

Production of Some Benthic Communities at Carrie Bow Cay, Belize

Paul E. Hargraves

ABSTRACT

The primary production of *Thalassia testudinum*, mixed algae on coral rubble, and coral sand in the vicinity of Carrie Bow Cay, Belize, was estimated from in situ oxygen flux (by titrimetry) in enclosed chambers. *Thalassia* beds were autotrophic, yielding a daily net production in the range of 2.22–42.3 mg O₂ per square meter (approximately equivalent to 0.67–12.7 g C per square meter). The other habitats were heterotrophic despite considerable microalgal development, with a production/respiration ratio (P/R) less than unity. Contribution by the phytoplankton was negligible. Diurnal oxygen flux in open waters over *Thalassia* beds was typical for similar tropical areas.

Introduction

In tropical coastal waters, coral reef ecosystems are generally considered to be highly productive in contrast to plankton communities, whose primary production is quite low or even negligible (Lewis, 1977; Milliman and Mahnken, 1969; Sournia, 1969). The metabolism of coral reefs as a unit has been the subject of numerous studies beginning with Sargent and Austin (1949) and Odum and Odum (1955). The remarkable fertility of reefs, their dynamic balance, and susceptibility to environmental perturbation have often been noted (see reviews by Lewis, 1977, and Johannes in Wood and Johannes, 1975).

The plants responsible for primary production in tropical coastal waters include mangroves, sea

grasses, macroscopic algae, boring and epipelagic algae, zooxanthellae, and phytoplankton. The relative importance of each group varies from area to area, but except for special environments such as enriched lagoons and upwelling areas (Sournia, 1969; Steeman-Nielsen, 1975), the contribution of phytoplankton is low. The techniques of investigating primary productivity have varied among investigators according to whether information is required on the productivity of the total community or its components, and according to the facilities and methods available. In general, chemical or polarographic measurements of oxygen flux are sufficiently precise for nonplanktonic biotopes, and these techniques have provided considerable information on the metabolism of tropical benthic communities (for instance, Lewis, 1977; McRoy and McMillan, 1977).

Reported here are results of production measurements in several habitats at and near Carrie Bow Cay, Belize. Topographic, oceanographic, and ecological characteristics of the area are presented elsewhere in this volume.

ACKNOWLEDGMENTS.—The technical assistance of D. Hargraves and K. Zimmerly is gratefully acknowledged. Partial support was provided by National Science Foundation Grant OCE-76-82280. N. Marshall reviewed an early draft of the manuscript.

Methods

Oxygen flux was measured in three habitats: seagrass beds (*Thalassia testudinum* Banks ex König with small amounts of *Syringodium filiforme* Kützling) at depths of 1 to 3 m on the lagoon side of

Paul E. Hargraves, Graduate School of Oceanography, University of Rhode Island, Kingston, R. I. 02881.

Carrie Bow Cay; mixed algal communities on coral rubble at depths of 0.5 to 1.0 m in the rubble and pavement zone behind the reef crest; and coral sand at a depth of 1 m in the back-reef zone. The coral rubble was composed of cobble-sized pieces of coral mixed with sand and with small (unidentified) filamentous, crustose, and thallose seaweeds. The coral sand first seemed devoid of organisms, but microscope examination revealed considerable numbers of blue-green algae, diatoms, Foraminifera with symbiotic algae, filamentous algae, and a multitude of other representatives of the micro- and meiobenthos.

Experiments were conducted over periods of dawn/noon, noon/sunset, and 24 h cycles with determinations at 1 or 2 h intervals, all during April/May 1977 and January 1978. For comparative purposes, the production of phytoplankton was also assessed.

For each experiment three transparent and two opaque polystyrene boxes of 500 cm² area were inverted over the substrate. The edges were pushed into the sediment to prevent leakage around the margin of the container. Water was withdrawn through sampling ports with a 50 ml capacity syringe. The total volume of enclosed water was 4.2 liters. For diurnal fluctuations in oxygen and phytoplankton production measurements, 300 ml biological oxygen demand (BOD) bottles were used.

Dissolved oxygen was measured titrimetrically by the Winkler method, using phenylarsine oxide (PAO) as titrant. PAO is superior to thiosulfate in its longer shelf life and resistance to bacterial decomposition, and produces results with comparable precision.

During the experiments water temperature varied from 26° to 29°C (by mercury immersion thermometer) and salinity varied from 34.4 to 35.2 ‰ (by Endeco refractometer type 102). As much as possible, all experiments were conducted on days that were cloud free, or nearly so.

Results and Discussion

Results of a preliminary experiment to determine the diurnal variation in dissolved oxygen in

the open water over a *Thalassia* bed are shown in Figure 71. During predawn hours, characteristically, minimum oxygen concentrations are exhibited. The subsequent rapid increase of dissolved oxygen reflects photosynthetic activity (as light intensity increases). The daily oxygen maximum occurs at or somewhat after noon, at which time minute streams of oxygen bubbles frequently issue from some *Thalassia* blades. A gradual decline in oxygen concentration occurs during the rest of the day, becoming more pronounced in the late afternoon. Minimum concentration is again reached in the predawn hours. This pattern is typical and well documented, not only for tropical seagrass communities (for instance, Odum et al., 1959; Qasim and Bhattathiri, 1971) but for coral reefs as well (for instance, Sournia, 1976a). For part of the day, the water is supersaturated, often in excess of 150%, with respect to oxygen. Some consequences of these conditions are discussed below.

Table 9 summarizes the production of the different communities. Oxygen data were converted to carbon assuming a photosynthetic quotient (PQ) of 1.25 (McRoy and McMillan, 1977; Westlake, 1963). The standing stock of *Thalassia* blades varied from about 34 to 126 g/m² dry weight, with a mean of about 47 g. Other organisms were not analyzed quantitatively.

Compared to published data for seagrass beds, summarized in Lewis (1977) and McRoy and

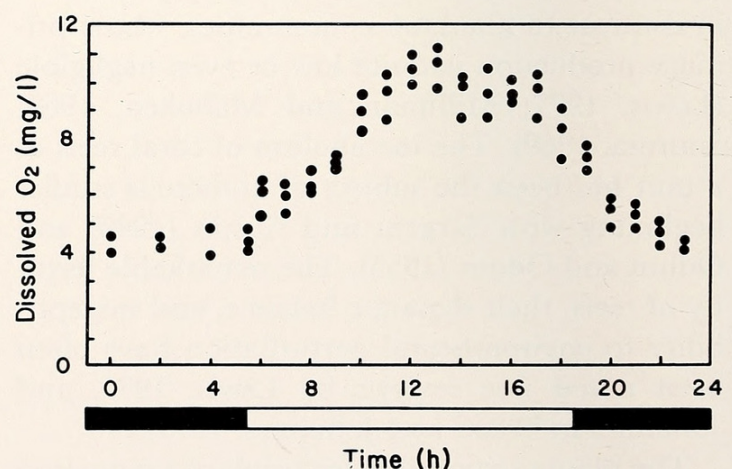


FIGURE 71.—Changes over a 24-hour period in dissolved oxygen over a *Thalassia* bed near Carrie Bow Cay, 28–29 April 1977.

TABLE 9.—Oxygen production of communities at Carrie Bow Cay, 26 April–5 May 1977, unless otherwise indicated (gross and net carbon production assumes $PQ = 1.25$ (Westlake, 1963); phytoplankton assumes 1 m water depth)

Community	Trials (n)	Production (mg O ₂ /m ² /d)		Respiration (mg O ₂ /m ² /d)	P/R	Production (g C/m ² /d)	
		Gross	Net			Gross	Net
<i>Thalassia</i> beds	5	19.3–118.1	6.03–42.30	13.27–75.80	1.45–1.56	5.79–35.43	1.81–12.69
<i>Thalassia</i> beds (Jan 1978)	3	14.9–33.2	2.22–14.50	12.68–18.70	1.18–1.78	4.47–9.96	0.67–4.35
Mixed algae/ coral rubble	3	60.0–94.3	-163.0–-31.6	223.0–125.9	0.27–0.75	18.00–28.29	-48.90–-9.48
Coral sand	2	75.5, 107.9	-11.3, -32.1	86.8, 140.0	0.87, 0.77	22.65, 32.37	-3.39, -9.63
Phytoplankton	2	0.48, 1.00	0.14, -0.07	0.34, 1.07	1.41, 0.93	0.14, 0.30	0.04, -0.02

McMillan (1977), the data for *Thalassia* at Carrie Bow Cay fall within previously noted ranges for gross and net production. The standing stock is rather low compared to several other localities in the Caribbean and Gulf of Mexico (refer to table 1 in McRoy and McMillan, 1977). In contrast to some *Thalassia* habitats in Puerto Rico (Odum et al., 1959), in the present case all measurements indicate a consistently autotrophic community, that is, ratio of production to respiration (P/R) in excess of 1. The wide range in measurements, in part attributable to density variations in *Thalassia* and seasonal differences, make extrapolations to an annual production uncertain. For comparative purposes the mean production for all *Thalassia* measurements may be estimated at 1800 g C/m²/y net production. This amount is higher than those reported from seagrass beds in Puerto Rico (Odum et al., 1959), but considerably less than those reported from Cuba and Florida (Buesa, 1972; Odum, 1957, 1963).

Differences in production were noted between late spring and winter. The extent to which these differences are significant is unknown because of the small number of replicates analyzed. Such variables as photoperiod (Marmelstein et al., 1968) and water temperature (citations in McRoy and McMillan, 1977) affect *Thalassia* production and add to the uncertainty of annual rate comparisons based on extrapolation.

A considerable area of the back-reef zone at Carrie Bow Cay consists of coral rubble and

pavement rock overgrown with a variety of small but conspicuous filamentous and thallose algae. Despite a gross production generally exceeding that of the *Thalassia* beds (Table 9), the community as a whole is heterotrophic, having a P/R less than 1. This habitat harbors a diverse and abundant fauna of burrowing invertebrates that contribute to the high community respiration. Grazing effects of fishes and large invertebrates, not considered here, are probably also significant in the consumption of primary producers (Marsh, 1976). The relative contribution of microalgal species in this habitat has generally been neglected, although Qasim et al. (1972) reported net production rates of 365–800 g C/m²/y for similar types of algae from the Laccadive Archipelago. Overall, the algal oxygen production in this habitat is less than oxygen consumption by herbivores and other animals.

Although the extensive coral sand areas north and northwest of Carrie Bow Cay appear to have few plant producers, microscopic examination revealed large numbers of benthic pennate diatoms and filamentous blue-green algae (or cyanobacteria), smaller numbers of Foraminifera with apparent endosymbiotic algae, and large numbers of micro- and meiobenthos metazoans. Community respiration slightly exceeded gross production, with P/R less than 1 (Table 9), although this habitat was closer to an autotrophic condition than the rubble-pavement habitat. The contribution of bacteria to community respiration

was not evaluated but it may be significant (see for instance, Edwards, 1978). The gross production approached that of the *Thalassia* beds, and therefore indicated the high photosynthetic activity here.

That such sand areas are not necessarily heterotrophic has been convincingly demonstrated by Sournia (1976b). Extensive development of the blue-green alga *Oscillatoria limosa* in sand at Moorea Island lagoon was responsible for an average gross production equivalent of over 6000 mg O₂/m²/d with P/R = 1.5–3.0, a highly autotrophic habitat. Although blue-green algae are not abundant at Carrie Bow Cay, the potential contribution of coral sand areas should not be ignored in calculations of production in reef areas. Under some circumstances Foraminifera with endosymbiotic algae may dominate coral sands. Sournia (1976a) described sands from Takapota Atoll with a net production of 115–354 mg O₂/m²/h (= 43–133 mg C/m²/h) and with populations consisting primarily of Foraminifera with endosymbionts. Small numbers of these protozoa were also present in sands at Carrie Bow Cay, but pennate diatoms dominated as primary producers.

These sands could potentially assume the autotrophic role that Sournia (1976a) described. A minor perturbation in the environment of organisms already under natural stress (by light and temperature thermal, among others) may shift community composition to one of low density consisting of eurytolerant species (Wood and Johannes, 1975). Several different species of blue-green algae, which certainly qualify as eurytolerant, can be observed in the sands of Carrie Bow Cay. Coral sand habitats have been largely neglected by ecologists, so that it would be useful to stress them experimentally in various ways in order to determine whether and how their trophic status is modified. Perturbation in the form of nutrient enrichment was attempted in one micro-atoll, resulting in significantly increased production (Kinsey and Domm, 1974).

As expected, the production of the phytoplankton was very low, and near the limits for accuracy

of the technique used (Table 9), supporting the conclusion that phytoplankton in the vicinity of coral reefs contribute a negligible amount to net production (Milliman and Mahnken, 1969; Sournia and Ricard, 1976). Although such shallow areas generally have, in addition to the normal complement of typically planktonic forms, a higher number of benthic diatoms swept into the water column by turbulence, net production remains negligible. For offshore Caribbean waters net production can be higher or lower than in reef areas, depending on locale. Beers et al. (1968) found 0.03–0.28 g C/m²/d offshore from Jamaica; Steeman-Nielsen and Jensen (1957) found 0.14 and 0.19 g C/m²/d in the south-central Caribbean Sea. In contrast, Ricard (1977) found higher production in the lagoon than in the open ocean at Tahiti, but the converse was true at Lakeba lagoon. Higher productivity is unquestionably possible under localized enriched conditions (Gordon et al., 1971; Margalef, 1975).

The limitations of technique and procedures used in this work deserve brief mention. Production in tropical benthic communities has been studied in several ways: by flow respirometry, which measures changes in the flux of carbon dioxide or oxygen (upstream-downstream); by in situ light/dark bottle methods using oxygen flux (titrimetric and polarographic) and various radioactive tracers; and by direct measurement of changes in standing stocks. All these methods are subject to errors and various assumptions (for discussion, see Lewis, 1977; Sournia, 1976c; Vollenweider, 1974) that will not be examined here, except to note that the technique used here appears to be satisfactory for benthic habitats. Unquestionably, accuracy decreases in the case of water supersaturated with oxygen; similarly, respiration of animals is affected by reduced oxygen levels. Recycling of oxygen in lacunae of *Thalassia* blades is another potential source of error (Hartmann and Brown, 1967).

The accuracy of conversion of oxygen flux to its equivalent carbon varies widely depending on the photosynthetic quotient assumed. This creates a problem in comparing the production rates

calculated by different authors. Photosynthetic quotients ranging from 0.86 to 3.00 are possible. This work follows Westlake (1963) in the assumption that $PQ = 1.25$ is valid for natural tropical communities in favorable conditions.

Two important sources of tropical primary production have not been considered here, namely the coral zooxanthellae and the larger seaweeds. The complex role of the former in reef trophic structure has been discussed by Lewis (1977) and Marsh (1976) among others, and the contribution of zooxanthellae at Carrie Bow Cay is certainly worthy of investigation. Under some conditions the larger seaweeds contribute significantly to primary production, even more so than *Thalassia* beds (Doty, 1971; Wanders, 1976), but their development around Carrie Bow Cay is not extensive.

Conclusions

Of the benthic habitats investigated at Carrie Bow Cay, *Thalassia* beds were most productive, yielding a maximum gross production of 35.4 g C/m²/d and a maximum net production of 12.7

g C/m²/d. Coral sand habitats and mixed algae with coral rubble habitats were heterotrophic in nature, despite considerable algal development. Net production by phytoplankton was negligible. The diurnal oxygen content of water flowing over *Thalassia* beds fluctuates in a manner typical of similar habitats previously described.

Given the problems inherent in comparing a wide variety of techniques and procedures, the pattern of primary production at Carrie Bow Cay is typical of similar tropical areas.

Addendum

Since the writing of this contribution three pertinent papers have appeared. Two center on reef community metabolism elsewhere in the Caribbean (Puerto Rico, U.S. Virgin Islands) and also employ the Winkler method for oxygen determinations (Rogers, 1979; Rogers and Salesky, 1981). The third deals with primary production by microalgae in North Sea sediments comparing various techniques, including platinum electrode measurements that allow recording of dissolved oxygen microprofiles (Revsbech et al., 1981).

Literature Cited

- Beers, J. R., D. M. Steven, and J. B. Lewis
1968. Primary Productivity in the Caribbean Sea off Jamaica and the Tropical North Atlantic off Barbados. *Bulletin of Marine Science*, 18:87-104.
- Buesa, R. J.
1972. Producción primaria de las praderas de *Thalassia testudinum* de la plataforma noroccidental de Cuba. *Cuba Centro de Investigaciones Pesquera, Revista Trabajos*, 3:101-143.
- Doty, M. S.
1971. The Productivity of Benthic Frondose Algae at Waikiki Beach, 1967-1968. *University of Hawaii, Botanical Science Paper*, 22: 119 pp.
- Edwards, R.R.C.
1978. Ecology of a Coastal Lagoon Complex in Mexico. *Estuarine and Coastal Marine Science*, 6:75-92.
- Gordon, D. C., R. O. Fournier, and G. J. Krasnic
1971. Note on the Planktonic Primary Production in Fanning Island Lagoon. *Pacific Science*, 25:228-233.
- Hartman, R. T., and D. L. Brown
1967. Changes in Composition of the Internal Atmosphere of Submerged Vascular Hydrophytes in Relation to Photosynthesis. *Ecology*, 48:252-258.
- Kinsey, D. W., and A. Domm
1974. Effects of Fertilization on a Coral Reef Environment—Primary Production Studies. In A. M. Cameron, B. M. Campbell, A. B. Cribb, R. Eudean, J. S. Jell, O. A. Jones, P. Mather and F. H. Talbot, editors, *Proceedings of the Second International Coral Reef Symposium*, 1:49-66. Brisbane, Australia: The Great Barrier Reef Committee.

- Lewis, J. B.
1977. Processes of Organic Production on Coral Reefs. *Biological Review*, 52:305-347.
- Margalef, R.
1975. Fitoplancton invernol de la laguna costera de Alvarado (Mexico). *Anales del Instituto Botanico Antonio Jose Cavanilles*, 32:381-387.
- Marmelstein, A. D., P. W. Morgan, and W. E. Pequegnat.
1968. Photoperiodism and Related Ecology in *Thalassia testudinum*. *Botanical Gazette*, 129:63-67.
- Marsh, J. A.
1976. Energetic Role of Algae in Reef Ecosystem. *Micronesica*, 12:13-22.
- McRoy, C. P., and C. McMillan
1977. Production Ecology and Physiology of Seagrasses. In C. P. McRoy and C. Helfferich, editors, *Seagrass Ecosystem, Scientific Perspective*, pages 53-87. New York: Marcel Dekker, Inc.
- Milliman, J. D., and C. V. Mahnken
1969. Appendix: Reef Productivity Measurements. *Atoll Research Bulletin*, 129:23-26.
- Odum, H. T.
1957. Primary Production of Eleven Florida Springs and a Marine Turtle Grass Community. *Limnology and Oceanography*, 2:85-97.
1963. Productivity Measurements in Texas Turtle Grass and the Effects of Dredging an Intracoastal Channel. *Publications of the Institute of Marine Science, University of Texas*, 9:45-58.
- Odum, H. T., P. R. Burkholder, and J. Rivero
1959. Measurements of Productivity of Turtle Grass Flats, Reefs, and the Bahia Fosforescenti of Southern Puerto Rico. *Publications of the Institute of Marine Science, University of Texas*, 6:159-170.
- Odum, H. T. and E. P. Odum
1955. Trophic Structure and Productivity of a Windward Coral Reef on Eniwetok Atoll. *Ecological Monographs*, 25:291-300.
- Qasim S. Z., and P.M.A. Bhattathiri
1971. Primary Production of a Seagrass Bed on Kavartti Atoll (Laccadives). *Hydrobiologia*, 38:29-38.
- Qasim, S. Z., P.M.A. Bhattathiri, and C.V.G. Reddy
1972. Primary Production of an Atoll in the Laccadives. *Internationale Revue des gesamten Hydrobiologie*, 57: 207-225.
- Revsbech, N. P., B. B. Jørgensen, and O. Brix
1981. Primary Production of Microalgae in Sediments Measured by Oxygen Microprofile, $H^{14}CO_3$ -Fixation, and Oxygen Exchange Methods. *Limnology and Oceanography*, 26:717-730.
- Ricard, M.
1977. Phytoplankton Contribution of Primary Productivity in Two Coral Reef Areas of Fiji Islands and French Polynesia. In D. L. Taylor, editor, *Proceedings of the Third International Symposium on Coral Reefs*, 1:343-348. Miami, Florida; Rosenstiel School of Marine and Atmospheric Science.
- Rogers, C. S.
1979. The Productivity of San Cristobal Reef, Puerto Rico. *Limnology and Oceanography*, 24:342-349.
- Rogers, C. S., and N. H. Salesky
1981. Productivity of *Acropora palmata* (Lamarck), Macroscopic Algae, and Algal Turf from Tague Bay Reef, St. Croix, U.S. Virgin Islands. *Journal of Experimental Marine Biology and Ecology*, 49:179-187.
- Sargent, M. C., and T. S. Austin
1949. Organic Productivity of an Atoll. *Transactions of the American Geophysical Union*, 30:245-249.
- Sournia, A.
1969. Cycle annuel du phytoplancton et de la production primaire dans les mers tropicales. *Marine Biology*, 3:387-303.
1976a. Primary Production of Sands in the Lagoon of an Atoll and the Role of Foraminiferan Symbionts. *Marine Biology*, 37:29-32.
1976b. Ecologie et productivité d'une Cyanophycée en milieu corallien: *Oscillatoria limosa* Agardh. *Phycologia*, 15:363-366.
1976c. Oxygen Metabolism of a Fringing Reef in French Polynesia. *Helgoländer Wissenschaftliche Meeresuntersuchungen*, 28:401-410.
- Sournia, A., and M. Ricard
1976. Phytoplankton and its Contribution to Primary Productivity in Two Coral Reef Areas of French Polynesia. *Journal of Experimental Marine Biology and Ecology*, 21:129-140.
- Steeman-Nielsen, E.
1975. *Marine Photosynthesis*. 141 pages. New York: Elsevier Scientific Publishing Company.
- Steeman-Nielsen, E., and A. Jensen
1957. Primary Oceanic Production: The Autotrophic Production of Organic Matter Production in the Ocean. *Galathea Report*, 1:49-136.
- Vollenweider, R. A., editor
1974. *A Manual for Measuring Primary Production in Aquatic Environments*. 213 pages. Oxford and Edinburgh: Blackwell Scientific Publications.
- Wanders, J.B.W.
1976. The Role of Benthic Algae in the Shallow Reef of Curaçao (Netherlands Antilles), II: Primary Productivity of the Sargassum Beds on the Northeast Coast Submarine Plateau. *Aquatic Botany*, 2:327-335.
- Westlake, D. F.
1963. Comparisons of Plant productivity. *Biological Reviews*, 38:385-425.
- Wood, E.J.F., and R. E. Johannes, editors
1975. *Tropical Marine Pollution*. 192 pages. Amsterdam, Oxford, New York: Elsevier Scientific Publishing Company. [Elsevier Oceanography Series, 12.]



Hargraves, Paul E. 1982. "Production of Some Benthic Communities at Carrie Bow Cay, Belize." *The Atlantic Barrier Reef Ecosystem at Carrie Bow Cay, Belize. I, Structure and Communities* 12, 109–114.

View This Item Online: <https://www.biodiversitylibrary.org/item/131277>

Permalink: <https://www.biodiversitylibrary.org/partpdf/387314>

Holding Institution

Smithsonian Libraries and Archives

Sponsored by

Biodiversity Heritage Library

Copyright & Reuse

Copyright Status: In Copyright. Digitized with the permission of the rights holder

Rights Holder: Smithsonian Institution

License: <http://creativecommons.org/licenses/by-nc-sa/3.0/>

Rights: <https://www.biodiversitylibrary.org/permissions/>

This document was created from content at the **Biodiversity Heritage Library**, the world's largest open access digital library for biodiversity literature and archives. Visit BHL at <https://www.biodiversitylibrary.org>.