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Light intensity, photoperiod duration, daily light flux and coral growth of *Galaxea fascicularis* in an aquarium setting: a matter of photons?

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Light is one of the most important abiotic factors influencing the (skeletal) growth of scleractinian corals. Light stimulates coral growth by the process of light-enhanced calcification, which is mediated by zooxanthellar photosynthesis. However, the quantity of light that is available for daily coral growth is not only determined by light intensity (i.e. irradiance), but also by photoperiod (i.e. the light duration time). Understanding and optimizing conditions for coral growth is essential for sustainable coral aquaculture. Therefore, in this study, the question was explored whether more light (i.e. more photons), presented either as irradiance or as light duration, would result in more growth. A series of nine genetically identical coral colonies of Galaxea fascicularis *L. were cultured for a period of 18 weeks at different light duration times (8 hours 150 μE m^{-2} s^{-1}:16 hours dark, 12 hours 150 μE m^{-2} s^{-1}:12 hours dark, 16 hours 150 μE m^{-2} s^{-1}:8 hours dark, 24 hours 150 μE m^{-2} s^{-1}:0 hours dark) and different irradiance levels (8 hours 150 μE m^{-2} s^{-1}:16 hours dark, 8 hours 225 μE m^{-2} s^{-1}:16 hours dark and 8 hours 300 μE m^{-2} s^{-1}:16 hours dark). Growth was determined every two weeks by measuring buoyant weight. Temperature, salinity and feeding levels were kept constant during the experiment. To detect possible acclimation of the corals to an increased light duration, rates of net photosynthesis and dark respiration were measured, hereby comparing coral colonies grown under an 8:16 hours light (150 μE m^{-2} s^{-1}):dark cycle with corals grown under a 16:8 hours light (150 μE m^{-2} s^{-1}):dark cycle. No increase in growth was detected with either increasing photoperiod or irradiance. Continuous lighting (24 hours 150 μE m^{-2} s^{-1}:0 hours dark) resulted in immediate bleaching and the corals died after 14 weeks. Hourly photosynthetic rates were significantly reduced in the 16 hour light treatment compared to the 8 hour light treatment. As a result, daily net photosynthetic rates were not significantly different, which may explain the observed specific growth rates. Acclimation to photoperiod duration appeared neither to be mediated by changes in chlorophyll-*a *concentration nor zooxanthellae density. Based on the results of this study, we can conclude that the enhancing effect of light on coral growth is not only a matter of photons. Obviously, the availability of light was not limiting growth in these experiments and was probably in excess (i.e. stressful amounts). Other factors are discussed that play a role in determining growth rates and might explain our results.*

Keywords: *Galaxea fascicularis*, coral growth, irradiance, photoperiod photo-acclimation, photosynthesis

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INTRODUCTION

Light is one of the most important factors influencing the growth and physiology of zooxanthellate scleractinian corals due to their symbiotic relationship with phototrophic microalgae, the zooxanthellae. When exposed to light, zooxanthellae perform photosynthesis, hereby producing oxygen and organic compounds. When their own respiratory needs are satisfied, zooxanthellae translocate the excess photosynthetic products to the coral host (Muscatine & Cernichiari, 1969; Muscatine *et al.*, 1981). Zooxanthellae can thus provide a considerable proportion of the resources needed for coral growth, both for soft tissue growth and for skeletal growth. The latter process is commonly referred to as light enhanced calcification. On average, calcification in light is found to be 3–4 times higher than in darkness (Gattuso *et al.*, 1999). Although the exact mechanisms of this enhancement are still a matter of debate (Gattuso *et al.*, 1999; Furla *et al.*, 2000; Allemand *et al.*, 2004; Moya *et al.*, 2006, 2008), the importance of light for coral growth is beyond doubt. Indeed, several studies have shown that a higher photon flux density (i.e. irradiance) results in increased skeletal growth (Marubini *et al.* (2001) for *Porites compressa* (80–700 μE m^{-2} s^{-1}), Reynaud-Vaganay *et al.* (2001) for *Stylophora pistillata* and *Acropora* sp. (130–260 μE m^{-2} s^{-1}), Reynaud

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et al. (2004) for *Acropora verweyi* (100–400 μE m^{-2} s^{-1}), Schutter *et al.* (2008) for *Galaxea fascicularis* (40–400 μE m^{-2} s^{-1})).

However, the quantity of light that is available for the zooxanthellae is not only determined by the photon flux density, but also by the length of the photoperiod. Until now, there have been no studies available that evaluate effects of increased photoperiod duration on coral growth under controlled conditions. If the enhancing effect of light on coral growth is related only to the amount of photons (i.e. light flux) received per day, then it can be expected that: (1) increasing irradiance will result in increased daily growth rates; (2) increasing photoperiod will result in increased daily growth rates; and (3) increasing daily light flux will result in increased daily growth rates.

The first aim of the current work was to test these hypotheses. For this, a series of nine genetically identical, 28-weeks-old, equal sized coral colonies of *Galaxea fascicularis* were cultured for a period of 18 weeks at different photoperiod durations (8 hours 150 μE m^{-2} s^{-1}:16 hours dark, 12 hours 150 μE m^{-2} s^{-1}:12 hours dark, 16 hours 150 μE m^{-2} s^{-1}:8 hours dark, 24 hours 150 μE m^{-2} s^{-1}:0 hours dark) and different photon flux densities (8 hours 150 μE m^{-2} s^{-1}:16 hours dark, 8 hours 225 μE m^{-2} s^{-1}:16 hours dark and 8 hours 300 μE m^{-2} s^{-1}:16 hours dark), of which some treatments were comparable in daily light flux (6.48 E/m^2/day: 8 hours 225 μE m^{-2} s^{-1}:16 hours dark and 12 hours 150 μE m^{-2} s^{-1}:12 hours dark, and 8.64 E/m^2/day: 8 hours 300 μE m^{-2} s^{-1}:16 hours dark and 16 hours 150 μE m^{-2} s^{-1}:8 hours dark).

Second, the acclimation of corals to different photoperiod durations (8 versus 16 hours light) was studied by measuring net photosynthetic rate, dark respiration, daily P/R ratio, zooxanthellae density and chlorophyll content. Whereas photo-acclimation to different photon flux densities has been studied extensively (Chalker *et al.*, 1983; Iglesias-Prieto & Trench, 1994; Titlyanov & Titlyanova, 2002; Anthony & Hoegh-Guldberg, 2003a), information on physiological adaptations to changes in the photoperiod duration remains scarce. It was expected that photosynthetic rates would not change under increased photoperiod duration, which would consequently result in higher daily photosynthetic rates with increased photoperiod duration. Considering the hypothesis that light enhanced calcification is mediated by photosynthesis, increased photoperiod duration was therefore expected to result in higher daily growth rates. To the best of our knowledge, this is the first description of acclimation of a zooxanthellate scleractinian coral to variation in photoperiod duration in a closed aquarium system.

MATERIALS AND METHODS

Experimental setup

PREPARATORY PHASE

Coral nubbins (single polyp clones) were created from *G. fascicularis* colonies that were grown at a light intensity of 60 μE m^{-2} s^{-1} (70W HQI) in a closed-circuit coral aquaculture system 'Quarantine system QU3' of Burgers Ocean, Arnhem, The Netherlands. QU3 is a 6000 l system consisting of four 1000 l aquaria and two 800 l sumps. The circulation system cycles 24 m^3 h^{-1} and the system is connected to a 23.5 l self made calcium reactor (pH 6.2–6.4; Q = 24 l h^{-1}), and a Schuran Aquafloater AQ250 protein skimmer.

Each coral nubbin was fixed to a 7 × 7 × 0.4 cm PVC plate using Reef Construct (Aquamedic). Nine PVC plates with coral nubbins were fixed to one single square plate and maintained for 28 weeks (7 months) in coral culture system QU3 at an irradiance of 150 μE m^{-2} s^{-1} which was provided by ATI lighting armatures containing 10.000K T5 Coral Light (Korallenzucht) bulbs. A light: dark cycle of 10L:14D was applied.

EXPERIMENTAL PHASE

After 7 months (28 weeks), each plate containing 9 small coral colonies was assigned to each of the following experimental light regimes (see also Table 1): 8 hours 150 μE m^{-2} s^{-1}:16 hours dark, 12 hours 150 μE m^{-2} s^{-1}:12 hours dark, 16 hours 150 μE m^{-2} s^{-1}:8 hours dark, 24 hours 150 μE m^{-2} s^{-1}:0 hours dark, 8 hours 225 μE m^{-2} s^{-1}:16 hours dark and 8 hours 300 μE m^{-2} s^{-1}:16 hours dark, and cultured for a period of 18 weeks. In addition to each plate containing 9 coral colonies, another 3 coral colonies were kept in each treatment explicitly for experimental use within respirometric flow cells. To facilitate adaptation to the new light regimes, all regimes were adapted in gradual steps (maximum 100 μE m^{-2} s^{-1} per day or 2 hours difference per day) during a time span of 7 days.

Lighting was provided by six ATI lighting armatures containing T5 Coral Light (Korallenzucht) bulbs (colour temperature: 10.000K, i.e. blue-end spectrum lighting) and adjusted to irradiance and light duration using a Profilux aquarium computer. Irradiance was measured weekly and adjusted if needed. Average values per treatment are shown in Table 1.

Experiments were done in semi-enclosed compartments that were constructed inside the coral aquaculture system QU3, to prevent lighting from one treatment to contaminate the other. As a consequence, no free movement of the water surface between experimental treatments and the overflow

Table 1. Description of experimental treatment (irradiance, photoperiod and daily light flux) and the average values for irradiance and water flow that were measured during the 18 week experimental period in each experimental treatment. Note: differences in water flow between treatments were not significantly different ($P > 0.10$).

	Irradiance (in μE/m^2/s)	Photoperiod (hours light:dark)	Daily light flux (in E/m^2/d)	Average irradiance (in μE/m^2/s)	Average water flow (in cm/s)
Treatment 1	150	8L:16D	4.32	149.7 ± 2.7	15.3 ± 3.5
Treatment 2	150	12L:12D	6.48	149.8 ± 4.4	16.3 ± 3.1
Treatment 3	150	16L:8D	8.64	151.0 ± 5.9	16.2 ± 2.6
Treatment 4	150	24L:0D	12.96	151.5 ± 6.2	15.2 ± 3.2
Treatment 5	225	8L:16D	6.48	223.0 ± 3.9	14.9 ± 2.6
Treatment 6	300	8L:16D	8.64	298.1 ± 6.2	16.9 ± 2.8

was possible. Skim boxes, connected to powerful circulation pumps (Aqua Medic Ocean runner 3500 and 6500, respectively 3500 and 6500 l h^{-1}), were installed and adjusted individually to allow for surface skimming (i.e. to keep the water surface free from algae). The water volume in each experimental treatment (~75 l) was estimated to be replaced every 5 minutes.

Within each experimental treatment, water flow was created by two small Eheim pumps (Type 1002; 1000 l h^{-1}) connected to a perforated PVC pipe. Flow velocity was measured weekly using a SENSA-RC2 electromagnetic current meter (Aquadata) and maintained around 15 cm/s. Average values per treatment are shown in Table 1.

Each experimental treatment was fed indirectly by daily feeding of the entire coral culture system (4000–8000 *Artemia* l^{-1}) and additionally twice a week directly inside each experimental treatment (approximately 250 *Artemia* l^{-1}). *Artemia* were hatched on site and subsequently enriched using Easy DHA Selco for 24 hours. Seawater was made up from Tropic Marine salt (Zoomix without bromide).

Temperature in the system was maintained at 25.8 ± 0.3 SD °C, salinity at 34.1 ± 0.1 SD ppt and pH 8.1 ± 0.1 SD. Water quality parameters were monitored on regular basis. During the experiment, the alkalinity in the system was 4.6 ± 1.0 SD mEq l^{-1}, calcium concentration 395.9 ± 17.7 SD mg l^{-1}, magnesium concentration 1203 ± 63.7 SD mg l^{-1}, nitrate concentration 0.195 ± 0.077 SD mg NO_3-N l^{-1} and phosphate concentration 0.018 ± 0.015 SD mg PO_4^{3-} l^{-1}.

Growth parameters

Growth was measured as increased buoyant weight (i.e. an approximation of skeletal weight), according to Schutter *et al.* (2008). Specific growth rates for buoyant weight were calculated between week 4 and week 18 (in weeks after the adjustment to the new light regimes), since it was assumed that corals need approximately 4 weeks to adapt to a new light regime (Falkowski & Dubinsky, 1981; Anthony & Hoegh-Guldberg, 2003b).

Respirometric measurements

NET PHOTOSYNTHESIS AND RESPIRATION

Net photosynthesis and dark respiration were determined for corals maintained at a photoperiod of 8 hours light and at a photoperiod of 16 hours light (irradiance: 150 μE m^{-2} s^{-1}). Three coral colonies of each treatment were measured on three different days by means of intermittent flow respirometry in a 1616 ± 5 ml respirometric flow cell, according to Schutter *et al.* (2008). The coral colonies in the 8 hour treatment were measured at the beginning and end of their photoperiod, while the coral colonies in the 16 hour treatment were only measured at the middle and end of their photoperiod due to restricted access to the experimental facilities of the public aquarium outside of normal working hours (see Figure 1).

Net photosynthetic oxygen production was measured at an irradiance of 150 μE m^{-2} s^{-1} (i.e. corresponding to the irradiance in the experimental treatment). Respiratory consumption of oxygen was measured in the dark. Lighting was provided by a T5 lighting system (ATI) containing eight 24 W coral light bulbs (Korallenzucht). A flow speed of ±10 cm s^{-1} was applied to ensure adequate mixing for respirometry.

DAILY P/R RATIOS

Daily P/R ratios were calculated to indicate whether the corals were self-supporting with respect to carbon. To be able to calculate daily P/R ratios, net photosynthetic and dark respiratory rates were converted to carbon equivalents, using the following equations:

$$P_c = P_{net} \times (12/32) \quad [\mu mol\ C\ min^{-1} cm^{-2}]$$

$$R_c = R_{dark} \times (12/32) \quad [\mu mol\ C\ min^{-1} cm^{-2}]$$

where P_c is net photosynthetic rate in carbon equivalents (μmol C min^{-1} cm^{-2}), P_{net} is net photosynthetic rate in oxygen equivalents (μmol O_2 min^{-1} cm^{-2}) and the factor (12/32) is the molar conversion factor to convert oxygen equivalents (O_2) to carbon equivalents (C). Analogously, R_c is dark respiratory rate carbon equivalents (μmol C min^{-1} cm^{-2}) and, R_{dark} is the dark respiratory rate in oxygen equivalents. Since we do not know the exact composition of substances that are produced during photosynthesis and that are respired during respiration, no further corrections were applied using metabolic quotients (Gattuso & Jaubert, 1990).

Daily P/R ratios were calculated using the following equation:

$$\text{Daily P/R ratio} = (P_c^* L)/(R_c^* D) \quad [\text{dimensionless}]$$

where P_c and R_c are expressed in mg C/hour/cm^2, and L and D correspond respectively to the number of hours of light and dark per day. Although interpretation of daily P/R ratios that are derived from short-term measurements is not justified according to Muscatine *et al.* (1981), it is used here as an approximation.

Analysis of coral tissue

TISSUE REMOVAL

At the end of the experiment, between 13:00 and 14:00, all corals were removed from their treatments, snap-fixed in formaldehyde (3 minutes 10% formaldehyde in 0.22 μm filtered

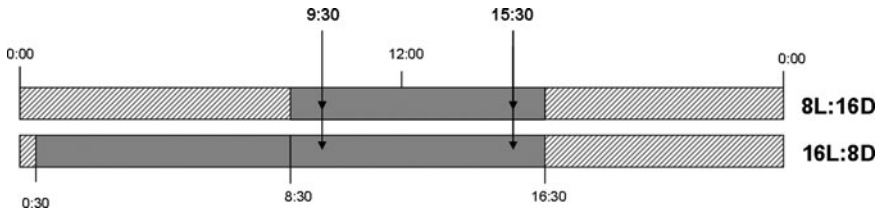

Fig. 1. Scheme explaining the time of respirometric measurements (see arrows at 9:30 and 15:30) relative to the experimental photoperiod duration (8L:16D and 16L:8D).

seawater (FSW) 34ppt), rinsed shortly in 0.22 μm FSW 34 ppt, wrapped in tin foil and frozen at −20°C until further processing (Broadbent *et al.*, 2002).

Corals (N = 9) from two treatments (8 hours light/150 μE m^{-2} s^{-1} and 16 hours light/150 μE m^{-2} s^{-1}) were taken from the freezer and soaked in Ca^{2+}-Mg^{2+}-free artificial seawater (ASW) with ethylene diamine tetracetic acid (EDTA) in a slowly moving water bath at 50°C overnight in order to facilitate tissue removal. This solution was prepared according to Rinkevich *et al.* (2005). Tissue was removed the next day using high pressured N_2 (maximum 1.5 bar within plastic bag). Cell suspensions were collected, diluted with 34 ppt ASW and centrifuged three times for 10 minutes at 4°C at 4000 rpm. The final tissue pellets of each coral were collected in one tube and total volume was determined using a 5 ml pipette. After homogenization using a LABOCAT X1030, samples were taken to count the number of zooxanthellae (200 μl) and for chlorophyll analysis (1 ml).

CHLOROPHYLL ANALYSIS AND ZOOXANTHELLAE COUNT

Chlorophyll was extracted by adding 9 ml 100% acetone to 1 ml tissue homogenate and storing it at −20°C overnight. The next day, this suspension was homogenized again using a LABOCAT X1030. After settlement of the pellet, the absorbance of the extract was measured in triplicate using a Beckman Coulter DU 530 Spectrophotometer at 750, 664 and 630 nm. 90% acetone in demiwater was used as a blank. The concentrations of chlorophyll-*a* and chlorophyll-C_2 were computed according to the equations given by Jeffrey & Humphrey (1975) for dinoflagellates. Each extinction value (OD664 and OD630) was corrected for the absorbance at 750 nm, which is a correction for the turbidity of the sample.

Zooxanthellae were counted using a Bürker–Turk counting chamber. Zooxanthellae density was expressed in amount of zooxanthellae per cm^2 surface area. Using the chlorophyll data, the amount of chlorophyll per zooxanthellae was also calculated.

Data analysis

Normality ($P > 0.05$) and homogeneity of variance ($P > 0.05$) of the growth and respirometry data were tested using the Shapiro–Wilk test and Levene's test in SAS 9.1. Since our growth, photosynthesis and respiration data did not satisfy the assumptions for analysis of variance testing, we used Kruskal–Wallis as a non-parametric test to detect statistical differences between treatments. A Student's *t*-test was used to detect statistical differences in chlorophyll content and zooxanthellae density between the 8 hours light and 16 hours light treatment.

RESULTS

Effect of photoperiod duration, irradiance and daily light flux on skeletal growth

PHOTOPERIOD

Specific growth rate did not change significantly with increasing photoperiod duration (8 hours, 12 hours and 16 hours). The corals in the 24 hours light treatment started bleaching after the change to the new light regime, but managed to stay alive and to keep growing until week 8. They died finally after week 14. Their specific growth rate (4–14 weeks) was significantly lower than the corals in the other light treatments ($P \leq 0.0005$) (Figure 2).

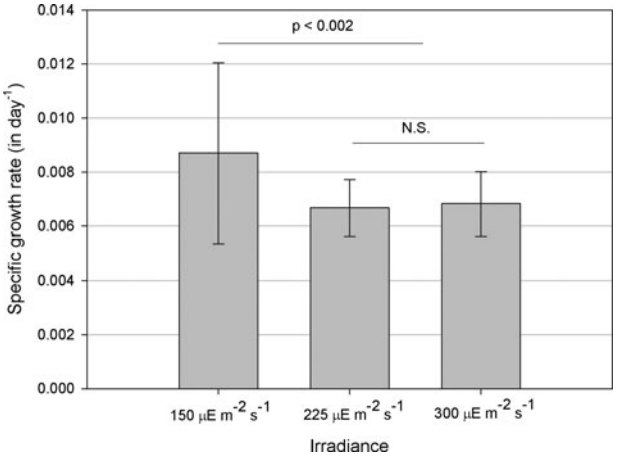

Fig. 2. Effect of photoperiod on the specific growth rate in terms of buoyant weight of *Galaxea fascicularis* between week 4 and week 18 of the experiment. Values are mean ± SD. N = 9.

IRRADIANCE

Specific growth rate decreased with increasing irradiance (150 μE m^{-2} s^{-1}, 225 μE m^{-2} s^{-1}, 300 μE m^{-2} s^{-1}). The corals in the 225 μE m^{-2} s^{-1} and 300 μE m^{-2} s^{-1} light treatment had a significant lower specific growth rate as buoyant weight compared to the 150 μE m^{-2} s^{-1} light treatment ($P < 0.002$) (Figure 3).

DAILY LIGHT FLUX

Specific growth rate did not change significantly with increasing daily light flux (6.48 E/m^2/day, versus 8.64 E m^{-2} day^{-1}) (Figure 4).

Respirometric measurements

No significant difference was found between our measurements of net photosynthesis and dark respiration measured

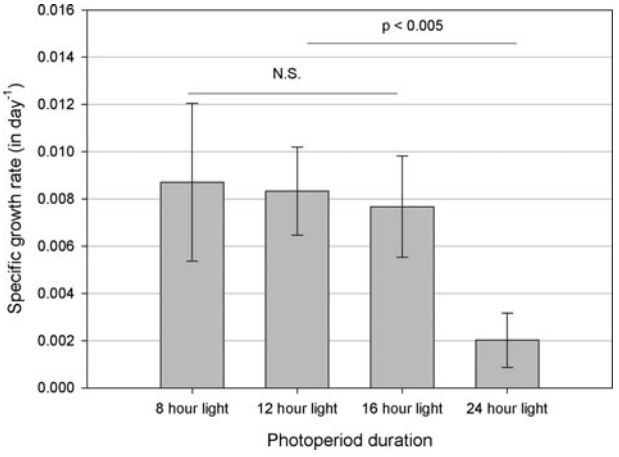

Fig. 3. Effect of irradiance on the specific growth rate in terms of buoyant weight of *Galaxea fascicularis* between week 4 and week 18 of the experiment. Values are mean ± SD. N = 9.

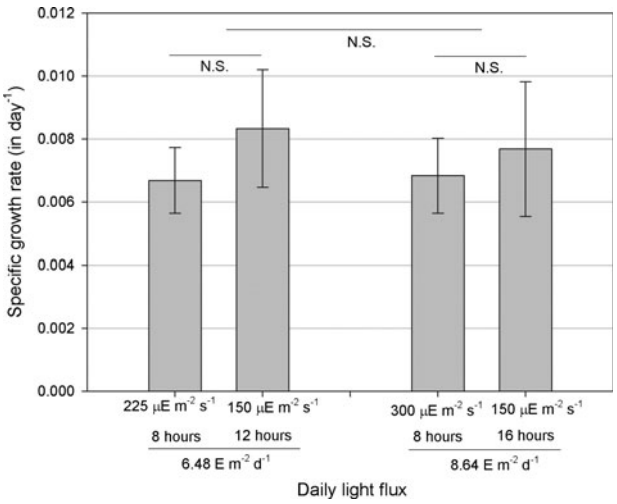

Fig. 4. Effect of daily light flux on the specific growth rate in terms of buoyant weight of *Galaxea fascicularis* between week 4 and week 18 of the experiment. Values are mean ± SD. N = 9.

at 9:30 and 15:30 for both the 8 hours light treatment and the 16 hours light treatment. Average net photosynthetic rate (in µmol O_2 min^{-1} cm^{-2}) was significantly higher for corals in the 8 hours light treatment compared to the 16 hours light treatment ($P = 0.0005$), while average dark respiratory rate was not significantly different ($P = 0.24$) (Table 2).

Despite the fact that the corals in the 16 hours light treatment were exposed to light twice as long compared to the corals in the 8 hours light treatment, the total amount of oxygen produced per day (i.e. daily net photosynthesis) was found to be not significantly different between treatments ($P = 0.48$). However, the total amount of oxygen respired in the night was significantly higher for the corals in the 8 hours light treatment ($P = 0.002$). Consequently, the average daily P/R ratio was significantly higher for the corals in the 16 hours light treatment ($P = 0.003$), i.e. the average daily P/R ratio for the corals in the 16 hours light treatment was above 1 (1.59 ± 0.66 SD), while the average daily P/R ratio for the corals in the 8 hours light treatment was below 1 (0.90 ± 0.44 SD) (Table 2).

Chlorophyll and zooxanthellae

No significant difference in chlorophyll-*a* content (in µg Chl a cm^{-2}) and chlorophyll-C_2 content (in µg Chl C_2 cm^{-2}) was detected between the corals in the 8 hours light and 16 hours light treatment (Student's *t*-test, respectively $P = 0.47$ and $P = 0.45$), despite visual observation suggesting that the corals in the 16 hours light treatment were less pigmented.

Zooxanthellae density (zoox cm^{-2}) and amount of chlorophyll per zooxanthellae (Chl a $zoox^{-1}$) were also not significantly different between the corals in the 16 hours light treatment and the corals in the 8 hours light treatment (Table 3).

DISCUSSION

Coral growth: a matter of photons?

No increase in specific growth rate was found with increasing irradiance, photoperiod duration or daily light flux. Continuous lighting (24 hours 150 µE m^{-2} s^{-1}:0 hours dark) resulted in immediate bleaching and death after 14 weeks. The specific growth rate of these corals was significantly decreased compared to the other treatments. Since several previous laboratory-based studies demonstrated that growth of scleractinian corals increases with increasing irradiance (Marubini *et al.* (2001): between 80 and 700 µE m^{-2} s^{-1} for *Porites compressa*; Reynaud-Vaganay *et al.* (2001): between 130 and 260 µE m^{-2} s^{-1} for *Stylophora pistillata* and *Acropora* sp.; Reynaud *et al.* (2004): between 100 and 400 µE m^{-2} s^{-1} for *Acropora verweyi*; Schutter *et al.* (2008): between 40 and 400 µE m^{-2} s^{-1} for *Galaxea fascicularis*), it can be concluded that light was not limiting for growth in this study. Rather it seems that light was in excess in certain experimental treatments, since the corals in the highest light treatments (225 and 300 µE m^{-2} s^{-1}) exhibited a significantly lower specific growth rate than the corals lowest light treatment (150 µE m^{-2} s^{-1}). Similar findings have been reported in field studies that measured coral growth rates along a depth gradient (Baker & Weber, 1975; Bak, 1976; Huston, 1985). For many coral species, optimal growth rates are found at intermediate depths, indicating that light is in excess at shallower depths. It should be noted that the concept 'saturating light intensity' is a relative property that varies between coral species and depends on the physiological status of the coral examined.

Obviously, the availability of photons alone cannot enhance coral growth. Besides the amount of photons, also other factors may play a role in determining coral growth rate. Factors known to be limiting for the growth of stony corals include water flow (Lesser *et al.*, 1994, Schutter *et al.*, 2011), aragonite saturation state (Gattuso *et al.*, 1998; Leclercq *et al.*, 2000; Schneider & Erez, 2006) and its associated components (Marubini *et al.*, 2008), the availability of essential trace metals such as copper and zinc (Ferrier-Pagès

Table 2. Overview of respirometric parameters of corals maintained at a photoperiod of 8 hours light (8 hours 150 µE m^{-2} s^{-1}: 16 hours dark) and at a photoperiod of 16 hours light (16 hours 150 µE m^{-2} s^{-1}: 8 hours dark). Values are mean ± SD. *P* values are given (Student's *t*-test).

		8 hours light		16 hours light		
		Mean	SD	Mean	SD	*P* value
Net photosynthesis	µmol O_2/min/cm^2	0.024	0.007	0.013	0.005	0.0005
Dark respiration	µmol O_2/min/cm^2	−0.017	0.006	−0.020	0.005	0.24
Daily net photosynthesis	µmol O_2/cm^2/day	11.627	3.419	12.756	4.799	0.48
Daily respiration	µmol O_2/cm^2/day	−16.303	5.414	−9.455	2.198	0.002
P/R ratio		0.90	0.44	1.59	0.66	0.003

Table 3. Overview of chlorophyll and zooxanthellae measurements of corals maintained at a photoperiod of 8 hours light (8 hours 150μE/m²/s: 16 hours dark) and at a photoperiod of 16 hours light (16 hours 150 μE/m²/s: 8 hours dark). Values are mean ± SD. *P* values are given (Student's *t*-test).

		8 hours light		16 hours light		
		Mean	**SD**	**Mean**	**SD**	***P* value**
Chlorophyll-*a*	*μg/cm2*	3.66	1.81	4.21	1.31	0.47
Chlorophyll-C_2	*μg/cm2*	1.12	0.52	1.31	0.51	0.45
Zooxanthellae density	*zoox/cm2*	2.58×10^6	9.85×10^5	3.17×10^6	7.69×10^5	0.32
Chlorophyll-*a* per zooxanthella	*μg/zoox*	1.81	0.67	1.54	0.67	0.57

et al., 2005) and/or the availability of essential nutrients such as aspartic acid (Allemand *et al.*, 1998) that are mostly supplied by heterotrophic feeding (Houlbreque & Ferrier-Pagès, 2009). While factors known to have an inhibiting effect on coral growth include elevated nutrient concentrations (Ferrier-Pagès *et al.*, 2000; Fabricius, 2005), increased iron concentration (Ferrier-Pagès *et al.*, 2001), increased temperatures (Jokiel & Coles, 1990; Marshall & Clode, 2004), competition (Rinkevich & Loya, 1985; Tanner, 1995) and sedimentation (Rogers, 1990).

The fact that the specific growth rate of *G. fascicularis* colonies grown at 8 hours 150 μE m^{-2} s^{-1}:16 hours dark was noticeably lower compared to *G. fascicularis* colonies grown at 10 hours 166 μE m^{-2} s^{-1}:14 hours dark during a similar time period in a previous study (0.0087 ± 0.0033 day^{-1} versus 0.0130 ± 0.0011 day^{-1}, based on data Schutter *et al.* (2008)), suggests that one or more factors were limiting or inhibiting in the current study. However, despite our efforts (see Table 4), the factor(s) limiting or inhibiting coral growth in this study could not be conclusively determined.

On the other hand, the unexpected response of our corals during the experimental phase of this experiment could also be due to the transition from the open aquarium system to the experimental setup (i.e. confinement of the corals, albeit within the same aquarium system) and/or the 'sudden' change in light regime. This seems plausible because of two observations: firstly, growth rates during the experimental phase of this experiment (0.0087 ± 0.0033 day^{-1} at 8h 150 μE m^{-2} s^{-1}:16h dark) were noticeably lower compared to *G. fascicularis* grown at 10 hours 166 μE m^{-2} s^{-1}:14 hours dark during a similar time period in a previous study (0.0130 ± 0.0011 day^{-1}, based on data from Schutter *et al.* (2008)); and secondly, growth rates during the experimental phase of this experiment were notably reduced compared to

Table 4. Comparison of growth (pre-culture and experimental phase) and aquarium parameters (experimental phase) during the present study with those during a previous study using the same genetic line of *Galaxea fascicularis* (Schutter *et al.*, 2008). Specific growth rate refers to specific growth rate as buoyant weight.

	This study				**Schutter *et al.* (2008)**			
	Mean	**SD**		**Notes**	**Mean**	**SD**		**Notes**
Specific growth rate								
Preculture phase	0.0144	0.0008	day^{-1}	150 μE/m²/s, 10L:14D, 28 weeks	0.0147	0.0017	day^{-1}	166 μE/m2/s, 10L:14D, 25 weeks
Experimental phase	0.0087	0.0033	day^{-1}	150 μE/m2/s, 8L:16D, 32–46 weeks	0.0130	0.0011	day^{-1}	166 μE/m2/s, 10L:14D, 25–42 weeks
Water quality								
Alkalinity	4.6	1	mEq/l		3.23	0.54	mEq/l	
Calcium	395.9	17.7	mg/l		393.75	14.36	mg/l	
Magnesium	1202	63.7	mg/l		1290	51.29	mg/l	
Nitrate	0.195	0.077	mg NO_3-N/l		0.19	0.08	mg NO_3-N/l	
Phosphate	0.018	0.015	mg PO_4^{3-}/l.		0.015	0.022	mg PO_4^{3-}/l.	
Aquarium settings								
General								
Temperature	25.8 ± 0.3 °C				26 °C			
Competition with algae	Reduced by regular maintenance				Reduced by regular maintenance			
Sedimentation	Not an issue				Not an issue			
Pre-culture phase								
Aquarium setup	Open inside aquarium system				–			
Artemia fed	Fed according to normal aquarium schedule (7 × a week)				–			
Water flow	Estimated at 5–15 cm/s				–			
Experimental phase								
Aquarium setup	Confined by PVC plates to treatment space				Open inside aquarium system			
Artemia fed (concentrated in aquarium)	4000–8000		*Artemia*/l	7 × a week in aquarium system	4000–8000		artemia/l	7 × a week in aquarium system
	253	*1*	*Artemia*/l	2 × a week inside each compartment				
Water flow	15.7	*2.5*	cm/s		5–15		cm/s	

the pre-culture phase (0.0144 $\pm$ 0.0008 day^{-1} at 10 hours 150 $\mu E\ m^{-2}\ s^{-1}$: 14 hours dark; see Table 4). It is possible, for example, that the sudden change in light duration in the photoperiod treatments caused a disturbance in the timing and phasing of cell division of zooxanthellae and/or coral host cells (Hoegh-Guldberg, 1994; Fitt, 2000), which could potentially result in decreased growth rates.

At any rate, it seems that the corals were under stress, which could explain their sensitivity to increased available light. It is well-known that different stressors can interact to reduce the tolerance to each individual stressor, e.g. temperature, salinity and light stress (Coles & Yokiel, 1978), temperature and light stress (Lesser & Farell, 2004), and thermal stress and ocean acidification (Anthony *et al.*, 2008; Muehllehner & Edmunds, 2009). It is recommended for future studies to use a longer experimental time (as in Schutter *et al.*, 2008) to cancel out potential stress effects due to (sudden) changes in light regime and transition between different systems.

Photo-acclimation to prolonged light duration

GROWTH AND PHOTOSYNTHESIS

Since light was not limiting for coral growth, corals in the 16 hours light treatment probably received excess light. Despite receiving excess light, the corals in the 16 hours light treatment managed to retain growth rates comparable to the corals in the 8 hours light treatment. Our respirometric data suggest that the corals in the 16 hours light treatment acclimatized to a longer photoperiod by decreasing their hourly rate of photosynthesis compared to the corals in the 8 hours light treatment. As a result daily net photosynthesis was not significantly different between treatments; this is in agreement with their similar specific growth rates. These results are in line with our original expectations that—if photosynthetic rates did not change with increased photoperiod duration—more hours of photosynthesis per day would result in a higher daily growth rate. Therefore, this result fits with the view that enhancement of calcification is mediated by photosynthesis (Gattuso *et al.*, 1999; Allemand *et al.*, 2004), since neither growth nor daily net photosynthesis were significantly different between the two treatments. Although no photosynthesis was measured in the different irradiance treatments, it is plausible that these treatments acclimatized to excess light by adjusting their photosynthetic rate accordingly. Photosynthesis was probably reduced with increasing irradiance levels, resulting in lower daily photosynthetic rates and—as we observed—lower daily growth rates at higher irradiance levels (225 $\mu E\ m^{-2}\ s^{-1}$ and 300 $\mu E\ m^{-2}\ s^{-1}$). However, this remains to be demonstrated in future studies.

Davies (1991) reported a higher total photosynthetic energy fixation of corals in the field on sunny days compared to cloudy days. On sunny days, total photosynthetic energy fixation was more than required for respiration and growth, while energy expenditure exceeded photosynthetic energy fixation on cloudy days. Although the daily amount of sunny hours is not the same as photoperiod duration, it can be said that the extra hours of light resulted in a higher daily net photosynthesis in the study of Davies (1991), which is in contrast to what we found in the present study. It is possible that receiving 'continuous lighting' (i.e. without occasional decreases in light intensity) for a prolonged period triggers a different physiological response and acclimation mechanism of the coral. Additionally, the 16 hours photoperiod duration that we applied in the present study is unnatural (i.e. never occurs in nature) and was only applied for aquaculture purposes.

Light stress is known to reduce photosynthetic rates as a result of oxidative stress (Lesser, 1996; Nakamura & Van Woesik, 2001; Finelli *et al.*, 2006), potentially impairing light-enhanced calcification. In response to excess irradiance, in general, corals will engage in mechanisms for photo-protection and limit their light capture to prevent photo-inhibition. Either by limited light availability or by photo-inhibition, this response will result in reduced photosynthetic rates (Titlyanov *et al.*, 2000; Anthony *et al.*, 2005). Moreover, light stress can also reduce coral growth rates (e.g. Baker & Weber, 1975; Bak, 1979; Huston, 1985) due to the allocation of energy to (costly) stress responses, such as the synthesis of heat shock protein and protecting pigments (Anthony *et al.*, 2002), instead of to coral growth. In fact, we found that the corals in the 16 hours light treatment had a significantly higher availability of photosynthetic carbon (i.e. higher daily P/R ratio) compared to the corals in the 8 hours light treatment, which did not make a difference for their growth. Possibly, the increased availability of photosynthetic carbon was allocated towards defence mechanisms against photo-oxidative stress instead of towards skeletal growth, explaining the absence of increased growth with increasing availability of photosynthetic carbon. Energy allocation to photo-protective mechanisms remains to be studied in future investigations.

ACCLIMATION MECHANISM

Based on zooxanthellae density and chlorophyll content, it is not possible to distinguish whether the adaption (photo-acclimation) to the longer light duration was host-controlled or symbiont-controlled, since neither a difference in zooxanthellae density nor in chlorophyll content was found. Generally, corals acclimate to increased light by regulating their light capture. This can occur either by limiting light harvest and utilization of their photosystems (i.e. by decreasing the amount of photosynthetic pigments per zooxanthellae, decreasing the zooxanthellae density in polyp tissue, or increasing non-photochemical quenching) and/or limiting light capture by self-shading of their photosynthetic surfaces (i.e. by changes in morphology and anatomy of coral colony) (Titlyanov *et al.*, 2000; Anthony *et al.*, 2005). Self-shading can be either a morphological response (i.e. expressed in colony architecture, long-term response) or a behavioural response (i.e. expressed as tissue retraction, short-term response). Tissue retraction is often a response to stress, e.g. in response to sub-aerial exposure, bright light or increased iron concentrations (Brown *et al.*, 1991) and can be expressed as polyp retraction or withdrawal of tentacles (Brown *et al.*, 1994, 2002). It is also known to occur in *G. fascicularis* (Brown *et al.*, 1994). Since self-shading does not involve the loss of either zooxanthellae or photosynthetic pigments (Brown *et al.*, 1994), it is possible that this occurred in the present study. Moreover, due to the sudden change in light regime, the corals in the present study neither had the time for morphological changes of the skeleton that normally occur during growth in a certain light regime (Anthony *et al.*, 2005). The reduced photosynthetic rates might therefore be explained by lower light levels as a result of self-shading,

and are hence host-controlled. Tissue retraction is likely an effective mechanism to keep irradiance within a physiologically optimal range, just like self-shading through morphological plasticity of skeletal architecture (Anthony *et al.*, 2005).

The mechanism to adapt to excess light might be the same for excess light received as irradiance and as light duration. The only difference might be in the time of onset of photo-adaptation or photo-inhibition, since if the irradiance itself is not stressful, the amount of photons can accumulate to stressful amounts during the day. However, this remains to be demonstrated.

The growth and physiological response of corals to increased light duration under light conditions that are limiting for coral growth remains to be investigated. The use of photosynthesis–irradiance curves and/or pulse-amplitude modulation measurements during daytime will provide more insight into the photo-acclimative responses.

CONCLUSION

The enhancing effect of light on coral growth is not only a matter of photons. No positive correlation between light availability and growth was observed under the given experimental conditions. Neither with increasing photoperiod duration, nor with increasing irradiance, nor with increased daily light flux. This indicates that light was not the limiting factor for coral growth and was most probably in excess. Continuous lighting (24 hours) resulted in immediate bleaching and finally death of the corals.

Corals were able to adapt to prolonged light duration under light saturating conditions by decreasing their hourly rate of photosynthesis. As a result, daily net photosynthesis was not significantly different between corals grown at 8 hours light and 16 hours light. Photo-acclimation to prolonged photoperiod was not achieved by changes in zooxanthellae density or chlorophyll content. It is proposed that the corals exhibited a form of self-shading that reduced the amount of photons reaching the coral, thereby reducing their photosynthetic rates and specific growth rates.

Obviously, light was not limiting for growth in this experiment. Factor(s) limiting or inhibiting coral growth in this study could not be conclusively determined. Our results do show that corals are able to adapt to a prolonged light duration under stressful condition and that daily growth rates seem to be correlated to daily photosynthetic rates. Therefore, for coral aquaculture, increasing light availability still seems promising, but remains to be explored under light-limited conditions.

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