PRODUCTIVITY OF FLORIDA SPRINGS
NONR 580 (02)

SECOND
Semi-annual Report to the
Biology Division
Office of Naval Research
Progress from February 1, 1953 to June 30, 1953

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Contents

ABSTRACT

During this second six months emphasis has been laid on developing a complete understanding of the metabolism of the Silver Springs ecosystem as an example of a community apparently in a steady state. Variation in phosphates, uptake of nitrates, and importance of boron have been estimated. Fluctuation of some major elements has been estimated. Examination of stomach contents has permitted trophic classification of dominant species and the standing crops have been estimated for these species by number and by dry weight. From these a pyramid of mass has been constructed. Special attention has been paid to bacteria using 3 methods for comparison of Silver Springs with lakes and estimation of the standing crop. The oxygen gradient method has been repeated at half hourly intervals. A carbon-dioxide gradient method has also been used to check the oxygen and to obtain a photosynthetic quotient. Black and light Bell jar experiments have been initiated to obtain checks on the other production measurements and to obtain a community respiration rate. An approximate balance has resulted from estimates of production, respiration, and downstream loss. A flow rate diagram has been constructed to clarify definitions of efficiency and their relationship to a steady state system. Mr. Sloan has statistically verified the increase of insect number and variety away from the boils and demonstrated the reliability of quantitative dipping for aquatic insects. Plans for the third half year include detailed and comparative study of the dominant algae and further estimates of rates of growth of all community components.

INTRODUCTION

Previous semi-annual report

In the introduction to the previous report the Florida Springs were described as an opportunity to study qualitative and quantitative productivity and the factors that control community structure and metabolism. The varied but constant temperature and chemical conditions in the different springs permit natural experiments and cumulative studies not possible in other types of natural environments. Work in the first six months as previously reported established a broad base by making initial surveys of the properties of a large series of springs and by developing techiques for study of productivity.

Personnel

During this half year William C. Sloan has continued as graduate assistant on the project. Mr. W. Hampton has served as an undergraduate assistant for several months. The Department of Biology has furnished as graduate assistant Bruce Parish for one month for the Boron work. Dr. Larry Whitford, phycologist from N.C. State College in Raleigh N.C. has joined us for full time study of the algae for the summer. We wish to acknowledge the continuing aid that we have received from many persons as partially indicated in the first report. Some of the results of these studies were presented in departmental seminar in March, at the association of Southeastern Biologists meeting in April, and at the Oceanographic Institute, Fla. State University July 3, 1953.

Purpose and scope of second half year

In the present report which includes work in the second six months, emphasis has been laid on developing as complete a picture as possible of the community structure and metabolism of one Spring: Silver Springs. In order to do this a number of additional techniques have been used. At least rough estimates of all the major components of Silver Springs have been completed and primary production measurements made by several methods. The measurement of production rates of the higher trophic levels has been started. As preparation for the future comparison of other springs with Silver, work has been continued on basic data for other springs such as oxygen, phosphate, nitrate, Boron, and Taxonomy. William C. Sloan has quantitatively confirmed his patterns of insect variation by analysis of variance.

PROGRESS: INTENSIVE STUDY OF SILVER SPRINGS

1. Characteristics and stability of non-living environment

Nitrates

Several series of nitrate determinations have been made in Silver Springs and a few other low chloride springs. An attempt has been made to compare the nitrate concentrations in the boil with those downstream during the day and night to determine the patterns of nitrate metabolism.

As with oxygen and carbon-dioxide discussed below the spring has been found to be horizontally slightly heterogeneous with respect to biologically active elements probably due to the local action of plants and varying rates of flow of water in some of the side pools and eddies. Thus to demonstrate boil--downstream differences a number of duplicate analyses have been run as summarized for nitrates in Table 1.

There is considerable variation inherent in our use of the phenoldisulfonic acid method as indicated by technique test. In spite of this variation and the variation in the spring there seems to be a significant drop in nitrate as one goes downstream especially during the day. Gordon Broadhead collected a series from a small spring run at Ichtucknee springs, and Hampton analyzed for nitrate and again found a significant drop.

If one uses the average nitrate daytime minus night uptake of .040 ppm one calculates from the rate of flow that 14,300 pounds per acre per year protein are being synthesized during the day.

In general the Spring has been found to be remarkably constant from day to day regarding nitrate. Additional determinations of inorganic phosphorus show continued constancy of these values for Silver Springsas shown in Table 2. The N/P ratio in the spring water is 10.8 by weight which is of the same magnitude as required for aquatic organisms. In other springs analyzed values of the same order of magnitude have been found although the N/P ratio tends to be somewhat lower and thus below that required in protoplasm. It seems that of the two, nitrate is more likely to become a limiting nutrient. Certainly the moderately large concentrations of both nitrate and phosphate are consistent with the obviously great fertility of the constant temperature streams.

Table I

NO_3-N and Inorganic P SILVER SPRINGS

Summary of data

ıte	Place	Time	number of analyses	NO_3-N mean ppm		Mean Inorganic Phosphorus ppm	
)il--Gauge Station Comparisons:							
ıy 18	Boil	Midnight	10	.499	10	--	
ıy 18	Gauge	Midnight	10	.468	10	--	
)ril 9	Boil	Noon	10	.453	10	.0384	
)ril 9	Gauge	Noon	10	.331	10	.0381	
ıy 25	Boil	Noon	5	.40	5	.0462	
ıy 25	Gauge	Noon	5	.34	5	.0446	
ıy 14	Boil	Noon	10	.462	10	.0506	
ıy 14	Gauge	Noon	11	.440	11	.0423	
Analysis of variance shows a significant Boil-Gauge decrease in day.							
ıriation during the day:							
ırch 7-8	Gauge	daylight	9	.41	3	.056	
ırch 7-8	Gauge	darkness	5	.45	3	.053	
ırch 26	Gauge	diurnal	22	.396	-	--	
	Boil		2	.49	-	--	
(Paired series; Analysis of Variance shows no significant difference between pairs and between the time of day)							
)b 19	Boil	day	1	.40	1	.013	
	Gauge	diurnal	12	.381	17	.0372	
ıriations down the run							
)b 12	whole run	day	12	.478	-	--	
)v 13	lower run		5	.548	-	--	
chnique test							
							Standard Dev.
)b 12	Boil		10	.416	-	--	.105
rch 24	standard		5	.592	-	--	.045
mparison Values from other low chloride springs							N/P
ekiwachee	June 6, 1953			.12		.018	6.7
ange	June 6, 1953			.22		.081	2.7
nlando	June 19, 1953			.17		.167 .179	.98
ue (Alachua Co)	June 26, 1953			.85		.092	9.2
htucknee	June 9, 1953			.40		.064	6.3
lver, Mean of above				.444		.0409	10.8

Boron in Springs and Other Florida Waters

by

H.T. Odum and Bruce Parish

As reported in the previous report the chemical composition f the springs with respect to the major elements has been shown o be fairly constant and data are available for most of the prings under study. Data on the trace elements however are largely bsent and information is needed to establish which trace elements may e limiting or otherwise biologically important to the spring communi- ies. It is an outstanding fact that many springs with essentially he same major element concentrations differ radically in the nature f the biological community.

A series of boron analyses was made of water in Silver Springs nd some other waters to establish general norms of the element for lorida. We are especially grateful to Mr. H.W. Winsor of the Florida gricultural Experiment Station for showing us his analytical methods nd thus getting us off to a rapid start.

The data on boron in Florida Waters are given in Table 2. These ata are arranged in order of the chlorinity of the water. It seems lear that there is a correlation between the boron and chloride as ight be expected from their similar high solubilities. The associa- ion of boron and chlorides is also consistent with the premise that he high salt content of peripheral Florida ground waters is largely ue to salt in pore spaces left during the last Pleistocene inundation. n surface waters some chloride-boron correlation may be expected from heir common source from marine salt brought down from the atmosphere y rain.

The P/B ratio in Silver Springs (2.8) is so small in comparison o the P/B ratio in plants that is seems unlikely that boron in lorida is limiting either in springs or other waters. However, the igh levels of Boron in these waters may be growth promoting although ot limiting. Baumeister in 1943 found .5--100 ppm B had a growth romoting effect on aquatic spermatophytes. (Jahr. Wiss. Botan. vol. 1, pp. 242-277)

Table 2
Boron in Florida Waters

ocality, Date	Boron ppm	Chloride ppm
reat Salt Lake, Utah, 1950*	43.5	149,224.
ea Water, mouth of Tampa Bay, May 30, 1953	4.4	34,400.
ea Water, Gulf	6.3	--
ea Water, Gulf	5.4	--
arm Salt Springs (Sarasota Co.) June 17, 1953	.304	9,350.
alt Springs (Marion Co.) June 14, 1953	.197	2,439.
ittle Salt Springs (Sarasota Co.) June 17, 1953	.200	1,430.
omosassa Springs (Citrus Co.) June 6, 1953	.186	570.
lue Springs (Volusia Co.) June 19, 1953	.125	775.
once De Leon Springs (Volusia Co.) June 19, 1953	.055	622.
hassahowitzka Springs (Citrus Co.) June 20, 1953	.024	53.
ake Okeechobee at Pahokee, June 18, 1953	.057	27.
range creek (out of Orange Lake) June 1, 1953	.019	9.
eekiwachee Springs, June 6, 1953	.013	5.
enhalloway River, Foley, June 9, 1953	.027	4.
uwannee River, Branford, June 9, 1953	.0116	7.
chtucknee Springs Run, June 9, 1953	.017	4.
ilver Springs, May 28, 1953 (mean of 4 analyses)	.015	8.
orris Lake,(Putnam Co.) June 1, (oligotrophic ?)	.011	5.
orth Twin Lake, (Putnam Co.) June 1, (oligotrophic?)	.0132	7.
ady Slipper Lake, (Putnam Co.) (oligotrohpic ?)	.0162	4.
agnesia Springs, (Alachua Co.) June 10, 1953	.015	8.
anta Fe River, June 9, 1953	.027	10.
ochloosa Lake outlet June 3, 1953 (eutrophic)	.0165	11.
anlando Springs,(Seminole Co) June 19, 1953	.032	8.
range Springs, June 1, 1953	.019	7.
mall pond in pine flatwoods 1/2 mile south of Devil's Mill Hopper, Alachua Co. Fla. Sept. 11, 1952	.018	17.
ainwater, thunderstorm, Gainesville, June 14,1953	.0085	2.
ainwater, thunderstorm, Gainesville, June 14, 1953	.015	-
ewmans lake, May 31, 1953	.012	7.
ogtown Creek, May 31, 1953	.012	7.
atchet Creek, May 31, 1953	.015	7.
oil at silver; mean of 5 analyses of 1 sample	.0154	8.
ownstream at Silver Springs; mean of 5 replications	.0170	8.
ilver downstream water: duplicate analyses(4)	.0145	8.

Boron in Silversprings epihpytic algae	2.0 mg/kg dry
Boron in Silver Springs Sagittaria	8.6 mg/kg dry
P/B ratio Silver Springs	2.8
P/B ratio in plants	544.

*water furnished by Dr. Willard Hartman, Univ. of California

Alkalinity, Hardness, Nitrites, and Chlorides

Although previous analyses have shown the concentrations of ajor elements in Silver Springs, additional analyses in Table 3 ere made to demonstrate the variation downstream. Rough values of itrites were also obtained. Apparently some appreciable water of utside origin enters the run in the lower two miles which accounts or the higher nitrite values which appear in the lower run. There s one ~~ob~~ [illegible] artesian well that flows in.

Table 3

Analyses of Water in Silver River
daytime February 12, 1953

	NO_3-N ppm	Cl ppm	NO_2-N ppm	Hardness ppm $CaCO_3$ versenate	M.O.* alkalinity
oil	.47	-	.0024	200.4	161.6
	.31	9.5	.0007	200.6	162.4
arrows	.46	9.9	.001	210.6	160.0
oat place					
(in plants)	.29	10.2	.0005	207.4	147.2
(in channel)	-	9.8	.0	216.0	158.8
eck before curve	.46	9.5	.0	205.8	149.2
aradise park	.54		.0	201.2	144.0
auge station	.50	8.7	.0	205.4	144.0
ta 7 (1 mile)	.32	9.9	.0	201.8	144.0
ta 8 (2 miles)	.38	10.3	---	203.6	144.0
ta 9 (3 miles)	-	9.5	.0035	200.8	131.2
ta 10 (3 1/2 miles)	.31	10.2	.0012	201.8	142.8
ta 11(4 1/2 miles)	.50	10.1	.0005	205.0	141.2
ta 12 mouth	124	10.2	.004	203.6	146.0

*Indicator used for methyl orange alkalinity was methyl purple.
Figures in ppm $CaCO_3$

Trophic level classification

The determination of the taxonomy and food chains for Silver Springs, although not completed, has proceeded to the point where tentative trophic levels can be drawn for the dominants with some confidence. Stomach contents have been examined to determine the positions of some organisms in the food web. Further detail will be added as obtained. A classification of dominants in Silver Springs is given in Table 4. The insects of lesser importance were listed in the first progress report by W.C. Sloan. At present a species is listed wholly in one trophic level or the other. Later it should be possible to indicate what percent overlap there is.

Table 4
Trophic Classification of Dominants in Silver Springs

PRIMARY PRODUCERS:

Sagittaria lorata	Stigeoclonium	Oscillatoria
Plectonema	Oedogonium	Cymbella
Cocconeis	Fragilaria	Amphora
Synedra	Melosira	Navicula
Spirogyra	Scenedesmus	Phizoclonium
Cladophora	Euglena	Terpsinoe
Gomphonema	Closterium	

HERBIVORES:

Gammarus sp.	Pseudemys nelsoni	Goniabasis sp.
Hyalella sp.	Pseudemys floridana	Aminicolae
Stylaria sp.	Mugil cephalus	Physa sp.
Tendipes sp.	Pomacea sp.	Hydroptila sp.
(1092 diatoms/gut)		Elophila sp.

REDUCERS:
Procambarus fallax
Bacteria (21 colony variants in gross aspect) 5-35% chromogens)

CARNIVORES:

Lucania goodei	Lepomis microlophus
Mollienisia latipinna	Lepomis macrochirus
Heterandria formosa	Lepomis punctatus
Gambusia affinis holbrooki	

SECONDARY CARNIVORES:
Micropterus salmoides, Lepisosteus platyrhyncus, Lepisosteus osseus

A fairly complete list including less predominant fishes is given by Hubbs and Allen (1943, Florida Academy of Science, vol 6, #3 & 4).

Identifications of spermatophytes are being made by Dr. A.M. Laessle; algae by Dr. Larry Whitford; and macrocrustacea by Dr. Horton Hobbs.

3. QUANTITATIVE COMPOSITION OF THE COMMUNITY (STANDING CROP)

Numbers and dry weights of dominant species

Figures 1 and 2 summarize detailed estimates of the numbers and biomass dry weights for the major components in Silver Springs. Notice that the biomasses have been grouped according to trophic levels. The various estimates have been made with a large variety of techniques; bacteria by direct counts as discussed below; plants by square foot harvest by hand with face mask; algae by scraping off periphyton from Sagittaria blades; periphyton animals by scrapings; larger snails by face mask cropping of 100 square feet quadrats; small nekton and loose periphyton with a 1/4 square foot plant sampling trap net; larger motile invertebrates with a screen box trap closed with a sliding door by hand; minnows by visual counts over marked quadrats; larger fished by visual face mask counts while towed swimming from a boat; and turtles assumed to be the same per area as in Rainbow springs where L. Marchand carried out extensive tagging. These various estimates are of course very rough but since we have heretofore had no remote idea of magnitudes, and since we are first interested in big differences, these data represent an advance. As discussed by E.P. Odum in his forthcoming text (Principles of Ecology, Saunders, Sept. 1953) data on whole communities suitable even for textbook illustrations of pyramids of mass are nearly non-existant. Because of the constancy and stability of Silver Springs it is here possible to build up such data.

Pyramid of Mass

Because pyramids of numbers reflect the interaction of two separate effects, they rarely indicate relationships with clear meaning. Pyramids of number are a result not only of the decreasing numbers with larger animals at the top of a food chain but the decreasing numbers with larger organisms at the bottom of the food chain also. The pyramid can widen up the chain.

Pyramids of biomass dryweight however are clear representations of standing crop with respect to energy relationships as discussed in the theory section below. The estimates of dominants have been lumped in figure 3 to produce a pyramid of mass for Silver Springs. The decreasing slope of the biomass decrease is similar to that found in lakes by Lindemann. The ratios of the standing crop masses are measures of this tendency. These for Silver Springs are:

H/P 3.9%; C_1/H 23%; C_2/C_1 54%; $R/P+H+C_1+C_2$ 1.2%

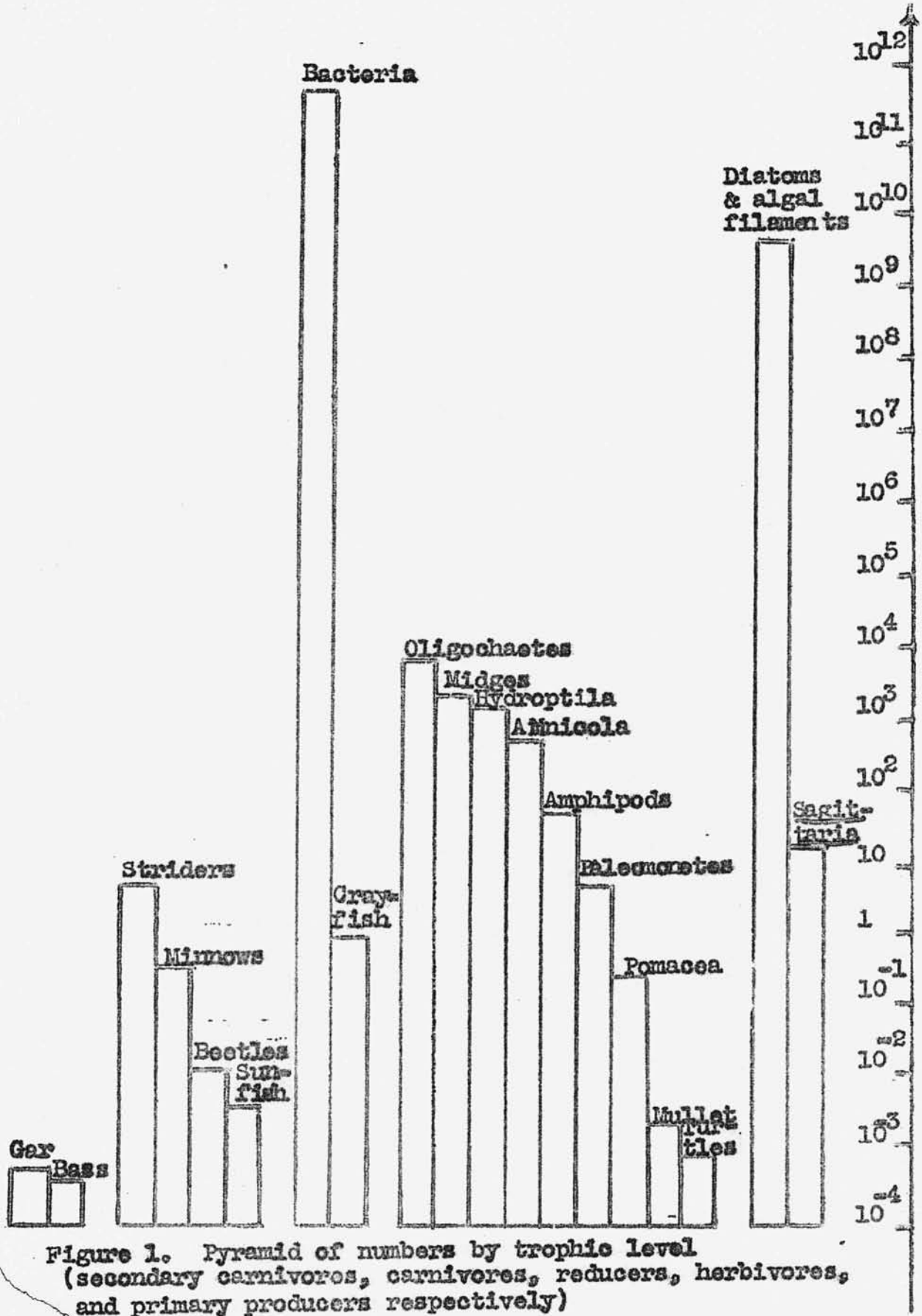

Figure 1. Pyramid of numbers by trophic level (secondary carnivores, carnivores, reducers, herbivores, and primary producers respectively)

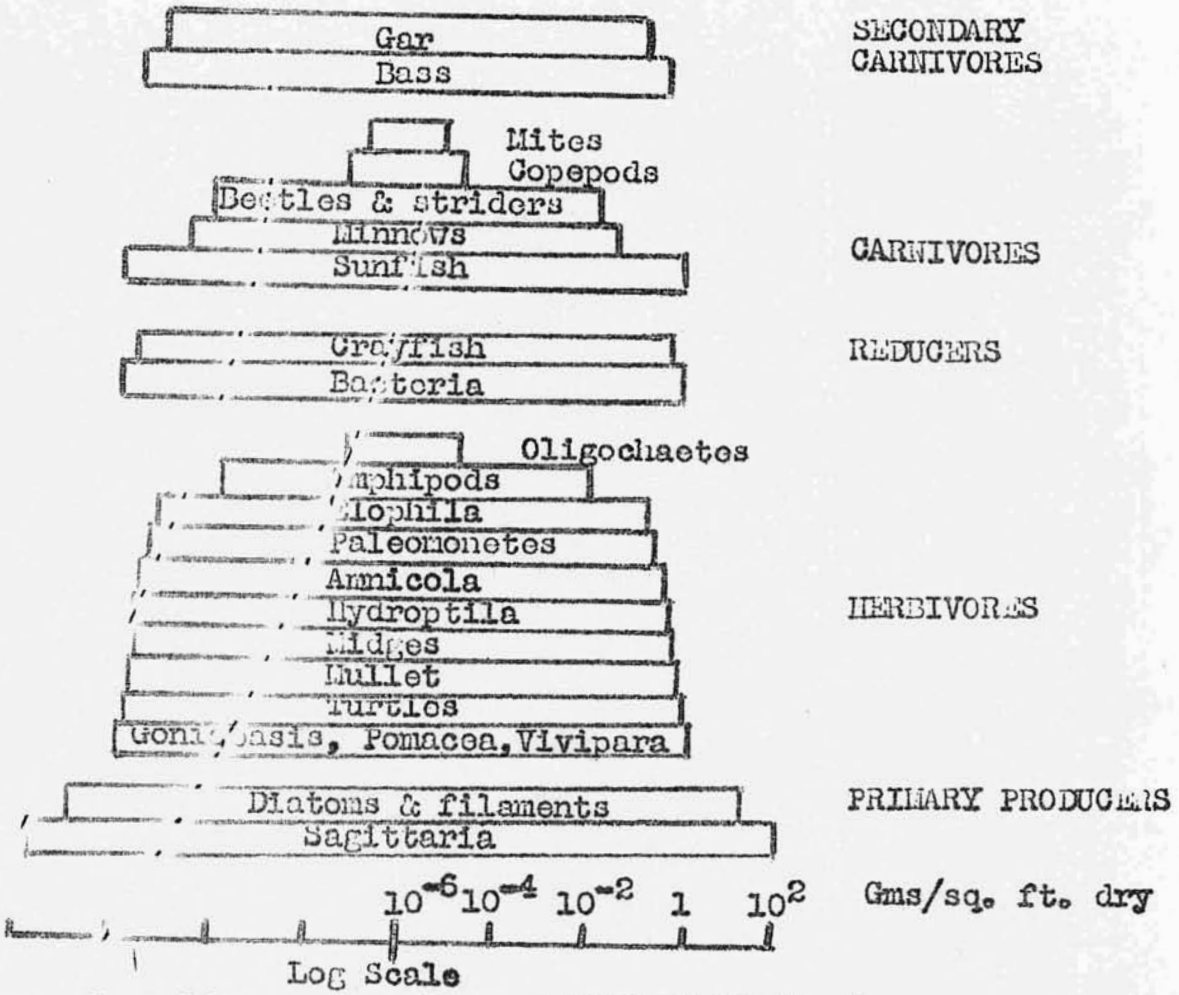

Figure 2. Estimates of Standing Crop of Dominants

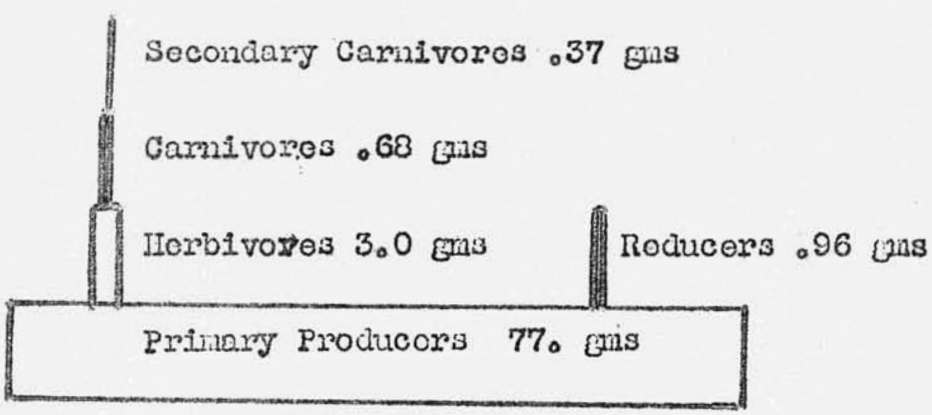

Figure 3. Pyramid of Mass in Silver Springs
gms/sq. ft. dry

Bacteria by H.T. Odum and Osilio Galindo

Several techniques used by Henrici and others were used in an effort to determine the standing crop of bacteria and something about the type of bacterial community as compared with lakes where these techniques were developed. First of all agar plates in pharmacy bottles were developed from periphyton scraped from Sagittaria blades and from mud samples. Second, counts were made of bacteria on glass slides after submersion in springs. Third, direct counts were made of aliquots of periphyton and mud suspensions using phase microscope. Finally, some counts were made of percent chromogens in the agar plates and the number of grossly different colony types. In this work we are grateful to Dr. Tyler and the Department of Bacteriology for advice and the loan of equipment and to Mr. J. Gonzalez who took an active interest and helped with the plating.

The data on the counts are summarized in Table 5. Just as found by Bere in Wisconsin lakes and others 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 error 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 - probably both.

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. In figure 4 the plot of frequency of species against the number of colonies per species shows a hollow curve that is often found in community analysis for reasons still obscure.

The glass slides showed numbers which 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 is apparently growth promoting even when the water is low in organic content.

In order to estimate the gms bacteria square feet in the Springs community the direct counts were multiplied by the volume calculated from a typical bacterium. The upper 1 cm of mud was arbitrarily included as part of the ecosystem. The large total surface in the Sagittaria supports periphyton bacteria that about equals the 1 cm deep mud bacteria in importance.

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

Table 5

BACTERIA IN SILVER SPRINGS

Material	Slides prepared	fields counted	mean estimate of number of bacteria
DIRECT COUNTS WITH PHASE MICROSCOPE 970x FRESH MATERIAL, LIVE			
10 x 1.4 cm	3	8	774. x 10^6
Sagittaria blade	2	6	757. x 10^6
with periphyton	1	5	468. x 10^6
1 cc mud 2 cm deep	2	9	276. x 10^6
	1	5	424. x 10^6
	1	5	398. x 10^6
1 cc mud 24 cm deep	1	5	226. x 10^6
COUNTS ON SLIDES SUBMERGED 72 HOURS AND STAINED			#bactera/mm^2/day
Slides on and near mud level	10	60	3277.
Slides 2 ft. below water surface	14	84	1281
PLATE COUNTS ON HENRICI CASEINATE AGAR	# dilution	# plates	number / % chromogens
10 x 1.3 cm blade of Sagittaria, still current	3	9	19.6 x 10^6 17.%
22 x 1.2 cm blade of Sagittaria, still current	5	15	17.6 x 10^6 15.%
10 x 1.2 cm blade of Sagittaria, swift current	2	5	21.9 x 10^6* .7%
1 cc mud, surface	6	18	5.7 x 10^6 10.%
1 cc Mud surface	3	9	4.9 x 10^6 9.%
1 cc Mud surface	3	8	1.6 x 10^6 20.%
1 cc Mud 9 cm deep	3	9	.26 x 10^6 6.%
1 cc Mud 18 cm deep	3	8	.24 x 10^6 7.%
1 cc Mud 27 cm deep	3	9	.40 x 10^6 7.%
1 cc water 1/4 mile	4	4	343. 5%

*excluding one plate count: 502 x 10^6.

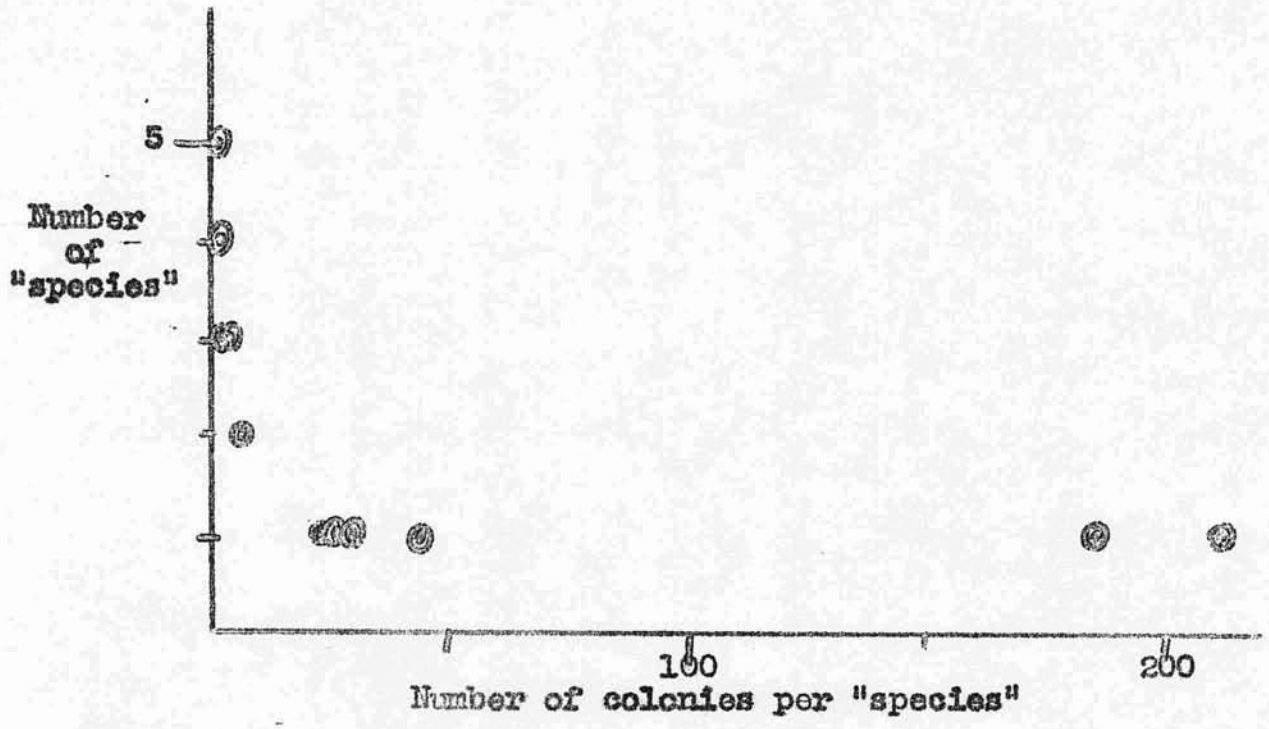

Figure 4. Relationship between the recognizable kinds of bacteria and their frequency in a periphyton sample plated on agar

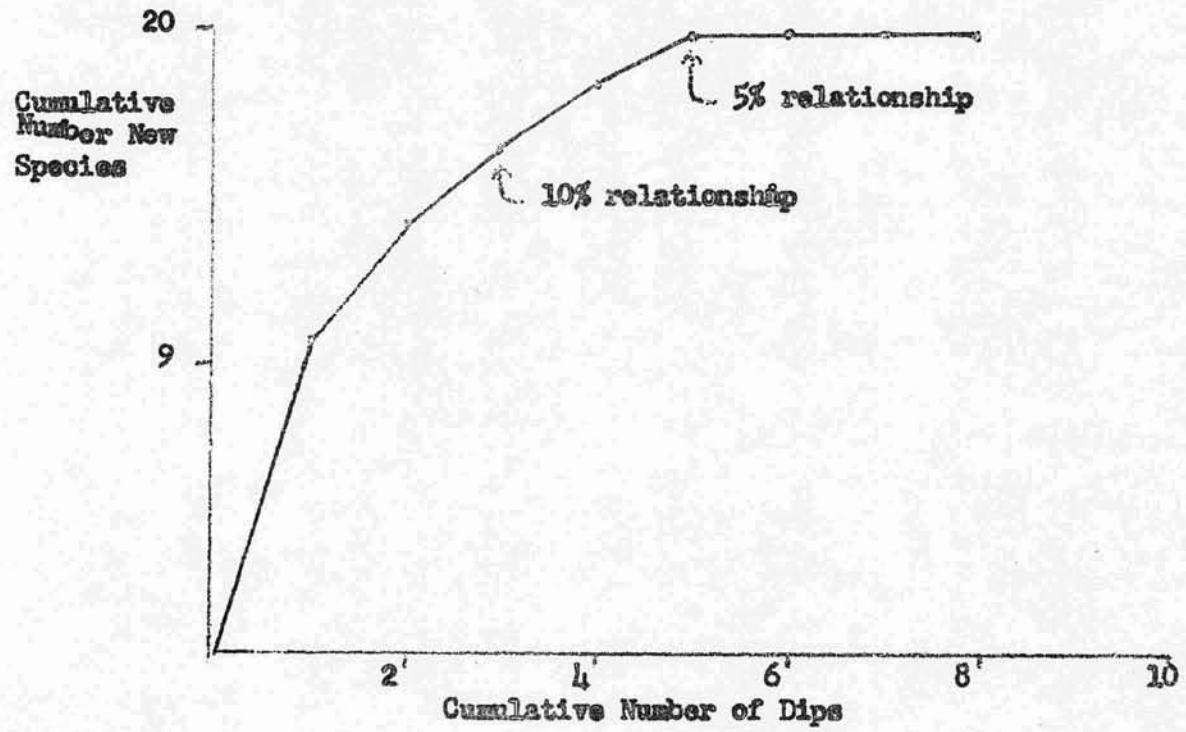

Figure 5. Relationship between increase in sampling area and number of new species collected.

Oxygen and Carbon-dioxide Gradient Measurements

In the first report a method for measuring primary productivity for the whole spring or stream community was described. The increase in oxygen between two stations at night was subtracted from the downstream increase during the day. Further study of this method has been carried out with analyses made every half hour. Results of these repetitions are shown in figures 6 and 7.

Similar curves have been obtained for carbon-dioxide as in figure 6. The area under the oxygen curve and the area above the dipping carbon-dioxide curve have been used to obtain photosynthetic quotients thus demonstrating the general validity of the interpretation of these changes as the result of differences in photosynthesis only. The meaning of these respiratory quotients are discussed in the section on theory below.

Considerable variation has been observed in both the oxygen and carbon-dioxide values from minute to minute indicating a considerable heterogeneity in the water. Some of this variation has been found in the boil also. However, the carbon-dioxide values are much more erratic. Part of this is due to the inherently less accurate end point of the carbon-dioxide titration used in comparison to the Winkler titration. However, there seem to be fluctuations which are greater than those due to technique and greater than fluctuations in oxygen. During the day under the intense subtropical sun in shallow clear water, oxygen is produced rapidly in the beds of Sagittaria and periphyton. These bubbles rising through the water may cause a more homogeneous distribution than in the case of carbon-dioxide. A tendency for carbon-dioxide fluctuation soon after dark observed on three occasions may be due to the trapped waters in eddies, shallow shelves, and side boils which become a few tenths of a degree cooler after dark and sink back into the main stream producing greater heterogeneity. In spite of these variations, by making larger series of analyses, curves such as those in figure 6 and 7 can be readily used as total community primary production.

It is likely that these estimates are minimum because in some of the less swift zones, face mask observation shows vast numbers of oxygen bubbles forming and breaking into the water. During the middle of the day some of these can be observed to reach the surface without becoming dissolved. Also a few places among plant mats become saturated during the day so that further production results in loss. Also during the day even in the main stream oxygen values are higher than at night so that not as much oxygen diffuses in from the atmosphere. Our procedure is to subtract the night values as though the day and night diffusion were the same. Since these effects all tend to cause an understimation of the primary production, it is all the more startling to find the enormous values such as those in table 6.

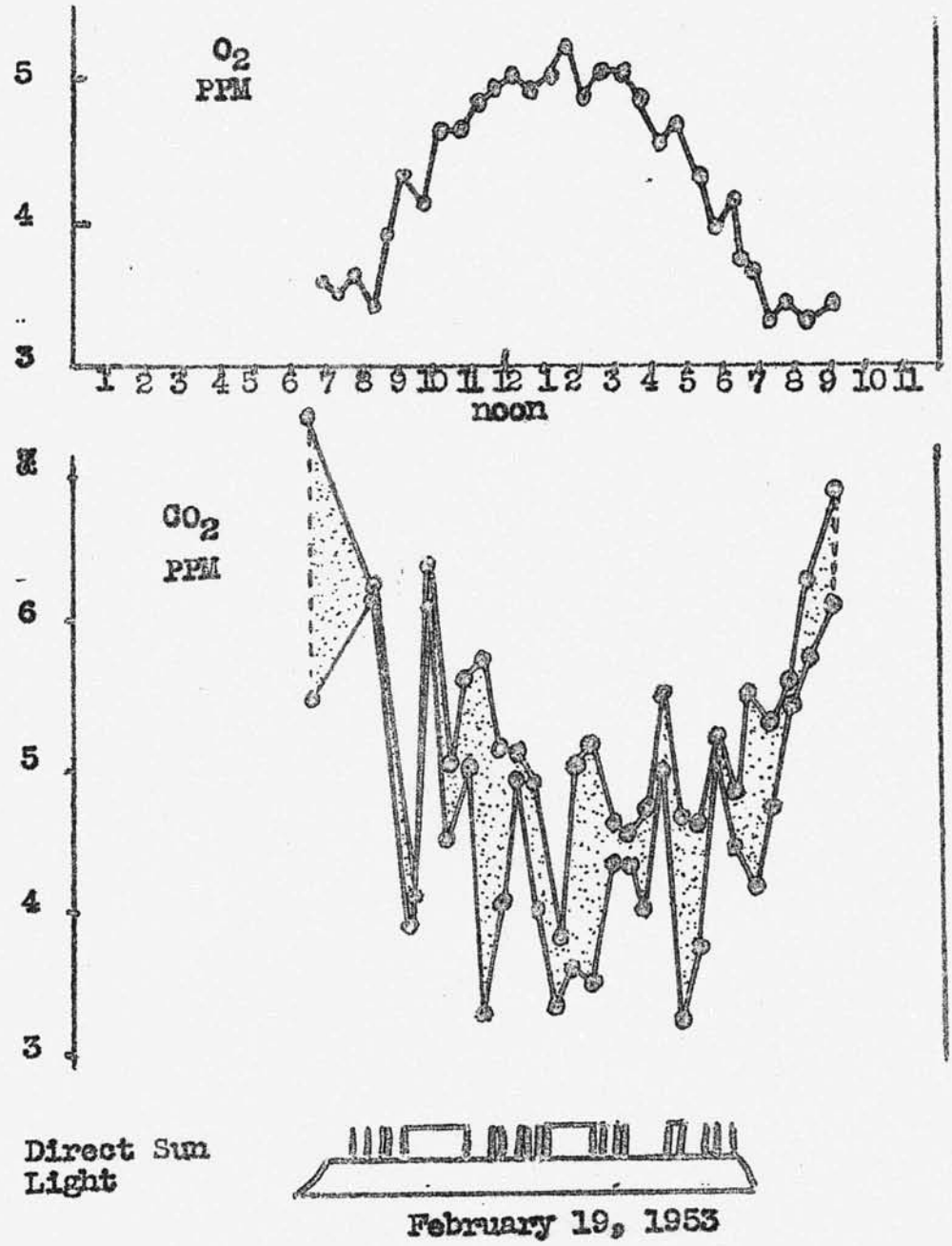

Figure 6. Oxygen and carbon-dioxide diurnal variation 3/4 mile downstream in Silver Springs (for oxygen gradient method of measuring primary productivity)

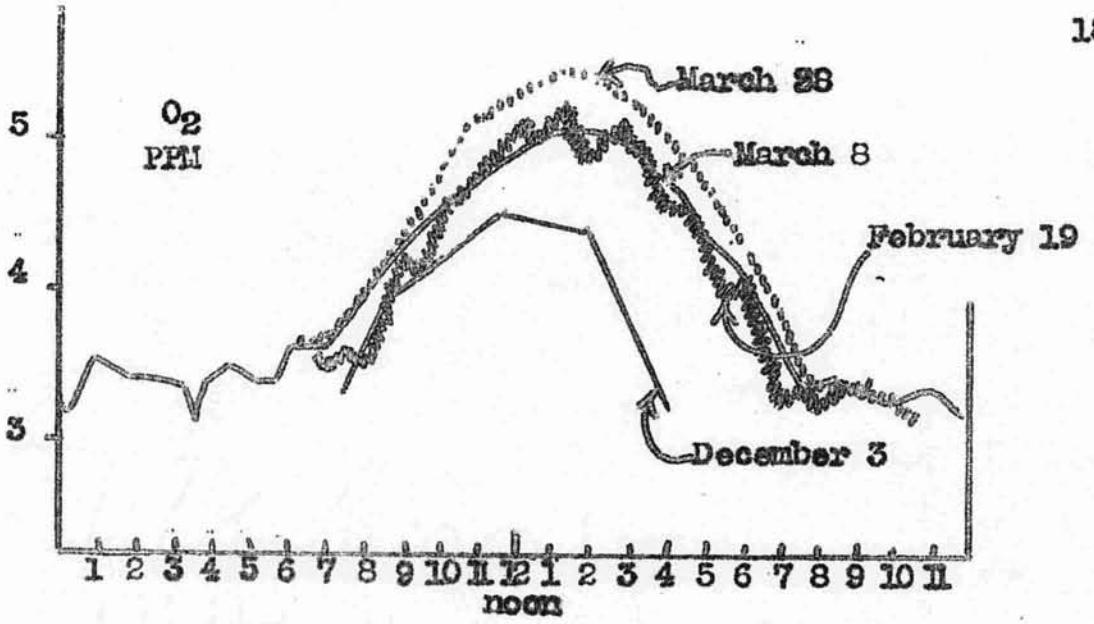

Figure 7. Seasonal oxygen variation 3/4 mile downstream in Silver Springs, Florida

Figure 8. Model of the thermodynamics of Silver Springs ecosystem

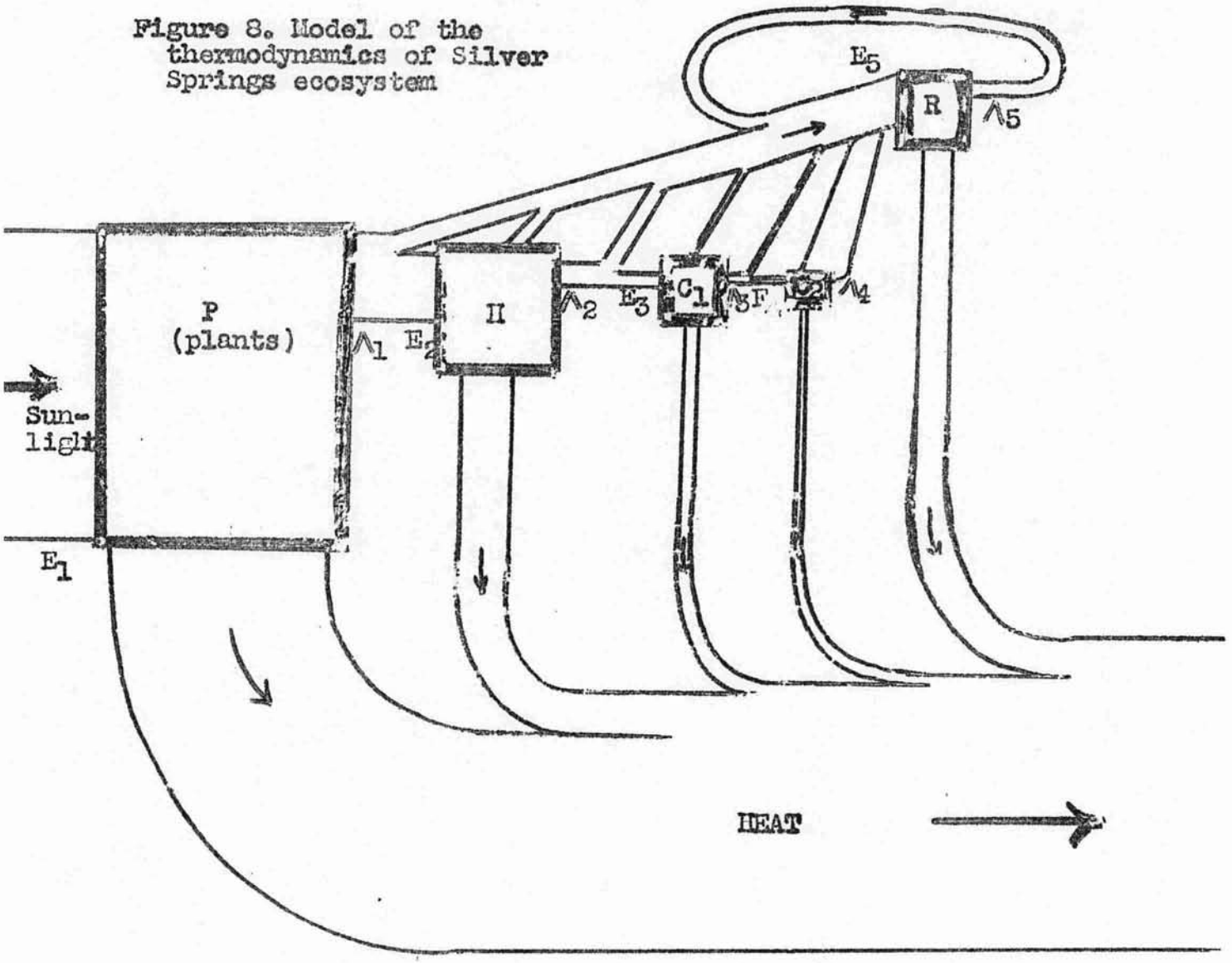

Table 6
Production Rates in Silver Springs

Method, Date	Operationally Determined figure	Uncorrected Primary Productivity converted to Pounds per acre per year
OXYGEN GRADIENT METHOD	area of O_2-time curve: ppm-hrs day minus night	Pounds per acre per year glucose
Dec. 3, 1952 cloudy	5.5	24,500.
Feb. 19, 1953 cloudy	12.1	54,000.
March 28, 1953 clear	13.1	58,200.
March 26, 1953 clear	16.0	71,400.
BELL JAR METHOD	ppm O_2 increase per jar per hour	Pounds per acre per year glucose
May 14, 1953	1.45	12,500.
1:00 p.m. clear	.60	8,300.
May 25, 1953	1.83	12,530.
1:00 p.m.	.85	8,100.
scattered cumulus	2.14	40,900.
	1.80	34,400.
Mean		19,500.
CAGE ENCLOSURE METHOD	% increase/day	lbs/acre/yr dry weight
Pistia Aug. 18-Oct. 9	1.9	19,600.
Oct. 9-Nov. 15	-1.8	decrease
Nov. 15-Feb. 12	-0.38	decrease
Feb. 12-March 7	.44	4,350.
March 7-April 9	.59	6,130.
April 9-May 11	2.8	28,900.
May 11-May 23	3.3	33,800
May 23-June 9	1.4	14,300.
June 9-July 2	.68	6,930.
Sagittaria		
Nov. 15-Feb 12	.19	5,800.
June 9-July 2	2.1	62,700.
N GRADIENT METHOD .040	ppm uptake, day-night	lbs/acre/yr Protein: [illegible]
DOWNSTREAM LOSSES		lbs/acre/yr dry [illegible]
3/4 mile downstream planktonic loss July 2	.112 mg/l (loss on ignition)	12,800.
Sagittaria clumps in gill net:		
March 25, 1953	286 gms. dry/hr	372.
March 30, 1953	312 gms. dry/hr	396.
RESPIRATION --BLACK BELL JAR	ppm decrease/jar/hr	lbs./acre/yr. glucose
May 14, 1953	.33	12,700.
May 25, 1953	.07	3,140.
	.22	9,400.
June 22, 1953	.71	18,180.
	77	18,740.
	1.24	58,400.
Mean		20,100.

Cage enclosure measurements

Further measurements have been made using the cage enclosure method of weighing wet and replanting. New data are included in table 6. Unfortunately two spring periods when the cloud cover is least and production is probably greatest are not represented because the big Pomacea snails found a hole in the small chicken wire and ate up the production. A second period was ruined by a Stenotheros turtle. (Parenthetically we note that under precisely known conditions of 2.8 ppm oxygen chicken wire lasts about 8 months; the opportunity to study corrosion under known conditions of oxidation potential and temperature should be obvious.)

The annual increase in growth rates of the Sagittaria indicated by the ten fold difference between January and June support the similar findings in the oxygen gradient methods in figure 7. To look at the community one would hardly guess that the ecosystem is turning over ten times as fast in the summer as in the winter and yet still is at the constant temperature of 23 deg C. The standing crop seems hardly to vary at all. The cage enclosure methods may give minimum results since the hardwarecloth top cuts out considerable light, and since the pulling up of roots diverts some growth energy.

Although not directly of interest in estimating the production in Silver Springs the estimates of growth rate of neuston, Pistia and hyacinths, have been continued. We think this is a powerful for estimating primary productivity in survey work in tropical areas. Where the temperature change in the air is not great either from week to week or from place to place, cages of neuston can be placed on unknown waters and a fertility value obtained in two weeks. The values of table 6 for Pistia indicate that in north Florida under air temperature conditions a climatic compensation point is exceeded only in the warm months.

As an additional check on other productivity measuring methods and in order to estimate respiration, the standard light-black bottle method has been adapted to the springs. Light and black bell jars were placed over typical areas of Sagittaria and its attached algae. A small tube leading from the center of the jar to the outside allows an oxygen sample to be drawn without disturbing the jar. The 100 cc used for analysis is small compared to the 12 liter capacity of the jar. Analyses are made about an hour apart so that changes in bacteria probably are minimized. The large surface on the plants included prevents the walls of the bell jar from having an appreciable effect. Smaller bell jars placed on the bare mud surface have been used to get some idea of the metabolism of the bacteria and diatoms on top of the mud. Again as in all springs work, the clear, relatively warm water permits intimate detailed work by hand with the face mask without the uncertainties of boat limnology. Results of bell jar measurements are given in table 6. These were calculated by refering the oxygen increase to the dry weight of the plants which were in the jar. Then this rate was multiplied by the average weight of plants per square foot.

It seems clear that the bell jar estimates are lower than the oxygen gradient method estimates. Although it is too soon to be sure, it is our inclination to regard the oxygen gradient figures as more correct. Blades of Sagittaria crumpled in a bell jar do not have fresh high nutrient water moved rapidly past as when they are waving in the current. Even so the similar order of magnitude by all these methods indicates that this at least is correct. Even in one hour some oxygen bubbles appeared at the top of the bell jar indicating underestimation.

The respiration rates from the bell jar experiments do not of course include respiration due to fishes.

Measurements of downstream loss

Further measurement of the amount of Sagittaria clumps drifting downstream have confirmed the magnitude of production loss due to this cause as given in table 7. Although impressive to the eye to see the endless stream of floating plants coming from an 18 acre producing area, this is not an appreciable part of the total production.

Having already noted that there was as little seston in Silver Springs water as perhaps any water in the world, we were astonished to find that although very small per liter that because the tiny plankton component breaking loose from the beds of plants was going downstream at the rate of 665 million gallons a day, a large fraction of the production was leaving the system hardly noticed as an occasional diatom, filament, or detritus fragment. The inference for lenitic limnology as discussed in the theoretical section of the first report is that stream productivities are probably on an acre basis among the highest even without allocthonous contributions.

One estimate of this invisible downstream loss was made by pouring 80 liters of water through a plankton net, drying in a crucible and ashing to get a loss on ignition as measure of the organic matter.

Dr. Nelson Marshall of the Oceanographic Institute Florida State University by running 12 gallon samples through his Foerst centrifuge obtained estimates of the chlorophyll going downstream. He found of course that all the values were extremely low but that water 3/4 mile downstream station contained .41 mg chlorophyll per cubic meter compared to a practically zero reading of .03 in the boil. If one uses a chlorophyll/organic mater ratio of .004 as in some Wisconsin lakes one obtains an organic matter content of .120 mg/l and a downstream loss similar to the one estimated from direct measurement as in table 6.

Silver Springs metabolic balance sheet

Although many estimates are as yet rough and tentative, it is now feasible to combine the various estimates to get an initial picture of the workings of the Silver Springs ecosystem and to locate contradictions and fallacies. First of all the uncorrected primary production rates must be corrected by adding the respiration rates for those hours during which photosynthesis was estimated. The respiration subtracted in the case of the oxygen methods is community respiration not just plant respiration.

If the hypothesis is correct that Silver Springs is in a steady state with no accumulation of organic matter or change in standing crop, then the following relationship must hold:

(corrected photosynthesis)-(total respiration)=(downstream loss)

$$\left(\begin{matrix}\text{uncorrected}\\ \text{production}\end{matrix}\right)+(\text{respiration})\left(\frac{\text{day hrs.}}{24}\right)-\left(\begin{matrix}\text{total}\\ \text{respiration}\end{matrix}\right)=\left(\begin{matrix}\text{downstream}\\ \text{loss}\end{matrix}\right)$$

The manipulations in Table 7 show that approximate balance is obtained with the lower estimates of primary production as in winter or in bell jars, for the calculated figures are then close to the observed estimates. For the high productivities, which must be real since they have been observed with more than one method, the calculated values are out of line with observed values. Whether this means that present measurement of respiration by bell jar is incorrect, that downstream loss is being underestimated, that organic matter is accumulated during summer and lost during winter, or that something else is wrong will have to be found from further investigations. It is interesting to notice the enormous values for corrected production even with observed respiration estimates. Where is this production going?

Table 7

Balance Sheet for Silver Springs

In each line two values are measurements and the one which is underlined is calculated by difference on the assumption of balance. All figures in pounds per acre per year.

Uncorrected Production:	Corrected Production:	Respiration: 24 hrs	Downstream Loss:	Agreement with Observed:
19,500 (bell jar)	29,550	20,100 (bell jar)	9,450	fair
----	62,700 (June) growth cage)	49,380	13,320 (June)	poor
71,400 (March, gradient)	129,480 (12 hrs)	116,160	13,320 (June)	none
24,500 (Dec. gradient,	30,090 8 hrs.)	16,770	13,320 (June)	none
71,400 (March, gradient)	81,450 (12 hrs.)	20,100 (bell jar)	61,350	none

A diagram for clarification of efficiency definitions

Because efficiencies mean so many things to different people, the diagram in figure 8 has been constructed to clarify definitions of three kinds of efficiencies at present in use in ecology. The diagram shows a community in steady state with the 1st and 2nd law of thermodynamics satisfied. The first is satisfied since the inflow energy and outflow energy are the same. The 2nd law is satisfied since most of the energy in each step is lost to heat since each step is a spontaneous irreversible energy transfer.

The first type of efficiency is the percent that the actual growth produced is of the inflowing food or radiant energy. This can be called the efficiency within the trophic level. On the diagram this is $\Lambda 2/E_2$ for example.

The second type of energy is the efficiency of energy transfer between trophic levels. This is the percent of the food produced which goes into the next step of the food chain instead of being "lost" to the reducers. In the diagram E_2/Λ_1 is an example. This efficiency between trophic levels can be considered 100% if one counts the reducers as part of the food chain.

The third type of efficiency is the percent that production at one level is of the production at the previous level. This food chain production efficiency is really the product of the other two efficiencies. An example on the diagram is $\Lambda 2/\Lambda 1$.

Relationship of standing crop to production rate

As shown in the diagram of Figure 8 the standing crop is the balance between the inflow and outflow rates so that there is a definite mathematical relationship when the system is in steady state.

Assume a simplified case as a model. Assume that all efficiencies within trophic levels (within organisms) are constant and equal (for example 10%). In this case the grams of standing crop are inversely proportional to the production rate per gram. There will thus tend to be many of those species with slow individual growth rates and few of those with rapid growth rates. Since the metabolic rate of organisms tends to decrease with size (Von Bertanlaffy, L.V. & J. Krywienczyk 1953. The surface rule in Crustacea. American Naturalist 87, pp. 107-110) the larger animals may tend to have higher standing crops relative to the amount of energy passing through the trophic level.

Productivity equation and photosynthetic quotients

The equation below is a summary or balance sheet for the process of primary production involving plant photosynthesis and growth, which are not separable in the ecosystem. This equation has been constructed using rough assumptions as to the ratios of elements in plankton from Fleming (1940, Proc. of 6th Pacific Science Cong. 3, pp. 535-539) and other sources. By means of the equation the large amount of oxygen that enters with nitrate becomes obvious. Under such an equation of either photosynthesis or respiration, the RQ is .73 due to a half protein composition and to the nitrate derived oxygen that does not show up in conventional means of measuring R.Q. If on the other hand protein growth were not appreciable the quotient would approach 1. The values for photosynthetic quotient observed in Silver springs were obtained from day curves of oxygen production and CO_2 uptake at the downstream station. The ratio of the curve areas indicates a photosynthetic quotient of .93 on Feb. 19 and .65 on March 26 possibly indicating a greater nitrogen metabolism at the later date. The estimated protein production of 14,500 lbs/acre/yr is consistent with a photosynthetic quotient between .65 and .93 and a total production of 30-50,000 lbs/acre/yr.

Eventually it will be possible by analyses of chemical composition of the plants to correct the equation above so that it fits Silver springs more than by assumption. Until this is done productivities obtained with oxygen measurements are reported as glucose rather than pounds calculated dry weight.

106 CO_2
+ 16 NO_3
+ 1 PO_4
+ 90 H_2O
+ 1,300,000 Calories radiant energy
+ 815 gms. minerals

→

Plankton (3258 gms)
106 C
16 N
1 P
180 H
46 O
minerals (815 gms.)
13,000 Calories energy content

+ 154 O_2
+ 1,287,000 Calories heat

WORK IN OTHER SPRINGS

Application of the analysis of variance to differential distribution of aquatic insects

by

William C. Sloan

In the first semi-annual report the scarcity of insects in spring boils as compared to spring runs was discussed. In order to substantiate those observations and also to determine the relative numbers of species and individuals per unit area, a standard collecting technique was devised and the resulting data were treated statistically by analysis of variance.

An area of the Homosassa run was chosen which was as nearly like the boil area as could be found. Five stations were then picked at random and at each station five sweeps each with a dip net and Needham scraper were made through one meter of vegetation. The same procedure was followed in the boil. The insects taken by different collecting methods were kept separate so that any variation could be tested for significance. Table 8 shows the mean number of individuals and species per twenty-five sweeps by both methods and for both areas. Standard deviations are also indicated. Analysis of variance for species and individuals is shown in table 9.

Analysis of variance showed the difference in both numbers of species and of individuals to be significant (P of species less than 3%; P of individuals less than 1%). The difference in methods of collecting was not significant.

Figure 5 seems to show that the number of dips used at each station was sufficient. At the three dip level, a 10% increase in number of new species is obtained for a 10% increase in sampling area; at the five dip level, only a 5% increase is obtained for a 10% increase in area. Five dips will continue to be the standard number.

This is believed to be of some importance since it now seems likely that quantitative differences in insect populations in the springs can be at least roughly measured without resorting to time consuming quadrat studies. Other quantitative methods for different types of habitats (logs, bottom) are being developed.

Table 8

		Boil		Run	
		Mean	St. Dev.	Mean	St. Dev.
Dip Net	# species	2.8	1.26	6.5	1.63
	# individuals	3.4	1.36	28.2	2.71
Needham scraper	# species	4.6	0.80	5.8	1.60
	# individuals	6.0	2.28	21.4	3.14

Table 9

Analysis of Variance

Source of variation	Degrees of freedom	Sum d^2	Variance	F value	P
between areas	1	31.25	31.25	6.146	< 3%
between methods	1	1.25	1.25	4.068	> 5%
residual or error	17	86.45	5.09		
total	19	118.95			
correction for mean	1	490.05			

Analysis of variance of number of species

Source of variation	Degrees of freedom	Sum d^2	Variance	F value	P
between areas	1	2020.05	2020.05	24.430	< 1%
between methods	1	22.05	22.05	3.750	> 5%
residual or error	17	1405.70	82.69		
total	19	3447.75			
correction for mean	1	4351.23			

Analysis of variance of number of individuals

Plan for the third half year

Dr. L. Whitford will complete a comparative study of the dominant algae in relation to the known differences in chemical media in ten to twenty of the most different springs during the summer. Mr. W. Sloan will complete his masters thesis on the relationship of insect numbers and variety to gradients of salinity and chemical stability in coastal runs. Main attention will be paid to completion of the metabolic understanding of Silver Springs, metabolism of organic matter, measurement of light intensities with community production, and rates of energy flow through higher trophic levels. As the imbalances in estimates for Silver Springs are resolved work will begin using the best of the techniques in comparing the varied spring productions in relation to their different chemical conditions such as N/P ratio. Plans will be made for subsequent check of production rates in these flow systems with P^{32}. As a corollary problem data will be accumulated next year on the seasonal reproduction variation in these constant temperature environments in relation to photoperiodic changes.