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Photosynthesis and Photoadaptation

The interplay of light, photosynthesis and photoadaptation plays an important role in reefkeeping.

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As reef hobbyists we are all very aware of the need for lighting our aquariums. Many of us have observed that when placed in our aquariums, the ability of small-polyped stony (SPS) corals to adapt depends on the lighting conditions. They thrive under certain light conditions, change color with differing locations in the tank, and, occasionally, shaded portions of the coral die when reoriented in the tank — just to name a few light related observations about the corals. We can get a better understanding of these observations by looking at the three interrelated phenomenon — light, photosynthesis and photoadaptation. By looking at the variation in light between nature and our aquariums, we can see the differences in the environment between natural coral reefs and our captive microcosms, and marvel at the adaptability of these creatures. This article primarily draws information from the scientific literature, but I have tried to keep the discussion at a level suited to average aquarists. Also, where possible, I have added information on its relevance and implications to the reef aquariums that we keep.

Light plays an important role in the development of coral reefs, as well as to the well-being of the corals. As early as the 19th century it was thought that light was a key variable in limiting coral reefs to shallow waters. Light influences the response to photosynthesis, the rate of calcification and also plays a role in the reproductive cycle.

Light

Without getting into the physics of light, let us take a look at the underwater light field in the ocean and see how well it is simulated or replicated in our aquariums. The two aspects of light that we are often concerned with are the quantity of light and the spectral quality of light.

Quantity of Light

The quantity of light is often termed irradiance and is defined as “the amount of light energy (radiant flux) incident on an infinitesimal element of a surface, containing the point under consideration, divided by the area of that element.” (Kirk 1994) Usually, two types of measures are used to measure the irradiance. One is quantum units — quanta (or photons) per square meter per second, where quanta are measured in micro-Einsteins, in which 1 Einstein is 1 mole of photons. Second is energy units — watts per square meter.

Quantum units are often used in photosynthetic measurements, while energy units are used in calculating energy budgets. Conversion between the two is possible, but requires knowledge of the spectral distribution of the light. Most common reef aquarium literature deals with light measurements in lumens, lux, watts/gallon — measures that are typically derived and based on standard lighting industry data. Because we are typically concerned with providing light to our aquariums primarily for the photosynthetic needs of the corals, the most appropriate measure is the quantum units, and, more specifically, we need to know the amount and quality of light available for photosynthesis. This measure of the amount of light that is frequently used is called photosynthetically available radiation (PAR), which I will discuss later when covering photosynthesis.

For excellent information on the lights we use and their PAR values, readers are directed to the writings by Dana Riddle and Richard Harker.

The underwater light at any given point depends on several variables that arise due to the physics of light traveling through the water, the water quality itself and the structure of the reef. When the light hits the water surface, some of it is reflected back and some of it enters the water. The amount of light entering the water depends on the angle of incident light and the surface characteristics of the water. The angle of incidence varies throughout the day as the sun moves across the sky. In addition, there are seasonal changes due to the movement of the sun between the two tropics. The angle of the sun impacts reef ecology — some reef organisms may be shaded during some part of the day, and in bright light during other parts of the day. This effect is more pronounced in shallower waters.

At greater depths the direction of light becomes less sensitive to the sun’s position and moves toward the vertical as depth increases. So, the direction of light reaching the deeper corals is not affected by the change in the sun’s position. However, the intensity of light may change due to the relationship between the angle of incidence and refraction.

The light reaching the corals is not consistent. This is one aspect of natural light that is not simulated in most of our aquariums. We typically subject the corals to almost constant light intensity with a fixed angle of incidence. So, clearly, our corals must adapt to this, and is one of the photoadaptations that the corals must accomplish.

The movement of the sun can be simulated to some extent through the use of light movers, which are available in the hydroponics gardening industry. Light movers that move light in a circular manner or linearly over rails may be used to provide the light variability throughout the day. However, given the fact that most home aquariums are less than 6 feet in length, the effect produced by moving the lights will not be as significant as in nature. Another approach that has been recently developed is the rotating aquarium (Gibbs 1998). Here, instead of rotating the lights, the aquarium is rotated along a central axis.

The light traveling from the top of the water surface toward the bottom is called downwelling light. Some of the downwelling light gets absorbed, and some is scattered by the dissolved and particulate matter in the water and by the water molecules themselves. Turbidity is a term used to describe the amount of particulate matter. The higher the turbidity, the more light that is scattered. The absorption and scattering results in reduction in the quantity of downwelling light as the depth increases.

Further, the scatter also creates some upwelling light (backscattering of light). On coral reefs, the upwelling irradiance is also increased by reflection from the “white” calcium carbonate substrate found on the reef floor. In fact, on coral reefs this upwelling irradiance may be a significant portion of the total irradiance (Dustan 1982). This upwelling light plays a critical role in allowing the growth of corals on the understory of the reefs. Thus, the addition of a white calcium carbonate substrate in a reef aquarium also helps in increasing the upwelling irradiance, while simultaneously increasing the biodiversity. Rather than covering all the sand with live rock, a good strategy would be to provide large open sand areas to increase upwelling irradiance.

In addition to these variations, other natural variations are introduced by meteorological and biological events. The clouds over the reefs modulate the intensity of light. Storms may directly reduce the amount of light reaching the reef and may also stir up the substrate, increasing the turbidity and cutting off light reaching the corals. Seasonal plankton blooms can also increase turbidity of the water. Typically, most home aquariums do not simulate these variations, although some aquarists do introduce a “midday” cloud simulation by shutting off some of the lights randomly during the day for a short period of time. Other devices, such as light dimmers, are also becoming available. These devices will dim the lights to about 25 percent and can also be programmed to create this simulated cloud cover at various times during the day. Whether these variations are beneficial to the corals has not yet been established.

Surface waves also affect the light intensity. The waves can act as a lens and focus the light, creating “glitter lines.” The glitter lines are intense and typically of short duration. They are very visible in shallow water. These glitter lines appear as flashes of light of high intensity and short duration, and have been measured as having up to twice the intensity of light incident on the water surface. This flashing light occurs only in direct sunlight, and does not occur when the light is diffused (as when a cloud obscures the sun). Whether this flashing light is advantageous to the corals or not is not known, but some researchers have found that it enhances photosynthetic performance in some unicellular algae (Falkowski 1982). In reef aquariums, these glitter lines or flashes can be created through the use of point source lights (e.g., metal halide bulbs) and surface agitation of the water. Florescent lighting is more diffuse and does not create these effects. I find the visual effect of dancing glitter lines to be very pleasing.

Spectral Distribution of Light

The word light in common usage typically refers to the electromagnetic radiation in the 400 to 700 nanometer (nm) wavelength range. This is the radiation to which the human eye is sensitive and also coincides with the radiation needed by plants for photosynthesis. The term PAR refers to the amount of light that falls in the range that is suitable for photosynthesis. In addition to the visible light, the sun is also a source of ultraviolet (UV) radiation (200 to 400 nm wavelength) and infrared radiation.

As light passes through the water column, it is attenuated exponentially, and this attenuation is not uniform across all wavelengths. So the water acts as a “filter,” reducing the spectrum of light that penetrates it. As depth increases, the waveband of light that penetrates narrows. The shorter wavelengths (reds and yellows) are the first to be absorbed, and the blue light penetrates the deepest. At a depth of 1 meter, only 50 to 60 percent of the higher wavelength light (600 to 700 nm) penetrates the water, and at a depth of 10 meters less than 10 percent of the higher wavelength light penetrates. By comparison, 92 to 97 percent of the irradiance in the 400 to 575 nm range is transmitted at 1 meter in depth, and 40 to 50 percent of the available spectrum in the range of 400 to 550 nm penetrates to depths of 10 meters (Jerlov 1976). Most of the SPS corals are found in waters less than 15 meters deep, but our reef aquariums are usually 24 to 30 inches deep.

So, we cannot rely on water to create the difference in spectral distribution in the tank and have to rely on the bulbs to provide a “correct” spectral distribution.

The amount of light and spectrum absorbed in the aquarium is often affected by the yellowing pigments or gelvin and the suspended particulate matter. Different wavelengths are absorbed differently. The use of activated carbon and ozone does, in fact, increase the irradiance transmitted through the water, especially in the UV range (Bingman 1996).

In our aquariums, the bulbs used have their own spectral distribution, which may differ considerably from the spectrum of light from the sun. It is very possible that two bulbs rated at the same Kelvin (K) color temperature may have very different spectral distributions.

So, given that the light used does not match the sunlight, this requires yet another kind of photoadaptation that the corals must go through. Figure 1 shows spectral scans of three different 6500 K, 250-watt Iwasaki metal halide bulbs. The plot in green shows the spectral distribution for a new bulb (after the burn in period). The yellow plot (Bulb A) shows the spectral distribution for a bulb that has been used for around 12 months, and the red plot is for another bulb used for 12 months. This is just some preliminary data toward understanding how the bulbs used in our aquariums behave and what their spectral distribution looks like over time. (This spectral scan data was provided by Dave Morgan using a LiCor LI-1800 spectroradiometer).Click image to enlarge

Figure 1.

Photosynthesis

The primary benefit of light to corals is the conversion of PAR into the energy required for photosythesis by the symbiotic zooxanthellae in the coral tissue to produce food. Photosynthetic pigments in the zooxanthellal cells carry out the collection of the light energy, such that they efficiently absorb light in the 400 to 700 nm range. The zooxanthellae contain various types of pigments: chlorophyll a, chlorophyll c and the carotenoids, such as Beta carotene, peridinnine and dinoxanthines. The pigments in the cells will absorb different wavelengths with different efficiencies. The absorption spectrum for zooxanthellae has been shown to have a broad peak in the 400 to 500 nm waveband (blue-green) and a narrow peak in the 650 to 700 (red) waveband.

The light used by the zooxanthellae is a function of the light field and the wavelength-specific absorption spectrum of the various pigments. The term photosynthetically useable radiation (PUR) has been defined as a means to quantify the capability of a cell to use the light available for photosynthesis. Thus, while PAR refers to total photosynthetically available radiation, the PUR concept is based on the speculation that not all cells use this available radiation uniformly, and some cells may be more/less efficient in using certain wavelengths of light. Dustan’s research (1982) states that isolated zooxanthellal cells from corals growing at shallow depths absorb less energy than those from deep waters. Higher absorption with increasing depth may partially offset the decrease in available light. In some corals the density of zooxanthellae may also increase with decreasing light, resulting in the often observed “browning up” of corals in light-deficient tanks.

How does irradiance affect photosynthesis? The rate at which photosynthesis occurs is dependent on the quality and quantity of light, density of zooxanthellae, composition of pigments, temperature and CO2 availability. The rate of photosynthesis is measured either by the O2 released or the CO2 fixed during photosynthesis. Without light, there is no photosynthesis and O2 is consumed and CO2 is released. As light is increased, some CO2 is consumed and O2 released. The point at which the CO2 consumption is the same as the O2 released is called the compensation point.

At the compensation point, the rate of photosynthesis equals the rate of respiration. As the light levels are increased beyond the compensation point, initially the rate of photosynthesis increases almost linearly with the increase in irradiance, but eventually the rate of photosynthesis begins to level off. The range of irradiance values where photosynthesis does not vary with irradiance is called light saturation. The light intensity required for saturation varies from species to species and also depends on other parameters, such as temperature and CO2 concentration.

The plot of photosynthesis as a function of irradiance is called a photosynthesis-irradiance (P-I) curve. These curves are of interest in understanding how an individual coral fares under a given light source. The P-I curves of photosynthesis are different for different corals living in shallow, well-illuminated areas when compared to corals living in shaded or deeper areas. The corals adapted to low illumination have steeper slopes in the initial part of their P-I curves, thus indicating that these corals can reach saturation sooner at lower light levels. This increase is primarily due to an increase in the number of zooxanthellae (Sorokin 1993). In general, these curves are hard to obtain. What is interesting is that photosynthesis may actually be inhibited at high irradiance levels, although photoinhibition has not been reported for corals in the natural environment.

UV radiation is harmful to most zooxanthellae, and the corals harbor pigments that screen out UV to protect the zooxanthellae from radiation damage. UV wavelengths below 300 nm have been shown to severely restrict photosynthesis. Research has shown that the presence of natural solar UV can decrease skeletal growth rate by 50 percent in Pocillopora damicornis (Dubinsky 1990). Corals contain pigments that can either block out UV, reflect UV or absorb the UV, and fluoresce the energy into visible portions of the spectrum. It has often been speculated that the colorful Acropora are colored due to the UV protecting pigments in the coral, and aquarists often try to increase the coloration of corals by providing more UV.

Although it has not been proven that all coloration in corals is due to these UV protecting pigments, the practice of adding UV (or increasing UV) in the reef aquarium should be generally avoided, because it is likely to cause more harm than good. Preliminary results from the lighting research conducted by Dana Riddle seem to indicate that it is not UV that is causing the coloration, but, in fact, it may have more to do with PAR and the spectral quality of light. I have noticed that corals tend to turn green in higher UV light, and it may be that green pigments are generated under UV light. For brilliant coral coloration (pinks, blues and purples) to show up, we may need to limit the stimulation of the “green pigment” response to the UV light.

A coral that is adapted to lower light conditions may often have a higher density of zooxanthellae and/or be capable of absorbing more energy. When such a coral is placed in the aquarium under intense light conditions, it is quite likely that the coral may become highly oxygenated during peak photosynthesis and undergoes stress due to oxygen poisoning. Corals from the deeper environment also are more sensitive to the lethal effect of UV than those taken from shallow waters.

In summary, not only is the intensity of light important, but so is its spectral distribution. The zooxanthellae in wild corals are adapted to a certain irradiance and spectral distribution, and when placed in a aquarium will have to adapt to its new lighting environment.

Photoadaptation

In the context of this article, the term photoadaptation is used to describe the ability of the organism to alter its structure and function in response to the characteristics of the light in its environment. When a coral from the wild or another tank environment is placed in a reef aquarium it has to photoadapt to the various aspects of light — the intensity, spectral distribution and direction of light. The basic adaptation mechanisms employed are various combinations of change in the chlorophyll content per unit surface area, change in the number and size of zooxanthellae, changes in coral morphology to increase the surface area available for light capture, and changes in respiration rate. More recent research is indicating that the corals may, in fact, harbor different types of zooxanthellae and the corals may be able to change the mix of the zooxanthellae as a photo adaptation response.

It has been shown that most of our aquariums are limited in light when compared to light in the natural reef environment. Often the light intensity may be one-third to one-quarter of what the coral receives in the wild. Yet we find that corals live and prosper (as far as growth is concerned) under these conditions.

The scientific literature has some interesting results on photoadaptation. For example, Porter et al. (1984) have provided data for Stylophora pistillata adapted to high and low irradiance levels, and examined photosynthetic parameters of intense light-adapted colonies at high and low light levels and low light-adapted colonies at high and low light levels. The results showed that low light-adapted colonies have much higher photosynthetic capacity at low light than the intense light-adapted colonies. Corals growing at higher light irradiance are often much lighter in color than colonies of the same species in lower irradiance regions. Interestingly, Falkowski and Dubinsky (1981) found that the difference in pigmentation in S. pistillata was not due to the density of zooxanthellae, but due to the average pigment content of the zooxanthellae. Another interesting result that could explain why corals live and grow well in our poorly lit aquariums is the research finding that the coral adaptation to low light was faster than adaptation to intense light.

Corals may also show morphological changes in response to irradiance. In the wild, colonies that are often hemispherical in shape in shallow waters become increasingly plate-like in deeper waters. In aquariums, most hobbyists have noticed that when fragments of the same coral are planted in different locations in a tank, they may often grow in different shapes. These morphological differences may not be completely attributable to irradiance, but may be a combination of several factors that include irradiance and water motion.

Corals in the wild are subject to light from various directions, and different parts of the coral may be photoadapted to different light characteristics based on its position and relative exposure to the light. When placed in an aquarium, the light is typically unidirectional (from the top), and parts of the coral that were once subjected to light may now be shaded, whereas parts that were shaded may be exposed to more light. Hence, different parts of the coral may have to photoadapt differently. Often we find that the underside or shaded portions of the coral colonies will bleach, and this is due to the change in the light reaching the bottom of the coral colony. Sometimes the tips may bleach, and this may be due to coral tips receiving too much light and its failure to adapt rapidly.

Conclusions

Light, photosynthesis and the incredible ability of the corals to photoadapt play an important role in the keeping of corals in our reef aquariums. Although the corals, by virtue of photoadaptability, may be forgiving, drastic changes in lighting should be avoided. Corals should be acclimatized to the aquarium lighting conditions in a gradual manner. Often, corals brought in from the wild will take two to three months before they adjust completely to the lighting conditions of the aquarium.

It has been my personal experience that smaller colonies tend to adapt better to new lighting conditions. There is less shading of the lower branches and hence less bleaching from the bottom up, and it is easier to orient it in a direction that it is accustomed to growing in the wild. I have also found that corals that are growing well in our reef aquaria also tend to adapt faster when moved to another reef. This may be due to the fact that the coral is already adjusted to the spectrum and intensity of the artificial lights, and only minor re-adaptation is required when moved to another aquarium.

Fragments of SPS corals grown under artificial lighting also adapt very quickly, and in fact may do better than larger colonies because they are also able to adjust their new growth morphology to the artificial lighting conditions. To avoid having the corals re-adjust to the lighting directions and intensity within an aquarium, frequent movement of the corals within a tank should be minimized. I find that the corals that are moved less frequently (or not moved at all) are able to maintain a consistent growth rate uninterrupted by the need to photoadapt when moved.

From the hobbyist point of view, it is very important to understand the light requirements of corals and be able to provide these requirements via artificial lighting. There is very interesting on-going research being conducted that I am sure will provide answers to the many light-related questions that are prevalent in the hobby. Someday we will be able to match the individual corals' P-I curves in our aquariums, be able to tweak the lighting spectrum so as to bring out the best colors in the corals, and bring science to the art of keeping coral reef aquariums.

The ability of the corals to adapt in such an incredible manner also raises some other interesting issues. Should we try to emulate the reef zones in our aquariums and make the effort to try to provide the light spectrum and intensity that the corals are accustomed to in the wild? Or, should we provide light that “enhances” the visual appearance and coloration of the corals and force the corals to adapt in a manner that we find appealing?