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Primary Production of an Atoll in the Laccadives

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I. Introduction

According to Yonge (1960) "an atoll raised to the surface in the midst of oceanic waters may be described as a large scale experiment in nature". Earlier studies have contributed to an understanding of primary production of atolls and coral reefs of the Pacific and Atlantic Oceans (Sargent and Austin, 1949, 1954; Odum and Odum, 1955; Kohn and Helfrich, 1957; Odum, Burkholder and Rivero, 1959; Gordon and Kelly, 1962). Comparable information on the atolls of the Indian Ocean has been completely lacking. Since Gardiner (1903—1906) published his classical work on the Maldive and Laccadive Archipelagoes, practically no knowledge has been added to the atolls of the Laccadives.

The Laccadive Archipelago consists of a group of islands and banks in the Arabian Sea (Fig. 1). Excluding Minicoy, which is the southernmost, the remaining islands are located between Lat. 10° N and 12° N and Long. 71°40′ E and 74° E. In all, there are 20 islands, of which 10 are inhabited. Of the 20 islands, at least 10 are atolls, each with a lagoon surrounded by a ring-shaped coral reef.

A growing interest in research on the atolls of the Laccadives prompted some of the biologists of the National Institute of Oceanography (India) to undertake several expeditions lasting 1—2 weeks to some of these atolls. So far, most of the work related to productivity has been confined to Kavaratti Atoll.

Kavaratti is a perfect atoll (Gardiner, 1903—1906). It is located along Lat. 10°33′ N and Long. 72°36′ E (Fig. 1), and has an island of 3.45 sq. km in area, which is largely covered by coconut palms. The northern end of the island is broad (about 1.2 km) and its southern end long and narrow, only about 40 m wide at the narrowest point (Fig. 2). On the western side it has a shallow lagoon,

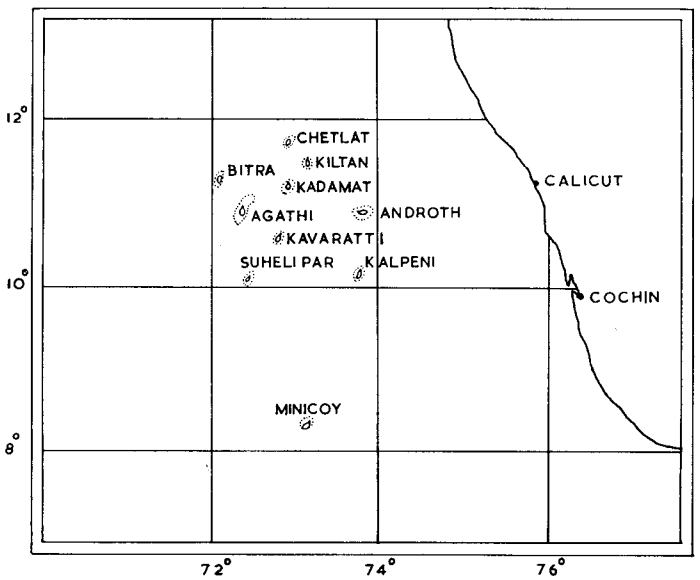

Fig. 1. Map showing the position of Kavaratti Atoll in the Laccadive Archipelago in relation to southwest coast of India

about 4500 m long and 1200 m wide, with depths ranging from 1.52 to 1.83 m at low water and 2.44 to 3.55 m at high water. Bordering the western margins of the lagoon, there is a ring-shaped coral reef with a width of about 250 to 300 m, except at the southwest point where it is more than 400 m wide. A gap in the coral reef, about 60 m wide, on the northwest point forms the main navigational entrance to the lagoon (Fig. 2). At low water the top portions of the reef are exposed, and the lagoon begins to look isolated from the surrounding sea, except at the navigational entrance and at a narrow break, about 5 m wide, at one point in the reef (Fig. 2). At high water the reef is submerged. The transport of water from the sea to the lagoon is maintained all the time by the action of surf, which breaks across the reef and is swept into the lagoon. At low water the depth over the reef, excluding the irregular pits, may not exceed 5 to 10 cm and at high water it largely depends upon the range of tides. The eastern side of the island (seaward) is exposed to high seas. The seaward beach has a steep slope with a substratum of loose coral blocks, coral limestones and debris, in addition to a sub-littoral zone of living corals in the reef adjoining the island (Fig. 2). These form break-water to the heavy surf which had a time frequency of 1 wave/8—10 seconds in November 1968.

The lagoon beach has a gentle slope with an exposure of about 60 m at the lowest low tide. The beach substratum is of coarse white sand and coral fragments. The floor of the lagoon toward the beach is somewhat different from

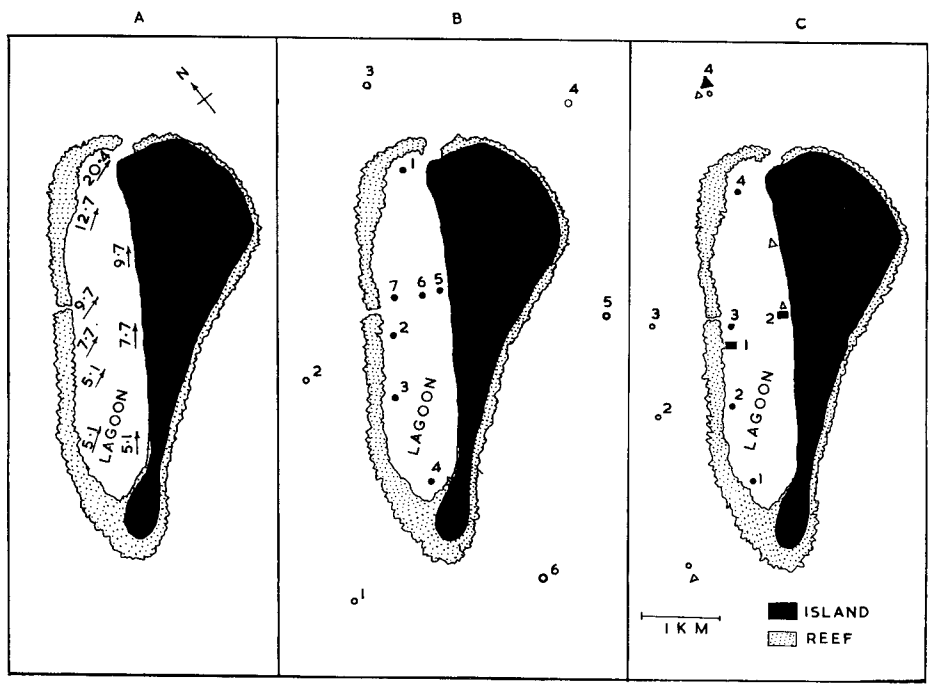

Fig. 2. Kavaratti Atoll showing the relative positions of Reef, Lagoon and Island.
(*A*) Current velocities (cm/sec) and direction of flow in the lagoon have been shown by arrows.
(*B*) Open circles show the position of stations 1—6 in the surrounding sea and closed circles show stations 1—7 in the lagoon, where concentrations of oxygen at different times of day and night were measured.
(*C*) Open and closed circles show the station positions in the sea and in the lagoon respectively, where changes in oxygen concentration were measured during the two runs; closed rectangles show the lagoon stations 1 and 2 where diurnal changes in oxygen were studied. Open triangles show the sites for C^{14} uptake and chlorophyll measurements and closed triangle the station where light penetration was measured

that leading to the leeward reef-mark and reef-flat. The former covers nearly 1/3 the area of the lagoon and consists of loose white sand with irregular surface formed of coral rocks and debris. The beach slope, from about low water neap tide, has a luxuriant growth of macrophytes — two species of seagrasses, *Thalassia hemprichii* and *Cymodocea isoetifolia* are most abundant and form a bed extending to a distance of 100 m into the lagoon. The former grows higher up along the beach and merges into a continuous bed with the latter and other plants growing lower down.

The portion of the lagoon toward the reef is characterised by living and dead corals, with irregular areas of coral rubble, algal beds and sand. Living corals are distributed in patches in between stretches of gravel and silt, which are probably derived from the attrition of outer reef. All along the lagoon-reef, corals are the dominant animals, although their growth is patchy. No corals are seen near the entrance to the lagoon, while a rich growth of corals exists at the southwest point of the lagoon.

In November the surface current in the lagoon had a velocity ranging from 5 cm/sec at the southwest point to 20.4 cm/sec at the entrance (Fig. 2 A). Field data on the currents in the lagoon, collected throughout the year by the Engineering Department, Laccadive Harbour Work, showed a unidirectional flow in all the seasons, accelerating enroute from the southwest corner to the entrance (Fig. 2 A). During the monsoon months, however, the average current velocity increases 3—5 times, depending upon the force of the prevailing winds and waves. The tides at Kavaratti are of mixed, semidiurnal type with a maximum range of about 1.7 m. Two high and two low water-marks occur each day, with a substantial difference in range and time (see bottom curve Fig. 5). From the field data on the pattern of circulation collected by the Engineering Department it appears that the current velocity in the lagoon remains largely unchanged by the tidal height.

II. Procedure and methods

Several different methods were combined to study the primary production of the atoll. At first an estimate of phytoplankton production in the surrounding sea and in the lagoon was made by using the radiocarbon technique of STEEMANN NIELSEN (1952) and by chlorophyll *a* determinations according to the method given by PARSONS and STRICKLAND (1963), by filtering 5—6 litres of water through Whatman GF/C pads and extracting the chlorophyll as suggested by UNESCO (1966). Then the rates of oxygen changes throughout day and night at two stations in the lagoon were measured, and from these, gross production and respiration were calculated after applying corrections for the diffusion of oxygen across the air-sea interface (see ODUM, 1956; KOHN and HELFRICH, 1957). Modifications in this method as suggested by GORDON and KELLY (1962) were incorporated, except that the changes in nitrogen were not studied in conjunction with oxygen. Fluctuations in other parameters such as temperature, salinity, nitrate-N, and phosphate-P were noted along with changes in oxygen. A third method, which makes use of oxygen changes in water during its transport over the reef (SARGENT and AUSTIN, 1949, 1954) and from which a sum total of photosynthesis and respiration of the reef community can be obtained, was also applied. Finally, several series of experiments were carried out on different plants and corals from the lagoon to determine their rates of oxygen production and consumption. Light penetration in the water near the reef was measured by a submarine photometer.

III. Results

1. Transparency of water

Although it is well known that the water near atolls and coral reefs is extremely clear, there are practically no published data on the vertical attenuation coefficient (k) in these waters. It was therefore considered desirable to make some measurements of light penetration and this was done on 9 November 1968 at the station shown in Fig. 2 C. The results obtained by using a Weston 865-RR (Whitney) photometer provided with neutral density filters, have been shown in Fig. 3. The instrument recorded the entire visible range of sun and skylight (300—750 mμ). The transmission of incident illumination at 20 m, 40 m and 60 m was 24%, 7% and 1%, respectively. The values of attenuation coefficients with depth were as follows:

Upper 10 m, $k = 0.066$; 10 to 20 m, $k = 0.075$; 20 to 30 m, $k = 0.076$; 30 to 40 m, $k = 0.045$; 40 to 50 m, $k = 0.101$; 50 to 60 m, $k = 0.118$.

The mean Secchi disc reading at this station was 23 m, which from the well known equation, $k = \frac{1.7}{D}$ gave the value of attenuation coefficient as 0.074. The transmission of surface illumination at the depth where the Secchi disc disappeared was 22%, and the compensation depth of the euphotic zone (1% of the surface illumination) was at 56 m.

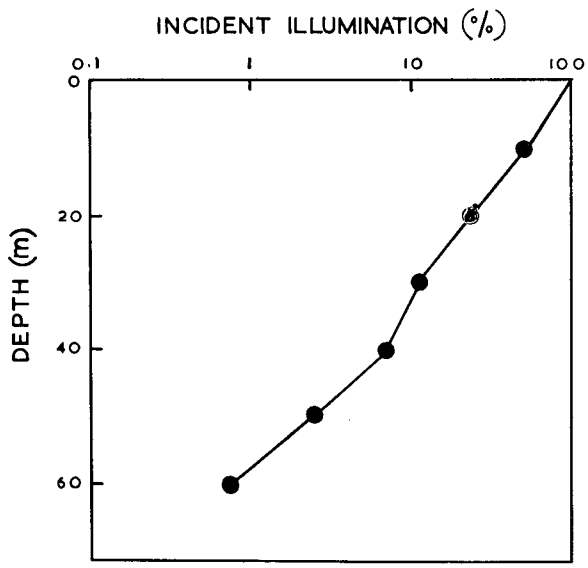

Fig. 3. Penetration of light near the reef on Kavaratti Atoll

These observations indicate that the transparency of water near the reef to a depth of 40 m was fairly high, but below this, probably the presence of some absorbing or scattering material gave rise to lower transparency. The clarity of these waters, however, can be understood better if a comparison is made with some other known values of attenuation coefficients of ocean waters. CLARKE and KELLY (1964) give $k = 0.070$ to 0.192 in the upper 30 m of the western Indian Ocean. For the Sargasso Sea which is well-known for its high transparency, the value of k is 0.050 (MENZEL and RYTHER 1961). The range in k in the upper 40 m at the station near the reef (0.075—0.045) suggests that the water near Kavaratti was clear, but certainly not so clear as the water near Rongelap Atoll where the Secchi disc reading was found to be 41 m (SARGENT and AUSTIN 1949).

Since the depth of the lagoon varies between 1.5 m and 3.0 m, it would appear from the attenuation coefficient of the upper 10 m that the illumination at the bottom of the lagoon would be 80—90% of that at the surface; but this will not be throughout the lagoon, as very often clouds of mucus and other suspended material could reduce the light to about 40% or even less in certain areas.

2. *Phytoplankton production*

Some estimates of primary production in waters outside and inside the lagoon have been given in Table 1. These estimates were made in November. The locations of the stations where C^{14} uptake and chlorophyll *a* determinations

were made, have been shown in Fig. 2 C. It can be seen from Table 1 that both in the open sea and lagoon, phytoplankton production was low and agreed with the rate of production of the western Indian Ocean determined by Steemann Nielsen and Jensen (1957—59). The values of chlorophyll *a* obtained at Kavaratti were fairly close to those found in waters of the Great Barrier Reef (Jeffrey, 1968). The phytoplankton counts were determined by net collections (0.065 mm mesh width) in December. Table 2 gives the counts of major groups in the surrounding sea and in the lagoon. It is clear from Table 2 that the crop in the lagoon was many times greater than that of the sea, and this was partly reflected by the C^{14} fixation and chlorophyll *a* values also (Table 1). The large

Table 1. Rate of photosynthesis and chlorophyll *a* in waters of Kavaratti. Each value given in the table is a mean of 3—4 measurements made in November 1968

	April		November		December	
	Sea	Lagoon	Sea	Lagoon	Sea	Lagoon
C^{14} assimilation mgC/m³/h	2,34	2.49	0.43	0.51	1.39	1.43
Chlorophyll *a* mg/m³	0.21	0.21	0.04	0.14	0.12	0.16

variation in the phytoplankton crop during December (Table 2) was not so well marked from the C^{14} uptake and chlorophyll *a* values in the preceding month (November). The counts, however, in the surrounding sea are of a similar order of magnitude as those reported from the other regions of the Indian Ocean (Zernova, 1962); but the counts in the lagoon are definitely high by oceanic standards. Probably the semi-enclosed nature of the atoll helps to retain the phytoplankton organisms within the lagoon for sometime, and this may help to maintain a higher phytoplankton biomass in the quiet waters of the lagoon.

To determine, however, how much phytoplankton growth the lagoon water can sustain, the following experiment was conducted: A plastic container of 500-litre capacity was filled with lagoon water, from which most zooplankton grazers had been removed by passing it through bolting nylon of 0.33 mm mesh width. This was allowed to stand under natural illumination (day and night), and each day, starting from the beginning of the experiment, the rate of photosynthesis of the water was determined at mid-day, along with its phosphate-P and nitrate-N contents. The C^{14} assimilation increased about 2-fold within 48 hours and then decreased (Fig. 4). The phosphate-P concentration during the

Table 2. Relative abundance of major groups of phytoplankton in waters of Kavaratti. Sea and lagoon values are based on 12 and 9 samples, respectively, collected from the surface in December 1968

Groups	Sea cells/m³)	Lagoon (cells/m³)
Diatoms	670	44440
Green algae	1800	8440
Blue-green algae	2300	210780
Dinoflagellates	4400	98330
Total organisms	9170	361990

same period decreased from 0.33 to 0.22 μg-at/l, but no corresponding decline occurred in the concentration of nitrate-N. The final nitrogen concentration after 72 hours was 0.42 μg-at/l compared with an initial 0.45 μg-at/l. These observations clearly indicate that the phytoplankton growth cannot occur beyond a certain point in the container probably because of the absence of some such substances which are continually produced and utilized in the lagoon and of which we have practically no knowledge.

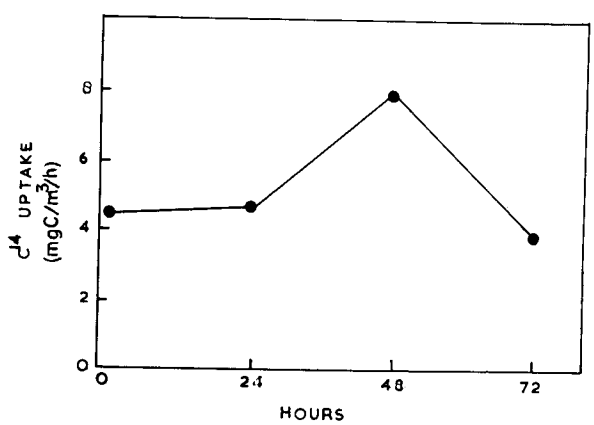

Fig. 4. Variation in the rate of carbon fixation with time in lagoon-water when kept in a large container and exposed to natural illumination

3. Lagoon production

The next step of our study was to make a series of *in situ* oxygen measurements of both oceanic and lagoon waters in replicates at different times of the day. All customary precautions were taken to ensure maximum sensitivity of the Winkler method. Table 3 gives the mean oxygen values obtained from replicate samples at different stations around the island and inside the lagoon. The station positions where oxygen measurements were made have been shown in Fig. 2 B. As can be seen from Table 3, while the oxygen values in the surrounding waters were subjected to little change at different times of the day, the values in the lagoon underwent marked fluctuations. These observations also make it clear that a close study of the changes in oxygen would perhaps be a satisfactory method of estimating the overall production of luxuriant communities of the atoll.

In November 1968, two stations were selected in the lagoon for the study of diurnal changes in the oxygen concentration. The positions of these stations have been shown in Fig. 2 C. Station 1 was at the lagoon-edge of the reef and station 2 near the beach, in the zone of seagrasses (*Thalassisa* and *Cymodocea*). The distance between the two stations was 1200 m. At each station, water samples were collected in replicates from a few centimeters below the surface, every three hours, over a 24-h period. These were fixed immediately and analysed the same day in a camp laboratory. Records of temperature, salinity, and nutrients were made along with oxygen.

Table 3. Concentrations of oxygen (ml/l) at different times of day and night in the surrounding sea (stations 1—6) and in the lagoon (stations 1—7) at Kavaratti. Each value given in the table is a mean of 3—4 replicate oxygen determinations

Time (h)	Sea Stations					
	1	2	3	4	5	6
1225 to 1330	4.26	4.25	4.37	4.09	—	—
2300 to 2320	—	—	4.46	4.30	—	—
0900 to 1200	4.41	4.37	4.34	4.64	4.35	4.39

	Lagoon Stations						
	1	2	3	4	5	6	7
1345 to 1430	5.57	4.60	5.72	4.12	—	—	—
2400 to 0035	—	—	4.48	3.96	—	—	—
0900 to 1300	6.12	4.61	5.32	—	—	—	—
1530 to 1800	—	—	—	7.83	5.63	4.88	4.75

Diurnal changes in all these parameters have been shown in Fig. 5 A and B from which it can be seen that the fluctuations in temperature at both the stations were almost similar. These were of the order of 1.5—2 °C. Maximum temperature was recorded at about 1600 hr and minimum at about 0300 h. The station situated at the grass bed was somewhat warmer than the reef station, but both stations recorded an increase and decrease in temperature at about the same time (Fig. 5 A). Diurnal changes in salinity were small (0.2%). The concentrations of both phosphate-P and nitrate-N were extremely low. The values of phosphorus decreased during the day and increased at night (Fig. 5 A) suggesting that probably some utilization of phosphorus occurs while photosynthesis is taking place. The concentrations of nitrate, on the other hand, showed a reverse trend i.e. the values increased during the day and decreased at night (Fig. 5 A). This was rather surprising and seems impossible to explain without further knowledge of the chemical and biological features of the environment.

The rates of changes of oxygen concentration in ml/cm strip/sec between the two stations were calculated by the formula given by Kohn and Helfrich (1957). These two stations were parallel to the direction of the currents and were up and down-stream because the entry of water into the lagoon is by the surf action across the reef and thus the water passes from station 1 to station 2. The correction for diffusion across the air-sea interface for each interval of 3-h was made by the equation:

$D = KS$, where K is the gas transfer coefficient and S is the saturation deficit between water and air.

Thus,

$$K = \frac{z\,(q_1 - q_2)}{s_1 - s_2}$$

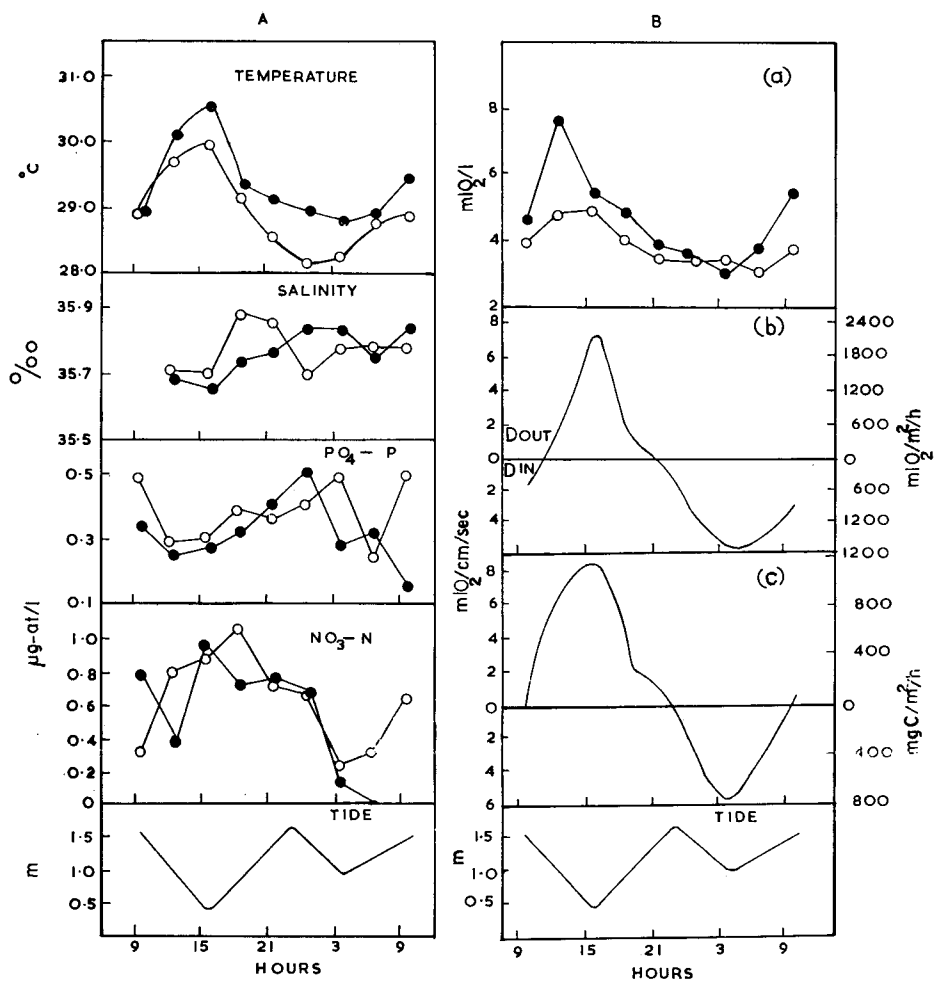

Fig. 5. *A*. Changes in temperature, salinity, phosphate-P and nitrate-N during day and night at the two stations in the lagoon (station 1, closed circles; station 2, open circles). *B*. Changes in oxygen concentrations at the two stations (*a*); Rate of diffusion of oxygen calculated from the values at the two stations (*b*); Changes in oxygen corrected for diffusion (*c*); Bottom curves give the tidal range during the period of observation

where z is the mean depth, q_1 and q_2 are the rates of changes in oxygen during a 3-h interval and S_1 and S_2 are the saturation deficits for the same period calculated from the equation of REDFIELD (1948) using the oxygen saturation values from the nomogram of GREEN and CARRITT (1967).

The calculated values of the gas transfer coefficient (K) for each interval of 3-h at the two stations have been given in Table 4. As can be seen from Table 4, at station 1 the short-term changes in the values of K were quite large and varied by factors 3—6. This can be attributed to seasurface roughness near the reef and to temporal variation in tidal height. GORDON and KELLY (1962) have

shown that these factors "change the area of the surface available for gaseous exchange with the atmosphere, thereby changing the effective value of the gaseous transfer coefficient". The two values which looked uncertain have been neglected from Table 4 because they were taken as artifact (see Gordon and Kelly, 1962).

Table. 4. Gas-transfer coefficients (K) of oxygen determined every three hours at two stations in Kavaratti Lagoon

Date	Period (hours)	K ($ml O_2/m^2/h/atm$)	
		Station 1	Station 2
3.11.68	1000–1300	12187	12295
	1300–1600	—	11820
	1600–1900	12969	12384
	1900–2200	5538	12802
	2200–0100	—	13053
4.11.68	0100–0400	25662	12779
	0400–0700	12690	10945
	0700–1000	20281	12721

It is interesting to note that the values of K at station 2 are fairly consistent probably because of the flat surface in the lagoon caused by its calm water. The average value of K is 9.6×10^6 $ml O_2/m^2/month/atm$, which is much higher than the value calculated for North Kapaa Reef (3.3×10^6 $ml O_2/m^2/month/atm$) by Kohn and Helfrich (1957) and comes close to the oxygen transfer coefficient of $20\,gO_2/m^2/h/atm$ determined for a Hawaiian coral reef (Gordon and Kelly, 1962). Our value in terms of $gO_2/m^2/h/atm$ is 19.

Fig. 5 B (a) gives the diurnal cycle of oxygen at the two stations from which it may be seen that the oxygen production was maximal at about mid-day. Since station 2 was situated just over the grass bed it gave rise to a greater amplitude in oxygen production than the station 1. The average current velocity for November has been taken as 10 cm/sec. Therefore, the time required for the water to pass from station 1 to station 2 would be approximately 3 hours. Hence according to the procedure suggested by Odum (1956), the curve for station 2 has been shifted to the left 3 hours. The average depth of the lagoon has been taken as 1.8 m.

Fig. 5 B(b) gives the rate of diffusion of oxygen calculated from the values at the two stations which would refer to a strip of lagoon, 1 cm wide and 1200 m long (the latter being the distance between the two stations). Therefore, in terms of area the strip will be equal to 12.0 m^2. The right ordinate of Fig. 5 B (b) shows the corresponding units on an areal basis.

Fig. 5 B (c) shows the cycle of oxygen corrected for diffusion rates. The areas of the curve above and below zero or "compensation line" give the community photosynthesis and respiration simultaneously. The two areas were measured by a planimeter, and the net production of the lagoon (top curve) was calculated as 219024 $ml O_2/cm/day$ or 8.15 $gC/m^2/day$ and the respiration (bottom curve) as 128088 $ml O_2/cm/day$ or 4.77 $gC/m^2/day$ (factor $\frac{0.536}{PQ}$ was used for converting

the oxygen values to carbon assimilation, where the value of PQ was taken as 1.2; see STRICKLAND (1960). Summing the values of community photosynthesis and respiration, the gross production of the lagoon would be 12.92 gC/m²/day. Assuming that respiration goes on at the same rate throughout day and night, and therefore multiplying the respiration value of 4.77 by a factor 2, the daily (24-h) net production of the lagoon would approximate 3.38 gC/m², and the ratio between photosynthesis (12-h) and respiration (24-h) P/R would be 1.35, which indicates that the lagoon community is autotrophic.

4. Production by plants

To get some idea of the photosynthetic and respiratory activities of the plants in the lagoon, several series of experiments were carried out on individual species. The procedure of these experiments was as follows: Freshly collected seagrasses and algae listed in Table 5 were taken. These were carefully washed with Millipore-filtered water from the lagoon and a small quantity of each (2—3 g) was weighed while still wet and kept in glass jars of 300 ml capacity containing filtered seawater, the oxygen concentration of which was carefully determined. They were immediately exposed to natural illumination (bright sunlight) for a period of 3 hours, except one experiment which was of 2 hours. The jars were completely filled, screw-capped and kept in a large trough containing freshwater, which was constantly changed to avoid any sharp increase in temperature in jars. In each experiment replicate sets of jars were used and from these, one set was kept in complete darkness parallel to those which were kept in light. At the end of the exposure, the water from each jar was siphoned off and analysed for oxygen. Increase and decrease from the initial value were taken as criteria for photosynthesis and respiration respectively. A set of two jars containing the same seawater was used as control in each experiment, and these were similarly exposed to light and darkness as the experimental jar. Winkler determinations of dissolved oxygen from the controls showed no appreciable change from the initial, whereas the changes in the experimental jars were very pronounced.

Table 5. Rates of oxygen production and consumption by different macrophytes and algae from Kavaratti Lagoon

Species	Wet weight used (g)	Time of incubation (h)	Net oxygen produced (ml/g/h)	Oxygen consumed (ml/g/h)	Net production (mgC/g/h)	Consumption (mgC/g/h)
Thalassia hemprichii	2.7	1400–1700	0.2119	0.0699	0.0946	0.03122
Cymodocea isoetifolia	2.7	1400–1700	0.0759	0.0880	0.0339	0.03931
Ulva lactuca	2.7	1400–1700	0.5340	0.0902	0.2385	0.04029
Cladophora fascicularis	2.7	1400–1700	0.3908	0.1043	0.1746	0.04659
Hypnea cervicornis	2.7	1400–1700	0.1447	0.0711	0.0646	0.03176
Halimeda incrassata	2.0	1530–1730	0.0250	0.0463	0.0112	0.02068
Mean			0.2304	0.0783	0.1029	0.03498

Table 5 shows the results of these experiments. As can be seen, different species gave different rates of oxygen production and consumption — i. e. their rates of photosynthesis were quite independent of their rates of respiration. In most cases, photosynthesis for 12 hours exceeded respiration for 24 hours. KANWISHER (1966) has shown that in several species of seaweeds, under op-

timum conditions of light and temperature, total respiration forms a small fraction of photosynthesis. The average values given in Table 5 were taken as an estimate of photosynthesis and respiration of the plant community. Since the experiments on which the average values are based were done in jars containing stagnant water, it is suspected that the values may only give an approximation of the estimate.

To estimate the plant biomass in the lagoon, a wooden quadrat (10 × 10 cm) was placed indiscriminately on different types of plant-beds of the lagoon at lowest low tide. Practically all plant material contained within this quadrat was scraped off, cleaned, wiped and weighed. Sixteen such measurements gave the weight of plant material ranging from 1000 to 4000 g/m² (average = 2320 g/m²). Prominent species contained in the scarpings were identified as follows:

Seagrasses: *Thalassia hemprichii* (Ehr.) Asch; *Cymodocea isoetifolia* Aschers and Graeb.

Green Algae: *Ulva lactuca* L.; *Enteromorpha prolifera* (Möller) J. Agardh.; *Chaetomorpha littorea* Harvey; *Cladophora fascicularis* (Mert.) Kützing; *Dictyosphaeria cavernosa* (Forsk.) Boergesen; *Boergesenia forbesii* (Harv.) Feldmann; *Halimeda incrassata* (Ellis et Sol.) Lamx. var. *simulans* (Howe) Boerg.

Brown Algae: *Colpomenia sinuosa* (Roth) Derbes et Solier.

Red Algae: *Fosliella lejolisii* (Rosan.) Howe; *Hypnea cervicornis* J. Agardh; *Spyridia filamentosa* (Wulf.) Harvey; *Laurencia papillosa* (Forsk.) Greville; *Acanthophora spicifera* (Vahl) Boergesen; *Leveillea jungermannioides* (Mert. et Her.) Harvey.

Primary production and consumption by the algae were determined in terms of area by multiplying the average values of photosynthesis and respiration given in Table 5 by the average biomass of plant material. This gave a gross production value of 8594 ml O_2/m²/day or 3.84 gC/m²/day and daily (24-h) respiration as 4360 ml O_2/m² or 1.94 gC/m².

5. *Production by corals*

Similar experiments were conducted on three species of corals. These were actively growing tips from freshly collected colonies. A known weight of these (7–9 g) was kept in replicate jars with freshly collected and filtered seawater from the lagoon, and Winkler determinations of oxygen were made before and after an exposure to light or darkness. The rates of oxygen production (net) and consumption by each species have been given in Table 6. Here again the two rates were different in the three species. In *Pocillopora damicornis* the production of oxygen was of the same order of magnitude as its rate of consumption, but in the other two species *P. verrucosa* and *A. indica* production far exceeded consumption. Their oxygen production when computed for 12 hours was greater than their respiration for 24 hours. These rates presumably included photosynthesis contributed by the zooxanthellae and filamentous algae residing in corals, and respiration of animal material plus all plant material contained in coral polyps and skeleton. Kanwisher and Wainwright (1967) by using a polarographic oxygen electrode have shown that in several species of Florida reef corals, photosynthesis is more than twice their respiration in the dark. It is of interest to note that there is a close

agreement between our results and the P/R ratios given by KANWISHER and WAINWRIGHT (1967). The ratios of gross photosynthesis (12-h) to respiration (24-h), P/R in the three species come to similar order of magnitude as those given by KANWISHER and WAINWRIGHT (p. 383) when their values of respiration for 12 hours are doubled to account for day and night respiration.

Table 6. Rates of oxygen production and consumption by three species of corals from Kavaratti Lagoon

Species	Weight used (g)	Time of incubation (h)	Net oxygen produced (ml/g/h)	Oxygen consumed (ml/g/h)	Net production (mgC/g/h)	Consumption (mgC/g/h)
Pocillopora damicornis (L.)	9	1530–1730	0.0219	0.0219	0.0098	0.0098
Pocillopora verrucosa (ELLIS and SOLANDER)	7	1400–1700	0.0290	0.0038	0.0130	0.0017
Acropora indica (BROOK)	9	1400–1700	0.0197	0.0040	0.0088	0.0018
Mean			0.0235	0.0099	0.0105	0.0044

6. *Production by reef*

The productivity of the reef was determined by measuring the oxygen changes in water during its transport over the reef (SARGENT and AUSTIN 1949, 1954). For these measurements four stations were selected outside the reef. Almost parallel and alongside to these were four stations in the lagoon as shown in Fig. 2 C. The first run was made on 6. 11. 1968 between 1225 and 1430 hours. Starting from station 1 during the run, samples for oxygen measurements were taken in replicates and fixed on board. The second run was made at night on 8.11. 1968 between 2300 and 0030 hours, but unfortunately due to turbulent conditions of the sea, only two stations could be worked outside the reef and two stations in the lagoon, which were opposite to the sea stations (see Table 7 and Fig. 2 C). It is clear from Table 7 that during daytime the oxygen values inside the lagoon were higher than those from outside, but at night the condition was reversed except at the entrance where the values at the two stations were almost the same. Thus, from the changes in oxygen of water flowing over the reef, the primary production of the reef community was calculated by:

Difference in O_2 (ml/cm^3) $\times$ mean depth (cm) $\times$ velocity (cm/sec)
= oxygen change by reef (ml O_2/cm/sec)
= production or consumption of oxygen.

The production was found to be 0.768 ml O_2/cm/sec and the consumption by reef 0.188 ml O_2/cm/sec. From these values, gross production of the reef community would be 6.15 gC/m^2/day and respiration 2.42 g C/m^2/24 h.

Using the value of oxygen consumption by the reef, an estimate of living corals over the reef can be made by the method of SARGENT and AUSTIN (1949) as follows:

Average oxygen consumption by the reef $= \frac{2.42 \times 10^3}{24}$ mgC/m^2/h (where factor 24 is used for converting the total respiration into hourly values).

Average rate of respiration by corals (from Table 6) = 0.0044 mgC/g/h. Therefore, average coral population over the reef $= \frac{2.42 \times 10^3}{24 \times 0.0044} = 2.3 \times 10^4$ g/m^2.

Table 7. Concentrations of oxygen obtained at different stations in the sea and in the lagoon during two runs

Date	Time (h)	Oxygen (ml/l) Day			
		Sea		Lagoon	
6. 11. 68 (First run)	1225 to1430	(St. 1)	4.263	(St. 1)	5.568
		(St. 2)	4.252	(St. 2)	4.601
		(St. 3)	4.368	(St. 3)	5.719
		(St. 4)	4.088	(St. 4)	4.123
	Mean		4.243		5.003
		Night			
		Sea		Lagoon	
8. 11. 68 (Second run)	2300 to 0035	(St. 3)	4.461	(St. 3)	4.484
		(St. 3)	4.298	(St. 4)	3.960
	Mean		4.380		4.222

IV. Discussion

The atolls of the Laccadives differ from those of the Marshall Islands in many ways. They invariably have shallow lagoons; Kavaratti Lagoon has an average depth of 2m, unlike the Eniwetok Lagoon and the lagoons of Bikini and Rongelap, which have depths averaging 48, 47 and 51 metres, respectively. Probably this feature alone would make the circulation pattern in the lagoon very different from that described by Von Arx (1948, 1954) for Bikini and Rongelap. The extreme shallowness of the lagoon and reef-flat makes the seagrasses, algae and the hermatypic corals live in a very strongly illuminated zone (see p. 211) and this encourages the biota of the lagoon to become massive. This is indeed a major factor that makes the lagoon and the reef on Kavaratti one of the most productive marine communities so far reported.

Almost all atolls of the Laccadives visited by us have been found to be oriented along a northsouth axis, with islands on the east and lagoon on the west. They thus lie directly along the path of the monsoons and receive the full force of the strong southwest monsoon from June to September and of the less forceful northeast monsoon from November to December. Thus, from season to season the direction of the winds keeps reversing and along with it the windward and leeward sides of the atolls, the distinction of which is based on unidirectional winds such as the trades, will also change. In a recent communication, Tranter and George (1969) while comparing the Indian Ocean atolls with those of the Pacific are of the opinion that since the western reef (bordering the lagoon) is exposed to full force of the southwest monsoon, it draws parallel to the Pacific windward reef.

The annual values of gross primary productivity and community respiration of some of the marine communities for which data are available have been given

in Table 8. It is clear from this table that the reef communities, though highly productive, are not always self-supporting. The non-autotrophic communities

Table 8. Comparison of estimates of primary production of coral reefs, atolls and seagrass beds made by different authors

Locality	Gross production ($gC/m^2/year$)	Community respiration ($gC/m^2/year$)	Authors
Hawaiian coral reef, Coconut Island	7300	12370	Gordon and Kelly (1962)
Fringing coral reef, North Kapaa, Hawaii	2427	2200	Kohn and Helfrich (1957)
Eniwetok Atoll, Marshall Island	3500[1])	3500[1])	Odum and Odum (1955)
El Mario Reefs, Puerto Rico	4450	4100	Odum, Burkholder and Rivero (1959)
Eastern Reef, Rongelap Atoll, Marshall Island	1250	1090	Sargen and Austin (1954)
Kavaratti Lagoon, Laccadives	4715	3482	Present authors
Bimini Lagoon, British West Indies	319	205	Odum and Hoskin (1958)
Kavaratti Reef, Laccadives	2250[1])	880[1])	Present authors
Turtle Grass-bed, Long Key, Florida	3880	2740	Odum (1956)
Turtle Grass-bed, West La Gata Reef, Puerto Rico	980	1290	Odum, Burkholder and Rivero (1959)
Thalassia bed, Channel north, Isla Magueyes, Puerto Rico	1350	1500	Odum, Burkholder and Rivero (1959)

Note: All values given in the table have been converted from oxygen to carbon by using $PQ = 1.2$.

[1]) Values uncorrected for diffusion.

in which respiration exceeds production largely include fringing reefs found adjoining the land-masses. The atoll reefs, on the other hand, found in the open ocean are generally autotrophic. Even among the fringing reefs, a few are self-supporting, while others are not. This may suggest that many of the fringing reefs are either dead or have become incapable of supporting large coral and plant populations. It may also suggest that the measurements of primary production of some of the fringing reefs were made during a period when the rate of production was probably at its seasonal minimum.

The reef community on Kavaratti Atoll produces more organic matter in a day than it consumes in 24 hours. This has been found to be true not only for the reef and lagoon but for several species of plants and corals.

This raises the fundamental question whether the reef can be nourished by its own production of organic matter. Corals are known to be specialized carnivores, feeding on zooplankton, especially at night (Yonge, 1930, 1963). Several earlier authors have found an abundance of zooplankton in waters near the reef (Russell, 1934), particularly at night (Emery, 1968), while others have noticed extremely low concentrations. The latter condition has probably led some authors to conclude that "corals must derive organic matter from the algae or die" (Sargent and Austin, 1954), or they must obtain nourishment from their associated plant material (Odum and Odum, 1955). Johnson (1954) found a greater abundance of zooplankton in the lagoons than in the surrounding seas of the Marshall Islands.

The zooplankton biomass recorded at Kavaratti Atoll during the different months of observations has been shown in Table 9 from which it is clear that in

Table 9. Average zooplankton biomass (wet weight) in waters of Kavaratti during different months of observation in 1968. Sea values refer to western side of the atoll. The figures in parenthesis show the number of hauls.

	Day		Night	
	Sea (mg/m^3)	Lagoon (mg/m^3)	Sea (mg/m^3)	Lagoon (mg/m^3)
April	6.4(2)	3.8(3)	—	—
October	—	—	426(8)[1]	189(6)[1]
November	65(3)	—	—	—
December	5.7(5)	2.0(3)	6.7(3)	28.7(2)

[1]) Mean value from the data of Tranter and George (1969).

April and December the zooplankton biomass was very low. There was an exceptional situation in April associated with a massive bloom of the blue-green alga, *Trichodesmium* (Qasim, 1970). In October the biomass values were very high, which was not so in November. Tranter and George (1969) have shown that the nocturnal abundance of zooplankton outside the reefs of Kavaratti and Kalpeni Atolls during the period of their survey was high even by neritic standards. They found significantly lower values of zooplankton biomass in the lagoons, especially at Kavaratti, and the difference they attributed to consumption by the corals, while the water was passing over the reef. They have thus concluded that the energy provided by zooplankton to the reef is of the order of 0.32 gC/m^2, which although falling considerably short of the total energy demand of the reef, is a major step to show that oceanic source of nutrition to corals in the form of zooplankton is by no means insignificant.

The question again arises that zooplakton energy does not remain consistent from season to season, as is evident from the wide variability of biomass at Kavaratti (Table 9) and from the recent findings of Johannes and Coles (1969) on Bermuda Reefs. How, then, do corals and other reef-dwelling animals continue to maintain themselves, and moreover, what is the next source of the remaining bulk of energy needed by the reef? The answer seems inevitable that it must come from the reef itself. Marshall (1965, 1968) reported an abundance of small detrital particles in the vicinity of coral reef, while Johannes (1967) has found similar "aggregates" composed largely of coral mucus in Eniwetok

Lagoon. We have confirmed the presence of large quantities of organic aggregates near Kavaratti Atoll, both by visual and microscopic examinations (QASIM and SANKARANARAYANAN, 1970). A growing literature showing the importance of small particles and organic aggregates as food in the sea (RILEY, 1963; SHELDON, EVELYN and PARSONS, 1967) would undoubtedly make them one of the important sources of potential energy for the filter feeders of the reef community. Since much of the reef productivity seems to be released in the form of particulate organic matter (QASIM and SANKARANARAYANAN, 1970), which is probably carried away into the surrounding sea, it is not surprising to find the production of the atoll communities substantially in excess of consumption, making them truly autotrophic communities.

Recent studies on the host-symbiont metabolic interaction, using elegant techniques, have indicated that soluble photosynthetic products (glucose or maltose) secreted by the green algae living in the gastrodermal cells of *Hydra* are, beyond doubt, passed into the animal tissue (MUSCATINE and LENHOFF, 1963; MUSCATINE, 1965), and thus the symbiont algae are of nutritional value to the host, particularly during the shortage of food or in starvation. Similarly, zooxanthellae of hermatypic corals, besides their important role in growth of corals and calcium deposition, as has been shown from the fine work of GOREAU and GOREAU (1960) and GOREAU (1961), also produce soluble organic material in appreciable quantities, which has been identified as glycerol (MUSCATINE, 1967). The extracellular product is excreted by the algae only in the presence of host-tissue homogenate (MUSCATINE, 1967). These findings have important implications not only in providing some answer to the well-debated question of coral nutrition but perhaps in giving an explanation of the extra source of much needed energy for the survival of the reefs in tropical waters.

V. Summary

1. In the midst of oceanic conditions, Kavaratti Atoll provided with a ring-shaped coral reef and a rich growth of attached algae and macrophytes in its shallow lagoon, forms a highly productive community.

2. The transparency of water near the coral reef is fairly high and the phytoplankton production in the surrounding sea is low. The lagoon seems to sustain a higher standing crop of phytoplankton than does the adjacent sea.

3. Estimates of gross production and community respiration made from diurnal changes in oxygen at two stations in the lagoon and from oxygen changes in water during its transport over the reef, showed that lagoon and reef communities are both autotrophic.

4. Experiments conducted on the oxygen exchange of several species of plants and corals confirmed that their rates of photosynthesis for 12 hours were greater than their rates of respiration for 24 hours. The conclusion that Kavaratti is among the most productive communities was drawn by a comparison of estimates made at Kavaratti with those of other marine communities.

5. The highly variable nature of zooplankton abundance in the surrounding sea and in the lagoon makes it apparent that in some seasons oceanic source of nutrition to corals in the form of zooplankton may be important, but zooplankton alone cannot meet the total energy needed by the reef community.

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Note added in proof

Prof. H. CASPERS drew the attention of the present authors towards the very interesting work done on hermatypic corals by Dr. LUDWIG FRANZISKET at the Hawaii Institute of Marine Biology, Coconut Island. In one of his papers, FRANZISKET (1969) gives the range in ratios of photosynthesis to respiration (24-h) in reef building corals as 2.9—4.3, which is close to our values. In another communication (FRANZISKET, 1970a), he concludes from his experiments on a number of corals that some corals definitely derive nutrition from the photosynthetic production of organic matter by zooxanthellae. He also shows that the presence of mucus gives very little error in Winkler determinations of dissolved oxygen (FRANZISKET, 1970b). These findings are of special interest to our work.

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