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Photosynthesis of Phytoplankton and Zooxanthellae on a Coral Reef

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Abstract

A carbon-14 assimilation method was used to determine action spectra and photosynthesis versus irradiance (*P* versus *I*) curves of natural populations of phytoplankton and zooxanthellae from a coral reef fringing Lizard Island in the Australian Barrier Reef. The action spectra were related to the phytoplankton species composition. The curves showed shade adaptation in phytoplankton from deeper waters and in the zooxanthellae. Rates of photosynthesis of zooxanthellae were shown to be highly but variably dependent on their host organisms. Photosynthetic production by zooxanthellae was about 0.9 gC m^{-2} day^{-1}, which is about three times higher than phytoplankton production in the waters close to the reef.

Introduction

The primary productivity of coral reef communities has been described by Odum and Odum (1955) as high, although the phytoplankton concentration in the associated waters is usually low (Sournia and Ricard, 1976). The presence of symbiotic zooxanthellae in many of the reef invertebrates has suggested that a major part of the primary productivity in the reef may be due to these algae. Therefore, it is important to determine the relative contributions of the phytoplankton and the symbiotic zooxanthellae, particularly those in the corals which compose a large proportion of the reef biomass. Phytoplankton photosynthesis versus irradiance (*P* versus *I*) curves can be used, together with measurements of submarine irradiance as described by Jitts *et al.*(1976) to estimate the *in situ* production. This method is more convenient than incubating samples of phytoplankton *in situ*; it also allows comparison of the productivity of phytoplankton samples from several locations and of symbiotic algae from several organisms. It was used in this study to compare phytoplankton production at several positions near Lizard Island near the northern end of the Australian Barrier Reef (14°40'S; 145°28'E), and to estimate the primary production of the coral zooxanthellae.

The photosynthetic response of phytoplankton to submarine irradiance depends not only on the level or irradiance, but also on the spectral distribution of the irradiance and the action spectrum of the phytoplankton. Action spectra of unialgal cultures of marine algae have previously been determined by Haxo (1960) and others (reviewed by Halldal, 1974), but there have been no such determinations for natural populations other than those for symbiotic zooxanthellae by Halldal (1968). Carbon-14 assimilation methods were used in this study to determine the action spectra for natural populations of phytoplankton and for symbiotic zooxanthellae in coral and clams.

Materials and Methods

Sampling

This study was carried out on board the R.V. "Alpha Helix" while moored at Lizard Island in April 1973. The three sampling positions are shown in Table 1. Samples from the water at the ship's anchorage and offshore were collected using a 6 l plastic water sampler (Jitts, 1964). A diver operated the sampler among the corals in calm waters in the reef area fringing the island close to the ship's anchorage.

Table 1. Details of sampling positions

Position	Depth of water (m)	Distance from Island (km)	Location
Reef area	3	0.2	14°39.8'S; 145°27.0'E
Anchorage	11	1.0	14°39.5'S; 145°26.8'E
Offshore	28	4.3	14°38.3'S; 145°25.4'E

Zooxanthellae Preparation

The zooxanthellae were extracted from both coral (*Pocillopora damicornis*) and clams (*Tridacna maxima*) in a manner similar to that employed by Muscatine (1967) and as further detailed by Smillie (1976). Clams 20 to 25 cm long were taken from the reef and kept no longer than one day in the open tanks supplied with a stream of surface seawater. Care was taken with the corals to avoid any exposure to the atmosphere, which would result in excessive mucus formation. After the zooxanthellae had been extracted and separated from the animal host tissue, a dilute suspension of the zooxanthellae was prepared using filtered seawater. For *in vivo* tests, uniform coral branch tips were cut off (2 cm long and 1 cm wide at the base) and placed in 50 ml incubation flasks with unfiltered seawater.

Carbon-14 Techniques

Samples of seawater containing natural populations of phytoplankton or zooxanthellae suspensions were incubated as described below in 50 ml round-bottomed Pyrex glass flasks. Before incubation, approximately 3.7 MBq (= 100 µCi) of carbon-14, in the form of $NaHCO_3$ solution was added to each flask. After incubation the samples were filtered through Millipore (type HA 0.45 µm) membrane filters using about 30 kPa vacuum, and both the filters and filtrates retained. The inorganic carbon-14 was removed from the filters by fuming with HCl, and after vacuum drying placed in a glass scintillation vial with 15 ml of toluene scintillant, and counted in a liquid scintillation counter (Beckman LS-100) at efficiencies of about 65%. The toluene scintillant contained: toluene, 390 ml; dioxane, 390 ml; ethanol, 234 ml; naphthalene, 50 g; PPO, 4.5 g; POPOP, 0.1 g. The filtrates were acidified with HCl to about pH 2, and the inorganic carbon-14 removed by aeration, than a 15 ml portion was shaken with 5 ml of "Aquasol" (New England Nuclear) and counted as before, with efficiencies of about 50%.

The coral pieces were removed from the seawater medium after incubation and ground with 50 ml methanol to a fine powder in a mortar. Five ml of the supernatant methanol extract was removed for the measurement of chlorophyll, and the remainder was acidified with 5 ml of concentrated HCl, and let stand until the carbon dioxide evolution from the dissolution of the coral carbonate had ceased. The sample was then filtered through a Millipore HA membrane filter. The total activity of the sample was measured by counting the filter in 15 ml of scintillant, and a 1 ml portion of the filtrate in 15 ml of scintillant. The seawater in which the coral pieces were incubated was examined for both particulate and soluble organic carbon-14 activity in the same manner as the phytoplankton.

The activity of the carbon-14 stock solution added to the samples was measured by counting aliquot portions under the same conditions as the samples. Quenching in the methanol extracts of the coral was determined using the carbon-14 stock solution as an internal standard.

The rates of photosynthesis were calculated by isotope dilution, and the *in situ* production rates were estimated, as described by Jitts *et al.* (1976), except that the dissolved inorganic carbon was not assumed to be a constant, and the measured values were used. During the study period, 23 samples were measured by the method described by Scott (1974); the dissolved inorganic carbon ranged from 21.5 to 22.7 gC m^{-3}. When calculating the daily rates of production from the P versus I curves, the underwater irradiance was assumed to have a noon maximum of 1300 x 10^{18} quanta m^{-2} sec^{-1} just below the surface, for a cloudless day of 12 h length. The extinction coefficient of the water was estimated to be 0.11 m^{-1}.

Incubation

Samples of phytoplankton were incubated *in situ* by suspending the incubation flasks from a buoy moored near the ship, at depths of 1, 3 and 7 m, from noon to sunset.

Artificial incubations were carried out for periods of 2 to 4 h at 25°C ± 0.5 C° in an incubator illuminated by a xenon arc lamp, as described by Jitts and Scott (1976). This incubator provided the samples with high levels of

white irradiance, which could be modified by the use of neutral and spectral filters.

Photosynthesis versus irradiance (*P* versus *I*) studies were carried out using spectrally neutral filters (Balzer) at 6 levels of irradiance, from (4 to 300) x 10^{18} quanta m^{-2} sec^{-1}. Action spectra at both low and high levels or irradiance were obtained by using interference filters (Schott) with about 30% peak transmission, and a half-band width of 15 nm. The irradiances at each wavelength were equalised using the neutral filters to about 3 x 10^{18} quanta m^{-2} sec^{-1} for low irradiance, and to about 50 x 10^{18} quanta m^{-2} sec^{-1} for high irradiance.

Dark uptake of carbon-14, measured on all samples for the same incubation periods, averaged about 1% of the uptake at high irradiance for phytoplankton samples, and 1.5% for zooxanthellae *in vivo* in coral.

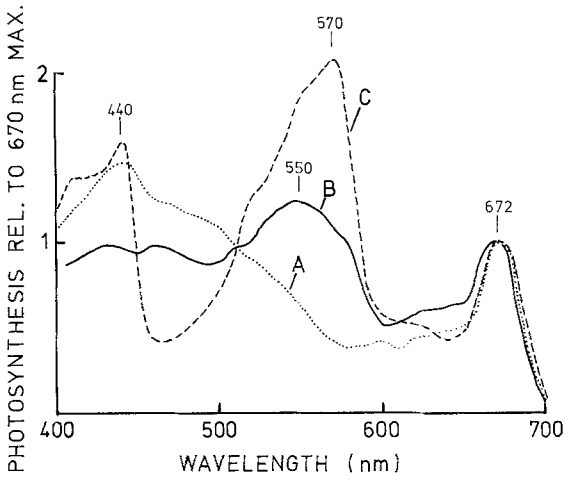

Fig. 1. Typical action spectra for major phytoplankton groups (abstracted from Haxo, 1960). A: Diatoms and dinoflagellates; B: cryptomonads; C: blue-green algae

Irradiance

The levels of irradiance used in the artificial incubations employing interference filters were measured with a Hewlett-Packard radiant flux meter (model 8330A). The levels of irradiance between 400 and 700 nm in those incubations employing neutral filters were measured with an ISCO spectroradiometer (model SR), which was calibrated against a standard tungsten lamp (ISCO, model SRC).

Chlorophyll

Chlorophyll *a* was measured by the fluorescence method described by Holm-Hansen *et al.* (1965).

Taxonomy

The dominant phytoplankton genera present in the water samples were determined by microscopic examination of a 50 ml sample, which had been concentrated to about 2 ml by centrifuging at about 500 x *g* for 15 min.

Results and Discussion

Relation between Phytoplankton Composition and Photosynthetic Action Spectra

Action spectra have previously been described for the major groups of marine algae, and related to the distribution of the principal accessory pigments among the groups (Haxo, 1960; Halldal, 1974). Typical examples of action spectra for diatoms and dinoflagellates, cryptomonads (small flagellates), and blue-green algae, are reproduced from Haxo (1960) in Fig. 1. The action spectra of natural populations of phytoplankton from Lizard Island are shown in Fig. 2. The latter are quite variable, particularly the maxima and shoulders, which occur at wavelengths that correspond with the maxima found for unialgal cultures as described by Haxo and Halldal, and thus allow these maxima and shoulders in the natural populations to be attributed to particular algal groups. The varying magnitudes of these maxima also suggest that they are related to the photosynthetic dominance of particular algal groups. The action spectra of the two samples from 10 m at the ship's anchorage (Fig. 2a, b) show maxima at 535 and 545 nm, respectively, which could be due to cryptomonads; maxima at 448 nm which are typical for diatoms, dinoflagellates and blue-green algae; and maxima at 671 nm which are common to all the major phytoplankton groups. The microscopic examination showed that these samples contained mostly small flagellates with species of the pennate diatoms *Nitzschia* and *Navicula* as the minor component. The action spectrum of the sample from 7 m at the ship's anchorage (Fig. 2c) showed a maximum at 500 nm which does not correspond with any of the typical spectra, but the small maximum at 445 nm together with the shoulder at 575 nm appeared to indicate that some blue-green algae were

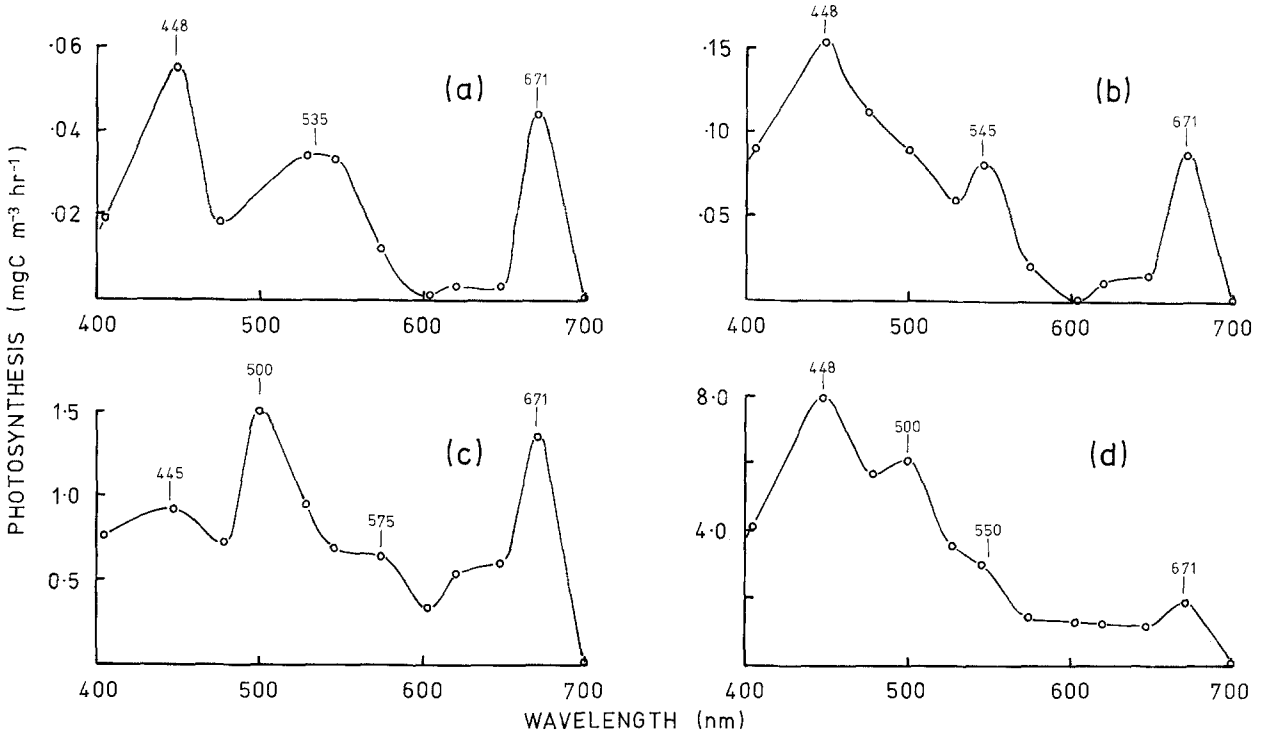

Fig. 2. Action spectra of 4 separate samples of natural phytoplankton populations. (a) from 10 m at the anchorage, containing 0.45 mg chlorophyll *a* m^{-3}; (b) from 10 m at the anchorage, containing 0.58 mg chlorophyll *a* m^{-3}; (c) from 7 m at the anchorage, containing 0.30 mg chlorophyll *a* m^{-3}; (d) from 2 to 3 m in the reef area, containing 3.43 mg chlorophyll *a* m^{-3}. The levels of irradiance for each wavelength band are 3 x 10^{18} quanta m^{-2} sec^{-1} for Samples (a) and (b), and 50 x 10^{18} quanta m^{-2} sec^{-1} for Samples (c) and (d)

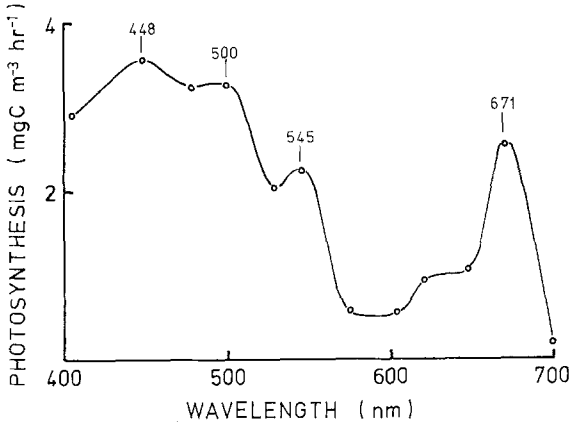

Fig. 3. *Tridacna maxima.* Action spectrum for zooxanthellae isolated from the clam and suspended in seawater. The suspension contained 9.43 mg chlorophyll *a* m^{-3}. The irradiance level for each wavelength band is 3 x 10^{18} quanta m^{-2} sec^{-1}

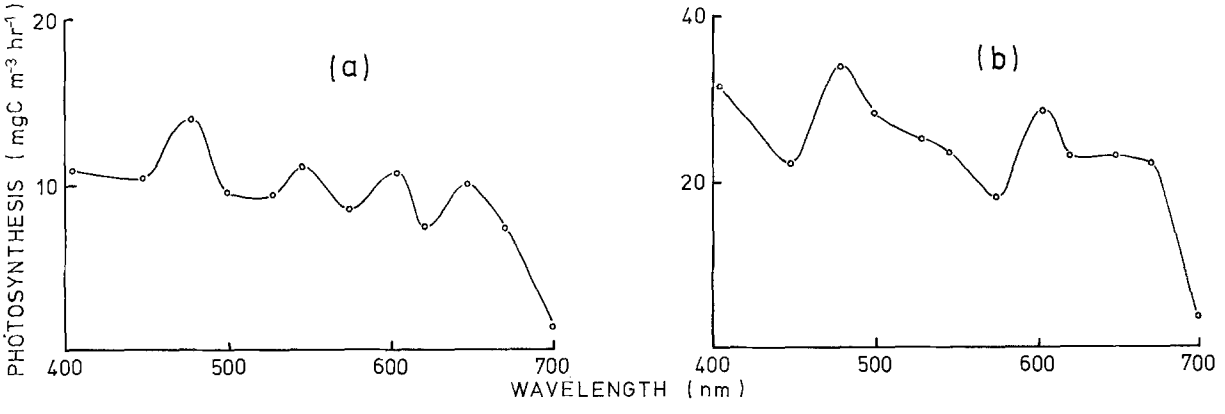

Fig. 4. Action spectra for isolated zooxanthellae suspended in seawater, using the higher irradiance level of 50 x 10^{18} quanta m^{-2} sec^{-1} for suspensions of (a) zooxanthellae isolated from the clam *Tridacna maxima*, containing 9.43 mg chlorophyll *a* m^{-3}; and (b) zooxanthellae isolated from the coral *Pocillopora damicornis*, containing 110.5 mg chlorophyll *a* m^{-3}

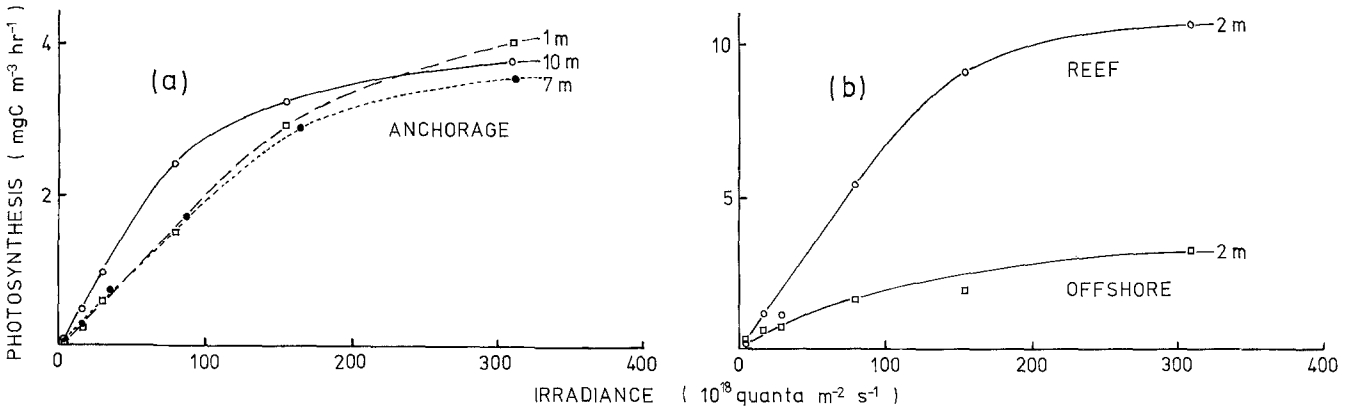

Fig. 5. Measurements of the rate of phytoplankton photosynthesis at 6 levels of irradiance (*P* versus *I*) using white light in the xenon incubator, for samples taken from (a) depths of 1, 7 and 10 m at the ship's anchorage; and (b) 2 m depth in the reef area and offshore

present. However, the microscopic examination showed mostly species of the dinoflagellate *Peridinium* and the diatom *Nitzschia*, with a minor component of species of the dinoflagellate *Ceratium* and the diatoms *Rhizosolenia* and *Amphiprora*, but no blue-green algae. The action spectrum of the sample taken at 2 to 3 m in the reef area (Fig. 2d) corresponds overall to that for the diatom and dinoflagellate group with a pronounced and broad maximum peaking at 448 nm, although the 671 nm maximum is less pronounced than in the typical spectrum, and there is a shoulder at 550 nm suggesting the presence of cryptomonads. There is also a small maximum at 500 nm which, like the spectrum in Fig. 2c, shows that there is an algal component present with an action spectrum which differs from those known for the common algal groups. The microscopic examination showed that this sample was composed of small flagellates, with species of the diatom *Nitzschia, Climacodium, Navicula* and *Chaetoceros*, and the dinoflagellate *Peridinium*. Thus all the samples appear to have action spectra which are consistent with the algal groups present, with the exception of the abnormalities noted in the spectra shown in Fig. 2c and d. Organic carbon-14 found in the filtrates for these four samples, and assumed to be photosynthetically derived from, and excreted by intact cells, averaged 5% of the carbon-14 found in the particulate fraction throughout the 400 to 700 nm range, and had the same action spectra for its formation.

The action spectrum at low irradiance for the suspension of zooxanthellae isolated from the clam *Tridacna maxima* is shown in Fig. 3. It is remarkably similar to that described by Halldal (1968) for zooxanthellae from the massive coral *Favia pallida*, even to the small peak at 545 nm.

The action spectrum at high irradiance for the suspension of zooxanthellae isolated from the clam (Fig. 4a) is quite different from that determined at low irradiance. The high irradiance spectrum has a more even response to light from 400 to 700 nm, and the maxima observed in the low irradiance spectrum can no longer be discerned. The high irradiance spectrum of the zooxanthellae suspension isolated from the coral *Pocillopora damicornis* (Fig. 4b) is similar to that for the isolated clam zooxanthellae at the same level of irradiance. This transformation of the action spectrum with changes of the level of irradiance is of importance in understanding photosynthetic behaviour of zooxanthellae in relation to both the level and the spectral characteristic of submarine irradiance.

Relation between Irradiance and Photosynthesis

The dependence of the rate of photosynthesis upon the level of irradiance for the phytoplankton samples is shown in Fig. 5. These *P* versus *I* curves, which were determined using white light in the xenon incubator, are very similar to those obtained by Jitts *et al.* (1976) in the Eastern Equatorial Pacific, and the Central Atlantic oceans. The *P* versus *I* curves vary with depth, and in the samples taken at the ship's anchorage (Fig. 5a) the deeper samples show some shade adaptation, approaching light saturation at lower levels of irradiance. This effect is probably due to the lower ambient irradiance level at the sampling

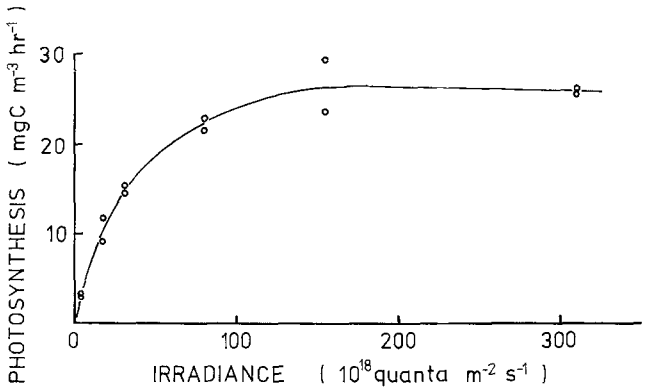

Fig. 6. *Tridacna maxima*. Measurements of the rate of photosynthesis at 6 levels of irradiance (*P* versus *I*) using white light in the xenon incubator, for a seawater suspension of zooxanthellae isolated from the clam, containing 9.43 mg chlorophyll *a* m^{-3}

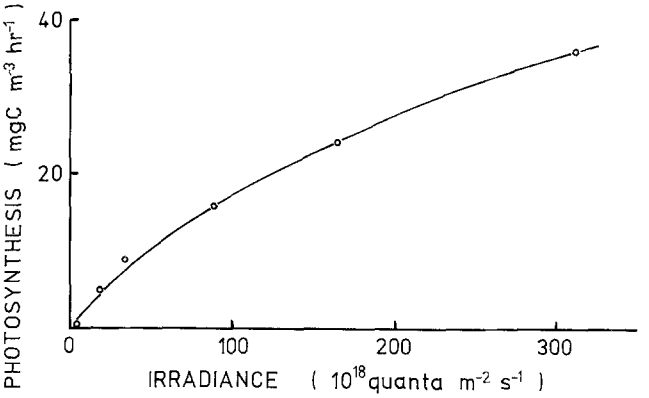

Fig. 7. *Pocillopora damicornis*. Measurements of *in vivo* rate of photosynthesis at 6 levels of irradiance (*P* versus *I*) for zooxanthellae in branch tips of the coral. Rates of photosynthesis have been corrected, using the chlorophyll *a* measurements, to rates for an average branch tip containing 27.3 µg chlorophyll *a*

Table 2. Daily *in situ* production rates for coral zooxanthellae and for phytoplankton in the reef waters

Sample	Position	Production rates calculated from *P* versus *I* curves: Particulate production gC m^{-2} day^{-1}	
		Cloudless day	Cloudy day
Phytoplankton	Reef area	0.30	0.29
Phytoplankton	Anchorage	0.35	0.25
Phytoplankton	Offshore	0.34	0.23
Coral zooxanthellae	Reef area	0.99	0.73

Sample	Position	Production rates measured by *in situ* incubations: Production gC m^{-2} day^{-1}	Date
Phytoplankton	Anchorage	0.27	6th April
Phytoplankton	Anchorage	0.29	13th April

point, as suggested by Steemann Nielsen (1974).

The maximum rates of photosynthesis at the three locations are quite different, and diminish with increasing distance from the island and with increasing water column depth. These differences are probably due to a higher nutrient flux in the shallow reef area, where nutrient regeneration in the sediments is more closely coupled to phytoplankton photosynthesis, as found by Rowe *et al.* (1975).

The *P* versus *I* curve for a seawater suspension of zooxanthellae isolated from the clam *Tridacna maxima* is shown in Fig. 6. This curve is almost identical to that obtained by Halldal (1968) for coral zooxanthellae, using different methods. When the *P* versus *I* curves for the isolated clam zooxanthellae and phytoplankton are compared, the clam zooxanthellae appears to be shade-adapted, and this may explain the change observed in the clam zooxanthellae action spectrum with change in irradiance level. The approach to saturating light conditions in the high irradiance action spectrum of the zooxanthellae is also indicated by the decrease in the photosynthetic efficiency (carbon-14 assimilated per quantum) to less than a third of that for the low irradiance action spectrum. Since the irradiance levels are high in the shallow waters in which these clams were found (up to 1000 x 10^{18} quanta m^{-2} sec^{-1} at noon), this shade adaptation must be due to self-shading in the clam mantle tissue, where the zooxanthellae are densely packed in

a thin layer. A clam 18 cm in length was found to contain 5 x 10^8 zooxanthellae, and a clam of similar size which was examined by Smillie (1976) yielded 3 x 10^9 zooxanthellae. The *in vivo P* versus *I* curve obtained for zooxanthellae contained in tips of the branches of the coral *Pocillopora damicornis* is shown in Fig. 7. This curve has a different shape to those for either phytoplankton or zooxanthellae. This difference is due to one side of the coral branch tip receiving the measured level of irradiance, while other parts of the coral will receive less due to shading, resulting in a *P* versus *I* curve which is the average of a family of *P* versus *I* curves differing only in their irradiance scales. This average curve will have a slightly lower maximum due to photoinhibition effects, and this maximum will occur at an apparently higher level of irradiance than is found for suspensions of zooxanthellae. The methanol extract contained about 90% of the carbon-14 fixed by the coral pieces, at all 6 levels of irradiance.

Dependence of Zooxanthellae Photosynthesis on the Host Organisms

Attempts to determine the *P* versus *I* curve for suspension of zooxanthellae isolated from the coral *Pocillopora damicornis* gave results which were suspect not only because the cells tended to form aggregates, but also because the percentage of dissolved organic products released to the water (20% of the particulate products) was much higher than for either phytoplankton or isolated clam zooxanthellae (5% mean). Also, the assimilation ratio, or carbon-14 assimilation rate to chlorophyll *a* (0.24 mgC h^{-1} mg chlorophyll a^{-1}) was much lower than the averages found for either phytoplankton (5.9) or isolated clam zooxanthellae (2.7). The assimilation ratio for phytoplankton is consistent with the ratios found by McAllister *et al.* (1964), and Curl and Small (1965), who found that the ratios above 5 are indicative of phytoplankton with an adequate nutrient supply, and that the normal range is from 1 to 10. Coral zooxanthellae *in vivo* give assimilation ratios of 1.6 or higher. These observations suggest that although the zooxanthellae in the corals and clams appear to be the same, and have the same pigment composition (Jeffrey and Haxo, 1968), those present in the coral are more dependent on their host, and are less readily extracted in a healthy state from the host tissue, and could even be regarded as different types of zooxanthellae. A further example of this was found in an unidentified tunicate which yielded a suspension of algal cells which resembled zooxanthellae and gave an assimilation ratio of about 0.02. Intact algal cells from this tunicate were also examined by Smillie (1976), using tetranitroblue tetrazolium as a Hill acceptor, and he found that not all of the cells were photosynthetically active, and that the photochemical activity could be misleading when expressed on a chlorophyll basis.

Photosynthetic Production on a Coral Reef

The daily production rates for phytoplankton in the water column, calculated from the *P* versus *I* curves, are shown in Table 2. These rates are calculated for a cloudless day, and also a day where half the level of solar irradiance is received. The phytoplankton production rates for the water column, which were measured by the *in situ* incubations at the ship's anchorage on two separate days, are also shown in Table 2, and are in agreement with the calculated values. During the period of study at Lizard Island none of the days was cloudless. Griffiths (1976) has also measured rates of phytoplankton photosynthesis at Lizard Island and found the rate of photosynthesis of surface samples at saturating light to be two to eight times lower than reported here, with abnormally high amounts of soluble organic products (30 to 50% of the total photosynthesis) and an unusually high assimilation ratio of 14.4. This assimilation ratio is above the normal range of 1 to 10, and is only comparable to those found by Malone (1971) for nannoplankton in eutrophic tropical surface waters. The production values shown in Table 2 are higher than the average of the range for oceanic waters, but may be considered normal for shallow waters on a wide continental shelf (F.A.O. Department of Fisheries, 1972).

The daily *in situ* photosynthesis rates for zooxanthellae in a coral branch tip at a depth of 3 m were calculated from the *in vivo P* versus *I* curve, in the same manner as for the phytoplankton. The production rate per square metre was estimated by assuming that actively growing coral, containing zooxanthellae, occupied 25% of the reef area giving the values shown in Table 2. Analysis of the unfiltered seawater used in the *in vivo* incubation of the coral pieces showed that there was no significant difference in the uptake of carbon-14 by the par-

ticulate fraction in the water (P_{max} = 3.5 mgC m^{-3} h^{-1}), when compared to other samples for the same depth on other days (P_{max} = 3.5 and 3.6 mgC m^{-3} h^{-1}). The absence of any apparent increase in the particulate production in the water shows that *Pocillopora damicornis* does not contribute significantly to particulate production by mucus excretion. Benson and Muscatine (1974) found that mucus from another coral, *Pectina lactuca*, contributed significantly to the particulate matter in the water, but this difference may be explained by their longer incubation period of 32 h, compared to the period of 2 h used in this experiment. The difference may also be explained by the large variation in mucus production by corals, as shown by Richman *et al.* (1975) who found that massive corals produced much more mucus than branched corals such as *Pocillopora damicornis*. Soluble organic carbon in the seawater medium used for the *in vivo* incubation was produced at the rate of 1.1 mgC m^{-3} h^{-1}, which is equivalent to 30% of the particulate photosynthesis rate or 0.1% of the photosynthesis rate for the coral zooxanthellae.

The estimated production rate of the coral zooxanthellae is about three times the measured rate of production for phytoplankton in the waters close to the reef. This difference suggests that the large and varied population of larger animals observed in the reef may be sustained mainly by production originated by the coral zooxanthellae and zooxanthellae of other symbionts, and the benthic algal community, with the phytoplankton production performing a minor function in the reef ecosystem. The close association of these larger animals with the corals, which also provide shelter, would ensure that a large proportion of the nutrients contained in the waste products of these animals is returned to the coral zooxanthellae and the benthic algae either directly, or by regeneration in the sediments (Rowe *et al.*, 1975).

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