

THE PRODUCTIVITY OF CORALS

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Summary

The symbiosis between corals and dinoflagellate algae of the genus *Symbiodinium* (“zooxanthellae”) underpins coral reefs, which are among the most productive ecosystems in the world. Their productivity is critically dependent on the illumination and temperature conditions. Corals live within a few degrees of their upper thermal limit, and elevated sea temperatures, often exacerbated by high solar radiation, damage the photosynthetic apparatus of the zooxanthellae and trigger bleaching. Much of the zooxanthella primary production is transferred directly to the coral tissues, where it is respired, stored or released into the surrounding water column as dissolved and particulate organic material. Overall, the excess production from the reef accounts, on average, for just 3% of the total primary production, and less than 1% of the total production is available in a form (e.g. invertebrates, fish) that can be harvested.

1. Introduction

Shallow water coral reefs are among the most productive ecosystems of the world, with gross primary productivity of $1-15 \text{ g C m}^{-2} \text{ day}^{-1}$ (*ca.* $0.4-5.5 \text{ kg C m}^{-2} \text{ year}^{-1}$). These exceptionally high levels of production are achieved principally by the symbiotic algae in reef-building corals and allied invertebrates (e.g. soft corals, sea anemones) and benthic algae, especially coralline rhodophytes and chlorophytes (e.g. *Halimeda*). The symbiotic algae in corals account for 50-70% of the total primary production on most reefs, although the algae are quantitatively more important on algal reefs’ where coral

growth is weak and at some high latitude sites. This article addresses the primary production of corals.

2. Zooxanthellae: The Primary Producers in Corals

Almost without exception, the primary producers in corals are dinoflagellate algae of the genus *Symbiodinium*, colloquially known as zooxanthellae. The type species of the genus *Symbiodinium* is *S. microadriaticum* Freudenthal, brought into axenic culture from the jellyfish *Cassiopeia xamachana*. *Symbiodinium* species have subsequently been isolated into culture from some corals, but the zooxanthellae in certain species appear to be intractable to cultivation. Molecular analyses based on rDNA complex have shown that *Symbiodinium* in corals and allied invertebrates are a monophyletic group within the gymnodinoid dinoflagellates. The functional differences among the various zooxanthellae is an area of active current research.

The zooxanthellae occupy 1-10% of the biomass of the living coral tissue, and their density is usually in the range $1-5 \times 10^6$ cells cm^{-2} coral surface area, although variations with many factors, including depth and season (low densities in deeper waters and in the summer), have been reported for some coral species. The relationship between the zooxanthellae and their coral host is very intimate. The zooxanthellae are intracellular, located in coral endodermal cells and separated from the surrounding coral cytoplasm by a membrane of coral origin, called the symbiosomal membrane. Inorganic carbon (C_i) and all other elements required by each zooxanthella must, therefore, traverse multiple animal membranes.

The enzyme responsible for CO_2 fixation in zooxanthellae and other dinoflagellate algae is ribulose biphosphate carboxylase (RuBisCo) and the pattern of short-term incorporation of photosynthetically-fixed radiolabeled CO_2 (administered as bicarbonate) has confirmed that the carbon is fixed by the C_3 pathway. Specifically, the dominant compound labeled within the first few seconds is 3-phosphoglycerate, the product of RuBisCo-mediated CO_2 fixation. However, the RuBisCo of zooxanthellae and other dinoflagellates is a form II enzyme, distinct from the form I RuBisCo in green algae and land plants, and with close sequence similarity to the RuBisCo in anaerobic purple nonsulfur bacteria *Rhodobacter* and *Rhodospirillum* of the α -Proteobacteria. Form II RuBisCo has a very poor capacity to discriminate against molecular oxygen, and the photosynthetic metabolism of zooxanthellae is predicted to be particularly predisposed to photorespiration and, consequently, reduced CO_2 fixation and depressed productivity in oxygenic environments. Oxygen tensions in illuminated corals are commonly high, as a result of oxygen evolution from zooxanthella photosynthesis, and zooxanthellae in isolation display photorespiration, as indicated by recovery of radiolabeled glycolate from $^{14}\text{CO}_2$. However, photorespiration in zooxanthellae in corals has not been reported, and the implications of the form II RuBisCo of zooxanthellae for coral productivity remain to be established.

The potential negative impact of photorespiration on coral productivity is compounded by physico-chemical limitations on the access of zooxanthellae to CO_2 . The core of the

problem is that the concentration of CO_2 (the form of C_i fixed by RuBisCo) in sea water is about $12 \mu\text{M}$, with most of the *ca.* 2.4 mM of dissolved C_i in the form of HCO_3^- , because of the high pH (8.2) of sea water. The enzyme carbonic anhydrase, which catalyzes the interconversion of HCO_3^- and CO_2 , is believed to play an important role in facilitating CO_2 uptake by the zooxanthellae. In a survey of over 20 species including some corals, the animal fraction of species containing zooxanthellae had, on average, 29 times higher carbonic anhydrase activity than non-symbiotic species. Animal carbonic anhydrase has been localized to the symbiosomal membrane, where it acts to promote delivery of CO_2 to the enclosed zooxanthella, and also the animal cytoplasm of the ectodermal cells, where it promotes transfer of C_i from the external sea water to the endodermal layer.

3. Factors Influencing the Rates of Photosynthesis by Zooxanthellae (see also Chemistry of the Oceans)

The zooxanthellae in corals are generally viable and photosynthetically-active, and their photosynthetic rates are broadly comparable to nonsymbiotic dinoflagellates. The chief determinants of their photosynthetic rates in corals are light and temperature; and the response of zooxanthellae to these factors and nutrients are considered in this section.

In many studies, photosynthesis is quantified from the flux of O_2 and not CO_2 , and then converted to units of carbon. Oxygen consumption in the light provides a measure of net primary production, and the gross primary production is the sum of net oxygen production under illumination and oxygen release by respiration in the dark. A major factor contributing to the use of oxygen data to study primary production in corals is that the flux of carbon (but not oxygen) is a function of calcification, as well as photosynthesis and respiration. Calcification produces net CO_2 (specifically 0.6 moles CO_2 per mole carbonate deposited) because the acid load arising from net H^+ production at calcification promotes carbonic acid formation and thence CO_2 gas.

3.1. Irradiance (see also *Physical Oceanography*)

The availability of light for photosynthesis by the zooxanthellae in corals in the reef environment is very variable and difficult to measure. In general terms, solar radiation is attenuated exponentially with depth and the spectral range of radiation is progressively reduced, with maximal penetration of radiation with wavelengths 400-490 nm. However, the underwater light field is affected by many factors, including the angle of incident light, absorption and scattering of light by particles in the water column and the three-dimensional topography of the reef. As a result, the irradiance incident on a coral surface shows regular diel and seasonal changes and irregular changes related to both weather (cloud cover, wave action etc.) and temporal changes on the reef (e.g. growth or death of other coral colonies competing for light).

The light field can be controlled and manipulated more readily in the laboratory than on the reef. Under laboratory conditions, the response of zooxanthella photosynthesis to

irradiance is non-linear. Photosynthesis-irradiance (P-I) curves of uniform general form are displayed by both isolated zooxanthellae and intact corals (Figure 1). At low irradiances, the photosynthetic rates vary in proportion to irradiance but, with increasing irradiance, the photosynthetic rates saturate and, with further increase in irradiance, decline through either photoinhibition (if the decline is reversible) or photodamage (irreversible decline). Photoinhibition reflects zooxanthella protective mechanisms, acting to reduce the amount of light reaching the photosynthetic reaction centers. In zooxanthellae, as in plants, xanthophylls in the antennae of photosystem II act to dissipate the excess energy as heat.

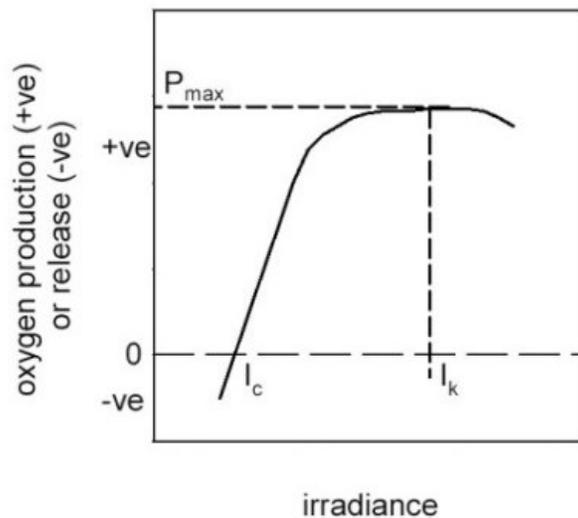


Figure 1. Generalized photosynthesis-irradiance curve for zooxanthellae

Many studies have demonstrated that corals from different depths or incubated at different irradiances vary in key photosynthetic parameters, as calculated from P-I curves. Corals acclimated to low irradiance tend to have a lower I_c and P_{max} than corals from high irradiance conditions (see legend to Figure 1 for explanation of terms). Detailed analyses of zooxanthellae in culture have demonstrated that the photosynthetic machinery of zooxanthellae for harvesting the radiant energy responds to irradiance through changes in both the size and number of photosynthetic units. These photoacclimatory responses of zooxanthellae are accompanied by other responses of the coral. In particular, the growth form of some coral species is not fixed, and colonies generally adopt a characteristic plate-like or encrusting morphology that maximizes light capture in deep waters and at low irradiance. These phenotypic responses of zooxanthellae and corals to variation in irradiance are compounded by genetic variation in both partners. Some instances of differences in the photosynthetic responses of corals from different depths may be a consequence of depth/irradiance-dependent distribution of zooxanthella genotypes with different photosynthetic properties or coral genotypes with different colony growth forms. With the availability of molecular techniques to study the coral-zooxanthella symbioses, the relative importance of phenotypic and

genotypic factors and their interaction, in shaping coral responses to irradiance are becoming increasingly amenable to analysis.

Ultraviolet (UV) radiation (200-400 nm) has deleterious effects on corals, related *inter alia* to their damage to DNA, proteins and membrane lipids. UV exposure is exacerbated by the stratospheric ozone depletion arising from the anthropogenic release of chlorinated fluorocarbons. UV radiation depresses photosynthesis in zooxanthellae, and its impacts on zooxanthella productivity is particularly significant in the top 5 m of the water column, but is detectable to 20 m in clear, tropical waters. Some protection against UV is provided by mycosporine-like amino acids which accumulate in the coral ectoderm cells and absorb UV radiation. These amino acids are derivatives of the shikimate pathway and may be synthesized by the zooxanthellae.

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Biographical Sketch

Angela Douglas is a Professor at the University of York, UK. She was a University Research Fellow of the Royal Society (1986-96), conducted postdoctoral research at the University of Oxford and East Anglia (1981-6), and her graduate studies were at the University of Aberdeen (1978-81).