

Primary Production of a Seagrass Bed on Kavaratti Atoll (Laccadives)

by

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INTRODUCTION

A considerable knowledge of marine phytoplankton productivity, in contrast with remarkably few investigations on the rate of production of naturally growing benthic plant communities in salt water, such as the vascular plants, prompted the present authors to report the primary production of a seagrass bed from the tropical zone. This study was considered important in two ways: (1) to determine the rate of production of a luxuriant macrophyte community growing in tropical waters on an atoll, and (2) to get some idea of the functions of this grass bed in the atoll community.

The grass bed is found in the lagoon on Kavaratti, an atoll of the Laccadive Archipelago, located along Lat. 10°33'N. and Long. 72°36'E. The lagoon is approximately 4500 m long, 1200 m wide, and has an average depth of 2 m. It is oriented in a north-south direction, with an island on the east and a coral reef, about 300 m wide, on the west (Fig. 1). A narrow break in the reef, about 60 m wide, forms an entrance to the lagoon at the north-west point. The grass bed consists mainly of turtle grass, *Thalassia hemprichii* (EHR.) ASCHERS (Hydrocharitaceae) and manatee grass, *Cymodocea isoetifolia* ASCHERS & GRAEB (Potamogetonaceae). The two species grow together along the beach-slope over a substratum of coarse white sand with coral rocks and debris. The growth of the seagrasses starts

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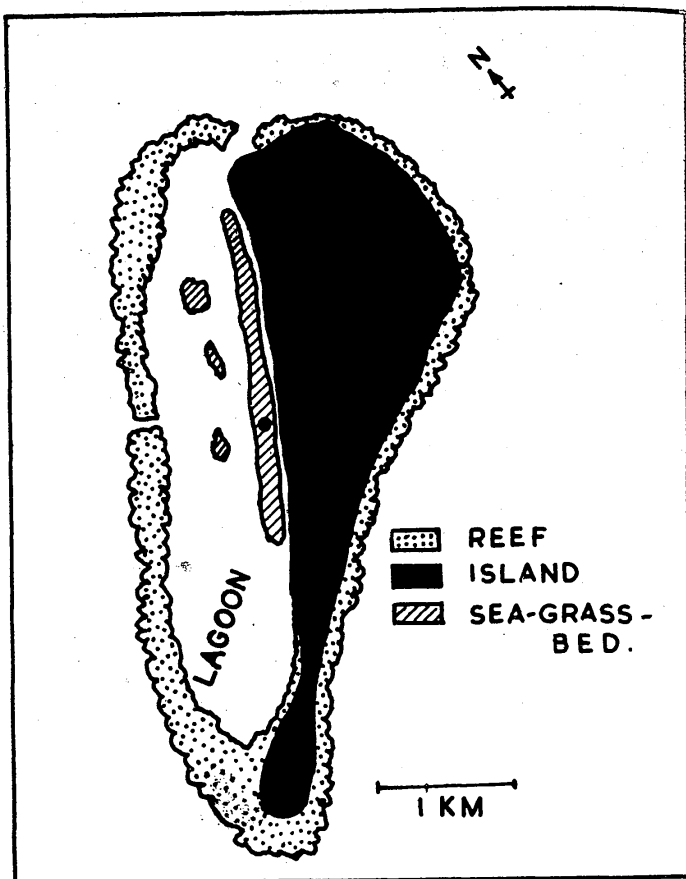


Fig. 1. Map of Kavaratti Atoll (Laccadives) showing the position of grass beds in the lagoon and the location of the station in the beach bed where diurnal changes in oxygen were measured.

from about low water neap tide and continues up to a distance of 100 m into the lagoon floor (Fig. 1). In certain parts it extends even farther than 100 m, forming smaller patches in the lagoon. Of the two species, *Thalassia* grows higher up along the beach. The maximum tidal range at Kavaratti is about 1.7 m, and the beach has an exposure of about 60 m at low tide. At the ebb, the grass bed becomes partially exposed and is thus subjected to desiccation and very wide fluctuations in temperature during sunlight. Similar beds of seagrasses were seen on several other atolls of the Laccadives, and as at Kavaratti, the seagrasses were largely confined to the beach side of the lagoon. In the intertidal zone, but farther into the lagoon, the grass bed also includes a rich flora of algae.

METHODS

Although in recent years the techniques of measuring primary production of phytoplankton have advanced considerably (see e.g. STRICKLAND, 1965), these methods are hardly applicable to situations where the bulk of primary production comes from benthic plants. For the grass bed, therefore, the most suitable procedure seemed to be that suggested by ODUM (1956) for measuring primary production in flowing waters, as the large bed of plants at shallow depth is subjected to a continuous unidirectional flow of seawater toward the entrance, with an average current velocity of 10 cm/sec at the surface, measured in November 1968 by using floats.

At one station over the grass bed (see Fig. 1), diurnal changes in oxygen were measured in November, 1968. Replicate water samples were collected from a few centimetres below the surface at 3-hour interval throughout 24 hours. These were fixed immediately for Winkler determinations of dissolved oxygen. All customary precautions were taken to ensure maximum precision in the oxygen measurements. The values for replicates were averaged. A diurnal curve of oxygen was constructed from the average values. The rates of change in oxygen were expressed according to the method suggested by ODUM (1956 & 1957) which states:

$$\begin{aligned} q &= p - r \mp d \\ \text{or} \quad p &= q + r \mp d \end{aligned}$$

where q is the rate of change of oxygen in ml/m^3 , p is the rate of gross production, r is the rate of respiration, and d is the rate of diffusion. The diffusion rates were calculated by multiplying the saturation deficits between water and air by the gas diffusion constants (K) for each 3-hour period (see GORDON & KELLY, 1962). The saturation deficits were determined from the equation given by REDFIELD (1948) using the saturation values of oxygen obtained from the nomogram of GREEN & CARRITT (1967).

In addition to the above method, a series of experiments were conducted on isolated plants collected from the grass bed for determining their rates of oxygen production and consumption.

RESULTS

Figure 2 shows the results of the study made on 3 and 4 November, 1968. The pronounced rate of change in oxygen from early morning until about 1600 hours is assumed to be a result of the excess photosynthetic activity of the benthic plants. The middle

curve in Figure 2 shows the rate of diffusion of oxygen (d) for each 3-hour interval. Community respiration (r) was calculated from the rates of change of oxygen between 0100 and 0700 hours, as indicated by the stippled area in the top curve, after making a correction for diffusion during the corresponding period. The rate of community respiration has been assumed to be the same during day and night.

The gross primary production is the sum of the areas under the curves (measured by a planimeter), taking due account of the algebraic sign for q and d . This is $26.80 \text{ l O}_2/\text{m}^2/\text{day}$, while respiration amounts to $13.80 \text{ l O}_2/\text{m}^2/\text{day}$ (24 hours). Using the well known

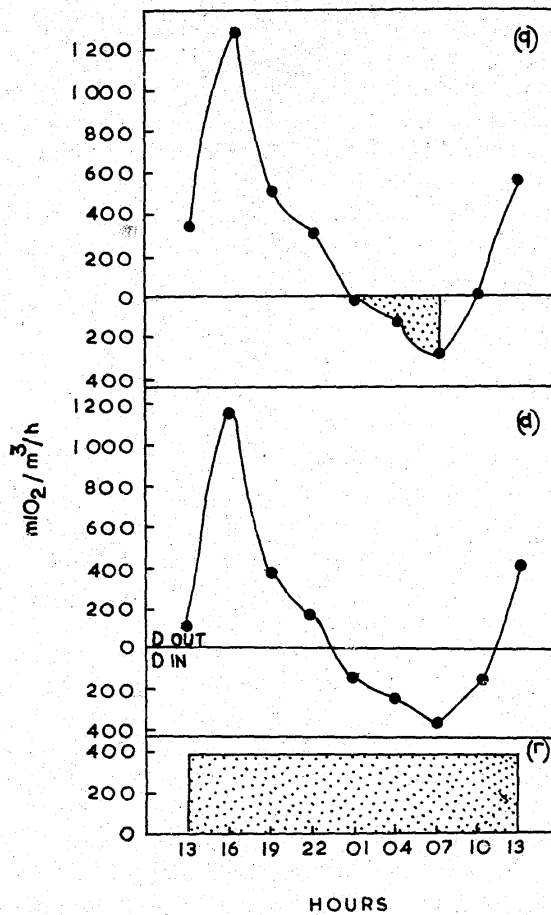


Fig. 2. (q) Rate of change in dissolved oxygen at the station situated over the grass bed. (d) Rate of diffusion of oxygen during day and night. (r) Community respiration calculated from the rate of change in oxygen between 0100 and 0700 hours (stippled area curve q).

conversion factor $\frac{0.536}{PQ}$ and taking the value of PQ as 1.2 (see STRICKLAND, 1960), the production and respiration will be equivalent to $11.97 \text{ gC/m}^2/\text{day}$ and $6.16 \text{ gC/m}^2/24 \text{ hours}$ respectively. The daily excess or net production of the community will be 5.81 gC/m^2 and the ratio between gross production and respiration (P/R) would be 1.94.

To make an approximation of the rate of primary production of the plants found in the bed, the following procedure was adopted: Some of the macrophytes and algae were collected from the grass bed. These were isolated and cleaned with Millipore-filtered seawater. A known wet weight of each species was then kept in replicate jars (300 ml capacity) containing filtered seawater and Winkler determinations were made of dissolved oxygen before and after an exposure to sunlight or darkness for a period of 2—3 hours. Special care was taken to ensure that the jars were completely filled and screw-capped and contained no air-bubbles. Similarly, after the experiments the water for oxygen analysis was gently siphoned off from the jars without creating any undue agitation. Control jars, which contained only filtered seawater, were taken with each set of experiment and these showed no appreciable change in the oxygen from the initial content either in the light or in the dark. The changes in experimental jars, on the other hand, were very substantial.

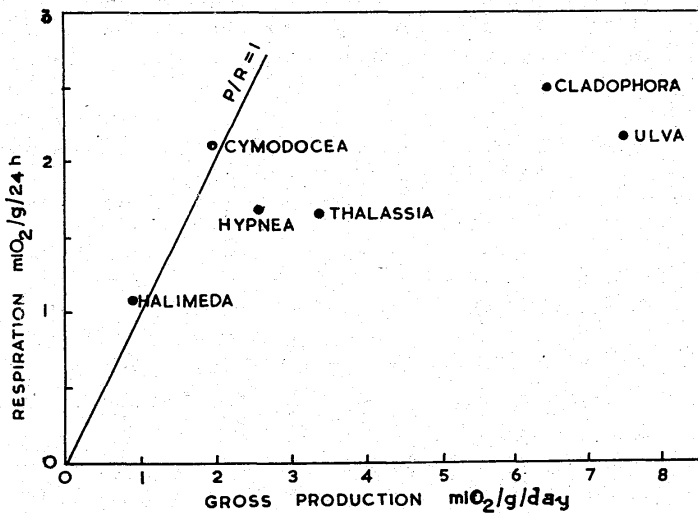


Fig. 3. Relation between production of photosynthetic oxygen for 12 hours and respiration for 24 hours in six species of plants taken from the grass bed on Kavaratti. The straight line demarcates the points where photosynthesis equals respiration. The units are based on wet weight of plants.

Photosynthetic production and respiration for each species were computed from the increase and decrease in the oxygen from the initial concentration respectively.

Figure 3 shows the relation between photosynthesis and respiration in six species of plants. In making these measurements, the main purpose was to determine whether the rates of photosynthesis and respiration of individual species would collectively approach the metabolic rate determined for the community. However, it is realized that the oxygen technique, though widely used for measuring algal metabolism, may not be fully applicable to aquatic angiosperms and thus might only give a crude approximation of the estimates. Also included in the figure is a straight line depicting the ratio of photosynthesis to respiration as unity. It is clear from the figure that, except *Cymodocea* and *Halimeda*, in all other species, the 12-hour photosynthesis exceeded 24-hour respiration. Plants such as *Ulva* and *Cladophora*, which have thin fronds, had a higher rate of photosynthesis than did *Cymodocea* and the calcareous alga, *Halimeda* with thick fronds (ODUM, 1959, KANWISHER, 1966). The numerical values of \bar{P} gross (12h)/ \bar{R} (24h) in different species have been given in Table I, along with the average value for all the six species. The mean value of 1.84 indicates that despite the individual variation in the P/R values, the group as a whole is autotrophic. A higher P/R ratio of 1.94 found for the natural grass bed probably indicates that the community includes more such plants which have thin and narrow fronds and in which the collective photosynthetic production is much greater than their combined respiration.

TABLE I

Ratios of gross photosynthesis for 12 hours to respiration for 24 hours (P/R) in some plants taken from the grass bed on Kavaratti.

Species	P/R
* <i>Thalassia hemprichii</i>	2.02
* <i>Cymodocea isoetifolia</i>	0.93
<i>Ulva lactuca</i>	3.46
<i>Cladophora fascicularis</i>	2.37
<i>Hypnea cervicornis</i>	1.52
<i>Halimeda incrassata</i>	0.77
Average	1.84
Entire seagrass and algal community	1.94

* The values for angiosperm indicate only an approximation.

DISCUSSION

In some isolated seaweeds, KANWISHER (1966) has shown that under optimum conditions of temperature and light, the instantaneous rates of photosynthesis are so high that values had to be disregarded on grounds of quantum efficiency and energetics, as the ideal conditions necessary for the attainment of this potential are never met in nature. However, the average rate of carbon fixation ($20 \text{ gC/m}^2/\text{day}$) found for some seaweeds, appears to be enough to make them double their weight within a few days. Thus, on many sea shores they attain such massive growth that mutual shading sets in, which restricts their photosynthesis and further growth.

In a large naturally growing community, there appears to be a combination of fast growing, slow growing and senile plants (ODUM, 1959), and therefore, the overall primary production of the community will largely depend upon the relative predominance of one type or the other. Table II gives a comparison of known estimates of primary production for such plant communities which are probably similar to that found on Kavaratti Atoll. It is clear from the table that all communities are not self-supporting. The non-autotrophic are those in which respiration for 24 hours exceeds photosynthesis for the daylight.

Seasonal differences in growth and attrition of seaweeds are also well known (KANWISHER, 1966). The estimates of production, therefore, made in different locations (Table II) for brief periods in one season are certainly not approximating an annual average. The high estimates of productivity for the grass bed on Kavaratti made by the present authors and for the turtle grass flat in Florida, given by ODUM (1956), could probably represent a seasonal maximum; and for the non-autotrophic communities indicated in Table II, they might well represent a seasonal minimum. From a more detailed study on the turtle grass communities at Texas, extended over a period of several years, it has been shown that the rate of production differs not only seasonally, but there are marked differences from one year to the other (ODUM, 1963).

The other factor which may control the growth and productivity of the plant communities is the grazing on flora by the herbivores, especially fishes. RANDALL (1961) reported intensive grazing by the surgeonfishes and parrotfishes on the two seagrasses, *Thalassia* and *Cymodocea* (*Syringodium*) from the coral reefs of West Indies. Similarly, STEPHENSEN & SEARLES (1960) by conducting controlled cage experiments at Heron Island, Great Barrier Reef, came to the conclusion that intense browsing of fish controls the rock beach flora. From these observations it could follow that the communities in

TABLE II

Estimates of gross primary production and respiration for some marine plant communities obtained by different authors.

Environment	Gross Production gC/m ² /day*	Respiration gC/m ² /24h*	Authors
Turtle grass flat, Long Key, Florida	10.63	7.50	ODUM (1956)
<i>Thalassia</i> bed, La Gata Reef, Puerto Rico	2.69	3.53	ODUM, BURKHOLDER & RIVERO (1959)
<i>Thalassia</i> bed, Channel north Isla Magueyes, Puerto Rico	3.70	4.11	ODUM, BURKHOLDER & RIVERO (1959)
<i>Thalassia</i> and <i>Cymodocea</i> bed, Kavaratti Atoll, Laccadives	11.97	6.16	Present authors

* PQ = 1.2 was used to convert oxygen values into carbon.

which the respiration of the community has been found to exceed its photosynthetic production may include those in which the plant biomass is always kept at a low level as a result of grazing.

What, then, could the ecological implications of the seagrass bed and its high primary production be? It is of interest to note that *Thalassia* and *Cymodocea* have been reported to grow on sheltered sandy beaches and are abundantly found near the coral reefs (DAWSON, 1966). They bind the loose coral sand with their root system and stabilize the otherwise rapidly shifting substratum. Their luxuriant growth offers shelter and protection to a very large number of animals (MOORE, 1958, STEPHENS, 1968). The association, therefore, between seagrasses and coral reefs does not seem merely an accident. The coral reefs occur in tropical waters of impoverished phytoplankton content (ODUM & ODUM, 1955), and therefore, if such an ecosystem with its diverse fauna, were to flourish in oligotrophic waters, it must have pockets of high productivity, like the seagrass beds, within itself. For this reason alone the varied fauna of the reef - excluding, of course, the corals and other well known carnivores (YONGE, 1963) - must depend on the food produced and made readily available to them within the ecosystem. It may even

be that such a dependence is on particular species of plants, in which case the grass bed with its high primary production would serve a most useful purpose to the reef-dwelling animals. In a recent communication, FENCHEL (1970) has shown that organic detritus derived from the turtle grass serves as food to animal communities.

SUMMARY

Along the intertidal zone of Kavaratti Lagoon, a seagrass bed, consisting largely of *Thalassia* and *Cymodocea*, grows on a substratum of loose coral sand and coral debris. Primary production of this grass bed was estimated from a study of diurnal changes in dissolved oxygen over the bed and experiments were conducted on some isolated plants to determine their rates of oxygen production and consumption. Both these studies showed that photosynthesis of the community during daylight is greater than its respiration during day and night combined.

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