

5

Interactions between Corals and their Symbiotic Algae

Gisèle Muller-Parker and *Christopher F. D'Elia*

The mutualistic relationship between corals and their algal endosymbionts is a key factor in the evolutionary success of hermatypic (reef building) corals. Corals that harbor endosymbiotic algae exhibit faster rates of calcification, photoautotrophy and many other attributes that are believed to contribute to the persistence of coral reefs in geologic time. Consequently, environmental and physiological conditions that result in changes in the relationship between the animal host and symbiotic algae may have profound ecological effects.

This chapter discusses the coral-zooxanthella symbiosis from the perspective of the nutrient dynamics and energetics of the association and in the context of the stability and adaptability of the symbiosis in the coral-reef ecosystem in which they are found. We examine aspects of the structure and function of the symbiosis that are believed to account for the high rates of calcification and productivity exhibited by reef corals. We discuss some of the factors that are believed to influence the density of symbionts and hence the physiological balance between the symbiotic partners. We consider the possible effects of both natural and anthropogenic events on coral reef ecosystems and how they might be expected to affect the stability and survival of the symbiosis. We also consider the possible costs and benefits associated with the symbiotic condition. We conclude by speculating about the value of using the coral symbiotic association as a measure of the "health" of coral reef ecosystems.

Although numerous animals in the coral reef community are hosts to zooxanthellae, here we focus our discussion on zooxanthellae in symbiosis with scleractinian corals. One must remember that each type or species of zooxanthellae is likely to have different adaptive capabilities and tolerances to environmental extremes (**Chapter 15**).

5.1 Description of the Symbiosis

5.1.1 Coral Anatomy and Location of Zooxanthellae

For our purposes here, a brief review of coral morphological features will suffice; a more complete description of coral morphology can be found in other recent publications (e.g., Veron, 2000; Borneman, 2001). Scleractinian corals are typically colonies of polyps linked by a common gastrovascular system, although some solitary, single-polyped forms exist (e.g. *Fungia* sp.). Polyps are small, fleshy extensions of the live coral tissue covering a non-living calcareous structure of the colony, referred to as the corallum. Although the living tissue is normally a veneer of just a few millimeters in thickness, the calcium carbonate it has deposited over time can be meters in

height or diameter (Fig. 5-1). Irrespective of the size colonies may attain, the thin layer of coral tissue itself is simply composed of two cell layers: the epidermis (sometimes referred to as ectodermis) and the gastrodermis (sometimes referred to as endodermis; Fig. 5-1). A thin connective-tissue layer, the mesoglea, composed of collagen, mucopolysaccharides, and some cells, separates these cell layers. The lower epidermal layer, the calicoblastic epidermis, secretes the calcareous external skeleton. The upper layer of epidermis (oral, or free epidermis) is in contact with seawater (Fig. 5-1). The individual polyps form corallites, i.e. skeletal tubes of deposited calcium carbonate that may be connected and fused in brain corals or are interconnected by what is referred to as the coenosteum. The tissues of imperforate corals are restricted to the surface of the skeleton. In perforate corals, the skeleton is penetrated by pores containing live coral tissues, but even in this case living tissues do not extend deeply into the corallum, and diffusive exchange of oxygen and other metabolites appears to occur quite readily, aided by many cilia in the coral's epidermal layer. Coral colonies grow by depositing new skeleton and budding additional polyps as the surface area of the tissues increases with size.

Many coral polyps are biradially symmetrical, with the central gut cavity lined by gastrodermis (Fig. 5-1). Tentacles, typically in multiples of six, surround the mouth and are used for capture of zooplankton. Food consumed by one polyp is shared with neighboring polyps via the gastrovascular system that functions in circulation and digestion of food particles. Polyp mouths also provide direct exchange of water and particulate food and wastes between the gastrovascular system and the external seawater.

The arrangement, density and size of polyps are characteristic for each coral species. However, coral species may exhibit different morphologies depending on environmental conditions such as water motion and light, and this causes problems in taxonomy of corals (Veron and Pichon, 1976; Veron, 2000).

5.1.2 *Zooxanthellae*

"**Zooxanthella**" is a general descriptive term for all symbiotic golden-colored algae that live in animals, including corals, sea anemones, molluscs and other taxa. Although the term has no taxonomic meaning, "zooxanthellae" is used primarily to refer to dinoflagellate symbionts, a group of diverse algae. It is a useful generic label, given the current state of uncertainty in the taxonomy of coral symbionts.

Zooxanthellae found in corals are typically 8-12 μm diameter cells that reside exclusively in membrane-bound vacuoles in the gastrodermal cells (Fig. 5-1). Their areal density normally ranges from $1 \times 10^6 \text{ cm}^{-2}$ to $2 \times 10^6 \text{ cells cm}^{-2}$ of coral surface, although this may be highly variable on both temporal and spatial scales. Some evidence suggests that seasonal differences exist in the density of zooxanthellae in corals; tropical corals during low light ("winter") months have greater numbers of

zooxanthellae. More information about the variability of zooxanthellae densities within colonies and among coral species is needed, especially given the critical role of zooxanthellae in coral nutrition, and the search for causes of coral bleaching, a phenomenon in which the host loses its symbionts under conditions of stress.

Based on early morphological studies, zooxanthellae in corals and other cnidarians were believed originally to belong to one species, *Symbiodinium microadriaticum*. The genetic diversity of zooxanthellae was first discovered by comparing the morphology and growth of symbionts isolated from different hosts in culture, resulting in the formal description of four species and the realization that different zooxanthellae were found in different animal hosts (reviewed by Trench, 1993; Rowan, 1991). This led to the concept of symbiont specificity, with one host selecting and maintaining one type of zooxanthella (its specific symbiont) over all other zooxanthellae. This concept, too, has changed. Our recent ability to distinguish among zooxanthellae through genetic analyses of molecular sequences (Rowan and Powers, 1992) has resulted in an explosion of different zooxanthella "taxa" (with some named species) belonging to very large diverse groups, and the discovery that different taxa inhabit the same host species and even the same host organism. One-third of scleractinian corals are now known to contain multiple *Symbiodinium* types, indicating that the symbiotic relationship is much more flexible than previously thought (Baker, 2003), and a given coral may acquire different types under different conditions.

Based on their genetic relatedness, zooxanthellae of corals and other invertebrate hosts are currently placed into seven groups (= clades; designated A through G), and others may yet be identified. Although members of a clade are more closely related to each other than to members of other clades, taxa within each clade exhibit broad genetic diversity. Zooxanthellae belonging to four of the clades (A-D) are common in corals. The individual genotypes of most zooxanthellae identified by their DNA sequences have yet to be formally described as new species.

The biogeographic distribution of members of the different clades of zooxanthellae in corals indicates the diversity of zooxanthellae is higher in the Caribbean (all 4 clades) than in the Indo-Pacific, where corals contain members of clades C and D. The reasons for these ocean-basin differences are, as yet, unresolved. In the Caribbean, clade A zooxanthellae are found in high light shallow water corals, and members of clade C are found in deeper corals than are A and B types, in the same coral or among different species. However, interpretation of ecological distribution patterns is complicated by the observation that some zooxanthellae are specialists, maintaining specific associations with only one host, while other generalist zooxanthellae associate with many hosts and have a wide biogeographic distribution. No strong relationship is evident between the types of zooxanthellae in closely related hosts, nor among the types of hosts inhabited by closely related zooxanthellae (Baker, 2003).

The dinoflagellates comprise a diverse group of mostly free-swimming single-celled microscopic typically planktonic algae that exhibit a variety of feeding modes ranging from photoautotrophy (photosynthetic carbon fixation) to heterotrophy (dissolved organic carbon uptake or feeding on particulate food). Zooxanthellae are able to photosynthesize and contain characteristic dinoflagellate pigments (diadinoxanthin, peridinin) in addition to chlorophylls *a* and *c*. They are brown or yellow-brown in color. Although zooxanthellae may be able to take up and assimilate dissolved organic carbon from host sea anemones, their own photosynthesis seems to contribute most to their energetic needs.

Zooxanthellae can live independently of their animal host. Cultures of free-living zooxanthellae established from isolates obtained from host tissues have been used to study growth rates and compare genetic and physiological characteristics of symbionts from different hosts. Some zooxanthellae never become established in laboratory cultures. Either they do not grow in algal media and under the culture conditions tested, or they are outcompeted by others better able to grow under specific culture conditions. Zooxanthellae living in animal cells are usually found in the coccoid stage (non-motile, lacking flagella); this differs from the free-living motile (dinomastigote) stage that possesses two flagella (Figure 5-2) and exhibits a characteristic swimming pattern. In culture, zooxanthellae alternate between the coccoid and dinomastigote stages. The dominant dinoflagellate feature evident on the ultrastructural level is the nucleus with permanently condensed chromosomes (dinokaryon; Figure 5-1). Free-living "wild" zooxanthellae have been isolated in a few instances from seawater and reef sediments and their genotypes characterized.

Santos and Coffroth (2003) showed that the life cycle of zooxanthellae, like that of most dinoflagellates, is dominated by asexual reproduction of haploid vegetative cells. The high genetic diversity of zooxanthellae suggests extensive recombination, although sexual reproduction has not been documented for these algae. As these authors point out, "questions pertaining to recombination in these enigmatic dinoflagellates, such as the factors that induce it and whether it occurs inside or outside a host, remain to be answered" (Santos and Coffroth, 2003).

5.1.3 Acquisition of zooxanthellae by corals

Zooxanthellae are well established in new corals derived from both asexual and sexual reproduction. In asexually produced (clonal) coral colonies, zooxanthellae are directly transmitted in coral fragments that form the basis of new colonies. In sexually produced corals, acquisition of zooxanthellae is either direct: from the parent, or indirect: from the environment. When zooxanthellae are acquired and whether or not the eggs contain zooxanthellae are characteristics of coral species. A confounding factor is the frequency of sexual versus asexual reproduction in each coral. A coral that relies almost exclusively on asexual reproduction (i.e. budding or fragmentation) for propagation, where direct transmission of

zooxanthellae is guaranteed, may not exhibit highly developed mechanisms for transmission of these algae during sexual reproduction.

During direct transmission via sexual reproduction, parental zooxanthellae are transferred to the eggs or to larvae brooded by the parent. The eggs of most corals do not contain zooxanthellae. For those that do, zooxanthellae from the gastrovascular cavity may be ingested by gastrodermal follicle cells and expelled near the oocytes by passing through temporary gaps in the mesoglea, where they are phagocytosed by the mature oocyte (Hirose *et al.*, 2001). Alternatively, cytoplasmic extensions of the gastrodermal cells that contain zooxanthellae may invade the egg plasm, as has been described for marine hydroids (Trench, 1987). These eggs may be released and fertilized in the water, or the larvae may develop within the mother coral. If eggs do not contain zooxanthellae, larvae brooded by the parent through the early stages of development (**Chapter 8**) may take up algae at any time prior to release. The presence or absence of zooxanthellae in eggs and planulae may affect their ability to persist in the plankton, as it appears that the photoautotrophic contributions of the zooxanthellae are potentially important factors in explaining the large distance of dispersion of some species (Richmond and Hunter, 1990).

Corals that do not inherit parental zooxanthellae must obtain them from seawater. The concentration of zooxanthellae in seawater over the reefs is likely to be quite low under normal conditions; positive chemotaxis of motile zooxanthellae towards the coral animal increases the probability of contact between appropriate partners. Free-living zooxanthellae may show preferential chemotaxis towards newly settled nonsymbiotic coral polyps. In experiments with the soft coral *Heteroxenia fuscescens*, motile zooxanthellae were attracted to animal extracts of juvenile nonsymbiotic polyps but not to extracts of adult symbiotic polyps and seawater controls (Pasternak *et al.*, 2004). Zooxanthellae also may be supplied indirectly to the coral by ingestion of fecal material released by corallivores and of zooplankton prey containing zooxanthellae. Regardless of the mechanism, indirect acquisition of zooxanthellae provides the potential for colonization by zooxanthellae that are genetically distinct from parental symbionts. Whether or not this actually occurs depends on host animal recognition of a suitable symbiont, and the chance encounter of the appropriate partners. There is no indication that host corals with direct, maternally transmitted zooxanthellae contain fewer zooxanthellae types than corals that acquire their symbionts by open acquisition (Baker, 2003). Together with recent evidence that the newly settled polyps of some species contain different zooxanthellae than their respective adult colonies, corals are likely to be able to acquire indirectly different zooxanthellae throughout their lives.

Coral "bleaching" also provides the potential for establishment of a new population of zooxanthellae in adult corals. Buddemeier and Fautin (1993) have proposed the "Adaptive

Bleaching Hypothesis" as a possible explanation for the ability of corals to change their algal flora from one clade to another.

Corals turn white (become bleached) when they lose most of their zooxanthellae; expulsion of zooxanthellae may involve loss of the host cells. Corals may also appear bleached when zooxanthellae are retained but lose their photosynthetic pigments. Corals that survive a bleaching event involving the loss of zooxanthellae eventually regain normal densities of zooxanthellae (they "re-brown") when environmental conditions improve. The source of zooxanthellae for the recovery and re-browning of a coral is unknown. Free-living zooxanthellae may invade corals after a bleaching event, residual zooxanthellae may re-populate their bleached host coral, or both may occur. The re-population of bleached tissues by free-living or residual zooxanthellae may change the genetic composition of the population of symbiotic algae within a coral. Field experiments have shown corals that may contain different zooxanthellae following a bleaching event.

Shifts in the composition of symbiont populations may result in an increased ability to survive future environmental stresses (Buddemeier and Fautin, 1993). Some evidence indicates that resistance to bleaching increases after symbiont populations change, but there is no information on how different zooxanthellae perform as symbiotic partners to the animal hosts under field conditions (Knowlton and Rohwer, 2003).

5.2 Nutrition and Adaptations to Environmental Factors

5.2.1 Coral nutrition

The success of corals in low-nutrient tropical waters is due largely to the variety of modes that corals utilize to obtain nutrition (Fig. 5-3). The animal has two primary feeding modes: capture of zooplankton by polyps and receipt of translocated photosynthetic products from its zooxanthellae. The amount of photosynthetic carbon translocated to the animal host is often sufficient to meet its metabolic respiratory requirements. Corals may also take up dissolved organic compounds from seawater, a process that is aided by the extremely high surface area to volume ratio of corals and the presence of cilia on their epidermal cells. However, the nutritional importance of this uptake, and of that of other food sources such as microplankton and bacteria, is uncertain. Animal metabolic waste products derived from holozoic feeding are retained within the coral, as they are a source of the nutrient elements (e.g. N, P) required by the zooxanthellae.

Zooxanthellae are photoautotrophs and thus require only inorganic nutrients, carbon dioxide, and light for photosynthetic carbon fixation. Inorganic nutrients may be acquired from animal waste metabolites, or from seawater, after passage through animal tissues. Zooxanthellae may also obtain organic nutrients from the animal, although the extent to which this occurs, and its significance, is not well understood.

The variety of coral nutritional modes suggests that corals are adaptively polytrophic and opportunistic feeders. This polytrophism seems to account for corals' ability to thrive in low-nutrient water (Muscatine and Porter, 1977). However,

environmental constraints and energetic costs associated with the maintenance of symbiotic algae, as discussed below, may under certain circumstances favor holozoic modes of nutrition.

Uptake of nutrient elements in an inorganic form from seawater by zooxanthellate corals was first observed by Yonge and Nicholls (1931) working with phosphate (PO_4^{3-}). Subsequently, such uptake has been observed by many authors for a variety of inorganic nutrient forms of nitrogen and phosphorus (PO_4^{3-} , NO_3^- , NH_4^+), and it has been firmly established that net uptake of inorganic forms occurs even at the characteristically low environmental concentrations observed in tropical seas. This mode of nutrient acquisition, once considered a curiosity, is now believed by many researchers to constitute a significant source of N and P to the symbiotic association (Fig. 5-3). However, the physiological mechanism by which this uptake occurs has been the subject of considerable debate.

Two alternatives exist to explain the uptake of dissolved inorganic nutrients even at low ambient concentrations, algal-mediated assimilation and host-mediated assimilation. This phenomenon has been investigated most extensively for ammonium. With respect to algal mediation of assimilation, D'Elia et al. (1983) proposed the "depletion-diffusion" hypothesis, suggesting that zooxanthellae reduce the coral intracellular concentration of inorganic metabolites such as NH_4^+ to such low levels that a concentration gradient is established resulting in an inward (perhaps enzymatically facilitated) diffusion of dissolved inorganic nutrient from the external seawater. In contrast, proponents of the host-mediated assimilation model (Rees 1987; Miller and Yellowlees 1989) suggest that the uptake of NH_4^+ (and by extension, other nutrient ions) is more likely transported and mediated by assimilatory enzymes in animal tissues, and then transported in an organic form to the zooxanthellae.

For ammonium uptake and assimilation, at least, several strong lines of evidence now suggest that the former mechanism is the more likely of the two alternatives. Kawaguti (1953) and Muscatine and D'Elia (1978) found that zooxanthellate, but not azooxanthellate corals take up ammonium. D'Elia et al. (1983) found that isolated zooxanthellae take up ammonium, and that uptake kinetics of isolated algae closely approximate those of intact symbioses. D'Elia and Cook (1988) provided indirect evidence that ammonium concentrations in host cytoplasm are indeed low enough to create a concentration gradient from seawater to the cytoplasm, and Szmant et al. (1990) showed that corals conserve N, which is consistent with establishing a low internal ammonium concentration. Most significantly, Swanson and Hoegh-Guldberg (1998) showed that ammonium is initially assimilated by the zooxanthellae of an anemone host model by demonstrating the incorporation of ammonium into the glutamate and glutamine pools of the zooxanthellae, and not of the host tissue.

The ramification of the algal-mediated nutrient uptake mechanism is significant: zooxanthellae, *in hospite*, are likely to be nutrient limited, as hypothesized by Cook and D'Elia

(1987), who provided a list of criteria for establishing nutrient limitation. Accordingly, increases in nutrient concentrations in ambient seawater that corals are exposed to, should, in fact, enhance cell division, growth rates and biomass of zooxanthellae, as observed by numerous authors (e.g. Hoegh-Guldberg, 1994).

5.2.2 Productivity of corals and role of zooxanthellae in calcification

Photosynthetic carbon fixation by zooxanthellae (P_{zx}) accounts for the high productivity of corals (Hatcher, 1988; **Chapter 7**). Any carbon fixed by zooxanthellae in excess of their own respiratory (R_{zx}) and growth requirements is potentially available to the host coral as a carbon and energy source. If the carbon fixed by zooxanthellae meets or exceeds the combined coral and zooxanthellae respiratory carbon requirement ($P_{zx} > R_{zx+animal}$; ratio of $P:R > 1$), the coral is potentially photoautotrophic with respect to carbon and does not require external carbon sources. When $P:R$ is less than one, carbon must be supplied from other nutritional sources, particulate or dissolved (Fig. 5-3). $P:R$ ratios derived from oxygen measurements generally show that shallow water corals have a $P:R > 1$, while the $P:R$ of deep water corals is less than one. Therefore, deep water corals are more likely to require external subsidies of organic carbon for maintenance than are shallow water corals.

Zooxanthellae enhance coral calcification and are responsible for much of the formation of the massive coral reef framework. The direct relationship between coral calcification rate and light indicates the fundamental importance of photosynthesis (Barnes and Chalker, 1990), although how photosynthesis enhances calcification is still unresolved. Models that have been proposed for the mechanism of enhancement of calcification by zooxanthellae consider the contribution of zooxanthella products to the process of calcification and the alteration of the physico-chemical environment by zooxanthellae to provide favorable conditions for calcification (Gattuso *et al.*, 1999). Photosynthesis may provide the energy for the active transport of calcium ions across the calcicoblastic epidermis for calcification, or promote the synthesis of the organic matrix upon which $CaCO_3$ is deposited. In turn, calcification generates protons (H^+) that are transported back into the coral tissues. The decrease in pH from the extra protons results in an increase in carbon dioxide, supplying the primary substrate needed for photosynthesis by zooxanthellae in the light (Al-Horani *et al.*, 2003). Photosynthesis raises the pH, providing more carbonate ions for calcium carbonate precipitation. Zooxanthellae, through the uptake of inorganic nutrients, may remove $CaCO_3$ crystal inhibitors such as phosphate from calcification sites. Despite the abundance of models, the significance of each one with respect to the link between calcification and symbiosis with zooxanthellae has not been determined.

The following section describes the factors that influence the productivity of zooxanthellae and hence the amount of carbon potentially available to the coral. The balance between primary

production and respiration (P:R) for a coral with a constant population density of zooxanthellae depends on environmental factors that affect both photosynthesis and respiration rates. The most important factors are light and temperature.

5.2.3 *Effect of Light and Temperature on Productivity of Zooxanthellae*

The reliance of corals on phototrophic nutrition and photosynthetically enhanced calcification favors the proliferation of corals in shallow, clear waters. Total daily production depends on the amount of light experienced by zooxanthellae, which is related to the light incident at their depth and transmitted through the coral animal tissues. Photosynthetic rates increase directly in response to increase in light intensity up to a certain light intensity, after which they are either independent of further increases in light or inhibited by high light (Hatcher, 1988). Consequently, mechanisms for regulating light capture and penetration through the coral could be advantageous and are evident in both the algal and animal partners.

Some corals grow well in the presence of high levels of ultraviolet (UV) radiation, while others are killed by exposure to high UV. The former include corals that are normally found in high light (in shallow water), while the latter include corals that live at greater depths or that are "shade-loving" species. Corals have UV-absorbing "sunscreen" compounds that protect against UV damage (Dunlap and Chalker, 1986). The quantity of their UV-absorbing sunscreens is related to the incident UV energy, and declines in corals with depth. The sunscreens, called mycosporine-like amino acids (MAAs), appear to be located primarily in the animal tissues and afford protection to the symbiotic zooxanthellae that do not make MAAs (e.g., members of Clade B) or that have low concentrations of these compounds.

Animal tissue pigments, contributed by four or more groups of color types of GFP-like proteins (GFP, green fluorescent protein), may serve to regulate the light received by zooxanthellae. In high light-adapted corals, fluorescent proteins are concentrated in the epidermis above the algae and may serve as a protective screen to scatter the light and remove excess light energy by fluorescence; the same proteins located below the algae in the gastrodermis in shade-adapted corals might help collect light under low light conditions by back-scattering and transformation of light to photosynthetically-active wavelengths (Salih *et al.*, 2000). However, Mazel *et al.* (2003) propose that the physical absorption, emission and reflection properties of GFPs do not function in optimizing light conditions for photosynthesis; instead, GFPs may help remove potentially damaging reactive oxygen species produced during photosynthesis.

By their location in a thin layer of photoprotective living tissue, supported by a strong skeleton formed by their animal partner (Fig. 5-1), zooxanthellae maximize light capture and are highly productive. Although they are unattached unicells, they enjoy many of the benefits of a macroscopic benthic lifestyle such as that of a seaweed. Such advantages

include maintenance in the photic zone with good water exchange. In addition, the coral may provide protection against herbivores.

As in trees, upper layers of the coral canopy receive more light than the understory surfaces of coral branches, and zooxanthellae in shaded and unshaded portions of the colony may exhibit different degrees of photoadaptation and exist at different population densities in coral tissues. This suggests that algae are localized like leaves on a tree, and that exchange of algae is limited between different parts of the coral colony.

Individual zooxanthellae acclimate to changes in light by changes in their photosynthetic systems, including the light-harvesting ability of photosynthetic units (amount of pigment) and the rate of carbon fixation (enzymatic adaptations). Zooxanthellae in corals from shaded habitats usually contain more chlorophyll and accessory light-harvesting pigments, held in larger chloroplasts with a greater number of chloroplast membranes, and thus are more efficient at light capture. The size of their light harvesting units is large. Zooxanthellae in corals in high light environments contain less photosynthetic pigment, in smaller light harvesting units in fewer chloroplast membranes, but have high rates of carbon fixation by containing more photosynthetic units. Light intensity also varies on a daily and seasonal basis, and zooxanthellae are likely to acclimate to these changes.

The ability of different coral species to photoadapt to prevailing light regimes via these mechanisms may limit the distribution of coral species in different light environments. Genetic differences in the photophysiology of different species or taxa of zooxanthellae are also likely to have a large effect on the optimal light regimes of individual coral species, and on that species distribution and ecological role. A coral's ability to host different algal symbionts, for example high and low light-adapted zooxanthellae taxa, may also influence its optimal light regime and distribution range. Clearly, proper quality and quantity of light are essential at the organismal level for (1) the overall stability of the association; (2) the ability of the symbiosis to exhibit net production ($P > R$); (3) the expression of photosynthetic pigments and the abundance of the zooxanthellae; and (4) diel behavioral aspects such as polyp expansion and contraction.

Temperature also affects metabolic rates of corals and their symbionts. The influence of temperature on productivity depends on how photosynthesis and respiration of both the algae and animal respond to changes in temperature. In general, corals are adapted to their ambient temperature conditions. For example, P:R ratios for the same species of corals in Hawaii and Enewetak across a temperature range (18-31°C) showed that Enewetak corals were adapted to their higher ambient temperatures (in Coles and Brown, 2003). Shallow corals may tolerate a wider range of temperatures than deep water corals. As was discussed for light, temperature tolerances may also depend on the individual coral species and the identity of the zooxanthellae retained by the animal host.

No given temperature causes coral bleaching (Coles and Brown, 2003). Instead, prolonged exposure to increases of 1-3°C above long-term annual maximum temperatures (ranging from 25°C to 35-36°C) are likely to induce bleaching (Coles and Brown, 2003). High light and ultraviolet light exposure may exacerbate the effects of high temperature, and other stressors may also initiate this phenomenon, which argues for caution in interpreting every bleaching event as the result of a temperature anomaly. Clearly, exposure to temperatures exceeding the tolerance range of the symbiosis affects its stability, generally resulting in the loss of zooxanthellae and possibly in the death of the host. Whether the loss is due to a direct temperature effect on the animal, zooxanthellae, or both, is not known. However, the rate of the temperature change and the duration of the temperature anomaly appear to be factors. As with changes in light, the ability of the coral to adapt to change in temperature or in other environmental factors depends on the acclimatory capability of one or more of the following: the animal, the zooxanthellae, and the symbiotic association as a whole.

5.3.4 *Effect of Nutrient Supply on Zooxanthellae in Corals*

Corals thrive in seawater where the concentrations (standing stock) of the major growth-limiting nutrient elements, nitrogen and phosphorus, are very low. A tenet of algal-animal symbiosis is that it evolved in response to relatively low ambient nutrient concentrations, and that accordingly, such conditions provide corals a competitive advantage over other benthic species. Corals conserve nitrogen by having low rates of protein catabolism and catabolizing translocated lipids and carbohydrates (Szmant et al., 1990).

Various sources of N and P exist for symbiotic zooxanthellae. The algae can obtain inorganic nutrients via recycling of waste products from their animal host, and "new" nutrients from the uptake of dissolved inorganic compounds from seawater and zooplankton capture by the coral (Fig. 5-3). In fact, early investigations of the role of symbiotic algae in corals suggested that they served as the kidneys for the animal (Yonge and Nicholls, 1931), although this is now considered highly unnecessary because of the proximity of the tissues to seawater and the relatively small thickness of the coral tissue layer. Although dissolved concentrations of nutrients are very low in most tropical waters, mass transport of nutrients via diffusion or transport across coral surfaces may be sufficient, when assimilated, to supply the nutrient requirements of the algae and its host (Hoegh-Guldberg and Williamson, 1999).

Although corals are undoubtedly adapted to waters containing very low levels of nutrients, corals can persist when nutrient levels around reefs become periodically elevated due to increased run-off from adjacent land, point source inputs (from sewage and industrial effluents), or periodic upwelling. Corals are unable to adapt to acute, high level nutrient enrichments and generally compete poorly with benthic macroalgae under such conditions. Excess nutrients may decrease calcification rates, presumably because phosphate interferes with aragonite crystal formation

during calcification (Simkiss, 1964).

Although some evidence suggests that elevated phosphate levels (exceeding about 1 μM) reduce calcification, and that high dissolved inorganic nitrogen levels (exceeding about 10 μM) destabilize the symbiosis by enhancing growth rates of the zooxanthellae, firm evidence is lacking that even these levels that would be considered extremely high for reef waters, directly benefit or affect the survival of the symbiosis. When growth rates of the zooxanthellae exceed coral growth or result in high population levels that are stressful to the coral animal, extra algae may be simply expelled. The expulsion of zooxanthellae may also represent a unique detoxification mechanism for the coral. For example, zooxanthellae have a high tolerance for heavy metals and accumulate them from seawater. Periodic expulsion of zooxanthellae could reduce the "body burden" of the heavy metals in the coral animal, as demonstrated for temperate sea anemones (Harland and Nganro, 1990).

Corals that survive direct effects of added nutrients may succumb to indirect effects such as reduction of light by increased phytoplankton biomass in the water column and overgrowth by fleshy seaweeds.

5.4 Stability of the Symbiosis

A stable symbiosis is defined as one in which the density of zooxanthellae in corals remains relatively constant under a given set of environmental conditions and the symbiotic partners do not change. This constancy may be important in balancing the benefits and the costs of the symbiosis (Table 5-1). Thus, the growth of zooxanthellae in corals is likely to be regulated somehow relative to the growth of the host. Either the growth rates of the zooxanthellae and the animal cells are comparable, or, if different, excess zooxanthellae are expelled from the coral.

Direct measurements of growth rates of zooxanthellae in coral tissue are difficult to make; doubling times have been estimated from diel measurements of the mitotic index (= the percent of dividing cells, Fig. 5-2) of zooxanthellae, while making assumptions about the duration and phasing of cell cycle stages. Doubling times for symbiotic zooxanthellae calculated by this approach show them to be at least an order of magnitude lower than for cultured zooxanthellae maintained in nutrient-enriched seawater.

Zooxanthellae densities may be regulated by the availability of nutrients. Resource limitation may help preserve the balance between zooxanthellae and animal biomass and growth rates. Upper density limits are likely controlled indirectly by the animal cell habitat, slowing zooxanthella division rates by limitations on space or diffusion of gases (CO_2 , O_2) through animal protoplasm. Some researchers have speculated that the host may produce a compound to inhibit algal growth once a certain density has been reached, but this compound has yet to be identified. Clearly, corals are known to expel zooxanthellae, and this is believed to be an important mechanism for controlling densities.

Furthermore, as numbers of zooxanthellae increase in coral tissue, self-shading of cells will reduce available light and there will be intense competition for limited resources, CO₂ and nutrients, potentially reducing net production and growth. In certain rapidly growing areas of the coral, animal growth rates may exceed those of the zooxanthellae, and populations of zooxanthellae are thus "diluted." For example, tips of branches of rapidly growing species often appear white and have reduced algal densities.

Environmental factors that are likely to affect both animal and algal growth include physical conditions and the availability of prey. Light directly affects photosynthetic productivity, while prey capture directly affects animal tissue growth and indirectly affects growth of zooxanthellae by its potential supply of nutrients and creation of new animal tissues, habitat for more zooxanthellae. Until recently, zooxanthellae were considered to live in a nutrient-rich environment by virtue of their intracellular habitat (Fig. 5-2). However, these algae display characteristics that suggest that their growth is normally nutrient-limited (Cook and D'Elia, 1987). The addition of dissolved inorganic nitrogen to seawater causes an increase in the growth rate of zooxanthellae (Hoegh-Guldberg, 1994) and in their nitrogen to phosphorus ratio (Muller-Parker *et al.*, 1994). The opposite trends are obtained when symbiotic associations are maintained with no particulate food resources in low nutrient seawater. It is unknown if the animal withholds nutrients from its algae, or if the supply is limited by the availability of nutrients (including animal prey and seawater as sources), or both. Nutrient limitation of the growth of zooxanthellae may favor the coral animal by creating an excess of photosynthetic carbon products that cannot be used for production of new cells and is therefore translocated to the animal host (Falkowski *et al.*, 1993).

Although the stability of the symbiosis is a useful concept, the diversity of zooxanthellae taxa in corals means we need to consider the possibility that apparently stable populations may be characterized by profound changes in the genetic composition of the zooxanthellae inhabiting corals over time. Furthermore, symbiont densities may follow predictable seasonal cycles, with highest densities of symbionts during low light winter months, highest animal tissue biomass in spring, and lowest population densities of zooxanthellae during late summer and fall months (Fitt *et al.*, 2000). These seasonal cycles may represent fine-tuning of the symbiosis in response to seasonal changes in light and temperature, with resultant effects on coral growth. As opposed to these normal cycles in zooxanthellae population dynamics, symbiont population densities may be disrupted by stressors that result in the mass expulsion of zooxanthellae, resulting in visibly bleached corals. Environmental stresses such as extreme temperatures, high light, air exposure, or rapid change in salinity cause coral bleaching. These large-scale disruptions in the symbiosis may provide positive or negative shifts in the balance between benefits and costs of the symbiosis

(Table 5-1). If the coral survives the stress and regains a normal population density of zooxanthellae, there may be a period during the re-population phase when algal growth rates exceed those of the animal tissue.

5.5 Cost-Benefit Analysis of the Symbiosis

Table 5-1 presents features that we consider to represent potentially significant benefits and costs of the symbiotic relationship between zooxanthellae and their coral animal hosts. These features are presented from the perspectives of both partners and of the complete association. We do not regard this table to be all-inclusive or complete, but we do suggest that this approach, albeit somewhat anthropomorphic, is a useful way to consider the symbiosis and may be helpful in framing future research directions.

From the animal's perspective, "sufficient" numbers of zooxanthellae must provide some input of energy towards offsetting respiratory requirements. A balance must exist between photosynthetic production and the metabolic cost of maintaining the algae. The costs include mechanisms to cope with high oxygen tension (activation and increase in levels of antioxidant enzymes) and possible regulation of the growth rate of zooxanthellae (Table 5-1). Since most corals contain 1×10^6 cm^{-2} to 2×10^6 zooxanthellae cm^{-2} , it is likely that this range represents an optimal algal density that balances the benefits and costs of the symbiosis. Rapid changes in densities of zooxanthellae in corals due to environmental perturbations, for example coral bleaching in response to high temperature and algal growth in response to increase in seawater nutrients, will upset this balance and may stress the coral by uncoupling algal and animal growth. From the alga's perspective, the coral must provide a good habitat. The "economic" benefit of the partnership may be viewed as the net return based on the relative costs of the symbiosis between zooxanthellae and the coral animal.

Although it is difficult to evaluate benefits and costs, obviously when benefits exceed costs there is a net benefit to sustaining the symbiosis, and the association might be expected to persist in a stable state. Conversely, when costs exceed benefits, net costs exist and the association might not persist. Thus, the persistence and stability of the symbiotic relationship at both ecological and evolutionary scales must depend on the net benefit of the symbiosis over relevant time scales with respect to its ability to withstand environmental stresses and to compete for space and other resources with other benthic organisms.

In some cases, benefits or costs of the partnership have been experimentally verified. For example, the enhancement of coral calcification by zooxanthellae is documented, both from comparison of calcification rates of symbiotic and non-zooxanthellate corals and by the light-enhanced calcification rates of symbiotic corals. In other cases, the relationships are less obvious. One must recognize that our knowledge of the costs and benefits of the relationship is limited, and that it can be

misleading to apply anthropomorphic interpretations of these. Subtle yet crucial benefits and costs may exist that we cannot yet identify or quantify. Moreover, the cumulative effect of different costs and benefits may not be simply additive. The interactive and synergistic effects between factors are not likely to be easily quantified.

The diversity and number of the entries in Table 5-1 suggest that the balance between benefit and cost for the relationship is highly dynamic and varies according to both previous and current conditions. Organisms have a physiological minimum and maximum tolerance to, and an optimum value for, any given factor. Within limits, such ranges of tolerance are useful constructs for the consideration of the environmental conditions both necessary and sufficient for survival. We can as yet only speculate whether the susceptibility of the coral to given stressors will be increased, decreased or modulated when compared to the susceptibility of the individual partners to the same stressors.

Factors that stress corals to a point where the relationship is disrupted seem to imply that the costs of maintaining a symbiosis have exceeded the benefits. This may provide for the short-term survival of the coral and of the zooxanthellae. When favorable conditions return, the symbiosis is re-established because the benefits to the coral are required in the long-term.

Disruption of the association by stressors may, in turn, have major consequences not only for the individual corals but also for the coral reef ecosystem. A particularly good example of this can be seen in the effect of temperature-induced coral bleaching on community structure in the Eastern Tropical Pacific (Glynn, 1991). In 1982-83, a very strong El Nino-Southern Ocean oscillation (ENSO) event resulted in severe warming and severe bleaching of corals in Costa Rica, Panama, Colombia and Ecuador.

Mass mortalities of corals occurred and reef structure changed substantially. Such severe effects notwithstanding, disruption of the symbiosis by stressors may also provide the opportunity not just to "weather a storm" but to "change partners" to other zooxanthella taxa or species that can provide better benefits and lower costs for particular environmental conditions (Buddemeier and Fautin, 2004a). For example, if zooxanthellae with high thermal tolerance successfully populate bleached corals, the new combination may be more resistant to subsequent high temperature stresses.

As we consider the factors affecting the costs and benefits of maintaining the symbiosis, which is a dynamic state in and of itself, it seems appropriate to consider three questions, namely: Is viewing symbiosis in terms of benefits and costs a practical way of assessing the ability of a symbiosis to persist? What are the known factors that shift the balance from benefit (+) to cost (-) to the symbiotic association? Are such factors interrelated?

Since we are only capable of making crude determinations of relative cost or benefit of a given factor, we cannot realistically provide numbers (limits) for the quantification of benefits and costs. Although this means that the answer to the first question is "no" in most cases, consideration of the relative benefits and costs does facilitate our ability to

conceptualize the response of the symbiotic association to changes in any factor.

Exposure to extremes in temperature, oxygen and salinity are all known to destabilize the symbiosis and result in the loss of zooxanthellae (coral bleaching). For each of these stressors, the cost of sustaining the zooxanthellae is likely to be too great so that either the host actively expels them or the zooxanthellae leave on their own accord. The stressor may damage the zooxanthellae, creating a liability for the host if the cells were to remain in their tissues. For example, disruption of photosynthetic membranes by high temperature leads to the uncoupling of photosynthetic energy transduction and the production of damaging reactive oxygen species, killing the zooxanthellae and damaging host cells (Tchernov *et al.*, 2004). Nutrients, on the other hand, seem to have a different effect that may also result in the active expulsion of zooxanthellae by the host. In this case, under conditions of nutrient repletion, algal expulsion seems only to keep the host from being overgrown by its endosymbionts. A disruption of the balance between the animal host and its zooxanthellae may result in reductions in productivity and coral growth, leading to possible overgrowth by faster-growing organisms (seaweeds). Below we discuss some practical examples of how natural and anthropogenic stresses to corals affect the stability of the symbiosis.

The final question posed above asked whether factors that affect the net benefit of the symbiosis interrelate with one another. It is possible to define a set of conditions under which a symbiosis will persist, and conversely, under which it will not. Nonetheless, we presently have almost no information regarding synergistic interactions and the effects of multiple stress factors on the net benefits to maintaining the symbiosis.

5.6 Environmental Effects on the Symbiosis

Other chapters in this book review general ecological features relating to corals and coral reefs. Here, we consider the stability of coral/zooxanthellae symbioses with respect to environmental stresses. We approach this topic first from the perspectives of local and regional effects, and then from the perspective of global environmental changes and effects through the alteration of the essential factors of sedimentation, light, nutrients, and temperature.

5.6.1 Local and Regional Stresses to Symbiotic Corals

In coastal areas, human population densities are increasing at an alarming rate, as people are migrating to within a few hundred kilometers of coasts as was dramatically illustrated by the tsunami tragedy of 2004. This demographic factor is having substantial environmental effects in all coastal areas in temperate and tropical regions, but to date most attention has been paid to temperate areas where more scientific study and environmental concern occur. That situation is beginning to change. Numerous meetings of international authorities on coral reefs over the last decade have concluded that the cumulative effects of local coastal development are presenting more

immediate problems than any present global effect such as ozone depletion or enhanced greenhouse effect due to the anthropogenic release of carbon dioxide. This is particularly important because much international policy concern has been focused on controlling greenhouse gases and climate change, while equivalent concern about recognizing on an international level the cumulative threat local stressors has only recently developed (see below).

Human coastal development brings with it increased inputs of nutrients from sewage and runoff. The process of over-enrichment by anthropogenic nutrient inputs (also referred to as "cultural eutrophication") is widely recognized and is becoming better understood in tropical environments where coral reefs are found. The classic example of this is Kaneohe Bay, Hawaii, where coral reefs suffered badly from increases in nutrient inputs and sedimentation (Smith, 1981). A remarkable advance in understanding of coral nutrition and maintenance of stable associations has occurred though almost without recognition or fanfare in the formal scientific literature. Aquarium hobbyists, building on the work of scientists seeking to improve public aquarium exhibits, have revolutionized the ability to maintain and grow corals in their own homes (Borneman, 2001). The works of Adey (1983), who recognized the importance of macroalgae in "scrubbing" excess nutrients from aquaria, and Jaubert and Gattuso (1989), who recognized the value of enhancing coupled nitrification and denitrification to maintain a low-N environment, have stimulated the adoption of devices such as the "Jaubert plenum," which is an undergravel biological filter that maintains low N levels in aquaria. The success of this system illustrates the value of controlling serious destabilizing effects of high N levels on zooxanthellate corals. The aquarium hobbyists have also learned how to maintain proper seawater chemistry to maintain and promote the growth (calcification) of corals.

Increased sedimentation and runoff are two of the most pronounced early effects of coastal development, and it has been recognized for some time that global sediment fluxes from land to sea are increasing (Milliman and Meade, 1983). In mountainous high precipitation areas especially, clear-cutting of forests and development of agrarian economies result in increased levels of water-borne sediments and nutrients, and decreases (or increases in the seasonal variation in) salinity. These activities have been associated with a reduction in coral cover and diversity (Kuhlmann, 1988). At the same time, symbiotic corals can provide a useful temporal record of environmental changes within a reef ecosystem because of the dependence of calcification on zooxanthellae; changes in calcification rate due to variation in parameters such as temperature, salinity, turbidity, and pollution are recorded in the density banding patterns of the coral skeletons.

Studies of terrestrial runoff in Kaneohe Bay, Hawaii, and other places suggest that turbidity (suspended sediment in the water) is one of the foremost enemies of reef corals (**Chapter**

15). Although the probable greatest effect of sediment on corals relates to the accumulation of particles on coral surfaces and interference with feeding, the effect of turbidity on the quantity and quality of light available for photosynthesis is also important, a matter of clear bearing on the persistence of the coral-zooxanthellae symbiosis. Alteration of light quality and quantity is due directly to the higher turbidity related to sediment loads and indirectly to turbidity resulting from the stimulation of phytoplankton growth by increased nutrient loadings associated with sedimentation and agricultural land practices (increased fertilizer and pesticide application, slash and burn and deep tillage agriculture) (see section 5.2.2 on coral nutrition and calcification).

In addition to the effects of increased run-off and sedimentation on nutrient levels, phytoplankton biomass, and turbidity, also to be considered are the effects on the trophic status of the water column overlying reefs that in turn may affect the nutrition and stability of the symbiosis. The predominant effect of elevated nutrient levels on corals and coral reefs seems to result from altered trophic structure resulting from overgrowth of corals by fleshy green algae, high bacterial biomass, increased disease (**Chapter 6**), etc., which are beyond the scope of this chapter.

5.6.2 *Global Stresses to Symbiotic Corals*

Scientists are increasingly concerned about the effects of global stresses and global change on corals and coral reefs (Hallock, 2001). With respect to the coral-zooxanthellae symbiosis, global stresses of particular relevance include: 1) increased UV light due to a reduction in the ozone layer; 2) temperature increases due to global warming and related changes in oceanic circulation patterns leading to variation in temperature and nutrient inputs; 3) cumulative increases in nutrients and turbidity due to industrial development in other areas; and 4) possible reductions in world ocean pH's due to CO₂-derived acidification.

The effect of chlorofluorocarbons (CFCs) on the depletion of the ozone layer and the subsequent increase in the flux of ultraviolet (UV) light to the Earth's surface have received substantial attention with respect to coral reefs. Conditions that favor photosynthesis by zooxanthellae expose corals to UV damage. Although corals contain pigments that may afford considerable protection from UV, the effective metabolic cost of UV protection for the animal and zooxanthellae with respect to the symbiosis is unknown. If the cost to the symbiosis is greater than the benefit of light-driven photosynthesis, then the symbiosis becomes a liability.

Temperature is a crucial factor affecting the stability of the coral/zooxanthellae symbiosis at the individual level, and certainly, in a larger sense, of coral reefs (Glynn, 1991). Limits of temperature tolerance for corals and well-developed coral reefs are considered to range from a winter minimum of approximately 18°C to a summer maximum of approximately 30°C, although to be sure, thriving reefs are found at either extreme

that appear to be uniquely adapted to such conditions. While initial interest in the ramifications of temperature stress on photosynthesis and respiration in corals and coral reefs developed as a result of concern about the thermal effects of electrical power generation on local biota (e.g. Coles and Jokiel, 1977), more recent interest in this topic is related to concerns about potential increases in global temperatures due to the enhanced greenhouse effect resulting from anthropogenic emissions of infrared-absorbing greenhouse gases (e.g. Jokiel and Coles, 1990).

Exposure to temperature extremes may or may not affect the stability of the symbiosis. Both the length of exposure to and the severity of a given temperature stress or anomaly are important factors. As an example, probably the best-known response that indicates a destabilization of the coral/zooxanthellae symbiosis, "bleaching," depends on both of these factors (Fitt *et al.*, 2001). Corals bleach, or actively expel their zooxanthellae most typically when temperatures increase sharply for a short period of time (+3-4°C, several days) or increase moderately for a longer period of time (+0.5-1.5°C, several weeks) (Glynn and D'Croz, 1990; Jokiel and Coles, 1990). Since coral calcification, and therefore reef growth, depends on the presence of zooxanthellae, a gradual rise in sea level with global warming might result in the demise of coral reefs at low latitudes and a shift to higher latitudes. The effects of low light and increased nutrient inputs from global changes in atmospheric deposition and oceanic circulation patterns factors are discussed in the previous section.

Whether the global extent of disruption of the coral symbiotic association with zooxanthellae will provide an accurate "barometer" of coral reef degradation due to global climate change remains an issue of debate and uncertainty. A recent report has concluded that secular increases in ocean temperatures are very likely to increase the number of coral bleaching episodes and that the combination of global climate change and local effects is a serious threat to coral reefs (Buddemeier *et al.* 2004b). Bleaching may simply represent a temporary disruption of the symbiosis that allows each partner to survive the stress on its own. As Baker (2004) states, "...in an era of climate change and global warming, the continued success of [coral reef] ecosystems is dependent on the stable association of these symbionts with the reef-building organisms which depend upon them." The potential for new and more tolerant combinations of partners after bleaching makes this issue more complicated, but does offer some hope that successful combinations may ensue.

A concern now looming on the horizon is the prospect of the "titration" of oceanic pH as a direct effect of anthropogenic CO₂ inputs. Brewer (1997) has calculated that by mid-century atmospheric CO₂ levels could approach 600 ppm with concomitant surface ocean pH reductions of approximately 0.3 units. This change in the ocean's carbonate buffer system could lead to an enhancement of photosynthesis in marine algae by increasing the pCO₂, but it may also decrease carbonate saturation and thereby

decrease calcification (Takahashi, 2004). The combination of these two effects would have profound effects on zooxanthellate-coral distribution by reducing the areal extent of the ocean suitable to sustain coral growth and survival.

5.8 Summary

The symbiotic association with zooxanthellae is clearly beneficial to corals. Increasing evidence has shown that the symbiotic state is accompanied by sensitivity to environmental stress, since a common response to a stress is the disruption of the symbiosis, resulting in coral bleaching. The response is complex, since zooxanthella taxa (or species) and different species or genotypes of coral animals may have different adaptive capabilities and tolerances to environmental extremes. As the host animal depends on its complement of zooxanthellae for reduced carbon compounds, coral death will ensue if stresses persist for long periods of time or if they are at levels outside of the tolerance range of the coral and of the zooxanthellae. Factors that induce a stress response include: light (quantity and UV), temperature, sewage and run-off inputs (high nutrients, increased turbidity), salinity (freshwater run-off from land due to deforestation and other land-use practices), and physical damage.

Disruption of the symbiotic association, in turn, has potential for use as an indicator of the health of the coral reef ecosystem. Drastic changes in the stability of the symbiosis, evidenced by changes in the ratio of zooxanthellae to animal biomass in corals, may turn out to be a useful diagnostic indicator of stresses to coral reefs. Present research is leading to improved understanding of how and when this can occur.

References

- Adey, W. H. 1983. The microcosm: a new tool for reef research. *Coral Reefs* 1:193-201.
- Al-Horani, F. A., S. M. Al-Moghrabi, and D. De Beer. 2003. The mechanism of calcification and its relation to photosynthesis and respiration in the scleractinian coral *Galaxea fascicularis*. *Marine Biology* 142 : 419-426.
- Baker, A. C. 2003. Flexibility and specificity in coral-algal symbiosis: Diversity, ecology and biogeography of *Symbiodinium*. *Annu. Rev. Ecol. Syst.* 34: 661-689.
- Baker, A. C. 2004. Symbiont diversity on coral reefs and its relationship to bleaching resistance and resilience. Pages 177-194 in E. Rosenberg and Y. Loya, editors. *Coral Health and Disease*. Springer-Verlag, Berlin.
- Barnes, D. J., and B. E. Chalker. 1990. Calcification and photosynthesis in reef-building corals and algae. In Z. Dubinsky (ed.), *Ecosystems of the world*, vol. 25: Coral reefs, pages 109-131. Elsevier Science Publishing, New York, 550 p.
- Brewer, P. G. 1997. Ocean chemistry of the fossil fuel CO₂ signal: The haline signature of "Business as Usual." *Geophys. Res. Letters* 24: 1367-1369.
- Borneman, E. H. 2001. *Aquarium Corals: Selection, Husbandry, and Natural History.*, Charlotte, Vermont, Microcosm Ltd. 464 p.
- Buddemeier, R. W. and D. G. Fautin. 1993. Coral bleaching as an adaptive mechanism. *BioScience* 43: 320-326.
- Buddemeier R.W., Baker A.C., Fautin D.G., and Jacobs J.R. 2004a. The adaptive hypothesis of bleaching. In E. Rosenberg and Y. Loya (eds.), *Coral Health and Disease*, pages 427-444. Springer-Verlag, New York, Berlin, p. xxx.
- Buddemeier, R. W., J. A. Kleypas, and R. B. Aronson. 2004b. *Coral Reefs & Global Climate Change: Potential Contributions of Climate Change to Stresses on Coral Reef Ecosystems*. Pew Center on Global Climate Change, Arlington, Virginia USA.
- Coles, S. L., and B. E. Brown. 2003. Coral bleaching - capacity for acclimatization and adaptation. *Adv. Marine Biology* 46: 183-223.
- Coles, S. L., and P. L. Jokiel. 1977. Effects of temperature on photosynthesis and respiration in hermatypic corals. *Mar. Biol.* 43: 209-216.
- Cook, C. B., and C. F. D'Elia. 1987. Are natural populations of zooxanthellae ever nutrient-limited? *Symbiosis* 4: 199-212.
- D'Elia, C. F., and C. B. Cook. 1988. Methylamine uptake by zooxanthellae/invertebrate symbioses: insights into host ammonium environment and nutrition. *Limnol. Oceanogr.*: 1153-1165.
- D'Elia, C. F., S. L. Domotor, and K. L. Webb. 1983. Nutrient uptake kinetics of freshly isolated zooxanthellae. *Mar. Biol.* 75: 157-167.
- Dunlap, W. C., and B. E. Chalker. 1986. Identification and quantification of near-UV absorbing compounds (S-320) in a hermatypic scleractinian. *Coral Reefs* 5: 155-159.

- Falkowski, P. G., Z. Dubinsky, L. Muscatine, and L. R. McCloskey. 1993. Population control in symbiotic corals. *BioScience* 43: 606-611.
- Fitt, W. K., F. K. McFarland, M. E. Warner, and G. C. Chilcoat. 2000. Seasonal patterns of tissue biomass and densities of symbiotic dinoflagellates in reef corals and relation to coral bleaching. *Limnol. Oceanogr.* 45: 677-685.
- Fitt, W. K., B. E. Brown, M. E. Warner, and R. P. Dunne. 2001. Coral bleaching: interpretation of thermal tolerance limits and thermal thresholds in corals. *Coral Reefs* 20: 51-65.
- Gattuso, J. P., D. Allemand, and M. Frankignoulle. 1999. Photosynthesis and calcification at cellular, organismal and community levels in coral reefs : a review on interaction and control by carbonate chemistry. *Amer. Zool.* 39: 160-183.
- Glynn, P. W. 1991. Coral reef bleaching in the 1980s and possible connections with global warming. *Trends Ecol. Evol.* 6: 175-179.
- Glynn, P. W., and L. D'Croz. 1990. Experimental evidence for high temperature stress as the cause of El Niño-coincident coral mortality. *Coral Reefs* 8: 181-191.
- Hallock, P. 2001. Coral reefs, carbonate sediments, nutrients, and global change. Pages 387-427 in J. George D. Standley, editor. *The History and Sedimentology of Ancient Reef Systems*. Kluwer Academic/Plenum Publishers, New York.
- Harland, A. D., and N. R. Nganro. 1990. Copper uptake by the sea anemone *Anemonia viridis* and the role of zooxanthellae in metal regulation. *Mar. Biol.* 104: 297-301.
- Hatcher, B. G. 1988. The primary productivity of coral reefs: a beggar's banquet. *Trends Ecol. Evol.* 3: 106-111.
- Hirose M., R. A. Kinzie III, and M. Hidaka. 2001. Timing and process of entry of zooxanthellae into oocytes of hermatypic corals. *Coral Reefs* 20: 273-280.
- Hoegh-Guldberg, O. 1994. The population dynamics of symbiotic zooxanthellae in the coral *Pocillopora damicornis* exposed to elevated ammonia. *J. Pacific Science* 48: 263-272.
- Hoegh-Guldberg, O., and J. Williamson. 1999. Availability of two forms of dissolved nitrogen to the coral *Pocillopora damicornis* and its symbiotic zooxanthellae. *Marine Biology* 133: 561-570.
- Jaubert, J., and J. P. Gattuso. 1989. An integrated nitrifying-denitrifying biological system capable of purifying seawater in a closed circuit system, p. 101-106. In: *Deuxieme Congres International d'Aquariologie (1988)*, Monaco. Bulletin de l'Institut Oceanographique, Monaco, No. special 5.
- Jokiel, P. L., and S. L. Coles. 1990. Response of Hawaiian and other Indo-Pacific reef corals to elevated temperatures associated with global warming. *Coral Reefs* 9: 155-162.
- Kawaguti, S. 1953. Ammonium metabolism of the reef corals. Pages 1:171-176 in *Biol. J. Okayama Univ.*
- Knowlton, N., and F. Rohwer. 2003. Multispecies microbial mutualisms on coral reefs: the host as a habitat. *American Naturalist* 162(Suppl.):S51-S62.
- Kuhlmann, D. H. H. 1988. The sensitivity of coral reefs to

- environmental pollution. *Ambio* 17 : 13-21.
- Mazel, C. H., M. P. Lesser, M. Y. Gorgunov, T. M. Barry, J. H. Farrell, K. D. Wyman, and P. G. Falkowski. 2003. Green-fluorescent proteins in Caribbean corals. *Limnol. Oceanogr.* 48 : 402-411.
- Miller, D. J., and D. Yellowlees. 1989. Inorganic nitrogen uptake by symbiotic marine cnidarians: a critical review. *Proc. R. Soc. (Ser. B)* 237: 109-125.
- Milliman, J. D., and R. H. Meade. 1983. Worldwide delivery of river sediment to the oceans. *J. Geol.* 91: 1-21.
- Muller-Parker, G., C. B. Cook, and C. F. D'Elia. 1994. Elemental composition of the coral *Pocillopora damicornis* exposed to elevated seawater ammonium. *Pacific Science* 48: 234-246.
- Muscatine, L., and C. F. D'Elia. 1978. The uptake, retention, and release of ammonium by reef corals. *Limnol. Oceanogr.* 23: 725-734.
- Muscatine, L., and J. W. Porter. 1977. Reef corals: mutualistic symbioses adapted to nutrient-poor environments. *BioScience* 27: 454-459.
- Pasternak, Z., A. Bchar, A. Abelson, and Y. Achituv. 2004. Initiation of symbiosis between the soft coral *Heteroxenia fuscescens* and its zooxanthellae. *Mar. Ecol. Prog. Ser.* 279 : 113-116.
- Rees, T. A. V. 1987. The green hydra symbiosis and ammonium I. The role of the host in ammonium assimilation and its possible regulatory significance. *Proc. R. Soc. Lond. B.* 229: 299-314.
- Richmond, R. H., and C. L. Hunter. 1990. Reproduction and recruitment of corals: comparisons among the Caribbean, the tropical Pacific, and the Red Sea. *Mar. Ecol. Prog. Ser.* 60: 185-203.
- Rowan, R. 1991. Molecular systematics of symbiotic algae. *J. Phycology* 27: 661-666.
- Rowan, R., and D. A. Powers. 1992. Ribosomal RNA sequences and the diversity of symbiotic dinoflagellates (zooxanthellae). *Proc. Natl. Acad. Sci. USA* 89: 3639-3643.
- Salih, A., A. Larkum, G. Cox, M. Kuhl, and O. Hoegh-Guldberg. 2000. Fluorescent pigments in corals are photoprotective. *Nature* 408 : 850-853.
- Santos, S. R., and M. A. Coffroth. 2003. Molecular genetic evidence that dinoflagellates belonging to the genus *Symbiodinium* Freudenthal are haploid. *Biol. Bull.* 204: 10-20.
- Simkiss, K. 1964. Phosphates as crystal poisons of calcification. *Biol. Rev.*:39: 487-505.
- Smith, S. V. 1981. Responses of Kaneohe Bay, Hawaii, to relaxation of sewage stress. Pages pp. 391-410. In: B. J. Neilson and L. E. Cronin [eds.], *Estuaries and Nutrients*. Humana Press. Clifton, New Jersey.
- Swanson, R. and O. Hoegh-Guldberg (1998). Amino acid synthesis in the symbiotic sea anemone *Aiptasia pulchella*. *Mar. Biol.* 131: 83-93.
- Szmant, A. M., L. M. Ferrer, and L. M. FitzGerald. 1990. Nitrogen excretion and O:N ratios in reef corals : evidence for

- conservation of nitrogen. *Mar. Biol.* 104: 119-127.
- Takahashi, T. 2004. The fate of industrial carbon dioxide. *Science* 305: 352-353.
- Tchernov, D., M. Y. Gorbunov, C. deVargas, S. N. Yadav, A. J. Milligan, M. Haggblom, and P.G. Falkowski. 2004. Membrane lipids of symbiotic algae are diagnostic of sensitivity to thermal bleaching in corals. *Proc. Nat. Acad. Sci.* 101: 13531-13535.
- Trench, R. K. 1987. Dinoflagellates in non-parasitic symbioses. In F. J. R. Taylor (ed.), *The biology of dinoflagellates*, pages 531-570. Blackwell, Oxford.
- Trench, R. K. 1993. Microalgal-invertebrate symbiosis - a review. *Endocytobiosis Cell Res.* 9: 135-175.
- Veron, J. E. N. 2000. *Corals of the World*. Townsville, Queensland, Australia, Australian Institute of Marine Science, Vol. 1, 463 p.
- Veron, J. E. N., and M. Pichon. 1976. *Scleractinia of Eastern Australia. Part I. Families Thamnasteriidae, Astrocoeniidae, Pocilloporidae*. Austr. Institute Mar. Sci. Monogr. Ser. I: 1-86.
- Yonge, C. M., and A. G. Nicholls. 1931. Studies on the physiology of corals. IV. The structure, distribution and physiology of zooxanthellae. *Sci. Rep. Great Barrier Reef Exped.* 1: 135-176.

Table 5-1. Putative Benefits and Costs of the Symbiotic Relationship for the Coral Animal and for Zooxanthellae

Benefits	Costs	Indirect (+/- effects)
A. Animal		
Supply of reduced carbon, providing low respiration costs and conservation of metabolic reserves	Regulation of algal growth and production of peri-algal vacuoles	High surface area-to-volume ratio favors both light capture and prey capture.
Increased growth and reproduction	Defenses against high oxygen tension, high light, and UV	Restriction to the photic zone
Increased calcification rate	Mechanisms for rejection of foreign or excess algae	
Conservation of nutrients	Vulnerability to environmental stresses that affect plants	
Sequestration of toxic compounds by algae		
B. Zooxanthellae		
Supply of CO ₂ and nutrients from host	Translocation of a significant fraction of photosynthetic carbon to animal	Nutrient supply is regulated
Maintenance in photic zone	Regulation of growth rate; growth slower in coral than in free-living state	Protection from grazers
Protection from UV damage by animal tissues	Expulsion from host	Dispersal by predators on animal tissue

Maintenance of a high population density of a single or few genotypes by host under uniform environmental conditions

Supply of CO₂ and nutrients limited by host

C. Coral symbiotic association

Increased growth, more competitive for space on reef

Compounded sensitivity to environmental stresses that affect algae, animals, or both

Increased ability to partition resources of food and space

Restricted tolerance range of light, temperature, and sedimentation conditions for growth

Increased resistance to water motion due to high calcification

Notes: Factors which are not direct benefits or costs are listed as indirect effects. The relative contribution of each factor to maintaining the balance between benefit and cost of the symbiotic association is unknown. Also, not all of these putative benefits have been documented, such as sequestration of toxic compounds by algae.

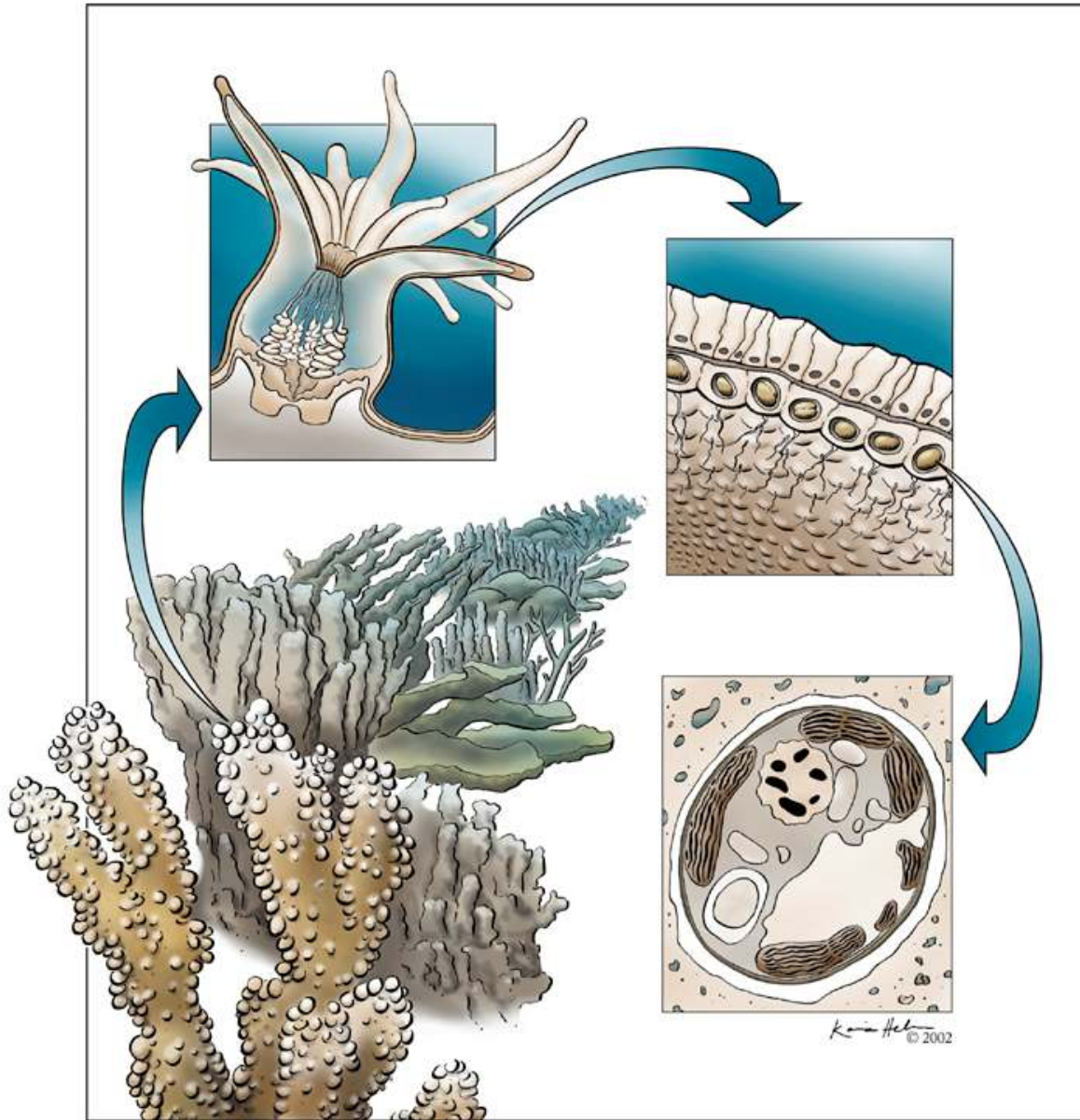


Figure 5-1. The coral symbiosis. A cross-section of a single coral polyp from a coral colony is shown in the upper left-hand boxed inset. The arrow leading from the coral polyp points to a section through the two tissue layers of the oral surface of the polyp (see also Fig. 5-2). The epidermis is the upper tissue layer in contact with the seawater, and the gastrodermis is the lower tissue layer in contact with the gastrovascular cavity. The gastrodermis contains zooxanthellae. The arrow from a zooxanthella points to a cross-section of the alga. The alga is enclosed in a peri-vacuolar animal membrane. Internal features shown in the cross-section include the nucleus with its permanently condensed chromosomes, sections of the chloroplast with banded photosynthetic membranes, a large (white) vacuole, and starch and lipid inclusions.

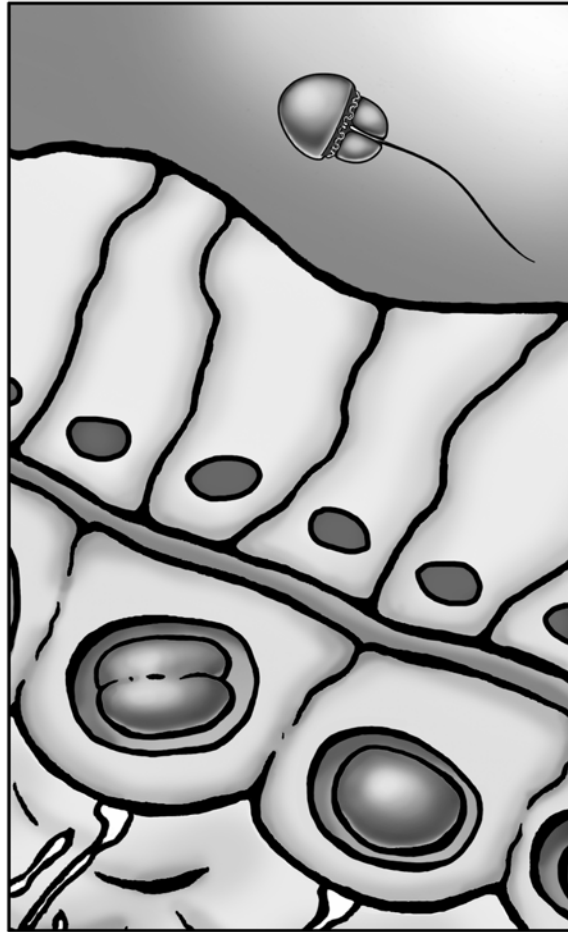


Figure 5-2: A section through the two tissue layers of the oral surface of the polyp showing the different life forms of zooxanthellae. A free-living motile cell (dinomastogote) is shown swimming in the seawater above the layer of nucleated oral epidermal cells. The two gastrodermal cells each contain one coccoid zooxanthellae; the cell on the left is in the process of dividing. The actual sizes of zooxanthellae range from 5 to 20 μm , depending on species and life form.

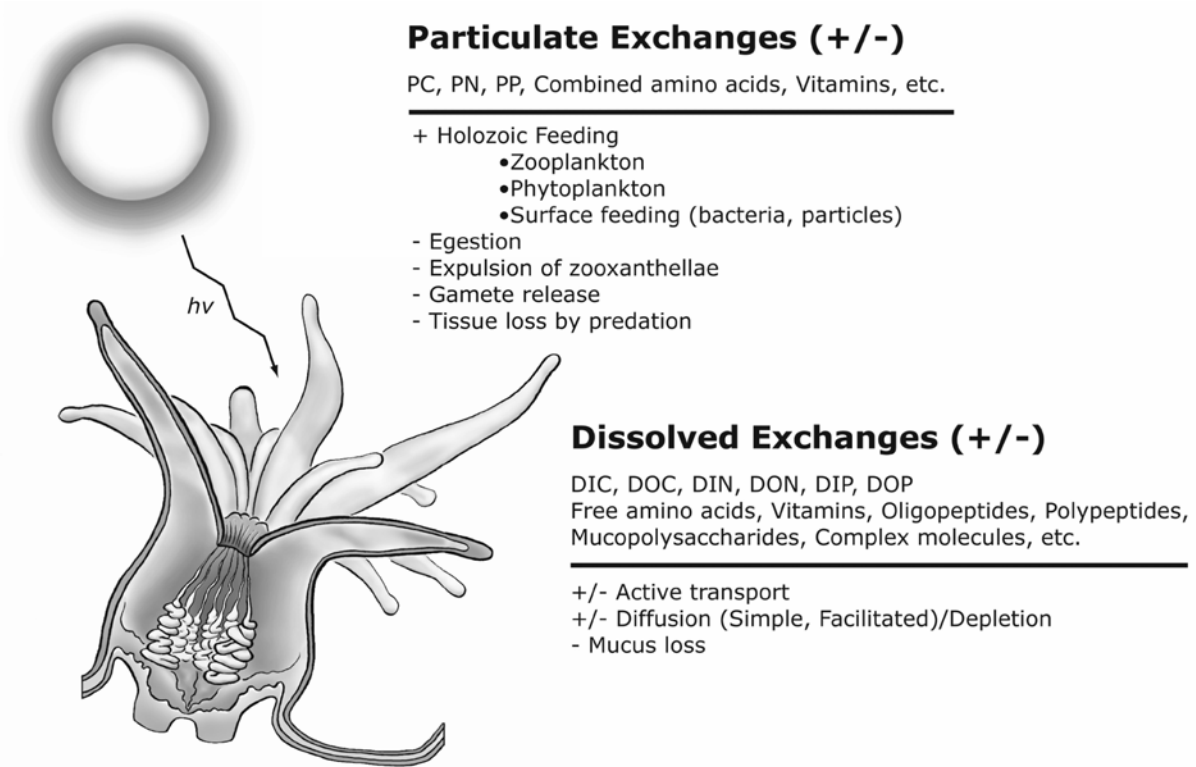


Figure 5-3: Particulate (P) and dissolved (D) exchanges of inorganic (I) and organic (O) carbon (C), nitrogen (N), and phosphorus (P) between a coral polyp and the seawater environment. "+" exchanges represent inputs from the environment to the coral, and "-" exchanges represent losses from the coral to the environment. Internal exchanges (not shown) include uptake by symbiotic algae and translocation between the algae and the host.