

Primary productivity of marine macrophytes in the coral reef lagoon of the Kadmat Island, Lakshadweep

V. K. Dhargalkar* and Nazima Shaikh

National Institute of Oceanography, Dona Paula, Goa 403 004, India

***In situ* primary productivity measurements were carried out with different macrophyte species (belonging to four groups) dominating the benthic communities in the coral reef lagoon of the Kadmat Island of the Lakshadweep Archipelago. The photosynthetic productivity and respiratory requirements in nine macrophytes were determined by measuring changes in dissolved oxygen concentration in light and dark bottles. The highest net productivity was recorded in *Laurencia papillosa* (Forsk.) Greville while the lowest was in *Dictyota bartayresiana* Lamour. More than 75% of the macrophytes studied had net photosynthetic productivity higher than 15 mg C (g dry wt)⁻¹ d⁻¹ and only one macrophyte, *Boergesenia forbesii* had net production and respiration ratio higher than 10. The results indicated that macrophyte species under investigation are most productive and both macroalgae and sea-grasses contribute equally to the carbon production of the coral reef lagoon of the Kadmat Island.**

ALTHOUGH phytoplankton contributes substantially towards the primary productivity of the coastal area, there are certain areas along the coastal belt where production of benthic macrophytes exceeds that of phytoplankton¹⁻⁵.

The primary productivity estimates of macrophytic population and communities of various marine ecosystems have been investigated⁶⁻¹³. Most of these investigations provided very little information on critical selective processes that determined photosynthetic properties and the relationship of algal morphology in respect of primary production.

Comparatively, very few estimates of macrophyte productivity have been reported from the Indian coast. Qasim and Bhattathiri⁸ estimated primary productivity in intertidal sea-grass beds of the Kavaratti lagoon and concluded that the photosynthesis of the benthic macrophyte communities during daylight was greater than its 24 h respiration.

The production budget of the Goa coast was estimated by using data on macroalgal standing crop biomass and the average net production in fourteen macroalgae from the intertidal areas of the Goa coast¹³. Ten benthic macroalgae from the Minicoy Atoll were studied to identify the productive species of the area. Results indicated that highly branched macroalgae were most productive in the lagoon area¹⁴.

It is known that coral and coral atolls are the most productive ecosystems in the marine environment¹⁵. The major contribution to primary productivity of the coral ecosystem is derived from benthic communities such as sea-grasses and macroalgae rather than phytoplankton². It has been estimated that the average rate of carbon fixation by the macroalgae from these ecosystems appears to be sufficient to double their weight within a few days, resulting into high standing crop⁸.

In the present investigation, net production (NP) and respiration (R) rates of 9 macrophytes (7 macroalgae and 2 sea-grasses), inhabiting coral reef lagoon of the Kadmat Island, Lakshadweep were assessed to identify the more productive macroalgae. The estimated average production in these macrophyte species was used to relate net productivity values to standing crop biomass as a basis for ecological assessment of the productivity of the lagoon.

Kadmat is one of the atoll islands of the Lakshadweep Archipelago (11°13'N and 27°47'E). It is a sausage-shaped island, about 8 km long with a width of 600 m at its broadest point (Figure 1). On the western side of the island there is a coral reef that encloses a lagoon. The area of the lagoon is 12.7 km². The lagoon has an average depth of 2.3 m. During the ebb tide, macrophyte beds towards the beach side get partially exposed. Large quantities of drifted sea-grasses and benthic macroalgae cover most of the sandy beach.

Macrophytes used in these experiments were collected from the intertidal and subtidal regions of the lagoon during low tide and were brought to the ship's laboratory. Seven benthic algae and two sea-grass species were selected on the basis of preliminary survey carried out to study their distribution, abundance, diversity and biomass in the lagoon. The species used were *Chaetomorpha linoides* (Ag.) Kuetz; *Boergesenia forbesii* (Harv.) Feldm. (Chlorophyta - Group I); *Padina boergeseni* Allender et Kraft, *Dictyota bartayresiana* Lamour. (Phaeophyta - Group II); *Gracilaria edulis* (Gmel.) Silva, *Acanthophora spicifera* (Vahl.) Boergs, *Laurencia papillosa* (Forsk.) Greville (Rhodophyta-Group III), *Cymodocea rotundata* Ehrenb. et Hemp. ex Aschers and *Thalassia hemprichii* (Her.) Aschers (Sea-grasses - Group IV). The macrophyte species were identified using the standard procedures.

The epiphytes and adhering sand particles of the macrophytes were washed thoroughly with sea water. They were then acclimatized for 24 h under laboratory conditions (temperature range 28 to 32°C, normal day light).

Although techniques for measurement of primary productivity of phytoplankton have advanced considerably¹⁶⁻¹⁸, these methods were not suitable for benthic macrophytes. In the present investigation, net primary productivity and respiration were measured by the light and dark bottle method¹¹ with slight modification as mentioned here.

*For correspondence. (e-mail: vinodd@csnio.ren.nic.in)

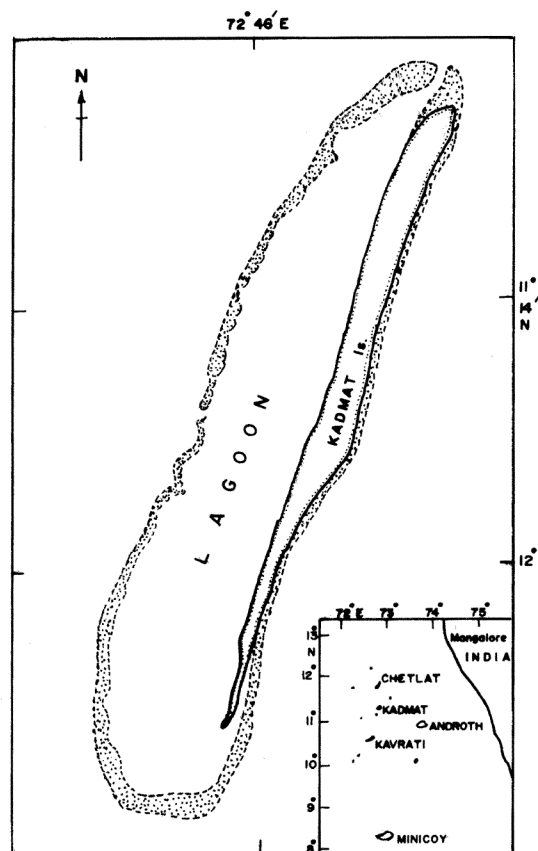


Figure 1. Map of the Kadmat Island enclosing coral reef lagoon. (Inset), Group of Lakshadweep Islands on the west coast of India.

Table 1. Average meteorological data of the study area collected during the experiment between 1000 and 1600 h.

Date	Air temperature (°C)	Water temperature (°C)	Humidity (%)	Solar radiation (mw/cm ²)
27-03-99	29.37	31.00	63.11	50.86
28-03-99	29.3	31.50	60.57	50.71
29-03-99	29.07	30.80	63.29	50.71
30-03-99	29.11	31.00	61.43	50.04
31-03-99	29.78	32.00	57.00	54.7

The size of the bottles, mass of the macrophytes to be used for the experiments and duration of the incubation period were standardized by conducting a series of experiments. It was found that one litre capacity glass bottles (light and dark), with 0.3 to 0.5 g macrophyte material and two hours incubation period were sufficient to obtain reproducible oxygen variation in light and dark bottles. All the experiments were conducted in triplicate.

The initial oxygen content of sea water was measured before and after every set of experimental bottles was filled with sea water. Three sets each of light and dark bottles were used for each macrophyte species, while a set of dark and light bottles incubated without macrophyte served as control. The oxygen values in light and dark bottles used as control remained constant, so blank corrections need not be applied.

Healthy, branched, clean fronds of known weight were selected from each acclimatized macrophyte and carefully transferred into the experimental bottles (light and dark) filled with sea water. To ensure that no light permeated, the dark bottles were wrapped with two layers of aluminium foil and finally covered with a black plastic bag. After transfer of the macrophytes, the bottles were tightly capped under water to avoid air bubbles.

All these bottles were incubated *in situ* for a period of two hours by suspending them from a triangular wooden frame at a depth of 0.5 m (± 0.2 m) from the surface, in such a way that none of the bottles was shaded. All incubations were carried out between 1000 and 1600 h. Solar radiation and relevant meteorological data that were recorded on board the ship *CRV Sagar Paschimi* are given in Table 1.

At the end of the incubation, water from each bottle was carefully siphoned with the help of a tube into two oxygen bottles and the dissolved oxygen concentration was determined by the Wrinkler method¹⁹. The macrophytes from the respective bottles were then removed, blotted dry and placed in labelled polyethylene bags and transported to the laboratory. They were dried at 60°C until constant weight. All oxygen values ($\text{ml l}^{-1} \text{h}^{-1}$) were converted into carbon values ($\text{g C l}^{-1} \text{h}^{-1}$) by using a factor of $0.375/\text{PQ}$ and the PQ value was taken as 1.2 (ref. 20). Further, these values were converted to $\text{mg C g}^{-1} \text{d}^{-1}$ and expressed on a dry weight basis.

The carbon production of the lagoon area was calculated from the average primary production of the macrophytes using macrophyte standing crop biomass of the lagoon area. The daily net productivity rate was estimated by subtracting 24 h of respiration from 12 h of gross production (GP) calculated from hourly rates²⁰. All the data were log transformed ($\log(x + 1)$), since this indicates heterogeneity.

The data were subjected to statistical analysis (one-way analysis of variance) to understand differences between groups/species for various photosynthetic production²¹.

In the naturally growing benthic community, there seems to be a combination of macrophytes, showing different growth rate (fast growing, slow growing and intermediately growing species). Therefore, overall primary productivity of the community will depend upon the relative predominance of one or the other type.

Although there is wide range of morphological variation in macrophytes, factors that regulate morphological plasticity and physiological and biochemical changes associated with different growth forms have not been known in many macrophytes. Littler²² reported that the relationship of macrophyte morphology and productivity under natural conditions has adaptive implication. In the present study, we have selected macrophytes with diverse morphological variations so that the photosynthetic productivity of fleshy and more highly branched,

Table 2. Net production (NP), respiration (R), gross production (GP) in mg C (g dry wt)⁻¹ d⁻¹ and GP/R ratio in different macrophytes from the coral reef lagoon of the Kadmat Island, Lakshadweep

Groups	Species	NP	R	GP	GP/R
Chlorophyta	<i>Chaetomorpha linoides</i>	23.396 ± (3.195)	8.359 ± (0.224)	31.755 ± (3.328)	3.799 ± (0.348)
	<i>Boergesenia forbesii</i>	19.634 ± (3.191)	1.142 ± (0.641)	20.776 ± (3.832)	18.193 ± (6.155)
Phaeophyta	<i>Padina boergesenii</i>	27.18 ± (2.603)	9.692 ± (0.960)	36.872 ± (3.136)	3.804 ± (0.301)
	<i>Dictyota bartayresiana</i>	11.441 ± (1.107)	6.231 ± (1.072)	17.672 ± (2.104)	2.836 ± (0.171)
Rhodophyta	<i>Laurencia papillosa</i>	35.896 ± (0.761)	9.986 ± (0.208)	45.882 ± (0.958)	4.595 ± (0.026)
	<i>Acanthophora spicifera</i>	13.509 ± (0.976)	6.474 ± (0.343)	19.983 ± (1.315)	3.087 ± (0.047)
	<i>Gracilaria edulis</i>	17.924 ± (2.501)	7.09 ± (2.043)	25.014 ± (4.544)	3.528 ± (0.483)
Sea-grass	<i>Cymodacea rotundata</i>	16.18 ± (0.367)	4.713 ± (0.275)	20.893 ± (0.619)	4.483 ± (0.139)
	<i>Thalassia hemprichii</i>	28.076 ± (0.307)	4.849 ± (0.117)	32.925 ± (0.334)	6.790 ± (0.152)

The figures in parentheses signify standard deviation.

less branched and thalloidal macroalgae were accounted for the estimation of overall productivity of the lagoon.

In the coral reef lagoon of the Kadmat Island, *G. edulis*, *A. spicifera*, *L. papillosa*, *C. linoides*, *B. forbesii*, *P. boergesenii*, *D. bartayresiana*, *C. rotundata* and *T. hemprichii* were found to be predominant. The net primary productivity in 9 macrophyte species ranged from 11.44 to 35.89 mg C (g dry wt)⁻¹ d⁻¹ and respiration from 1.14 to 9.981 mg C (g dry wt)⁻¹ d⁻¹ (Table 2). The average rate of carbon fixation in these macrophytes was 21.47 mg C (g dry wt)⁻¹ d⁻¹, which appears to be quite sufficient to double their mass within a few days⁸.

In Chlorophyta, *C. linoides*, a finely branched alga, showed primary production (synonymous with photosynthetic productivity in this investigation) 1.20 times higher than that of the less branched and thick thalloid of *B. forbesii*. Littler²² pointed out that all the biomass in the finely-branched forms is photosynthetic and resulted in a close functional relationship between primary productivity and thallus dry weight. A problem of thallus crowding in the experimental bottles was ruled out by using few thalli.

Similar to our observations, Kaladharan and Kandan¹⁴ reported that more branched macroalgae such as *Enteromorpha compressa* (Linn.) Grev and *Hypnea valentiae* (Turn.) Mont had higher productivity in the lagoons of the Minicoy atoll. Similarly, Paalme²³ recorded very high productivity in branched macroalgae *E. intestinalis* (Linn.) Link, *Cladophora glomerata* (Linn.) Kuetz, and *Ceramium tenericome* from the Gulf of Finland.

In the Chlorophyta, no significant relation was observed in the net production within the species ($f_1, 4 = 2.1; P > 0.05$) in spite of the morphological variation and thallus structure. However, respiration showed significant relationship within the species ($f_1, 4 = 85; P < 0.01$). This could be due to the presence of reproductive cells in the filaments of *C. linoides* resulting in a high respiration rate. The rate of respiration in *C. linoides* was 7-fold higher than the *B. forbesii*²⁴. Despite high respiration rate in *C. linoides*, net production was higher. This indicated that reproductive cells also contribute to photosynthetic production²⁵.

Net production/Respiration (NP/R) ratio in *B. forbesii* was 6.9-fold higher than *C. linoides*, indicating that the former is a subtidal species and prefers low light intensity for photosynthesis. Our experiments were performed at a depth of 0.5 m (± 0.3 m) from the surface of the water where sufficient light was available for photosynthesis. A different condition than that prevailed at subtidal area. In the Kadmat lagoon, the average depth was 2.3 m and due to the clear water sufficient light was available for algal photosynthesis. Perhaps, *B. forbesii* regulates proportionately more non-photosynthetic structural tissue to allow the required light for photosynthetic production. In nature, this alga occupies sheltered habitats such as rock crevices and shaded surfaces of the rocks.

The two phaeophyta members used in this experiment varied in morphological structure. *P. boergesenii* had greater weight per unit area (8.6 mg cm⁻²) compared to *D. bartayresiana* (4.2 mg cm⁻²). The net photosynthesis in *P. boergesenii* was 2.4-fold greater than that of *D. bartayresiana* and net productivity was a highly significant ($f_1, 4 = 115; P < 0.01$). These two species were found to grow mostly in similar habitats (subtidal) and there was no obvious difference in substrata, wave exposure and light regime, except for thallus thickness. However, difference in productivity could be due to the presence of more non-photosynthetic tissue that reduced the weight-based production by thin thallus of *D. bartayresiana*²².

The net productivity in the Rhodophyta varied from 13.5 to 35.89 mg C (g dry wt)⁻¹ d⁻¹ with *L. papillosa* showing the highest production. Respiration in all the three species of Rhodophyta did not exhibit significant variation ($f_2, 6 = 4.9; P > 0.05$). In *L. papillosa*, photosynthetic production was 3.5-fold greater than respiration. The macrophytes growing in similar habitats having fleshy and highly branched thallus have greater photosynthetic productivity than the poorly-branched macrophytes¹¹. Highly branched, flattened and tougher *L. papillosa* showed significantly greater photosynthetic productivity than fleshy and less branched *G. edulis* ($f_2, 6 = 87; P < 0.01$). However, in the present study, de-

spite morphological variations, species belonging to Rhodophyta showed comparatively higher photosynthetic production than the other macrophytes studied.

Sea-grasses have been reported to grow in sheltered sandy beaches and are abundantly found in the coral reefs²⁶. These luxuriantly growing sea-grasses offer shelter and protection to a variety of organisms of the coral ecosystems²⁷. In the coral reef lagoon of the Kadmat Island, sea-grasses occupy comparatively larger area than macroalgae. Extensive sea-grass beds cover intertidal and subtidal areas of the lagoon. The average biomass recorded for the two species of sea-grasses was 0.830 kg m⁻² (wet wt).

The photosynthetic productivity in *C. rotundata* and *T. hemprichii* was estimated to be 16.18 and 28.078 mg C (g dry wt)⁻¹ d⁻¹, respectively. In *T. hemprichii* the production was 5.7-fold higher, whereas in *C. rotundata* it was 3.4-fold higher than respiration. Highly significant relationship between NP, GP and GP/R was observed within the sea-grass species ($f_{1, 4} = 1324$; $f_{1, 4} = 649$; $f_{1, 4} = 385$; $P < 0.01$, respectively). This indicates that these sea-grasses make substantial contribution to the carbon fixation of the lagoon ecosystem.

The average production of all the groups (Groups I to IV) studied was 21.47 mg C (g dry wt)⁻¹ d⁻¹. For all the groups 75% had photosynthetic production higher than 15 mg C (g dry wt)⁻¹ d⁻¹ and only one species showed NP/R ratio greater than 10. Highly significant relationship was noticed between GP, NP and GP/R ratio in the Rhodophyta species. This indicates that specific standing crop biomass is the most important factor for the larger productivity of macrophytes.

The benthic plant communities in which respiration exceeds its photosynthetic production indicated that the biomass of the plant remains always at low level as a result of grazing⁸. In this study we have observed that the average photosynthetic productivity was 4.7-fold higher than the respiration, suggesting that the rate of grazing was comparatively lower than the biomass production of the dominant species in the lagoon area.

It has been known that coralline ecosystem is one of the most productive ecosystems of the world and a major contribution to the productivity is from sea-grasses⁸. Similarly, it has been shown that a single macrophyte plant *T. testerdium* is capable of fixing 11 times more carbon than the phytoplankton and when compared to the coastal area its relative productivity is up to 35 times higher². However, in the present study it was observed that sea-grasses (av. primary productivity 22.12 mg C (g dry wt)⁻¹ d⁻¹ and macroalgae (av. primary productivity 21.25 mg C (g dry wt)⁻¹ d⁻¹) contribute equally to the productivity of the lagoon ecosystem.

The carbon production of the lagoon area was calculated assuming that 56% of the area was occupied by

sea-grasses and macroalgae, and the average primary production for sea-grasses and macroalgae was 21.47 mg C (g dry wt)⁻¹ d⁻¹ during the post-monsoon month of March 1999. In terms of biomass, it works out to a reasonable 56.3 kg C d⁻¹ for the 12.7 km² coral reef lagoon of the Kadmat Island. This high production rate by the macrophytes might be a representative figure.

1. Westlake, D. F., *Biol. Rev.*, 1963, **38**, 385–425.
2. Buesa, R. J., *Cent. Invest. Pesqueras, Reun. Bal. Trab. CIP*, 1972, **3**, 101–143.
3. Littler, M. M., *J. Exp. Mar. Biol. Ecol.*, 1973, **11**, 103–120.
4. Mann, K. H., *Science*, 1973, **182**, 975–981.
5. McRoy, C. P. and McMillan, C., *A Scientific Perspective* (eds McRoy, C. P. and Helfferich, C.), Marcel Dekker, New York, 1977, pp. 53–87.
6. Odum, E. P., *Fundamentals of Ecology* (eds Phillips, R. C. and McRoy, P. C.), Saunders Co., Philadelphia, 1953, pp. 1–384.
7. Johnston, C. S., *Int. Rev. Gesamten Hydrobiol.*, 1969, **54**, 473–490.
8. Qasim, S. Z. and Bhattathiri P. M. A., *Hydrobiologia.*, 1971, **38**, 29–38.
9. Littler, M. M. and Murray, S. N., *Mar. Biol.*, 1974, **27**, 131–135.
10. Burries, J. E., Holm-Hansen, D. and Black, C. C., *Aus. J. Plant Physiol.*, 1976, **3**, 87–92.
11. Littler, M. M. and Arnold, K. E., *Aquat. Bot.*, 1980, **8**, 141–156.
12. Ogden, J.C., *Handbook of Sea-grass Biology*, Garland STPM Press, New York, 1980, pp. 177–198.
13. Dhargalkar, V. K., *Marine Plants, their Biology, Chemistry and Utilization* (eds Krishnamurthy, V. and Untawale, A. G.), Seaweed Research and Util. Association of India, 1985, pp. 79–88.
14. Kaladharan, P. and Kandan, S., *Seaweed Res. Util.*, 1997, **19**, 25–28.
15. Wells, S. M., *Coral Reefs of the World Indian Ocean, Red Sea and Gulf*, IUCN, 1988, vol. 2, pp. 1–77.
16. Strickland, J. D. H., in *Chemical Oceanography* (eds Riley, J. P. and Skirrow, G.), Academic Press, London, 1965, pp. 477–610.
17. Qasim, S. Z., *Indian J. Mar. Sci.*, 1977, **6**, 122–137.
18. Pant, A., Dhargalkar, V. K., Bhosale, N. B. and Untawale, A. G., *Mahasagar Bull. Natl. Inst. Oceanogr.*, 1980, **13**, 225–234.
19. Strickland, J. D. H. and Parsons, T. R., in *Practical Handbook of Seawater Analysis*, Bull. Fish. Res. Board, Canada, 1968, p. 167.
20. Strickland, J. D. H., *Bull. Fish. Res. Board, Canada*, 1960, 122.
21. Sokel, R. R. and Rohlf, F. J., *Biometry*, Freeman, New York, 1995, p. 887.
22. Littler, M. M., *Bot. Mar.*, 1980, **22**, 161–165.
23. Paalme, T., in *Marine Biologists Symposium*, 5–8 August, Paernu, Estonia 1997, pp. 184–194.
24. Haxo, F. T. and Clendenning, K. A., *Biol. Bull. Mar. Biol. Lab.*, 1953, **105**, 103–114.
25. Kremer, B. P., *Helgol. Wiss. Meeresunters.*, 1975, **27**, 115–127.
26. Dawson, E. Y., *Marine Botany*, Holt, Rinehart and Winston, Inc, New York, 1966, p. 371.
27. Stephens, W. M., *Nat. Hist. J. Am. Mus. Nat. Hist.*, 1968, **77**, 51–57.

ACKNOWLEDGEMENTS. We thank the Director, NIO for his encouragement and interest in this work. We also thank Ms Deepali Komarpant for her assistance in the field, Shri R. A. Sreepada for statistical analysis, and Dr P. M. A. Bhattathiri for his valuable comments on the manuscript (NIO contribution no. 3579).

Received 29 April 2000; revised accepted 11 August 2000