

How are coral populations structured by light? Marine light regimes and the distribution of *Madracis*

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ABSTRACT: We studied the relation of light with coral colony morphology and coral distribution over a 5 to 50 m reef slope. We describe the characteristics of 6 species of the genus *Madracis* in relation to the light (photosynthetically active radiation [PAR]: 400 to 700 nm) colonies receive at a small spatial scale (1 to 10 cm). Species differ in their response to light but we could distinguish 3 strategies: (1) Species strive for maximum light capture and colonies occur above a threshold light value. This limits the distribution of such species toward greater depths. These species are found in shallow (<15 m) water and their morphological variation is not related to variation in the amount of light they receive. (2) Species strive for maximum light capture but all colonies occur below a threshold light value. Such species occur only on the deeper parts (>30 m) of the reef slope. Colony morphological variation is also unrelated to variation in the amount of light the colonies receive. (3) Species prefer low light habitats. Such species are found over the entire reef slope and they show a bimodal light preference. One part of the population (1st mode) prefers the maximum amount of light available at a particular depth. The other part of the population (2nd mode) prefers cryptic habitats with low light levels (5 to 60 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$). In these species, morphological variation in colony shape relates to light availability. Structural complexity of the reef surface within the same depth causes such variation in local light availability. This variation ranges between the maximum value at a depth predicted by physical laws and the minimal values encountered in cryptic habitats. The large variation in available light occurring over spatial scales as small as 10 cm distorts the direct relation between depth and light. Depth and light are only correlated as ecological factors for species that strive for maximum light capture (Strategy 1 or 2). A large depth distribution does not imply adaptation to a large light range when species have a strict preference for cryptic light environments. For such species (Strategy 3) depth is not a proxy for light. The different light strategies of species are related to morphological variation and species exploration of the reef habitat.

KEY WORDS: Marine light regimes · Coral populations · *Madracis* · Distribution · Life-history strategy

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INTRODUCTION

Environmental factors influence the ecology, physiology and morphology of zooxanthellate scleractinian corals. Frequently studied factors include: salinity (Coles & Jokiell 1988), temperature (Coles 1988,

Meesters & Bak 1993), dissolved oxygen concentration (Coles & Jokiell 1988), water motion (Jokiell 1978, Dennison & Barnes 1988), light quality (Falkowski et al. 1990) and quantity (review by Falkowski et al. 1990, Barnes & Chalker 1990). Although corals respond to the entire suite of factors mentioned above, light has been regarded to play a key role in coral ecology (Veron 1995). Light affects aspects such as coral settle-

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ment (Maida et al. 1994, Mundy & Babcock 1998), movement (Yamashiro & Nishihara 1995) and competition with other organisms (Baynes 1999), but, above all, light is an essential requirement because it enables photosynthesis and calcification of the symbiotic coral-zooxanthellate complex (Chalker et al. 1983, Gattuso 1985, Jokiel 1986, Hidaka 1988, Falkowski et al. 1990, Iglesias-Prieto & Trench 1997, Romaine et al. 1997, Ferrier-Pages et al. 1999, Ilan & Beer 1999).

A change in the amount of light received by a colony has physiological consequences and often requires morphological adaptations to maximize light capture (Graus & McIntyre 1982). Recent advances in computer modeling of coral colony growth support the notion that colony morphology is indeed dependent on light as a structuring factor (Muko et al. 2000, Kaandorp & Kubler 2001). In short, the dependence of corals on light is an axiom, but information on the amount of light corals receive in a reef setting is surprisingly lacking.

The underwater light environment has been thoroughly described by physical oceanographers and their formulas allow the calculation of the amount of light received at any depth (Jerlov 1966). In theory, light decreases exponentially with depth, which results in equal amounts of light received at any point within the same depth facing the same direction. However, since reef systems are characterized by structural complexity, the amount of light received by organisms at the same depth will vary depending on their position on the reef framework. Brakel (1976) in his study on Jamaican coral reef benthos was among the first to recognize the influence of structural complexity, and the organism's immediate surroundings, on the amount of light it receives. Different positioning of colonies within the same depth and shading, or reflection by other reef inhabitants or substrate-elements, provides organisms with light other than would be expected from physical laws. Changes in colony position within the same depth or changes in surrounding substrate types can result in a change in light that is equivalent to substantial change in depth. Roos (1967, 1971) first established the role of submarine light in the ecology of corals. Roos (1967) and Brakel (1976) clearly indicate that spatial heterogeneity, at the 1 to 10 cm scale, affects the distribution of light on a coral reef. This variation must be taken into account in studies of benthic phototrophic organisms. However, not much is known about the amount of light coral colonies receive at a small spatial scale and the consequences for their physiology and morphology are largely unstudied (but see Titlyanov et al. 1990). They found that 3 Pacific coral species occurred over different but greatly overlapping light ranges, ranging between 90–50 and 5–1% surface light (PAR). This large range has been

attributed to adaptational mechanisms at the cellular level.

Nevertheless, a species light range provides only limiting values. It provides no information on the relation between colony characteristics and the variation in the amount of light present between these limits. Linking colony characteristics to the specific amount of light the colony receives would provide such information, which is an important first step to explore the role of light in scleractinian coral demography and morphological plasticity.

The coral genus *Madracis* (Pocilloporidae) currently comprises 6 species (Wells 1973a,b, Vermeij et al. unpubl.) on Caribbean reefs. Morphological diversity between species, morphological plasticity within species and large environmental tolerance characterize the genus (Fenner 1993, Wells 1973a). The species have specific depth distributions and are dominant species of the deeper (>50 m) reef slope (Vermeij & Bak in press). Despite the large depth range all species harbor type-B zooxanthellae (Diekmann et al. 2002). All species are easily distinguished based on colony morphology and number and shape of septae (see 'Materials and methods'). The morphological species distinction corresponds to genetical species for all species except for *M. pharensis* and *M. decactis* (Diekmann et al. 2001). *M. pharensis* and *M. decactis* show morphological overlap and their separation as different species is debated (Zlatarski & Estalella 1982, Fenner 1993, Diekmann et al. 2001). Their phenotypic plasticity ranges from encrusting colonies in cryptic positions (*M. pharensis*) to nodular colonies at exposed positions on a reef (*M. decactis*). The different amount of light received at these positions has been suggested to cause the observed morphological differences (Fenner 1993). The description of *M. pharensis* and *M. decactis* as 2 ecomorphs by Fenner (1993) is not supported by our observations. On the reefs we studied, sometimes up to 50% of the colonies belonging to the *M. pharensis/decactis* complex did not match the proposed morphotype-environment combination. This demands a reevaluation of the relation between morphology and light in this complex.

Variation in depth distribution and colony morphology makes the genus *Madracis* well suited to address questions such as: (1) What is the variation in light that colonies receive at a certain depth? (2) How is the distributional pattern of a species related to its light preference? (3) Is variation in colony morphology really related to light? And (4) Is the relation between ecological and morphological characteristics with light species-specific? To answer these questions we relate the distribution and colony morphology of 6 *Madracis* species to the amount of light they receive at a small spatial scale at various depths over a reef slope from 5 to 50 m.

MATERIALS AND METHODS

Sampling. The characteristics of *Madracis mirabilis* Duchassaing and Michelotti 1861, *M. decactis* Lyman 1859, *M. pharensis* Heller 1868, *M. formosa* (Wells 1973a), *M. senaria* (Wells 1973b) and *M. carmabi* (n. sp.; Vermeij et al. unpubl.) were determined by measuring 50 colonies of each species in each of 6 isobathic transects over a 50 m depth gradient. Transects were placed at 5, 10, 20, 30 and 50 m over the fringing reef near Buoy 1 (Bak 1977) on the leeward coast of Curaçao (Fig. 1), Netherlands Antilles (12°05' N, 69°00' W). Each colony was measured for a number of parameters.

Relief: Relief is the shortest distance between 2 peripheral points divided by distance between the same points over the colony's surface. Relief is independent of the position of these points at the colony periphery provided that the line between them passed through the center of the colony (Kruskal-Wallis 1-way ANOVA, $p > 0.72$, $n = 200$). Because of the relatively simple growth forms (from 1st order branching to encrusting) we used relief as an indicator of colony morphology

Position on the substrate: Colonies were classified according to their position on the substrate. We distinguished 5 different positions: (1) on a horizontal surface receiving direct sunlight (angle of light, $\alpha = 0^\circ$); (2) On top of the substrate but receiving light at angles $90^\circ > \alpha > 0^\circ$; (3) against vertical walls, receiving little or no direct sunlight ($\alpha \approx 90^\circ$); (4) under overhangs, receiving no direct sunlight; and (5) in small caves or holes, receiving no direct sunlight.

Light environment: Light environment is defined as the light a colony receives from the 3 main spatial directions and determined according to the following

protocol. The local light environment was measured for each colony using a cosine LI-192SA underwater quantum sensor (LI-COR) connected to a LI-1000 data-logger (LI-COR). The sensor measures the quantum flux in the photosynthetically active range of 400 to 700 nm. The sensor is cosine-corrected to provide a measure of the irradiance in $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ passing through a plane. The meter was mounted in a Plexiglas instrument housing and the entire apparatus could be operated *in situ* by a SCUBA diver. The light, radiant flux in $\mu\text{mol photons m}^{-2} \text{s}^{-1}$, reaching a colony was measured *in situ* in 3 directions: (1) coming in straight from above ($\alpha = 0^\circ$); (2) coming from aside ($\alpha = 90^\circ$); and (3) coming from below ($\alpha = 180^\circ$; only possible for colonies under overhangs).

All light measurements were done during days with low cloud cover (<5%) around midday (12:00 to 14:00 h) in May and June 1998. We measured light at every second and integrated every measurement with the 5 previous ones to minimize the effects of fast light fluctuations caused by refraction at the sea surface. Since weather or water column conditions differed slightly between days, we standardized our data following Jaubert & Vasseur (1973, 1974). All measurements of light reaching the colony were expressed as a proportion of the downcoming light received at the same depth away from the reef in open water. This reference value was obtained away from the reef, a position where structural elements of the reef framework have no effect on its value. The reference value was then used to express the amount of light a colony receives as the amount it would receive under the conditions on May 6, 1998, assuming that the proportion between the measurements and the reference value was identical. On May 6, a light curve was made under a cloudless sky with no wind. The curve was based on 541 measurements of the light coming from each of 3 different directions ($\alpha = 0^\circ, 90^\circ$ and 180°) taken at 10 cm depth intervals over a 50 m depth range.

The reference value was determined before and after each set of measurements on the colony. The measurements were only used if the reference value had not changed. The calculation can be given in formula as:

$$\text{Light colony}_{(d,t,z)} = [\text{Measurement value}_{(d,t,z)} / \text{Reference value}_{(t,z)}] \times \text{Value}_{(\text{May } 6, z)}$$

where t = time, z = depth and d = direction

$$\begin{aligned} \text{if } & (1) \ 95\% \text{ Value}_{(\text{May } 6, z)} < \text{Reference value}_{(t,z)} < 105\% \text{ Value}_{(\text{May } 6, z)}; \\ & (2) \ \text{Reference value}_{(t,z)} \text{ before measurements} \\ & \quad = \text{Reference value}_{(t,z)} \text{ after measurements} \end{aligned}$$

Morphospecies definition. For *Madracis mirabilis*, *M. senaria* and *M. formosa*, we used the morphological

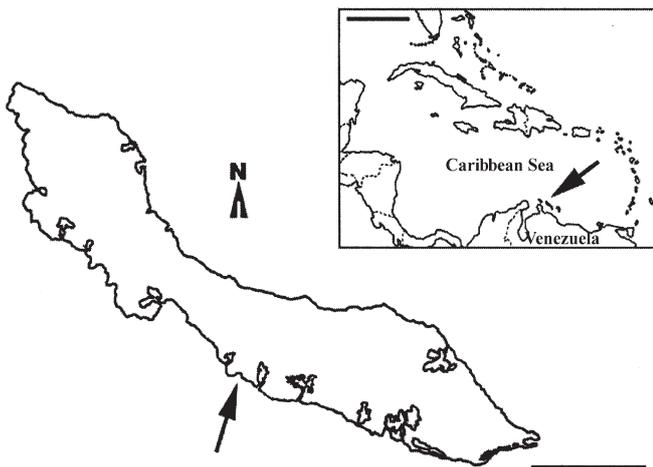


Fig. 1. Location of Curaçao (Netherlands Antilles) and the study site Buoy 1. Scale bars are 500 and 10 km respectively

descriptions from Wells (1973a,b). Based on genetic data (Diekman et al. 2001), *M. pharensis* and *M. decactis* are considered as a species complex. The Latin names are used to indicate the 2 types in colony morphology, corresponding to the proposed ecotypes by Fenner (1993): encrusting and nodular colonies were classified as *M. pharensis* and *M. decactis*, respectively. *M. pharensis* occurs in a spectacular variety of colormorphs and we included the 2 most abundant colormorphs of *M. pharensis* in our study: the brown morph (*M. pharensis* 1) and the green morph (*M. pharensis* 8). One particular group of colonies showed characteristics of *M. decactis* (10 septs) and *M. formosa* (branching morphology). We distinguish this morph as *M. carmabi* (described by Vermeij et al. unpubl.).

Statistical analysis. Regression analysis was used to examine the relation between environmental parameters and the occurrence and characteristics of *Madracis* species/morphs. All statistical tests were performed in SYSTAT 9.0. Light preference curves for 3 species showed bimodal distributions with 1 mode corresponding to colonies receiving high light levels at exposed positions and a second mode corresponding to colonies at low light positions (cryptic or deep). Because of the large differences in light received by colonies in the 2 modes, we treat the modes separately. This results in a subdivision of these 3 species in a cryptic (cr) and an exposed (ex) fraction. *K*-means clustering was used to assign individual colonies to each fraction. *K*-means clustering splits a set of objects into a selected number of groups by maximizing between-cluster variation relative to within-cluster variation. It is similar to a 1-way analysis of variance where the groups are unknown and the largest *F*-value is sought by reassigning members to each group (Systat 9.0).

RESULTS

Light distribution

The light distribution for May 6, 1998, over a 50 m depth gradient ($n = 541$ measurements for each direction) is shown in Fig. 2. The largest decrease in ambient light occurs in the first 10 m, where 65 to 70% of the incident surface light is absorbed or reflected. The extinction coefficient (k') of the local water column was -0.063 for downfalloffing light ($\alpha = 0^\circ$), -0.054 for light from aside ($\alpha = 90^\circ$) and -0.048 for light from below ($\alpha = 180^\circ$). The relative proportion of light coming from aside and below increases with depth, relative to the light coming from above ($R^2 = 0.33$ and 0.62 respectively, $p < 0.000$, $n = 541$). This reduces the asymmetry in the irradiance pattern with depth. In shallow water

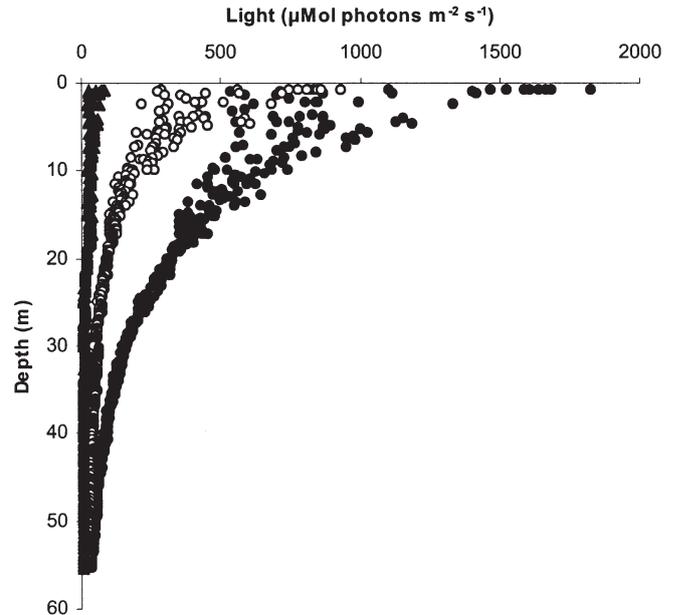


Fig. 2. Light gradient measured on May 6, 1998, at Buoy 1, Curaçao. Different markers indicate light coming from different directions. (●) The light coming in straight from above ($\alpha = 0^\circ$). (○) The light coming from aside towards the reef in a 90° angle with the light coming from above ($\alpha \approx 90^\circ$). (▲) The light coming from below, reflected by the reef ($\alpha = 180^\circ$). All measurements in $\mu\text{mol photons m}^{-2} \text{s}^{-1}$

this asymmetry results from a bulge in the irradiance pattern towards the sun.

The increased symmetry of the irradiance pattern with depth also has consequences for seasonal fluctuations in solar energy. In Fig. 3 the yearly fluctuation of solar irradiance is calculated for various depths at Buoy 1 (data Curaçao Meteorological Service) using the extinction coefficient for Buoy 1 of May 6, 1998. Obviously, irradiate solar energy shows no seasonality in deeper water.

A wide light range is available for organisms, within 1 depth, in shallow water (Fig. 2). The available light range rapidly narrows and at 30 m it is 18% of the 5 m values. The lower limit of the available light range at any depth is below that suggested by the line for light coming from below (far left in Fig. 2). That line is more indicative of the reef's reflectance. Low light levels are not synonymous with greater depth because values approaching $0 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ can be found in cryptic habitats at every depth over our 50 m depth gradient. It follows that at any depth there is a significant light range, from the maximum light present at a depth to absolute darkness in cryptic habitats, available to organisms. This available light range decreases with depth since maximum light (i.e. downcoming, $\alpha = 0^\circ$) decreases exponentially (Fig. 2).

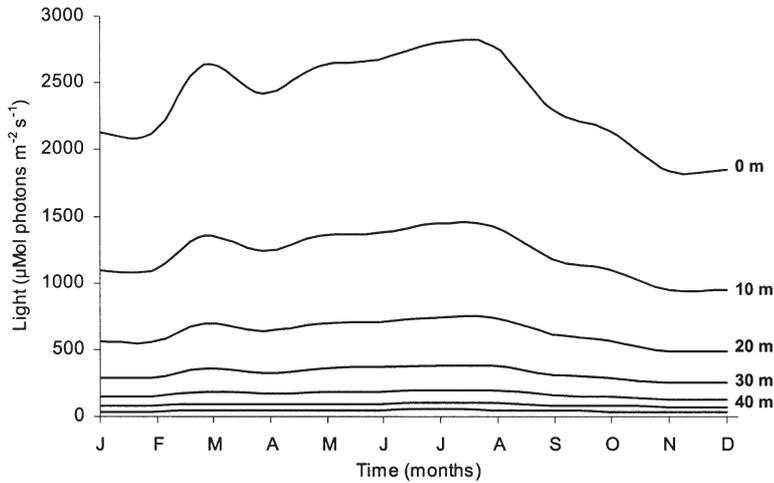


Fig. 3. Seasonal change in irradiance pattern at 10 m isobaths from the surface to 60 m depth (50 and 60 m not indicated in graph)

Species light preferences

Three species, *Madracis mirabilis*, *M. carmabi* and *M. formosa*, show a preference for maximum light capture. Their colonies are mostly (>73%) found in Position 1 (Fig. 4). Two other species, *M. pharensis* and *M. senaria*, occur over a broad isobathic light range but most colonies occupy low light habitats (Positions 3, 4 and 5). The strategy of *M. decactis* is intermediate and approximately half of the colonies is found in exposed, the other half in cryptic positions. The positions on the substratum for all species are given in Fig. 4.

The majority of colonies of species that prefer direct sunlight, such as *Madracis mirabilis* above 20 m and *M. formosa* below 30 m, are found at Positions 1 and 2. Colonies of species preferring cryptic environments, such as *M. pharensis*, occur mainly in Positions 3 to 5. The light variation at Positions 3 and 1 starts overlapping below 30 m (186 to 5 and 61 to 2 µmol photons m⁻² s⁻¹ respectively) and therefore the terms 'exposed' and 'cryptic' no longer characterize different light habitats below this depth. The fraction of colonies found at the exposed positions is increased in populations >30 m. However, 'exposed' and 'cryptic' become meaningless in relation to the amount of light received and in fact only refer to different topographical positions.

Reef surfaces oblique to surface light (Position 2) are relatively rare, because the transition from horizontal surfaces to vertical ones is usually a sharp angle. Fur-

thermore, *Madracis* colonies compensate for small differences in substrate angle by changing their growth direction towards the sun, consequently receiving direct sunlight as if occurring in Position 1.

Small-scale light habitat

Small positional changes can result in major changes in incoming light. A shift in position from horizontal (Position 1) to

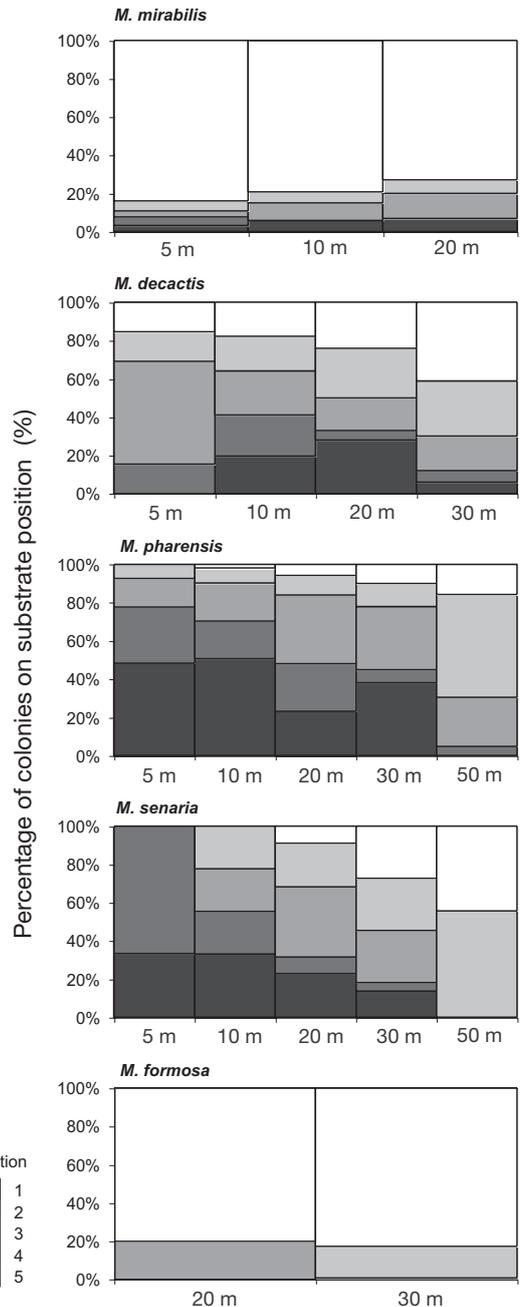


Fig. 4. Positions of colonies per depth as the percentage of the population occupying each of 5 positions. The positional range includes light-exposed positions (Position 1) to low light habitats (Position 5)

a position on a vertical wall (Position 3) results in a decrease of 60% in the light a colony receives ($SD = 9.0\%$, $n = 541$, all depths pooled). Positions in intermediate light levels (Position 2) are scarce on the reef and this causes bimodality in the light preference distributions of species that occur over a broad isobathic light range, such as *Madracis pharensis* (Fig. 5). One mode corresponds to the maximum light at a certain depth (Position 1) and the second mode corresponds to the low light environments (Positions 3 to 5).

For bimodally distributed data averages and standard deviations carry no biological meaningful information. Therefore, we described the 2 modes individually. We used *K*-means clustering (Systat 9.0) to assign the colonies to each mode (Table 1). The different strategies of *Madracis mirabilis*, *M. formosa* and *M. carmabi* on one side and of *M. pharensis*, *M. decactis* and *M. senaria* on the other are illustrated in Fig. 6. The unimodal distribution of the first 3 species is indicated by 1 marker per depth (Fig. 6). The second group of species shows a bimodal distribution of colonies over successive light classes. The 2 modes are indicated by 2 markers per depth (Fig. 6), representing the exposed and cryptic fraction of the population at each depth. The light received by colonies in the cryptic fraction (cr), which contains most individuals (Table 1), is identical between species at the same depth (ANOVA, $df = 2$, $n = 397$, $F = 0.001$, $p < 0.97$) and differs between depths (ANOVA, $df = 3$, $n = 397$, $F = 6.702$, $p < 0.00$), although differences are very small (Fig. 6). The light received by colonies in the exposed part of the popula-

tion (ex; white markers in Fig. 6; see Table 1) is also identical for species at the same depth (ANOVA, $df = 3$, $n = 259$, $F = 1.086$, $p < 0.37$), but differs greatly between depths (ANOVA, $df = 3$, $n = 259$, $F = 467.34$, $p < 0.00$). In *M. decactis* the preference for cryptic or exposed positions is less obvious compared to the other *Madracis* species (Table 1) since approximately half of the colonies is found in the exposed fraction, and the other half in the cryptic fraction. We found no difference in the light preferences of the brown and the green morph of *M. pharensis* (ANOVA, $df = 1$, $n = 300$, $F = 0.073$, $p < 0.79$).

Light strategies

In general *Madracis* species are able to survive over a broad light range, but they show strong preference for a subset of the total light range over which a species is found. Since some species strive for maximum light capture (*M. mirabilis*, *M. formosa* and *M. carmabi*), and because maximum available light depends on depth, such preferred subsets of light values depend on depth. Other species prefer a cryptic light regime, which is a subset of the light range found at every depth (*M. pharensis* and *M. senaria*).

In the genus *Madracis*, 3 light strategies in relation to light availability emerge: (1) Species strive for maximum light capture and occur above a threshold light value. This limits their distribution towards greater depths (*M. mirabilis*). (2) Species strive for maximum light capture but occur below a threshold light value.

Their distributions are therefore limited to the deeper parts (>30 m) of the reef slope (*M. formosa* and *M. carmabi*). (3) Species occur over the entire reef slope in low light habitats (*M. pharensis* and *M. senaria*). Although positional shifts, from cryptic to exposed positions, occur at greater depths (>30 m, Fig. 4), the amount of light received in these positions is the same at greater depth (Fig. 6). The positional shift therefore does not result in increased light capture and probably results from: (1) a decrease in the number of Positions 3 to 5, due to a simpler reef morphology at great depths; and (2) reduced competition for exposed positions at great depths. The characterization of a species light strategy is essential if one wants to relate a species' morphological or ecological characteristics to light.

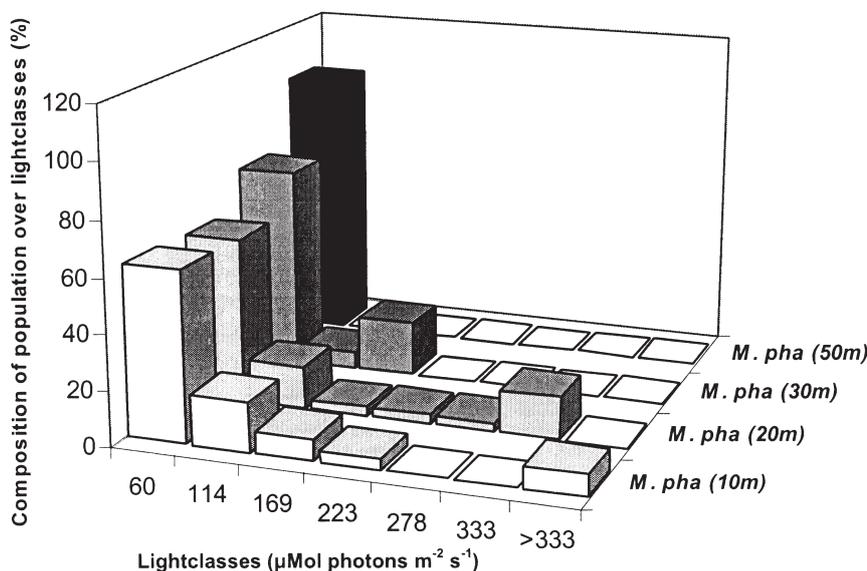


Fig. 5. The bimodal light distribution of *Madracis pharensis* colonies at depths 10, 20, 30 and 50 m

Table 1. Results of the *K*-means clustering of bimodal light distributions for *Madracis pharensis* (morphotypes 1 and 8), *M. decactis* and *M. senaria*. There is no separation in the populations of *M. mirabilis*, *M. carmabi* and *M. formosa* since these species only occur in well-lit positions on the reef. ex: exposed; cr: cryptic

Species	Depth (m)	F-value	% Diff.	Position	n	Minimum	Maximum	Mean	SD	% frac
<i>M. pharensis</i> (1)	10	320.0	749.5	cr	46	10.5	191.3	58.3	45.1	92.0
				ex	4	447.8	595.9	495.4	68.1	8.0
<i>M. pharensis</i> (1)	20	815.6	489.6	cr	51	1.5	127.0	48.7	23.9	78.5
				ex	14	191.1	320.4	287.0	38.8	21.5
<i>M. pharensis</i> (1)	30	570.2	509.7	cr	40	4.6	87.6	25.8	17.0	80.0
				ex	10	145.3	165.9	157.4	6.7	20.0
<i>M. pharensis</i> (1)	50	362.9	182.7	cr	36	10.4	28.2	16.0	5.0	69.2
				ex	16	31.6	48.2	45.3	5.3	30.8
<i>M. pharensis</i> (8)	20	595.6	497.0	cr	39	12.1	140.6	48.2	28.4	75.0
				ex	13	225.3	334.7	287.5	36.9	25.0
<i>M. pharensis</i> (8)	30	1506.7	642.0	cr	41	2.1	48.9	21.7	10.5	80.4
				ex	10	146.1	172.2	160.9	8.8	19.6
<i>M. pharensis</i> (8)	50	428.7	-65.0	cr	24	10.4	31.3	17.1	6.8	48.0
				ex	26	38.0	54.7	48.9	3.8	52.0
<i>M. senaria</i>	20	1153.2	633.1	cr	34	5.2	160.9	42.1	27.2	66.7
				ex	17	218.7	332.6	308.3	24.6	33.3
<i>M. senaria</i>	30	744.3	429.7	cr	25	10.9	84.6	30.4	18.0	48.1
				ex	27	104.8	186.8	161.0	16.6	51.9
<i>M. senaria</i>	50	295.3	125.5	cr	26	10.5	33.5	21.4	7.9	44.1
				ex	33	39.3	55.0	48.1	3.8	55.9
<i>M. decactis</i>	10	333.7	451.9	cr	20	9.1	293.2	94.9	74.8	37.0
				ex	34	327.0	626.6	523.5	87.8	63.0
<i>M. decactis</i>	20	651.9	420.6	cr	16	13.9	163.5	57.1	38.5	30.2
				ex	37	210.3	341.1	297.4	28.0	69.8
<i>M. formosa</i>	50	-	-	ex	48	39.3	52.3	47.3	2.6	100.0
<i>M. mirabilis</i>	5			ex	50	804.8	804.8	804.8	0.0	100.0
<i>M. mirabilis</i>	10			ex	23	588.9	590.1	589.5	0.3	100.0
<i>M. carmabi</i>	20			ex	12	263.6	349.7	314.6	27.6	100.0
	30			ex	24	157.7	166.9	163.4	2.8	100.0

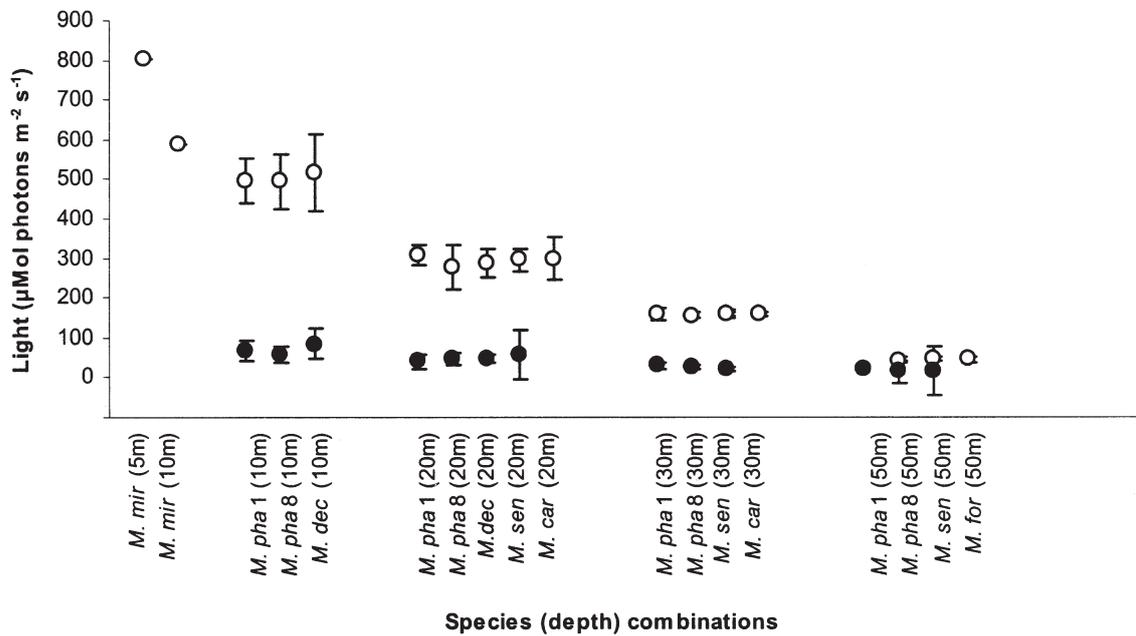


Fig. 6. Mean light (± 1 SD, in $\mu\text{mol photons m}^{-2} \text{s}^{-1}$) received by colonies in the exposed (O) and cryptic (●) fractions of the population for 6 *Madracis* species over their depth range

Table 2. The relation between morphology (colony relief) and irradiance (PAR) for 6 *Madracis* species

Species	R ²	n	p-value
Strategy 1: Species striving for maximum light capture, limited at lower end of depth distribution			
<i>M. mirabilis</i>	0.01	100	0.24
Strategy 2: Species striving for maximum light capture, limited at upper end of depth distribution			
<i>M. formosa</i>	0.00	55	0.67
<i>M. carmabi</i>	0.03	50	0.23
Strategy 3: Species striving for low light habitats, large depth distribution			
<i>M. pharensis</i>	0.37	217	<0.01
<i>M. senaria</i>	0.38	215	<0.01
<i>M. decactis</i>	0.47	100	<0.01

Morphological variation

The 3 different light strategies are reflected in the relation between colony morphology and light availability (Table 2). There are 2 main strategies. Species that strive for maximum light capture (*Madracis mirabilis*, *M. formosa* and *M. carmabi*) show morphological invariability under different light regimes ($R^2 < 0.03$), whereas in cryptic species (*M. pharensis*, *M. senaria* and *M. decactis*), colony morphology changes in relation with light. In the 3 cryptic species, 37 to 47% of the variation in colony morphology is related to the amount of light they receive (Table 2).

Only in *Madracis decactis* and *M. pharensis* does this change in morphology result in taxonomic problems, because of overlapping species definitions in the species descriptions of Wells (1973a). Here, we treat the 2, namely *M. decactis* and *M. pharensis*, as a species complex, with the original Latin names indicating the 2 most dominant morphologies. The characterization of *M. decactis* and *M. pharensis* as 1 entity is supported by genetical data (Diekmann et al. 2001).

Our data show that the use of depth as a proxy for light easily results in wrong conclusions. For example, variation in the morphology (i.e. relief) of *Madracis pharensis* and *M. senaria* does not change with depth (ANOVA, $df = 3$, $n = 200$, $F > 6.702$, $p > 0.81$). The range of light values available at 1 depth is important. Table 2 indicates that colony morphology relates to the amount of light that colonies receive, within 1 depth, on a small spatial scale.

In the species with a large depth distribution, preferring low light habitats, colonies tend to occur in 2 modes (at Positions 1 and 3). The colonies in these modes, exposed and cryptic (Fig. 6) in *Madracis pharensis*, *M. senaria* and *M. decactis*, differ in colony relief (Fig. 7). The relief in the cryptic fraction is always lower (i.e. closer to 1) than that in the exposed fraction. This difference is significant for all 3 species (Mann-Whitney *U*-test, $U > 179$, $p < 0.011$).

DISCUSSION

Light distribution

Within any depth, all light habitats between the maximum (i.e. downcoming) light, described by the extinction coefficient (k'), and values near absolute darkness can be found. With increasing depth, surface irradiance fluctuations become damped (Fig. 3) and the spatial asymmetry in irradiance pattern decreases. Absolute differences in the amount of light received at different positions become small below 30 m (Fig. 2). The overall reduction in light variability with depth has

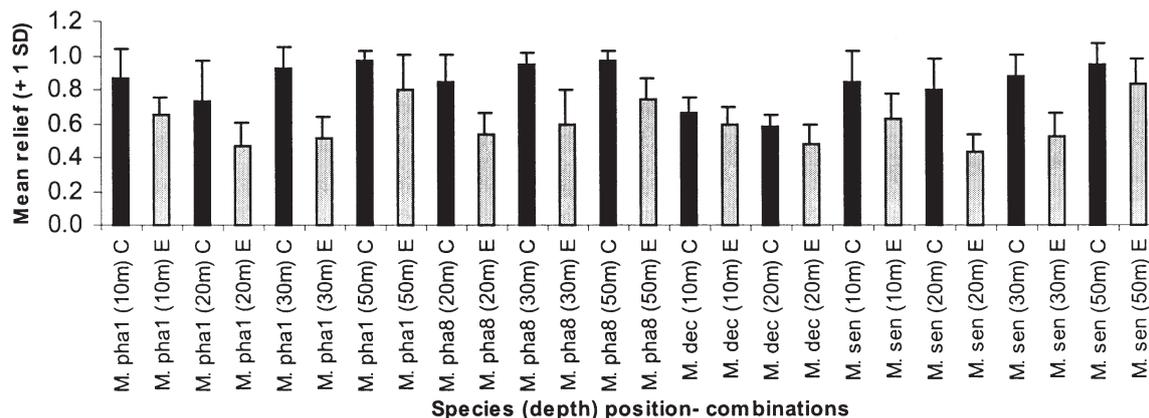


Fig. 7. Mean colony relief (± 1 SD) for the exposed (E) and cryptic (C) fractions of the population for 3 *Madracis* species, including 2 *M. pharensis* morphotypes. A value near 1 indicates a flat surface, a value near 0 maximum relief

consequences for processes that use changes in light as a temporal cue (e.g. timing of reproduction, Van Veghel 1994), as a spatial indication (e.g. coral settlement; Maida et al. 1994, Mundy & Babcock 1998) and as a directional aid (e.g. in determining colony morphology; Muko et al. 2000).

Small differences in light regimes, e.g. in water transparency, have their greatest effect at the deep reef. An extreme example of a zooxanthellate reef coral at the lower limit of its depth distribution was a *Madracis pharensis* colony we observed at a depth of 133 m (M.J.A.V. pers. obs.). When k' is -0.063 , this species appears to survive at 0.26% surface light. With a decrease in transparency, i.e. a small increase in k' of 0.01 (i.e. higher extinction value), the depth corresponding to 0.26% surface light moves upward with 18.2 m. If transparency increases, i.e. k' decreases (0.01), the depth corresponding to 0.26% surface light moves downward 25.1 m. Such small changes result in a difference in the depth, corresponding to the 0.26% surface light value, of >40 m (18.2 + 25.1 m). The unequal difference in depth change, caused by the 2 respective changes in k' , is due to the exponential decrease of light with depth. The example of our deep *M. pharensis* colony shows that the underlimit of coral species, expressed in depth (m), depends on subtle differences in the optical conditions of their overlying water column.

Changes in light variation during the year (Fig. 3) affect the behavior of organisms that use local light intensity to identify suitable habitats for settlement (Maida et al. 1994, Mundy & Babcock 1998). The suitability of such habitats is partially determined by the minimum amount of light needed for survival. This minimum value can only be determined during the period when light levels reach their yearly minimum values. In the Caribbean, this occurs in November-December, directly after the reproductive period of the majority of coral species (October-November). The offspring of these species settle during the yearly minimum in irradiance. Recruits that select future habitats based on light quality consequently reduce the chance of choosing a death trap, i.e. a habitat where light intensity drops below the minimum level to survive later in the year.

Depth as a proxy for light

The data clearly illustrate that the use of depth as a proxy for light can result in misinterpretations of the relation between coral species and light. Relating morphological/ecological information to depth is only allowed for species that show strict preference for exposed positions (Position 1), growing towards the downcoming light (e.g. *Madracis mirabilis*, *M. formosa* and *M. carmabi*). Furthermore, colonies must be free-standing, i.e. free from shading or reflectance by other reef components. For *M. pharensis* and *M. senaria*, depth cannot even approximately be used as a proxy for light. Analyzing the colony morphology (relief) of *M. senaria* and *M. pharensis* with depth as an indicator of light, would lead to a Type II error. We would conclude that these species have a broad light range given their large depth distribution and that their morphology is insensitive to light since variation in colony relief is the same at all depths. Both conclusions prove to be false. Firstly, we see that *M. pharensis* (Fig. 5, Table 1) and *M. senaria* (Table 1) colonies prefer a restricted light range and are found mostly ($68 \pm 16\%$, mean \pm SD, $n = 10$) in the lowest light category (5 to 60 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$). Secondly, the morphology of both *M. pharensis* and *M. senaria* relates to small scale, isobathic light differences (Table 3). It is a surprising paradox that species which live over the smallest light ranges also have the greatest depth range.

A second mistake that is easily made when differences in light strategies are not considered can be illustrated using *Madracis mirabilis*. This species occurs in an absolute light range of 491 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ (313 to 804 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$), almost 7 times wider than that of *M. pharensis* and *M. senaria*. *M. mirabilis* survives in a wide light range but occurs in a relative restricted depth range of 15 m (5 to 20 m), whereas *M. pharensis* and *M. senaria* occur from 5 m until >50 m.

The presence of various light strategies shows that a proper determination of a species' relation to light is essential to understanding related aspects in the ecology/morphology of corals. Failure to recognize these strategies (Table 4) will result in: (1) an underestima-

Table 3. Increasing sensitivity to irradiance of *Madracis pharensis* (morphotypes 1 and 8) and *M. senaria*. With increasing depth, expressed as the variation in colony relief explained by differences in irradiance received

Depth (m)	Species: <i>M. pharensis</i> 1		<i>M. pharensis</i> 8		<i>M. senaria</i>	
	R^2 ($\times 100\%$)	p-value	R^2 ($\times 100\%$)	p-value	R^2 ($\times 100\%$)	p-value
10	26.00	0.000	No data		27.00	0.000
20	28.00	0.000	31.00	0.000	26.00	0.000
30	28.00	0.000	28.00	0.000	41.00	0.000
50	66.00	0.000	68.00	0.000	75.00	0.000

Table 4. Overview of light strategies present within the genus *Madracis*

Strategy	Main light preference	Distribution on reef	Morphology
1	Maximum	Shallow	Insensitive to light
2	Maximum	Deep	Insensitive to light
3	Minimal	Entire reefslope	Sensitive to light

tion of species' light-related morphological variation; and (2) an overestimation of species' light tolerance.

Evolutionary implications

The characterization of corals into separate species is not always easy (e.g. Lang 1984) and in *Madracis*, the distinction between *M. pharensis* and *M. decactis* as different species is debated (e.g. Diekmann 2001). They have an overlapping distribution (Vermeij & Bak unpubl.) over the reef slope. *M. decactis* has a light strategy close to *M. pharensis* and *M. senaria* (Strategy 3). Approximately half of the *M. decactis* colonies prefers exposed positions while the other half is found in cryptic habitats. *M. decactis* becomes rare at 30 m and is not often found in deeper reef parts.

Fenner (1993) and Zlatarski & Estalella (1982) state that based on morphological similarities at the corallite level, *Madracis pharensis* and *M. decactis* are identical species. Diekmann et al. (2001), analyzing colonies from our study site, found no genetic difference between the 2 species using ITS sequences of rDNA. The absence of genetic differentiation indicates that *M. pharensis* and *M. decactis* form a species-complex. Fenner (1993) suggested that *M. pharensis* and *M. decactis* represent 2 ecomorphs with different light preferences. *M. pharensis* would be the cryptic morph and *M. decactis* would be the morph that prefers exposed positions. This is not confirmed by our results. We found many *M. decactis* in cryptic habitats (Figs. 4 & 6), which indicates that the phenotype-environment match is not as strict as proposed by Fenner (1993).

Other factors, besides light, that can influence colony morphology in corals are water movement (Kaandorp 1999) and sedimentation (Young & Elias 1999). These processes are of minimal importance at our study site relative to the role of light (Vermeij & Bak in press). Increased water movement should result in more compact growth forms on exposed positions; however, this is opposite to what we observe, i.e. high relief (nodular) colonies are found at these positions. No relation was found in Curaçao (Van Veghel 1994) between morphology and sedimentation due to large fluctuations in sedimentation rate over both horizontal and

vertical scales. In addition, sedimentation depends on water movement (Jokiel & Morrissey 1993) and therefore cannot explain the presence of nodular colonies in both exposed and cryptic positions, if such morphology was dependent on the degree of sedimentation.

Moran (1992) shows that developmental systems, such as morphological growth patterns, are often flexible enough to establish simple polyphenisms if environmental conditions are favorable. However, many factors can prevent the evolution of a strict phenotype-environment matching. The relative frequencies of the different environments (i.e. exposed and cryptic habitats in our case), the fitness relations of the alternative phenotypes in the different environments and the possible cost of plasticity, all determine the outcome of this interaction. An increase in colony relief relates to increasing light for both *Madracis pharensis* and *M. decactis*, suggesting overall morphological sensitivity to light within the species-complex (Fig. 7). Selection leads to genetical fixation if each of the 2 phenotypes has a higher fitness in its particular light environment (i.e. being flat is more advantageous in cryptic habitats than a nodular morphology and vice versa for exposed habitats; Moran 1992). The isobathic bimodal distribution of the colonies of each species over a light range (Fig. 6) can therefore indicate the onset of speciation (Stearns 1992). This suggests the possible evolutionary role of light in the formation of new coral species.

We therefore consider *Madracis pharensis* and *M. decactis* as 1 species complex whose morphological plasticity is related to, but not totally explained by, differences in light that colonies receive.

CONCLUSION

Our results show that variation in light levels caused by reef structural complexity at a small spatial scale (1 to 10 cm) is as important as light differences related to depth. Over an isobathic light range, 3 of 6 species are characterized by bimodal distributions, where one part of the population prefers light exposed positions and the other part cryptic low light positions. Three different light strategies were found in the genus *Madracis*, which may also characterize the relation between morphology, distribution and light availability in other coral species. If differences in light strategies are ignored, coral behavior or dependence on light may be misunderstood. We show that light Strategies 1 and 2 (colonies striving for maximum light capture, colony morphology independent of light) can be confused with Strategy 3 (colonies in cryptic light habitats, colony morphology related to light). Light availability depends on 2 factors, depth and isobathic light variation caused by structural complexity. Each of

these can be the deciding factor in understanding the morphology and distribution of a coral species. In addition, the overall importance of light in coral biology is indicated by its possible role in evolutionary processes, as shown in the *M. pharensis/decactis* species-complex.

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