TROPHIC STRUCTURE AND PRODUCTIVITY OF SILVER SPRINGS, FLORIDA[1]

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INTRODUCTION

SPRINGS OF FLORIDA; A NATURAL LABORATORY FOR STREAM LIMNOLOGY

By a remarkable circumstance of nature there are many large springs in central Florida (29° N. Lat.) each with relatively constant temperature of 21 to 25° C. There are many varied types, and all contain aquatic communities in their basins and their outflow channels. Each spring differs from the others by a few factors. Thus there are chloride springs, calcium springs, sulfate springs, springs with high and others with low oxygen tensions, saline springs, soft water springs, and other types. Analyses of many of the major chemical elements in these waters have already been published (Ferguson, Lingham, Love & Vernon 1947).

Because of their special properties these springs are collectively a giant constant temperature laboratory. In spite of the actions of the community that tend to modify the water a constant medium is maintained by the fresh flow from underground. In this rare situation it is possible to compare whole communities in a ready made experimental design.

[1]A project carried out primarily from the Department of Biology, University of Florida, Gainesville, Fla. These studies, the 13th publication of the Springs project, were aided by a contract between the Office of Naval Research, Department of the Navy, and the University of Florida NR 163-106 (580-02).

The spring "runs" provide gradients of conditions from the "boil" downstream. Because the rate of flow of each run is relatively constant, a distance down the run corresponds to a time interval following the first meeting of sunlight and water. Thus the spring run can be used to study rates of water change. Several of the runs involve a transition from fresh water to sea water of the ocean. Some springs have oxygen gradients. Some have fish populations and some are isolated from such populations.

Thus there exists a marvelous opportunity to study community metabolism and productivity in the ready-made natural laboratory in which whole communities can be studied under controlled conditions. The series of natural experiments that have been set up seem ideal for studying the role of the factors that control productivity.

The purpose of this research was to study the basic workings of stream ecosystems and factors controlling individual, population, and community productivity by an analysis of the unique conditions supplied by outflow from the largest and best known of these chemostatic springs, Silver Springs (Figs. 1-6).

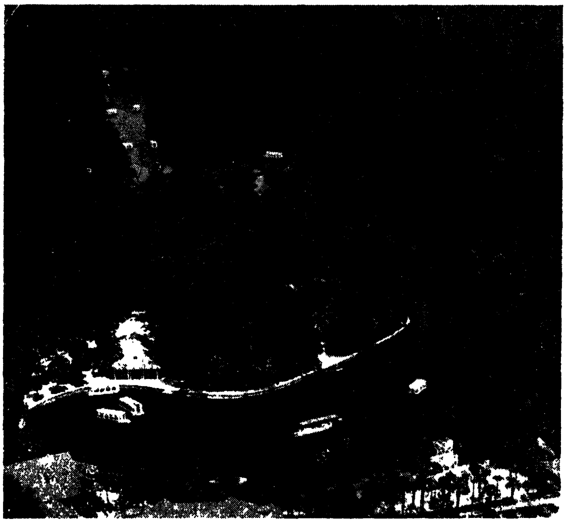

FIG. 1. Aerial view of the main boil and headwater region of Silver Springs, Marion County, Florida, looking eastward and downstream.

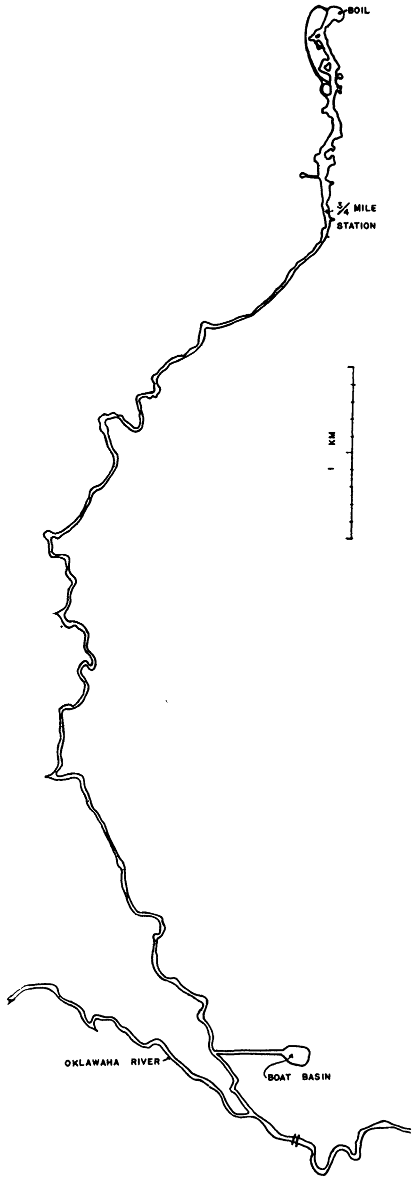

FIG. 2. Map of Silver River including the headwater region, the 5 mile "spring run," the artificial boat basin, and the mouth on the Okeawaha River (based on an aerial photograph).

The general plan was to characterize the chemostatic flow, to establish the qualitative and quantitative community structure, to measure the production rates, and to study the mechanisms by which the community metabolism is self-regulated.

Throughout the study an effort was made to apply a large variety of techniques to one stable environment. In order to do this in most cases, methods were not applied with the repetitions necessary to achieve the maximum accuracy possible with these procedures. However efforts are made to specify the levels of accuracy and to draw conclusions properly based on reproducible results of sufficient magnitude. Since Silver Springs was located 40 miles from the laboratory, the work at times took on the characteristics of expeditions.

EARLY RECORDS AND THE STEADY STATE IN SILVER SPRINGS

Although De Soto camped near Ocala, there is apparently no recorded evidence that either he or Ponce de Leon visited Silver Springs. Although good accounts of some of the other springs are found in the writings of both the elder Bartram and son, no description of Silver Springs is included (Harper

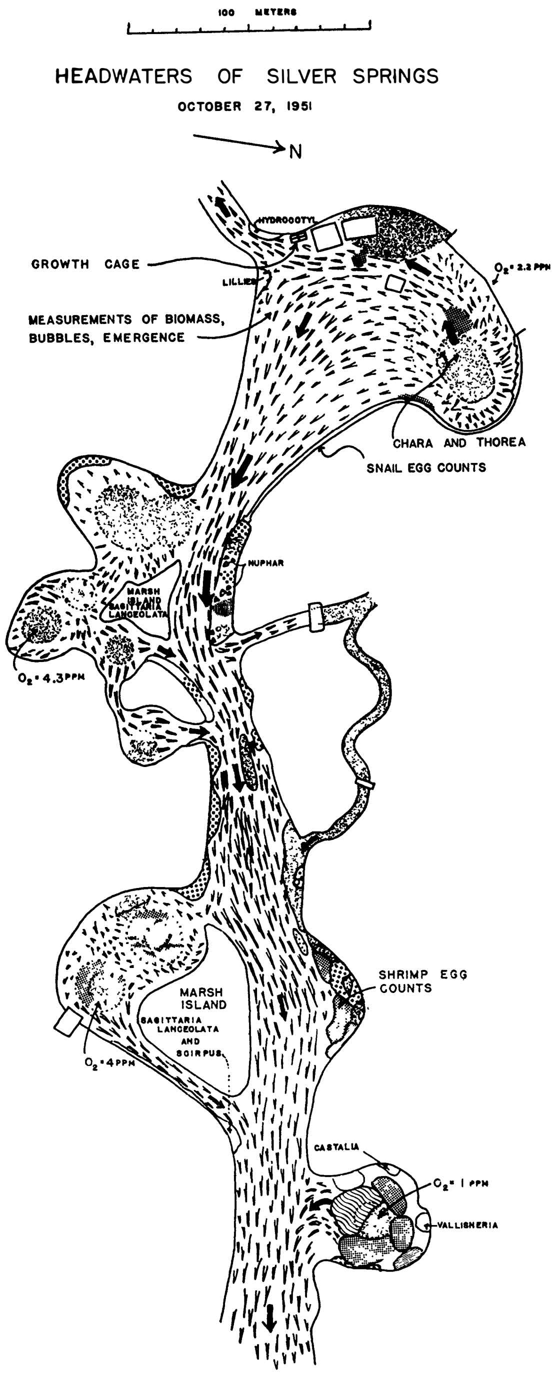

FIG. 3. Map of the upper headwater region of Silver Springs showing plant communities, general current patterns, study stations, and oxygen concentrations. The map was contructed October 27, 1951 with hand compass and string. Large dots, Pontederia; small dots, Najas; fine bars, Eichornia; wavy lines, Ceratophyllum.

1942). However, some more recent accounts of Silver Springs have been found in the literature. J. Leconte in 1860 visited the beautiful Silver River and wrote

FIG. 4. Underwater view in the main boil area of the typical Sagittaria and epiphytic aufwuchs community showing the waving grass, the splendid visibility, and herbivorous turtles held by the observers (William Ray, Jr. and Ginger Stanley).

a scientific paper in the American Journal of Science (1861) on the optical properties of this unusally clear stream and described "moss like" plants on long waving grass blades. Brinton (1859) describes moss and "dark green sedge waving its long tresses" and large catfish from a visit in 1856. He also recorded a boil depth of 41 ft., a temperature of 73.2 deg. F. and a main boil discharge of 300 million gallons a day all essentially similar to recent figures. In May, 1864 a Confederate soldier wrote a letter to his wife describing the "thick carpet of perfectly green grass" (Anon. 1868).

There is enough in these descriptions to indicate that then as now the broad expanses of stream bottom were dominated by dense waving blades of fresh water eelgrass (Sagittaria) coated with growths of algae (Fig. 4). A continuing prevalence of the grass communities since 1900 is recorded in a succession of underwater photographs in the phamphlets and circulars advertising Silver Springs (filed in Florida room; Univ. of Florida Library, Gainesville). These early observations, added to the evidence of little change during the 4 years work on the present project, are direct evidences that remarkable stability exists in a very rich and fast growing community. Apparently for long periods of time there is a steady state. Evidence given below shows the extent to which the geological sources of the outflow water provide a constant hydrographic climate and the

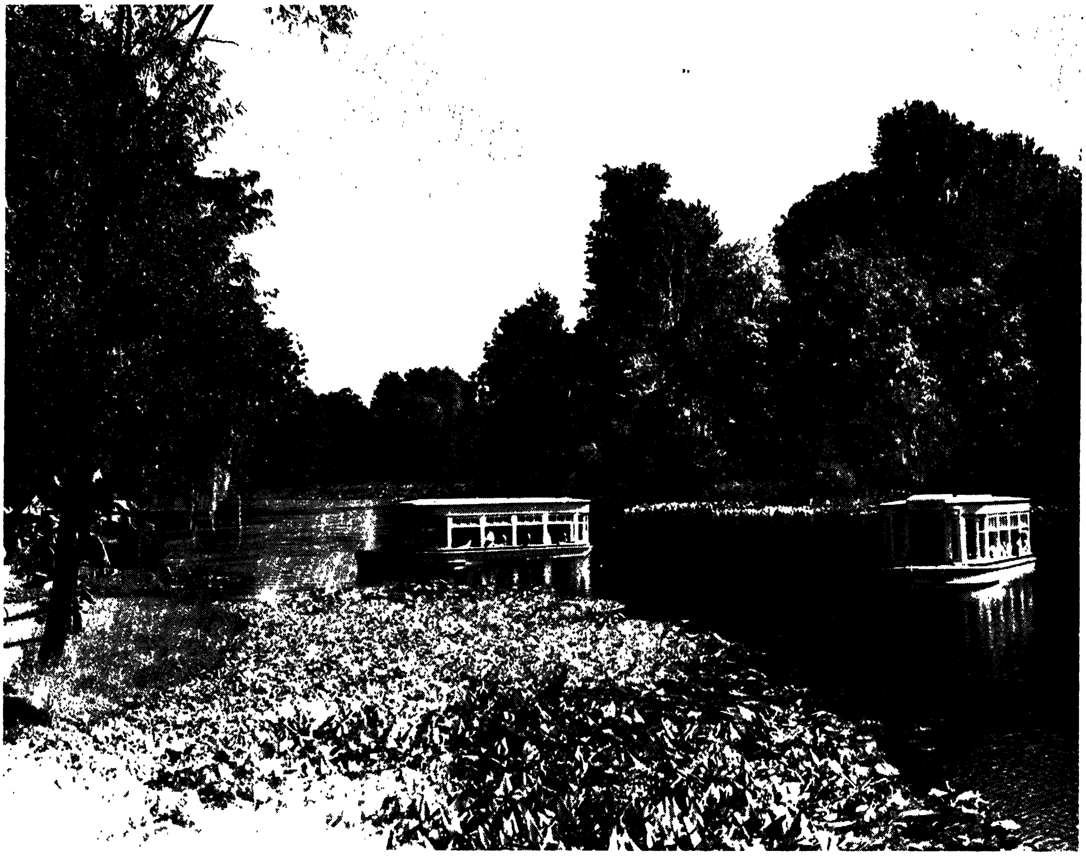

FIG. 5. View looking downstream from the narrows below the main boil showing patches of littoral macrophytes (Pontederia, Nuphar, and Pistia).

degree to which a climax community has resulted. It is symbolic that an old boat captain who guides on the river should ask if the waving grass ever grew. To him it has always seemed the same.

If a steady state exists, powerful new approaches and methods are possible. Data are cumulative and things not measured one day may be measured later. New methods of thermodynamics of the steady state apply as cited below. Rate techniques involving flow systems are directly applicable. Most terrible and healthy for the poor ecologist is the realization that anyone can check his field work at any later time, a rare situation indeed heretofore. The principal change in the upper mile zone, where most of the study has been made, is the enclosure of the boil with a wall along the northern border with a corresponding reduction in the area of shallow, somewhat more stagnant littoral waters. Hubbs and Allen (1943) indicated a decrease in fish species associated with the removal of this habitat. Apparently the main flowing stream community has not, however, been much modified.

A long history of permanency is of course no guarantee of a future, for when industry and large municipalities locate nearby, large springs cease flow as the demands on the artesian ground water lower the table. This has already happened at Kissingen Springs, Polk County, Fla. and Palma Ceia Springs, Hillsborough County, Fla. (Cooper, Kenner & Brown 1953).

PRODUCTION PROBLEMS IN FLOWING WATERS

In recent years rapid advances in techniques and thinking have led to conceptual schemes based on much evidence as to the workings of aquatic communities in lakes, estuaries, and oceans. By measuring the flux of energy, the energy partition, the controlling factors, and associated resulting biological phenomena, overall and characteristic quantitative patterns have been discovered. In contrast few attempts have been made to study overall community metabolism, to measure production rates, or to develop community concepts for streams.

The study of Silver Springs reported here has been made with the purpose of determining the basic structure and workings of flowing water ecosystems by the careful study of one stream under some unusually favorable conditions provided. In recent years such holistic consideration of the energy flux and biomass have provided a fruitful approach to the understanding of many types of ecological communities. A general account of the concepts in-

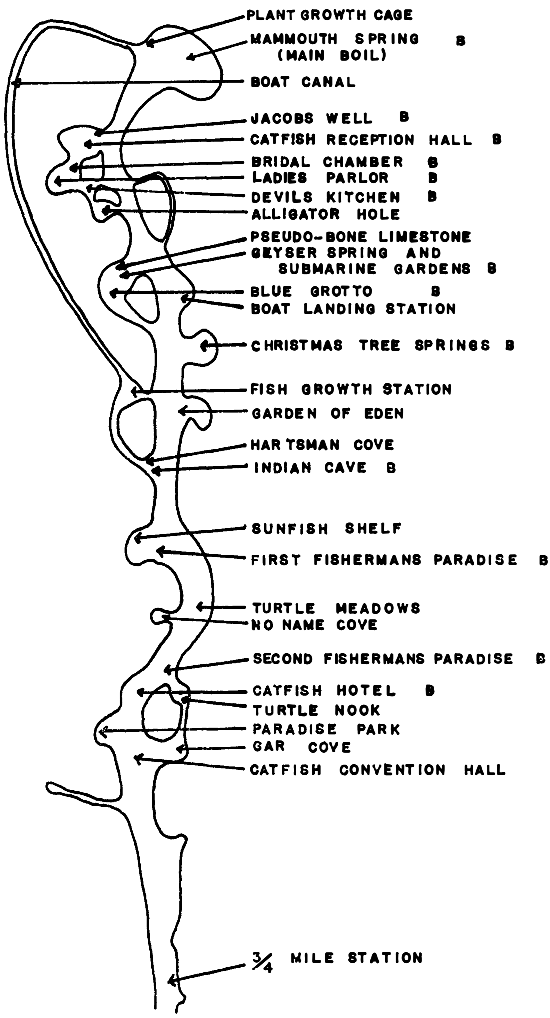

FIG. 6. Map of the upper ¾ mile zone of Silver River showing principal "boils," tourist points, the side canals, and study stations. The traditional names were supplied by Mr. William Ray, Jr. Active boils are designated by "B."

volved is given by H. T. Odum and E. P. Odum (1953). Diagrammatically, the object of the energy approach may be said to be the complete quantitative determination of the states and flow in Figure 7 as well as the control mechanisms by which such a picture is sustained. The story in this paper concerns the details and workings previewed in Figure 7.

A review and summary of the scattered but extensive literature on productivity of flowing water communities have been presented elsewhere (Odum 1956a, 1956b), but some principal hypotheses as to the workings of streams may be restated here before data are presented from Silver Springs.

1. A hypothesis was presented by Odum and Pinkerton (1955) based on theoretical reasoning that in ecological systems there is an optimum but low efficiency that gives the maximum productivity (power output) and that climax communities as well as other steady states tend to be adjusted to this state.
2. The productivity per area under the above adjustment thus is fixed but the productivity per gram biomass varies inversely with the size of the organisms. Since the photosynthesis per gram biomass may be roughly determined from the size of the cell under optimum efficiency maximum power adjustment, the standing crop and productivity become related and one may theoretically determine productivity from standing crop and vice versa.
3. The efficiency with which the energy of sunlight is fixed into organic matter by the photosynthesis of the primary producers may be increased by the action of the current. Thus the optimum efficiency for maximum power adjustment may depend on the current velocity. In a sense the current acts as an auxiliary energy source. Very high productivities may occur in streams.
4. The ratio of total community production to total community respiration determines the character of the biological community present by determining the relative standing crop biomass of the producer and consumer trophic levels.
5. The difference between the photosynthesis and community respiration is the difference between imports and exports of organic matter. Thus a balance sheet may be constructed.
6. Longitudinal succession (upstream to downstream) is directed towards a community of mixed autotrophs and heterotrophs and an organic content of the water of the order of magnitude of 1 to 15 ppm.
7. Under some conditions of climax or steady state a community may be established in spite of seasonal differences in the input of light energy and in spite of a rapid turnover.
8. The metabolism of a stream community may be readily determined by an analysis of the differences between the concentrations of the substances upstream and downstream from the communities.

In this study the remarkable natural situation in Silver Springs is utilized to measure the overall productivity of the community as a basis for checking the above hypotheses and developing other conceptual schemes as to the thermodynamics of streams. Another study (Odum & Odum 1955) on the flowing water community of a coral reef provides data from a marine environment. A similar approach has been used by E. P. Odum (1954) in terrestrial successional communities. Comparative studies on other Florida springs are in press (Odum, 1957).

CHEMICAL METHODS AND REPRODUCIBILITY

A fairly large number of replicate analyses were made of biologically active chemical constituents in the course of the study of community metabolism. It was immediately evident from the visible behavior of dye in the turbulent current that the mixing of water of slightly different trajectory would be expected to produce heterogeneity in successive samples. It became necessary therefore to assay both the variation inherent in the routine chemical methods as used and the variation due to real water differences associated with the heterogeneity of the flowing water from second to second. In Table 1 are given successive duplicate analyses from relatively homogeneous water. The standard deviations and confidence limits given indicate the variation inherent in the analytical techniques. The variations inherent in the water heterogeneity are presented in the section on chemostatic characteristics that follows.

Oxygen was measured with a direct Winkler method in 125-cc screw capped bottles. Reagents were added with dropping pipettes; titrations were done back in the laboratory. Water samples were taken with a U. S. Public Health Sewage Sampler: a Kemmerer bottle; a sampler consisting of two bottles on a stick; and in a few cases by direct filling. The various shortcuts used sacrificed some accuracy for speed although the errors introduced are far less than the large changes observed and the considerable minute to minute fluctuation as between successive duplicate samples. The Ohle (1953) method of running a control indicated that there were few interfering substances in Silver Springs water thus justifying the unmodified Winkler method (Table 1). Water taken from the floor of the boil was not significantly lower in oxygen than that at the surface (Table 1).

During the first two years carbon dioxide was collected in 250-cc glass-stoppered bottles and measured by the phenolphthalein titration in 100-cc samples in 125-cc glass bottles surrounded by matching samples representing water before and after the endpoint. Mr. Gordon Broadhead cooperated in a test of technique reported in Table 1. The inherent difficulty with the very faint endpoint and the difficulty with the rapid diffusion out of carbon dioxide from these carbon dioxide rich waters caused the analytical accuracy to be much lower for carbon dioxide than for oxygen (see Table 1). The pH determined carbon dioxide values from the Moore (1939) equations were somewhat more accurate and were used in the last of the study. Where large diurnal series of samples were collected as a part of other operations it was necessary to hold samples 6 to 18 hours. This practice is less serious in Silver Springs than in most waters because of the low total organic matter content of 0.8 ppm. The low BOD of the water is discussed subsequently. The main error arises from the diffusion loss in handling. The main difficulty encountered with carrying an electronic pH meter into the field was the drift due to the mists and fog over the water during night work in a moist subtropical area.

A very expensive effort was directed at nitrate metabolism. Nitrates were first determined with the phenol-disulfonic acid method (American Public Health Association 1936) and subsequently with the more reproducible and rapid strychnidine method of Zwicker & Robinson (1944). Because of small biological utilization (compared to oxygen) and be-

TABLE 1. Variation Inherent in Analytical Procedures[a]

	Mean	Standard Deviation	Maximum percent deviation expected for 95% of the analyses
CARBON DIOXIDE			
Titration of 100 cc samples with .02N NaOH and phelnopthalein. ppm			
Twenty duplicate samples were drawn from the same gallon jug and titrated by two persons.			
(1). Silver Springs Water:			
By Broadhead: 7.8, 7.6, 7.9, 8.1, 7.7, 8.1, 8.0, 8.3, 7.6, 7.8,	7.89	.226	6
By Odum: 6.9, 7.6, 8.3, 7.4, 7.5, 7.9, 7.3, 7.1, 7.7, 7.1,	7.48	.397	11
(2). Crystal Springs Water			
By Broadhead: .97, .88, 1.75, 1.50, 1.14, 1.41, 1.14, 1.41, 1.50, 1.14, 1.14,	1.28	.259	40
By Odum: 1.14, .88, .88, 1.06, 1.14, 1.58, .88, 1.14, 1.49, 1.14,	1.23	.229	37
OXYGEN			
Unmodified Winkler Method; 125 cc bottles Direct			
Winkler procedure as routinely carried out using 125 cc screw cap bottles and dropping bottles			
duplicate analyses on water from the same gallon jug			
5.22, 5.25, 5.31, 5.27, 5.32, 5.38, 5.28, 5.37	5.30	.052	2.0
duplicate analyses on water from the same carbuoy			
7.40, 7.35, 7.39, 7.38, 7.41, 7.41, 7.33, 7.28, 7.36, 7.31,	7.362	.109	1.5
Comparison of sampling methods: Homosassa Springs Boil bridge, Feb. 2, 1954, W. Sloan. This includes variation due to water heterogeneity.			
filled by hand (air escaping in bubbles)			
4.60, 4.90, 5.25, 5.15 ppm	4.97	.251	10
filled with Sampler			
4.78, 5.12, 5.00, 4.98	4.98	.102	4
Comparison of Direct Winkler method with Ohle Iodine-iodide method			
All samples from downstream station at Silver Springs			
Direct method:			
5.19, 5.48, 5.15, 5.20, 5.28, 5.34,	5.27	.113	4.3
Ohle method:			
5.18, 5.37, 5.58, 5.38, 5.21, 5.36,	5.34	.116	4.3
Test of boil samples taken at 1 ft. depth and 30 ft. depth			
1.82, 1.77, 1.66, 1.78, 1.33	1.672	.179	21
1.79, 1.88, 2.44, 2.09, 1.79	1.998	.246	25
pH with Beckman model G, and thus a test of pH determined CO_2, duplicate analyses from the same carbuoy			
8.22, 8.28, 8.29, 8.32, 8.33, 8.33, 8.34, 8.33, 8.33, 8.33,	8.310	.036	1

[a] Also see Table 8 for duplicate analyses of Silver Springs water, separate samples collected simultaneously at one station.

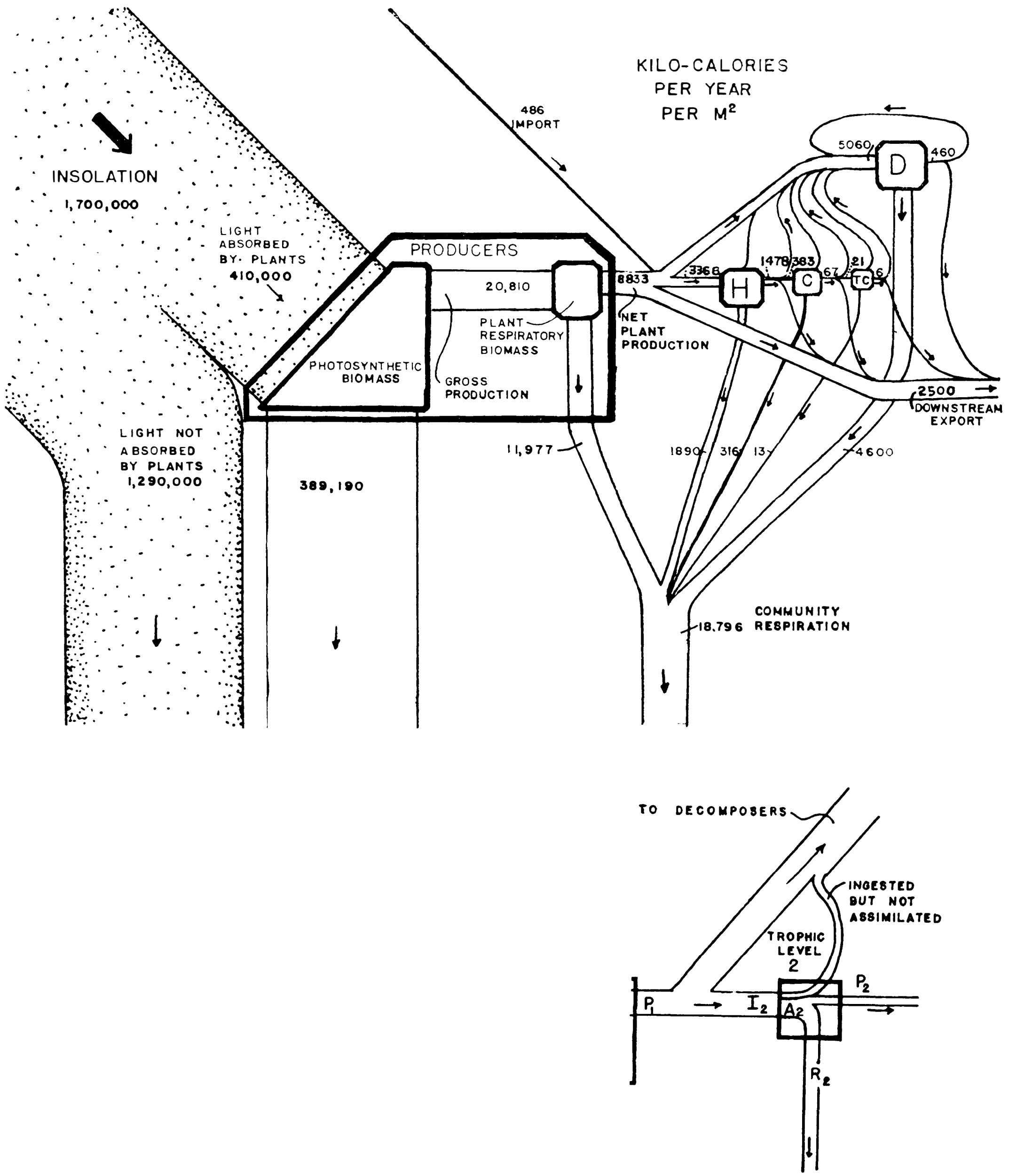

FIG. 7. Energy flow diagram with estimates of energy flows in kilo-calories per square meter per year in the Silver Springs community. The small diagram contains symbols used in text discussion (P, production; I, energy intake; A, consumer assimilation; R, respiration).

Energy flows are estimated very roughly for purposes of indicating orders of magnitude only on the basis of data given below: Conversion factors used are: 5.8 Cal/gm protein; 4.0 Cal/gm carbohydrate; 3.1 Cal/gm oxygen metabolized as protein; 3.4 Cal/gm oxygen metabolized as carbohydrate; 23% ash in Sagittaria-aufwuchs.

Incident light of visible, usable wave length: 4.1 x 10^5 Cal/m^2/yr (Mean incident insolation of 1.7 x 10^5 Cal/m^2/yr for 29.2° N. Lat. from Kennedy, 1949, for the 10 days on which diurnal curves were obtained in Table 10; ½ taken as usable for photosynthesis; 60% penetration to mean productive depth of 1.8 m; 10 to 30% diminished by shading of the trees).

Gross primary production: 20,810 Cal/m^2/yr (6390 gm/m^2/yr from Table 15 minus 1470 gm ash; 13.3% protein from quotients of Table 10).

Import of allocthonous organic matter as bread fed to the fishes every day: 486 Cal/m^2/yr (70 loaves per day; 365 gm/loaf, mostly carbohydrates).

Total community respiration: 18,796 Cal/m^2/yr (6000 gm/m^2/yr from Table 15; 23% ash; 13.3% protein. The 4% discrepancy in Table 15 is taken up here for purposes of balancing the diagram by substracting 794 Cal/m^2/yr).

Total herbivore production: 1478 Cal/m^2/yr (Sum of production of larger and smaller herbivores).

Production by larger herbivores: 268 Cal/m^2/yr (Mean of 141% turnover/yr for some of the dominant herbivores from Table 13: mostly protein: 34 gm dry/m^2 standing crop of larger herbivores from Table 7).

TABLE 1. (Continued)

	Mean	Standard Deviation	Maximum percent deviation expected for 95% of the analyses
NITRATE			
(analyses prior to Sept. 1, 1953 by phenoldisulphonic acid method; after this date by the strychnidine method)			
Phenoldisulphonic acid method:			
5 duplicate analyses on samples from the same bottle, March 24, 1953.			
.57, .65, .53, .59, .62 ppm	.592	.105	35
10 duplicate anelyses on samples from the same bottle, Silver Springs, Feb. 12, 1953.			
.57, .31, .54, .44, .46.			
.32, .41, .51, .32, .28	.416	.045	22
Strychnidine Method			
10 samples from the same carbuoy optical densities:			
.110, .095, .088, .097, .094, .120,			
.139, .102, .110, .090	.015	.0149	28

cause of the inherent variation both in the water and in the methods, it was possible to show differences only statistically with whole series. Consequently, the conclusions about nitrate metabolism are only tentatively drawn. The large series of values do, however, give a good general picture as to the fluctuation of a biologically active trace element in a stable ground water outflow and in the stream after a ¾ mile flow. 5 cc of water, 5 cc of strychnidine reagent and 5 cc of low nitrate sea water were added uniformly in 20-cc glass vials and read in a Klett-Summerson colorimeter after about 5 hours. With each series of about 20 samples were run 2 blanks and 3 unknowns. A graph was thus plotted for each series. Interference from contamination from glass is not so serious with the high nitrate levels of Silver Springs as with marine waters.

Inorganic phosphate determinations were made with the ammonium molybdate method (Robinson & Kemmerer 1930). A series of digestions on Silver Springs waters (Odum 1953a) indicated that 93% of the dissolved phosphorus was inorganic so that subsequent analyses were made of inorganic phosphorus only. As with the nitrate analyses the biological action of the community was too small relative to the fluctuations in the methods and waters to show anything but small statistical trends. Three standards were run with each series of analyses.

Attempts to use polyethylene bottles were entirely unsuccessful and all data with these were discarded when it was found that nitrates and phosphates are very rapidly removed by those bottles, far more rapidly than in ordinary glass bottles.

Versenate hardness was determined with Taylor Co. reagent and procedure; alkalinity was determined with methyl purple indicator. pH was determined with a Beckman Model G. instrument. Dissolved organic matter was determined with a hot acid permanganate oxidation method (1937 standard methods) as well as by BOD.

Chlorophyll was determined with a Beckman spectrophotometer by procedure of Richards & Thompson (1952). Pseudoplankton was caught on millepore filters; the whole filter was then dissolved in acetone and centrifuged. The supernatant was then dissolved in acetone and centrifuged. The supernatant was then compared in the spectrophotometer with a blank made from the filter alone. Other methods are as indicated subsequently.

ACKNOWLEDGEMENTS

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Production by smaller herbivores: 2110 Cal/m²/yr (9100% turnover per year from Table 13; 2.3 dry gm/m² standing crop of smaller herbivores from Table 7).

Herbivore respiration: 1890 Cal/m²/yr (1.5 mg/gm dry/hr oxygen metabolism obtained from an average of .35 for midges and caddisflies with tubes, .60 for snails, 3.54 for gammarids; mostly protein).

Total intake by herbivores: 3368 Cal/m²/yr (Sum of herbivore respiration and production).

Carnivore respiration: 316 Cal/m²/yr (1.10 mg/dry gm/hr oxygen metabolism from .39 for stumpknockers and 1.81 for Lucania as possibly representative of carnivores; mostly protein; 10.7 gm/m² standing crop of carnivores from Table 7).

Carnivore production: 67 Cal/m²/yr (110% turnover/yr for stumpknockers as representative although partly herbivorous; 10.7 gm/m² standing crop).

Carnivore intake: 383 Cal/m²/yr (Sum of carnivore respiration and production).

Top carnivore respiration: 13 Cal/m²/yr (.065 mg/gm wet/hr or .33 mg/dry gm/hr oxygen metabolism for black bass from Clausen quoted by Hart (1952); mostly protein;1.5 gm/m² standing crop of dry top carnivores from Table 7

Top carnivore production: 6 Cal/m²/yr (Turnover 69.5% from tagging recovery (Caldwell et al., 1956; mostly protein).

Top carnivore intake: 21 Cal/m²/yr (Sum of top carnivore respiration and production).

Decomposer respiration: 4600 Cal/m²/yr (Sum of mud and aufwuchs bacterial respiration estimates).

Mud surface bacterial respiration: 2300 Cal/m²/yr (.079 gm oxygen/m²/hr from bell jars in Table 11; assumed half protein).

Aufwuchs bacterial respiration: 2300 Cal/m²/yr (.3 gm dry/m² standing crop of grass bacteria the same as the bacterial standing crop in the upper 1 cm of mud; see Tables 7 and 9; metabolism of grass bacteria assumed in Table 13 to equal that of the mud).

Decomposer production: 460 Cal/m²/yr (Assumed 9% bacterial efficiency).

Decomposer intake: 5060 Cal/m²/yr (Sum of production and respiration estimates).

Producer plant respiration: 11,491 Cal/m²/yr (Difference between total community respiration and that of other respiration components in Figure 7).

Export of organic matter: 2500 Cal/m²/yr (766 gm/m²/yr exported from Table 15; 13% protein, 23% ash).

Net plant production: 8833 Cal/m²/yr (Difference between gross production and plant respiration estimates).

See text section on energy flow diagram for further discussion.

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PROPERTIES OF THE CHEMOSTATIC OUTFLOW

SILVER RIVER

Silver Springs and its river are pictured from aerial view in Figure 1 and from an underwater view in Figure 4. The map in Figure 6 indicates the names of the boils following the custom of the boat guides as they carry their tourists about in glass bottom boats. The communities of aquatic plants in the upper zone are pictured in some detail in Figure 3. Some views of the shores mostly in their natural condition are given in Figure 5.

There is an extensive and interesting series of boat trips in glass bottom boats as the main attraction in this highly commercialized area. A running account of the sights is given by the boat captains. Most of what is said is picturesque and designed to entertain. The large volume of tourism has actually been an advantage as it has provided continual observation by interested boat guides who have made many interesting comments. The boats are almost all electrically driven so that the water is not affected by exhausts. The large volume of boat-hours is itself a pretty constant factor throughout the year during daylight hours.

Five miles downstream the river joins the humic-watered Oklawaha River and loses many of its unusual properties. In times of drought, however, (as in the summer of 1955) the river flow is so minor that the clear spring water dominates the community for many more miles.

THERMOSTATIC CHARACTERISTICS

In the bulletin on the chemical character of Florida Springs (Ferguson *et al.* 1947) 19 temperature measurements were reported for Silver Springs for 1945 and 1946 between 22.2 and 23.3° C. A few temperature measurements made during this study showed a continuing thermostatic condition through the 5 years studied 1950-1955. Temperature observations for the boil are as follows:

Observations made from a boat trip down the Silver River before dawn on a cold night in winter when the maximum degree of cooling would be expected revealed a drop of 1° C in 5 miles. In the middle of a clear hot day in summer (June 30, 1952), when heating might be expected to be maximal, there was only a 1° C rise in 5 miles in spite of an air temperature over 100° F. The turbulent flow of the stream is adequate to mix throughly all the waters except in a few nooks along the shore. A thermistor bridge was constructed and a horizontal map was made of the temperatures of the surface waters of the head region. The thermistor was hung from the bow. The boat was rapidly criscrossed through the stream with one observer reading the thermistor readings and another plotting the values on a map as shown in Figure 8. In spite of some heating in the areas of more slowly moving water, the water does not remain stationary or stratified enough to develop more than about 1° F rise in the backwaters. There is an opportunity here for study of rates of heat transfer across thermostated water surfaces that should be followed further.

On some of the carbon dioxide graphs described below a series of sharp fluctuations around sunset in downstream valves suggested that cooling is permitting some water trapped among plants to eddy back into the main stream causing heterogeneity. Unlike the hot springs which have been studied or the rather cold springs of northern Europe, Silver Springs has a sufficiently high temperature so that the spring phenomena are comparable to the phenomena of interest in other communities during their main growth seasons.

CURRENT AND DISCHARGE

Half of the volume of the Silver Springs discharge arises from the main head boil and the rest from a number of smaller boils in the head region. The smaller boils are a complicating factor in many measurements, but provide additional natural experimental situations.

The U. S. Geological Survey has made a careful study of the total discharge relative to stage height and makes regular measurements of the stage at the same station where most of the downstream measurements of this study were made. The seasonal picture of this discharge during the period of study is given in Figure 9. It has been previously demonstrated that the Silver River reflects the erratic rainfall and evaporation balance (Ferguson *et al.* 1947). Thus the outflow, although far more stable than that in surface rivers, is not constant (Fig. 9) but has a tendency toward a maximum discharge in the fall and minimum at the end of the hot dry spring. After some quick rains there is, rarely, an influx of some nonartesian, darkly-stained and turbid water, although this is minor and restricted to a few places and a few hours following rain. Small changes in stage of the stream result in relatively large differences in flow volume although the current velocities are less affected. The mean flow at a representative cross section is .7 ft per second

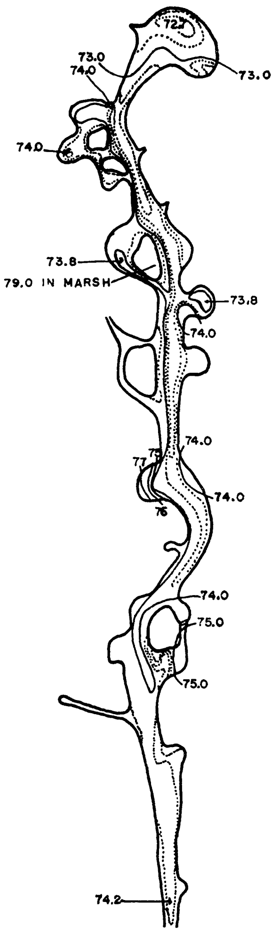

FIG. 8. Map of the horizontal distribution of water temperature on a hot summer day, 3:00 p.m., June 8, 1955. The isotherms are based on 500 plotted temperature readings in degrees Fahrenheit made rapidly with a thermistor suspended 6 inches below the prow of a small boat. The boat driven by an outboard motor was rapidly crisscrossed, one observer reading the microammeter and one plotting the figures. The entire area was covered in about an hour in a downstream direction so as to keep approximately abreast of the drift of the same water mass.

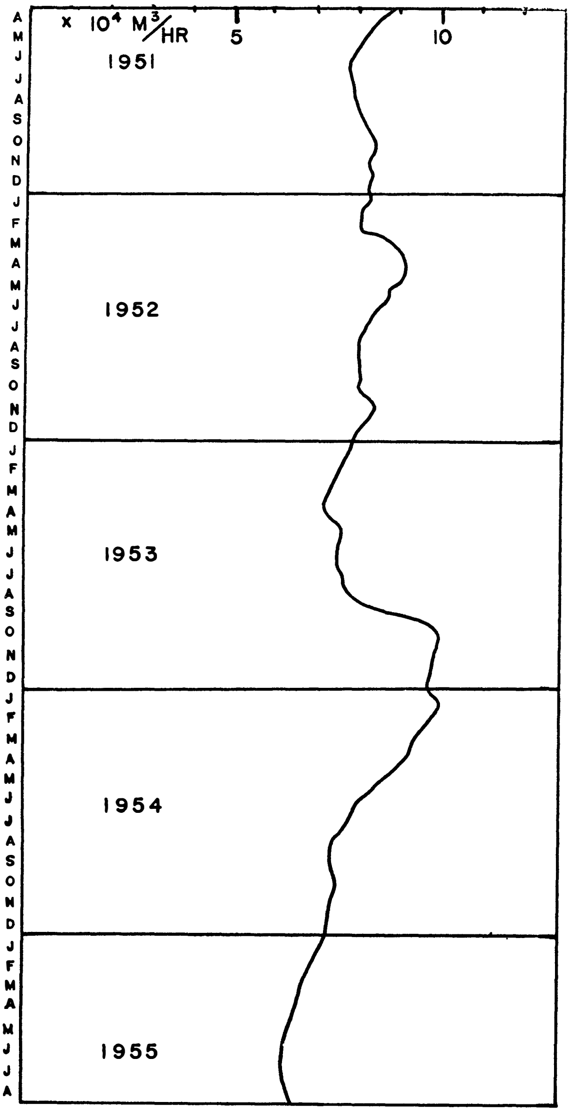

FIG. 9. 5 year record of water discharge from the ¾ mile headwater zone of Silver Springs River; data obtained by the U.S.G.S., Ocala, Fla. (see acknowledgement). Discharge in cubic meters per hour.

(.21 m/sec). If one may judge from chemical data below on trace elements, there is little qualitative difference in the outflow during the annual cycle.

The horizontal distribution of current velocity may be inferred from the horizontal map of temperature in Figure 8 on hot summer days where the stagnant water becomes a few tenths of a degree warmer before it finally passes out of the head region. These detailed patterns of current trajectory are important in relating overall community metabolism to its component parts, and are a major controlling principle in the community.

Vertical patterns of current (Fig. 10) were determined with visual observations of fluorescein dye from a dropping bottle pipette carried by an underwater observer and with a propeller-type midget current meter.

Considerable variation in velocity is found even in the main current due to the different depths as indicated by the longitudinal profile in Figure 11.

The total discharge of about 600 million gallons per day is often cited as equal to the total industrial, agricultural, and municipal water use of the state of Florida. Of course as rivers go this is a small river, but as springs go this is among the largest in the world.

CHEMOSTATIC PROPERTIES; THE VARIOUS BOILS

In their study of the chemical characteristics of Florida Springs, Ferguson *et al.* (1947) cited many

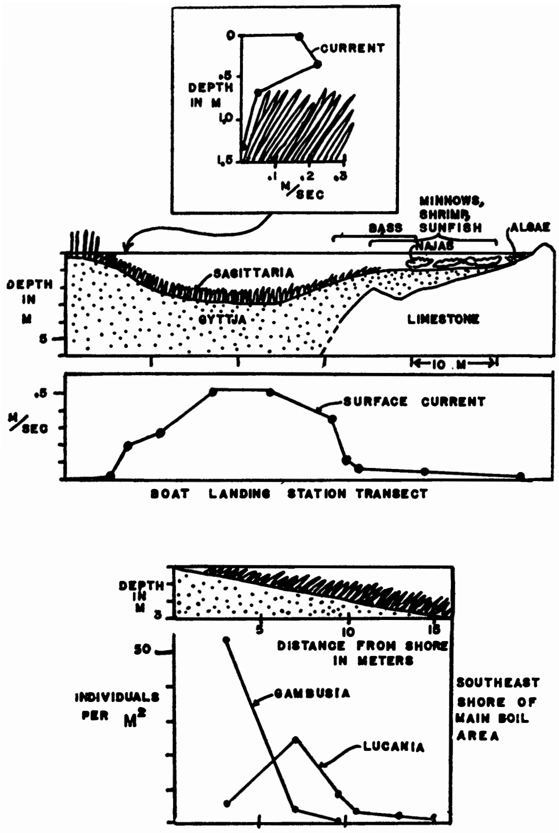

FIG. 10. Transects across Silver Springs showing the distribution of current velocities and some principal organisms. The transect at the boat landing station was made June 29, 1955; the current velocities were measured visually 1 ft below the surface with dye. Counts of the small fishes along the shore were made with a 10 x 10 ft frame visually on April 9, 1953. Littoral algal mats on April 5, 1954 were dominated by Spirogyra, Oedogonium, and Rhizoclonium.

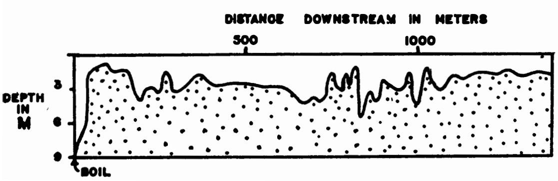

FIG. 11. Bottom profile in the middle of the channel of the headwater zone of Silver Springs, measured by Caldwell and Hellier in June, 1955.

cases where chemical analyses of the major dissolved ions as much as 40 years apart showed within the error of the methods little or no change in chemical composition. Two such analytical series for Silver Springs' main boil have been copied in Table 2 along with spectrographic analyses by J. A. Fiskel and a few determinations made during the course of this study. The general constancy seems established for the major constituents. To further confirm the chemostatic nature of the ecosystem, efforts

TABLE 2. Characteristics of the Main Boil in Silver Springs, Florida, Expressed in ppm Unless Otherwise Specified.

Constitutent	Dec. 16, 1907[a]	Oct. 21, 1946	1950-1955[b]
Calcium	73	68	72
Magnesium	9.2	9.6	..
Sodium	9.8	4.0 } 5.1	..
Potassium		1.1	..
Total Hardness (as $CaCO_3$)	220	209	200[c]
Temperature	...	...	23.0
Radioactivity	...	...	Not detected[d]
Total Alkalinity (as HCO_3)	219	201	195[e]
Free CO_2	...	5[f]	8.8[g]
pH	...	7.8[f]	7.53
Sulfate	44	34	....
Chloride	7.7	7.8	9.6[h]
Silica	13	9.2	....
Dissolved Oxygen	..	...	2.24[j]
Oxidation Potential (volts)	..	...	0.436
Dissolved Solids	274	237	241
Bacteria colonies per ml plated on caseinate agar	...	...	99
Algal cells per ml	...	...	4
Specific Conductance Micromhos at 25 deg. C.	...	401	.
Color (USGS Scale)	...	4	.
Minor Constituents in Parts Per Million			
Strontium	...	...	0.78[l]
Boron	...	...	0.0145[n]
Nitrate-Nitrogen	.2	1.3	0.46[m]
Nitrite-Nitrogen	...	...	0.0015[o]
Kjeldahl N	...	...	0.002
Phosphate-Phosphorus	...	...	0.054[m]
Dissolved Organic Matter	...	...	0.62[i]
Iron (Fe)	...	.04	0.29[p]
Chlorophyll	...	...	0.00029[m]
Aluminum	...	...	0.30[p]
Manganese	...	...	0.0010[p]
Copper	...	...	0.007[p]
Silver	...	...	0.002[p]
Molybdenum	...	...	0.002[p]

Cobalt, tin, mercury, zinc, lead, beryllium, arsenic, nickel, palladium, cadmium, germanium, indium and bismuth were not detected in the spectrographic analysis by Dr. Fiskel.[p]

[a] Ferguson, Lingham, Love, and Vernon, 1947.
[b] Most measurements were made on water taken in the boil near the surface. Some mixing has already taken place here with previously emerged water recirculating in eddies so as to be drawn into the main stream of newly emerging water. Thus a few cells could be found in the turbulent outflow of the boil. See Table 4 for oxygen differences between the surface and bottom of the main boil.
[c] Versenate, Feb. 12, 1953.
[d] Determined roughly with a survey meter by H. Moul. The residue from the evaporation of 4 liters was not different from background of 32 counts per minute. 5 different samples were evaporated.
[e] Methyl purple indicator, Feb. 12, 1953.
[f] Delayed analysis. Since this property changes with time as described in the text the e act value may be questioned.
[g] Phenolpthalein titration with KOH; see Table 8.
[h] Feb. 12, 1953; see Figure 26.
[i] Feb. 25, 1954.
[j] Winkler, method, see Table 8.
[l] Odum (1951).
[m] See Table 8.
[n] Odum and Parrish (1954).
[o] Alpha napthylamine acetate method (standard methods).
[p] Spectrographic analysis by John G. A. Fiskel, Univ. of Florida Agricultural Experiment Station, Gainesville, Fla., of an evaporated and ashed four liter sample. These figures should be considered as orders of magnitude. Quantitative estimations were based on densitometer comparisons with standards consisting of mixtures of constituents in proportions often found in soils.

have been made to establish the magnitude and variation in the minor and biologically active elements.

It has been shown by Ferguson *et al.* (1947) that adjacent boils a few yards apart may or may not have similar chemical composition. A striking case of this phenomenon was analyzed in the present project at Chassahowitzka Springs, Citrus County, Florida (Odum 1953b) where one boil contained a flow with 53 ppm chloride and a nearby boil contained a flow with 750 ppm chloride. The various small boils that contribute water to Silver River are marked on the map in Figure 6 and some data on water from the boil basins are given in Table 3.

TABLE 3. Biologically active constituents in the various boils of the headwater area of Silver Springs, Fla. For boil locations see Figure 6.

Name of Boil	Oxygen[b] ppm night	Oxygen[b] ppm day	Carbon Dioxide[c] ppm night	Carbon Dioxide[c] ppm day	Nitrate-N[d] ppm night	Nitrate-N[d] ppm day
Main Boil[a]	2.26	2.65	9.58	9.15	.463	.491
Smaller side boils:						
Reception Center	3.20[e]	4.10[h]	9.2[f]	7.9[h]	.48[e]	.36[h]
	4.03[e]	4.10[h]	10.0[f]	11.7[h]	.47[e]	.36[h]
			10.9[g]			
Bridal Chamber	4.05[e]	4.75[h]	10.6[f]	7.7[h]	.43[e]	.37[h]
	4.22[e]	4.70[h]	10.6[f]	8.3[h]	.53[e]	.41[h]
Ladies Parlor	4.15[f]	4.57[h]	7.9[f]	9.3[h]	.52[g]	.25[h]
	4.27[f]	4.30[h]	9.6[g]	7.2[h]	.50[g]	.40[h]
Devils Kitchen	4.03[f]	4.86[h]	10.2[f]	7.1[h]	.50[g]	.42[h]
	4.20[f]	4.39[h]	9.6[f]	8.0[h]	.50[g]	.56[h]
			9.6[g]			
			8.9[g]			
Blue Grotto	4.25[k]	3.51[i]	8.0[l]	8.7[j]	....	.42[i]
	4.14[k]	3.48[i]	12.1[f]	8.7[j]	....	.46[i]
	4.75[l]	4.33[n]		8.8[j]		
	4.79[l]			8.6[j]		
Christmas Tree Springs	1.00[f]	1.66[h]	7.1[g]	5.2[h]	.36[g]	.24[h]
	1.13[f]	2.05[h]		5.9[h]		.18[h]
Fisherman's paradise 1	3.36[e]	4.35[h]	9.6[g]	7.6[h]	.45[e]	.26[h]
	3.40[e]	4.35[h]	10.6[g]	7.1[h]	.41[e]	.42[h]
Fisherman's paradise 2	3.22[l]	3.20[h]	8.8[g]	....	.33[g]	.33[h]
	3.53[l]	3.96[h]	8.3[g]	....	.38[g]	.33[h]
Mean of smaller boils[m]	3.548	3.895	9.34	7.87	.444	.360
	3.721		8.60		.402	

[a] Mean of data in Table 8.
[b] Direct Winkler method.
[c] Phenolpthalein titration.
[d] Strychnidine colorimetric method.
[e] March 15, 1954, 2-3 a.m.
[f] March 29, 1954, 3 a.m.
[g] May 20, 1954, 11:30 p.m.
[h] Feb. 25, 1954, noon.
[i] Feb. 18, 1954, noon.
[j] April 5, 1954, noon.
[k] March 13, 1954.
[l] May 23, 1954.
[m] Average of the mean analysis for each boil.
[n] April 5, 1954, 6:00 p.m.

Clearly some boils are distinctive and different from the main flow. Also it is apparent that some boils have a strong enough flow relative to the volume of the boil basins so as to be independent of day and night changes associated with the dense communities flooring the basins and boil sides.

Table 4 indicates the changes which occur in the 5 miles of run downstream due to ground water flows from rock fissures and some actions of the community. Like the temperature, the major chemical properties are little changed in the 5 miles of run. The headwater region where the main study was made is even more constant.

That the trace and biologically active elements as well as the major elements are relatively constant over long periods of time may be inferred from data from the main boil in Figure 12. There seems to be some trend in the oxygen curve and possibly other curves that is related to the total discharge indicated in Figure 9. The sampling of water was done from a boat above the main outflow. Because of the large eddies within the spacious boil area pictured in Figure 1, the water sampled included some water that had emerged previously and passed along the plants to be drawn into the outflow again. This is known to occur because plankton tows in the outflow water yield a few algae typical of the main communities. Thus the short time variability observed as indicated in the data in Figure 13 may involve a heterogeneity in the outflow water as well as heterogeneity created by drawing in lateral water. The relative action of these two possible sources of heterogeneity was not ascertained. From the standard deviations in Table 8 the percent variations of 95% of the samples are given.

From the point of view of the organisms, the microhabitat concentrations are of importance. Some

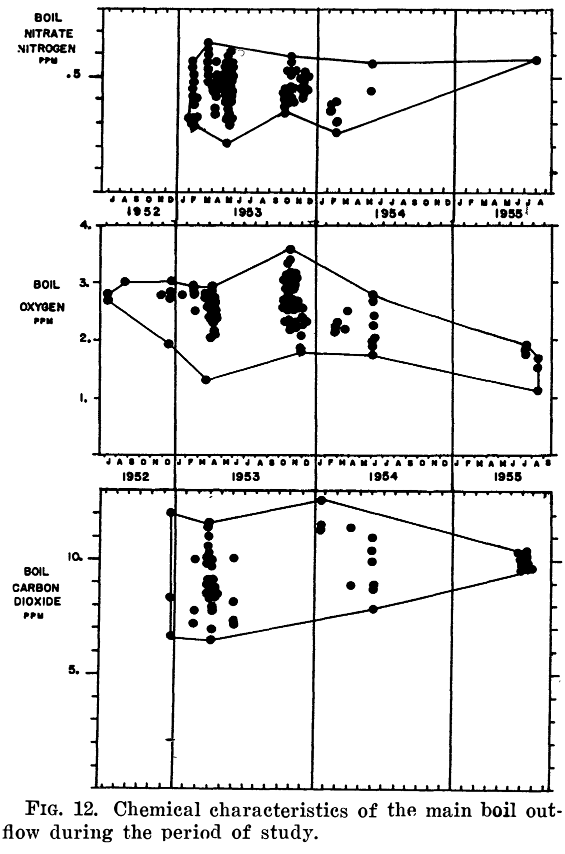

FIG. 12. Chemical characteristics of the main boil outflow during the period of study.

TABLE 4. Characteristics of the water as it flows down Silver River in the main channels.

Distance below the main boil							Phosphorus[b]		Oxygen ppm					Temperature deg C				Carbon-dioxide ppm		pH	
miles	km	NO_3-N[a] ppm	Cl[a] ppm	NO_2-N[a] ppm	Hardness[a] ppm $CaCO_3$ versenate	M. O.[a] alkalinity (methyl purple) ppm HCO_3	Inorganic ppm	Total ppm	winter dawn e	winter dawn d	day f	summer day b	summer day h	winter dawn e	day f	summer afternoon g	summer afternoon h	afternoon f	dawn e	dawn e	afternoon f
Boil	0	.47	.....	0.0024	200.4	161.6	0.041	0.047	2.7	2.8	2.0	3.0	......	23.0	23.0	23.4	......	12.0	13.9	7.7	7.4
		.31	9.5	0.0007	200.6	162.4	.....	.....	3.4	3.0	2.8	3.1	......	23.0	.....	23.8	......	......	11.1	7.7	7.1
.13	.21	.46	9.9	0.001	210.6	160.0	0.045	......	3.4	3.3	3.4	3.9	......	......	......	23.8	......	5.7	8.4	7.8	......
.25	.40	......	9.8	0.0	216.0	158.8	......	......	......	......	......	......	......	23.0	.....	23.8	23.4	......	......	......	......
.50	.80	.46	9.5	0.0	205.8	149.2	0.045	0.047	3.4	3.3	3.0	......	......	......	......	......	......	7.5	7.0	7.8	......
.63	1.00	.54	....	0.0	201.2	144.0	......	......	......	......	3.2	4.3	......	23.0	23.0	24.0	......	6.6	6.9	......	7.7
.75	1.20	.50	8.7	0.0	205.4	144.0	......	......	3.9	......	......	......	......	......	......	......	......	......	......	......	......
1.0	1.6	.32	9.9	0.0	201.8	144.0	0.040	0.046	4.1	3.7	3.6	4.9	......	22.5	......	......	......	6.2	6.2	7.8	7.7
1.5	2.40	......	......	......	......	......	0.051	0.053	......	......	5.1	5.2	......	22.3	......	......	......	7.6	6.2	7.8	7.8
2.0	3.20	.38	10.3	......	203.6	144.0	0.043	0.046	......	......	......	5.4	......	......	......	......	......	......	......	......	......
2.5	4.00	......	......	......	......	......	0.042	0.046	4.3	4.0	5.4	5.7	6.78	22.2	......	......	24.0	5.6	5.3	7.7	7.8
3.0	4.8	......	9.5	0.0035	200.8	131.2	0.041	0.041	4.3	......	5.0	......	......	22.2	23.0	......	......	5.2	5.8	7.8	7.8
3.5	5.6	.31	10.2	0.0012	201.8	142.8	......	......	......	4.0	......	5.3	......	......	......	......	......	......	......	......	......
4.0	6.4	......	......	......	......	......	0.040	0.048	4.0	......	5.3	......	......	22.1	......	......	......	4.0	7.1	7.7	7.9
4.5	7.2	.50	10.1	0.0005	205.0	141.2	......	......	3.9	4.4	6.2	5.3	6.32	22.1	23.0	......	24.0	6.3	6.7	7.7	7.7
5.0	8.0	.24	10.2	0.004	203.6	146.0	0.043	0.046	3.74	3.56	4.50	4.61	......	22.5	23.0	23.3	23.8	6.7	8.6	7.8	7.7
Mean	.....	.408	10.76	0.0013	204.35	148.4	0.0431	0.0466													

[a] February 12, 1953, daytime. [b] August 9, 1952, 2:30 p.m., cloudy. [c] Inflow of 6 ft. artesian well. [d] Nov. 12, 1952, 7:30 a.m., air, T12.0 deg C.
[e] Dec. 3, 1952, 7:30 a.m., air T, 13.0 deg C. clear. [f] Dec. 3, 1952, afternoon cloudy air T, 22.5 deg C. [g] May 23, 1954, clear 2:00 p.m.
[h] June 30, 1952, clear.

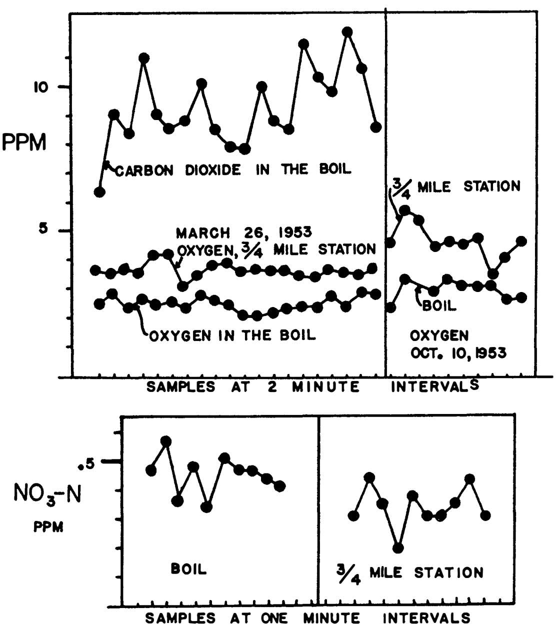

FIG. 13. Fluctuation of water quality in Silver Springs over short periods of time. Nitrate data were obtained April 9, 1953.

analyses were made in a few representative microhabitats to gain some idea of the extreme range of these localized effects. These are given in Table 5. The action of the community photosynthesis in the day and respiration at night is large although there is enough exchange even in plant beds in the back waters to prevent the lethal ranges of oxygen and complete nutrient depletion that result when communities are entirely enclosed. A typical community bottom portion enclosed in a bell jar at night had depleted the nitrate and oxygen in 8 hrs. The downstream changes of the community as a whole are considered in detail as a device for studying community metabolism in a later section. Although there are fluctuations associated with eddies, slight seasonal patterns of change described below, and microhabitat differences, the chemical character at any one place is essentially constant. On the average the hydrographic climate is more chemostatic than most lakes, streams, and marine environments.

The higher phosphorus values in Table 8 for Nov. 27, 1953 are atypical, unexplained and possibly due to experimental errors. On Oct. 1, 1953 after general heavy rains there occurred one of the periods when Silver Springs reaches a temporary maximum high water for a day or two. Phosphorus measurements were made which did not differ significantly from those made at other times.

LIGHT AND TRANSPARENCY

The extreme clarity of the Silver Springs water permits intense insolation of the sub-tropical sky to reach the entire community. One can read print on the bottom of the spring from the surface. The transparency of the water is indicated by the data on light transmission in Figure 14. A comparison of winter and summer indicates slight differences in percent transmission due to the angle of the sun and due to localized effects of trees around this community. Because of the bits of pseudo-plankton that are stirred into the outflow the measurements in Figure 14 represent the boil community but not the actual nature of the overflowing underground water. A comparison of the data with averages given by Grice and Yentsch (1956) shows that, clear

TABLE 5. Characteristics of Microhabitats. Concentrations in ppm.

Location	Oxygen	Carbon-dioxide	NO_3-N	PO_4-P
Main boil values for comparison (from Table 8):	2.46	9.37	.48	.055
Among plants in Pontederia marsh, Daytime:	6.74	0.0	....	....
In heavy Najas beds at the boat landing station (see figure 3 and 6), Daytime:	8.15[f]	4.4[f]	.15[f]	.027[g]
	8.07[f]	2.5[f]	.15[f]	
	8.00[h]	2.8[h]	....	
	6.70[j]	4.4[k]	....	
	6.16[g]	2.0[g]	....	
	7.26[o]	0.0[o]	....	
	6.34[o]	1.1[o]	....	
mean:	7.24	2.5	.15	
Night'time:	1.13[e]	12.5[c]	.13[e]	
	1.38[c]	11.6[a]	.16[e]	
mean:	1.25	12.1	.15	....
In Sagittaria beds on the southeast side of the boil: Daytime:	2.69[p]	9.9[d]	.33[b]	
	2.79[p]	10.6[d]	.36[b]	
	3.02[b]	11.2[b]	.34[b]	
	2.69[b]	8.6[b]	.35[b]	
	.....	11.1[b]	....	
mean:	2.80	10.2	.35	....
Night'time:	1.75[a]	14.7[c]	.39[c]	
	1.30[a]	12.5[c]	.42[c]	
mean:	1.53	13.6	.41	....
In bell jars over Sagittaria beds on the southeast side of the boil Daytime, after 240 minutes enclosure in the afternoon May 2, 1954:	6.80	6.7	.15	.031
	6.25	6.7	.22	.028
	7.02	4.8	.22	.038
mean:	6.69	6.1	.20	.033
Night'time after 310 minutes May 13, 1954:	.75	14.1	.27	.040
	.98	13.8	.21	.022
	1.10	16.4	.12	.080
mean:	.94	14.7	.20	.047

[a] March 29, 1954, 3:00 a.m.
[b] May 2, 1954, 2:30 p.m.
[c] May 20, 1954, 11:30 p.m.
[d] April 9, 1954, 10:30 a.m.
[e] March 15, 1954, 3:00 a.m.
[f] February 25, 1954, clear noon.
[g] June 30, 1952.
[h] December 3, 1952, 3:30 p.m., cloudy.
[j] November 13, 1952, 8:00 a.m.
[k] December 3, 1952, 7:30 a.m.
[l] August 9, 1952, 2:30, cloudy.
[m] May 23, 1954, 2:00 p.m., scattered cumulus.
[n] May 15 1953.
[o] December 17, 1952, 2:30 p.m., clear.
[p] October 22, 1953, 2:00 p.m., clear.

as it is, Silver Springs absorbs more light than some marine waters. It is possible to use a Secchi disc since the spring is only 40 ft deep in any place other than some crevices in side boils. However, a horizontal Secchi disc reading may be made by a swimming observer underwater with a face mask. In the upper zones of the Silver Run this horizontal Secchi disc reading is about 105 m and fluctuates rapidly as the turbulent eddies of the flow bring water masses of slightly different trajectory. The clarity and warmth of the water is a great advantage. One may work with face mask in this community with as much intimacy as in terrestrial environments and coral reefs. One has a much higher degree of confidence with sampling here than in turbid streams. Light measurements were made with a photometer containing a Weston cell No. 594YR with visible spectral sensitivity. An extinction coefficient of 0.06 below one meter was computed following Sverdrup *et al.* (1946). Grice and Yentsch (1956) found 0.077 in Wakulla Springs.

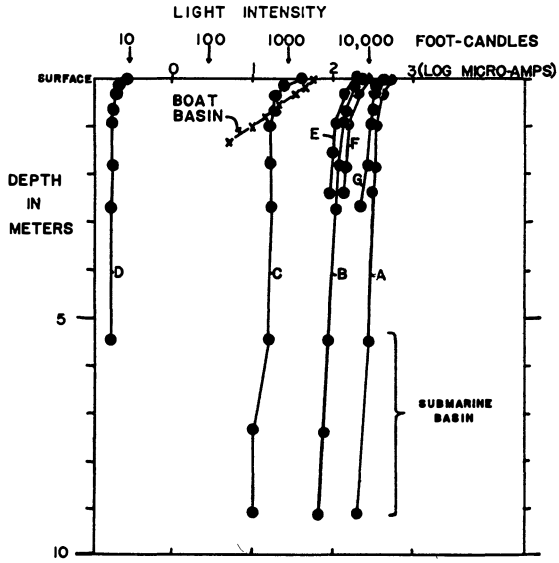

FIG. 14. Light transmission in Silver Springs. Log of the visible light intensity (in microamperes registered by a submarine photometer) plotted against depth. A rough estimate of foot candles is also plotted using .25 foot candles per microampere (calibrated with a standard lamp). A diaphragm with a shielding of 1/103 and a frosted glass filter with 63% transmission were used. Times and locations were: A. Boil, 1:10 p.m., May 23, 1954, clear sky. B. Main boil, 2:40 p.m. December 19, 1953, clear, windy. C. Main boil, 4:45 p.m., December 19, 1953, clear, windy. D. First Fisherman's Paradise boil, 5:45 p.m., December 19, 1953, dusk, clear, windy, without diaphragm shield, values divided by 103. E. ¾ mile station, May 23, 1954, 4:50 p.m. F. Bridal Chamber boil, 4:30 p.m., May 23, 1954, clear sky. G. Catfish Reception Hall, 12:20 p.m., February 25, 1954. Boat Basin, 2:30 p.m., overcast, August 11, 1955 (see Figure 2).

Because of the clarity of the water there is little diffraction and the light reaching the photometer is direct sunlight. The ripples on the surface act as lenses as described by Minnaert (reprinted 1954) producing rapid fluctuations in the microammeter recording the rapid variation of light. Thus the community is one of flashing light except on cloudy days. Light reflection also is increased by ripples of windy days. The flashing was averaged by eye in obtaining the readings plotted in Figures 14 and 15. In Figure 14 a rough pattern of transmission with depth is given which is somewhat similar to curves found in open waters. However, the relatively narrow walls of the deeper portions modify the light fields.

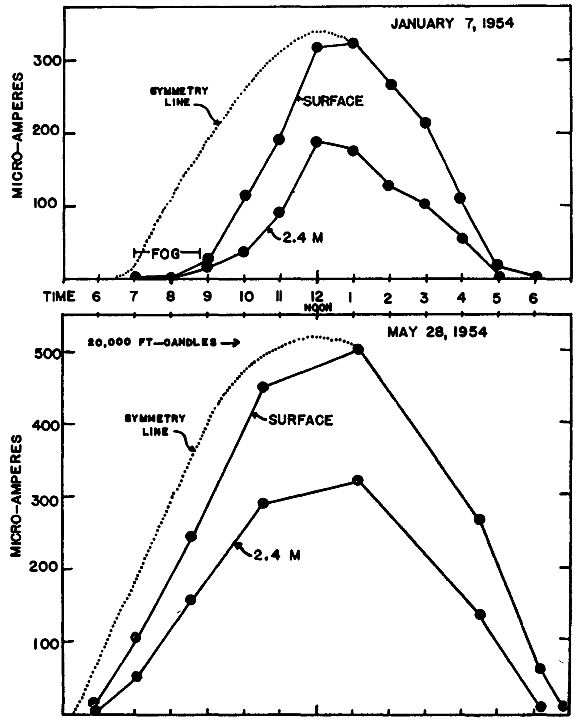

FIG. 15. Comparison of summer and winter light curves at the surface and at plant level in Silver Springs. Roughly equivalent foot candle values are given (see Figure 14). The dotted symmetry lines indicate the mirror reflection of the afternoon light curve for the morning. The area between the morning light curve and the symmetry line indicates the magnitude of shading by trees which is especially shadowing in the morning because of the springs orientation in a west-southwest to east-northeast axis.

One of the most elegant characteristics of these springs as a natural laboratory is the ability to separate the ecological effects of light from those of temperature at the community level for the temperature is constant and the light varies seasonally both in intensity and in photoperiod as shown in Figure 15.

The following procedure was used to calculate useful photosynthetic energy reaching the plant levels. First the energy for a given type of sky for this latitude and day of the year was obtained, and then the percent of the photosynthetic range of wave lengths reaching the community was found. The trees are an irregular factor in the calculation acting more when the sun is low on the horizon than when it is overhead. When the sun sets in the west in the afternoon it shines down the stream so as to strike the community directly with few trees interfering. Since the sunlight curves would be symmetrical if there were no trees, one may draw a morning curve as a mirror image of the afternoon curve in order to determine what percent of the day's insolation is caught by the trees during the morning. This is done in Figure 15; the shading effect is about 29% in winter and 10% in summer.

The aerial photograph in Figure 1 shows the spring as very dark, indicating that the light was absorbed and not returned. This phenomenon is easily demonstrated by inverting the photometer over the community surface under water. A negligible reading is found. The waving blades of eelgrass (Sagittaria) and algae in Figure 4 are highly efficient in absorbing the light. As a bed of waving greenery the community stands about 3 ft off the bottom of the muck (Fig. 4) even though many blades may be much longer. If the photometer is let down into the plant bed 2 ft the reading is again 0, indicating that the natural and mobile thatching serves as an opaque roof to the muck surface. Fishes and other organisms pass unnoticed through these bottom tunnels.

Work at night was carried out with battery operated headlights. In the low conductivity of this fresh water, these devices work readily for the underwater swimmer. In general all the fishes were repelled by these lights and usually remained out of sight in the twilight at the end of the beam.

HYDROGRAPHIC MICROCLIMATES

Among the Sagittaria beds, which range from 0 to 15 feet in depth below the surface, there is a characteristic micro-environment. The water among the plants tends to be retarded, to exchange with the surface areas less rapidly, to be depleted of nutrients, and in a sense to acquire properties suggestive of a hypolimnetic environment. Some idea of this microstratification may be obtained from the measurements of current and chemical properties in Figure 16 and Table 5. From metabolism experiments discussed in subsequent sections it is clear that this bottom water is actually not isolated for long and must be exchanged entirely every few hours since otherwise entirely anaerobic conditions would develop. On Feb. 12, 1953, versenate hardness was 207 ppm in littoral plant beds and 216 ppm in the channel. The percentage modifications of major chemical constituents are small. However, it is quite a contrast to the very rapid exchange of the water at the plant tips where no water is in contact with the plant surfaces for more than a fraction of a second. Because of the low oxygen concentrations in the plant beds at night, some possibility of a limit to fish may exist in these upper spring areas. This is discussed relative to the presence of larger fish in particular boils.

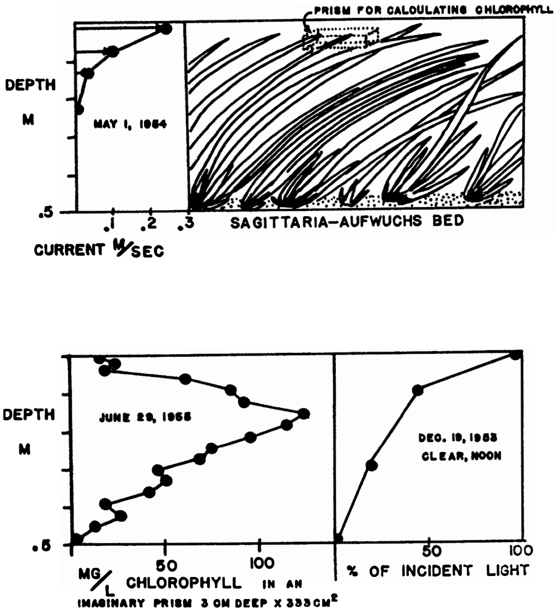

FIG. 16. Characteristics of the Sagittaria microhabitat, including curves of the vertical distribution of current, light, and benthic chlorophyll. Current velocity was determined with a propeller-earphone type midget current meter. A submarine photometer was used to determine light penetration. Chlorophyll extracted from the grass blades was calculated so as to indicate the average benthic chlorophyll in a volume of space in the Sagittaria bed.

THE SILVER SPRINGS COMMUNITY

THE AREAL PATTERN

Except for the littoral patches of plants of other types mapped in Figure 3, the springs community in the upper ¾-mile head water zone of main study is remarkably uniform with the complex of waving Sagittaria and aufwuchs encrustations. The area of the bottom community is determined from the map in Figure 3 as 18.5 acres, of which 1 acre is made up of sand, littoral macrophytes, and crevices. It is in this area that the overall standing crop, trophic structure, productivity, and metabolism are studied in the discussions that follow. There are also differences in the animal distributions and in the form of plant growth which will be described.

PRIMARY PRODUCERS

In Table 6 are summarized the species of principal primary producers. Dr. A. M. Laessle, Dept. of Biology, Univ. of Florida, has participated by retaining specimens in his aquatic plant herbarium and provided identifications. Dr. L. Whitford, N. C. State College, Raleigh, N. C., spent a summer working on this springs project and has made a general ecological study of these algae (Whitford 1956). The algae were identified by him.

The predominant producers are the matted diatoms and filamentous greens and blue-greens

TABLE 6. Community Dominants by Trophic Level[ab]

PRIMARY PRODUCERS:

DOMINANTS:

Sagittaria lorata, Cocconeis placentula, Synedra ulna, Melosira granulata, Melosira varians, Melosira italica, Fragilaria sp., *Terpsinoe musica, Plectonema wollei, Achnanthes lanceolata, Eunotia pectinalis, Navicula minima.*

OTHER SPECIES:

Lobelia cardinalis, Panicum paludivagum, Pistia stratiotes, Najas guadalupensis, Ceratophyllum demersum, Vallisneria neotropicalis, Potamogeton illinoiensis, Ludwigia natans, Colocasia antiquorium, Gomphonema sphearophorum, Cymbella mexicana, Gomphonema longiceps, Pontederia cordata, Fragilaria construens, Pinnularia interrupta, Fragilaria brevistriata, Gomphonema acuminatum, Fragilaria capucina, Amphora proteus, Epithemia sp., *Nitschia amphibia, Pleurosigma elongatum, Cyclotella* sp., *Biddulphia leavis, Amphithrix* sp., *Lyngbya epiphytica, Lyngbya nordgardhii, Chara zeylanica, Lyngbya kutzingii, Microspora floccuosa, Stigeoclonium* sp., *Oscillatoria splendida?, Calothrix* sp., *Entocladia* sp., *Schizomeris leibleinii, Mougeotia* sp., *Xenococcus* sp., *Audouinella violacea, Spirogyra* sp., *Rhizoclonium fontanum, Spirogyra* sp., *Cladophora* sp., *Oedogonium* sp., *Scenedesmus dimorphus, Scenedesmus bijuga, Euglena* sp., *Closterium* sp., *Pseudoluvella lens, Vaucheria* sp., *Compsopogon coerulens, Leptodictyum riparum, Eichornia crassipes, Hydroctyle* sp., *Thorea ramosissima, Nuphhar* sp.

HERBIVORES (AND ALGAL PARASITES):

DOMINANTS:

Pseudemys nelsoni, Pseudemys floridana, Mugil cephalus, Pomacea paludosa[e], *Viviparus georgianus, Oxytrema catenaria, Littoridinops* sp., *Amnicola* sp., *Gammarus* sp., *Hyalella* sp., *Mollienesia latipinna*[f], *Tendipes* sp.,[g], *Calopsectra* sp.[h], *Polypedilum* sp., *Tendipes decorus, Hydroptila* sp.[j], *Elophila* sp., *Lepomis microlophus* (young)[k], *Lepomis punctatus* (half)[k], *Paleomonetes paludosus*[l].

OTHER SPECIES (trophic level less certain):

Tendipes (Synchironomus) sp., *Glyptotendipes senilis, Anopheles quadrimaculatus, Cryptochironomus* sp., *Spaniotoma* sp., *Leptocella albida, Calibaetis floridanus, Signalosa pelenensis*[c], *Dorosoma cepedianum, Erimyzon sucetta, Mugil curema, Notemigonus crysoleucas, Tipula* sp., *Cladopelma* sp., *Stylaria* sp., *Arcella* sp., *Ancylus* sp., *Rhizophydium schroeteri* (on *Asterionella*), *Lagenidium rabenhorstii* (on *Spirogyra*), *Chytridium olla, Entophlyctis confervaeglomeratae* (on *Spirogyra*), *Phlyctochytrium chaetiferum* (on *Spirogyra*), *Rhizophydium globosum* (on diatom), *Chytridium* sp. (on diatom). Occasional *nematodes, tardigrades, rotifers, oligochates, and flatworms* were found in the aufwuchs.

CARNIVORES:

DOMINANTS:

Lucania goodei, Gambusia affinis, Lepomis punctatus (half)[k], *Lepomis microlophus (half)*[k], *Lepomis macrochirus, Ictalurus lacustris, Ictalurus catus, Dyneutes carolinus, Dyneutes angustus, Gyrinus rockinghamensis, Gyrinus pachysomas, Rhagovelia choreutes, Metrobates nomalus, Mesovelia mulsanti, Microvelia bueni.*

OTHER SPECIES (trophic level less certain; some belonging to two levels):

Craspedacusta sowerbii (Microhydra), Hydra sp. (green). *Hydra* sp. (brown), *Unidentified mites* and *leeches, Argia sedula, Ischnura ramburii, Enallagma* sp., *Nehalennias* sp., *Anamalagrion hastatus, Copelatus caelatipennis, Copelatus copelatus, Copelatus chevrolati, Pentancura* sp., *Macrobrachium carcinus, Pelecoris carolinensis, Belostoma lutarium, Ranatra drakei, Dolomedes okefenokensis, Macrocyclops albidus, Eucyclops agilis, Jordanella floridae, Lucania parva, Elassoma evergladesi, Notropis* sp., *Hybopsis* sp., *Leptolucania ommata, Heterandria formosa, Aphredoderus sayanus, Esox americanus, Esox niger, Strongylura marina, Ameiurus natalis, Anguilla bostoniensis, Fundulus chrysotus, Fundulus dispar, Labidesthes sicculus, Hadropterus nigrofasciatus, Chaenobryttus coronarius, Lepomis auritus, Poxomis nigromaculatus, Steontheros odoratus*[m], *Stenotheros minor*[m], *Thamnophis sauritus*[m], *Natrix taxispilota*[m],

[a] Other species found in the side run but not in the main spring headwater zones: *Odontomyia* sp., *Leptocella candida, Tendipes* sp., *Triaenodes* sp., *Argia fumipennis, Baetis spiethi, Hydrometra australis, Tricorythodes abilineatus, Baetis spinosus, Argia sedula.*

[b] See acknowledgements for sources of identifications. Dominance was assigned on the basis of the counts summarized in Table 7, Figure 18 and Figure 19, and from data obtained by J. Yount, University of Florida.

[c] Not recorded during this study but reported by Hubbs and Allen (1943) as irregular, rare or occasional visitant.

[d] Only an occasional individual was seen or taken. It is not a regular part of the fauna.

[e] Two guts contained 4140 diatoms, 570 filaments and 4% plant tissue.

[f] 6 guts contained 2030 diatoms and 1800 algal filaments.

[g] One gut contained 1092 diatoms and algal filaments.

[h] 4928 diatoms and filaments in one gut.

[j] One gut contained 162 diatoms.

[k] Since more than half of the guts contained plant material, half of the species is considered as an herbivore and half as a carnivore.

[l] The recognizable parts of the gut contents was of plant origin.

[m] The herpetofauna listed were taken from a detailed, annotated list for Silver Springs kindly supplied by Wilfred T. Neil in personal communication.

TABLE 6. (Continued)

Natrix sipedon[m], *Amyda ferox*[m], *Chelydra serpentina*[m], *Siren lacertina*[m], *Amphiuma means*[m], *Rana catesbeiana*[m], *Rana grylio*[m], *Rana heckscheri*[m], *Hyla cinerea*[m], *Butorides virescens, Florida caerulea, Ardea herodias, Fulica americana, Aramus pictus, Gallinula chloropus.*

SECONDARY CARNIVORES:

DOMINANTS:

Micropterus salmoides, Lepisosteus platyrhyncus.

OTHER SPECIES:

Alligator mississippiensis, Abastor erythrogammus, Lepisosteus osseus, Amia calva.

DECOMPOSERS (defined as a miscellaneous trophic level):

DOMINANTS:

Bacteria (21 colony variants in gross examination of plates; 5—35% *chromogens*), *Procambarus fallax* (25% of the contents of 3 guts was recognizable; 2/3 of this was plant and 1/3 animal)[b].

encrusting the eelgrass blades. The diagram of the aufwuchs in Whitford's paper (1956) closely resembles the diagrams for European aufwuchs in Ruttner (1952). Quantitatively the bottom plants were estimated by placing a metal square of bent concrete reinforcing rod over the plants and cropping by hand all plants whose bases were within the 1 ft square. These were then drained 1-2 minutes and weighed wet. A sample of this Sagittaria-algae complex was then dried and a dry-wet weight equivalent obtained (6.1%). A number of samples were averaged. For other purposes counts were made as to the number of blades per clump, the average length blade, and the number of clumps per square foot. From these estimates, summarized in Table 7, can be computed the total surface of blades based on one square meter. About 24.3m^2 surface is supported per 1m^2 mud surface.

The percent of this large biomass that is algae was determined by scraping most of algae off the blades with a knife and obtaining an equivalent dry weight on an area basis. In a few places there are large mats of algae (Fig. 3) which are attached littorally lying like blankets on the rest of the community in less swift water. These mats although individually very distinctive are not large enough to figure in the overall community estimates.

The aufwuchs is continually growing and breaking off so that a small component of tychoplankton or pseudo-plankton develops as one passes down stream as indicated by the upstream and downstream comparisons of Table 8. On an area basis this is a negligible part of the standing biomass of primary producers (.025%) per area. From the enormous standing crop one would suppose, as is demonstrated below, that the community is very fertile and possesses a high productivity.

In freshwater it can be reasoned that the processes of concentrating the minerals that make up ash require expenditure of energy. Thus no effort has been made to correct biomass for ash since the ash may be largely a necessary component.

AUFWUCHS SUCCESSION

The Sagittaria blades grow from their bases in spurts. That this is so can be seen from the results of a simple experiment pictured in Figure 17. Small wires twisted into the base of a Sagittaria plant on April 5, 1954 were allowed to remain during growth for 26 days. One blade already having completed maximum elongation grew very little as evidenced by the unchanged spacing of the wires. The small basal tip however, was pushed far out by growth between two wires at the base.

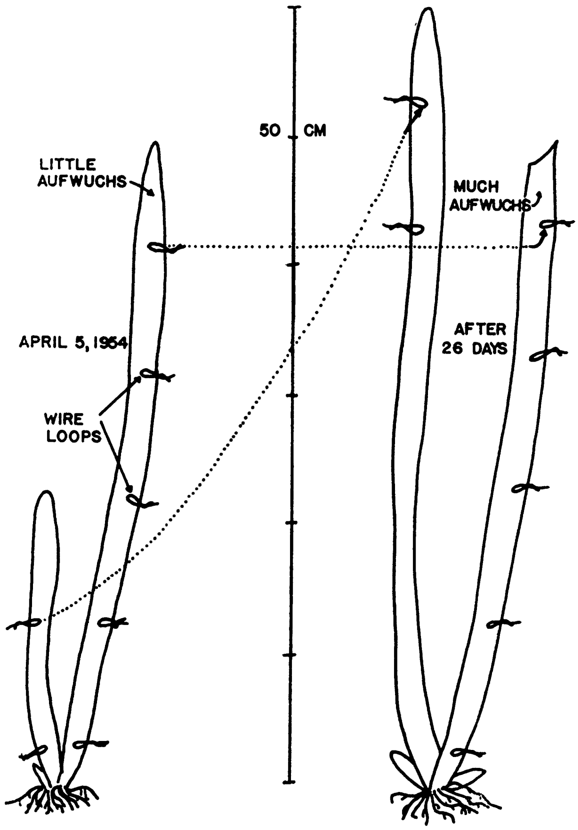

FIG. 17. Growth patterns in Sagittaria blades marked with wire loops. Rapid growth from the base is followed by heavy aufwuchs accumulation.

This growth from the bottom means that the aufwuchs organisms in their attachment will have been attached longest on the tip portions and most recently have invaded the basal portions. Thus within the overall steady state of the community, the length of the eelgrass blades has a microcosmic time succession laid out in a space succession.

Although individual blades grow irregularly in the manner described above, it is apparent that there is an average growth rate for blades since the community remains in approximate steady state year after year. By cutting whole bunches of blades into groups of segments, one may average the effects of irregular blade growth. For example one may assume that the basal segments of many blades together collectively represent the average aufwuchs that attaches first whereas the group of segments

TABLE 7. Estimates of Biomass in the 18.5 Acre (7.6 x 10^4 m^2) Headwater Area of Silver Springs from the Boil to ¾ mile station. 17.5 Acres of Sagittaria and 1.0 Acre of Macrophytes, Crevices and Sand; Islands Excluded.

Component	Measurement and basis for calculation	Biomass averaged over the spring area gm/m²
PRODUCERS:		
Sagittaria	2.8 (3.0, 2.9, 3.7, 1.5, 2.9, 2.3. 3.7, 2.7) lbs/sq. ft. wet Sagittaria and aufwuchs; 6.1% dry of wet; additional dry weight measurements from bell jar work: 28.2 (18.6, 40.7, 25.3) gm/.033 m² May 14, 1953; 23.9 (37.0, 18.4, 16.4) gm/.033 m² May 25, 1953; 23.7 (27.4, 28.8, 15.0) gm/.033 m² June 22, 1953; mean 812 gm/m² Sagittaria-aufwuchs. 94% of area is Sagittaria-aufwuchs. 75.5% of Sagittaria-aufwuchs is Sagittaria	578
Algae on Sagittaria (Aufwuchs)	24.5% of dry Sagittaria (above) is aufwuchs	188
Algae in boils, bare spaces	1/2 acre not estimated	. . .
Other macrophytes	Total coverage 3% of spring. Mean dry weight, 1441 gm/m² (Najas, 1950; Pontederia, 980; Scirpus, 1970; Pistia, 463)	43
Total biomass of producers		809
HERBIVORES		
Microfauna which drains off the Sagittaria and aufwuchs when the clumps are removed from water. Collected in Cornell Plant net. 94% coverage of the *Sagittaria* complex		
Hydrobiidae	109 (64, 65, 192, 56, 176)/.13 m² .00005 gm dry tissue/individual	.04
Oligochaetes	36 (16, 29, 45, 29, 61) individuals/.13 m²; .0000008 gm dry/individual	.0002
Midges (mostly herbivorous)	31 (12, 39, 83, 3, 17)/.13 m² .00004 gm dry/individual	.01
Gammarids	.75 (28, 70, 200, 8, 69) individuals/.13 m²; .001 gm dry/individual	.06
Copepods and ostracods	21 (57, 13, 7, 11, 19) individuals/.13 m²; .000001 gm dry/ individual	.00015
Flatworms	7 (2, 9, 7, 5, 12) individuals/.13 m² .00001 gm dry/individual	.00005
Paleomonetes	6 (5, 25, 1, 0, 0) individuals/.13 m²; .040 gm dry/ individual	1.7
Microfauna which does not drain from clumps of Sagittaria but which must be scraped from the leaves 18.7 (13, 23, 18, 21) clumps Sagittaria/ft.²; 10.0 (110/13, 294/23, 166/18, 201/21) blades/clump or 2000 blades/m² of Sagittaria covering 94% of the spring; 120 cm² surface/blade.		
Hydroptila	98 (8, 281, 5) individuals/10 blades .00004 dry gm/individual	.78
Midges	111 (78, 49, 205) individuals/10 blades; .00004 gm dry/individual	.90
Elophila	5 (0, 15, 0) individual/10 blades .00021 dry gm/individual	.21
Hydrobiidae	28 (53, 2, 27) individuals/10 blades; .00005 gm dry tissue/individual	.3
Oligochaetes	51 (23, 5, 126) individuals/10 blades; .0000008 gm dry/individual	.007
Arcella	1.5 individuals/cm² blade surface (Figure 19); .000001 gm/individual dry	.3
Larger Herbivores		
Mullet	590 individuals counted visually/25,000 m²; 1191 gm/wet individual (mean of 6 speared fish); 20% dry of wet	5.6
Pomacea	3.7 individuals/m² quadrat (15/2.2 m² shallow quadrat); (1/1.73 m² deep quadrat); 1.1 gm tissue/individual	4.0
Turtles	From tagging and recapture work by L. J. Marchand (1942) in Rainbow Springs, Marion Co., 12,000 pseudemys were estimated for about .92 km² area of spring and spring run. 5 x 10² gm dry/turtle	6.7
Stumpknockers	1/2 of biomass as calculated in carnivore section	6.3
Intermediate Sized Herbivores; sampled with sliding door box sampler devised by W. C. Sloan placed over plants and mud by hand		
Oxytrema	1 (3, 4, 0, 0, 0, 0, 0, 9, 0, 0, 0, 0, 0, 0, 0, 0) individuals/.085 m² 29 gm dry tissue/ individual (mean of 30) individuals	2.9
Viviparus	26/2.23 m² shallow quadrat; 2/1.73 m² deep quadrat .15 gm dry tissue/individual	1.0
Paleomonetes	12 (47, 6, 2, 1, 4)/.085 m² .041 gm dry/ individual	5.8
Total biomass of Herbivores		36.8
CARNIVORES		
Water Striders	Counts from crisscrossing boat (June 9, 1953) in rafts: 30, 275 individuals/18 acres plus the scattered: 6 individuals/.093 m²; .0019 gm dry/individual (mean of 16)	.12
Gyrinid Beetles	10,050 individuals counted/18 acres (June 9, 1953); .022 gm dry/individual (mean of 9 Copelatus, 3 Dyneutes)	.0028
Leeches	1.4 (0, 0, 7, 0, 0) individuals/.13 m² in plant drain net of Sagittaria complex 94% coverage of Sagittaria; .016 gm dry/ individual	.12
Lucania	11 (12, 45, 16, 6, 4, 0, 5, 0) individuals/ 1.73 m² visual quadrat; 0.60 gm dry/individual	.39
Gambusia	13 (100, 4, 0, 0, 0, 0, 0, 0) individuals/.73 m² visual quadrat; .060 gm dry/individual	.45
Heterandria	3 (25, 0, 0, 0, 0, 0, 0, 0) individuals/1.73 m²; (large count along banks): .040 gm dry/ individual	.07
Stumpknockers (L punctatus) and other sunfish	Half taken as Carnivore; 2.0 individuals/m² visual quadrat (mean of 31 estimates on 3 days ranging 0-5 fish/m²; 30 gm wet/ 85 mm individual; 21.0% dry of wet (85 mm is mean length in the population on a weight bases, Caldwell et al. manuscript)	6.3
Larger Stumpknockers and other sunfishes above grass	1403 individuals/25,000 m² visual survey, March 9, 1953; 85 gm wet/individual; 21% dry of wet	1.0
Catfish	520/18 acres in visual survey (mean of 3 observers in glass bottom boat) 1430 gms wet/fish (mean of 21 speared)	2.0
Notropis and Hybopsis	20% dry of wet assumed 1 school/10 m of shore; 3 km shoreline. 50 individuals/school .1 gm dry/individual	.02
Hydra and Craspedacusta	.1 individuals/cm² attachment surface (Figure 19); 2000 blades/m²; 120 cm²/ blade; 24 m² attachment surface/m² bottom; .1 cm dimension .00001 gm dry/individual calculated by volume	.24
Mites	Drainage of Sagittaria through Cornell plant net; 7.2 (5, 2, 16, 2, 11)/.13 m²; .00009 gm dry/individual	.005
Total biomass of Carnivores		10.7

TABLE 7. (Continued)

Component	Measurement and Basis for calculation	Biomass averaged over the spring area gm/m²
TOP CARNIVORES		
Bass (larger)	139 individuals/25,000 m² visual survey; 510 gms wet/individual (mean of 18 speared); 20% dry of wet	.57
Lepisosteus platyrynchus	116 individuals/25,000 m² visual survey; 1045 gm wet/fish (mean of 2 speared); 20% dry of wet	.93
Lepisosteus osseus	3 individuals/7.6 x 10⁴ m² visual survey 3800 gm wet/fish (mean of 8 speared); 20% dry of wet	.03
Total biomass of Top Carnivores		1.53
DECOMPOSERS (defined as organisms utilizing parts of several trophic levels		
Bacteria on plant surfaces	Direct count method with phase, oil immersion examination of scrapings, shreded and diluted; 25,000,000. Individuals/cm² of Sagittaria blade tip; surface (774,000,000/26; 757,000,000/28; 468,000,000/28; 24.3 m² plant surface/m² bottom area; density of bacteria in whole blade 50% 1.77 x 10^{-12} cm³ volume/individual; 5% dry of wet volume; 94% coverage of Sagittaria	.30
Bacteria in bottom mud	Direct count method on diluted mud under oil immersion phase microscope; 331,000,000 individuals/cc mud (276,000,000; 424,000,000; 398,000,000; 226,000,000); depth of main bacterial activity taken as 1 cm; 1.77 x 10^{-12} cm³ volume/individual; 5% dry of wet volume	.29
Crayfish	.81 individual/.075 m² (0, 0, 6, 0, 0, 2, 0, 1, 0, 2, 1, 1, 0, 0, 0, 0); .37 gm dry/individual (mean of 3)	4.0
Total biomass of Decomposers		4.6

2 inches out but next to the base represent the aufwuchs on blades which have grown 2 inches on the average and are thus slightly older in succession of attachment. From data below it is possible to determine the average blade growth rate and thus determine the ages of these fractions of aufwuchs under natural conditions. The result of scraping these fragments and making counts of the species is given in Figure 18.

It was found by Whitford that the complex of algae attaching to glass slides was very similar to the algae attaching to the natural substrate of Sagittaria blades. Thus by placing out glass slides in boxes among the plant tips the succession could be studied by counts of organisms on the glass slides at different time intervals. The results of such studies are summarized in Figure 19. The glass appears to become etched after several months exposure. The results of the counts on the blades and on glass slides are similar. The successional series is roughly as follows:

Bacteria-cocconeis type diatoms—larger diatoms—algal green and blue-green filaments—herbivorous animals (*Arcella,* midges)—carnivorous animals

FIG 18. Longitudinal distribution of aufwuchs on Sagittaria blades as an indicator of chronological succession.

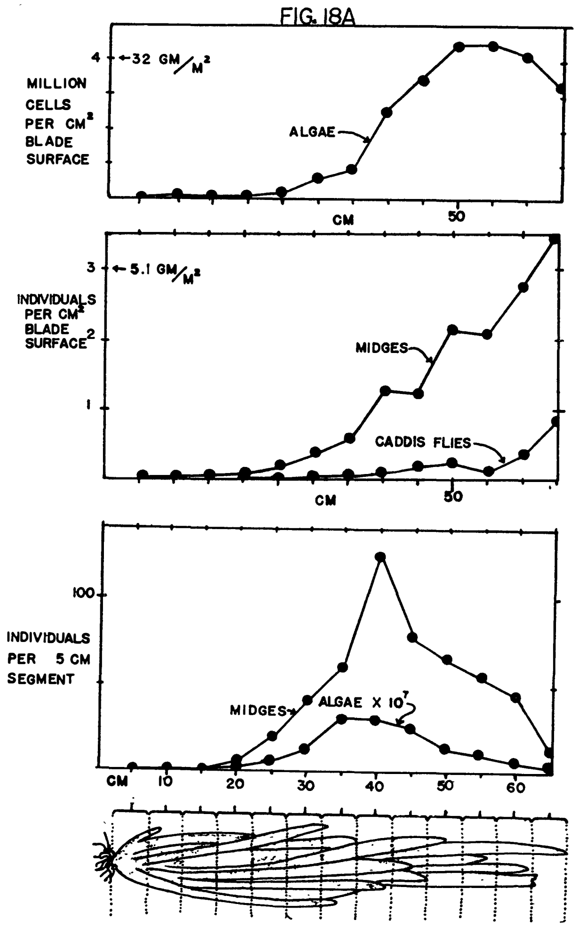

FIG. 18a. The two upper graphs show the increase in density of algae, midges, and caddisflies per blade area toward the tips, October 1, 1953. The lower graph shows the algae and midges as a function of distance from the base of the grass clump. Fewer organisms are found at the extremity of the clump because of the small number of long blades in spite of the high density on the few blades protruding. The manner of cutting the clumps before scraping off the aufwuchs is shown at the bottom.

(*Craspedacusta, Hydra*)—breaking-off and bitten-off tips reaching the fishes. This is a beautiful example of the way in which a macrocosm may be in a steady state due to the component multiple summation of successional phases.

The extractions of chlorophyll on the segments in Figure 18 indicate that the maximum chlorophyll per area of blade occurs some distance from the tips. If the chlorophyll of the aufwuchs is a measure of the productive rate, then the tips are being removed by the breaking off in the zone of maximum production. The system is thus in a steady state analogous to the optimum catch in fisheries. The

FIG. 18B

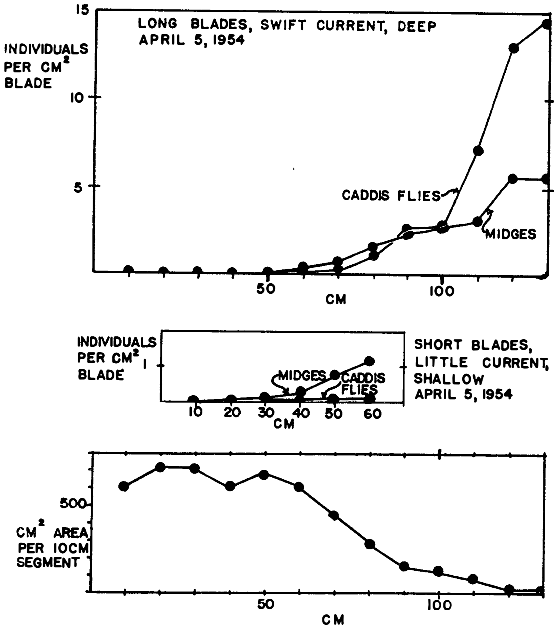

FIG. 18b. The two upper curves contrast the distributions of midges and caddisflies on the long narrow blades of swift water in the narrows below the main boil with some thick, short blades found littorally in slowly moving water. The lower graph shows the decrease in blade area per longitudinal interval of cutting towards the extremities of Sagittaria clumps.

FIG. 18C

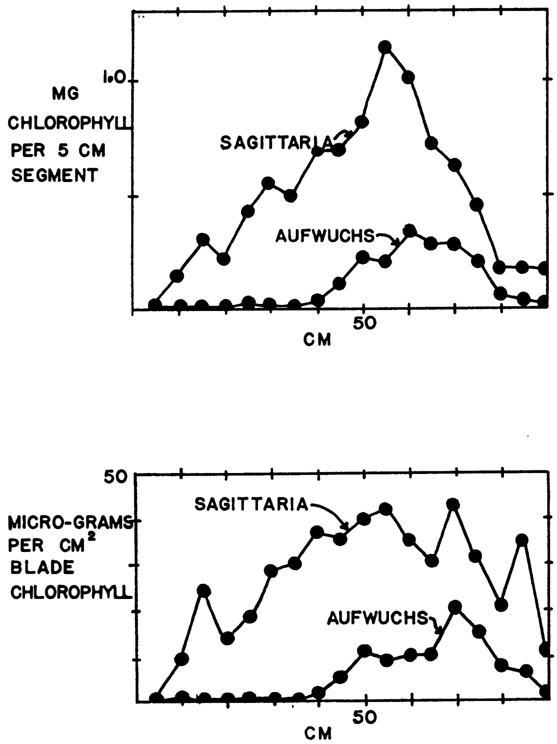

FIG. 18c. Chlorophyll distribution according to longitudinal zones of Sagittaria blades on June 29, 1955 (see Figure 16). In the upper curve the chlorophyll extracted from the aufwuchs and scraped blades is reported according to the longitudinally measured distance of the zone from the base of the clumps as shown in the sketch in Figure 18a. In the lower curve the chlorophyll is reported in terms of its concentration per area of blade.

maximum chlorophyll of the Sagittaria is also at a maximum at an intermediate level presumably reflecting the decrease of light cited in the light section.

The rate of growth of aufwuchs down among the plant bases was lower. The slow current, dim light, and nutrient depletion are factors. After 30 days in place glass slides showed only 27% coverage of *Cocconeis*, .7 *Arcella*/cm², and .17 midges/cm² whereas slides suspended at the same time at plant tip level had acquired an average of 95% coverage of *Cocconeis*; 2.2 *Arcella*/cm² and 3.5 midges/cm².

There is in Figures 18 and 19 some evidence for a maximum standing crop of some algae before the herbivores become established and subsequently a herbivore maximum before the carnivores begin to take a maximum harvest. The distribution of organisms on the slides is generally contagious and concentrated more on the upper sides of the glass.

The standing crops of algae and other aufwuchs on the blades of Sagittaria are not a measure of the production there. In swift water a great fraction of the algae and small animals grown there is carried away downstream. On the other hand in the still shallows the production of algae and animals stays in situ and may support additional food chains and a dense but not necessarily vigorously growing community.

BACTERIA AND OTHER DECOMPOSERS

By H. T. Odum and Osilio Galindo

Several techniques used by Henrici (1939) and others were used in an effort to determine the standing crop of bacteria and to compare the type of bacterial community in the spring with those in lakes where these techniques were developed. First of all, agar plates in pharmaceutical bottles were developed from water samples and from periphyton scraped off Sagittaria blades, and from mud samples. Second, counts were made of bacteria on glass slides after submersion in springs, flaming and dipping in Gentian violet. Third, direct counts were made of aliquots of periphyton and mud suspensions using a phase microscope. Finally, some counts were made of percent chromogens in the agar plates and of the number of grossly different colony types. In this work we are grateful to the Department of Bacteriology, University of Florida, for advice and the loan of equipment and to Mr. J. Gonzalez who took an active interest in and helped with the plating.

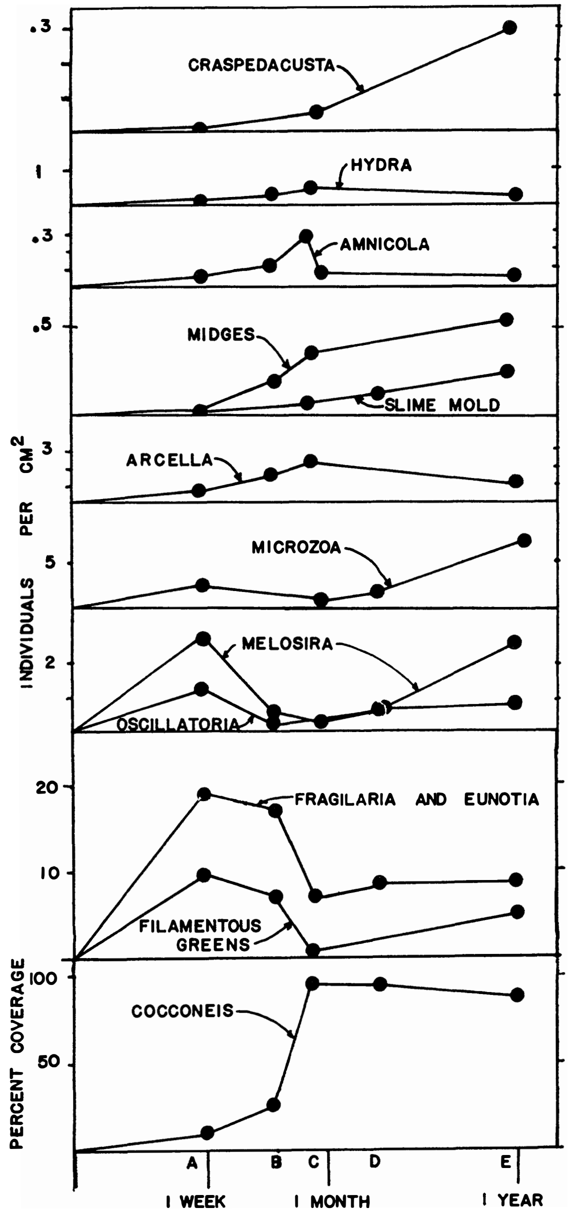

FIG. 19. Succession of aufwuchs on glass slides submerged at the level of the Sagittaria blades tips from the growth cage (see Figure 3) in slide boxes wrapped with hardware cloth. The data are reported on a logarithmic scale of time. Dates are indicated by letters on the abscissa: A. May 5 to 12, 1954. B. May 5 to 20, 1954. C. April 5 to May 1, 1954. D. September 1 to November 13, 1952. E. July, 1953 to April 5, 1954.

The culture and dilution bottles covered with aluminum foil under the caps were autoclaved in the laboratory and carried into the field. The medium used is as follows: sodium caseinate, .05%; peptone, .05%; starch, .05%; glycerol, .05%; dibasic potassium phosphate, .05%; agar, 1.50%; tapwater (Gainesville, hard water partly of artesian origin), 1 liter. The agar in the bottles was melted on the stove in the Silver Springs kitchen. Pipettes, knife for scraping, and glass tube for initial mud samples were wrapped in paper sterilized and opened in the field at the time of use. 1-cc samples of mud or measured periphyton samples were collected by the underwater worker by hand and immediately placed in sterile dilution bottles. After vigorous shaking dilutions were made and introduced into the agar prior to its solidification. For the vertical sampling in the mud, a Hiller peat corer was used by the underwater observer. Immediately upon opening the corer out of water a mud sample was taken from within the corer where no contact occurred between the mud and metal surfaces. Because of the low concentrations of bacteria in the water, there was no larger contamination possible from this source.

The data on the counts are summarized in Tables 8 and 9. Just as found by Bere (1933) in Wisconsin lakes the direct counts are much greater than plate counts. To what extent we are counting dead bacteria in direct counts of fresh material is not known but in the periphyton where there is a rapid turnover of energy it seems likely that the erorr due to dead bacteria is not large. In the mud in one preliminary series the direct counts as one goes down in the mud did not decrease whereas the plate counts were much less. Whether this reflects the presence of dead bacteria or the presence of anaerobic bacteria that just don't grow in the agar is not clear. The correct figure for bacterial biomass is probably between estimates derived from direct counts and those from plate counts.

The periphyton was characterized by beautiful chromogens which developed in the plates after about two weeks. These were less abundant in the mud. Thus again the pattern in lakes is confirmed for the springs. The plot of frequency of colony types against the number of colonies per type shows a hollow curve that is often found in community analysis for reasons still obscure.

The numbers of bacteria found on glass slides are of the same order of magnitude as found in lakes. This is especially interesting since the counts from the water are low even after passing over beds of Sagittaria and periphyton. The action of a strong current may be growth promoting even when the water is low in organic content. Thus the bacteria on slides after a short time period are a measure of growth conditions and water fertility rather than the number of bacteria in the water.

In order to estimate the grams of bacteria per area in the springs community the direct counts were multiplied by the dry weight calculated for a typical bacterium. The upper 1 cm of mud was arbitrarily included as part of the ecosystem in the first calculation. The large total surface in the Sagittaria supports periphyton bacteria that about equals the 1 cm deep mud bacteria in numbers. It is sup-

TABLE 8. Changes Between the Boil and the ¾ Mile Downstream Station

Measurement	Boil			¾ Mile Downstream		
	Mean	S	Separate analyses	Mean	S	Separate analyses
OXYGEN, ppm Daytime (sunrise to sunset) 1952-1955	2.656	.400	58 analyses (Fig. 12)	2.8 - 6.3		(Fig. 23-31)
Night samples (midnight to dawn) Nov. 13, 1952	2.80	....	2.80	....	....	....
Feb. 19, 1953	2.84	....	2.84	3.56	.078	3.58, 3.50, 3.59
March 8, 1953	2.30	....	2.80, 1.80	3.12	.193	2.85, 2.83, 3.31, 3.21, 3.10, 2.85, 3.20, 3.28, 3.11, 2.97, 3.31, 3.40
Nov. 28, 1953	1.90	.109	1.85, 1.80, 2.05	3.45	.107	3.30, 3.55, 3.50
Jan. 7, 1954	....	....	....	3.40	.075	3.39, 3.48, 3.34
March 13, 1954	2.35	....	2.20, 2.50	....	....	....
May 23-24, 1954	2.59	.217	2.80, 2.28, 2.68	3.37	.369	4.03, 3.62, 2.82, 3.45, 3.12, 2.88, 3.58, 3.59, 3.25
July 12, 1955 9:00 p.m.	1.85	.057	1.90, 1.77, 1.88	2.87	.107	2.82, 2.91, 2.87
Aug. 11, 1955 10:30 p.m.	1.45	.208	1.17, 1.67, 1.51	2.55	.132	2.57, 2.53, 2.57
Mean of 8 nights	2.26	.460	....	3.19	.337	....
Mean of night values	2.13	.505	....	3.20	.343	....
March 26, 1953 day in boil; night downstream	2.485	.236	4:00 p.m. (Fig. 13)	3.665	.241	6:10 a.m. (Fig. 13)
CARBON DIOXIDE Daytime (sunrise to sunset)	9.155	....	29 analyses (Fig. 12, 13)	2.4 - 11.5		(Fig. 23-30)
Night samples (midnight to dawn) Feb. 13, 1953	....	....	....	6.40	....	7.4, 5.4
Feb. 19, 1953	8.60	....	7.2, 10.0	5.67	.88	5.9, 4.5, 6.6
March 8, 1953	7.60	.86	7.7, 6.5, 8.6	7.34	1.06	8.1, 7.0, 8.4, 8.9, 5.5, 7.0, 7.0, 9.3, 6.6, 5.7, 8.4, 6.5, 7.8, 7.9, 6.8, 6.6
Jan. 7, 1954	11.90	.50	12.6, 11.5, 11.6	11.17	.39	11.3, 11.3, 10.9, 10.7, 11.9, 11.3
March 29, 1954	10.15	....	11.4, 8.9	....	....	....
May 20, 1954	10.70	....	10.4, 11.0	10.15	....	10.4, 9.9
May 23, 1954	8.83	.50	9.8, 8.7, 7.9, 8.9	10.10	.69	11.3, 10.1, 9.6, 9.2, 9.6, 9.9, 11.1, 10.0
July 12, 1955 (CO_2 determined from pH) 9:00 p.m.	9.98	.42	9.7, 9.7, 9.7, 9.9, 9.9, 10.3, 10.3, 10.2, 10.2	8.82	.60	8.8, 8.6, 9.2, 9.4, 7.9, 9.0, 8.0, 9.7
Mean of 7 nights	9.680	1.33	....	8.521	2.00	....
Mean of all values	9.704	1.40	....	8.587	1.83	....
March 26, 1953 day in boil; night downstream	9.26	.54	4:00 p.m. (Fig. 13)	7.20	.266	6:10 a.m. 7.4, 7.0, 6.5, 8.4, 5.5, 7.7, 7.5, 7.0, 6.9, 7.0, 8.3, 6.8, 6.2, 8.2, 8.5, 6.3
NITRATE-NITROGEN[a], ppm *Night'time* March 7-8, 1953	.51	....	.56, .45	.45	.091	.42, .29, .49, .56, .49
March 27, 1953	.49	....	.50, .48	.41	....	.41, .41
May 8, 1953 1:00 a.m.	.498	.055	.43, .59, .49, .56, .47, .40, .50, .48, .55, .51	.468	.041	.51, .49, .38, .40, .49, .50, .49, .47, .48, .47

[a] Phenoldisulphonic acid method to September 1953; strychnidine method thereafter.

TABLE 8. (Continued)

Measurement	Boil			¾ Mile Downstream		
	Mean	S	Separate analyses	Mean	S	Separate analyses
Nov. 27, 1953	.463	.034	.41, .49, .45, .45, .42, .49, .49, .48, .52, .43	.439	.018	.42, .42, .45, .41, .45, .47, .45, .42, .45, .44, .45
Mean of 4 days	.490	.023		.442	.015	
Overall mean	.483	.049		.449	.050	
Daytime						
Feb. 19, 1953	....	....	.40	.381	.081	12 analyses (Fig. 26)
March 7-8, 1953	....	....	....	.389	.109	.40, .39, .14, .38, .44, .50, .47
March 26, 1953	....	....	....	.396	.060	22 analyses (Fig. 28)
April 9, 1953 noon, clear 1 minute apart	.453	.064	.47, .57, .36, .48, .34, .51, .47, .47, .44, .42	.333	.062	.31, .44, .35, .19, .38, .31, .31, .35, .38, .31
May 14, 1953 1:30 p.m. clear	.462	.086	.55, .33, .62, .48, .35, .51, .41, .46, .40, .51	.440	.091	.52, .37, .41, .55, .38, .60, .31, .45, .43, .32, .51
May 25, 1953 1:30 p.m. clear	.396	.113	.57, .49, .28, .32, .32	.340	.080	.37, .27, .42, .22, .42
Oct. 10, 1953 noon, clear	.401	.030	.43, .44, .43, .42, .39, .37, .34, .38, .41, .40	.380	.014	.36, .36, .38, .41, .38, .38, .38, .37, .40, 38
Oct. 22, 1953 noon, clear	.493	.065	.53, .53, .58, .53, .56, .45, .39, .52, .45, .39	.374	.057	.38, .45, .42, .45, .42, .33, .29, .36, .35, .29
Mean of days	.441	.032		.3791	.031	
Mean of all day values	.445	.079		.3841	.077	
PHOSPHATE PHOSPHORUS (inorganic) *Night'time*						
Aug. 9, 1952	....	....	.041	....	....	.040
March 7-8, 1953	....	....	....	.057	.0042	.052, .056, .062
Feb. 19, 1953	....	....	.013	....	....	.027
Nov. 27, 1953	.0836	.0065	.085, .093, .085, .075, .076, .088	.0859	.0063	.093, .087, .081, .090, .077, .086, .078, .095
Mean of all night values	.0695	.026	....	.0711	.0208	
Daytime						
Aug. 9, 1952	....	....	.041	....	....	.040
Feb. 19, 1953	....	....	....	.0372	.0108	17 analyses (Fig. 26)
March 7-8, 1953	....	....	....	.0563	.0224	.048, .087, .034
April 9, 1953 noon, clear	.0384	.012	.035, .069, .034, .041, .036, .033, .028, .039, .045, .024	.0381	.0159	.037, .026, .031, .039, .084, .032, .033, .041, .031, .027
May 14, 1953 noon, clear	.0506	.0070	.052, .053, .051, .049, .042, .051, .046, .069, .049, .044	.0423	.0063	.044, .045, .036, .042, .037, .033, .054, .038, .047, .051, .038
May 25, 1953 noon, clear	.0462	.010	.060, .056, .044, .037, .034	.0446	.0085	.033, .044, .038, .052, .056
Oct. 1, 1953 noon, broken clouds; high water; some runoff	.0621	.0091	.061, .056, .076, .070, .068, .046, .054, .066	.0585	.0077	.056, .068, .061, .056, .062, .043, .054, .068
Oct. 10, 1953 noon, clear	.0558	.0057	.055, .059, .058, .061, .064, .055, .051, .058, .042, .055	.0546	.0090	.042, .051, .066, .055, .064, .047, .048, .047, .071, .055
Oct. 22, 1953 2:00 p.m., scattered clouds	.0498	.0075	.044, .050, .062, .043	.0430	.0051	.049, .037, .047, .037, .048, .040
Mean of days	.0505	.0074	....	.0470	.0071	....
Mean of all day values	.05033	.0117	....	.04483	.0096	....

TABLE 8. (Continued)

Measurement	Boil Mean	Boil S	Boil Separate analyses	¾ Mile Downstream Mean	¾ Mile Downstream S	¾ Mile Downstream Separate analyses
CLUMPS OF FLOATING SAGITTARIA-AUFWUCHS						
dry gms/hr						
Jan. 4, 1953	....	....	....	289	....	....
March 25, 1953 7:15 p.m.	....	....	....	176	....	....
March 26, 1953 7:30 a.m.	....	....	....	184	....	....
Mean				216		
Oxidation Potential Beckman Model G platinum-calomel						
May 28, 1954 5:30 p.m.	.436	.002	.436, .438, .436, .437, .433	.432	.001	.431, .432, .433, .432, .433
BACTERIA						
Colonies/cc						
Oct. 15, 1953	99	24	64, 71, 91, 69, 126, 97, 106, 130, 127, 109	988	436	277, 1072, 650, 1037, 725, 1227, 1033, 1926, 604, 1328
CHLOROPHYLL						
mg/M³						
July 2, 1953 (by N. Marshall with 10 liters through Foerst centrifuge)	.03	....	....	.43	....	....
3 liters through millepore filter; Beckman Model DU spectrophotometer: Richards & Thompson (1952) method.						
July 10, 1955	.29	....	....	1.57	....	See diurnal curves in Fig. 29.
Aug. 11, 1955	.48	....	....	1.68	....	See Fig. 30
NO. 10 NET SESTON						
mg dry/l						
July 2, 1953	....	....	....	.11	....	....
Aug. 28, 1954 (dye and net method)	.017	....	....	.118	....	.145, .091
May 28, 1954	.01	....	....	.06	....	....
SAND AND SESTON						
Millepore filter (increase of filter weight) (includes sand)	.5	....	July 12, 1955	.85	....	July 21, 1955 (noon)
NO. OF ALGAL CELLS						
individuals/cc						
No. 10 net						
July 2, 1953 (84 l concentrate)	2.2	....	....	67	....	....
Millepore filter						
June 8, 1955	4.1	....	....	113	....	....
TOTAL ORGANIC MATTER						
Acid permanganate method ppm oxygen used						
Oct. 1, 1953 (some surface drainage)	.533	.144	.70, .55, .35	1.13	.35	1.00, 1.60, .80
Oct. 10, 1953	.688	.155	.50, .70, .60, .73, 1.09, .50, .55, .62, .72, .82, .75, .68	.807	.18	.89, .79, 1.11, .70, 1.15, .70, .70, .61, .70, .72
Alkaline permanganate method (Benson and Hicks, 1931)						
Feb. 25, 1954	.62	....	....	.76	....	....
May 23, 1954 noon	....	....	....	.79	....	....
BOD method, 25 deg. C.						
June 8, 1955 after 33 days, oxygen in ppm						

TABLE 8. (Continued)

Measurement	BOIL			¾ MILE DOWNSTREAM		
	Mean	S	Separate analyses	Mean	S	Separate analyses
Unfiltered	7.097	.046	end: 7.15, 7.11, 7.04, 7.12, 7.21, 6.95	7.308	.189	end: 7.22, 7.69, 7.17, 7.29, 7.21, 7.27
Millepore Filtered	4.827	.228	end: 5.18, 4.89, 4.93, 4.51, 4.54, 4.91	5.163	.257	end: 5.41, 5.45, 5.16, 4.68, 5.16, 5.12
July 12, 1955 after 21 days, oxygen change in ppm						
Unfiltered	−.77	.176 .131	start: 5.27 (5.22, 5.36, 5.23) end: 4.53 (4.65, 4.58, 4.37)	....	....	....
Millepore Filtered	−.81	.120 .042	start: 5.07 (4.94, 5.04, 5.23) end: 4.16 (4.10, 4.17, 4.20)	....	....	....
July 20, 1955 after 26 days, oxygen change in ppm						
Unfiltered	....	....	....	−.75	.010 .057	start: 5.31 (5.31, 5.28, 5.33) end: 4.56 (4.49, 4.58, 4.62)
Millepore Filtered	....	....	....	−.62	.47 .36	start: 3.03 (3.68, 2.53, 2.89) end: 2.41 (2.87, 2.39, 1.97)

posed that bacteria below 1 cm in the many feet of organic muds are not contributing much to the metabolic activity of the community. The calculations are given in Table 7.

Early in the plating it was found that the spring bacteria plated out more rapidly at the natural temperature of 23° C than at 37° C again in agreement with behavior of aquatic populations elsewhere. The chromogens appeared late, after two weeks, and developed whether the cultures were in the light or dark.

The counts of bacteria in the water, like the counts of phytoplankton, show the extreme sparsity of plankton components. The steady increase downstream shown by the increase in counts in Table 8 by a factor of ten in ¾ mile is an indication of the contribution of the substrate community to the water. Assuming a steady state it is also a measure of the community net production as described below. The low counts in these springs waters are consistent with a summarizing statement by Whipple (1899). It should be remembered that the water in the boil area includes some water recirculated by eddies from the community floor.

In the intense light of this community, it may be that a considerable number of the bacterial sized cells counted in the direct counts are photosynthetic. In the periphyton counting but not in the deeper mud samples a large proportion of the individuals were spheres larger than most bacteria although smaller than Chlorella-sized algae. What the classification or metabolism of these dominants may be was not determined.

Decomposition of dead animal tissue was very rapid. Crabs, turtles, and fish which died in the course of experiments conducted in cages where the oxgen was maintained by the .1 m/sec flow of the water at 2.8 ppm day and night were mostly decomposed in 3 days. Ordinary chicken wire oxidized in 8 months and ¼-inch galvanized hardware cloth oxidized partially in about 2 years. Slow decomposition in the Christmas Tree Spring with its low oxygen tension (1.1 ppm) may be indicated somewhat by a photograph shown by E. Ross Allen (Hubbs & Allen 1943) of a characteristic shaped log which looks visibly little changed in June 1955. The untreated and unpainted pine two by fours of the experimental cage on the edge of the main boil were half-rotten at the end of 3 years in a flowing current of 2.9 ppm oxygen.

To gain some idea of the fungal populations, hemp seed were placed in open glass vials in several situations underwater and allowed to develop for three weeks. These were sent to Dr. Terry Johnson, Dept. of Botany, Duke University. He reported only the algal parasites (see Table 6) on the attached algae and an absence of fungi that attack hemp. Most waters provide growth on hemp seed with this method. Also found but not identified were large amoeboid "slime molds" 2 cm in size covering the sheets of diatoms on the glass slides.

As a result of various estimates described above,

TABLE 9. Bacteria in Silver Springs 1953.

Direct Counts With Phase Microscope, 970X, Fresh Material, Live, June 9.

Material	Slides Prepared	Fields Counted	BACTERIAL COUNTS X 10^6 mean	range
Sagittaria blade with periphyton, 28 cm² surface	3	8	774	270-1520
	2	6	757	470-1000
	1	5	468	270-600
1 ml mud located 2 cm below the mud surface	2	9	276	40-440
	1	5	424	200-660
	1	5	398	130-600
1 ml mud located 24 cm below the mud surface	1	5	226	130-270

Counts on Slides Submerged 72 hours and Stained With Gentian Violet, May 12.

Location	Slides Prepared	Fields Counted	Bacteria /mm²/day	
Slides on and near mud level	10	60	3277	2186-5760
Slides .6 m below water surface	14	84	1281	613-2480

Plate Counts of Aufwuchs and Mud on Henrici Caseinate Agar, 1953.

Material location and date	Number of Samples	Number of Plates	BACTERIAL COUNT X 10^6 mean[a]	range	Percent Chromogens
Sagittaria blade					
In shallows, little current:					
May 28, 26 cm²	3	9	19.6	4.1-35	17
May 9, 57 cm²	5	15	17.6	7.3-22	15
In deeper water, swift current:					
May 28, 24 cm²	2	5	21.9[b]	9.7-34	0.7
Mud, 1 ml:					
Mud surface:					
May 9	6	18	5.7	0.6-15	10
May 28	3	9	4.9	3.1-5	9
June 1	3	8	1.6	.6-2.6	20
9 cm deep in mud					
June 1	3	9	.26	.12-.33	6
18 cm deep in mud					
June 1	3	8	.24	.07-.5	7
27 cm deep in mud					
June 1	3	9	.4	.11-.7	7

Plate Counts on Water, 1 ml (no dilutions)

Distance from boil and date	Number of Samples	Number of Plates	BACTERIAL COUNT X 10^6 mean	range	Percent Chromogens
Boil, Oct. 15	10	10	99	79-130	..
¼ mile, June 1	4	4	343	277-1926	5
¾ mile, Oct. 15	10	10	989		..

Summary of Bacterial Distribution in Silver Springs

	Percent Chromogens	Agar Plates X 10^6	Direct Counts X 10^6	Ratio of Counts to Plates
Sagittaria blade with aufwuchs	16	19.6	666	34
Mud, on the surface, 1 ml	10	4.0	366	91
Mud, 27 cm below the mud surface, 1 ml	7	0.4	266	665
Water, 1 ml	5	0.00048	...	...

[a] Mean of 1/10,000, 1/100,000, and 1/10^6 dilutions; 3 replications each.
[b] Excluding one plate count 502 x 10^6.

the bacterial and decomposer biomass is found to be small relative to the primary producer biomass. However, it will be found in the metabolism discussions below that although small in biomass, the total part in the utilization of energy is enormous.

A few of the animal components should probably be classified with the decomposers since their source of nutrition is miscellaneous including dead organic matter or bacteria. Crayfish are thus included in the overall decomposer biomass in the construction of pyramids of biomass below.

BOTTOM SEDIMENTS

Unlike the situation in lakes, streams send most of their excess production of unused organic matter downstream as seston. Silver Springs is no exception. However, much organic matter is also decomposed in situ. The stability of its current regimes has apparently allowed a relatively steady state to develop regarding the bottom sedimentation as well as with other phases of community process. The sedimentation of organic matter down among the Sagittaria blades develops a rich algal gyttja that almost qualifies as a sapropel since disturbance of the bottom releases large volumes of gases. Some data on the nitrogen content of the mud were obtained by Kjeldahl analyses. .38% was found on the surface and .23% was found 25 cm deep. These values are about half of those in the sediments of eutrophic Linsley Pond (Hutchinson & Wollack 1940). The rapid decomposition of this organic matter as well as the downstream losses apparently balances the sedimentation rate, since the bottom beds of Sagittaria and the muck in which they are rooted have been reasonably stable over the 5 years of study.

The underwater observer walking among the plants usually sinks into the ooze at the base of the plants over the ankles and sometimes to the knees in spite of the shells in the muck. Depending on the irregular base of limestone the muds vary from zero to more than 16 ft in thickness as probed with a rod. The large numbers of Pomacea and Vivipara snails which are sedimented among the gyttja make it highly calcareous. Since it has been demonstrated that the rate of growth of rooted aquatic plants is a function of the nutrients in the substrate, the nature of the bottom mud is as important to the ecosystem here as in a lake. Thus this community is like a coral reef or a terrestrial one in building up its substrates so as to support a high climax production. Except for its thick bed of rich muck Silver River would be a rushing canal through a pipe of limestone rock. Further downstream below the study area it is of this nature. A screen cage filled with Najas coated with aufwuchs growth was suspended for 6 months at the station with 2.8 ppm oxygen so that a pint jar would collect sedimenting organic matter. It completely filled with a rich black ooze similar in appearance to that formed in rich lakes. The loss on ignition of this ooze was 37.6%. No detectable radioactivity was found in the dried peat.

In a few places there are short sand beaches mostly introduced for bathing. A fairly typical psammon was found here with green algae concentrated a few millimeters below the sand surface and a variety of oligochaetes, tardigrades, ostracods, amnicola and a few ciliates. These are very minor relative to the representative community.

INVERTEBRATES AND OTHER HERBIVORES

By and large the herbivore trophic level is made up of immense numbers of small invertebrates eating the aufwuchs algae. The waving surfaces on the blades of Sagittaria support a rich invertebrate aufwuchs living in and on the algal growths. Others climb and swim in the more sheltered waters at the bases of the plants. In addition the mullet continually nibble the plant tips and the large plant-eating turtles (*Pseudemys*) make considerable inroads. The flop of jumping mullet and the slipping of turtles off their logs are frequent events in the life of the spring when the sun shines.

The sampling of the various components of the herbivore populations for purposes of rough biomass estimates in Table 7 required a variety of methods as follows:

1. Large bottom snails (*Viviparus, Oxtrema,* and *Pomacea*) were picked by hand from a 10 ft by 10 ft square placed on the bottom.

2. Mullet were counted from a small aluminum boat by eye by observer hanging on the bow of the boat with a face mask towed rapidly in criscrossing circuits.

3. Turtles were assumed to have the same density per area as in Rainbow Springs, another very large spring with somewhat similar vegetation in the same county similarly disturbed with boats and tourism. Dr. Lewis Marchand (1942) tagged 1200 turtles and was getting at the end of his study about 10% recovery, thus permitting an estimate of about 12,000 *Pseudemys* on the river.

4. Gammarids, copepods, mites, and other organisms around the bases as well as that fraction of the aufwuchs which drains off of the plants when removed from the water were collectively estimated with the Cornell plant net obtained from Foerst Co. The underwater observer placed the net down over an area of Sagittaria and closed the metal jaws about the bases of the plants, pulling them up by the roots, inverting the whole mass underwater and bringing it up out of water so that the drainage of the plants and the water which had been about the bases of the plants passed through the bolting silk part of the net. Then the plants were removed with shaking. The residue in the bolting silk of the net was worked into one spot and transferred to a specimen jar. The contents were preserved and counted later.

5. The extremely numerous invertebrate components of the aufwuchs which did not drain off with the above procedure were estimated by scraping the contents with a razor blade into bottles. The number of blades and the areas of blade surface were estimated. From previously estimated number of blades per average bottom mud area, the total number of each dominant per area of spring was determined.

Once a rough count of the number of each dominant per area of the spring was obtained, a rough biomass was obtained by determining the average dry weight of each component organism. The results of these estimations and calculations are given in Table 7.

The current velocity has a considerable effect on the microenvironment and thus on the invertebrate population. Distance from shore and exposure to fish predation are part of this pattern. In order to get representative estimates, the quadrat methods described above were made as a series out from shore on the south side of the boil area where a complete range of conditions may be expected to exist. These results were averaged in Table 7. One obvious pattern was the presence of very large caddis fly populations in the faster currents with an almost complete absence in the slower currents in spite of similar Sagittaria blade communities. The immense insect emergence at dusk is described below.

Water spiders and gyrinid beetles were counted visually from the small boat while crisscrossing the stream in typical areas.

FISHES AND CARNIVORE TROPHIC LEVELS

The main secondary consumers (carnivores) in Silver Springs are the fishes. As already considered some of the fishes, especially the mullet, are herbivores, but most derive their food supplies from the abundant small invertebrates described above. The fishes present in Silver Springs have been described earlier by Hubbs & Allen (1943) and Allen (1946). As part of this general project Caldwell, Odum, Hellier & Berry (1956) have collected information on the annual cycle of the fishes from the point of view of their growth, life history, and populations. The dominant fishes and their approximate trophic classification are listed in Table 6.

Quantitative estimates of larger fishes were made visually by an observer towed by a boat as described above for mullet. This was done in the early morning hours before the glass bottom boats began operations and when the oxygen in the Sagittaria beds was least so as to minimize the error due to fish hidden in the beds. This method seemed good for most species but not for the dominant species, the stumpknocker, (*Lepomis punctatus*) which resides in the Sagittaria beds in large numbers. For these and for the minnow-sized fishes some quadrats were laid out in the beds and an observer made direct counts by sneaking up through the waving blades, parting the grass and peering among the dark interior. There seemed to be dual reactions of the stumpknockers to the observer. Some moved closer simulating curiosity; others moved away. It is hoped that these responses were equivalent and that an estimation of some value resulted. The number of these fishes per area was then multiplied by a rough figure for the dry weight of an average sized fish as seined. The resulting estimates are given in Table 7.

One of those very characteristic features of the springs which interest the tourist are the large (10-50 lb) Channel catfishes that school in some of the side boils and in some of the bare places about ½ mile downstream. These are shown in Figure 20. These fishes have been observed to hang head down in the rising water from the side boils and a number of suggestions have been made as to possible purpose or meaning in terms of the life history of these fishes. Dr. Coleman Goin thought there might be underground cave fauna occasionally emerging to be eaten. Some have thought there was a diurnal pattern with fishes in the caverns during the day and out at night (Hubbs & Allen 1943). However, our fairly extensive night operations failed to discover any clear cut pattern although possibly more feeding in shallow areas was observed at night. Some catfishes were in the boils both day and night.

FIG. 20. Catfishes schooling in the sandy cavern called the Catfish Convention Hall. A school is invariably found here at all seasons. Note the algae mixed with the sand.

Another hypothesis that merits consideration is the respiration advantage. For a fish to fall nose-down into the rising current of fairly oxygenated water would require little respiratory work. In Table 2 are given the oxygen tensions of the various boils. It is very obvious that the catfishes do not hover in the main boil and only in some of the side boils. It is very interesting that they should frequent the boils with larger oxygen contents. It may be that these fishes rest in these currents. Especially if they build up deficits while feeding in some of the plant zones of the springs where the content drops below 1 ppm, they might use these deep boils as places to replace their oxygen deficits.

The same phenomenon was observed in Lithia, Springs, Hillsborough County with a few Bullheads (*Ameiurus*). The water in Lithia Springs emerged with 2.1 ppm oxygen and 3.8 ppm CO_2 and increased downstream (no side boils), so the fishes with only one boil to use were selecting the lowest oxygen concentration area in the stream. However, it may be that by falling head-first down into this strong upflow, no work is required, so that the excess of oxygen intake over utilization is less than for a fish swimming horizontally or pumping water through the gills in slightly higher oxygen tensions.

In the course of each of the glass bottom boat trips one or more balls of wadded bread is tossed to the catfish schools that are always opposite Paradise Park in a deeper section of the stream. Much of this bread is observed to be eaten by the catfish and bluegills with some being dispersed. The 70 loaves ordered by the Silver Springs management each day for this purpose represents 486 Cal/m^2/yr over the whole spring area. Although negligible compared to the overall energy production (Fig. 7), this is a very large energy source to be entering the food chain at the herbivore level. It seems likely that the large schools of catfishes and to some extent the bluegills are receiving considerable nutrition from this special food source.

A top carnivore or tertiary consumer trophic level in Silver Springs exists in Silver Springs in the larger bass and gars. These were estimated visually as with the other large fishes and the data included in Table 7. The centrarchid population studies made as part of the project on Silver Springs are published elsewhere (Caldwell, Odum, Hellier & Berry 1956) but some conclusions pertaining to the role of the stumpknockers and bass are restated as follows:

a. Colored plastic tags with individual color combinations can be used to follow individual fish visually for as long as a month, but evidence indicates a high mortality of tagged fish. Tagged sunfish do not move far but bass do move up and down the river for at least several miles.

b. Breeding extends over a long period from February to September but diminishes to only scattered reproduction during the winter in spite of the constant temperature.

c. Distinct year classes are absent but there are modes in frequency distributions of the young fishes.

d. Rings in the scales are distinct and are apparently formed at almost any time of the year. The frequency of ring formation is too great in stumpknockers relative to their growth to be annuli. In bass the rings do appear on the average at about yearly intervals.

e. Stumpknockers of all ages, winter and summer, have their guts with two-thirds algae and one-third animal material.

f. Caged stumpknockers grow .31% per day in summer; recaptures of tagged bass indicate .19% weight increase per day. Some evidence for decreased winter growth was found.

g. All the stumpknockers whose visceral cavities were opened contained conspicuous parasitic infestions.

MICROHYDRA (CRASPEDACUSTA)

One of the many surprises provided by Silver Springs was the appearance of the sessile stage of the fresh water jellyfish Craspedacusta on glass slides. Three to 6 individuals appeared on any slide which had been submerged for three weeks or longer. These tiny individuals were observed to stun and eat small midge larvae that were abundant in loose tubes on the same slides. No evidences of a medusa stage were found, but asexual budding was observed. Because of the stability, the Silver Springs community is suggested as a reliable source of the interesting animal. A few counts are given in Figure 19.

PARASITE PYRAMID

The larger fishes were found to be regularly infested with parasites. In energetic terms these parasites belong in the same trophic level with the top carnivores. Dr. Wanda Hunter and Dr. Winona Vernberg of Duke University carried out the following tedious study to help estimate whether the parasites of the dominant species of fish were important energy consumers relative to the carnivores.

Parasites, mainly acanthes, strigeids, and trematodes, were isolated from one group of ten individuals in the winter and one group of ten individuals during summer. In the group of fishes collected in May 1954 there were 222 worms with a collective dry weight of 36.2; in the group of fishes collected in December, 1954 there were 161 worms with a total dry weight of 22.7 mg. There was no distinct difference in the composition of the parasitic populations.

The ratio of dry standing crop of parasites under these conditions approximating a steady state was .036% parasites in the total fish by dry weight. Thus the parasitic pyramid is very steep. Some idea of the possible energy utilization may be obtained from metabolism measurements of a small trematode by Hunter & Vernberg (1955). Allowing 10% of the wet parasite volume as dry weight, the respiration of adults was about 2 mg oxygen/gm dry parasite/hr for the adults and about 60 mg oxygen/gm dry/hr for the cercariae. If a metabolic rate figure of 10 mg oxygen/gm dry weight/hr is used with the estimate of .036% parasites by weight in 13 gm stumpknockers per m^2, one finds an intake of energy by the parasites of about 1 Calorie/m^2/year, which is not important in comparison to the Carnivore energy utilization. Thus in spite of a high metabolic rate per gram, the parasites in this climax situation are not energy dominants.

TROPHIC STRUCTURE AND BIOMASS PYRAMIDS

The rough estimates of biomass by trophic levels outlined in previous paragraphs are summarized in the calculations of Table 7. One main difficulty comes from overlapping species which draw energy sources from two or even more trophic levels. Where the food was mostly in one trophic level, the whole animal was assigned to that trophic level. Where partition of food sources involved a second source of importance, the species was divided and placed in two trophic levels according to the percent of the food derived from each. Unfortunately fragmentary information exists as to the food sources and it was not possible to carry out detailed food studies on each species. Some basis for placing the animal in a particular trophic level is given in the list of community dominants in Table 6. The general significance of pyramids is given in Odum & Odum (1953). There is a possibility that communities which adjust to some kind of steady state tend to resemble each other in basic properties such as biomass pyramids because of basic laws common to steady state community systems. Further discussion relating the shape of pyramids to the size of organisms and community structure in streams is given elsewhere (Odum 1956b). Since one is here mainly interested in order of magnitude, the trophic classification should not receive too detailed a use without further studies. In Figure 21 are summarized the estimates of biomass in a pyramid of biomass by trophic level. Notice that a clear pyramid results just as have been found for other communities so far investigated where the dominant producers are not all small in individual size. The decomposers are seen to rank following carnivores as far as actual biomass of protoplasm. Their metabolic importance is discussed below and found to be great relative to their mass.

A single blade of aufwuchs has its own pyramid of biomass with a decrease in biomass from plants to herbivores to carnivores.

PHOTOPERIODISM AND REPRODUCTION

As described in the environmental section, the temperature is constant but the light changes seasonally. With this regime the annual changes in energy flux associated with changes in production are due to light and not temperature. The individual species might be expected to be adjusted to this pulse in energy in their own individual life histories by a coincidence of periods of the extra energy drains of reproduction with the seasons of greatest energy flux through the community. The mechanisms by which their physiological cycles are externally controlled cannot be related to temperature but must be controlled by light either by direct photoperiodic

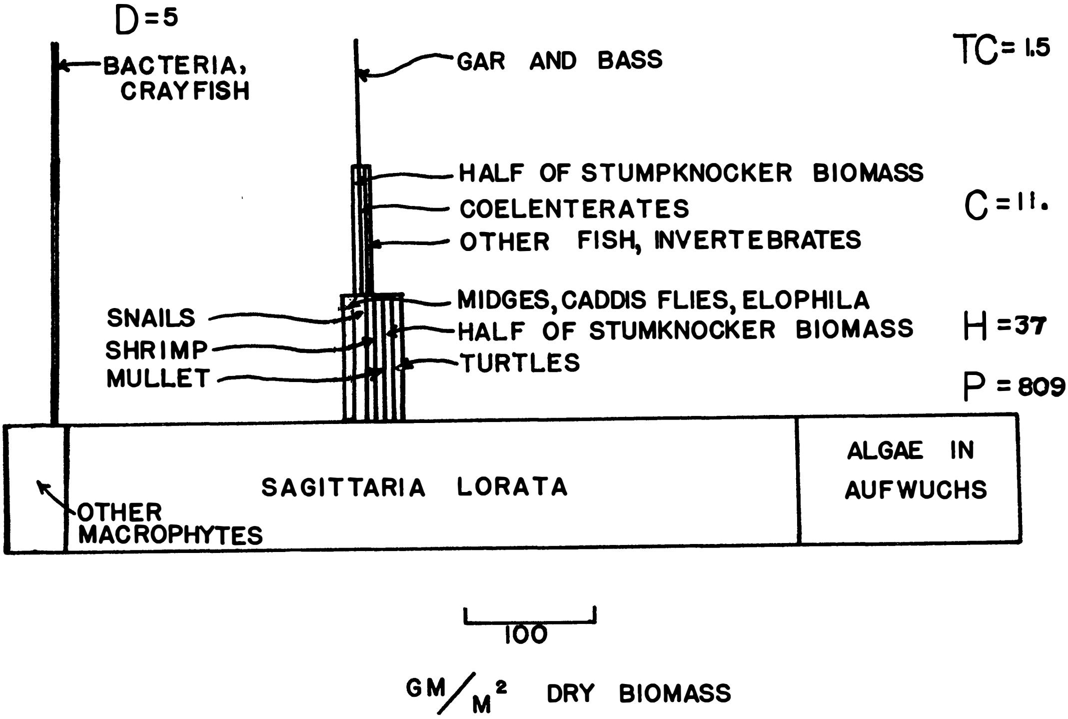

FIG. 21. Pyramid of biomass for the Silver Springs community based on the estimates in Table 7. P, primary producers; H, herbivores; C, carnivores; TC, top carnivores; D, decomposers.

control or indirect control through effects on the production rate.

In Figure 22 are given seasonal patterns of reproduction for snails, shrimps, and fishes. A similar curve is given by Caldwell, Odum, Hellier & Berry (1956) for the stumpknocker. Surprisingly there is some breeding all the year in some species but an enormous increase occurs during the spring. Photoperiodism is clearly implied although not proved. It is interesting that *Paleomonetes paludosus* here behaves differently from its behavior in experiments in North Carolina (Jenner, personal communication) where increased dark period leads to sharp starts and stops in the seasonal reproduction pattern. Hildebrand (1921) found Gambusia and Mollienesia from Beaufort, N. C. and Augusta, Georgia breeding from May through September. In Key West, Florida he reported Gambusia breeding at all seasons but much less in winter. Apparently a flexibility in timing of reproduction exists in these ranging species so that their life cycles can be readily kept in pace with food supply.

Barney & Anson (1921) had long ago noted the decline of breeding in Gambusia in September and October in Louisiana prior to a decrease in temperature.

That the apple snails did continue some winter laying was indicated by the continual presence of pink, recently laid egg clusters that normally turn white after a week or two. In the summer hatching occurs in two to three weeks.

These results on photoperiodism suggest ways by which the community as a whole is integrated so as to maintain so stable a state in spite of the seasonal pulse of productive energy. Those species whose reproductive cycles are geared to the seasonal pulse may be expected to excel in competition over any species which is not regulated to take advantage of the excess production of the spring and summer. With predators being less specific in their diets than their food, the prey organisms which can reproduce least will either be maintained at low levels or by the Allee minimum population effect be eliminated.

By these adjustments a pulse in production need not result in excessive changes in population numbers at any trophic level, for the excess young at one level are rapidly eaten by the excess young in the next level. Where the ecosystem is so precisely adjusted, it may be that fewer species will be found. Those which cannot compete may be eliminated here, whereas in fluctuating environments like many streams, conditions change so rapidly that species which are one day losing out in competition may begin to gain under other conditions so that more species may be present any instant. See Hutchinson (1953) for an account of this hypothesis.

This in a way is an extension of the generality that where environments become extreme for any reason the number of species present decreases. Silver Springs is not extreme in the usual senses of temperature, light, or chemical environment. However, this spring is extreme in being stable, and

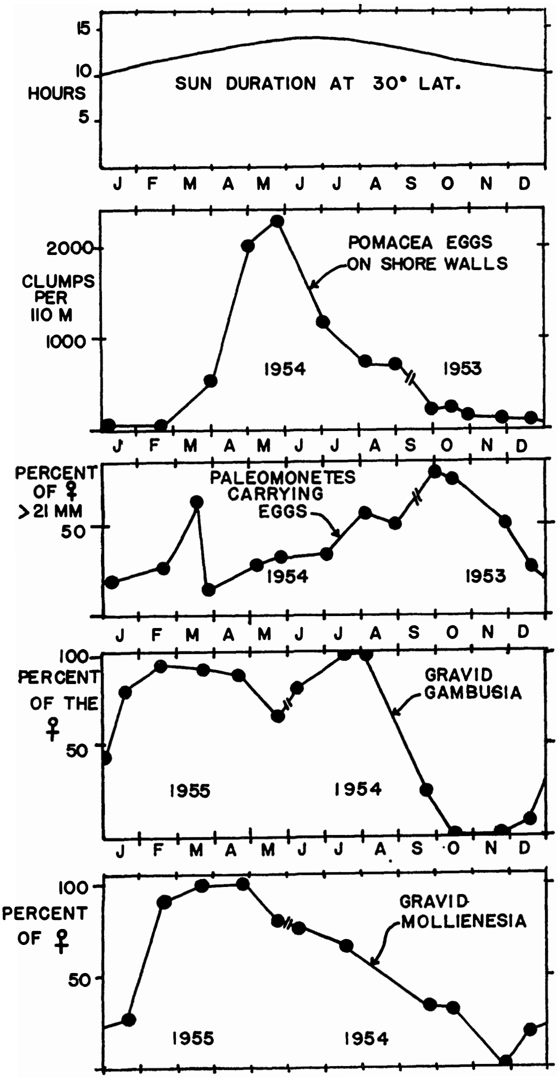

FIG. 22. Seasonal distribution of breeding in representative species. The approximate day period is given in the upper graph. Counts of apple snail eggs were made on the wall pictured in Figure 3.

thus has fewer species. Dr. Yount's hypothesis (1956) of greater competition for greater productivity is certainly in harmony with the fewer species in the springs.

Caution is thus urged in the use of species number for pollution classifications. According to criteria of the small number of insect species, Silver Springs would be described as a polluted stream. One cannot imagine a stream which in all its properties is less affected by man and which by its organic content and other chemical conditions is more nearly the perfect biological environment. Other springs (Blue Springs, Volusia Co.; Orange Springs, Marion Co.; Green Cove Springs, Clay Co.) in Florida with more extreme conditions of oxygen have even less species and yet are in no way polluted but possess low bacterial and organic matter contents in their water and are unaffected by man's activities.

BIOSTATIC CHARACTERISTICS AND COMPETITION

Measurements and sampling at different times have shown that remarkable consistency exists except for some diurnal and annual effects. Evidences for stability in the physical and chemical environment of the spring were given in earlier sections. Evidences of biological stability in Silver and other springs may be cited as follows:

1. The dominant algae covered eelgrass noted in the last century is still present (see section on early records.) Dry weights of samples in May-June, 1953 (Table 7) averaged 765 gm/m^2. Those made in August 1952 were similar (860 gm/m^2).

2. The map of Silver Springs (Fig. 6) made in 1951 was little changed in 1955. Only 1% of the spring area had changed in type of vegetation.

3. The taxonomic composition of the algae in Silver Springs was not found to vary during a year (Whitford 1956). Further examination by J. Yount and the author showed no change in 1955.

4. Glass slides kept in identical positions in the springs and examined at different seasons (Nov., April, May, June, July, Fig. 19) showed no differences in composition of glass slide aufwuchs with its dominance of Cocconeis.

5. Some unpublished evidences of stability and instability of macrophytes in other springs have been collected by D. Swindale and H. T. Odum. Maps were made of spring headwater areas before and after 3 years. In these smaller springs greater disturbance of plant beds occur than in Silver Springs. Considerable shifting of patches and beds occurs, but there is considerable stability of the major floral composition.

6. Analysis of variance of insect populations in Weekiwachee and Homosassa spring boils (Sloan 1956) showed no significant change in populations seasonally. Comparisons in Silver Springs by Mr. Sloan with the same method indicated no seasonal variation for Silver Springs either. On May 28 Mr. Sloan using his 5 sweep procedure in the plants in four places in the boil area found 2, 1, 3, 0 individuals. He had previously shown with a curve of number of species versus number of net sweeps that a point of diminishing returns in turning up new species was reached with about 5 sweeps.

7. The careful description of the fish populations given by Hubbs & Allen (1943) for Silver Springs when compared with the recent status of the fish populations (Table 6 & 7) indicate that no change has occurred in dominants or minor constituents of the main channel communities. Essentially constant patterns of length frequency for the dominant stumpknocker (*L. punctatus*) were found by Caldwell, Odum, Hellier & Berry (1956) during 1954-55.

The most stable areas are apparently those nearest to the current and thus most independent of the seasonal and man made changes. Hubbs & Allen

(1943) cite the decrease in marshy area around the boil with the building of a wall and cleaning up of the margins for tourist purposes prior to 1943. A general impression of decrease in *Mollienesia, Micropterus, Esox, Amia,* and *Elassoma* is recorded. On an area and biomass basis the littoral associations are minor even below the main boil where the littoral zones have been less affected. The removal of the headwater marshes apparently made the spring more homogeneous by removing littoral and variable environments which are more like non spring environments.

8. Measurements of snail eggs on the boundary walls in 1954 were similar to those at the same time of year in 1953.

9. Primary production of the entire spring in December 1953 was similar to that in December 1954 (See Annual Cycle of Production).

10. Counts of invertebrates in the aufwuchs and Sagittaria beds in 1955 (Table 7) were similar to those made in 1952. The constancy of the macroinvertebrates and small fishes was qualitatively verified during the year of seining that was part of the fish study.

11. Similar bacterial populations were found in the water in October and June, 1953.

One of the most fascinating, unsolved problems in the springs is the competition between the similar eelgrasses *Sagittaria lorata* and *Vallisneria neotropicalis.* Laessle (1953) discovered the simple diagnostic way of separating these species in the field by the branching of the roots in Sagittaria. The two species were found in some springs in alternating patches and occasionally in intimate associations of both. Silver Springs contains mostly Sagittaria although some patches of Vallisneria were found (Fig. 3) and in the downstream area by Dr. D. Swindelle. In 1953 a 4′ x 3′ cage was planted with Vallisneria in Silver Springs with plants brought up from Homosassa Springs. A dense growth was maintained for over a year. The factors maintaining the great dominance of Sagittaria in Silver Springs are not yet known. Some other springs with no consistent chemical similarity as yet detected are dominated by Vallisneria.

Side Run and Species Variety

In Figure 2 is shown a small spring run, the boat canal, through which some of the main boil water flows with an average current in June, 1955 of .14 m/sec. This run is partially shaded and possesses a different biota from the main spring mainly in having a greater variety of additional species represented in small numbers. (Insect variety measured by W. C. Sloan and algae by L. A. Whitford and J. Yount). On May 15, 1953 at 3:30 pm on a clear day the oxygen down the run was as follows: Boil, 2.50; first boat house, 3.78; last of boat houses, 4.01; sharp bend, 4.70; at old bridge, 4.51; at mouth of side run, 5.53 (5.52, 5.54). Thus the oxygen pattern resembles that in the main run (Table 3). This little spring situation considered as a natural experiment tends to refute the idea that the low variety of species in the main Silver Springs run and other similar Florida springs is due to the moderately low oxygen or other property of the water acting directly. Instead some other hypotheses must be offered such as a direct action of the greater main stream productivity; competition according to the Yount hypothesis (Yount 1955); shading; or the lower current velocity of the side run (.14 m/sec) compared to the main run (.21 m/sec).

Zoogeography

In other springs of the world a big point has been made of the presence of relicts. Thus Neilsen (1950) reports arctic forms relict in the cold springs of Germany and Tuxen (1944) reports tropical forms relict in the hot springs of Iceland. In Silver Springs however the temperature and aquatic conditions tends to be an average of the general regime in aquatic environments of Florida and to be in the general region of optimum biological conditions as far as temperature. Thus it is no surprise that relict faunas have not been described for Silver Springs.

There are few endemics in the springs. The large animals can readily move down the spring river and thus into the waters of the rest of the state so that gene isolation is apparently not great. For example the mullets must move from the sea 100 miles up the St. Johns river from their breeding grounds in order to reach Silver Springs. The algae and smallest species belong to the groups which have their distribution dominated by a tendency to be carried or blown over vast areas. Only the intermediate sized species may be expected to develop an isolation long enough to develop races.

Dr. J. P. E. Morrison, U. S. National Museum, identified the mollusks from a number of Florida springs and indicated that the larger species (*Pomacea paludosa, Viviparus georgianus, Oxytrema catenaria,* and *Physa microstoma*) were distributed throughout the spring communities without the development of races. On the other hand he found some evidence of races in the small Hydrobiidae.

Pseudo-Plankton

The turbulent outflow emerges apparently without plankton but quickly picks up fragments of algae and small animals as it rushes through the beds of weaving plants. The increase in chlorophyll, organic matter, bacteria, and algae is cited for the upper ¾ mile zone in Table 8. This is a useful pattern since one can here infer what magnitudes of organisms are contributed to stream waters. In ordinary streams these contributed fractions tend to be matched by the steady state removal of similar amounts by sedimentation and organismal capture. Even at the ¾ mile zone the plankton is extremely small (.2 gm/m^3). Another reason for a relatively small number of species of some groups of organisms in Silver

River compared to some other rivers may be the absence of the plankton feeding niche.

Since the water flushes the entire upper zone in about an hour it is not possible for any true plankton or reproducing plankton (Potamoplankton) to develop. It is therefore interesting to consider the populations found in the boat basin. The boat basin is a dead end canal leading out from the side of the Silver River about 5 miles downstream (Fig. 2). The end of the canal is a circular pool used for launching boats. This water is in exchange with the main Silver River but may receive local significant drainages in time of rain even though there are no definite inflowing streams. This back water possesses about the same alkalinity (155 ppm) and versenate hardness (202 ppm) as the main channel (alkalinity, 141 ppm; hardness, 205 ppm). The basin possesses a regular and rich plankton population showing something of the potential of the spring water.

It is also interesting to report that when Silver Springs water is placed in the light, intense green blooms of plankton algae develop after several weeks. The Silver Springs water is suggested as an excellent medium for culture work related to ecology since it is a well-balanced medium similar to other natural waters except in being very low in organic content. It is chemically defined and barring unexpected events will always be there for repetitive work or for future analyses. It is likely that chemically defined conditions can be achieved in this way more readily than mixing a medium with chemicals whose purity is never completely known and whose content can never be exactly duplicated. Dr. R. Short, Florida State University, has found reproducible results with culture of parasitic worm stages using Wakulla Springs water where similar stability apparently exists.

Besides the small particles, there are the large fragments of plants that continually drift conspicuously downstream. Most of this is Sagittaria that has been broken off by current, boats, or turtles. These blades float at the surface and the impression is one of large magnitude. A gill net was stretched across the stream at the ¾ mile station at the surface on three occasions so that the magnitude of this downstream loss could be measured. As indicated in Table 8 this loss is very small compared to the losses in particulate and dissolved organic matter. No difference was observed between the early morning and late evening. There may be some difference in the amount of cutting by boats but by the time these fragments catch on the margins and become released again, the diurnal pulse seems to be removed. The breaking of the rotted tips and the cutting by turtles may be of equal magnitude.

Discussion of diurnal plankton is included in the chlorophyll section.

VERTICAL DISTRIBUTIONS

In the deeper boils, especially in the large main boil which has a floor 40 ft deep, there are distinct vertical stratifications of flora. Whitford (1956) found that the pattern of red algae in deeper and darker waters which occurs in some other aquatic environments especially the sea, held here also. The bottom of the main pool is characterized by Chara and red algae without the heavy beds of Sagittaria. The Sagittaria blades are filled with gas bubbles that permit the tips to wave upward into the water and which float the whole plant to the surface when the roots are dislodged. It is possible that pressure is a factor for nowhere in the spring does the Sagittaria go below about 15 ft. This cannot be due to light alone since the light intensities in the bottom are 58% of those at a depth of one meter, and in some wooded overhanging side channels Sagittaria grows in this light intensity.

The distribution of chromogenic bacteria in the euphotic zones was cited previously. The stratification of light and chlorophyll within the plant beds is shown in Figure 16. In shallow water short but numerous blades may by their encrustations indicate an age similar to that of long waving blades of deeper, swifter water.

COMMUNITY METABOLISM AND PRODUCTION MEASUREMENTS

UPSTREAM-DOWNSTREAM METHODS

According to one ideal for studying ecology one should lift up a whole community, place it in a respirometer, measure the whole metabolism, and yet not disturb the normal influx and outflow of raw materials, energy, and waste products. It has perhaps been this ideal that has motivated workers who have laid the emphasis on plankton in ecological work where one could enclose representative samples of whole communities. Valuable advances have resulted from these methods in biological limnology and oceanography.

When one thinks twice about the spring's laboratory with its thermostatic, chemostatic, and biostatic conditions, it may be realized that one actually has a giant flow-system respirometer that encloses the entire community of 18 acres. As the water emerges from the boil and flows over the community the changes in the water between the boil and downstream stations are a measure of the metabolism of the whole community. By multiplying the volume of the discharge by the change in the concentration of the constitutents in the water one may determine the whole effect of the community. This may then be prorated on area, volume, or biomass basis depending on the purpose. It should be possible to compare chemical effects by comparing springs whose constant flows differ in initial content.

In another paper elsewhere (Odum 1956a) the author summarizes previous work on upstream-downstream measurements in flowing waters and methods for estimating atmospheric diffusion. A summary of the main metabolic processes indicated that the upstream-downstream change of oxygen over any stretch of stream community is the algebraic sum of the primary production, the respiration, the diffusion into or out of the water, and the accrual from tributary inflows. By subtracting the night changes from the day changes, the gross primary production may be estimated. Thus one may measure the metabolism of the whole community directly and instantaneously. The production rate may be followed, hourly, daily, and by seasons. As discussed subsequently, special methods may be used to estimate the role of diffusion, respiration, and accrual in the night metabolism. The springs thus are a flow system in which the steady flux of nutritive, clear water is mixed at the boil with sunshine to start a biological chain of reaction as in some chemical kinetic apparatus. Some comparisons and differences between this system and the balanced aquarium are discussed elsewhere (Odum & Johnson 1956). Data on community metabolism as measured by the upstream-downstream changes of several biologically active water constituents follow.

Oxygen Metabolism and Diffusion

In Table 4 is the pattern of oxygen change down Silver River. The 11-ft aluminum boat and 5-horsepower motor were used so as to collect from the entire run in about an hour. The ¾ mile station was chosen as the most suitable place to make continuous measurements to determine metabolism of the headwaters. This spot was at the lower end of the broad expanses and thus at the end of the zones where the trees constitute a minimum shading problem. Below the ¾ mile study station the increase in velocity of current and shade apparently prevented the development of the broad homogenous community found above. This 4 mile section of rapid flow through a gorge of rock and primarily sandy bottom acts as a barrier separating the fertile headwater zones of less rapid flow and the Oklawaha River with its ordinary brown water, seasonal fluctuations, and more complex populations.

In Figures 23-31 are given curves of the oxygen at the downstream station during the course of the day. Clearly there is a diurnal increase due to primary production with a return to lower values at night. There is considerable heterogeneity in the water due to the turbulent eddies and slight differences in trajectory, yet these variations are minor compared to the large magnitudes involved. By multiplying the volume of water discharged by the difference between daily values and night values one obtains the day's gross primary production. The night values serve as ones black bottle with which to compare the day values. The increasing production with increasing light intensity, day length or with clear skies as opposed to overcast skies can be inferred from the graphs. The daily maximum in the oxygen curves comes about an hour after the maximum sunlight at noon on clear days. This is probably an indication of the time it takes for the water to reach the downstream station. An average velocity of 0.21 m/sec estimated in the discussion on current would carry boil water to the ¾ mile station in 1.6 hrs.

One of the conspicuous phenomena in the metabolism of the springs is the formation of enormous numbers of bubbles in and among the aufwuchs, especially in the moderate or slow current areas less than about 0.3 m/sec. These bubbles form during the day and are then observed to rise to the surface. These are probably initially oxygen bubbles. In the swifter waters there are fewer of these bubbles presumably because the water in the aufwuchs microclimates gets replaced before supersaturation is achieved. The rising of these bubbles to the surface during the times of intense sunlight of clear days in May or June could lead to an error in production measurements. In an effort to assess the magnitude of this error, glass funnels were suspended from stakes as shown in Figure 32 so that bubbles rising from below would be trapped in the small end of a graduated centrifuge tube at the water level where standard pressure conditions would permit an estimation of the gas volume.

On theoretical grounds it seems likely that these bubbles are not pure oxygen. Once a gaseous phase has formed the other gases in the water may be expected to exchange dissolved gases with the bubble according to their solubilities in the water. Thus the bubbles rising may have a composition closer to that of air than to that of the initial oxygen bubble that formed. Supporting this interpretation is the following observation: As described below a circulating microcosm was built containing a blade of Sagittaria with aufwuchs. When a light was turned on the glass tube with its circulating water, bubbles formed among the aufwuchs presumably as a result of photosynthesis. However, when the light was turned off and the community allowed to go all night the bubbles were unchanged in size. When the water was tapped the oxygen had dropped to zero. The gases had apparently exchanged with the bubbles without diminishing their size. In spite of a fair flow through the tube of 2 cm/sec the bubbles among the aufwuchs algae were seldom displaced as long as their size remained small.

In Figure 32 are given the measurements of bubble volumes trapped showing the diurnal pattern. From the time lapse and area of the funnel one may obtain a correction for oxygen loss. From the area under the diurnal bubble curve in Figure 32 the gas volume released is estimated for the month of May as 224 ml/m^2 day oxygen lost if the bubbles are entirely oxygen (0.30/m^2). The oxygen production for similar days in May is seen from Figure 32 to be about 28 gm/m^2/day.

Thus the bubble loss in Silver Springs is apparently less than 1% and is neglected in further calculations.

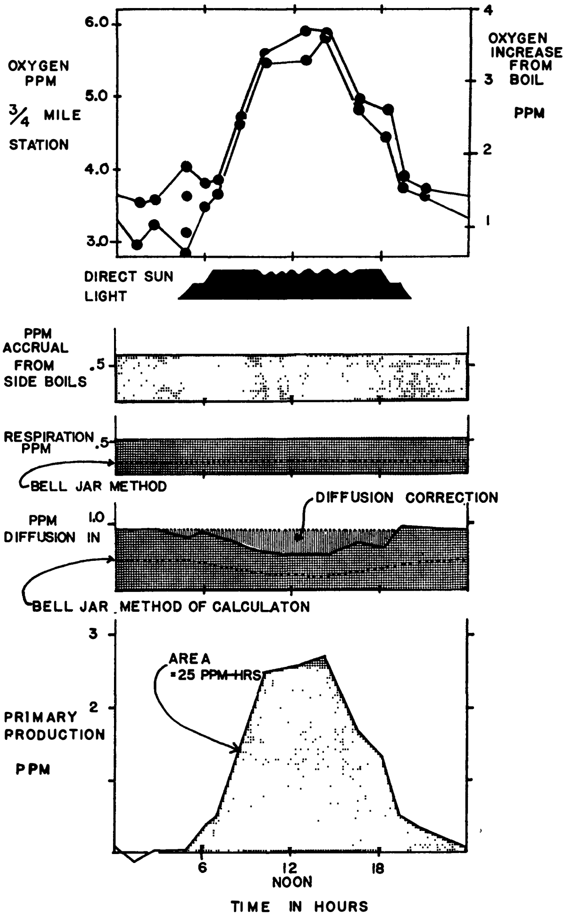

FIG. 23. Diurnal pattern of oxygen at the ¾ mile station May 23-24, 1954 with sample calculation of components of community metabolism. In the upper graph the ppm oxygen as measured is indicated on the left ordinate. On the right ordinate is given the ppm oxygen increase over the average boil value. In the second graph is plotted the average oxygen increase due to water of higher oxygen entering from lateral boils. Respiration is indicated as estimated from bell jars (underestimation suspected) and as estimated in the discussion of oxygen metabolism and diffusion. In order to illustrate balance sheet methods of calculation, diurnal diffusion curves are given as calcuated from the bell jar respiration estimate and as calculated from the higher respiration estimates made. Another somewhat different and intermediate diffusion rate is used subsequently for Silver Springs calculations (see text in oxygen section). The vertical hatching is the diffusion correction which must be added to the area under a diurnal oxygen curve to obtain the primary production. The lowermost graph shows the primary production resulting from the algebraic sum of the downstream changes, accrual, respiration, and diffusion.

Another source of error is the difference in diffusion gains between day and night. Some oxygen is added to the headwater zone from the atmosphere both day and night since the oxygen concentration in this zone is always below saturation except in a

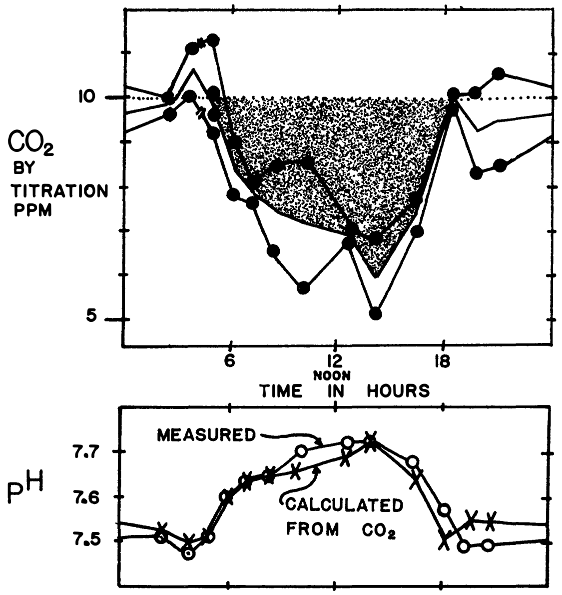

FIG. 24. Diurnal curve of phenolpthalein-titrated carbon dioxide and pH at the ¾ mile station, May 23-24, 1954 (oxygen curves in Figure 23). In the lower graph is given the electrometrically measured pH curve and the pH curve calculated from the carbon-dioxide using the Moore equations (1939). The shaded area is used to calculate production (Table 10).

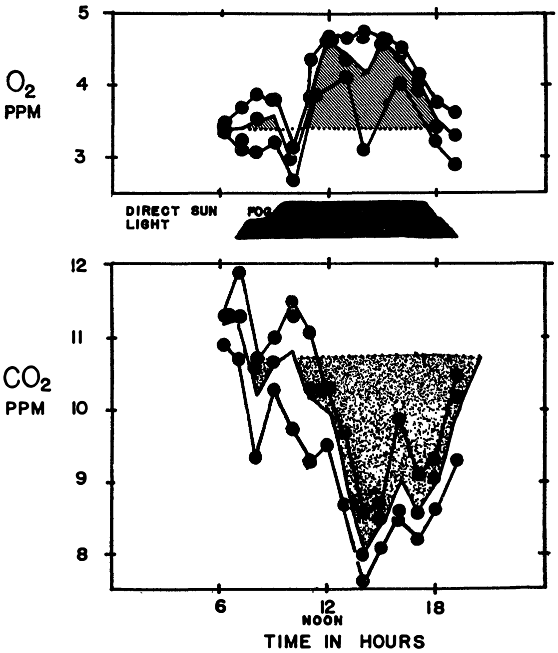

FIG. 25. Diurnal sequence of oxygen and carbon-dioxide for January 7, 1954. The black bar graph indicates the time when the community was receiving direct sun and diffuse light.

few minor plant beds in isolated backwaters. Although the boil outflow is always around 2-3 ppm the oxygen tension is as high as 6 ppm at the ¾

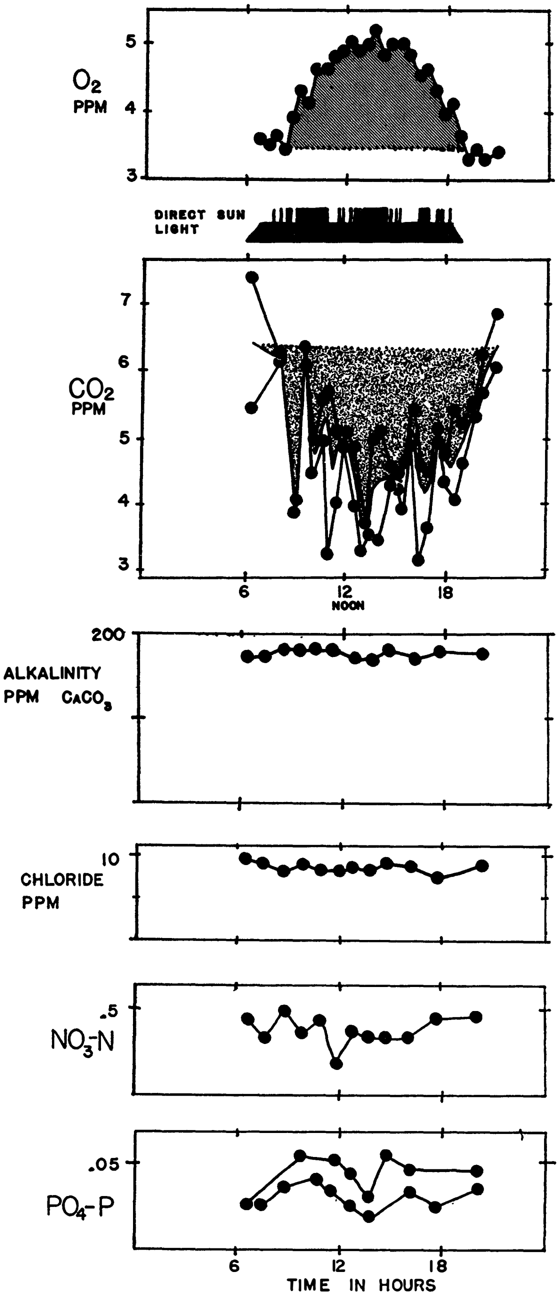

FIG. 26. Diurnal sequence of oxygen, carbon-dioxide, alkalinity (methyl purple), chloride (Mohr method), nitrate-nitrogen (phenoldisulphonic acid method), and inorganic phosphorus at the ¾ mile station, February 19, 1953.

mile station in the middle of very productive days and down to 3.5 ppm at night. Thus the gradient of oxygen into the spring differs. If one assumes that the diffusion into the spring at night is the same as that in the day one underestimates the productivity since the gradient is less in the day and less actually diffuses in. Thus the oxygen measured at the ¾

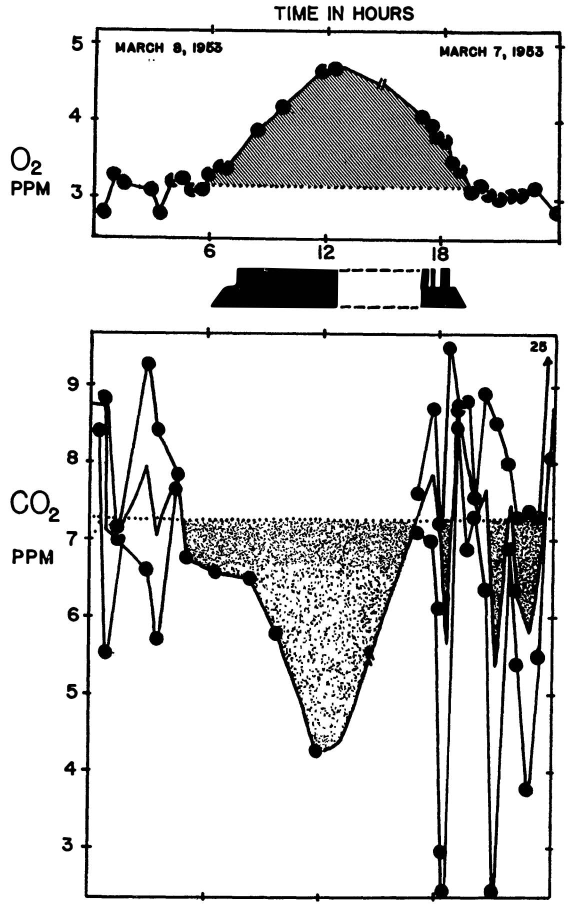

FIG. 27. Diurnal sequence of oxygen and carbon-dioxide March 7-8, 1953 at the ¾ mile downstream station.

mile station downstream is more due to production than would be indicated by subtracting the night value as a black bottle value.

In a previous discussion (Odum 1956a) ways of estimating diffusion in flowing waters were summarized. In Silver Springs two methods have been applied. In one method the diffusion rate was estimated from the rate of downward diffusion of the surface film as observed visually. Fluorescein sprinkled over the surface was watched from below by an observer wearing a face mask and the time for equal distribution with depth determined. The oxygen gas transfer coefficient (defined as the grams oxygen transferred per square meter per hour for a zero saturation) was estimated from the turnover time following a theoretically derived procedure given by Phelps (1944). In the channel in 2.8 m water the turnover times estimated were 2.7 m in 57 sec; 2.1 m in 47 sec and 3.0 m in 81 sec. These were computed for 2.77 m depth, 23 deg temperature, and a gaseous diffusion coefficient of 2.0. A gas transfer coefficient of .92 gm/m²/hr for 0% saturation was obtained.

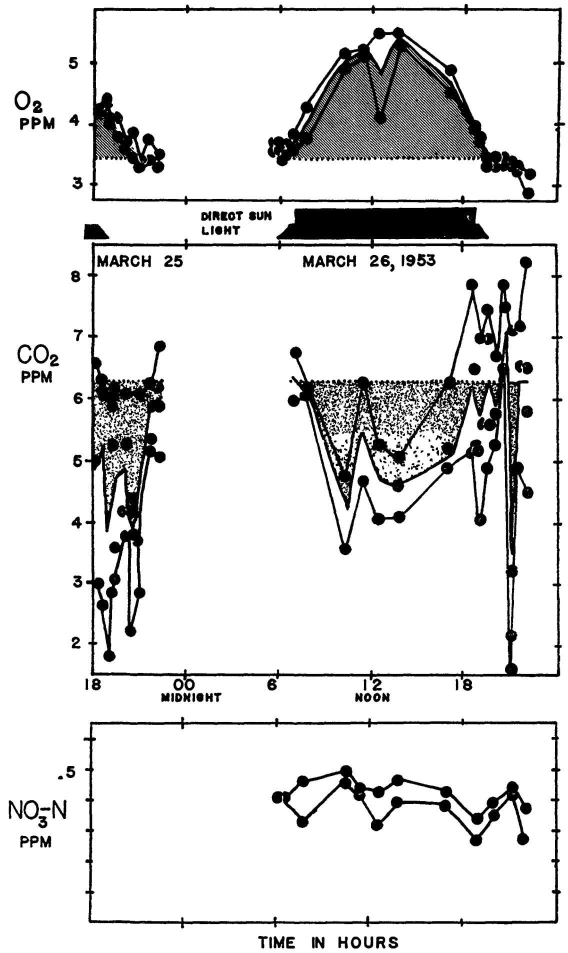

FIG. 28. Diurnal sequence of oxygen, nitrate-nitrogen (phenoldisulphonic acid method), and carbon-dioxide at the ¾ mile downstream station, March 25-26, 1953.

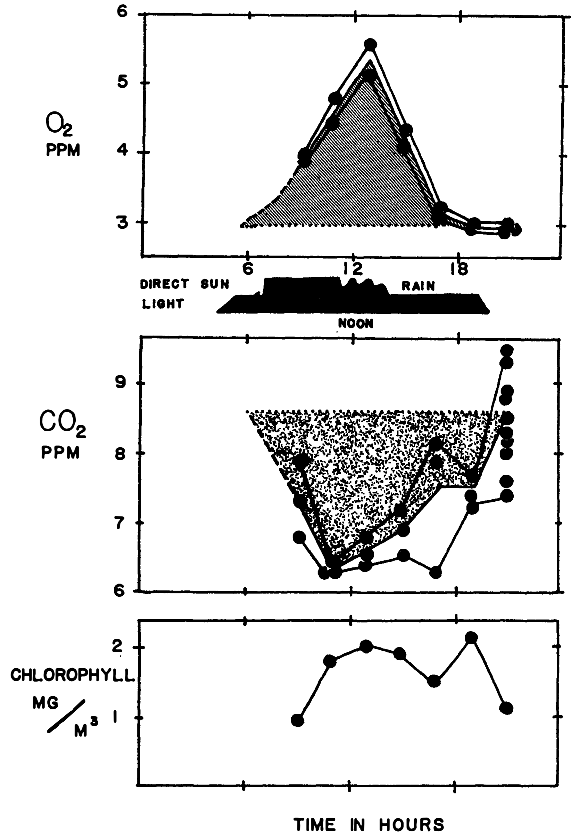

FIG. 29. Diurnal sequence of oxygen, carbon-doxide (determined from pH), and chlorophyll at the ¾ mile station, July 12, 1955.

In the second method independent measurements of community respiration in bell jars and in a circulating respirometer were combined as subsequently described (.61 gm/m^2/hr; .54 ppm). Then the accrual of oxygen due to the inflow of smaller side boils was estimated as .61 ppm (Table 2) from separate analyses in these flows. From the night oxygen change of 1.1 ppm (Table 8) was subtracted the respiration (.54 ppm) and the accrual (.61 ppm) to obtain the rate of oxygen diffusion for the nighttime saturation deficit (1.03 ppm/68%). These relationships are illustrated in Figure 23. A gas transfer coefficient of 1.51 gm/m^3/100% saturation deficit or 2.72 gm/m^2/100% deficit results for an average depth of 1.8 m (discharge of 8.5 x 10^4 m^3/hr x 1.6 hr $\div$ 7.6 x 10^4m^2). The respiration value here (.54 ppm) used is higher than the value for bell jars (.19 ppm) used by Odum (1956a) in a similar calculation because an attempt is made here to correct for the underestimation of the bell jar method as discussed in the community respiration section.

From a gas transfer coefficient of .92 gm/m^2/hr for 0% saturation by the dye method and 2.72 gm/m^{2}hr for 0% saturation by the balance sheet method one obtains an average of 1.82 gm/m^2/hr for 0% saturation (.21 gm/m^2/hr/ppm deficit or .19 ppm/ppm deficit). This value has been used in Figure 24, Table 10, and elsewhere, where diffusion is estimated for the spring. Since the diffusion rate is linearly proportional to the saturation deficit, the rate of oxygen diffusion was readily estimated for each hour of the day according to the saturation deficit existing over the headwater region at that time. In Figure 23 are given the respiration, accrual, and diffusion curves thus calculated for one day as an example.

In Silver Springs with its fairly deep waters (Fig. 11) the difference between day and night diffusion is not great and the error in estimating gross primary production is only 2.3 ppm hrs/day on May 23, 1954 and thus about 10%. Since the diffusion correction for production is dependent on the diurnal change in diffusion rate and not the diffusion itself, the correction is little modified by changes in the gas transfer coefficient used.

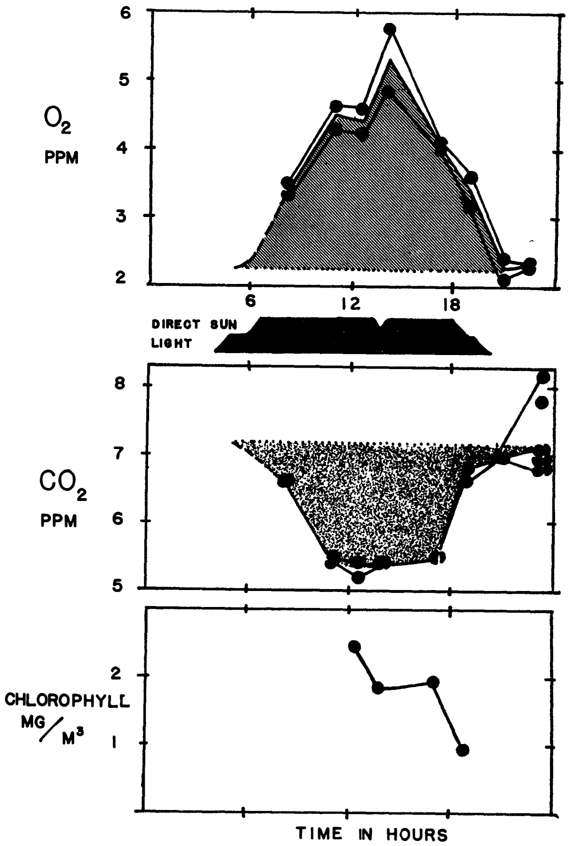

FIG. 30. Diurnal sequence of oxygen, carbon-dioxide (pH method), and chlorophyll for August 11, 1955.

OXIDATION-REDUCTION POTENTIALS

Some measurements with still platinum and saturated calomel electrodes are given in Table 8. It is interesting that there is relatively little change in going from boil to ¾ mile station in spite of the increased oxygen. The increase of dissolved oxygen downstream is accompanied by a concurrent increase of reduced substances such as the organic matter from the photosynthetic community. Apparently the sum of actions of substances which act at the platinum surface is unchanged. Thus the free energy differences between dissolved oxygen and organic matter, both within the same water, are increased by the action of the community.

CARBON DIOXIDE METABOLISM AND pH

The upstream-downstream method was used also for carbon dioxide. As indicated in the chemical methods section the accuracy of these methods is considerably less than the Winkler method for oxygen. Thus a greater number of samples was necessarily analyzed. Some diurnal patterns are given in Figures 24-30.

The free carbon dioxide content of 6 to 10 ppm in the water rapidly diffuses out of the stream as can be readily demonstrated by the steady rise of pH in a sample of Silver Springs boil water standing

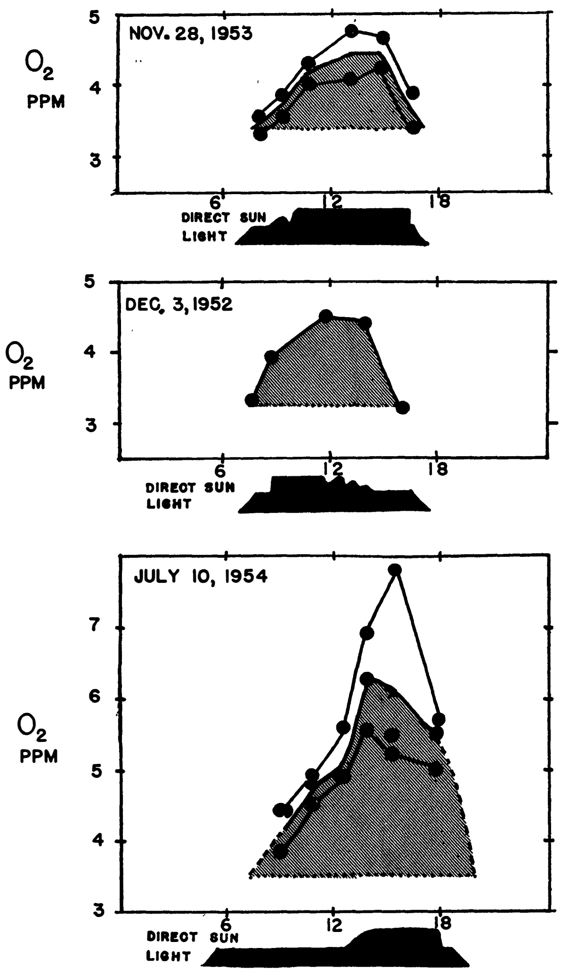

FIG. 31. Diurnal sequences of oxygen on three days: November 28, 1952, December 31, 1952, and July 10, 1954 at the ¾ mile downstream station.

open. The loss of carbon dioxide in these waters is larger than the inflow of oxygen. In the first 5 hours the diffusion was found to be in an O_2/CO_2 ratio by atoms of .91 where the ratio of saturation deficits in the water by atoms was 1.04. When waters are temporarily isolated in eddies along the margins of the stream, photosynthesis and diffusion work in the same direction, tending to lower concentrations in the case of carbon dioxide and raise them in the case of oxygen. The diffusion is much less in the margins, however, than in the main flow because with little current the gas transfer coefficient is small, as shown experimentally by Streeter, Wright & Kerr (1936).

The gas transfer coefficient for the diffusion out of the carbon dioxide may be estimated in several ways as was done for oxygen. The calculation by the theoretical procedure from the dye turnover times differs only in the use of a gaseous (non-turbulent) diffusion coefficient for carbon dioxide instead of for oxygen. Since the ratio of the CO_2

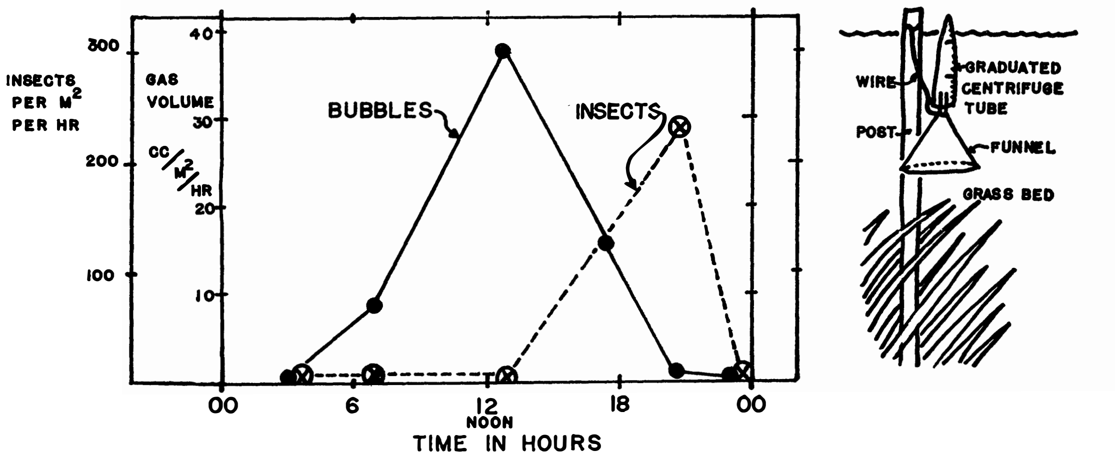

FIG. 32. Diurnal sequence of rising bubbles and emerging insects as indicated by catches in suspended funnels. The funnel arrangement is shown on the right. Each point on the curve is the mean from 4 stations for the preceding 5 hours. See Figure 3 for location of stations. The stations were located at .35 m, .6m, .9m, and 1.3 m depth between 4m and 12m from shore.

diffusion to oxygen diffusion in stationary vessels of Silver Springs water (.91 by atoms O_2/CO_2) is similar to the ratio of the saturation gradients (by atoms 1.04 O_2/CO_2 it seems that the gas transfer coefficient for carbon dioxide is essentially the same as that of oxygen within limits of these rough estimations.

The carbon dioxide diffusion in the field may also be estimated from the few bell jar measurements of carbon dioxide (Table 11) and upstream and downstream changes as was done for oxygen. The mean upstream-downstream change in carbon dioxide at

TABLE 10. Community Quotients and Production Rates

Date and cloud conditions	Area Under Oxygen Curve[a] ppm-hrs/day	Area Under Carbon Dioxide Curve[b] ppm-hrs/day	Daytime community quotient by atoms O_2/CO_2 x 1.37	Discharge x 10^4 m^3/hr (Fig. 9)	% Protein[c]	Production of organic matter[d] (ash free) gm/m²/day	Dry weight including ash[e] gm/m²/day
WINTER							
Nov. 28, 1953 (Fig. 31) broken stratocumulus clearing	6.5	....	(1.0)	9.8	0	8.0	10.4
Dec. 3, 1952 (Fig. 31) clear becoming overcast stratocumulus	6.5	....	(1.0)	8.2	0	6.6	8.6
Jan. 7, 1954 (Fig. 25) clear except early morning fog	8.6	15.4	.77	9.8	0	10.4	13.5
Feb. 19, 1953 (Fig. 26) broken stratocumulus	11.0	14.3	1.05	7.6	5	10.0	13.0
March 8, 1953 (Fig. 27) clear	14.4	19.0	1.04	7.5	4	12.9	16.8
Mean for winter:			.95				
SPRING AND SUMMER:							
March 26, 1953 (Fig. 28) clear	17.3	15.7	1.5	7.7	51	12.9	16.8
May 23, 1954 (Fig. 24) few scattered cumulus	25.2	26.3	1.3	8.5	31	23.4	30.4
July 10, 1954 (Fig. 31) broken cumulus and middle clouds	21.3	....	(1.5)	7.8	51	16.0	20.8
July 12, 1955 (Fig. 29) scattered cumulus becoming overcast nibostratus and rain	14.4	20.5	.97	6.4	0	11.3	14.7
Aug. 11, 1955 (Fig. 30) clear	26.7	21.0	1.75	6.4	77	13.7	17.8
Mean for spring and summer:			1.38		27		
Mean of all measured values:			1.20				

[a] 8% added for diurnal diffusion correction of oxygen as indicated in text.
[b] 10-17% added for diurnal diffusion correction of CO_2 as indicated in text.
[c] Inferred from the community quotient.
[d] Calculated on the basis of the protein-carbohydrate proportions indicated by the community photosynthetic quotient, 7.6 x 10^4 m^2 area, and the discharge. Carbohydrate figured with a PQ of 1 and .94 gm organic matter/gm O_2; protein figured with a photosynthetic quotient of 1.97 for a nitrate-nitrogen source and .51 gm organic matter/gm CO_2.
[e] A constant ash/organic ratio of 23% was assumed for lack of information on annual variation.

night is −1.1 ppm/hr from Table 8. The carbon dioxide release due to respiration is estimated from a few bell jar measurements in Table 11 as .30 $gm/m^2/hr$ (.27 ppm). The accrual due to the addition of half of the water from the side boils is obtained from the mean of the carbon dioxide values of the lateral boils in Table 2 (9.34 ppm) and prorated on a 1 to 1 basis with the boil water (9.58 ppm). This leads to an accrual effect of −.12 ppm. Diffusion is determined from the relationship $q=a+r-d$, where q is the rate of change of carbon dioxide per area, a is accrual, r is respiration, and d is diffusion. The diffusion rate is found to be 1.27 ppm/hr for 8.6 ppm average saturation excess (.5 ppm is saturation), which is computed as a carbon dioxide transfer coefficient of .17 $gm/m^2/hr/ppm$ deficit (.15 ppm/ppm deficit). Since the bell jar respiration estimate may be too small, this estimate of the gas transfer coefficient for carbon dioxide is probably also too small. All estimates of CO_2 diffusions are made with a gas transfer coefficient of 0.21 ppm/ppm deficit gradient (mean of the value from the bell jar method, 0.15 and from the oxygen coefficient, 0.26).

The carbon dioxide gas transfer coefficient is used to correct the carbon dioxide production curves for diurnal differences in diffusion by the hour in Table 10. For example on May 23, 1954 (Fig. 24) this correction summed over the whole day is only 5.9 ppm/hrs or 22%. As in the oxygen case there tends to be a decrease in diffusion correction with decrease in the production.

The uptake of carbon dioxide during the day as in the case of oxygen is strikingly correlated with the daily passage of the sun. However, the carbon dioxide values are extremely variable from sample to sample. The range of variation and functuation is greater than that inherent in the analytical technique as determined by the comparison of standard deviations in Table 4 or 8. Why the oxygen curves should be smoother than the carbon dioxide curves is not clear. It may be that the bubbles of oxygen that rise from the plants before being dissolved help to distribute the oxygen production uniformly, whereas the carbon dioxide taken up occurs only at the plant surfaces thus permitting isolated eddies of different carbon dioxide to develop depending on the trajectory. The winter curves for both oxygen and carbon dioxide have less variability than the summer curves. It may be that in summer the backwaters tend to become heated and thus to form microstratifications which serve to isolate the water longer. In winter the cooling at the surface maintains more vigorous turbulence in the stream. The turbulence seems noticeably greater in the small 11 ft. aluminum boat on cold winter mornings as compared to the warmer seasons. At sunset some of the carbon dioxide curves (Figs. 23-31) in the warmer seasons show erratic variations that are wider in range than at other times of the day. With cooling in the evening the heated, trapped, water in some of the backwaters may tend to break out and join the main circulation. When water becomes isolated in the margins, the diffusion diminishes as concentrations approach saturation relative to the air whereas in the main stream concentrations remain unsaturated. In the case of oxygen, 6 ppm may diffuse in from the air before saturation is reached but 9 ppm of carbon dioxide can diffuse out. Thus waters in the shallows may lose more carbon dioxide than they gain oxygen. When such water mixes back into the main channel especially at sunset, the possible modification of concentrations there may be greater for carbon dioxide than for oxygen. This effect may partially account for the greater fluctuations observed in the carbon dioxide curves in Figures 23 to 30. Waters from Silver Springs standing for long periods of time lose even more carbon dioxide by the concurrent precipitation of calcium carbonate which is supersaturated.

The loss of carbon dioxide from Silver Springs water is illustrated by the rise in pH from 7.5 to 8.15 in an open carbuoy in 33 days with concurrent deposition of both acid soluble and acid insoluble crystals on the sides. If diffusion in the shallows is greatest when mixing is occurring as at night, there may be a higher oxygen (and lower CO_2) before dawn than after sunset in the main flow. Some suggestion of a difference is observed in Figures 23-31.

A very interesting characteristic of two winter curves (Figs. 25 and 26) was the rapid return of the oxygen curve to a night value in contrast to the slow return of the carbon dioxide to night values. The implication of this pattern if it is a real one is that carbon dioxide is being fixed after sunset by dark reactions. Other curves showed some tendency for a carbon dioxide post-sunset lag (Figs. 27, 28 and 29).

Since the alkalinity at any one place is essentially constant as indicated in Table 1 and Figure 13, the changes in carbon dioxide should produce corresponding changes in pH. In Figure 21 the pH is calculated with the Moore (1939) equations for an alkalinity of 144 ppm characteristic of the downstream station after side flows have entered. The pH was also measured with the Beckman pH meter model G. It was found that because of the low organic matter of the water, pH and carbon dioxide determinations could be delayed several hours in closed bottles so that accurate work could be done back in the laboratory. The measured and calculated values of pH are very similar (Fig. 24) showing the manner by which the pH may be used to measure stream carbon dioxide and thus production, as done in lakes by Verduin (1951).

In Figures 25, 26, and 28 just after sunrise there is evidence of a burst of photosynthetic activity and an irregular pattern of the oxygen and carbon dioxide curves. It is possible that this pattern in nature is similar to some patterns recorded in algal cultures following dark periods when the release and

TABLE 11. Light and Dark Bell Jar Experiments in the Field.

		OXYGEN				CO_2			NITRATE-NITROGEN			INORGANIC PHOSPHATE PHOSPHORUS		
	Start	lapse minutes	Start ppm	Change ppm	gm $O_2/m^2/hr$	Start	Change	gm $CO_2/m^2/hr$	Start	Change	gm $N/m^2/hr$	Start	Change	gm $P/m^2/hr$
I. TALL BELL JARS OVER SAGITTARIA. .0326 m^2/jar 11.6 1/jar volume														
Light bell jars:														
May 14, 1953, clear														
1	2:30 p.m.	150	5.02	3.62	.52	...	...	...	...	...	...	...	...	...
2	1:00 p.m.	300	4.57	2.99	.21	...	...	...	...	...	...	...	...	...
May 25, 1953, scattered cumulus														
1	1:00 p.m.	95	2.71	2.09	.47	...	...	...	...	...	...	...	...	...
	3:00 p.m.	60	2.35	.85	.30	...	...	...	...	...	...	...	...	...
2	1:00 p.m.	100	2.71	3.57	.76	...	...	...	...	...	...	...	...	...
	3:06 p.m.	60	2.38	1.62	.58	...	...	...	...	...	...	...	...	...
May 2, 1954, few cumulus														
1	1:35 p.m.	245	2.84	3.96	.35	11.2	−4.5	−.39	.35	−.20	−.017	.048	−.017	−.0015
2	1:45 p.m.	245	4.17	2.08	.18	9.5	−3.8	−.33	.34	−.14	−.012	.035	−.007	−.0006
3	2:15 p.m.	240	6.25	.77	.07	8.6	−3.8	−.34	.36	−.14	−.012	.041	−.003	−.00027
4	2:35 p.m.	210	3.49	2.99	.30	11.1	−3.3	−.34	.35	−.09	−.009	.066	−.031	−.0032
Mean					.225			−.325			−.0125			−.00114
Mean of light					.374									
Dark bell jars:														
May 14, 1953	2:30 p.m.	150	3.84	− .84	−.12	...	...	...	...	...	...	...	...	...
June 22, 1953														
1	4:35 p.m.	60	2.56	− .77	−.28	...	...	...	...	...	...	...	...	...
2	4:35 p.m.	60	2.48	− .77	−.28	...	...	...	...	...	...	...	...	...
3	4:35 p.m.	60	2.57	−1.24	−.44	...	...	...	...	...	...	...	...	...
Mean					−.28									
Nov. 28, 1953, 3 consecutive samples in each jar														
1	11:27 a.m.	60	3.10	.21	.07	...	...	...	...	...	...	...	...	...
	12:37 p.m.	108	3.31	−1.51	−.30	...	...	...	...	...	...	...	...	...
	2:25 p.m.	95	1.80	− .89	−.20	...	...	...	...	...	...	...	...	...
2	11:29 a.m.	75	2.92	.03	.01	...	...	...	...	...	...	...	...	...
	12:44 p.m.	106	2.95	− .78	−.16	...	...	...	...	...	...	...	...	...
	2:30 p.m.	90	2.17	− .51	−.12	...	...	...	...	...	...	...	...	...
3	11:31 a.m.	57	3.03	.06	.02	...	...	...	...	...	...	...	...	...
	12:28 p.m.	114	3.09	− .87	−.16	...	...	...	...	...	...	...	...	...
	2:32 p.m.	92	1.43	− .79	−.18	...	...	...	...	...	...	...	...	...
Mean of last two in each set					−.14									
May 13-14, 1954														
1	8:55 p.m.	310	2.50	−1.52	−.10	11.1	3.0	.21	.37	−.10	.0070	.040	0	0
2	9:08 p.m.	318	2.60	−1.50	−.10	8.9	4.9	.33	.51	−.30	.020	.044	−.022	−.0015
3	9:30 p.m.	307	1.71	− .96	−.06	11.1	5.3	.37	.24	−.12	.0084	.040	.040	.0028
Mean					−.082			.30			.0115			.0004
Mean of dark					−.21									
II. SHORT BELL JARS OVER MUD SURFACE. (No Sagittaria-aufwuchs) 1.8 1/jar; area, .020 m^2/jar.														
Light bell jars:														
May 14, 1953	2:30 p.m.	300	2.99	1.23	.022	...	...	...	...	...	...	...	...	...
May 25, 1953	12:35 p.m.	133	2.65	− .40	−.016	...	...	...	...	...	...	...	...	...
Dark bell jars:														
May 25, 1953														
1	12:35 p.m.	128	2.50	− .70	−.027	...	...	...	...	...	...	...	...	...
2	12:35 p.m.	130	2.55	− .60	−.025	...	...	...	...	...	...	...	...	...
April 5, 1954, after 20 min. in place														
1	3:10 p.m.	95	6.28	−1.87	−.11	...	...	...	...	...	...	...	...	...
2	3:15 p.m.	95	6.06	− .75	−.043	...	...	...	...	...	...	...	...	...
3	3:20 p.m.	95	4.28	−3.32	−.19	...	...	...	...	...	...	...	...	...
Mean					−.079									

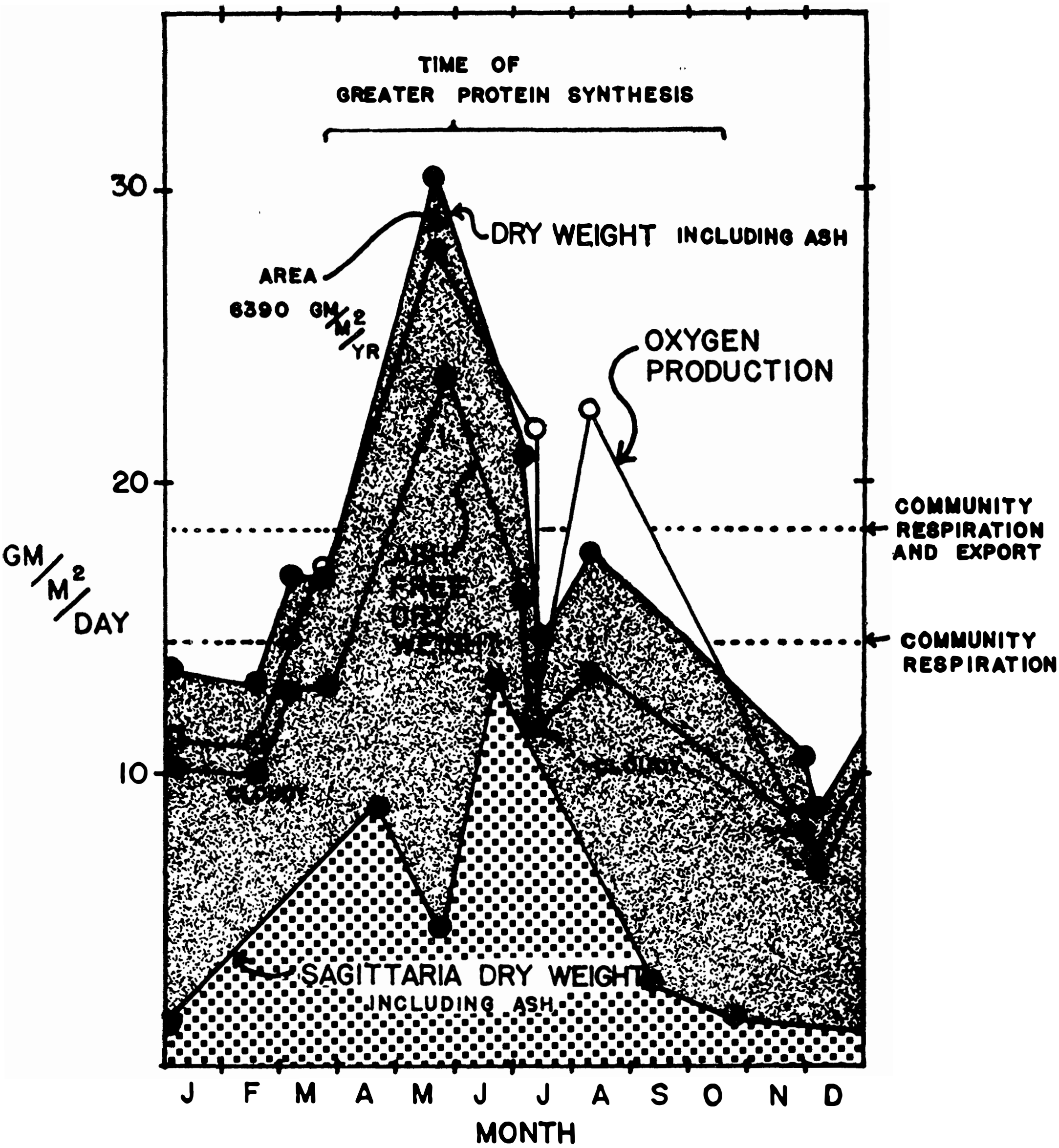

FIG. 33. Annual sequence of primary production. The lowermost curve is the net production of Sagittaria from growth measurements in cages reported in Table 12. The gross primary production of the entire community as estimated from detailed diurnal curves of Figures 23 to 31 are plotted on the basis of calculations in Table 10. Times of protein synthesis are indicated on the basis of photosynthetic quotients. Community compensation points are indicated by horizontal dashed lines. The annual production is obtained from the shaded area under the curve of dry weight production.

uptake of carbon dioxide is at first irregular (Rabinowitch 1951).

PHOTOSYNTHETIC QUOTIENT

Ryther (1956) has recently reviewed the information on naturally occurring photosynthetic quotients indicating that because of the nature of the organic matter produced by the community, quotients of about 1.25 are usual, and even higher values occur if the nitrogen is supplied as nitrate. In a study of oxygen and carbon dioxide curves in Swiss streams Schmassman (1951) found similar values of the photosynthetic quotient for natural stream communities.

The area under each diurnal oxygen curve was used to measure oxygen production after corrections were applied for diffusion and bubble loss. Similarly the area above the curve of carbon dioxide was utilized to measure the carbon dioxide uptake. The photosynthetic quotients from the two measurements are given in Table 10 and are used to calculate production values in Figure 33. There is apparently a higher photosynthetic quotient in the seasons of greater production possibly because of more protein synthesis in summer. Winter metabolisms may be mainly maintenance in the form of carbohydrate metabolism. Myers (1949) reported a possibly similar phenomenon in Chlorella culture. The photosynthetic quotient was near one when photosynthesis did not much exceed respiration but increased as the P/R ratio increased. More light produced higher protein content.

As indicated in the section on nitrogen metabolism, the main source of nitrogen is nitrate. Thus the oxygen produced relative to the carbon dioxide used is different from that where nitrogen is supplied as ammonia or organic nitrogen. As described in the section on the annual cycle of production, photosynthesis is about 70% algal and 30% by Sagittaria. If the nitrogen content is respectively 8% (assumed) and 2.0% (Kjeldahl) there is about 6.2% total nitrogen being assimilated or about 39% protein (6.2% x 6.25). If the nitrogen source was ammonia, the photosynthetic quotient might be expected to be 1.17. With nitrate as source a quotient of 1.38 is expected. Metabolism of this latter type was observed on sunny days in spring and summer (Table 10).

Bell Jar Measurements

Since the springs community is mainly attached to the bottom rather than suspended in the water the light bottle-dark bottle method can be applied only if a typical sample area of the bottom can be placed in the bottles for measurements. Glass and plastic bell jars, therefore, were adapted for in situ measurements as shown in Figure 34. The underwater observer wich face mask placed the bell jars over the community. The edges of the jar settled several centimeters into the soft muck bottom thus sealing the jar. Then by means of a tube held within the jar by a stiff wire, water was drawn from the bell jar by means of the sampling device. The air within the two 125-cc bottles on the stick rose to the surface through the outlet tube and was replaced with water drawn from the bell jar. To speed up the process, the observer applied mouth suction to the outlet tube. The water was drawn from the outside up into the bell jar through the mud at the rim creating a slight disturbance and turbidity in the lower few centimeters of the bell jar. The upper volume of water was undisturbed. After a measured interval of time, about an hour, the sampler was again attached to the bell jar tube and another sample was taken. From the change in chemical content between the first and second sample and from the volume and area of the base of the bell jar, the metabolism per area was computed. It was found that one observer working continuously could set four such bell jars and sample at hourly intervals. Black cloth was used for making black bell jar measurements of respiratory metabolism.

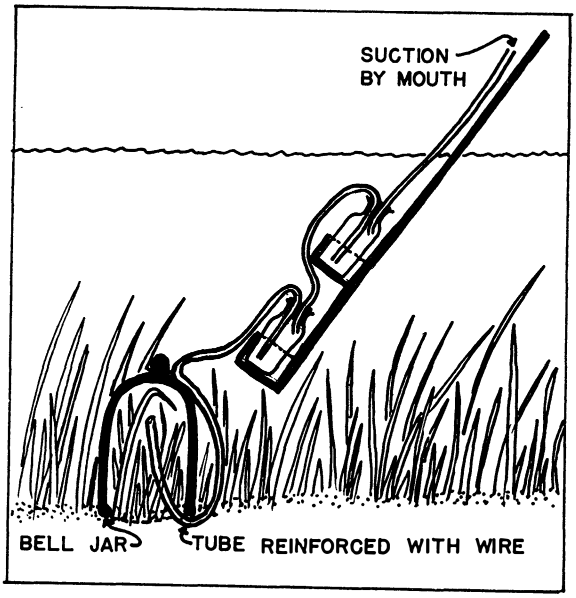

FIG. 34. Position of bell jar and sampler in field experiments.

This method has produced considerable variation in values due to a number of difficulties that seem inherent in the method. Heterogeneity of community is one source of error that arises due to the difficulty of placing the bell jar over the waving blades so as to exactly include a representative fraction. The disturbance of mud in drawing the first sample may also introduce errors.

In the Silver Springs bell jars and in similar work done on coral reef substrates (Odum & Odum 1955) a lag effect was observed. If in the middle of the day one places a black bell jar over the reef or Sagittaria substrates the oxygen in the water continues to rise for the first half hour. This is apparently due to diffusion of the oxygen from bubbles in the aufwuchs and reef substrates into the water even though the plant cells are no longer releasing oxygen. As seen from the data for Nov. 28, 1952 in Table 11, measurements in subsequent time periods after an adjustment period are more consistent. One cannot therefore use short time measurements made immediately after placing the jars over the community.

The bubbles found in the top of the bell jar are another source of error. A few bubbles come from the mud due to disturbance in placing the jars, but most are released from the community and form very large pools of air of as much as 15 cc at the top of the jar in the light bottles. Much of this is oxygen but the bubbles are likely to have a ratio of gases more like air as discussed above in the section of bubble formation in the aufwuchs. This may not be too serious if bubbles already formed are being released upward by production of more bubbles. At times the bubbles form a considerable volume even though the oxygen in the bell jar water is not super-saturated.

Most serious of all is the lowering of metabolic rates that may result from the stoppage of current flow. That current makes a big difference in aquatic plant metabolism was shown by Gessner (1937). A discussion of this error is included in the community respiration section that follows.

From the comments on sources of error it is plain that the method is exceedingly rough and may not be as useful as the black and light bottle method in planktonic communities. Nevertheless, averages of these values give one some kind of check on the orders of magnitude of photosynthesis and an independent estimate of respiratory metabolism. It should be emphasized that the biomass of this community in each bell jar is enormous. All of the oxygen disappears from a black bell jar after several hours. The productivity and metabolism are very high.

An excess of photosynthesis over respiration is indicated by bell jar experiments over 3 days. From 5:00 p.m. May 25 to 5:00 p.m. May 28, three light jars had extensive bubbles in the top. The water at 23° C had 8.91, 12.90, and 13.81 ppm oxygen indicating supersaturation. The dark bottles had .98, 0, and 0 ppm and a few gas bubbles.

Bacterial Metabolism

In the description of the community above, quantitative counts showed a high bacterial population in the periphyton and in the ooze. The periphyton bacteria were inseparably bound in with the algae so that it was not possible to separate and measure their metabolism. Part of this may be autotrophic. To estimate the bacterial metabolism on the ooze surfaces, small bell jars 6 inches high were rigged with tubes as described for the tall jars. The ooze surface under the plants was skimmed off so that the upper centimeter was removed. This was done to remove algae which may have sedimented there. Then the small bell jars were placed down with black cloth covers and the oxygen uptake measured. These measurements were converted into respiration rates per area as given in Table 11, averaging .079 gm $O_2/m^2/hr$. If this metabolic rate is divided by .3 gm dry bacteria biomass/m^2 estimated in Table 7 as populating the upper cm of mud, a dry weight-based metabolic rate estimate is obtained. This value, 270. mg O^2gm dry bacteria/hr, is higher than might be expected for active bacterial populations according to their size. A discussion of organismal size and biomass structure is given by Odum (1956b) including a graph of size and metabolism based on data in Zeuthen (1953). Either the bacteria are fully active in a layer deeper than 1 cm or the bacterial metabolic rate is large.

An equal biomass of bacteria (.3 gm/m^2) was estimated to inhabit the aufwuchs (Table 7). These bacteria, unlike those in the upper mud, are well exposed to circulation and presumably possess as great a metabolism per individual and per gram biomass. In absence of data as to the fraction of the aufwuchs metabolism due to heterotrophic bacteria, the metabolism of the aufwuchs bacteria was assumed to equal that of the mud bacteria (see Table 13). If this metabolic rate is of the right order of magnitude, the bacteria are of great importance metabolically in spite of their insignificant biomass.

As the oxygen falls below 1 ppm the rate of respiration falls as has been previously shown for marine waters (Zobell 1940) and sewage waters (Pomeroy 1938). Thus the respiration deep in the mud can be inferred to be negligible relative to that in the surface mud. The usefulness of the black bell jar method is thus also restricted to short aerobic periods of 20 minutes to 3 hours. Criticisms of the short bell jar results because of the artificial current stoppage are not so serious, since the current is normally very small at the base of the heavy bed of plants above the Silver Springs mud.

Cage Enclosure Experiments

In order to measure the growth rates and production by the Sagittaria, four large cages (3′ by 6′ by 4′) were built and submerged in the spring almost to the top. The hardware cloth tops hinged upward so that one could enter the cage and work with face mask in about 3 feet of water. Following a suggestion of Dr. A. M. Laessle, Univ. of Florida, Sagittaria plants were taken from other areas and replanted within the cages. Short bladed plants of 6 to 10 inches length were selected, dead blades were removed and a wet weight was taken by measuring the weight with a milk scale reading in lbs and tenths after 1 minute drain. The root systems were intact and the plants were readily thrust into the muck in the floor of the cage much as one plants rice plants. After 1 to 2 months the plants were pulled out, washed and reweighed. The wet weight increase was then converted into dry weight equivalent. Natural conditions of growth were maintained by the current that flowed continually through the cage. Even after the cage became covered with filamentous algae, the current within the cage was .03 m/sec. Outside the current was .21 m/sec. The temperature and nutrient conditions were remarkably constant since the same spot always gets about the same trajectory of water except for some eddies. It was found that the hardware cloth walls of the cage kept out larger fishes but for some behavioristic reason caused the minnows to concentrate. 800 minnows were estimated in one cage. The continual nibbling at the aufwuchs by these fishes tended to keep the algae fairly constant so that the weight increases observed are mainly that of the Sagittaria rather than the aufwuchs. The aufwuchs was undoubtedly experiencing a greater production, but its rate of turnover and utilization was so high that it did not affect these weight measurements made at the start and end of a months time.

TABLE 12. Plant Growth in Cage Enclosures.

Species	Starting date	Time lapse days	% Increase per day[a]	Net growth dry gm/m²/day (in a continuous raft)
PISTIA				
in 1.67 m² cage 7.7% dry of wet; 10.0 kg wet in 1.67 m² raft 1952-1953	Aug. 18	53	1.9	8.9
	Oct. 9	37	−1.8	−8.4
	Nov. 15	89	− .38	−1.82
	Feb. 12	23	.44	2.04
	Mar. 7	33	.59	2.75
	Apr. 9	32	2.8	13.0
	May 11	12	3.3	15.3
	May 23	17	1.4	6.5
	June 9	23	.68	3.1
SAGITTARIA LORATA				
in 1.67 m² cage 636 gm/m² in natural density 1952	Aug. 16	55	.46	2.9
	Oct. 9	37	.30	1.9
	Nov. 15	89	.19	1.2
1953	June 9	23	2.1	13.4
1954	Apr. 5	27	1.4	8.9
	May 2	40	.75	4.8
EICHORNIA				
in 1.17 m² cage 380 dry gm/m² in a raft 1953	May 14	9	2.7	10.3
8.9% dry of wet	May 23	17	2.6	9.9
7. 1 kg wet/1.67 m²	June 9	23	1.35	5.2
CERATOPHYLLUM DEMERSUM				
in a .0016 m³ cage at .3m depth. Growth calculated on a basis of 1116 dry gm/m² in a natural density[b] 1952-1953	Dec. 3	71	1.2	13.4
	Feb. 12	24	2.2	24.6
	Mar. 8	32	1.71	19.1
	Apr. 9	32	− .57	−6.4
NAJAS GUADALUPENSIS				
in a .125 m³ cage suspended 1 ft. below water in Blue Spring, Alachua Co., Fla. 850 gm/m² dry[b] 1951-52	Dec. 23	7	2.1	17.9
	Dec. 23	7	2.1	17.9
	Jan. 13	14	.8	6.8
	Jan. 13	14	1.4	11.9
In Silver Springs 1953	Aug. 18	36	.41	3.5
ALGAL MATS				
natural accumulation on the bottom of a 2.24 m² cage; 544 gms/m² wet; 20.5% dry of wet 1955	Feb. 12	58	3.6	3.9

[a] Daily increment of change referred to mean biomass during the period of time in order to compute the percent change.
[b] Measurement of dry weight per area in natural patches in springs by J. H. Davis.

The snails were a problem especially in the spring of the year. The hardware cloth kept the adults out but in the spring small juvenile Pomacea could enter and grow to important size in a couple of weeks. Two series had to be discarded when large snails were found inside at the close of the period. These measurements were repeated, however, a year later so that a years cycle of cage enclosure measurements of Sagittaria was obtained. These are given in Figure 33 and Table 12.

These results show a definite seasonal pattern in growth measurements in spite of constant temperature, current, and chemical media. The hydrographic microclimate in the cage is shown in Table 5. Two main factors due to the experimental procedure probably caused an underestimation of growth. One was the effect of pulling up the plants and replanting. Root systems were found to be reestablished after two weeks but growth was presumably partially inhibited during this time. Also the hardware cloth kept out considerable light as indicated in the light meter readings taken from within the enclosures. At 11:15 May 2, 1955 the top was found to remove 19% of visible light. 52% of direct sunlight reached the bottom in the cage through the top and 3 ft of water. Thus the light conditions within the cage resembled those at usual Sagittaria depths, 6-8 ft (Fig. 14). Since some of the community was somewhat shaded and in deeper water than the cage enclosure it may be that the conditions in the enclosure were not too far from an average condition. At least the order of magnitude is shown and the measurements are of comparable value. The replanted clumps seemed normal in every way with rapid elongations to three times planted length in some blades in three weeks. Blooming of the Sagittaria occurred in these enclosed communities at all seasons. Also reported in Table 12 are some high growth rates for Ceratophyllum.

PLEUSTON NUTRIENT BIOASSAY

Some growth measurements were made of the floating macrophytes Pistia and Eichornia. These plants are not a major part of the community but served as a means of making a nutrient bioassay of the potential fertility of waters. With the constant flow of similar water underneath the plant roots, the growth at different times of the year would be expected to be a function of air temperature and light only. As seen in Table 12 the growths observed were large. In winter the growth of Pistia retrogressed with the decay of leaves and loss to some insects causing a decrease in weight even though there were always small centers of fresh new growth branching out. The winter decrease was correlated with the growth pattern of the species outside of the cages where the Pistia almost disappeared during the winter to grow forth in considerable patches in the summer. A summer growth minimum was also observed. Penfound (1956) interprets summer minima in net growth rates as a result of higher summer respiration. The enormous productions here with all the pleuston may be reasonable since high light intensities are available to emergent plants and since the roots are continually bathed in high nutrient water. Penfound in a review (1956) summarizes available data in suggesting that the primary productivity of emergent aquatic plants is as high or higher than that entirely in water or entirely on land.

It is suggested that for assay of nutrient conditions one needs only to transplant some of these floating aquatics in enclosures and measure their increase in wet weight after three weeks. If careful record is kept of air temperature, it should be possible to develop a rapid and significant bioassay of total lake conditions. This is especially important for tropical areas where emergent aquatic plants dominate and where temperature ranges are minimal.

ANIMAL GROWTH RATES AND METABOLISM

Conceptually determination of the energy entering a trophic level is not difficult since this input energy is roughly equal to the metabolic rate of the organisms plus their net growth rate. From estimates of the standing biomass per area and the respiration per gram biomass obtained from physiological data one may calculate the flux of energy into a trophic level. In pioneer work by Lindemann (1942) Juday (1940) and Dineen (1953) various assumptions are made as to growth rate per organism in order to determine the productivities and efficiencies of each trophic level.

Measurement of the outflow of organic matter from a trophic level is more tedious and estimation of the growth rate of the varied animal components by trophic levels is rarely achieved. Usually, direct determinations have been mostly restricted to one trophic level because of the extensive amount of work required to get satisfactory measurements.

In this study, some efforts have been made to estimate the growth rates of a few of the main consumer components of all trophic levels directly. It must be realized that in spite of the efforts expended and the constancy and reproducibility of ecosystem a really satisfactory series of measurements of herbivore and carnivore production has not been obtained. Whether these estimates of dominants can be used to represent the entire trophic level is also uncertain.

Measurements and calculations of turnover rates (steady state assumed) were made as follows as summarized in Table 13. Viviparus snails were enclosed in a hardware cloth. The wet volume displacement was measured at the start and at the end of a period of 31 days. Najas and Sagittaria were placed in the cage which was placed down on the muck under the plants in the normal environment for these water breathing snails. A similar experiment was conducted with Pomacea snails in a cage which was partly out of water and filled with duckweed.

The growth rates of small aufwuchs animals are estimated in Table 13 from the data on the rate of growth of the Sagittaria blades. If the plant blades and populations of animals on the blades are in a steady state and stable on the average, the rate of blade growth indicates the rate of replacement of the heavily encrusted populations on the blade tips. Some of the animals emerge, some are eaten, and some drift downstream but the rate of replacement is the rate of growth.

The growth estimates of stumpknockers and bass were obtained only after extensive efforts that are reported in detail elsewhere (Caldwell, Odum, Hellier & Berry, 1956).

A few metabolism estimates were made of animals placed in bottles of Silver Springs water Aug. 24, 1955. Winkler oxygen determinations were made before and after short periods of time. The respiration rates in mg oxygen/gm/hr dry weight of tissue are given as follows: *Lepomis punctatus*, .39 mg/gm/hr; *Gammarus*, 3.54 mg/gm/hr; midges and caddis flies (including tubes and cases), .35 mg/

TABLE 13. Estimates of Turnover Rates (Population turnover: net production/standing crop)

Component	Basis for Calculation	Turnover % per year
Producers:		
Sagittaria	599 gm dry/m² standing crop[a], 1900 gm/m²/yr. production[b]	317%
Algae	177 gm dry/m² standing crop[a], 4490 gm m²/yr. production[b]	2540%
Total	ratio of total production and standing crop	1212%
Herbivores:		
Viviparus	40 individuals kept in a bottom cage; 6%/month wet volume increase per surviving individual. Alternative approach: 6 individuals died in 31 days; 15% replacement required per month. Mean estimate	120%
Pomacea	5 individuals in a cage with duckweed; 27% wet volume increase/individual/month	324%
Turtles	From Marchand (1942) about 7% growth/yr. for turtles of intermediate size (170mm)	7%
Stumpknockers (half carnivore)	See below	113%
Mean of the representative larger herbivores		141%
Midges and Caddisflies (representative of small herbivores)	.16 (.23, .09) mg dry flies per cm² of blade tip in the zone of breaking off (Fig. 18); 1% replacement of lost tips/day due to outgrowth of Sagittaria (Table 12); 25.5 m² blade area/m² bottom; thus .42 gm/m²/day replacement; standing crop[a], 1.7 gm/m²	9100%
Carnivores		
Stumpknockers (half herbivore)	Growth of 22 fish in experimental enclosures[c]; .31% weight increase/day	113%
Top Carnivores		
Bass	Recovery of 6 tagged individuals[c]; .19% increase in weight/day	69%
Decomposers		
Bacteria		
Mud Surface	Standing crop in upper cm of mud[a] .3 gm dry/m²; metabolism (Table 7) .079 gm oxygen/m²/hr (Table 11)	230,000%
Aufwuchs	standing crop in aufwuchs[a], .3 gm dry/m²; metabolism assumed to equal that of the mud bacteria	230,000%

[a] See Table 7.
[b] See text of the section on annual cycle of production.
[c] Data from Caldwell, Odum, Hellier, and Berry (1956).

gm/hr; *Viviparus,* .45 mg/gm/hr; *Oxytrema,* .75 mg/gm/hr; *Lucania,* 1.81 mg/gm/hr.

These values suggest that animals in the Silver Springs environment possess the same rates of energy intake as found in similarly adapted animals elsewhere at the same temperature. (For example, see values given by Prosser 1950).

For the dominant carnivore, the stumpknocker, the above respiration (9.4 mg/gm/day) plus growth (Table 13, 3.1 mg/gm/day) when divided into the growth produces a growth efficiency estimate of 25%. (One gram dry weight is taken as roughly equivalent to a gram of oxygen). For the midges and caddis flies this procedure leads to an estimate of 23% growth efficiency (8.4 mg/gm/day respiration; 2.5 mg/gm/day growth). For Viviparus there is an efficiency of 23% (10.8 mg/gm/day respiration; 3.3 mg/gm/day growth).

INSECT EMERGENCE

A few measurements of the insect emergence were made, at first inadvertently, with the funnel device which was set up for the measurement of oxygen bubbles. The funnel device (Fig. 32) catches the pupae as they rise to the surface to emerge. Measurements were made at 4 stations at different distances from shore on stakes in .3, .45, .6, and 1.3 m depths. Jonasson (1954) has recently described a similar device.

The emergence of insects is very heavy and mainly restricted to the hours between dusk and midnight. The daily cycle is indicated by the graph in Figure 32. Maximum emergence as visually observed was at 7:45 pm March 26, 1953. On March 6, 1953 the emergence began at 7 pm and was gone at 9 pm. The emergence seems to be as large on cold winter nights as in the summer. However, in the winter the clouds disappeared rapidly so that one hour after dark there were few to be seen. In the summer the clouds persisted longer. Almost no dawn emergence was noted in the headwater zones where mainly midges and caddis flies dominate. On one occasion (Dec. 3, 1952) a small dawn emergence of may flies was noted in winter 4 miles downstream both at dawn and at 4:30 pm. May flies are almost absent from the upper spring regions. The insect emergence when converted into a grams per area per time basis (.01 gm/m^2/day) is found to be small relative to the growth of aquatic insects (.42 gm/m^2/day) as estimated from the calculated rate of aufwuchs replacement (Table 13). With 41,800 individual midges and caddis fly larvae per square meter and a emergence of about 236 individuals per square meter per day the emergence involves only .6% of the population/day. There is apparently a very high turnover as indicated in Table 13 (25%/day).

NITROGEN METABOLISM

The waters emerging from the ground contain a relatively high nitrate concentration of about .46 ppm as indicated in Table 1, 2, 3, and 8. The Kjeldahl nitrogen was only .002 ppm in the boil and .08 ppm downstream as measured approximately on Feb. 25, 1954. Nitrates were measured with two methods whose accuracy is discussed in the chemical methods section.

Evidences of several kinds indicate that the nitrate is decreased by the plant beds both during the day and night so that the nitrate reaching the ¾ mile downstream station decreases in concentration slightly but significantly. Where water passes through the plants relatively slowly as in the microhabitats along the bottom and edges, the nitrate falls markedly as indicated by the low values in Table 5 in comparison to those of the open flow. Similarly when bell jars were placed over the plant beds and samples extracted before and after a period of time as described in the section above on bell jar experiments, a rapid nitrate uptake was indicated by the rapid drop of nitrate in the jar (Table 11).

In Figure 35 is shown a circulating water system containing a blade of Sagittaria with its aufwuchs community of algae, bacteria, and animals. Silver Springs water was circulated over this community for several hours. Then the composition of water was again determined. The nitrate was rapidly decreased. The oxygen was also rapidly removed from this community. Whether nitrate was assimilated or reduced was not determined in this case. However, nitrate was decreased from 0.4 to 0.2 ppm while the dissolved oxygen was still above 5.0 ppm. These various measurements suggest that these communities remove nitrate nitrogen during both day and night. On March 26, 1955 there was not a significant difference between samples at different times of the day as compared with variation within pairs of samples collected at the same time (Table 7).

Data are given in Table 8 which indicate that

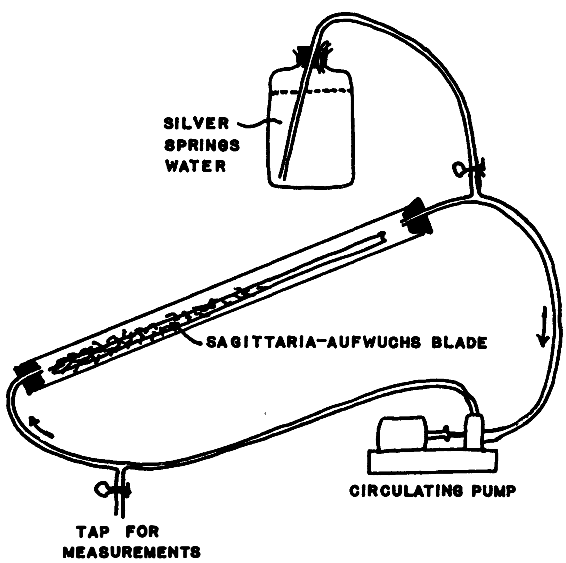

FIG. 35. Circulating stream apparatus used as a flowing respirometer.

TABLE 14. Nitrate Changes in Aerobic and Anaerobic Springs

	Mean	NITRATE NITROGEN S	Separate analyses
Nitrate Decrease in an Aereated Spring Ichatucknee Springs, Mill Spring Boil, Flow through bed of eel grass; Data from Gordon Broadhead April 17, 1953[a]			
Above plant bed	.155	.039	.17, .10, .13, .22, .13, .18
Below plant bed	.098	.033	.14, .13, .05, .12, .08, .07
Difference[c]	.057		
Nitrate Increase in Anaerobic Springs Beecher Springs, Welaka, dominated by blue-green algae and white sulfur bacteria. Oxygen values given in Odum and Caldwell (1955)			
Feb. 6, 1953[a]			
Boil	.000	. .	. . . .
200 m downstream	.015	. . . .	. . . .
350 m downstream	.040	. . . .	. . . .
Aug. 2, 1955[b]			
Boil, 11:30 p.m.	.23	.086	.12, .38, .18, .24, .22
200 m downstream night, 10:30 p.m.	.35	.141	.23, .53, .46, .19, .105, .38, .38
daytime, 1:30 p.m.	.45	.052	.41, .52, .41
Green Cove Springs, dominated by blue-green algae and white sulfur bacteria in the run below a swimming pool.			
Jan. 27, 1953, 8:30 p.m.[a]			
Boil	.000	. . . .	. . . .
40 m (below swimming pool)	.000	. . . .	. . . .
70 m downstream	.024	. . . .	. . . .
100 m downstream	.085	. . . .	. . . .
145 m downstream	.165	. . . .	. . . .
Mar. 4, 1953[a]			
Boil	.010	. .	. . . .
40 m (below swimming pool)	.045	. . . .	. . . .
45 m	.065	. . . .	. . . .
70 m	.090	. . . .	. . . .
100 m	.065	. . . .	. . . .
145 m	.075	. .	.105, .045

[a] Phenoldisulphonic acid method.
[b] Strychnidine method.
[c] Significant at P = 5%.

there is a significant difference between analyses made in the main boil and those made downstream. This decrease seems to be a result of two processes, one the community action described above and the other the mixing of the lateral boils. The average nitrate nitrogen in the side boils (Table 2) is 0.402 ppm which is 0.061 ppm less than that in the main boil (0.463 ppm, Table 8). Since half of the water is from the main boil and half from the side flows, a nitrate content of 0.433 ppm would be expected downstream from the mixture of all the water sources. The observed nitrate at the ¾ mile station is 0.408 (Table 8). Thus there is apparently a nitrate removal by the community of about 0.025 ppm.

Mill Springs, one of the Ichatucknee Springs, Columbia Co., Fla. was studied by Gordon Broadhead to further test the action of the eelgrass—aufwuchs beds on nitrate. The spring outflow of water is somewhat similar in quality to that of Silver Springs (Ferguson *et al.* 1947). Measurements of nitrate were made above and below a uniform bed of Vallisneria about 0.3 m deep. In this situation there is little complication due to stagnating water and side inflows. As indicated from the data in Table 14, there was a definite nitrate decrease in the water both during the night and during the day.

Some nitrite-nitrogen measurements made upstream and downstream in Silver Springs are included in Table 3. There were no changes of sufficient magnitude to account for chemical reduction of nitrate to nitrite. Thus some living components in the plant beds are apparently assimilating nitrate. Some of this may be bacterial denitrifying activity where oxygen is low in the mud and some is the nitrate assimilation in photosynthesis.

In Silver Springs the main part of the community is composed of a complex of Sagittaria and aufwuchs. A Kjeldahl nitrogen determination of this material indicated 2.12% nitrogen. Thus one may infer that about 13.3% (6.25 x 2.12) is protein. 23% of the dry material is ash (600° C). Thus if half of the production is protein, then the following equation adequately describes the relative utilization of carbon dioxide and nitrogen in terms of oxygen production: By weight for 100 gm dry biomass: 7.1 gm NO_3 + 117.3 gm CO_2 + 45.9 gm H_2O +23 gm minerals $\rightarrow$100 gm biomass (31.9 C; 2.1 N; 37.9 O_2; 5.1 H; 23 ash) + 94 gm O_2. If a day's oxygen release averages 16.6 gm/m^2/day, as taken from the data in Figure 33, then a day's nitrate-nitrogen assimilation fixation according to the equation just given is about 1.23 gm/m^2/day or for 8.5 x 104 m^3/hr discharge, 0.046 ppm. This allows the nitrate to be fixed both day and night as suggested by the data. This also accounts for the oxygen that is part of the nitrate which is released in photosynthesis. The required nitrogen fixation is thus very similar when estimated from the content of the community (0.046 ppm) to that estimated on the assumption that the downstream decrease is mainly due to the fixation of nitrate by the plants (0.025 ppm). One thus has a measure of protein production as well as of carbon fixation.

Although the single Kjeldahl values are only approximate, the 0.078 ppm increase in Kjeldahl nitrogen downstream is at least of the same order of magnitude as the 0.060 decrease in nitrate nitrogen. The steady state postulated for the Silver Springs would require an annual balance between these figures.

Whereas nitrate is removed in partly oxygenated Ichatucknee Springs and Silver Springs, some of the more reduced springs which are populated with more blue green algae may fix more than they use. Some suggestion of this may be found in the increases of nitrate in going downstream in Green Cove Springs and Beecher Springs in Table 14 although the downstream change on the night of Aug. 2 is not significant. Both of these springs begin initially with small or negligible nitrate concentrations and zero oxygen tensions. These waters do not have appreciable nitrite concentrations.

In Silver Springs the nitrate utilization may be partially accompanied by a turnover and regeneration of nitrate in some parts of the community. Because of the nitrogen uptake day and night, nitrogen is not a sensitive indicator of photosynthesis in streams.

PHOSPHORUS METABOLISM

As indicated in Tables 3 and 8 the phosphorus is present mainly as inorganic phosphorus and is maintained at a high and fairly constant concentration all the way down the run. Just as the uptake of nitrate was detected in water in plant beds in closed bell jars and in the upstream-downstream main flow, so phosphate phosphorus decreases were found in bell jars (Tables 5 and 11). A small significant upstream-downstream decrease was found on the average (Table 8). The slight decrease in phosphorus downstream (0.0055 ppm) includes both the effects of the side boils, which were not measured and the small uptake of phosphorus by the plants.

THE NITROGEN-PHOSPHORUS RATIO

The ratio of nitrogen to phosphorus is sometimes useful as an indication of which nutrient will tend to be limiting. This is complicated by the self-adjustment by some plants of the relative ratio of requirement depending on the ratio in the water. Even though the absolute quantities of both elements are large and not much depleted within the area under study, this does not eliminate the possibility that one or the other limit growth more than the other. In the microhabitats and along the actual cell surfaces deficiencies may readily develop.

The N/P ratio (by weight) in Silver Springs is 8.05 (.435/.0542, Table 8). By atoms this is 17.8. In microhabitats in plant beds (Table 5) the ratio by atoms may change to about 10. It seems likely that of the two nitrogen is more likely to be limiting. It is probably coincidental that the N/P of the outflow water is so close to plant requirement ratios.

Similar inferences made regarding boron (Odum & Parrish 1954) indicate that boron is far less limiting than is phosphorus in Silver Springs.

Fifty phosphorus and nitrate-N analyses were made on the same 50 samples in the course of the study. A graph of nitrogen versus phosphorus did not suggest any correlation of these elements within the limits of the methods used.

CHLOROPHYLL; DIURNAL PSEUDOPLANKTON VARIATION

Chlorophyll "A" measurements, using methods cited in the methods section, were made of the aufwuchs, the Sagittaria blades scraped free of aufwuchs, and the pseudoplankton as caught on a millepore filter. The longitudinal distribution of chlorophyll in and on a Sagittaria grass blade were presented in Figure 18. The vertical distribution of chlorophyll in a waving bed of Sagittaria was given in Figure 16 relative to the penetration of light.

When these estimates are placed on an area basis a value of 2.95 gm/m^2 of chlorophyll is found (15.3 mg/10 blade plant clumps; 193 clumps/m^2). This is only somewhat larger than the values of 0.9-1.6 gm/m^2 found by Gessner (1949) not only for aquatic communities in lakes but terrestrial forests.

Because of its sensitivity, the chlorophyll method was used to determine the diurnal cycle of release of pseudoplankton. In Figures 29, 30, and 36 are given diurnal curves of chlorophyll as caught on millepore filters from 3 liters of water at the ¾ mile downstream station. The comparison between the boil and the downstream station is given in Table 3. Blum (1954) describes a diurnal pulse in stream planktonic algae. The diurnal curves in Silver Springs provide convincing support for the diurnal fluctuation in the releasing of pseudoplankton from the thick benthic communities. This diurnal pattern may include effects due to boats as well as the cell divisions. The chlorophyll values obtained in the 1955 millepore filter work with 1 to 2 mg chlorophyll/m^3 are somewhat higher than the value of 0.41 mg/m^3 found by Nelson Marshall on July 2, 1953 with the Foerst centrifuge in a 10-liter sample following a one day delay. The lower value may reflect a loss of nannoplankton with the Foerst centrifuge.

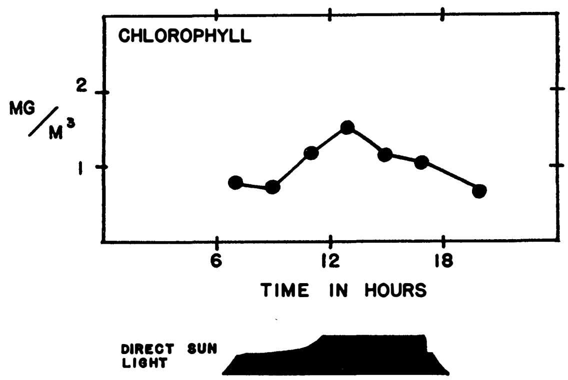

FIG. 36. Diurnal chlorophyll content of water at the ¾ mile downstream station on a winter day, January 26, 1956. Data obtained by J. Yount.

From the diurnal curve of chlorophyll a two-fold variation in downstream loss of organic matter is indicated. From the rough estimates of total organic matter going downstream in the water during the day of about 0.8 ppm (Table 8), the chlorophyll/organic matter ratio is 0.002 (1.6 mg/m^3/.8 gm/m^3). This is not far from the ratio of 0.004 given by Manning & Juday (1941) for Wisconsin lakes. In the Sagittaria-aufwuchs of the community itself the chlorophyll to organic matter ratio is 0.0038 (2.95 gm/m^2/775 gm/m^2). The ratio of chloroyphyll to organic matter for the aufwuchs algae which are the plants most readily swept downstream is higher

(0.012 gm chlorophyll/gm dry). For the Sagittaria blades after scraping the ratio is lower (0.0030 gm chlorophyll/gm dry).

A comparison of the diurnal curve of chlorophyll export for winter (January 26, 1956 in Fig. 36) with a curve for summer (July 12, 1955 in Fig. 29) suggests a somewhat greater export during the summer correlated with the higher production at that time. The mean chlorophyll export on the winter day is 1.01 mg/m^3, on the summer day 1.57 mg/m^3. The utilization and export of organic matter is less subject to fluctuation than is the production. Whereas the summer production is 2 to 3 times that in the winter, the chlorophyll export is only 1.5 times greater in the summer than in the winter.

COMMUNITY BUDGET

Annual Cycle of Production

The daily gross production including that compensated for by respiration is given in the graphs in Figures 23-31 where the downstream oxygen or carbon dioxide is followed through a day. These gas production values were converted into ash-free dry weight using the observed photosynthetic quotient (Table 10). These were then converted into dry weight by including 23% ash (x 1.3). When the individual day production values are plotted on a graph according to the month of the year, either as oxygen or as dry weight, a rough curve of annual production may be drawn (Figure 33). Included in this are overcast and clear days as indicated. The graph is representative since the annual cycle includes an alternation of clear, partly cloudy, and overcast skies. Spring is especially clear whereas summer is cloudy. That a similar value of production was obtained in 1952 as in 1953 is another indication of the steady state character of the community.

Drawn horizontally are two lines representing community compensation points of two types. One is the total respiration estimate for the community from the next section. According to the equation given in the nitrogen section 0.54 $gm/m^2/hr$ O_2 is equivalent to 0.61 gm dry weight including ash m^2/hr (14.6 $gm/m^2/day$). This is based on 1.13 gm dry/gm O_2 respired where nitrogen is not oxidized to nitrate. Respiration in the bell jars was accompanied by nitrate decrease rather than increase. The second horizontal line drawn in Figure 33 is the total organic losses from the community including downstream export loss as well as respiration. It will be noted that the gross primary production in winter does not equal community losses so that there must be some retrenchment in total community biomass and sediments although it is not conspicuous enough to be noted in rough biomass measurements made so far.

Thus the Silver Springs community may maintain its great mass of individual producers if they maintain a production above their individual compensation points all the year. This is possible by exporting organic matter representing the excess production of summer. This situation suggests that communities in order to be stable in a region of large annual light variation must store or export considerable organic matter during the summer. Alternatively the communities themselves must die out during the winter in the familiar way of many environments.

Community Respiration

In the bell jar experiments in natural situations cited in a previous section 0.37 $gm/m^2/hr$ oxygen net production was obtained for sunny spring days (Table 11). For a 12 hour day this is 4.45 $gm/m^2/day$ oxygen net primary production. A glance at the oxygen production measurements by the upstream-downstream method of 15 to 28 $gm/m^2/day$ in Figure 33 suggests that the bell jar method has underestimated about 4 fold. If the up-stream-downstream method is correct, then the placing of the bell jar and consequent cessation of the current flow has depressed metabolism. In this case it may be suspected that the respiration measurements by bell jars of the Sagittaria-aufwuchs complex is similarly too small due to the enclosing effect. The method of estimating respiration in streams from diurnal curves suggested previously (Odum 1956a) is not applicable here because of the constancy of the night saturation deficit.

In the circulating water apparatus pictured in Figure 35 a blade of aufwuchs Sagittaria with a dry weight of 0.64 gm used up 2.08 mg/l oxygen per hour under conditions of 0.022 m/sec flow. The flow chamber with only water and bacteria used up 0.87 mg/hr. Subtracting this 0.87 mg one obtains 1.21 mg/l oxygen which for a .68 liter capacity gives a respiration estimate of 1.3 mg/gm/dry/hr (1.01 gm oxygen/m^2/hr). This is much higher than the respiration obtained with the bell jar measurements. As indicated in Table 11 0.22 gm oxygen/775 gm dry Sagittaria-aufwuchs was used over 1 m^2 (or about 0.28 mg oxygen/gm dry/hr).

There is thus a dilemma in arriving at a respiration value for the community with a 4 or 5 fold difference in the two estimates. Actually the larger values are more like those of other tissues. It is possible that without current the oxygen in the thick aufwuchs micro-environment becomes locally limiting even though the bell jar as a whole still has adequate oxygen.

Two Sagittaria blades with aufwuchs scraped off were placed in BOD bottles for respiration measurements. These blades (dry weight 0.18 and 0.26 gm) used 0.58 and 0.55 mg oxygen/gm dry weight/hr over a four hour period. For 578 gm/m^2 Sagittaria (without aufwuchs) this constitutes a respiration of 0.33 gm oxygen/m^2/hr. Thus this respiration alone is greater than the estimate from bell jars (.22 $gm/m^2/hr$). The addition of the aufwuchs and mud surface respiration will raise the figure.

For purposes of these calculations (Table 15) an average value of 0.79 mg oxygen/gm dry/hr

(0.61 gm/m^2/hr oxygen) is used in overall budget calculations (mean of 1.3 and 0.28 mg oxygen/gm dry/hr). Choosing an intermediate value may have a basis if plants in stillwater margins differ in respiration markedly from those in the flow.

DOWNSTREAM CHANGE OF ORGANIC MATTER

One of the special aspects of the headwater springs area which make possible an understanding of the metabolism is the initial very low organic matter content of the waters emerging from the boil. As the water passes downstream particulate and possibly dissolved organic matter are added as the contribution of the community to the downstream area. Some measurements were made of organic matter by permanganate oxidation and biochemical oxygen demand at the boil and downstream as reported in Table 8. Also estimated were number of algal fragments, chlorophyll from this pseudoplankton, and the weights of large plants floating as caught with a gill net.

The various measurement methods given in Table 8 are in concurrence on the level of total organic matter as ordinarily between .6 and .9 ppm in the upper section of Silver River. Although the magnitudes of the concentrations are small, being less than 1/10th of the organic matter of the usual lake or stream environment, the volume of flow is so large that the total flux of organic matter passing in 24 hours is very large. It is readily obvious to the observer in Silver Springs that pseudoplankton is breaking off the benthic community and passing downstream as large fragments of particulate matter, and smaller components. A nice qualitative demonstration of the increase in organic matter in the water is provided by the color of the dry evaporating dish after 4 liters of water had been evaporated. Water from the boil yields light buff. Downstream the dishes are darker and more of humic tan color. As evidenced in Table 8 the seston caught in a #10 net increases 6 to 10 times; the bacteria increase 10 times; the number of algal cells as counted on a cedar oil treated millepore or taken in plankton net increases about 30 times in the first ¾ mile; and the chlorophyll of Foerst centrifuge concentrate or of millepore filter collected samples shows a 5 to 10 fold increase. From these evidences there can be no question that the organic content in recognizable and particulate fractions increases downstream so that the community is exporting this type of organic matter from its production.

However, the picture for colloidal and dissolved organic matter is not clear. When efforts were made to estimate the total organic matter including dissolved and colloidal fractions, some anomalous results were obtained. Permanganate oxidations of water samples yielded small but not significant increases between the boil and downstream water and biochemical oxygen demand measurements showed if anything a reverse effect. In the July 12 and July 20 BOD series in Table 8 the filtering had more effect on the downstream water than on the boil water. In the June 8 series filtering increases the difference between boil and downstream. Because the differences of .1 to .3 ppm under consideration are at the limit of accuracy of the methods, it is very difficult to account for these results. It is possible that there are some oxidizable, dissolved constituents of the boil water which becomes oxidized or absorbed before reaching the downstream station. Whether these are inorganic or are organic compounds adding to the trophic base of the community is not known. Enough iron was found by Fiskel (Table 1) although its state of reduction has not been determined. Since there is little proof that non-particulate organic matter is quantitatively important to the nutrition of most aquatic communities, the interpretation of the BOD values remains perplexing. It is interesting that Sargent & Austin (1949) similarly reported an unexplainable BOD decrease across their coral reef community. It must be kept in mind that the small magnitudes of organic matter involved here, although unimportant as a food source in a standing water, are potentially of much greater importance to a benthic community because of the amount of water flow per day. If the boil were receiving dissolved but usable nutrient constituents from underground to the extent of 0.3 ppm, the effect would equal the tremendous and obvious primary production documented in previous sections. Even a smaller component of organic matter being taken from inflow would profoundly influence production.

As summarized in Table 15 part of the community's primary production passes downstream as small particulate organic matter.

From Table 8 0.09 mg dry/1 increase in #10 net seston implies 878 gm/m^2/yr export of small particulate organic matter. The large clumps and fragments of Sagittaria-aufwuchs complex that float conspicuously down the stream are insignificant (25 gm/m^2/yr) as indicated by measurement. A gill net stretched across the upper 3 ft. of the stream at the ¾ mile downstream station was used to measure these fragments which float at the surface. A mean of 216 gm/hr was obtained in three measurements (Table 8).

An alternative computation of the magnitude of the downstream export of aufwuchs material was obtained from the chlorophyll measurements and the chlorophyll to organic matter ratio of the aufwuchs (.012). An average chlorophyll value (1.25 mg/m^3 was obtained from the diurnal curves of Figures 29, 30, 36 and during low water when the discharge was 6.4 x 10^4 m^3/hr. The magnitude of export obtained in this way (766 gm/m^2/yr) is similar in order of magnitude.

A computation of the organic matter increase downstream as measured by the permanganate oxidation changes of about .13 mg/1 (Table 8) leads to an estimate of total organic matter export of 1280 gm/m^2/yr.

The estimates of particulate organic export derived from chlorophyll is used in Table 15. These values are about equal to the slight excess of production over the respiration estimates. How the peculiar BOD results fit with this is unknown. Neither import nor export of the dissolved organic matter is clearly proved so that only the particulate organic matter is included in the balance sheet in Table 15.

BALANCE SHEET

In any community the influx of energy must be entirely accounted for in the passage through the community and in the outflow if an understanding of the community metabolism is to be obtained (Clarke 1946). In a steady state community, this objective may in part be realized. By constructing a balance sheet, the various estimates of biomass or energy flux which have been estimated in previous sections must be mutually consistent within the crude limits of estimation. Table 15 is such an annual balance sheet. The gross production is obtained from the diffusion corrected upstream-downstream oxygen flows as represented in Figure 33. The bubble loss is negligible as discussed in the section on oxygen metabolism. The only definitely demonstrated allochthonous organic input is the 70 loaves of bread (365 gm each) fed to the fish each day. This import is neglected in Table 15. Respiration estimates are taken from an average of the bell jar measurements and the flowing respirometer measurement. The organic matter added to the water by the community and then exported is estimated in the previous section.

Although an exact agreement between production and respiration-organic matter loss is not found, the difference of 4% can presumably serve as some estimate of the reliability of the orders of magnitude. The estimates of respiration and organic export are certainly rough approximations, whereas the production measurements may be more accurate.

ENERGY FLOW DIAGRAM

In Figure 7 the flow of energy through the community in Silver Springs was shown according to trophic levels. The use of the diagram is applicable in general form to any system. It shows distinctly the workings of the first two laws of thermodynamics. According to the first law the total influx of energy equals the total flux out. According to the second law, especially as interpreted with the optimum efficiency maximum power hypothesis (Odum & Pinkerton 1955), wherever an energy transformation occurs most of the energy is dispersed into heat that is unavailable for further use by the organisms in the community.

Since the overall metabolism has now been estimated as summarized in the balance sheet in Table 15, it is now possible to make some rough estimates of the component flow rates. Where estimates are complete, the diagram may be used as a check since the parts must agree with the whole. Where estimates are incomplete the diagram may be used to fill in the part from the total. The figure must be regarded as extremely tentative because of the many possible errors and incomplete data.

TABLE 15. Mean Annual Balance Sheet of Organic Matter in Silver Springs for the Upper ¾ Mile Zone of 18 Acres.

		Dry Weight (including ash) gm/m²/yr.
INCOME		
Primary Production.......	Calculated as the area under the annual curve of gross primary production in Figure 33, which is in turn based on daily oxygen curves, observed photosynthetic quotients, and ash corrections (Table 10)	6390
Bread fed fish....	See section on fishes	120
Total Income...		6510
LOSSES		
Community Respiration.......	Mean of short duration bell jar experiments (underestimate; see text) and flowing respirometer measurement (overestimate). Bell jar respiration for less than 150 minutes duration, .28 mg oxygen/gm/dry/hr; flowing respirometer metabolism, 1.3 mg oxygen/gm dry/hr. 1.13 gm dry/gm oxygen used as a conversion factor where nitrogen is not oxidized to nitrate (see text section on nitrogen)	6000
Downstream Export of Organic Matter..........	Estimates from Table 8, 1.25 mg/m³ chlorophyll exported (see organic matter section); ratio of dry weight to chlorophyll, .012 (see text of chlorophyll section). 6.4 x 10^4 m³/hr. discharge; 7.6 x 10^4 m² area. (See organic matter section for other estimates of similar order of magnitude.)	766
Total losses......		6766
Discrepancy Between Income and Loss		256

As discussed in the animal growth rate section, there are several procedures required to work out the flow rates of production at the various trophic levels. To obtain the respiration of a trophic level one determines the standing crops, estimates the respiratory metabolism per gram, and multiplies to obtain the total respiratory metabolism in each trophic level. The net production of the trophic level follows from the determination of the growth rates (output) directly using varied means depending on the organisms. As described in sections on animal growth rate above, this has been done in some cases and reported as turnover in Table 13. The best estimates from this table are used in the energy flow diagram in Figure 7. The input of energy into a trophic level is mainly the sum of the respiration and net production if one neglects egested unassimilated matter. The flow picture in Figure 7 shows the relationship of growth, utilization, assimilation, and heat loss for each trophic level. From these concepts one may also derive the several types of efficiencies (ratios x 100) useful in describing ecological systems. These are defined as follows using symbols from the flow diagram:

P=production rate (rate of net organic synthesis in the form of the species of the trophic level or in storage products)

A=rate of assimilation

I=rate of ingestion (consumption) or energy intake

R=rate of respiration

$$E_u = \text{utilization efficiency} = \frac{I_2}{P_1} = \frac{I_3}{P_2} = \frac{I_4}{P_3} = \frac{I_5}{P_4}$$

$$E_a = \text{assimilation efficiency} = \frac{A_2}{I_2} = \frac{A_3}{I_3} = \frac{A_4}{I_4} = \frac{A_5}{I_5}$$

$$E_t = \text{tissue growth efficiency} = \frac{P_2}{A_2} = \frac{P_3}{A_3} = \frac{P_4}{A_4} = \frac{P_5}{A_5}$$

$$E_e = \text{ecological growth efficiency} = \frac{P_2}{I_2} = (E_t)\ (E_a)$$

$$E_l = \text{Lindeman efficiency (ratio of intakes of trophic levels)} = \frac{I_2}{I_1} = (E_e)\ (E_u)$$

$$E_p = \text{trophic level production ratios} = \frac{P_2}{P_1} = (E_u)\ (E_e) = (E_u)\ (E_t)\ (E_a)$$

The data in Figure 7 permit the calculation of the ecological growth efficiencies (E_e) and the trophic level production ratios (E_p, synonomous with Lindeman's usage of trophic level efficiencies only in the first trophic level). The ecological growth efficiencies E_e and the trophic level production ratios are given as follows:

	E_e	E_p	E_l
Plant Net Production	$\frac{8,833}{20,810}$=42%	$\frac{8,833}{20,810}$=42%	$\frac{20,810}{410,000}$=5%
Herbivores	$\frac{1,478}{3,368}$=44%	$\frac{1,478}{10,395}$=14%	$\frac{2,380}{20,810}$=11%
Carnivores	$\frac{67}{383}$=17%	$\frac{67}{490}$=45%	$\frac{383}{2,380}$=16%
Top Carnivores	$\frac{6}{21}$=29%	$\frac{6}{67}$=9%	$\frac{21}{383}$=6%

Great confusion often results from misunderstanding as to which efficiency is meant. The energy flow diagram is a help in this clarification. In another communication some current uses of the term production as synonomous with assimilation are questioned (Odum 1956b).

The general principle from Lindeman (1942) and Dineen (1953) that trophic level efficiency (E_l or E_p) increased along the food chain was not entirely confirmed for Silver Springs although the estimates of rates at the higher trophic levels are probably not accurate enough to test the relationship definitely.

LIGHT INTENSITY AND EFFICIENCY OF PRIMARY PRODUCTION

The visible and usable light intensities reaching the community plants were estimated as reported in the environmental section. The gross primary production for different days during the year was summarized in Figure 33. The relationship of the primary production and the light intensities are related in Figure 37. All estimates of light intensity received the tree correction previously discussed in the light section. The points in Figure 37 are in a rough line corresponding to 5% efficiency of photosynthesis. A similar graph was found for eleven other springs (Odum 1957).

Apparently the production of the whole community is proportional to the light intensity even at these relatively high light intensities. In contrast, physiological experiments on single plants show decreasing efficiencies at high light intensities. The community metabolizes below its overall com-

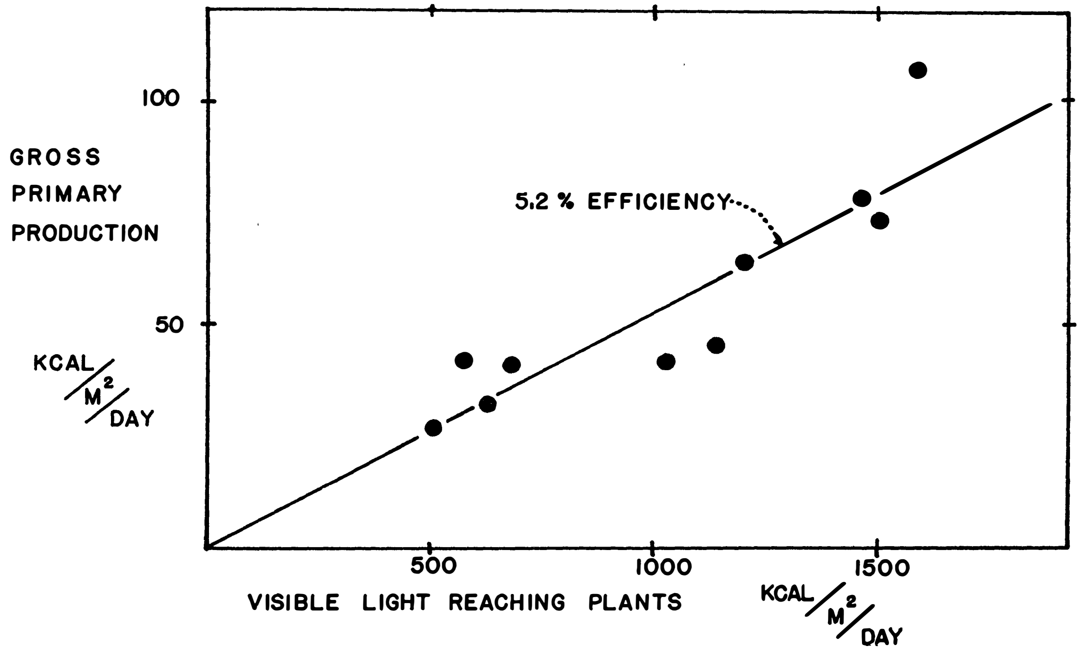

FIG. 37. Gross primary production as a function of light intensity which is absorbed by the plant beds of the community. Each point is based on one of the detailed diurnal oxygen curves of Figures 23 to 31. Ash free dry weights from Table 10 are converted into Calorie values on the basis of the percent protein estimates in Table 10. 5.8 Cal/gm protein and 4.0 Cal/gm carbohydrate conversions are used. Total insolation reaching the ground is calculated from Kennedy (1949) on the basis of cloud cover and season. Half of this is taken as visible and usable light energy; 60% is assumed to reach the plant level of 1.8m and be absorbed. A correction for tree shading is applied: 30% in December, 10% in July, and interpolation between these values for other months.

pensation point on cloudy winter days, but this does not mean that all of the individual plants do. The community compensation point includes not only plant respiration but downstream losses and consumer respiration. A possible explanation of the dumping of much of the production downstream lies in a requirement that at steady state the single plants must not long be exposed to conditions below the individual's compensation point. Perhaps there is generalization that temperate communities must produce excess organic matter as soil or peat or downstream loss which tropical communities need not do.

TURNOVER, CLIMAX AND STEADY STATE

With a gross primary production during a year of 6390 gms/m^2 and with a standing crop biomass of all components of 819 gms/m^2 it is clear from the ratio that the community turnover is 8 times/ year. As discussed elsewhere (Odum 1956b) the smaller the component organism, the more rapid the turnover. Thus the overall community turnover has meaning only in that it expresses the relationship of the size of the community and the total productivity.

Where all of the components of a community turn over several times a year there would be ample opportunity for changes to occur if there were no self regulative mechanisms. In Silver Springs there is apparently a fairly high degree of stability. Shelford & Eddy (1929) presented evidence that the climax concept was applicable to streams. The Silver Springs community is strong evidence that where the hydrographic climate is constant the community may develop a steady state. The possible relationship to the balanced aquarium idea is discussed elsewhere (Odum & Johnson 1955).

It is suggested that the stability of a system be measured by the number of times it turns over without change. Thus communities of small organism which persist for a year with a daily turnover may be considered as stable in this sense as a community of large organisms which lasts 300 years while turning over once per year.

The summer pulse of primary production due to the greater influx of light mainly leads to an increase in reproduction in the consumers rather than to pulses, blooms, and changes in populations. The increases in rates at any one trophic level are accompanied apparently by increases in utilization at other trophic levels so that the standing crops do not change markedly.

BOAT BASIN BACKWATER—A NATURAL EXPERIMENT

In the section on pseudoplankton the boat basin was described. The diurnal pattern of oxygen and carbon dioxide 1 meter below the surface of this still pool is shown in Figure 38. Also calculated is the rate of change curve. Since the water stratified thermally somewhat during the day (surface temperature 29.1° C; 1 meter temperature 27.9°), the gas transfer coefficient is likely to be minimal. Taking a value typical of quiet water of about .1 gm/m^2/hr at 0° saturation (Table in Odum 1956a), the amount of diffusion into and out of the water is calculated (depth 1.3m) and found to be less than .03 ppm/m^2/hr (maximum saturation deficit, 32%) and thus negligible relative to the photosynthesis. The area under the corrected oxygen-change curve corresponds to an estimate of 6.5 gm oxygen m^3/day primary production. This is about 26 KCal/m^3/day organic production (x 4.0). The light energy absorbed within the top meter is estimated to be 87% as shown by the light curve for the boat basin given in Figure 14. Starting with a light intensity reaching the ground on a cloudy day in July from Kennedy (1949) and allowing 50% energy to be of usable wave length, the useful energy absorbed in the top meter is calculated to be 2400 KCal. Thus an efficiency of about 1.1% is obtained. At the same time in the main flowing community of Silver Springs the efficiency is about 5%. In the boat basin at 1.1% efficiency the production from all the usable incident light (2740 KCal/m^2/day) would be about 7.5 gm oxygen/m^2 day. On a similar day in the main stream even though half of the light was absorbed before reaching the producers, the production was larger (12 gm oxygen/m^2/day) due to the greater efficiency.

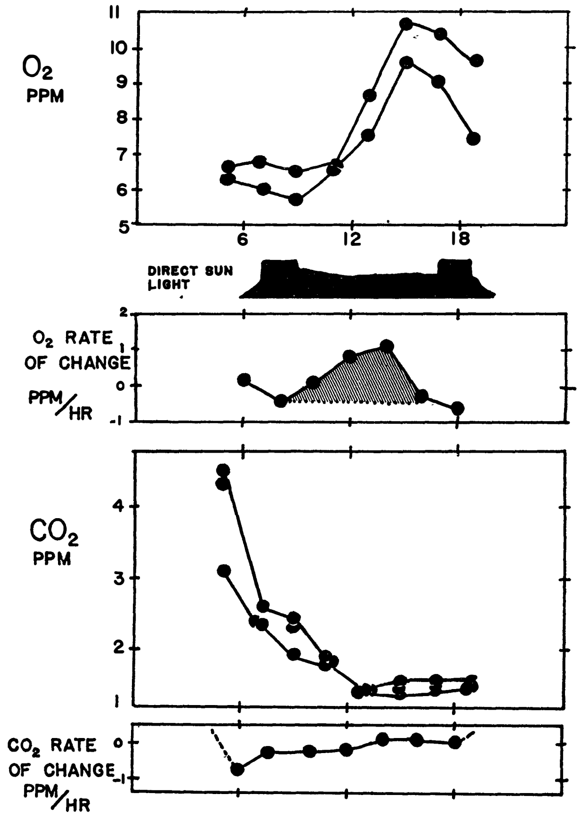

FIG. 38. Diurnal curves of oxygen and carbon-dioxide in the boat basin on Silver Springs River (see Figure 2). The oxygen values are given in the upper graph. The rate of oxygen change in the upper curve is calculated and plotted in the second graph. In the lower part of the figure is plotted the carbon-dioxide as calculated from the pH and the rate of change of carbon-dioxide.

EFFICIENCY AND CURRENT

The production of Silver Springs is clearly large. It has been suggested elsewhere in a review of existing data (Odum 1956a) that flowing waters in general are usually more productive than marine, lake, or terrestrial situations. Ruttner (1953) and many others since have pointed to the action of current in renewing media and removing wastes in micro-environments. Gessner (1937) experimentally showed increased production. It seems reasonable to consider the energy due to flowing water over aquatic plants provided by the current as an auxillary source aiding the productive process.

If the hydrostatic drop in head in Silver Springs is transferred into frictional heat energy without acceleration of the water while passing over the ¾ mile study zone, the potential energy difference between the boil and the ¾ mile station may be considered the energy available to the community in driving the current. In Silver Springs at times of lowest stage a drop of .144 m per km occurs from the boil (39.2 ft above sea level) to the Oklawaha river (34.6 ft) (U. S. Corp. of Engineers 1938). Such a drop over the headwater zone involves a dispersion of 5.2 x 10^5 KCal/m^2/day potential energy for a flow of 6 x 10^4 m^3/hr. This is about a tenth of the gross primary production of the 18 acre area (Fig. 37).

From the previous section the backwaters of the boat basin were considered as a case of production in still waters of the same nutrient supply. The primary production was estimated as 5 times less efficient than that in Silver Springs headwater run at the same time. One wonders if a large increase in efficiency is obtained in exchange for a small energy expenditure necessary to increase circulation rate or whether the actual total volume of nutrients is the important difference.

SUMMARY

1. Silver Springs, Marion County, Florida is a thermostatic, chemostatic, and biostatic ecological community in seasonally pulsing steady state climax.
2. The annual primary production is 6,390 gms/m^2 or 57,100 lbs/acre of organic matter, including 13% protein and 23% ash.
3. The efficiency of primary production relative to the incoming light in usable wave lengths reaching plant level is about 5.3%.
4. The efficiency of production in a still water backwater without current is estimated as 1.1% on the basis of a diurnal oxygen curve.
5. The rate of primary production of the whole

community is linearly proportional to the light intensity under natural conditions.

6. The community experiences an annual turnover of 8 times. In view of an apparent stability of gross features of at least 100 years, the stream constitutes a climax.
7. Most of the production goes into respiration, but 12% goes downstream as organic matter mainly in seston form.
8. A pulse of productive energy due to the greater influx of light passes through the community in the spring and summer and is expressed at the plant level as a higher percentage production as protein and at higher trophic levels by breeding or increase in breeding activity. Productivity in the springtime is 2 to 3 times winter production.
9. Measurements of community metabolism in Silver Springs and probably in other springs may be made readily by comparison of upstream and downstream measurements.
10. In the main flow, in the retarded flow of plant beds, and in bell jars inorganic phosphorus and nitrate nitrogen was found to be removed from the water day and night.
11. A large midge and caddisfly emergence occurs in the evening at all times of the year. Counts of pupae caught in funnels suggest that only a relatively small proportion of the midge population ever emerges.
12. Water lettuce and hyacinth growth in cages may be used as a simple direct bio-assay of potential primary production. Growths are maximum in spring and fall.
13. Transplantation experiments with Sagittaria indicate that 1/3 of the primary production is due to the Sagittaria although ¾ of the standing crop biomass is eelgrass.
14. Bacteria constitute a relatively small part of the standing crop biomass, but next to the plants are the main consumers in terms of energy utilization. Chromogens are numerous in the algae but not in the mud. Plate counts, slide counts, and direct counts are reported.
15. Efficiency concepts and flow rate estimates may be checked for consistency with the flow rate diagram.
16. In Silver Springs the titration of carbon-dioxide and the measurement of pH are alternatively useful in determining the carbon-doxide fixation and release during community metabolism between the boil and the downstream station.
17. The community metabolic quotient as measured and corrected for oxygen losses varies markedly during the day, but on an average is about 1.38 in summer and .95 in winter. This agrees with the expectation for carbohydrate and for 39% protein where nitrate fixation is involved.
18. Some of the main invertebrate components and fish species (*Pomacea, Paleomonetes, Mollienesia, Gambusia, Lepomis punctatus*) exhibit a strong photoperiodism in breeding cycles in this constant temperature environment.
19. The downstream increase in oxygen during the night may be used as a measure of the diffusion where an independent estimate of respiration is available.
20. Respiration estimates of .22 gm/m^2/hr were obtained from bell jar measurements of submerged communities. Lag effects, high variability and elimination of current reduce the reliability of these estimates. Higher respiration values were obtained in a flowing respirometer.
21. Hydrographic microclimates within the plant beds experience considerable diurnal range in oxygen, nutrient concentration and carbon-dioxide.
22. Varied sampling methods were used to estimate the biomass of dominants. The community of organisms possesses a pyramid of dry biomass structure with C_2/C_1 ratio 14%; C_1/H ratio 31%; H/P ratio 4.4%. This compares well with other attached communities (nonplanktonic) where such rough measurements have been made.
23. The aufwuchs community is dominated by the sessile generation of *Craspedacusta* (*Microhydra*) and hydra as carnivores, midges and caddisflies as herbivores, and mats of diatoms and blue green algae as producers.
24. The individual boils differ in chemical properties. A change in oxygen associated with decreased flow was observed in the main boil in the 1955 drought.
25. Species lists, distributional maps, and a rough trophic classification is given for the community.
26. Patterns and variations of biologically active chemical properties, oxygen, carbon-dioxide, phosphate phosphorus, and nitrate nitrogen have been studied over one minute intervals, upstream, downstream, day, night, in micro environments, and in bell jars. Variation in methods was established with technique tests.
27. Diffusion of oxygen and carbon-dioxide was estimated with a dye turnover method and from balance sheet estimations. Bubble losses were estimated in suspended funnels.
28. Oxidation-reduction potentials were unchanged upstream and downstream.
29. Study of the downstream oxygen and carbon-dioxide curves permits a study of the instantaneous progress of total community photosynthesis. Oxygen and carbon-dioxide curves are not synchronous.
30. Biochemical oxygen demand measurements suggest a slight decrease in total organic matter in spite of the increase in particulate organic matter as the water flows downstream over the community.
31. The trace element and nutrient contents of Silver Springs water are more reproducible than are most laboratory-synthesized media.
32. Light penetration curves are given indicating a greater transparency than in most marine waters.
33. The chlorophyll of the benthic community was determined as 2.95 gm/m^2. This chlorophyll is

concentrated about 1/3 of the distance from the eelgrass tips in a zone of somewhat lower light intensity than found at plant-tip level.

34. A thermistor temperature map is given for a summer day, which portrays the rate of flow and heating.
35. Diurnal patterns and patterns over the 5 mile spring run are given for versenate hardness, alkalinity, chloride, and nitrite.
36. The catfish nose-dive behavior is postulated to produce a respiratory advantage.
37. A diurnal increase of chlorophyll in the pseudoplankton was observed with assays of millepore filtered samples winter and summer.
38. The N/P ratio and utilization suggests that nitrogen is the more limiting.
39. Succession of aufwuchs organisms on individual blades occurs continually as the Sagittaria blades grow out from the bottom. In any one area blades and their biota are in various successional stages but the whole area is in steady state and a kind of stable succession distribution possibly analagous to a stable age distribution.
40. Silver Springs constitutes a regulated natural laboratory containing a community in which data are cumulative and studies may be repeated.

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