs in the Anthropocene

Coral reefs are the most spectacular and taxonomically diverse marine ecosystems, thriving in tropical waters with low levels of nutrients and high light penetration (Marubini and Davies 1996; Jackson et al. 2001; Koop et al. 2001). They form huge, heterogeneous structures, providing habitat for various reef organisms of which invertebrates contribute dominantly to the high diversity (Glynn and Enochs 2011). Key organism is the hermatypic, zooxanthellate coral, since it creates the reef framework by accretion of calcium carbonate ($CaCO_3$). This accretion (also by molluscs, foraminifera and algae) determines the biogenic production, which together with sediment import and cementation as well as carbonate loss processes like biological and mechanical erosion, sediment export and dissolution make up net reef growth (Kleypas et al. 2001; McClanahan 2002). The most common type of reef, "production-dominated reefs", shows an continuous accumulation of biologically produced $CaCO_3$ by the local community (Kleypas et al. 2001). These modern reefs had their origin 65 million years ago and expanded and contracted due to a variety of extrinsic factors such as sea level and climatic changes (Pandolfi 2011; Richmond and Wolanski 2011). A new era began when humans evolved, adding new stressors (Fig. 1) on top of persistent natural events such as hurricanes or *Acanthaster* outbreaks (Richmond and Wolanski 2011).

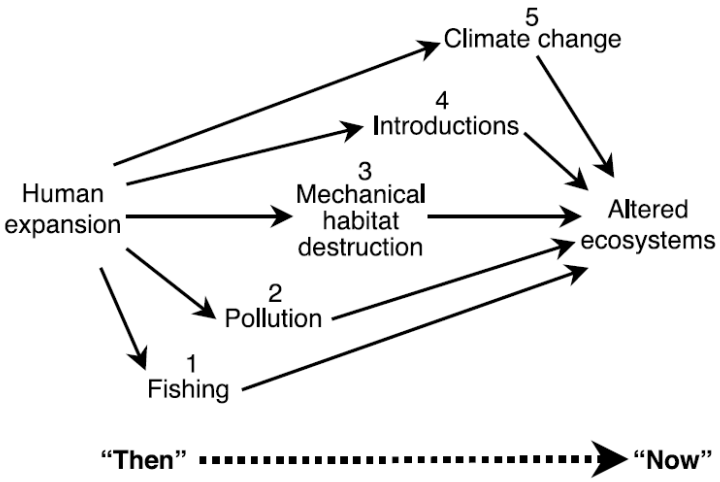

Figure 1. Historical sequence of human disturbances affecting coastal ecosystems. Pollution highlighted as ancient and long-term operative influence. (Jackson et al. 2001)

Human disturbances began when the development of coastal zones collided with the distribution of coral reefs (Jackson et al. 2001). In these tropical and subtropical areas (Fig. 2), reefs provide numerous ecosystem services to millions of people (McClanahan 2002). Coral reefs contribute to the economy of at least 100 nation states with values up to US$ 6,075 ha^{-1} y^{-1} in 1997 (Duarte et al. 2008), being among the most valuable ecosystems on earth (McClanahan 2011). Since coastal urbanization is increasing with growing population density, frequency and intensity of disturbances and their ecological effects on coastal ecosystems have increased and accelerated (Jackson et al. 2001; WHO 2005). 37% of mankind live within 100 km of the coastline and 70% of the world's megacities are now in coastal zones (Duarte et al. 2008).

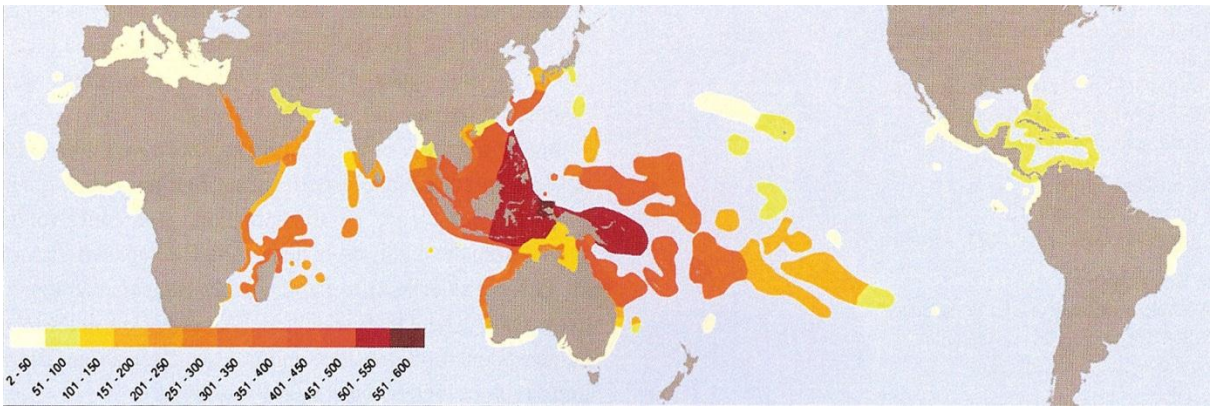

Figure 2. Global biodiversity of zooxanthellate corals. Colours indicate total species richness. (Veron et al. 2011)

Besides global threats, such as ocean acidification and sea surface temperature (SST) rise, changing water quality due to pollution is still one of the major localized threats to coral reef ecosystems (Fabricius 2005). Increasing exposure to loads of nutrients, organic matter and sediments discharged from land either by coastal watersheds or by untreated sewage discharge have the potential to seriously impact and degrade coastal reefs at local scale (Koop et al. 2001; Fabricius 2005; Cooper and Ulstrup 2009). Although not a classical pollutant, increased nutrient concentrations (inorganic and particulate forms of nitrogen and phosphorus) are considered to decrease water quality significantly by increasing turbidity and bacterial densities. Furthermore, inorganic nutrients and organic matter foster fast growing algae and filter feeder abundances, respectively, which may lead to coral reef community shifts towards a lower complexity, diversity and hence reduced resilience (Shimoda et al. 1998; Fabricius et al. 2005; Costa Jr. et al. 2008). Worldwide, coastal waters become more eutrophic due to land runoff and it has been shown that eutrophication can act as single most significant pressure on coastal coral reefs similar in severity as bleaching an overfishing (Spalding et al. 2001; Fabricius 2005).

In addition to short-term impacts, land-based pollution acts as stress-reinforcing factor of large scale disturbances (e.g. ocean acidification) by undermining the resilience of the ecosystem (Hoegh-Guldberg et al. 2007; Maina et al. 2011). The whole ecosystem response is therefore likely to be much greater than the sum of individual disturbances and a sudden transition in community composition is possible (Jackson et al. 2001). In 1998, 30% of reefs worldwide were considered to be threatened by coastal development (Fig. 3) and 22% by land-based pollution (e.g. waste water and agricultural run-off) (Bryant et al. 1998). It is therefore of extreme importance to understand and consequently reduce the influence of local stressors to assist coral reefs through the decades of climate change (Hoegh-Guldberg et al. 2007).

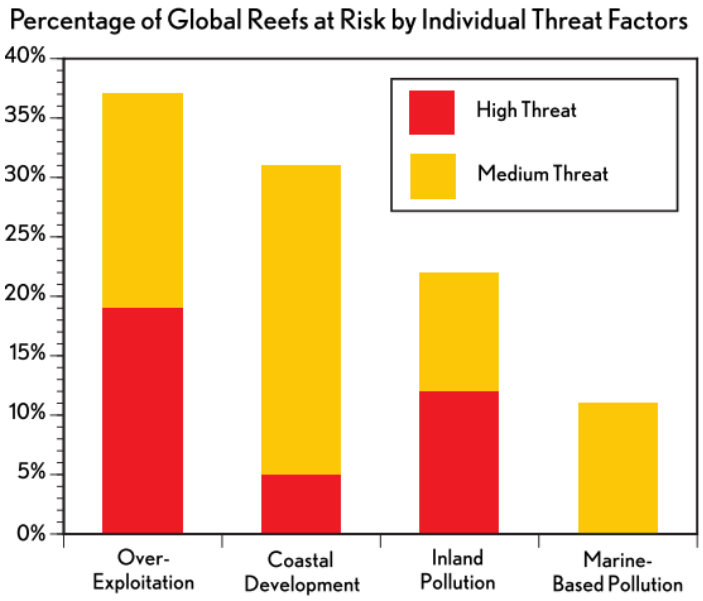

Figure 3. Reefs at risk (Bryant et al. 1998)

1.2 The coral holobiont

Most hermatypic corals consist of the host polyp animal and endosymbiotic, unicellular dinoflagellate algae (commonly referred to as zooxanthellae; Cooper and Ulstrup 2009). The zooxanthellae are located in vacuoles (symbiosomes) within the host's endoderm cells (Fig. 4; Trench 1987) and the transport of gases and carbon compounds occurs through and in conjunction with the membranes of algae and the host (Wakefield et al. 2000). The dinoflagellates are usually arranged in a monolayer with millions of cells per square centimetre of coral-colony surface (Drew 1972) and the population can include one or more genotypes in different abundance (Stambler 2011).

Zooxanthellae belong to the genus *Symbiodinium*, an diverse genus with eight lineage, of which six clades (A-D, F, G) are found in scleractinian corals (Baker 2003; Stambler 2011). These clades are widespread in shallow water tropical and subtropical cnidarians and one square meter of reef might easily contain $>10^{10}$ algal symbionts (Baker 2003; Stambler 2011). This high number emphasizes the importance of them as primary producers in oligotrophic reefal waters where the polyp animals depend on the photosynthetic products of zooxanthellae to cover their energetic and carbon requirements (Muscatine 1990). In this mutualistic symbiosis, up to 95% of the photosynthetically fixed carbon is translocated to the polyp, contributing up to 100% of daily metabolic requirements (Muscatine et al. 1984; Dubinsky and Jokiel 1994). Glycerol, sugars, organic acids, amino acids, lipids and polyunsaturated fatty acids produced by the zooxanthellae are transferred to the host, stimulated by a compound described as host-release factor (HRF) (Grant et al. 2006; Venn et al. 2008).

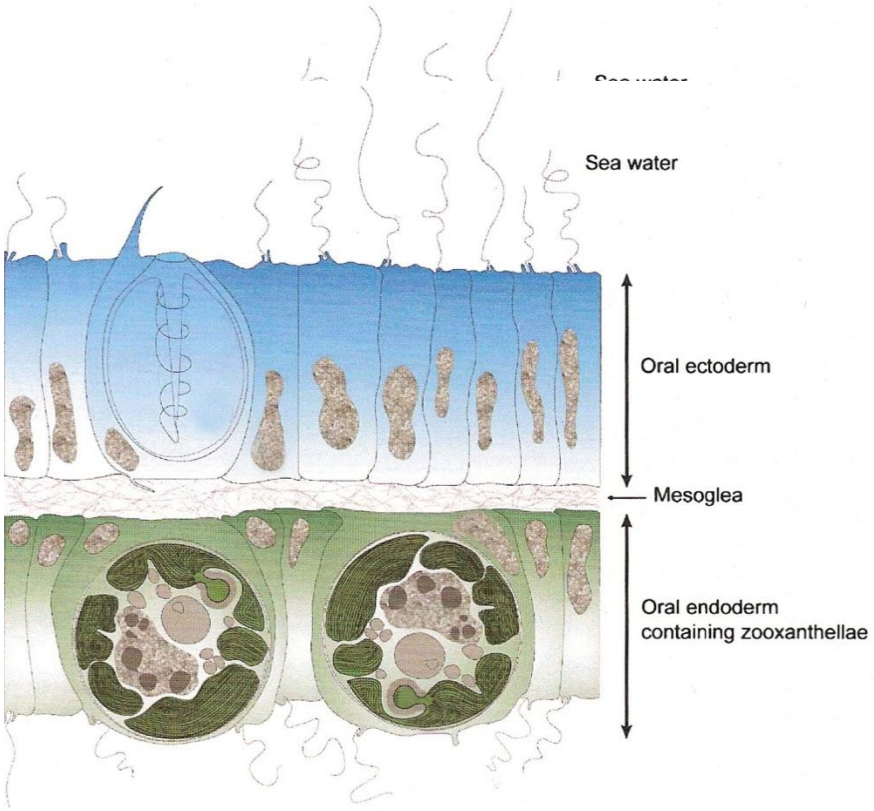

Figure 4. Schematic section of the histology of a zooxanthellate coral across its oral ecto- and endoderm. Derived from Allemand et al. (2011)

Besides autotrophy of the zooxanthellae, polyp animals are able to ingest organic matter and capture prey items, providing a variable but rich source of nutrients such as nitrogen, phosphorus and essential amino acids. Received material from zooplankton, bacteria, suspended particles and dissolved matter is partitioned between animal host and its algal symbionts (Anthony and Fabricius

2000; Piniak et al. 2003) via a translocation of nutrients from the coral animal to the symbionts (Dubinsky and Jokiel 1994; Piniak et al. 2003).

In consequence, the coral holobiont is potentially mixotrophic and carbon and nutrient fluxes between the host, the algae, and the environment are based on the tight symbiotic relationship (Anthony and Fabricius 2000). The fluxes allow coral reef communities to succeed in oligotrophic waters (Muscatine and Porter 1977) and to be spread all over the tropical oceans (Stambler 2011). Additionally, the interaction of autotrophy and heterotrophy forms a mechanism to sustain an optimal energy balance during changing environmental conditions and offset stress from varying water quality (Anthony and Fabricius 2000). Enhanced feeding, for example, counteracts reduced photosynthesis and can maintain physiological functioning even under turbid conditions and during bleaching events (Houlbrèque and Ferrier-Pagès 2009).

1.3 The coral response to pollution and eutrophication

The vulnerability of a coral reef is often described as a function of the capacity of physiological acclimatization and genetic adaptation of the perturbed reef organisms (Maina et al. 2011). This capacity can be highly variable between species, and although degrading water quality is considered as an overall threat to coral reefs, it may be harmless or even beneficial for some reef species, including coral species (Fabricius 2005; Cooper and Ulstrup 2009; Sawall et al. 2011). Some corals have the ability to acclimatize to extreme conditions, hence showing a wide physiological niche (Anthony and Fabricius 2000; Maina et al. 2011; Sawall et al. 2011). The magnitude and speed of species-specific responses strongly depends on the type and duration of pollution. Terrestrial runoff, including sewage discharge, leads to a change in various water quality parameters at the same time and while eutrophication (up to a certain nutrient concentration) can be beneficial for at least some coral species, other types of pollution like heavy metals, pesticides or hydrocarbons are always deleterious and significantly affect the health of reefs (Fabricius 2005).

1.3.1 Effect of dissolved inorganic nutrients

Enrichment of inorganic nutrients may act as fertilizer and support zooxanthellae growth (Hoegh-Guldberg 1994; Marubini and Davies 1996; Ferrier-Pagès et al. 2000, 2001) or it may be harmful by impacting e.g. the balance between host and zooxanthellae exchange rates (Dubinsky and Jokiel 1994) or coral gamete fertilization success (Koop et al. 2001). Diverse responses and acclimatization reactions have been observed in laboratory experiments using single parameter manipulations as well as in situ measurements including several stressors, reviewed in Fabricius (2005). Increased levels of dissolved inorganic nitrogen (DIN, as nitrate, nitrite or ammonium) at constant photosynthetically active radiation (PAR) lead to an increase in zooxanthellae density (Hoegh-Guldberg 1994; Marubini and Davies 1996; Ferrier-Pagès et al. 2000, 2001; Koop et al. 2001). DIN from the surrounding water is assimilated by the symbiotic algae and used for the synthesis of nitrogen-containing molecules such as amino acids and nucleotides. Since nitrogen is very limited in oligotrophic reef systems, zooxanthellae produce compounds with high C:N ratios which they mainly translocate to the host animal for use of respiration (e.g. glycerol). Access to nitrogen by anthropogenic sources allows algae to decrease their C:N ratio, which leads to a higher utilization of the nutrients and energy for zooxanthellae growth (Fig. 5) and a lower rate of translocation to the coral host (Dubinsky and Jokiel 1994; Ferrier-Pagès et al. 2000). Since both, chlorophyll a and total protein per unit surface increase with increasing dinoflagellate density, the photosynthetic rates are increased (Fabricius 2005). In contrast, elevated level of dissolved inorganic phosphorus (DIP) seems to have only little effect on zooxanthellae population, while the effect on coral growth and calcification are discussed controversially (Fabricius 2005).

On community level, hard corals are virtually unrivalled in their nutrient-poor environment. With degrading water quality at sewage outfalls or river mouth, macroalgae species can form dense mats, increase their standing crop and compete with coral communities (Koop et al. 2001; Fabricius 2005). They use dissolved inorganic nutrients to build up their fleshy organic matter and may hence outcompete corals, increase sediment trapping and restrict gas exchange below the sediment creating anoxic conditions when algal mats collapse (Fabricius 2005). Additionally, macroalgae inhibit coral recruitment by space occupancy and shading. It is of general acceptance that increased nutrient supply support a shift from coral- to algal-dominated reefs (Koop et al. 2001), in particular in co-occurrence with coral stressing conditions, such as temperature rise, diseases and the removal of herbivores (Szmant 2002; Bruno et al. 2003).

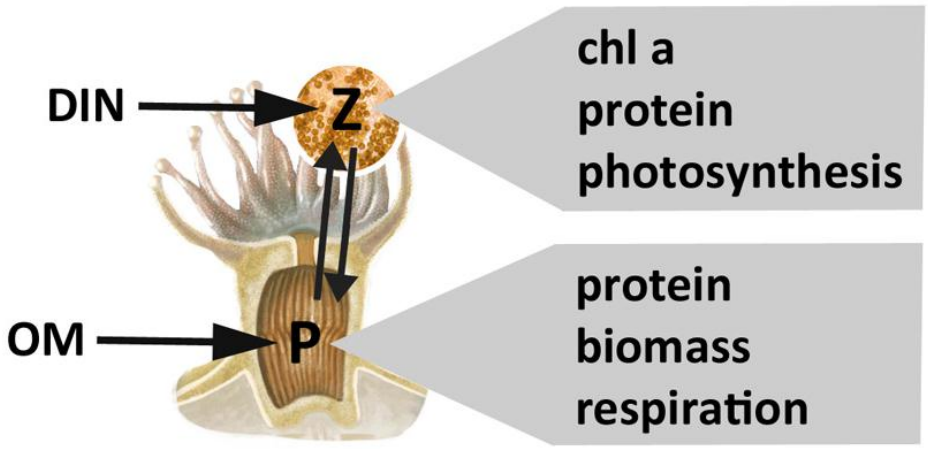

Figure 5. Nutrient pathways in pristine reef systems (oligotrophic, high light). Dissolved inorganic nutrients (DIN) are incorporated by zooxanthellae while organic matter (OM) is taken up heterotrophically by the polyp animal. Energy and nutrients are translocated between symbionts and host and determine the tissue composition and metabolic rates of the coral holobiont.

1.3.2 Effect of particulate and dissolved organic matter

Dissolved inorganic nutrients from external sources (e.g. sewage discharge) are rapidly taken up by bacteria, flagellates, micro-algae and benthic primary producers in oligotrophic reef waters, where production is strongly nutrient limited (Fabricius 2005). The planktonic community exists at ambient DIN concentrations between 0.02 – 0.05 µM. Even slight increases in inorganic nutrients of about 0.1 µM are sufficient to support maximal division rates and bloom formation can begin immediately (<1 day) after nutrient input (Furnas et al. 2005). Dissolved nutrients thereby support plankton biomass and organic matter production while DIN and DIP pools have fast turnover times from hours to days. Consequently, only a small fraction of land-based nutrients gets into direct contact with benthic corals and is available for zooxanthellae uptake for a short time. Large benthic organisms like corals are hence thought to respond more intense to organic matter produced from inorganic nutrients in reef waters than from inorganic nutrient stocks (Furnas et al. 2005). In consequence, measuring fast incorporated inorganic nutrients usually underestimates terrestrial nutrient input while chlorophyll a concentrations, reflecting actual primary production, seem to result in a more accurate determination of the nutrient supply (Bell 1992).

Increased levels of organic matter (OM), either in particulate live (LOM), dead or dissolved form (DOM), can enhance heterotrophic feeding (Fig. 5) of corals and lead to enhanced tissue growth

(Anthony and Fabricius 2000; Fabricius 2005). Up to eight times increased tissue biomass were found in corals fed by particulate matter (Anthony and Fabricius 2000) or live organic matter (Ferrier-Pagès et al. 2003) compared to starved corals after six weeks. Is has been shown for some coral species that the number of ingested zooplankton is proportional to prey density (Anthony and Fabricius 2000; Grottoli et al. 2006) and starved corals feed more prey items than fed corals (Ferrier-Pagès et al. 2003). Some species are efficient predators of zooplankton and able to ingest from 0.5 to 2 prey items per polyp per hour of ingestion, as found for the polyps of *Madracis mirabilis*, *Montastrea cavernosa* and *Porites porites* (Sebens et al. 1996; Houlbrèque and Ferrier-Pagès 2009). In addition, increased heterotrophic feeding increases nutrient translocation to the zooxanthellae, hence increasing zooxanthellae density and consequently areal zooxanthellar protein and chlorophyll a, which further increases photosynthetic rates (Fig. 3; Ferrier-Pagès et al. 2003; Houlbrèque et al. 2003). However, zooxanthellae density appears to increase to a lesser extent than in response to direct incorporation of dissolved nutrients because of a nutrient partitioning between host and algae (Dubinsky and Jokiel 1994).

1.3.3 Effect of turbidity

In every water body, the availability of light is a function of water depth and particle concentration. Due to anthropogenic disturbances, in particular terrestrial runoff, coastal waters show increased loads of particles in suspension which decrease water clarity and light penetration depth (Telesnicki and Goldberg 1995; Fabricius 2005). Accelerated phytoplankton growth and sediments, discharged from land or resuspended from the seafloor reduce visibility and the amount of light available for coral photosynthesis (Fabricius 2005). Eventually, this may cause coral death and hence a lower hard coral cover, as it was found e.g. in Hawaii, close to a sewage outlet (Hunter and Evans 1995). Near Puerto Rico, five weeks of shading altered the community structure and functioning of a coral reef, by decreasing net primary production and respiration and by causing bleaching and death of several hard coral species (Rogers 1979).

In order to cope with daily or seasonal light fluctuations, corals are able to adjust their photophysiology to some degree, a process called photoacclimation (Fabricius 2005; Hoogenboom et al. 2009). It allows corals to persist in variable light environments and must be strictly separated from changes in photophysiology due to elevated nutrients (e.g. increase in zooxanthellae density). Photoacclimation includes a change in number of thylakoids per zooxanthellae cell and size of photosynthetic units (i.e. number of pigment molecules) thereby altering the light absorption

capability (Maritorena et al. 2002; Cooper and Ulstrup 2009). Regarding a P-E curve (photosynthesis vs. irradiance) there is evidence that with decreasing light, whether due to turbidity or depth, the initial slope (α) is increasing, while the maximum photosynthetic rate is decreasing. Consequently, optimum photosynthetic rates are reached under lower light levels, expressed in a decreased E_K (light intensity of incipient saturation; Mass et al. 2007). Thereby, corals usually show a greater photochemical efficiency in turbid waters. Despite separation of these acclimation processes from nutrient responses, the extent of photoacclimation may also be dependent on the concentration of available nutrients, since an increase in light-harvesting pigment-protein complexes requires nutrients (Maritorena et al. 2002).

1.3.4 Effect of sedimentation

Increased sediment loads do not only affect corals by the reduction in light, but also by settlement on the coral surface. Indeed, this is usually the more severe impact on corals, since it can kill exposed corals tissue within a period of a few days (Riegl and Branch 1995). Coral communities are easily smothered, their capacity to capture prey items is reduced and abrasion takes place in turbulent waters (Stafford-Smith 1993; Fabricius 2005).

The coral response is an active sediment rejection by hydrostatic pumping, ciliar movement and mucus production. Particles are bound by mucus globules and strands, secreted by mucus glands on the surface and rejected from the colony surface as large flocculent particles (Telesnicki and Goldberg 1995; Brown and Bythell 2005). This is an energy-consuming process, which may lead to compromises in energy allocation towards tissue growth, calcification and reproduction. Respiration rates are usually increased and photosynthetic rates decreased, leading to P:R ratio below 1 where more carbon is respired than accumulated by photosynthesis (Riegl and Branch 1995). Sediments enriched with transparent exopolymer particles (TEP, “marine snow”) produced by phytoplankton and bacteria in nutrient-enriched coastal waters kill newly settled coral recruits and increases coral respiration dramatically (Fabricius et al. 2003). In contrast, intermediate amounts of clean sediment do not affect corals as much as low-level sedimentation with TEP (Fabricius and Wolanski 2000). Generally, as lower the organic content of settled sediment as lower the hazardousness for the hard corals, given at less anthropogenic effected coastlines.

1.4 The objectives

Eutrophication of coastal ecosystems due to terrestrial runoff is an ancient, but still potent threat to coral reefs (Jackson et al. 2001; Fabricius 2005). Especially in times of increasing human population density and coastal urbanization, it can act as single most significant pressure and exceed global change prospects. If not such severe, eutrophication in combination with turbidity and sedimentation stress, acts as a stress reinforcing interactive stressor which is influencing the overall recovery rate and resilience to climate disturbances (Maina et al. 2011). The degree of sensitivity and capability of physiological acclimatization will determine how scleractinian corals counter these stresses. Most scientists discussing the future of coral reefs (Jackson et al. 2001, McClanahan 2002, Hoegh-Guldberg et al. 2007, Joseph and McClanahan 2011) are aware of the synergistic effects and the threat to exceed a “tipping point” where an alternative state of reefs is reached and a return would be difficult. Enhancement of the knowledge base of the physiological response of corals to environmental stimulus, can help to increase future models and reduce local stressors by effective management (Duarte et al. 2008; Maina et al. 2011).

Recent research has shown that a loss of diversity and shifts in food webs within coral reefs as an ecosystem response to land-based pollution does not necessarily imply a negative impact for every coral species (Koop et al. 2001; Bongiorni et al. 2003; Sawall et al. 2011). Thus, it is important to assess species-specific stress tolerance and metabolic performance. In situ investigations of the acclimatization potential of dominant frame-building corals to water quality changes under realistic conditions are needed.

Within the "Jeddah Transect Project", investigations of coral acclimatization to the North-South water quality gradient in the Red Sea were now complemented by in situ experiments along a cross-shelf (near- to off-shore) nutrient gradient in front of the city of Jeddah. The study serves to improve our understanding of acclimatization potential and speed of scleractinian corals to anthropogenic land-based pollution. For this purpose, the widely distributed reef-building coral *Pocillopora verrucosa* (Ellis and Solander, 1786) was transplanted from off- to near-shore and vice versa and its physiological plasticity to cope with changing water quality in terms of nutrient concentrations, turbidity and sedimentation was investigated. This includes in situ incubation for metabolism measurements (photosynthesis, respiration) and coral tissue analyses (photopigments, protein concentration and biomass). To the best of our knowledge, this is the first study demonstrating the stress resistance and acclimatization speed of a widely distributed reef-building coral to acute sewage discharge in Saudi Arabia.

Central research questions:

(1) Do coral colonies from eutrophic (near-shore) and oligotrophic reefs (off-shore) show differences in nutritional status (biomass, total protein, zooxanthellae density, chl a concentration) and metabolic rates (photosynthesis, respiration)?

(2) Do transplanted corals acclimatize to changed water quality (from off- to near-shore and vice versa) and approximate native corals in terms of nutritional status and metabolic rates?

(3) How fast do corals acclimatize to changed water quality and is the speed depending on the transplantation direction (from off- to near-shore and vice versa)?

2 Material and Methods

2.1 Study Sites and Sampling Design

The study was conducted from February to May 2012 at the Red Sea coastline of Saudi Arabia. The linear oceanic basin is separating Africa from the Arabian Peninsula and terminates to the south at the strait of Bab al Mandeb (Fig. 6A). Due to its enclosed situation only limited seawater exchange takes place through the Gulf of Aden and thereby limiting the nutrient supply. Additionally, located between deserts, there is no riverine and only low rain input, reducing the flushing of terrigenous, nutrient-rich material into the Red Sea. The upper water column is highly oligotrophic and chlorophyll content of pelagic waters is 0.1-0.2 mg m^{-3} in large areas of the Northern and Central Red Sea (Acker et al. 2008). Primary production is mainly limited by nitrate and phosphate, whereas iron is introduced by dust from the surrounding deserts. According to warm sea surface temperature (SST) and nutrient limitation, large coastal areas possess extensive coral reef complexes, which are some of the healthiest in the world due to low human population and the minimal development in these desertic conditions (Acker et al. 2008).

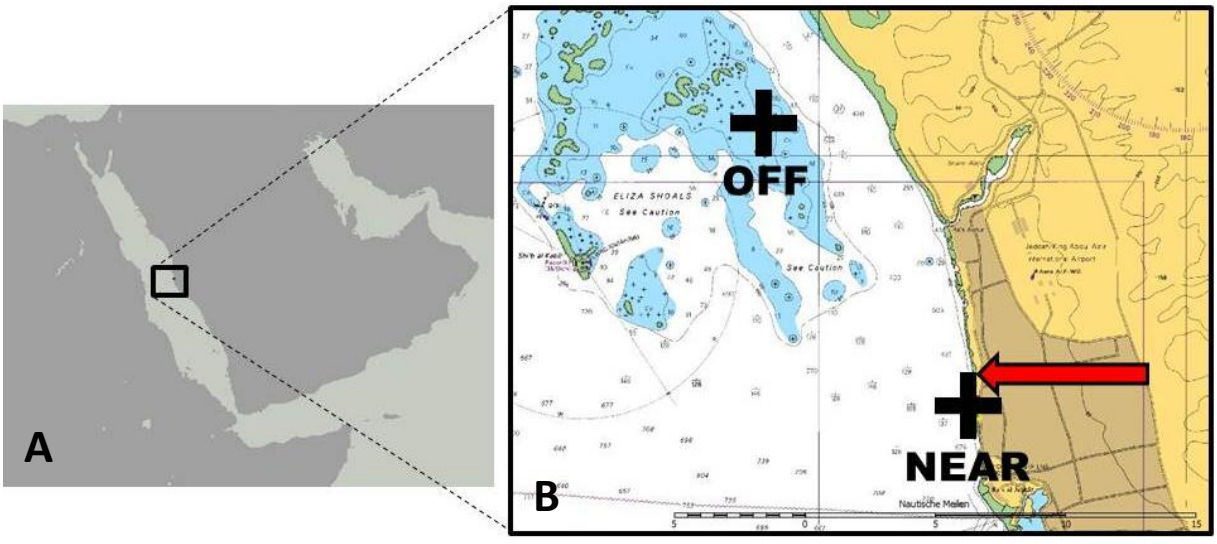

Figure 6. Marine charts of the Red Sea (A) and the coastal waters of Jeddah (B) with sewage outlet (red arrow). Study sites: "OFF" non-impacted off-shore reefs, "NEAR" impacted near-shore reefs. Green patches are coral reefs.

After the discovery of vast reserves of oil and a second oil boom in 2009 due to a rapid increase in oil prices 2008-2009, Saudi Arabia is economically one of the fastest growing countries, leading inter alia to rapid development of coastal areas. The second largest city of Saudi Arabia is Jeddah, located at the central coast of the Red Sea, with an increase of population from 381 000 in 1971 to more than 3 million people until now (Abdu et al. 2002). One of the greatest challenges is the waste water processing, where only a small share of households feature connectivity to the municipal sewage treatment plans (Risk et al. 2009; personal conversation). Consequently, a large volume of untreated sewage is discharged into coastal waters. On the narrow continental shelf, extensive coral reefs have developed and form a fringing reef in front of the promenade. The reef flat extends about 30 m from the promenade to the reef crest, where the reef drops quickly to 15-20 m depth. Further away from the coast, separated by a deep channel, patch reefs exist, in particular in the Northern end of Jeddah (Fig. 6B).

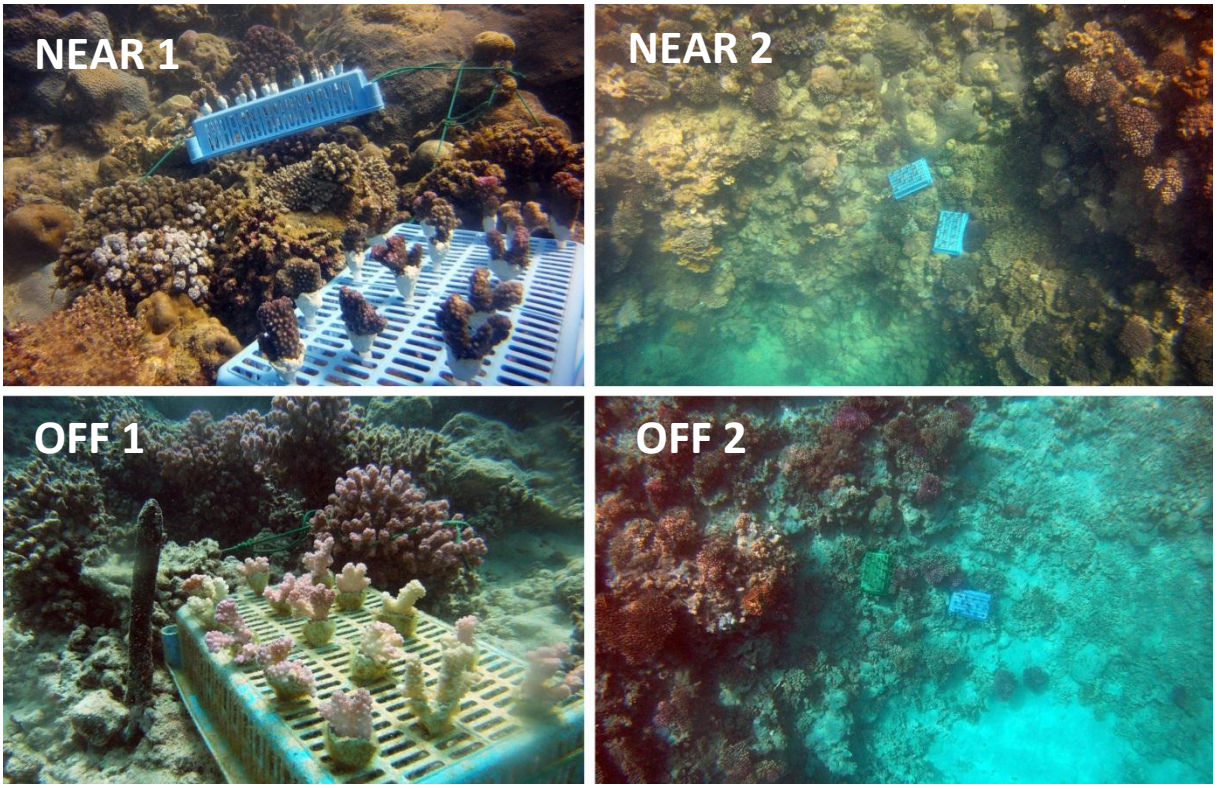

Figure 7. Appearance of coral fragments on baskets before transplantation. Near-shore corals (NEAR 1) look greenish-brownish with a thick tissue layer while off-shore corals (OFF 1) appear brighter and less fleshy. Experimental site at eutrophic near-shore conditions (NEAR 2) in comparison to the non-impacted pristine reef site (OFF 2).

Four experimental sites were established with two strongly impacted eutrophic near-shore reefs (*NEAR1*: 21°35.36' N 39°6.16' E ; *NEAR2*: 21°35.41' N E39°6.17' E; Fig. 7B) and two sites at pristine oligotrophic off-shore reef patches about 15km northeast of the city and 7km away from coast (*OFF1:* 21°46.74' N 38°57.42' E ; *OFF2*: 21°46.32' N 38°57.42' E). Examined reefs (Fig. 7) at similar water quality levels had at least a distance of 120 m ensuring a genetic variety of sampled colonies. While the prevailing currents are directed towards south along the coastline, eutrophic wastewater does not reach Northern off-shore sites. At each site, 20 sun-exposed colonies of *Pocillopora verrucosa* (Ellis and Solander, 1786) were sampled between 4-5 m water depths, depth at which highest coral cover is found. Colonies were sampled with a distance of at least 5 m between colonies at comparable reef spots (in terms of current and wave exposure). An apical branch (5-8 cm high) was removed from the centre part, attached to a PVC screw with underwater epoxy (ORCA Construct: Coral Glue) and labelled with colour-coded numbered tags. Prepared coral fragments were fixed at the corresponding experimental site to installed PVC baskets (Fig. 7) in the reef (20 fragments / basket) and left to recover from handling for two weeks. For transplantation experiments, one out of two prepared baskets per study site was transferred to the site with oppositional nutrient conditions (NEAR ↔ OFF), in order to identify acclimatization processes. The remaining non-transplanted fragments, further referred to as “native” colonies, served to identify existing differences between corals from off- and near-shore (results averaged over all times of sampling) as well as to show potential effects of the method of fragmentation (changes within experimental period). In situ incubations were conducted in the coral reef adjacent to installed baskets right after transplantation (t=0), after three (t=3) and six weeks (t=6). The incubation device (Fig. 8) consisted of four cylindrical acrylic chambers equipped with oxygen sensors (DIGISENSE Optical Dissolved Oxygen Sensor, PONSEL, France) for dissolved oxygen measurements and valves for water sampling. Each chamber had a stirrer and was flushed with surrounding seawater by a pump every 45 min for 2 min (47 min = 1 incubation cycle), automatically. The device was positioned by SCUBA-diving at the investigated reef spot and three labelled fragments from the basket were inserted by their screws in one chamber each (Fig. 9A+B; screws cleaned from fouling organisms). The 4^{th} chamber served as coral-free control to determine oxygen evolution by planktonic organisms in the water column.

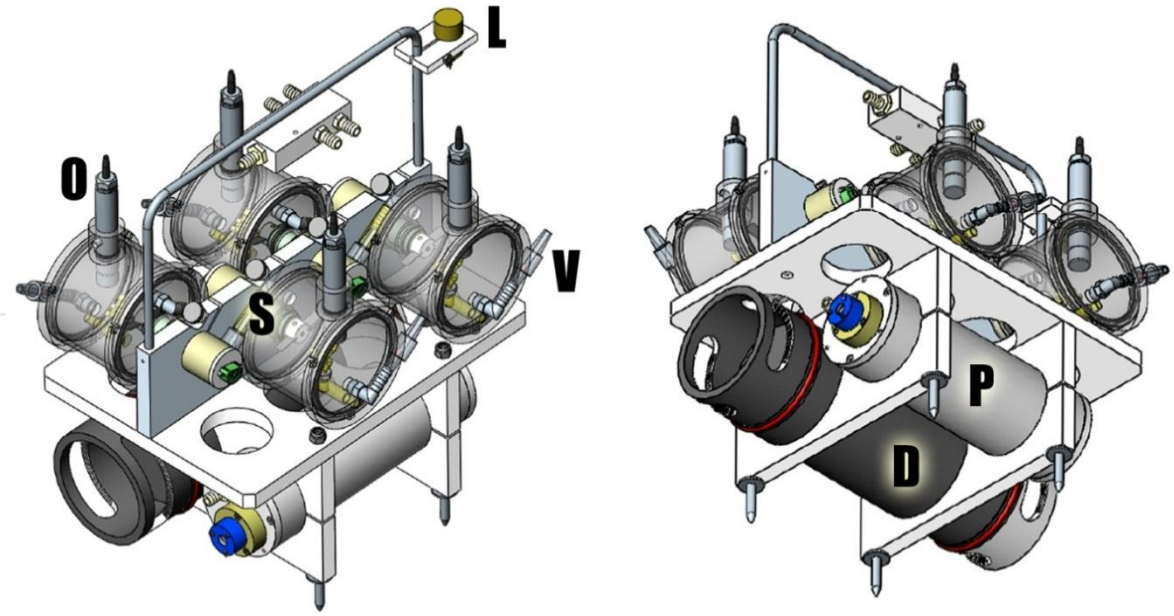

Figure 8. Construction drawing of the in situ incubation device (without tubes and cables). Four cylindrical incubation chambers equipped with a stirrer (S) and oxygen optode (O) are in connection with a data logger (D) and a pump below (P). A light sensor (L) continuously records incoming PAR while water can be sampled via valves (V).

Oxygen and incoming PAR were measured continuously (SDL Submersible data logger, NEXSENS, USA) every minute during the five incubations cycles per day from approximately 08:00 low light to 13:00 high light conditions. Every second cycle the entire device was covered by black cloth for respiration measurements. After incubation, coral fragments were transferred into the laboratory for measurements of maximum quantum yield and tissue analyses. Four days of measurement at one experimental site allowed replicating six non- and six transplanted fragments (n=6) with two controls each. One complete set of incubation including all sites lasted 16 days.

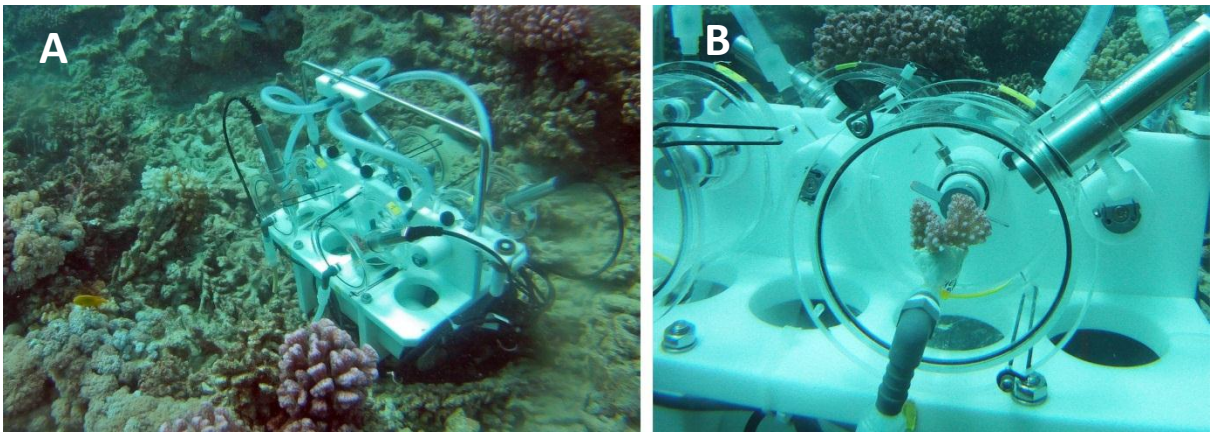

Figure 9. Incubation device in the field (A). Coral fragment in a single incubation chamber (B) representing one replicate (B).

2.1 Environmental parameters

In order to quantify the influence of sewage discharge on water quality and compare impacted- and non-impacted reef complexes, water samples were taken during the experiment with 10-l folding bags at the time of fragment investigations. Triplicate samples (2-l) for chlorophyll a (chl *a*) were filtered on glass-fibre filters (Whatman GF/F) and for particulate organic nitrogen (PON), particulate carbon (PC) and total suspended solids (TSS) on pre-combusted and pre-weighted glass-fibre filter (Whatman GF/F). Filters were stored lightproof at -20°C. Triplicate filtrate (10-ml) was filled in glass jars with a Teflon lid and acidified with H_3PO_4 (pH<2) for dissolved organic carbon (DOC) analysis. Triplicate water samples (15-ml) were gravity filtrated through a 0.2 µm membrane filter and filled into scintillation vials for dissolved inorganic macronutrient determination (phosphate PO_4^{3-}, ammonium NH_4^+, nitrate NO_3^{2-}, nitrite NO_2^-, silicate SiO_4) and triplicates of original seawater samples (50-ml) were filled into PE-bottles for total N and P analysis, all stored at -20°C.

Chl a was extracted from the filter with 90% acetone in a lightproof 4°C fridge over 24 h, centrifuged at 4°C, 4000 rpm for 10 minutes and the supernatant was filled in 1 cm glass cuvettes. Concentration of chl a was determined fluorometrically at an emission wavelength of 668 nm and an extinction wavelength of 430 nm (10-AU Fluorometer, KONTRON Instruments). Fluorometer calibration was conducted with a chlorophyll a standard (Fluka, Sigma-Aldrich, Switzerland).

Filters for PON and PC were dried in an oven (50°C, 24 h) and weighted. Difference between pre- and post-filtration resulted in the TSS value. Afterwards, filters were folded in tin casings, nitrogen and carbon content were determined with an elemental analyser (Fisons CN-Analyser NA 1500N) and molar C/N ratios were calculated. DOC was determined with a total organic carbon analyser. Inorganic nutrients were measured photometrically (Spectra-Photometer U-2900, Hitachi) in a 10 cm quartz cuvette, after standard procedures described by (Grasshoff et al. 1983). Total nitrate and phosphate was measured with the same methods as for PO_4^{3-} and NO_3^{2-}, after the complete oxidation of organic material in the water sample.

2.2 Coral metabolism

Oxygen data from the incubation device was used to calculate net photosynthesis (PS_n) as the sum of gross photosynthesis (PS_g, positive) and dark respiration (R, negative). PS_n and R were obtained by the difference in dissolved oxygen at the beginning and the end of an incubation cycle, while the first 10 min of each incubation cycle was excluded due to unstable oxygen values. PS_n and R rates were corrected for the contribution of the planktonic metabolism by subtracting the values of the control chamber. By construction of photosynthesis – irradiance (P-E) curves, the maximum net photosynthesis (PS_nmax) and net photosynthetic rate at 400 PAR (PS_n400) were determined by a nonlinear regression analysis. A single exponential decay function with an exponential rise to maximum (Function 1; three parameters: y_0, a, b) was used, with "f" as coral oxygen production at a given PAR "x" using the software SigmaPlot 10.

Function 1: $f=y_0+a*(1-\exp(-b*x))$

For further assessment of the properties of the photosynthetic apparatus, the maximum quantum yield of the photosystem II (F_v/F_m) was measured in the laboratory for all coral fragments with a pulse amplitude modulation fluorometer (Diving-PAM, Walz, Germany). For this, the fragments were dark adapted for 10 min, the minimum fluorescence (F_0) was measured after dark adaptation and the maximum fluorescence (F_m) after treatment with a saturation pulse. From these parameters maximum quantum yield was calculated (Function 2).

Function 2: $F_v/F_m = (F_m - F_0)/ F_m$

2.3 Tissue parameter

All extractions of the tissue from the entire coral fragments were performed immediately after return from in situ incubation and the PAM measurements. Tissue was removed efficiently with an air jet by fixing the fragment in a bag with filtered seawater, the exact volume was recorded and the

tissue slurry was stored at -20°C until analyses. The skeleton was labelled and stored until determination of the surface area.

Frozen tissue slurry was transferred to Kiel, Germany, and following analyses were performed on defrosted and homogenized (Ultra Turrax, Janke & Kunkel, Germany) samples in the laboratories of GEOMAR. Coral biomass was determined gravimetrically. 2-ml of tissue slurry was filtered on a pre-weighted GF/F filter and dried for 24 h at 50°C before weighing again. The difference of weight before and after tissue application was calculated and the weight differences represented the dry weight of the biomass.

Zooxanthellae and polyp cells were separated by centrifugation (4000 rpm, 10 min, 4°C) while opened polyp cells (by previous homogenisation) stayed in dilution and unaffected dinoflagellates were spun down. The zooxanthellae pellet was collected, rinsed and centrifuged two times (4000 rpm, 10 min, 4°C) in order to clean it from remains of polyp cells. Afterwards zooxanthellae cells were opened with SDS treatment (sodium dodecyl sulphate). With a calorimetric measurement the protein concentration of the host polyp ($Prot_P$) and the zooxanthellae ($Prot_Z$) were determined separately. Bicinchoninic acid (BCA) was used to quantify total protein content by a colour change, detected by a photometer (Pierce BCA Protein Assay Kit, Thermo Scientific). Calibration was conducted with bovine serum albumin standard (Pierce BCA Protein Assay Kit, Thermo Scientific). Chlorophyll a was measured fluorometrically like described in “water parameters” though 500 µl of tissue slurry was used instead of filters.

2.4 Measurement standardization

The surface area of the dried corals skeletons were determined by the waxing method (Naumann et al. 2009a). Skeletons were dipped into hot melted candle wax (Paraffin, 65°C) for 3 s and left to dry for 24 h. After weighing, waxing was repeated and difference between first and second weighting offered a wax amount proportional to the area of the coral fragment. A standard curve was constructed with differently sized wooden cubes of known surface area. The surface area was used as standardization for all measured metabolism and tissue parameter. Therefore, all parameters are expressed as cm^{-2}. The wax coating technique ensures an objective area determination without being dependent on the surface consistence.

2.5 Statistical Analysis

All data is displayed as mean ± standard error. Statistical analyses were conducted with the software STATISTICA 8. General differences between the two sites (water quality, metabolic and tissue parameter) were analysed as single factors using a t-test. Both off-shore sites and both near-shore sites were merged since water quality revealed no differences. A correlation matrix was used to find significant dependencies in transplantation data between factor trends.

3 Results

3.1 Environmental data

Water quality differed between near- and off-shore reefs (Table 1). The concentration of all measured dissolved inorganic nutrients in the water column was significantly higher near-shore. Mean concentration of nitrate was 7.4-fold greater near-shore, followed by the concentration of nitrite which was 2.3-fold higher close to the shore. Phosphate and Silicate had 1.2- to 1.3-fold higher concentrations near-shore compared to off-shore reef waters. Similarly, mean concentration of particulate nitrogen and carbon were generally 1.3-fold higher near-shore. Chlorophyll a concentration was 1.5 times higher and levels of total suspended solids were 1.1-fold higher close to the shore. Same applies for concentrations of total nitrate (1.8-fold) and phosphorus (1.2-fold) which were significantly higher near-shore. Total incoming PAR differed by 163 µmol photons m^{-2} s^{-1} with 27% lower radiation (during incubations between 11:00-12:00) near-shore (595 ± 33 µmol photons m^{-2} s^{-1}) compared to off-shore (756 ± 25).

Table 1. Contrasting water quality between near-shore and off-shore reefs including dissolved inorganic nutrients, particulate organic nitrogen (PON) and particulate carbon (PC), chlorophyll a (chl a), total suspended solids (TSS) as well as total nitrogen (N) and phosphate (P). Mean ± SE. Significant differences (p<0.05) = *

Parameter	n	near-shore	off-shore	diff. (off → near) [x-fold]	t value	*P*
Nitrate [µmol l^{-1}]	12	1.18 ± 0.17	0.16 ± 0.03	7.38*	5.80	<0.001
Nitrite [µmol l^{-1}]	12	0.07 ± 0.01	0.03 ± 0.00	2.33*	3.87	0.001
Phosphate [µmol l^{-1}]	9	0.19 ± 0.01	0.15 ± 0.01	1.29*	3.24	0.004
Silicate [µmol l^{-1}]	9	1.49 ± 0.09	1.24 ± 0.05	1.20	2.08	0.052
PON [µg l^{-1}]	9	18.00 ± 1.05	14.15 ± 0.75	1.27*	2.47	0.021
PC [µg l^{-1}]	9	141.63 ± 7.83	112.70 ± 4.98	1.26*	2.53	0.018
Chl a [µg l^{-1}]	9	0.40 ± 0.01	0.26 ± 0.01	1.54*	16.88	<0.001
TSS [mg l^{-1}]	21	8.90 ± 0.19	8.01 ± 0.24	1.11*	2.97	0.005
Total N [µmol l^{-1}]	6	11.52 ± 1.68	6.41 ± 0.20	1.80*	2.80	0.018
Total P [µmol l^{-1}]	9	0.51 ± 0.02	0.42 ± 0.02	1.22*	3.67	0.002

3.2 Metabolic rates

Metabolic rates of native fragments remained constant over time and time-averaged rates of PS_nmax were ~2-fold higher near-shore (0.14 ± 0.02 mg O_2 cm^{-2} h^{-1}) compared to off-shore (0.07 ± 0,01) while PS_n at 400 PAR was 1.8-fold higher near-shore (near: 0.05 ± 0.01; off: 0.03 ± 0.01) (Fig.10). In addition, a slightly higher (2%) but still significant maximum photosynthetic yield (F_v/F_m) was observed near-shore (0.664 ± 0.003) compared to off-shore corals (0.651 ± 0.004). Respiration, averaged over both dark incubations per day, also showed a clear trend with 1.3-fold higher respiration rates in native near-shore corals (near: -0.03 ± 0.01 mg O_2 cm^{-2} h^{-1}; off: -0.02 ± 0.01). Set into relation, near-shore corals had a higher PS_nmax/R ratio (5.3) than off-shore colonies (3.4).

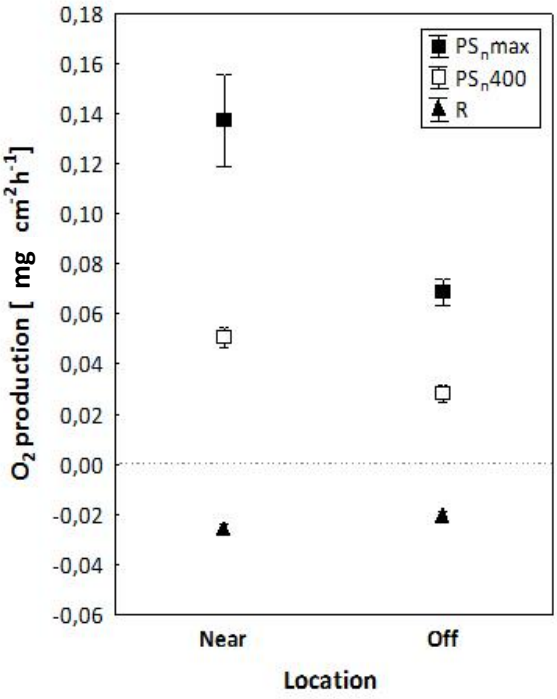

Figure 10. Maximum net photosynthesis (PS_nmax; n=16), net photosynthesis at 400 PAR (PS_n400; n=16) and respiration (R; n=16) at both locations, averaged over all times of sampling for native coral fragments. Mean ± SE

During the transplantation experiment, corals altered their metabolic rates rapidly and significantly (Fig. 11). More than a doubling of photosynthesis (PS_nmax and PS_n400) within six weeks was evident for corals moved towards the coast into eutrophic near-shore waters while respiration rate increased 1.4-fold (Tab. 2). Corals transplanted into oligotrophic off-shore waters showed a weaker response and photosynthesis decreased 1.3- to 1.5-fold (PS_nmax and PS_n400) while respiration decreased 1.1-fold (Tab. 2). Consequently, the ratio of PS_nmax:R increased in corals transplanted to near-shore (5.15), achieving ratios of native near-shore fragments, whereas the ratio slightly decreased (4.03) in contrary transplantation direction. All metabolic changes from off- to near-shore presented

significant increases within six weeks while responses from near- to off-shore showed a clear although not statistical significant. Strongest metabolic response to changing water quality took place within the first 3 weeks after transplantation already (Fig. 11).

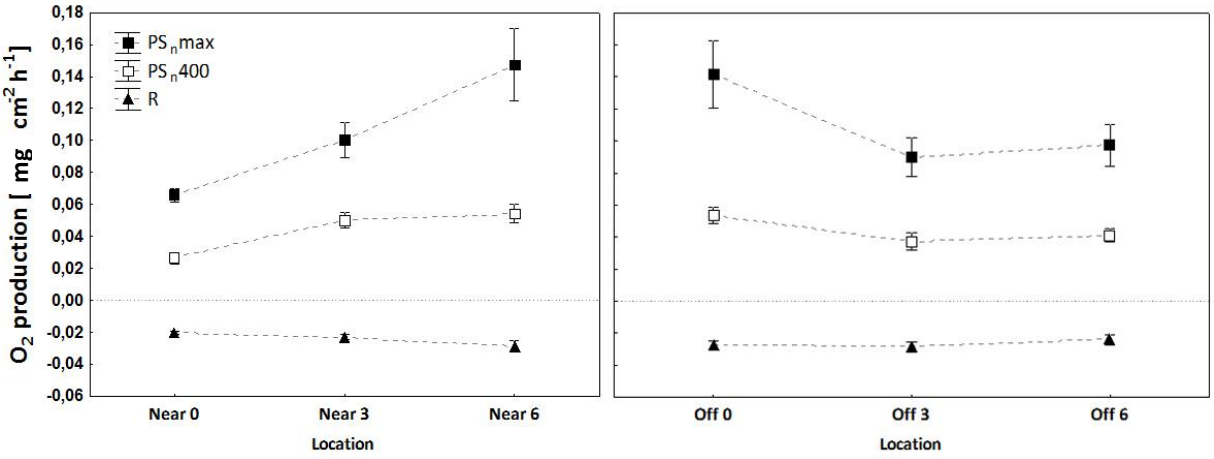

Figure 11. Metabolic changes in maximum net photosynthesis (PS_nmax; n=5-11), net photosynthesis at 400 PAR (PS_n400; n=5-11) and respiration (R; n=5-11) during 6 week period after transplantation. Respiration rates display averaged daily dark respiration. Mean ± SE

Table 2. Changes in maximum net photosynthesis (PS_nmax), net photosynthesis at 400 PAR (PS_n400*)* and respiration (R) during six week period after transplantation. Mean ± SE. Significant differences (p<0.05) = *

Parameter [mg O_2 cm^{-2} h^{-1}]	**Near 0**	**Near 6**	**diff. (0 → 6) [x-fold]**	**n**	***t value***	***P***
PS_nmax	0.066 ± 0.00	0.148 ± 0.02	2.2*	10	-3.55	0.002
PS_n400	0.026 ± 0.00	0.054 ± 0.01	2.1*	10	-4.13	0.001
R *(-1)	0.020 ± 0.00	0.029 ± 0.00	1.4*	10	2.48	0.023

Parameter [mg O_2 cm^{-2} h^{-1}]	**Off 0**	**Off 6**	**diff. (0 → 6) [x-fold]**	**n**	***t value***	***P***
PS_nmax	0.142 ± 0.02	0.097 ± 0.01	0.5	8	1.63	0.121
PS_n400	0.053 ± 0.01	0.041 ± 0.00	0.3	8	1.82	0.086
R *(-1)	0.027 ± 0.00	0.024 ± 0.00	0.1	8	-0.87	0.397

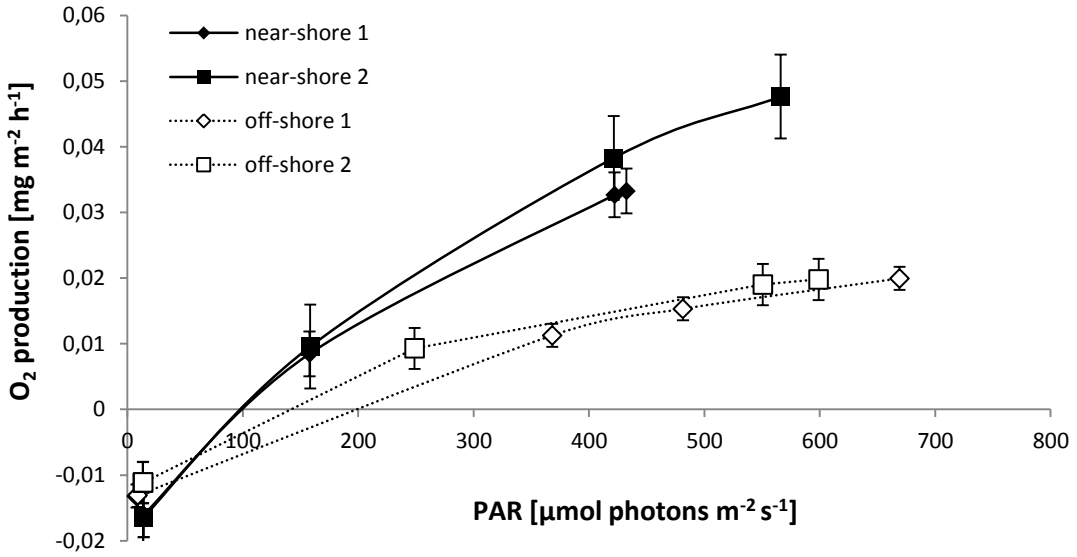

Figure 12. P-E (Photosynthesis – Irradiance) curves for native fragments from near- and off-shore reefs at t=0. Each data point contains three replicates (=colonies), while a curve consists of five data points (two dark and three light incubations) taken between 8 and 12 am. Near-shore fragments show a higher O_2 production at lower PAR.

Maximum quantum yield of PSII, assessed with the PAM, increased in all transplanted corals after 3 weeks independent of the direction of transplantation (Fig. 13). After 6 weeks, corals moved from off- to near-shore showed an increase from 0.659 ± 0.003 to 0.667 ± 0.004 in maximum quantum yield compared to a decrease from 0.663 ± 0.002 to 0.637 ± 0.004 in individuals moved from near- to off-shore.

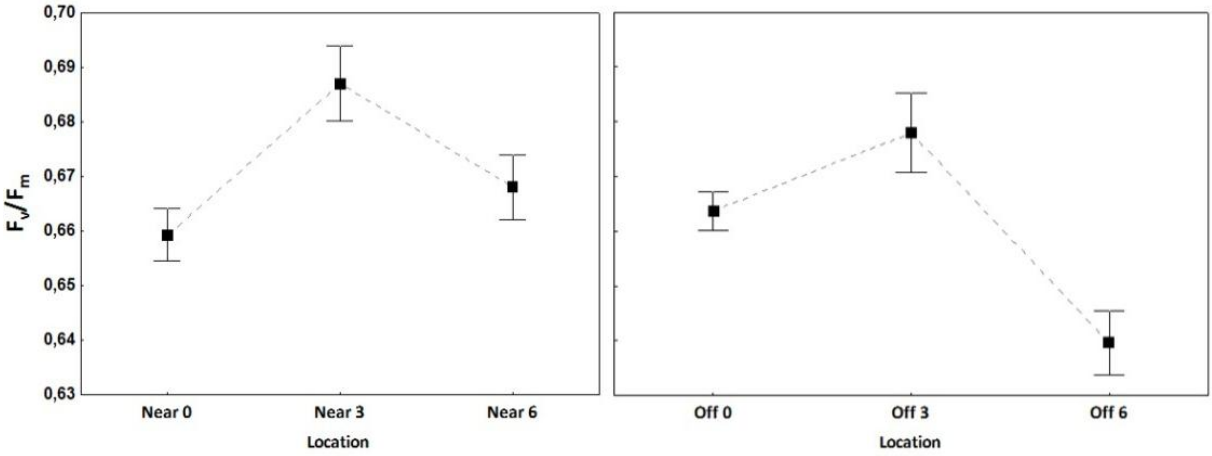

Figure 13. Changes in maximum quantum yield (F_v/F_m) within six weeks period after transplantation. Mean ± SE

3.3 Tissue parameter

In native fragments, tissue parameters except of chlorophyll remained constant over time. Chl a concentration increased significantly from 4.50 ± 0.50 µg cm^{-2} to 6.56 ± 0.65 (p=0.018) in near-shore corals and from 1.83 ± 0.23 µg cm^{-2} to 2.97 ± 0.37 (p=0.014) in off-shore corals.

Time averaged rates of tissue chl a concentration followed the pattern of photosynthesis with ~2.3-fold higher concentration in native near-shore fragments (5.48 ± 0.45 µg cm^{-2}) compared to off-shore fragments (2.35 ± 0.23) (Fig. 14). Biomass (DW) was ~1.2-fold higher in near-shore corals (3.85 ± 0.21 mg cm^{-2}) compared to off-shore corals (3.23 ± 0.16). Both results confirmed personal observations where off-shore corals appeared brighter and less fleshy. Near-shore corals looked more greenish-brownish with thicker tissue. Almost twice as much protein concentration of the symbiotic dinoflagellates was found in near-shore corals (near: 29.41 ± 2.35 µg cm^{-2}; off: 17.28 ± 1.34) whereas polyp protein content was only 1.3-fold higher (near: 0.43 ± 0.02 mg cm^{-2}; off: 0.39 ± 0.02).

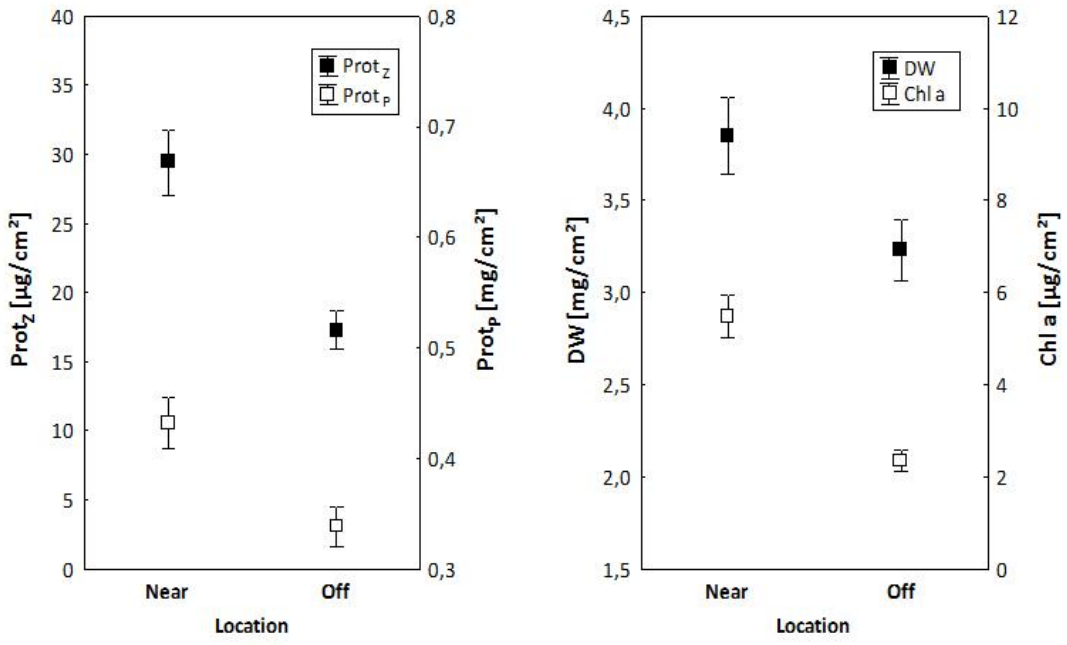

Figure 14. Tissue characteristics of native near- and off-shore corals including protein concentration of symbiotic zooxanthellae ($Prot_Z$) and the host polyp ($Prot_P$), tissue dryweight (DW) as a proxy for biomass and chlorophyll a concentration (chl a). Mean ± SE

A change of all tissue parameters was evident in transplanted coral fragments (Fig. 15). In accordance to the metabolic rates, corals transplanted from off- to near-shore waters displayed a dramatic and rapid increase in areal chl a, DW and protein concentrations of zooxanthellae and coral host, with the most dramatic increase in zooxanthellae features, such as chl a (3.6-fold) and protein (2.1-fold) (Tab.3). Fragments transplanted from near- to off-shore showed a weaker response to water quality changes (Fig. 15). Fragments had ~0.5-fold decrease in chlorophyll a and zooxanthellae protein concentration (Tab. 3), as well as a decline in polyp protein content of 20%. In contrast, dryweight showed a slight increase from 3.85 ± 0.21 mg cm^{-2} to 4.71 ± 0.31. At the end of the experimental period, six out of 40 fragments, transplanted from near- to off-shore, were partially bleached or even dead, with up to 70% colonies surface area without symbionts or tissue. In contrast, no bleaching occurred in corals, transplanted from off- to near-shore.

Table 3. Changes in tissue parameters chlorophyll a (chl a), dryweight (DW) as a measurement for biomass and protein concentration of zooxanthellae ($Prot_Z$) and polyp ($Prot_P$) during six week period after transplantation. Mean ± SE. Significant differences (p<0.05) = *

Parameter	**Near 0**	**Near 6**	**diff. (0 → 6) [x-fold]**	**n**	***t value***	***P***
Chl a [µg cm^{-2}]	2.35 ± 0.24	8.48 ± 0.47	3.6*	12	12.87	<0.001
DW [mg cm^{-2}]	3.23 ± 0.17	4.31 ± 0.26	1.3*	12	3.65	0.001
$Prot_Z$ [µg cm^{-2}]	17.28 ± 1.37	36.13 ± 4.12	2.1*	12	5.32	<0.001
$Prot_P$ [mg cm^{-2}]	0.34 ± 0.02	0.46 ± 0.02	1.4*	12	4.57	<0.001

Parameter	**Off 0**	**Off 6**	**diff. (0 → 6) [x-fold]**	**n**	***t value***	***P***
Chl a [µg cm^{-2}]	5.48 ± 0.45	3.01 ± 0.40	0.5*	10	3.36	0.002
DW [mg cm^{-2}]	3.85 ± 0.21	4.71 ± 0.31	(-1.2)*	9	2.23	0.033
$Prot_Z$ [µg cm^{-2}]	29.41 ± 2.35	15.10 ± 1.66	0.5*	10	3.81	0.001
$Prot_P$ [mg cm^{-2}]	0.43 ± 0.02	0.36 ± 0.02	0.2	10	1.87	0.071

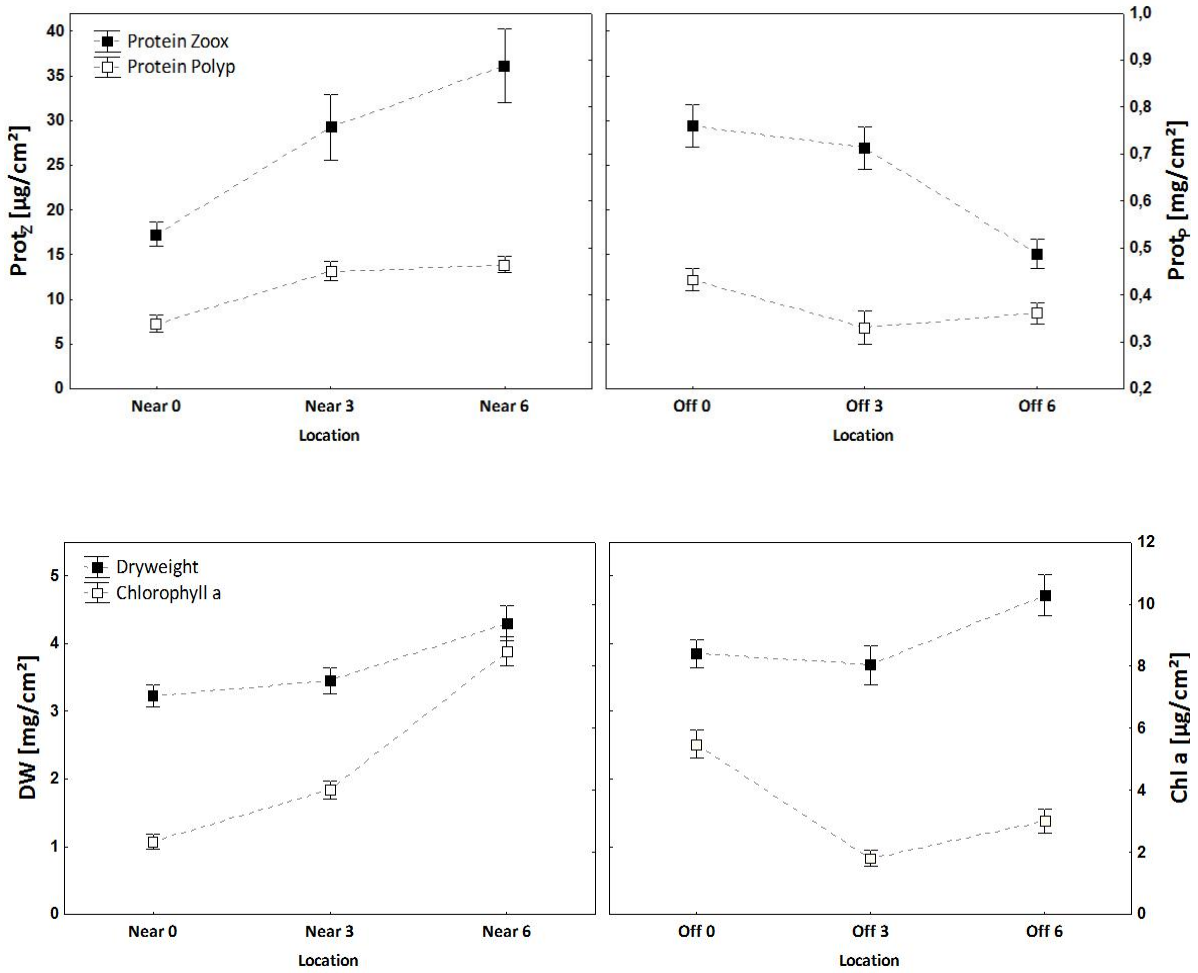

Figure 15. Changes in tissue chlorophyll a (Chl a), dryweight (DW) and protein concentration of zooxanthellae ($Prot_Z$) and polyp ($Prot_P$) within six weeks period after transplantation. Mean ± SE

4 Discussion

The primary objective of this study was to assess the impact of anthropogenic pollution on coral metabolic performance, define their physiological plasticity and measure the speed of acclimatization processes. Enhanced terrestrial runoff, leading to increased concentrations of inorganic nutrients and particulate organic matter as well as higher turbidity and sedimentation stress, is one of the major threats to coral reefs (Jackson et al. 2001; Fabricius 2005). In spite of significant ecosystem responses as increasing proportions of macroalgae and a shift to heterotrophic filter feeders (reviewed in Fabricius 2005), studies have shown no inevitable negative effects of eutrophication on coral individuals in situ (Koop et al. 2001). Some corals actually profiting from nutrification and terrestrial runoff by showing higher growth and reproduction rates at constant survival rates (Bongiorni et al. 2003) as well as higher energetic gains through increased auto- and heterotrophy (Anthony 2006; Sawall et al. 2011). However, other aspects of coral acclimatization are less well known (e.g. acclimatization speed) and in situ measurements are still rare. The results of this study revealed fast and efficient acclimatization of the species *P. verrucosa* to eutrophication, whereas interestingly, acclimatization from eutrophic to oligotrophic conditions seemed to be slower and transplantation even stressful for some specimen. This possibly indicates a weaker acclimation potential for near-shore corals or harmful effects of increased light intensity on high zooxanthellae loaded specimen. The different aspects of acclimatization are discussed in the following.

4.1 Environmental parameters

Eutrophication of near-shore reefal waters is evident by enhanced chlorophyll a, particulate organic matter, high concentrations of inorganic nutrients (in particular NO_3^{2-}) and decreased PAR. Measured data indicate high concentrations of nitrogen compounds from untreated sewage such as domestic and industrial effluents (Risk et al. 2009). A high chlorophyll a concentration at the impacted site pointing at a fast incorporation of available inorganic nutrients by nitrogen-limited plankton (Furnas et al. 2005). However, elevation in chl a is less pronounced than previously assumed by reason of strongly increased nitrogen concentrations. Prevailing coastal currents from the north may push primary production to the south and parts of the production might be bound rapidly by the benthic reef community (e.g. corals and bivalves). In summary, the near-by dumping of wastewater

(21°35.73' N 39°6.20' E) strongly alters the water quality of the fringing near-shore reef system and its impact appears to be chronic as it is already persistent for decades (Risk et al. 2009).

4.2 Effect of fragmentation

As measurements of nutritional status and metabolism in native fragments revealed, fragmentation had probably only a small effect on colonies of *P. verrucosa*. Assumed stress of removal and fixation did not lead to a loss of zooxanthellae and biomass, or tissue already recovered from handling within two weeks prior t=0. Here, the comparison to unfragmented colonies would reveal the pure effect of fragmentation (analyses are in progress). Until then, the observed, uniform increase in chl a (1.5- to 1.6-fold) in near-shore as well as off-shore colonies could be interpreted as prolonged recovery from fragmentation while other tissue parameter and even metabolic rates seemed to be unaffected or already recovered. Consequently, elevated chl a concentrations in transplanted colonies have to be evaluated in respect of the fragmentation effect but the overall effect seems to be low.

4.3 Response of zooxanthellae

The finding of significantly enhanced photosynthetic rates in eutrophic near-shore waters suggests a linkage between nutrient access and zooxanthellar autotrophy. The symbiotic dinoflagellates are in a permanent state of nitrogen limitation at oligotrophic off-shore reef conditions, while they find access to large amounts of dissolved inorganic nutrients (Muscatine et al. 1989; Dubinsky and Jokiel 1994; Hoegh-Guldberg 1994) such as NO_3^{2-} (elevated > 7-fold) in the near-shore reefs. This contributes to zooxanthellae growth, as reflected in increased areal chl a and zooxanthellar protein. This is in agreement with results of Muscatine et al. (1989), Hoegh-Guldberg (1994), Marubini and Davies (1996), Koop et al. (2001) and Sawall et al. (2011), showing increased zooxanthellae densities with increasing nutrient concentrations. More chl a at same coral surface (elevated > 3-fold) significantly increases catchment of photons hence increases photosynthesis of the coral. An increase in PS with increasing inorganic nutrients has been previously reported for the corals *Stylophora pistillata* (Ferrier-Pagès et al. 2000, 2001), *Stylophora subseriata* (Sawall et al. 2011) and whole coral

communities of the Great Barrier Reef (Koop et al. 2001). Consequently, more incoming PAR could be utilized resulting in higher energy availabilities and hence more photosynthates, primarily used by the zooxanthellae themselves for further division. Higher algae densities also explain, at least partly, enhanced respiration rates of near-shore corals (elevated 1.3-fold) by more oxygen consumption per unit surface area.

Since turbidity and hence light intensity (decreased 1.3-fold) are low in eutrophic waters due to plankton growth and particulate organic matter, photoacclimation of zooxanthellae may also impact areal chl a concentration and hence photosynthetic rates. Many previous studies have shown an increase of the intracellular pigment concentration with diminishing light in *P. verrucos*a, independent of zooxanthellae density changes (Maritorena et al. 2002; Cooper and Ulstrup 2009). These processes cannot be identified here, since chl a concentration could not be calculated per cell basis. It is assumed that photoacclimation to changing light conditions plays a minor role in *P. verrucosa* near-shore populations due to the fact that areal chl a and zooxanthellae protein concentrations rise commensurately and light intensity decreases comparatively little (27%). Additionally, available nutrients and hence zooxanthellae multiplication is assumed to cover and exceed the effect of photophysiological acclimation processes on a cell basis in respect of maximum photosynthetic rates.

Another source of nutrients is the polyp host, also contributing to zooxanthellae growth and hence photosynthetic rates. Increased translocation processes from the animal to the symbionts provide the near-shore algae population with additional resources (Dubinsky and Jokiel 1994). Within days, digestion of organic matter by the polyp will lead to excretion of N-rich compounds (e.g. NH_4) and be ready for incorporation by the adjacent zooxanthellae population. Already within hours, zooxanthellae receive nutrients from the coelenteron before assimilated by host polyp (Houlbrèque and Ferrier-Pagès 2009). Both pathways are likely to be enhanced at eutrophic near-shore stations, where heterotrophy of the polyp is increased. Piniak et al. (2003) and Piniak and Lipschultz (2004) revealed a rapid arrival (~30 min) of stable isotope tracer (^{15}N) in the symbiotic dinoflagellates after heterotrophic feeding. In the same experiment, zooxanthellae acquired 10 to 20% of the ingested prey nitrogen mass while the host retained the bulk of the ingested label (Piniak et al. 2003). It is assumed that polyp animals can upregulate the inorganic nutrient acquisition to stimulate zooxanthellae growth by increased feeding (Dubinsky and Jokiel 1994). This hypothesis confirms the idea of a regulated algae population and polyps in eutrophic waters may provide their symbionts population with nutrients in order to regain photosynthetic rates in a low-light environment. A higher photosynthesis in near-shore corals in spite of less PAR therefore could be explained not only by

dissolved inorganic nutrient uptake but by an upregulated support of the zooxanthellae with nutrients gained by heterotrophy (Houlbrèque et al. 2004; Houlbrèque and Ferrier-Pagès 2009).

In addition to the effect of nutrient availability, differences in photophysiology between near- and offshore colonies could also be based on a different set of zooxanthellae (Baker 2003). For *P. verrucosa* it has been shown that photosynthetic rates decreased in some corals during periods of elevated temperature whereas other individuals were not affected (Rowan 2004). A different set of *Symbiodinium* taxa accounted for this difference and it is assumed that symbiosis recombination may be one mechanisms by which corals adapt to a changing environment (Rowan 2004). Unfortunately, genetic identification of existent taxa is missing due to logistical constraints but investigations on *Stylophora pistillata* in the Northern Red Sea (Gulf of Aqaba) have shown no effect of eutrophication on clade identity (Lampert-Karako et al. 2008).

Maybe the most remarkable finding is the acclimatization speed of the zooxanthellae population. In contrast to revealed differences in nutritional status and metabolic rates between long-term acclimatized native near- and off-shore populations, transplanted corals faced a steep and rapid nutrient gradient during translocation. The increase in zooxanthellae density and hence photosynthesis within six weeks (elevated > 2-fold) at the eutrophic site clearly point at a perception and quick response to new environmental conditions. Already after three weeks of exposure, photophysiology approached values of native near-shore colonies. Zooxanthellae seem to utilize available nutrients very quickly, leading, along with a changed light regime, to a rapid adjustment of the nutritional status and metabolism (Fig. 16). These findings correspond to results of Cooper and Ulstrup (2009) who demonstrated an increasing PAR-absorptivity with decreasing light and increasing nutrient concentrations and a greater photochemical efficiency in near-shore corals. Their findings are confirmed here and transplanted colonies seem to increase the efficiency of PS II in eutrophic conditions within 6 weeks. Ferrier-Pagès et al. (2000) revealed increased rates of photosynthesis and increased zooxanthellae densities within nine weeks of elevated nutrient concentrations and Hoegh-Guldberg (1994) attested an up to 3-fold increase in the mitotic index of zooxanthellae within eight weeks of exposure to high concentrations of ammonium.

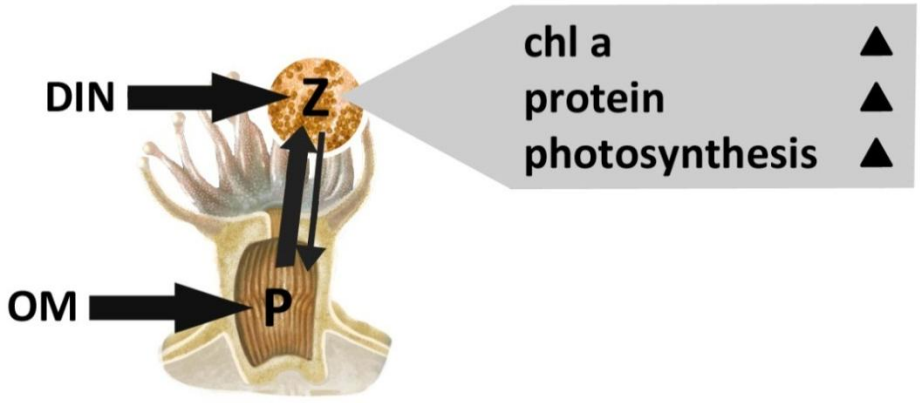

Figure 16. Effects of elevated dissolved inorganic nutrients (DIN) and organic matter (OM) on tissue composition and metabolism of the zooxanthellae population. Thick arrows represent a large flux/effect, while small arrows represent a small flux/effect.

Six weeks after transplantation from off- to near-shore, zooxanthellae growth and photosynthesis actually exceeded characteristics of native near-shore fragments (chl a: 1.6-fold; protein: 1.3-fold; PSmax: 1.05-fold). A likely reason for this unexpected finding is an unbalanced growth of the symbionts. It has been suggested that the host animal keeps zooxanthellae in a near-permanent nitrogen limitation to control cell numbers and avoid space competition (Hoegh-Guldberg 1994; Maritorena et al. 2002). Unlimited nutrient access due to eutrophication therefore may results in a perturbation of the mutualistic symbiosis by a reduced translocation of carbon to the host and uncontrolled algae multiplication (Dubinsky and Jokiel 1994). Unfortunately, an extension of the experimental period was not feasible due to logistical constraints but would possibly reveal a tipping point, followed by a reduction in zooxanthellae numbers to densities of native near-shore colonies.

Same mechanisms of acclimatization are able to explain the reverse changes in zooxanthellae for corals transplanted from near- to offshore (Fig. 17). A rapid decline in nutrients led to a critical shortage to maintain high density algal populations and led to a loss of zooxanthellae (protein and chl a decreased 0.5-fold). In addition, high light conditions are likely to push low-light acclimatized zooxanthellae in conditions of photoinhibition or even cause photodamage (Ralph et al. 2005). This hypothesis is supported by data of the PAM measurements, where F_v/F_m dropped significantly in corals transplanted to high light off-shore waters (Cooper and Ulstrup 2009; Warner et al. 2011) and further by visual signs of bleaching at some specimen. However, the decline in zooxanthellar nutritional status and metabolism is moderate and not achieving values of native off-shore populations within the experimental period. An explanation may be found in mobilization of reserves, which are able to maintain zooxanthellar cell functioning for at least six weeks. Lipids represent a major energy reserve and corals originating from near-shore waters with plenty of

nutrients should hold a stock of lipids (Harland et al. 1993; Anthony 2006; Ferrier-Pagès et al. 2011). So far, comparative studies are missing, however data offers first insights in variable response speeds of the photophysiology to changing nutrient and light conditions, although an elongation of the experiment would have shown us, if corals can acclimatize an sustain on the long run.

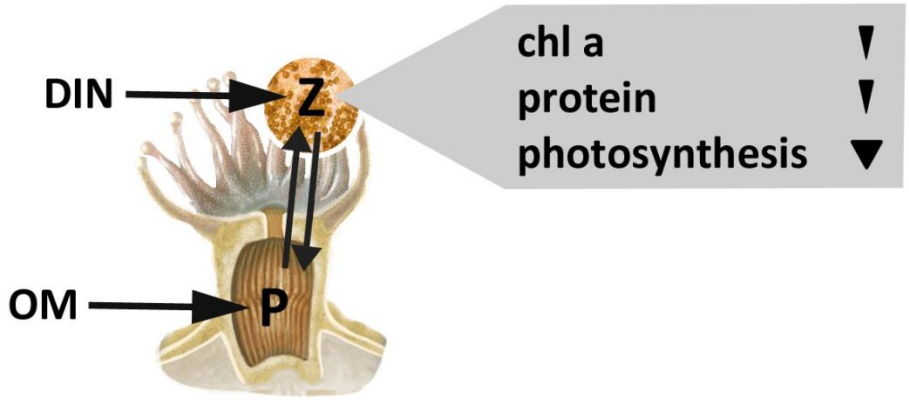

Figure 17. Effects of reduced dissolved inorganic nutrients (DIN) and organic matter (OM) on tissue composition and metabolism of the zooxanthellae population. Thick arrows represent a large flux/effect, while small arrows represent a small flux/effect.

4.4 Response of coral host

While elevated levels of dissolved inorganic nutrients in eutrophic waters are rapidly utilized by the zooxanthellae population, host polyps are unable to use this nutrient source. In addition, a lower translocation of carbon-enriched compounds from the zooxanthellae to the host may take place due to higher symbiotic algae growth (Dubinsky and Jokiel 1994). Recent studies could also not support the theory of a substantial translocation of nitrogen from the algae to the host (Piniak and Lipschultz 2004), even at high inorganic nitrogen supply (Lipschultz and Cook 2002).

The significant higher biomass (elevated 1.2-fold) and protein concentration (elevated 1.3-fold) of near-shore polyps therefore suggests heterotrophic feeding as an alternate nutrient source (Fig. 14). Prey capture by nematocysts, tentacles or mucus may provide a rich source of essential nutrients, leading to observed tissue growth (Piniak et al. 2003; Houlbrèque and Ferrier-Pagès 2009). Possible feeding occurs on organic matter (OM), either in particulate live (LOM), dead or dissolved form (DOM). Nevertheless, an enrichment of near-shore reefal waters with PON (elevated 1.3-fold) and PC

(elevated 1.3-fold) is evident and the high primary production (chl a elevated 1.5-fold) should provide food for extensive grazer populations. Most reefs house a complex mixture of pelagic (Heidelberg et al. 2004) and demersal zooplankton (Alldredge and King 1977), which stocks are depleted by benthic reef fauna in a layer <1m above the bottom (Yahel et al. 2005). Therefore, potent heterotrophic feeding appears to be very likely at the eutrophic near-shore site and could explain differences in host animal tissue parameters.

LOM depletion rates were shown for comparable reef systems in the Red Sea by Yahel et al. (2005) and since corals feed primarily during the night when zooplankton densities are highest, daytime water quality data is unfortunately not reflecting actual LOM supply (Heidelberg et al. 2004; Yahel et al. 2005). Additionally, high current velocity as well as wave action at the reef crest near-shore most likely increase the flow rates around the colonies and again amplify heterotrophic feeding (Sebens et al. 1998).

High polyp growth rates in eutrophic waters have also been demonstrated by Anthony and Fabricius (2000), which showed a positive energy balance of corals in turbid waters due to an increase of the feeding rates on SPM, compensating the energy loss due to lower photosynthetic rates. Higher protein concentration, thicker tissue and higher biomass with feeding were already demonstrated for numerous tropical corals (reviewed in Houlbrèque and Ferrier-Pagès 2009). In addition, microorganisms like pico- and nanoplankton, which account for the bulk of pelagic planktonic biomass and also dominating the planktonic community of coral reefs, should contribute to the heterotrophic feeding at the impacted reef spots here (Houlbreque et al. 2004; Naumann et al. 2009b). In the central Red Sea, picoplankton account for 76-77% of chl a and primary production in epipelagic waters (Gradinger et al. 1992). The production of mucus nets, also observed and measured in our investigation (analyses in progress), serves to catch these small prey items (Lewis and Price 1975). First data indicate higher mucus productions of near-shore corals, supporting the hypothesis that microorganisms once more promoted by eutrophication account for tissue characteristics and good nutritional status.

In near-shore corals, enhanced biomass and protein content were associated with higher respirations rates (elevated 1.3-fold). On the one hand, higher polyp biomass and cell densities are considered to increase areal oxygen consumption even at constant cell respiration. On the other hand, energy-consuming behaviors, related to eutrophic conditions, are likely to enhance metabolic rates on a cell basis. Prey capture (e.g. by mucus production) has been shown to increase metabolic rates significantly (Telesnicki and Goldberg 1995). Active sediment rejection as a consequence of a higher

particle input and enhanced particle settlement near-shore (TSS elevated 1.1-fold) is likely to affects metabolic rates and hence respiration.

Like the acclimatization potential in zooxanthellae, host polyps of transplanted colonies showed a rapid response to changed water quality (Fig. 18). Protein concentration (elevated 1.4-fold) and biomass (elevated 1.3-fold) increased within six weeks after movement into eutrophic waters, followed by increased respiration (elevated 1.4-fold). The heterotrophic plasticity seems to allow *P. verrucosa* to respond to organic matter availability and utilize new resources (LOM, SPM, DOM) for growth. In addition to a substantial nutrient contribution, heterotrophically gained carbon also might become important. Transplanted corals faced a turbid, low-light environment and translocation from the symbionts probably decreased. Carbon gained by feeding therefore could present a significant energy source, especially during short-term water quality changes (Houlbrèque and Ferrier-Pagès 2009). Remarkable, again, is the speed of acclimatization and polyp nutritional status, like in zooxanthellae, exceeded performance of native near-shore populations. Again, this finding might not only be beneficial on the long run, pointing at a perturbation of the mutualistic symbiosis and uncontrolled growth.

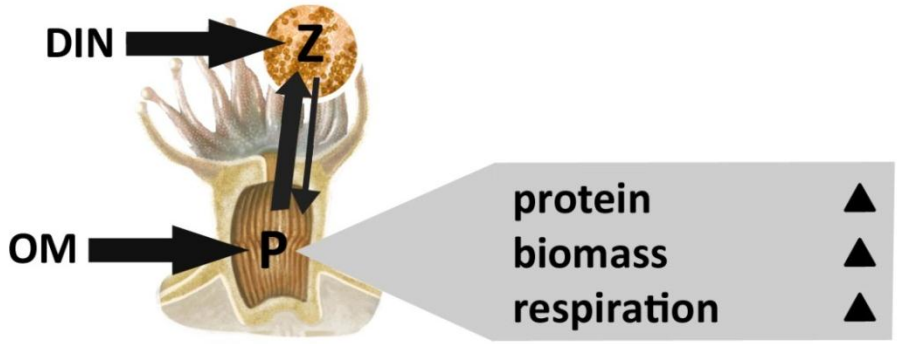

Figure 18. Effects of elevated dissolved inorganic nutrients (DIN) and organic matter (OM) on tissue composition and metabolism of the host polyp. Thick arrows represent a large flux/effect, while small arrows represent a small flux/effect.

Corals transplanted from near- to off-shore reefs displayed a slower acclimatization (Fig. 19), not reducing protein concentration (decreased 0.2-fold) to levels of native off-shore colonies. Again, lipid reserves stored during eutrophic conditions eventually act as buffer and supply animal cells with energy to maintain biomass at least for six weeks of experiments (Harland et al. 1993; Anthony 2006; Ferrier-Pagès et al. 2011). An extension of the experiment might have revealed further decline of nutritional status, assuming that after a depletion of reserves, polyp as well as zooxanthellae cells

would die until a stock of cells remains which reflects nutrient availability of the new environment and possibly show values of native populations.

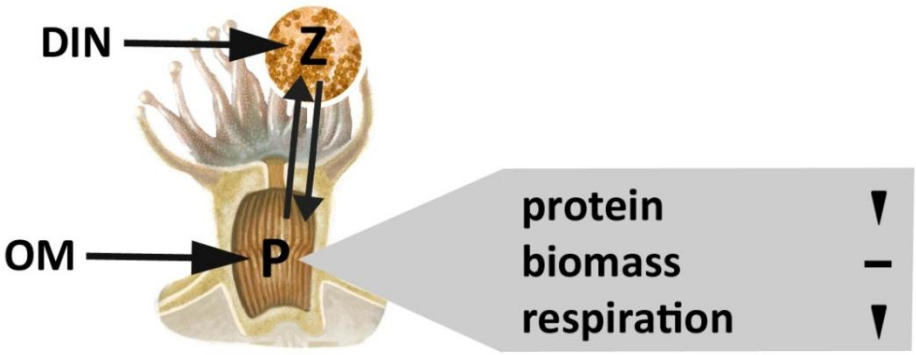

Figure 19. Effects of reduced dissolved inorganic nutrients (DIN) and organic matter (OM) on tissue composition and metabolism of the host polyp. Thick arrows represent a large flux/effect, while small arrows represent a small flux/effect.

4.5 Conclusion

Regardless of the detrimental effect of terrestrial runoff on coral reef ecosystems as a whole, this study demonstrates that there are scleractinian coral species that are able to resist a human land-based degradation of water quality. Actually, results point at a rapid short-term acclimatization potential, revealing coral responses and resilience in a different light. Changes in nutrient concentration, light availability and particle settlement appear to be tolerated by individuals of *Pocillopora verrucosa*, and zooxanthellae as well as host polyps are able to adjust nutritional status and metabolism within a few weeks. While acclimatization to eutrophic conditions occurred fast and measured parameters exceeded characteristics of native colonies, a switch to oligotrophic conditions aroused a slower adjustment towards native colonies and induced several bleaching spots. Therefore, high zooxanthellae loaded specimens seem to be more susceptible for varying water quality. All in all, the mixotrophic nutrition and the variable energy and nutrient fluxes between polyp, zooxanthellae and surrounding water, lead to a high stress resistance against, and rapid acclimatization potential to land-based eutrophication so that colonies of *P. verrucosa* de facto thrive in anthropogenic affected near-shore reef systems.

The following mechanisms appear to allow *P. verrucosa* to acclimatize to impoverished environments:

(1) In response to high availability of nutrients, either by inorganic nutrient uptake or translocation from the host, zooxanthellae enhance their nutritional status and increase growth rates.

(2) Higher algae numbers lead to a compensation of the loss in light availability in turbid near-shore areas and actually increases, enlivened by the nutrient supply, the production of photosynthates.

(3) Enrichment in organic matter enhances feeding rates and increases the nutritional supply of the polyp animal. A higher protein content and biomass per area are the consequence of an increase in heterotrophy.

(4) A translocation of heterotrophically gained nutrients towards the symbionts increases rates of photosynthesis and hence, in the long term, increases the transfer of photosynthates from the algae to the host.

(5) Rapid changes in water quality should be buffered by energy reserves in form of lipids, stored during periods of high nutrient supply. Mobilization of these compounds helps the corals to keep their stock of zooxanthellae and biomass in times of need.

Further efforts should be concentrated on identification of species-specific acclimatization potentials to various co-operating environmental stressors. Since stress resistance has been specified for a great many of scleractinian corals, the speed of physiological responses defines the sensitivity of a species in a cumulative anthropogenic affected ocean. In spite of existing data for *P. verrucosa*, other scleractinian corals might appear as less-tolerant species. It also remains an open question, if corals acclimatized and even profiting from eutrophic conditions are more or less resilient to further stressors of global extent, e.g. SST rise or ocean acidification. This study highlights the need of further in situ measurements on various species as well as under various combined water quality changes (e.g. nutrient and temperature) in order to improve future models which help to detect actual threats and minimize local stressors effectively.

My personal prospect is a study about the coral energy budget in which the contribution of auto- and heterotrophy is defined for different environmental conditions. Physiological acclimatization processes could be attended by a shift in energy input and hence a change in trophic level, altering the whole benthic-pelagic coupling. Transplantation experiments with isotope analyses would reveal the dependence of corals on organic sources across human-affected reefal waters (overfishing, eutrophication, warming etc.).

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A movie about my work in Saudi Arabia…

www.vimeo.com/kolleproductions/researchinsaudiarabia

Statutory Declaration

I declare that I completed this work on my own and that information which has been directly or indirectly taken from other sources has been noted as such. Neither this, nor a similar work, has been published or presented to an examination committee. I agree to publish this work in the library of GEOMAR and I attest that this document is in accordance with the electronic version.

Kolja Beisiegel

Attachment

Table 4. Change in oxygen concentration [mg/chamber] during 38 min of incubation in light (L) and dark (D). Light given in prevailing photosynthetic active radiation (PAR) averaged over incubation periods.

		Kammer				
Light / Dark	PAR	1	2	3	4	Location
L	368	1,03	0,8	0,64	0,23	01.04 O1-1-A
D	8	-0,61	-0,62	-0,77	0,06	
L	481	1,2	0,92	1,02	0,12	
L	669	1,31	1,08	1,12	0,07	
D	9	-0,76	-0,79	-0,82	-0,06	
L	249	0,71	0,47	0,26	0,05	02.04 O1-1-B
D	13	-0,65	-0,72	-0,35	-0,05	
L	551	1,19	1,13	0,54	0,02	
L	599	1,15	1,19	0,5	0,05	
D	14	-0,64	-0,72	-0,4	-0,07	
L	746	1,22	1,2	0,18	-0,02	03.04 O1-1-C
D	9	-0,6	-0,32	-0,84	0,05	
L	675	1,33	0,83	1,8	0,07	
D	9	-0,55	-0,29	-0,79	0,02	
L	775	1,23	0,74	1,61	0,04	
L	319	1,06	0,86	0,61	0,15	04.04 O1-1-D
D	11	-1,28	-0,81	-0,66	0,08	
L	618	1,33	1,31	1,1	0,04	
L	722	1,55	1,37	1,11	0,03	
D	9	-0,9	-0,8	-0,67	0,03	
L	838	1,47	1,3	1,02	0,02	
L	378	0,7	0,73	0,84	0,12	08.04 N1-1-A
D	9	-0,59	-1,14	-0,73	0,04	
L	645	1,21	1,74	1,61	0,02	
D	9	-0,57	-0,99	-0,69	0,03	
L	746	1,25	2,31	1,46	-0,02	
L	381	1,02	0,84	0,71	0,09	09.04 N1-1-B
D	11	-0,71	-0,58	-0,42	0,07	
L	538	1,5	1,23	0,93	0,03	
D	11	-0,78	-0,66	-0,49	0,04	
L	748	1,78	1,62	0,95	0,04	
L	158	0,55	0,6	0,24	0,08	14.04 N2-1-C
D	14	-0,72	-0,73	-0,49	0,05	
L	432	1,61	1,59	1	0,05	
D	14	-0,79	-0,78	-0,62	0,04	
L	422	2,02	1,92	1,24	0,05	
L	158	0,48	0,6	0,63	0,06	15.04 N2-1-D
D	14	-0,57	-0,91	-0,91	0,01	
L	421	1,46	2,16	2,6	0,05	
D	14	-0,68	-1	-1,09	0,02	
L	566	1,92	2,8	2,95	0,04	
L	458	1,39	1,36	0,64	0,1	16.04 O2-1-A
D	13	-0,91	-0,29	-0,44	-0,06	
L	628	1,6	0,54	0,76	0,06	
D	14	-0,85	-0,74	-0,42	0,07	
L	612	1,62	1,58	0,72	0,05	
L	594	1,4	2,5	0,71	0,01	16.04 O2-1-B
D	13	-0,78	-1,17	-0,86	0,03	
L	412	1,44	2,43	0,63	0,03	
D	12	-0,84	-1,16	-0,84	0,04	
L	188	0,97	1,53	0,23	0	
L	400	0,91	2,52	0,11	1,37	17.04 O2-1-C
D	13	-0,49	-1,78	0,03	-0,79	
L	647	1,04	3,75	-0,01	1,67	
D	14	-0,48	-2,05	0,06	-0,84	
L	757	1,12	3,95	0	1,58	
L	662	0,65	1,5	0	0,91	17.04 O2-1-D
D	14	-0,4	-0,85	0,05	-0,4	
L	476	0,59	1,4	0,02	0,85	
D	13	-0,41	-0,75	0,01	-0,43	

		Kammer				
Light / Dark	PAR	1	2	3	4	Location
L	444	1,43	2,69	1,86	0,13	24.4 O1-2-A
D	13	-0,71	-1,58	-1,11	0,05	
L	694	1,63	3,95	2,48	0,06	
D	13	-0,71	-1,81	-1,05	0,01	
L	837	1,61	3,91	2,7	0,02	
L	411	2,5	1,94	0,93	0,12	25.4 O1-2-B
D	13	-1,57	-1,11	-0,54	-0,26	
L	561	3,12	2,63	1,04	0,01	
D	13	-1,49	-1,12	-0,6	-0,1	
L	915	3,03	2,87	1,06	-0,04	
L	480	0,76	0,77	0,56	0,05	26.4 O1-2-C
D	12	-0,92	-0,59	-0,45	-0,12	
L	726	0,92	0,88	0,69	0,09	
D	11	-0,84	-0,57	-0,43	-0,14	
L	818	0,92	0,99	0,75	-0,04	
L	461	0,73	0,7	0,41	0,04	27.4 O1-2-D
D	12	-0,44	-1	-0,2	-0,13	
L	720	0,86	1,36	0,39	0,1	
D	13	-0,44	-1,1	-0,21	-0,16	
L	818	0,93	1,54	0,38	0,02	
L	374	0,79	3,02	0,66	0,06	28.4 N1-2-A
D	14	-0,74	-2,19	-0,67	-0,19	
L	657	0,99	4,89	1,23	0,04	
D	13	-0,72	-2,24	-0,65	-0,28	
L	669	1,01	5,2	1,39	-0,03	
L	385	1,99	2,74	0,79	0,04	29.4 N1-2-B
D	15	-1,32	-1,43	-0,45	-0,1	
L	655	3,13	4,6	1,03	0,01	
D	13	-1,1	-1,16	-0,64	-0,05	
L	663	3,03	4,63	0,93	0,08	
L	422	1,14	1,99	1,3	0,02	30.4 N1-2-C
D	13	-0,77	-1,35	-0,72	-0,06	
L	641	1,79	3,13	1,69	0,07	
D	14	-0,81	-1,06	-0,72	-0,07	
L	675	1,86	3,22	1,63	-0,02	
L	401	0,68	3,82	1,37	0,32	01.5 N1-2-D
D	13	-0,77	-2,86	-0,86	-0,24	
L	648	1,3	7,54	2,09	0,14	
D	14	-0,76	-3,81	-0,88	0,1	
L	757	1,37	8,6	1,94	-0,1	
L	259	0,41	0,71	0,75	-0,01	02.5 N2-2-A
D	13	-0,36	-0,9	-0,45	-0,1	
L	511	0,73	2,04	1,28	0	
D	13	-0,39	-1,08	-0,56	-0,08	
L	555	0,69	2,16	1,29	0,08	
L	243	1,42	0,72	0,67	0,03	03.5 N2-2-B
D	14	-1,41	-0,72	-1,07	-0,11	
L	422	2,77	1,59	1,53	0,14	
D	14	-1,38	-0,7	-1,08	-0,08	
L	444	3,14	0,74	1,47	0,03	
L	218	0,59	0,8	1,04	-0,03	04.5 N2-2-C
D	12	-0,48	-1,09	-1,25	-0,05	
L	318	0,88	1,74	1,82	0,1	
D	13	-0,48	-1,5	-1,29	-0,15	
L	575	1,24	2,59	2,51	0,05	
L	223	2,12	0,83	0,53	0,02	05.5 N2-2-D
D	13	-1,83	-0,67	-0,48	-0,18	
L	574	3,84	1,72	0,98	0,09	
D	13	-1,78	-0,86	-0,53	-0,23	
L	615	4,17	2,01	0,79	-0,08	

		Kammer				
Light / Dark	PAR	1	2	3	4	Location
L	477	0,67	3,42	2,15	0,03	06.5 O2-2-A
D	13	-0,36	-1,67	-1,44	-0,08	
L	836	0,72	3,93	2,6	0,04	
D	13	-0,34	-1,9	-1,45	-0,08	
L	807	0,72	3,79	2,84	0,1	
L	462	0,83	1,25	1,36	0,05	07.5 O2-2-B
D	12	-0,47	-0,75	-1,26	-0,06	
L	599	0,9	1,39	1,78	0,05	
D	14	-0,45	-0,53	-1,15	-0,07	
L	665	0,77	1,15	1,69	0	
L	490	0,99	1,36	0,61	0,06	08.5 O2-2-C
D	13	-0,57	-0,46	-0,39	-0,16	
L	769	1,17	1,76	0,7	0,04	
D	14	-0,54	-0,44	-0,4	-0,1	
L	718	1,18	1,81	0,7	0	

Table 5. Incoming PAR [µmol m^{-2} s^{-2}] at the near-shore and off-shore reef site during all incubations between 11 and 12 am.

near-shore	off-shore
669	669
663	746
675	722
757	837
422	915
566	818
555	818
444	612
575	757
615	807
	665
	718

Table 6. Volume of filtered seawater used for tissue extraction. Surface area of the whole coral derived from wax coating technique.

Coral	Seawater [mL]	Surface [cm-2]
N1-1-A1	33	43,39
N1-1-A2	35	75,27
N1-1-A3	37	52,26
N1-1-B1	28	47,92
N1-1-B2	26	48,46
N1-1-B3	23	46,42
N1-1-C1	29	58,63
N1-1-C2	34	66,47
N1-1-C3	28	56,02
N1-1-D1	47	70,20
N1-1-D2	23	54,10
N1-1-D3	27	42,66
N2-1-A1	32	57,87
N2-1-A2	36	46,04
N2-1-A3	28	30,10
N2-1-B1	41	77,82
N2-1-B2	48	80,79
N2-1-B3	29	60,38
N2-1-C1	33	44,80
N2-1-C2	33	54,07
N2-1-C3	30	38,74
N2-1-D1	29	43,36
N2-1-D2	32	45,69
N2-1-D3	30	73,96
O1-1-A1	28	**57,52**
O1-1-A2	32	51,04
O1-1-A3	48	58,82
O1-1-B1	29	47,51
O1-1-B2	32	53,79
O1-1-B3	26	35,81
O1-1-C1	33	40,37
O1-1-C2	27	25,77
O1-1-C3	48	56,14
O1-1-D1	42	69,69
O1-1-D2	39	63,89
O1-1-D3	30	49,20
O2-1-A1	37	75,75
O2-1-A2	33	46,93
O2-1-A3	27	46,01
O2-1-B1	26	70,01
O2-1-B2	27	73,36
O2-1-B3	26	64,72
O2-1-C1	30	38,58
O2-1-C2	34	77,22
O2-1-C3	28	46,04
O2-1-D1	37	28,35
O2-1-D2	34	29,14
O2-1-D3	27	39,06

Coral	Seawater [mL]	Surface [cm-2]
N1-2-A1	26	46,01
N1-2-A2	26	73,96
N1-2-A3	25	46,13
N1-2-B1	24	75,91
N1-2-B2	22	56,49
N1-2-B3	23	37,75
N1-2-C1	27	50,53
N1-2-C2	36	52,16
N1-2-C3	25	49,51
N1-2-D1	27	40,88
N1-2-D2	29	98,99
N1-2-D3	26	46,39
N2-2-A1	25	24,71
N2-2-A2	24	35,97
N2-2-A3	21	36,38
N2-2-B1	29	96,15
N2-2-B2	25	35,84
N2-2-B3	23	116,68
N2-2-C1	22	35,33
N2-2-C2	27	40,14
N2-2-C3	36	76,90
N2-2-D1	36	114,93
N2-2-D2	22	26,56
N2-2-D3	28	33,45
O1-2-A1	33	**53,72**
O1-2-A2	32	61,79
O1-2-A3	41	83,14
O1-2-B1	42	102,88
O1-2-B2	38	57,74
O1-2-B3	29	39,44
O1-2-C1	24	67,45
O1-2-C2	32	27,61
O1-2-C3	20	37,94
O1-2-D1	25	42,12
O1-2-D2	20	57,30
O1-2-D3	25	11,46
O2-2-A1	23	32,46
O2-2-A2	30	77,28
O2-2-A3	35	104,69
O2-2-B1	30	35,33
O2-2-B2	24	38,17
O2-2-B3	34	87,45
O2-2-C1	24	36,03
O2-2-C2	27	19,15
O2-2-C3	27	22,96
O2-2-D1	29	31,11

Table 7. Measured water quality parameter at the impacted station near-shore and the off-shore reef. Chlorophyll a (Chl a), total suspended solids (TSS), particulate organic nitrogen (PON) and particulate carbon (PC) data were derived from filters while the inorganic nutrients were gravity filtrated.

Station	Chl a [µg/L]	TSS [mg/L]	PON [µg/L]	POC [µg/L]	Nitrate [µmol/L]	Nitrite [µmol/L]	Phosphate [µmol/L]	Silicate [µmol/L]
Near	0,388117888	8,1	14,5125898	106,433341	1,40452	0,0567744	0,1772828	1,1188306
Near	0,431865432	8,34	15,041248	105,803382	0,986614	0,0682274	0,1575194	1,2181158
Near	0,388117888	7,92666667	13,4750414	107,020963	0,6105406	0,0521932	0,1509316	1,2961256
Near	0,388117888	7,81333333	14,0347115	120,543467	0,6116276	0,0224154	0,1964584	1,216442
Near	0,431865432	7,9	14,9766843	116,867116	0,576065	0,0292872	0,1964584	1,2448092
Near	0,388117888	7,88	18,8969183	144,865417	0,664428	0,0269966	0,2623364	1,2589928
Near	0,388117888	8,65333333	20,3269259	154,56206	2,1429232	0,1025864	0,203634	1,9769384
Near	0,388117888	10,0533333	19,3263737	151,517665	2,053072	0,1254924	0,2233974	1,8776532
Near	0,388117888	9,43333333	19,7117583	172,195892	2,0501796	0,1140394	0,2233974	1,9769384
Near		7,88666667	20,6744067	194,963951	1,1136326	0,0750992	0,1838706	1,5372468
Near		8,76666667	20,3459676	186,366234	1,0834536	0,0957146	0,1838706	1,601073
Near		8,08	24,61332	154,149996	0,8123792	0,0750992	0,1509316	1,5443386
Near		9,99333333	26,1559502	173,117968				
Near		10,2	23,6829535	183,502973				
Near		9,44	13,1803338	125,553958				
Near		10,22	12,5437681	103,60225				
Near		9,14	14,3063863	106,619867				
Near		9,69333333						
Near		9,18666667						
Near		9,35333333						
Near		8,88666667						
Off	0,256875257	6,44	13,8196214	113,556913	0,1451012	0,0155436	0,1443438	1,3812272
Off	0,300622801	5,84	12,3408286	100,417906	0,1502842	0,024706	0,1838706	1,4025026
Off	0,256875257	5,81333333	12,7637553	106,494211	0,1648302	0,0292872	0,1904584	1,0833716
Off	0,256875257	8,10666667	16,7153629	128,877652	0,071689	0,060265	0,1311682	1,140106
Off	0,256875257	6,95333333	16,5798887	131,321729	0,107012133	0,029723667	0,1443438	1,0550044
Off	0,256875257	8,40666667	17,8680738	130,844866	0,037359	0,037359	0,1311682	1,3244928
Off	0,256875257	9,36	12,9567202	113,349126	0,2436296	0,0269966	0,1641072	1,2961256
Off	0,256875257	9,2	12,0468473	92,3426119	0,2078664	0,0292872	0,1443438	1,2606666
Off	0,256875257	9,38	12,2840635	97,0603879	0,3134672	0,0384496	0,104817	
Off		9,07333333			0,2191188	0,013253		
Off		8,39333333			0,1741932	0,024706		
Off		8,81333333			0,1646296	0,024706		
Off		8,17333333						
Off		8,97333333						
Off		8,42666667						
Off		7,50666667						
Off		7,16666667						
Off		7,55333333						
Off		7,74						
Off		8,68666667						
Off		8,25333333						

Table 8. Dryweight (DW), chlorophyll a (Chl a) as well as protein content of the zooxanthellae (Zoox) and the animal polyp per unit surface area for each sampled colony after 3 weeks (t=3).

			Protein	
Coral	DW [mg/cm²]	Chl a [µg/cm²]	Zoox [µg/cm²]	Polyp [mg/cm²]
O1-1-A1	3,675561171	2,087553223		
O1-1-A2	4,200298111	1,920163147	26,17127449	0,47443054
O1-1-A3	3,219204575	0,499878413	27,59109924	0,444227891
O1-1-B1	3,064477658	2,617662165	20,97740348	0,567085804
O1-1-B2	4,462175975	1,093375903	19,07898857	0,36979102
O1-1-B3	3,717730632	2,224030694	9,544532046	0,353668445
O1-1-C1	3,732051279	2,00322451	29,45621179	0,745562145
O1-1-C2	3,222327811	1,283859233	20,38988009	0,501677735
O1-1-C3	5,471613547	2,618594552	27,26868637	0,554834375
O1-1-D1	2,690838112	0,369172141	22,11370087	0,460730087
O1-1-D2	2,795723998	1,12179341	13,39266378	0,458901066
O1-1-D3	4,192488159	2,2413682	48,39902425	0,543404738
N1-1-A1	4,600917796	3,726849882	29,67037253	0,422835046
N1-1-A2	3,517645608	4,84233561	47,13736445	0,517772583
N1-1-A3	4,584700483	5,204934341	19,47856823	0,430068008
N1-1-B1	4,037558392	4,295214216	48,63226454	0,398410392
N1-1-B2	3,189512005	2,629209438	36,89958412	0,473078636
N1-1-B3	3,084216993	2,428054163	36,55873695	0,509810452
N1-1-C1	5,569435082	7,574876871	33,18636805	0,458387384
N1-1-C2	3,941030379	4,38659954	30,7542786	0,38806319
N1-1-C3	4,196240528	5,205367646	26,54704217	0,453755795
N1-1-D1	4,264688879	1,640479192	30,34661302	0,400935879
N1-1-D2	3,328577817	3,385346436	50,18860943	0,451899898
N1-1-D3	4,240472036	5,040174429	41,7749681	0,333582603
N2-1-A1	2,690368732	4,403876467	16,72408033	0,401830116
N2-1-A2	3,307608431	3,353007898	17,43126146	0,383594143
N2-1-A3	3,427815075	2,849132915	17,35356516	0,287229805
N2-1-B1	3,587863976	5,486565807	17,06214888	0,447875079
N2-1-B2	2,691580889	5,095655782	6,040853973	0,46788726
N2-1-B3	2,701462576	3,824569827	8,109146729	0,413100386
N2-1-C1	3,734923019	5,415240575	36,53307919	0,45847452
N2-1-C2	2,807351807	4,112392015	17,85281	0,261341996
N2-1-C3	3,484817579	2,371921725	34,62727924	0,454301375
N2-1-D1	4,042859173	6,555036354	16,80586567	0,338185474
N2-1-D2	3,456437549	3,003325552	19,8033063	0,362889614
N2-1-D3	2,62020923	5,217777582	36,75576475	0,485184552
O2-1-A1	2,522882547	1,795315458	18,66898954	0,270529651
O2-1-A2	4,011453796	3,015136646	24,27625469	0,395802627
O2-1-A3	2,133242392	1,437999036	13,64955306	0,279703549
O2-1-B1	2,647876769	2,957429532	25,78088875	0,337958491
O2-1-B2	2,311407623	1,127326498	13,16395298	0,235048103
O2-1-B3	2,062910855	1,230475103	21,96180892	0,324316502
O2-1-C1	3,97744028	2,858064946	21,99454218	0,394106603
O2-1-C2	2,509874602	1,618419983	16,64605671	0,170176616
O2-1-C3	4,500502147	3,725564331	38,68386642	0,381384655
O2-1-D1	4,920703614	0,799555602	27,02412149	0,352466721
O2-1-D2	3,884781405	1,429272909	28,49641268	0,18714577
O2-1-D3	2,339966948	1,693845735	27,48507117	0,118356933

Table 9. Dryweight (DW), chlorophyll a (Chl a) as well as protein content of the zooxanthellae (Zoox) and the animal polyp per unit surface area for each sampled colony after 6 weeks (t=6).

			Protein	
Coral	DW [mg/cm²]	Chl a [µg/cm²]	Zoox [µg/cm²]	Polyp [mg/cm²]
O1-2-A1	4,263084628	1,881470016	24,85446917	0,389560578
O1-2-A2		5,393464224	39,18488666	0,432650196
O1-2-A3	4,726551067	2,718676669	42,42303482	0,43298489
O1-2-B1	3,419164886	4,001455811	46,39166826	0,488124115
O1-2-B2	4,185792808	2,015827798	22,85069182	0,22174181
O1-2-B3	5,529304095	2,252088499	12,02385268	0,175250315
O1-2-C1	2,524572322	2,397678315	31,23597651	0,499965694
O1-2-C2	10,92183749	2,83946916	25,03526334	0,537678603
O1-2-C3	3,2444409	2,26033424	10,80601432	0,378889871
O1-2-D1	4,321148107	3,272450572	27,82471071	0,57015156
O1-2-D2	2,207517351	0,641398093	28,52094441	0,47815423
O1-2-D3	8,78110075	1,336428993	24,77134732	0,487543501
N1-2-A1	5,786891378	5,192774298	32,27752558	0,465348116
N1-2-A2	2,490550786	6,890779282	19,81117608	0,41894059
N1-2-A3	4,738816382	8,298753973	19,19186369	0,372183997
N1-2-B1	2,54992698	10,07139269	31,51775225	0,433522015
N1-2-B2	2,651917836	5,248055831	11,99160654	0,364612951
N1-2-B3	2,668518294	2,985718606	8,492779889	0,114773936
N1-2-C1	5,038393584	9,818936824	52,01128276	0,423083687
N1-2-C2	5,255782669	10,14709079	44,71950858	0,470671289
N1-2-C3	3,97615619	5,567345735	45,15678789	0,430553486
N1-2-D1	4,719606124	8,902029256	45,32407666	0,378162038
N1-2-D2	2,928212677	8,614376893	62,74763934	0,495500137
N1-2-D3	4,887265032	8,239928843	35,38407497	0,420330136
N2-2-A1	5,639608711	7,436150323	10,92693289	0,253069956
N2-2-A2	4,260669921	8,992956299	21,10343448	0,470339277
N2-2-A3	3,942488431	6,36480412	11,71487961	0,30097998
N2-2-B1	3,30416185	6,836179667	17,95906701	0,355908756
N2-2-B2	4,848115584	3,845860115	15,03923535	0,300182196
N2-2-B3	1,275382313	1,328286038	10,88180704	0,327266754
N2-2-C1	4,032139934	9,155243049	19,00724624	0,385039807
N2-2-C2	4,755361097	8,652591389	29,91199121	0,318638913
N2-2-C3	4,566933134	7,743262047	24,63437097	0,274108547
N2-2-D1	2,874035688	8,059316059	14,1011121	0,344009732
N2-2-D2	5,449796442	11,16194509	1,621846071	0,092225806
N2-2-D3	3,17688182	5,640852942	33,92724117	0,156185964
O2-2-A1	3,996339461	3,906506852	22,83992287	0,379963017
O2-2-A2	3,245393395	4,280518606	27,82143729	0,418897969
O2-2-A3	2,998768198	3,071881978	18,57563977	0,298879382
O2-2-B1	4,267076834	4,681658377	21,18092512	0,40250686
O2-2-B2	3,530920234	3,081704174	13,54944232	0,292966237
O2-2-B3	2,723576069	2,143565176	16,55045491	0,311285977
O2-2-C1	4,589517787	4,488521751	25,09706611	0,435380751
O2-2-C2	4,709629781	1,727559887	13,85729599	0,340729898
O2-2-C3	6,655819275	2,16107161	7,871452337	0,464696891
O2-2-D1	4,329864684	3,426120786	16,50546515	0,358297468
O2-2-D2				
O2-2-D3				

Table 10. Minimum fluorescence (F) and maximum fluorescence (F_m) measured with the Diving-PAM. From these parameters maximum quantum yield was calculates.

Coral	F	Fm'	Yield
O1-1-A1	356,00	1059,33	0,663
O1-1-A2	449,67	1309,33	0,656
O1-1-A3	282,00	705,00	0,607
O1-1-B1	287,33	813,67	0,646
O1-1-B2	327,67	977,33	0,666
O1-1-B3	247,67	688,67	0,638
O1-1-C1	387,33	1303,00	0,703
O1-1-C2	343,33	1150,67	0,701
O1-1-C3	485,33	1579,67	0,691
O1-1-D1	345,33	1080,33	0,677
O1-1-D2	500,00	1583,67	0,684
O1-1-D3	439,33	1522,33	0,711
N1-1-A1	449,00	1450,33	0,689
N1-1-A2	361,33	1164,67	0,689
N1-1-A3	421,00	1290,33	0,673
N1-1-B1	429,33	1388,33	0,691
N1-1-B2	335,00	1097,33	0,694
N1-1-B3	338,67	901,33	0,620
N1-1-C1	464,33	1427,33	0,675
N1-1-C2	427,67	1269,67	0,663
N1-1-C3	429,00	1352,00	0,682
N1-1-D1	447,33	1438,33	0,688
N1-1-D2	453,67	1374,00	0,669
N1-1-D3	431,33	1316,67	0,671
N2-1-A1	389,00	1297,33	0,700
N2-1-A2	433,33	1481,67	0,707
N2-1-A3	418,67	1421,67	0,706
N2-1-B1	409,00	1331,67	0,692
N2-1-B2	427,67	1318,33	0,676
N2-1-B3	445,67	1527,33	0,708
N2-1-C1	464,67	1328,33	0,649
N2-1-C2	415,67	1158,33	0,641
N2-1-C3	468,33	1475,33	0,682
N2-1-D1	463,67	1449,67	0,680
N2-1-D2	381,67	1097,00	0,651
N2-1-D3	422,33	1254,33	0,662
O2-1-A1	358,67	975,67	0,633
O2-1-A2	350,33	1001,67	0,651
O2-1-A3	316,33	957,67	0,670
O2-1-B1	296,00	802,67	0,630
O2-1-B2	294,00	863,67	0,658
O2-1-B3	314,00	944,67	0,668
O2-1-C1	410,00	1180,00	0,651
O2-1-C2	316,67	843,33	0,624
O2-1-C3	387,33	1136,00	0,659
O2-1-D1	383,67	1207,00	0,682
O2-1-D2	417,33	1361,00	0,693
O2-1-D3	400,33	1181,00	0,660

Coral	F	Fm'	Yield
O1-2-A1	353,00	967,67	0,637
O1-2-A2	460,00	1219,67	0,622
O1-2-A3	406,33	1048,33	0,610
O1-2-B1	409,33	1147,33	0,640
O1-2-B2	401,67	1145,00	0,649
O1-2-B3	312,00	922,67	0,658
O1-2-C1	311,00	894,33	0,651
O1-2-C2	265,33	647,33	0,588
O1-2-C3	254,00	654,67	0,612
O1-2-D1	284,67	804,67	0,645
O1-2-D2	256,67	738,33	0,652
O1-2-D3	237,33	622,33	0,619
N1-2-A1	470,33	1425,33	0,669
N1-2-A2	413,00	1154,67	0,641
N1-2-A3	459,00	1307,33	0,647
N1-2-B1	470,00	1312,33	0,640
N1-2-B2	403,67	1130,67	0,642
N1-2-B3	374,33	1034,67	0,637
N1-2-C1	347,33	973,67	0,643
N1-2-C2	444,00	1270,67	0,651
N1-2-C3	390,67	1118,67	0,650
N1-2-D1	437,67	1296,67	0,662
N1-2-D2	438,00	1286,00	0,659
N1-2-D3	386,33	1075,00	0,640
N2-2-A1	448,33	1349,67	0,667
N2-2-A2	421,67	1317,00	0,679
N2-2-A3	422,67	1286,67	0,671
N2-2-B1	411,33	1243,33	0,668
N2-2-B2	470,00	1521,33	0,690
N2-2-B3	417,00	1291,67	0,678
N2-2-C1	434,33	1372,67	0,683
N2-2-C2	457,00	1512,00	0,698
N2-2-C3	479,33	1535,00	0,687
N2-2-D1	447,67	1465,33	0,693
N2-2-D2	448,67	1428,67	0,685
N2-2-D3	420,00	1259,33	0,666
O2-2-A1	370,33	1129,67	0,671
O2-2-A2	376,67	1071,33	0,648
O2-2-A3	401,33	1215,33	0,669
O2-2-B1	332,00	1014,33	0,670
O2-2-B2	332,67	979,67	0,660
O2-2-B3	364,67	1092,33	0,660
O2-2-C1	377,00	1022,33	0,633
O2-2-C2	340,00	943,67	0,639
O2-2-C3			
O2-2-D1	366,00	1112,00	0,668
O2-2-D2			
O2-2-D3			