POND SUCCESSION ON THE KAIBAB PLATEAU, ARIZONA

A Thesis Submitted to the Faculty of

Baylor University

In Partial Fulfillment of the

Requirements for the Degree

of

Master of Science

in

Biology

By

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Waco, Texas

August, 1969

ABSTRACT

Quantitative data were obtained for a seral comparison of five sinkhole ponds on the Kaibab Plateau, Arizona. Species diversity, community metabolism, primary production, and relative seral rank were assayed.

Information theory and non-information theory species diversity indices were used to compare the phyto- and zooplankton, benthos, and emergent vegetation both within and among ponds. Species diversity of these four pond features showed large fluctuations, hence diversity indices afford distinction only between early versus late seral stages.

The ponds were divided into early versus late categories based on community metabolism estimates, as calculated by the diel oxygen curve method. Primary production values, derived from diel oxygen curve values, indicate that primary production increases during succession to a certain point, then decreases as the aquatic ecosystem approaches senescence.

Methods of estimating seral stage based on measurements of individual characteristics were ineffective, so a systems analysis approach was developed. Species diversity, photosynthesis-respiration ratio, and mean depth were related mathematically to produce a seral ranking value which varies directly with seral stage. Values calculated with this formula correspond well with presumed seral stages of the ponds.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

ACKNOWLEDGMENTS

Greatest thanks are due Dr. Frederick R. Gehlbach, who drew up the overall plan for this study, arranged for funding, and provided direction during the course of the study. I wish to thank my wife, Jerry Lynn Kimmel, for her help as a field and laboratory assistant.

Dr. Owen T. Lind gave valuable advice and assisted by loaning equipment, as did Dr. W. Eugene Crowder. Mr. Charles Poe, Mr. Bert Moulden, and Dr. Howard Rolf, of the Baylor University Data Processing Center, developed computer programs and provided assistance in developing mathematical formulae.

Mr. Merrill D. Beal and Mr. Larry Henderson of the National Park Service, Grand Canyon National Park, Arizona, provided great assistance in arranging laboratory and living space and in handling certain administrative details of the project. Dr. Helen B. Correll identified plants, and Mr. George Beck and Mr. Peter Bennett provided advice in the field. Dr. O.T. Hayward read the manuscript.

Primary funds were provided by the Grand Canyon Natural History Association, and equipment funds by the National Science Foundation.

INTRODUCTION

Little is known concerning the interrelationships of the kinds of organisms and numbers of individuals (community structure) in terms of pond succession. Nor is the relationship of community structure with photosynthesis-respiration ratios and primary production (community metabolism) well understood. Shelford (1911) offers criteria for the various stages of pond succession and considers ponds as complex communities. Unfortunately, many subsequent papers do not build on Shelford's levels of integration, but revert to classical, descriptive studies of ponds (Ball and Hayne, 1952; Eggleton, 1931; Jewell, 1927; Kenk, 1949; Lindeman, 1941; Lippert and Jameson, 1964; Mozley, 1932; Petersen, 1926).

Dineen (1953) offers the most comprehensive study of a small body of water. The number of samples taken and his effort to deal with both population dynamics and energetics in a Minnesota pond is impressive, but the treatment of community structure goes no further than describing various population fluctuations, and lacks synthesis.

The purpose of this study is to elucidate successional changes in five natural ponds on the Kaibab Plateau, Arizona, as a possible basis for practical consideration of water resources in Grand Canyon National Park. Comparative species diversity of phyto- and zooplankton, benthos, and emergent vegetation, on both seasonal and among-pond bases is one criterion emphasized. Photosynthesis-respiration ratios and primary production, both calculated from diel oxygen curves, comprise other criteria.

Measurable characteristics of each pond are related in a simple systems analysis approach to seral ranking of the five ponds. Two non-information theory diversity indices are compared to two information theory diversity indices to help establish quantitative ecological criteria.

My first hypothesis is that clear-cut differences exist between different seral stages on the basis of within- and among-pond comparisons of species diversity.

Margalef (1958) indicates that as an ecosystem matures, community structure becomes more complex. The number of species increases, the distribution of individuals in species becomes more even, food webs increase in complexity, and species become more specialized. Several theoretical indices of relationship of number of species and number of individuals have been advanced (Fisher, Corbet, and Williams, 1943; Odum, Cantlon, and Kornicker, 1960; Preston, 1948), but it seems advantageous to measure species diversity directly.

Margalef (1956, 1958) was the first to apply information theory to the study of community structure, and has been followed by many recent investigators (Lloyd, Zar, and Karr, 1968; Pielou, 1966a, 1966b; Wilhm and Dorris, 1968).

Diversity indices based on information theory account for the distribution of individuals in species.

Lloyd et al. (1968) define the information content of a community as being "... equivalent to the uncertainty involved in predicting which species an animal would be confronted with by the next random encounter -- assuming that it wanders freely over the entire community." The greater the information content, that is, the more species present and the more even the distribution of individuals among the species, the greater is the diversity.

My second hypothesis is that ponds in different seral stages have different photosynthesis-respiration ratios, with early stages having P/R in excess of 1, later stages with P/R less than 1 (Odum, 1956).

The diel oxygen curve method of measuring photosynthesis-respiration ratios was developed by Odum (1956), Odum and Hoskin (1958), and modified by McConnell (1962). It is based on the calculation of total community respiration over a 24 hr. period by extrapolating the rate of oxygen consumption in a pond from sunset to the following sunrise through to the next sunset. Photosynthesis rate is determined by measuring the change in the dissolved oxygen concentration from sunrise to sunset. Gross photosynthesis is derived by taking the algebraic difference between the end of the extrapolated respiration line and the last measured sunset oxygen value.

Goldman (1968) relates primary production and seral stage by a bell-shaped curve. Primary production increases with succession to a certain point, then decreases as the aquatic ecosystem becomes senescent. Thus, primary production seems limited in usefulness as a seral indicator due to its non-linear relationship with succession, but it may serve to substantiate other seral indicators.

The third hypothesis is that several pond characteristics can be related in a simple non-cumulative manner to give a useful seral ranking formula.

Different characteristics must be considered in conjunction if generalizations are to be made concerning ecosystem factors (Goldman, 1968; Odum, 1969; Rawson, 1960). Some factors have inverse relationships, some have synergistic effects, and others are only indirectly related (Odum, 1969). If the variety of biological features of Kaibab Plateau ponds are useful measures in assessing water resource dynamics in that area, some effort must be made to relate them in a meaningful way.

Goldman, Gerlelli, Javornicky, Melchiorri-Santolini, and DeAmezaga (1968) relate eleven parameters in a progressive multiple correlation, and indicate that after correlating oxygen, light, species diversity, temperature, and silicates, little information was gained by including other factors. Additional, similar work is necessary to limit the number of variables necessary in a general formula. Rawson (1960) relates a number of factors in a simple cumulative formula and establishes scores for twelve northern Saskatchewan lakes. A cumulative relationship does not seem valid without detailed analysis of the factors cumulated.

DESCRIPTION OF STUDY AREA

The study ponds, locally called lakes, are located between $36^{o}10'$ to $36^{o}25'$ north and $111^{o}55'$ to $112^{o}10'$ west, on the Kaibab Plateau, Coconino County, Arizona. Three of the ponds are in Grand Canyon National Park, two in the Kaibab National Forest.

The Kaibab Plateau has an elevation of ca. 2400 to 2700 m (8000-9000 ft.), abruptly truncated on the south by the Grand Canyon. The surface structure is the southwardly dipping Permian Kaibab limestone.

Merkel (1962) divides the Kaibab Plateau into three biotic communities. Below ca. 8250 ft. the dominant community consists primarily of ponderosa pine, *Pinus ponderosa*. Above ca. 8250 ft. a mixed white fir, *Abies concolor*, and ponderosa pine forest occurs, with the fir as the dominant species. Aspen, *Populus tremuloides*, occurs in groves in this community. The third community comprises the natural meadows which occur in shallow valleys on the Kaibab Plateau. Dominant plants of this community are the grasses *Muhlenbergia montana*, *Sitanion hystrix*, *Festuca ovina*, *Koeleri cristata*, and *Blepharoneuron tricholepis*. In grazed meadows in the Kaibab National Forest all grass species are reduced except *Blepharoneuron tricholepis*, which occurs more abundantly than in the ungrazed meadows.

Greenland Lake and Harvey Meadow Pond are in aspen groves in the white fir-ponderosa pine community, Little Park Lake lies between ungrazed meadow and white fir-ponderosa pine forest, and Indian Lake and Boundary Pond are in grazed meadows.

Most summer precipitation is in August, although in 1967 and 1968 (the years of the study) considerable rain fell in July. December through March precipitation rates are high due to the large snowfall, often accumulating to 3 m (9 ft.). Mean minimum temperatures range from -12 C (9 F) in February to 8 C (47 F) in July. Mean maximum temperatures range from 2 C (35 F) in January to 25 C (77 F) in July (Grand Canyon National Park data). The large amount of snow and low temperatures probably impose severe limitations on community structure and metabolism in the ponds, though no sampling has been attempted during the winter.

Figures 1 through 10 show extensive emergent vegetation in Boundary Pond, Little Park Lake, and Greenland Lake, smaller amounts in Indian Lake, and none in Harvey Meadow Pond. Glyceria borealis, Sparganium simplex, and Potamogeton grammiueus x illinonesis are the dominant species. Greenland Lake exhibits patchy zonation, probably resulting from its very flat shallow basin. Boundary and Little Park ponds have concentric zonation, Indian Lake has only G. borealis scattered in the shallow portions. Based on the criteria of Lippert and Jameson (1964) Boundary, Little Park, and

FIGURE 1. HARVEY MEADOW POND

FIGURE 2. INDIAN LAKE

FIGURE 3. BOUNDARY LAKE

FIGURE 4. LITTLE PARK LAKE

FIGURE 5. GREENLAND LAKE





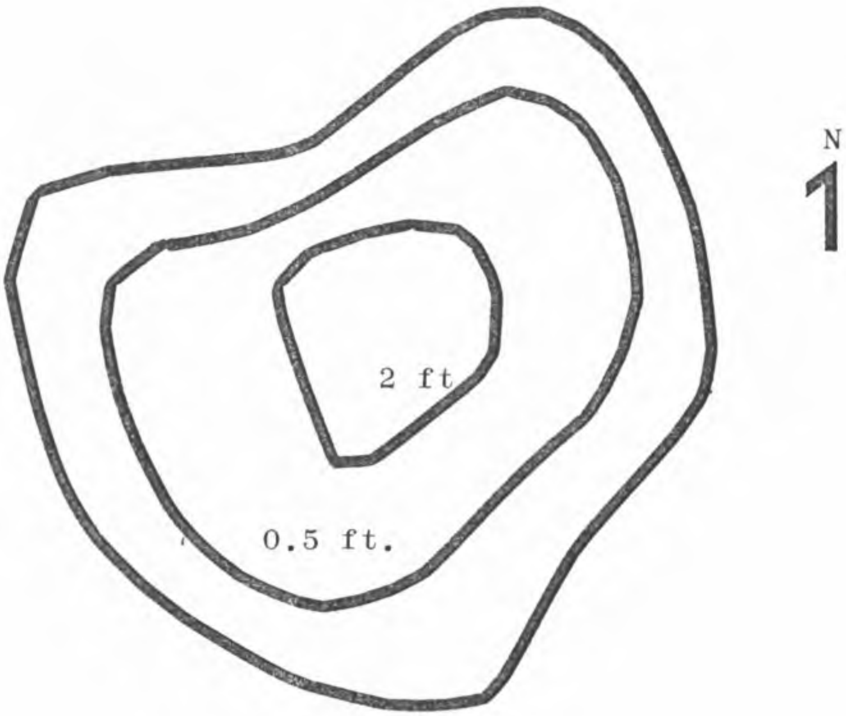


FIGURE 6. HARVEY MEADOW POND

Scale: 1" = 20'

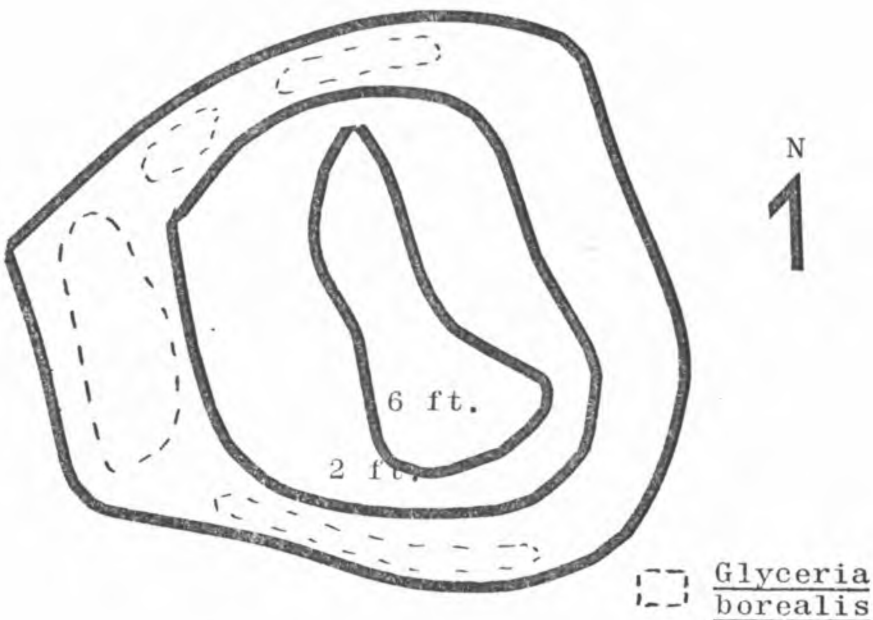


FIGURE 7. INDIAN LAKE

Scale: 1" = 40'

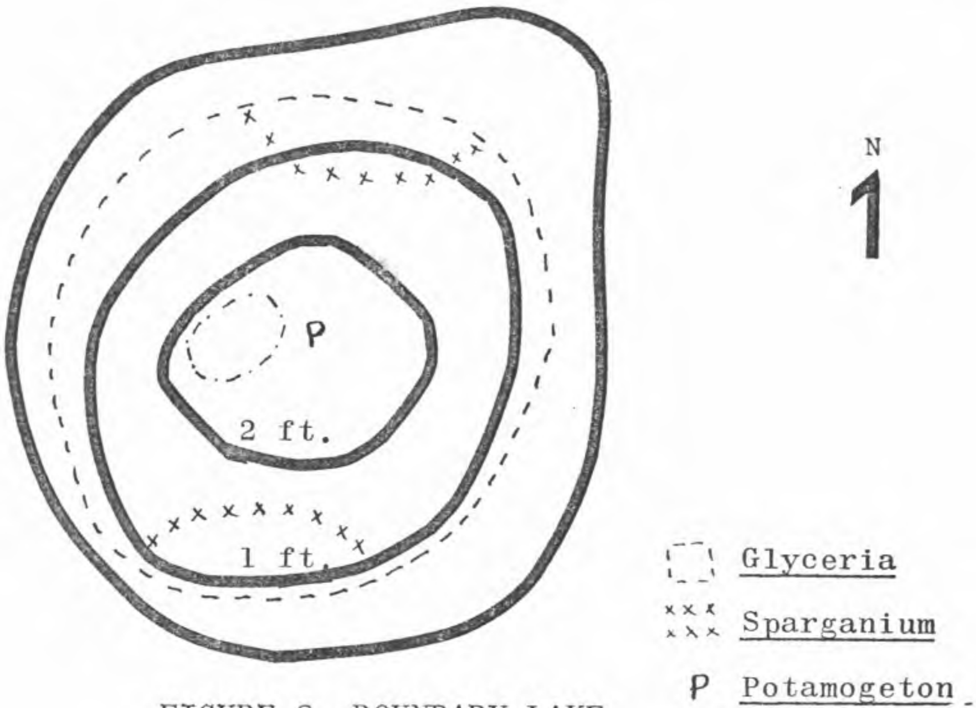


FIGURE 8. BOUNDARY LAKE
Scale: 1" = 40'

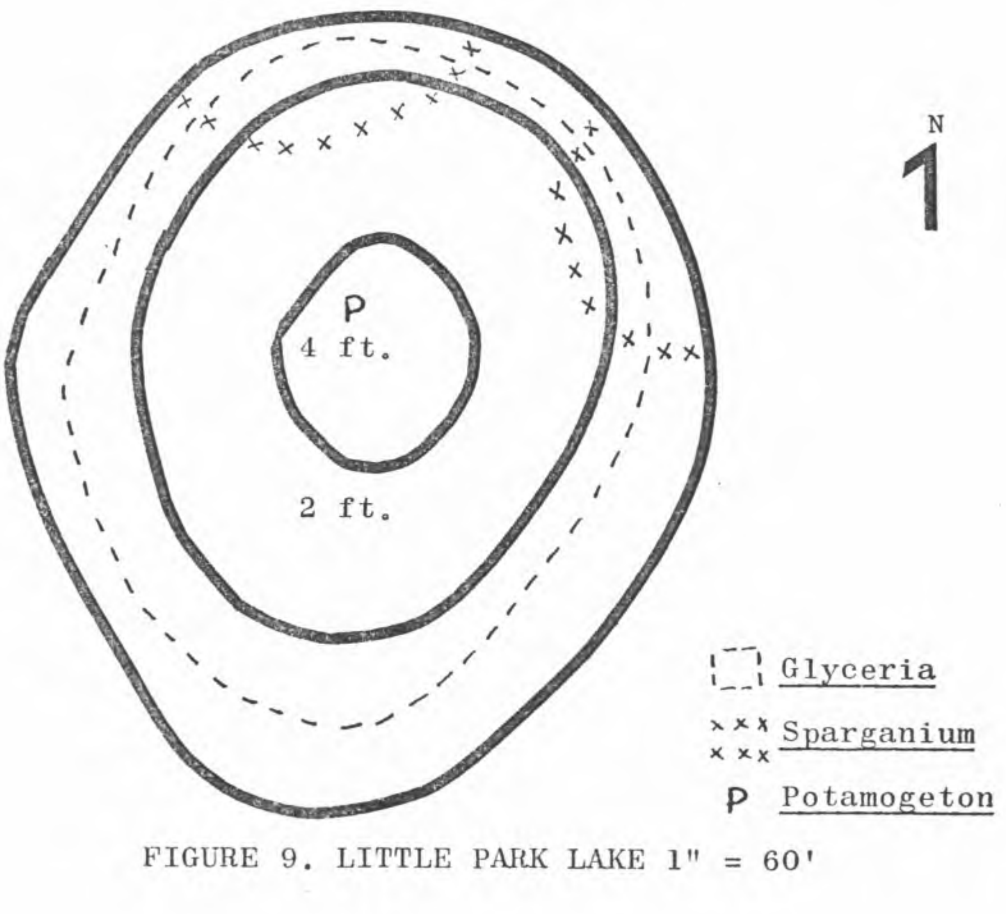


FIGURE 9. LITTLE PARK LAKE 1" = 60'

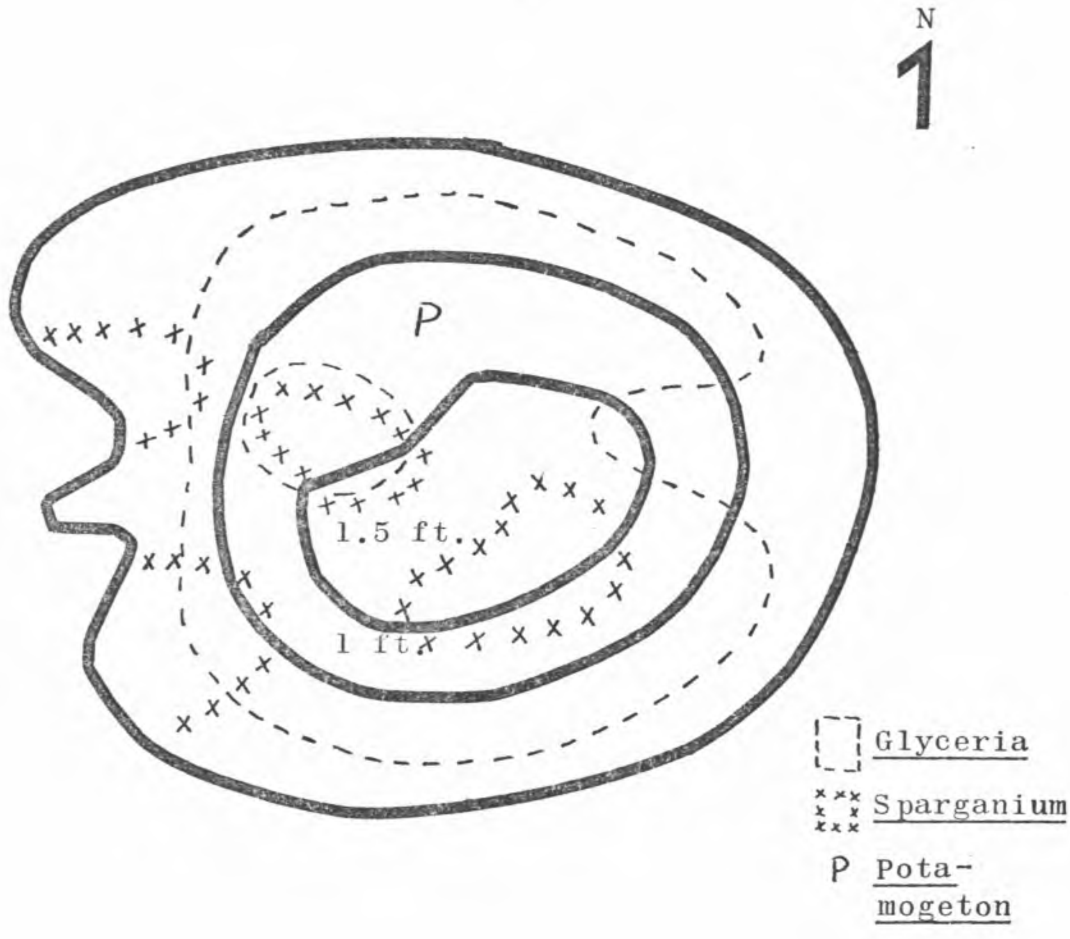


FIGURE 10. GREENLAND LAKE

Scale: 1" = 40'

Greenland ponds are late seral stages, while Indian Lake and Harvey Meadow Pond are presumed to be early seral stages.

The ponds are either unmodified natural depressions (sinkholes) or sinkholes modified by low earthern dams. Their morphological characteristics (Table 1) are important, since the main successional trend includes topographic change. European limnologists (Ruttner, 1966) have used mean depth (volume/surface area) as a seral criterion; because this ratio is an expression of basin shape. The higher the ratio, the more conical the basin (e.g. Indian Pond, Table 1). As a pond proceeds toward a terrestrial ecosystem, the basin fills in and becomes less conical. Though it is invalid to compare a series of ponds strictly on the basis of mean depth because ponds initially may have different basin shapes, mean depth is an indicator of relative longevity of the aquatic ecosystem.

The study ponds did not vary significantly ($P > 0.05$) in water temperature (Table 2) nor did they have thermal stratification, due to their shallow basins.

Harvey Meadow Pond (Figs. 1 and 6) is located ca. 1.6 km (1 mi.) north of the Grand Canyon National Park North Rim Ranger Station. The east shore is formed by a limestone cliff. An unpaved road (NPS W-2) is tangential to the pond on its west side. Roadside drainage ditches and a culvert under the road drain runoff into and overflow out of the pond from adjacent Marble Flats and Harvey Meadow.

TABLE 1. MORPHOMETRIC DATA

Pond	Surface Area		Volume		Max. Depth		Mean Depth	
	m^2	$ft.^2$	m^3	$ft.^3$	m	ft.	m	ft.
Harvey	366	3944	107	3767	0.76	2.5	0.29	0.95
Indian	977	10,512	932	32,895	1.83	6.0	0.95	3.13
Boundary	483	5199	184	6484	0.76	2.5	0.38	1.25
Little Park	3689	39,690	2167	76,491	1.22	4.0	0.58	1.90
Greenland	1914	20,593	679	23,949	0.76	2.5	0.35	1.16

TABLE 2. TEMPERATURES (C) OF NORTH RIM PONDS, SUMMER, 1968

Pond	Sunset Mean	Range	Sunrise Mean	Range
Harvey	21	15-26	14	11-18
Indian	20	13-23	15	10-18
Boundary	21	13-24	13	9-17
Little Park	21	13-23	13	8-15
Greenland	20	15-26	15	11-21

Harvey Meadow Pond was turbid, with Secchi disk readings less than 10 cm. Heavy siltation from the drainage probably accounts for the turbidity and for ca. 50 cm (1.5 ft.) of soft sediment on the bottom. Harvey Meadow Pond is the only pond studied that was exceptionally turbid, and the only one subject to heavy man-induced drainage.

Indian Lake (Figs. 2 and 7) is east of Arizona highway 67, ca. 6.5 km (4 mi.) north of the North Rim Entrance Station, in the Kaibab National Forest. It is a large sinkhole deepened to an undetermined extent by the roadbed which is tangential to the pond on the west. All sides are steep, and the basin shape is almost conical except for a shelf on the west shore. Secchi disk readings were usually ca. 1 m (3 ft.). The bottom is firm and covered with small stones.

Indian Lake is subject to livestock use, and in summer, 1967, ca. 400 l/week (100 gal.) of water were pumped from it. Such pumping was not observed in 1968.

Boundary Pond (Figs. 3 and 8) is west of Arizona highway 67, ca. 0.5 km (0.25 mi.) north of the North Rim Entrance Station, in the Kaibab National Forest. The pond is apparently an unmodified sinkhole, with a steep west shore and a gently sloping east shore. The pond is subject to cattle grazing and watering. Secchi disk readings were usually to maximum depth. The bottom is soft mud and decaying vegetation.

Little Park Lake (Figs. 4 and 9) is located east of

Arizona highway 67, ca. 1.2 km (0.75 mi.) south of the North Rim Entrance Station in Grand Canyon National Park. The pond is on the edge of Upper Little Park (meadow) with a steep forested slope east of the pond. The main body of the pond is surrounded by meadow. The basin is apparently a sinkhole, modified by a low earthern dam on the west side. The dam is ineffective in increasing pond capacity. Turbidity was low, with Secchi disk readings to maximum depth. The water was shaded by emergent vegetation, and the bottom covered by decaying vegetation.

Greenland Lake (Figs. 5 and 10) is located on the Walhalla Plateau of Grand Canyon National Park, a peninsula of land extending into Grand Canyon from the Kaibab Plateau. The pond is west of the National Park Service road leading to Cape Royal, on the narrowest part of the Walhalla Plateau, ca. 0.8 km (0.5 mi.) from the canyon rims to the north-northeast and south-southwest. It is in a shallow draw, with an ineffective earthern dam on its west side. Turbidity was low, with Secchi disk readings to maximum depth. The water was shaded by emergent vegetation, and the bottom covered by decaying vegetation.

METHODS

Field Methods

Field work was conducted from mid July until late August, 1967, and from early June until late July, 1968. Five ponds were selected to represent presumed stages of succession from early to late. Only ponds with populations of larval tiger salamanders (*Ambystoma tigrinum*) were chosen, since this study is part of a broader ecological study of the salamander.

Ponds were mapped and sounded in 1967. Percent cover of emergent vegetation was measured by lines of 2 ft. square quadrats, set to cross and include all vegetation zones. Plankton and benthos were sampled in 1967 at three-week intervals for reconnaissance and were not included with 1968 data. In 1968 plankton was sampled at weekly intervals, and benthos at biweekly intervals. Plankton was sampled by pouring 40 liters of pond water through a #25 plankton net. Benthos was sampled by one haul of a 0.02 m^2 (0.25 $ft.^2$) Ekman dredge. Samples were preserved in 10% formalin and examined later. Sample stations were selected so that no sample would be affected by a previous one. All samples were taken in water ca. 0.5 m (1.5 ft.) deep, in locations where emergent vegetation would not foul the dredge or net.

Turbidity (visibility) was measured by occasional Secchi disk readings. Temperature was measured with a thermistor each sunrise and sunset, when a diel oxygen curve was run. Water samples for dissolved oxygen were taken at sunset, sunrise, and the following sunset on all days which met climatic conditions required for the diel oxygen curve method of community metabolism estimation (lack of strong wind and no rain for 24 hours) (Lind, 1966). Samples were taken with a 3 l PVC Kemmerer sampler. The ponds were divided into two sampling groups based on proximity: Harvey Meadow Pond and Greenland Lake as one group; Little Park Lake, Boundary Pond, and Indian Lake as the other. Each group was sampled on alternate appropriate days to avoid an artifact of sample time in the data.

Laboratory Methods

Plankton counts were made by eight sweeps through 1 ml of sample using a compound microscope (100X). Benthos samples were washed through soil seives (smallest diameter 0.5 mm) and examined under a dissecting microscope. In both cases, identifications were made as completely as possible (Edmondson, 1959), and number of individuals of each taxon was counted. The 1968 benthos samples were kept for ash-free weight determinations (American Public Health Association, 1965) for biomass species diversity indices (Wilhm, 1968). Flotation methods of benthos enumeration

(Anderson, 1959) were not effective on samples from Boundary Pond, Little Park, and Greenland Lakes because of the great amount of plant detritus in the samples. Thus, flotation was not used for enumeration of any of the samples to prevent introducing a variable.

All dissolved oxygen samples were titrated by the azide modification of the Winkler method (American Public Health Association, 1965), further modified by use of phenylarsene oxide as a titrant and 200 ml samples for titration. Titrations were made to the nearest 0.05 ml with an automatic buret.

Analytical Methods

Menhinick (1967) maintains that

$$D = m/N^{1/2} \tag{1}$$

where: D = diversity

m = total number of species in sample

N = total number of individuals in sample

is sensitive to varying distributions of individuals in species, but other workers indicate that provision must be made for the number of individuals in each species (Margalef, 1958b).

The interspecies contact index (Menhinick, 1967b)

$$IC = 1 - \sum_{i=1}^{m} n_i^2 - \sum_{i=1}^{m} n_i/N(N - 1) \quad (2)$$

where: IC = interspecies contacts

n_i = number of individuals in the i^{th} species

m and N as in (1)

seems to account for the distribution of individuals in species, but has not been widely applied.

Pielou (1966a) classifies common ecological sampling procedures and categorizes diversity indices derived from information theory according to various sampling techniques. The index derived by Brillouin (1956) and modified by Margalef (1958, 1968)

$$D = 1/N \log_2 N!/n_a!n_b!\ldots n_m! \quad (3)$$

where: D, m, N as in (1)

$n_a, n_b, \ldots n_m$ = number of individuals in species a, b,...m

is believed to be useful only when all individuals in a collection can be identified and counted, as with benthos and emergent vegetation samples. The index derived by Shannon and Weaver (1949)

$$D = \sum_{i=1}^{m} n_i/N \log_2 n_i/N \quad (4)$$

where: D, n_i, N as in (2)

is useful when the collection is too large to allow all individuals to be counted, and a smaller sample must be used for enumeration, as in plankton samples.

Both formulae (3) and (4) are to be used only when the number of species in the sample is known or reasonably represented. This last criterion is met as long as there is not a large number of species each with only one or two individuals (Pielou, 1966a).

The indices of Brillouin (1956) and Shannon and Weaver (1949) were used for situations which both meet and fail to meet Pielou's (1966a) criteria in an effort to show the relationship between diversity indices and sampling methods. For correlation coefficients and seral rank calculations the indices were used in accord with Pielou. In addition to the calculated indices, the Odum et al. (1960) diversity curves were plotted for each sample, but offered no additional information.

Species diversity indices can be "swamped" by an over abundance of one species, producing a misrepresentation of community structure. Dickman (1968) has proposed a method to alleviate swamping, but it is not sound due to an excess of derived variables. For my three samples of Greenland benthos, diversity values including the chironomid, *Podonomus*, are 1.20, 0.85, and 0.96; without *Podonomus* the corresponding values are 2.36, 1.80, and 1.71. *Podonomus* is the only organism in the present study which produces this effect; nevertheless, it is evident that cognizance must be taken of all species in a community when considering calculations of species diversity. Diversity calculations used in synthesis in this paper omitted Podonomus.

A Fortran computer program (Appendix) was written to compute formulae (1), (2), (3), and (4). Computations were made on a Honeywell 1200 computer in the Baylor University Data Processing Center. Other calculations, including means, standard errors, standard deviations, and Pearson Product Moment Correlation Coefficients, were made on a Monroe Epic 3000 calculator in the Baylor Department of Biology.

Gross photosynthesis and respiration values derived from 7 diel curves per pond were used to calculate mean photosynthesis-respiration ratios and primary production values for each pond.

To better approximate true primary production in the five ponds, gross photosynthesis values were converted to a m^2 basis by multiplying m^3 values by the mean depth. None of the ponds has a mean depth equal to one meter, and the photic zone includes the entire pond in all cases.

A simple formula was derived to relate species diversity, mean depth, and community metabolism and so provide an ordinal value by which to rank the five ponds according to seral stage. The following value varies directly with seral stage.

$$SR = \sum \text{div. indices}^{1/2} - \text{mean depth}^{1/2} - \text{mean } P/R^{1/2} \quad (5)$$

An SR (seral rank) value was calculated for each pond, using appropriate (Pielou, 1966a) diversity indices for phyto- and zooplankton, benthos, and emergent vegetation. Square roots of all values were used to reduce the size effect of any individual value. Mean depth and mean P/R are inversely related to species diversity, hence are subtracted from diversity values.

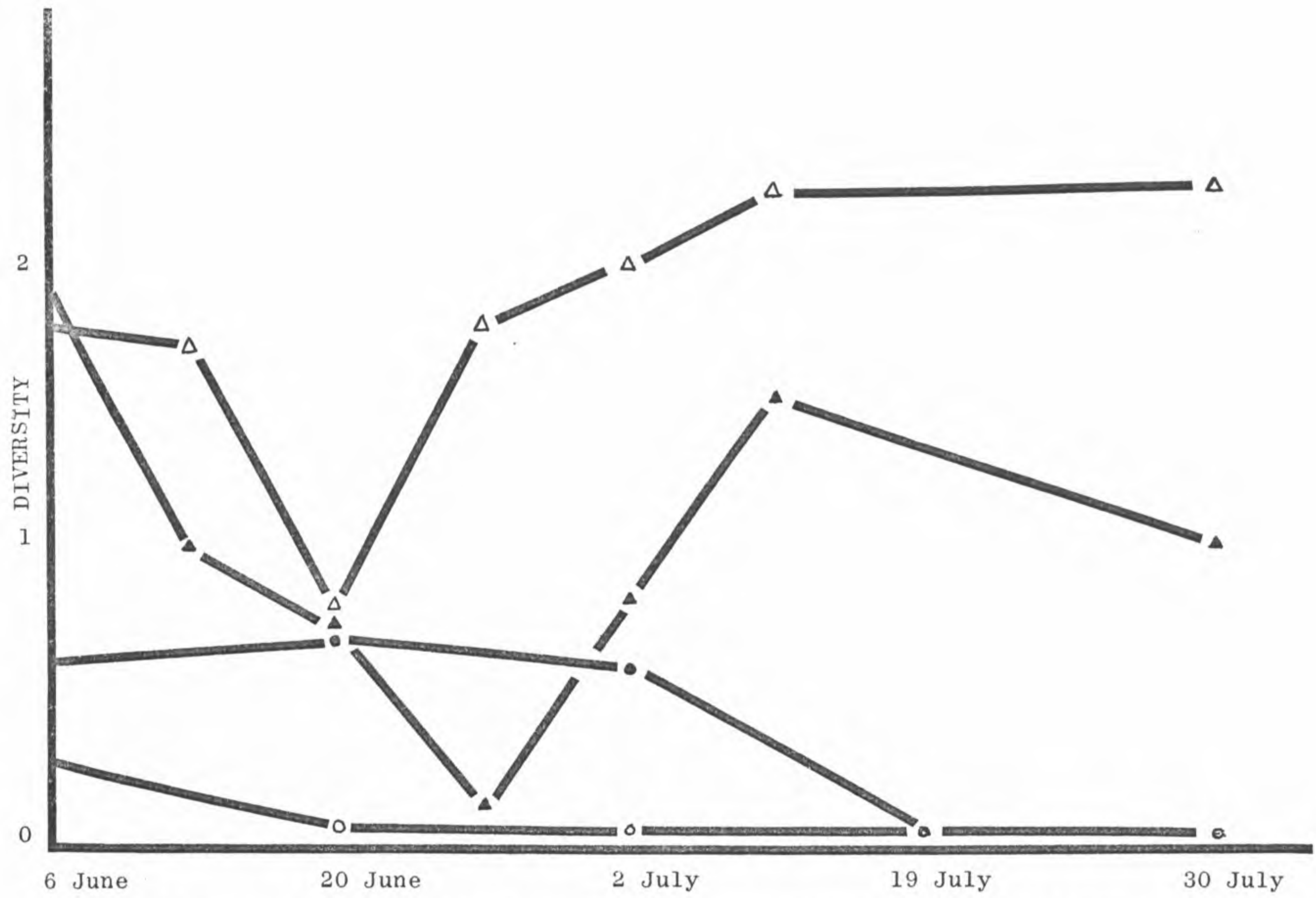
RESULTS

Figures 11 through 15 show seasonal succession and indicate a wide divergence in both direction and amplitude of species diversity for the samples plotted. Phyto- and zooplankton diversity was, in most cases, greater than that of benthos (Table 3). This is the reverse of the concept of Margalef (1963) in that the benthos, with relatively fixed spatial positions between each of its members, has a presumed potential of a greater diversity than the highly labile plankton.

A low diversity was maintained in the phytoplankton in relation to the zooplankton. This agrees with Margalef (1968) because energy passes from the phytoplankton to the zooplankton thus increasing the information level in the zooplankton at the expense of the phytoplankton. This further separates the two in information content, hence diversity.

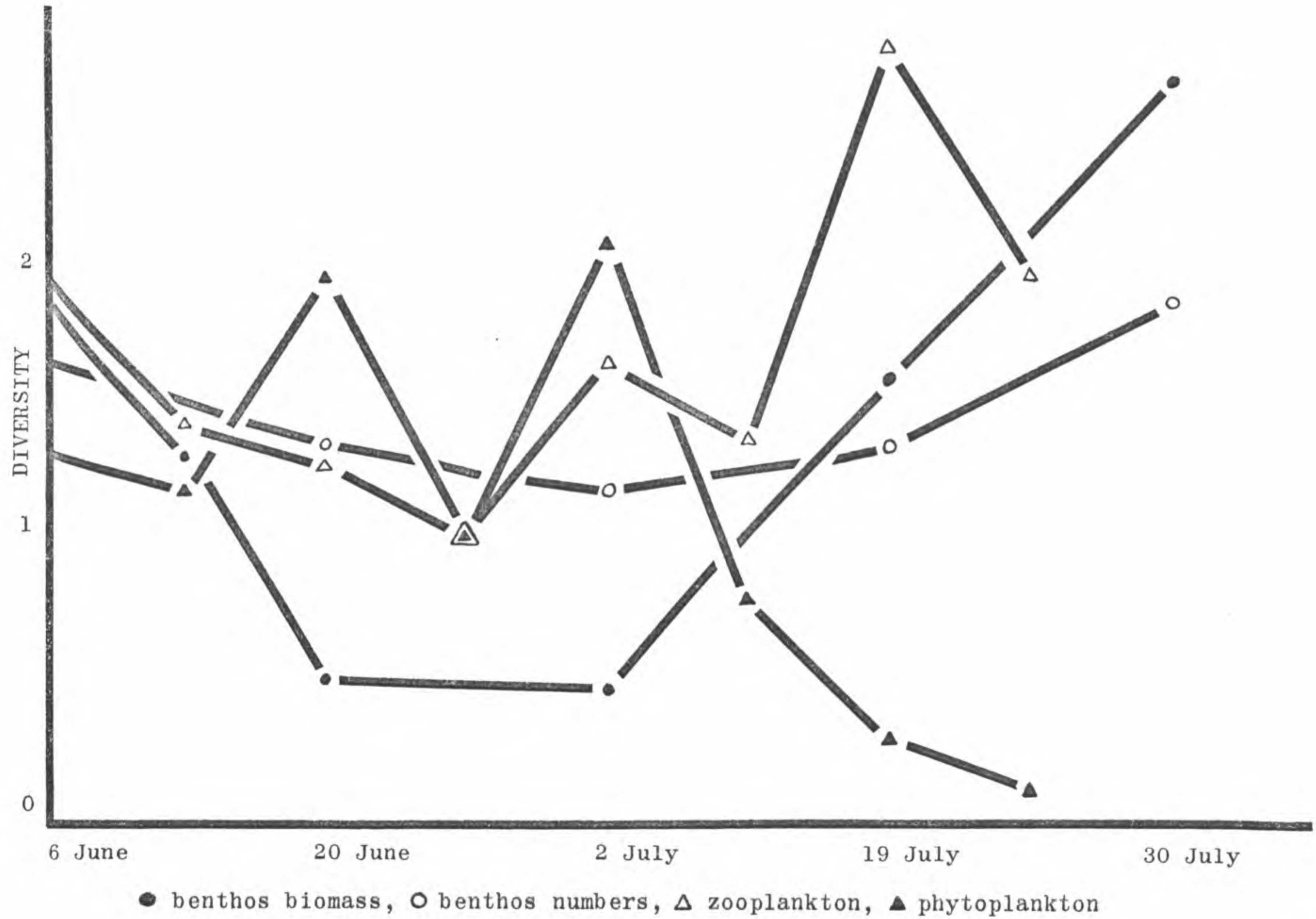
Figures 11 through 15 indicate wide fluctuations of seasonal species diversity in all ponds. A slight reduction of fluctuations during the latter part of the season is evident in Boundary Pond phyto- and zooplankton (Fig. 13), Little Park Lake benthos individuals and phytoplankton (Fig. 14), and Greenland Lake phyto- and zooplankton (Fig. 15) species diversity curves. No other seasonal successionary trends are common among the five ponds.

FIGURE 11. SEASONAL SUCCESSION CURVES, HARVEY MEADOW POND



● benthos biomass, ○ benthos numbers, △ zooplankton, ▲ phytoplankton

FUGURE 12. SEASONAL SUCCESSION CURVES, INDIAN LAKE

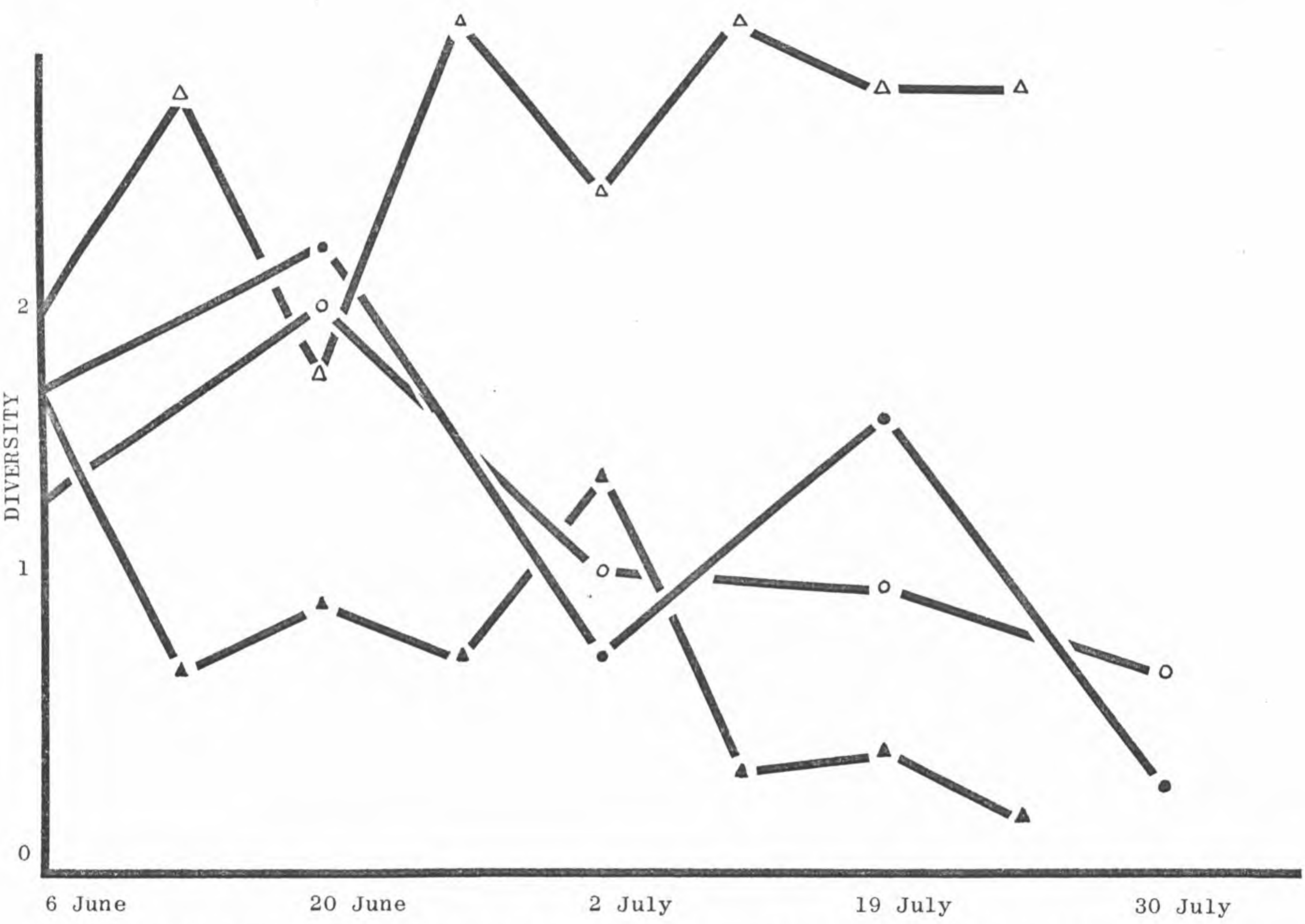


DIVERSITY
2
1
0
6 June
20 June
2 July
19 July
30 July
● benthos biomass, ○ benthos numbers, △ zooplankton, ▲ phytoplankton

FIGURE 13. SEASONAL SUCCESSION CURVES, BOUNDARY POND

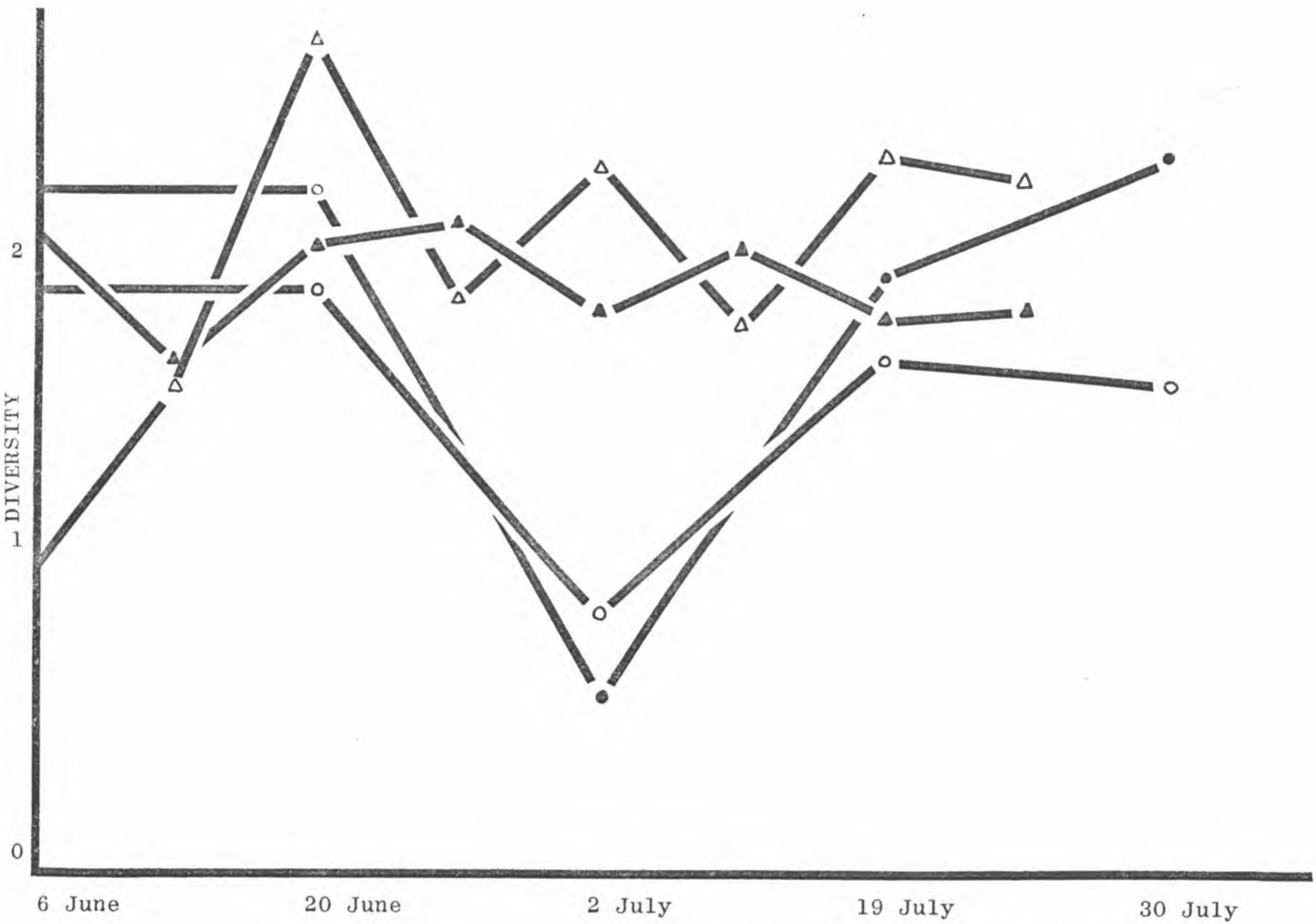

DIVERSITY
2
1
0
6 June
20 June
2 July
19 July
30 July
● benthos biomass, ○ benthos numbers, △ zooplankton, ▲ phytoplankton

FIGURE 14. SEASONAL SUCCESSION CURVES, LITTLE PARK LAKE



● benthos biomass, ○ benthos numbers, △ zooplankton, ▲ phytoplankton

FIGURE 15. SEASONAL SUCCESSION CURVES, GREENLAND LAKE



● benthos biomass, ○ benthos numbers, △ zooplankton, ▲ phytoplankton

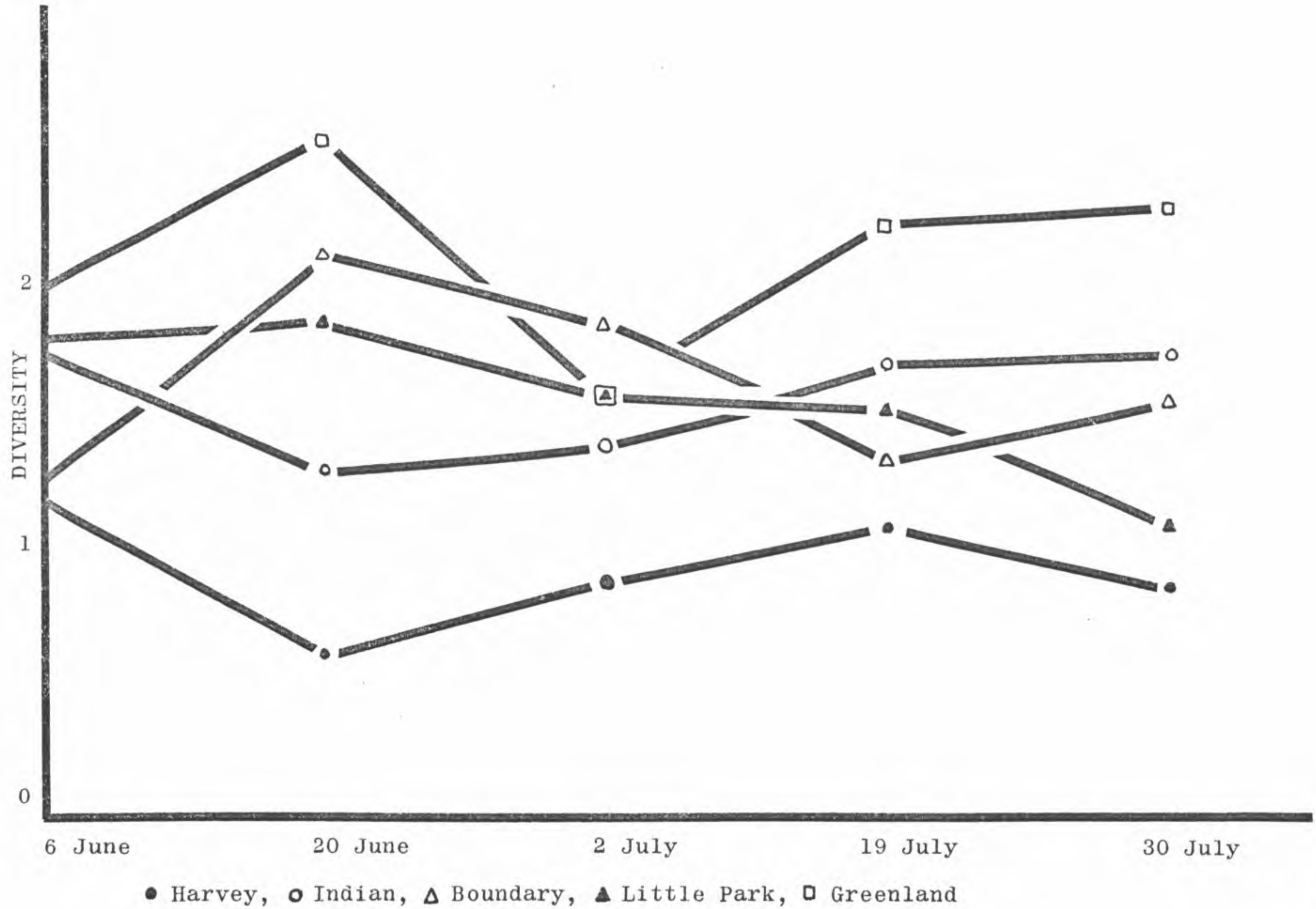
TABLE 3. SPECIES DIVERSITY VALUES FOR EACH POND

Pond	Phyto-plankton Mean N=8	Zoo-plankton Mean N=8	Benthos Numbers Mean N=5	Benthos Biomass Mean N=5	Emergent Vegetation
Harvey	1.04	1.75	0.06	0.37	0.0
Indian	1.08	1.60	1.45	1.39	0.0
Boundary	1.99	2.37	1.01	0.93	0.78
Little Park	0.78	2.68	1.25	1.37	1.42
Greenland	2.07	2.11	1.68	1.99	1.34

Differences in the possibility of adequately sampling benthos and plankton, in the possibility of completely enumerating certain samples, and probable inherent differences in community dynamics such as competition, grazing, predation, and cooperation (Yount, 1956) cause (1) large fluctuations in values of species diversity, and (2) different seral ranking dependent upon the pond's communities sampled (phyto- and zooplankton, benthos, or emergent vegetation). When diversity indices for each sample at a given sample time are added (e.g., phytoplankton diversity + zooplankton diversity + benthos diversity) fluctuations are damped and trends are apparent (Fig. 16). These cumulative seasonal diversity curves fall into two general categories: Harvey and Indian Ponds show a decrease in diversity in late June, while Boundary, Little Park, and Greenland Ponds show a concomitant increase in diversity. These two categories correspond to the early versus late division shown below by community metabolism data, and imply that seasonal trends differ with seral stage. The complete meaning of this is difficult to determine with the information available, but it is evident that direct correlation of diversity with age possibly does not hold true during all stages of succession.

The criteria of Pielou (1966a) prohibit use of plankton, benthos, and emergent vegetation data in a cumulative species diversity index because the samples must be enumerated

FIGURE 16. CUMULATIVE SEASONAL SPECIES DIVERSITY CURVES


DIVERSITY
2
1
0
6 June
20 June
2 July
19 July
30 July
● Harvey, ○ Indian, △ Boundary, ▲ Little Park, □ Greenland

differently.

Table 4 indicates significant ($P < 0.05$) correlation between information theory indices and non-information theory indices when used for zooplankton and benthos samples; results were the same for other types of samples. Index (1), the simple diversity formula, failed to correspond with the other indices in ranking all samples, but every other index produced the same ranking, though the magnitude was different due to mathematical differences in calculation. I did not observe the errors indicated by Pielou (1966a) when the formulae were misused with my data.

Odum (1956) indicates that P/R values should fluctuate around 1, with autotrophic communities being greater than 1, heterotrophic communities less than 1. Odum (1956) and Margalef (1963) indicate that photosynthesis decreases per unit plant biomass in later stages of succession; therefore, P/R should be inversely related to seral stage. Table 5 indicates a decrease in P/R from Harvey Meadow Pond to Greenland Lake, roughly corresponding inversely with species diversity (Table 3, Fig. 16). Due to the large range of P/R values, sampling period limitation as result of rain, and relatively few samples, it is dangerous to rank the ponds by P/R in more than an early versus late division.

TABLE 4. PEARSON PRODUCT MOMENT CORRELATION COEFFICIENTS FOR DIVERSITY INDICES

	Species-individual Ratio (1)	Interspecies Contact (2)	Brillouin (3)	Shannon-Weaver (4)
Benthos				
(1)	-	0.91**	0.89*	0.99***
(2)		-	0.99***	1.00***
(3)			-	0.99***
(4)				-
Zooplankton				
(1)	-	0.55	0.75*	0.77*
(2)		-	0.97***	0.98***
(3)			-	0.99***
(4)				-

*, **, *** indicate $P < 0.05, < 0.01, < 0.001$, respectively

TABLE 5. MEAN P/R CALCULATED BY THE DIEL OXYGEN CURVE METHOD

Pond	Mean P/R N=7	Variance	Standard Error	Range
Harvey	1.07	0.015	0.023	0.93-1.32
Indian	1.05	0.018	0.051	0.90-1.33
Boundary	0.97	0.005	0.028	0.86-1.07
Little Park	0.96	0.022	0.056	0.74-1.20
Greenland	0.94	0.004	0.023	0.84-1.01

Table 6 indicates first an increase followed by a decrease in primary production as related to presumed seral stage (cf. Tables 3 and 4). This agrees with the concept of Goldman (1968). The five study ponds fit a unimodal curve: Harvey Meadow Pond represents an early sere with low primary production, Little Park Lake represents a middle sere, with high primary production, and Greenland Lake is a late sere with low primary production.

Assuming the validity of the relationship discussed by Goldman, primary production values can serve as a possible check on seral ranking formulae. However, since we do not know the form of the non-linear relationship of primary production with succession, primary production values are of limited use in seral ranking.

The seral ranking formula (5) produces the following values: Harvey Meadow Pond, 1.62; Indian Lake, 2.68; Boundary Pond, 4.16; Little Park Lake, 4.20; and Greenland Lake, 5.10. Harvey Meadow Pond is the earliest sere, which is corraborated by its complete lack of emergent vegetation and low species diversity. However, the man-induced turbidity probably introduces an unnatural effect. The calculated successional sequence of the ponds corresponds to the presumed seral stages. While this seral ranking formula is based on consideration of only a few important criteria, it suggests that systems analysis approaches to studies of aquatic ecosystems are useful.

TABLE 6. GROSS PRIMARY PRODUCTION IN FIVE PONDS ON THE KAIBAB PLATEAU, ARIZONA

Pond	Mean gm O_2 m^{-2} day^{-1} N=7	Range
Harvey	1.08	0.20-8.55
Indian	2.53	0.45-6.45
Boundary	3.18	7.45-11.30
Little Park	5.10	5.75-11.90
Greenland	1.73	2.80-6.90

DISCUSSION

P/R values show a definite trend of moderate to high negative correlation with all other biological characteristics (Table 7). A negative correlation is to be expected, according to Margalef (1963) and Odum (1956), because in succession photosynthesis tends to decrease per unit biomass, and organic matter tends to accumulate. P/R shows a significant ($P < 0.01$) correlation with emergent vegetation. Likewise, zooplankton species diversity shows a significant ($P < 0.05$) correlation with emergent vegetation species diversity. The high correlation of P/R and zooplankton species diversity with emergent vegetation species diversity is probably related to a fourth factor of seral stage.

P/R values are not correlated with mean depth (Table 7). P/R is not influenced by this physical factor to the extent that it is invalid as an estimate of biological characteristics. Mean depth tends toward negative correlation with biological characteristics, which, though insignificant ($P > 0.05$), indicates that physical filling-in of a pond increases the successionary trend toward a terrestrial community.

Benthos species diversity calculated using biomass values rather than numbers of individuals indicates a significant ($P < 0.01$) correlation with benthos individuals

TABLE 7. PEARSON PRODUCT MOMENT CORRELATION COEFFICIENTS FOR ALL MEASURED CHARACTERISTICS

	P/R	Phyto-plankton Diversity	Zoo-plankton Diversity	Benthos Numbers Diversity	Benthos Biomass Diversity	Emergent Vegetation Diversity	Heat Budget	Mean Depth
P/R	-	-0.54	-0.79	-0.65	-0.68	-0.96**	0.26	0.28
Phytopl. Div.		-	0.09	0.44	0.35	0.31	-0.47	-0.45
Zoopl. Div.			-	0.24	0.22	0.85*	-0.26	-0.30
Benthos No. Div.				-	0.95**	0.56	0.46	0.46
Benthos Biomass Div.					-	0.63	0.29	-0.03
Emergent Veg. Div.						-	-0.27	-0.29
Heat Budget							-	0.99***
Mean Depth								

*, **, *** indicate $P < 0.05, < 0.01, < 0.001$, respectively

species diversity. Use of biomass rather than numbers of individuals for species diversity calculations does not seem to have the advantage indicated by Wilhm (1968).

Efforts to assess the comparative successional status of ponds by use of either species diversity estimates or estimates of community metabolism are frustrated by several inherent difficulties with each method, and by incomplete understanding of the methods. It thus seems desirable to relate several factors mathematically in a systems analysis approach. Moreover, it is natural to do so, since all factors are interrelated in the ecosystem concept. Though each of the factors independently offered some information, when related to one another in a way which seemed legitimate, they resulted in a meaningful successional sequence indication.

For assessment of water supply and long range planning, information must be available concerning the expected longevity of existing water supplies. In general, longevity of an aquatic ecosystem and its ecological age, expressed by its relative seral stage, are inversely proportional.

SUMMARY

Observable differences occur in five sinkhole ponds on the Kaibab Plateau, Arizona, when compared on the basis of species diversity of phytoplankton, zooplankton, and benthos; and community metabolism and primary production. Diversity tends generally to increase with the ecological age of the system. Community metabolism tends to change from greater than 1 to less than 1 with increasing maturity of the ecosystem, and primary production shows an increase with age to a certain point, followed by a decrease.

When species diversity was used to rank the series of five ponds, an ambiguous order resulted. Assessment of seral stage based on species diversity criteria varies depending on the part of the ecosystem used for comparison. Phyto- and zooplankton, benthos, and emergent vegetation seem to have basically different species diversity characteristics in terms of succession. When the species diversity for all samples taken from a community were added, a less ambiguous ranking resulted.

Several variables, including sampling and enumeration difficulties, were found to influence estimates of species diversity. Unbiased samples of either plankton or benthos are difficult to take, and benthos samples from ponds with large amounts of detritus are unreliable. A "swamping"

effect by very abundant species, and the undetermined effect of succession on all members of an aquatic ecosystem are intrinsic factors which limit the usefulness of species diversity alone as a seral criterion.

Information theory and non-information theory diversity indices were compared. No major disagreement was observed, though indices which account for the distribution of individuals in species seem to be the more reliable.

Estimates of community metabolism rank the five ponds, with Harvey Meadow Pond and Indian Lake having P/R values in excess of 1; Boundary Pond, Little Park Lake, and Greenland Lake with P/R values less than 1. However, seral ranking more precise than this early versus late division was not warranted by either the method or results.

Primary production is not linerally related to succession, and therefore, is limited as a seral criterion when used alone. Results from the five ponds correspond in terms of presumed seral stage with similar comparisons in the literature (Goldman, 1968).

A seral ranking formula was derived which relates species diversity, P/R, and mean depth to give a value which is directly proportional to seral stage. The results of this systems analysis approach seem to correspond with the seral stages of the ponds based on emergent vegetation, and offer a much clearer division than any of the individual characteristics.

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FORTRAN COMPUTER PROGRAM FOR SPECIES DIVERSITY

The following program calculates the formulae of Shannon and Weaver (1949) providing values for mean diversity, minimum diversity, maximum diversity, and redundancy. It also calculates values for the indices of Margalef (1958), Menhinick (1967b), and the simple ratio of number of species to square root of number of individuals. Values on the computer printout for each of the above are headed DBAR, DMIN, DMAX, R, DM, IC, DG, respectively.

Input format is as follows:

Card Column	
1-4	sample date, numerical
5	sample location, alphabetical
6-8	number of individuals in species 1
9-11	number of individuals in species 2

etc, through column 80.

All input values must be right-aligned.

```
SEQ#  LABEL FORTRAN STATEMENT

            DIMENSION Y(25),XN(25),XFAC(25)
            IMPLICIT DOUBLE (X,D,S)
            WRITE(3,101)
      101   FORMAT(1H1,5X,:DBAR:,10X,:DMAX:,13X,:DMIN:,12X,:R:,11X,:DM:,
          1  14X,:IC:,14X,:DG:)
            READ(2,LIST)A
            XM = A
        1   READ(2,10,END = 500)M,I,B,Y
       10   FORMAT(2I2,A1,25F3.0)
            WRITE(3,99)M,I,B
       99   FORMAT(1H2,I2,1X,I2,5X,A1/)
            DO 11 I = 1,25
         11 XN(I) = Y(I)
            SUMN = 0.0
            SUMN2=0.0
            DO 20 I = 1,25
            SUMN = SUMN + XN(I)
            SUMN2 = SUMN2 + (XN(I)*XN(I))
            J = I -1
            IF(XN(I).EQ. 0.0) GO TO 24
        20 CONTINUE
        24 DBAR = 0.0
            DO 30 I = 1,J
            D = (XN(I)/SUMN)*(DLOG(XN(I)/SUMN)/DLOG(XM))
            DBAR = DBAR + D
        30 CONTINUE
            DBAR =-DBAR
            DF = DLOG(1.0D0)
      CDF IS LOG OF N FACTORIAL
            N = SUMN
            DO 40 I =1,N
            SN = I
            DF = DLOG(SN)+DF
        40 CONTINUE
            DF = DF/DLOG(XM)
            S = J
            DN = SUMN/S
            N = SNGL(DN)
            DM = DLOG(1.0D0)
            DO 50 I = 1,N
            DN = I
            DM = DLOG(DN) + DM
        50 CONTINUE
            DM = DM/DLOG(XM)
            DMAX = (1.0/SUMN)*(DF-(S*DM))
            XY = SUMN -(S-1.0)
            N = SNGL(XY)
            DFN = DLOG(1.0D0)
            DO 60 I =1,N
            XY=I
            DFN=DLOG(XY)+DFN
        60 CONTINUE
            DFN = DFN/DLOG(XM)
```

SEQ# LABEL FORTRAN STATEMENT

```
      DMIN = (1.0/SUMN)*(DF-DFN)
      SR = (DMAX - DBAR)/(DMAX -DMIN)
      DO 104 I=1,25
      N= SNGL(XN(I))
      IF(N.EQ.0)GO TO 102
      XFAC(I) = DLOG(1.0D0)
      DO 104 M=1,N
      XF=M
      XFAC(I) = XFAC(I) + DLOG(XF)
104   CONTINUE
102   J = I - 1
      DM = DLOG(1.0D0)
      DO 103 M = 1,J
      DM = XFAC(M) + DM
103   CONTINUE
      DM= DM/DLOG(XM)
      XF = DF-DM
      DM = (1.0/SUMN)*XF
      SIC = 1.0-((SUMN2-SUMN)/(SUMN*(SUMN-1.)))
      DG = S/DSQRT(SUMN)
      WRITE(3,100) DBAR,DMAX,DMIN,SR,DM,SIC,DG
  100 FORMAT(1H ,7(F10.5,5X))
      GO TO 1
  500 STOP
      END
```

	Harvey		Indian		Boundary		Little Park		Greenland	
	1	2	1	2	1	2	1	2	1	2
Bacillariales		C	C	R		R		R		R
Cyanophyta	R		C	C	C	C	A	A		R
Volvocales		A			R	R	R			C
Rotifera	R	C		R	C	R	C	R		R
Copepoda		C	C	R	A	C	C	C		R
Diptera	C	C	C	C	C	C	R	R	A	A
Odonata					R	R				
Anellida	A	C	C	R	C	A	R	R		
Mollusca							R	R		R
Parasitengona									C	R

1 and 2 refer to 31 July, 1967, and 17 August, 1967, respectively

R, C, A refer to 1-10, 11-100, above 100 individuals per sample, respectively

1967 PHYTO-, ZOOPLANKTON, AND BENTHOS TAXA, SEASONAL OCCURRENCE, AND RELATIVE ABUNDANCE

	Harvey								Indian								Boundary								Little Park								Greenland							
	1	2	3	4	5	6	7	8	1	2	3	4	5	6	7	8	1	2	3	4	5	6	7	8	1	2	3	4	5	6	7	8	1	2	3	4	5	6	7	8
<u>Navicula</u> sp.					R	R					R		R		R	R									R		C				R					R	C			
<u>Scenedesmus</u> sp.											R	C	R	R	R			C		C	C	C	R			R	R				R	R	R	R	A	C	C	A	A	A
<u>Anabena</u> sp.					A										A	A				R	R	C	C	A														A	A	A
<u>Dinobryon</u> sp.									R	C	C		C	C			C	C		C	C	C	C	A	C	C	A	A	A	C			C	C	C	A	C	A	C	C
<u>Microspora</u> sp.					C				C	C	R		C	R			R	C	C	C	C	C	C	C	C	A	C	C	A	A	A	A	C	R	C	A	C	A	C	C
<u>Volvox</u> sp.																	R		R									R		C	R				R	R	R			
<u>Closterium</u>																																								
sp. A.																		R	R														C		C	A		C	C	C
sp. B.									R	R	R	C					C			C					R				R											
sp. C.	R	R	R								R		R					R	C	C	C	C	R											R			R	C		
sp. D.	R	R	C	R	R	R	C	A																					R	R	C	A								
<u>Staurastrum</u>																																								
sp. A.									R				C	R	R				R		C	C					C													
sp. B.																			R								C													
sp. C.																																	C	R	R		R	R		
<u>Zygnema</u>												R	R								C	C			C		C		A											

1, 2, 3, 4, 5, 6, 7, 8 refer to 6, 12, 20, 26 June, 1968, and 2, 11, 19, 25 July, 1968, respectively

R, C, A refer to 1-10, 11-100, above 100 individuals per sample, respectively.

1968 NET PHYTOPLANKTON TAXA, SEASONAL OCCURRENCE, AND RELATIVE ABUNDANCE

	Harvey								Indian								Boundary								Little Park								Greenland							
	1	2	3	4	5	6	7	8	1	2	3	4	5	6	7	8	1	2	3	4	5	6	7	8	1	2	3	4	5	6	7	8	1	2	3	4	5	6	7	8
Eubranchipus									R										C		R						C		R						C		C		C	
Camptocercus			R									R		C						R		C		C		R		C		C		A		R		R		C		
Chydorus						R		C			R		C						R			C		C		R	C		C		C			R						
Daphnia	C		R	R	C		R								R				R									R		C	C	C			R				R	R
Diaphanosoma																					C								A											
Eurycercus																																								R
Leptodora	R	C	C	C	C	C	C		R	R	C	A	C	A	C	C	R	R	C	C	C	C	C	C	C	C	R	C	C	C	C	C	C		C	C	R	C	C	C
Simocephalus						R									R	C				C	R	R	C	R	C	R			R	C	A	C			C			R	C	C
Cyclops	R	R		R	C	R	C		C	R	R	R	C	R	C				R		C		R	R	R	C	R	R	R	C	C	C	R	R	R	R	R	R	C	C
Cypria																					R					C		R	C	C						R		R		
Astramoeba									R												R														R					R
Conochilus									R		C		A		C		R		R		C	C	R		C		C				C	C		R						
Cupelophagis																R						R						C		R	R	C								
Dicranophorus																			C		C	R								R	R	R					R			
Euchlanis																			C			C						C		R	C									
Filina	R			R	C	R	C						R												R								R		R					
Kellicottia						R																						C												
Keratella		R	R	R	R	C	C	R				C		R		R		R		C					C							R							C	R
Lecane												R	C	R																										
Notholca																						R																		
Platyias																							R					R		C										R
Polyarthra		R														R					R	R	R		R		R				R	R								
Testudinella			R		R													R		R		R		C		R		R			C									

symbols as on preceding page

1968 NET ZOOPLANKTON TAXA, SEASONAL OCCURRENCE, AND RELATIVE ABUNDANCE

	Harvey					Indian					Boundary					L.P.					Greenland				
	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5
Ambystoma tigrinum			R																						
Dytiscidae																							C	R	
Elmidae																						R		R	R
Helodidae													R							R					R
Rhantus														R						R					R
Culcoides										R		R	R			R	C	R	R	R	C	R	R		
Meringodixa						R	R					R			R		R		R			R			
Podonomus	R	C	A	A	A		C	C	C	C	R	C	C	C	C	R	C	C	C	A	R	C	A	A	A
Corixidae																								R	
Hirudidae						C			R																
Gyraulus													R												
Nemata	C	A	A	A	A	R			C	R	C	A	A	A	C	C	A	C	A	C	C	R	C	C	C
Aeschna												R		R			R								
Sympetrum																						R			
Oligochaeta																									
sp. A.	R					R	R	C	R	C	C	A	C	C	R	C	A	A	C	A	C	A	C	C	C
sp. B.		R			R			R			R	C	R												
sp. C.																	R		R						
Cypria						R	R														R	C	C		
Parasitengona						R		R														R	R		R
Limenphilus						R	C	C	R	R															

1, 2, 3, 4, 5 refer to 6, 20, June, 1968, and 2, 11, 30 July,1968, respectively
other symbols as on preceding pages

1968 BENTHOS TAXA, SEASONAL OCCURRENCE, AND RELATIVE ABUNDANCE

EMERGENT VEGETATION, KAIBAB PLATEAU PONDS

Carex rostrata Stokes

Danthonia californica Boland

Elocharis acicularis (L.) Roem. and Schult.

Glyceria borealis (Nash) Betchelder

Hordeum jubatum L.

Juncus badius Suksd.

Phleum pratense L.

Potamogeton grammineus L. x P. illinoensis Morong

Rumex sp.

Sparganium simplex (S. multipedunculatum (Morong) Rydb.)

Umbelleferae sp.

INTERPRETATIVE OUTLINE FOR NATIONAL PARK SERVICE USE

I. Sinkholes

   A. Description and history of Kaibab limestone

   B. Cave formation: simple description of chemical reaction between carbonic acid and limestone

   C. Sinkhole formation: diagrams and explanation

   D. Springs: description of Roaring Springs and simple explanation of percolation, aquifers, etc.

II. Dynamics of pond life

   A. Community concept: energy transfers

      1. Exchanges with surrounding environment

         a. Sunlight for photosynthesis

         b. Emergent insects and salamanders

      2. Interrelations within the community: food webs

         a. Producer organisms: function and common names of dominant species

            (1) Phytoplankton

            (2) Emergent vegetation

         b. Consumers: description of dominant interesting species

            (1) Zooplankton: 1st order

            (2) Benthos: 2nd order

            (3) Salamanders: 3rd order

B. Succession: description of changes in the community with emphasis on visual factors such as emergent vegetation and surface area, stressing encroachment of terrestrial vegetation

1. Harvey Meadow Pond as an early sere
2. Little Park Lake as a well developed sere
3. Greenland Lake as a late sere
4. Reference to extinct ponds visible in several places on the Kaibab Plateau

III. Effect of man on succession

A. Man-induced drainage in Harvey Meadow Pond

B. Effect of livestock on pond succession

C. Terrestrial examples

1. Kaibab deer herd
2. Effect of fire control on white fir-ponderosa pine forest community (Merkel, 1962)

VITA

James Ross Kimmel was born on 15 April, 1943, in Waco, Texas. He is the only son of Mr. and Mrs. Ross Kimmel Jr. The author has one sister, Martha Christine Kimmel.

The author attended Texas public schools, graduating from Waco High School in 1961. In June, 1961, he entered Abilene Christian College, where he attended until January, 1963, when he entered Baylor University. Upon graduation with a Bachelor of Science degree in biology from Baylor in June, 1964, the author entered the Peace Corps, and taught science in Ghana, West Africa, until July, 1966.

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