# PRODUCTIVITY STUDIES ON SOME HERMATYPIC CORALS BY MEANS OF BOTH OXYGEN MEASUREMENTS AND $^{14}C$ METHOD

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## ABSTRACT

The hermatypic corals harbour boring filamentous algae in their skeleton as well as symbiotic zooxanthellae in their soft tissue. These imprisoned algae produce much more quantity of oxygen by photosynthesis than the respiratory needs of the coral. Various attempts have been made in the past to estimate the oxygen production of corals and there was apparently disagreement among authors on the role of boring algae in the total production. In this work an attempt is made to evaluate the percentage of oxygen production contributed by the boring algae and the symbionts of a few species of reef building stony corals from Palk Bay and Gulf of Mannar around Mandapam (S. India). The gross production was estimated by dark and light bottles by Winkler technique, converting the oxygen values into carbon equivalents. The share of zooxanthellae was then determined by incubating the isolated symbionts with $NaH^{14}CO_3$. A marked difference was observed in the two sets of values thus obtained. In the light of the present results the role of the boring algae in the productivity of reef corals is discussed.

## INTRODUCTION

Hermatypic scleractinian corals are known to produce more quantity of oxygen than is needed for their respiration during day time, by the photosynthetic activity of their imprisoned algae (Yonge, 1937, 1957; Yonge *et al.*, 1932; Odum and Odum, 1955; Kanwisher and Wainwright, 1967). The imprisoned algae in a coral colony comprise the symbiotic zooxanthellae and the boring filamentous algae found in the subsurface skeleton and between the polyps (Odum and Odum, 1955). Kawaguti (1944) has shown that in *Acropora corymbosa* the symbiont is *Gymnodinium symbiodinium*. A large number of organisms such as sponges, bryozoans, polychaetes and molluscs may be found as epizoites or as borers along with several microscopic acellular organisms, on a coral skeleton. Odum and Odum (op. cit) working on the trophic structure and productivity of a windward coral reef community on Eniwetok Atoll, have concluded that "the zooxanthellae (in the coelenterate polyps) comprised only about 6% of the total plant portion, filamentous algae embedded in the skeleton making up the bulk of the plant material". They thus attributed comparatively negligible role to the

symbionts in the total plant matter in a coral colony. Recently Kanwisher and Wainwright (1967) have reported that "in the Florida reef corals, the boring green algae contribute very little indeed" to the productivity. According to these authors, the symbiotic zooxanthellae contribute about 90% of the total productivity of corals. The present study is an attempt to determine the primary production of a few species of reef corals of Palk Bay and Gulf of Mannar around Mandapam in South India, by both oxygen measurements by Winkler method and $^{14}C$ technique, and to compare the values.

## MATERIAL

The following species of corals were selected for the present study.

Order Scleractinia
Suborder Astrocoeniina
Family Pocilloporidae

1) *Pocillopora damicornis* (Linnaeus)

Family Acroporidae

2) *Acropora corymbosa* (Lamarck)
3) *A. erythraea* (Klunzinger)
4) *Montipora divaricata* Brüggemann

Suborder Fungiina
Family Poritidae

5) *Goniopora stokesi* Milne Edwards and Haime
6) *Porites solida* (Forskål)

Suborder Faviina
Family Faviidae

7) *Favia pallida* (Dana)
8) *Favites abdita* (Ellis and Solander)
9) *Goniastrea pectinata* (Ehrenberg)
10) *Cyphastrea microphthalma* (Lamarck)

The corals were collected from the fringing reefs of Palk Bay and Gulf of Mannar during low tides and brought to the aquarium in large polythene buckets. The associated animals such as sponges, bryozoans, polychaetes and the larger attached algae as far as possible were carefully removed from the surface. Specimens whose skeletons were found to be attached by borers were discarded. The specimens were then cut into convenient size. In the case of large massive species the upper living zone with the band of filamentous algae was chipped out. Exposure to air was completely avoided except for a few minutes when

they were taken out to chisel to pieces. The corals were then kept in an open aquarium tank for 2 to 4 days to get them acclimatised to the conditions and to let them recover from any injury to the tissues during transportation and subsequent handling. All the corals used in the present experiments were collected more or less at a depth of 50 cm at low tide.

## METHODS

Each specimen was subjected to two sets of experiments, to determine 1) the gross production and 2) the production by the symbiotic zooxanthellae alone, both for a unit time. The gross production was estimated by the usual dark and light bottle method and the share of symbionts by $^{14}C$ method. For each species the experiments were repeated with two samples and the average value was taken for interpretation of the results.

### *Oxygen estimation*

Air-tight dark and light atlas jars with a capacity of 1040 ml were used in oxygen estimations. To make them light-proof the outer side was coated with black paint and then covered with a black cloth. The weight of the corals used ranged from 64 to 125 grams (weight and volume were determined at the cessation of the experiments). The respirometers were set in large plastic buckets and were tightly closed under water. The bottles were then left in a large open tank 6x3½x1½ metres at a depth of about 50 cm. The depth was adjusted to be almost the same at which the specimens were collected. Since corals show a higher rate of activity at about noon (Sargent and Austin, 1954; Goreau, 1961) our experiments were conducted mostly between 10.30 a.m. and 12.30 p.m. in the months of February, June, July and September, all under bright sunlight. On introduction into the respirometer it has been noted that the polyps of most of the species got fully expanded. The water temperature of the aquarium tank during the season of the experiments varied from 30 to 31.5°C but showed no marked change during the experimental period for a single species. The water in the experimental tank was emptied and refilled at intervals to prevent any marked rise of temperature. All the experiments were precisely adjusted for one hour. At the termination of the experiment the bottles were gently shaken and about 160 ml of water were siphoned out for oxygen estimation by the Winkler technique. Corrections for the volume of the coral were applied in calculating the total production or consumption by the coral. Controls were invariably run concurrently and necessary corrections to the values were made. The production and consumption for a specimen were estimated on adjacent days almost at the same time and same temperature and light intensities. Details of the species, weight and volume of the specimens used, the average of water temperature and the initial and final oxygen values are listed in Tables 1 and 2. Table 3 shows total production and the ratio of production by consumption for the various species.

*Estimation of carbon fixed by zooxanthellae*

The weight and volume of the corals that were used for the estimation of their oxygen production and consumption, were determined and the corals crushed in a porcelain mortar with filtered sea water generally within 24 to 48 hours after the oxygen estimation. The supernatant yellow solution containing the zooxanthellae was decanted. The decantation was repeated until the microscopic examination of the decant showed no more zooxanthellae. The whole solution was then centrifuged at high speed, the resulting pellet was repeatedly washed to remove the animal tissue and the attached mucus and made up to 100 ml in filtered sea water. In most of the species the decanted yellow solution was very thin but in some cases it was thick due to the presence of excessive quantity of mucus. The extraction of the zooxanthellae was completed within 1 to 1½ hours after crushing of the corals. The symbionts in the various species ranged from 8 to 12 $\mu$ in diameter. A few microscopic, actively moving organisms were seen in some species along with the zooxanthellae. The residue in the mortar (i.e. the skeleton) still retained the green colour indicating that most of the boring algae were left in the skeleton. Moreover microscopic examination of the extract did not reveal any broken pieces of filamentous algae. 5 ml of the aliquot was then added to the filtered sea water in a pyrex light bottle with a capacity of 265 ml. One ml of $NaH^{14}CO_3$ was added after covering the bottle with a black cloth. A control was set concurrently. The bottles were then incubated after removing the cover, under bright sunlight in the same tank almost at the depth where oxygen estimation was carried out. They were shaken at intervals to keep the algae in suspension and the incubation was stopped exactly after one hour, by covering the bottles again with a black cloth. The bottle was then well shaken and 20 ml of the water with the algae was filtered through a membrance filter in a filtering unit under a pressure of + 1.5 kg. The control was also suitably filtered. The filters were dried in a dessicator and the radioactivity was determined by a $2\pi$ Proportional Counter using Burshane gas. In calculating the total radioactivity of the zooxanthellae of any sample, necessary correction for both control and background was applied.

One ml of the filtrate was acidified with HCl in a tinfoil container and evaporated to dryness and then tested for radioactivity. But in most of the cases no appreciable count was detected indicating the loss through filtrate was comparatively negligible. Preliminary experiments showed a steady increase in the radioactivity of the filters in the first three hours. But after three hours the increase was not significant. This shows that the zooxanthellae were alive during our experimental period and were actively incorporating radioactive carbon by photosynthesis. As in the case of oxygen estimation the average values of two experiments were used for the interpretation of the results. All values were corrected to two decimal places. The whole experiment, i.e. from crushing to filtering, lasted about 2 to 2½ hours. The details of the results are

presented in Table 4. The equivalent carbon of oxygen was calculated assuming a PQ of 1.25.

## Discussion of the Results

The results of the present experiments presented in Tables 1, 2 and 3, also clearly indicate that, as already pointed out by Kanwisher and Wainright (1967), neither the weight nor the volume of a coral colony is in proportion to its productivity. The surface area may be a more reliable parameter but its estimation in several cases especially in slender ramose forms is likely to go wrong to a marked degree. The production and consumption, needless to say, are factors regulated by the quantity of the imprisoned plankton and the animal tissue present and the physiological state of them. This is also influenced by several other external factors (vide infra). In the ten species of corals which we used in the experiments of short duration the ratio of production to consumption varied from 1.97 to 3.58. The lowest ratio of 1.97 was shown by *Goniastrea pectinata* and the highest of 3.58 by *Porites solida*. In most of the other species the values ranged from 2.3 to 3.58. *Acropora, Pocillopora* and *Goniopora* showed a very high rate of production as well as consumption indicating a high metabolic rate. The ratio of production by consumption is more fluctuating, if the results of the twenty experiments are considered separately, where they are from 0.58 to 4.27.

Goreau and Goreau (1959) have shown that the rate of calcification in corals is in part dependent on the presence of zooxanthellae, though several other factors such as light and 'inherent species specific factors' may influence (Goreau, 1961). The present results also indicate that the zooxanthellae of the faster growing genera like *Acropora* and *Pocillopora* have a comparatively higher rate of photosynthetic activity when compared to the slower growing genera such as *Favia, Favites, Goniastrea* and *Porites*.

The carbon fixed by the different corals per hour, measured by both the Winkler technique and $^{14}C$ methods, are presented in Table 5. The carbon values obtained by the latter method are adjusted to net by multiplying the experimental values by 0.96 (Steemann Nielsen, 1964). Except in the case of *Goniastrea pectinata* and *Goniopora stokesi* the net values of carbon fixed by the zooxanthellae is always less than the net production measured by light bottle. In *Goniopora stokesi* the two values are almost similar, allowing for a small percentage of experimental error. In the case of *Goniastrea pectinata* it is possible that the potential production of the specimens used might not have been realised in the light bottle, or the zooxanthellae might have multiplied during the intervals (Kanwisher, 1966). But the latter possibility is found in all species used. *Montipora divaricata* shows a very low value with $^{14}C$ incubation in spite of the higher values obtained by light and dark bottles. We are unable to explain this wide discrepancy, though the experiments were repeated, but always showed a very low radioactivity. The wide range of ratio of the net productions measured

by the two methods in the different genera and species is also noteworthy. While the net production of carbon obtained by the light bottle is by both the zooxanthellae and the boring filamentous algae (whatever may be the share of the latter) the $^{14}C$ values account only for the zooxanthellae. While Odum and Odum (1955) attributed 94% of the total plant matter of a coral head to the boring algae in the Eniwetok Atoll, Kanwisher and Wainwright (1967) attributed only less than 10% of the total productivity of a coral to the boring algae in the Florida reefs. We could not attempt to estimate separately the production of boring algae but our preliminary experiments clearly indicate that the filamentous algae are a major constituent of the total plant matter of the reef corals and are capable of photosynthesising. However, it is apparent that the difference in the net productions obtained by the light bottle and the $^{14}C$ method is not attributable to the boring algae, as may be clear from the following general discussion.

## General Discussion

There has been much variability in the carbon production values of the tropical oceanic waters, estimated by $^{14}C$ and light and dark bottles using Winkler reagents. The former technique though regarded as more sensitive, the values obtained thus were lower by a factor of 10-100 (Ryther, 1954). This discrepancy in the values had been mainly because of use of inappropriate value for PQ (McAllister *et al,* 1961) and also because of undue prolongation of the experimental time (Steemann Nielsen and Kholy, 1955), and the physiological state of the phytoplankon. Recent investigations have also pointed out the importance of proper standardisation of the $^{14}C$ stock solutions which is an essential pre-requisite for the proper assessment of the values (Steemann Nielsen, 1965; Nair, 1966). Even though, there is controversy as to what exactly is being measured by $^{14}C$ technique (cf. Strickland, 1960) it has now been agreed that in short term experiments the value obtained is something between gross and net production for phytoplankton, but probably near to the net. The above investigations, however, are on the marine phytoplankton or cultures of phytoplankton in the laboratory conditions. With regard to the symbiotic zooxanthellae no previous similar work is known to the present authors and very little is actually known on the physiological changes that may take place on the algae on their separation from the host tissue. Even if the values of respiration is added to the net values of carbon fixed by the zooxanthellae and adjusted to gross in the values given in Table 5, excepting in *Goniastrea pectinata* and *Goniopora stokesi* such an adjusted gross value is less than the gross production obtained by light and dark bottle technique. In other words the oxygen consumption values being constant in both cases, the net production measured by light bottle, as already indicated, is of a higher order. The higher values obtained for the two species are, however, not in agreement with the result with the other species. This disparity in the two sets of values obtained for net productions in corals can be due to the effect of several factors either acting independently or collectively.

TABLE *Oxygen production by reef corals- light bottle experiments. Genera and species are listed in alphabetical order*

| No. | Name of species | Wt. in grams | Vol. in ml | Vol. of respirometer in cc | Date | Time | Average water temp | Control | | Coral | | Difference from control | Net production of oxygen mg/hr. |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | | Initial oxygen mg/l | Final oxygen mg/l | Initial oxygen mg/l | Final oxygen mg/l | | |
| 1a. | *Acropora corymbosa* | 90 | 40 | 1045 | 1-7-'68 | 10.35-11.35 | 29.5 | 5.33 | 5.33 | 5.33 | 8.03 | 2.70 | 2.71 |
| 1b. | " " | 72 | 33 | -do- | 2-7-'68 | 10.35-11.35 | 29.5 | 5.22 | 5.22 | 5.22 | 8.14 | 2.92 | 2.96 |
| 2a. | *Acropora erythraea* | 72 | 36 | -do- | 16-2-'68 | 11.40-12.40 | 30 | 6.70 | 6.70 | 6.70 | 9.96 | 3.26 | 3.29 |
| 2b. | | 70 | 35 | -do- | 19-2-'68 | 11.40-12.40 | 30 | 7.01 | 7.05 | 7.01 | 9.39 | 2.34 | 2.36 |
| 3a. | *Cyphastrea microphthalma* | 110 | 56 | -do- | 5-9-'68 | 10.20-11.20 | 30.5 | 5.43 | 5.52 | 5.43 | 6.86 | 1.34 | 1.33 |
| 3b. | " " | 102 | 52 | -do- | 5-9-'68 | 11.30-12.30 | 30.5 | 5.43 | 5.43 | 5.43 | 6.31 | 0.88 | 0.87 |
| 4a. | *Favia pallida* | 142 | 84 | -do- | 17-7-'68 | 10.30-11.30 | 29.5 | 5.59 | 5.59 | 5.59 | 7.38 | 1.79 | 1.72 |
| 4b. | " | 115 | 68 | -do- | 18-7-'68 | 10.30-11.30 | 29.5 | 5.70 | 5.70 | 5.70 | 7.20 | 1.50 | 1.46 |
| 5a. | *Favites abdita* | 88 | 48 | -do- | 23-2-'68 | 11.20-12.20 | 30 | 5.49 | 5.49 | 5.49 | 5.79 | 0.30 | 0.30 |
| 5b. | " | 84 | 45 | -do- | 24-2-'68 | 11-30-12.30 | 30 | 5.57 | 5.57 | 5.57 | 6.68 | 1.11 | 1.11 |
| 6a. | *Goniastrea pectinata* | 98 | 49 | -do- | 21-2-'68 | 11.40-12.40 | 30 | 4.82 | 6.12 | 4.82 | 6.46 | 0.34 | 0.34 |
| 6b. | " " | 102 | 51 | -do- | 22-2-'68 | 11.30-12.30 | 30 | 5.49 | 5.49 | 5.49 | 6.05 | 0.56 | 0.56 |
| 7a. | *Goniopora stokesi* | 125 | 82 | -do- | 22-7-'68 | 10.40-11.40 | 30 | 5.62 | 5.73 | 5.62 | 10.66 | 4.93 | 4.74 |
| 7b. | " | 90 | 50 | -do- | 23-7-'68 | 10.25-11.25 | 29.5 | 5.51 | 5.51 | 5.51 | 7.95 | 2.44 | 2.43 |
| 8a. | *Montipora divaricata* | 107 | 60 | -do- | 28-8-'68 | 9.45-10.45 | 30.0 | 5.36 | 5.36 | 5.36 | 8.81 | 3.45 | 3.43 |
| 8b. | " " | 70 | 35 | -do- | 28-8-'68 | 11.00-12.00 | 30.0 | 5.39 | 5.39 | 5.39 | 8.92 | 3.53 | 3.56 |
| 9a. | *Pocillopora damicornis* | 64 | 31 | -do- | 31-8-'68 | 10.25-11.25 | 30.5 | 5.36 | 5.36 | 5.36 | 9.32 | 3.96 | 4.02 |
| 9b. | " " | 90 | 40 | -do- | 31-8-'68 | 11.35-12.35 | 30.5 | 5.35 | 5.35 | 5.35 | 10.09 | 4.74 | 4.76 |
| 10a. | *Porites solida* | 100 | 56 | -do- | 21-6-'68 | 10.45-11.45 | 30 | 4.99 | 4.99 | 4.99 | 6.07 | 0.08 | 1.07 |
| 10b. | " | 107 | 60 | -do- | 22-6-'68 | 11.00-12.00 | 30 | 4.99 | 4.99 | 4.99 | 6.47 | 1.48 | 1.46 |

TABLE 2. *dark bottle experiments with corals. The weight and volume of corals and the volume of the respirometer are same as indicated against the respective numbers in Table* 1.

| No. | Name of species | Date | Time | Average temperature | Control | | Coral | | Difference | Oxygen in mgs. used by corals | Gross production in mg. (i.e. net production plus consumption) |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | Initial oxygen mg/l | Final oxygen mg/l | Initial oxygen mg/l | Final oxygen mg/l | | | |
| 1a. | *Acropora corymbosa* | 2-7-'68 | 10.35-11.35 | 29.5 | 5.22 | 5.22 | 5.22 | 2.92 | 2.30 | 2.31 | 5.02 |
| 1b. | " " | 1-7-'68 | 10.35-11.35 | 29.5 | 5.33 | 5.33 | 5.33 | 3.37 | 1.96 | 1.98 | 4.94 |
| 2a. | *Acropora erythraea* | 19-2-'68 | 11.40-12.40 | 30 | 7.01 | 6.86 | 7.01 | 5.19 | 1.67 | 1.68 | 4.97 |
| 2b. | " " | 16-2-'68 | 11.40-12.40 | 30 | 6.7 | 6.44 | 6.7 | 4.90 | 1.54 | 1.55 | 3.91 |
| 3a. | *Cyphastrea microphthalma* | 5-9-'68 | 11-30-12.30 | 30.5 | 5.43 | 5.39 | 5.43 | 4.48 | 0.91 | 0.90 | 2.24 |
| 3b. | " " | 5-9-'68 | 10.20-11.20 | 30.5 | 5.43 | 5.43 | 5.43 | 4.75 | 0.68 | 0.67 | 1.57 |
| 4a. | *Favia pallida* | 18-7-'68 | 10.30-11.30 | 29.5 | 5.69 | 5.69 | 5.69 | 4.55 | 1.14 | 1.10 | 2.82 |
| 4b. | " | 17-7-'68 | 10.30-11.30 | 29.5 | 5.59 | 5.55 | 5.59 | 4.77 | 0.78 | 0.76 | 2.22 |
| 5a. | *Favites abdita* | 24-2-'68 | 11.30-12.30 | 30 | 5.31 | 4.90 | 5.31 | 4.38 | 0.52 | 0.52 | 0.82 |
| 5b. | " | 23-2-'68 | 11.20-12.20 | 30 | 5.49 | 5.08 | 5.49 | 4.82 | 0.26 | 0.26 | 1.37 |
| 6a. | *Goniastrea pectinata* | 22-2-'68 | 11.20-12.20 | 30.0 | 5.49 | 5.30 | 5.49 | 5.04 | 0.26 | 0.26 | 0.60 |
| 6b. | " " | 21-2-'68 | 11.40-12.40 | 30.0 | 6.12 | 6.05 | 6.12 | 5.38 | 0.67 | 0.67 | 1.23 |
| 7a. | *Goniopora stokesi* | 23-7-'68 | 10.25-11.25 | 29.5 | 5.51 | 5.51 | 5.51 | 3.51 | 2.00 | 1.93 | 6.67 |
| 7b. | " " | 22-7-'68 | 10.30-11.30 | 29.5 | 5.70 | 5.70 | 5.70 | 4.22 | 1.48 | 1.42 | 3.85 |
| 8a. | *Montipora divaricata* | 28-8-'68 | 11.00-12.00 | 30 | 5.39 | 5.39 | 5.39 | 3.56 | 1.83 | 1.82 | 5.25 |
| 8b. | " " | 28-8-'68 | 9.45-10.45 | 30 | 5.36 | 5.36 | 5.36 | 4.07 | 1.29 | 1.30 | 4.86 |
| 9a. | *Pocillopora damicornis* | 31-8-'68 | 11.25-12.25 | 30.5 | 5.28 | 5.28 | 5.28 | 3.30 | 1.98 | 2.01 | 6.03 |
| 9b. | " " | 31-8-'68 | 10.25-11.25 | 30.5 | 5.28 | 5.28 | 5.28 | 2.94 | 2.34 | 2.35 | 7.11 |
| 10a. | *Porites solida* | 22-6-'68 | 11.00-12.00 | 30 | 4.99 | 4.99 | 4.99 | 4.40 | 0.59 | 0.58 | 1.65 |
| 10b. | " | 21-6-'68 | 10.45-11.45 | 30 | 4.99 | 4.92 | 4.99 | 4.51 | 0.41 | 0.40 | 1.86 |

TABLE 3. *Oxygen production by reef corals, calculated from two experiments each. Details of separate experiments are as in Table 1 and 2.*

| No. | Name of species | Total weight in gms. | Total vol. in ml. | Average water temp °C | Net production of oxygen in mg/hr | Oxygen consumed in mg/hr | Grass production in mg/hr | Production / Consumption |
|---|---|---|---|---|---|---|---|---|
| *1a+1b. | *Acropora corymbosa* | 162 | 73 | 29.5 | 5.67 | 4.29 | 9.96 | 2.32 |
| 2a+2b. | *Acropora erythraea* | 142 | 71 | 30 | 5.65 | 3.23 | 8.88 | 2.75 |
| 3a+3b. | *Cyphastrea microphthalma* | 212 | 118 | 30.5 | 2.20 | 1.57 | 3.77 | 2.40 |
| 4a+4b. | *Favia pallida* | 257 | 152 | 29.5 | 3.18 | 1.86 | 5.04 | 2.71 |
| 5a+5b. | *Favites abdita* | 172 | 93 | 30 | 1.41 | 0.78 | 2.19 | 2.81 |
| 6a+6b. | *Goniastrea pectinata* | 200 | 100 | 30 | 0.90 | 0.93 | 1.83 | 1.97 |
| 7a+7b. | *Ganiopora stokesi* | 215 | 152 | 29.5 | 7.17 | 3.35 | 10.52 | 3.14 |
| 8a+8b. | *Montipora divaricata* | 154 | 71 | 30 | 6.99 | 3.12 | 10.11 | 3.24 |
| 9a+9b. | *Pocillopora damicornis* | 154 | 71 | 30.5 | 8.78 | 4.36 | 13.14 | 3.01 |
| 10a+10b. | *Porites solida* | 207 | 116 | 30 | 2.53 | 0.98 | 3.51 | 3.58 |

* Numbers refer to Tables 1 & 2.

TABLE 4. *Details of incubation of zooxanthellae with* $NaH^{14}CO_3$. *Genera and species are listed alphabetically*

| No- | Name of species | Weight gms. | Vol. ml | Date | Duration | Average water temp. °C | Counts* p/m | Carbon fixed by zooxanthellae mg/hr. Adjusted to net |
|---|---|---|---|---|---|---|---|---|
| 1a. | *Acropora corymbosa* | 90 | 40 | 3-7-'68 | 10.45-11.45 | 30 | 184250 | 0.64 |
| 1b. | " " | 72 | 33 | 4-7-'68 | 10.45-11.45 | 30 | 188375 | 0.65 |
| 2a. | *Acropora erythraea* | 72 | 36 | 19-2-'68 | 11.40-12.40 | 30 | 132000 | 0.46 |
| 2b. | " " | 70 | 35 | 20-2-'68 | 11.40-12.40 | 30 | 150700 | 0.52 |
| 3a. | *Cyphastrea microphthalma* | 110 | 56 | 7-9-'68 | 11.00-12.00 | 30.5 | 67100 | 0.24 |
| 3b. | " " | 102 | 52 | 6-9-'68 | 11.00-12.00 | 30.5 | 95150 | 0.33 |
| 4a. | *Favia pallida* | 142 | 84 | 19-7-'68 | 11.15-12.15 | 30 | 67650 | 0.24 |
| 4b. | " | 115 | 68 | 20-7-'68 | 11.15-12.15 | 30 | 45375 | 0.15 |
| 5a. | *Favites abdita* | 80 | 48 | 28-2-'68 | 11.30-12.30 | 30 | 20900 | 0.07 |
| 5b. | " | 84 | 45 | 27-2-'68 | 11.30-12.30 | 30 | 60775 | 0.21 |
| 6a. | *Goniastrea pectinata* | 98 | 49 | 24-2-'68 | 11.35-12.35 | 30 | 46750 | 0.17 |
| 6b. | " " | 102 | 51 | 23-2-'68 | 11.35-12.35 | 30 | 52250 | 0.18 |
| 7a. | *Goniopora stokesi* | 125 | 82 | 25-7-'68 | 10.40-11.40 | 30 | 422125 | 1.46 |
| 7b. | " " | 90 | 60 | 24-7-'68 | 10.40-11.40 | 30 | 22000 | 0.77 |
| 8a. | *Montipora divaricata* | 100 | 50 | 28-8-'68 | 10.40-11.40 | 30 | 4675 | 0.02 |
| 8b. | " " | 70 | 35 | 29-8-'68 | 10.40-11.40 | 30 | 2200 | 0.01 |
| 9a. | *Pocillopora damicornis* | 64 | 31 | 2-9-'68 | 10.30-11.30 | 30.5 | 308550 | 1.07 |
| 9b. | " " | 90 | 40 | 3-9-'68 | 10.30-11.30 | 30.5 | 291775 | 1.01 |
| 10a. | *Porites solida* | 100 | 56 | 24-6-'68 | 11.00-12.00 | 30 | 27500 | 0.09 |
| 10b. | " | 107 | 60 | 25-6-'68 | 11.00-12.00 | 30 | 31350 | 0.11 |

* Counts are given after making the necessary correction for the control and the back ground.

TABLE 5. *Comparison of values of primary production of reef corals estimated by oxygen method and $^{14}C$ technique*

| No. | Name of species | Weight in gms. | Carbon equivalent to net $O_2$ (PQ=1·25) mg. | Carbon equivalent to respiration mg. | Gross Carbon mg. | $^{14}C$ values of carbon adjusted to net, mg. | Percentage realised by $^{14}C$ against the net production measured by l. bottle |
|---|---|---|---|---|---|---|---|
| 1. | *Acropora corymbosa* | 162 | 1.70 | 1.29 | 2.99 | 1.29 | 75.88 |
| 2. | *Acropora erythaea* | 142 | 1.69 | 0.97 | 2.66 | 0.98 | 57.99 |
| 3. | *Cyphastrea microphthalma* | 212 | 0.66 | 0.47 | 1.13 | 0.57 | 86.36 |
| 4. | *Favia pallida* | 257 | 0.95 | 0.56 | 1.51 | 0.39 | 41.10 |
| 5. | *Favites abdita* | 172 | 0.43 | 0.23 | 0.66 | 0.28 | 65.10 |
| 6. | *Goniastrea pectinata* | 200 | 0.27 | 0.28 | 0.55 | 0.35 | 129.60 |
| 7. | *Goniopora stokesi* | 215 | 2.16 | 1.00 | 3.16 | 2.23 | 103.20 |
| 8. | *Montipora divarticata* | 170 | 2.09 | 0.94 | 3.03 | 0.03 | 1.44 |
| 9. | *Pocillopora damicornis* | 154 | 2.63 | 1.31 | 3.94 | 2.08 | 79.10 |
| 10. | *Porites solida* | 207 | 0.76 | 0.29 | 1.05 | 0.20 | 26.31 |

A proper assessment of PQ value is essential in converting the oxygen values into equivalent carbon. Ryther (1956) has pointed out that a PQ of 1 is largely an experimental artifact and suggested a value of 1.25 for phytoplankton of natural waters. Based on the results of $^{14}C$ and oxygen measurments of the coastal waters, Prasad and Nair (1962) suggested a PQ of 1.3. It appears from our results that a PQ of 1 is too low for the symbiotic zooxanthellae and a value of 1.25 is more reasonable and is adopted in this work.

Interference of chemical agents in the Winkler technique is a factor that might influence the results obtained (Kanwisher and Wainwright, 1967). The role of micro-organisms in the respiration of corals is a factor that needs consideration. There are a large number of them present in a coral head and they are observed along with the isolated zooxanthellae. If they respire both in the dark and light bottles this should introduce no systematic errors (Strickland, 1960) in the oxygen values. Yonge (1937) has noted that about 34.3% of the apparent respiration of the *Acropora* is due to the rapid consumption of mucus by bacteria during the experimental period. But as pointed out by Sargent and Austin (1954), for short term experiments where the corals are subjected to minimum disturbance, correction for mucus oxidation is of only secondary importance.

The algae are known to excrete a part of their photosynthetic product in the form of soluble products like glycerol aminoacids and peptides (Hellebust, 1965; Muscatine, 1965, 1967) when incubated with radioactive carbon. According to Hellebust (1965) the different algae on incubation, under full sunlight with radioactive carbon at a temperature of 18 °C for five hours, excreted as much as 9 to 52% of their photosynthate as soluble by-products. Muscatine (1967) working with the symbionts of *Pocillopora* has stated that, on incubation at a temperature of 25° C they lost as much as 12% of their photosynthetic product into the medium in the absence of any tissue homogenate, in the first hour of incubation at a light intensity of 4400 to 6600lu/$m^2$. The rate of excretion was shown to be of the magnitude of 36.8% in the presence of the host tissue homogenate. Separation of the zooxanthellae from the host tissue might have marked effect on their physiological activities that might result in a retardation of their photosynthetic activity in the free medium.

The host tissue is believed to accelerate the photosynthetic activity of the symbionts either by shading and providing optimum conditions of light or directly by chemical catalysis (Muscatine, 1967). Goreau and Goreau (1960) have suggested that *in vivo* these soluble by-products will be transferred to the host tissue and will be utilised. As we could not detect any marked loss as soluble products of photosynthesis in our experiments, our results can be modified only in the light of earlier findings. It appears to be only reasonable to allow a loss of 5% of the total photosynthetic product of the zooxanthellae as soluble

by-products in the present series of experiments (Muscatine, personal communication).

When zooxanthellae are isolated and left in a free medium for incubation, they are suddenly subjected to a much greater intensity of light than in their natural habitat. It is quite likely that the optimum conditions are not met with in the free medium. Further, the present experiments were carried out under full sunlight at a depth of about 50 cm of water. It has already been pointed out by Hellebust (1965) that intense light may do damage to the cells during incubation with $^{14}C$. But cell lysis may be regarded negligible during short periods of incubation (Muscatine, 1965). But as already been mentioned, a steady increase in carbon uptake in comparison with the controls for the first three hours of our incubation of zooxanthellae is suggestive that the cell lysis is negligible in the present cases. Yet another possibility is the loss of a few zooxanthellae during isolation and subsequent manipulation. This, however, will not be of any considerable measure since extreme care has been taken to avoid, as far as possible, such waste in the present set of experiments.

In spite of giving allowances for all these it is evident from the present results that the production measured by $^{14}C$ is generally less than what is obtained by oxygen measurements, though in two cases, viz., *Goniastrea pectinata* and *Goniopora stokesi*, the values by the former method were higher. If such difference could be an indirect evidence to the share of the boring algae in the overall productivity of the coral head, it would appear that this share would be rather high in certain cases (see Table 5).

We are at present unable to suggest the exact share of the filamentous algae in the gross production of corals of this area. Kanwisher and Wainwright (*op. cit*) attribute only 10% of the total production in Florida reef corals but it may be pointed out that there is always danger in extrapolating results from one place to another, for the content of symbiotic algae and the boring algae in corals may vary from region to region and even in different species.

## Summary and Conclusions

The primary production of a few species of hermatypic scleractinian corals are estimated by both Winkler method and $^{14}C$ technique. The results emphasise that neither the weight nor the volume of corals can be taken as a unit for comparison of the production values of various species or even within the different specimens of a single species or part of the same specimen. The faster-growing genera like *Acropora* and *Pocillopora* have a higher metabolic rate than the slower-growing genera like *Favia, Favites, Goniastrea* and *Porites*.

In the ten species of corals used, the ratio of gross production by consumption varied from 1.97 to 3.58. The symbiotic zooxanthellae when isolated and incubated with radioactive carbon in filtered sea water under bright sunlight

at a temperature of about 30° C, actively incorporated carbon by photosynthesis in the first two to three hours during which cell lysis is comparatively negligible.

The net values of incorporated carbon obtained by $^{14}C$ method are mostly less than the values obtained by the oxygen technique. It is probable that in the case of symbionts the $^{14}C$ values are nearer to the net production than to the gross.

The various external and internal factors that might have influenced the present results either directly or indirectly are briefly reviewed.

The boring filamentous and attached algae on a coral colony are decisively contributing towards the total production, but their share may vary in different species.

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## DISCUSSION

MUSCATINE I wonder if you have considered the possibility that zooxanthellae after removal from the corals may show retardation in activity. I mean, you cannot expect it to act as under natural conditions.

PILLAI This is a factor that needs experimental confirmation for which we made no attempt. But it may be borne in mind that our incubation of zooxanthellae with $^{14}C$ was done for only one hour and invariably the experiments were terminated within 2 to 2½ hours from crushing of the coral to the final filtering. Separation of zooxanthellae from the host tissue might be influencing their photosynthetic activities. Moreover the illumination is not the same in natural and experimental conditions. These problems need further investigations.