Evolutionary Ecology of the coral genus Madracis - an illustration of the nature of species in scleractinian corals
Vermeij, M.J.A.

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Chapter 5

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

Vermeij M.J.A. and R.P.M. Bak
ABSTRACT We studied the relation of light with coral colony morphology and coral distribution over a 5 to 50m reef slope. We describe the characteristics of 6 species of the genus Madracis in relation to the light (PAR, 400-700nm) colonies receive at a small spatial scale (1-10cm). Species differ in their response to light but we could distinguish three strategies: (1) Species strive for maximum light capture and colonies occur above a threshold light value. This limits the distribution of such species towards greater depths. These species are found in shallow (<15m) 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 (>30m) 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 (5-60 μMol photons m² 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 is ranging 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 10cm 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.

INTRODUCTION

Environmental factors influence the ecology, physiology and morphology of zooxanthellate scleractinian corals. Frequently studied factors include: salinity (Coles and Jokiel 1988), temperature (Coles and Jokiel 1988, Meesters and Bak 1993), dissolved oxygen concentration (Coles and Jokiel 1988), water motion (Jokiel 1978, Dennison and Barnes 1988), light quality (Falkowski et al. 1990) and quantity (review by Falkowski et al. 1990, Barnes and Chalker 1990). Although corals respond to the entire suite of factors mentioned above, light has been regarded to play a key role.
role in coral ecology (Veron 1995). Light affects aspects such as coral
settlement (Maida et al. 1994, Mundy and Babcock 1998), movement
(Yamashiro and 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-
zoanthellate complex (Chalker et al. 1983, Gattuso 1985, Jokiel 1986,
Hidaka 1988, Falkowski et al. 1990, Iglesias-Prieto and Trench 1997,

A change in the amount of light received by a colony has physiological
consequences and often requires morphological adaptations to maximize
light capture (Graus and McIntyre 1992). 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 and 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. For corals, Roos (1967, 1970) pioneered the role of submarine
light in their ecology. Roos (1967) and Brakel (1976) clearly indicate that
spatial heterogeneity, at the 1-10cm 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 three pacific coral species
occurred over different but greatly overlapping light ranges, ranging
between 90-50% to 5-1% surface light (PAR). This large range has been attributed to adaptational mechanisms at the cellular level. However, 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 six species (Wells 1973a, b, Vermeij et al. submitted) 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 reef slope (> 50m, Vermeij and Bak, submitted). Despite the large depth range all species harbour type-B zooxanthellae (Diekmann et al. in press). All species are easily distinguished based on morphology. 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 (Fenner 1993, Zlatarski and Estalella 1982, 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 two 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 asks for 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:
- What is the variation in light (that colonies receive at a certain depth)?
- How is the distributional pattern of a species related to its light preference?
- Is variation in colony morphology really related to light?
- Is the relation between ecological and morphological characteristics with light species specific?

Chapter 5 Marine light environment and *Madracis*
To answer these questions we relate the distribution and colony morphology of six *Madracis* species to the amount of light they receive at a small spatial scale at various depths over a reef slope from 5 to 50m.

**MATERIAL 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. subm.) were determined measuring 50 colonies of each species in each of 6 isobathic transects over a 50m depth gradient. Transects were placed at 5, 10, 20, 30, and 50m 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:

(1) **relief:** (shortest distance between two 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 1$^{st}$ order branching to encrusting) we used relief as an indicator of colony morphology.
(2) **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, (5): in small caves or holes, receiving no direct sunlight.

(3) **light environment:** defined as the light a colony receives from the three main spatial directions and determined according to the following protocol:

**Light measurements:** 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 400-700nm. The sensor is cosine corrected to provide a measure of the irradiance in $\mu$Mol photons m$^{-2}$ 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 $\mu$Mol photons m$^{-2}$ s$^{-1}$, reaching a colony was measured *in situ* in three directions:

1. coming in straight from above ($\alpha=0^\circ$);
2. coming from aside ($\alpha=90^\circ$);
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 (12h00-14h00) in May and June 1998. We measured light at every second and integrated every measurement with the five previous ones to minimise the effects of fast light fluctuations caused by refraction at the sea surface. Since weather- or watercolumn conditions differed slightly between days we standardised our data following Jaubert and 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 at May 6$^{th}$ 1998, assuming that the proportion between the measurements and the reference value was identical. On May 6$^{th}$, 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 three different directions ($\alpha=0^\circ$, $\alpha=90^\circ$, $\alpha=180^\circ$) taken at 10cm depth intervals over a 50m 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:

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

with $t =$ time; $z =$ depth; $d =$ direction

if (1) $95\% \text{Value}_{(\text{May 6th},z)} < \text{Reference value}_{(t,z)} < 105\% \text{Value}_{(\text{May 6th},z)}$

(2) Reference value$_{(t,z)}$BEFORE MEASURING = Reference value$_{(t,z)}$AFTER MEASURING

**Morphospecies definition.** For *M. mirabilis*, *M. senaria* and *M. formosa* we used the morphological descriptions from Wells (1973a,b). Based on genetic data (Diekman et al. 2001), *M. pharensis* and *M. decactis* are considered as one species complex. The latin names are used to indicate the two 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 two 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 sept) and *M. formosa* (branching morphology). We distinguish this morph as *M. carmabi* (described by Vermeij et al. submitted).

**Statistical analysis.** Multiple 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 three species showed bimodal distributions with one 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 two modes, we treat the modes separately. This results in a subdivision of these three 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 maximising between-cluster variation relative to within-cluster variation. It is similar to a one-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 6th 1998 over a 50m depth gradient (n = 541 measurements for each direction) is shown in Fig. 2. The largest decrease in ambient light occurs in the first 10m, where 65-70% of the incident surface light is absorbed or reflected. The extinction-coefficient ($k'$) of the local watercolumn was -0.063 for downfalling 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 irradiance pattern with depth. In shallow water this asymmetry results from a bulge in the irradiance pattern towards the sun. The increased symmetry of the irradiance pattern with depth has also consequences for seasonal fluctuations in solar energy. In Fig. 3 the yearly fluctuation of solar irradiance is calculated for various depths at Buoy 1.
Figure 3. Seasonal change in irradiance pattern at 10m isobaths from the surface to 60m depth (50 and 60m not indicated in graph).

(data Curacao Meteorological Service) using the extinction-coefficient for Buoy 1 of May 25th 1998. Obviously, irradiate solar energy shows no seasonality in deeper water.

A wide light range is available for organisms, within one depth, in shallow water (Fig. 2). The available light range is rapidly narrowing and at 30m it is 18% of the 5m 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 μMol photons m⁻² s⁻¹ can be found in cryptic habitats at every depth over our 50m-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 is decreasing with depth since maximum light (i.e. down coming, α=0°) is decreasing exponentially (Fig. 2).

**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 (position 3, 4 and 5). The strategy of *M. decactis* is intermediate and approximately half of the colonies are found in exposed, the other half in cryptic positions. The positions on the substratum for all species are given in Fig. 4.
Figure 4. Positions of colonies per depth as the percentage of the population occupying each of five positions. The positional range includes light exposed positions (position 1) to low light habitats (position 5).
The majority of colonies of species that prefer direct sunlight, such as *M. mirabilis* above 20m and *M. formosa* below 30m, are found at position 1 and 2. Colonies of species preferring cryptic environments, such as *M. pharensis*, occur mainly in positions 3 to 5. The light variation at position

3 and 1 starts overlapping below 30m (respectively 186-5 and 61-2 µMol photons m\(^{-2}\) s\(^{-1}\)) 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 below 30m. However, “exposed” and “cryptic” are 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. Furthermore, *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 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 *M. 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 (position 3 to 5).

For bimodally distributed data averages and standard deviations carry no biological meaningful information. Therefore we described the two modes individually. We used K-means clustering (Systat 9.0) to assign the

Table 1. Results of the K-means clustering of bimodal light distributions for *M. 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 on well lit positions on the reef.

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<td>100.0</td>
</tr>
<tr>
<td><em>M. mir</em></td>
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<td>-</td>
<td>-</td>
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<td>50</td>
<td>804.8</td>
<td>804.8</td>
<td>804.8</td>
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<tr>
<td><em>M. mir</em></td>
<td>10</td>
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<td>-</td>
<td>ex</td>
<td>23</td>
<td>588.9</td>
<td>590.1</td>
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<td><em>M. car</em></td>
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<td>-</td>
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<td>163.4</td>
<td>2.8</td>
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</table>
colonies to each mode (Table 1). The different strategies of *M. mirabilis*, *M. formosa* and *M. carmabi* on one side and of *M. pharensis*, *M. decactis* and *M. senaria* on the other are illustrated by Fig. 6. The unimodal distribution of the first three species is indicated by one marker per depth (Fig. 6). The second group of species shows a bimodal distribution of colonies over successive light classes. The two modes are indicated by

![Graph showing mean light (+/- 1 SD, in µMol photons m² s⁻¹) received by colonies in the exposed (○) and cryptic (●) fractions of the population for six *Madracis* species over their depth range.]

Figure 6. Mean light (+/- 1 SD, in µMol photons m² s⁻¹) received by colonies in the exposed (○) and cryptic (●) fractions of the population for six *Madracis* species over their depth range.

two 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 (Tab. 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 population (white markers in Fig. 6, regular lettering in Tab. 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 (Tab. 1) since approximately half of the colonies is found in the exposed fraction, the other half in the cryptic fraction. We found no difference in the light

Chapter 5 Marine light environment and *Madracis*
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, M. carmabi*), and because maximum

<table>
<thead>
<tr>
<th>Table 2. The relation between morphology (colony relief) and irradiance (PAR) for 6 <em>Madracis</em> species.</th>
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</thead>
<tbody>
<tr>
<td>Species</td>
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<tr>
<td>-------------------------------------</td>
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<tr>
<td><strong>Strategy I:</strong> Species striving for maximum light capture, limited at lower end of depth distribution</td>
</tr>
<tr>
<td><em>M. mirabilis</em></td>
</tr>
<tr>
<td><strong>Strategy II:</strong> Species striving for maximum light capture, limited at upper end of depth distribution</td>
</tr>
<tr>
<td><em>M. formosa</em></td>
</tr>
<tr>
<td><em>M. carmabi</em></td>
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<tr>
<td><strong>Strategy III:</strong> Species striving for low light habitats, large depth distribution</td>
</tr>
<tr>
<td><em>M. pharensis</em></td>
</tr>
<tr>
<td><em>M. senaria</em></td>
</tr>
<tr>
<td><em>M. decactis</em></td>
</tr>
</tbody>
</table>

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, M. senaria*). In the genus *Madracis* three 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 (>30m) of the reef slope (*M. formosa, M. carmabi*). (3) Species occur over the entire reef slope in low light habitats (*M. pharensis, M. senaria*). Although positional shifts, from cryptic to exposed positions, occur at greater depths (>30m, 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, (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.
Morphological variation
The three different light strategies are reflected in the relation between colony morphology and light availability (Table 2). There are two main strategies. Species that strive for maximum light capture (*M. mirabilis*, *M. formosa*, *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 three cryptic species 37-47% of the variation in colony morphology is related to the amount of light they receive (Table 2).

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

Our data shows 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 *M. 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 one depth is important. Table 3 indicates that colony morphology relates to the amount of light that colonies receive, within one depth, on a small spatial scale.

![Figure 7. Mean colony relief (+ 1 SD) for the exposed (E) and cryptic (C) fractions of the population for three Madracis species, including two M. pharensis morphotypes. A value near 1 indicates a flat surface, a value near 0 maximum relief.](image-url)
In the species with a large depth distribution, preferring low light habitats, colonies tend to occur in two modes (at positions 1 and 3). The colonies in these modes, exposed and cryptic (Fig. 6), in *M. 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 one) than that in the exposed fraction. This difference is significant for all three species (Mann Whitney U-test, U > 179, p < 0.011).

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

| Species | *M. pharensis* 1 | | | *M. pharensis* 8 | | | | *M. senaria* | |
|---------|-----------------|---|---|-----------------|---|---|-----------------|---|
| depth (m) | \( R^2 \times 100\% \) | 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 |

**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 30m (Fig. 2). The overall reduction in light variability with depth has 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 and 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 *M. pharensis* colony we observed at a depth of 133m (Vermeij, pers. obs.). With \( k' \) being -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 18.2m. If transparency increases, i.e. \( k' \) decreases (0.01), the
depth corresponding to 0.26% surface light moves downward 25.1m. Such small changes result in a difference in the depth, corresponding to the 0.26% surface light value, of more than 40m (18.2 +25.1m). The unequal difference in depth change, caused by the two respective changes in k', is due 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 watercolumn.

Changes in light variation during the year (Fig. 3) affect the behaviour of organisms that use local light intensity to identify suitable habitats for settlement (Maida et al. 1994, Mundy and 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 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 settles 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 = light?**

The data clearly illustrates 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. M. 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 can not even approximately be used as a proxy for light. Analysing 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. We see that M. pharensis (Fig. 5 and Tab. 1) and M.senaria (Tab.1) colonies prefer a restricted light range and are found mostly (68±16%, mean ± SD, n = 10) in the lowest light category (5 – 60 μmol photons m⁻² s⁻¹). Secondly, the morphology of both M. pharensis and M. senaria relates to small scale, isobathic light differences (Tab. 3). It is a surprising paradox that the species living over the smallest light ranges, have the greatest depth range.
A second mistake that is easily made when differences in light strategies are not considered can be illustrated using *M. mirabilis*. This species occurs in an absolute light range of 491 µMol photons m\(^{-2}\) s\(^{-1}\) (313-804 µMol photons m\(^{-2}\) s\(^{-1}\)), almost seven 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 15m (5-20m), whereas *M. pharensis* and *M. senaria* occur from 5m till more than 50m. The presence of various light strategies shows that a proper determination of a species relation to light is essential to understand related aspects in the ecology/morphology of corals. Failure to recognise these strategies (Tab. 4) will result in: (1) an underestimation 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 and Bak, submitted) over the reef slope. *M. decactis* has a light strategy close to *M. pharensis* and *M. senaria* (Strat. III). Approximately half of the *M. decactis* colonies prefer exposed positions while the other half is found in cryptic habitats. *M. decactis* becomes rare at 30m and is not often found in deeper reef parts.

Fenner (1993) and Zlatarski and Estalella (1982) state that based on morphological similarities at corallite level *M. pharensis* and *M. decactis* are identical species. Diekmann et al. (2001), analyzing colonies from our study site, found no genetic difference between the two species using ITS-sequences of mDNA. 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 two 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 (Fig. 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 1999). These processes are of minimal importance at our study site relative to the role of light (Vermeij and Bak subm). Increased water movement would result in more compact growth forms on exposed positions, which is opposite to what we observe: high relief (nodular) colonies are found at these positions. No relation was found in Curaçao (Van Veghel 1994) between morphology and sedimentation due large fluctuations in sedimentation rate over both horizontal and vertical scales. Also, sedimentation depends on water movement (Jokiel 1993) and therefore can not explain the presence of nodular colonies in both exposed as 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 *M. 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 two 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 be an onset to speciation (Stearns 1992). This suggests the possible evolutionary role of light in the formation of new coral species.

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

Our results show that variation in light levels caused by reef structural complexity at a small spatial scale (1-10cm) is as important as light differences related to depth. Over an isobathic light range, three of six species are characterised 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 characterise the relation between morphology, distribution and light availability in other coral species. If differences in light strategies are ignored, coral behaviour or dependence on light may be misunderstood. We show that light strategies 1 and 2 (colonies striving for maximum light capture, colony morphology independent on light) can be confused with strategy 3 (colonies in cryptic light habitats, colony morphology related to light). Light availability depends on two 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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CITED LITERATURE

Jaubert JM and Vasseur P (1973) Essai d'interprétation de la répartition de certain peuplements sciaphiles du "Grand Recif" (Tulear, Madagascar) a partir d'


Vermeij MJA and Bak RPM (Submitted) Species-specific population structure of closely related coral morphospecies along a depth gradient (5-60m) over a Caribbean reef slope. Bull Mar Sc.


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