APPENDIX: REEF PRODUCTIVITY MEASUREMENTS

by John D. Milliman and Conrad V. W. Mahnken

Oxygen Uptake on Reef Flats

Hydrographic observations were taken on transects across the reef flats of Courtown and Albuquerque cays. Three stations comprised the transect at Courtown (between East and Sand cays); four stations comprised the Albuquerque transect (south of South Cay). Each station was marked by two anchored buoys, placed at approximately equally spaced intervals across the reef flat. The outermost station (referred to as Station 1) of both transects was about 75 m leeward of the outer reef margin; the innermost (Station 3 at Courtown, 4 at Albuquerque) was on the leeward margin of the inner reef (Figure A-1). Observations were taken at approximately three-hour intervals for 25 hours at Courtown Cays (23-24 May). The outer reef stations were not sampled at night due to hazardous navigation; values, however, could be inferred from sunset and pre-dawn values.

Water and air temperatures were measured with a "bucket" thermometer, the accuracy being about ± 0.5°C. Current direction and velocity were estimated by measuring the direction and time for a partially submerged small float to traverse a distance of 10 m. Salinity and oxygen samples were taken; the oxygen samples were then "pickled," using the standard Winkler technique, and stored in a dark, cool place until return to the laboratory.

Temperature, salinity and oxygen variations over the outer and inner reef flats of Courtown and Albuquerque cays are shown in Figures A-2 and A-3. The ranges of oxygen and temperature values generally were greater at the inner stations (higher values in daytime, lower at night). Salinity remained more or less constant, indicating the relatively rapid passage of water over the reef flat. Currents on the reef flat stations at Courtown Cays ranged from 26 to 36 cm/sec and at Albuquerque Cays, from 13 to 15 cm/sec.

Oxygen change in flowing waters is expressed as the product of mean current velocity, mean water depth, and the difference in oxygen concentrations between the up- and down-stream stations (Sargant and Austin, 1954). In calculating the oxygen uptake on the outer reef

1/ Bureau of Commercial Fisheries, Biological Laboratory, 2725 Montlake Blvd. East, Seattle, Washington 98102.
<table>
<thead>
<tr>
<th></th>
<th>NET OXYGEN GAINED (ml/cm/day)</th>
<th>NET OXYGEN LOST (ml/cm/day)</th>
<th>NET OXYGEN GAIN (ml/cm/day)</th>
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<tr>
<td><strong>Total reef flat</strong></td>
<td></td>
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<tr>
<td>(sta. 4 - ocean sta.)</td>
<td>69,000</td>
<td>8,200</td>
<td>60,900</td>
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<td>(sta. 1 - ocean sta.)</td>
<td>83,000</td>
<td>0</td>
<td>83,000</td>
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<tr>
<td><strong>Inner reef flat</strong></td>
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<td></td>
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<tr>
<td>(sta. 4 - sta. 1)</td>
<td>9,800</td>
<td>30,600</td>
<td>-20,800</td>
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<td><strong>ALBUQUERQUE CAYS</strong></td>
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<td><strong>Total reef flat</strong></td>
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<td>7,300</td>
<td>67,700</td>
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<td>(sta. 1 - ocean sta.)</td>
<td>67,300</td>
<td>0</td>
<td>67,300</td>
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<td><strong>Inner reef flat</strong></td>
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<tr>
<td>(sta. 3 - sta. 1)</td>
<td>37,200</td>
<td>36,400</td>
<td>-800</td>
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Table A-1. Computation of oxygen gain and loss on the reef flats of Albuquerque and Courtown Cays.

<table>
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<tr>
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<th>REEF STATIONS</th>
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<tr>
<td></td>
<td>OCEAN 1 2 3 4</td>
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<tr>
<td>Courtown</td>
<td>---- 2.87 3.15 3.18 ----</td>
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<tr>
<td>Albuquerque</td>
<td>---- 2.37 2.23 4.47 5.38</td>
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<td>Western Caribbean</td>
<td>2.21</td>
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Table A-2. Twenty-four hour mean surface carbon fixation (g/Carbon/m³/day) at stations across the windward reef of Courtown and Albuquerque Cays and oceanic waters of the western Caribbean.
flat, open-ocean and outer reef flat values represent up- and down-stream values, respectively \( \frac{1}{1} \); for the inner reef, outer reef and inner reef values represent up- and down-stream values. Oxygen uptake across the entire reef flat is reflected by the difference in open ocean (up stream) and inner reef (down stream) oxygen values. The calculated oxygen changes in the reef waters at Courtown and Albuquerque Cays are shown in Figures A-4 and A-5. Integration of the area above the zero lines quantifies the net gain in oxygen; similarly, the area below the line represents the net loss. These values (for 24 hours) are given in Table A-1.

At Courtown Cays most of the oxygen uptake occurred on the outer reef; the net oxygen gain on the inner reef flat was negligible. At Albuquerque Cays, waters flowing across the inner reef flat actually lost oxygen; the entire oxygen uptake occurred on the outer reef.

If the oxygen influx had been strictly due to biologic activity, a net loss of oxygen would have been expected at night. The fact that incoming ocean waters continually gained oxygen on the outer reef suggests that oxygen is entering from a non-biologic source. Blanchard and Woodcock (1957; cf. Gordon and Kelly, 1962) showed that the trapping of air bubbles by breaking waves can cause oxygen saturations up to 115 percent. With surf almost constantly crashing on the outer reefs of both atolls, oxygen can be continuously forced into the incoming waters.

Without a proper measure of the amount of oxygen physically put into the outer reef waters, no measure of reef productivity can be made. However, these observations lend support to the opinion that most oxygen uptake takes place on the outer edge of the reef (Gordon and Kelly, 1962).

**Plankton Productivity**

At each station the plankton productivity of the ambient reef waters was determined by measuring the C-14 uptake (Steeman-Nielsen, 1952). Dark and light bottles were inoculated with C-14 and incubated in situ in a series of short-term experiments corresponding in time to the periods between oxygen sampling. The bottles at each station were hung from lines attached between two buoys. Upon retrieval, the water in each bottle was filtered through an HA Millipore filter (0.45 μm pore opening). The individual filters were stored and later counted at

\(^{1/}\) In these calculations it is assumed that open ocean water approaching the atoll is in equilibrium with the atmosphere (that is saturated with oxygen). Indeed, oxygen values in the upper 20 m of nine oceanographic stations occupied by the U.S. Fish and Wildlife service GERONIMO during October 1965, in the vicinity of Courtown Cays, are essentially at saturation levels (101 - 1 percent; 4.45 ± 0.01 ml/l), with a diurnal range of hundredths of a ml/l (unpublished data).
the U.S. Bureau of Commercial Fisheries Radiobiological Laboratory, Beaufort, N.C.

Two trends of plankton productivity are apparent at both atolls: there is a marked diurnal variation in carbon fixation, and there is a net increase in carbon fixation from the windward to leeward stations across the reefs (Figures A-6, A-7; Table A-2). Because no synoptic oceanic measurements were taken for comparison, we have used a mean production estimate of five ocean stations occupied in October 1965, by the F. W. S. GERONIMO, along a section extending 700 km to the windward of Courtown and Albuquerque Cays. Since light inhibition is characteristic of shallow surface waters at all five ocean stations (maximum productivity is at 10 to 15 m) (unpublished data) the strong light must also tend to inhibit planktonic productivity on the shallow reef stations at the two atolls. Consistent with this assumption is the similarity between mean surface carbon fixation rates for the oceanic and windward reef stations (Table A-2). The successive increase in carbon fixation across the reefs in the direction of flow therefore may not be attributed to planktonic algae, but instead may be related to the presence of benthic algae, torn loose from the reef flat, which are not inhibited by high irradiance. The reef water possibly accumulates more benthonic fragments as it passes across the reef, accounting for the increase in net carbon fixation at the innermost stations. Thus the relative contribution of planktonic forms to the overall productivity of the reef flat is probably nil; Odum and Odum (1955) reached a similar conclusion.

References Cited


1. Chart of western Caribbean and Central America.

2. Study area chart.
3. Chart of Courtown Cays, based on aerial photographs, H. O. Chart 2077, and observations made during the cruise.
4. Chart of Albuquerque Cays, based on aerial photographs, H. O. Chart 2077, and observations made during the cruise.

5. Chart of Roncador Bank, based on aerial photographs, H. O. Chart 1374, and observations made during the cruise.
6. Chart of Serrana Bank, based on aerial photographs, H. O. Chart 1374, and observations made during the cruise.

7. Locations of hydrographic stations occupied at Courtown Cays (A), Albuquerque Cays (B), Roncador Bank (C) and Serrana Bank (D).
8. Idealized plan and cross sectional views of the ecologic zonations at Courtown Cays. The other atolls have similar zonations.

9. Profiles of the lagoon at Roncador Bank, based on soundings made during the cruise. These profiles depict the great number of patch reefs within the lagoon, and also show the lack of any apparent sill (profile AB).

10. Profiles of Serrana Bank lagoon. These profiles show the contrast of the great number of patch reefs in the eastern part of the lagoon, and the relatively flat, shallow lagoon bottom to the west (profile FF').
1. The Millepora zone, composed primarily of the flat hydrocoral Millepora alcicornis (labeled ma in picture), the soft coral Palythoa mammillosa (pm) and encrusting red algae (ra); *Halimeda opuntia* (ho) is also common.

2. A panoramic photograph of the Millepora zone in the heavy surf zone (left) of the outer windward reef. This picture was taken at Roncador Bank during spring low tides; similar, but somewhat less well-developed colonies are found at the other atolls.
3. A large colony of Diploria, located in the Diploria zone on the outer reef, is seen exposed about 1/2 m above low tide. The upper 10 cm of the coral is dead, perhaps reflecting the limit to which normal waves can bathe it.

4. Depths in the inner reef flat (foreground) are significantly greater than on the outer reef flat (background).
5. At all atolls the majority of lagoon reefs are scattered, low-lying patches. The bottom depth in this photograph is about 13 m; the diver is 5'10" tall.

6. Patch reefs often have an abundance of foliose and pinnacle growth forms of Montastrea annularis, the latter shown in the center of this picture.
7. Bands of beachrock extend windward from East Cay at Courtown Cays, seemingly indicative of the lagoonward migration of the cay. Tall palm trees characterize the vegetation on East Cay. In the background is the wreck of a Colombian ship, awash on the reefs.

8. Close-up picture of the beachrock bands. Fissures are parallel and perpendicular to the strike of the rock.
9. Elevated beachrock at North Cay, Albuquerque Cays. Recent beachrock is in the foreground of the picture.

10. Dense Ficus forest at South Cay, Albuquerque Cays.
11. Rocks emergent at low tide line the windward rim of the outer reef at Roncador Bank. Roncador Cay is seen in the background.

12. Roncador Cay is covered with a rubble of coral heads. Piles of these dead corals were once used as walls.
A-1 Locations of reef productivity stations at Courtown and Albuquerque Cays.

A-2. Time plot of temperature, salinity and oxygen variations on the reef flats of Courtown Cays.

A-3. Time plot of temperature, salinity and oxygen variations on the reef flats of Albuquerque Cays.
A-4. Calculated oxygen gain and loss on the reef flats of Courtown Cays.

A-6. Carbon fixation rates across the windward reef flat of Courtown Cays.