Primary Production Measurements in Eleven Florida Springs and a Marine Turtle-Grass Community

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Reprinted from Limnology and Oceanography
Vol. II, No. 2, April, 1957
Printed in U.S.A.

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ABSTRACT

During July and August, 1955, primary production measurements were made in eleven Florida spring communities and a marine turtle-grass community in the Florida Keys by means of the diurnal curve method. Diurnal measurements of oxygen and carbon dioxide made at a station downstream from the main springs were used in estimating gross primary production and community photosynthetic quotients. These curves show in detail the course of production hour by hour under various conditions in whole natural communities.

The primary production values obtained ranged from 0.7 g oxygen/m²/day in a small, heavily shaded, anaerobic spring on a rainy day to 64 g oxygen/m²/day on a sunny day in an aerobic spring where the plant beds trailed at the water surface. A comparison of the chemostatic properties in the springs studied suggests that oxygen, phosphate, nitrate, and carbon-dioxide levels are relatively unimportant in determining the magnitude of primary production in these spring communities. Light as influenced by cloud cover, trees, and water depth is the main controlling factor. Approximate efficiencies found were 0.5 to 10% (mean 4%) of the visible light energy reaching plant level. Downstream increases in planktonic chlorophyll and oxygen suggested a steady state in 7 km of longitudinal succession in Rainbow Springs River. Net production of benthic algae of 1.5 g/m²/day was estimated in Orange Springs from the rate of bubble release into funnels placed on the bottom.

INTRODUCTION

The large artesian springs of Florida are collectively a giant laboratory for the study of natural communities. All are maintained at constant temperature and relatively constant chemical condition by the strong flow from underground. Although the temperatures of about 23°C are similar, the chemical conditions of each spring are somewhat different (see Ferguson *et al.* 1947). Since many properties are similar from spring to spring, it is possible to compare the productivity of springs in an effort to determine the effects of those factors that do differ.

In a previous paper (Odum 1956a) some methods were described for measuring primary production in flowing waters from an analysis of diurnal curves for oxygen and carbon dioxide. The results of testing this method closely in Silver Springs, Florida, are reported elsewhere (Odum 1957). In this paper similar studies are reported for eleven other Florida Springs, as well as a marine turtle-grass community whose tidal waters flow over the benthic community in a way that suggests comparison with the freshwater spring communities. Some properties of these thermostatic and chemostatic communities are given in Table 1.

The diurnal curve method of measuring production as applied to springs consists of measuring oxygen and carbon dioxide throughout a day at a station below the spring outflow (boil). Since the boil is constant in properties, the action of the community on the water is indicated by the downstream differences. By subtracting the night values from the day values and applying a correction for diffusion differences between day and night, one obtains the gross primary production.

In some streams the changing degree of saturation at night permits an estimate of diffusion and respiration to be obtained from the diurnal curves themselves (Odum

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[1] These studies carried out at the University of Florida were aided by a contract NR 163-106 between the Biology Branch, Office of Naval Research and the Department of Biology, University of Florida. The author is grateful to James B. Messerly for his effective research assistance in carrying out the field collections and analyses.

TABLE 1. *Characteristics of the communities studied*[a]

Name of spring and location	Depth of plants[b] m	Shading by trees[b] %	Oxygen[a] ppm	Carbon dioxide ppm	NO_3-N ppm	PO_4-P ppm	N/P by atoms
Anaerobic Springs							
Beecher Springs, Welaka, Putnam Co.	1	80	0.8	4.5	0.11	0.112	2.3
Blue Springs, Volusia Co.	1	50	0.25	7.9	—	0.123	—
Aerobic Springs							
Weekiwachee Springs, Hernando Co.	2	10	1.3	4.8	0.12	0.018	15
Manatee Springs, Levy Co.	0.5	60	1.8	13.2	—	0.037	—
Silver Springs, Marion Co.	1	10	2.6	9.7	0.46	0.054	23
Green Cove Springs, Clay Co., zone below pool	0.05	50	2.8	1.8	0.09	0.005	42
Chassahowitzka Springs, Citrus Co., oligohaline side boil	0.1	10	3.8	9.2	—	0.013	—
Blue Spring, Alachua Co., small side boil with "*Utricularia*"	1	90	3.9	7.5	—	—	—
Blue Spring, Alachua Co., main boil	0.2	70	4.2	6.8	0.85	0.092	21
Homosassa Springs, Citrus Co., fish-bowl spring, oligohaline	0.1	30	4.3	4.9	0.080	0.008	23
Rainbow Springs, Marion Co.	1.5	10	5.2	4.9	0.080	0.008	23
Marine Turtle Grass,							
Long Key, Fla.	0.5	0	4.2	—	—	—	—

[a] The springs are arranged in order of increasing oxygen concentration of the water (values).

[b] Visual estimation.

[c] From boil to downstream measurement station.

1956a). However, in springs with their constant outflows, diffusion must be determined independently. In this paper a value of the diffusion correction obtained in work in Silver Springs (Odum 1957) is used. The diffusion estimate itself, however, is not crucial for the determination of gross primary production. Diffusion is subtracted along with respiration when the night values are subtracted from the daytime values. It is only the change in diffusion resulting from the change in saturation deficit for which correction must be made. Judging from studies on Silver Springs, the correction for changing diffusion apparently amounts to only about 10 to 15% of the total production in spring communities.

In this paper as in previous papers small letters designate metabolic rates on a water-volume basis and capital letters metabolic rates on a community-area basis.

CHEMICAL METHODS

Oxygen was measured by the un Winkler method, the samples be in the field. Carbon dioxide wa mined from pH and methyl purple a by means of an alkalinity nomogram 1945: 288). Because of the low matter content of the water (less ppm) it was possible to bring th back to the laboratory for pH de tions. These were made within hours of the time of sampling. Chl determinations of the plankton we from 3-liter samples. After the w passed through millipore filters, t was then dissolved in acetone and ment concentration estimated with man Spectrophotometer following cedure of Richards with Thompson

THE DIURNAL CURVES OF OXYGE CARBON DIOXIDE

In Figures 1–10 are given the curves made in 10 springs at stations

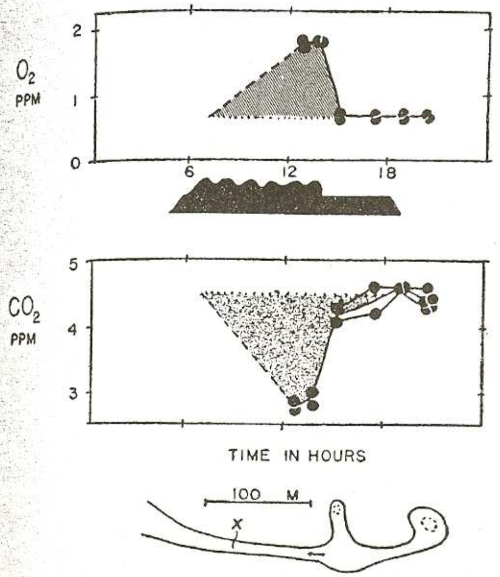

FIG. 1. Diurnal curves of oxygen and carbon dioxide at a downstream station marked *x* in Beecher Springs, Welaka, Putnam County, Florida, August 2, 1955. This spring is anaerobic and characterized by blue-green algae and white sulfur bacteria.

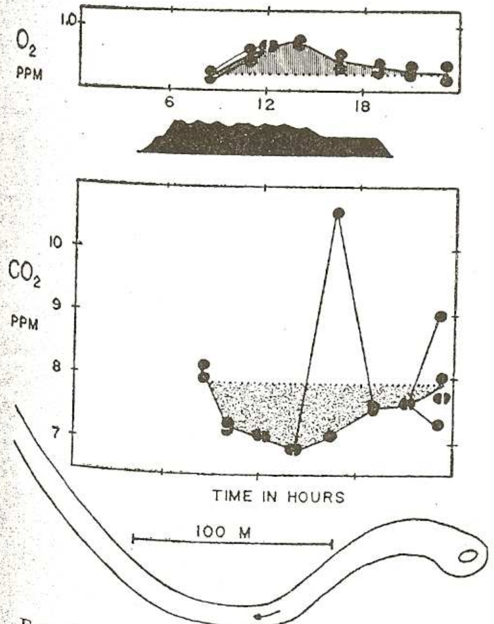

FIG. 2. Diurnal curves of oxygen and carbon dioxide from a station 450 meters downstream in Blue Springs, Volusia County, Florida, August 9, 1955. The spring is anaerobic and characterized by blue-green algae.

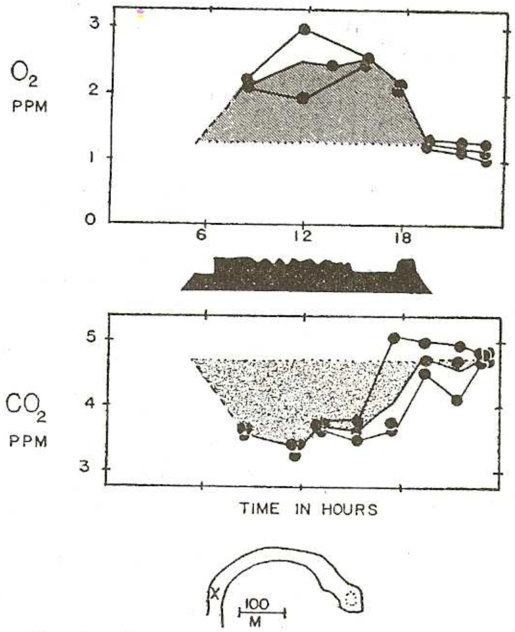

FIG. 3. Diurnal curves of oxygen and carbon dioxide at a station marked *x* downstream from Weekiwachee Springs, Hernando County, Florida, July 26, 1955. The spring is very deep and floored with *Sagittaria* and algae, especially *Hydrodictyon*.

in each case a short distance below the main boil. For reasons of economy complete 24-hour series were not obtained, but the field work was planned so that a representative night value was obtained either late at night or early in the morning. All sampling was done in duplicate or triplicate. The shaded areas between the mean curves and the horizontal lines representing the night values are a measure of the gross production. The lower part of the horizontal black bar graph indicates the duration of light. The upper margin of the black bar is straight and horizontal when the sun was shining directly without interference from clouds as indicated by descriptive notes made in the field. It should be realized that the curves are records of the hour to hour changes in production, which reflect the weather and cloud changes intimately. No clear cut evidence was found of a midday depression in production as known for isolated land plants.

As also reported in the Silver Springs

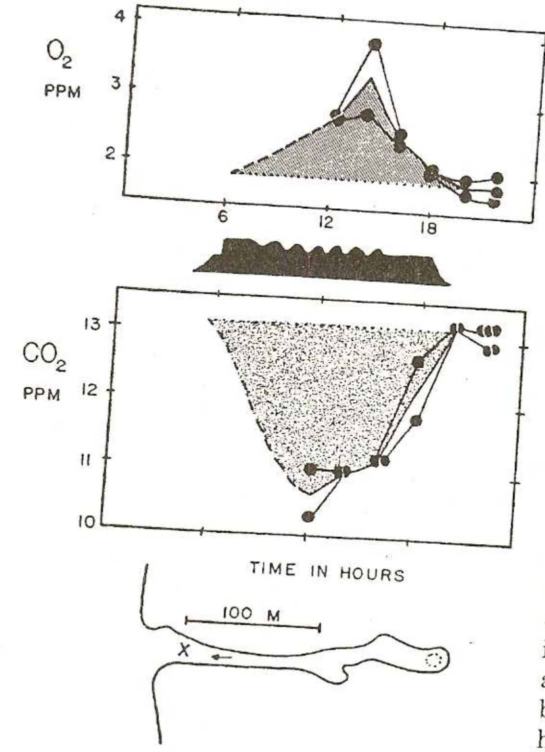

FIG. 4. Diurnal curves of oxygen and carbon dioxide at a downstream station marked *x* in Manatee Springs, Levy County, Florida, August 15, 1955.

work, the oxygen and carbon-dioxide curves are not entirely symmetrical in that the carbon-dioxide curves show irregular behavior after sunset. Whereas the oxygen release by the community ceases at sunset, the carbon dioxide uptake seems to continue longer as indicated in the graphs for Rainbow, Homosassa, Beecher, and Blue Springs (Figs. 1, 2, 9, and 10). In contrast, the Alachua Blue Springs (Fig. 7) show some kind of over-compensation after sunset with the carbon dioxide rising temporarily to a higher value than typical of the nighttime. It is not certain whether these effects represent the behavior of the plants or are an artifact due to some differences in mixing that occur along the shores as some of the backwaters cool.

In Green Cove Springs (Fig. 5) the water from the boil flows in part into a swimming pool and over a falls before flowing over the community of organisms in the stream. In this situation the large of the swimming pool relative to the troduces complex lag factors affect water that enters the downstream zo such a situation where the properties water entering the zone are not cc the two-station analysis must be resor As shown in Figure 5, diurnal curves obtained at both ends of a short segm the stream. The upstream values then subtracted from the downstream to get the rate-of-change curves for ox and carbon dioxide.

In Figure 11 are presented data for m turtle grass off Long Key, Florida, obta by the modification of the diurnal c method referred to previously as the method (Odum 1956a). The thick characteristic beds of *Thallassia* were loc in 3 ft of flowing water which was conti ally changing in direction and velo because of the tide. The procedure u here was for the wading observer to fol a spot of fluorescein dye in the water about ten to twenty minutes, using flashlight at night. The enormously hi production rate of this dense grass co munity produced significant oxygen chang in short time intervals. Duplicate samp of water were taken adjacent to the dye sp at the start and completion of a run. T fluorescein spot was renewed periodical from a dropping bottle as the dye disperse The oxygen values obtained are given Table 2. An oxygen rate-of-change cur (Q) was computed as given in Figure 1 Respiration and diffusion were then obtaine using the methods given previously (Odu 1956a). When these estimates of rates respiration and diffusion are subtracted fro the oxygen rate-of-change curve the primar production curve obtained is shown at th bottom of Figure 11. Because differen degrees of saturation were found at di ferent times of night, the change in oxyge rate-of-change had to be related to th change in saturation deficit in order compute the diffusion coefficient. This wa not possible in the case of the springs.

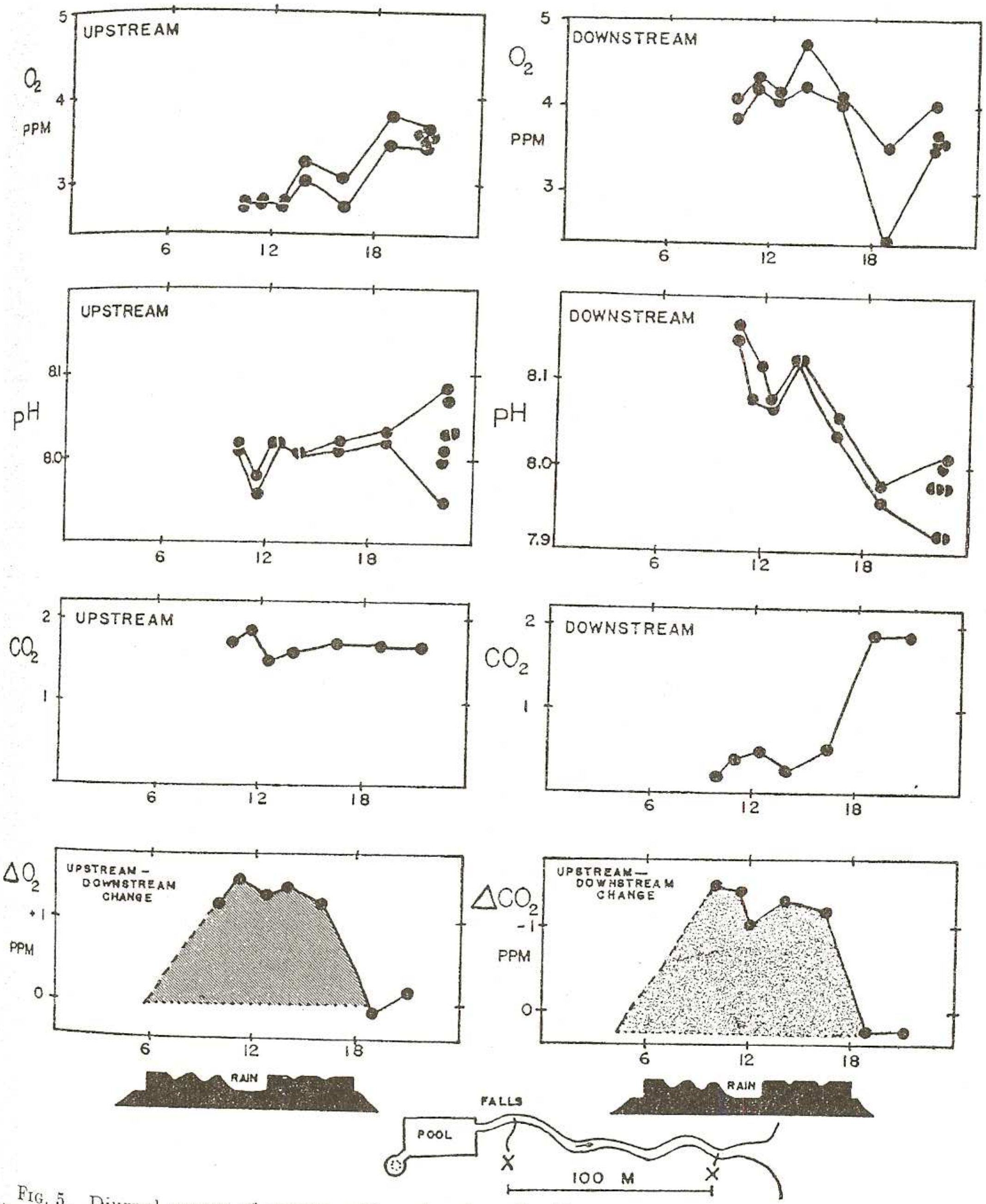

FIG. 5. Diurnal curves of oxygen, pH, and carbon dioxide as computed from pH at two stations (marked *x*) in the run below Green Cove Springs, Clay County, Florida, July 7, 1955. In the lower graphs are plotted curves of oxygen and carbon dioxide change between the upstream and downstream stations. This shallow brook contains *Vallisneria* beds.

COMPUTATION OF PRIMARY PRODUCTION AND COMMUNITY PHOTOSYNTHETIC QUOTIENTS

In Table 3 is listed the primary production computed for each pair of diurnal oxygen and carbon-dioxide curves. The computation consists in multiplying the area under the diurnal oxygen curve (Figs. 1–11) in ppm-hrs/day by the discharge in m³/hr and

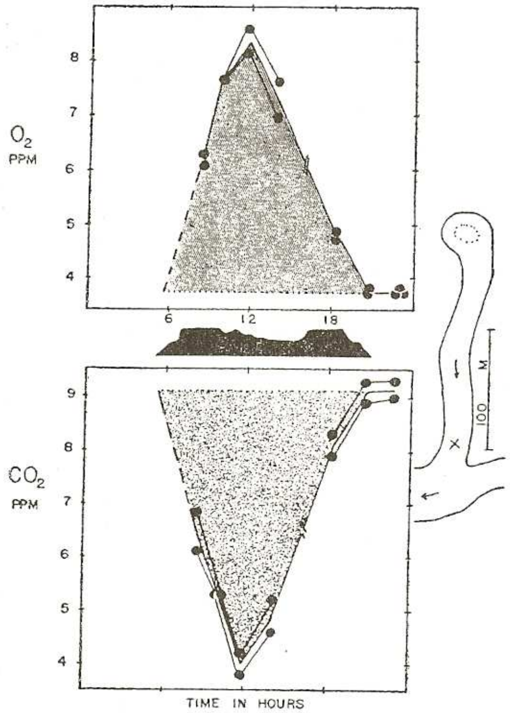

FIG. 6. Diurnal curves of oxygen and carbon dioxide at the mouth (marked x) of the first of the smaller oligohaline springs that flows into the main Chassahowitzka Springs run from the North a few hundred feet below the main fish-camp area, August 3–4, 1955. The water is filled with heavy beds of *Potamogeton pectinatus*, *Vallisneria*, and algae, which trail at the surface.

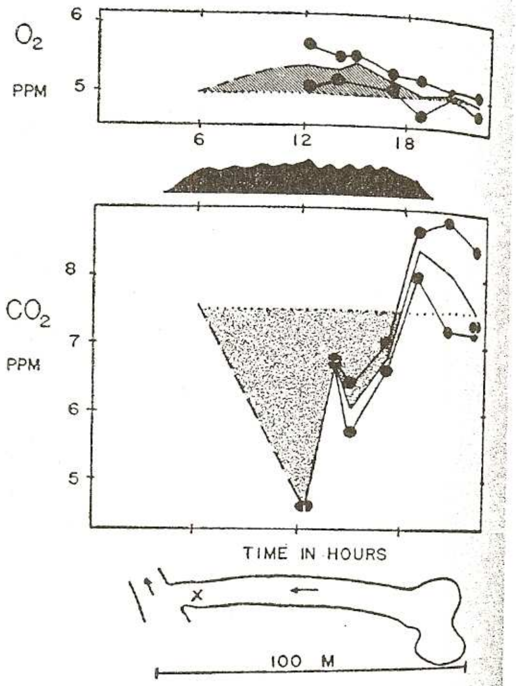

FIG. 7. Diurnal curves of oxygen and carbon dioxide at the mouth (marked x) of a small shaded boil full of *Utricularia* at Blue Springs, Alachua County, Florida, July 28, 1955.

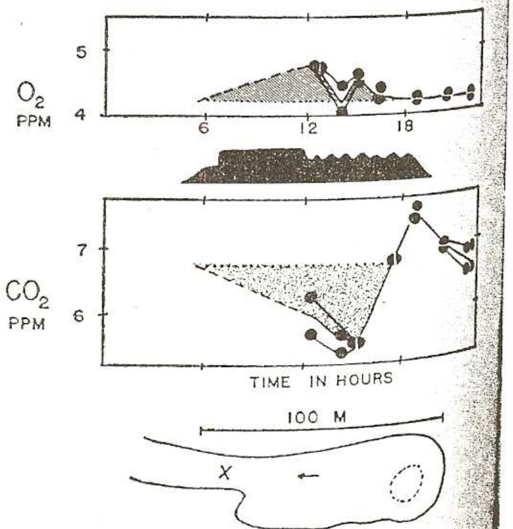

FIG. 8. Diurnal curves of oxygen and carbon dioxide at a station marked x in the main boil of Blue Springs, Alachua County, Florida, July 28, 1955. The spring contains mixed vegetation: *Vallisneria*, *Najas*, *Ceratophyllum*, and surface vegetation.

dividing by the area of the community between the boil and the downstream station in m^2. For example, in Weekiwachee Springs 14.5 ppm-hrs times 10.7×10^3 m^3/day divided by 16×10^3 m^2 is 9.7 g/m^2/day oxygen production. In the Silver Springs study the oxygen production was shown to be more closely proportional to the energy storage than was the dry weight or ash-free dry weight because of the possible shift from glucose to protein production with changes in light intensity. Consequently production values are reported as oxygen measured. Based on Silver Springs a 10% uniform correction for change in diffusion rate between night and day was added to obtain the production values in Table 3. Since the range in saturation deficit of oxygen during night and day is

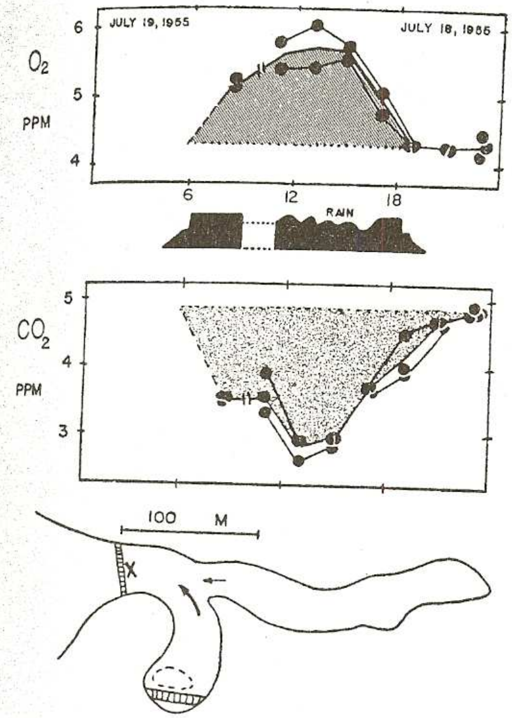

FIG. 9. Diurnal curves of oxygen and carbon dioxide at the station marked *x* in Homosassa Springs, Citrus County, Florida, July 19, 1955. Most of the discharge comes from the main fishbowl boil as indicated by the heavy arrow in the sketch. The area of the small springs to the right is mostly shaded and covered with floating aquatics. Only the area of the main flow is used in computations. This main spring is oligohaline and perpetually a place of milling about for marine fishes.

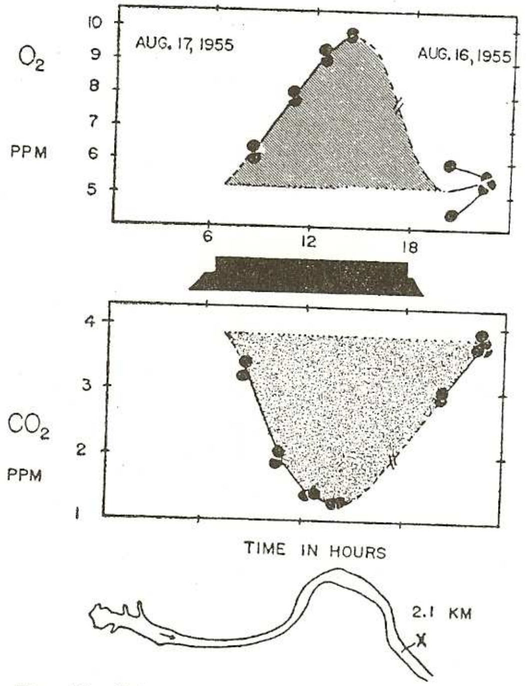

FIG. 10. Diurnal curves of oxygen and carbon dioxide at a downstream station marked *x* on a clear day in Rainbow Springs River, Marion County, Florida, August 16, 1955.

similar in each spring, the diffusion effects are likely to be similar.

The calculation of carbon-dioxide assimilation was made in the same way as described for oxygen. Then the ratio of the oxygen production to the carbon-dioxide production was reported as a community photosynthetic quotient as already done for Silver Springs (Odum 1957).

FACTORS AFFECTING PRIMARY PRODUCTION

In Table 1 are listed some of the main properties of the community that might be expected to modify the primary production: the degree of shading of the stream by trees, the approximate depth of the water to the main level of photosynthesis in the plant beds, the nitrate-nitrogen, the phosphate-phosphorus, the N/P ratio, the carbon-dioxide concentration, and the oxygen concentration.

It is clear from the diurnal curves and the computed production values in Table 3 that there is an enormous range of production within the springs studied. In considering the factors responsible for these differences, one should think of these communities as being in steady-state equilibrium due to a thermostatic, chemostatic, and remarkably constant biological environment. Thus the productions that are reported represent the productivity of the stabilized steady state and presumably represent the maximum production possible under the conditions of the particular outflow. Hypothetically communities will adjust to the maximum production that can be sustained since such a community may be expected to have maximum survival value following Lotka's maximum power principle (Odum and Pinkerton 1955).

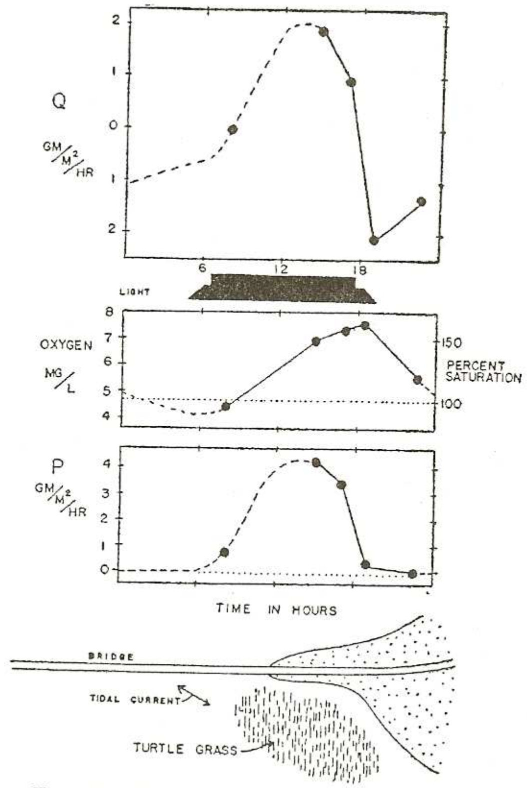

FIG. 11. Rate of oxygen change (*Q*) and primary production (*P*) on an area basis in masses of water moving over beds of turtle grass along the causeway on Long Key, Florida, August 14, 1955. The oxygen curve (middle graph) is used to correct for diffusion loss during the day so as to derive the production curve (*P*) from the oxygen rate-of-change curve (*Q*). Parcels were followed with fluorescein dye by a wading observer. Points are the mean differences between duplicate samples (Table 3). Current velocity varied from 0 to 0.22 m/sec.

TABLE 2. *Oxgyen changes (mg/L) near moving dye spots over* Thallassia *grass flats Aug. 14, 1955, Long Key, Fla.*

Time of start	Time lapse in minutes	Depth m	Oxygen at start	Oxygen at end	Oxygen change	Rate of oxygen change gm/m²/hr
2:35 pm	7	0.9	6.85	7.05		
			6.81	7.10	0.25	1.86
3:56 pm	14	0.9	7.24	7.49		
			7.20	7.44	0.25	0.96
6:41 pm	5.5	0.9	7.79	7.80		
			8.04	7.62	—0.21	—2.1
10:24 pm	10.4	0.75	5.67	5.45		
			5.80	5.40	—0.32	—1.4
7:53 am	4.8	1.05	4.47	4.43		
			4.48	4.52	0	0

An examination of the carbon-dioxi nitrogen, and phosphorus values in Tabl suggests no correlation with the prima production. That the nutrients which lin production under transient conditions a not important in steady state seems reaso able since the large and continuous flows a continually renewing the aquatic mediu so that no real deficit of nutrients ca develop. If nutrients are not limiting, on next looks to light as the limiting factor. I previous papers Odum and Pinkerton (1955 and Odum (1956b) presented a theory tha in steady state when light is the limitin factor an adaptation for maximum power output (production) is developed at a moderately low efficiency. This efficiency is lower than the maximum possible efficiency. These springs may provide real cases to test the operation of this principle. It is not unreasonable that the springs represent the maximum power adjustment to the available light. The efficiencies may represent the optimum efficiency postulated in the aforementioned theory as a requirement of Lotka's principle and the second law of thermodynamics.

An examination of the data in Table 1 shows that the light reaching the community is the main factor controlling production. In Silver Springs the maximum cloudiness in rainy summer days lowered the primary production by half. Whereas this effect is clearly indicated and the effect of the trees is also clearly apparent in the Beecher and Alachua Blue Springs, the cloud effects and tree effects cannot account for the differences in the productivity of relatively unshaded springs studied on sunny days. An examination of the depths of the water over the plant beds, however, revealed that the springs with maximum production have long streamers of rooted plants that support Aufwuchs within a few centimeters of the surface, such as in Chassahowitzka Side Boil and Homosassa Springs. It also seems possible that the anaerobic springs have lower efficiencies, as in Blue Volusia and Beecher Springs, Welaka.

Starting with an insolation for August 1 of about 7000 kCal/m²/day (Kennedy 1949), some rough estimations of light intensity at

TABLE 3. *Production measurements during July and August*

Community	Date 1955	Clouds	Discharge × $10^3 m^3$/day	Oxygen production[a] gm/m^2/day	Carbon-dioxide assimilation[a] gm/m^2/day	Community photosynthetic quotient by atoms (O_2/CO_2 × 1.37)
Beecher	Aug. 2	broken to overcast, rain	0.44	0.68[c]	1.2[c]	0.9
Blue, Volusia	Aug. 9	scattered cumulus	11.7[b]	5.4[e]	14.1[c]	0.5
Weekiwachee	July 26	broken clouds	10.7[b]	10.7[e]	9.4[e]	1.5
Manatee	Aug. 15	scattered clouds	15.0[b]	19.4[e]	51.7[e]	0.5
Silver	Mean of 3 measurements during July–Aug., 1954–55 (Odum, 1957)		68.0[c]	18.0	17.4	1.4
Green Cove	July 7	broken clouds	0.49[d]	15.5	21.2	1.0
Chassahowitzka Side run	Aug. 3–4	broken clouds	2.7[d]	26.7[e]	28.5[e]	1.3
Blue (*Utricularia*)	July 29	broken clouds	0.66[d]	2.0[e]	35.2[e]	0.8
Blue, Alachua	July 28	broken clouds	3.7[d]	5.2[e]	9.1[e]	0.8
Homosassa	July 19	broken clouds	18.6[b]	63.8[e]	95.0[e]	0.9
Rainbow	Aug. 16	clear	70.0[b]	23.9[e]	18.0[e]	1.8
Long Key	Aug. 14	almost clear	—	34.0	—	—

[a] $\frac{\text{(ppm-hrs from graphs) (discharge)}}{\text{area}}$.
[b] Ferguson *et al.* (1947).
[c] Courtesy, U. S. Geological Survey.
[d] Measured with dye and watch at a cross section.
[e] Includes 10% addition for diffusion difference between day and night.

plant level can be made. The following are the factors used for calculating the light energy reaching the plants relative to the light energy reaching the ground on a clear day. Half is considered of wave length suitable for photosynthesis, ¼ is considered removed for broken cloudiness, ½ is considered removed by 100% heavy tree shading, and about 40% is considered removed for the first meter of water (includes surface reflection and refraction). From the estimates of water depth, cloudiness, and tree shading listed in Tables 1 and 3 and the assumptions stated above, an estimate of the visible light energy reaching the plant beds in each spring at the time of the production measurement was computed. In Figure 12 the production measurements and the computed light intensities are plotted. The distribution of points indicates a rough correlation of gross primary production with visible light intensity as thus estimated. The efficiencies seem to be about 4%, with little sign of decreasing efficiencies at the higher production rates. Ten measurements made in every season in Silver Springs (Odum 1957) showed a similar correlation of production and light intensity at about 5% efficiency. That so many varied communities with high production should have so similar efficiencies under conditions of continuously renewed medium supports the theory of an optimum and moderate efficiency requirement for maximum production under naturally adapted and competitive conditions. These results are similar to the seasonal correlations of production with light in naturally adapted lakes found by Verduin (1956).

The absence of light saturation effect in Figure 12 suggests that these permanently fixed benthic algal communities like pine trees on land (Rabinowitch 1951) are sun tolerant at high light intensities, and thus differ from plankton communities studied (Ryther 1956a). Manning, Juday, and

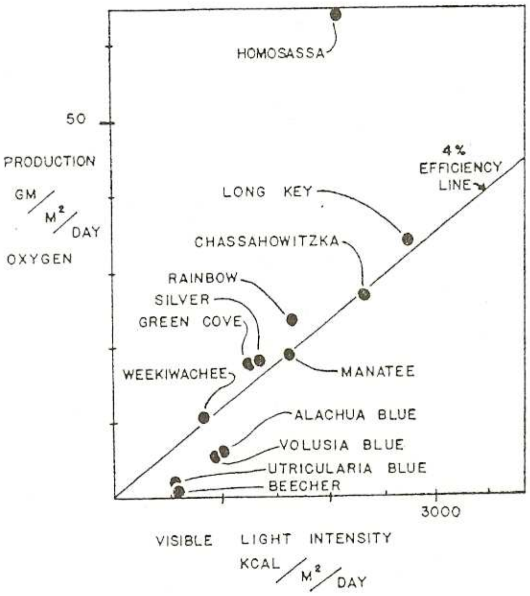

FIG. 12. Gross primary production on an area basis as a function of visible light intensity reaching the level of main plant beds. The production values in Tables 1 and 3 are obtained from areas under oxygen curves in Figures 1–11. A 4%-efficiency line has been drawn on the basis of 3.4 Calories production per gram oxygen released.

Wolf (1938) showed a similar sun tolerance in littoral *Cladophora*.

The range in photosynthesis due to changes in light intensity is apparently greater than that found in plankton communities (Edmondson 1956). The larger range in the spring communities may be due to the absence of a light saturation effect in the normal range of light intensities.

COMMUNITY PHOTOSYNTHETIC QUOTIENTS

The photosynthetic quotients (O_2/CO_2 by atoms) as estimated from the areas under the diurnal curves in Figures 1–10 are presented in Table 3. Like the quotients reported for Silver Springs, the quotients in these varied environments show a correlation with the magnitude of production, suggesting a greater per cent protein production at times of maximum light intensity.

That the quotients are as close to 1 as they are is in one sense a rough confirmation of the order of magnitude of the production values. However, the quotients below 1 are not easily accounted for. Ryther (1956b) summarized data on photosynthetic quotients in populations which resemble those in nature and found that values of about 1.25 were usual. Schmassmann (1951) using diurnal oxygen and carbon-dioxide curves in a Swiss stream obtained a community quotient greater than one.

One possible factor that could lower the community quotient in some springs is a diurnal shift from anaerobic metabolism at night to aerobic metabolism during the daytime, as a result of slight daytime rises in oxygen tension in microenvironments.

Variation in type of nitrogen source can also produce differences in community photosynthetic quotients. As previously suggested on the basis of some nitrate increases observed in two springs, there may be some nitrogen fixation where nitrate-nitrogen is scarce (Odum 1957). More oxygen is released where the nitrogen source is of the nitrate type. Burstrom (1956) summarizes the complex effects on the photosynthetic quotients due to variations in nitrogen metabolism.

HOMOSASSA SPRINGS

The Homosassa Springs is a very peculiar environment. That the enormous primary production in Table 3 is valid seems likely from some large upstream-downstream oxygen increases observed on two other occasions. The area in Figure 9 to the right of the main outflow contains some minor spring inflows which were not included in the computation. If this area had been included, the production per m² would have been lower and more like those in the other springs. However, it was visually obvious to the observer that the water passing the downstream station did not include appreciable quantities of water from the minor spring. The strong flow through the long plant tresses marks its passage because the plant blades form stream lines. Thus we must search for some other explanation for the very high efficiency and production in this spring.

The Homosassa Springs is unusual in another respect that may be related to the high production. Large populations of marine fishes mill about in the boil area where they form the basis of a very fascinat-

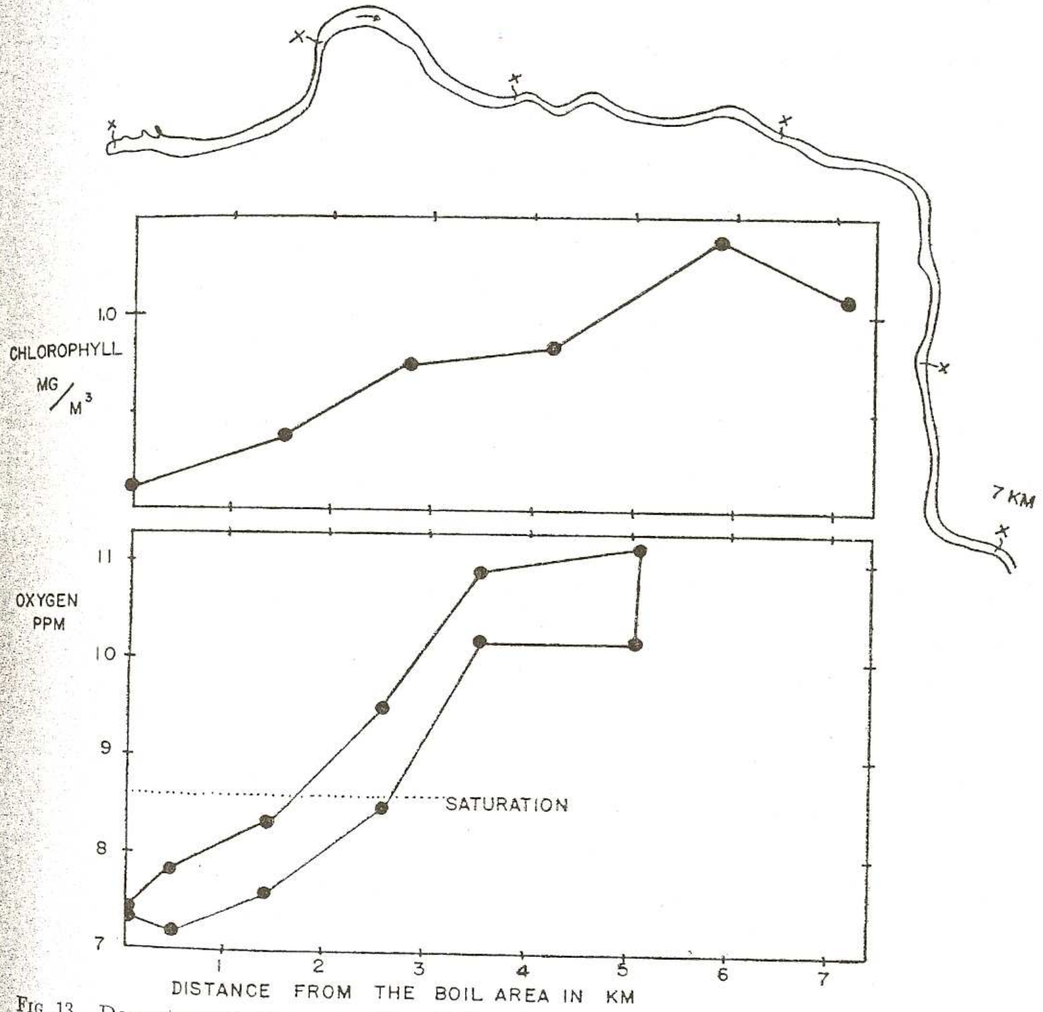

FIG. 13. Downstream increases in chlorophyll and oxygen in the water of Rainbow Springs River. The stations at which chlorophyll samples were made on August 16, 1955, are indicated by x's. Two oxygen samples were made at each station on May 16, 1954, between 1 and 2 p.m. with scattered cumulus clouds. The temperature downstream was 25.5°C. The spring in its upper zones is characterized by beds of *Sagittaria*, shifting to *Chara* and other benthic algae, and visibly increasing turbidity. These data were obtained with Dr. L. J. Marchand.

ing tourist attraction. A cause for the fish concentrations has been previously suggested (Odum 1953). An enormous number of large fishes, far more than are functionally part of the community (possibly 1000) are ever present in the boil. The wastes from these fishes could conceivably provide an unusual nutrient source of heterotrophic energy supplement or important organic requirements. Another peculiarity is the fine, flocculant, reddish, iron precipitate. The water has a green color in gross appearance.

CALCULATIONS BASED ON STEADY STATES IN LONGITUDINAL SUCCESSION

In a previous paper (Odum 1956a) the concept of excess of production over respiration in the spring headwaters was described, with the implication that particulate organic matter was exported from this zone. Further downstream the increasing organic content of the water was thought to increase respiration until a balance of production and respiration was achieved. In Figure 13 are plotted a longitidinal series of chlorophyll determinations made in Rainbow Springs River. The boat floated downstream with the water during sampling so that the values obtained represent the change in the water mass in its passage. A suggestion of leveling off at something over 1 mg/m³ chlorophyll is observed 6 km downstream as the character of the river shifts from a predominantly benthic type community to a planktonic one.

Another type of temporary steady-state balance that was observed was the daytime pattern of oxygen from the boil downstream. The water emerging from the boil area during the day receives oxygen at first by production and diffusion. Then as the water attains and exceeds the saturation value a balance develops between production, respiration, and loss by diffusion. This is reached on a sunny day about 5 km below the boil area as observed in Figure 13. If leveling off of the chlorophyll means that exports balance imports at this station, it may be inferred that production balances community respiration at this point also.

The downstream distribution of oxygen on a sunny day in the Rainbow Springs river (Fig. 13) makes possible a rough computation of production, respiration, and diffusion. Consider the zone about 1.8 km downstream from the boil (Fig. 13) where the water is approximately saturated with respect to the oxygen of the air. If the rate of flow is about 0.2 m/sec, the oxygen is increasing at a rate of about 1.2 ppm/hr. Since there is no diffusion in this zone, the following relationship holds:

$$p - r = 1.2 \text{ ppm/hr}$$

where p is the production and r the respiration on a volume basis.

From the chlorophyll graph (Fig. 13) the rate of export of organic matter may be calculated on the assumption that the pseudoplankton has a ratio of chlorophyll to organic matter of 0.002 as in Silver Springs. Twelve hours of photosynthesis and 24 hours of respiration are apparently producing an export of 1.4 mg chlorophyll/m³/6 km, as estimated from the upper graph in Figure 13. At a flow of about 0.2 m/sec and a depth of 2 m the export is estimated as 0.17 g/m²/hr dry organic matter. Therefore over a 24-hour period

$$12P - 24\,R = 24(0.17)\text{g/m}^2$$

where P and R are production and respiration on an area basis. By combining this relation with the equation above inferred from the oxygen graph in Figure 13, R is calculated to be 0.28 g/m²/hr and P 1.48 g/m²/hr during the middle of the day. This value is similar to the approximately 2 g/m²/hr (23.9 g/m²/day) obtained in Table 3 with the diurnal curve method based on Figure 10. The use of data obtained at different times here is justified by the chemostatic nature of the oxygen and chlorophyll conditions. Evidence that chemostatic conditions exist in such springs is given for Silver Springs by Odum (1957).

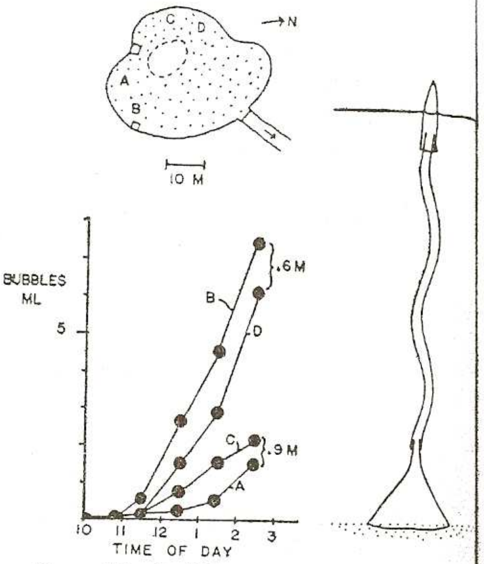

FIG. 14. Bubble production in Orange Springs, Putnam County, Florida. The type of apparatus used to collect bubbles is shown at right. Letters *A–D* indicate locations of funnel apparatus in the map of the springs headwater area at the top. The graph shows the bubble readings at the tip of the apparatus on a sunny day, August 1, 1955. Stations *B* and *D* were at 0.6 m depth; Stations *A* and *C* were at 0.9 m depth.

NET PRODUCTION MEASUREMENTS OF BOTTOM ALGAE IN AN ANAEROBIC SPRING BY MEANS OF BUBBLE ACCUMULATIONS IN FUNNELS

In Orange Spring, Putnam County, Florida, the head pool is partially enclosed by a wall and dam so that the clear anaerobic water emerging from caverns is held temporarily above a sandy bed about one meter below the surface. This sand is a dusky olive-brown due to a heavy film of *Cladophora*, *Gomphonema*, *Lyngbya*, and *Microspora* (Whitford 1956). As shown in Figure 14, funnels (230 cm^2 in area) were placed upon the bottom ooze with extension tubes to the surface terminating in graduated centrifuge tubes. Four such funnel devices were placed on the sand at 10:00 a.m. on August 1, 1955. During the first two or three hours the oxygen produced dissolved in the 275 cc of water in the funnels, and no bubbles appeared. By 1:00 and 2:00 p.m., however, a steady release of bubbles was occurring. The curves of Figure 14 for water 0.6 m deep indicate a rate of gas release 5 times that at 0.9 m depth. The water initially contains about 1 ppm H_2S and 1 ppm free CO_2. The rate of gas release into the shallower funnels in sunlight was 0.15 $g/m^2/day$, which is similar in magnitude to the low estimates for the two other anaerobic springs reported in Table 3. Thus the several methods for measuring in situ community production in nature yield similar estimates.

These measurements establish the range and magnitude of primary production in streams under unusually well defined conditions. It is hoped that many more such measurements in the future may help determine which are the main factors controlling energy flows in trophic systems.

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