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ORIGINAL PAPER

Variation in colony geometry modulates internal light levels in branching corals, *Acropora humilis* and *Stylophora pistillata*

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Abstract Colonial photosynthetic marine organisms often exhibit morphological phenotypic plasticity. Where such plasticity leads to an improved balance between rates of photosynthesis and maintenance costs, it is likely to have adaptive significance. To explore whether such phenotypic plasticity leads to more favourable within-colony irradiance for reef-building branching corals, this relationship was investigated for two coral species *Acropora humilis* and *Stylophora pistillata*, along a depth gradient representing light habitats ranging from 500 to 25 µmol photons m^{-2} s^{-1}, during 2006 at Heron Island, Great Barrier Reef (23.44°S, 151.91°E). In the present study changes in flow-modulated mass transfer co-varied with light as a function of depth. In low-light (deep) habitats, branch spacing (colony openness) in *A. humilis* and *S. pistillata* was 40–50% greater than for conspecifics in high-light environments. Also, branches of *A. humilis* in deep water were 40–60% shorter than in shallow water. Phenotypic changes in these two variables lead to steeper within-colony light attenuation resulting in 38% higher mean internal irradiance (at the tissue surface) in deep colonies compared to shallow colonies. The pattern of branch spacing was similar for *S. pistillata*, but this species displayed an alternate strategy with respect to branch length: shade adapted deep and cave colonies developed longer and thinner branches, allowing access to higher mass transfer and irradiance. Corals in cave habitats allowed 20% more irradiance compared to colonies found in the deep, and had a 47% greater proportion of irradiance compared to colonies in the shallow high-light environment. Such phenotypic regulation of internal light levels on branch surfaces partly explains the broad light niches of many branching coral species.

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Introduction

Many species of scleractinian coral display intra-specific variation in colony architecture among habitats (Willis 1985; Bruno and Edmunds 1997). Phenotypic plasticity occurs across a range of taxa and it is thought to confer benefits under environmental variability (Via et al. 1995). Light and water flow are important variables for the biology of scleractinian corals as they both affect rates of photosynthesis and respiration (Dennison and Barnes 1988; Patterson et al. 1991). Similar to plants, corals need to manage external irradiance levels to a favourable amount for acquiring sufficient light energy via photosynthesis for survival, growth and reproduction (Chalker et al. 1983; Anthony and Connolly 2004) but avoid higher light levels potentially causing photoinhibition and photo-damage (Brown et al. 1999; Jones and Hoegh-Guldberg 2001; Winters et al. 2003; Hoogenboom et al. 2006). It is common for terrestrial plants to use plant geometry and physiology to optimize their photosynthetic response (reviewed by Herbert 1996). Reef-building corals are found across light habitats (e.g., Goreau 1959; Veron 1995) ranging from extremely shaded cave (Anthony and Hoegh-Guldberg 2003a), deep (Mass et al. 2007) or turbid-water environments (Anthony and Connolly 2004) receiving <50 µmol

photons m^{-2} s^{-1} to shallow-water reef crests exposed to >2,000 μmol photons m^{-2} s^{-1} (Jones and Hoegh-Guldberg 2001). Reef-building corals can acclimatize to sub- or supra-optimal variable light regimes at multiple levels: on a long time scale they can modify their morphology by growing and, over a shorter time, by altering their pigmentation within the host or dinoflagellate. However, it is likely that in extreme shaded habitats corals may be light limited and must supplement their energy requirement with substantial predation (Mass et al. 2007). In resolving the nature of coral photoacclimation, several studies have been concerned with the effects of changes in pigmentation (Dubinsky et al. 1984; Muscatine et al. 1984; Dove et al. 2006) and numerous studies investigated the correlation between colony morphology and ambient light levels (e.g., Dustan 1975; Graus and Macintyre 1976; Jaubert 1981; Graus and Macintyre 1982; Brakel 1983; Dubinsky and Jokiel 1994; Vermeij and Bak 2002; Mass et al. 2007). The few studies that have focused on morphological effects on within-colony light levels have been limited to plating (Anthony et al. 2005; Hoogenboom et al. 2008) and massive (Muko et al. 2000) corals, providing insight into adaptive variation in colony geometry (Hoogenboom et al. 2008). However, to date no studies have examined the relationship between light habitat, colony architecture, and within-colony irradiance budgets in branching corals such as the genus *Acropora* that is the largest group of reef builders and represents >70% of the coral species on Indo-Pacific reefs (Wallace 1999).

Some coral species adopt more "open" geometries in low-light environments, in particular in deep water (e.g., Willis 1985; Titlyanov and Titlyanova 2002; Anthony et al. 2005). Such openness for higher light capture can also facilitate a higher degree of colony convection, improving mass transfer in deep or cryptic, low-flow habitats (Patterson et al. 1991; Bruno and Edmunds 1997, 1998) thereby potentially enhancing rates of photosynthesis (Lesser et al. 1994; Sebens et al. 1997). Conversely, tight packing of colony structures in shallow, high-flow habitats (Helmuth et al. 1997; Sebens et al. 1997) increases self-shading and reduces convection of coral tissues. Higher water flow can also increase contact with particulate matter such as zooplankton for ingestion, (Fabricius et al. 1995; Sebens 1997; Sebens et al. 1997), increase uptake of dissolved nutrients (Atkinson and Bilger 1992; Thomas and Atkinson 1997), and remove sediments from coral surfaces (Rogers 1990). Because light availability as well as flow energy generally both decrease from shallow to deep water, phenotypic changes in coral geometry along light gradients are likely to also favour within-colony flow environments.

Scleractinian corals form a symbiosis with unicellular dinoflagellates that inhabit cells in the coral oral gastrodermis (Muscatine and Porter 1977). Since these symbiotic dinoflagellates are distributed over the entire surface area of the 3D coral architecture, variation in the spacing, angle or length of the structural elements will affect the amount of self-shading, and hence the light regime experienced by different parts of the colony (Anthony et al. 2005). Here, we test the hypothesis that observed variation in the spacing, length and diameter of branches in colonies of two common coral species, *Acropora humilis* and *Stylophora pistillata* along light gradients in situ, represent morphological solutions to achieving physiologically favourable internal irradiances. The two branching species differ in that *Stylophora pistillata* is a highly successful species and is found in a more diverse range of habitats than is *Acropora humilis* (Falkowski and Dubinsky 1981; Veron 2000; Titlyanov et al. 2001; Wolstenholme et al. 2003; Mass et al. 2007). *Stylophora pistillata* also harbors a suite of symbiotic dinoflagellate strains (Sampayo et al. 2007) while *A. humilis* forms a symbiosis with C3 only (LaJeunesse et al. 2004). These attributes may affect the extent of geometric variation capabilities of the two species.

As a theoretical basis for identifying favourable irradiance levels we use the point at which light harvested equals the turnover rate of photosystems, quantified by the subsaturating irradiance, Ek, of the photosynthesis-irradiance relationship (Falkowski and Raven 1997; Anthony and Hoegh-Guldberg 2003b). Based on experimental work with foliose corals (*Turbinaria mesenterina*), Ek at the level of the polyp (i.e. without considering structural self-shading) ranges from 50 to 150 μmol photons m^{-2} s^{-1} (Anthony and Hoegh-Guldberg 2003b).

Analogous to the leaf arrangement in terrestrial plants that affects the light field within the leaf crown (Pearcy et al. 2005), branch-to-branch self-shading in corals is likely to affect internal light fields in the colony. Specifically, reduced branch spacing, thicker branches, and increased branch length all contribute to enhanced colony self-shading. Mechanistically, these geometric changes will narrow the angles of incident light impinging on any given point on the tissue surface (Anthony et al. 2005), effectively causing a steeper light attenuation from the tip to the base of the branch. In high-light environments, tighter packaging of branches can be an advantage because it reduces the amount of tissue surface area subjected to supra-optimal irradiance, potentially leading to photoinhibition. Conversely, greater branch spacing, thinner and shorter branches will increase the angles of incident light reaching further down the branch and reduce self-shading. Here, we will explore the pattern of change in these geometric parameters along a light and mass transfer gradient in situ for *Acropora humilis* and *Stylophora pistillata*, and test whether resulting changes in internal colony light fields have significance for the photophysiology of the coral symbiosis.

Materials and methods

Study site and study species

The present study was undertaken at Heron Island Reef (23.44°S, 151.91°E) on the Southern Great Barrier Reef, Australia. We chose two sites with similar depth (light) range but different flow environments to assess the relative importance of light and mass transfer in driving morphological variation. The low-flow site (Harry's Bommie) is located on the southern, wave-protected side of Heron Reef, whereas the high-flow site (Tenements) is situated on the northern, wave-exposed side. *Acropora humilis* and *Stylophora pistillata* both occur within the depth range 5–18 m at the two sites, with the water column on average attenuating approximately 75% of available light (Fig. 1). Two main light environments were investigated for each site and species distribution: shallow (5 m) and deep (18 m) below lowest astronomical tide. As *S. pistillata* is also abundant under overhangs (with irradiance levels of only 5–10% of those in open shallow habitats, Anthony and Hoegh-Guldberg 2003a) at both Harry's Bommie and Tenements, we included such cave habitats for this species. The two species display different colony morphologies at the two depths and in the cave habitat (Fig. 2).

Environmental irradiance

We estimated the yearly ambient photosynthetically active irradiances (PAR) in the different habitats using underwater light loggers (Odyssey, Z412, Christchurch, New Zealand). The loggers were deployed at 5 and 18 m below lowest astronomical tides (LAT) and in the cave environment at Harry's Bommie and Tenements. They were deployed between 5 November 2005 and 10 November 2006 and recorded mean irradiance from readings taken every second in a 30-min period and the 30-min means were averaged. The cosine-corrected light sensor was calibrated against a manufacturer-calibrated sensor (LI-COR, LI-192S). Mean irradiance was calculated for each day (excluding the dark hours) during the logged period, using only the 7-day period following the cleaning of the sensors once a month.

Flow regime

Flow or mass transfer near the individual coral colonies ($n = 10$ colonies depth^{-1}, site^{-1}) was measured using a plaster-dissolution technique previously applied to subtidal environments (Dennison and Barnes 1988; Jokiel and Morrissey 1993; Kawamata 1998). The protocol of Fulton and Bellwood (2005) was followed to produce the plaster balls and to estimate plaster weight loss as a result of mass transfer. Plaster balls were made by mixing 470 g casting plaster

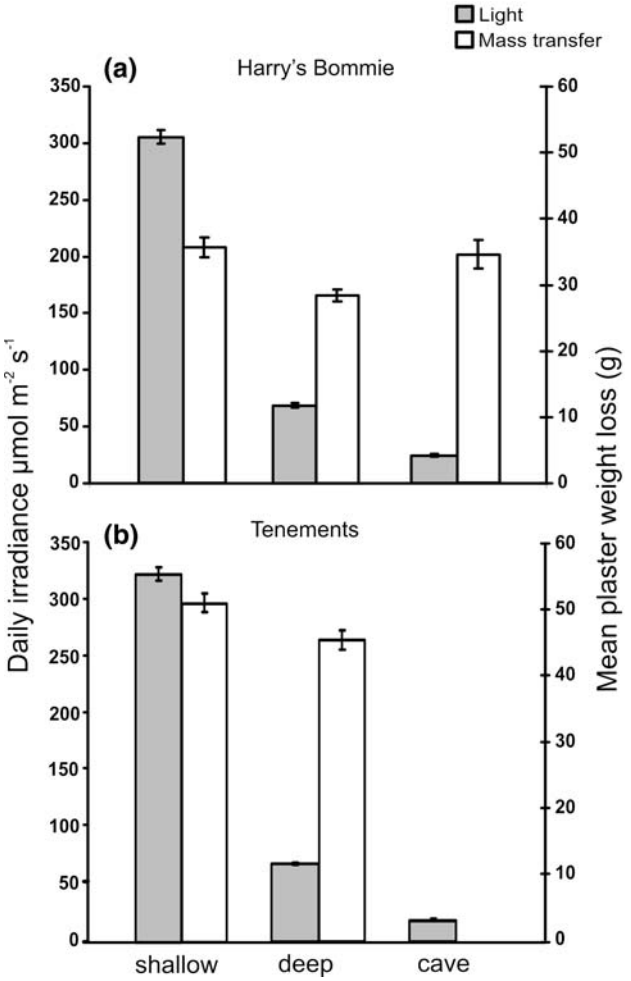

Fig. 1 Differences in ambient daily irradiance µmol m^{-2} s^{-1} and mean plaster weight loss (g) as a function of depth and cave environment at **a** Harry's Bommie and **b** Tenements. *Error bars* represent SE of the mean

(CSR Limited) and 250 g cold water. The mix was poured into spherical moulds made out of tennis balls, and a galvanized wire (210 mm long and 2.5 mm thick) was added as an attachment point. Plaster balls in moulds were left to set for 2 h and then left to dry until repeated weight measurements showed consistency. Plaster balls that were deployed were within the mass range of 117.0 ± 1.0 g, and they were attached upright in the field next to the tagged *Acropora humilis* and *Stylophora pistillata* colonies using the galvanized wire. After a deployment time of 24 h plaster balls were retrieved, left to dry and the final weight was measured. During this 24 h period no plaster ball weight loss exceeded 65% of its original weight. The final weight loss was used as a proxy for the flow regime or mass transfer at sites near the tagged colonies. This was repeated on three occasions (March, July and November) in 2006 to include variability in water motion at each site. A mean plaster weight loss, representing a relative measure of mass

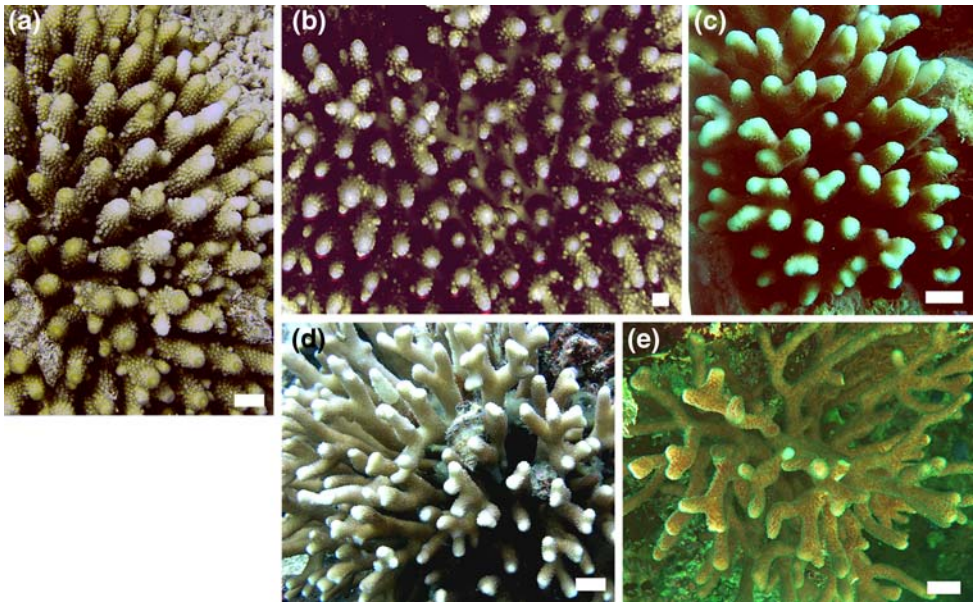

Fig. 2 Type morphologies of the two branching corals in different light habitats (shallow, deep, cave) at Harry's Bommie on Heron Island, GBR. **a** *Acropora humilis* at 5 m (shallow) **b** *Acropora humilis* at 18 m (deep) **c** *Stylophora pistillata* at 5 m (shallow) **d** *Stylophora pistillata* at 18 m (deep) **e** *Stylophora pistillata* at 5 m (cave). *Scale bars* represent 1 cm

transfer or flow energy (Porter et al. 2000) at sites near the coral colonies, was determined by an average of the values from the three different times in 2006.

Colony morphology

Solar radiation distributed along the tissue surface of a branching coral colony is constrained by a suite of variables. For branches found in the central part of a colony, irradiance at points along each branch will depend on: (1) the ambient light field (diffuse vs direct), (2) angles of incident light with respect to vertical and geographical direction, (3) position along the branch and (4) distance to neighboring branches. As the mathematical modeling of light distribution within a branching colony is highly complex, this study approached the problem empirically and focused on three main geometric parameters. Based on light models for foliose corals (Anthony et al. 2005) and studies investigating phenotypic plasticity in branching species as a function of water flow regimes (Bruno and Edmunds 1997; Helmuth et al. 1997; Sebens et al. 1997), we chose branch spacing, length and diameter as the main parameters affecting within-colony light climates, as changes in these three parameters are likely to have effects on self-shading within branching coral colonies.

For each coral species in each habitat ($n = 15$ colonies depth^{-1}, site^{-1}), we tagged coral colonies and measured the lengths and diameters of six central branches and the spacing between six central branch pairs. Because both species display minimal within-colony variation in branch characteristics, six measurements provided good representation of each colony. Also, by using central branches, our measurements represented 70–80% of the colony. In order to minimize variation due to colony size, we only used colonies in the size range 25–35 cm diameter for *A. humilis* and 18–30 cm for *S. pistillata*.

Within-colony light measurements

To characterize irradiance distributions within coral colonies, light attenuation profiles were determined along central branches of the tagged study colonies above. Preliminary analyses indicated that inclusion of peripheral branches in the analysis would only improve colony representation by 30%, and this representation would only strengthen the self-shading trend for shallow colonies and show a profile maximising openness in deep colonies. Five irradiance profiles were measured on each colony and were carried out at mid-day (11:00–14:00 h) on cloudless days. Irradiance (PAR) was measured at 5–8 points down each branch using a cosine corrected quantum sensor with a 2 × 2-mm head at the end of a 1-mm diameter fiber optic cable (Diving-F1, Walz, Germany) connected to a submersible fluorometer (Diving-Pam, Walz, Germany). Incident downwelling irradiance at the branch tip (sensor held horizontally) provided an estimate of environmental (ambient) irradiance and was used as a reference point for attenuation profiles. Five to eight consecutive irradiance measurements were made with the sensor disc held parallel to the tissue surface, the sensor was held by the cable away from the colony as to prevent shading. Light profiles thus represented an integrated "polyp view" of the light distribution within the colony (Anthony et al. 2005). In the absence of a formal theory for light attenuation within branching coral colonies we used linear and exponential empirical best fits to the data.

Data analysis

Effects of habitat (light) and site (flow) on branch spacing, branch length and branch diameter were tested using a two-way analysis of variance (ANOVA). Similarly, variations in irradiance and flow among habitats were tested using a two-way analysis of variance (ANOVA). Data were tested for normality and homogeneity of variance, and data were transformed where these assumptions were violated. Non-parametric equivalents of tests were used in cases where assumptions were violated despite transformations. Non-linear estimation was used to determine rate of within-colony light attenuation. Irradiance attenuation profiles within colonies were analysed using non-linear regression, and performed using STATISTICA 7.0 (StatSoft Inc). The attenuation model that provided the best fit was used (mean ± SE of model coefficients) to generate light distributions over branch surfaces for the different coral morphologies and in the different light habitats through Monte Carlo simulations using Excel (Microsoft Inc.) and Pop tools (CSIRO) in which the daily maximum irradiance (mean ± SE) was used as the input variable. The assumptions for the Monte Carlo simulations were that the residuals were normally distributed and that the ratio of direct to diffuse light remained constant over the entire branch surface.

We used maximum rather than average daily ambient irradiance because in shallow water habitats corals are more likely to adjust to the highest and potentially damaging irradiances. Also the maximum daily irradiance can be present for up to 5 h day^{-1}, which is almost half the daily light period. One-way ANOVA and a t-test of light distribution kurtosis were used to determine differences in the PAR distributions over branch surfaces among light attenuation models for both species in all habitats.

Results

Ambient environmental conditions

Irradiance levels varied among deep and shallow habitats (Kruskal–Wallis test, $H_{2,701} = 601.1$, $P < 0.001$). At both sites, the mean daily irradiance at 5 m was 4-fold that at 18 m and 12-fold that in the cave habitat (Fig. 1). The ambient irradiances at the two sites were highly comparable: although mean daily irradiance values in shallow waters at Tenements were slightly higher (<5%) than those at Harry's Bommie (Kruskal–Wallis test, $H_{1,701} = 10.8$, $P < 0.001$) they were within 1% similar in the deep and cave habitats between the two sites (Fig. 1).

Mass transfer, as measured by plaster dissolution, was higher in shallow waters compared to deep waters (two-way ANOVA, $F_{2,78} = 20.5$, $P < 0.001$) and 56% higher at Tenements compared to Harry's Bommie (two-way ANOVA, $F_{1,78} = 238.8$, $P < 0.001$) (see Fig. 1), while no interaction between depth and site was found (two-way ANOVA, $F_{2,78} = 1.3$, $P = 0.254$). Within sites, mass transfer in shallow waters was 16 and 25% greater than in deep waters at Tenements and Harry's Bommie, respectively. There was no significant difference in mass transfer between the cave and open habitats at 5 m.

Colony morphology

The two coral species showed similar morphological responses for branch spacing, but contrasting responses for branch length and diameter (see Table 1). Specifically, branch spacing of *Acropora humilis* at 18 m depth at the two sites was 44 and 67% greater than in the shallow sites at Tenements and Harry's Bommie, respectively. *Stylophora pistillata* had the smallest branch spacing in the shallow high-light habitat, with a 28% decrease in branch spacing at Harry's Bommie and a 42% branch spacing decrease at Tenements compared to the cave and deep habitats (Tables 1, 2). Branch lengths of *A. humilis* colonies were 41% greater at Harry's Bommie and 58% longer at Tenements, in the shallow habitat at 5 m compared to the deep habitat at 18 m. Conversely, branches of *S. pistillata* colonies were longer at 18 m than at 5 m: by 28% at Harry's Bommie and 34% at Tenements. Similarly, in cave habitats *S. pistillata* branches were 12% longer at Harry's Bommie and 37% at Tenements compared to those in the high-light environment at 5 m (Tables 1, 2). Interestingly, *S. pistillata* colonies in shallow water had 40% thicker branches than colonies in deep water and cave habitats. In contrast, *A. humilis* displayed no difference in branch diameter between habitats or sites (Tables 1, 2).

Within-colony light attenuation

Overall the exponential irradiance model accounted for most of the observed variance in both species and in all cases explained more of the variation than the linear model (see Appendix 1) and analysis of residuals indicated that they were approximately normally distributed. Within-colony light attenuation, an indicator of degree of colony self-shading, decreased with ambient irradiance (i.e. increased at depth and in the cave habitat). The best fit equations of the exponential irradiance model showed that in *Acropora humilis*, light attenuation between branch tip and branch base was 40% greater in the shallow habitat at Harry's Bommie and 43% greater at Tenements, compared to that of colonies in deep water (Fig. 3). Colonies of *Stylophora pistillata* in the cave habitats showed minimal light attenuation consistent with their extreme low light

Table 1 Means (±SE) of morphological parameters, branch length, branch spacing and branch diameter, for colonies (n = 15) of *Acropora humilis* and *Stylophora pistillataat* two sites (Harry's Bommie and Tenements) and in different habitats (shallow = 5 m; deep = 18 m; cave at 5 m)

	Branch length	Branch spacing	Branch diameter
	Mean ± SE (mm)	Mean ± SE (mm)	Mean ± SE (mm)
Harry's Bommie			
Acropora humilis			
Shallow	76.3 (2.6)	18.4 (0.9)	8.8 (0.1)
Deep	54.2 (2.9)	29.7 (0.6)	8.5 (0.2)
Stylophora pistillata			
Shallow	57.5 (3.2)	18.3 (1.0)	9.0 (0.3)
Deep	73.6 (2.0)	25.1 (1.2)	5.1 (0.2)
Cave	64.5 (3.5)	25.6 (1.3)	5.5 (0.2)
Tenements			
Acropora humilis			
Shallow	77.0 (1.7)	22.7 (1.1)	8.6 (0.2)
Deep	50.3 (1.7)	28.7 (1.0)	8.7 (0.2)
Stylophora pistillata			
Shallow	45.7 (2.7)	14.5 (0.3)	9.8 (0.3)
Deep	61.2 (4.1)	25.1 (0.9)	5.6 (0.3)
Cave	62.7 (3.2)	27.6 (0.6)	5.7 (0.2)

Table 2 Summary of two-way ANOVAs and Kruskal–Wallis tests for *Acropora humilis* and *Stylophora pistillata* branch length, branch spacing and branch diameter, with source of variance being habitat (shallow, deep and cave) and site (Harry's Bommie and Tenements)

Source of variance	Branch length			Branch spacing			Branch diameter		
	df	*F*	*P*	*df*	*H*	*P*	*df*	*F*	*P*
Acropora humilis									
Habitat	1	123.6	**<0.001**	1	59.3	**<0.001**	1	0.24	0.63
Site	1	0.55	ns	1	6.42	**0.013**	1	0.02	0.9
Habitat × Site	1	1.04	ns				1	1.50	0.23
Total	67			76			67		
	df	*F*	*P*	*df*	*F*	*P*	*df*	*F*	*P*
Stylophora pistillata									
Habitat	2	13.9	**<0.001**	2	0.4	**<0.001**	2	146.6	**<0.001**
Site	1	11	**<0.001**	1	3.8	ns	1	5.4	**0.023**
Habitat × site	2	1.6	ns	2	53.5	**0.026**	2	0.3	ns
Total	84			96			84		

Significant results are highlighted in bold

environment. In contrast, colonies in shallow-water open environments had maximum light attenuation, 33 and 30% greater than for conspecifics in the deep habitat, and 40 and 41% greater than for colonies found in the cave habitat, at Harry's Bommie and Tenements respectively (Fig. 3).

Branch light distributions

For *Acropora humilis*, branch light distributions from Monte Carlo analyses indicated that the more open colony morphology typical of corals in deep waters facilitates a 38% increase in mean irradiance and results in a 2-fold greater proportion of irradiances >25 µmol photon m^{-2} s^{-1} compared to the type morphologies in shallow waters (Fig. 4, Table 3). The cave type morphology for *Stylophora pistillata* increases the light in the higher irradiance categories at both sites and all environmental irradiance conditions. Corals in cave habitats also increase the mean irradiance distribution by 20% and specifically allow a 3-fold greater proportion of irradiance >20 µmol photon m^{-2} s^{-1} (Fig. 4, Table 3) compared to model results with colonies exhibiting a deep water morphology. The cave type morphology also increases the mean irradiance distribution by 47% and allows a 5-fold greater proportion of irradiance >20 µmol photon m^{-2} s^{-1} compared to model results for shallow water colony morphologies. For both species, the tighter packing of branches in shallow water reduced the proportion of tissue surfaces

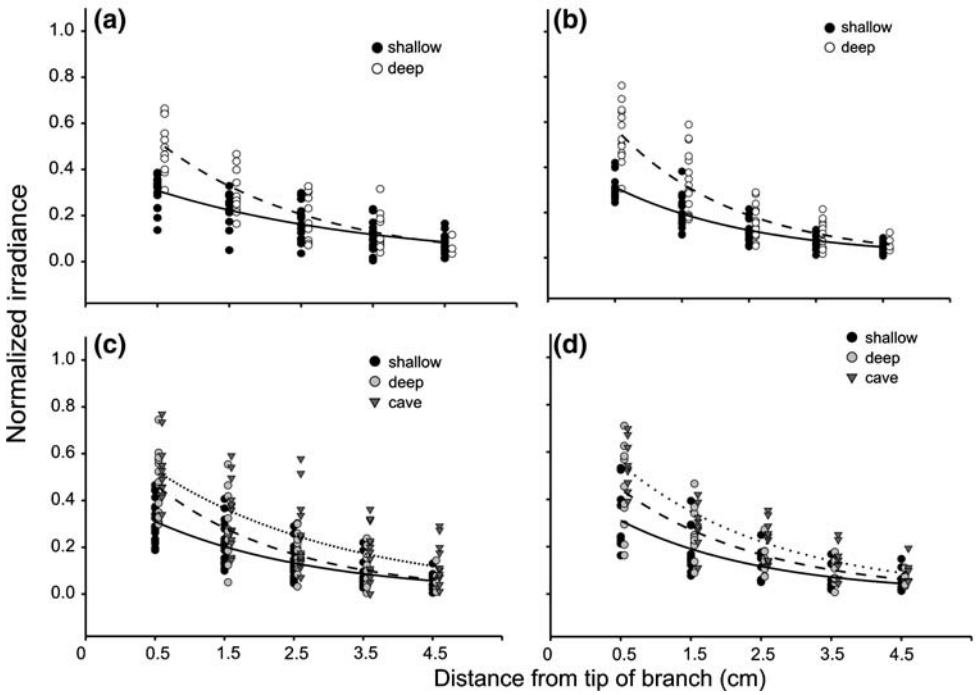

Fig. 3 Within-colony light attenuation profiles for *Acropora humilis* and *Stylophora pistillata* **a** *A. humilis* at Harry's Bommie **b** *A. humilis* at Tenements **c** *S. pistillata* at Harry's Bommie and **d** *S. pistillata* at Tenements. Irradiance is normalized to irradiance at the top of the colony ($n = 15$). *Lines* represent exponential irradiance models depicted in Appendix 1, where *solid lines* are shallow models, *broken lines* are deep models, and *dotted lines* are cave models

exposed to high, and potentially damaging, light levels (>350 µmol photon m^{-2} s^{-1}). Specifically, in shallow-water *A. humilis* colonies, tight branching resulted in a 36% decrease in the irradiance distribution mean, and in a 5-fold reduction in the proportion of tissue surfaces exposed to higher irradiances (>350 µmol photon m^{-2} s^{-1}) compared to the model for deep water colonies. Similarly, *S. pistillata* colonies at 5 m reduced the proportion of irradiance >350 µmol photon m^{-2} s^{-1} by 3- and 5-fold compared to model results for corals in deep water and caves. The mean PAR distribution was reduced by 23 and 43% compared to corals in deep water and caves, respectively (Fig. 4, Table 3).

Discussion

The interaction of reef-building corals with the surrounding light environment is critical to our understanding of some of the most fundamental aspects of their biology. The present study reveals that variation in colony morphology represents an important strategy for achieving favourable light environments within coral colonies. The colony design of these branching corals contributes strongly to protecting the colony against excessive light in shallow waters. These variations are likely to be a consequence of both light and flow aspects of the habitat. Although this study did not test the relative contribution of mass transfer variations to changes in colony morphology, when comparing the two external drivers, the external light environment varied by a greater magnitude, i.e., by 400–500% compared to a flow regime that only differed by 16–25% (Fig. 1). Also, although mass transfer was ~50% higher at Tenements compared to Harry's Bommie, colony geometry did not vary between sites for both species.

Within-colony light attenuation curves were steeper for colonies in shallow, high light environments compared to low-light environments. Branch light distributions demonstrated that both species adopted a type morphology that shifted irradiance distributions to either increase or reduce light levels within the colony relative to ambient levels and achieved a more favourable within-colony light environment for a given habitat (shallow, deep or cave) (Fig. 4). In this study the patterns of morphological changes varying within-colony light levels in *Acropora humilis* and *Stylophora pistillata* with ambient light, is somewhat analogous to that found in terrestrial and aquatic plants. For example, structural variation in forest understorey plants maximizes light capture (Herbert 1996; Pearcy and Yang 1996, 1998). Also, seagrass species can vary their amount of self-shading by changing shoot density and shoot size (e.g., Enriquez and Pantoja-Reyes 2005).

For the two branching study species *Acropora humilis* and *Stylophora pistillata*, simple morphological parameters such as branch spacing, length and diameter varied with ambient light environment and to some extent with external flow conditions. In shallow, high-light environments, narrowing of the space between branches in both *A. humilis* and *S. pistillata* promoted greater self-shading from potentially damaging light levels such as photoinhibition and UV-R damage (Hoogenboom et al. 2006; Levy et al. 2006). Tighter branch spacing in high flow environments also

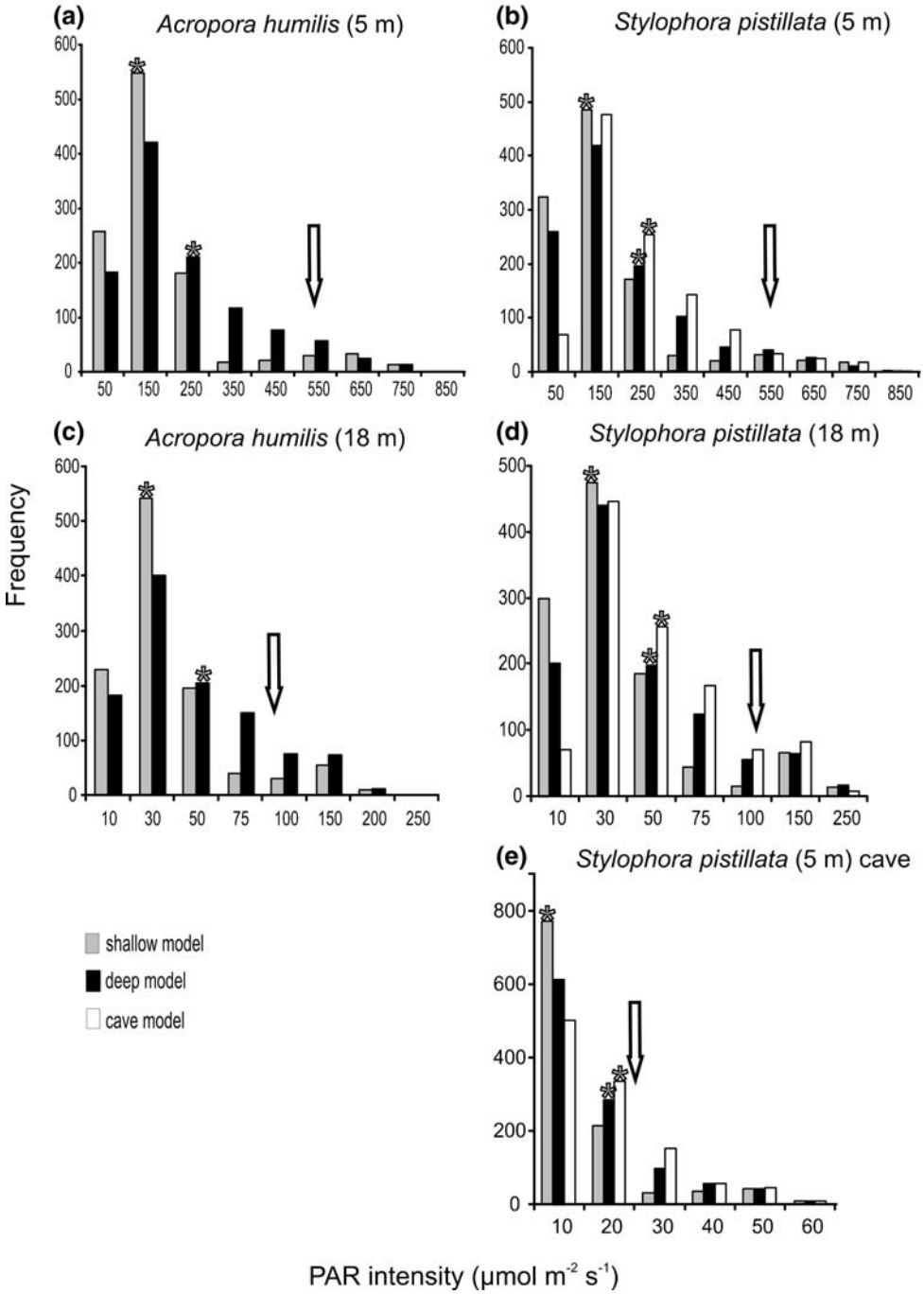

Fig. 4 Estimated whole-branch irradiance distribution for *Acropora humilis* and *Stylophora pistillata* colonies in respective light habitats (shallow, deep, and cave), using daily maximum irradiance (mean ± SE) as input value. Each distribution is obtained using the exponential irradiance model in Appendix 1. Type morphologies for **a** *A. humilis*; shallow (mean = 135.9) and deep (mean = 183.8), and **b** *S. pistillata*; shallow (mean = 132.8), deep (mean = 161.8) and cave (mean = 193.2) at shallow (5 m) ambient light level. Type morphologies for **c** *A. humilis*; shallow (mean = 29.5) and deep (mean = 40.3), and **d** *S. pistillata*; shallow (mean = 28.8), deep (mean = 35.4) and cave (mean = 42.7) at deep (18 m) ambient light level. Type morphologies for (c) *S. pistillata*; shallow (mean = 9.8), deep (mean = 12.4) and cave (mean = 14.7) at cave (5 m) ambient light level. *Arrow* indicates ambient irradiance level. *Star* indicates mean of the light distribution

thickens the diffusive boundary layer and reduces mass flux to the tissue surface area of the colony (e.g. Sebens et al. 1997; Kaandorp et al. 2005). This structural change also reduces the impact of wave forces (Madin and Connolly 2006). In deep, low light environments, the wider spacing of branches observed in this study would permit more light to reach deeper parts of the colony. Wider spacing of branches also promotes higher mass fluxes (the rate of mass flow across a unit area) and is favorable for corals in low-flow environments in deep water (e.g. Helmuth et al. 1997; Bruno and Edmunds 1998; Kaandorp 1999; Kaandorp et al. 2005). *Stylophora pistillata* found in the cave had widely spaced branches in a high flow regime. Corals found in these habitats live in very low ambient light levels (≥25 µmol photon m^{-2} s^{-1}) and it may be that there is a tradeoff between the reduction of impact of physical forces with higher mass transfer, and the need to compensate their potential light limitation by spreading out into the current to

Table 3 Summary of t-tests and one way ANOVAs for *Acropora humilis* and *Stylophora pistillata* of light distribution kurtosis derived from different irradiance models (shallow, deep and cave), at 3 different ambient light levels (shallow, deep and cave)

Source of variance	Shallow ambient light			Deep ambient light			Cave ambient light		
	df	*t*	*P*	*df*	*t*	*P*			
Acropora humilis kurtosis									
Model	1	−2.33212	**0.031**	1	−11.1139	**<0.001**			
Total	18			18					
	df	*F*	*P*	*df*	*F*	*P*	*df*	*F*	*P*
Stylophora pistillata kurtosis									
Model	2	5.2708	**0.012**	2	33.07791	**<0.001**	2	2406.82	**<0.001**
Total	27			27			27		

Significant results are highlighted in bold

maximize mass transfer and particle capture, while at the same time increasing light capture.

Branches of *Acropora humilis* were longer in the shallow waters and shorter in the deep waters, which would increase self-shading in the sunlit shallows and reduce self-shading within colonies growing at deeper sites. *Stylophora pistillata* shows a different strategy in that it exhibits longer and thinner branches in deep waters and in caves. This may be a result of reduced calcification in the low-light environment and maximization of the surface area to volume ratio to increase particle capture. In terms of effects on within- colony self-shading in ambient low light levels, the thinning of branches may be counteracting the self-shading effects of branch lengthening. From a flow perspective longer branches are beneficial in low-flow environments as they facilitate high mass flux and shorter branches present in high-flow environments decrease mass flux (Kaandorp et al. 2005) and reduce the impact of physical forces created by high water flow (Madin and Connolly 2006). Branch length variation in the pocilloporid coral *S. pistillata* thus appears to depend more on water flow than the light at Heron Island. This is consistent with *Madracis mirabilis*, a Caribbean relative of the pocilloporid family, where the determining factor for morphological plasticity is the flow regime and diffusion limitation (Kaandorp et al. 2005).

In the present study *Stylophora pistillata* colonies in the deep and cave habitats also had thinner branches compared to colonies found in the shallow open environment, which would help reduce the self-shading effect of longer branches, a trend that was not found in *Acropora humilis*. Also, colonies found in the cave environment extended their branches horizontally, not vertically like colonies found in other habitats, so the increase in branch length would not promote greater self-shading. Overall, despite differences in branch lengths between *A. humilis* and *S. pistillata*, light attenuation curves were similar for both species between depths, implying that changes in colony morphology can modulate the internal light environment.

The light distribution mean was surprisingly low in all habitats and for both species. Colonies in deep water had a mean branch light level of 30–50 μmol photon m^{-2} s^{-1} and 130–140 μmol photon m^{-2} s^{-1} in the shallow. This indicates that branching colonies are strongly self-shaded to <10% of their maximum environmental irradiances, and will have a greater part of the colony shade-adapted, as the within-colony light attenuation is steep and most of the ambient light is lost within the first 2 cm from the tip (Fig. 3). This results in sun-adapted areas at the top of branches and shade-adapted areas at the base of branches. These differences in light climate within coral colonies often result in differences in gross photosynthetic activity for various parts of coral colonies (Helmuth et al. 1997; Ulstrup et al. 2006) so that photoacclimation and adaptation across a coral colony will be heterogenous (Falkowski et al. 1990; Jones et al. 1998; Ralph et al. 2002). According to previous studies, colonies in shaded environments (deep, cave) may have an energetically suboptimal light level (Anthony and Hoegh-Guldberg 2003b), and it has been shown that colonies exposed to such low PAR intensities may be light limited and need energy supplementation through feeding (Mass et al. 2007). The trend in this study was also different from that found in *Turbinaria mesenterina* where the modal irradiance at all depths was 100–200 μmol photon m^{-2} s^{-1} (Anthony et al. 2005). It may be that branching corals in shaded environments are limited by the extent to which they can modify their morphologies, as there may be genetic constraints. This study assumed that growth changes were phenotypic rather than genetic, but without a transplant study it is not possible to differentiate between them. Also the within-colony surface irradiance measured in this study might not reflect the internal light environment experienced by the photosynthetic symbiotic dinoflagellates. The coral-dinoflagellate complex can adopt other photoacclimatory mechanisms, such as adjusting photosynthetic pigment concentrations to maximize low irradiance (Falkowski and Dubinsky 1981; Dubinsky et al. 1984; Porter et al. 1984) or regulate GFP-like protein and mycosporine-like amino acid concentrations

to minimize potential photoinhibition and UV-R induced tissue damage at high ambient irradiance levels (Shick et al. 1996; Dove 2004). In addition, the highly reflective properties of the skeleton make it an efficient light trap extending the path length of a photon (Enriquez et al. 2005). Moreover, within the coral tissue multiple scattering and diffuse reflection result in within-tissue light climates being higher than expected compared to incident irradiance (Kuhl et al. 1995). These additional photoacclimatory mechanisms may interact with structural phenotypic plasticity in adjusting light levels reaching the symbiotic dinoflagellates. To compare optimal irradiances between species one would need to compare the light levels reaching the photosynthetic unit in the symbiotic dinoflagellate. Such a study might show that the favourable irradiance levels for the *Stylophora pistillata* and *Acropora humilis* in the present study are comparable to those in *Turbinaria mesenterina*. Our study revealed the importance of variation in colony geometry on within-colony surface irradiances in branching coral species. The relative importance of colony architecture at the macro scale may be less important in other coral species with a massive colony morphology.

Distribution differences between the two branching species may explain to some extent the difference in morphology across the external light/mass transfer gradient. *Stylophora pistillata* has a broader light niche compared to *Acropora humilis* as it is often found in more shaded habitats (~1% surface light intensity) such as deep waters at 65 m (e.g., Mass et al. 2007), or cryptic habitats in shallow waters (this study), while the *A. humilis* depth range only extends to 20 m (Wolstenholme et al. 2003), which is a less shaded habitat. In the more shaded habitats where *S. pistillata* is found, it is likely that colonies are light limited and must supplement their energy requirement with a larger contribution from heterotrophy (Mass et al. 2007). As a result, regulating external flow regimes for *S. pistillata* to a colony optimum would be important. This might further explain why in this study the branch length variation in *S. pistillata* was apparently more related to mass transfer than light, compared to the pattern for *A. humilis*. In addition, *S. pistillata* harbors a greater diversity of symbiotic dinoflagellate strains (Sampayo et al. 2007) compared to *A. humilis* (LaJeunesse et al. 2004). This, combined with its greater level of geometric variation, might explain its broader light niche.

The present study demonstrates that structural changes in branching scleractinian corals can enhance light capture or increase self-shading to modulate ambient light intensities to more favourable within-colony surface light levels.

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References

Anthony KRN, Hoegh-Guldberg O (2003a) Variation in coral photosynthesis, respiration and growth characteristics in contrasting light microhabitats: an analogue to plants in forest gaps and understoreys? Funct Ecol 17:246–259. doi:10.1046/j.1365-2435.2003.00731.x

Anthony KRN, Hoegh-Guldberg O (2003b) Kinetics of coral photoacclimation. Oecologia 134:23–31. doi:10.1007/s00442-002-1095-1

Anthony KRN, Connolly SR (2004) Environmental limits to growth: physiological niche boundaries of corals along turbidity-light gradients. Oecologia 141:373–384. doi:10.1007/s00442-004-1647-7

Anthony KRN, Hoogenboom MO, Connolly SR (2005) Adaptive variation in coral geometry and the optimization of internal colony light climates. Funct Ecol 19:17–26. doi:10.1111/j.0269-8463.2005.00925.x

Atkinson MJ, Bilger RW (1992) Effects of water velocity on phosphate uptake in coral reef-flat communities. Limnol Oceanogr 37:273–279

Brakel WH (1983) Depth-related changes in the colony form of the reef coral *Porites astreoides*. The ecology of deep and shallow reefs. Symp Ser Undersea Res 1:21–26

Brown BE, Ambarsari I, Warner ME, Fitt WK, Dunne RP, Gibb SW et al (1999) Diurnal changes in photochemical efficiency and xanthophyll concentrations in shallow water reef corals: evidence for photoinhibition and photo-protection. Coral Reefs 18:99–105. doi:10.1007/s003380050163

Bruno JF, Edmunds PJ (1997) Clonal variation for phenotypic plasticity in the coral *Madracis mirabilis*. Ecology 78:2177–2190

Bruno JF, Edmunds PJ (1998) Metabolic consequences of phenotypic plasticity in the coral *Madracis mirabilis* (Duchassaing & Michelotti): the effect of morphology and water flow on aggregate respiration. J Exp Mar Biol Ecol 229:187–195. doi:10.1016/S0022-0981(98)00050-1

Chalker BE, Dunlap WC, Oliver JK (1983) Bathymetric adaptations of reef-building corals at Davies Reef, Great Barrier Reef, Australia. II. Light saturation curves for photosynthesis and respiration. J Exp Mar Biol Ecol 73:37–56. doi:10.1016/0022-0981(83)90004-7

Dennison WC, Barnes DJ (1988) Effect of water motion on coral photosynthesis and calcification. J Exp Mar Biol Ecol 115:67–77. doi:10.1016/0022-0981(88)90190-6

Dove S (2004) Scleractinian corals with photoprotective host pigments are hypersensitive to thermal bleaching. Mar Ecol Prog Ser 272:99–116. doi:10.3354/meps272099

Dove S, Ortiz JC, Enriquez S, Fine M, Fisher P, Iglesias-Prieto R et al (2006) Response of holosymbiont pigments from the scleractinian coral *Monipora monasteriata* to short-term heat stress. Limnol Oceanogr 51:1149–1158

Dubinsky Z, Jokiel P (1994) The ratio of energy and nutrient fluxes regulates the symbiosis between zooxanthellae and corals. Pac Sci 48:313–324

Dubinsky Z, Falkowski PG, Porter JW, Muscatine L (1984) Absorption and utilization of radiant energy by light and shade-adapted colonies of the hermatypic coral *Stylophora pistillata*. Proc R Soc Biol Sci Ser B 222:203–214

Dustan P (1975) Growth and form in the reef-building coral *Montastrea annularis*. Mar Biol (Berl) 33:101–107. doi:10.1007/BF00390714

Enriquez S, Pantoja-Reyes NI (2005) Form-function analysis of the effect of canopy morphology on leaf self-shading in the seagrass *Thalassia testudinum*. Oecologia 145:235–243. doi:10.1007/s00442-005-0111-7

Enriquez S, Mendez ER, Iglesias-Prieto R (2005) Multiple scattering on coral skeletons enhances light absorption by symbiotic algae. Limnol Oceanogr 50:1025–1032

Falkowski PG, Dubinsky Z (1981) Light-shade adaptation of *Stylophora pistillata*, a hermatypic coral from the Gulf of Eilat. Nature 289:172–174. doi:10.1038/289172a0

Falkowski PG, Raven JA (1997) Aquatic photosynthesis. Blackwell Science, Malden

Falkowski PG, Jokiel PL, Kinzie RAIII (1990) Irradiance and corals. Coral Reefs 25:89–107

Fabricius KE, Genin A, Benayahu Y (1995) Flow-dependent herbivory and growth in zooxanthellae-free soft corals. Limnol Oceanogr 40:1290–1301

Fulton CJ, Bellwood DR (2005) Wave induced water motion and the functional implications for coral reef fish assemblages. Limnol Oceanogr 50:255–264

Goreau TF (1959) The ecology of Jamaican coral reefs I. Species composition and zonation. Ecology 40:67–90. doi:10.2307/1929924

Graus RR, Macintyre IG (1976) Control of growth form in colonial corals: computer simulation. Science 193:895–897. doi:10.1126/science.193.4256.895

Graus RR, Macintyre IG (1982) Variation in growth forms of the reef coral *Montastrea annularis* (Ellis & Solander): A quantitative evaluation of growth response to light distribution using computer simulation. Smithson Contrib Mar Sci 12:441–464

Helmuth BS, Sebens KP, Daniel TL (1997) Morphological variation in coral aggregations: branch spacing and mass flux to coral tissues. J Exp Mar Biol Ecol 209:233–259. doi:10.1016/S0022-0981(96)02687-1

Herbert TJ (1996) On the relationship of plant geometry to photosynthetic response. In: Mulkey SS, Chazdon RL, Smith AP (eds) Tropical forest plant ecophysiology. Chapman & Hall, London, pp 139–161

Hoogenboom MO, Anthony KRN, Connolly SR (2006) Energetic cost of photoinhibition in corals. Mar Ecol Prog Ser 313:1–12. doi:10.3354/meps313001

Hoogenboom MO, Anthony KRN, Connolly SR (2008) Energetic implications of phenotypic plasticity in foliose corals. Ecology (in press)

Jaubert J (1981) Variations of the shape and of the chlorophyll concentration of the scleractinian coral *Synaraea convexa* Verrill: Two complementary processes to adapt to light variations. Proc of the 4th Int Coral Reef Symp 2:55–58

Jokiel PL, Morrissey JI (1993) Water motion on coral reefs: evaluation of the clod-card technique. Mar Ecol Prog Ser 93:175–181. doi:10.3354/meps093175

Jones RJ, Hoegh-Guldberg O (2001) Diurnal changes in photochemical efficiency of the symbiotic dinoflagellates (Dinophyceae) of corals: photoprotection, photoactivation and the relationship to coral bleaching. Plant Cell Environ 24:89–99. doi:10.1046/j.1365-3040.2001.00648.x

Jones RJ, Hoegh-Guldberg O, Larkum AWD, Schreiber U (1998) Temperature-induced bleaching of corals begins with impairmentof the CO_2 mechanism in zooxanthellae. Plant Cell Environ 21:1219–1230. doi:10.1046/j.1365-3040.1998.00345.x

Kaandorp JA (1999) Morphological analysis of growth forms of branching marine sessile organisms along environmental gradients. Mar Biol (Berl) 134:295–306. doi:10.1007/s002270050547

Kaandorp JA, Sloot PMA, Merks RMH, Bak RPM, Vermeij MJA, Maier C (2005) Morphogenesis of the branching reef coral *Madracis mirabilis*. Proc R Soc Biol Sci Ser B 272:127–133. doi:10.1098/rspb.2004.2934

Kawamata S (1998) Effect of wave-induced oscillatory flow on grazing by a subtidal sea urchin *Strongylocentrotus nudus* (A. Agassiz). J Exp Mar Biol Ecol 224:31–48. doi:10.1016/S0022-0981(97)00165-2

Kuhl M, Cohen Y, Daalsgard T, Jorgenen BB, Revsbech NP (1995) Microenvironment and photosynthesis of zooxanthellae in scleractinian corals studied with microsensors for O_2, pH and light. Mar Ecol Prog Ser 117:159–172. doi:10.3354/meps117159

LaJeunesse TC, Bhagooli R, Hidaka M, de Ventier L, Done T, Schmidt GW et al (2004) Closely related *Symbiodinium* spp differ in relative dominance in coral reef host communities across environmental, latitudinal and biogeographic gradients. Mar Ecol Prog Ser 284:147–161. doi:10.3354/meps284147

Lesser MP, Weis VM, Patterson MR, Jokiel PL (1994) Effects of morphology and water motion on carbon delivery and productivity in the reef coral, *Pocillopora damicornis* (Linnaeus): Diffusion barriers, inorganic carbon limitation, and biochemical plasticity. J Exp Mar Biol Ecol 178:153–179. doi:10.1016/0022-0981(94)90034-5

Levy O, Achituv Y, Yacobi YZ, Stambler N, Dubinsky Z (2006) The impact of spectral composition and light periodicity on the activity of two antioxidant enzymes (SOD and CAT) in the coral *Favia favus*. J Exp Mar Biol Ecol 328:35–46. doi:10.1016/j.jembe.2005.06.018

Madin JS, Connolly SR (2006) Ecological consequences of major hydrodynamic disturbances on coral reefs. Nature 444:477–480. doi:10.1038/nature05328

Mass T, Einbinder S, Brokovich E, Shashar N, Vago, Erez J, Dubinsky Z (2007) Photoacclimation of Stylophora pistillata to light extremes: metabolism and calcification. Mar Ecol Prog Ser 334:93–102. doi:10.3354/meps334093

Muko S, Kawasaki K, Sakai K (2000) Morphological plasticity in the coral *Porites sillimaniani* and its adaptive significance. Bull Mar Sci 66:225–239

Muscatine L, Porter JW (1977) Reef corals: mutualistic symbiosis adapted to nutrient-poor environments. Bioscience 27:454–460. doi:10.2307/1297526

Muscatine L, Falkowski PG, Porter JW, Dubinsky Z (1984) Fate of photosynthetic fixed carbon in light-adapted and shade-adapted colonies of the symbiotic coral *Stylophora pistillata*. Proc R Soc Biol Sci Ser B 222:181–202

Patterson MR, Sebens KP, Olson RR (1991) In situ measurement of flow effects on primary production and dark respiration in reef corals. Limnol Oceanogr 36:936–948

Pearcy RW, Yang W (1996) A three-dimensional crown architecture model for assessment of light capture and carbon gain by understory plants. Oecologia 108:1–12. doi:10.1007/BF00333208

Pearcy RW, Yang W (1998) The functional morphology of light capture and carbon gain in the redwood forest understorey plant *Adenocaulon bicolor*. Funct Ecol 12:543–552. doi:10.1046/j.1365-2435.1998.00234.x

Pearcy RW, Muraoka H, Valladares F (2005) Crown architecture in sun and shade environments: assessing function and trade-offs with a three-dimensional simulation model. New Phytol 166:791–800. doi:10.1111/j.1469-8137.2005.01328.x

Porter JW, Muscatine L, Dubinsky Z, Falkowski PG (1984) Primary production and photoadaptaion in light- and shade-adapted colonies of the symbiotic coral, *Stylophora pistillata*. Proc R Soc Biol Sci Ser B 222:161–180

Porter ET, Sanford LP, Suttles SE (2000) Gypsum dissolution is not a universal integrator of "water motion". Limnol Oceanogr 45:145–158

Ralph PJ, Gademann R, Larkum AWD, Kuhl M (2002) Spatial heterogeneity in active chlorophyll fluorescence and PSII activity of coral tissues. Mar Biol (Berl) 141:639–646. doi:10.1007/s00227-002-0866-x

Rogers CS (1990) Responses of coral reefs and reef organisms to sedimentation. Mar Ecol Prog Ser 62:185–202. doi:10.3354/meps062185

Sampayo EM, Franceschinis L, Hoegh-Guldberg O, Dove S (2007) Niche partitioning of closely related symbiotic dinoflagellates. Mol Ecol 16:3721–3733. doi:10.1111/j.1365-294X.2007.03403.x

Sebens KP (1997) Adaptive responses to water flow: Morphology, energetics, and distribution of reef corals. Proc 8th Int Coral Reef Symp 2:1053–1058

Sebens KP, Witting J, Helmuth B (1997) Effects of water flow and branch spacing on particle capture by the reef coral *Madracis mirabilis* (Duchassaing and Michelotti). J Exp Mar Biol Ecol 211:1–28. doi:10.1016/S0022-0981(96)02636-6

Shick JM, Lesser MP, Jokiel PL (1996) Ultraviolet radiation and coral stress. Glob Change Biol 2:527–545. doi:10.1111/j.1365-2486.1996.tb00065.x

Thomas F, Atkinson MJ (1997) Ammonium uptake by coral reefs: effects of water velocity and surface roughness on mass transfer. Limnol Oceanogr 42:81–88

Titlyanov EA, Titlyanova TV (2002) Reef-building corals–symbiotic autotrophic organisms: 2 Pathways and mechanisms of adaptation to light. Russ J Mar Biol 28(Supplement 1):S16–S31. doi:10.1023/A:1021833821493

Titlyanov EA, Titlyanova TV, Yamazato K, van Woesik R (2001) Photo-acclimation dynamics of the coral *Stylophora pistillata* to low and extremely low light. J Exp Mar Biol Ecol 263:211–225. doi:10.1016/S0022-0981(01)00309-4

Ulstrup KE, Berkelmans R, Ralph PJ, van Oppen MJH (2006) Variation in bleaching sensitivity of two coral species across a latitudinal gradient on the Great Barrier Reef: the role of zooxanthellae. Mar Ecol Prog Ser 314:135–148. doi:10.3354/meps314135

Vermeij MJA, Bak RPM (2002) How are coral populations structured by light? Marine light regimes and the distribution of *Madracis*. Mar Ecol Prog Ser 233:105–116. doi:10.3354/meps233105

Veron JEN (1995) Corals in time and space. Cornell University Press, Ithaca

Veron JEN (2000) Corals of the world. Australian Institute of Marine Science, Townsville

Via S, Gomulkiewicz R, De Jong G, Scheiner SM, Schlichting CD, Van Tienderen PH (1995) Adaptive phenotpic plasticity: consensus and controversy. Trends Ecol Evol 10:212–217. doi:10.1016/S0169-5347(00)89061-8

Wallace CC (1999) Staghorn corals of the World: a revision of the coral genus *Acropora*. CSIRO Publishing, Collingwood

Willis BL (1985) Phenotypic plasticity versus phenotypic stability in the reef corals *Turbinaria mesenterina* and *Pavona cactus*. Proc 5th Int Coral Reef Symp 4:107–112

Winters G, Loya Y, Roettgers R, Beer S (2003) Photoinhibition in shallow-water colonies of the coral *Stylophora pistillata* as measured in situ. Limnol Oceanogr 48:1388–1393

Wolstenholme JK, Wallace CC, Chen CA (2003) Species boundaries within the *Acropora humilis* species group (Cnidaria; Scleractinia): a morphological and molecular interpretation of evolution. Coral Reefs 22:155–166. doi:10.1007/s00338-003-0299-0