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Measuring Photosynthesis in Symbiotic Invertebrates: A Review of Methodologies, Rates and Processes

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1. Introduction

Several marine invertebrate species live in symbiosis with phototrophic organisms, mostly cyanobacteria and dinoflagellate algae. Such symbioses occur among different animal phyla, such as Porifera, Cnidaria, Mollusca and Plathyhelminthes (Venn et al. 2008). Animal host and phototrophic symbiont together are usually referred to as holobiont. Many of these holobionts act as net primary producers when growing in shallow waters (Wilkinson 1983; Falkowski et al. 1984) and thus have an important role in element cycling in marine ecosystems (Muscatine 1990). In addition, symbiont photosynthesis is often very important for the energy budget of the host animal (Davies 1984; Falkowski et al. 1984; Edmunds & Davies 1986; Anthony & Fabricius 2000). Hence, both from an ecological and a physiological point of view, it is important to have accurate, quantitative estimations of photosynthesis in symbiotic animals. In this chapter, we will provide an overview of methods to characterize photosynthesis in these animals, highlight important data obtained with these methods and present conceptual frameworks that describe how photosynthesis is controlled in marine symbiotic invertebrates. Hereby, we will be particularly focusing on zooxanthellate Scleractinia (stony corals, Fig. 1), a symbiosis that will be described in the next section.

2. The phototrophic symbiosis in stony corals

The fact that light affects the growth of many stony corals has been described already in the first half of the previous century (Vaughan 1919). The discovery that unicellular algae reside in the living tissue of corals (Fig. 2) even dates back further, to the late nineteenth century. The algae were termed zooxanthellae and the symbiosis was extensively studied in the first half of the twentieth century (e.g. Boschma 1925; Yonge & Nicholls 1931a,b). More recent works have established that all zooxanthellae found in scleractinian corals are dinoflagellates belonging to the genus *Symbiodinium* (see reviews by Baker 2003 and Stat et al. 2006). *Symbiodinium* is subdivided in several phylotypes (clades), termed A, B, C, D, E, F, G and H, which all have different properties in terms of pigmentation and heat tolerance,

thus providing their coral hosts with flexibility with regards to differences in light and temperature regimes, an aspect that will be further outlined in Section 4. *Symbiodinium* has also been found in other taxa (e.g. other cnidarian groups, Molluscs). In sponges, the photosynthetic microsymbionts are usually cyanobacteria (Venn et al. 2008).

The photosynthetic processes taking place in zooxanthellae inside coral cells in principle do not differ largely from photosynthetic processes in other plants. The main difference is the constraints impeded by the animal cell environment on the zooxanthellate cell. All supplies that are needed to perform photosynthesis have to cross several additional cell membranes (cell membranes of the different coral cell layers and the symbiosome). Therefore, the host cell can modify the surrounding environment and control the activity of the symbiont.
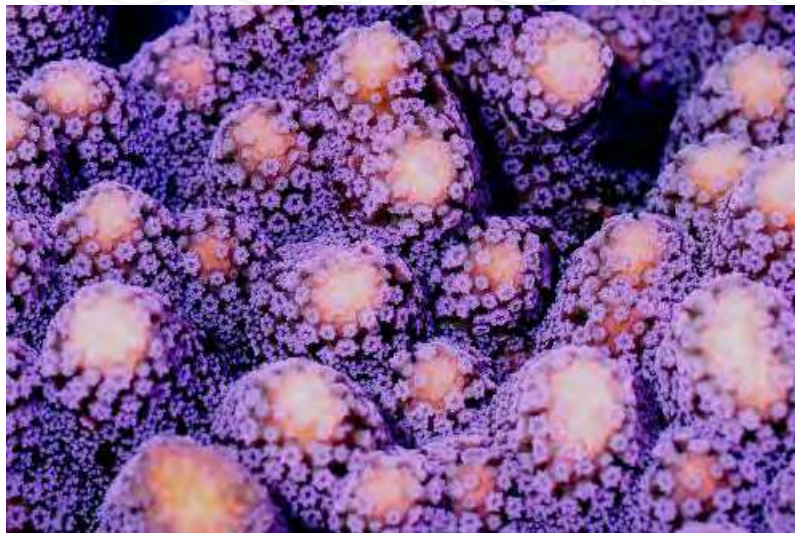

Fig. 1. Branch tips of the branching zooxanthellate stony coral *Stylophora pistillata*. The white tips of the branches, where the most active accretion of new calcium carbonate skeleton takes place, do not contain zooxanthellae. Photography by Tim Wijgerde.
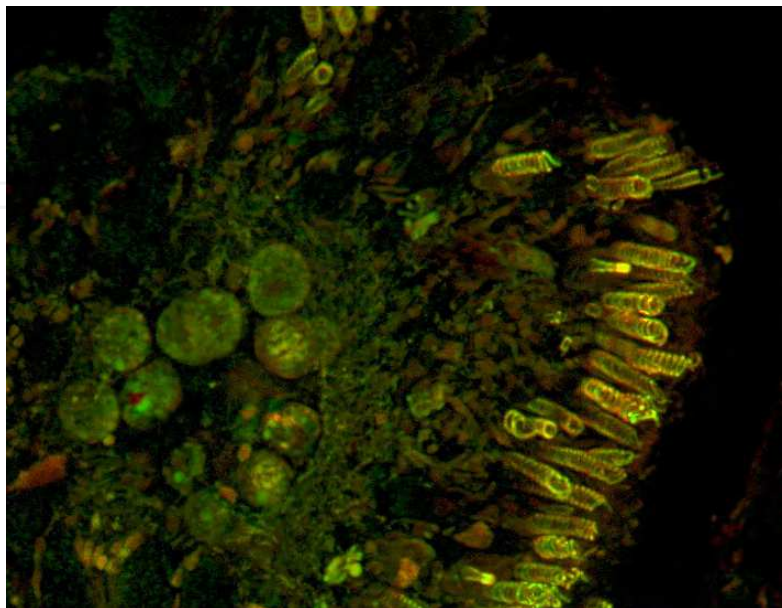

Fig. 2. Zooxanthellae *in hospite* in *Porites asteroides*. Photography by M. en C. Alejandro Martínez Mena, Laboratorio de Microcine, Facultad de Ciencias, UNAM.

Coral-zooxanthellae associations are regarded as mutualistic symbioses, implying that there are benefits for both components. The coral host provides a sheltered environment for the symbiont and provides the algae with essential nutrients such as nitrogen and phosphorus, whereas the coral receives carbohydrate fuel and amino acids for protein synthesis (Dubinsky & Jokiel 1994). Initially, it was believed that the coral host would mainly acquire nutrients from the algae by digesting them (Boschma 1925; Goreau & Goreau 1960). Muscatine & Cernichiari (1969) were the first to demonstrate *in hospite* that photosynthesis products were actively translocated from the zooxanthellae to the host cells. Later, it became apparent that this process of translocation represents the main carbon flux between symbiont and host, and that zooxanthellae digestion is quantitatively of minor importance (Muscatine et al. 1984). The translocation of photoassimilates between symbiont and host is a host-controlled process. Muscatine (1967) discovered that host homogenates were able to release organic molecules from zooxanthellae suspensions, glycerol being the main constituent of the excreted materials. Later, Ritchie et al. (1993) added ^{14}C labelled glycerol to isolated zooxanthellae in suspension and found that glycerol was metabolized rapidly by zooxanthellae. It was concluded from this study that the hitherto unidentified host factor induces changes in the metabolism of the zooxanthellae rather than altering membrane permeability, as had previously been suggested. Studies on isolated zooxanthellae may not always reflect their behaviour *in hospite*, as was demonstrated by Ishikura et al. (1999). The composition of the translocated carbon in the intact host-symbiont association may vary among species and comprises sugars, glycerol, amino acids, fatty acids and other organic acids (see overview by Venn et al. 2008).

In zooxanthellate stony corals, photosynthesis is closely coupled to calcification (Gattuso et al 1999; Moya et al. 2006). The mechanism responsible for this coupling, which is also termed Light Enhanced Calcification (LEC) has been debated since its early discovery by Kawaguti & Sakamoto (1948). Most likely, calcification is stimulated in the light due to the simultaneous supply of oxygen and metabolic energy through photosynthesis (Rinkevich & Loya 1983; Colombo-Palotta et al. 2010), herein aided by the concurrent increase in pH in the calicoblastic fluid layer (Al Horani et al. 2003), which facilitates the deposition of calcium carbonate.

3. Measurement of photosynthetic processes in corals

The following sections provide descriptions of methods that are commonly used to characterize photosynthesis-related parameters in symbiotic marine invertebrates, including critical reflections on the use of these methods.

3.1 Relating photosynthesis to light

Measurements on photosynthetic processes are usually related to a quantification of the light field under which the photosynthesis takes place. Albert Einstein introduced the concept of photons, universal minimal quantities of light, comparable to molecules of mass. As such, light can be quantified in mole photons or mole quanta, also termed Einsteins (E). To describe the light field on a projected surface area, it is recommended to use the parameter Quantum Irradiance (E), to be expressed in µmole quanta $m^{-2} s^{-1}$ (often written as µE $m^{-2} s^{-1}$). Quantum Irradiance is often referred to as Photon Flux Density (PFD) or light intensity.

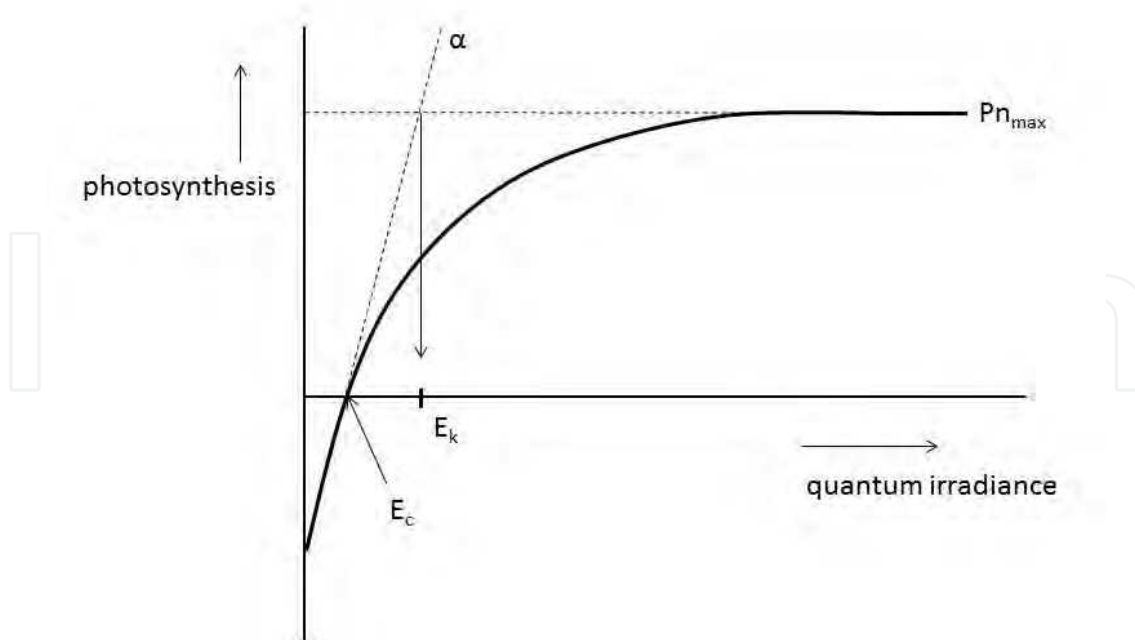Fig. 3. Example of a curve that relates net photosynthesis to irradiance, showing the compensation point E_c, the Talling Index E_k, α and Pn_{max}.

Only photons with a wavelength between approximately 400 to 700 nm can be used in photosynthesis. This part of the light spectrum is termed photosynthetic active radiation (PAR) or photosynthetic usable radiation (PUR) if the available light spectrum is corrected for the spectrally variable capacity of the organism to absorb light (PAR x Absorptance). Throughout this text, the term quantum irradiance will be used to denominate the flux of photons within the PAR spectrum per m² per s, a parameter that is often referred to as Photosynthetic Photon Flux density (PPFD). Each photon carries a level of energy that is determined by its wavelength. Despite the energetic differences among photons, each photon within the PAR range is able to promote one photochemical excitation event. The energy that is in excess of the energy required for excitation transfer is dissipated as heat. For a more detailed list of quantities and units relating to light, we refer to a mini-review by Osinga et al. (2008).

Many studies on coral photosynthesis show photosynthesis rates under different irradiances, resulting in curves such as presented in Fig 3. Curves of this type are generally referred to as photosynthesis/irradiance curve, or shortly: P/E curve. It should be noted here that P/E curves obtained in the field (see for example the data obtained by Anthony & Hoegh-Guldberg 2003) reflect the actual photosynthetic response of corals to a natural light field (PAR) and daily light cycle, whereas P/E curves measured on aquarium corals (e.g. Goiran et al. 1996; Houlbrèque et al. 2004; Schutter et al. 2008) under laboratory conditions usually reflect the photosynthetic potential of the coral, since most aquarium corals are grown under a fixed quantum irradiance. Several descriptors can be derived from the P/E curves: 1) the compensation point (E_c), which is the irradiance at which photosynthesis equals respiration; 2) the maximal photosynthesis (P_{max}); 3) the photosynthetic efficiency (α), which is the slope of the linear increase in the photosynthetic rates as irradiance increases, and 4) the onset of saturation or Talling index (E_k), which is the point on the X-axis of the

curve where the initial, linear slope of the curve intersects with the horizontal asymptote resembling P_{max}.

The Talling index is often used as a measure to characterize the acclimation of a photosynthetic organism to its light regime (Steeman-Nielsen 1975). The most commonly used model to describe P/E curves and to estimate P_{max} and E_k is the hyperbolic tangent function (Chalker & Taylor 1978):

$$P = P_{max} \times \tanh(E/E_k) \qquad (1)$$

where P is the actual rate of photosynthesis measured at a given irradiance, P_{max} is the maximal photosynthetic capacity and E_k is the Talling Index.

Although this model provides accurate estimations of P_{max} and E_k, its assumption that photosynthesis increases with irradiance up till a horizontal asymptote is false: at high quantum irradiance levels, photosynthesis will decrease due to damage of the photosystems by excess light. An alternative (and probably better) approach is to use independent estimations of these parameters to allow better comparison between determinations obtained from the use of different equations (i.e., quadratic, exponential, etc.). A linear regression is required to determine α, paying attention that the incubations at low light levels need to be in the linear phase of the photosynthetic increment with irradiance. A minimum of four determinations are needed for a confident determination of α. Assessment of Pmax requires at least three consecutive measurement points at saturating irradiance. E_k and E_c can then be derived from those determinations as follows:

$$E_k = P_{max}/\alpha \qquad (2)$$

and

$$E_c = R_d/\alpha \qquad (3)$$

where R_d is the dark respiration.

3.2 Relating photosynthesis to size

When determining photosynthetic rates, it is necessary to relate the data to a size parameter. Several methods have been developed to assess the size of sedentary organisms such as corals. Selection of an appropriate method depends on the species (sensitive or robust, small or large, plate, boulder or branched), the circumstances (aquarium, *in situ*, is the colony fixed or can it be taken out of its environment) and the desired precision.

Two approaches to quantify coral size can be distinguished: estimating biomass (i.e. volume and weight-related parameters) and estimating surface area (see overview of related techniques in Table 1). The major difference between both approaches is that biomass measurements document mostly added coral skeleton, which does not contribute to biological activity, whereas surface-area measurements mainly reflect the amount of live coral tissues. As such, the surface area parameters serve as prime descriptors for standardization and quantification of physiological and biochemical parameters allowing comparative work of different experimental conditions, in particular work that relates to photosynthesis. When determining P/E curves, rates should always be related to surface parameters. Nevertheless, measurement of corals' surface area can be restricted by morphological variation and highly complex architectural structures that reduce accuracy. In addition, in complex structures such as branching corals, the light field within the colony varies largely. Hence, overall colony photosynthesis is an average rate reflecting

Size parameter	method	description	applications	advantages	limitations
Surface area	2D photometry	Top view pictures of corals are taken and analysed either by hand or by software to estimate the projected 2D surface area. A reference object of defined length (usually used is a ruler) must be included on the pictures to normalize the surface to values in square meters.	Encrusting and plate-shaped species with a regular shape (such as hemispherical boulders); assessment of % coverage; crude assessment of coral biomass on natural reefs.	Accurate for species with a flat surface or a simple, regular shape; applicable everywhere; non-destructive; no impact on organisms.	Not easily applicable to branching species and species with complex morphologies; the 2D projection of 3D organisms may lead to underestimations of the real surface area.
Volume	3D photometry[1]	Stereo-photography (3D) with two underwater cameras mounted on a fixed frame. The pictures are analysed using specific software.	Measurements of *in situ* growth rates of irregularly shaped species.	Very accurate, applicable everywhere, non-destructive, no impact on organisms.	Expensive, time-consuming technique.
Volume	replacement	The coral is positioned in a beaker glass (or similar) after filling this beaker up to an indicated level. Due to the incoming coral, the water level in the beaker will rise. The volume of the coral is now determined by siphoning off the excess water above the indicator level with a syringe (or similar) and by measuring the volume of the water in the syringe, which is equal to the coral volume.	Estimation of the volume of corals for incubation studies; a biomass estimate for branching and plate-shaped corals that can be related to a biological activity.	A quick, low-cost, non-destructive method with a reasonable precision.	The method can only be applied to corals that can be removed from their environment; the corals have to be taken out of the water to remove water that is attached to the coral surface – this step causes variability in the results and may inflict stress to the corals.
Volume	ecological volume[2]	A coral colony is converted to a cylindrical shape using 2D photography of coral colonies (one picture taken from the side, another from the top of the colony). A reference object of defined length must be included on the pictures to assess the height and the width of the colony. Image analysis (assessment of height and width) is done using simple software (note: height and width can also be measured directly by hand using a ruler). Biological volume is defined as $V = \pi r^2 h$, in which V is the ecological volume, r is the radius (calculated by dividing the average width of the colony by 2) and h is the height of the colony.	"Quick and dirty" measurements of (*in situ* and *ex situ*) growth rates and/or standing stocks. May be used as an efficient and comparative estimator for the total volume in the aquarium that is occupied by resident corals.	Relatively simple method using commonly available non-specialist materials; applicable everywhere, non-destructive, no impact on organisms.	Not a true size estimate: colonies having the same ecological volume may differ considerably in volume, weight, surface area and polyps numbers; slightly interpretation sensitive (comparative measurements should preferably done by the same person).
Weight	(drip dry) wet weight	Direct weighing of corals that are taken out of the water and have been shaken until no more drops fall off.	Measurements of *in situ* growth rates of irregularly shaped species.	Quick and easy, non-destructive method.	The method can only be applied to corals that can be removed from their environment; the corals have to be taken out of the water to remove water that is attached to the coral surface – this step causes variability in the results and stresses the corals.

Size parameter	method	description	applications	advantages	limitations
Weight	Buoyant weight3	Corals are weighed underwater, using a balance with an under-weighing device; a ring which is positioned on the bottom side of the balance to which a hook can be attached. The balance is positioned above an aquarium, bucket or anything that can hold a volume of water. The coral is hung onto the under-weighing ring-device using fishing line and two metal hooks.	Measurements of growth rates and/or standing stocks in aquaria.	Reasonably precise, easy, non-destructive method with low impact on organisms (that can be kept underwater; hence, water attached to the surface of the coral is also no issue here).	The method can only be applied to corals that can be removed from their environment; buoyant weight is a relative measure (although it can be converted into dry weight if the specific density of the coral material is known).
Weight	Dry weight	Corals are oven-dried (130 °C; incubation time varies depending on the size of the sample and the type of coral, but is usually around 24 h) and weighed regularly until they do not decrease in weight anymore.	Determination of biomass without water; first step to determine the separated weights of organic, living tissue and skeleton.	Very accurate.	Destructive, the coral has to be sacrificed.
Weight	Ash-free dry weight	Second step to determine separated weights of organic, living tissue and skeleton. Dried corals are ashed in a muffle furnace at 550 °C. By subtracting the weight of the remaining ashes (skeletal weight) from the previously obtained dry weight (skeleton + organic tissue), the dry weight of the organic fraction is obtained.	Comparative studies on growth, reference value for biological processes.	Very accurate; discriminates between organic tissue and skeletal weight	Destructive, the coral has to be sacrificed.

Table 1. Overview of methods to determine coral size.

photosynthetic activity under a wide range of quantum irradiance levels. P/E curves obtained for larger branching colonies as reported in the literature should be considered as the relation between colony photosynthesis and the ambient light field and should be termed differently.

3.3 Oxygen evolution techniques

Oxygen evolution techniques estimate net photosynthesis and dark respiration from changes in the oxygen concentration in an enclosure holding the targeted primary producer (Fig 4). When incubated in darkness, respiration rates can be assessed from the measured decrease in oxygen concentration. Incubation in light provides estimates on net photosynthesis (Pn): the observed change in the concentration of oxygen is the sum of production of oxygen due to photosynthesis and concurrent consumption of oxygen due to respiration by the algal population and the host. Determinations of respiration require distinction between respiration rates of dark-adapted samples (dark respiration, R_{dark}) and respiration rates of previously illuminated samples (light respiration R_{light}).

Incubations for oxygen evolution measurements should always be run concurrent with a blank control to correct for background activity in the water surrounding the targeted organism. In the case of corals, we found that the actual background in the water

surrounding the coral is prone to change after one hour of incubation (Fig. 5). Production of mucus by the corals may stimulate bacterial activity in the surrounding water, thus increasing the actual background activity when compared to the blank control. Therefore, we recommend a regular (hourly) exchange of incubation water when performing oxygen evolution measurements on corals.

When related to an appropriate size measure (see Section 3.2), oxygen evolution measurements are currently the best method available to obtain quantitative data on net primary production in corals. Oxygen evolution can also be used to estimate gross primary production (Pg). To calculate Pg, it is necessary to add values for respiration losses during illumination (R_{light}) to values for Pn. This is due to the fact that light respiration is usually higher than dark respiration as photosynthesis stimulates both algal and host respiration. Light respiration is highly variable in corals and can be six times higher than dark respiration (Kuhl et al. 1995). Hence, in order to asses Pg from oxygen evolution measurements, an adequate measurement of light respiration is required. A suitable approach is to measure respiration immediately upon darkening at the end of the incubation under the highest irradiance level, which is termed Post-illumination respiration (R_{pI}). The average between R_d and R_{pI} is used to calculate gross-photosynthesis from net photosynthesis determinations. Section 3.4 deals with alternative techniques to assess Pg.
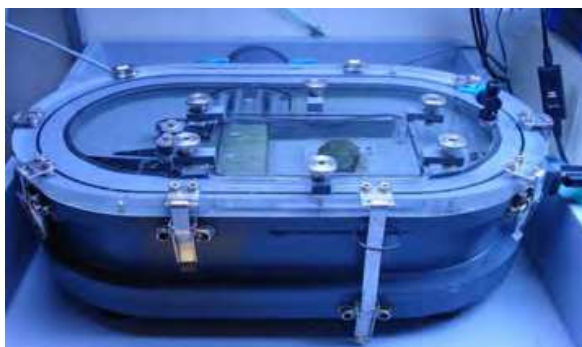

Fig. 4. Measurement of oxygen evolution. A coral colony is held in an enclosure equipped with an oxygen sensor, a paddle wheel, and a water jacket for temperature control. Light is supplied from the top.
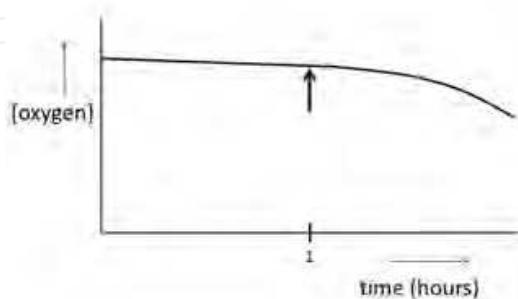

Fig. 5. Real-life example of increasing background respiration: the arrow indicates when the background sample was replaced with water in which a coral had been incubated for 1 hour.

When oxygen evolution is applied to generate P/E curves, the curve will show the relation between net photosynthesis and irradiance. The following modification of the hyperbolic tangent function (Equation 1) can be used to describe the data (Barnes & Chalker 1990):

$$Pn = R_{dark} + Pg_{max} \times tanh(E/E_k) \qquad (4)$$

where Pn is the net rate of photosynthesis, R_{dark} is the rate of respiration measured in darkness and Pg_{max} is the maximum gross photosynthetic rate (defined as $Pn_{max} - R_{dark}$, i.e. maximum net photosynthetic rate minus dark respiration). This equation also allows for calculation of the compensation point, at which Pn equals zero.

3.4 Measuring light respiration and gross photosynthesis

The rate of light respiration can be assessed either through the use of oxygen microsensors or by applying methods based on stable isotopes of oxygen. Oxygen microsensors can be applied to characterize the oxygen profile within biologically active layers that either produce or consume oxygen, such as sediments, microbial mats and living tissue (Revsbech & Jorgensen 1983). Oxygen production and consumption are deduced from the oxygen profiles using Fick's first law of diffusion:

$$J_{(x)} = -D_0 (\delta C_{(x)}/ \delta_x) \qquad (5)$$

where $J_{(x)}$ is the diffusive flux of oxygen at depth x, D_0 is the temperature- and salinity-dependent molecular diffusion coefficient for oxygen in water, and $\delta C_{(x)}/ \delta_x$ is the slope of the oxygen profile at depth x.

Light respiration can be assessed using the so-called light/dark shift method (Revsbech & Jørgensen 1983), hereby measuring the depletion of oxygen immediately after an abrupt switch from ambient light to full darkness. During the first few seconds to minutes (the time depending on the thickness of the tissue layer involved) after the onset of darkness, the respiration rate will shift from a stable light respiration value to a stable dark respiration value. Hence, the initial rate of oxygen depletion will closely resemble the preceding rate of light respiration (Fig 6). Oxygen microsensors were used by Kuhl et al. (1995) to assess
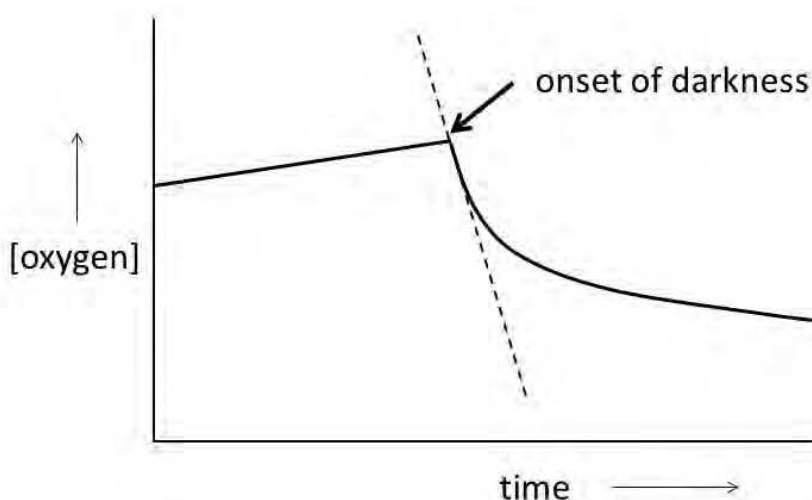

Fig. 6. Measuring light respiration using the light/dark shift method. The dashed line indicates the rate of light respiration.

photosynthetic parameters in *Acropora* sp. and *Favia* sp., hereby including measurements of the light respiration using the light/dark shift method. Their results show that the often used approach to take the dark respiration value for calculation of Pg may lead to a considerable underestimation of Pg and hence, provide an incorrect view on coral energetics, a consideration that had already been made several decades earlier in plant sciences.

Kana (1990) established an alternative technique where O^{18} labelled oxygen is used to assess respiration independently from oxygen production through photosynthesis. The technique is based upon two principles: 1) photosynthetic oxygen is produced from water through the Hill reaction (not from CO_2), and 2) during respiration, oxygen is used to produce CO_2 (and not water). Therefore, the O^{18} label is not likely to re-appear rapidly as photosynthetic oxygen. Using these principles, Mass et al. (2010) measured light respiration in colonies of *Favia veroni* by online membrane inlet mass spectrometry as the decline in O^{18} after a small spike of O^{18} labelled oxygen to the incubation chamber.

3.5 Measuring light respiration and gross photosynthesis

Pulsed Amplitude modulated (PAM) fluorometry has become one of the standards for the research on photosynthesis. The technique is based upon measuring the chlorophyll *a* fluorescence emission by Photosystem II of short, saturating pulses of light emitted onto photosynthetic active surfaces in relation to the fluorescence signal of continuously emitted light (Schreiber et al. 1986; Van Kooten & Snel 1990). PAM fluorometry is nowadays routinely applied to estimate a series of photosynthesis-related parameters, such as the maximum and effective photochemical efficiency (Fv/Fm and $\Delta F/Fm'$) of photosystem II (PSII), non-photochemical quenching (the amount of excess excitation energy dissipated as heat), sustained quenching of fluorescence (qI) and the proportion of PSII that remain temporally or permanently closed and fail to reduce Q_B, the second quinone electron acceptor. PAM fluorometry has also become increasingly popular among coral scientists. Since the first application of this technique to corals in the late nineties of the previous century, a plethora of papers has been published on this topic.

The principles of PAM fluorometry and its suitability for application on marine organisms were reviewed recently in the book by Sugget et al. (2010). In this book, Enríquez & Borowitzka (2010), provide a thorough analysis of PAM fluorometry, which is briefly summarized below.

The principle of PAM measurements is depicted in Fig. 7. First, background fluorescence (F_0) is measured by supplying a moderated quantity of background light that is insufficient to induce photochemistry (all photosystems are open). Then, a saturated pulse is given, leading to a peak that represents maximal fluorescence (Fm; all photosystems are closed). The ratio between the observed increase in fluorescence over the background level (Variable fluorescence, Fv = Fm – F_0) and the maximal fluorescence (Fm) is a proxy for the probability for a photochemical event to occur (photochemical efficiency, Fv/Fm). If this parameter is determined after the sample was maintained under dark conditions and all the non-photochemical quenching activity has been relaxed, Fv/Fm represents the maximum photochemical efficiency of PSII. If this descriptor is determined under steady-state illuminated conditions, it represents the effective photochemical efficiency of PSII for this specific irradiance ($\Delta F/Fm'$). A decrease in the maximum Fv/Fm over time implies that the rate of photodamage is exceeding the rate of repair of the damaged PSII. Photosynthetic

organisms exposed to light usually show a decrease in $\Delta F/Fm'$ associated with the increment in light exposure and a recovery after the peak of irradiance at noon. The initial maximum of the day Fv/Fm can be reached at the end of the light period or incomplete recovery or higher values can be observed depending on the amount of light in excess absorbed during the day: higher values lead to incomplete recovery and the accumulation of photodamage, but lower values allow better recovery and lead to higher initial Fv/Fm values. A recent study by Schutter et al. (2011b) shows that corals are exposed to continuous light (i.e. 24 hours per day) bleached and died after 7 weeks.

Under a range of assumptions, PAM can also be applied to estimate rates of electron transport (ETR), which is a proxy for gross photosynthesis under subsaturating light conditions (Genty et al. 1989). The apparent quantum yield is converted to ETR by multiplying it by the quantum irradiance, the absorptance (i.e. the fraction of the quantum irradiance absorbed by the photosynthetic apparatus) and the fraction of the corresponding energy delivered to PSII or the absorbed light that is utilized by PSII. Absorptance can be assessed through reflection measurements (Shibata 1969; Enríquez et al. 2005; see next subsection). The fraction of light energy delivered to by PSII is generally assumed to be 50%, based on an assumed balanced condition between PSII and PSI. ETR can simply be converted into oxygen evolution rates by assuming that four electrons are needed to produce one molecule of oxygen from water. Whereas this approach might work under non-saturating quantum irradiance levels, ETR values may overestimate oxygen evolution rates under saturating light due to an increasing proportion of non-photochemical quenching as a sink for excitation energy. In addition, since a PAM measurement represents only a small fraction of the total surface of an organism, many measurements will be needed to accurately quantify gross photosynthesis at the level of the whole organism if the colony has a large variation in tissue condition. Such an analysis should also take into account that the light field and tissue photoacclimatory condition will be highly variable in colonies with a complex architecture.
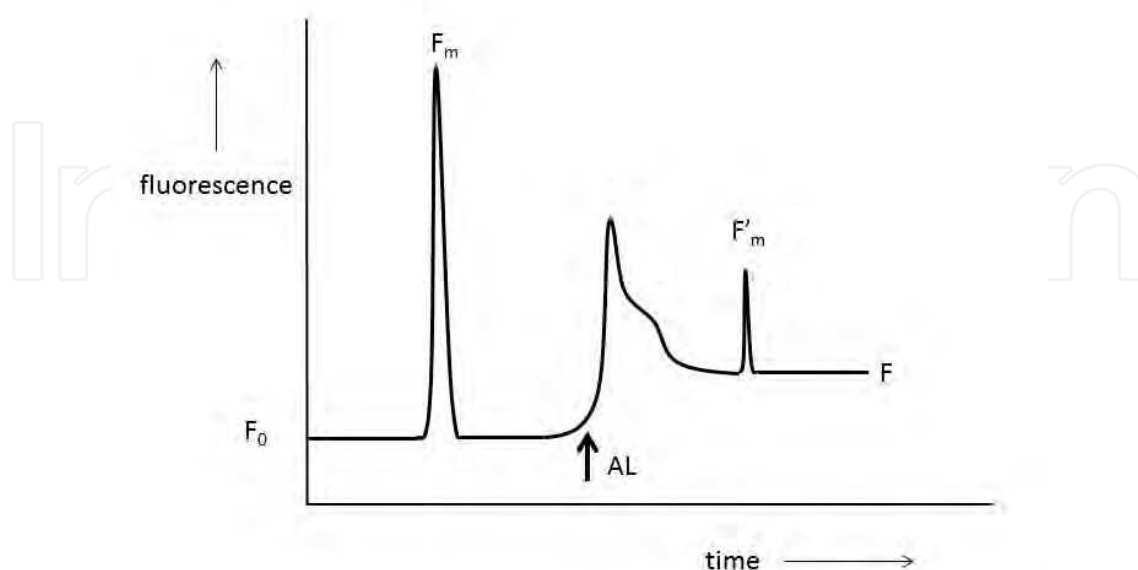

Fig. 7. Principle of PAM fluorometry. Arrow and AL indicate the moment when the actinic light is switched on. See text for further explanation.

As a more qualitative measure, indicative for changes in photosynthetic activity (i.e. to generate P/E curves), Beer et al. (2001) introduced the **relative ETR** (rETR). The use of this approach is limited and not recommended if the absorption cross-section of coral tissue changes among organisms, treatments or during the experimental approach. As the amount of light absorbed by a photosynthetic tissue is highly variable in most marine organisms the lack of control of this source of variation over ΔF/Fm' changes does not allow the comparison of relative changes in ETR. The use of this approach is limited and not recommended, because adsorptance is highly variable in most marine organisms. Acquiring rETR values through the making of rapid light curves (RLC, Ralph & Gademann 2005) is not recommended in particular, because the time needed for a photosynthetic organism to reach photosynthetic steady-state is much longer than the time intervals applied in the RLC method (Enríquez & Borowitzka 2009).

3.6 Measuring light respiration and gross photosynthesis

Reflection of light falling onto photosynthetic active biological surfaces can be quantified using a spectrometer and a small waveguide detector attached to it to collect the reflected light (Enríquez 2005, Enríquez et al. 2005, Terán et al 2010). It is hereby important to relate the measurement to a standard representing 100% reflection, for example white reference materials such as Teflon or a high reflecting materials supplied by manufacturers of light meters and spectrometers. Reflection measurements can provide information to quantify the light dose absorbed by a coral surface from absorptance determinations. Absorptance (A) is defined as the fraction of incident light absorbed by a surface and can be quantified from reflectance (R) measurements assuming that coral skeleton has minimal transmission (Enríquez et al. 2005) as A = 1 - R. In addition measurement of the percentage of light reflected can serve to quantify coral acclimation, coral paling and adaptive coral bleaching, and potentially, to indicate the onset of non-adaptive coral bleaching.

4. Rates and mechanisms: What controls coral photosynthesis?

Many researchers have carried out experiments to unravel how photosynthesis is controlled in stony corals. Limiting factors include the photon flux density and the availability of inorganic nutrients such as dissolved inorganic carbon (DIC), nitrogen (DIN), phosphorous (DIP) and iron. Additional factors that have been reported to influence coral photosynthesis are temperature, water flow, pH and oxygen. Table 2 summarizes photosynthetic rates that have been measured in stony corals *in situ* and *ex situ* in aquaria under a large variety of conditions. Using the data and experiments listed in Table 2, we will outline the mechanisms by which the different factors influence photosynthesis rates in stony corals.

4.1 Light

Light is the primary factor distinguishing photosynthesis from other assimilatory metabolic processes. Light is harvested by antenna molecules that are part of large light harvesting complexes termed Photosystem I (PSI) and Photosystem II (PSII), which are present on the thylakoid membranes of the chloroplasts residing in photosynthetically active cells. In the antenna molecules, an electron is excited by a photon to a higher energetic state. Through a cascade of events that take place in the thylakoid membrane and will not be discussed in

Species	conditions	Rdark	P and/or Pmax*	I_k (μE m^{-2} s^{-1})	reference
Goniastrea retiformis	Shaded, incubated with filtered seawater	25.9 (μg O$_2$ cm^{-2} h^{-1})	127.6* (μg O$_2$ cm^{-2} h^{-1})	263.4	Anthony & Fabricius 2000
	Shaded, incubated with high loads of suspended matter	29.4	137.6* (μg O$_2$ cm^{-2} h^{-1})	261.4	
	Unshaded, incubated with filtered seawater	25.1	105.7*	310.6	
	Unshaded, incubated with high loads of suspended matter	22.3	104.1*	321.2	
Porites cylindrica	Shaded, incubated with filtered seawater	22.3	141.4*	350.3	
	Shaded, incubated with high loads of suspended matter	21.1	130.6*	306.8	
	Unshaded, incubated with filtered seawater	21.4	130.0*	390.7	
	Unshaded, incubated with high loads of suspended matter	23.0	92.2*	334.0	
Montipora monasteriata	Open water corals, simulated natural light cycle	1.33 (μmol O$_2$ cm^{-2} h^{-1})	3.92* (μmol O$_2$ cm^{-2} h^{-1})	211	Anthony & Hoegh-Guldberg 2003
	Corals growing under overhang, simulated natural light cycle	0.70	3.24*	127	
	Corals from cave, simulated natural light cycle	0.43	2.94*	80.8	
Porites porites	Branch tips obtained from 10 m depth	11.91 (μl O$_2$ cm^{-2} h^{-1})	82.34 (μl O$_2$ cm^{-2} h^{-1})	456	Edmunds & Davies 1986
	Constant PPFD of 500 μE m^{-2} s^{-1}, 0.5 mM HCO$_3^-$		12 (nmol O$_2$ mg chl *a*$^{-1}$ h^{-1})		Herfort et al. 2008
	Constant PPFD of 500 μE m^{-2} s^{-1}, 1.0 mM HCO$_3^-$		24		
	Constant PPFD of 500 μE m^{-2} s^{-1}, 2.0 mM HCO$_3^-$		43.5		
	Constant PPFD of 500 μE m^{-2} s^{-1}, 4.0 mM HCO$_3^-$		52.5		
	Constant PPFD of 500 μE m^{-2} s^{-1}, 6.0 mM HCO$_3^-$		61.5		
	Constant PPFD of 500 μE m^{-2} s^{-1}, 8.0 mM HCO$_3^-$		56		
Acropora sp.	Constant PPFD of 500 μE m^{-2} s^{-1}, 1.0 mM HCO$_3^-$		5		
	Constant PPFD of 500 μE m^{-2} s^{-1}, 2.0 mM HCO$_3^-$		8		
	Constant PPFD of 500 μE m^{-2} s^{-1}, 4.0 mM HCO$_3^-$		12		
	Constant PPFD of 500 μE m^{-2} s^{-1}, 6.0 mM HCO$_3^-$		15		
	Constant PPFD of 500 μE m^{-2} s^{-1}, 8.0 mM HCO$_3^-$		12		
Stylophora pistillata	Constant PPFD of 350 μE m^{-2} s^{-1}, low feeding, low flow (0.6-1 cm s^{-1}), measured after 3 weeks	0.44 (μmol O$_2$ cm^{-2} h^{-1})	0.57* (μmol O$_2$ cm^{-2} h^{-1})	403	Houlbrèque et al. 2004
	Identical as above, high feeding	0.43	0.20*	203	
	Constant PPFD of 300 μE m^{-2} s^{-1}, low feeding, low flow (0.6-1 cm s^{-1}), measured after 9 weeks	0.229	0.30		Houlbrèque et al. 2003
	Constant PPFD of 300 μE m^{-2} s^{-1}, high feeding	0.495	1.20		
	Constant PPFD of 200 μE m^{-2} s^{-1}, low feeding	0.134	0.22		
	Constant PPFD of 200 μE m^{-2} s^{-1}, high feeding	0.449	0.70		
	Constant PPFD of 80 μE m^{-2} s^{-1}, low feeding	0.186	0.15		
	Constant PPFD of 80 μE m^{-2} s^{-1}, high feeding	0.438	0.20		

Species	conditions	Rdark	P and/or Pmax*	I_k ($\mu E\ m^{-2}\ s^{-1}$)	reference
Coral assemblage	Mesocosm experiment, high flow (20 cm s^{-1}), natural solar cycle, peak PPFD ~ 1200, ambient CO_2		37 (mmol $O_2\ m^{-2}\ h^{-1}$)	586	Langdon & Atkinson 2005
	Mesocosm experiment, high flow (20 cm s^{-1}), natural solar cycle, peak PPFD ~ 1200, 1.7 x ambient CO_2		36		
	Mesocosm experiment, high flow (20 cm s^{-1}), natural solar cycle, peak PPFD ~ 700, ambient CO_2		23		
	Mesocosm experiment, high flow (20 cm s^{-1}), natural solar cycle, peak PPFD ~ 700, 1.3 x ambient CO_2		31		
	Mesocosm experiment, high flow (20 cm s^{-1}), natural solar cycle, peak PPFD ~ 700, 2 x ambient CO_2		21		
	Mesocosm experiment, high flow (20 cm s^{-1}), natural solar cycle, peak PPFD ~ 700, enriched with DIN & DIP, 0.6-1.9 x ambient CO_2		29-34		
Montastrea annularis	Constant PPFD of 250 $\mu E\ m^{-2}\ s^{-1}$, natural oligotrophic seawater	14.8 ($\mu l\ O_2\ cm^{-2}\ h^{-1}$)	39.5* ($\mu l\ O_2\ cm^{-2}\ h^{-1}$)	119	Marubini & Davies 1996
	Constant PPFD of 250 $\mu E\ m^{-2}\ s^{-1}$, seawater + 1 $\mu M\ NO_3$	13.6	37.9*	111	
	Constant PPFD of 250 $\mu E\ m^{-2}\ s^{-1}$, seawater + 5 $\mu M\ NO_3$	14.4	46.4*	88	
	Constant PPFD of 250 $\mu E\ m^{-2}\ s^{-1}$, seawater + 20 $\mu M\ NO_3$	15.0	49.5*	104	
Porites porites	Constant PPFD of 250 $\mu E\ m^{-2}\ s^{-1}$, natural oligotrophic seawater	10.9	44.2*	215	
	Constant PPFD of 250 $\mu E\ m^{-2}\ s^{-1}$, seawater + 1 $\mu M\ NO_3$	10.2	45.8*	232	
	Constant PPFD of 250 $\mu E\ m^{-2}\ s^{-1}$, seawater + 5 $\mu M\ NO_3$	9.6	58.6*	304	
	Constant PPFD of 250 $\mu E\ m^{-2}\ s^{-1}$, seawater + 20 $\mu M\ NO_3$	8.5	61.8*	382	
Stylophora pistillata	Constant PPFD of 300 $\mu E\ m^{-2}\ s^{-1}$, pH = 7.6, 2 mM HCO_3^-		38 ($\mu mol\ O_2\ g^{-1}$ buoyant weight d^{-1})		Marubini et al. 2008
	Constant PPFD of 300 $\mu E\ m^{-2}\ s^{-1}$, pH = 8.0, 2 mM HCO_3^-		47		
	Constant PPFD of 300 $\mu E\ m^{-2}\ s^{-1}$, pH = 8.2, 2 mM HCO_3^-		38		
	Constant PPFD of 300 $\mu E\ m^{-2}\ s^{-1}$, pH = 7.6, 4 mM HCO_3^-		66		
	Constant PPFD of 300 $\mu E\ m^{-2}\ s^{-1}$, pH = 8.0, 4 mM HCO_3^-		66		
	Constant PPFD of 300 $\mu E\ m^{-2}\ s^{-1}$, pH = 8.2, 4 mM HCO_3^-		80		
	In situ, 5 m depth, winter	0.25 ($\mu mol\ O_2\ cm^{-2}\ h^{-1}$)	0.87* ($\mu mol\ O_2\ cm^{-2}\ h^{-1}$)	659.5	Mass et al. 2007
	In situ, 65 m depth, winter	0.04	0.15*	5.8	
	In situ, 5 m depth, summer	0.41	1.19*	1084.5	
	In situ, 65 m depth, summer	0.08	0.42*	108.9	
	Constant PPFD of 380 $\mu E\ m^{-2}\ s^{-1}$, 450 $\mu atm\ CO_2$, T = 25.3 ^oC	0.34 ($\mu mol\ O_2\ mg$ protein$^{-1}\ h^{-1}$)	0.24 ($\mu mol\ O_2\ mg$ protein$^{-1}\ h^{-1}$)		Reynaud et al. 2003
	Constant PPFD of 380 $\mu E\ m^{-2}\ s^{-1}$, 470 $\mu atm\ CO_2$, T = 28.2 ^oC	0.39	0.41		
	Constant PPFD of 380 $\mu E\ m^{-2}\ s^{-1}$, 734 $\mu atm\ CO_2$, T = 25.1 ^oC	0.39	0.20		
	Constant PPFD of 380 $\mu E\ m^{-2}\ s^{-1}$, 798 $\mu atm\ CO_2$, T = 28.3 ^oC	0.44	0.27		

Species	conditions	Rdark	P and/or Pmax*	I_k (μE m^{-2} s^{-1})	reference
Galaxea fascicularis	Constant PPFD of 90 μE m^{-2} s^{-1}, flow = 10 cm s^{-1}	9.0 (nmol O_2 cm^{-2} min^{-1})	11.7 (nmol O_2 cm^{-2} min^{-1})		Schutter et al. 2010
	Constant PPFD of 90 μE m^{-2} s^{-1}, flow = 20 cm s^{-1}	10.0	10.4		
	Constant PPFD of 90 μE m^{-2} s^{-1}, flow = 25 cm s^{-1}	10.4	8.2		
	Constant PPFD of 280 μE m^{-2} s^{-1}, flow = 5 cm s^{-1}		49		Schutter et al. 2011
	Constant PPFD of 560 μE m^{-2} s^{-1}, flow = 20 cm s^{-1}		42		
	Constant PPFD of 280 μE m^{-2} s^{-1}, flow = 5 cm s^{-1}		30		
	Constant PPFD of 560 μE m^{-2} s^{-1}, flow = 20 cm s^{-1}		57		

Table 2. Overview of photosynthetic rates measured in zooxanthellate stony corals.

detail here, the excitation energy is converted to metabolic energy (ATP) and reducing power (NADPH), which enables the conversion of CO_2 to organic carbon and the release of oxygen. Eight photochemical events, four per reaction centre in each photosystem, are needed to release one molecule of oxygen (i.e. eight photons), hence the maximal theoretical yield (also termed maximal quantum yield) of photosynthetic oxygen production from light energy is 12.5% (the evolution of 1 oxygen molecule requires 8 photons).

In the sea, the availability of light for photosynthesis depends largely on depth. In clear tropical waters, at a depth of 100 m, the PFD is only 2% of the PFD at the surface (Lesser et al. 2009). Zooxanthellate corals have been found up till depths exceeding 150 m. According to Lesser et al (2009), the deepest living photosynthetic coral specimen ever found so far being a colony of *Leptoseris hawaiiensis* growing at a depth of 165 m at Johnston Atoll (Maragos & Jokiel 1986). In order to cope with these highly variable light conditions, corals and their symbionts have developed a myriad of adaptation mechanisms (generally referred to as **photoadaptation** mechanisms), such as variation in the level of pigmentation, the number of zooxanthellae, pigmentation per cell, antenna size, coral morphology (Tissue and skeleton), polyp size and polyp behaviour (Dustan 1982, Iglesias-Prieto & Trench 1994; 1997a,b; Titlyanov et al. 2001; Levy et al. 2003; 2006; Hennige et al. 2008). When a coral is transferred to another location, the symbiotic population will respond to this change by modifying its photosynthetic apparatus to the new light conditions (Titlyanov et al. 2001). Changes in photosynthetic activity and the underlying photophysiology induced by diverse adjusting mechanisms upon changes in the light regime are generally referred to as **photoacclimation** processes. For example, in specimen of *Stylophora pistillata*, both the number of zooxanthellae per cm^2 coral surface and the amount of chlorophyll *a* per zooxanthellate cell doubled within 40 days upon translocation from an area exposed to 95% of the ambient surface irradiance to an area exposed to 30% of surface irradiance. The same response was observed upon translocation of corals from 30% surface irradiance to 0.8% surface irradiance (Titlyanov et al. 2001).

Under high light, down-regulation mechanisms are needed to prevent that the excess light causes large levels of damage to the photosynthetic apparatus. Several mechanisms for photoprotection have evolved in photosynthetic organisms (see mini-review by Niyogi 1999). Among these are pathways to safely dissipate the excess of energy absorbed as heat (non-photochemical quenching) or that allow to maintain the flow of electrons through both

photosystems under Ferredoxin sinks limitation such as the cyclic electron flow and the water-water cycle (Asada 2000). The water-water cycle acts as a sink for electrons through a cyclic series of reactions involving superoxide dismutase and ascorbate. Photorespiration, which is basically the oxigenase instead of the carboxilase activity of the enzyme Rubisco, can also be considered as an alternative photoprotective mechanism that enables the maintenance of Rubisco activity under carbon limitation conditions (Niyogi 1999). These general photoprotective mechanisms also exist in zooxanthellate corals (e.g. Jones et al. 2001; Gorbunov et al. 2001), and will not be explained in detail here. Other adaptive mechanisms to high light include the synthesis of antioxidant molecules and host pigments that protect the symbiont photosynthetic membranes (Dove et al. 2008), efficient systems to repair photodamage, and the controlled expelling of zooxanthellae, which is also termed **adaptive bleaching** (Fautin & Buddemaier 2004).

Anthony & Hoegh-Guldberg (2003) studied photoacclimation by measuring photosynthesis and respiration in specimen of *Montipora monasteriata* from different habitats, hereby comparing corals growing in an open area (peak irradiance > 600 µmole quanta m^{-2} s^{-1}) to corals growing in caves (peak irradiance < 50 µmole quanta m^{-2} s^{-1}). Shade-adapted corals had a lower compensation point and a lower Pn_{max} than their light-adapted conspecifics, but a higher photosynthetic efficiency (Fig 8). In contrast to the study by Titlyanov et al. (2001), Anthony & Hoegh-Guldberg (2003) did not find an increase in the number of zooxanthellae per unit of coral surface, and no increase in the amount of chlorophyll a per cell at lower irradiances. However, the shade-adapted coral had a thinner tissue layer, and may thus have had a higher density of zooxanthellae per unit of tissue volume. Not hampered by secondary effects of high light such as photorespiration, formation of reactive oxygen species, and non-photochemical quenching, low light corals may be optimally adapted to perform photosynthesis with a very high efficiency. Indeed, the quantum yield of nearly 10% estimated by Anthony & Hoegh-Guldberg (2003) in shade-adapted corals is close to the theoretical maximum of 12.5%. In addition, the shape of the corresponding P/E curve closely resembled a solely light-limited process, Pn_{max} already being reached at a quantum irradiance of approximately 100 µmole quanta m^{-2} s^{-1}. The first quantification of the minimum quanta requirements of photosynthesis ($1/\Phi_{max}$) for intact corals, using a correct methodology for the determination of coral absorptance and the amount of energy absorbed by the coral surface was reported by Rodríguez-Román et al. (2006), who quantified an average value of 15.4 ± 2.3 quanta absorbed per O_2 molecule evolved. This represents a quantum efficiency of 6.5% (Φ_{max} = 0.065) for the species *Montastraea faveolata*.

These findings, together with the description of the optical properties of intact coral structures done by Enríquez et al. (2005) confirm that corals are very efficient light collectors and users and can rely they metabolic needs on the symbiotic relationship even at low irradiance values. Thanks to multiple scattering of light by the coral skeletons, effects of self-shading are small. Hence, photosynthesis in coral holobionts or in isolated zooxanthellae will exhibit saturation under relatively low levels quantum irradiance (100-200 µmole quanta m^{-2} s^{-1}, see for example Iglesias-Prieto & Trench 1994; Anthony & Hoegh-Guldberg 2003). Positive effects of higher quantum irradiance values on coral growth and photosynthesis reported for example by Schlacher et al. (2007) and Schutter et al. (2008) may relate to self-shading effects due to the increasing colony size of the growing coral (Fig. 9).
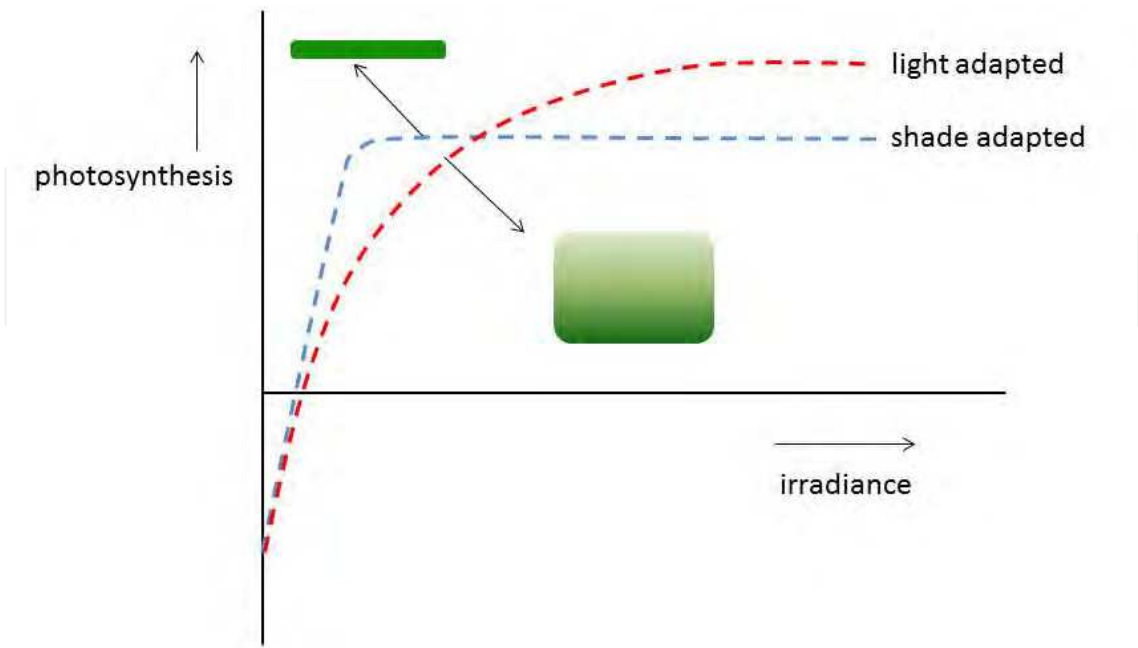
Fig. 8. Schematic representation of the results found by Anthony & Hoegh-Guldberg (2003) on photoadaptation by shade-adapted and light-adapted specimen of *M. monasteriata*. P/E curves for shade-adapted corals (blue line) and light-adapted corals (red line) are shown. The presumed thickness and pigmentation of the coral tissue corresponding to shade-adapted and light-adapted P/E curves is indicated.
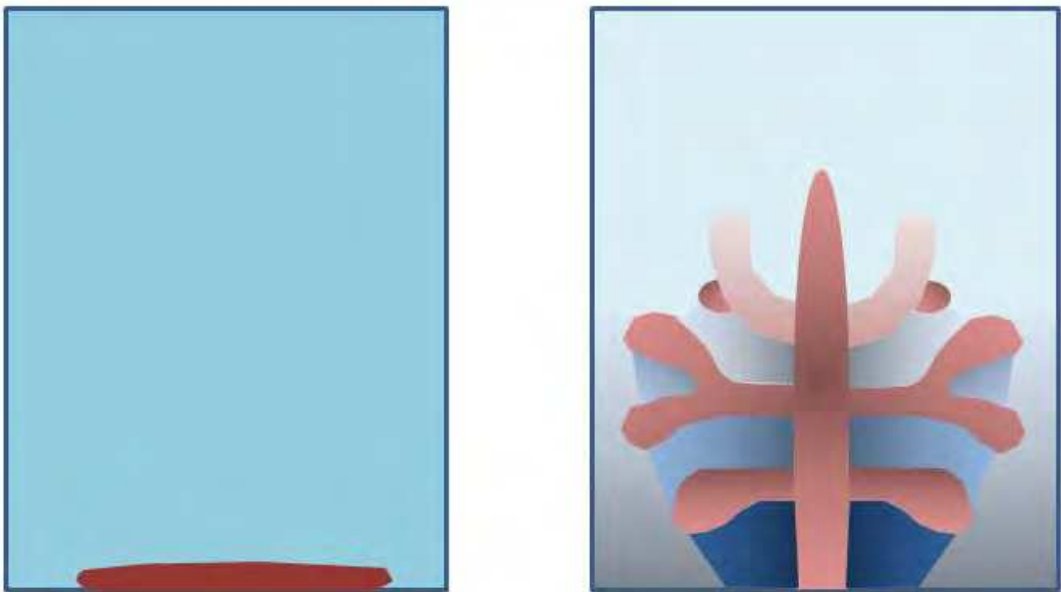

Fig. 9. Schematic representation of different light fields around a shade-adapted, plate-shaped coral (left) and a light adapted branching coral (right).

The strength of the light field is usually measured around the top of the coral colony, but the quantum irradiance at the bottom end of a colony may be tenfold lower. This may cause light limitation of photosynthesis in the lower parts of the colony, and hence, further increasing the quantum irradiance will further enhance the growth of these corals. In agreement to this view is the work of Schutter and coworkers on *Galaxea fascicularis* (Schutter et al. 2010, 2011). Schutter et al. (2010) found very high growth rates of 2.5% per day for small nubbins of *G. fascicularis* that were grown under a quantum irradiance of 90 µmole quanta m^{-2} s^{-1}, which corresponds to the afternoon peak irradiance at a depth of approximately 50 to 60 m (Mass et al. 2007). In another study, which was executed under much higher quantum irradiance levels (300 and 600 µmole quanta m^{-2} s^{-1}), a positive relation between SGR and quantum irradiance was observed, although the growth rates obtained were lower than the 2.5% per day that had been observed for small nubbins grown at 90 µmole quanta m^{-2} s^{-1}.

4.2 Inorganic nutrients

In shallow waters (on average, until a depth of nine metres), light is available in excess and may control coral photosynthesis through inhibitory mechanisms rather than limitation. Under saturating light, the availability of nutrients may as well become a limiting factor for coral photosynthesis. Experimental results suggest that photosynthetic rates of the zooxanthellae are limited by the availability of DIC, whereas the size of the symbiotic population and pigmentation per cell (i.e. the thickness of the coral tissue, the number of zooxanthellae per cm^2 of coral surface and the number of zooxanthellae cells per coral cell) is determined by the availability of inorganic nitrogen (Falkowski et al. 1993). Addition of DIC (e.g. Marubini & Thake 1999; Marubini et al. 2003) enhances photosynthesis and calcification, by increasing the rate of photosynthesis per cell. An increased availability of DIN without concurrent increased supply of DIC apparently disrupts the delicate balance of the symbiosis: additions of ammonium and nitrate increase the biomass of the zooxanthellae and lead to lower rates of calcification (Stambler et al. 1991; Marubini & Davies 1996), whereas concurrent addition of bicarbonate restores the calcification (Marubini & Thake 1999). Addition of planktonic food (i.e. carbon, nitrogen and phosphorous in a natural ratio) enhances tissue growth in corals and increases the size of the symbiotic population and pigmentation per cell leading to thicker tissue (cf Trench & Fisher 1983) and higher photosynthetic rates per unit of coral surface under increasing light than their food-limited conspecifics (Houlbrèque et al. 2004; Fig. 10A). This enables highly fed corals to calcify faster under high light than food-limited corals (Osinga et al. 2011). In contrast to these findings, corals exposed to increased DIN levels displayed a higher P$_{max}$ without a corresponding increase in calcification, despite the denser population of zooxanthellae residing in those corals (Marubini & Davies 1996; Fig 10B). There are two possible explanations for this apparent paradox. First, high DIN loadings reduce translocation of photosynthetic products from the algae to their host. Second, DIN-enriched corals respond to the enrichment by increasing the number of zooxanthellae per cm^2 without a concurrent increase in coral tissue and calcification capacity. Hence, DIN fed corals exhibit a higher zooxanthellae to coral tissue ratio than DON enriched corals, in which both the thickness of the coral tissue and the number of zooxanthellae per cm^2 increase. This implies that the algae are perhaps suboptimally packed in a more dense concentration in DIN-enriched corals.

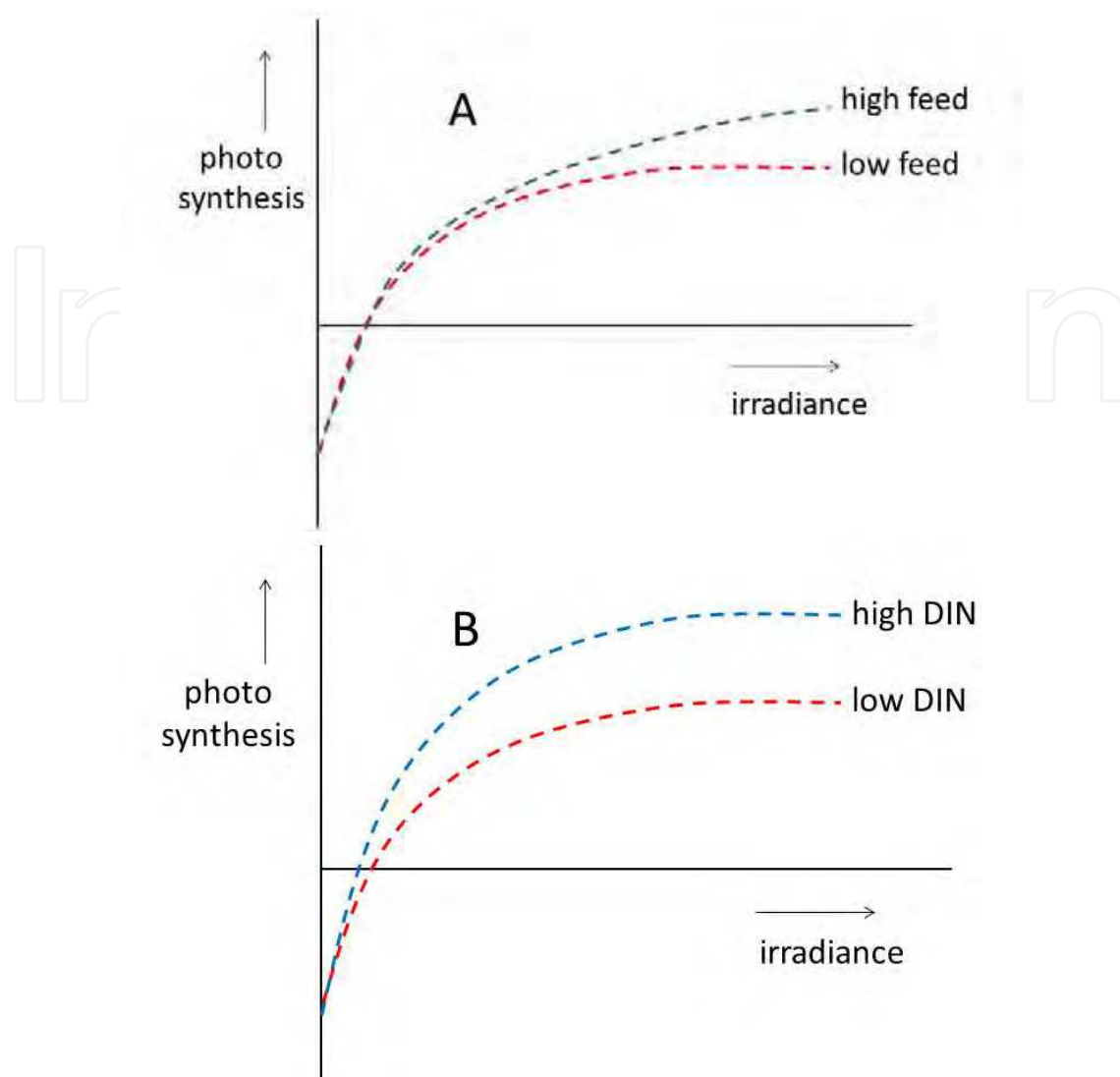Fig. 10. Schematic representation of the findings of Houlbrèque et al. (2004) on the effects of feeding on photosynthesis in *Stylophora pistillata* (A) and the findings of Marubini & Davies (1996) on the effects of DIN enrichment on photosynthesis in *Montastrea annularis* and *Porites porites* (B).

4.3 The role of water flow and oxygen

Water flow around a sessile organism regulates the rate of gas exchange between the organism and the surrounding water by affecting the thickness of the diffusive boundary layer – a thin, stagnant layer of water around the surface of the organism that determines the rate of mass transfer via diffusion (Patterson 1992). In flume experiments allowing a controlled variation in flow, Dennison & Barnes (1988) found that flow stimulated photosynthesis in corals, which was attributed to an improved influx of DIC, thus relieving DIC limitation of photosynthesis. Recent studies (Mass et al. 2010; Schutter et al. 2011) have related the enhancement of photosynthesis by flow to an increased efflux of oxygen. Under low flow, photosynthetic produced oxygen accumulates in the coral tissue (Gardella & Edmunds 1999; Mass et al. 2010). A concurrent flow-limited influx of DIC will lead to a high oxygen / DIC ratio in the zooxanthellate cell, which will induce high rates of

photorespiration, in particular in organisms that contain Type II Rubisco. Photorespiration reduces the efficiency of carbon fixation, but allows maintaining a minimum of carbon fixation under conditions of carbon limitation and high oxygen availability. The impact of photorespiration may be reduced by increasing the flow (Mass et al. 2010; Schutter et al. 2011) or by increasing the availability of DIC, thus reducing carbon limitation of coral photosynthesis. Indeed, several authors reported on increased photosynthetic activity in corals under elevated DIC levels (e.g. Herfort et al. 2008; Marubini et al. 2008; see next subsection).

Fig. 11 depicts a predicted change in P/E curve following an increase in flow. Under high flow, P_n will linearly increase until Pn_{max} has been reached, whereas under low flow, inhibition of net oxygen evolution due to photorespiration will increase with increasing irradiance, thus resulting in a lower Pn_{max} and a quantum yield (slope) that decreases with increasing irradiance.
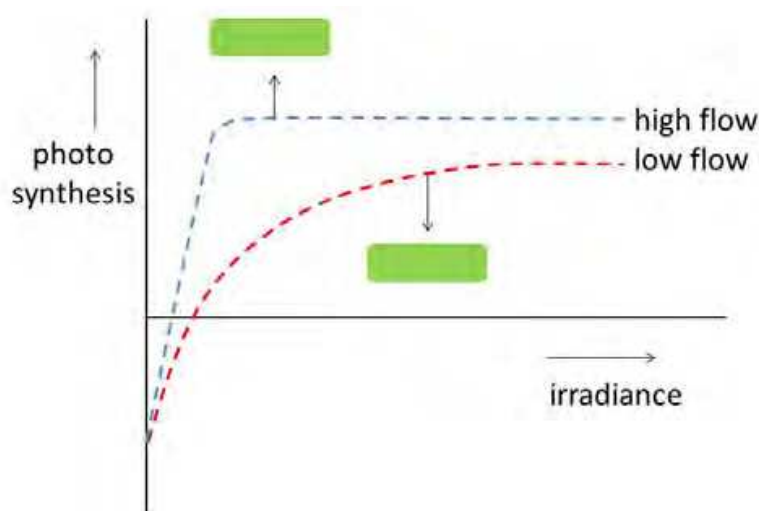

Fig. 11. Predicted effect of flow on photosynthesis in corals. The presumed thickness and pigmentation of the coral tissue corresponding to the P/E curves is equal in both conditions as indicated.

4.4 pH and dissolved inorganic carbon

Due to increasing atmospheric carbon dioxide concentrations, the ocean pH is decreasing. Almost 30% of the anthropogenic CO_2 emissions have been already removed from the atmosphere by the oceans. An increased availability of CO_2 may stimulate photosynthesis in DIC-limited corals (i.e. corals receiving non-limiting quantities of light), because CO_2 diffuses freely through the cell membrane and does not require carbonic anhydrase activity (the conversion of bicarbonate HCO_3^- into CO_2, Langdon & Atkinson 2005). However, doubling the concentration of dissolved CO_2 slightly reduced net photosynthesis in colonies of *Stylophora pistillata* cultured under a quantum irradiance of 380 µmole quanta m^{-2} s^{-1}, even though the number of zooxanthellae per coral cell increased (Reynaud et al. 2003). Several other studies also failed to demonstrate an effect of pH on photosynthesis (Marubini et al. 2008; Goiran et al 1996; Schneider & Erez 2006). It should be noted that these studies all evaluated the effect of pH on net photosynthesis. Hence, it cannot be excluded that the higher [CO_2] simultaneously stimulated to the same extent both algal photosynthesis and coral respiration, so that no increase in Pn could be detected. Indeed, Langdon & Atkinson

(2005) found an increase in net photosynthetic carbon fixation in an experimental coral community upon an increase in $[CO_2]$ without a concurrent increase in the net production of oxygen. Several studies found that calcification was impaired by high $[CO_2]$ (Reynaud et al. 2003; Langdon & Atkinson 2005; Marubini et al. 2008), although Reynaud et al. (2003) only observed such a negative response under elevated temperature. The studies by Langdon & Atkinson (2005), Schneider & Erez (2006 and Marubini et al. (2008) showed that photosynthesis and calcification are uncoupled under high CO_2 availability (a higher photosynthetic production concurrent with a lower calcification), which raises the question for what alternative purpose the excess photosynthetic carbon is being utilized within the holobiont under high $[CO_2]$ conditions. We hypothesize that part of the excess carbon is being respired to provide additional energy needed to maintain a high pH in the calcifying fluid.

Contrasting results have also found with respect to the effect of total [DIC] on coral photosynthesis. Marubini et al. (2008) found that a doubling of the ambient seawater [DIC] nearly doubled the rate of P_n in *Stylophora pistillata*. In agreement with these results, Herfort et al. (2008) found an optimal [DIC] of 6 mM for photosynthesis in *Porites porites* and *Acropora* sp. This concentration is well above the ambient seawater [DIC], which is approximately 2 mM. Other studies failed to show such an effect (Goiran et al. 1996; Schneider & Erez 2006). The contrasting findings may have been caused by differences between species, but also by differences in experimental approaches, such as pre-incubation time (Marubini et al. 2008), effects of limited mass transfer of gases due to low flow (e.g. Dennison & Barnes 1998; see also Section 4.3) and changes in Pg that are not reflected in Pn. Further studies in this field should focus on these aspects and should elucidate the relative importance of CO_2 and HCO_3^- as substrates for photosynthesis in corals.

4.5 Temperature; its role in coral bleaching

Bleaching of zooxanthellate corals, the partial or total expelling by a coral of its zooxanthellae population, is beyond doubt the most intensively studied subject within coral science (see reviews by Lesser 2007; Weis 2008). Whereas bleaching is mainly associated with thermal anomalies (Hoegh-Guldberg 1999; Lesser & Farrell 2004), it must be noted here that with respect to coral bleaching, light and temperature act as partners in crime: they both induce the same type of stress (Iglesias-Prieto 2006). For example, high light and high temperature both have a negative effect on Photosystem II. Re-oxidation of the first quinone electron acceptor Q_A is considered as the rate limiting step in the electron transport reactions in PSII. Over-excitation of Q_A under high light can cause a double reduction of Q_A. This over-reduction induces the formation of reactive oxygen species (ROS), which can cause damage in PSII (Smith et al 2005). High temperature reduces the rate at which Q_A is re-oxidized (Lesser & Farrell 2004; Suggett et al. 2008). Hence, by slowing down re-oxidation of Q_A, high temperature increases the probability that a Q_A molecule becomes over-reduced under high light. Moreover, both high light and high temperature cause an increase in the respiratory demand of a coral, which implies that the proportion of translocated photosynthetic carbon that can be used by the coral for tissue growth becomes smaller. The growing respiratory demand thus causes the coral tissue to become thinner, which makes the zooxanthellae more vulnerable to bleaching (Enriquez et al. 2005), so that the photosynthetic activity is even further reduced. In this way, the bleaching process accelerates rapidly, ultimately resulting in a complete loss of zooxanthellae from the tissue.

Some corals may survive the current era of rapid climate change. The combination of high light and high temperature is restricted to the upper zone of the coral reef environment. Corals usually remain safe from temperature-induced bleaching at depths below 10m. In addition, corals have the potential to adapt to chronic thermal stress, which makes them less vulnerable to acute thermal stress (Mumby et al. 2011). Zooxanthellae play an important role in the responses of corals to thermal stress (Rowan et al. 1997; Ulstrup et al. 2006), although symbiont identity does not fully explain the variation in coral tolerance to thermal stress (Fitt et al. 2009). The different phylotypes (clades) of *Symbiodinium* residing in corals exhibit strong differences in thermo-tolerance (Bhagooli & Hidaka 2003; Baker et al. 2004; Robison & Warner 2006; Suggett et al. 2008). Berkelmans & Van Oppen (2006) were the first to describe a shift in abundance of different *Symbiodinium* types upon transplantation of corals to different light/temperature habitats. Previous work had not documented such shifts in *Symbiodinium* types after coral transplantation to contrasting light environments (Iglesias-Prieto et al. 2004). Shifts in relative abundance in *Symbiodinium* types have been attributed to changes in the relative abundance of the genetic varieties already present in the coral rather than to uptake of new types from the environment. It is not clear yet if corals hosting a mixed population of Symbiodinium would have higher potential for thermal acclimation than corals hosting a single type. The effect of symbiosis plasticity on symbiosis robustness and specifically on holobiont capacity to cope with thermal stress has not been fully elucidated yet. Using real-time PCR techniques, Mieog et al. (2007) found that minute numbers of different types were present in 78% of the samples taken from species that were previously believed to host only one *Symbiodinium* type. Coffroth et al. (2010) recently reported that some corals are capable of taking up *Symbiodinium* from the environment, thus increasing their potential for acclimation through symbiont shuffling. Coffroth et al. (2010) were also the first to note that this uptake of foreign zooxanthellae may not necessarily cause a stable thermo-tolerant symbiosis, and hence, may not prevent the occurrence of bleaching.

Another recent study suggest that the thermo-tolerant *Symbiodinium* type D1a is a rather selfish organism that hardly translocates photosynthetic carbon to its host (Smith et al. 2010), which puts another constraint to symbiont shuffling as a mechanism of thermo-adaptation.

5. Summary and conclusions

1. Photosynthesis in corals is affected by many, often interacting factors.
2. Zooxanthellate corals possess a myriad of mechanisms to adjust their photophysiology to changing environmental conditions, including symbiont shuffling.
3. P/E curves represent a useful characterization of the photosynthetic responses of zooxanthellate corals, the shape and the associated parameters P_{max}, α, E_c and E_k being good indicators for photo-acclimation.
4. Oxygen evolution measurements are the easiest and most reliable way to obtain information on net photosynthesis and dark respiration.

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7. References

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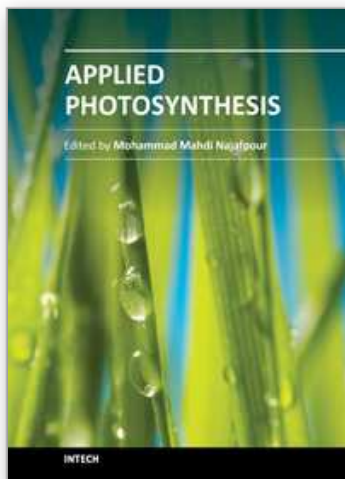
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Edited by Dr Mohammad Najafpour

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