PRODUCTIVITY OF FLORIDA SPRINGS

NR 163-106

(NONR 580-02)

First Annual Report
(3rd semi-annual report)
to Biology Branch
Office of Naval Research
Progress from January 1 to December 31, 1953

by

Howard T. Odum

With sections by
Cailio Galindo
Bruce Parrish
Richard Pinkerton
William Sloan
Larry Whitford

Dept. of Biology
University of Florida
Gainesville, Fla.

CONTENTS

INTRODUCTION

Prepared by: Howard T. Odum with sections written by W.C. Sloan and Larry Whitford

NR: 163-106

CONTRACT: NONR 580 (02)

ANNUAL RATE: $5000 (4 years)

CONTRACTOR: Dept. of Biology, University of Florida Gainesville (with Biology Branch, Office of Naval Research)

PRINCIPLE INVESTIGATOR: Howard T. Odum (In the course of the original application this project became administratively listed under W. C. Allee, Head of the Biology Dept.)

Collaborators during current period:
John H. Davis, Dept. of Botany
Larry A. Whitford, N.C. State College, full time during summer 1953
Richard C. Pinkerton, Dept. of Chemical Engineering

Assistants:
William C. Sloan, June 1, 1952 to present
Osilio Calindo, June 1953, financed by Dept. of Biology
Bruce Parrish, June 1953, financed by Dept. of Biology
Wade Hampton, Feb. to May, 1953

TITLE OF PROJECT: PRODUCTIVITY OF FLORIDA SPRINGS

Objectives: A study of the basic factors controlling individual, population, and community productivity by an analysis of the unique conditions supplied by outflows from selected constant temperature springs

ABSTRACT:

a. During current report period (Jan. 1, 1953 to Dec. 31, 1953)

By means of new methods it has been possible to measure theover-all community metabolism as well as the standing state community in Silver Springs. Photosynthetic rates have been determined by downstream gradient methods, transplantation growth plots, and bell jars diurnally and annually. Respiration rates have been estimated with bell jars. The downstream losses of particulate, and dissolved organic matter have been found to balance the excess of photosynthesis over respiration. The community has thus been demonstrated to be in a constant temperature steady state somewhat comparable to a climax on land. Nitrate, phosphate, and major chemical constitutents are essentially constant. There is an approximate constancy of standing crop of organisms although the production rates in summer are three times those in the winter. Some evidence suggests that there are photoperiodic

changes in reproduction rates in spite of constant temperature. Rates of protein synthesis estimated from nitrate uptake downstream agree (1) with photosynthetic quotients obtained from carbon dioxide and oxygen uptake downstream and (2) with the nitrogen content of the community. The overall annual production of 50,000 lbs./acre is the greatest productivity we know of on land or sea. Such high figures seem reasonable with the flow of high nutrient, warm water, and high light intensity over a dense periphyton community. Theoretical concepts of stady state thermodynamics have been applied to show that self maintaining ope systems tend to adjust to high power and low efficiency output. The 3% photosynthetic efficiency observed in Silver Springs is in agreement with this principle. Pyramids of weight and pyramids of number have been determined including bacteria. These pyramids are similar to some in the literature. The contribution of an acre of a fertile stream annually is readily inferred from data obtained on downstream increase of bacteria, chlorophyll, and organic matter.

In other springs Mr. Sloan has related stability of insect populations to chlorinity and to gradients of stability of environmental factors. Dr. L. A. Whitford during the summer made an ecological and taxonomic study of the distribution of algae in 26 contrasting springs. From his lists and from analytical data on the chemostatic water in these springs one can infer culture conditions necessary for many species.

Where consistent with accuracy ~~necessary~~ to prove a point, some of the maximum accuracy that might be obtained is sacrificed in any one technique to permit the study of all aspects of the community.

b. Since start of project

This contract was begun June 1, 1952. In the first 6 months which preceded the current report period, the oxygen gradient and transplant productivity methods were developed. Maps were constructed and comparative chemical and biological data were obtained for 40 constrasting springs. Miscellaneous exploratory experiments were conducted as reported in the first progress report. Experiments begun earlier in the springs on chlorinity control of marine invasion were completed. Intensive work on Silver Springs was begun.

PLANS FOR FUTURE:

Immediate: Measure production rates of higher trophic levels:

a. periphyton animals by glass slide growth and succession rates on *Sagittaria* blades.

b. fish by tagging, visual tracing of colored tags, and recapture with gig; growth in cages

Construct a laboratory periphyton, flow-system, algal culture as a stream model.

Complete nitrogen picture with total nitrogen analyses; check some nitrate patterns.

Long Range: Compare production rates of different springs with the best of the techniques.
Compare production differences with chemical differences in the thermostatic chemostats.
Devise experiments to demonstrate relative roles of competition, incidence, time lag factors, and physical composition on community structure.
Compare productivities, efficiencies, and community structure of springs with other possibly steady state communities such as coral reefs, tropical streams and equatorial estuaries.

REPORTS AND PUBLICATIONS:

A study begun earlier but completed as part of this project:
Odum, H.T. 1954. Factors controlling marine invasion into Florida waters. Bull. of Marine Science of the Gulf and Caribbean, vol. 3, pp.134-156.

Stimulated by this project although not directly supported:
Laessle, A.M. 1953. The use of root characteristics to separate various ribbon-leaved species of Sagittaria from species of Valisneria. Turtox News, vol. 31, (12) Dec. 2 pp.

The second semi-annual progress report was distributed in July 1953. Because of the change in policy to an annual report system, copies of the 2nd semi-annual report are attached aspart of this report and referred to within to avoid duplication. Oral papers on aspects of springs work were presented at the AIBS, Assoc. of SE Biologists, and Fla. Acad. of Science meetings.

PROGRESS:

A. COMMUNITY METABOLISM OF SILVER SPRINGS

Nitrates

In the 2nd semi-annual report(p.4-5) is reported 145 nitrate analyses made with the laborious phenol-disulfonic acid method. These analyses had a high variability inherent in the method but established the general nitrate level, demonstrated a seasonal constancy, and a small downstream uptake statistically.

The strychnidine method for determining nitrates was then adopted with improved reproducibility and reduced cost. The pattern previously shown has been confirmed. The nitrate uptake is found to decrease both at night and during the day. This new data is summarized with the old in Table 1. Note the approximate constancy of the nitrates seasonally.

Table 1. Nitrate Analyses in Silver Springs in ppm

Day, time, sky	Boil: # of analyses	Boil: mean	3/4 mile downstream: # of analyses	3/4 mile downstream: mean
Strychnidine Method:				
Nov. 27, 1953 night (2:30 a.m.)	10	.463	10	.439
Oct. 22, 1953 day (2:00 p.m.) almost clear	10	.493	10	.374
Oct. 10, 1953 day (1:00 p.m.) clear	10	.401	10	.380
Phenol-disulfonic Acid Method				
April 9, 1953 day, noon, clear	10	.453	10	.330
May 8, 1953 night	10	.499	10	.468
May 14, 1953 noon clear	10	.462	10	.440
May 25, 1953 1:30 p.m. few cumulus	5	.40	5	.34
Mean		.457		.400

Phosphates

Additional inorganic phosphate determinations were carried out in Silver Springs. The data in Table 2 shows a small significant uptake of phosphate between the boil and downstream. (The possibility that the decrease of phosphate and nitrate is in part due to the entrance of different quality water from small side boils is now being checked.)

Table 2. Dissolved Inorganic Phosphorus in Silver Springs in ppm

Day, time, sky	Boil: # of analyses	Boil: mean	3/4 mile station: # of analyses	3/4 mile station: mean
April 9, 1953, noon clear	10	.0384	10	.0381
May 14, 1953, noon, clear	10	.0506	10	.0423
May 25, 1953, noon, few cumulus	5	.0462	5	.0446
Oct. 1, 1953, noon, broken clouds	8	.0621	8	.0587
Oct. 10, 1953, noon, clear	10	.0558	10	.0546
Oct. 22, 1953, 2:00 p.m., cumulus	4	.0498	6	.0430
Nov. 27, 1953, night	6	.0836	8	.0861
Mean		.0543		.0525

Nitrogen-phosphorus ratio, comparisons between springs

The downstream decrease of nitrate is .057 ppm and the downstream decrease of phosphorus is .0026. The uptake ratio is therefore 21.9/1 by weight if it can be assumed that the downstream decrease is entirely uptake. The ratio in the water is .457/.0543 or 8.4/1. Thus relative to the water the nitrogen decreases twice as fast as phosphorus and thus should limit first. Full confidence in this result cannot be placed until the contribution of the side boils is checked and the downstream organic nitrogen is measured. From Table 3 below it is interesting that Silver Springs has a higher N/P ratio than other springs analyzed. Thus nitrate-N may be limiting in many springs.

The very striking differences in the communities in the different springs in spite of similarities in the chemical composition of the major elements and similarity of temperature and light is one of the most fascinating aspects of the whole project. Constituents that might be responsible are nitrate-N and phosphate and the N/P ratio. There are wide and radical differences in N/P ratios. The adoption of the strychnidine method has permitted nitrate determinations on the high chlorinity springs as in some cases in Table 3. As a beginning to the comparative study of various springs (which is the main objective of next years study) some N/P ratios are shown in Table 3. Some idea of the large community differences can be obtained from Dr. Whitford's algal lists in subsequent sections below.

Table 3. N/P ratios in various springs

Spring, date	NO_3-N ppm	Inorg. P ppm	N/P by weight
1953:			
Juniper, Dec. 4.	.040	.024	1.66
Wekiva (Orange Co.), Dec. 4	.062	.132	.47
Ponce De Leon (Volusia Co.), Dec. 4.	.157	.052	3.00
Alexander, Dec. 3	.034	.050	.68
Silver Glenn, Dec. 3	.023	.022	1.00
Salt, Dec. 3	.060	.012	5.00
Homosassa, Nov. 1953	.080	.008	.10
Rock, Dec. 6, 1953	.112	.127	.89
Silver, mean of 300 analyses	.444	.0409	10.8
Weekiwachee, June 6.	.12	.018	6.7
Orange, June 6.	.22	.081	2.7
Sanlando, June 19.	.17	.172	.98
Blue (Alachua Co.), June 26.	.85	.092	9.2
Ichtucknee, June 9.	.40	.064	6.3

Light Intensity

Measurement of light intensities has just commenced, but some initial figures enable an estimate to be made of the magnitudes. Measurements were made with a submarine photometer obtained from Fred Schueler, 30 Albemarle Road, Waltham 54, Mass. containing a Weston photronic cell #594YR. A diurnal curve of light intensity at the surface and 8 ft. deep on a clear winter day is given in Figure 1 with light intensity expressed in microamperes as read. Approximately 1/4 foot-candles are equivalent to a microampere. As shown approximately half of the incident radiation penetrates to the photosynthetic surfaces of the community which are mostly in shallower water than 8 ft. The bed of plants is 2 to 3 ft. thick and 99% or more of the light reaching the plants is absorbed in the first 1 1/2 ft. When the photometer is inverted at the water surface no appreciable light intensity is measured so that 99% or more of the light is absorbed. Of the light incident on the water much is deflected by refraction and reflection in connection with ripples, for there is a strong flicker in the microampere reading when the wind ripples the surface. As is known in other waters the absorption in the first meter of the very clear water is not logarithmic. Further measurements are in progress to determine whether or not this water is more transparent than that in the Sargasso Sea. From the point of view of vertical stratification the largest intensity differences occur in the first meter. In Figure 1 note that the length of day at 8 ft. depth is only slightly shorter than at the surface even in the winter.

Photosynthetic Efficiency

At the same time that light was measured in Figure 1, the productivity was determined by the downstream gradient method of oxygen measurement as outlined in previous reports and corrected for simultaneous respiration on bell jar estimates. This production gives an estimate of 10 % of the incident light in the photosynthetic range is taken as 1/4 foot candles/microampere in Figure 2. If a calculated intensity is obtained for a clear day from Kennedy (1949. Computation of daily insolation energy. Bull. of Amer. Meteorol. Soc., vol. 30, pp. 208--213.), an efficiency of 3.2% is obtained. If the annual production of 50,000 lbs./acre is used with an annual insolation figure from Haurwitz and Austin (1944, Climatology, McGraw Hill.), 3.3% is obtained.

Photoperiodism

In an effort to understand how the greater plant production of spring and summer is translated into animal production without gross changes in the community, two series of measurements are being made as indexes to reproductive activity of two invertebrate populations. The percent of female shrimps (Paleomonetes) with eggs and the number of clumps of Pomacea (Ampullaria) eggs on 125 meters of rock and board walls which constitute one border of the boil area. Although incomplete there is data enough in Table 4 to suggest a definite photoperiodic pulse in breeding intensity although some breeding occurs winter and summer. At constant temperature it is very likely that the stimulus involves light directly or indirectly.

Table 4. Seasonal Variation in Egg Counts in Silver Springs

Date	Paleomonetes % of females with eggs	Pomacea # of egg clumps per 125 meters of shore
1953		
Oct. 1	79	227
Oct. 15	74	253
Oct. 22	-	194
Nov. 23	50	136
Dec. 19	27	105
Jan. 7, 1954	19	78

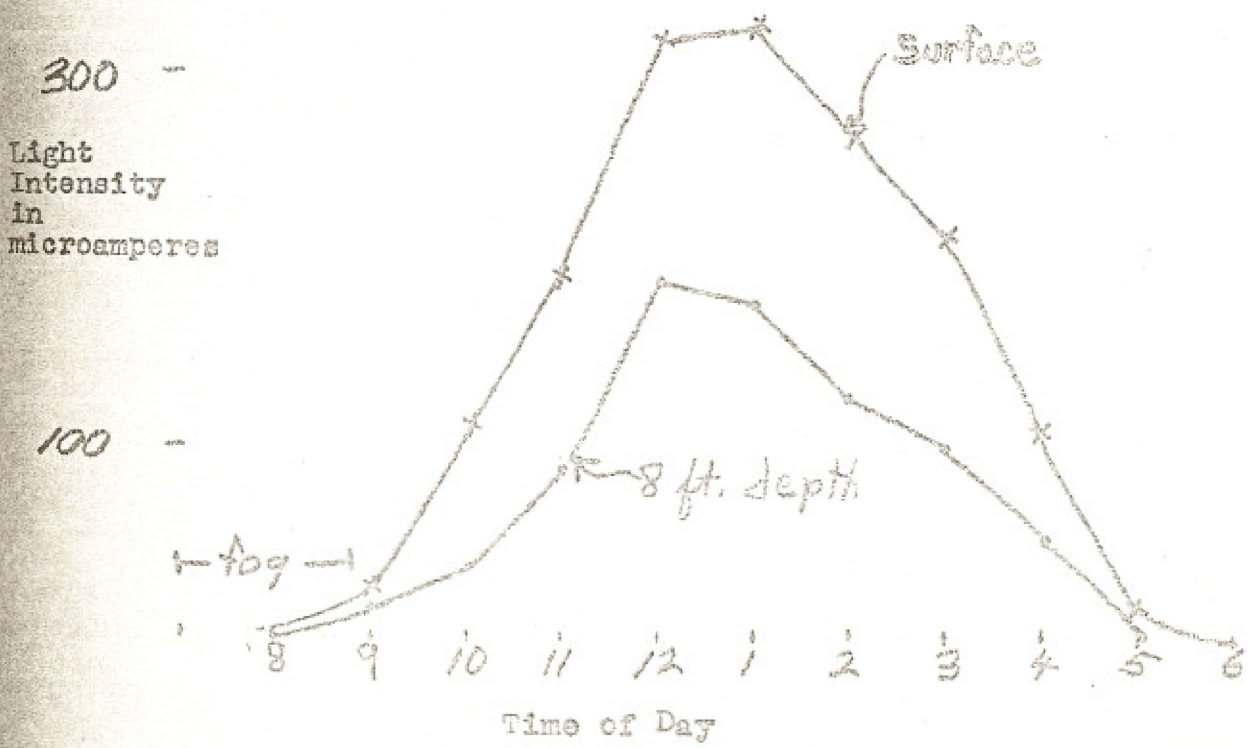


Figure 1. Diurnal March of Light Intensity in Silver Springs Dec. 19, 1953

Further measurements of production and respiration

The methods for measuring overall productivity by oxygen g adient methods, cage transplants, and bell jars were outlined in the first progress report and detailed data is reported from the early part of the current report period in the 2nd semi-annual report (attached) on pp. 16-21. Since that time two additional full day curves of oxygen and carbon-dioxide have been obtained which confirm the previous patterns. Some additional summer data is all that is now needed to show a detailed picture of the overall community production rates relative to annual changes in length of day and light intensity.

Another series of 6 black bell jar respiration measurements were conducted Nov. 28. This timerubber tube was used rather than copper (The use of copper was potentially a stupid blunder) for extracting water from inside the bell jars. As listed in Table 5 below, these measurements fortunately agree with the previous measurements on p. 19 of the 2nd progress report. The bell jar measurements were made during the day. In the first hour after the jars were lowered over the plants there was a net oxygen increase. This may be accounted for by the suggestion that oxygen diffused into the water from the tiny visible bubbles imbedded in the periphyton. In the second and third hour the oxygen decreases at about the same rate and it is these rates that are used as respiration estimates.

Table 5. Further Bell Jar Respiration Measurements

Time lapse between oxygen measurements in minutes	Oxygen decrease per hr. per jar ppm	lbs./acre/yr glucose*
108	.84	22,400.
95	.61	16,200.
106	.44	11,720.
90	.34	9,060.
114	.46	12,240.
92	.52	13,840.
	mean:	14,240

*If 1 ppm O_2 = .66 ppm dry weight instead of
1 ppm O_2 = .94 ppm glucose, mean respiration is 10,000 lbs/acre/yr

The diurnal curves of oxygen and carbon dioxide at the down-stream station on Jan. 7, 1953 again showed the lag between oxygen release and carbon-dioxide uptake. The oxygen curve follows the light curve with a rapid return to night values at sundown whereas the carbon-dioxide uptake reaches a peak later than the oxygen and does not return to night values until several hours after dark. Thus the timing of light and dark reactions of photo-synthesis show up even in this overall community respirometryy Peculiarly a phötosynthetic quotient greater than 1 was obtained.

Pyramids of weight and number

Quantitative estimates of the main community components were made and analyzed in the first part of this report period and are included on pp. 10-15 of the attached 2nd progress report. Included in this are estimates of bacteria. Further estimates of standing crop are planned.

Downstream losses from community production

A major part of work this fall has been an estimation of the downstream loss of production. As indicated in the balance sheet section below these estimates indicate that the overall metabolism estimates now roughly balance. Estimates of downstream loss include: BOD values, permanganate organic matter, bacteria, chlorophyll (by Nelson Marshall, Fla. State Univ.), particulate organic matter, and gross plant clumps. The BOD values were inconsistent and thus the permanganate method was adopted. These data were summarized in Table 6. It is quite clear that there is a very small downstream increase in content of organic matter which appears insignificantly small per liter until one multiplies by the large water discharge. It is then apparent that the steady downstream loss of organic matter mainly as invisible dissolved substances plus microscopic particulate organic matter is half of the production of the 3/4 mile headwater region (See Table 7). Just as in the terrestrial community, possibly the coral reef, or the lake, the community is adjusted to produce considerable excess organic matter over that needed to balance respiration.

Table 6. Changes 3/4 mile downstream

Measurement, method	Boil		3/4 mile downstream	
	# of analyses	mean	# of analyses	mean
Bacteria (Henrici Agar)	10	99/cc	10	988./cc
Chlorophyll (centrifuge and extract 10 liters, by Nelson Marshall)				
July 3, 1953	1	.03 mg/M^3	1	.43mg/M^3
Dissolved Organic Matter (Permanganate method, values in ppm O_2)				
Oct. 1, 1953	3	.54	3	1.10
Oct. 10, 1953	10	.69	10	.81
Oct. 22, 1953	5	.57	5	.62
Mean:		.603		.802
5 day BOD (values in ppm O_2 used up)				
Oct. 1, 1953	5	.15	5	-.04
Oct. 10, 1953	5	-.134	5	-.04
Particulate organic matter (plankton net concentrate of 84 liters)				
July 2, 1953	-	-	1	.11 mg/l.
Algal cells (84 liter concentrate)	1	2.2/cc	1	67./cc
Clumps of Sagittaria (dry weight)	-	-	3	296 gms/hr.

Long range stability

In 1861 Leconte visited Silver Springs and wrote a paper describing the optical effects observed and some aspects of the community. (Leconte, J. 1861. On the optical phenomena presented by the Silver Spring in Marion Co., Fla., Amer. J. of Sci., 2nd Series, vol. 31, pp. 1--12.) His description of the dominant plants as "water grass and moss-like plants" with blades 3-4 ft. long suggests that the community in its gross aspects is in the same condition as it was in 1861.

Balance sheet for Silver Springs

The estimates of dissolved organic matter lost downstream in Table 6 account for the excess of production over respiration. Thus the problem discussed in the 2nd progress report (p. 22) seems solved. The annual balance sheet is given in Table 7. Some further data will be obtained to check these estimates. Perhaps for the first time the overall community metabolism of a steady state natural community has been determined. It is both exciting and sobering to know that the community does not change radically so that data now obtained can be repeated by anyone later or made the basis for further work without repitition. Anything that one forgets to measure today can be measured tomorrow or next year. This reproducibility should permit rapid advances not possible in the successive studies in famous localities such as L. Mendota, L. Lindimere, and Linsley pond.

Table 7. Annual Balance Sheet For Silver Springs

	lbs./acre/yr.
Photosynthesis corrected for respiration	45,950.
with diffusion correction, approximately	50,000.
Respiration	15,100.
Downstream loss	
Clumps	590.
Particulate	13,320.
Dissolved	15,000.
unaccounted for	1-6000.
Protein production	20,800.
I.C.	.6-1.2

B. The Species of Algae and their Distribution in Florida Springs
by Larry A. Whitford, Department of Biology
N. C. State College, Raleigh

The dominant species of algae of the typical Florida spring and run are two species of blue-green algae and five or six species of diatoms. Plectonema wollei, a large filamentous blue-green alga is by far the most conspicuous. It is found to a depth of 30 feet in the boils, throughout the pools, and is abundant in the runs. Amphithrix sp. is more abundant in areas of lower light deep in the boils and in masses of vegetation. Plectonema forms extensive mats and clumps on sand, ooze and rock, and smaller masses occur in and on all types of aquatic flowering plants. On it and on the leaves of aquatics, Cocconeis placentula, Achnanthes lanceolata, Gomphonema longiceps, Gomphonema sphaerophorum and Synedra ulna, and its varieties, grow abundantly as epiphytes. These five species of diatoms, together with a few others account for, it is estimated, over one half the organic matter produced in Florida springs. Every leaf, stem, Plectonema filament, rock, or wood surface exposed to the sunlight for a few days has a complete cover of diatoms. Within a few weeks the layer is several cells thick. Light is the most important variable. The under side of leaves has only 10-15% of the number found on the upper surface. Surfaces within a plant mass likewise have much less, and although the water is exceptionally clear, numbers are greatly less in the deep boils (over 20 feet).

There is little difference in the dominant algae of boil, pool and run. The shallows of the pool and the edges of the run have more filamentous diatoms and green algae because they are not washed away as rapidly by the current, but the standing crop is little greater especially in beds of flowering plants. There is some shift in the dominants toward the filamentous diatoms Fragilaria, Melosira and Nitschia and the green algae Rhizoclonium and Spirogyra.

The dominants tolerate a wide variation in chemical conditions. Apparently very low dissolved oxygen prevents abundant growth of most of them in the boil, but in the presence of a few ppm of oxygen there can be a wide variation in nitrate, phosphorus, calcium, chlorides, total dissolved solids and hardness without any marked change in the flora. Growth of Plectonema is abundant where there is only a few parts of chloride per million and where there is nearly 200 ppm. Most of the dominant diatoms grow well at chloride concentrations definitely in the oligohaline range (up to 600 ppm).

The apparent complete absence of Plectonema in Manatee spring and its abundance in the very similar Fanning spring nearby cannot be explained unless it is due to oxygen deficiency in the former spring. Similarly, the factors which allow the growth of Hydrodictyon in abundance in a few springs and apparently prevent its growth in others are unknown. The same is true of the genera Vaucheria and Dichotomosiphon which are present and abundant in only a few springs. The genus Cladophora should be mentioned here also. As a gunus it should be placed among the dominants even in the salt springs. Since it is a very large genus, however, with species adapted to a wide range of conditions it is not listed as a dominant because no one species is abundant and widespread in the springs. Apparently one species is present in Silver spring, another in Wakulla, and still others in saline waters. An accurate knowledge of the species and their distribution might help determine some of the important factors bearing on algal distribution. Concentration of chlorides, and speed of current may be important here. The great diminution in amount of the species of Cladophora in Wakulla run between July 4 and August 1, 1953, cannot as yet be explained.

The quieter water at the edges of the spring pool and along the edges of the run support a much more varied flora than that of the boil and run channel. As pointed out above, there is no great variation in the species of dominants or their total abundance but the total number of species is much greater. Rhizoclonium is abundant only here, as are certain species of Spirogyra and other filamentous algae. The unattached filamentous diatoms and some single-celled and colonial green and blue-green algae are much more abundant or sometimes present only here.

There is no true plankton in the springs or their runs. There is, however, a considerable pseudoplankton or tychoplankton composed of microorganisms constantly being detached and carried down the runs. (See Odum, Second Semi-annual Report p. 22). That a true plankton flora would develop in the spring waters under pond or lake conditions is proved both by the floras of nearly lake waters with similar chemical composition and by a few cases where spring waters are impounded. An excavated boat basin about 150 feet long off Silver Springs run contains many phytoplankton species in such genera as Endorina, Dictyosphaerium, Ankistrodesmus, Kirchneriella, Micratinium, and Pediastrum. Very small embayments along other runs, and even the water in submerged boats indicate that a true, and rich, plankton flora would develop under empoundment.

The dominant algae of the springs and their runs constitute what seems definitely a permanent vernal flora. Widespread collections from more than ten springs at all seasons indicate almost no seasonal changes in dominance. There is possibly a migration upward in winter of shade species (see below) but this cannot, as yet, be definitely confirmed. Such genera as Microspora, Stigeoclonium, Oedogonium and narrow-celled species of Mougeotia which are abundant only in spring in most habitats are abundant in the springs the year round. No sexual reproduction in the common green algae has been observed at any season in boil, pool or swift run.

Certain species of algae in the springs seem definitely to be shade plants, since they are found only in deep boils or in masses of vegetation and since temperature is not a variable here. All the fresh-water red algae such as Audouinella, Compsopogon and Thorea belong here. Thorea has been collected in Silver Springs only at a depth of 30 feet or more. Amphithrix, Xenococcus and possibly a few diatoms are also shade forms.

The rapidity with which the dominant algae attach themselves to leaves, stems, and other surfaces is amazing. Planted glass and wood strips have several hundred diatoms per sq. mm at the end of five days. Observations of young and older leaf surfaces indicate that attachment is as rapid here, or more so. In about 15 days there is an average of 100% coverage one cell thick. Within a month there is a tangle of epiphytes several cells thick. The type of attachment surface is important and there is also a fairly definite order of attachment. On smooth surfaces such as glass or plastic strips, certain algae and Naias leaves Cocconeis placentula and Achnanthes lanceolata are the pioneers. On leaves, especially of Vallisneria and Sagittaria all three are pioneers with more Cocconeis than the others.

Next, Xenococcus and Pseudoulvella attach in considerable numbers but apparently are soon covered and greatly reduced in numbers. Gomphonema longiceps, G. sphaerophorum and Synedra ulna attach over the pioneer species and all remain in large numbers from then on. Among these the unattached filamentous diatoms become abundant. The chief ones are Fragilaria construens, F. capucina, Melosira italica and M. granulata. Several other diatoms and several green algae, especially species of Stigeoclonium, Microspora, and Oedogonium, make up a minor part of the permanent algal mat together with a few less abundant blue-green algae.

This permanent mat continuously loses cells to the flowing water but growth keeps it relatively uniform in thickness and composition. Deeper in the masses of vegetation and on the under side of leaves Cocconeis placentula is the chief diatom and Xenococcus and Amphithrix are present in some abundance. The total flora in the shaded areas is only about 5 to 15% of that on the top side of leaves or in better lighted areas.

Some study has been made of the types of algae attaching to other surfaces than plants in the springs. Bare wood is the most common such material. A rather wide variety of species are found on wood. Synedra is the commonest diatom along with Stigeoclonium, Rhizoclonium, Cladophora certain species of Spirogyra and Oedogonium in the green algae, and Phormidium, Lyngbya, and Chroococcus among the blue-greens.

Painted wood seems to have a much smaller variety of species. Apparently the chief ones are blue-greens such as Schizothrix that form tough gelatinous layers over the paint surface. In this mat the diatom Rhopalodia is sometimes abundant and a number of green algae such as Spirogyra and Oedogonium attach to it.

Iron surfaces seem to favor green algae although the diatom Synedra ulna attaches directly to iron. The genera Rhizoclonium and Stigeoclonium are most abundant together with the blue-greens Phormidium and Anabaena. Epiphytic diatoms on the algae attached to the iron are abundant.

A copper screen submerged in Silver Springs pool for several months had a surprisingly large amount of algae on it. All were green algae. The filamentous species, Microspora stagnorum formed a mat in which Sphaerocystis shroeteri, Scenedesmus obliquus, S. dimorphus, and S. bijuga were abundant. There were no other algae or epiphytic algae present. Apparently even in running water copper inhibits the attachment or growth of most species.

Changes in the algal flora down run are not marked where conditions are not modified by such things as shady banks, ingress of surface water, water from other springs, or sea-water intrusion. After the first mile Silver Springs run becomes narrow and the banks heavily wooded. It also receives some brown surface water down run. Consequently about 2 1/2 miles from the boil flowering plants largely disappear probably due to reduced light. Mats of Vaucheria, with some filamentous blue-green algae, and a few of the usually dominant diatoms, are abundant in the shallows. The deeper channel has relatively little plant life.

Wakulla run apparently receives some saline water from springs along it, with consequent modification of its flora toward the oligohaline type discussed below. Weekiwachee run soon receives considerable brown surface water and later sea-water from the Gulf. The diatoms at first dominant are replaced by others (Epithemia turgida and Synedra radians). Then as the run nears the Gulf a species of Rivularia becomes very abundant, and certain salt-tolerating diatoms such as Melosira borreri, Biddulphia sp. Stephanodiscus barkleyi, Nitschia paradoxa, and Cyclotella meneghiniana become abundant.

In the slightly salty (oligohaline) springs, and in the runs as they near the Gulf, the increase in salinity is first marked by the presence of the above-mentioned diatoms and not by the dropping out of typically fresh-water species. The only exception seems to be Plectonema wollei. It disappears when the chloride level exceeds 200 ppm. It is surprising to find, near the Gulf, typically fresh-water genera like Spirogyra, Oedogonium, and Mougeotia, abundant, and in healthy condition, along with typically marine genera such as Enteromorpha, Batotophora, and Polysiphonia. When such species as Cladophora graminea, Enteromorpha plumosa, and Cyclotella meneghiniana are common or abundant in the boil along with the usual fresh-water dominants it definitely indicates an oligohaline condition.

Two definitely saline springs have been studied; Salt Springs (chlorides 2,400 ppm) and Warm Salt Spring (chlorides 9,300 ppm). The first has several species of diatoms common to abundant which are dominants in the fresh-water springs. These are Cocconeis placentula, Gomphonema longiceps, and Achnanthes lanceolata. The chief dominants in Salt Springs are Enteromorpha plumosa, Cocconeis placentula, Licmophora flabellata, Nitschia paradoxa, and Melosira borreri. The algal flora indicates it should be placed on the border between oligohaline and brackish.

Warm Salt Spring, like the other springs, has a dominant algal flora of blue-greens and diatoms, but it does not have a single important species in common with any fresh-water spring studied. Both high temperature (86°F) and salinity are probably important, along with low dissolved oxygen. Dominant here are the blue greens Spirulina? platensis, Oscillatoria sp., Chroococcus limneticus; a single green alga, Chara hornemanni; and two diatoms, Amphora eulensteinii and Nitschia gandersheimiensis. Other important algae, especially in the run, are Vaucheria (a marine species), Nitschia linearis, and Cocconeis pediculus.

Collections from three "sulfur" springs have been studied. Sulfates are known to be high in two of them and all are characterized by a hydrogen sulfide odor and a very low oxygen tension (0.0 to 0.7 ppm). One is oligohaline. In all cases the dominant flora is filamentous blue-green algae, chiefly species of Phormidium and Lyngbya. A few diatoms, notably the ubiquitous Synedra ulna, are present. As the water moves down the run, it becomes better oxygenated and probably loses some of the dissolved sulfur compounds due to the action of the abundant sulfur bacteria. Within a short distance a species of Spirogyra becomes abundant, at first at the surface, and later on the bottom of the run. The blue-green species characteristic of the boil begin to drop off and are replaced by larger species of filamentous blue-greens chiefly Oscillatoria sp. and other species of Phormidium. The tolerant diatoms, Gomphonema longiceps and Eunotia pectinalis come in. Within a half mile (in Beecher Spring run) the flora is quite similar to that of the quieter portions of a typical run. The algae in deeper water, however, are still largely blue-greens. At the surface filamentous blue-greens are the chief dominants along with Cocconeis placentula and Gomphonema longiceps. It is worth noting that the species <u>Plectonema wollei</u> has not been collected in these springs nor their runs. After further oxygenation the entirely typical springs flora should certainly develop.

Apparently only fairly high salinity prevents any spring from supporting a rich algal flora in its lower run. These studies tend to confirm previous ones as to the high productivity of Florida Springs.

Detailed lists have been prepared for 26 contrasting springs. Some sample lists follow:

Number of Taxa (genera, species, varieties, forms) Identified from all Springs Areas

Chlorophyceae (green algae)	53
Cyanophyceae (blue-green algae)	32
Bacillariophyceae (diatoms)	66
Rhodophyceae (red algae)	4
other groups of algae	3
Total	158

Many species of filamentous green algae cannot be identified except when fruiting. Probably a total of 65 taxa or more present.

Many species of blue-green algae yet remain to be identified. The total will approximate 50 taxa or more.

Only a few species of diatoms remain unidentified. Probably 75 taxa are present.

Estimated total taxa inhabiting springs studied 190-200.

List of Algae in a Sulfur Spring and Pool
(Beecher Spring)

Phormidium sp.
Lyngbya sp.
Spirulina subsalsa
Aphanocapsa sp.
Synedra sp.
Navicula sp.
Spirulina gomontii
Chroococcus turgidus?
Aphanothece sp.
Gleocystis gigas?

List of Algae in a Salt Spring
(Warm Salt Spring)

Spirulina ? platensis
Amphora eulensteinii
Chara hornemannii
Oscillatoria sp.
Nitschia gandersheimiensis
Spirulina tenuissima
Aphanothece nidulans

Aphanocapsa stagnina
Chroococcus sp.
Phormidium sp.
Amphora coffaeformis
Amphora proteus
Achnanthes exigua
Navicula radiosa
Cocconeis pendiculus
Lyngbya sp.
Synechococcus elongatus
Amphiprora pulchra
Phormidium tenue?
Euglena sp.

List of Algae Typical of Most Springs and their Upper Run

The list is in approximate order of abundance, by volume of species. The first six species constitute 80-90% of the total average volume.

Cocconeis placentula
Synedra ulna (& vars.)
Gomphonema longiceps (& vars.)
Plectonema wollei
Achnanthes lanceolate var. elliptica
Gomphonema sphaerophorum
Amphithrix sp.
Fragilaria construens
Cladophora spp.
Spirogyra spp.
Rhizoclonium spp.
Nitschia amphibia
Cymbella spp.
Stigeoclonium spp.
Oedogonium spp.
Pseudoulvella sp.
Xenococcus sp.
Lyngbya spp.
Chara zeylanica (& fors.)
Vaucheria sp.
Hydrodictyon reticulatum
Mougeotia spp.
Microspora spp.
Scenedesmus spp.
Melosira spp.

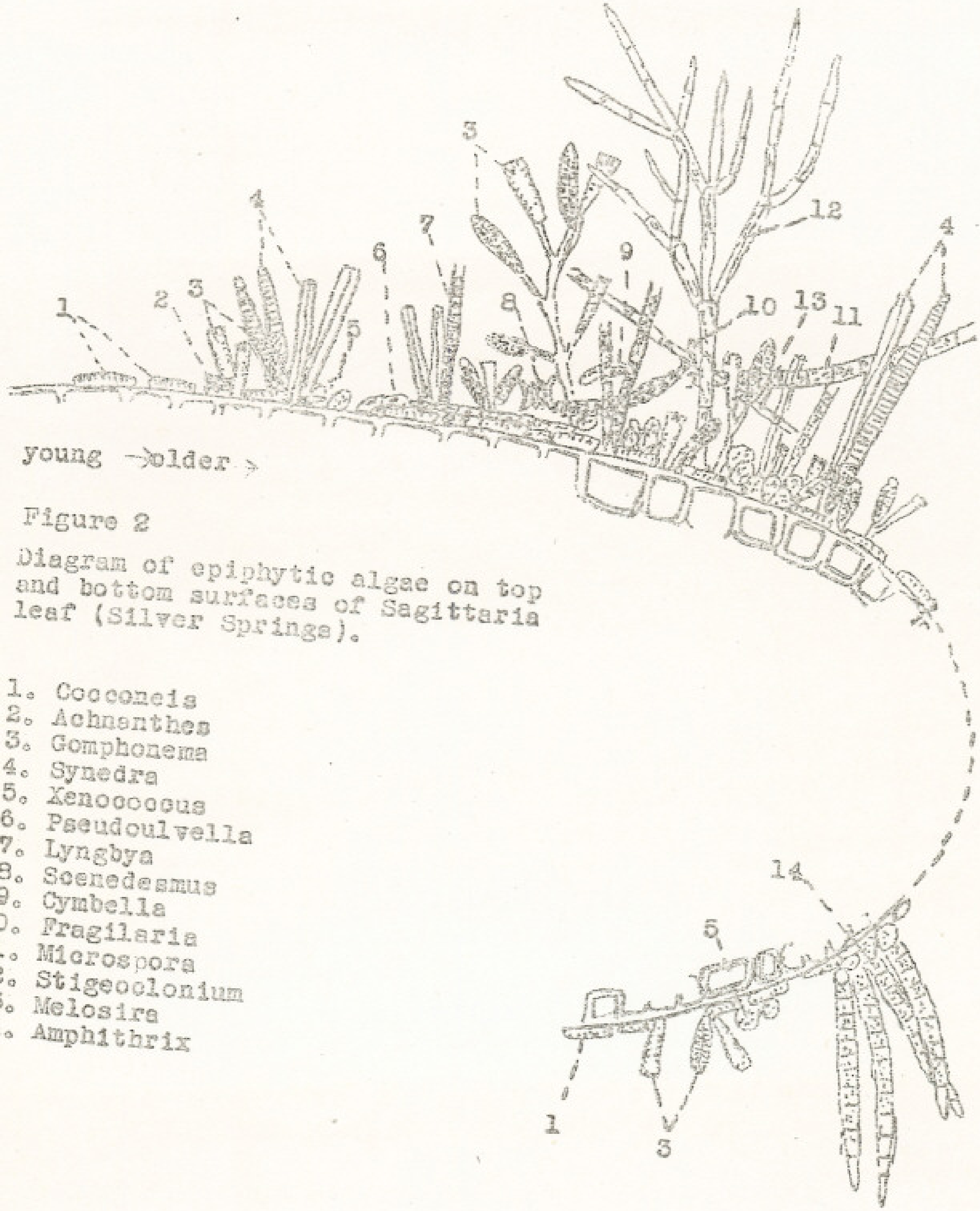


Figure 2

Diagram of epiphytic algae on top and bottom surfaces of Sagittaria leaf (Silver Springs).

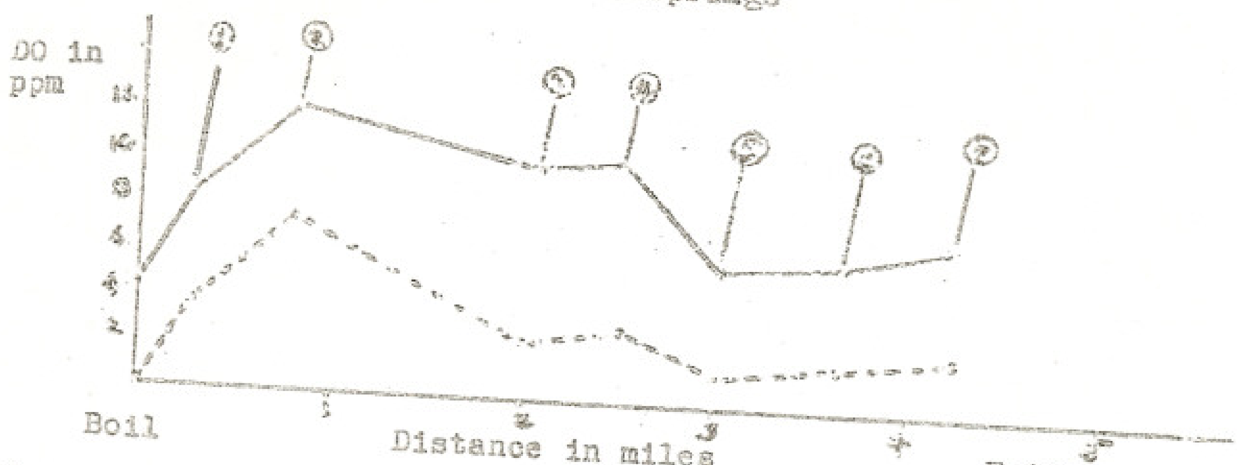
1. Cocconeis
2. Achnanthes
3. Gomphonema
4. Synedra
5. Xenococcus
6. Pseudoulvella
7. Lyngbya
8. Scenedesmus
9. Cymbella
10. Fragilaria
11. Microspora
12. Stigeoclonium
13. Melosira
14. Amphithrix

6. DISTRIBUTION OF AQUATIC INSECTS IN RELATION TO ENVIRONMENTAL GRADIENTS

In the previous semi-annual progress reports, patterns of insect distribution in Homosassa and Weekiwachee Springs were discussed. Variance analysis of this distribution showed that population density as well as species number increases with distance downstream from the spring boils. The decrease in species number as the estuaries are approached was also noted. It was suggested that this differential distribution is correlated with environmental gradients. Graphs of these gradients based on additional data are shown below.

Figure 3. Dissolved oxygen in parts per million. Maximum, solid line, range, dotted line. Maximum represents the mean value of DO samples taken throughout the year within two hours of the suns zenith. Range is the maximum minus the minimum values, all of which were taken before dawn. Each locus on the curves represents a collecting station which is designated by an encircled number.

a) Dissolved oxygen in Homosassa Springs



b) Dissolved oxygen in Weekiwachee Springs

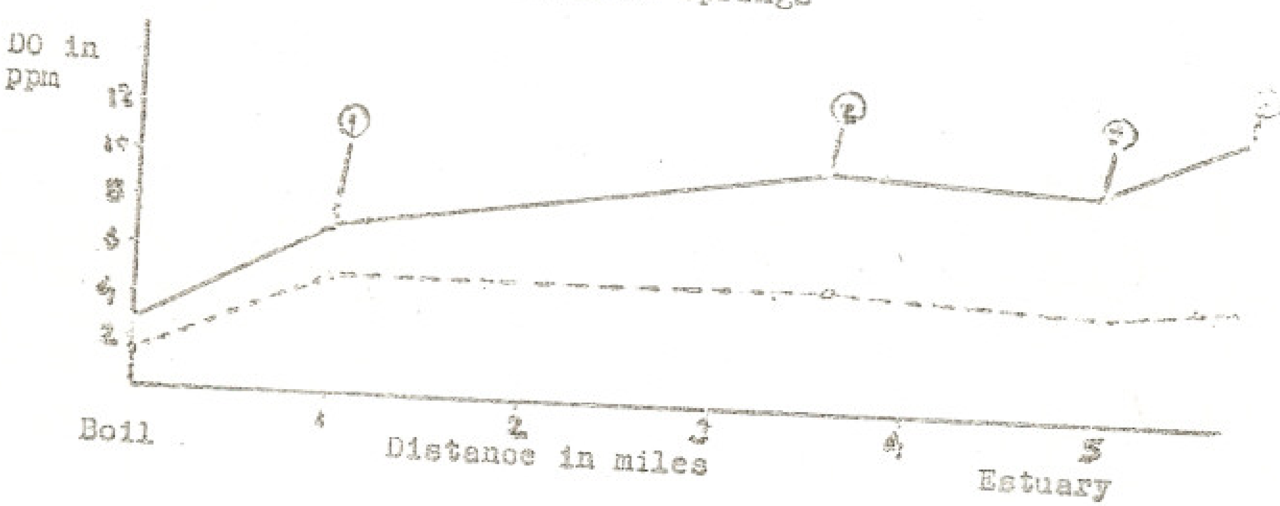
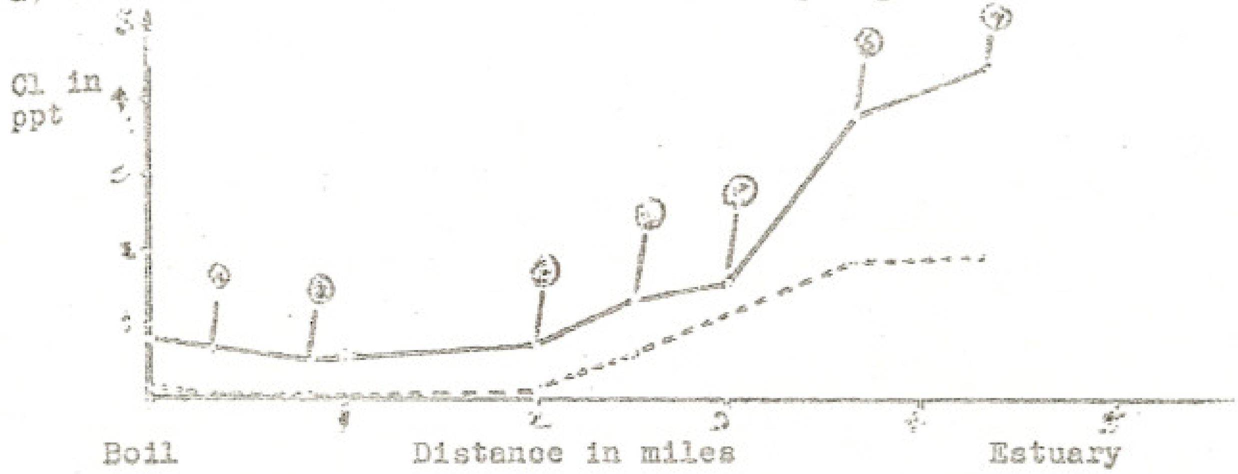
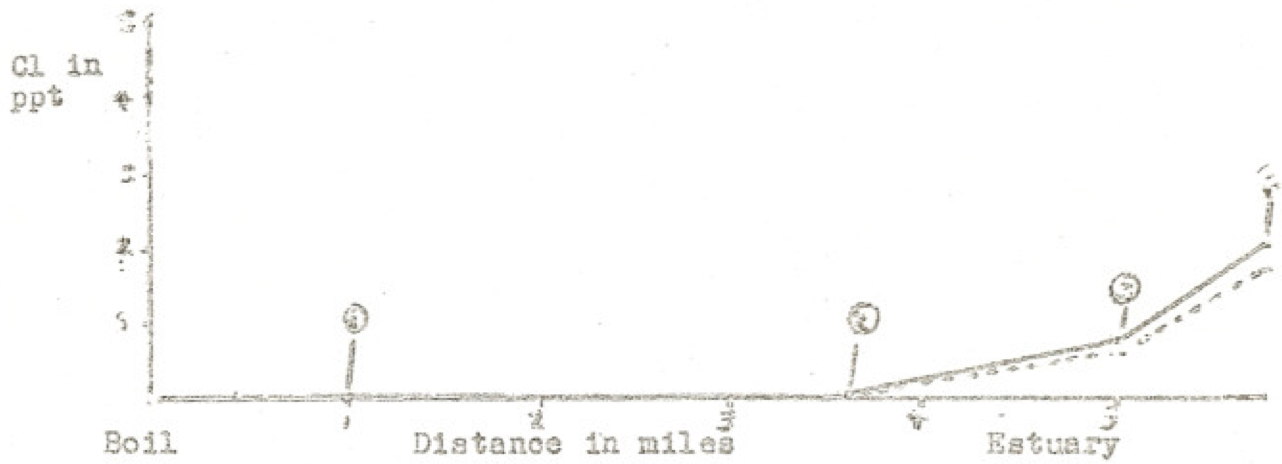


Figure 4. Chloride values in parts per thousand. Maximum = solid line, range = dotted line. Maximum is the mean value for chloride samples collected at high tide. Range means the difference between high and low tide values and thus shows the tidal effect.

a) Chloride concentrations in Homosassa Springs



b) Chloride concentrations in Weekiwachee Springs

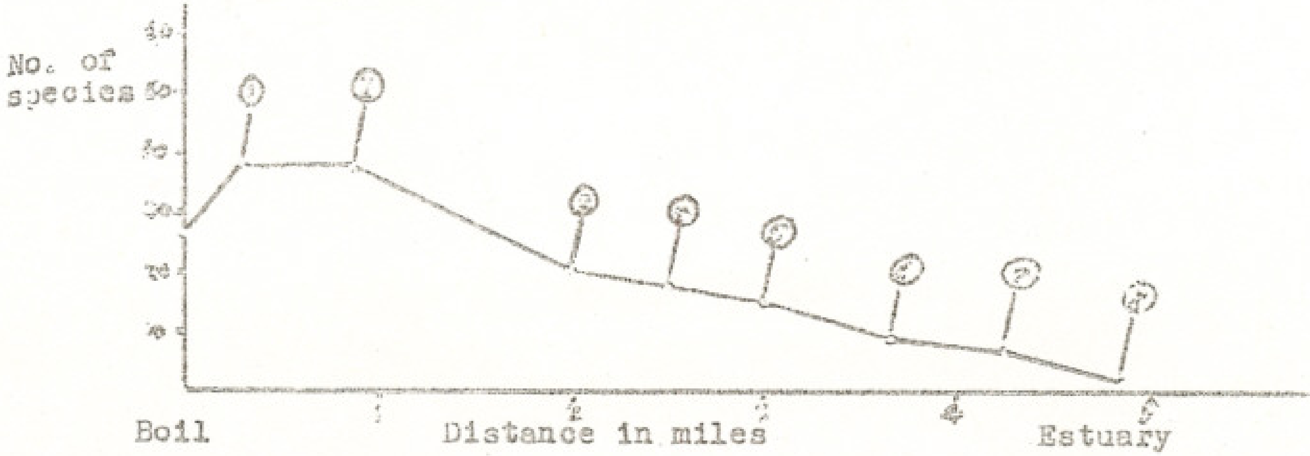


Species Distribution

The total number of species per station is shown below in figure 5. Table 2 shows the number of species per order for each station and total number of species for each spring system. No seasonal variation in species composition has been noted although not all of the data have been consolidated.

Figure 5. Number of species plotted against distance down run.

a) Homosassa Springs



b) Weekiwachee Springs

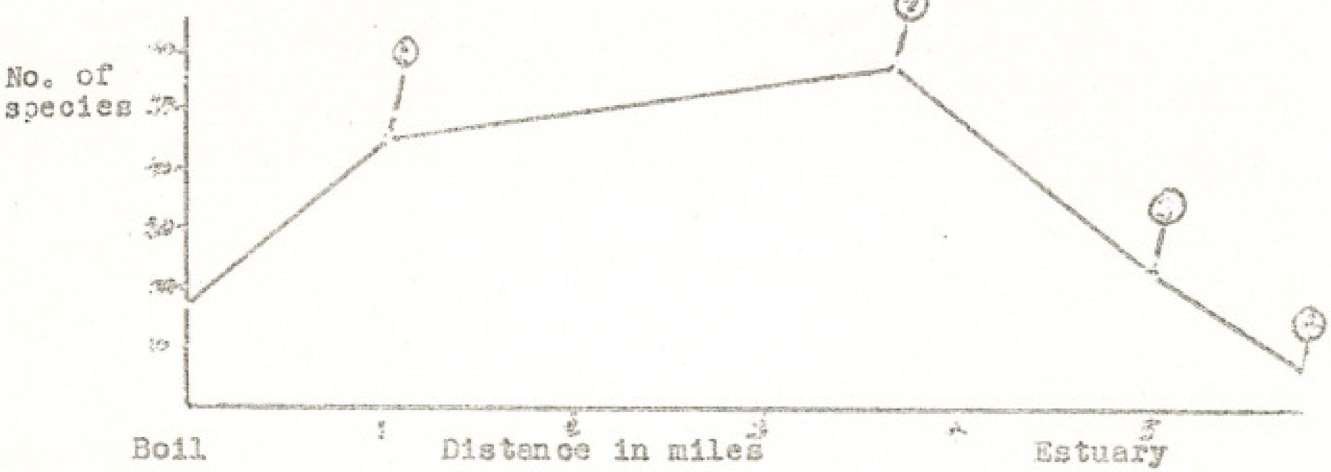


Table 8

Number of species per order found at each station and total number of species for each spring.

Order	Homosassa station number								
	Boil	1	2	3	4	5	6	7	8
Ephemeroptera	4	5	5	2	3	2	1	1	0
Trichoptera	9	9	9	7	1	3	0	0	0
Odonata	5	7	7	4	5	4	3	3	1
Diptera	4	9	7	8	5	5	4	2	0
Lepidoptera	1	1	1	0	0	0	0	0	0
Hemiptera	3	7	7	0	5	3	2	1	1
Coleoptera	1	0	2	0	0	0	0	0	0
Total	27	38	38	21	19	17	10	7	2

Total for river = 54

Order	Weekiwachee station number				
	Boil	1	2	3	4
Ephemeroptera	2	10	11	4	1
Trichoptera	1	7	15	10	2
Odonata	6	9	13	3	1
Diptera	4	7	8	5	3
Lepidoptera	0	1	1	1	0
Hemiptera	3	7	4	1	1
Coleoptera	1	4	3	0	0
Total	17	45	55	24	8

Total for river = 74

It is seen that curves for both maximum oxygen and oxygen range seem to resemble the species curves fairly well; at least in the upper parts of the rivers. It seems unlikely, however, that oxygen in excess of 6 or 7 ppm could affect the insect distribution although the low DO in the boil areas proper may be limiting. Investigations of other lotic systems have shown that large numbers of species are able to exist in situations whose DO content never exceeds 6 or 7 ppm.

It appears fairly certain that the increase in chloride content in the lower runs is serving to control insect distribution. It is difficult to determine, however, whether the total chloride concentration or the tidal effect is more important in this respect. In general, it seems that chloride concentrations in excess of 0.5 ppt may serve as a limiting factor. In waters containing more that 1.0 ppt chloride, typical brackish water forms are most common. Some of these are Enallagma durum (Hagen), Trochopus plumbeus (Uhler), and the brine fly, Ephydra sp.

Stability

The hypothesis that spring boil areas are stable was proposed in previous reports. Data on Homosassa and Weekiwachee Springs confirm this general pattern. The oxygen range curves seen in figure 3 are reflections of the stability of the environment; these show the boil regions to be the most stable parts of the systems. The extremely small seasonal changes in temperature in these regions as seen below also indicate stability in the headwaters.

	Boil	1/2 way down	Estuary
Homosassa	1	8	8
Weekiwachee	1	5	6

Seasonal range of temperature in degrees centigrade

Evidence of long term stability of insect populations is shown by the fact that the numbers of individuals per sample collected during different seasons in the boil areas of both rivers do not differ significantly. This is shown in the table below.

Table 9. Analysis of variance of number of individuals collected in boil areas.

Stations compared	Date	# sweeps	Mean # insects/5 sweeps	p value
Homosassa	April	25	3.8	>.05
Homosassa	Nov.	25	10.0	
Homosassa	April	25	3.8	>.05
Weekiwachee	July	25	7.4	
Homosassa	Nov.	25	10.0	>.05
Weekiwachee	July	25	7.4	

However, a significant difference is found in the numbers of individuals per sample collected at different seasons downstream.

If those species having the best chance for survival are those whose optima fall within the small range of environmental fluctuations exhibited by the boil regions, the difference in numbers of species between boil and downstream areas may be, at least in part, a function of this environmental stability.

Ordinarily, the reduction of species variety by limiting factors results in large populations of the few surviving species since these are now relieved of a certain amount of competition and predation pressure. This is not the case in boil areas where small populations of the existing few species is the rule. Possible population limiting factors were discussed in the first progress report and include available food and predation. An attempt will be made to evaluate the importance of these in the final report.

D. Productivity theory

Productivity measurements and atmospheric diffusion in streams

Heretofore where the gradient method of measuring productivity has been applied, atmospheric diffusion has been assumed to be constant during both night and day. Because the gradient flow method promisesto be of general applicability to springs, to coral reefs (Sargent, M.C. and T.S. Austin 1949 Organic productivity of an atoll, Trans. Amer. Geophysics. Union, vol. 20 (2), p. 245-249.), to estuaries, and to streams, it is necessary to consider the night and day changes in atmospheric diffusion as a further refinement. It may be expected that the rate of diffusion of oxygen into or out of a flowing system in the course of a 24 hour cycle will depend primarily on the oxygen concentration in the flow. It should be possible to determine the function relating the rate of diffusion of oxygen per area to oxygen concentration for a particular flow system so that thereafter a correction might be applied to production measurements in the same place.

Consider an average square unit area of stream community. Let P be the rate of photosynthesis, R the rate of respiration, D_1 the rate of diffusion of oxygen into the stream and O the oxygen concentration. Then:

$$dO/dt = P - R + D_1$$

If the difference between daytime and nighttime oxygen concentrations is very small then both R and D_1 can be assumed constant as has been done heretofore in the springs. Then the difference between day and night values of dO/dt is the productivity(uncorrected). dO/dt can always be evaluated by measurements at two stations on a flowing system at an interval of time between upstream measurement and downstream measurement to permit the water to pass.

If oxygen content is alternately supersaturated and undersaturated the oxygen concentration is momentarily in equilibrium with the atmosphere each day. At this time D_1 can be assumed zero and the rest of the equation evaluated using other measurements.

In springs or in the majority of streams which do not become supersaturated it is necessary to evaluate D_1 for a given section of stream with independent measurements of R and P with black bottle experiments, etc. For Silver Springs at night at the downstream station dO/dt is .5 ppm, which amounts to 68 mg/sq. ft./hr. Respiration based on bell jars is 18 mg/sq. ft./hr. Substitution in the above equation gives

$$D_1 = 68 - 0 + 18 = 86$$ mg/sq. ft/ hr when the oxygen concentration is 3.0 ppm and the temperature is 72 deg. F.

This calculation of course neglects fish respiration whose magnitude has yet to be determined.

The diffusion rate into Silver Springs during the day as the values at the downstream station reach 5 ppm may be expected to be less than at night when oxygen concentration is at 3 ppm. Using night values of diffusion as has been done in production measurements thus underestimates the production. The maximum error that could result assuming that nod diffusion in took place during the day amounts to 10,000 lbs./acre. The error is probably about half this.

Another kind of loss involving oxygen bubbles in the shallower water on summer days which rise to the surface without dissolving has been visually observed but not yet measured.

Timés ' Speed Regulator; The optimum efficiency for maximum power output in physical and biological systems

by H. T. Odum and R. C. Pinkerton (Dept. of Chem. Eng.)

Because the second law of thermodynamics does not indicate the magnitudes of rates of entropy increase, a general theoretical expression has been derived with the use of concepts of steady state thermodynamics to supply a"times speed regulator" to mathh "times arrow". Our proposition is that natural systems tend to operate at that efficiency which produces a maximum power output, which is less than the maximum efficiency. An expression relating efficiency and maximum power was developed which was applied to: (a) Atwood's machine, (b) a water wheel turning a grindstone, (3) one battery charging another battery, (4) a thermocouple running an electric motor, (5) a thermal diffusion engine, (6) the metabolism of an organism, (7) food capture by an organism for its maintenance, (8) photosynthesis, (9) a self sustaining climax community, (10) growth and maintenance of a civilization. The essence of the general derivation, and the application to a steady state community like Silver Springs is extracted from the manuscript and summarized below.

A driving process coupled to a driven process can be geared at one extreme of no work being accomplished in the driven process or at another extreme of so great a strain that the system is stopped. Both extremes, the first with 0% efficiency and the 2nd with 100% efficiency produce a zero useful power output. If power output in the form of growth and maintenance is at a premium in the survival of systemsin nature, they may be expected to be adjusted for an optimum efficiency that is not maximum. The expression for efficiency in terms of maximum power adjustment is derived below:

$$T\,dS/dt = J_1X_1 + J_2X_2$$

$$J_1 = (\ell + cf^2)X_1 - cfX_2$$

$$J_2 = -cfX_1 + cX_2$$

$f = X_2/X_1$ when $J_2 = 0$; When $X_1 = 0$ $J_2 = c\,X_2$

$J_1 = \ell X_1$ when $X_2 = fX_1$ and $J_2 = 0$

If $R = X_2/fX_1$

$$P_2 = cf^2X_1^2\ R(1-R)$$

$$E = P_2/P_1$$

at maximum power output (P_2 = maximum); $R = 1/2$ and

$$E = \frac{1}{2(1 + 2\ell/cf^2)}$$

The symbols represent the following:
J_2 is the output flux; X_2 is the thermodynamic "force" of the out process; J_1 is the input flux; X_1 is the input thermodynamic "force"; ℓ is the leakage giving the value of J_1 when J_2 is 0; c is the conductivity giving the value of J_2 when X_1 is 0; f is the factor of proportionality relating X_1 and X_2; E is the output efficiency; P_1 is the useful power input; P_2 is the usefu power output; t is the time; T is the absolute temperature; and S is the entropy. (For methods used see Denbigh, K. G. 1951. Thermodynamics of the Steady State. Methuen, London, 103 pp.)

Now let us apply this to an ecological steady state community like Silver Springs where the exergonic driving "force" is the absorption of radiation and the endergonic process is the maintenan and self replacement of the community. If all the power output is replacement, the maximum replacement and thus the maximum size that can be supported in steady state occurs when the thermodynamic force ratio adjustment (R) is 50%. One can visualize that a community not in climax would have a net growth output and thus would increase in density until its maintenance replacement requirement balanced death and dissipative rates at R = 50% Communities which did not follow this scheme might be expected not to have equal survival value. It is thus suggested that the largest size system that can be maintained in steady state on a given potential energy source is one whose replacement costs approach 50% of the power input. This result suggests that there is a definite ratio to be expected between standing crop and productivity(as empirically observed) that corresponds to that rate of entropy increase that results in maximum power. Similar ratios might be expected in widely variant types of communities.