Variation in Coral Photosynthesis, Respiration and Growth Characteristics in Contrasting Light Microhabitats: An Analogue to Plants in Forest Gaps and Understoreys?
Author(s): K. R. N. Anthony and O. Hoegh-Guldberg
Source: *Functional Ecology*, Vol. 17, No. 2, (Apr., 2003), pp. 246-259
Published by: British Ecological Society
Stable URL: http://www.jstor.org/stable/3599181
Accessed: 16/07/2008 10:34

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at http://www.jstor.org/page/info/about/policies/terms.jsp. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at http://www.jstor.org/action/showPublisher?publisherCode=briteco.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

JSTOR is a not-for-profit organization founded in 1995 to build trusted digital archives for scholarship. We work with the scholarly community to preserve their work and the materials they rely upon, and to build a common research platform that promotes the discovery and use of these resources. For more information about JSTOR, please contact support@jstor.org.

http://www.jstor.org

Functional Ecology 2003
17, 246–259

Variation in coral photosynthesis, respiration and growth characteristics in contrasting light microhabitats: an analogue to plants in forest gaps and understoreys?

K. R. N. ANTHONY*† and O. HOEGH-GULDBERG‡

**Centre for Coral Reef Biodiversity, School of Marine Biology and Aquaculture, James Cook University, Townsville, Queensland 4811, and ‡Centre for Marine Studies, University of Queensland, Brisbane, Queensland 4072, Australia*

Summary

1. The often complex architecture of coral reefs forms a diversity of light microhabitats. Analogous to patterns in forest plants, light variation may drive strategies for efficient light utilization and metabolism in corals.

2. We investigated the spatial distribution of light regimes in a spur-and-groove reef environment and examine the photophysiology of the coral *Montipora monasteriata* (Forskål 1775), a species with a wide habitat distribution. Specifically, we examined the variation in tissue and skeletal thickness, and photosynthetic and metabolic responses among contrasting light microhabitats.

3. Daily irradiances reaching corals in caves and under overhangs were 1–5 and 30–40% of those in open habitats at similar depth (3–5 m), respectively. Daily rates of net photosynthesis of corals in cave habitats approximated zero, suggesting more than two orders of magnitude variation in scope for growth across habitats.

4. Three mechanisms of photoadaptation or acclimation were observed in cave and overhang habitats: (1) a 20–50% thinner tissue layer and 40–60% thinner skeletal plates, maximizing light interception per unit mass; (2) a two- to threefold higher photosynthetic efficiency per unit biomass; and (3) low rates of dark respiration.

5. Specimens from open and cave habitats displayed a high capacity to acclimate to downshifts or upshifts in irradiance, respectively. However, specimens in caves displayed limited acclimation to further irradiance reduction, indicating that these live near their irradiance limit.

6. Analogous to patterns for some plant species in forest gaps, the morphological plasticity and physiological flexibility of *M. monasteriata* enable it to occupy light habitats that vary by more than two orders of magnitude.

Key-words: Energy balance, photoacclimation, reef coral, spur-and-groove

Functional Ecology (2003) **17**, 246–259

Introduction

Light is the key source of energy for reef-building, zooxanthellate corals (Muscatine 1990). The high gross productivity of coral reefs (see review by Hatcher 1990) is, in part, attributable to the high irradiances in shallow oceanic waters. Numerous studies have focused on the role of light in the photophysiology and energetics of reef corals (Falkowski *et al.* 1984; Spencer-Davies 1991; Hoegh-Guldberg & Jones 1999; Anthony & Fabricius 2000; earlier studies reviewed by Falkowski, Jokiel & Kinzie 1990; Muscatine 1990). Common to most studies, however, is the notion that light and associated responses of coral photosynthesis and growth vary mainly with depth (Chalker, Dunlap & Oliver 1983; Oliver, Chalker & Dunlap 1983; Barnes & Chalker 1990) or turbidity (Anthony & Fabricius 2000; Anthony, Connolly & Willis 2002).

The often complex architecture of coral reefs produces a diversity of light microhabitats within distances of only one to a few metres, for example beneath tabular corals (Sheppard 1981), in cavities (Dinesen 1983), and at sites near steep slopes and under overhangs (Brakel 1979). Based on similarities in spatial complexity, the light variation in reef environments may be analogous to that of forest habitats. Plants

†Author to whom correspondence should be addressed. E-mail: kenneth.anthony@jcu.edu.au

© 2003 British Ecological Society

in canopy gaps and in the understorey can often be characterized as either sun or shade plants, displaying physiological as well as morphological adaptations (or acclimations) to their light environment (reviewed by Chazdon *et al.* 1996; Lambers, Chapin & Pons 1997). Whereas photophysiological and morphological responses to microsite light variation are well established for plants, little is known about the temporal and spatial profile of irradiances in structurally complex reef habitats, and what the implications are for the physiology and energetics of coral symbioses.

Species of plants, corals and macro-algae that occur in a wide range of light habitats are faced with contrasting photophysiological challenges. For example, the growth of plants in forest understoreys (review by Chazdon *et al.* 1996) and of phototrophic corals in shaded (review by Muscatine 1990) or turbid (Anthony & Fabricius 2000) reef habitats may be limited by light availability. Conversely, in open forest gaps (Kitao *et al.* 2000) or on reef crests (Hoegh-Guldberg & Jones 1999; Jones & Hoegh-Guldberg 2001), high irradiances may cause photoinhibition or photodamage. Given that light limitation and light stress are both likely to influence key fitness components such as growth and reproduction, plasticity in light responses is likely to have a selective advantage for coral species with wide light-habitat distributions. For instance, species that are able to occupy extreme low or high light regimes may have reduced competition in those habitats. Also, a greater physiological tolerance of light-habitat dynamics (e.g. after physical disturbances) will increase the physiological potential for colonization of newly formed light gaps.

We investigated the microhabitat light variation in a reef groove environment and the associated variation in growth characteristics (tissue and skeletal thickness), photophysiology and respiration of hermatypic corals, using the common species *Montipora monasteriata* as a case study. The foliaceous (plate-like) growth form of this species allows comparison of the roles of tissue thickness and photopigment concentration in light capture, and of the photosynthetic capacity of corals and plants. First, we characterized the light regimes within a groove habitat to allow comparison with light regimes of contrasting light environments in other habitats, for example forest gaps and understoreys. Second, we investigated the implications of such contrasting habitats for the energetics of *M. monasteriata*, and to what degree corals can photoacclimate to changes in growth irradiance. Specifically, we tested the hypothesis that corals in groove habitats display morphological and physiological adjustments to spatial variation in light regimes by varying the thickness and composition of the tissue layer and parameters of the net photosynthesis–irradiance (P–I) curve. Such a pattern would be consistent with that found in forest gaps and understoreys, where plants generally exhibit light acclimation via two mechanisms: changes in leaf anatomy (e.g. thickness); and physiological and biochemical changes in cells and chloroplasts (e.g. Chazdon & Kaufmann 1993).

Materials and methods

STUDY SITES

The field work was conducted in reef grooves along the northern front of Wistari Reef (Fig. 1a) near Heron Island in the southern section of the Great Barrier Reef (23°27′S, 151°54′E). Reef habitats along north-facing reef slopes were chosen because they are likely to display the highest variation among light microhabitats during the day. Specifically, the orientation of groove walls and overhangs is perpendicular to the path of the sun, shading west-facing groove walls in the morning and east-facing walls in the afternoon. The depth within the grooves was 2–4 m below the lowest astronomical tide (3 m tidal range) and the width of the groves ranged from 3 to 6 m. Based on an initial survey of light regimes and coral distributions within five groove systems, the one that represented most microhabitat characteristics of all grooves was selected for further study (Fig. 1).

LIGHT MEASUREMENTS

To characterize the variation in light regimes within the groove during the day, a set of five light loggers (392, Dataflow Systems, Cooroy, Australia) with cosine-corrected PAR sensors (400–700 nm wavelength) were deployed along a transect running east–west across the groove floor (Fig. 1b). All sensors had been calibrated under water against a manufacturer-calibrated quantum sensor (Li 192s, LiCor, Lincoln, NE, USA). All sensors were placed next to specimens of *M. monasteriata* (except in the western cave which was without scleractinian corals) with the sensor orientation similar to that of the colony surface. The orientation of colonies was generally horizontal in open habitats and vertical in cave habitats (Fig. 1c), indicating the predominant direction of incident light in those microhabitats. Thus two loggers were placed horizontally (sensor pointing outwards) in a west- or east-facing cave (loggers A and E, Fig. 1b). Two loggers were placed under the edge of overhangs in the eastern and western side of the groove (loggers B and D), and one logger was placed in the centre of the groove (logger C). For comparison, a logger was also deployed in open habitat 10 m away from the slope at 5 m depth (logger F, not shown). The loggers were deployed for 9 days (11–19 January 2001) during which they stored integrated records of irradiance every 5 min.

STUDY SPECIES AND CORAL SAMPLING

One of the most prevalent corals in the spur-and-groove systems of Wistari Reef is *Montipora monasteriata* (Forskål 1775), a species that forms plating colonies

© 2003 British Ecological Society,

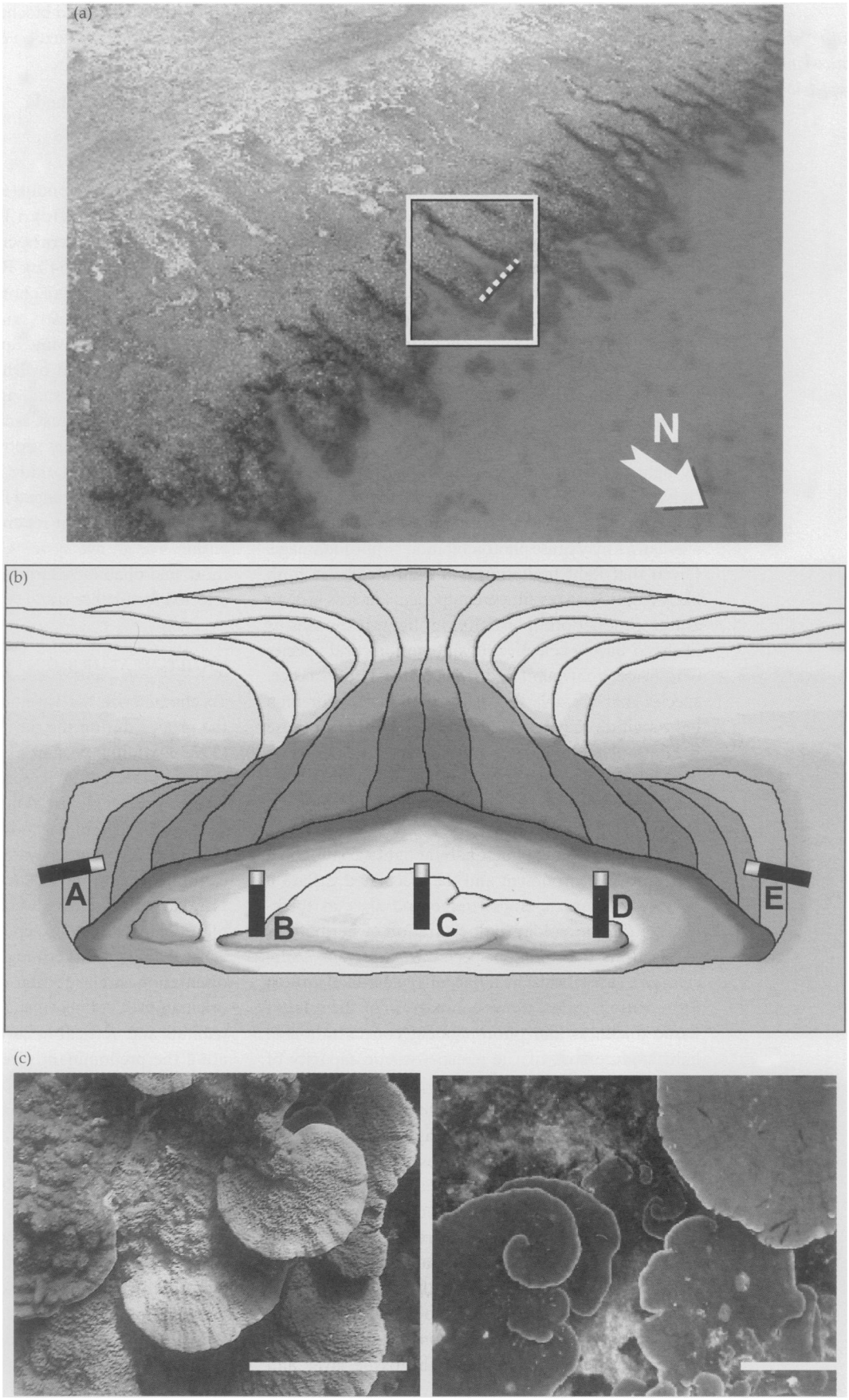

Fig. 1. (a) Aerial photograph of the northern front of Wistari Reef, southern Great Barrier Reef, Australia. Inset shows main study site with the location of the logger transect (approximately 6 m long). (b) Schematic profile of reef groove at Wistari Reef, indicating the spatial arrangement of loggers. (c) *Montipora monasteriata* growing on the walls of the eastern wall of a typical groove (left panel, vertical orientation) and in open habitats (right panel, horizontal orientation). Scale bar ≈ 20 cm in both panels.

© 2003 British Ecological Society,

up to 50 cm in diameter. *Montipora monasteriata* is common throughout the Indo-Pacific (Veron 1986) and is found in most reef microhabitats. To determine the photophysiological responses, tissue components and growth characteristics of *M. monasteriata* from different light microhabitats, we collected colony fragments (≈8 × 8 cm, using bone-cutters) from habitats within the groove. Three habitats could be defined: (a) open habitats, which were free from any shading by the walls of the groove; (b) overhangs, which were sites directly underneath the edge of the shelf-like overhang of the groove walls; and (c) caves, which were sites under the overhangs and were permanently shaded.

PHOTOPHYSIOLOGICAL RESPONSES

To determine *P–I* response curves of *M. monasteriata* from the groove habitats, oxygen-respirometry runs were conducted in the laboratory at Heron Island Research Station under two metal halide lamps (each 400 watts, EYE, Japan) using a system with six closed chambers. Individual chambers (35 cm long, 11 cm wide, 8 cm high) were designed as flumes and produced a unidirectional flow of 5–6 cm s^{-1}. The system was submerged in a jacket of running seawater to buffer temperature fluctuations and to allow periodic flushing of chambers (4 min flushing between every 20 min recording interval). The chambers were fitted with Clark-type oxygen electrodes connected to a signal conditioner (Cheshire Systems, Adelaide, Australia) and a logger (DataTaker 50, Chesterland, Ohio, USA). To control for photosynthesis and respiration of biofilm and micro-organisms, two chambers in each run were left empty.

Irradiance was adjusted by elevating or lowering the lamps, exposing the corals to 10 irradiances for 24 min each (ranging from 0 to 1300 μmol photons m^{-2} s^{-1}). Each respirometry run started with a dark incubation at 7:00–8:00 am using fully dark-adapted corals, through stepwise increasing irradiance, and concluded with a dark incubation at 02:00–03:00 pm following exposure to maximum irradiance. The second dark incubation was used to examine the effect of high irradiance on animal host respiration (R'_{dark}). We assumed that the increase in coral metabolism due to its immediate light history would persist for at least 20 min (the duration of each recording window) after the light was turned off.

To normalize *P–I* curve parameters to colony surface area, all colonies (and a ruler for scale) were photographed using a digital camera (Sony DSC-P1). Surface areas were determined from the digital images using the software package Mocha (Jandel Scientific, San Rafael, CA, USA). Each coral was then wrapped in foil and frozen at –70 °C for later morphometrical and biochemical analysis. *P–I* curve parameters and associated standard errors were estimated by fitting the model (Jassby & Platt 1976)

$$P_n = P_{max} \tan h \frac{\alpha I}{P_{max}} + R_{dark} \qquad \text{(eqn 1)}$$

to the net photosynthesis-irradiance dataset using iterative non-linear estimation (Statistica 1999). P_{max} is the maximum rate of photosynthesis (gross); α is the initial slope of the *P–I* curve (a proxy for quantum yield); and R_{dark} is the rate of respiration at night. In addition, subsaturation irradiance (I_k) was calculated as $I_k = P_{max}/\alpha$. Standard errors for parameters in each individual curve fit were <10% of the parameter estimates, and were not included in the calculation of standard errors for each coral group.

PHOTOSYNTHETIC CARBON GAIN

Daily rates of net photosynthesis (P_{nD}, a proxy for carbon balance) were estimated by integrating hourly rates of net photosynthesis (equation 2) over the day, using the 9-day light data for cave west and central groove. Because *M. monasteriata* rarely extends its polyps, we assume that it relies on a minimal amount of heterotrophy and thus that its carbon acquisition is mainly governed by phototrophy. However, excretion can represent a substantial carbon loss (Crossland 1987), and P_{nD} may thus underestimate the carbon balance. P_{nD} was calculated as

$$P_{nD} = \frac{1}{9} \sum_{t_d=1d}^{t_d=9d} \sum_{t_h=1h}^{t_h=24h} \left[P_{max} \tan h \frac{\alpha I_{(t)}}{P_{max}} + R_{dark} \right], \qquad \text{(eqn 2)}$$

where t_h and t_d are time in hours and days, respectively. Note that irradiance is here parameterized by time of day. To compare the relative importance of each *P–I* curve parameter with respect to its regulatory effect on the daily net photosynthesis (P_{nD}) in each habitat, we subjected equation 2 to a series of sensitivity analyses. Briefly, sensitivity was determined as the relative change in P_{nD} caused by a 10% change in a given parameter, while other parameters were kept constant.

TISSUE AND SKELETAL PROPERTIES

For protein analysis, a frozen subsample (2–3 cm^2) of each colony was solubilized in 10 ml 1 M NaOH at 90 °C for 1 h. Subsamples (0·1 ml) of the slurries were assayed for protein (DC protein assay kit, Bio-Rad Laboratories, Regents Park, NSW, Australia) using bovine serum albumin (Bio-Rad) as a standard. Absorbances were measured at 750 nm wavelength in a spectrophotometer (Agilent 8453, Agilent Technologies, Palo Alto, CA, USA). The surface areas (polyp side only) of the remaining skeletal fragments from the protein assay (and the assays below) were determined by foil wrapping (Marsh 1970).

Chlorophyll was extracted from coral samples (≈4 cm^2) in darkness using cold (4 °C) acetone (100%) during three consecutive extractions, each of 4–6 h duration. Absorbances were determined at 630 and

© 2003 British Ecological Society,

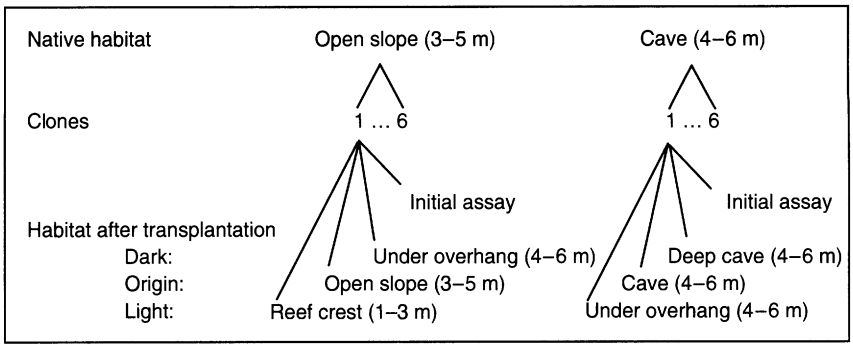

Fig. 2. Experimental design of the 3-week transplantation experiment for *Montipora monasteriata* between light environments in a groove at Wistari Reef. The light environments of the five different habitats are depicted in Fig. 3. In each habitat, six fragments from the different clones were attached to racks. In addition, one fragment from each clone was transplanted to the reef substrate in either the shaded or open habitat to control for effects of rack.

663 nm, and chlorophyll *a* concentrations were calculated using the formula of Jeffrey & Humphrey (1975).

To determine concentrations of zooxanthellae per unit surface area, the tissue of coral samples was separated from the skeleton using an airbrush connected to a reservoir of filtered (0·45 μm) seawater. A 5% buffered formalin solution (4–6 ml) was added to the resulting homogenate (20–30 ml). The concentration of zooxanthellae was measured using a haemocytometer and 10 replicate cell counts per sample. The counts were adjusted to sample volume and normalized to cm^2 colony surface area.

To examine morphological mechanisms of photoacclimation, the thickness of the skeletal plates of coral samples was determined under a dissecting microscope fitted with an eyepiece graticule. Three replicate points were measured along the broken edge approximately 2 cm from the leading edge of the coral colony, the latter to standardize thickness comparisons. Skeletal density (ρ_S) was estimated as the ratio of skeletal dry weight to skeletal volume (Anthony *et al.* 2002) using fragments from each coral from the assays above.

TRANSPLANTATION EXPERIMENT

To investigate photoacclimative responses in *M. monasteriata* from contrasting light habitats, a transplantation experiment between shaded (cave and overhang) habitats and open groove habitats was conducted. Four large fragments (approximately 10 × 10 cm) were cut from each of six clones in both cave and open habitats (total of 48 fragments). One fragment from each clone was used for initial photophysiology assays in the laboratory (see below). The remaining fragments were then transplanted to three habitats: a less-shaded habitat; a more shaded habitat; and their native habitat as control (Fig. 2). A full reciprocal transplantation between light extremes was avoided because such transitions are unlikely to occur naturally. For attachment, a 3–4 mm hole was drilled (underwater) in one corner of each coral colony, which was then secured with cable ties to a PVC rack fixed horizontally to a concrete block. The orientation of the coral colonies was kept similar to that of conspecifics growing naturally in each habitat (horizontal in open habitats, vertical in caves). To control for effects of manipulation, additional coral fragments were transplanted back to the reef substrate.

As a measure of state of photoacclimation, corals were assayed for apparent electron transport rates (apparent ETR) as a function of irradiance. Apparent ETR *vs I* curves provide a proxy for *P–I* curves, but do not allow direct comparison with these (Maxwell & Johnson 2000). Corals were assayed for apparent ETR using a pulse amplitude modulation (PAM) chlorophyll fluorometer (Diving PAM, Walz, Effeltrich, Germany) in the laboratory. In addition, maximum quantum yield (F_v/F_m, dark-adapted) was determined to assess whether photosystem II was adversely affected by the treatments (Hoegh-Guldberg & Jones 1999). Assays were conducted under the same light set-up and protocol as described above for the respirometry runs. To provide a pretransplantation baseline, one fragment per clone (total of 12) was assayed in the laboratory on day 1 (Fig. 2); and to test for treatment effects all transplanted corals and controls (total of 48) were assayed in the laboratory on day 21.

STATISTICAL ANALYSES

Confidence intervals for daily, net rates of photosynthesis (P_{nD}, equation 2) were estimated by Monte Carlo simulations of P_{nD} using the 9-day irradiance dataset and the means and standard deviations of individual *P–I* curve parameters. Briefly, at hourly time stamps, a random-normal generator (programmed in MatLab 5·11) sampled randomly from within the normal distribution defined by the mean and standard deviation for each of the *P–I* curve parameters for corals from each of the groove habitats. The hourly outputs were then entered sequentially into equation 2 to produce one replicate estimate of P_{nD}, and the procedure was repeated 500 times to estimate standard deviation.

© 2003 British Ecological Society,

Table 1. Daily irradiances at five different locations within a reef groove and on an open slope on the northern side of Wistari Reef (southern Great Barrier Reef)

	Light regime (mol photons m^{-2} day^{-1})			
Habitat	Logger	Mean	SE of 9 days	Percentage of central groove
Cave east	A	0·2	0·01	1·1
Cave west	E	0·9	0·04	4·7
Overhang east	B	7·3	0·37	40·4
Overhang west	D	6·0	0·35	33·1
Central groove	C	18·4	0·55	100
Open slope	F	14·3	0·51	78·8

Estimates based on accumulated 5 min records between January 10 and 19 2001.

Results

LIGHT ENVIRONMENT

The daily, integrated irradiance in the two caves was only 1–5% of that in the central part of the groove (Table 1; Fig. 3). No zooxanthellate corals were found near the light logger in the darkest cave (logger A, Fig. 1); and logger E represented the darkest habitat that sustained colonies of *M. monasteriata*. Corals under overhangs at the entrance to caves, on the other hand, received 30–40% of corals in the open (central groove) habitat. In addition to general shading, the low irradiance in caves and under overhangs was also due to shorter day-lengths (≈50%) because direct irradiance occurs only in the morning for east-facing caves or in the afternoon for west-facing caves (Fig. 3). The surface irradiance during the 9-day period was typical for summer in the region, based on insolation data from the AIMS weather station on Great Keppel Island (23°09′S, 150°56′E, ≈100 km north-west of Heron Island).

EFFECTS OF LIGHT REGIME ON TISSUE AND SKELETAL PROPERTIES

Specimens of *M. monasteriata* in the contrasting light habitats differed strongly in biomass per unit surface area, chlorophyll *a* per unit biomass, zooxanthella density per unit biomass, and colony plate thickness (Table 2). Most notably, the surface-specific mass of protein of colonies in cave microhabitats was only half that of colonies in open habitats and around 60% that of corals under overhangs. Also, the plate thickness of colonies in caves and under overhangs was 40–60% that of colonies in the open groove habitat. (Plate thickness under overhangs did not differ significantly from those in open habitat.) The densities of skeletal plates in all three habitats, however, were almost identical (Table 2), and concentrations of chlorophyll *a* and zooxanthellae did not differ significantly between

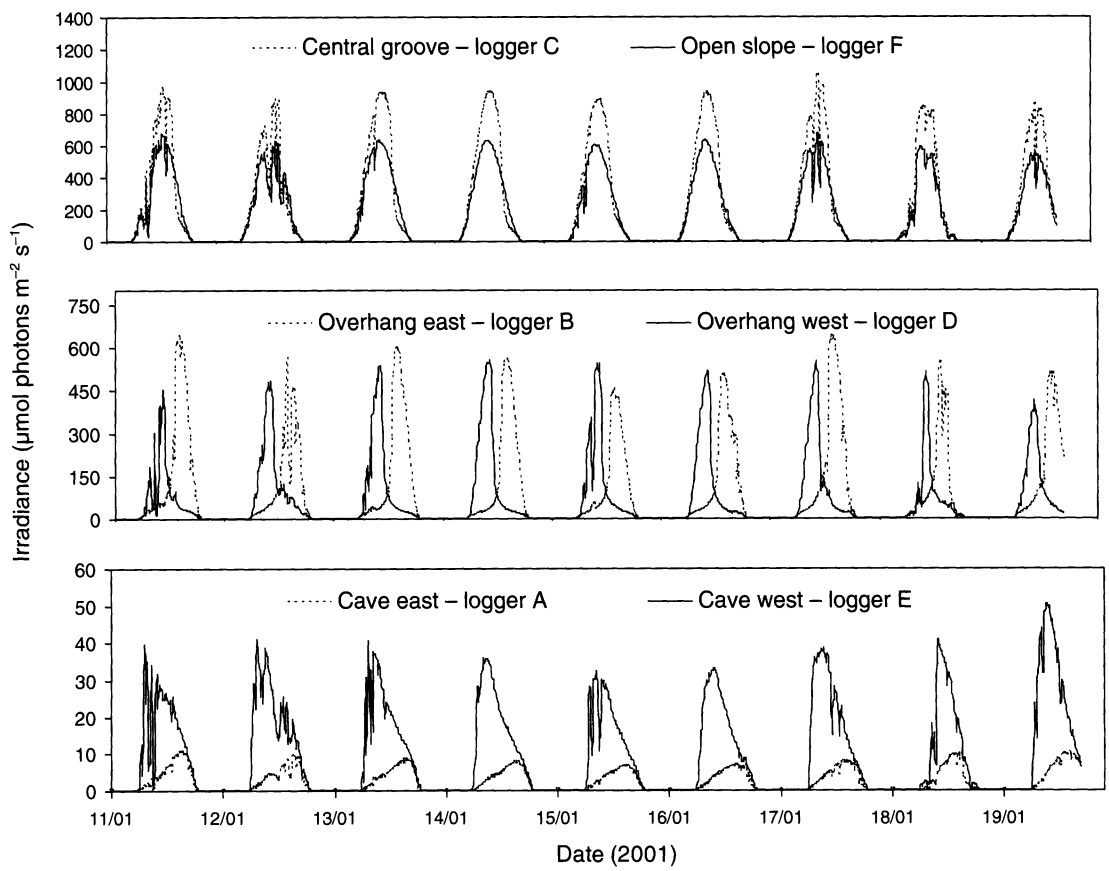

Fig. 3. Daily irradiances at five different positions within a groove environment on the north slope/crest of Wistari Reef on the southern Great Barrier Reef. Note the different scales on *y* axes.

© 2003 British Ecological Society,

© 2003 British Ecological Society,
Functional Ecology, 17, 246–259

Table 2. Estimates of photosynthetic, tissue and skeletal parameters for *Montipora monasteriata* sampled from open (op), overhang (oh) and cave (c) habitats in a reef groove at Wistari Reef; also shown are the results of one-way ANOVAs for comparisons of parameter values between habitats

	Open			Overhang			Cave					
Response parameter	Mean	SE	*N*	Mean	SE	*N*	Mean	SE	*N*	*F*	*P*	*Post hoc* test
Tissue composition and growth characteristics												
Protein (mg cm^{-2})	6·86	0·59	9	5·69	0·75	8	3·46	0·42	8	8·29	0·002**	oh > ca, op > ca
Chlorophyll *a* (μg cm^{-2})	35·0	4·03	9	36·6	3·44	8	41·2	4·49	8	0·64	0·537 NS	
Ratio of chlorophyll *a* to protein (μg mg^{-1})	5·34	0·63	9	7·66	1·60	8	14·1	3·03	8	9·70‡	<0·001***	ca > oh, ca > op
Zooxanthella concentration (10^6 cells cm^{-2})	1·56	0·14	8	2·00	0·21	8	1·61	0·20	8	1·75	0·200 NS	
Zooxanthellae per unit protein (10^6 cells mg^{-1})	0·25	0·04	8	0·40	0·06	8	0·58	0·11	7	4·81	0·020*	ca > op
Chlorophyll *a* per zooxanthella (pg)	20·8	1·33	8	19·1	1·92	8	22·0	2·03	7	0·71	0·506 NS	
Thickness of skeletal plate 2 cm from edge (mm)	7·12	0·65	9	4·24	0·73	8	2·87	0·33	8	13·4†	<0·001***	op > oh, op > ca
Skeletal density (g cm^{-3})	2·07	0·01	9	2·03	0·02	8	1·98	0·03	8	2·00	0·763 NS	
Photosynthetic parameters												
α (mol O_2 mol $photons^{-1}$)	0·052	0·002	8	0·071	0·010	6	0·096	0·013	8	7·90‡	0·003**	ca > op
α (mol O_2 mg $protein^{-1}$ mol $photons^{-1}$)	0·008	0·001	8	0·015	0·002	6	0·030	0·005	8	23·4‡	<0·001***	ca > oh > op
P_{max} (μmol O_2 cm^{-2} h^{-1})	3·92	0·12	8	3·24	0·40	6	2·74	0·31	8	4·83†	0·020*	op > ca
P_{max} (μmol O_2 mg $protein^{-1}$ h^{-1})	0·60	0·06	8	0·67	0·08	6	0·89	0·16	8	1·89	0·179 NS	
I_k (μmol photons m^{-2} s^{-1})	211	7·88	8	127	3·15	6	80·8	2·85	8	209‡	<0·001***	op > oh > ca
R_{dark} (μmol O_2 cm^{-2} h^{-1})	–1·33	0·13	8	–0·70	0·19	6	–0·43	0·09	7	13·26	0·001***	op > oh, op > ca
R_{dark} (μmol O_2 mg $protein^{-1}$ h^{-1})	–0·21	0·04	8	–0·15	0·04	6	–0·13	0·04	8	1·49	0·251 NS	
R'_{dark} (μmol O_2 cm^{-2} h^{-1})	–1·65	0·12	8	–1·35	0·18	6	–1·21	0·20	8	1·81	0·190 NS	
R'_{dark} (μmol O_2 mg $protein^{-1}$ h^{-1})	–0·25	0·02	8	–0·28	0·04	6	–0·40	0·10	8	1·60	0·227 NS	

Key to symbols: P_{max}, maximum rate of photosynthesis (gross); α, initial slope of the *P–I* curve; I_k, subsaturation irradiance; R_{dark}, rate of dark respiration at night; R'_{dark}, rate of dark respiration following exposure to maximum experimental irradiance (≈1300 μmol photons m^{-2} s^{-1}). Assumptions of normality and variance homogeneity were tested using the Kolmogorov–Smirnov one-sample test and Levene's test, respectively (Sokal & Rohlf 1995).

†Data showed variance heterogeneity regardless of transformation, and were analysed untransformed.

‡Data were log-transformed prior to statistical analyses to remove variance heterogeneity. Means and SEs are untransformed.

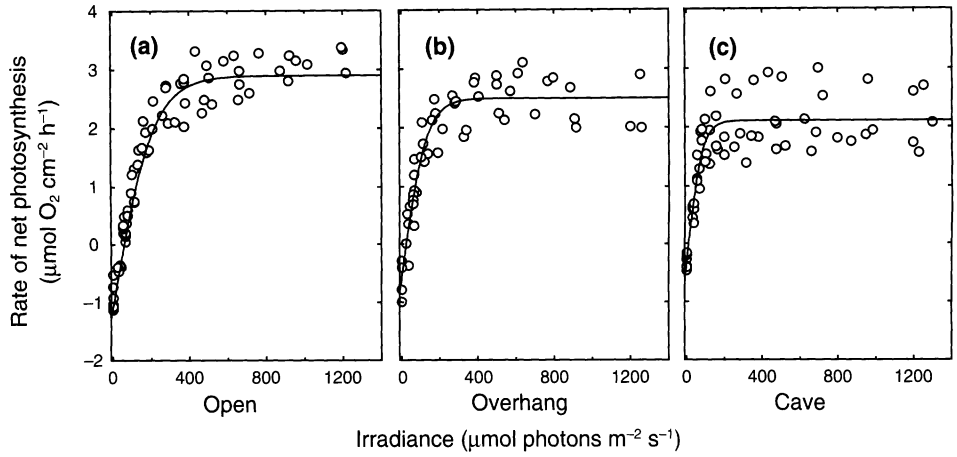

Fig. 4. Photosynthesis–irradiance (*P–I*) curves for *Montipora monasteriata*, indicating the state of photoadaptation of corals from open (a), overhang (b) and cave (c) habitats in a reef groove (Wistari Reef, Great Barrier Reef). Each graph represents six to eight colonies. See Table 2 for comparisons on *P–I* model parameters. The *P–I* model (equation 1) provided a good fit to all data sets (R^2 = 96·4, 86·8 and 79·5% for a–c, respectively).

groups when normalized to surface area. Overall, these results indicate that growth in the shaded microhabitats maximizes the ratio of surface area to coral biomass and skeleton, as well as the content of algae and photopigment per unit biomass, in combination maximizing light interception per unit biomass and per unit mass of photosynthetic pigments.

PHOTOPHYSIOLOGICAL RESPONSES

The P_n *vs* I curves of *M. monasteriata* in cave microhabitats were characteristic of shade-adapted corals, for example with I_k values of around 80 μmol quanta m^{-2} s^{-1} (Table 2; Fig. 4a). For *M. monasteriata* in open habitats, I_k values were approximately 210 μmol quanta m^{-2} s^{-1}, characteristic of light-adapted corals. Under overhangs, I_k values (≈143 μmol photons m^{-2} s^{-1}) were intermediate of those in open and cave habitats (all comparisons significant by ANOVA, Table 2). When normalized to surface area, the apparent quantum yield (α, the initial slope of the *P–I* curve) of colonies in caves (0·168 mol O_2 mg mol $photons^{-1}$) only marginally exceeded that of colonies in open and overhang microhabitats (0·108 and 0·114 mol O_2 mol $photons^{-1}$, respectively). However, per mg protein, α of corals from caves and under overhangs was more than twice that of corals from open habitats. Interestingly, the maximum rate of photosynthesis (P_{max}) varied significantly across habitats when normalized to surface area (from 4·76 to 8·40 μmol O_2 cm^{-2} h^{-1}), but the comparison was not significant for data normalized to protein (from 1·14 to 1·47 μmol O_2 mg $protein^{-1}$ h^{-1}; Table 2).

Area-based rates of dark respiration (R_{dark}, before sunrise) of cave and overhang corals were significantly lower than those of conspecifics from open habitats. However, when normalized to biomass (protein), R_{dark} in cave and overhang corals did not differ significantly. In both cave and overhang corals, rates of dark respiration on exposure to maximum experimental irradiances (R'_{dark}) were about 150 and 100% higher than R_{dark}. In contrast, R'_{dark} of corals in open habitat was only about 40% higher than R_{dark}. Respiration rates of cave and overhang corals thus responded more strongly to maximum irradiances than did those of conspecifics in open habitats. The shapes of the *P–I* curves showed no evidence of photoinhibition in corals from open or overhang habitats, indicated by the net rates of photosynthesis following the predicted asymptote [$P_n = P_{max} - R_{dark}$] for irradiances greater than I_k (Fig. 4b). The cave corals showed some tendency to become photoinhibited at the highest irradiance (Fig. 4c).

Table 3. Monte Carlo estimations of daily rate of net photosynthesis (P_{nD}) ± SD of *Montipora monasteriata* in open, overhang and cave habitats based on 9 days of irradiance records (Fig. 3) and *P–I* curve parameters (Table 2)

Habitat	Surface-specific (μmol O_2 cm^{-2} day^{-1})	Biomass-specific (μmol O_2 mg $protein^{-1}$ day^{-1})
Cave west (logger E)	−0·05 ± 0·99	−0·21 ± 0·24
Overhang east (logger B)	5·46 ± 0·96	0·87 ± 0·23
Overhang west (logger D)	4·49 ± 1·33	0·72 ± 0·23
Central groove (logger C)	6·57 ± 1·28	1·22 ± 0·21

The model was run using equation 2. Cave west was the most shaded habitat in which specimens of *Montipora monasteriata* were found.

DAILY RATES OF NET PHOTOSYNTHESIS

The Monte Carlo estimates of net photosynthesis predicted that the daily photosynthetic carbon gain (P_{nD}) of corals in cave microhabitats was less than 5% that of corals in open habitats (Table 3), suggesting that these corals are at the boundary of their light niche. When normalized to protein, however, P_{nD} of cave corals was around 12% of P_{nD} in open habitats. Simulations using light data from logger A (cave east) produced highly negative estimates of P_{nD}, consistent with the fact that

Table 4. Sensitivities of net photosynthesis (P_{nD}, daily rates) to variation in individual *P–I* curve parameters

	Percentage change in net photosynthesis (P_{nD})		
Parameter*	Cave	Overhang	Open
P_{max}	53	53	64
α	395	40	20
R_{dark}	−453	−87	−77

Sensitivity was determined as the relative change in P_{nD} (equation 2) caused by a 10% increase in a given parameter (P_{max}, α or R_{dark}) while other parameters were kept constant. The 9 day irradiance data sets (Fig. 3) and mean parameter values (Table 2) for each habitat were used as input variables for each sensitivity estimate.
*Normalized to protein.

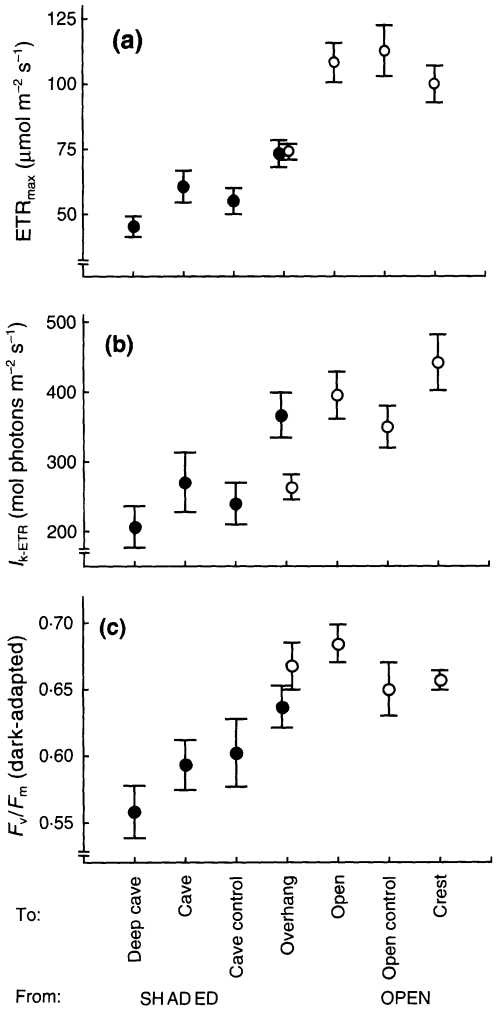

Fig. 5. Effects of habitat shift (increase or decrease in growth irradiance) on photosynthetic parameters of *Montipora monasteriata*. Corals from: ○, open habitats; ●, cave habitats. Effects of transplantation between light microhabitats were tested using a two-way, repeated-measures ANOVA with treatment as the repeated measure (clone fragments distributed to different habitats were dependent samples). See Table 5 for analyses.

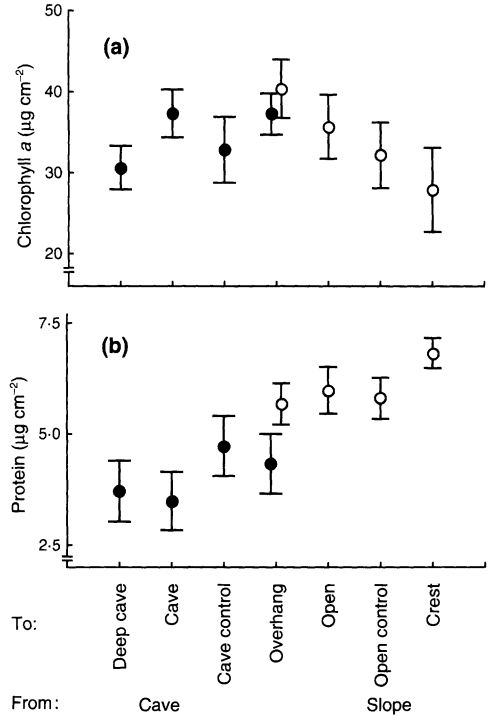

Fig. 6. Effects of habitat shift (increase or decrease in growth irradiance) on area-based chlorophyll *a* and protein content in *Montipora monasteriata*. See Table 5 for analyses and Fig. 5 for keys to symbols.

no hermatypic (photosymbiotic) corals could be found in such dark microhabitats. Surprisingly, P_{nD} under overhangs ranged from 60 to 83% of that in open habitats. The low standard deviation for all estimates of P_{nD} was due, in part, to the low variability in daily irradiance during the 9-day period.

The results of sensitivity analyses indicated that P_{nD} of all coral groups was more sensitive to changes in R_{dark} than to any other *P–I* curve parameter, but more so for corals in caves than for those under overhangs and in open habitats (Table 4). Specifically, a 10% change in R_{dark} of cave specimens produced an almost 10-fold greater effect on P_{nD} than did changes in P_{max}. In contrast, changes in R_{dark} and P_{max} of corals in open habitats produced largely similar effects (although in opposite directions). Also, P_{nD} of the cave corals was highly sensitive to changes in apparent quantum yield (α), whereas the opposite was the case for corals in open habitats.

EFFECTS OF TRANSPLANTATION

Groups of *M. monasteriata* transplanted from cave and open habitats showed acclimation responses mainly through changes in maximum apparent electron transport rate (ETR_{max}) and subsaturation of ETR ($I_{k\text{-ETR}}$, Fig. 5). However, during the 3-week experiment there were no significant changes in chlorophyll *a* content (Fig. 6). Three main points are worth noting. First, the apparent ETR_{max} of corals transplanted from open habitats to under the overhang reached values similar to those of conspecifics transplanted from shaded habitats to under the overhang (comparison not significant by ANOVA, Table 5). Second, the point of subsaturation ($I_{k\text{-ETR}}$) for open-habitat corals

© 2003 British Ecological Society,

Table 5. Results of ANOVA for effects of transplantation on apparent ETR *vs I* curve parameters and tissue properties for *Montipora monasteriata* among light microhabitats within a reef groove (see Fig. 2 for details of design)

	Habitat		Transplantation		Habitat × Transplantation	
	F	*P*	*F*	*P*	*F*	*P*
Response parameters	(1,10)		(3,30)		(3,30)	
ETR_{max} (μmol electrons m^{-2} s^{-1})	32·47	<0·001***	38·96	<0·001***	2·96	0·075 NS
$I_{k\text{-}ETR}$ (μmol quanta m^{-2} s^{-1})	18·91	0·001**	19·33	<0·001***	3·51	0·027*
F_v/F_m (dimensionless)	9·51	0·012*	26·00	<0·001***	4·09	0·032*
Chlorophyll *a* (μg cm^{-2})	0·388	0·547 NS	0·93	0·441 NS	3·14	0·040*
Protein (mg cm^{-2})	21·45	<0·001***	2·76	0·056 NS	0·86	0·475 NS

The factor Transplantation was analysed as repeated measures because specimens transplanted across microhabitats originated from one colony (N = 6 colonies per transplant group). Because one to three control samples were lost from each habitat group, their cells were replaced by the means of the remaining control samples to maintain a balanced design. Degrees of freedom are given in parentheses (effect, error). See Figs 5 and 6 for comparison of transplant groups.
†Data showed variance heterogeneity (Levene's test) regardless of transformation, and were analysed untransformed.

moved to under the overhang was significantly lower than that of cave corals moved to under the overhang (Table 5), signifying overcompensation by the open-habitat corals in terms of photoacclimation. Third, maximum quantum yield (F_v/F_m, dark-adapted) varied significantly between habitat groups and among transplant groups, but there was also significant interaction between these factors (Table 5), the latter indicating that the two groups responded differently to light variation. Specifically, F_v/F_m of open-habitat corals was approximately 20% higher than that of cave conspecifics. However, F_v/F_m of transplanted cave corals was maximized under the overhang (near logger D) and minimized in the darkest cave near logger A (approximately 15% relative decrease), indicating that photosystem II of zooxanthellae in the dark-cave transplants was stressed relative to that of symbionts under the overhang. Conversely, F_v/F_m did not vary significantly among transplant groups in the open habitat.

Within the shaded and open habitat groups, the three photophysiological parameters did not vary significantly among dark cave, cave and control transplants, or among open control and crest. The most shaded group had marginally lower apparent ETR_{max}, $I_{k\text{-}ETR}$ and F_v/F_m than the remaining groups; however, comparisons were not significant by ANOVA. These results indicate, first, that specimens in the most shaded, native cave habitats (near logger E) have limited ability to photoacclimate to further reductions in light regime, but acclimate well to a light increase (cf. gap opening). Second, variations in light habitats in the open regime (except under overhangs) produced only minor variation in photophysiological parameters.

There was no main effect of habitat and transplantation on the concentration of chlorophyll *a* (Fig. 6; Table 5). However, the interaction term for these factors was significant, indicating that the transplantation had different effects on the two groups. Specifically, chlorophyll *a* tended to decrease with an increase in light habitat (overhang to crest habitats) in the open habitat, but was relatively invariant in the shaded regime (overhang to cave habitats). Consistent with the generic open-*vs*-shade comparison above, the protein concentrations of the open-habitat corals were significantly higher than those of the shade-habitat conspecifics, but transplant groups did not vary significantly.

Discussion

The two orders of magnitude lower growth irradiance in cave compared to open microhabitats of the groove environment corresponds to the light attenuation occurring over more than 50 m depth of open water in offshore locations (Kirk 1994). Also, such irradiance variation between the groove microhabitats approximates that found among canopy, gap and understorey in rainforests (Chazdon & Fetcher 1984; Pearcy 1987). Our results suggest that the broad light niche of *M. monasteriata* is a consequence of physiological flexibility and morphological plasticity, consistent with the patterns found for leaves of forest plants in gaps and understoreys (reviewed by Chazdon *et al.* 1996). Combined physiological, cellular and morphological strategies for optimizing light capture in spatially and temporally varying light regimes have been studied extensively in rainforest plants (Oberbauer & Strain 1986; Pearcy 1987; Chazdon & Kaufmann 1993). In corals, previous studies have focused mainly on cellular responses of the symbionts (Chang, Prezelin & Trench 1983; Iglesias-Prieto & Trench 1994).

MORPHOLOGICAL ACCLIMATIONS TO LIGHT HABITAT

Variations in morphological and biochemical characteristics of *M. monasteriata* across groove microhabitats were largely analogous to those reported for sun and shade plants. Specifically, cave specimens had high chlorophyll *a* content per unit biomass and low biomass

© 2003 British Ecological Society,

per unit surface area, and displayed a growth pattern directed towards expanding colony surface area rather than volume (indicated by thin skeletal plates). Also, colonies in caves and under overhangs formed vertical or oblique plates, further maximizing the capture of incident light. Similarly, leaves of shade plants are generally thin, and have a relatively large amount of photosynthetic material and a low proportion of nonphotosynthetic tissue (Chazdon & Kaufman 1993; reviewed by Lambers *et al.* 1997). Further, understorey plants may display leaf orientations that maximize light capture (Takenaka, Takahashi & Kohyama 2001). In contrast to patterns found for chloroplasts in leaves of shade plants (Lambers *et al.* 1997) and zooxanthellae of other species (Chang *et al.* 1983; Porter *et al.* 1984), shaded colonies of *M. monasteriata* in this study did not have a significantly higher chlorophyll *a* concentration per algal cell. Recent studies of cultured zooxanthellae from *Montipora*, however, show only 20% variation in chlorophyll *a* content across a broad range of light regimes (Iglesias-Prieto & Trench 1994). It is possible that different within-colony distributions of zooxanthellae in the two habitats may have masked variations in cellular pigments. Specifically, the undersides of colonies in open habitats had tissue and contained zooxanthellae, but most corals in caves did not. Morphological plasticity to maximize light interception and use has been suggested previously for corals across depth ranges (Barnes 1973), in particular in inshore turbid habitats (Willis 1985). These studies, however, drew inferences from comparisons of colony shape and did not measure photophysiological parameters.

PHOTOSYNTHETIC CHARACTERISTICS ACROSS LIGHT MICROHABITATS

Phototrophic organisms in shaded and semishaded microhabitats, such as reef grooves and forest gaps and understories, are facing two major challenges: maximization of irradiance capture, and protection from short periods of peak irradiances. First, in cave habitats (this study) irradiance is severely reduced throughout the day. This is also true for forest understories, except for the occurrence of sunflecks (Pearcy 1994; Watling *et al.* 1997). To sustain a positive (or zero) energy balance in habitats that are largely permanently shaded, phototrophs must maximize their capture and utilization of weak irradiance and minimize their energy costs (Chazdon & Kaufmann 1993; Mulkey, Wright & Smith 1993). In this study, cave specimens of *M. monasteriata* demonstrated all such responses: thinning and widening of tissue and skeleton normal to the direction of irradiance; a high apparent quantum yield (α); low subsaturation irradiance (I_k); and low rates of dark respiration (R_{dark}). Moreover, on a per-biomass basis, the photosynthetic capacity (P_{max}) of cave corals was slightly higher than that of conspecifics in open habitats, an opposite response to that reported for forest plants (Mulkey *et al.* 1993). Second, for corals under reef overhangs or for plants in forest gaps, the effective day-length may be shortened significantly depending on the orientation of the reef walls relative to the path of the sun (Brakel 1979) or the size of the gap (Chazdon & Fetcher 1984). Under overhangs in the reef groove of this study, the daily light *vs* time profile was compressed to only 2–3 h above the subsaturating irradiances. Photosynthetic responses in such habitats are therefore likely to be a compromise between maximum light capture during the shaded window of the day, and protection from excess light during the unshaded window. The lack of photoinhibition at irradiances up to 1300 μmol m^{-2} s^{-1} in specimens from under overhangs (Fig. 4b) suggests that these corals are capable of avoiding photosynthetic stress during short periods of irradiance, allowing a relatively high photosynthetic efficiency (high α, low I_k). As a result, despite 70% lower growth irradiances under overhangs relative to open habitats; the daily rates of net photosynthesis (P_{nD}) in corals under overhangs were 60–83% of those in open habitats.

DAILY RATES OF NET PHOTOSYNTHESIS

Our study is unique in demonstrating that specimens of a photosymbiotic coral species, separated by only a few metres, inhabit light regimes that differ by two orders of magnitude, resulting in contrasting scopes for growth and reproduction. Despite the photophysiological, metabolic and morphological plasticity of *M. monasteriata*, daily rates of net photosynthesis in the most shaded habitats are likely to cover only maintenance costs and a minimal growth rate. Such contrasts in resources and scope for energy investment across a wide niche suggest an opportunistic strategy of habitat use whereby only part of the local population maintains high productivity (open-habitat corals), while the remainder of the population (cave corals) escapes competition at the expense of productivity. Several studies have suggested similar diversification of scope for growth and reproduction within populations of rainforest plants along successional gradients (Strauss-Debenedetti & Bazzaz 1996), but not previously in coral populations.

The results of the sensitivity analyses indicate that a reduced rate of dark respiration (R_{dark}) is the key mechanism for maintaining a positive rate of daily net photosynthesis in shaded and semishaded habitats. Because dark respiration represents a relatively high tax on the daily energy budget of corals with low rates of energy acquisition and/or short periods of irradiance, even a small reduction in the hourly rate of dark respiration has major implications for the energy balance in marginal light habitats. The daily rates of net photosynthesis of corals in caves were also highly sensitive to changes in apparent quantum yield (α), but this pattern was reversed for corals in open habitats and under overhangs. In marginal light habitats such

© 2003 British Ecological Society,

as caves, mechanisms for downregulating dark respiration and maximizing photosynthetic efficiency are thus likely to be more critical for coral energetics than mechanisms for maximizing P_{max}. The lower area-based R_{dark} of corals in caves and under overhangs was largely explained by their lower tissue mass (60% protein relative to the open-habitat conspecifics), as also found for shade plants (Chazdon & Kaufmann 1993). Other factors explaining the lower dark respiration of shaded corals are their thinner tissue layer and lower levels of respiratory substrate (e.g. glycerol translocation from zooxanthellae to host), and lower growth rates, analogous to the pattern found in vascular plants (Lambers *et al.* 1997). The greater increase in rate of respiration by corals from caves and overhangs following exposure to high irradiance may indicate a high capacity for metabolic activity or growth once irradiance increases. Such light-induced metabolic activity has been observed for plants in forest understoreys following the opening of tree-fall gaps (Strauss-Debenedetti & Bazzaz 1996), and may also, tentatively, facilitate rapid growth following disturbances that enhance the local light regime (e.g. gap openings) in coral reef habitats (Stimson 1985). It is likely, however, that the strong light response of respiration rates in shade corals represents a stress response by both zooxanthellae and coral host, in that maximum experimental irradiance was several-fold that experienced naturally by the cave corals.

ACCLIMATION TO CHANGE IN LIGHT MICROHABITAT

The results of the transplantation from shaded to semi-open habitat illustrated a high capacity in *M. monasteriata* to acclimate to upshifts and downshifts in growth irradiance such as those likely to occur following physical disturbances on reefs (Stimson 1985) or resulting from competition for space (Lang & Chornesky 1990). Specimens transplanted from open habitats to underneath the overhang (about 70% reduction in growth irradiance) acclimated fully within 3 weeks of transplantation. [We argue that, based on the results of previous transplantation experiments across light regimes (Anthony & Hoegh-Guldberg 2003), 3 weeks is ample time for full biochemical photoacclimation to occur.] Most notably, colonies from the open habitat reached significantly lower points of subsaturation ($I_{k\text{-ETR}}$) than did colonies transplanted from caves to under the overhang (Fig. 5; Table 5), indicating different photoacclimative responses following upshifts or downshifts in growth irradiance. The relative overcompensation of $I_{k\text{-ETR}}$ by cave specimens moved out under overhangs is likely to signify a protective mechanism against photodamage during peak irradiances. Conversely, the relatively large reduction in $I_{k\text{-ETR}}$ of specimens transplanted from the open habitat to underneath the overhang may indicate an adaptive mechanism to offset energy deficits. Based on the respirometry results, predicted $I_{k\text{-ETR}}$ for overhang corals would be intermediary between cave and open-habitat corals. The difference in acclimated $I_{k\text{-ETR}}$ of the two groups under the overhang cannot be explained by differences in tissue thickness, as the relatively thick tissue of open-habitat corals would counteract a reduction in their I_k, and area-based protein did not change significantly during the experiment. The latter is expected, given the relatively short duration (3 weeks) of the experiment. Further, the hypothesis that differences in $I_{k\text{-ETR}}$ were attributable to differences in symbiont taxonomy (Iglesias-Prieto & Trench 1994) could not be supported in this study, as symbionts of all coral samples belonged to the same clade (C17 of *Symbiodinium* sp., T. LaJeunesse, unpublished results). Colonies of *M. monasteriata* found in their most shaded microhabitat (western cave) showed only limited acclimation to further reduction in growth irradiance, as indicated by a lack of change in $I_{k\text{-ETR}}$. Also, the slight reductions (≈15%) in maximum electron transport rate, maximum quantum yield and concentrations of chlorophyll *a* collectively indicate a degree of photosynthetic stress induced by light limitation. Conversely, colonies moved from open-slope habitat to reef crest showed a slight increase in $I_{k\text{-ETR}}$ (relative to open-habitat controls), signifying photoacclimation to increased growth irradiance.

In conclusion, these results demonstrate that the habitat distribution of *M. monasteriata* in spur-and-groove reef environments spans a continuum from extreme low- to high-light environments, analogous to the habitat distribution of some plant species in forest gaps and understories. The wide light niche of *M. monasteriata* is facilitated by physiological as well as morphological acclimations, but results in contrasting scope for growth across light environments. The capacity of cave specimens to acclimate well to increasing irradiances (and to respond to high irradiance by increased metabolism) suggests that *M. monasteriata* may share the strategy of understorey plants that rely on future opportunities to invade more favourable habitats (Strauss-Debenedetti & Bazzaz 1996). The adaptive significance of extreme niche widths for the population biology of corals is unclear and deserves further attention.

Acknowledgements

This study was funded by the Australian Research Council (grant no. A00105071 to K.R.N.A. and A10009109 to O.H.G.). We thank Roberto Iglesias-Prieto, Ross Jones, Pia Anthony and Melissa Varoy for their critical reading and valuable comments. This is contribution number 71 of the Centre for Coral Reef Biodiversity at James Cook University.

References

Anthony, K.R.N. & Fabricius, K.E. (2000) Shifting roles of heterotrophy and autotrophy in coral energetics under

varying turbidity. *Journal of Experimental Marine Biology and Ecology* **252**, 221–253.

Anthony, K.R.N. & Hoegh-Guldberg, O. (2003) Kinetics of coral photoacclimation. *Oecologia* **134**, 23–31.

Anthony, K.R.N., Connolly, S.R. & Willis, B.L. (2002) Comparative analysis of tissue and skeletal growth in corals. *Limnology and Oceanography* **47**, 1417–1429.

Barnes, D.J. (1973) Growth in colonial scleractinians. *Bulletin of Marine Science* **23**, 280–298.

Barnes, D.J. & Chalker, B.E. (1990) Calcification and photosynthesis in reef-building corals and algae. *Ecosystems of the World: Coral Reefs*, Vol. 25 (ed. Z. Dubinsky), pp. 109–131. Elsevier, Amsterdam.

Brakel, W.H. (1979) Small-scale spatial variation in light available to coral reef benthos: quantum irradiance measurements from a Jamaican reef. *Bulletin of Marine Science* **29**, 406–413.

Chalker, B.E., Dunlap, W.E. & Oliver, J.K. (1983) Bathymetric adaptations of reef-building corals at Davies Reef, Great Barrier Reef, Australia. II. Light saturation curves for photosynthesis and respiration. *Journal of Experimental Marine Biology and Ecology* **73**, 37–56.

Chang, S.S., Prezelin, B.B. & Trench, R.K. (1983) Mechanisms of photoadaptation in three strains of the symbiotic dinoflagellate *Symbiodinium microadriaticum*. *Marine Biology* **76**, 219–229.

Chazdon, R.L. & Fetcher, N. (1984) Photosynthetic light environments in a lowland tropical rainforest in Costa Rica. *Journal of Ecology* **72**, 553–564.

Chazdon, R.L. & Kaufmann, S. (1993) Plasticity of leaf anatomy of two rain forest shrubs in relation to photosynthetic light acclimation. *Functional Ecology* **7**, 385–394.

Chazdon, R.L., Pearcy, R.W., Lee, D.W. & Fetcher, N. (1996) Photosynthetic responses of tropical forest plants to contrasting light environments. *Tropical Forest Plant Ecophysiology* (eds S.S. Mulkey, R.L. Chazdon & A.P. Smith), pp. 5–55. Chapman & Hall, London.

Crossland, C.J. (1987) *In situ* release of mucus and DOC-lipid from the coral *Acropora variabilis* and *Stylophora pistillata*. *Coral Reefs* **6**, 35–42.

Dinesen, Z.D. (1983) Shade dwelling corals of the Great Barrier Reef, Australia. *Marine Ecology Progress Series* **10**, 173–186.

Falkowski, P.G., Dubinsky, Z., Muscatine, L. & Porter, J. (1984) Light and the bioenergetics of a symbiotic coral. *Bioscience* **34**, 705–709.

Falkowski, P.G., Jokiel, P.L. & Kinzie Iii, R.A. (1990) Irradiance and corals. *Ecosystems of the World: Coral Reefs*, Vol. 25 (ed. Z. Dubinsky), pp. 89–107. Elsevier, Amsterdam.

Hatcher, B.G. (1990) Coral reef primary productivity: a hierarchy of pattern and process. *Trends in Ecology and Evolution* **5**, 149–155.

Hoegh-Guldberg, O. & Jones, R.J. (1999) Photoinhibition and photoprotection in symbiotic dinoflagellates from reef-building corals. *Marine Ecology Progress Series* **183**, 73–86.

Iglesias-Prieto, R. & Trench, R.K. (1994) Acclimation and adaptation to irradiance in symbiotic dinoflagellates. I. Responses of the photosynthetic unit to changes in photon flux density. *Marine Ecology Progress Series* **113**, 163–175.

Jassby, A.D. & Platt, T. (1976) Mathematical formulation of the relationship between photosynthesis and light for phytoplankton. *Limnology and Oceanography* **21**, 540–547.

Jeffrey, S.W. & Humphrey, G.F. (1975) New spectrophotometric equations for determining chlorophyls *a*, *b*, *c*1 and *c*2 in higher plants, algae and natural phytoplankton. *Biochemie und Physiologie der Pflanzen* **167**, 191–194.

Jones, R.J. & Hoegh-Guldberg, O. (2001) Diurnal changes in the photochemical efficiency of the symbiotic dinoflagellates (Dinophyceae) of corals: photoprotection, photoactivation and the relationship to coral bleaching. *Plant, Cell and Environment* **24**, 89–99.

Kirk, J.T.O. (1994) *Light and Photosynthesis in Aquatic Ecosystems*, 2nd edn. Cambridge University Press, Cambridge, UK.

Kitajima, K. (1994) Relative importance of photosynthetic traits and allocation patterns as correlates of seedling shade tolerance of 13 tropical trees. *Oecologia* **98**, 419–428.

Lambers, H., Chapin Iii, F.S. & Pons, T.L. (1997) *Plant Physiological Ecology*. Springer, Berlin.

Lang, J.C. & Chornesky, E.A. (1990) Competition between scleractinian reef corals: a review of mechanisms and effects. *Coral Reefs*, Vol. 25 (ed. Z. Dubinsky), pp. 209–252. Elsevier, Amsterdam.

Marsh, J.A. (1970) Primary productivity of reef-building calcareous red algae. *Ecology* **51**, 255–263.

Maxwell, K. & Johnson, G.N. (2000) Chlorophyll fluorescence – a practical guide. *Journal of Experimental Botany* **51**, 659–668.

Mulkey, S.S., Wright, S.J. & Smith, A.P. (1993) Comparative physiology and demography of three neotropical forest shrubs – alternative shade-adaptive character syndromes. *Oecologia* **96**, 526–536.

Muscatine, L. (1990) The role of symbiotic algae in carbon and energy flux in reef corals. *Ecosystems of the World: Coral Reefs*, Vol. 25 (ed. Z. Dubinsky), pp. 75–87. Elsevier, Amsterdam.

Oberbauer, S.F. & Strain, B.R. (1986) Effects of canopy position and irradiance on the leaf physiology and morphology of *Pentaclethra macroloba* (Mimisaceae). *American Journal of Botany* **73**, 409–416.

Oliver, J.K., Chalker, B.E. & Dunlap, W.E. (1983) Bathymetric adaptations of reef-building corals at Davies Reef, Great Barrier Reef, Australia. I. Long-term growth responses of *Acropora formosa*. *Journal of Experimental Marine Biology and Ecology* **73**, 11–35.

Pearcy, R.W. (1987) Photosynthetic gas exchange responses of Australian tropical forest trees in canopy, gap and understory micro-environments. *Functional Ecology* **1**, 169–178.

Pearcy, R.W. (1994) Photosynthetic response to sunflecks and light gaps: mechanisms and constraints. *Photoinhibition of Photosynthesis: from Molecular Mechanisms to the Field* (eds N.R. Baker & J.R. Bowyer), pp. 255–271. BIOS Scientific, Oxford.

Porter, J.W., Muscatine, L., Dubinsky, Z. & Falkowski, P.G. (1984) Primary production and photoadaptation in light-adapted and shade-adapted colonies of the symbiotic coral, *Stylophora pistillata*. *Proceedings of the Royal Society of London Series B* **222**, 161–180.

Sheppard, C.R.C. (1981) Illumination and the coral community beneath tabular *Acropora* species. *Marine Biology* **64**, 53–58.

Sokal, R.R. & Rohlf, F.J. (1995) *Biometry*, 3rd edn. W.H. Freeman, New York.

Spencer-Davies, P. (1991) Effect of daylight variations on the energy budget of shallow-water corals. *Marine Biology* **108**, 137–144.

Statistica (1999) *Release 5.1*. StatSoft Inc., Tulsa, OK, USA.

Stimson, J. (1985) The effect of shading by the table coral *Acropora hyacinthus* on understory corals. *Ecology* **66**, 40–53.

Strauss-Debenedetti, S. & Bazzaz, F.A. (1996) Photosynthesic characteristics of tropical trees along successional gradients. *Tropical Forest Plant Ecophysiology* (eds S.S. Mulkey, R.L. Chazdon & A.P. Smith), pp. 162–186. Chapman & Hall, London.

Takenaka, A., Takahashi, K. & Kohyama, T. (2001) Optimal leaf display and biomass partitioning for efficient light

© 2003 British Ecological Society,

capture in an understorey palm, *Licuala arbuscula*. *Functional Ecology* **15**, 660–668.

Veron, J.E.N. (1986) *Corals of Australia and the Indo-Pacific*, 2nd edn. University of Hawaii Press, Honolulu, Hawaii.

Watling, J.R., Robinson, S.R., Woodrow, I.E. & Osmond, C.B. (1997) Responses of rainforest understorey plants to excess light during sunflecks. *Australian Journal of Plant Physiology* **24**, 17–25.

Willis, B.L. (1985) Phenotypic plasticity versus phenotypic stability in the reef corals *Turbinaria mesenterina* and *Pavona cactus*. *Proceedings of the Fifth International Coral Reef Congress, Tahiti*, Vol. 4, pp. 107–112. Antenne Museum National d'Histoire Naturel, Moorea.

Received 22 July 2002; revised 28 November 2002; accepted 1 December 2002

© 2003 British Ecological Society,