Chapter 5

IRRADIANCE AND CORALS

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INTRODUCTION

Ironically, confusion existing prior to the 19th century concerning whether corals were plants or animals, in a sense has persisted to modern times. Demonstration of the animal nature of the polyp clearly placed corals in the animal kingdom insofar as taxonomists were concerned. The plant-like nature of reef corals is due to the presence of symbiotic, photosynthetically competent dinoflagellate algae (commonly called zooxanthellae) that live within the ectodermal cells of the coral animals. The existence of zooxanthellae has been known since Brandt (1883) coined the term for the symbionts of radiolarians. Discussions of the taxonomic status, and past and current research on the nature of the symbionts, can be found in publications by McLaughlan and Zalh (1959), Taylor (1973), Muscatine (1974), and Blank and Trench (1985).

The algal component of the coral symbiosis requires light for photosynthesis; therefore reef forming, or hermatypic, corals are predominantly found in the euphotic zone. Reef corals are generally restricted to depths between the surface and 100 m (Wells, 1957a, b) and are only occasionally found much deeper. While some species, such as Leptoseris hawaiiensis, occur at 165 m in the Pacific (Maragos and Jokiel, 1986), and Schlichter et al. (1988) have found L. fragilis at depths between 100 and 145 m in the Red Sea, the richest reef coral development generally occurs at depths of less than 20 m. Presumably a major factor influencing the depth distribution of corals is light.

While studies of the effects of light on reef corals often are concerned with their photosynthetic response, light also influences the rate of calcification of hermatypic corals and plays a role in their reproductive cycle. It should be kept in mind, however, that in the natural environment light covaries with other ecological factors, such as turbulence and temperature, which may make it difficult to isolate the importance of any single factor in the ecophysiology of corals.

The purpose of this chapter is to present an overview of what is known and unknown about the effects of irradiance on reef-forming corals. We begin with a brief historical overview of coral photobiology. Next, the major aspects of ambient light fields are discussed along with problems in measuring light. Finally, we consider the morphological and physiological aspects of photoadaptation in reef corals, and the consequences of photoadaptation to coral growth.

Historical development of coral photobiology

The first scientific visitors to coral reefs observed that true reef-building corals are restricted to relatively shallow waters. Differences between the fast growing reef corals and deep living corals were recorded early in the 19th century (Quoy and Gaimard, 1825), and it was thought that light might be one of the factors responsible for limiting reef corals to shallow waters. The notion that reef corals were creatures of shallow water was of fundamental importance for all theories of coral-reef morphogenesis, and particularly the controversy surrounding the formation of atolls. Darwin's subsidence theory (1842), the submarine mound theory of Murray (1880) and the antecedent platform theory (Davis, 1928) are based on the idea that reefs and atolls cannot develop unless there is a solid substratum in shallow water on
which corals could grow. Regardless of the major differences in opinions concerning the origin of atolls, it was universally recognized that models of atoll development must take into account the fact that reef-building corals are restricted to relatively shallow water. Darwin frequently put the lower depth limit for reef growth at 20 to 30 fathoms (36 to 54 m), and this limit was not questioned by later workers.

In 1916, T.W. Vaughn listed six ecological factors that appear to influence the vertical distribution of reef corals: (1) removal of silt by the action of water motion in shallow water; (2) occurrence of greater abundance of planktonic food of corals in shallow water; (3) depth to which light penetrates; (4) temperature; (5) salinity; and (6) exposure to air during low tides. Exposure to air at low tide as well as associated temperature and salinity fluctuations in shallow water could limit upward growth, while the depth to which wave-induced water motion and light penetrates might determine the lower limit. Also, temperature can limit the lower distribution of reef corals because below the thermocline it may be too cold for reef-coral growth, even at lower latitudes. Vaughn stated that “strong light is essential for the vigorous growth of shoal water corals”, but most of his discussion centered on temperature as a controlling factor. He gave no indication of how light might control the lower limit of coral distribution.

Vaughn believed that corals are strictly heterotrophic animals, obtaining all of their nutrition from animal prey in the water column (Vaughn, 1916, 1919). Consequently, he suggested that abundance of planktonic food in shallow water is a factor controlling the distribution of corals, while admitting to a lack of evidence to support this statement. J. Stanley Gardiner (1898) had previously demonstrated that reef corals liberate oxygen in the presence of sunlight, and noted that oxygen production only occurred in pigmented corals (that is, corals containing zooxanthellae).

During the Great Barrier Reef Expedition (1928–1929), C.M. Yonge studied the nutrition of corals, and in 1931 Yonge and Nicholls published the first description of the oxygen metabolism of reef corals over 24 hours. They concluded that diurnal oxygen production by zooxanthellae was not sufficient to meet diel respiratory requirements. They also conducted the first studies of the relation of photosynthesis to depth, and thereby showed a relationship between light intensity and photosynthesis by the corals.

By the late 1940s the general consensus was that reef corals were restricted to shallow water by the photic requirements of their symbiotic algae but the nature of this limitation was still a matter of debate. The experimental studies of Verney (1930, 1931), Yonge (1930, 1931) and Kawaguti (1944, 1969) demonstrated the capacity of the symbiosis to produce surplus oxygen during daylight hours. The role of light in the enhancement of coral growth was noted fairly early (Yonge and Nicholls, 1931), but the first clear experimental demonstration of the effect was carried out by Goreau (1959). These studies supported Verney’s hypothesis that the lower limit of reef-coral distribution was determined by water clarity, and hence the ability of the system to produce oxygen in sunlight (Verney, 1930, 1931). Yonge (1930, 1931) concluded that coral reefs were probably dependent on light for metabolism of the zooxanthellae, but maintained that reef corals did not obtain nutrition from the algae. He believed that algae were important to coral physiology because they removed the waste products of animal metabolism (carbon dioxide, phosphorus, and nitrogen compounds).

Goreau (1961) supported Yonge’s idea (1930, 1931) that the primary importance of zooxanthellae was removal of the metabolic waste products of the coral animal. Further, he attributed light-enhanced calcification to the removal of carbon dioxide by zooxanthellae, which accelerated a proposed inorganic process of calcium carbonate precipitation. Subsequently, he referred to “the zooxanthellae problem” and reiterated that light-enhanced removal of animal metabolites and enhancement of calcification by carbon dioxide removal were the important light-mediated functions of the zooxanthellae in the reef-coral symbiosis.

The “zooxanthellae problem” was reopened by the studies of Franzisket (1964, 1969a, b) who designed a flow-through system that allowed oxygen measurements to be taken every 30 minutes with minimum manipulation of the coral. From these measurements he produced what appears to be the first published photosynthesis-irradiance
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curve for corals as well as an estimate of the 24-h oxygen budget for reef corals. The corals produced enough surplus oxygen on a diurnal cycle to live as autotrophs. Subsequent investigations using in situ respirometers have clearly shown that the ability of a coral to live totally autotrophically, or its need to supplement autotrophic carbon fixation with heterotrophic metabolism, strongly depends on the light regime in which the coral lives (Porter et al., 1984).

THE UNDERWATER LIGHT FIELD

While light is one of the most important variables to quantify in studying the effects of irradiance on coral ecophysiology, it is also one of the most difficult variables to measure, especially in relation to corals. An excellent review of the submarine light field in relation to corals is presented by Weinberg (1976). The measurement of the light field requires subjective decisions by the investigator, which ideally should be based on the application of the measurement to the process under investigation. Two factors should be considered when measuring light in the marine environment, namely quantity and spectral quality, and we will discuss each in turn.

Generally, one is interested in quantifying the amount of light incident on some particular area. If one points a narrow tube at a light source (such as the sun) and varies the angle of the tube from the nadir to zenith, one can obtain measurements of the flux of light at various angles. This flux, called the radiant flux (with units of quanta m⁻² s⁻¹, or joules m⁻² s⁻¹), is seldom measured in biological experiments, but has been used in a study of the growth of the coral Porites astreoides (Roos, 1967).

The most frequently measured property of light is irradiance. Strictly speaking, irradiance is the flux of light energy (radiance) incident on an infinitesimally small element of surface containing the point under consideration divided by the area of that element (Jerlov, 1968). This flux, with units of quanta m⁻² s⁻¹ or watts m⁻², is often used because it contains information about the integrated areal distribution of radiant energy. Irradiance is commonly measured with a light sensor consisting of a calibrated photodiode and an amplifier connected to a recording device. The geometry of the light sensor is important. Because of scattering, some of the light which penetrates into the sea is reflected back to the surface. Typically, light sensors are available in two designs: one is spherical, which measures light in all directions (approximately 4π steradians), and the other is a flat sensor which measures light with a 2π steradian field (Kirk, 1983). The spherical or "scalar" light sensor measures both forward-scattered (downwelling) and back-scattered (upwelling) light simultaneously. The flat or "cosine" sensor may be used to measure the downwelling light independently of the upwelling light. By summing the measurement of the downwelling and upwelling light, one can calculate the integrated or scalar light field. On coral reefs, upwelling irradiance may be a significant portion of the total irradiance (Dunstan, 1982) because corals and calcium carbonate sediments, which are often found on reefs, may reflect relatively large proportions of the downwelling light. In fact, from an ecological perspective, upwelling irradiance is critical for the growth of coral species colonizing the understorey of reefs (Roos, 1967).

There are many units one can choose in measuring light. Usually two types of units are of interest: energy units and quantum units. The conversion from one type of light unit to another requires knowledge of the spectral distribution of the light field, which is sometimes not well characterized. Energy units, such as watts or joules, are frequently useful if one is interested in calculating energy budgets, such as the efficiency of photosynthesis. Quantum units are often used in photosynthetic measurements because they can be stoichiometrically related to photochemical reactions.

The underwater light field is modified by the angle of the incident light, the absorption and scattering of light by dissolved and particulate materials in the water, and by water molecules themselves. The temporal distribution of light in the sea varies on many scales, from that of the millisecond to the year (Falkowski, 1984). The first-order influence is related to the angle of the sun as it crosses the sky. The angle of the sun is especially important in coral-reef ecology, not only because it is closely related to the total irradiance at the surface, but because reefs are not uniform in
all directions (that is, isotropic). Many reef organisms may be shaded during some part of the day, while in bright light during other parts of the day (Brakel, 1979). The angular distribution of downwelling light incident on reef corals is controlled by azimuth of the sun, reflection, refraction, scattering, and shading. The resulting irradiance distribution pattern in shallow water is a prolate spheroid, with the long axis pointing toward the sun (Whitney, 1941). Surfaces pointing directly upward receive considerably more light than slanted surfaces. Vertical surfaces typically receive 25% of horizontal surface irradiance at the same depth. The direction of maximum sunlight intensity becomes less sensitive to sun direction and moves toward the vertical with increases in water depth (Pettersson, 1938; Roos, 1967).

As direct sunlight penetrates the water column, it is scattered, causing a rapid increase in the relative amount of diffuse downwelling light in relation to the amount of direct sunlight. The directional properties of the refracted sun and sky light at the water surface become more important as light reaches greater depths. Corals growing at depth experience a more uniform directional field, with most of the light coming from the vertical.

Superimposed on the first-order changes in irradiance are second-order phenomena, which cannot be predicted from regular seasonal or diel changes. These variations are induced largely by meteorological events. For example, clouds modulate the surface intensity of light. Storms can reduce light for many days, as a direct result of reduction of light reaching the sea surface, or the indirect result of increasing turbidity cutting off light penetration to the corals. Storms can stir up local sediments or increase runoff of terrestrial sediments into the water. Phytoplankton blooms can also occur due to increased storm runoff.

A wave can act as a lens and focus light. This effect is most pronounced in shallow water because scattering diffuses the beam with depth. Movement of waves across a reef creates "flashes" of light that can be very intense and of short duration. Using a submersible sensor connected directly to an oscilloscope, P. Griffiths and R.A. Kinzie III (pers. commun.) measured these flashes on the Coconut Island reef in Hawaii. When photosynthetically available radiation (PAR) incident on the surface was 2100 to 2500 \( \mu \text{E m}^{-2} \text{s}^{-1} \), flashes in excess of 4000 \( \mu \text{E m}^{-2} \text{s}^{-1} \) occurred at a rate of 1 to 3.5 flashes s\(^{-1}\). Flash durations were 0.05 to 0.30 s, averaging about 0.10 s. Flashing did not occur if the sun was obscured by a cloud, because light reaching the surface of the water was diffuse, and not focussed by the wave. It is not known if rapidly modulated natural PAR is advantageous to coral photosynthesis, or if it has any influence whatsoever. Short-term variations in irradiance may enhance photosynthetic performance in unicellular algae (Phillips and Myers, 1954; Abbott et al., 1982; Falkowski, 1984).

Visible wavelengths

In the sea, water molecules, and particulate and other dissolved materials in the water, absorb and scatter light. Light is attenuated exponentially with depth. Light attenuation is not uniform over all wavelengths, however, and the water column behaves like a monochromator, narrowing the spectrum of the light which penetrates farthest to a relatively narrow waveband.

The first spectral measurements of visible radiation in deep ocean water were made by Hjort (1911) using a combination of colored filters and photographic paper. Subsequently, the measurement techniques were greatly refined, and spectral curves of major water types were defined. Attenuation of visible light with depth (Fig. 5.1) is accompanied by alteration of spectral composition (Jerlov, 1968; Dustan, 1982). The relative spectral contribution is a function of the optical properties of water, dissolved materials, and particulate content.

The spectral distribution of light is most conveniently measured with a spectroradiometer, an instrument that scans across some portion of the electromagnetic spectrum. Spectroradiometers are expensive and there is relatively little information about the spectral nature of the underwater light field, especially on coral reefs (Dustan, 1982). In oligotrophic oceans, the waveband of maximum penetration is between 440 and 490 nm, giving the open ocean the appearance of being blue. In many coastal waters, however, the waveband of maximum penetration is shifted towards the green and is centered around 550 nm, because of the absorption of light by humic substances and phytoplankton which are often relatively abundant in coastal
waters. On coral reefs, the spectral nature of the light field is most likely to resemble that of an oligotrophic ocean, because humic substances and free-living phytoplankton are generally sparse in reef waters (Fig. 5.1).

The conversion of photosynthetically active radiation into chemical bonds requires that the light be absorbed and transferred to reaction centers which form the heart of the photosynthetic machinery (reviewed by Prezelin, 1981). The absorption spectrum for zooxanthellae shows a broad peak between 400 nm and 550 nm and a second, narrower peak between 650 nm and 700 nm (Fig. 5.2). The broad peak in the blue-green portion of the spectrum is attributable to the absorption of light by chlorophyll a, chlorophyll c, and the carotenoid, peridinin. The narrow red absorption band is attributable almost entirely to chlorophyll a and to a much lesser extent to chlorophyll c. Fluorescence excitation spectra clearly indicate that the light absorbed by chlorophyll c and peridinin is transferred to chlorophyll a with efficiency close to 100%.

The light utilized by zooxanthellae (or any photosynthetic organism) is a function of the light field ($E$) and the wavelength-specific absorption spectrum ($A$) of that cell. The product of these two variables is called the photosynthetically usable radiation or PUR (Morel, 1978) and is represented by the equation:

$$\text{PUR} = \int_{400}^{700} A_\lambda \cdot E_\lambda$$

where $A_\lambda$ is the absorption of light normal to the cell at wavelength $\lambda$ and $E_\lambda$ is the downwelling spectral irradiance at wavelength $\lambda$. Dustan (1982) calculated PUR for isolated zooxanthellae, and found that cells taken from corals growing at shallow depths absorb less light energy (Fig. 5.3). Cells taken from deep waters show greater whole-cell absorption, resulting from an accumulation of pigments. Higher absorption partially offsets the decrease in available light with increasing depth. In addition, in some corals the density of zooxanthellae may increase with decreasing depth, which also results in overall increased light absorption.

**Non-visible wavelengths**

In addition to photosynthetically active radi-
Fig. 5.3. Photosynthetically usable radiation (PUR) of zooxanthellae isolated from Montastrea annularis. Discovery Bay, Jamaica. Note that the algae from different depths vary with respect to their absorbance of light energy and its spectral quality (after Duxton, 1982).

The presence of natural solar UV can decrease skeletal growth by 50% in the coral *Pocillopora damicornis*, while increasing larval production by 80% (Jokiel and York, 1982). Natural levels of UV radiation have been shown to reduce $^{44}$Ca uptake *in situ* for *Porites damicornis* (Roth et al., 1982). Ultraviolet-tolerant and ultraviolet-resistant genetic strains of zooxanthellae are known (Jokiel and York, 1982). Zooxanthellae are sensitive to long-wavelength UV-A (320 nm to 400 nm) as well as short-wavelength (<320 nm) radiation (Jokiel and York, 1982, 1984). Corals taken from deep (low ambient UV) environments are far more sensitive to the lethal effects of UV damage than corals taken from shallow (high ambient UV) environments (Siebeck, 1981).

MacMunn (1903) pointed out that corals contain pigments that absorb and block UV radiation. He concluded that “in this way they probably act as a screen, protecting the delicate organisms from the irritating effects of the rays of short wavelength.” The UV-blocking substances are now known to be mycosporine-like amino acids (Dunlap and Chalker, 1986).

Other UV-active pigments absorb UV radiation and fluoresce the energy into the visible portion of the spectrum (Kawaguti, 1944, 1969; Catala, 1959). The chromophores of the UV-reflecting and UV-fluorescing pigments appear to be large organic molecules which are disrupted when extracted with solvents other than water. Hence, they are very difficult to analyze and little is known about their structure (B.E. Chalker, pers. commun.). The UV-fluorescent pigments absorb UV radiation with strongest absorption near 320 nm, but with some absorption to 400 nm. Energy absorbed at 380 nm fluoresces in a waveband ranging from 450 to 530 nm (Kawaguti, 1969; 1973).

The UV-absorbing, reflecting, and fluorescing pigments persist in corals that have lost their symbiotic zooxanthellae (Jokiel and Coles, 1974). The substances appear to be concentrated as granules in the coral ectoderm (Kawaguti, 1944, 1969) where they are most effective in shielding the symbionts from UV damage. Although UV-active pigments are located in the animal portion of the symbiosis, they probably are produced by the zooxanthellae (Kawaguti, 1944). The mycosporine-like amino acids which serve as UV-
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blockers in corals are most likely derived from the shikimic acid pathway of the zooxanthellae (B. Chalker and W. Dunlap, pers. commun.). An analogous situation is found in the sarcoglossan mollusc Placobranchus. Carbon fixed by the chloroplasts in the animal’s tissues is incorporated into the UV-absorbing compound that presumably shields the symbiosis from UV damage (Ireland and Scheuer, 1979).

Infrared radiation is rapidly absorbed by seawater and does not penetrate very far into the water column. Little is known about infrared radiation and reef corals, but there is reason to believe that studies in this area would be informative. Infrared photographs reveal that living corals emit large amounts of infrared radiation compared to other reef substrata. Reef corals located on reef flats (to depths of 2 m) are readily discerned as bright red areas in these photographs. Possibly this represents the energy from the visible portion of the spectrum that has been modified by photochemical reactions (that is, fluorescence). Comparisons of absorption spectra and emission spectra could provide clues concerning the energy budget of corals.

Light sensors typically have a spectral response that is not uniform over all wavelengths. Most commercially available sensors are capable of measuring light between 400 and 700 nm. It is difficult to find sensors with high sensitivity and suited for aquatic use that measure near-UV or infrared wavelengths. Thus, there are few published measurements of light in the oceans outside of the visible spectrum. It is possible to measure light outside of the visible wavelengths without a photoelectronic sensor, by using an actinometer, which is a photochemical reaction sensitive to a specific waveband of light (Seliger and McElroy, 1965).

Lunar cycles

Night irradiance has a component related to the phases of the moon. The release of planulae by some species of reef corals follows a monthly cycle (see, for instance, Marshall and Stephenson, 1933; Atoda, 1947; Harrigan, 1972; Stimson, 1978; Harriott, 1983). This oscillation has been termed “lunar” periodicity, but without any direct evidence as to its cause. Many potential forcing functions show oscillations with a similar frequency. The monthly cycle of larva release in the reef coral Pocillopora damicornis is clearly responsive only to the night irradiance signal (Jokiel et al., 1985). Cycles can be shifted by changing the pattern of night irradiance, and synchronization breaks down when the corals are given either continuous night irradiance or none. The mechanism by which corals can respond to such low levels of irradiance as are found at night is unknown.

Most species of corals spawn gametes rather than brood planulae (Fadallah, 1983; Harrison et al., 1984), and most corals are simultaneous hermaphrodites, with an annual gametogenic cycle. Annual spawning on the Great Barrier Reef occurs during one or two months when the water temperature is approaching maximum. Time of spawning appears to be controlled by night irradiance, because extending day length with an artificial light source will cause a delay in spawning (Harrison et al., 1984). The planula larvae of several species of reef corals delay attachment until dark, while in the ahermatypic species Tubastraea coccinea spawning and attachment is not influenced by the diurnal light cycle (Kawaguti, 1944).

The effects of light intensity on photosynthesis

The effects of irradiance on corals are most frequently studied with regard to photosynthesis. The overall relationship between light intensity and photosynthesis is nonlinear (Fig. 5.4). A number of different equations have been used to describe the photosynthesis–irradiance (P–I) curve, and comparisons between the various equations (Jassby and Platt, 1976; Chalker, 1981) suggest that a hyperbolic tangent function or an exponential function can provide reasonable fits to experimental data.

Numerous studies have shown that P–I curves have a similar shape for a multitude of photosynthetic organisms (Talling, 1957; Jassby and Platt, 1976) including corals (Chalker, 1981) and cultures of zooxanthellae (Haldal, 1968; Scott and Jitts, 1977). The initial rate of photosynthesis increases in direct proportion to increasing irradiance, but eventually photosynthesis becomes saturated by light and approaches an asymptote which is the
maximum net photosynthetic rate, \( \Phi_{\text{net}} \). Oxygen consumption in the dark, or dark respiration (\( R \)), is negative by convention. The maximum gross photosynthetic rate is given by:

\[
\Phi_{\text{gross}} = (\Phi_{\text{max}} - R)
\]

The level of irradiance at which the initial linear portion of the curve intersects \( \Phi_{\text{max}} \) is termed the saturation "constant", \( I_s \). The point at which the P–I curve crosses the abscissa is the instantaneous compensation intensity, \( I_c \), or the intensity of light required to maintain a photosynthetic rate equal to respiratory demands.

Photosynthetic rates may be expressed in relation to a variety of parameters, such as chlorophyll \( a \), protein, surface area, algal cell number, polyp size, and so on. In coral ecophysiology usually two types of parameters are selected, one which reflects photosynthetic or algal processes, such as chlorophyll \( a \), and one which reflects the physiological or "ecophysiological" responses of the whole coral, such as surface area. For example, P–I curves may be very similar for two organisms when expressed per unit chlorophyll, but entirely different when expressed per unit surface area (Fig. 5.4). Such differences obviously reflect differences in the chlorophyll/surface area ratio, which may, in turn, be related to the surface density of zooxanthellae, to the pigmentation of the individual algal cells, or both. When one is interested in understanding how an individual coral is faring under a given light regime, P–I curves normalized to surface area are usually very informative.

When the initial slope (\( \alpha \)) of the P–I curves is normalized to chlorophyll, the result is related to the efficiency with which light is used in photosynthetic reactions:

\[
\alpha = K_c / \Phi_{\text{max}}
\]

where \( \Phi_{\text{max}} \) is the maximum quantum yield (\( O_2 \) per quantum) and \( K_c \) is the spectrally averaged absorption cross-section of chlorophyll (m\(^2\) per milligram chlorophyll). It is commonly thought that the maximum quantum yield (\( \Phi_{\text{max}} \)) of photosynthesis is relatively constant, averaging 0.10 \( O_2 \) per quantum. Thus, changes in \( \alpha \) are usually attributed to changes in \( K_c \), the meaning of which will be discussed.

The calculation of meaningful \( \alpha \), \( I_s \), \( I_c \) or \( \Phi \) values requires knowledge of the light incident on or absorbed by a coral in situ. Measuring incident irradiance may be problematic, especially on reef walls, but measuring the light absorbed is almost impossible. The living tissue of the coral is distributed over a highly irregular surface, hence the microenvironment of the zooxanthellae may be extremely variable. Because of shadows cast by the calcium carbonate structure, reflection or backscattering of light from the calcium carbonate of hermatypic corals or light focussing, and the occurrence of animal and algal pigments, it is extremely difficult to characterize, let alone generalize upon, the level of the light to which zooxanthellae are exposed. Turning a coral head upside down in a chamber may result in significant changes in photosynthesis–irradiance curves. Measurements of light intensity to which corals are exposed are likely to vary significantly from experiment to experiment, and are difficult to
normalize. Some of the variations in $z$, $I_e$, and $\phi$ reported within and between species are undoubtedly due to the problems in measuring incident and absorbed light.

At high irradiance levels photosynthesis is often inhibited in many photosynthetic organisms. Photo-inhibition is a function of intensity, and of duration of exposure (that is, the dose of light absorbed). Photo-inhibition has not been reported (to our knowledge) for corals in situ, and it is difficult to say if photo-inhibition ever occurs in reef corals in the natural environment. Coral planulae are not photo-inhibited even at maximum solar irradiance levels (Richmond, 1983).

It should be pointed out that observations of reduced photosynthetic rates at high irradiance levels are not necessarily an indication of photo-inhibition per se, but may be due to factors associated with high light, such as high temperature, elevated oxygen tensions, or high water motion. For example, high oxygen concentration inhibits photosynthesis (Turner et al., 1956; Black et al., 1976; Downton et al., 1976). Coral tissues may become highly oxygenated during a period of peak photosynthesis (Crossland and Barnes, 1977). Water motion may be a critical factor in the removal of this metabolic waste (Jokiel, 1982). Corals show skeletal adaptations that modify the flow of water at the tissue-water interface, and thereby allow a single species to adapt to a relatively wide range of external hydrodynamic and photic conditions (Chamberlain and Graus, 1975; Jokiel and Cowdin, 1976; Jokiel, 1982).

In addition to influencing photosynthesis, light intensity also influences calcification of corals (Barnes and Chalker, Ch. 6). Corals with zooxanthellae calcify several times faster in light than in darkness, while corals that have lost their zooxanthellae calcify at low rates that are not influenced by light (Kawaguti and Sukamoto, 1948; Goreau, 1959; Goreau and Goreau, 1959). Calcification rates in hermatypic corals appear to be controlled primarily by photosynthetic rate (Goreau, 1961; Vandermeulen et al., 1972).

PHOTOADAPTATION IN CORALS

The photosynthesis-irradiance relationship in corals is dynamic — that is, it can change in response to the average irradiance in which the organism is growing, which we will call the “growth irradiance”. Such changes generally help to optimize the efficiency with which light is harvested and used in photosynthetic reactions. The general term “photoadaptation” is often used to denote changes in photosynthetic performance with changes in irradiance during growth. In the broadest sense of the term, photoadaptation in reef corals occurs at every level of biological organization from the molecular to the community level. By this definition one might be concerned with photoadaptive changes that take minutes (expansion of a polyp), hours (changes in photosynthetic pigments in a zooxanthellae), days (changes in the density of zooxanthellae), years (changes in growth form or size) or thousands of years (genetic selection).

At the molecular level, adaptation to growth irradiance by zooxanthellae is a response of the protein-synthesis machinery to prolonged changes (on the order of days to weeks) in irradiance regimes. In all algal cells, chlorophyll molecules are bound by weak forces to specific proteins intimately associated with lipids. There are numerous chlorophyll-protein complexes which, together with prosthetic groups on other proteins, comprise the elements of the light-harvesting and electron transport system. This system, often called the “photosynthetic apparatus”, can respond to changes in growth irradiance. For simplicity we shall consider a typical cell to contain three chlorophyll-protein complexes, namely a light-harvesting chlorophyll protein, a photosystem I (PS I) chlorophyll-protein and a photosystem II (PS II) chlorophyll-protein. The chlorophyll-protein complex constituting PS I contains chlorophyll $a$ molecules which can donate electrons to an acceptor (that is, they can become oxidized). Upon oxidation the chlorophyll in this pigment-protein complex undergoes a reversible bleaching at 700 nm and is therefore called P700. The reaction centers of PS II also contain chlorophyll $a$ and can be assayed by measuring the oxygen flash yield. Oxygen is evolved only by PS II, and during a long train of short saturating flashes (as provided by xenon strobes, for example) each reaction center will become oxidized on every flash. As four electrons are photooxidized from water in the evolution of one oxygen molecule, any given
reaction center will evolve one oxygen molecule on every fourth flash.

The light-harvesting chlorophyll complex contains the bulk of the chlorophyll $a$ and chlorophyll $c$ of the cell, and in zooxanthellae it also contains the carotenoid, peridinin. The molar ratio of peridinin to chlorophyll $a$ is four. This complex is associated primarily with PS II, but some excitation energy absorbed by the light-harvesting chlorophyll–protein can “spill over” into PS I. The light-harvesting chlorophyll complex serves as an antenna for the reaction center chlorophyll–proteins. One can conceive of the light-harvesting chlorophyll–proteins as forming the collecting area of a dish antenna, the focal point of the antenna being reaction-center chlorophyll–proteins. By measuring the ratio of chlorophyll $a$ to P700 and the number of molecules of chlorophyll $a$ per molecule of oxygen evolved per flash, one can estimate the average “size” of the antenna. This was done for zooxanthellae from high- and low-light adapted *Stylophora pistillata* by Falkowski and Dubinsky (1981) and by Titlyanov et al. (1980). Falkowski and Dubinsky found that, as zooxanthellae adapted to lower growth-irradiance levels, the number of PS I reaction centers per cell remained relatively constant, but the chlorophyll to P700 ratio increased from 425 in high-light adapted cells to 1650 in shade-adapted cells. They concluded that the “size” of the photosynthetic unit changed in response to growth irradiance in zooxanthellae from *S. pistillata*. Similar data and conclusions were obtained by Zvalinskii et al. (1980), who assayed PS II reaction centers by measuring oxygen flash yields. They reported that the zooxanthellae from *Pocillopora verrucosa* grown at 20 m had 1300 chlorophyll molecules per oxygen molecule per flash, while corals from colonies grown at 45 m had 1800 chlorophyll molecules per oxygen molecule per flash. These data suggest that the average chlorophyll per PS II reaction center is 325 molecules for *Pocillopora verrucosa* grown at 20 m and 450 molecules for corals at 45 m. If the data from *Stylophora pistillata* for PS I and from *P. verrucosa* for PS II are comparable, then the ratio of PS II to PS I reaction centers in zooxanthellae is greater than 1.0 [see Falkowski et al. (1981) for discussion].

Changes in the antenna size of the photosynthetic units imply that there is a change in the absorption cross-section of the photosynthetic apparatus. Simply put, if the number of chlorophyll molecules per reaction center doubles, the probability of a photon being absorbed by the antennae should also double if all other things are equal. Under such conditions one might expect that the initial slope of the P–I curve would increase when the curve is normalized per cell. This has been quantified in whole-colony P–I responses (Wehter and Porter, 1976; Falkowski and Dubinsky, 1981; McCloskey and Muscatine, 1984; Porter et al., 1984; Kinzie and Hunter, 1987) and in isolated P–I responses (Chang et al., 1983; Muller-Parker, 1984). Furthermore, it has been repeatedly shown that the maximum rate of photosynthesis (at light saturation) is almost always lower for colonies or cells grown at lower irradiance levels. Variations in initial slopes as well as in $P_{\text{max}}$ results in ample variability within P–I curves, so that it is sometimes difficult to describe “typical” P–I curves for light- and shade-adapted zooxanthellae or whole corals.

While the data show that P–I responses are more complex than might be predicted on the basis of simple changes in the “size” of photosynthetic units, it is possible to account for some of the variability reported. First, we shall consider the optical properties of photosynthetic units. As the average size of each photosynthetic unit increases, the unit appears to harvest less light per unit chlorophyll $a$, so that a doubling of the chlorophyll per reaction center does not, in fact, lead to a doubling of light-harvesting capability. The non-linearity of light harvesting can be quantified by measuring the apparent optical cross-section of zooxanthellae normalized to chlorophyll, the so-called $K_s$ values (Dustan, 1979; Dubinsky et al., 1984). $K_s$ differs from PUR [in eqn (1)] primarily in that whole-cell absorption is normalized to chlorophyll $a$ [see Dubinsky (1980) for a discussion of the relationship between $K_s$ and PUR]. As cells become increasingly shade-adapted the membrane surface area increases within the chloroplasts, resulting in increased stacking of thylakoid membranes. The probability that chlorophyll molecules in the center of a thick stack of membranes will ever intercept a photon is small because incoming photons are likely to be absorbed by molecules in the distal portions of the stack, closer to the light source. Thus, when in vivo absorption curves are
normalized to chlorophyll a, it appears that the "target" for photons is smaller (normalized per chlorophyll a) for shade-adapted cells with highly stacked thylakoids. This phenomenon results in a decreased initial slope in P–I curves when normalized to chlorophyll a. It should be pointed out that \( K_e \), like PUR, depends on the spectral quality of light. Spectral quality is incorporated in the calculation of \( K_e \) by the following expression:

\[
K_e = \frac{\sum (k_{e_i} \cdot I_{\lambda_i} \cdot \Delta \lambda_{n_i})}{\sum (I_{\lambda_i} \cdot \Delta \lambda_{n_i})}
\]

where \( k_{e_i} \) is the average absorbance over the wavelength interval \( \Delta \lambda_{n_i} \), and \( I_{\lambda_i} \) is the irradiance in that spectral interval (Falkowski et al., 1985). As the spectral quality shifts from broad irradiance near the surface to blue light deeper in the water column, overlap in the blue region between the absorbance spectra of photosynthetic pigments and the spectral quality of light actually increases. This does not mean that more photons can be absorbed per unit time deep in the water column, but it does imply that those photons which penetrate deep in the water column have a greater probability of being absorbed by photosynthetic pigments. As a consequence, \( K_e \) is spectrally corrected using eqn (4).

It would appear that the decrease in \( K_e \) due to increased stacking of thylakoid membranes may be offset by the shift in the spectra of the incident light (Wyman et al., 1987). In addition to changes in \( K_e \), some of the variability in P–I curves can be accounted for by changes in the turnover time of the reaction centers. For example, high-light adapted algae have greater photosynthetic rates at high light, due, in part, to the fact that each photosynthetic unit turns over at faster rates. Zvalinskii et al. (1980) calculated that the turnover of a photosynthetic unit for high-light adapted zooxanthellae was 200 s\(^{-1}\), while for a cell more adapted to shade the rate was only 87 s\(^{-1}\). The decrease in rate of turnover of the photosynthetic units is possibly related to a decrease in cellular content of ribulose (bis) phosphate carboxylase and perhaps other enzymes involved in carbon fixation (Beardall and Morris, 1976; Falkowski, 1980; Sukenik et al., 1987).

In addition to alterations in pigmentation and molecular reorganization of pigment proteins, there are a few data showing that zooxanthellae exhibit changes in respiration with changes in irradiance. Dubinsky (pers. commun.) observed that zooxanthellae freshly isolated from high-light adapted Stylolophora pistillata had higher specific respiration rates than those obtained from shade-adapted specimens.

The depth distribution of some species of corals is often broad, and can range over two orders of magnitude in irradiance level. Corals adapt to changes in growth irradiance, but it is often difficult to sort out adaptation to irradiance level per se from adaptation to depth, which potentially includes changes in spectral quality, nutrient regime, and temperature (see, for instance, Coles and Jokiel, 1978). There are numerous terms used in the literature to denote the adaptation to irradiance, including “sun−shade”, “light−shade”, and “photoadaptation”. In most studies of the effects of irradiance on coral ecophysiology, the sampling scheme usually encompasses specimens taken over a wide range of depths and consequently includes changes in both quantity and quality of light.

It should be noted that “photoadaptation” implies that an organism expends some energy to change some aspect of its physiology and/or morphology to become better suited to some light regime. By this criterion, some species will “adapt” better than others. The degree of adaptation should not be determined on an absolute scale; it is desirable to compare two organisms, either of the same species or two species, within similar light regimes. For example, Porter et al. (1984) have provided data for Stylolophora pistillata adapted to high- and low-growth irradiance levels. They examined photosynthetic parameters of high-light adapted colonies in high- and low-light regimes, and low-light adapted colonies in low- and high-light regimes. The data clearly show that low-light adapted colonies have much greater photosynthetic capacity at low light than their high-light adapted counterparts. It is interesting to note, however, that shade-adapted colonies did as well at high light as the high-light “adapted” colonies.

In some studies (see, for instance, Falkowski and Dubinsky, 1981) irradiance level was clearly separated from changes in spectral composition, while in other studies (such as Wethey and Porter, 1976; McCloskey and Muscatine, 1984) the spectral
quality and irradiance levels covaried. On the whole-colony level photoadaptation is manifested in a variety of ways, including changes in pigmentation, zooxanthellae density, photosynthesis–irradiance responses, dark respiration, polyp density and gross morphology (such as surface area/volume ratios). Perhaps the most obvious indication of photoadaptation is often the variation in the degree of pigmentation within a coral species with either irradiance (Redalje, 1976; Falkowski and Dubinsky, 1981) or depth (McCloskey and Muscatine, 1984).

Corals growing at high irradiances are often markedly lighter in color than the same species found at low irradiance, such as in grottos and under ledges. For example, Falkowski and Dubinsky (1981) found that colonies of *Stylophora pistillata* growing at high irradiances had little pigmentation, while those found at low growth irradiance levels were almost black. The differences in pigmentation are manifested at the cellular level. The density of zooxanthellae per unit surface area was nearly the same in specimens of the hermatypic coral *Stylophora pistillata* grown in high-light and shade-adapted. The differences in pigmentation could be attributed to differences in the average pigment content of the zooxanthellae; in colonies grown at high light there was 2 pg chlorophyll a per cell, while in colonies adapted to low growth irradiance levels there was 8 pg chlorophyll a per cell. It should be noted that there were no significant changes in chlorophyll a/c ratios with growth irradiance.

Since hermatypic corals have an ability to adapt to growth irradiance, high-light and low-light adapted colonies should not be considered ecotypes. This is most readily shown by cross-transplantation studies. With *Stylophora pistillata* for example, colonies found at high growth irradiance levels could become “shade-adapted” within a few weeks and vice versa (Falkowski and Dubinsky, 1981). Gattuso and Jaubert (1984) reported that adaptation to high light was slower than adaptation to low light.

**MORPHOLOGICAL RESPONSES TO IRRADIANCE**

Expansion is a means for the polyp to capture more light. Ultraviolet radiation will cause the polyps of some corals, such as *Goniopora*, to expand during darkness when they normally are closed (Catala, 1959). Polyp expansion in reef corals is related to irradiance, but is highly variable within species (Lasker, 1979) and between species (Abe, 1938, 1939). Most of the species in the following genera show daytime polyp expansion: *Acropora, Euphyllia, Fungia, Goniopora, Halomitra, Madracis, Montipora, Pavona, Physogyra, Pleurogyra, Pocillopora, Porites* and the hydrocoral *Millepora*. Corals that normally have their tentacles expanded only in darkness include the following genera: *Agaricia, Caulastrea, Echinopora, Hydathora, Isophyllia, Montastrea, Oxyopora, Siderastrea, Tridacophyllia* and the ahermatype *Tubastrea*. There can be considerable variability within a species. A number of diverse factors influence day–night polyp expansion. Yonge (1930) suggested that night expansion of polyps is a feeding response to increased abundance of zooplankton. A test of this hypothesis by Abe (1939) showed that expansion of polyps in the reef coral *Caulastrea furcata* is not related to the abundance of its zooplankton food source, but is related only to light. He proposed that expansion was a means of dissipating respiratory carbon dioxide in darkness.

Branching species of corals often outgrow and “overtop” their neighbors (Connell, 1973, 1976, 1978; Porter, 1974, 1976). The most successful canopy species belong to the genus *Acropora* and form thickets, tables or brackets. Corals often are hemispherical in shape in shallow water and become increasingly plate-like in deeper water. Also, shallow communities tend to be dominated by branching forms, while deeper communities tend to consist of massive, encrusting and plate-like forms. In general, highly phototrophic species with small polyps (such as *Acropora, Porites, Pocillopora, Stylophora*, and *Millepora*) seem to be more successful in competing for light by outgrowing competitors (Porter, 1976). These species form the canopy, while the more heterotrophic species having larger polyps (such as *Montastrea*, faviids, musiids) can persist in the understory layer of corals between the branches (Porter, 1974; Graus and MacIntyre, 1976). Sheppard (1981) observed that shading caused by these “canopy” corals does not seem to influence the diversity or abundance of the understory community.
Porter (1976) noted that photosynthesis (P) to respiration (R) ratios in reef corals are inversely related to polyp size. An exception to this rule is seen in the solitary coral *Fungia scutaria* which has an extremely large polyp (up to 10 cm diameter), but is highly phototrophic and has a very high P/R ratio (Franzisket, 1969a, b). This exception has been explained as a necessary hydrodynamic adaptation for life on unstable substrata in shallow, turbulent environments (Jokiel and Cowdry, 1976). Porter (1976) reasoned that corals having large polyps are better adapted to capture plankton and lead a heterotrophic existence, while small polyps are an adaptation for the increased capture of light. A reduction of polyp size as a mechanism of increasing light capture seems unlikely. For example, 99.9% of incident light is absorbed by the living tissues of the massive coral *Favia pallida*, which has very large polyps. Less than 0.1% penetrates to the skeleton (Halldal, 1968). In addition, small polyps such as are found in *Acropora* and *Pocillopora* can become light-saturated at extremely low light intensities. Rather, reduction in polyp size appears to be an adaptation that increases the surface/volume ratio of the polyp to allow higher rates of exchange of dissolved metabolic materials (especially oxygen and carbon dioxide) in highly phototrophic organisms (Jokiel, 1982). Canopy development by species with small polyps overcomes their inability to capture light while maintaining a high surface area for gas exchange (Jokiel and Morrissey, 1986).

The relationship between photosynthesis and irradiance (P–I curve) in the branched reef coral *Pocillopora damicornis* is modified by the size of the colony (Jokiel and Morrissey, 1986). Net photosynthesis of the colony increases with size more rapidly than total respiration. The P/R ratio, net primary production and production efficiency increase with size, along with chlorophyll per unit reef area. The initial slope of the P–I curve and the maximum photosynthetic rate are inversely related to size. Jokiel and Morrissey (1986) regarded increased canopy development as a photoadaptive characteristic that increases efficiency of energy utilization by overcoming the energetic limitations resulting from the fact that individual cells are saturated at low light intensity.

Relatively little attention has been given to the effect of light on populations and communities of reef corals. Corals show genetic differentiation of photoadaptive characteristics within the same species. Colonies of *Montastrea cavernosa* transplanted to different depths with new light regimes did not fare as well as resident colonies after a 2-year period (Dustan, 1979). Differences in growth, numbers of algae, plant pigment concentration and mortality were attributed to genetic differences between the shallow- and deep-water populations of zooxanthellae (Dustan, 1979).

**MODELING THE EFFECTS OF IRRADIANCE**

There are different probabilities of finding some coral species at different irradiiances. Assuming that the depth distribution of corals is not random and that irradiance influences distribution through differential effects on growth, one can develop a simple conceptual model in an attempt to understand the effects of irradiance on growth of a given species. Let us assume that symbiotic hermatypic corals obey this simple growth equation:

\[ G = ((P_e)(T) + (H) - (R + e)) \]

where \( G \) is growth rate (t\(^{-1}\)), \( P_e \) is daily integrated gross photosynthesis, \( T \) is the fraction of the gross photosynthesis which is translocated from the zooxanthellae to the host (see Muscatine, Ch. 4), \( H \) is the heterotrophic incorporation of reduced carbon, \( R \) is whole coral respiration and \( e \) is excretion or secretion of organic carbon (including the production of mucus and planulae and losses of zooxanthellae).

One can examine the effects of irradiance on \( P_e \) by examining the light-harvesting capacity of a species:

\[ P_e = (K_s)(\text{chl m}^{-2})(I)(\phi) \]

where \( K_s \) is the absorption cross-section normalized to chlorophyll \( a \), chl m\(^{-2}\) is the areal concentration of chl, \( I \) is the average growth irradiance (daily integrated value), and \( \phi \) is the quantum yield of photosynthetic carbon assimilation at the growth irradiance. In reality it usually is not practical to measure \( \phi \), so \( \phi \) is calculated from other measurable variables.

In considering the problem of interspecific differences in light-harvesting, Wyman et al. (1987) examined \( K_s \) and chl \( a \) per unit area for six species
of hermatypic corals from Discovery Bay, Jamaica. The data (summarized in Table 5.1) indicate that neither $K_e$ nor chlorophyll per unit area varies significantly between species at a given depth. However, the product of $K_e$ and chlorophyll per unit surface area, which is the absorbance (that is, a dimensionless number proportional to the light-harvesting capacity of the coral), varies significantly between species. These data suggest that different species of corals growing at the same depth could be expected to differ in light-harvesting properties. However, for each species there may be an optimal depth (or irradiance level) for light-harvesting. For example, Acropora cervicornis has a maximum light-harvesting capability at approximately 10 m, while Montastrea annularis and M. cavernosa have optima near the surface (Table 5.1).

Using measured P-I curves (Porter et al., unpublished data), Wyman et al. (1987) calculated $\phi$ as a function of irradiance for a variety of species. In each case the maximum $\phi$ values for corals growing near the surface were invariably lower than for the same species growing deeper in the water column (Fig. 5.5). Differences in $\phi$ between surface and deep corals may be due to the absorption of PAR by carotenoids and perhaps other UV-blocking molecules which do not transfer excitation energy to photosynthetic reaction centers.

There are very few data available for numerical solution of eqn (5). Perhaps the most difficult term to measure is $H$, the heterotrophic intake of organic carbon. Through use of in situ respirometers (Porter, 1980; McCluskey and Muscatine, 1984) it is possible to determine daily integrated $P/R$ ratios. If $P/R$ ratios are less than 1.0 it is inferred that the coral must assimilate organic carbon to meet its metabolic demands. If $P/R$ ratios exceed 1.0, then presumably photosynthetically derived carbon could meet the metabolic needs of the coral.

### Table 5.1

<table>
<thead>
<tr>
<th>Species</th>
<th>Depth (m)</th>
<th>Chl cell (pg chl a cell$^{-1}$)</th>
<th>Chl area (ug chl a cm$^{-2}$)</th>
<th>$K_e$ (m$^2$·mg chl a$^{-1}$)</th>
<th>$K_e$ (Chl a area)$^e$</th>
<th>1/$\phi_{max}$ (O$_2$/quanta)</th>
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*The chl cell and $K_e$ data were measured from isolated zooxanthellae from each species at the designated depth.

*Chl area was calculated for chl a cell and the surface density of zooxanthellae.

*The product of $K_e$ and chl a area is a dimensionless number which corresponds to the absorbance of the coral.

*1/$\phi_{max}$ is the minimum quantum requirement for oxygen evolution, calculated from $K_e$ and $\phi$ (data not shown).
demands of the coral, if $T$ was sufficiently large (see Muscatine et al., 1984; Muscatine, Ch. 4). However, if the $P/R$ ratio is less than 1.0, then one cannot conclude that $H=0$.

The range of $P/R$ is relatively small, so it is important to know the daily integrated values of $P/R$ for the species under question with a high degree of precision. It should be pointed out that we refer to the $P/R$ ratio measured at growth irradiance, not the maximum $P/R$ obtained at light saturation. Obviously, values of $P/R$ will decrease with decreasing irradiance, and values less than 1.0 imply that the organism must acquire organic carbon from heterotrophy. In examining $P/R$ as a function of depth (and consequently irradiance), McCloskey and Muscatine (1984) showed that the $P/R$ ratio declined less than would be predicted on the basis of P-I curves derived from surface corals and extrapolated to lower irradiance levels. An important aspect of adaptation to lower irradiance is a reduction in whole-coral respiration (McClosky and Muscatine, 1984; Porter et al., 1984; Kinzie and Hunter, 1987). A reduction in respiration often implies that the growth rate of the organism is decreased proportionally. Therefore, a decrease in growth irradiance is probably accompanied by a decrease in growth rate and a decrease in respiration. Because $P/R$ ratios decrease with depth, corals deep in the water column often appear to be heterotrophic.

Falkowski et al. (1984) calculated that excretion in the coral *Stylophora pistillata* is proportionally higher in shade-adapted colonies, and that shade-adapted colonies could not meet their metabolic demands from photosynthetic carbon assimilation alone. It seems that corals living at low irradiance may excrete organic carbon, and so must simultaneously ingest organic carbon from heterotrophic sources. In assessing the adaptive patterns in different species with respect to growth irradiance, it is possible to dissect light-harvesting from other physiological parameters such as respiration.

**CONCLUDING REMARKS**

In this review of irradiance and corals we attempted to show that the subject area is rich in unanswered questions. Although there are many studies of various aspects of the effects of irradiance on corals, it is not possible to relate irradiance quantitatively to growth, or to the distributions of individual species. The effects of irradiance on corals are intimately related to the role of zooxanthellae in the coral's energy requirements (Falkowski et al., 1984). In this regard, irradiance is also addressed in other chapters of this volume — those on carbon metabolism (Muscatine, Ch. 4), calcification (Barnes and Chalker, Ch. 6), and species distribution (Achituv and Dubinsky, Ch. 1). While irradiance is not the only abiotic forcing function in coral reef development, it is probably one of the most important. This factor has certainly been a major influence on the evolution of this important marine symbiosis.

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