ly shaded by jungle trees lie farther inland, in the area of heavier rainfall. This explanation would link the correlation between Monilia pod rot and sunlight with the already established correlation between Monilia and rainfall.

Effect of area of plantation in cacao and of area of land per tree

A highly significant negative correlation appears between yield and area of plantation in cacao. This is to be expected, for it is the relationship that usually exists between extensive and intensive agriculture. On small plantations, labor is likely to be more closely supervised than on large plantations, and maintenance is usually better. Many of the large plantations have large areas in cacao that are difficult to reach and are given no attention except at harvest time. There is, however, a tendency towards larger plantations in the inland areas and smaller ones nearer the coast; and, part of the effect attributed to plantation size may actually be the effect of other factors already discussed.

Most cacao in Ecuador is much too closely planted, and a reduction in the stand of trees per hectare might logically be expected to result in an increase in yield. In this analysis, however, this effect did not appear. The lack of correlation between area per tree and yield might be due to there not being enough plantations with sufficiently reduced stands to make a mathematical relationship appear.

Summary

An evaluation of certain factors affecting the yield of cacao in Ecuador is discussed. Among the factors considered are: amount of rainfall, incidence of witches' broom disease and Monilia pod rot disease, per cent of total sunlight falling on the cacao trees, area of plantation in cacao, and area of land per tree.

Correlation coefficients indicate a rather complicated interrelationship among rainfall, witches' broom disease and Monilia pod rot disease. A highly significant negative correlation is shown to exist between yield and rainfall, yield and witches' broom, and between yield and area of plantation. The data, however, indicate no correlation between yield and incidence of Monilia pod rot disease although Monilia pod rot disease is highly significantly correlated with witches' broom disease. An explanation is offered for this curious relationship as well as for the lack of correlation between Monilia pod rot and yield.

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THE DISTRIBUTION OF AQUATIC INSECTS IN TWO FLORIDA SPRINGS[1]

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Introduction

It has been previously noted (Berner 1950) that fewer species of immature aquatic insects are

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found per unit area at the sources, or boils, of spring-fed Florida rivers than in the rivers themselves. This phenomenon is by no means a local one. Ide (1935) found species gradients in the streams of Central Ontario as did Sprules (1947). Seurat (1922 *in* Brues, 1928) studied the species gradient in a large North African spring. These workers (with the exception of Berner) were investigating waters whose temperatures varied considerably even over small distances, and their conclusions that the insect distributions were in various ways correlated with temperature gradients were no doubt correct. Most Florida springs, however, by virtue of their large volumes of flow, maintain nearly constant temperatures over long distances from the sources. Solutions other than temperature gradients must therefore be sought to explain the distribution of insects in these springs. The present study is an attempt to determine qualitatively and quantitatively the extent of this differential distribution in two constant-temperature springs and their rivers, and to correlate the distribution patterns with measured environmental factors.

The constant-temperature springs of Florida provide their inhabitants with an environment of unusual stability. At any one point in a spring or its river the annual change in most measured chemical and physical factors is very small. The springs systems so far studied by H. T. Odum (1952, 1953, 1953a) indicate that they are, in fact, in steady states. This stability in time does not always, of course, extend to space; that is, gradients of certain environmental factors exist linearly in the rivers of the springs. The two major gradiently arranged elements whose effects were studied during the present investigation are chloride and dissolved oxygen.

The following terms will be employed throughout this paper. Since some of these are used in rather limited senses, their restricted definitions are given here.

Boil: that part of the spring, usually near the center of the pool, where the outflow actually occurs. This is generally marked by surface turbulence.

Pool: the remainder of the spring, or source, area.

Springhead: the area composed of the boil and its pool.

Run: the river of the spring.

Estuary: from the first part of the river to exhibit chloride fluctuations as a function of tidal effect, to the Gulf of Mexico.

Diel period: this refers to a section of time which includes one light (day) and one dark (night) period (Carpenter 1934 *in* Allee *et al.* 1949).

Throughout the following discussion, the term "springs" may be used to designate an entire river system. Whenever the source areas are specifically referred to, however, one of the above definitions will be used.

Methods

The springs chosen for study were Homosassa Springs in Citrus County and Weekiwachee Springs in Hernando County, both on the middle west coast of Florida. These were selected because of their contrasting features and because of their relatively short rivers which could be travelled by boat in the space of half a day. The proximity of both rivers to the Gulf of Mexico, into which they flow, provided an opportunity to study the effects of chloride gradients and fluctuations due to tides on the aquatic insect populations.

Collecting stations were established at points in the rivers where decided differences exist in the environmental factors under consideration. Figures 1a and 1b are maps showing locations of collecting stations on both rivers. Collecting was done with a dip net containing 25 meshes per inch and having a bag opening of 13 x 10½ inches, a Ward's Needham scraper with a ⅛ inch mesh, and three strainer buckets having 1⁄16, ⅛, and ⅜ inch mesh screens, respectively, and diameters of 9¼ inches. Collections were made at each spring about every six weeks from November, 1952 to February, 1954.

In order to determine the distribution of the various species in terms of occurrence frequency of their individuals, it was necessary that a reliable quantitative collecting method be devised. As quadrat studies in water of any depth are not necessarily accurate and are often very time consuming and since many of the forms encountered were vegetation dwellers which could easily be taken with a dip net, a prescribed number of dip net sweeps was taken as a composite standard sample. The number of sweeps necessary to obtain an adequate sample was determined in the following manner: By making single sweeps at random in the aquatic vegetation and then plotting the cumulative number of species collected against each increase in sampling area (successive sweeps), characteristic species-area curves were obtained. Three examples of these are shown in Figure 2. As can be seen, the curves have begun to level off to the left of five sweeps. The arrows indicate those points on the curves at which a 10 percent increase in sampling area results in only

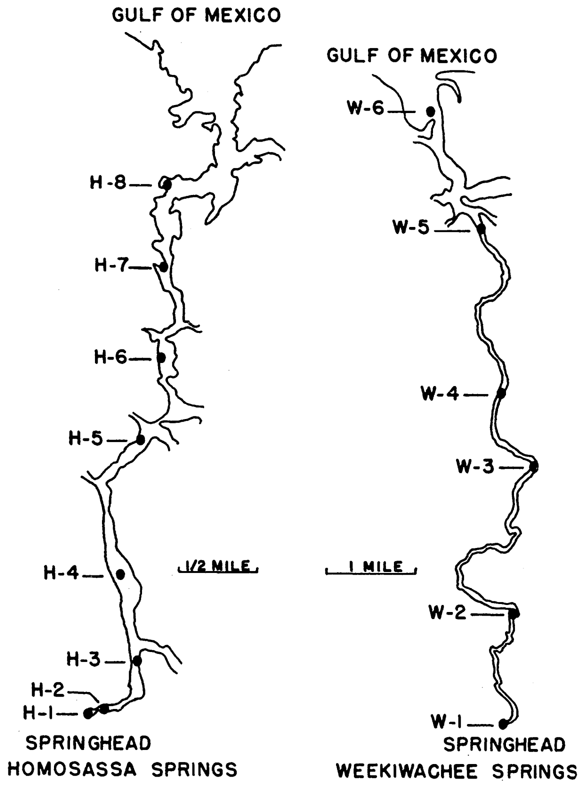

FIG. 1. Maps of (*a*, left) Homosassa Springs, and (*b*, right) Weekiwachee Springs, showing collecting stations. tions.

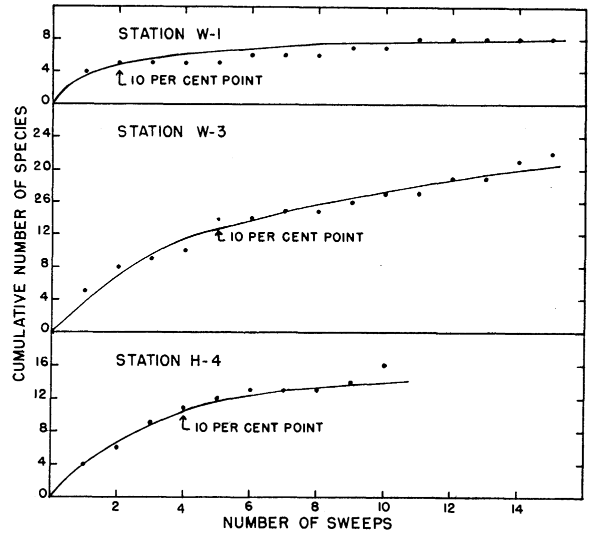

FIG. 2. Species-area curves showing minimum points of collecting adequacy.

a 10 percent increase in species number. This point was obtained by Cain's method (1938). It was assumed that sweeps in addition to five would be unprofitable and upon this assumption a five-sweep sample was adopted as the standard unit. Subsequently, when sampling quantitatively, at least five sweeps were made on each habitat. By applying analysis of variance to the data obtained in this fashion, it was possible to separate sampling error from actual variation in distribution.

Water temperature was measured with a standard centigrade mercury thermometer and was taken among the vegetation. Current velocity was determined with a Leopold and Stevens midget current meter and some values were also obtained from the U. S. Geological Survey, Surface Water Branch.

In order to determine the concentration of dissolved oxygen at maximum and minimum light intensity, water samples were taken among the plants during clear weather within the period 11 A.M. to 3 P.M. and before sunrise. The samples were fixed in the field and titrated upon returning to the laboratory. A test was made to determine the difference between results obtained using the Winkler method of analysis and the Rideal-Stewart modification of this method. Thirty water samples were collected from five stations in both rivers, and each method of analysis was used for half of the samples from each station. A total difference of 3.2 percent between the two methods was observed, with the Rideal-Stewart modification giving the highest values in all but one case. In view of this small difference and because of the slow procedure involved in the Rideal-Stewart modification, the Winkler method of analysis was employed throughout this study.

Chloride samples were collected at high and low tides as predicted by Coast and Geodetic Survey tide tables. Since samples were taken in the rivers and estuaries, however, and not on the coast, actual high and low tides were difficult to predict. Chloride analyses were made using the Mohr method.

The oxygen and chloride analyses were carried out as outlined in "Standard Methods for the Examination of Water and Sewage," 9th ed. (1946). Hydrogen ion concentration was measured by the color comparison method; bromthymol blue and cresol red were used as indicators. This was determined infrequently as other springs studies indicated that the pH variation with time at any one point was very slight.

HOMOSASSA SPRINGS

The Homosassa River has as its main origin Homosassa Springs, which is located on the Florida west coast in Citrus County about two miles west of U. S. Highway 19. It empties into the Gulf of Mexico after flowing five miles successively through mesic hammock, swamp, and coastal marsh. The boil area is utilized as a tourist attraction but neither swimming nor boating is allowed in this part of the river and consequently it is relatively undisturbed. An interesting feature of the boil is the large number of marine fish that congregate there. Odum (1953b) has suggested that these fish enter the boil from nearby feeding areas which are somewhat lower in chloride concentration and that the result of this movement may be a replenishing of their salt supply. At no point sampled in the entire river system does the chloride concentration fall below the lower limit of the oligohaline range (0.1 to 1.0 parts per thousand), and in the boil area the mean value found during this study is 0.74 $^0/_{00}$. The dissolved oxygen concentration in this region remains about 5 parts per million with extremely little variation during a diel period.

Around the edge of the pool, station 1, the dominant rooted aquatic plants are *Vallisneria neotropicalis, Potamogeton pectinatus* and *Najas guadalupensis* in that order of abundance. This part of the spring is scarcely disturbed by the current. As the water flows from the pool into the narrow channel, which at this point is about 15 yards wide, the current velocity approaches 0.5 ft/sec and the vegetation changes to predominantly *P. pectinatus*. Here *V. neotropicalis* and *N. guadalupensis* are found only in scattered patches. Up to this point, the bottom is composed about two and a half feet. The bottom now becomes softer and contains a large amount of partially decayed plant material which has a faint odor of hydrogen sulfide. Within one-half mile from the springhead, the current velocity has subsided to less than 0.3 ft/sec, the chloride concentration has become reduced to about 0.5 $^0/_{00}$ and the average dissolved oxygen has increased to approximately 7.5 ppm. The vegetation is composed mainly of *V. neotropicalis* having heavy epiphytic algal growths; smaller amounts of *P. pectinatus* are found in the deeper parts of the run. The width of the channel increases to about 150 yards. The river continues its broad, slow course with little apparent change for about one and one-half miles. The swamp through which the river has been flowing now rapidly gives way to saw-grass (*Mariscus jamaicensis*) marsh. This is probably the most inland part of the river to receive tidal water; the chloride concentration shows a daily fluctuation for the first time. At about this point, the water becomes more turbid; this turbidity increases downstream to the Gulf. The bottom here is composed of finely divided black silt, probably organic in origin, and the odor of hydrogen sulfide in the bottom material is considerably stronger than it was further upstream. The dominant rooted aquatics are *P. pectinatus* and *N. guadalupensis*. Within one mile the saw-grass is replaced by blackrush (*Juncus roemerianus*) and the silt, which was found overlying a very soft mud bottom in the saw-grass area, is now underlain by marine shell deposits. *Potamogeton pectinatus* is still the dominant rooted aquatic but *N. guadalupensis* and *V. neotropicalis* are found in small patches. These conditions persist for approximtaely two miles and then the marine alga *Sargassum* sp. becomes common and rooted aquatics disappear. This area is the farthest downstream from which collections were made. Table I summarizes the major physical features of each station in the Homosassa River. Current velocity refers to average surface velocity in the channel. The stations may be located by referring back to Figure 1a. The detailed data on chloride and dissolved oxygen concentrations, current velocity among plants, and pH may be found by consulting the section on Enviromental Features.

Weekiwachee Springs

This spring is located in Hernando County about twenty-five miles south of Homosassa Springs. The Weekiwachee River winds through nearly fourteen miles of scrub, swamp, and coastal marsh before flowing into the Gulf at Bayport, a resort village.

The springhead is situated about 100 yards west of U. S. Highway 19, and, like Homosassa, serves as a tourist attraction. Swimming is allowed in one section of the pool but this is confined to a small area some distance from the collecting station (station 1) and thus probably has little or no disturbing effect. The major features of this river system are in sharp contrast to those of Homosassa. The pool area is only sparsely covered by plants, the dominant rooted aquatic being *Sagittaria lorata*. The water movement to which the collecting site at the pool is subjected is that from the backwash of the boil. This is very slight. Unlike Homosassa, the chloride content is quite low in this area. The average concentration recorded during this study was 0.007 $^0/_{00}$, which is considerably below the oligohaline range. The dissolved oxygen has never been known to exceed 2.5 ppm in any part of the collecting station at the springhead, but, unlike Homosassa, may vary as much as 1 ppm during a diel period. The bottom is composed of firm, white sand not noticeably different from that of Homosassa except for color.

Two miles below the springhead the mean dissolved oxygen concentration has increased to about 4.5 ppm. The current is about 1 ft/sec and this remains nearly constant from the pool outflow

TABLE I. Major environmental features of the collecting stations in Homosassa Springs. The abbreviations V. n., P. p., and N. g. stand for *Vallisneria neotropicalis, Potamogeton pectinatus,* and *Najas guadalupensis,* respectively

Station and miles from Boil	Dominant Submerged Rooted Aquatics			Temperature °C		Current Velocity (Surface of Channel)
	Order of Dominance	Percent Bottom Covered	Bottom Composition	Extreme Maximum	Extreme Minimum	Feet/Second
H−1 (0)......	V.n., P.p., N.g.	30	Fine yellow sand	23.3	22.5	Less than 0.01
H−2 (.20)....	P.p., N.g., V.n.	50	Above type plus areas topped with organic detritus	24.0	22.8	0.53
H−3 (.70)....	V.n. with heavy algal growth	40-50	Sand and silt topped with organic detritus	24.9	22.0	0.27
H−4 (1.5)....	P.p., N.g., V.n.	70	Sand topped with fine black silt. H_2S odor	26.2	23.9	0.13
H−5 (2.0)....	P.p., N.g., V.n.	30	Organic detritus and black silt. H_2S odor	27.8	20.0	0.19
H−6 (3.0)....	P.p., V.n., N.g.	15	Black silt merging into silt-covered shellbar	29.0	19.0	Less than 0.01
H−7 (4.0)....	P.p., V.n., N.g.	10-15	Shellbar covered with black silt. H_2S odor	29.0	18.5	Less than 0.01
H−8 (4.5)....	Sargassum sp.	5-10	Shellbar covered with black silt.H_2S odor	....	17.5	Less than 0.01

to the estuary. The channel width varies from approximately thirty to fifty feet for the entire course of the river. The average depth of the entire run is estimated to be about five or six feet. The dominant rooted aquatics are *S. lorata* and *Najas guadalupensis* and the bottom ranges from firm, white sand to soft, black silt and organic detritus. Six miles down the run (station 4) the situation is much the same except that *N. guadalupensis* has replaced *S. lorata* as the dominant rooted plant, and the average dissolved oxygen concentration has increased to 7 ppm.

The next noticeable change occurs starting at a point about nine miles from the springhead. Here the tidal effect, as evidenced by increasing chloride concentrations, first becomes obvious. This is reflected in the changing vegetation. *Potamogeton pectinatus* first appears and *S. lorata* slowly becomes replaced with *Vallisneria neotropicalis* while *N. guadalupensis* becomes increasingly sparse. The swamp, through which the river has been flowing, changes abruptly to saw-grass marsh which merges quickly into black-rush marsh. The bottom ranges from white sand to soft, brown silt. The river now enters the area of estuarine conditions where *P. pectinatus* is dominant, although *V. neotropicalis* and a small amount of *Najas* are still found. The current slows to less than 0.1 ft/sec as the estuary broadens, and the depth is reduced to three to four feet. The bottom now consists of sand mixed with finely divided, black silt which has a strong hydrogen sulfide odor. Just before the open Gulf is reached, *P. pectinatus* is replaced with *Ruppia maritima* and the other rooted aquatics disappear. At high tide, the chloride concentration here (station 6) approaches one third that of sea water.

The major physical features of each station in Weekiwachee Springs are shown in Table II and the stations may be located in Figure 1b. The chloride and dissolved oxygen concentrations for each station are discussed and graphed in the section on Environmental Features.

Major Environmental Features

The major environmental factors studied during this investigation were concentrations of dissolved oxygen and chloride. Gradients of these are present in both river systems but differ considerably in each. Temperature and pH were measured only occasionally since a study made by the Florida Geological Survey (Furguson *et al.* 1947) indicated that these features are remarkably constant for springs in general. Current velocities were measured infrequently. The five environmental factors cited above will be discussed in the following paragraphs.

Homosassa Springs

DISSOLVED OXYGEN. Figure 3 shows the mean dissolved oxygen and the change in dissolved oxygen concentrations at the collecting stations in the Homosassa River. Mean dissolved

TABLE II. Major environmental features of the collecting stations in Weekiwachee Springs. The abbreviations S. l., N. g., P. p., V. n., and R. m stand for *Sagittaria lorata, Najas guadalupensis, Potamogeton pectinatus, Vallisneria neotropicalis,* and *Ruppia maritima,* respectively

Station and miles from Boil	Dominant Submerged Rooted Aquatics: Order of Dominance	Dominant Submerged Rooted Aquatics: Percent Bottom Covered	Bottom Composition	Temperature °C: Extreme Maximum	Temperature °C: Extreme Minimum	Current Velocity (Surface of Channel): Feet/Second
W−1 (0)......	S.l. with some epiphytic algae	10-15	White sand covered sparsely with plant detritus	24.0	23.2	Less than 0.01
W−2 (2.0)....	S.l., N.g.	30	From firm white sand to black silt and detritus	25.3	23.3	0.90
W−3 (6.4)....	N.g., S.l.	45	Same type as W−2	26.0	19.0	0.90*
W−4 (8.5)....	N.g., S.l.	30	Same as W−2 except silt lighter in color	28.0	18.0	0.72
W−5 (11.7)...	P.p., V.n., S.l. (drops out in this station), N.g.	15-25	From fine white sand to brown silt	28.0	....	....
W−6 (13.6)...	V.n., P.p., N.g., small amount of R.m.	30-40	Sand mixed with black silt. H_2S odor	30.8	15.7	Less than 0.01

*Average of USGS cross-sectional values.

oxygen is the average of mean day and night values and dissolved oxygen change is the mean day minus the mean night value. Figure 3 also shows all of the actual values recorded at the stations.

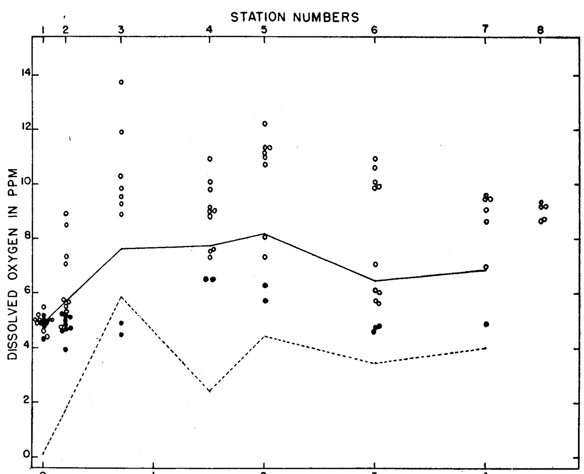

FIG. 3. Dissolved oxygen concentrations in Homosassa Springs. Black points are night values, open points day values. Solid line, average of mean-day and mean-night values; dotted line, difference between mean-day and mean-night values.

The dissolved oxygen concentration of the boil and pool is relatively high compared to springs such as Weekiwachee and Silver (Odum 1953). No value below 4.3 ppm was recorded from this station (station 1) during the study. Like the headwaters of many other Florida springs, a striking feature connected with dissolved oxygen is the nearly constant concentration exhibited through a diel period. Apparently the water, which has just emerged from subterranean crevices and is fairly homogeneous with respect to dissolved oxygen concentration, is not in contact with the plants of the pool area for a sufficient length of time to allow an increase in dissolved oxygen content due to photosynthetic activity to occur. Similarly, during the dark period, the respiration effect is not reflected in a dissolved oxygen decrease.

As the channel narrows and approaches station 2, the water becomes more turbulent and diffusion may take place more readily. The rooted aquatic plants increase in density and the photosynthetic and respiratory potentials per unit area thus increase. These three effects, diffusion, photosynthesis, and respiration, are reflected in the higher average dissolved oxygen concentration and a larger change per diel period. The environment here, at least with respect to dissolved oxygen, is decidedly less constant than that of station 1.

At station 3, there is no turbulence and the current is so slight as to be immeasurable by the method employed. The growth of rooted aquatics is heavy and the epiphytic algal growth is extremely dense. These algae, mostly *Cladophora* sp., sometimes completely cover the upper side of the leaves of *Vallisneria* plants, which are dominant at this station. Although growths of epiphytic algae are common in most parts of the run, they are no-where else nearly so luxuriant as at this station. Among the plants, dissolved oxygen is sometimes found in concentrations exceeding 13 ppm and it is at this station that the most variable dissolved oxygen concentrations have been recorded per diel period for the entire river system.

At station 4, the mean night dissolved oxygen concentraton is considerably higher than that of station 3 while the mean day dissolved oxygen content is lower. The fluctuation in dissolved oxygen concentration is thus less than at station 3.

At station 5 the average dissolved oxygen concentration is higher than at station 4. The rooted aquatic coverage is less as is the epiphytic algal growth, so the increase is probably not a function of local photosynthetic activity. The current is comparable to that of station 4 and there is no observable turbulence.

Station 6 has generally lower dissolved oxygen concentrations than the preceding station. The smaller values may be a function of the increased salinity (Sverdrup *et al.* 1949), the larger amounts of organic matter as evidenced by the increased turbidities, the decrease in aquatic plant density, or a combination of these. The diel change in dissolved oxygen is somewhat less than at station 5 though not markedly so.

The tendency toward lower dissolved oxygen concentrations seen at station 6 continues through stations 7 and 8 (see Figure 3). Due to the difficulty of reaching station 8 before sun-up, minimum dissolved oxygen values were never obtained from that area; however, the diel change in dissolved oxygen is probably about the same as at station 7.

CHLORIDE. Figure 4 shows the actual chloride values recorded at each station. These are enclosed in histogram fashion so that the extent of fluctuation may easily be seen. Although most of the chloride samples were taken at high and low tides as given in the U. S. Coast and Geodetic Survey Tide Tables, these designations apply only to the point at which the estuary meets the Gulf. Consequently, there is considerable lag between apparent and actual tide stages in the estuary itself. At stations 7 and 8, high tide water was apparently never sampled although several attempts were made to do so, and the tidal fluctuation is no doubt greater than is shown in Figure 4. The maximum chloride values from these stations are not known but it would seem that they should be in excess of those at station 6, whose maximum recorded value was 5.1 $^0/_{00}$.

At the river's source, station 1, the chloride content averages 0.74 $^0/_{00}$. This high concentration comes from ground water and is not due to marine tidal invasion (Odum 1953b). The fluctuation in concentration is probably due to dilution of groundwater after periods of rain.

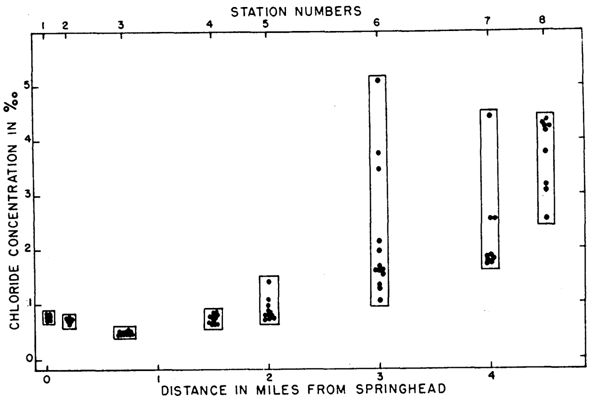

FIG. 4. Chloride values in Homosassa Springs.

Although station 2 shows a slight drop in chloride concentration, which may not be significant, the range of fluctuation is about the same as at station 1. If the drop represents a real decrease, it may indicate that there are other, fresher springs contributing to the river somewhere between stations 1 and 2.

The concentration at station 3 is still lower, and the values here show less fluctuation than the previous two stations. The variation between maximum and minimum values obtained from eleven samples taken at different apparent tide stages was 0.048 $^0/_{00}$.

Between stations 3 and 4 a stream known locally as the Hall River flows into the run of Homosassa. The three water samples obtained from the channel of this river contained 1.15, 1.77, and 1.76 $^0/_{00}$ chloride. The inflow of this brackish water probably explains the rise in chloride concentration from station 3 to 4. The fluctuation here is possibly due to incomplete mixing of the slightly brackish water from upstream and the more brackish water from the Hall River. The maximal values recorded from station 4 are the same as those from the boil while the minima are somewhat lower.

Station 5 is probably the first station to receive tidal water of marine origin; the tidal effect here produces an observed fluctuation of 0.67 $^0/_{00}$ chloride. For the purpose of this study, the estuary begins at this station. Figure 4 shows the large increase in fluctuation that takes place between stations 5 and 6. The minimum chloride values steadily increase through station 8 although the maximum values seemingly decrease past station 6. As mentioned in the opening paragraph of this discussion, this is probably because the last two

TABLE III. pH values at collecting stations in Homosassa and Weekiwachee Springs

	H−1	H−2	H−3	H−4	H−5	H−6	H−7	H−8	W−1	W−2	W−3	W−4	W−5	W−6
November 1953......	7.5	7.5	7.5	...	7.7	8.4	8.1	8.1	...	7.5	7.4	7.4	7.4	...
February 1954.......	...	7.7	7.6	7.6	7.7	8.0	8.0	8.3	7.6	...	7.6	7.6	...	7.5

stations were apparently not visited during actual high tide; therefore, the true maximal values are probably considerably in excess of the concentrations shown.

CURRENT VELOCITY. Because of mechanical difficulty encountered in using the current meter, only two series of velocity measurements were made. The values in Table I are averages of these and refer to surface velocities in the channel. The lowest reading that the meter will register is 0.01 ft/sec. Therefore, where no current was encountered it is reported as being less than 0.01 ft/sec.

At station 1, the backwash from the boil is the only observable current to which the inhabitants of the pool edge are subjected. This is very slight and not at all obvious. As the water flows from the pool toward station 2, however, the current quickly increases to an average of 0.53 ft/sec. Since the channel is narrow and there are no protected areas, all parts of the station are subjected to current of this average velocity. By the time the river has progressed to station 3, the mid-channel velocity has decreased to an average of 0.27 ft/sec and the current among the plants at the collecting site is less than 0.01 ft/sec. The current velocity at station 4 is again less than 0.01 ft/sec among the plants and averages 0.13 ft/sec in the channel. At station 5 the velocity averages 0.08 ft/sec among the plants and 0.19 ft/sec in the channel. The velocity reported for station 5 must be viewed with some reservation, however, because on one occasion the "current" was seen to be flowing upstream. This was probably due to a combination of backing up of water from the incoming tide and a strong wind which was blowing in an upstream direction. Station 5 was the last station at which velocities were measurable. The current at stations 6, 7, and 8 are therefore considered to be less than 0.01 ft/sec., although during incoming and outgoing tides and periods of high wind, these stations are probably subjected to a slight irregular current.

HYDROGEN ION CONCENTRATION. Since a survey of all the major Florida springs by Furguson *et al.* (1947) showed the variation of pH to be slight for springs in general even over long periods of time, only two series of pH readings were made at each station. Like most other Florida springs, Homosassa is alkaline due to the leaching of its waters through limestone before reaching the surface. Table III shows the pH values at each of the stations for the two series taken during this study. The fluctuations shown in this table for stations 1, 2, 3, 4, and 5 are small enough to be within the range of reading error. The variation between values at stations 6, 7, and 8 is probably due to the changes in chemical composition of the water with high and low tides. A correction for salt-error was applied to stations 6, 7 and 8 using the correction factors employed by Harvey (1928).

TEMPERATURE. Temperatures were recorded among the plants with a centigrade mercury thermometer. Table IV shows values which were recorded over a nine-month period. Stations 1, 2, and 3 are seen to approach constant temperature while the lower stations, although varying somewhat between summer and winter months, still have at the most a ten degree change between these seasons.

TABLE IV. Water temperature values (°C) recorded at collecting stations in Homosassa and Weekiwachee Springs

	June 1953	July 1953	Aug. 1953	Oct. 1953	Nov. 1953	Jan. 1954	Feb. 1954
H−1.......	23.2	....	....	....	22.5	23.3	....
H−2.......	23.3	....	23.5	....	24.0	....	24.0
H−3.......	24.0	....	....	....	22.0	23.3	24.9
H−4.......	....	....	26.2	....	....	....	23.9
H−5.......	27.0	....	27.8	....	20.0	....	22.5
H−6.......	27.0	....	29.0	....	19.0	....	22.0
H−7.......	....	....	29.0	....	18.5	....	20.3
H−8.......	....	....	....	....	17.5	....	20.8
W−1......	....	24.0	23.5	23.5	....	23.9	24.0
W−2......	24.0	24.6	23.5	24.8	....	....	....
W−3......	26.0	26.0	....	....	....	....	23.5
W−4......	26.0	28.0	27.0	22.5	....	18.0	22.4
W−5......	27.0	28.0	....	....	....	....	....
W−6......	27.4	30.8	....	24.8	....	15.7	20.5

WEEKIWACHEE SPRINGS

DISSOLVED OXYGEN. Figure 5 shows the mean dissolved oxygen concentrations and changes in dissolved oxygen at the collecting sites in the Weekiwachee River system, and also indicates the actual values recorded at these stations.

The dissolved oxygen of the headwaters of this spring is among the lowest of the non-anaerobic

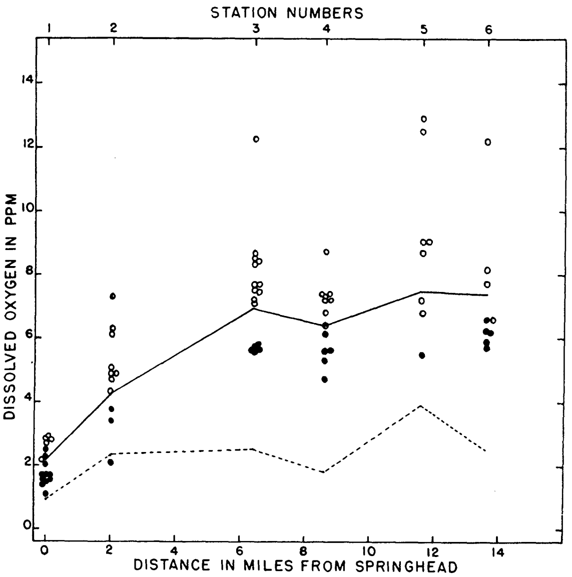

FIG. 5. Dissolved oxygen concentrations in Weekiwachee Springs. Black points are night values, open points day values. Solid line, average of mean-day and mean-night values; dotted line, difference between mean-day and mean-night values.

Florida springs. The mean dissolved oxygen concentration is 2.20 ppm and, unlike Homosassa which has practically no diel fluctuation, has a dissolved oxygen change of almost 1 ppm. This is probably because Weekiwachee has a larger pool and the water from the boil, instead of flowing immediately to the run, as in Homosassa, can stand at the edge for some time. This water may then be acted upon by photosynthesis and respiration. The fluctuation is still small, however, in comparison with many other aquatic situations, and the environment in the pool (station 1), in terms of dissolved oxygen, is still unusually constant. At no other known point in the river does the dissolved oxygen descend to the level of that of the springhead.

At station 2, although this is two miles below the river's source, the mean dissolved oxygen concentration has increased only to 4.3 ppm with mean minima and maxima of 3.08 and 5.46 respectively. The minimum values used for this station were obtained from samples collected on rainy days since night water samples were very difficult to obtain in this part of the river. The low concentration found here is probably due to the fairly low densities of rooted aquatics throughout the two mile course. Even though the dissolved oxygen content remains low at this station, the diel fluctuation as shown in Figure 5 is considerably greater than that of the previous station.

The steady increase in dissolved oxygen content continues through station 3, the mean here being almost 7 ppm. The diel fluctuation, 2.55 ppm, is slightly greater than that of station 2. One very high value was recorded from this station (see Fig. 5). This sample was probably taken in water that had somehow been standing long enough among plants, perhaps in a small whirlpool, to become supersaturated with respect to oxygen.

Station 4, whch is approximately two miles below the previous station, shows a slight drop in mean dissolved oxygen content. This may be a reflection of the 15 percent decrease in plant density. Compared to station 3, this station exhibits a fairly large drop in diel fluctuation of dissolved oxygen.

No water samples were collected from station 5 during the dark hours but the one rainy-day sample taken probably approaches the night concentration. The mean day values are generally high compared to upstream stations even though there is a large decrease in plant density.

Station 6 is located in the broad, shallow bay shown in Figure 1b. The aquatic plant growth is very dense in parts of this area and the dissolved oxygen concentration is correspondingly high; not so high, however, as at station 5. The chloride content of the water at high tide becomes almost a third that of sea water but this seems to have little effect on the dissolved oxygen concentration. The change in dissolved oxygen per diel period is somewhat less than at station 5.

CHLORIDE. Figure 6 shows chloride values from all stations. These, as in the chloride diagram of Homosassa Springs, are enclosed in order to show ranges in fluctuation.

Stations 1, 2, and 3 are definitely in the fresh water range. None of these stations reach the "nearly oligohaline" (Odum, 1953b) range of 0.025 to 0.100 $^{0}/_{00}$. The fluctuation shown at all these stations is very small and probably within the range of experimental error.

Station 4 shows a slight increase in chloride content over the previous three stations. On two occasions, values falling in the "nearly oligohaline" range were recorded. There is a possibility that this increase is due to inflow of water of marine origin, but the distance of this station from the Gulf and the high current velocity throughout the entire run would seem to indicate that this is not the case.

Station 5 shows a definite chloride fluctuation and this is no doubt due to marine tidal water. During low tide the chloride content at this station is comparable to that of station 4. However, one sample indicates that at high tide the concentration increases well into the oligohaline range.

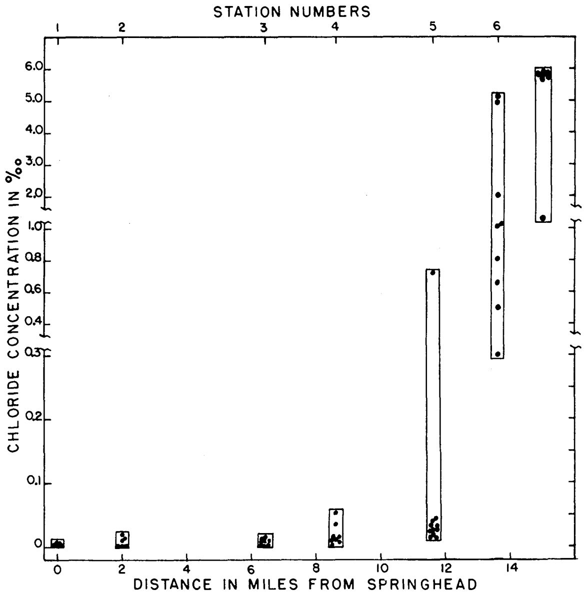

FIG. 6. Chloride values in Weekiwachee Springs.

At station 6, the concentration during high tide becomes nearly one third that of sea water. At low tide, however, values in the low oligohaline range have been recorded. The measured extremes in chloride content at this station are 0.30 and 5.28 ‰. The last block of values in Figure 6 are from samples taken at the mouth of the river about one-eighth of a mile from station 6. These values range from 1.3 to 5.8 ‰.

CURRENT VELOCITY. Table II shows the surface current velocity in the channel at the various stations. Since these (with the exception of the U. S. Geological Survey readings) are averages of measurements made at the same time, no information is available on fluctuation of current velocity throughout the year. However, the USGS values show that cross-sectional averages taken ¾ mile downstream from the springhead range from a low of 0.75 ft/sec in November, 1952 to 1.12 ft/sec in June, 1953. The values shown in Table II are probably comparable to the current to which the plants and their inhabitants are subjected since all collecting sites were in areas which are exposed to current.

No measurable river current was found in the bay, but upon one occasion a water velocity of 0.34 ft/sec was recorded flowing into the estuary. This was during the tidal inflow. Apparently this area, like that of Homosassa, is subject to reversal of current with change in tidal flow and wind direction.

HYDROGEN ION CONCENTRATION. pH was measured in the same manner as for Homosassa. A correction for salt-error was made for station 6. Table III shows the two series taken during this study. These seem very similar to the values recorded in Homosassa except for the estuary samples.

TEMPERATURE. Table IV shows temperatures as recorded over a nine-month period. There is practically no temperature fluctuation until station 3 is reached, and even then the observed seasonal variation is less than three degrees. The bay shows the greatest range of seasonal fluctuation, slightly in excess of fifteen degrees. This is somewhat more than for the Homosassa estuary.

SPECIES DISTRIBUTION AND POPULATION DENSITY

Previous mention has been made of the occurrence of smaller numbers of species in spring pools in comparison with the runs. It is also true that there are fewer individuals in these source areas than in the runs. In the following discussion estimates of relative density for those species whose populations were not quantitatively measured are necessarily somewhat arbitrary. General estimates will be given for some of these species, however. Species distribution in Homosassa and Weekiwachee Springs is shown in Figures 7 and 8; Figure 9 shows the species distribution broken down to orders. Because of its length, a table showing the species present at each station is omitted. This information is available in thesis form in the University of Florida libraries. Dissolved oxygen and chloride concentrations at the collecting sites are shown in Figures 3 through 6.

Population density in this study refers to the mean number of individuals collected per unit area. Actual numbers of insects collected were used in calculations of population density. Only two groups, the Ephemeroptera and Odonata, were studied from a quantitative standpoint since the structural adaptations of other groups, such as

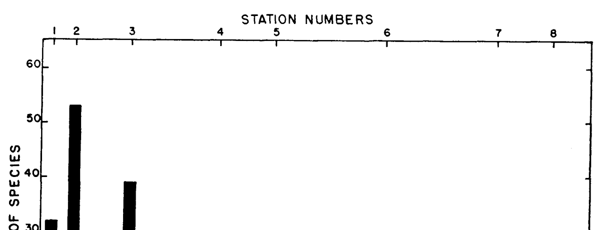

FIG. 7. Numbers of insect species taken from collecting stations in Homosassa Springs.

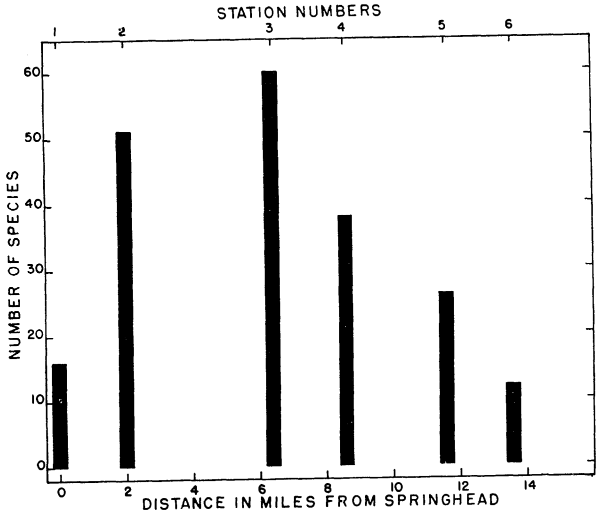

FIG. 8. Numbers of insect species taken from collecting stations in Weekiwachee Springs.

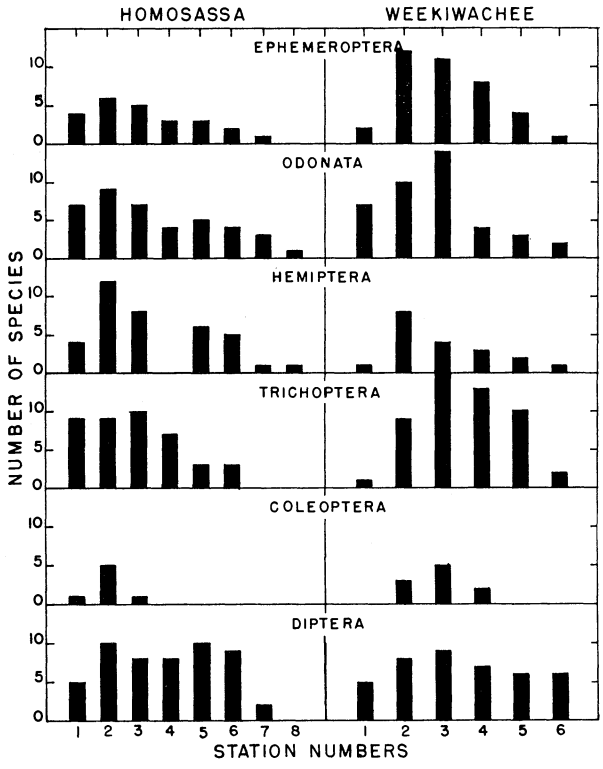

FIG. 9. Number of species per order of insects taken in Homosassa and Weekiwachee Springs.

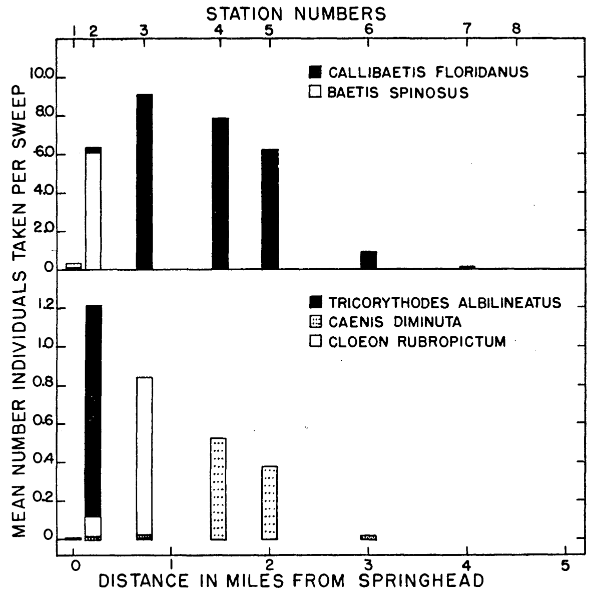

FIG. 10. Relative population densities of five species of mayflies. Homosassa Springs.

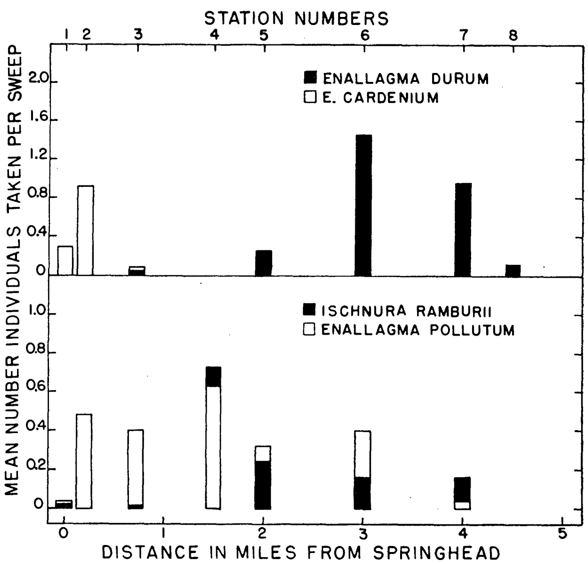

FIG. 11. Relative population densities of four species of damselflies. Homosassa Springs.

the vegetation-adhering cases of the Diptera and Trichoptera, would not permit a valid numerical comparision of their populations with those of the first two groups mentioned without devising other collecting methods. The mean number of individuals per sweep, shown in Figures 10 through 13, was determined by dividing the total number of individuals collected by the number of sweeps made at that station. The values shown in these figures are based on a total of 697 sweeps.

HOMOSASSA

DIPTERA. In the omitted table, mentioned above, some of the dipterous forms were grouped into categories higher than species. For the purpose of this study, the Chironomidae include all forms in this family with the exception of the Chironominae and the Tanypodinae, since these were considered separately. The Chironominae include all of the genus *Tendipes* (= *Chirono-*

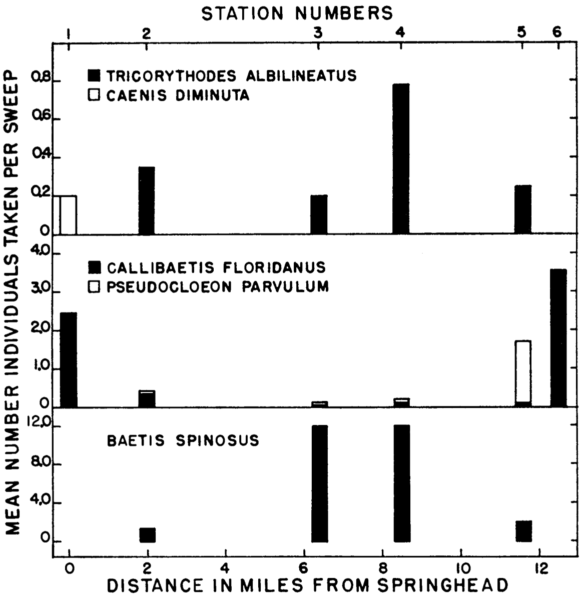

FIG. 12. Relative population densities of five species of mayflies. Weekiwachee Springs

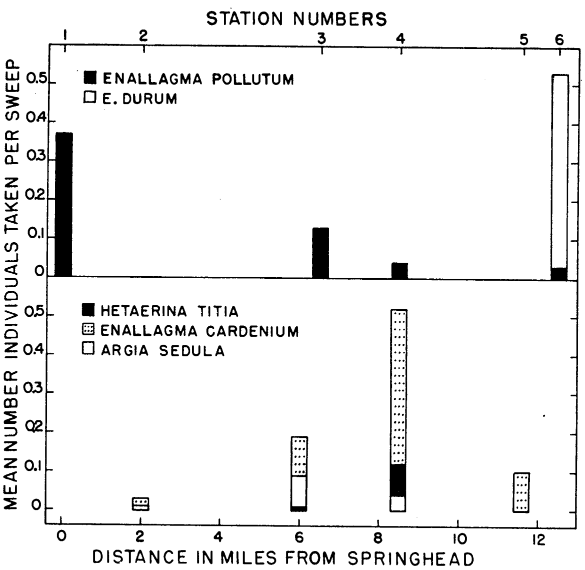

FIG. 13. Relative population densities of five species of damselflies. Weekiwachee Springs.

mus) with the exception of the *Tendipes decorus* and *T. militaris* groups. The Tanypodinae include all those in this subfamily. *Tanytarsus* includes all members of this group. The above mentioned forms, along with the *Palpomyia* and *Bezzia* groups, are very evenly distributed in the Homosassa River.

None of the groups mentioned above are found in large numbers at any station but seem to be present in smaller numbers in the pool (station 1) than at other stations. As might be expected, the predaceous Tanypodinae, *Palpomyia,* and *Bezzia* groups were fewer in number than most other forms. The *Tendipes militaris* group is rarest, having been taken at only one station on one occasion. The two species of Culicidae recorded were probably victims of surface-water run off from an adjacent swamp, as these are characteristic of stagnant water. The empidids *Hemerodromia* and *Roederiodes,* which were taken only at the swift-water station (station 2), are typically swift-water forms in North America although species of the former have been reported from stagnant water in Europe (Bischoff *in* Johannsen 1935). The stratiomyid *Odontomyia* is generally found in still waters but in this study they have been repeatedly taken from logs in fairly swift waters at station 2. They are, however, more common at downstream stations where the current velocity is less. The ephydrid *Ephydra* sp. belongs to the same genus as the well-known brine fly that occurs in Great Salt Lake. The species present in Homosassa, however, is probably *E. subopaca* which, although a brackish-water form and found in salt concentrations up to 11 $^0/_{00}$ (Johannsen 1935), is not present in Great Salt Lake. In Homosassa it was found in salt concentrations of over 8 $^0/_{00}$.

EPHEMEROPTERA. The mayflies are represented in Homosassa by seven species, five of which occur in numbers large enough for comparison of their populations (see Fig. 10). *Callibaetis pretiosus* occurs only at station 2 and in very small numbers while *Baetis intercalaris* was taken rarely and only at station 3. *Callibaetis floridanus* is the most widely distributed and abundant mayfly in Homosassa Springs. Its range extends far into the high-chloride waters of the estuary but the numbers of individuals are small in this area. The occurrence of this species in brackish water has been reported by Berner (1950) and Berner and Sloan (1954). *Baetis spinosus* is found at stations 1, 2, 4, and 5 but only in abundance at station 2, the swift-water station. It was rarely taken at slow-water stations although it commonly occurs in quiet water elsewhere (Berner 1950). The distribution of *Tricorythodes albilineatus* is similar to that of *B. spinosus* but the number of individuals collected was considerably smaller. *Cloeon rubropictum* has somewhat the same pattern of distribution as does *T. albilineatus* except that the peak of the density curve of the former is at station 3 instead of 2. *Caenis diminuta,* although present at all stations except 7 and 8, is found in greatest number at station 4. It is apparently fairly tolerant as a species although its populations are seen to be quite small in areas of environmental extremes such as the pool and estuary.

Many species of this order are very sensitive to low concentrations of dissolved oxygen, and for this reason they are sometimes used as indicators of "clean water" (waters of relatively high dissolved oxygen concentrations).

TRICHOPTERA. The Hydroptilidae are the most widely distributed family of the caddisflies with the Leptoceridae being next. Because of the case building habits of this group and the resulting difficulty of collecting quantitatively by the method employed for other insects, little has been learned of the relative abundance of the various species. Like the mayflies, the Trichoptera are generally found in waters which are well aerated; they, too, are sometimes used as "clean water" indicators. The presence of nine species of this insect in the pool at Homosassa out of a total of ten found in the entire river seems to indicate that the dissolved oxygen concentration in the springhead is probably not seriously limiting to this order.

HEMIPTERA. Unlike the other groups of aquatic insects (with the exception of the Coleoptera), the Hemiptera are able to range for considerable distances and are not dependent upon dissolved oxygen. Since nearly all of the Hemiptera are predaceous and their food for the most part consists of aquatic and terrestrial insects and entomostraca, they are found in greatest number, as might be expected, where the concentration of other insects is greatest; that is at stations 2 and 3. *Mesovelia mulsanti* is the most widely distributed species, being found from station 2 to 8. The others have a rather spotty distribution but this is probably due as much to insufficient sampling because of the extreme mobility of these insects as to actual difference in distribution. One form, *Metrobates hesperius ocalensis,* was formerly known only from the Rainbow River in Marion County (Herring 1950). Only four species have been taken in the pool and this may be a reflection of the small numbers of other insects in this area.

COLEOPTERA. Five species of Coleoptera have been collected. All of these are present at station 2; four of them exclusively. Beetles are very few in number and on several collecting trips were not recorded.

LEPIDOPTERA. There are two genera of aquatic Lepidoptera, *Nymphula* and *Elophila,* both of which occur in Homosassa. They are very rarely taken, however, and then at stations 1 and 2 only. Since this order is so poorly represented, it is not included in the frequency histogram (Fig. 9).

ODONATA. The Anisoptera are sparsely distributed in the river. The greatest number of species are found at stations 2 and 1 where the bottom is for the most part firm and free from hydrogen sulfide such as occurs in the substrate of the downstream stations.

The Zygoptera are rather few in number of species but some of these are represented by fairly large populations at certain stations. *Argia sedula* and *A. fumipennis* are the only species limited to the upper region of the run; they are taken but rarely. Others are well distributed in the river as can be seen in Figure 11. This figure also shows the relative sizes of nymphal populations of the Zygoptera. *Enallagma cardenium* is limited to the first four stations and is more frequently taken in the pool than the other species. It attains its maximum abundance at station 2, the swift-water station. *Ischnura ramburii* is more common at station 4 but is completely absent only at station 8. Its presence in waters of high salinities was noted by Pearse (1934) and Wright (1943). *Enallagma pollutum* has the same range as *I. ramburii* (stations 1 through 7) but is much more evenly distributed numerically. It, too, is tolerant of fairly high chlorinities although no reference to this effect has been found in the literature. In fact, Wright (1943) indicates that *E. pollutum* is characteristic of strictly fresh water. *Enallagma durum* has perhaps the most interesting distribution among the damselflies. It is present at all stations except 1 and 2, but is found in greatest numbers in the estuary where the other species are either absent or represented by only a few individuals. Wright (1943) mentions that in the marshes of the Central Gulf Coast, this species reaches its greatest abundance in brackish water. *E. durum* was the only damselfly nymph found at station 8 but here it is present in very small numbers.

Weekiwachee Springs

DIPTERA. The distribution of the Diptera in Weekiwachee Springs is remarkably similar to that in Homosassa; the chief differences being in the near elimination of slow-water forms such as *Odontomyia* and *Ephydra* and the increase in swift-water forms. More species are found in the estuary than is the case in Homosassa.

EPHEMEROPTERA. Only two species of mayflies, *Callibaetis floridanus* and *Caenis diminuta* occur in the pool where the concentration of dissolved oxygen is always low (maximum recorded, 2.5 ppm). *C. floridanus* reaches greatest abundance in the pool and estuary; these are perhaps the two most extreme stations, with respect to environmental factors, in the entire river. The presence of *Callibaetis* in numbers in waters poor in dissolved oxygen is interesting because Gaufin and Tarzwell (1952) recorded no other mayfly but *Callibaetis* sp. from the recovery zone of a polluted stream (min. dissolved oxygen conc., 1.6 ppm), and Dr. F. P. Ide (personal communication) reports two species of *Callibaetis* as being more tolerant than other mayfly forms in a polluted stream in Ontario. The paucity of *C. floridanus* in the stations of the run can probably be accounted for by the fact that this species is primarily a slow to stagnant-water form and the swift current of the run is therefore limiting.

At the station below the boil (station 2), the number of species increases to twelve. From this point on, there is a gradual decrease in species number until at the estuary station only *C. floridanus* is found. *Baetis spinosus* is present in fairly large numbers at stations 3 and 4 but is completely absent at stations 1 and 6. *Tricorythodes albilineatus,* being a swift-water form, is present at all of the swift-water stations in roughly the same numbers but is absent at stations 1 and 6. *Caenis diminuta* is present at station 1 but is found here only in small numbers. A very few specimens were taken at station 2. This is typically a still-water species and its absence from the run is not surprising. *Pseudocloeon parvulum* is found in greatest numbers in the lower regions of the run. It does not occur at station 1 and is found only in small numbers in the middle section of the run.

The peaks of the population curves for the mayflies of Weekiwachee are somewhat different than for Homosassa, partly because of the swift current of the former.

TRICHOPTERA. Only one species of caddisfly, *Leptocella* sp. A, is found in the pool of Weekiwachee Springs as contrasted with nine in Homosassa. The distribution of this order in Weekiwachee is very similar to that of the mayflies except that the greatest number of species of Trichoptera are found at station 3 instead of 2 as for mayflies. The similar distribution of the two groups, at least in the pools, may be due to the generally high oxygen requirements of both. Two species, *Leptocella* sp. A and *Oecetis cinerescens,* persist in the high chloride waters of the estuary. Their absence in the lower Homosassa stations is therefore probably due to some factor other than chloride concentration. The increase in species number over Homosassa may be explained by the presence of more rheophilic forms. There seems to be little difference in numbers of individuals of the same species in the two rivers.

HEMIPTERA. The water striders are more sparsely distributed in this river than in Homosassa. Only one species has been taken in the pool; this, again, may reflect the low level of available food in the springhead area. As in Homosassa, there is a sudden increase in species number below the boil area. It is interesting to note that one form, *Metrobates hesperius depilatus,* is known only from the Weekiwachee River and Salt Creek, a stream which flows into the estuary of Weekiwachee (Herring 1950). This subspecies occurs at all stations but the last. Only *Hydrometra australis* was collected in the estuary.

COLEOPTERA. As in Homosassa, this order is represented by only a few species and by small populations. It is as difficult to explain the paucity of beetles here as in Homosassa. None was taken in the pool, possibly for the same reason as was suggested for the Hemiptera. Three species were found at station 2, five at station 3 and two at station 4. Below this point, none was collected.

LEPIDOPTERA. Both of the aquatic genera are present but not at the same stations. *Elophila* is found only at stations 2 and 3 while *Nymphula* was taken only from stations 4 and 5. As in Homosassa, the numbers of individuals are small in all habitats where these insects occur.

ODONATA. More species of the Odonata, both Anisoptera and Zygoptera, occur in Weekiwachee than in Homosassa. The presence of more dragonfly nymphs may be because the swift current prevents accumulation of large amounts of organic detritus on the bottom of Weekiwachee resulting in less hydrogen sulfide in the substrate. The increase in damselfly nymphs over the number found at Homosassa is difficult to explain as these insects are more often found in waters of less current velocity than that found in Weekiwachee. The number of species in the boil area is the same as for Homosassa; these species are, for the most part, also the same. The low dissolved oxygen in the pool of Weekiwachee is obviously not a limiting factor to these forms. The number of species is greatest at station 3, and then subsides until, in the estuary, only *Enallagma durum* and *Ischnura ramburii* are found. As has been reported by Wright (1943), both of these species are tolerant of brackish water. These forms were also found in the Homosassa estuary along with *Enallagma pollutum.* As may be seen in Figure 13, the observed population densities of the species of Zygoptera are greater in Homosassa than in Weekiwachee Springs.

Statistical Treatment of Quantitative Data

In order to show that the differences in numbers of individuals obtained at the different stations were real and not a result of sampling error, a statistical treatment, analysis of variance, was applied to data obtained from quantitative sampling. The standardized sampling method was as follows: five or more areas were picked at random at a given station. Within each of these areas a five-sweep sample was made (five sweeps has been shown to be an adequate sample; see Fig. 2) and the insects from each of these samples were kept separate. The specimens were later counted and the numbers compared statistically with those of collections made (1) at different times but at the same stations, (2) at different times and at different stations, and (3) near the same times but at different stations. The results of these analyses substantiated the conclusion that population density gradients exist in the runs of both rivers. For example, numbers of individuals in samples taken from H-1 were significantly (P less than .01) less than those from H-2 and from H-3, both in April and in November. Numbers were not significantly different (P. greater than .05) in samples taken at H-1 at different seasons (April and November). The same was true for samples taken from W-1 at different times. Numbers were, however, significantly lower at W-1 than at W-2 or at W-3. Significant differences were shown to exist between numbers present in samples taken from H-3 in April and in November. The greater seasonal fluctuation in temperature at station H-3 may, in part, account for this observed seasonal variation in density while the more constant temperatures at W-1 and H-1 are probably instrumental in compressing population density fluctuation in these areas.

Discussion

The two major features that are similar in both Homosassa and Weekiwachee Springs are temperature and pH (see Tables III, IV). Dissolved oxygen (Figs. 3, 5) and chloride concentrations (Figs. 4, 6) differ considerably in the springheads of the two springs. Dissolved oxygen concentrations are essentially the same in the lower halves of both rivers but chloride concentrations are alike only in the estuaries. The only point in Homosassa at which the current velocity is somewhat comparable to that of Weekiwachee is at station 2. Another condition which is no doubt common to both springs, at least in the springhead areas, is a limited number of ecological niches. Because of the nearly constant conditions which exist in these areas, available niches should be relatively few in both (H. T. Odum *in* E. P. Odum 1953, p. 251).

By referring to Figures 7, 8, and 9, it can be seen that the general trend in both rivers is for species numbers to be initially low at the pool, to increase rather sharply at the next one or two stations below the springhead, and then gradually to decline as the estuary is approached. In the freshwater sections of both rivers there is a striking correlation between this distribution and dissolved oxygen concentrations. Since experimental evidence concerning the oxygen requirements of the species in question is lacking, the existence of a real relationship must remain speculative until such evidence is forthcoming. However, many observations regarding the paucity of related species in waters of low dissolved oxygen concentrations seems to suggest that, at least in the springhead areas, this may be an important limiting factor. (Campbell 1939; Gaufin and Tarzwell 1952).

The phenomenon of species number reduction in boil areas is more obvious in Weekiwachee (Fig. 8) than in Homosassa Springs (Fig. 7). Since the dissolved oxygen concentration is considerably higher in the pool of Homosassa while many other factors are common to both pools, this would seem to lend weight to the suggestion that dissolved oxygen concentrations of these magnitudes are insufficient for some species. There is a complicating factor, however, which cannot be ignored. That is that small fish (primary carnivores) are commonly observed in the springhead of Weekiwachee Springs but are only rarely seen in this area of Homosassa where the larger fish (secondary carnivores) presumably prevent their establishment. Predation pressure by the small fish in Weekiwachee may have the effect of eliminating those insect species whose eggs and larvae or nymphs are most easily seen and captured.

In the mid-sections of both rivers conditions are not nearly so invariable as near the sources. This variability is shown in part by the dissolved oxygen fluctuations in the downstream areas (Figs. 3, 5) and by slight but significant temperature fluctuations in these sections (Table IV). It seems reasonable that the increased number of ecological niches provided by this variety could result in establishment of larger numbers of species in these areas. Conversely, the limitation of species in springheads is possibly in part due to the nearly constant environmental conditions found there. This may serve to limit all but those species whose developmental optima fall within these narrow limits of variation.

The reduction in species numbers as the estuaries are approached is almost as striking as the similar phenomenon at the sources. There is good agreement between this reduction and the increase in chloride concentration. Here again, however, experimental evidence regarding chloride tolerances of the species under consideration is meager. Pearse (1934) made observations on insect distribution in brackish-water pools at Dry Tortugas. He found *Microvelia borealis, Trichocorixa sellaris,* and larvae of *Chironomus* sp. in a pool whose salinity range was recorded as 20.30 to 73.32 $^0/_{00}$ (11.2 to 40.6 $^0/_{00}$ chlorinity) through the summer months. *Ischnura ramburii,* which in the present study was found in waters of approximately 4.5 $^0/_{00}$ chlorinity, was taken by Pearse from pools in which the recorded salinity range was 19.38 to 23.65 $^0/_{00}$ (10 to 13.1 $^0/_{00}$ chlorinity). Osburn (1906) found that *I. verticalis* could survive (for an undisclosed period) in sea water whose density was 1.01 at 72 F. (chlorinity approximately 8 $^0/_{00}$) but died within a day or two when placed in sea water of density 1.015 (chlorinity approximately 11 $^0/_{00}$).

These data are pitifully few but they indicate that at least two of the species recorded from the Florida springs, along with several related species, can tolerate chlorinities considerably in excess of those in the estuaries of the two rivers. One possibly important difference in these studies is that Pearse and Osburn worked in ponds whose salinities were not subject to tidal fluctuation. The species that are found in the lower stations of the Homosassa and Weekiwachee estuaries must, however, withstand daily chloride fluctuations of 1 to 5 parts per thousand. Although the osmotic stress is not so great as in fresh or sea water, the insect still must solve the problem of periodic fluctuation and differing ion ratios from that of its body fluid (Buck *in* Roeder 1953). This is perhaps as important a barrier as concentration itself. Other factors, such as decreases in the amounts of vegetation (and thus a decrease in protected areas) and changes in the nature of the substrate, are probably contributory to the formation of distribution patterns in the lower reaches of both rivers.

For those species whose densities were quantitatively compared (Figs. 10-13) the frequency distribution was found to follow roughly the same pattern as the species distribution. That is, small populations in the springheads, increasing numbers downstream, and reduction again as the estuaries are approached. The latter phenomenon is partly a result of the elimination of many groups, presumably by the high chloride concentrations and fluctuations of the estuaries. The population peaks of a few species, such as *Enallagma durum,* are in the higher chloride ranges but these, too, soon decline. In the estuary of Weekiwachee Springs, *E. durum* and the mayfly *Callibaetis floridanus* reach the peak of their densities at chloride concentrations which approach 5.5 $^0/_{00}$ at high tide. The chloride fluctuation due to tide in this area is about 5 $^0/_{00}$.

Because of the presence of small fish in the pool of Weekiwachee, as was discussed above, fish predation may be instrumental in keeping the numbers of insects depressed. This cannot explain, however, the correspondingly small numbers of individuals found in the Homosassa pool. In Florida springs in general, planktonic forms are practically absent in boil areas. The lack of this important food source should certainly limit the numbers of individuals of those species which are dependent, either primarily or secondarily, on such a food source. But it is difficult to understand how this could affect those species, such as some mayflies, which feed on the epidermis and epiphytic algae of higher plants.

The question of species being restricted to certain plants as a factor explaining distribution should be mentioned. Although it is known that a few species of aquatic insects are limited to one or a few host plants, this condition is far less common than among terrestrial species. McGaha (1952) reports that even though some emergent plants may shelter restricted insect species, those species which inhabit totally submerged plants show practically no specificity. Even species frequenting emergent plants have a wide range of food plants (Frohne 1938). In the present study no restricted plant-insect species associations were noted although it must be admitted that this aspect was not given detailed consideration.

There are certain similarities between the fauna of the pools of the two springs studied and that of organically polluted water. Some forms, such as blood worms (*Tendipes*) and the mayfly nymph *Callibaetis,* which are known to be tolerant of varying degrees of organic pollution, are found in springheads. On the other hand, forms such as most of the other mayfly species and caddisflies, which are sometimes used by sanitation biologists as "clean water" indicators (Claassen 1932; Campbell 1939), are notably few, especially in the pool of Weekiwachee. These data do not, of course, suggest that the springheads are at all polluted but perhaps only that one of the major results of organic pollution, low concentrations of dissolved oxygen, is common to both situations.

The chemical constancy of springheads has been demonstrated by dissolved oxygen determinations and pH and temperature measurements during this study and by many chemical analyses made by the Florida Geological Survey over a period of several years. Evidence that insect population sizes do not change significantly in these pools with the seasons was presented in the section on statistical treatment. Thus the nearly constant environmental conditions seem to be reflected in the constant sizes of populations found in these areas.

Summary

Two constant-temperature Florida springs, Homosassa and Weekiwachee Springs, have been studied and an attempt has been made to correlate the spatial and temporal distribution of aquatic insects with measured physical and chemical environmental factors. This investigation was conducted from November 1952 to February 1954. The major results of the study may be briefly summarized as follows:

1. The dissolved oxygen concentrations form gradients in both springs but this is more pronounced in Weekiwachee than in Homosassa. The dissolved oxygen content is typically lowest in the springhead areas but increases fairly rapidly with distance down the runs.

2. In the lower parts of the runs, the chloride concentration increases due to the effect of marine tidal invasion. The chloride content in Homosassa Springs begins in the oligohaline range and the concentration becomes gradually greater in the estuary. In Weekiwachee Springs, however, the chloride concentration is low and never reaches the oligohaline range in the run. The change from fresh to brackish water is very abrupt in the estuary.

3. Temperature was found to be essentially constant in the springheads of both rivers; the daily and seasonal changes in temperature at downstream stations, even those several miles below the pools, were not of large magnitudes.

4. The pH is nearly constant in the springheads and runs but varies somewhat in the estuaries; this is probably due to changes in the salt concentrations during tidal inflow and outflow.

5. By using as indices dissolved oxygen fluctuation and temperature variation, areas of environmental variability were found to lie at points considerably below the springheads.

6. Gradients of both numbers of species and densities of populations exist in both rivers. The numbers of species and individuals are fewer in springhead and estuarine areas than in mid-sections of the rivers. This is statistically verified. Factors which may in part explain the observed distribution patterns are discussed.

7. The similarities between certain of the fauna of springhead areas and that of organically polluted waters is pointed out. This may be accounted for by the fact that in both situations dissolved oxygen concentrations are low.

8. Evidence is presented which indicates that, at least with respect to insect populations, springheads are areas of biological as well as chemical constancy.

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ECOLOGICAL ASPECTS OF THE SYMPATRIC DISTRIBUTION OF MEADOWLARKS IN THE NORTH-CENTRAL STATES[1]

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Students of avian distribution have long been intrigued with the sympatric relationship of the two species of meadowlarks in the central region of the United States.[2] The eastern meadowlark (*Sturnella m. magna*) and the western meadowlark (*Sturnella n. neglecta*) have overlapping breeding ranges extending from Oklahoma northward into southern Ontario. This paper is the report of a study of historical and ecological aspects of this sympatric distribution and proposes an hypothesis to explain the distributional changes that have occurred within recent years. The equally intriguing relationship between *S. n. neglecta* and other races of *S. magna,* south of Oklahoma, will be omitted from the present discussion due to the paucity and conflicting nature of the reports from that area.

I am greatly indebted to numerous amateur and professional ornithologists who have contributed distributional data for this analysis, and I regret that lack of space permits only a listing of their names in an appendix at the end of the paper. I am especially grateful to the following individuals who have given generously of their time to various aspects of the study: Mr. Vincent Batha, Mrs. A. J. Binsfeld, Mr. and Mrs. George Crossley, Miss Doris Gates, Mr. and Mrs. Kenneth Krumm, Mr. Philip Mallow, Mr. Thomas Morrissey, Miss Margarette Morse, Mr. Russell Mumford, Mr. Alvin Peterson, and Mr. and Mrs. George Spidel. Special thanks are due to Dr. John T. Emlen, Jr., Department of Zoology, University of Wisconsin, for his contribution to the study and assistance in preparation of the manuscript. For a critical reading of the manuscript I would like to express thanks to Dr. John T. Curtis of the University of Wisconsin, Dr. Ernst Mayr of Harvard University, and Dr. Harrison B. Tordoff of the University of Kansas.

Former Distribution

Early records of meadowlark distribution are inadequate for a detailed account of progressive changes. As an alternative all available records made before 1900 have been pooled to provide an approximate picture of the breeding ranges of the two species at the turn of the century. The range maps are based in part on published material and in part on extensive personal communication with current workers in strategic localities. Because of the many irregularities of distribution and reporting techniques, it seemed desirable to present the ranges in a generalized form. Those readers who are interested in the details of local distribution should refer to the original sources of documentation as listed in the appendix.

The approximate limits of the critical zone of overlapping breeding ranges of eastern and western meadowlarks, at the turn of the century, are indicated in Map 1. The eastern species could be found breeding regularly and commonly throughout most of the area east of line E. In addition it was recorded as present in isolated, peripheral colonies beyond this region in the limited area indicated by the horizontal lines extending west-

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[2] The taxonomic relationship of these species is, in itself, an interesting problem and in some contention among contemporary ornithologists. Though this aspect will not be treated here, the author is convinced, by virtue of his own research, of the wisdom of their recognition as full species. It is with that understanding and interpretation that this paper is presented.