STRUCTURE AND FUNCTION OF ZOOPLANKTON COLONIZATION IN TWELVE NEW EXPERIMENTAL PONDS

by

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(ABSTRACT)

This study examined the structural and functional development of zooplankton communities in 12 new experimental ponds for one year and tested four predictions derived from the Random Placement Hypothesis (Coleman 1981). Physico-chemistry, zooplankton colonization dynamics, zooplankton community structure and function were analyzed every two weeks from 5 February 1988 to 10 February 1989. Ponds varied in physico-chemistry at points in time but followed similar patterns during the study year.

Ponds were not colonized by zooplankton similarly. Some species occurred in all ponds with about the same timing, but many species exhibited variable timing among ponds or never occurred in more than a few ponds. Colonization curves varied among ponds and through time, and species accrual curves differed in both accrual rates and the numbers of species accrued. Observed colonization curves did not closely match the curve expected according to the Random Placement Hypothesis.

Zooplankton community structure also varied among ponds. Multivariate analyses could not discern similar trends in zooplankton community structure among ponds due to the disparity of species trends among ponds. Species data were pooled into taxa (Copepoda, Cladocera, Rotifera, Ostracoda and *Chaoborus*) and analyzed. Rotifers dominated zooplankton communities in densities and biomass, and ponds differed in taxa densities and biomasses.

Zooplankton community function was more similar among ponds than community structure. Multivariate analyses indicated ponds generally followed similar trajectories in zooplankton community function through the year.

Zooplankton did not colonize experimental ponds equally and did not develop similar zooplankton community structure among ponds. Dispersal processes probably limited colonization and development of zooplankton community structure. Zooplankton community function was generally more similar among ponds than community structure, probably due to the functional redundancy of zooplankton species. Implications of these results for experimental pond studies are discussed.

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1.0 PROLOGUE

This research was conducted as part of an interdisciplinary project at the VPI&SU experimental pond facility, located at the Southern Piedmont Agricultural Experiment Station, Blackstone, Virginia. The ponds were constructed for the purpose of conducting studies on pesticides according to guidelines established by the U.S. Environmental Protection Agency (USEPA). My research focused on colonization of the ponds in their first year and did not involve application of pesticides. This section briefly describes: (a) the USEPA program for hazard evaluation of pesticides and the role of experimental ponds in that program, (b) the goals and development of the VPI&SU experimental pond project, and (c) construction of the experimental pond facility.

Pesticides must be tested and evaluated prior to registration with the USEPA and distribution by a company for use. The USEPA uses a four-tiered system of tests to evaluate pesticides for potential ecological hazard (Urban and Cook 1986, Jenkins et al. 1989). This brief summary of that system considers only tests on aquatic organisms. The testing tiers system begins with relatively simple acute bioassays with fish, conducted in the laboratory. Results of bioassays are compared to prescribed decision criteria. Should a pesticide be judged sufficiently toxic according to these criteria, the next level of testing is required. For example, if the expected environmental concentration exceeds the LC_{50} of the bioassay test organisms, the next level of testing is required. The testing tiers progress through invertebrate partial life cycle studies and fish early life stage studies to fish full life cycle tests at tier 3. If a pesticide is found to be toxic at this level, then tests for effects in the field are required.

Field tests on pesticides can be conducted in experimental ponds (mesocosms) according to USEPA guidelines (Touart 1988). Mesocosms must contain representative biota, including phytoplankton, benthic invertebrates, zooplankton, and fish. Biota can be introduced to experimental ponds by inoculation from an established pond or by natural colonization. EPA guidelines (Touart 1988) recommend circulation of water among ponds prior to a pesticide test to enhance similarity among ponds. A mimimum of four treatment levels is recommended (control + 3 pesticide levels), and at least three replicate ponds are needed per treatment level. Test duration depends on degradation rates of the chemical and its toxicity. Data to be collected include physico-chemical parameters, phytoplankton dominant taxa and biomass, periphyton biomass, zooplankton dominant taxa densities, and benthic macroinvertebrate densities. Data on fish populations are also collected at the end of a study, including density and biomass of size classes and fecundity.

Construction of the VPI&SU experimental ponds began in late 1986. Timber was cleared and stumps removed by May 1987. Topsoil was scraped from the site and stockpiled, an underground plumbing system put in place, and the ponds were excavated during 1987. Excavated clay was also stockpiled. Several wells were drilled at the facility during this time. Two wells were successful and were connected to the underground plumbing. The wells permitaddition of groundwater to ponds (individually) to maintain water level. In addition, the plumbing will permit draining of the ponds and refilling from the reservoir in preparation for future pesticide studies. Following excavation, the ponds were lined with stockpiled clay, the clay was compacted, and the ponds were lined again with stockpiled topsoil. The ponds were filled with municipal water from a fire hydrant near the site during the last week of January 1988 and were filled on 31 January 1988. Further details of the construction process were described by Layton (1989).

Sampling for my study began on 5 February 1988 and continued through 11 February, 1989. My study tested a prediction of the Random Placement Hypothesis (Coleman 1981) and evaluated the extension of that hypothesis to zooplankton community structure and function in early colonization. While testing a basic, ecological hypothesis, this study also documented the early development of pond mesocosms and evaluated the replicability of these ponds prior to "homogenization" efforts (e.g., drain ponds and refill from reservoir) and pesticide testing.

2.0 INTRODUCTION

The overall goal of this study was to investigate zooplankton colonization. Colonization is an important component of succession, but one that is difficult to separate from other interactions occurring during succession. The 12 new experimental ponds provided the opportunity to examine early colonization of relatively simple communities.

Colonization is, by definition, a structural event and traditionally has been considered in simple, structural terms (i.e., number of species present). Community structure can also be considered in more complex terms, such as population density, biomass, diversity, etc. Parallel to the development of community structure is the development of community function (e.g., energy flow and nutrient cycling). Four hypotheses relevant to colonization dynamics exist: Random Placement Hypothesis (Arrhenius 1921, Coleman 1981), Equilibrium Theory (MacArthur and Wilson 1967), Habitat Diversity (Williams 1964), and Disturbance (Connell 1978). All four hypotheses consider only the number of species present and do not consider other structural or functional measures of developing communities. The Random Placement Hypothesis (RPH) is considered the null hypothesis (Connor and McCoy 1979, McGuinness 1984a) and was tested in this study. I also evaluated its extension to zooplankton community structure and function. relationships between selected environmental variables, community structure, and community function were evaluated to indicate factors important in setting the direction of community development.

2.1 LITERATURE REVIEW

Succession: Structure and Function

Clements (1916) viewed succession as an orderly, predictable process of progressive change, with development from pioneer stages to a single, stable climax community (McIntosh 1980). An ecosystem was considered a dynamic entity, reacting to changes in the environment as a unit (O'Neill et al. 1986). Although Clements (1916) described succession in structural terms (species), he recognized the importance of processes and function in succession (McIntosh 1980).

The Clementsian (holistic) view of succession has been further developed into a functional or ecosystem approach. Odum (1960) examined both structure and function in ecological succession in a six-yr study of fallow agricultural fields He and his colleagues found that primary production of the "old-fields" began at a high rate, then declined and stabilized. At the same time, species numbers started low but increased and became relatively stable. These trends continued in the same fields at the next stage of succession (Golley 1965). Odum (1960) concluded that: (a) a change in productivity does not necessarily correspond with a change in species, and (b) productivity does not necessarily increase during succession.

Odum (1969) graphically compared successional energetics in a forest and a laboratory microcosm. He noted the following common trends: (a) an initial increase in production, followed by decrease or stabilization, and (b) a gradual, asymptotic increase in biomass. Again, function (productivity) did not correspond to structure (biomass) during succession.

In the same paper, Odum defined the ecosystem as a unit of organization undergoing an orderly and predictable trend of development toward a stable, mature system. He provided a list of expected trends in ecosystem development, including functional attributes such as production, energy flow, nutrient cycling, etc. Although Odum prefers the term "mature system," the similarity to Clements' successional climax is apparent.

Gleason (1926) disagreed with Clements' concept of an orderly, predictable succession. Often called the individualistic approach, Gleason's focus was on the behavior of individual populations. He considered succession to be far from orderly and predictable, dependent only on the species present and their responses to environmental changes. The result is an extremely variable process with no single predictable outcome.

Gleason's view has also extended to the present. Recent proponents include Drury and Nisbet (1973) and Horn (1975, 1976). This "reductionistic" view is exemplified by Horn's discussion of the Markov model; a statistical process of replacement probabilities for individual organisms by other individuals of the same species or different species. The reductionistic approach depends heavily on competition, and according to McIntosh (1975), is now one of the most influential concepts in ecology.

In summary, the history of successional theory in the U.S. has been characterized by a dichotomy between the holistic/ecosystem (functional) approach and the individualistic/reductionistic (structural) approach. McIntosh (1980) stated that this "embarassing heterogeneity creates great difficulties in assessments of community and succession."

More recently, a general ecosystem theory has developed (Webster 1979, Allen and Starr 1982, O'Neill et al. 1986) that incorporates the holistic and individualistic approaches by considering them as two viable but separate hierarchies: one structural and the other functional. To borrow an analogy by O'Neill et al. (1986), holistic and individualistic groups view the same complex object (ecosystem) hidden behind a two-paneled screen, but the two groups see different projections of the ecosystem on their panels. Neither view is incorrect, but are simply different perspectives of the same subject. Within this dual hierarchy framework, the historical debate between approaches becomes unnecessary (and is perhaps unresolvable anyway). The difference made by the dual hierarchy concept is that new predictions and hypotheses can be formulated by coincident consideration of both structure and function. In addition, traditional hypotheses can be tested within the dual hierarchy framework for more complete understanding of ecosystem complexity.

Hypothesis Testing in Ecology

Hypothesis testing lies at the heart of statistical experimentation (Popper 1968, Platt 1964, Green 1979), but much controversy has been raised concerning the value of hypothesis testing in ecology. This debate revolves around those who favor the hypotheticodeductive appproach (e.g., Strong et al. 1979, Strong 1980, Connor and Simberloff 1983) and those who favor the inductive approach (e.g., Diamond and Gilpin 1982, Quinn and Dunham 1983, Roughgarden 1983). Debate has largely focused on the relationship between an area's size and the number of species in that area, and the role of competition in regulating species richness.

Proponents of hypothesis testing assert that properly-formed null hypotheses are valuable in ecology and are especially needed to study complex systems. Opponents (inductive approach) claim that reliable null hypotheses are too difficult to construct, testing is often infeasible, and null hypotheses will necessarily be rejected due to excessive simplicity relative to natural systems. One opponent (Roughgarden 1983) states that theories of science other than the "Popperian" approach exist and that it may be hasty to align ecology with that approach. However, in his review of species-area literature, McGuinness (1984a) found only two studies of MacArthur and Wilson's equilibrium theory (1967) that tested a null hypothesis. Ecology does not seem to have rushed to the "Popperian" approach, at least in species-area studies.

Connor and McCoy (1979) reviewed the species-area literature and critically appraised progress. The authors stated, "the idea that the species-area relationship is purely a sampling phenomena [sic] should be considered a null hypothesis, and all hypotheses invoking biological processes to explain the species-area relationship should be considered alternatives." McGuinness (1984a) repeated this position more forcefully, claiming an "almost universal lack of an appropriate null hypothesis" in species-area studies. The implication is that many studies supporting species-area hypotheses might have been explained by random chance alone.

Succession and Species-Area Hypotheses

Ecologists have long recognized a relationship between area and species number (Connor and McCoy 1979, McGuinness 1984a). More species (and numbers of individuals) can occupy large areas than small ones, and so a species-area curve can be derived. Organisms inhabit (colonize) an area over time, and this colonization is the common link between species-area and succession concepts. Colonization can be discussed solely in terms of succession or species-area (e.g., Nicholson and Monk 1974, Coleman et al. 1982), but tests of species-area hypotheses can provide information on succession by indicating factors that influence succession (Sousa 1979, 1980).

Four species-area hypotheses have been proposed (and changed names) over the last century: (1) Random Placement (Passive Sampling); (2) Habitat Diversity (Habitat Heterogeneity); (3) Equilibrium Theory (Area per se); and (4) Disturbance. Each of these hypotheses is briefly described below in approximate chronological order.

1. **Random Placement (Passive Sampling):** Generally attributed to Arrhenius (1921), this hypothesis states that placement of species in a region is simply a function of region size. Larger regions collect larger samples of species and by sampling statistics alone would be expected to contain more species. This hypothesis assumes (1) a lack of correlation in the location of individuals and (2) statistical homogeneity between regions for the distribution of environmental influences (sunlight, habitats, predators, prey, etc.) (Coleman 1981, Coleman et al. 1982, McGuinness 1984b).

2. **Habitat Diversity (Heterogeneity):** Williams (1943) sought to explain species-area curves by hypothesizing that larger areas support more species due to the inclusion of more habitats than smaller areas. This hypothesis has been invoked a number of times to at least partially explain results (e.g., Schoener and Schoener 1981, Gunnill 1982) but has never been shown

experimentally to result in a species-area curve. Simberloff (1976) considered the hypothesis invalid for his experiments with small mangrove islands.

3. **Equilibrium Theory (Area per se):** This hypothesis is most commonly encountered in discussions of species-area relationships. Largely based upon theories of MacArthur and Wilson (1967) and the modification made by Simberloff (1969), this hypothesis proposes that (1) species immigration rates from a source pool to an "island" are related to distance between the points and (2) species become extinct faster on small islands due to smaller population sizes. When immigration rates balance extinction rates, an equilibrium number of species is reached for that island size. A large number of studies have used this hypothesis to explain the species-area curve, but many studies have not actually tested the hypothesis or adequately demonstrated it (Connor and McCoy 1979, Simberloff 1974, McGuinness 1984b).

4. **Disturbance:** Natural environmental disturbances (e.g., storms, etc.) affect ecosystems by reducing diversity (number of species) in a region, and "the frequency and intensity of these events is thought to decrease with increasing area" (McGuinness 1984a). This hypothesis is apparently derived from observations and

common sense. For example, if subjected to the same storm, Lake Superior should be less affected overall than a nearby pond. The relative impact of disturbance is simply a matter of scale, and so the consequence of disturbance (decrease in diversity) is also a function of scale. Osman (1977), Sousa (1979), and McGuinness (1984b) demonstrated the importance of disturbance in intertidal systems, but this hypothesis does not seem to have been applied to other ecosystems. Perhaps this is because intertidal systems are so dominated by wave action that only one form of disturbance need be considered. Other systems may have greater complexity of disturbances, making the hypothesis more difficult to study.

Species-area hypotheses are related to succession by their treatments of colonization dynamics. MacArthur and Wilson's equilibrium theory (1967) explicitly addressed colonization as the integral of immigration and extinction rates. Other hypotheses (Random Placement, Habitat Diversity and Disturbance) do not require measurements of immigration/extinction rates, depending instead on extrinsic factors (randomness, habitat, disturbance) to explain colonization curves and the results of colonization. It should be noted that none of the above hypotheses are concerned with structural measures more complex than number of species present over time. Population densities/biomass and community or ecosystem function are not considered.

Of the four hypotheses, the null hypothesis is the Random Placement Hypothesis (Connor and McCoy 1979, McGuinness 1984a,b). It is the simplest explanation for the species-area relationship. The presence of more species in larger areas is the result of random colonization, with larger areas "sampling" more colonists. Habitat differences, biological interactions, and disturbances are assumed to be inconsequential. Should this null hypothesis be rejected, other hypotheses can then be tested in the order of increasing complexity (Green 1979).

Random Placement Hypothesis: Recent Literature

Coleman (1981) refined the Random Placement Hypothesis (RPH) of Arrhenius (1921) and showed that this was a mathematical statement of Connor and McCoy's (1979) null hypothesis. Coleman derived formulae for the expected species-area curve and the variance of the curve, thus permitting tests of goodness-of-fit of data to the model. McGuinness (1984b) stated that this method "is likely to give a more accurate estimate of the expected species-area relationship since the shape the curve should not be influenced by sampling variability."

Coleman et al. (1982) tested this null hypothesis with birds nesting on islands in a lake and found results were explained by random placement. They explained that the concepts of immigration and extinction are inappropriate for islands that are strongly interactive in their population fluxes and that verification of the RPH requires complete censuses of individuals through time.

Haila (1983) examined bird populations on islands by considering the colonization process as a sampling metaphor, with ponds "sampling" birds. He assumed that colonization follows a Poisson distribution, with the expected mean population sizes of species determined by (1) the average regional abundance of species and (2) the "sampling efficiency" of an island. He also applied Coleman's (1981) Random Placement Model and found agreement within but not between island-type groups. Habitat composition was an important "sampling efficiency" factor, and groups of islands with similar habitats "sampled" birds similarly.

McGuinness (1984b) tested the RPH with intertidal communities. No single hypothesis accounted for all diversity patterns; the RPH was a "good" model for more than half the communities sampled.

Ryti (1984) studied perennial plants on boulder "islands" in Baja, California. Data were compared to results of random colonization simulations. These simulations were analogous to Coleman's (1981) model, but also allowed for different colonization abilities of species. Random colonization was found to be the "most parsimonious explanation for the density and diversity patterns."

Boecklen (1986) mentioned the RPH, but specifically tested the Habitat Diversity Hypothesis, without considering random placement as the null hypothesis. By applying multivariate analysis to factor out area, Boecklen found habitat heterogeneity to be a significant predictor of species number.

Stevens (1986) evaluated the Equilibrium, Random Placement and Habitat Diversity Hypotheses simultaneously for wood-boring insects and their host plants. The RPH was considered a test of scientist sampling bias. Stevens found only the Habitat Heterogeneity Hypothesis was consistent with the data.

Clearly, no single hypothesis best explains all results, and that in only a few cases has the RPH been specifically tested as the null hypothesis. In addition, all of the papers state and test hypotheses in simple structural terms, such as number of species per area, diversity, and colonization curves. These hypotheses have not been applied to densities/biomass or functional measures of a community or ecosystem.

Experimental Ponds

Experimental ponds (mesocosms) may be valuable for studying succession in complex communities. Multiple ponds permit replication and experimental manageability in relatively large scale systems. Experimental ponds have been used to study a variety of phenomena, including fish foraging (e.g., Werner et al. 1983), anuran predation (Wilbur et al. 1984), fish production (Geiger 1983), and nutrient loading - predation interactions (Hall et al. 1970). Ponds have also been used to evaluate effects of chemicals on multiple populations under natural conditions (e.g., Hurlbert et al. 1972, deNoyelles et al. 1982, Giddings et al. 1984, and Crossland and Wolff 1985). No studies have explicitly examined the variability/replicability of experimental ponds (i.e., their suitability as statistical replicates in experimentation). In addition, pond studies have focused primarily on structural parameters. No pond studies analogous to Odum's (1960) old-field study seem to have been undertaken, in that structure and function have not been considered together. In the context of O'Neill et al. (1986), only a partial view of pond succession exists.

Hall et al. (1970) conducted an extensive study over 3 yrs on 18 replicate ponds. After the ponds had been filled 2 yrs and "had a well-developed flora and fauna," they were treated with different nutrient and predation levels. Hall et al. (1970) provided much information on the interaction of nutrient levels and predation, but data were not presented on the pretreatment period (before successional trends were confounded by treatments). Considerable variability between replicate ponds is apparent from data (e.g., Fig. 6, 7, 19 and Tables 11, 12, and 14; Hall et al. 1970) and may indicate different successional conditions among ponds.

Successional studies in experimental ponds also have implications for regulatory pesticide risk assessment. The U.S. Environmental Protection Agency recently developed guidelines for testing ecological effects of pesticides in experimental ponds (Touart 1988), and several such studies have been conducted to date. Protocols involve replicate ponds per treatment level. If pretreatment succession of ponds should lead to significantly different structure and function between replicate ponds, treatment effects may be confounded with successional differences. A study of potential reasons for differences between ponds may prove beneficial to pesticide risk assessment.

2.2 HYPOTHESIS STATEMENT AND RESEARCH OBJECTIVES

Hypothesis Statement

Zooplankton communities in replicate experimental ponds will develop the same structural and functional characteristics. According to the Random Placement Hypothesis, this is due to random colonization by organisms in ponds of equal dimensions and successional age.

Definitions. For this project, I defined zooplankton communities as Rotifera, Cladocera, Copepoda, Ostracoda, and *Chaoborus* larvae. Structural characteristics were defined as number of species present, species density, biomass, and community diversity and evenness. Functional characteristics were defined as community productivity, respiration and nutrient regeneration rates.

Assumptions. The RPH makes two assumptions: environmental homogeneity among areas and no correlation in the location of individuals (Coleman 1981). For the experimental ponds, I tested the assumption of environmental homogeneity by measuring physico-chemical parameters. I tested the second assumption by evaluating correlations among species' locations.

Research Objectives

Objectives for this research project were to test the following predictions for zooplankton communities in the experimental ponds:

1. Ponds will have similar colonization curves. If species number is a function of area, then same-sized ponds should collect species similarly.
2. Observed colonization curves will closely correspond to an expected colonization curve based on Coleman's (1981) mathematical statement of the RPH.
3. Ponds will have similar zooplankton community structure. This prediction tested the generality of the RPH to measures of community structure beyond species number.
4. Ponds will have similar zooplankton community function. This prediction tested the generality of the RPH to community measures not usually considered in colonization studies.

Another objective was to evaluate the physico-chemistry of the ponds for comparisons among ponds and assessment of trends during the first year.

3.0 COMPARATIVE PHYSICOCHEMISTRY OF TWELVE NEW EXPERIMENTAL PONDS

3.1 INTRODUCTION

Experimental ponds have been used in a variety of ecological studies, including studies of fish habitat use (Werner et al. 1983), fish production (Geiger 1983), and nutrient loading and predation (Hall et al. 1970). Experimental ponds have also been used to test effects of chemical contamination (e.g., Hurlbert et al. 1972, deNoyelles et al. 1982, Giddings et al. 1984, Crossland and Wolff 1985). In addition, the U.S. Environmental Protection Agency recently finalized guidelines for experimental pond studies as part of the pesticide registration process (Touart 1988): some studies have already been conducted for this purpose (e.g., Hill 1985).

Experimental ponds (mesocosms) are considered to have greater complexity and scale than laboratory-scale systems while maintaining some control of experimental conditions and replicability (Odum 1984). However, enhanced environmental realism of outdoor experiments may be gained at the expense of replicability, depending on the extent of control over conditions that is retained. While it is unreasonable to expect outdoor ponds to be exact replicates, it is necessary to know the extent of natural variation among ponds in order to (a) better develop management techniques for control of experimental conditions and (b) correctly interpret experimental results.

Hall et al. (1970) observed substantial variation among experimental ponds after 2 yrs of unmanaged development. Hurlbert et al. (1972) assigned treatments to ponds to purposely maximize between-pond variation within treatments. This conservative approach was based on knowledge of prior manipulations to ponds and zooplankton samples collected 1 week prior to treatment. Others have drained and refilled their ponds with water from an adjacent pond to increase similarity among ponds prior to treatments (e.g., deNoyelles et al. 1982). Unfortunately, no explicit evaluation of replicability among multiple experimental ponds appears to have been conducted.

The initial development of experimental ponds and pre-experiment conditions directly affect replicability but have not been documented. Ponds are usually examined up to 3 weeks immediately preceding treatment (e.g., Hall et al. 1970, Hurlbert et al. 1970, 1972, Hanazato and Yasuno 1987, deNoyelles et al. 1982) but have not been examined beyond this brief pre-test period.

New experimental ponds also offer opportunity to study colonization dynamics, although very few studies of colonization have been conducted in ponds. Hubbard (1973) constructed colonization curves of two new experimental ponds for up to 86 days after initial filling. Hubbard considered his results consistent with the species equilibrium model of MacArthur and Wilson (1967). Clement et al. (1977) examined chironomid colonization of new rice paddies for 30 days, but the paddies were connected by slowly flowing water, thereby eliminating discussion of results in terms of island biogeographic theory.

This paper represents part of a study of 12 experimental ponds during their first year of existence and prior to manipulation or treatments. The study was a "natural experiment" on colonization dynamics and evaluated a prediction of the Random Placement Hypothesis (Connor and McCoy 1979, Coleman 1981, McGuinness 1984a). Twelve experimental ponds of equal dimensions will collect equal numbers of species, simply as a function of size. An assumption of the hypothesis is that environmental factors are homogeneous among ponds. This paper evaluates that assumption of environmental homogeneity (replicability).

3.2 MATERIALS AND METHODS

Study Site

An experimental ponds facility was constructed during 1987-1988 at the Southern Piedmont Agricultural Experiment Station near Blackstone, VA. The site is in the Piedmont physiographic province ($77^{o}57'30"W$, $37^{o}5'30"N$) at an elevation 128 m above mean sea level. The facility consists of 12 ponds and a reservoir (Fig. 3-1). The reservoir was constructed after the ponds and was not included in this study.

Prior to construction, the site was a mixed pine and deciduous forest. After removal of the vegetation, topsoil and subsurface clay from the site were saved for use in the ponds. PVC pipe was installed underground to connect ponds to the reservoir and two wells. Valves permitted the addition of well water individually to any pond.

Pond excavations began in late June 1987 and ended in November 1987. All 12 ponds were constructed according to the same specifications: square, with 404.8 m^2 surface area (20.12 m on a side), 2.13 m depth, 2.5:1 slope ratio (Fig. 3-1). Each pond was bermed at the top to prevent surface runoff from entering the pond. The ponds were sealed with about 15 cm of compacted clay and

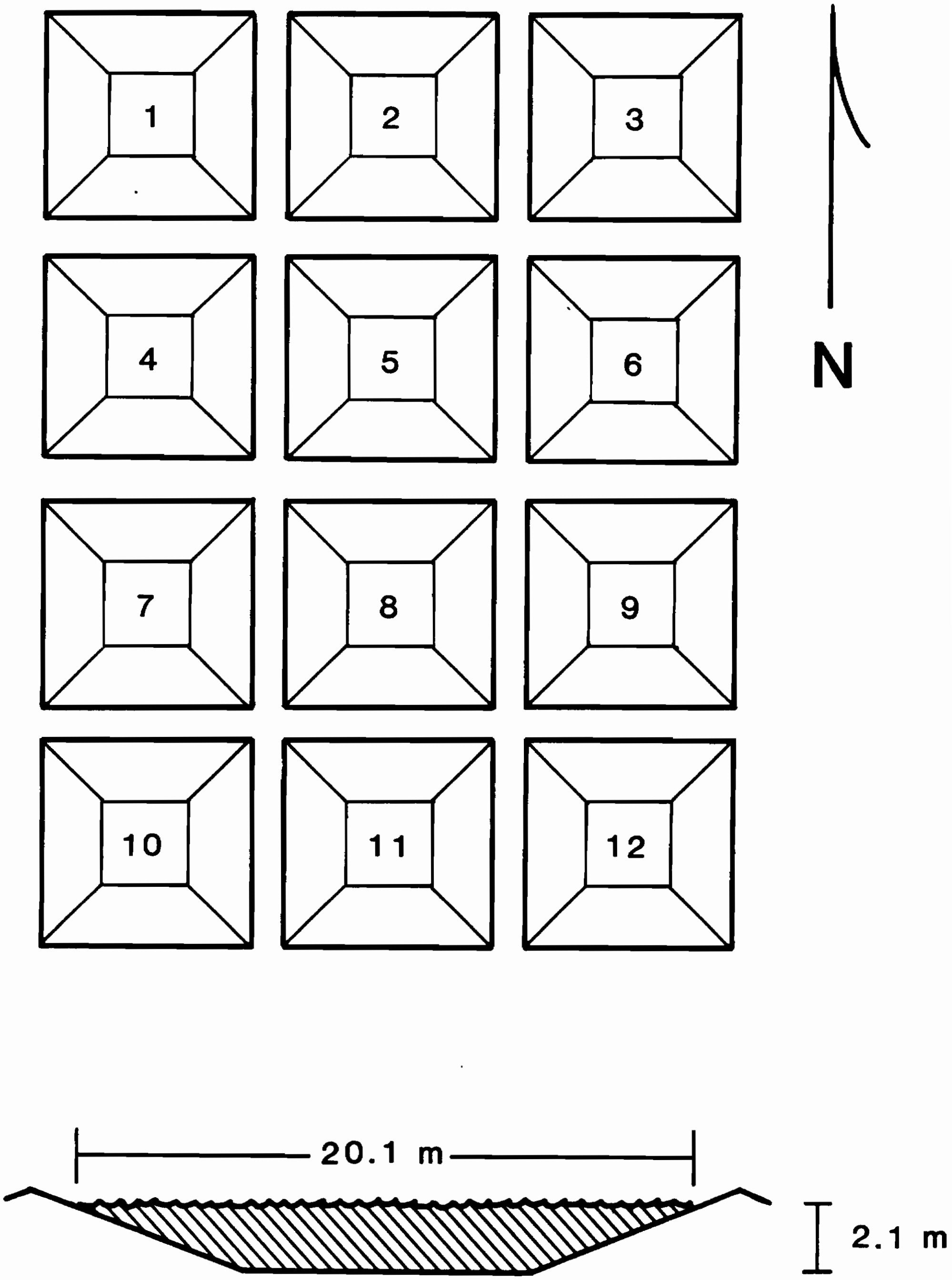


Figure 3-1. Experimental Pond Facility. The reservoir was located west of Ponds 1, 4, and 7. Slopes were 2.5:1.

lined with about 15 cm of topsoil from the site prior to filling with water. Ponds were excavated in the following order: 3,2,1,4,5,6,9,8,7,10,11,12 (Fig. 3-1). Excavation was interrupted for about 2 months between ponds 8 and 7. Following excavation of all ponds, the berms and tops of inner slopes were seeded with grass and mulched with straw to reduce erosion.

All twelve ponds were filled with chlorinated municipal water (source: Nottoway Reservoir) from a nearby fire hydrant in late January 1988. This water was used because wells did not produce enough water to fill the ponds in a short time period. Water entered the ponds through the underground pipes, so that all 12 ponds received water simultaneously. Ponds were filled over the course of 6 days, ending on 31 January 1988.

This study preceded any treatments of the ponds. The only manipulation of the ponds was the addition of well water to individual ponds to compensate for evaporation and/or loss of water through the soil-clay liners. At no time was water transferred from one pond to another during this study, and no reservoir water was added to any ponds.

Sampling and Analyses

Sampling and analyses were conducted every 2 weeks for 1 yr, starting on 5 February 1988 and ending on 10 February 1989, except for one three-week interval in November 1988. Biweekly sampling events spanned two days, often with 7 ponds sampled on the first day and 5 on the second. Data were graphed and analyzed as if all 12 ponds were sampled on the same day, with the assumption that changes in weather conditions, etc. within 24 hours would not alter physico-chemical conditions significantly.

In addition to the biweekly sampling trips, limited sampling and analyses (temperature, dissolved oxygen, pH, Secchi depth) were made during intervening weeks from March through October 1988. The criterion for starting and ending these one-day sampling trips was a 10^{o} C water temperature. This criterion was considered more representative of seasonal conditions than a calendar-based criterion. Data from these trips were not used in statistical analyses, but were included in some graphs of general trends.

All sampling was done according to a set of random sampling sequences prepared prior to the study to ensure no patterns would be established among ponds due to sampling activities. Each pond was sampled at three stations: always at the center (2.13 m depth) and at 2 of the 4 sides (1.07 m depth). The two sides were chosen each sampling trip by coin toss (East vs. West, North vs. South). Sampling stations within ponds were consistent throughout the study by the use of ropes suspended over the ponds. The intersection of the ropes marked the center, and a position on the ropes at 1.07 m depth marked the side stations.

Sampling was conducted with two goals: (a) collect sufficient data to accurately represent each pond for the purposes of this study, and (b) do so quickly and efficiently to permit sampling all 12 ponds within two days. Sampling equipment and procedures were derived with the additional constraints of practicality and reliability in inclement weather: no shelter was available at the ponds.

Ponds were sampled from an inflatable raft. Upon entering the pond, sampling started at the center station, then proceeded to the two side stations. Dissolved oxygen and temperature were measured at the center station at surface, 1-m, and 2-m depths with an air-calibrated dissolved oxygen meter (YSI Model 407A). Secchi depth was also recorded at the center station.

Whole-water samples were obtained with a tube sampler at all stations. The tube sampler was a 1-m long plexiglass tube (5.1 cm i.d.), fitted with a cable through the tube. A racquetball was attached to the bottom end of the cable. The ball fit in the end of the tube for a water-tight seal when the cable was pulled taut. The tube was lowered vertically into the water, the cable pulled taut, and then the tube was lifted out of the water. The collected vertical "core" of water was then emptied into a bucket by releasing tension on the cable. Five tube samples were collected at each station. Tube samples were taken to 2 m depth at the center station and 1 m depth at side stations. The volume of water collected at the two side stations equalled the volume collected at the center station. All water samples from a pond were combined into one bucket for an integrated sample.

The integrated sample was then mixed and subsampled, with subsamples filtered through Whatman GF/C filters. Filters were stored in stoppered test tubes on dry ice until return to the laboratory for chlorophyll a analyses. Filtrate was poured into an acid-washed, borosilicate glass bottle and stored on ice until laboratory analyses for water chemistry. One such bottle was prepared for each pond at each sampling date.

Concurrent with this procedure, pH was measured on another subsample with an Orion model 407A meter. Data collected in the field were: dissolved oxygen and temperature at the surface, 1-m, and 2-m depths, Secchi depth, and pH.

Analyses conducted in the laboratory were: chlorophyll a, hardness, alkalinity, conductivity, ammonia (NH_3-N), nitrate (NO_3-N), nitrite (NO_2-N) and soluble reactive phosphate (SRP). All analyses were conducted according to APHA (1985). Chlorophyll a samples were assayed with a Gilford model 250 spectrophotometer. Total hardness and total alkalinity were measured titrimetrically. An Orion model 399A pH meter was used for alkalinity titrations. Conductivity was measured with a YSI model 32 conductance meter; all values were standardized to 25° C. Ammonia and SRP were assayed colorimetrically with a Gilford Response spectrophotometer. Nitrate and nitrite were assayed with a Dionex Model 14 ion chromatograph.

Weather data (daily maximum and minimum air temperatures and precipitation) were collected at Fort Pickett, located adjacent to the study site. I obtained weather data from the Virginia State Climatology Office, Charlottesville, Virginia. Wind speed and direction data were not available.

Soil analyses were conducted on samples collected before the ponds were filled (October 1987) and after the ponds were 1-year old (March 1989). Samples were collected from the approximate midpoint of slopes and bottom of each pond and combined into one sample per pond. October samples were collected with a hand trowel and March samples were collected with a sediment corer. Soil samples were mixed, air-dried, and then analyzed by the Soil Testing Laboratory of the VPI&SU Cooperative Extension Service.

Data Manipulation & Statistical Analyses

Data were compiled into three-dimensional matrices: ponds x dates x variables. Several data points were missed during the year-long study, due to instrument failure or human error. Because multivariate techniques require that all data be present for analysis of a pond-date combination, averages of values from preceding and following dates were used to represent a missing value in multivariate statistical analyses. All data were log-transformed (log(x+1)) prior to analyses, except pH because it is already logarithmic. Statistical analyses were conducted with the Statistical Analysis System (SAS, SAS Institute 1985). Statistical analyses of variation in log-transformed univariate data included:

- Coefficients of variation (CV = standard deviation/mean) for each variable at each biweekly sampling date. A CV > 10% was considered a priori to indicate significant variation about the mean. The 10% criterion was arbitrary but I considered it a reasonable range for judging similarity among ponds.
- Shapiro-Wilk statistic (test of H_0: normal distribution) for each variable at each biweekly sampling date. This statistic is sensitive to both dispersed and clumped distributions about the mean. All values are shown in tables but only those values corresponding to dispersed distributions (as indicated by CVs > 10%) are discussed.
- Analyses of variance (ANOVA) for each variable, with pond and time as treatments (without replication). Duncan's multiple range tests were computed for variables found to have significant differences among ponds.
- Paired comparison t-tests of soil analyses, testing the hypothesis that differences between pre- and poststudy soil chemical analyses were zero.

3.3 RESULTS

Univariate Trends and Variation

Evaluation of general trends in univariate data was based on plots of overall (all 12 ponds) means and standard deviations of each measured variable through time.

Water temperatures exhibited an obvious and expected seasonal cycle (Fig. 3-2). The ponds were unshaded, exposed to wind, and shallow, ensuring similar temperature among ponds. Thermal stratification was transient in the ponds, primarily in the spring and following marked increases in air temperature. Water at 2-m depth was slower to warm up at these times. Water temperatures reached about 30° C during late July and August, then declined uniformly for all depths to winter temperatures of about 5° C. Differences among ponds in surface temperatures were largely due to timing of measurement during the day. Ponds sampled in early morning were cooler at the surface than those sampled in the afternoon.

Water temperature CVs never exceeded 7% and were usually less than 5% (Table 3-1). All significant Shapiro-Wilk statistics (Table 3-2) were due to narrow distributions about means and no significant differences among ponds were found by ANOVA.

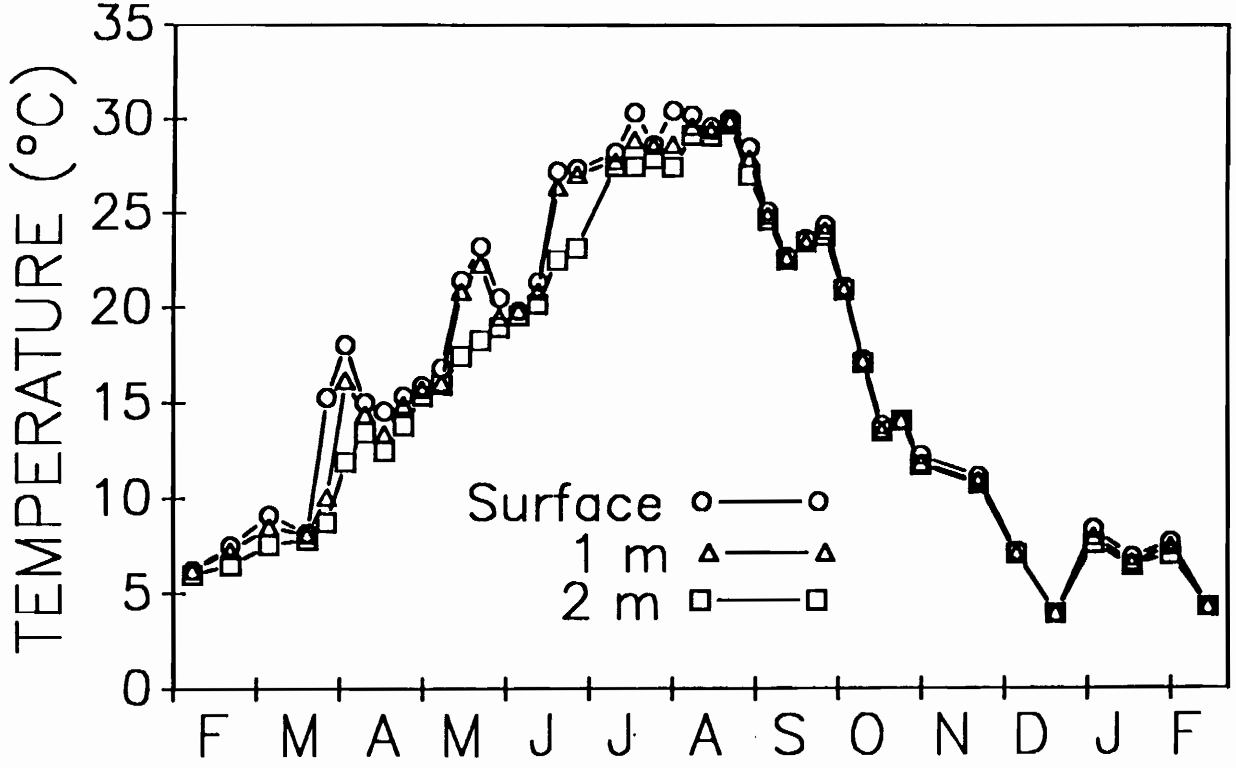


Figure 3-2. Mean water temperature

Table 1. Coefficients of Variation (a)

Sample Dates	Week	Temperature			Dissolved Oxygen			pH	Alkalinity	Hardness	Conductivity	NH3	NO3	NO2	PO4	Chlorophyll a	Secchi Depth
		Surf.	1 m	2 m	Surf.	1 m	2 m										
Winter 88																	
Feb 05,06	1	7.0	5.2	5.7	3.0	2.9	2.7	0.7	1.3	0.8	0.9	103.5	48.3	103.9	105.4	244.0	15.3
Feb 19,20	3	1.8	1.9	4.6	0.9	0.9	0.8	1.5	1.1	0.6	1.0	176.5	48.3	103.9	49.4	245.4	11.3
Mar 04,05	5	3.2	2.0	4.1	0.9	1.0	1.2	1.1	2.0	1.1	0.4	74.3	23.8	163.1	47.4	176.0	7.4
Mar 18,19	7	1.1	1.4	1.5	0.8	0.8	0.8	1.1	2.0	0.7	0.7	156.2	14.8	55.0	--	156.8	8.3
Spring 88																	
Apr 01,02	9	1.9	1.7	3.9	1.4	1.4	2.5	1.6	2.4	0.7	0.6	89.9	30.5	64.9	92.1	98.1	11.6
Apr 15,16	11	3.4	1.7	1.7	1.4	1.2	1.1	1.4	2.5	1.3	0.8	67.8	33.4	247.4	135.2	44.8	16.2
Apr 29,30	13	1.4	1.3	1.3	1.8	1.8	2.1	1.3	2.0	1.1	1.1	129.2	93.8	24.3	70.9	34.9	10.7
May 13,14	15	1.2	0.5	2.1	3.8	4.2	11.5	2.4	3.8	1.3	1.1	85.2	93.8	24.3	74.9	45.0	21.1
May 27,28	17	2.1	1.0	1.4	4.1	4.3	26.1	1.6	2.9	1.5	1.2	37.1	111.0	17.4	77.2	29.4	22.9
Jun 10,11	19	1.9	1.0	1.9	5.3	5.4	11.2	1.4	2.9	1.4	1.2	39.9	80.1	18.4	202.5	31.3	12.9
Jun 24,25	21	1.2	1.0	2.2	5.3	5.3	28.4	1.6	2.5	1.3	1.4	234.8	332.9	--	50.5	19.0	19.3
Summer 88																	
Jul 08,09	23	1.2	0.8	0.4	3.6	3.6	3.7	2.3	2.3	1.4	1.3	93.5	75.8	--	29.3	23.9	10.3
Jul 20,21	25	0.7	0.9	1.6	1.3	1.3	7.3	4.0	2.1	2.0	1.5	145.3	234.6	287.3	72.5	32.2	9.8
Aug 05,06	27	0.7	0.3	1.0	2.9	2.8	17.5	3.2	2.3	2.7	1.9	314.2	162.4	207.4	63.8	35.0	13.9
Aug 19,20	29	0.7	0.5	0.6	4.5	4.4	7.2	2.1	1.9	2.3	1.8	166.7	260.3	227.2	77.9	49.7	14.1
Autumn 88																	
Sep 02,03	31	0.6	0.2	0.7	2.5	2.6	2.9	3.8	2.8	2.1	1.5	308.7	298.5	176.6	--	41.6	12.7
Sep 16,17	33	0.9	0.6	0.6	3.0	3.4	3.6	4.0	2.1	2.7	1.9	92.0	216.7	205.0	--	65.1	12.6
Sep 30,01	35	0.7	0.4	0.4	1.9	1.9	2.1	4.6	3.4	4.2	1.9	71.6	164.3	344.9	--	46.9	14.5
Oct 14,15	37	1.6	0.8	0.9	1.5	1.5	1.5	2.5	2.3	4.2	1.7	64.0	98.5	--	--	60.0	14.5
Oct 28,29	39	2.0	1.1	0.9	10.0	2.1	1.6	14.2	1.3	3.1	1.8	120.8	--	--	--	53.3	15.6
Nov 18,19	42	1.8	1.4	1.2	1.3	1.4	1.4	1.9	1.1	4.1	1.9	91.4	215.4	346.6	119.4	39.8	21.0
Winter 89																	
Dec 02,03	44	3.3	3.0	2.9	1.6	1.6	1.5	2.6	3.9	4.2	1.8	72.8	346.4	249.9	211.2	39.9	22.3
Dec 16,17	46	1.9	2.0	2.0	1.2	1.2	1.2	1.6	2.0	4.2	2.2	105.8	141.6	346.5	44.1	49.3	18.5
Dec 28,29	48	5.1	5.6	5.8	5.3	4.7	4.3	2.4	2.3	3.2	1.9	63.7	--	23.0	168.1	36.8	16.0
Jan 13,14	50	6.7	5.5	4.7	0.8	0.8	0.8	4.6	1.5	2.8	1.8	200.7	153.8	81.9	81.9	40.0	13.5
Jan 27,28	52	3.2	2.8	1.6	1.0	1.0	0.9	1.9	2.0	2.0	2.0	46.9	129.1	81.7	61.3	35.2	13.0
Feb 10,11	54	4.3	4.2	4.3	1.2	1.2	1.2	1.5	2.6	2.4	1.7	68.1	206.6	148.0	23.3	34.0	13.9

(a) C.V.s could not be calculated for dates with means of 0.

Table 2. Shapiro-Wilk Statistics (p values for test of Ho: normal distribution of log-transformed data).

Week	Temperature (C)			Dissolved Oxygen (mg/L)			pH	Conductivity (umhos/ /cm)	Alkalinity (mg/L CaCO3)	Hardness (mg/L CaCO3)	NH3-N (mg/L)	NO3-N (mg/L)	NO2-N (mg/L)	PO4-P (mg/L)	Chlorophyll a (mg/m3)	Secchi Depth (ft)
	Srfc.	1 m	2 m	Srfc.	1 m	2 m										
1	0.15	0.27	0.06	0.43	0.41	0.20	<0.01	0.84	<0.01	<0.01	0.04	<0.01	<0.01	0.02	<0.01	0.04
3	0.05	0.25	0.35	0.24	0.45	0.10	0.34	0.02	<0.01	<0.01	<0.01	<0.01	<0.01	0.64	<0.01	0.06
5	0.68	0.04	0.29	0.02	0.05	0.17	0.40	1.00	0.19	<0.01	0.05	<0.01	<0.01	0.39	<0.01	<0.01
7	<0.01	0.02	<0.01	0.16	0.25	0.08	0.04	<0.01	0.01	<0.01	<0.01	0.16	<0.01	<0.01	<0.01	<0.01
9	0.03	<0.01	0.68	<0.01	0.09	0.54	0.03	0.34	0.10	<0.01	0.25	0.82	0.04	0.01	0.05	0.40
11	0.10	0.03	0.02	0.65	0.65	0.89	0.09	0.43	0.02	<0.01	0.73	0.96	<0.01	<0.01	0.90	0.37
13	0.35	0.27	0.02	0.02	0.04	0.03	0.02	0.63	0.07	<0.01	<0.01	0.19	0.34	0.36	0.47	<0.01
15	0.06	<0.01	0.26	0.88	1.00	0.08	0.17	0.45	0.10	0.01	0.33	0.19	0.34	0.19	0.20	0.06
17	0.02	<0.01	0.40	0.07	0.08	<0.01	0.25	0.30	0.36	<0.01	0.55	0.05	0.08	0.05	<0.01	0.34
19	0.01	0.21	<0.01	0.50	0.59	0.28	0.06	0.25	0.43	0.08	0.16	0.10	0.01	<0.01	0.47	0.32
21	0.02	<0.01	0.68	0.16	0.16	0.23	0.44	0.67	0.41	0.09	<0.01	<0.01	<0.01	0.71	<0.01	0.35
23	0.10	0.04	0.01	0.28	0.44	0.41	0.41	0.21	0.24	0.09	0.18	0.66	<0.01	0.70	0.40	0.54
25	0.10	0.08	0.10	0.03	0.09	<0.01	0.24	0.63	0.52	0.16	<0.01	<0.01	<0.01	0.21	0.42	0.30
27	0.04	0.09	<0.01	0.70	0.87	<0.01	0.23	0.47	0.12	0.27	<0.01	<0.01	<0.01	0.93	0.83	0.48
29	0.01	0.05	0.05	0.35	0.36	0.03	0.06	0.12	0.16	0.05	<0.01	<0.01	<0.01	0.07	0.68	0.26
31	0.03	<0.01	<0.01	0.30	0.22	0.26	<0.01	0.40	0.41	0.05	<0.01	<0.01	<0.01	<0.01	0.87	0.46
33	0.02	<0.01	<0.01	0.02	<0.01	<0.01	<0.01	0.54	<0.01	<0.01	0.19	<0.01	<0.01	<0.01	0.92	0.05
35	<0.01	0.06	0.02	0.98	0.98	0.81	0.88	0.38	0.20	<0.01	0.53	<0.01	<0.01	<0.01	0.98	<0.01
37	0.17	0.55	0.35	0.51	0.51	0.51	0.03	0.50	0.18	<0.01	0.43	0.04	<0.01	<0.01	0.07	<0.01
39	0.09	0.03	0.01	<0.01	0.05	0.40	<0.01	0.49	0.34	0.04	<0.01	<0.01	<0.01	<0.01	0.89	0.35
42	0.48	0.69	0.51	0.77	0.58	0.58	0.26	0.45	0.02	<0.01	0.15	<0.01	<0.01	0.01	0.57	<0.01
44	0.28	0.27	0.25	0.57	0.56	0.59	0.08	0.57	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	0.60	0.07
46	<0.01	<0.01	<0.01	0.22	0.22	0.22	0.48	0.20	<0.01	<0.01	0.04	<0.01	<0.01	<0.01	0.65	0.14
48	0.02	<0.01	<0.01	<0.01	<0.01	<0.01	0.49	0.89	0.94	<0.01	0.15	<0.01	0.23	<0.01	0.67	0.32
50	<0.01	0.03	<0.01	0.04	0.07	0.06	0.01	0.39	<0.01	<0.01	<0.01	<0.01	0.06	<0.01	0.89	0.72
52	0.45	0.30	0.16	0.69	0.25	0.24	0.17	0.28	0.43	<0.01	0.09	<0.01	0.15	0.34	0.93	0.37
54	0.01	0.02	0.03	0.16	0.07	0.07	0.44	0.37	0.17	<0.01	0.65	<0.01	<0.01	<0.01	0.98	0.48

Dissolved oxygen followed a trend inverse to temperature, with relatively little variation among ponds and no appreciable stratification for much of the year (Fig. 3-3). Dissolved oxygen at 2 m in early April (Fig. 3-3) was greater than at surface and 1-m depths because surface waters were warmer at that time. Lower D.O. values at 2 m in May and early August were due to placement of the D.O. probe near the sediment surface when some pond depths had dropped due to evaporation or leakage. Variation among ponds at other times and for other depths was generally minor. Dissolved oxygen CVs exceeded 10% only five times during the study (Table 3-1). Only two of these events corresponded to significantly non-normal distributions (Table 3-2) of 2-m D.O. values, and all of these high CVs occurred when D.O. was measured near the sediment surface. Annual mean D.O. values were not significantly different among ponds.

A general increase was observed in pH during the study year, changing from slightly basic to slightly alkaline (Fig. 3-4). Initial pH of pond water was about 6.8 and gradually increased to a maximum of about 7.8 in October 1988, varying thereafter between about 7.6 and 7.8. Coefficients of variation exceeded 10% only once, corresponding with a significant non-normal distribution

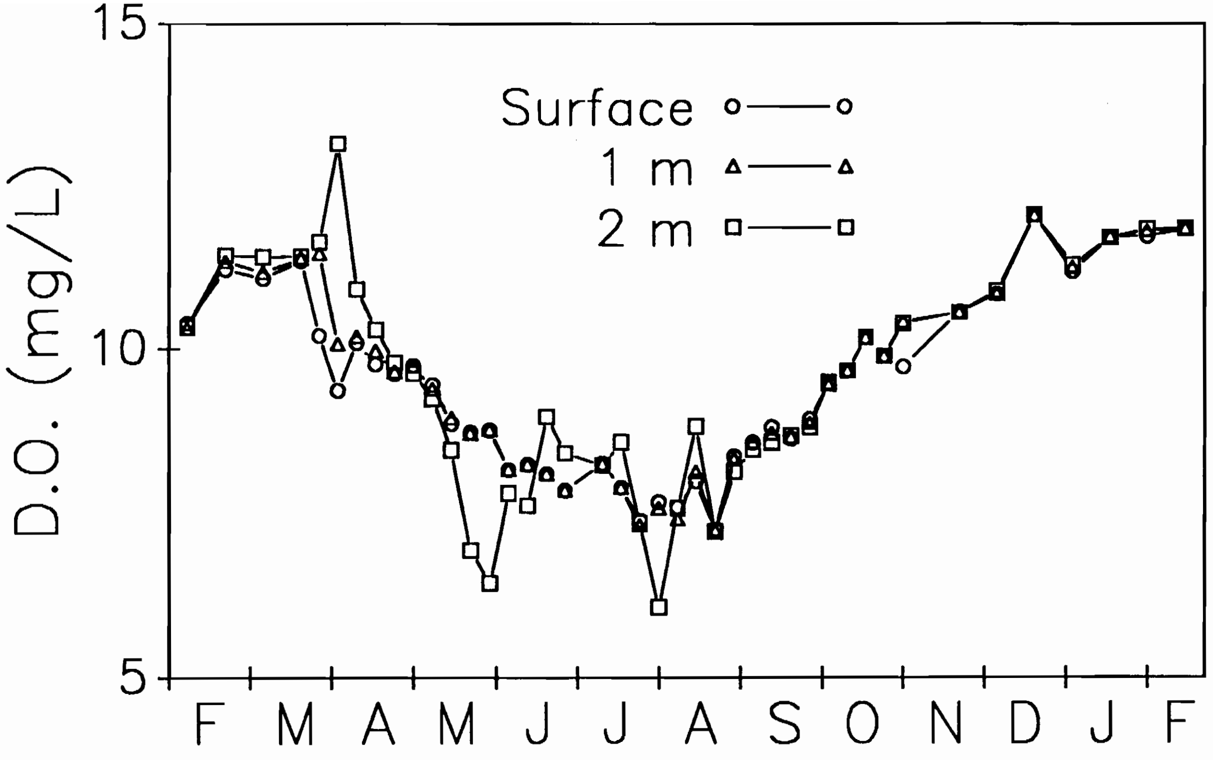


Figure 3-3. Mean dissolved oxygen.

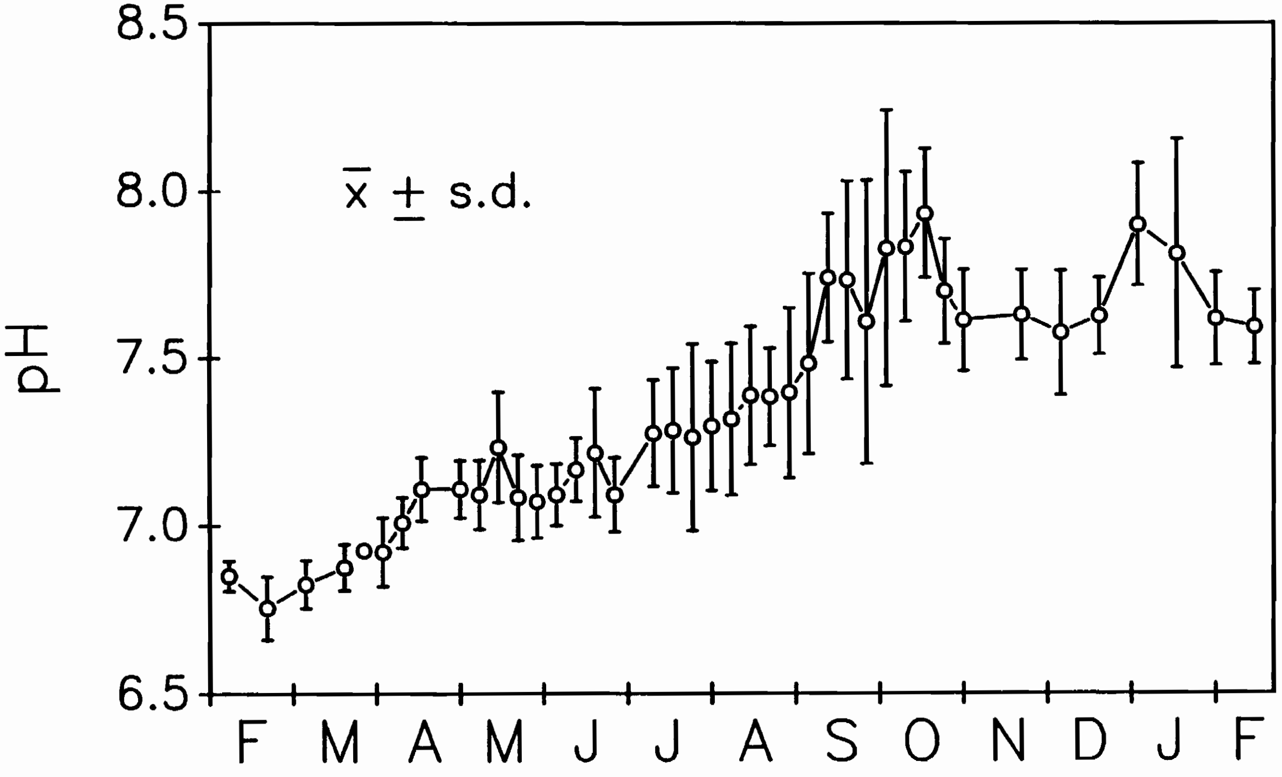


Figure 3-4. Mean pH.

of pH values (Tables 3-1, 3-2). Annual mean pH values of ponds were not significantly different (p=0.061), with two overlapping groups identified by Duncan's test (Table 3-3).

A general increase in total alkalinity was observed (Fig. 3-5), although the ponds never developed a large buffering capacity. Alkalinities increased from 30 mg/L as $CaCO_3$ to a maximum of about 55 mg/L as $CaCO_3$ during Autumn 1988. Alkalinities decreased during Winter 1989 to about 45 mg/L as $CaCO_3$. Alkalinity CVs never exceeded 4%. Only one date showed a significant non-normal distribution due to a clumped distribution about the mean (Tables 3-1, 3-2). However, ponds were significantly different by ANOVA (p=0.0001), and four overlapping groups were identified by Duncan's test (Table 3-3).

Water hardness was generally steady at about 75 mg/L as $CaCO_3$ until Fall 1988 (Fig. 3-6). Erroneous water hardness data were collected during September through December 1988 and are omitted from Figure 3-6. Despite this error, hardness apparently declined from about 75 to about 55 mg/L as $CaCO_3$ during Fall 1988, as evidenced by the values from January and February 1989. Coefficients of variation never exceeded 5%, and most dates after July 1988 exhibited non-normal distributions

Table 3-3. Duncan's Multiple Range Test Results(a).

Variable	Ponds											
pH	11	4	8	10	12	9	3	1	6	7	5	2
	A	A	A									
		B	B	B	B	B	B	B	B	B	B	B
Alkalinity	9	8	12	6	4	7	11	10	5	1	2	3
	A	A	A	A	A					D	D	D
		B	B	B	B	B	B	B	B			
					C	C	C	C	C	C		
Hardness	11	12	7	4	1	9	10	2	6	5	3	8
	A	A	A	A	A	A	A	A	A	A	A	
			B	B	B	B	B	B	B	B	B	B
Conductivity	12	7	11	1	4	2	3	10	9	5	6	8
	A	A	A	A	D	D	D	E	E	E	F	G
			B	B	B							
				C	C	C						
NH_3	7	12	10	11	8	9	6	1	3	5	4	2
	A	A	A	A	A	A						
				B	B	B	B	B	B	B	B	B
NO_3	7	10	5	3	12	4	2	11	1	6	8	9
	A	A	A	A	A	A	A	A	A			
		B	B	B	B	B	B	B	B	B	B	B
Chlorophyll a	9	7	6	12	2	11	4	1	10	3	8	5
	A	B	B	B	B	B	B	B	B			
			C	C	C	C	C	C	C	C	C	
				D	D	D	D	D	D	D	D	D
Secchi Depth	5	8	3	1	4	6	2	11	10	7	12	9
	A	A	A	A	A		D	D	D	D	D	D
				B	B	B	B					
						C	C	C	C	C	C	C

(a) Ponds are ranked in descending order (left to right) of variable means. Ponds connected by the same letter were not significantly different. Variables with one grouping for all ponds were: temperature, D.O., NO_3 and PO_4.

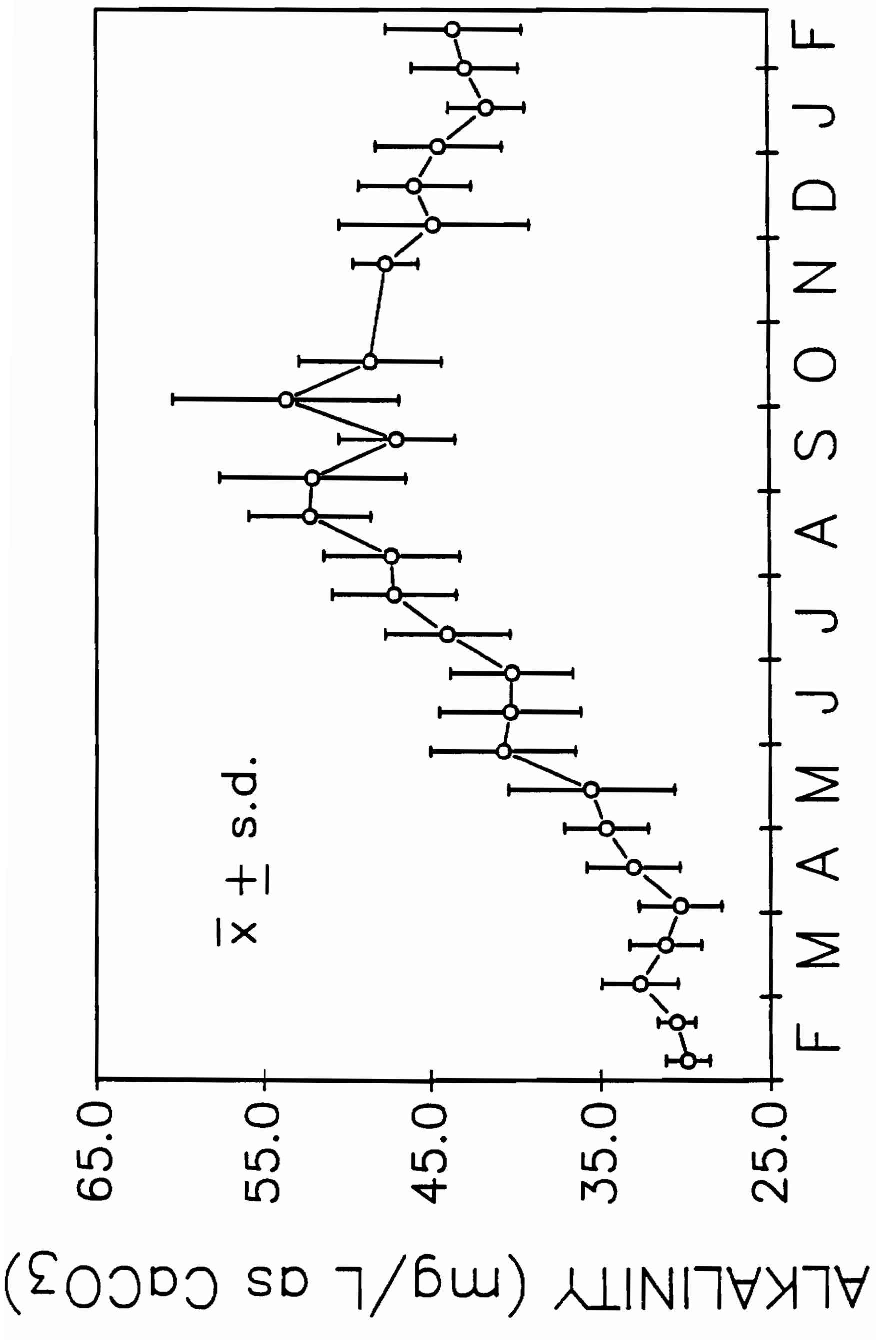


Figure 3-5. Mean alkalinity.

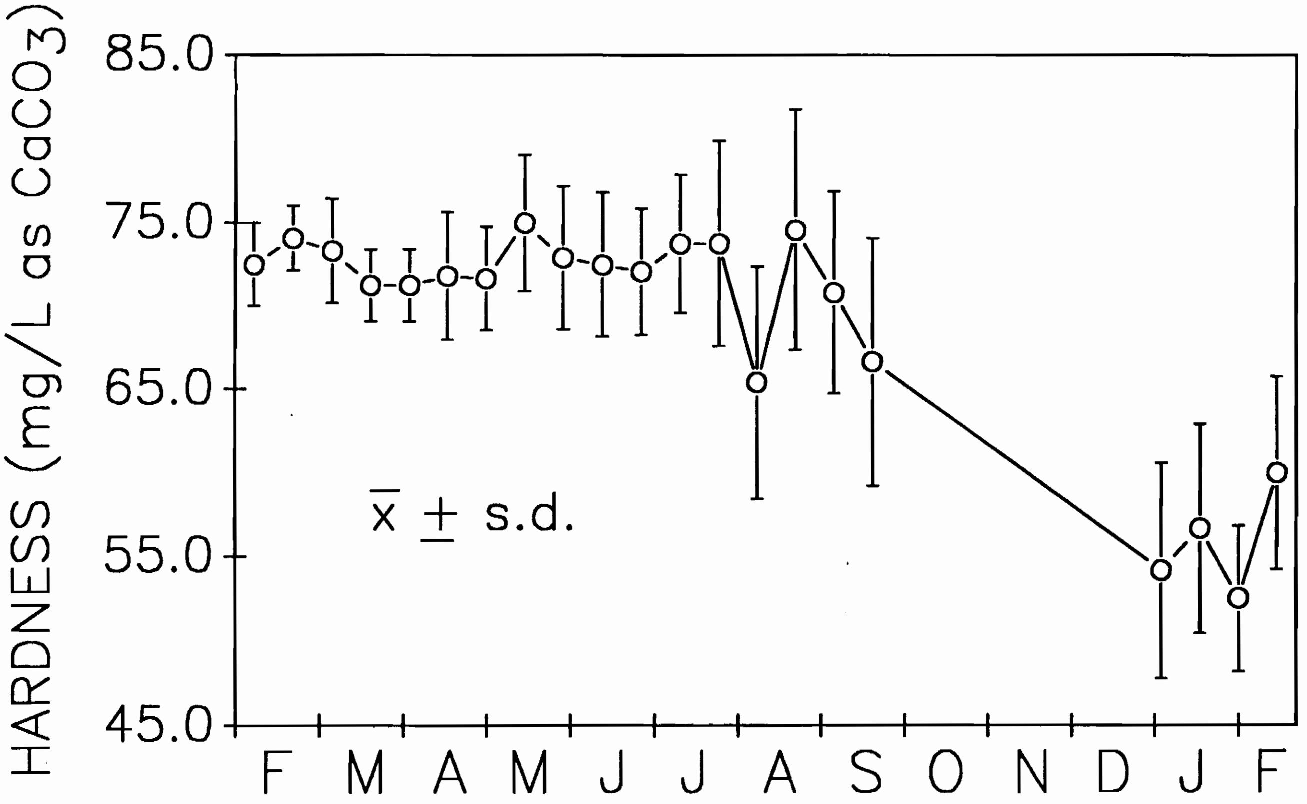


Figure 3-6. Mean hardness.

due to clumped distributions about the mean (Tables 3-1, 3-2). Annual mean water hardness values for ponds were not significantly different by ANOVA.

The general increase and apparent stabilization of pH and alkalinity may have been related to the transition of formerly terrestrial topsoil into aquatic sediment with benthic micro- and macroorganisms. Sediments and benthic organisms probably had a strong influence on water column chemistry, due to the high surface-to-volume ratio of these small, shallow ponds. Significant increases in sediment Ca and pH (Table 3-4) and the absence of an increase in water hardness indicate that increases in alkalinity were not due to leaching of $CaCO_3$ from sediments. Alkalinity and pH trends may have been related to increased respiratory output of CO_2 as soils turned to sediments.

Contrary to the trends in pH, alkalinity, and hardness, a general decline in conductivity occurred throughout the study year (Fig. 3-7). This decline was roughly linear and did not resemble the bimodal trends of pH and alkalinity or the trend for hardness. This result indicates a loss of ions from the water column, perhaps by sequestering in plankton and settling into sediments. Coefficients of variation were very low (Table 3-1) and all dates after July 1988 had

Table 3-4. Pre- and poststudy sediment chemistry[a].

Variable	Pre-study mean (± sd)	Post-study mean (± sd)	
pH	5.5 (0.2)	5.9 (0.2)	***[b]
P	1.2 (0.4)	1.0 (0.0)	
K	33.9 (4.6)	36.6 (2.2)	
Ca	308.0 (66.0)	519.0 (56.1)	***
Mg	53.7 (15.9)	53.3 (4.5)	
S	1.0 (0.0)	1.0 (0.0)	
NO_3-N	5.2 (1.9)	3.3 (0.8)	**
Zn	0.96 (0.27)	1.32 (0.22)	
Mn	7.04 (0.94)	7.15 (1.10)	
% Organic Matter	2.11 (0.40)	2.33 (0.24)	

[a] All units are mg/kg, except pH and % organic matter.

[b] Asterisks denote significant differences of pre- and post-study means by paired t-test: *** = $p < 0.001$, ** = $p < 0.01$.

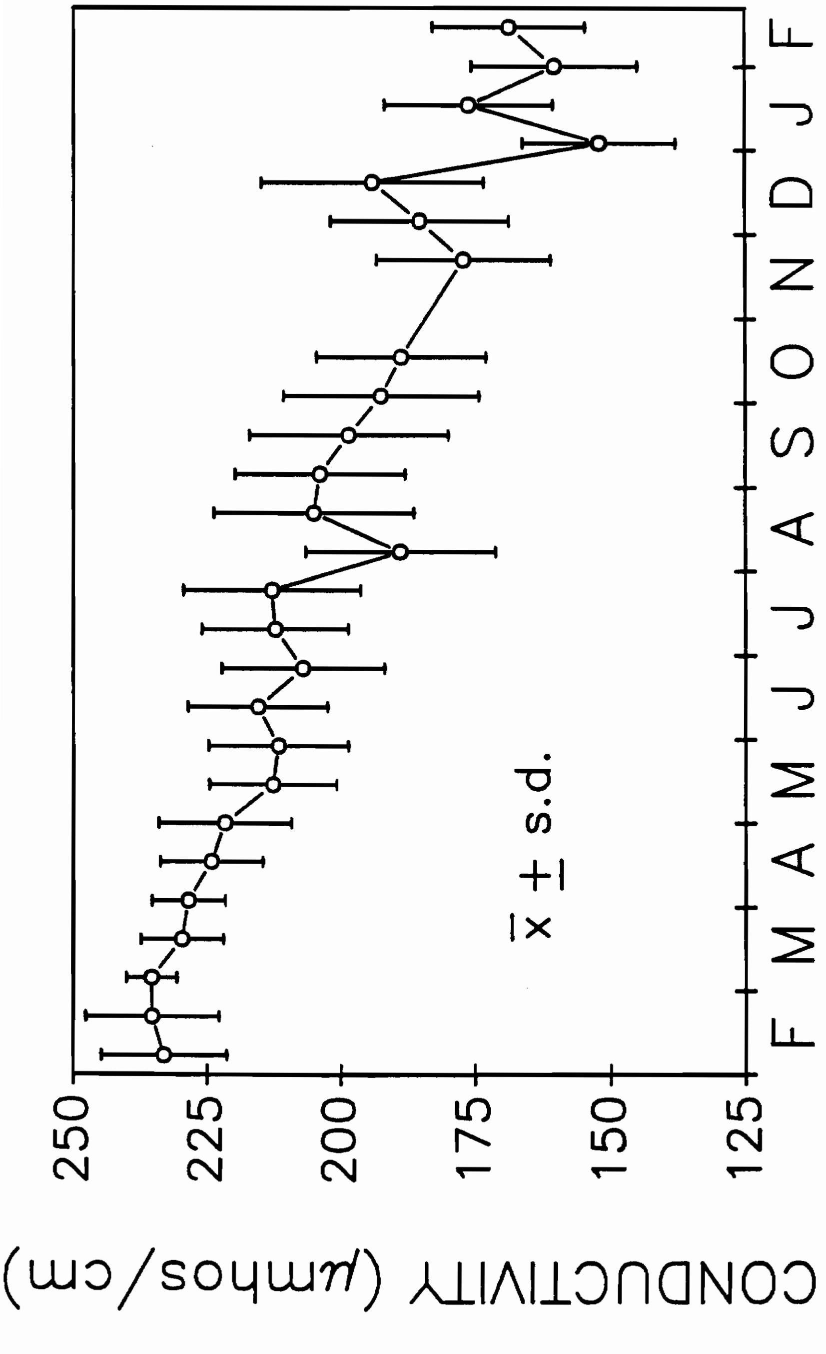


Figure 3-7. Mean conductivity.

significantly non-normal distributions due to clumped distributions about the mean (Table 3-2). However, annual mean values of ponds were significantly different (p=0.0001, ANOVA), and significantly different groups existed (Duncan's: p=0.05, Table 3-3). Ponds with significantly lower annual mean conductivity were the ponds that received the most groundwater to maintain water levels throughout the year. Water used to fill the ponds initially (municipal water) was almost twice as conductive as groundwater (203 and 115 micromhos/cm, respectively). The progressive replacement of initial water with groundwater in some ponds was probably responsible for the differences in conductivity.

The remaining variables (NH_3, NO_3, NO_2, SRP, chlorophyll a, and Secchi depth) are more closely linked to biological activity and environmental changes and should vary depending on population cycles, productivity, weather, etc. (Wetzel 1979). This was apparently the case in the ponds, although it is difficult to discern clear relationships among variables.

Ammonia concentrations varied widely among ponds and over time (Fig. 3-8). The lowest detection limit was 0.02 mg/L and NH_3-N was at or below this limit for much of the study. Ammonia generally increased soon

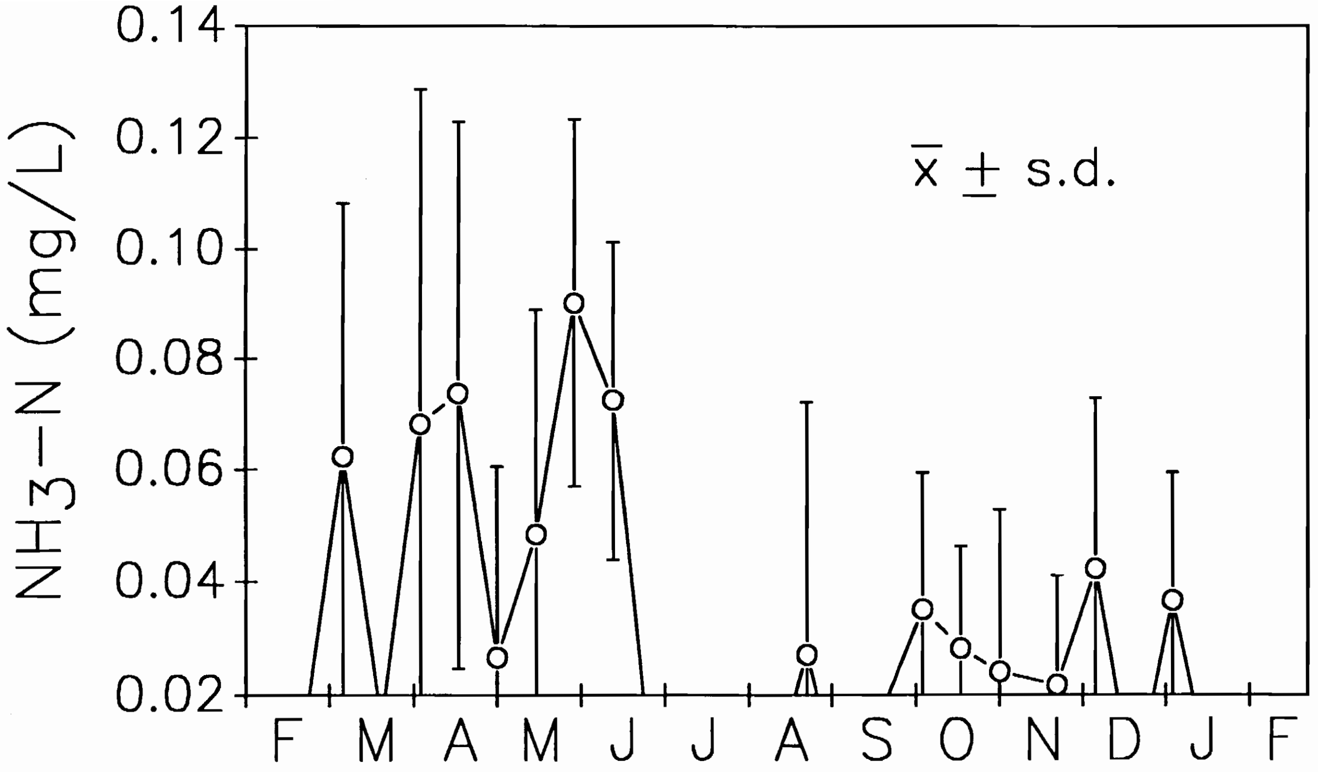


Figure 3-8. Mean ammonia concentrations.

after the ponds were filled, then declined sharply in June 1988, varying at or above detection limits thereafter. These early, higher NH_3 levels may have been due to release from sediments. All ammonia CVs were greater than 10%, ranging from 37% to 314% (Table 3-1). Ammonia levels were non-normally distributed on about one-half of the sample dates (Table 3-2). Ponds were significantly different in annual mean NH_3-N levels (p=0.0001, ANOVA), and two overlapping groups were identified by Duncan's test (Table 3-3).

Nitrate concentrations also varied considerably, but a general trend is apparent from Figure 3-9. Nitrate levels were high after the ponds were filled, peaking at an average of 1.25 mg/L NO_3-N in early March. Concentrations dropped through Spring 1988 and remained low for the remainder of the study. As with NH_3, the nitrates trend may have been related to sediment release. Nitrate CVs ranged from 15% to 346% (Table 3-1), and 20 of 27 sample dates showed non-normal distributions (Table 3-2). However, ponds were not significantly different by ANOVA.

Nitrite levels were low throughout the study, except for several weeks in Spring 1988 and Winter 1989 (Fig. 3-10). The two peaks in nitrite occurred with

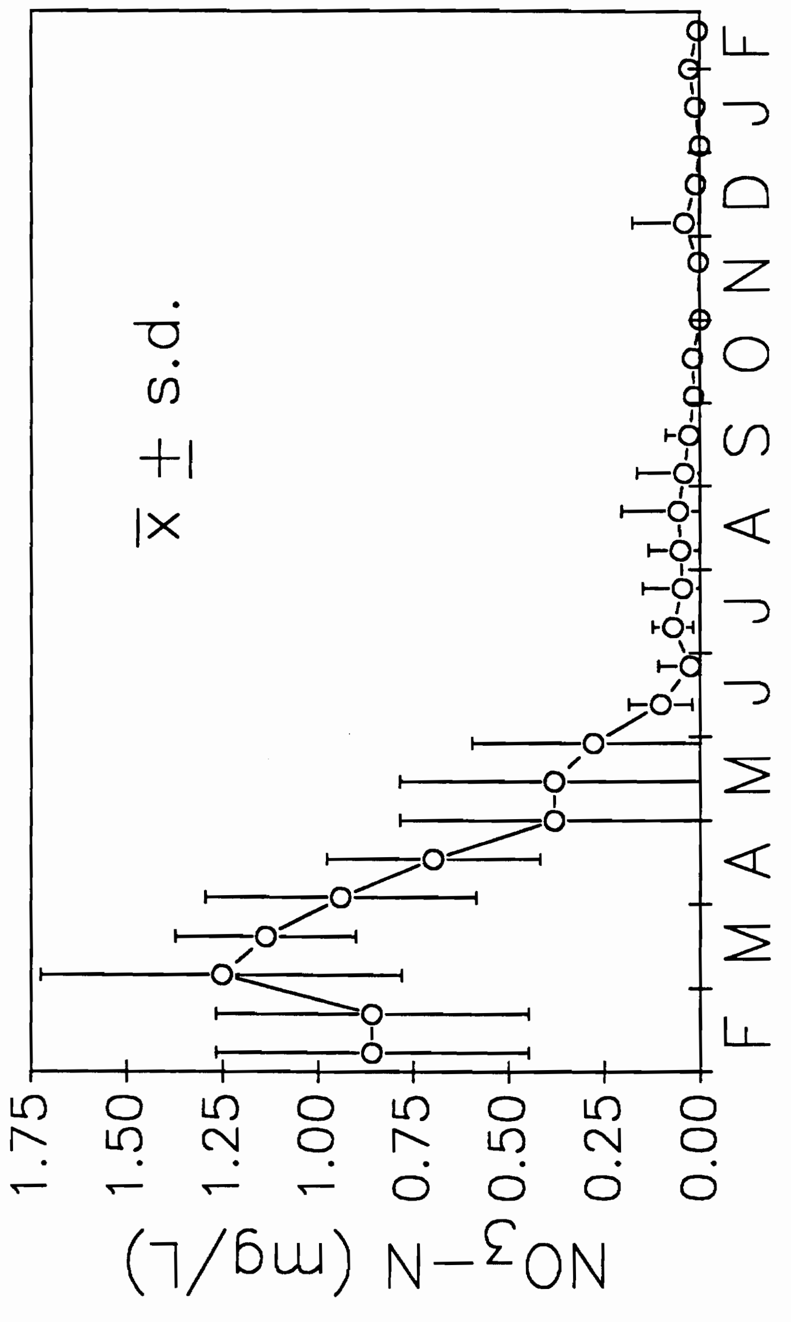


Figure 3-9. Mean nitrate concentrations.

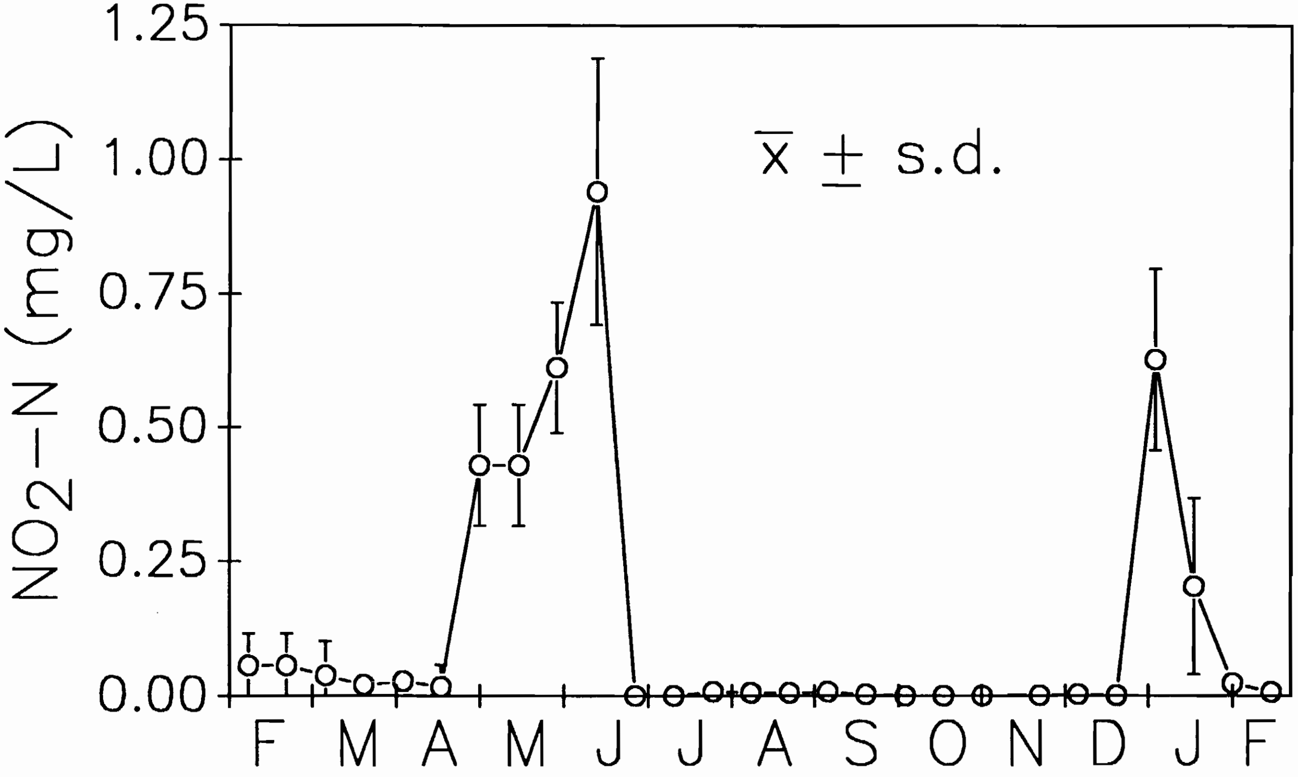


Figure 3-10. Mean nitrite concentrations.

comparatively low variability among ponds, as evidenced by the error bars in Figure 10. All CVs were greater than 10%, but the two nitrite peaks had the lowest CVs of about 20% (Table 3-1). The maximum CV was 347%, with 21 of 27 dates exhibiting non-normal distributions (Table 3-2). Annual mean nitrite levels of ponds were not significantly different by ANOVA.

Soluble reactive phosphate (SRP) was at or below detection limit (0.02 mg/L) for most of the study, with three notable exceptions (Fig. 3-11). High initial values were probably related to release of phosphates from sediments. Ponds varied greatly in a second peak in mid-May 1988 and again in November 1988. The November peak included three exceptionally high values (0.68, 0.49, 0.42 mg/L). Other values were comparable to previous peaks. The May and November peaks can not be explained by comparison to other data. Exceptionally high SRP values may have been due to contamination or analytical error. It should be noted that only a fraction of total phosphates was measured, with presumably more PO_4 present in other forms. Changes in SRP were probably related to changes in the distribution of phosphate among forms. All dates exhibited CVs > 10%, and 17 of 27 dates exhibited non-normal distributions (7 of these 17 dates had mean

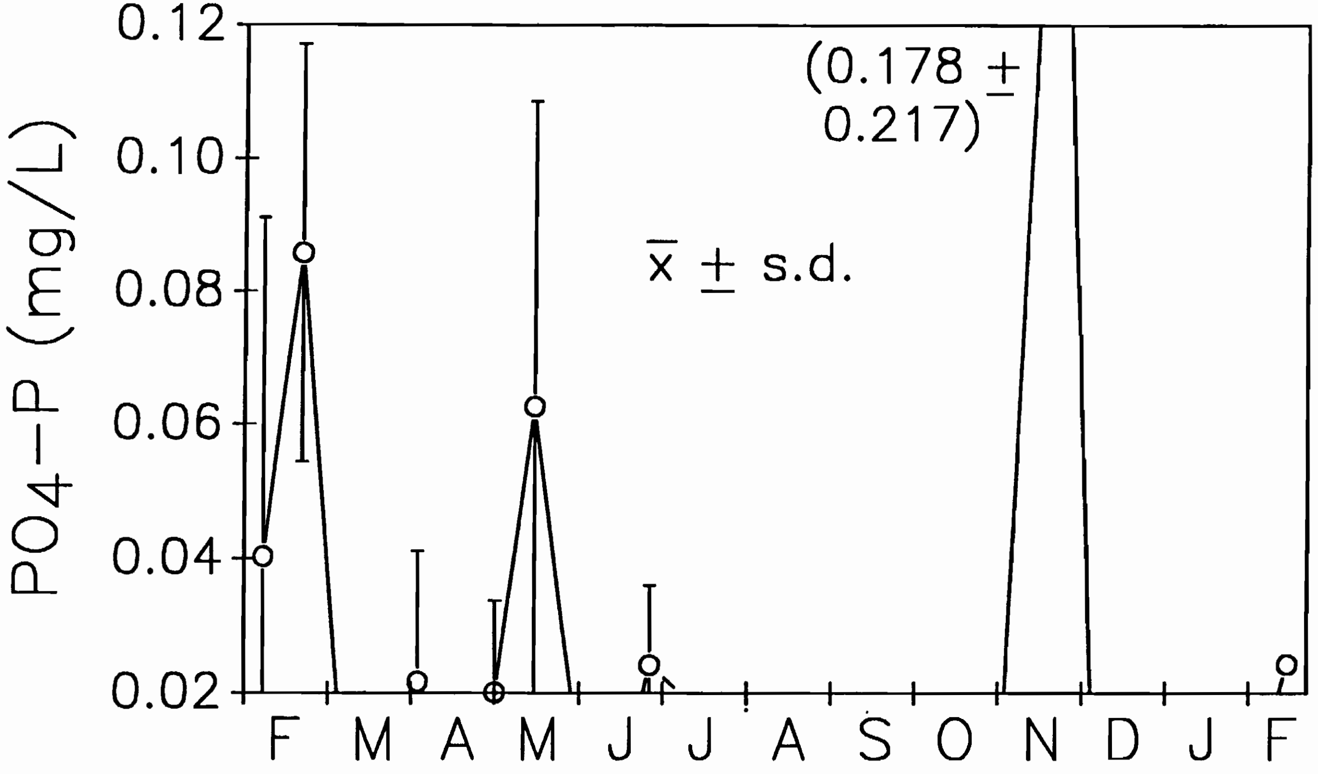


Figure 3-11. Mean soluble reactive phosphate concentrations.

concentrations of 0.0 mg/L). Ponds did not have significantly different mean annual SRP.

Chlorophyll a was variable among ponds, but all ponds exhibited increases in Spring 1988, sharp reductions in late Summer 1988 after temperatures approached 30^{o} C, and increases again after temperatures returned to < 25^{o} C (Fig. 3-12). Pond 9 annual mean chlorophyll a was significantly greater than all other ponds (Table 3-3). Reasons for Pond 9's high chlorophyll levels are not clear. Pond 9 was not greater than other ponds in measured nutrients and received less groundwater than several other ponds. Chlorophyll a is an integrative measure, incorporating all chlorophyllous phytoplankton populations within a pond into one value. It appears that phytoplankton biomass was constrained by temperature, but other unmeasured factors were responsible for increasing phytoplankton biomass, depending on the requirements of individual populations. All CVs were > 10%, ranging from 19 to 245 %. Chlorophyll a data were non-normally distributed among ponds on 6 of 27 sample dates, but 4 of those 6 dates were during the first 2 months of the study (Table 3-2). Data were normally distributed after early July 1988. Ponds were significantly different (p=0.001, ANOVA) and Pond 9 was significantly different

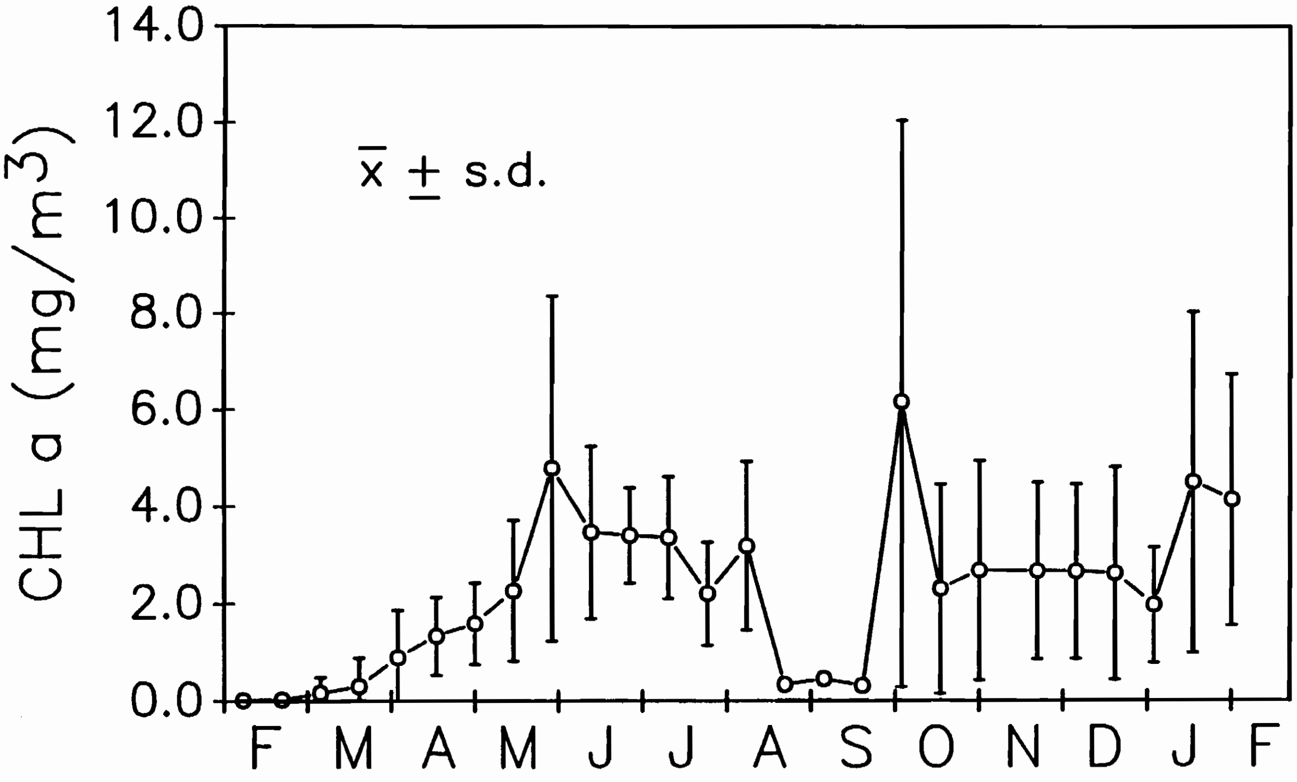


Figure 3-12. Mean chlorophyll a concentrations.

(p=0.05) from three other highly overlapping groups by Duncan's test (Table 3-3).

Secchi depths were fairly stable and shallow for the first two months of the study (Fig. 3-13), probably due to turbidity from initial filling. Secchi depths then varied through time, with a fairly stable mean depth maintained from August through October 1988. Secchi depth CVs exceeded 10% for all but three sample dates (Table 3-1). Only 7 of 27 sample dates exhibited non-normal distributions (Table 3-2) and two of these 7 corresponded to CVs < 10% (March 1988), indicating clumped distributions about the mean. Ponds were significantly different (p=0.0001) for mean annual Secchi depths and four overlapping groups were identified by Duncan's test (Table 3-3).

Several reductions in transparency (especially in late July and November, 1988) were immediately preceded by large rainstorms (Fig. 3-14). It is very likely that strong winds associated with storms at these times increased turbidity in the ponds. Surface runoff may have contributed to increased runoff but was probably a minor factor because drainage areas of ponds were only slightly larger than pond surface area. Wind data were not available, but winds might also have contributed to other changes in Secchi depths during the study.

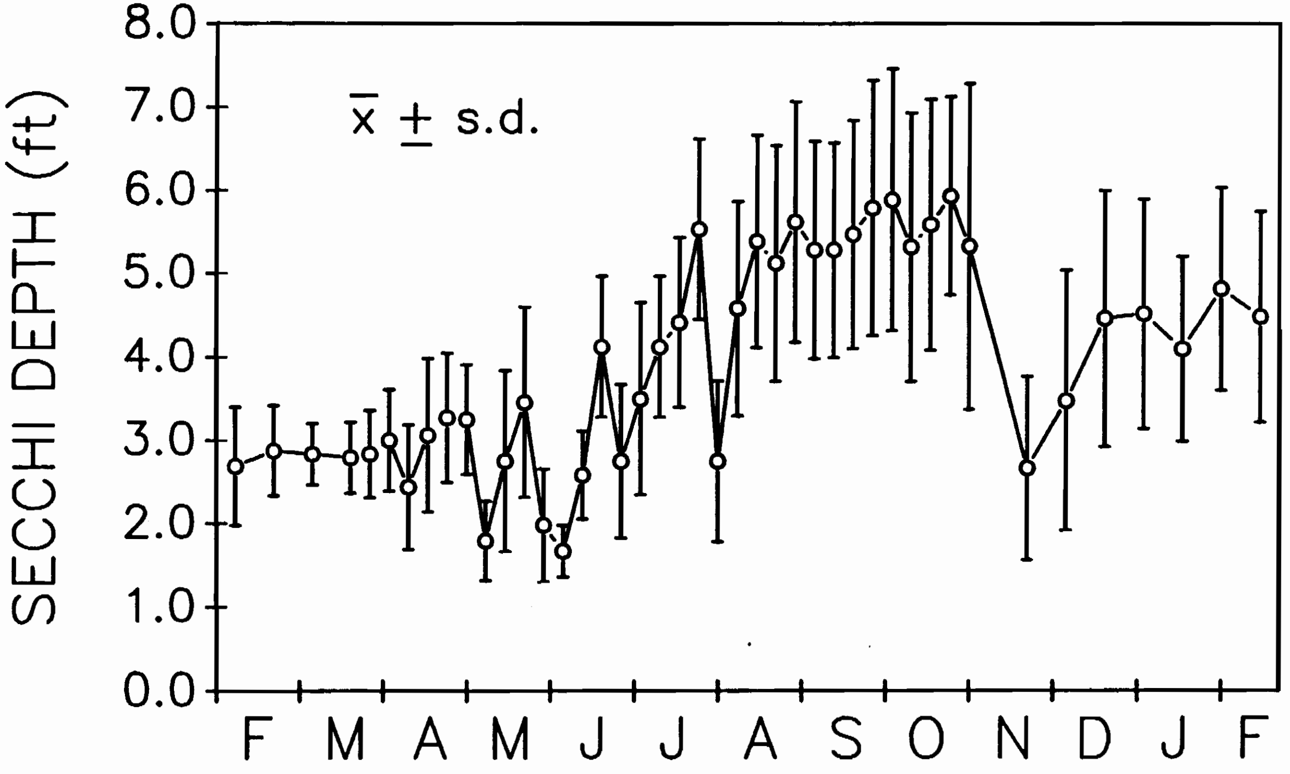


Figure 3-13. Mean Secchi depth values.

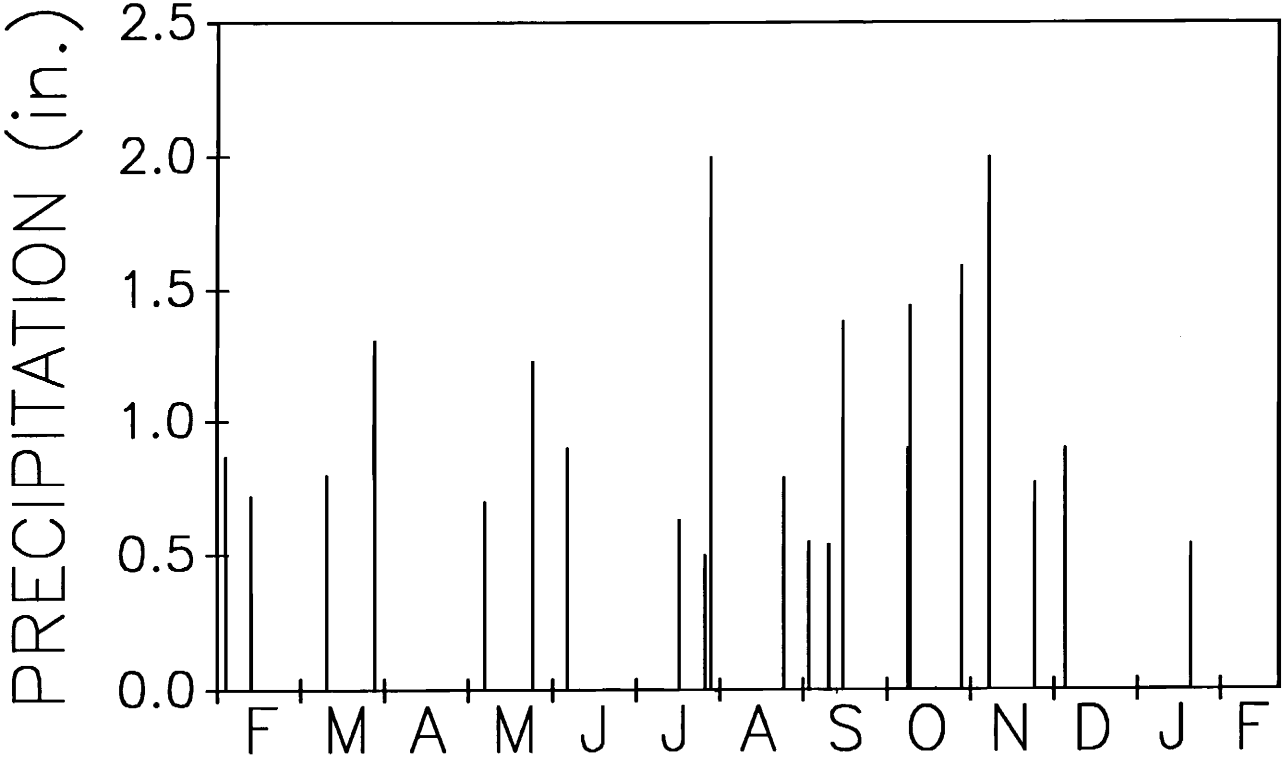


Figure 3-14. Major precipitation events (≥0.5 in.).

3.3.2 Multivariate Trends and Variation

Multivariate analyses were used to summarize patterns and enhance description of general trends. Two types of multivariate analyses were used:

- Principal Components Analysis (PCA), conducted on data for all ponds at all sample dates. By connecting the sample date principal component scores for each pond, a plot of successional trajectories in multivariate space is derived (Austin 1977). This permits graphical comparisons of trajectories among ponds and the identification of common and divergent trends. Only principal components (PCs) representing > 10% of total variation were plotted.
- Hierarchical cluster analyses, using centroid linkage clustering on Mahalanobis distances and conducted on data for all ponds by season. Centroid clustering defines the distance between two clusters as the squared Euclidean distance between their centroids. Centroid clustering has the following advantages over single and complete linkage methods: it is (1) more robust to outliers, (2) less prone to creating chains of units rather than groups, and (3) is not restricted to giving spherical clusters (Digby and Kempton 1987).

Mahalanobis distances are useful for variables of different scales, as is the case for physico-chemical parameters (Digby and Kempton, 1987). Months were assigned to seasons based on water temperatures during the study.

Surface temperatures were omitted from multivariate analyses because variation among ponds during sampling was simply a function of the time of day when sampling occurred.

Principal components analysis presented summary views of physico-chemical trends for each pond through the study year. The first three principle components (PCs) represented 68% of the variation for all 15 variables in 12 ponds over one year (Table 3-5). Principal component 1 was heavily dominated by temperature and dissolved oxygen and was interpreted as representing seasonal changes. Principal component 2 represented all other parameters except NH_3, NO_2, and SRP and was interpreted as representing general chemical conditions. The third PC represented primarily NH_3, NO_2, chlorophyll a, and Secchi depth and was interpreted as representing nutrient and productivity conditions. The fourth PC was heavily dominated by SRP but was responsible for only 7% of total variation.

Table 3-5. Physicochemistry principle components analysis.

	PC 1	PC 2	PC 3	PC 4
Variables		Eigenvectors		
Temperature (1 m)	0.4347	-0.0547	-0.0267	0.0071
Temperature (2 m)	0.4333	-0.0884	-0.0369	0.0115
D.O. (surface)	-0.4443	0.0214	0.0543	0.0344
D.O. (1 m)	-0.4435	0.0405	0.0559	0.0464
D.O. (2 m)	-0.3452	0.0235	-0.1442	0.1068
pH	0.1037	-0.4214	0.0809	0.0784
Alkalinity	0.0936	-0.4350	0.0369	-0.0530
Hardness	0.2406	0.2975	-0.0091	0.1284
Conductivity	0.1416	0.3811	-0.1257	-0.0354
NH_3	0.0330	0.1644	0.4495	0.2657
NO_3	-0.0649	0.4441	-0.0964	0.0960
NO_2	0.0704	0.0858	0.5652	0.1528
S.R.P.	-0.0374	0.0897	0.0319	-0.8846
Chlorophyll *a*	0.0081	-0.2406	0.4782	-0.1310
Secchi Depth	0.0276	-0.2973	-0.4323	0.2355
Eigenvalues	4.6787	3.8707	1.6533	1.0575
Proportion (%)	31.19	25.80	11.02	7.05
Cumulative Proportion (%)	31.19	56.99	68.02	75.07

Figure 3-15 shows PC 1 plotted against PC 2, representing 57% of total variation. Each line represents the trajectory of a pond through the study period. Considerable variation exists among ponds at any point in time and along the trajectories, but a common trend is obvious. A general seasonal trend is apparent for all ponds, due to the strong influence of temperature and dissolved oxygen on PC 1. Within this annual cycle are trajectories of the ponds along PC 2, representing a developmental change in water chemistry during the year. Most progression of trajectories along PC 2 occurred in the first half of the study period, with little change along PC 2 after Fall 1988. This result reflects the apparent stabilization of variables such as pH, alkalinity, and NO_3.

Also shown in Fig. 3-15 is a plot of PC 3 over time for all of the ponds. Little net change in PC 3 occurred over the year, with values fluctuating about 0. However, most ponds exhibited a large deflection along PC 3 during mid-May through early June 1988. This change in PC 3 was apparently related to coincident changes in several variables at this time: NH_3, NO_2, and chlorophyll a increased while Secchi depths decreased (Figures 3-8, 3-10, 3-12, and 3-13). A second, lesser deflection occurred in most ponds at the end of

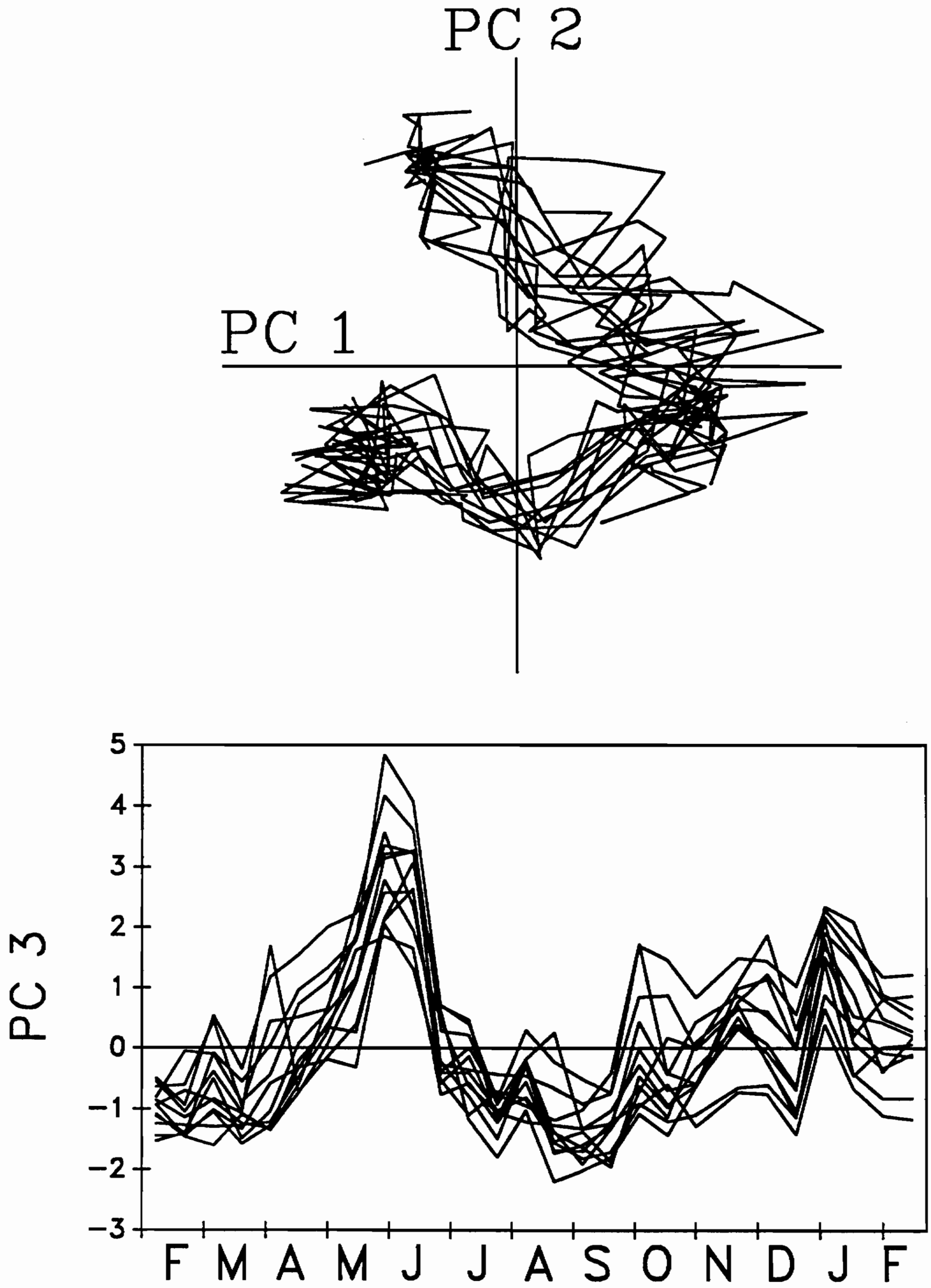


Figure 3-15. Principal component analysis of physicochemical parameters. See text for explanation of axes.

December, apparently related to a spike in NO_2 levels at this time (Fig. 3-10).

Seasonal cluster analyses are shown in Figure 3-16. Major separations among clusters show only 1 - 3 ponds as being unique during the first four seasons (Winter 1988 through Fall 1988). In addition, no one pond was consistently different from the others across seasons and no spatial patterns of groupings were consistent across seasons. The major separation in Winter 89 grouped five ponds (4, 11, 12, 7, and 9) apart from all others, and Pond 9 was only weakly associated with this group. However, this major separation occurred at a lesser distance between clusters than the major separations of earlier seasons, indicating that differences among ponds were less marked in Winter 89.

3.4 DISCUSSION

Six variables (temperature, D.O., pH, alkalinity, hardness, and conductivity) followed stable trends through time with relatively low variability among ponds. Significant differences among ponds for conductivity seem to be due to differential addition of groundwater to ponds to compensate for water loss. Alkalinity, hardness, pH, and conductivity are often used as general descriptors of systems and do not change

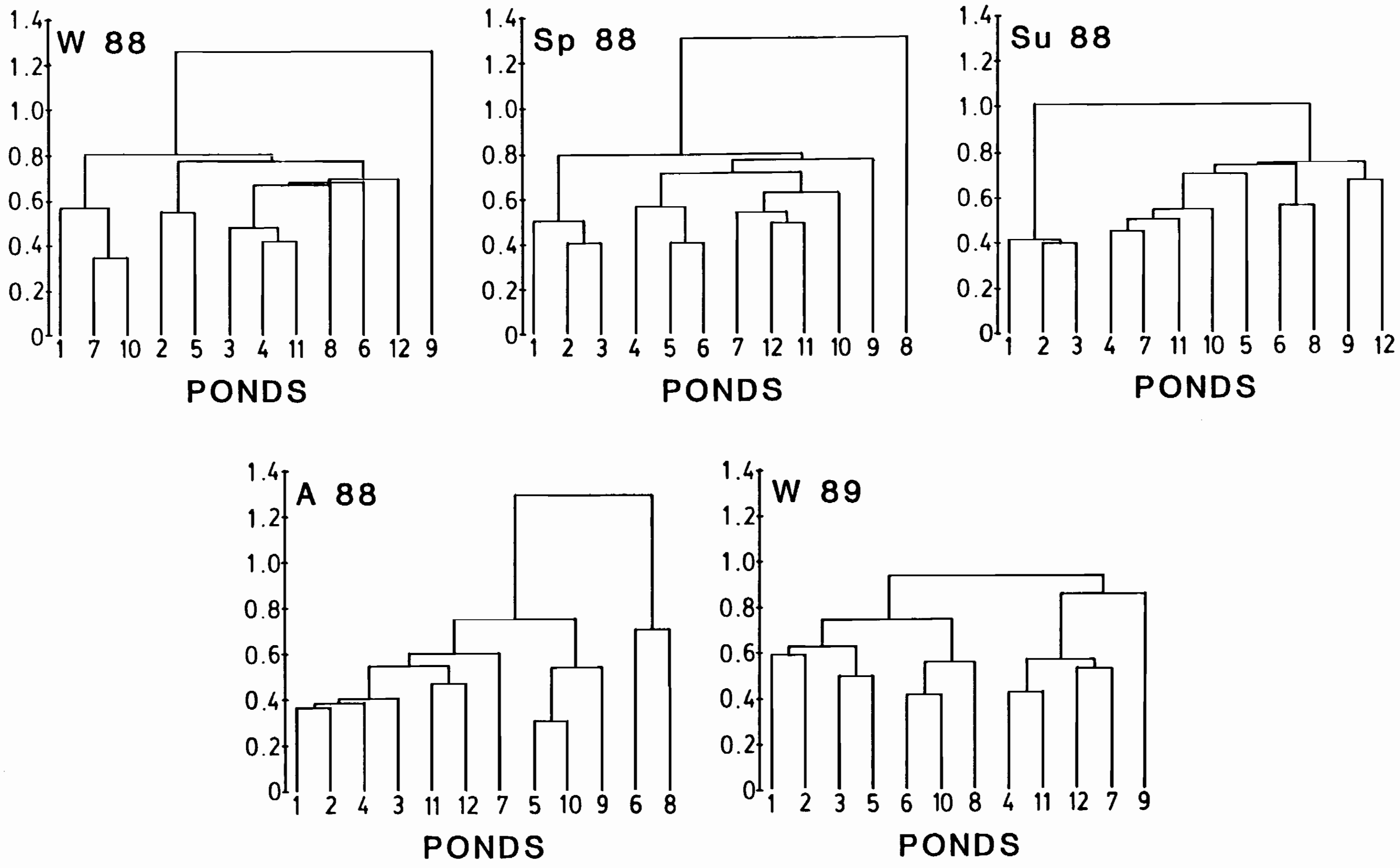


Figure 3-16. Seasonal cluster analyses of physico-chemical parameters. See text for description of clustering method. W88= Winter 1988, Sp88= Spring 1988, Su88=Summer 1988, A88=Autumn 1988, W89= Winter 1989.

markedly unless in highly productive systems (Wetzel 1979). Other parameters (nutrients, chlorophyll a and Secchi depth) were far more variable among ponds and through time. Nitrate, ammonia, phosphate and Secchi depth were all affected by initial conditioning of sediments after the ponds were filled with water. It is also very likely that weather contributed to fluctuations in some of these variables, especially Secchi depth. Secchi depth did not correlate with chlorophyll a in any of the ponds (all $r^2 \leq 0.05$, lowest $p = 0.23$) and major decreases in Secchi depths were apparently due to storms. Nutrients and chlorophyll a are closely related (directly for chlorophyll a) to biological processes, and fluctuations in these data were probably related to biological events (population peaks and crashes, changes in growth rates, and productivity).

Inspection of univariate data yields different impressions of variation among ponds, depending on the parameter of interest. In addition, different parameters exhibit their highest variation among ponds at different points in time. Within this range of variation among ponds are common temporal trends: seasons, general increases in pH and alkalinity, general decrease in conductivity and declines of NH_3, NO_3, and

SRP after flooding of the soils. The overall impression for all the univariate data is one of general trends for all ponds through the year but with variation among ponds for some parameters at some points in time.

Multivariate analyses present summary graphic representations yielding the same overall impression. At any point in time, principal components trajectories indicate variation among ponds, but the trajectories follow the same general pattern. In addition to seasonal changes in the ponds (PC 1), most major changes in water chemistry (PCs 2 and 3) occurred in the first half of the study period. Seasonal cluster analyses indicate only a few ponds as being greatly different from others per season, and no pond was consistently different across seasons. In addition, no consistent spatial patterns of clusters existed.

Were the ponds environmentally homogenous? The answer to this question must be qualified for the length of time under consideration. If one is interested in brief time periods (i.e., < 1 month), my answer is no: ponds differed in various ways at different times, and these differences were more likely to be maintained during a short time interval. However, if one is interested in the entire year, my answer is a cautious yes. Ponds were generally similar, although not identical. Some ponds differed in annual mean conductivity and one differed in chlorophyll a, but these ponds were similar in other variables. Considering all variables collectively, differences among ponds tended to average out over the year, and the same general trends occurred in all ponds with about the same timing of changes. For the purposes of a year-long study of zooplankton colonization, I considered ponds sufficiently similar to meet the assumption of environmental homogeneity.

This conclusion carries three caveats and several implications. Only a subset of all environmental variables were measured, and other ecologically-important variables, such as microbial production, dissolved organic carbon, total phosphate, etc. may contribute to a different conclusion. Secondly, this study was conducted in the first year of the ponds. No "homogenization" of ponds (e.g, drain and refill) was done, and macrophytes had not yet developed. Trends through a year and patterns among ponds may be different following "homogenization" and development of macrophytes. Finally, environmental homogeneity does not necessarily mean that populations of interest (zooplankton, benthic macroinvertebrates, fish, etc.)

will also exhibit homogeneity among ponds. Environmental homogeneity is a subset of all the parameters under consideration in community- and ecosystem-level experiments, and does not imply that other parameters will be replicable among ponds.

These results and conclusions imply that short term experiments (e.g., < one month) in these ponds run the risk of having results confounded by within-treatment variations in environmental conditions. Experiments should be conducted over longer periods (e.g., $\geq$ 6 months) to reduce chances of consistent environmental differences among ponds.

Manipulations of ponds should be made with caution, to ensure that further heterogeneity is not introduced. Ponds differed in conductivity, apparently due to addition of groundwater to some ponds to compensate for water loss (presumably due to leakage). If water loss cannot be stopped by additional clay, compaction, etc., it may be worth the effort to repeatedly drain the ponds to the level of the lowest pond and add equal amounts of supplemental water to all ponds. If efforts are not made to minimize this artifactual heterogeneity, ponds will continue to differ in some variables according to their sources of water.

4.0 COLONIZATION DYNAMICS: COMPARISONS AMONG PONDS AND OVERALL TRENDS

4.1 INTRODUCTION

As a phenomenon central to studies of species-area relationships and succession, colonization has been directly or indirectly studied for many years (e.g., Arrhenius 1921, Gleason 1922, Williams 1943, Maguire 1963, Simberloff and Wilson 1969 & 1970, Rey 1981, McGuinness 1984a) and continues to attract research and discussion (e.g., Gray et al. 1987, Roughgarden 1989). Much of the research on species-area relationships has addressed or claimed to be consistent with the Equilibrium Hypothesis of MacArthur and Wilson (1967), although some reviewers claim little actual support has accumulated for the theory (Gilbert 1980, McGuinness 1984b).

As stated by McGuinness (1984a), the Equilibrium Hypothesis is but one alternative hypothesis; other alternative hypotheses are the Habitat Diversity (Williams 1943, 1964) and Intermediate Disturbance (Connell 1978) Hypotheses. The Random Placement Hypothesis (RPH) is the null hypothesis and accordingly should be considered before invoking alternative hypotheses (Connor and McCoy 1979, Strong 1980, McGuinness 1984b). The RPH is generally attributed to

Arrhenius (1921) and was expressed mathematically by Coleman (1981).

The RPH states that the number of species present in a location is simply a function of area, assuming environmental homogeneity among locations and a lack of correlation in the presence of individuals (Coleman 1981). Coleman et al. (1982) found the number of birds breeding on islands varied with island size according to the RPH. McGuinness (1984a) considered the RPH a good predictor for over half of the intertidal communities he sampled, but no single hypothesis adequately described all observed patterns. If a data set is fully explained by the RPH, alternative hypotheses need not be invoked. However, acceptance of the null hypothesis does not imply that non-random processes did not occur, only that results fit the null conditions (Cale et al. 1989).

I conducted a study testing a prediction of the RPH for zooplankton in twelve new experimental ponds of equal dimensions. If, according to the hypothesis, locations of different size collect different numbers of species simply as a function of area, then ponds of equal dimensions should collect the same numbers of species. I constructed colonization curves for the ponds and compared them to address this prediction. Colonization curves plot species number at each point in time over the study period. As an alternate approach, I also constructed and compared species accrual curves (cumulative number of species observed).

The RPH addresses species-area relationships. All twelve ponds had the same area and a species-area curve was not relevant. Instead, I applied Coleman's (1981) formulae for mean and variance of the expected species number to each sample date throughout the study. I could then construct an expected colonization curve for comparison to observed curves for the ponds.

My objectives for this study were to answer the following questions: 1) Were ponds of equal dimensions colonized by zooplankton similarly, as predicted by the RPH? 2) Did the RPH (as described by Coleman 1981) adequately predict the colonization of zooplankton in these ponds? 3) If not (for either question), what factors may have contributed to the results? 4) What overall, general trends were apparent in the colonization of twelve "replicate" ponds?

4.2 MATERIALS AND METHODS

Study Site

An experimental pond facility was constructed during 1987-1988 at the Southern Piedmont Agricultural Experiment Station near Blackstone, Virginia. The site is in the Piedmont physiographic province (77°57'30"W, 37°5'30"N) at an elevation 128 m above mean sea level. The facility consists of twelve ponds and a reservoir (Fig. 3-1). The reservoir was constructed after the ponds and was not included in this study.

Prior to construction the site was a mixed pine and deciduous forest. After removal of vegetation, topsoil and subsurface clay from the site were saved separately for use in the ponds. Pipes were placed underground to connect ponds to the reservoir and two wells. Valves permitted addition of well water to each individual ponds.

Excavation of ponds began in late June 1987 and ended in November 1987. All twelve ponds were constructed according to the same specifications: square, with 404.8 m^2 surface area (20.12 m on a side), 2.13 m depth, 2.5:1 slope ratio. Each pond was bermed at the top to prevent surface runoff from entering the pond. The ponds were sealed with about 15 cm of compacted clay and lined with about 15 cm of topsoil from the site. Ponds were excavated in the following order: 3,2,1,4,5,6,9,8,7,10,11,12 (Fig. 3-1). Excavation was interrupted for about 2 months between ponds 8 and 7. Following excavation, the berms and tops of inner slopes were seeded with grass and mulched with straw to reduce erosion. Areas between ponds were fertilized but inner slopes of ponds were not fertilized.

Two ropes were suspended over each pond, each traversing the pond from the mid-point of opposite sides (East-West and North-South) and crossing in the center. Small docks were also built on the west side of each pond.

All twelve ponds were filled with water in late January 1988. Chlorinated tap water (source: Nottoway Reservoir) from a nearby fire hydrant was used. Water entered the ponds through the underground pipes, so that all twelve ponds received water simultaneously. Ponds were filled over the course of 6 days, ending on 31 January 1988. Sampling started on 5 February 1988 and continued for one year, ending on 10 February 1989.

The only manipulation of the ponds was the addition of well water to maintain water levels. At no time was water transferred from one pond to another during this study, and no reservoir water was added to any ponds. No fish were stocked in the ponds and fish were never observed in any pond during the study.

Sampling Strategy

Sampling and analyses were conducted biweekly for one year, starting on 5 February 1988 and ending on 10 February 1989. One three-week interval occurred in November 1988. In addition, limited sampling was conducted during intervening weeks from March through October 1988. The criterion for starting and ending these shorter sampling trips was a 10^{o} C water temperature. The 10^{o} C criterion was arbitrary but was considered representative of seasonal changes.

All sampling was done according to a set of random sampling sequences prepared prior to the study. These random sequences ensured that no patterns would be established among ponds due to sampling activities. Each pond was sampled at three stations: always at the center (2.13 m depth) and at 2 of the 4 sides (1.07 m depth). The two sides were chosen each sampling trip by coin toss (East vs. West, North vs. South). Sampling stations were kept consistent throughout the study by using the suspended ropes as guides. The intersection of the ropes marked the center, and a position on the ropes at 1.07 m depth marked the side stations.

Sampling Procedures

Sampling procedures were consistent for all ponds at all sampling dates. Ponds were sampled from an inflatable raft. Upon entering the pond, sampling started at the center station, then proceeded to the two side stations. Two types of samples were collected at each station: tube and net samples.

Tube samples collected whole water for use in analyses of phytoplankton taxa, chlorophyll, and water chemistry. Four liters of this water were also used to collect and preserve rotifers. Five tube samples were collected at each station. Tube samples were taken to 1.83 m depth at the center station and 0.91 m depth at side stations. Tube samples were collected with a 1.83 m-long plexiglass tube (5.08 cm i.d.) fitted with a cable through the tube. A rubber ball was attached to the bottom end of the cable. The ball fit in the end of the tube for a water-tight seal when the cable was pulled taut. The tube was lowered into the water, the cable was pulled taut, and then the tube was lifted out of the water. The collected vertical "core" of water was then emptied into a bucket by releasing tension on the cable. Two 20-L buckets were filled this way in each pond.

Bucket contents were combined in a larger container upon exiting the pond. Four L were subsampled and sieved through 35-um plankton netting. Collected organisms were rinsed from the sieve into a jar and preserved with about 4% formalin. Formalin was buffered with 5% sodium acetate (Steedman 1976) and contained 5 g/L sugar (Haney and Hall 1973).

Quantitative net samples were collected to estimate crustacean and Chaoborus densities. Net samples were collected at each station via vertical tows from the bottom with a Wisconsin-style plankton net, (80-um mesh: Wildlife Supply Co.). The net was gently placed on the bottom and allowed to lie there for about 2 min before being hauled up. This was done to obtain a representative sample of the whole water column, with minimal disturbance of the bottom water. Two net samples were collected at each station. Collected organisms were rinsed from the net into a second jar and preeserved with 4% formalin (as above).

Pond depth was recorded and used in calculations of water volume collected for quantitative estimates of zooplankton densities. Pond depth applied to calculations for net tows at the center station only: net tows at side stations were always in 1.07 m of water, regardless of pond depth.

Six of 648 samples were accidentally not preserved during the study. The average of preceding and subsequent samples was used to represent densities for a missing data point in analyses. If available (March - October), samples from intervening weekly trips were used in averaging. The following rules were used for assignment of species presence/absence to these missing samples:

Preceding Sample	Missing Sample	Subsequent Sample
Present	(Present)	Present
Present	(Absent)	Absent
Absent	(Absent)	Present
Absent	(Absent)	Absent

Spatial heterogeneity and within-pond variance could not be evaluated because tube samples were pooled and subsampled and net samples were pooled for each pond. However, the purpose of this study was to compare colonization trends of ponds, with each pond serving as an experimental unit (Hurlbert 1984). Three sampling stations per each small pond and about 100 L of sampled water provided sufficiently representative data to evaluate colonization trends.

Sample Processing and Analyses

Preserved zooplankton were counted and identified at 40 X with a Sedgwick-Rafter chamber and a Nikon binocular microscope. Greater magnifications were used to aid identifications. Samples were examined before counting and sample volumes were adjusted for the concentration of organisms. Entire samples were counted if depauperate, while dense samples were counted using at least three subsamples. Subsamples were obtained by mixing the sample and transferring 1.0 mL to the Sedgwick-Rafter chamber with a calibrated autopipette. Entire subsamples were counted. Original densities (organisms/L) were calculated using sample volumes, number of subsamples, and volumes of water represented in net tows. Quantitative data were converted to binary data (presence = 1, absence = 0) for use in calculations of species present. Statistical analyses were conducted using SAS (SAS Institute 1985).

4.3 RESULTS

Colonization Curves

Colonization curves (species present over time) for the twelve ponds are shown in Figure 4-1. All ponds had a low number of zooplankton species initially and increased in species number after several weeks.

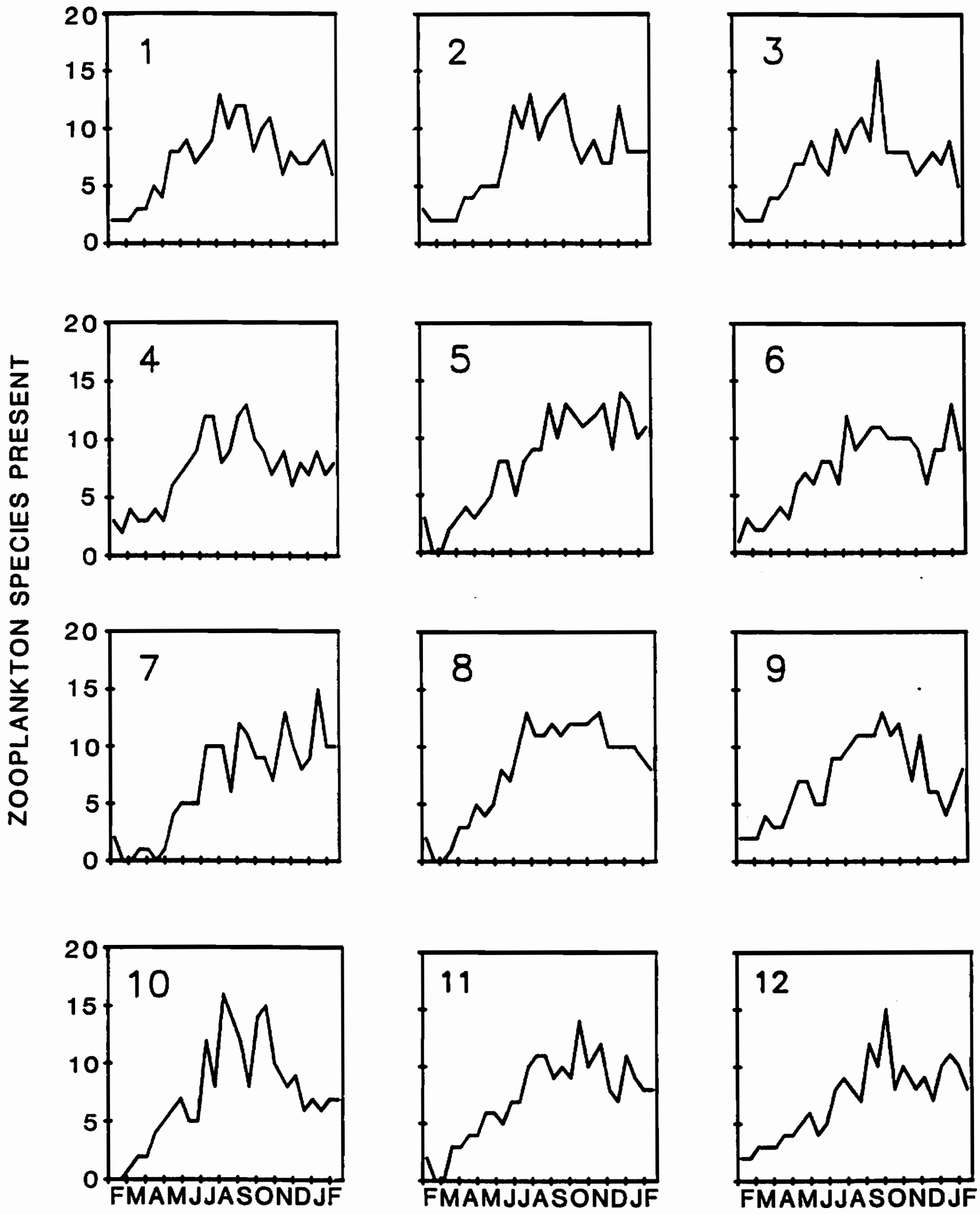


Figure 4-1. Zooplankton colonization curves. Plots are arranged in the configuration of ponds at the facility.

Zooplankton species numbers started at values greater than zero for all ponds except Pond 10. Zooplankton species present at the beginning of the study were apparently present in puddles prior to filling of the ponds. Some of the species present at Week 1 were not present at Week 3, likely due to changes in conditions following filling of the ponds. There was a definite lag period during Winter 1988 for several ponds (e.g., Ponds 2, 4, 7) while other ponds (e.g., Ponds 6, 12) did not exhibit a strong lag period (Fig. 4-1).

Colonization curves exhibited considerable variation among ponds and through time within a pond (Fig. 4-1). Some ponds exhibited sharp spikes in zooplankton species number (e.g., Ponds 3, 4, 7, 10, 12) while other ponds exhibited less marked variability over time (e.g., Ponds 5, 6, 8). Large changes in zooplankton species number were not synchronous among ponds and did not coincide with environmental changes such as rainstorms (Section 3.0). This variability precluded statistical comparisons of curves by dummy-variable regression analysis (Kleinbaum et al. 1988) and analysis of covariance (Sokal and Rohlf 1981).

Most of the ponds exhibited declining species numbers during Autumn 1988 and Winter 1989 (Fig. 4-1). However, Ponds 5, 6 and 7 did not exhibit this decline, and some decreases in species number were much greater than others. The apparent effect of seasons on colonization was not consistent among ponds.

Species Accrual

Another approach to considering colonization is a cumulative record of initial species detections, providing a plot of species accrual per pond through time. This analysis assumes sampling methods were adequate to detect species presence upon colonization and ignores possible extinctions. A species was recorded as present in a pond upon its first appearance in a sample and thereafter through the study. I analyzed the logistic species accrual trends (Fig. 4-2) by dummy-variable regression analysis (Kleinbaum et al. 1988) and compared species accrual rates (r) and numbers of species accrued (K). Dummy-variable regression analysis (DVRA) is a technique for comparing regressions and provides estimates of regression coefficients with 95% confidence limits. DVRA is often used to compare experimental treatments to controls. Because no treatment groups existed in this study, I arbitrarily designated Pond 1 as the reference for DVRA.

All regressions were highly significant ($p < 0.001$) and the lowest correlation coefficient for the

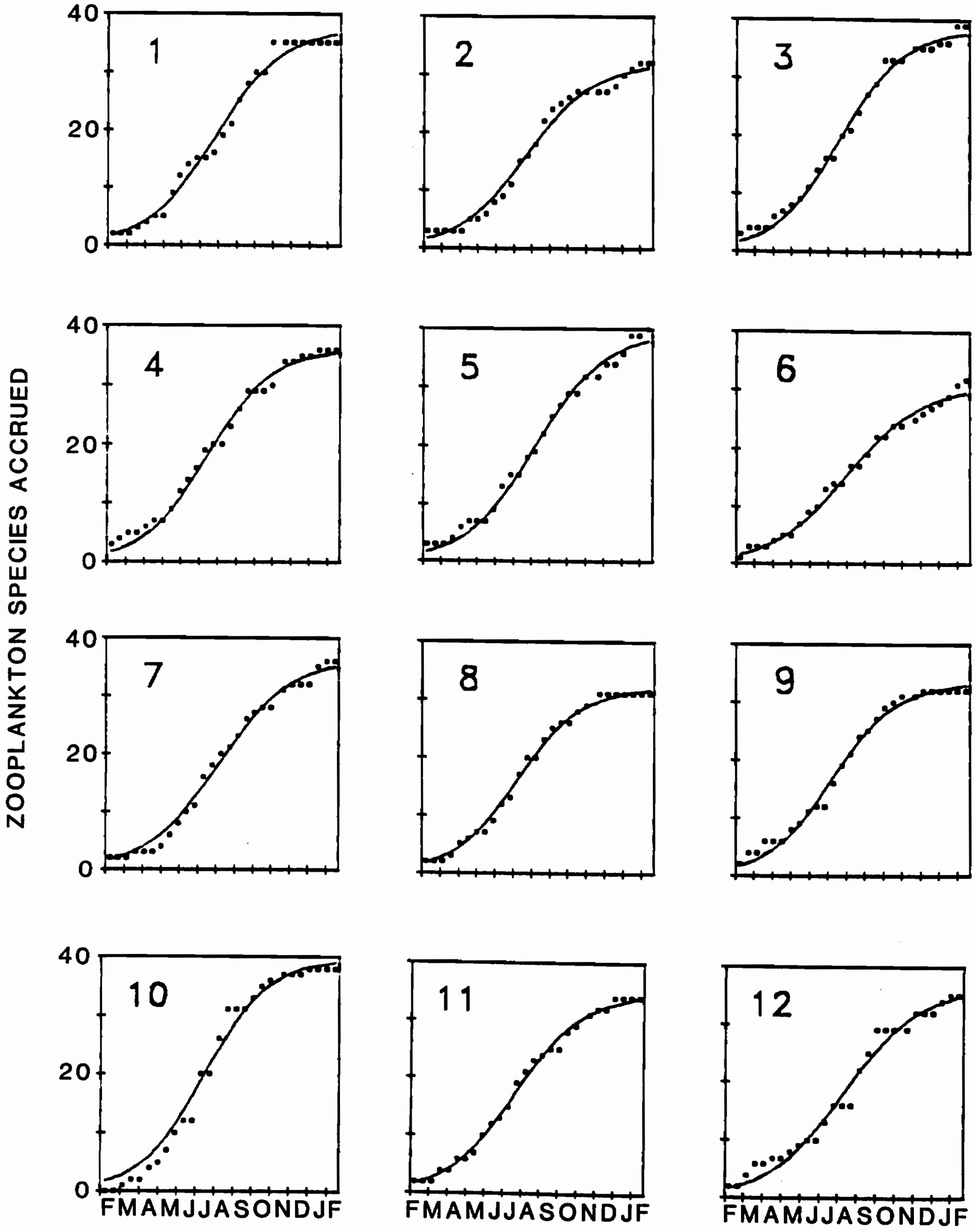


Figure 4-2. Zooplankton species accrual curves. Plots are arranged in the configuration of ponds at the facility.

regressions was 0.953. The logistic species accrual curves were significantly different among ponds ($p < 0.001$) and ponds differed in both estimated species accrual rates and estimated numbers of species accrued (Fig. 4-3). It is interesting to note that a greater accrual rate did not necessarily lead to a greater estimate of species accrued. For example, Pond 9 had a relatively high accrual rate but did not have a corresponding high estimate of species accrued. Asymptotes also depended on the timing of the inflection point for the curve.

Observed and Expected Species Numbers

Coleman (1981) provided the following equations to calculate the expected number of species for an area $\mathbf{s(a)}$ and its variance $\mathbf{o^{2}(a)}$ according to the RPH:

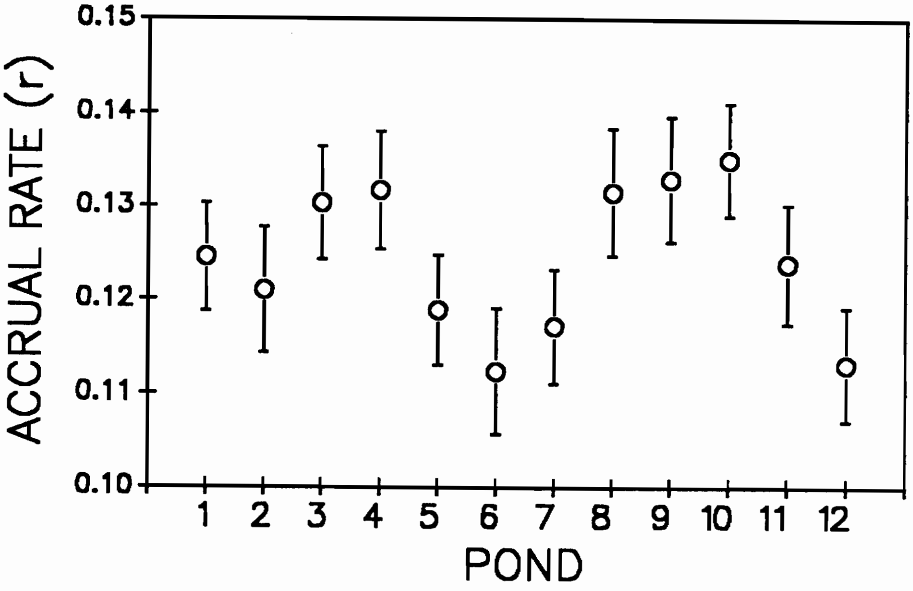
$$\bar{s}(\alpha) = S - \sum_{i=1}^{s}(1-\alpha)^{n_i} \qquad \text{(Eqn. 1)}$$

$$\sigma^{2}(\alpha) = \sum_{i=1}^{s}(1-\alpha)^{n_i} - \sum_{i=1}^{s}(1-\alpha)^{2n_i} \qquad \text{(Eqn. 2)}$$

where $\mathbf{a}$ = relative area of the site,

$\mathbf{S}$ = set of all species present at all sites,

n_i = overall abundance of each species in S.



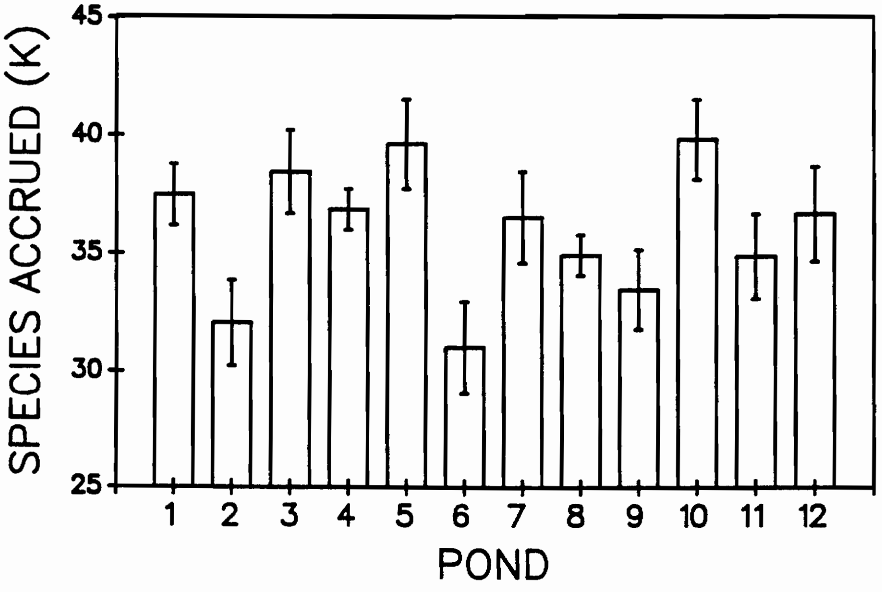


Figure 4-3. Zooplankton species accrual rates and species accrued per pond. r and K estimates are from logistic regressions fitted to data.

Relative area **a** = 1/12 for all ponds and therefore (1-a) = 0.916667 was a constant for all ponds. The value **S** was calculated by counting the number of species present over all ponds at each sampling date. Overall abundances $\mathbf{n_i}$ were calculated as the sum of densities (organisms/L) over all ponds for each species. The expected number of species **s(a)** and its variance $\mathbf{o^2(a)}$ were calculated at each of 27 sample dates. If the ponds were colonized according to the RPH, about 2/3 of the observed species numbers should fall within the bounds of **s(a)** ± one standard deviation (Coleman 1981). Systematic or large differences between expected and observed points would indicate the colonizing zooplankton did not follow the RPH.

Table 4-1 shows that observed species numbers rarely fell within one standard deviation of expected values. Observed species numbers did not match expected values according to this criterion on 23 of 27 sample dates. Average observed and expected species numbers were similar early in the study and some values were roughly similar again late in the study. Differences between observed and expected species numbers were greatest during summer months (weeks 17-35, Table 4-1). Observed zooplankton colonization did not correspond to the trend predicted by the RPH due to

Table 4-1. Observed and Expected Species Numbers. According to Coleman (1981), 8 of 12 ponds (2/3) should fall within one standard deviation (s.d.) of the expected species number.

	Observed Species Numbers in Ponds												Observed		Expected		Number of Ponds Within Expected
Week	1	2	3	4	5	6	7	8	9	10	11	12	Avg.	s.d.	Avg.	s.d.	Std. Dev.
1	2	3	3	3	3	1	2	2	2	0	2	2	2.1	0.9	2.2	0.5	6
3	2	2	2	2	0	3	0	0	2	0	0	2	1.3	1.1	0.9	0.5	0
5	2	2	2	4	0	2	0	0	2	1	0	3	1.5	1.3	0.9	0.8	1
7	3	2	2	3	2	2	1	1	4	2	3	3	2.3	0.8	1.0	0.7	2
9	3	2	4	3	3	3	1	3	3	2	3	3	2.8	0.7	2.3	0.8	9
11	5	4	4	4	4	4	0	3	3	4	4	4	3.6	1.2	2.5	0.6	2
13	4	4	5	3	3	3	1	5	5	5	4	4	3.8	1.1	2.3	0.5	0
15	8	5	7	6	4	6	4	4	7	6	6	5	5.7	1.2	6.8	1.0	6
17	8	5	7	7	5	7	5	5	7	7	6	6	6.3	1.0	9.5	1.1	0
19	9	5	9	8	8	6	5	8	5	5	5	4	6.4	1.8	10.3	1.3	2
21	7	8	7	9	8	8	5	7	5	5	7	5	6.8	1.4	10.9	1.1	0
23	8	12	6	12	5	8	10	10	9	12	7	8	8.9	2.3	12.1	1.4	3
25	9	10	10	12	8	6	10	13	9	8	10	9	9.5	1.8	15.3	1.2	0
27	13	13	8	8	9	12	10	11	10	16	11	8	10.8	2.3	16.3	1.3	1
29	10	9	10	9	9	9	6	11	11	14	11	7	9.7	2.0	16.2	1.4	0
31	12	11	11	12	13	10	12	12	11	12	9	12	11.4	1.0	15.7	1.4	0
33	12	12	9	13	10	11	11	11	11	8	10	10	10.7	1.3	17.0	1.6	0
35	8	13	16	10	13	11	9	12	13	14	9	15	11.9	2.4	16.3	1.7	2
37	10	9	8	9	12	10	9	12	11	15	14	8	10.6	2.2	12.5	1.5	4
39	11	7	8	7	11	10	7	12	12	10	10	10	9.6	1.8	11.2	1.6	8
42	6	9	8	9	12	10	13	13	7	8	12	8	9.6	2.3	12.9	1.7	4
44	8	7	6	6	13	9	10	10	11	9	8	9	8.8	2.0	11.1	1.5	3
46	7	7	7	8	9	6	8	10	6	6	7	7	7.3	1.2	8.2	1.2	8
48	7	12	8	7	14	9	9	10	6	7	11	10	9.2	2.3	11.4	1.6	4
50	8	8	7	9	13	9	15	10	4	6	9	11	9.1	2.8	10.6	1.7	5
52	9	8	9	7	10	13	10	9	6	7	8	10	8.8	1.8	10.3	1.6	6
54	6	8	5	8	11	9	10	8	8	7	8	8	8.0	1.5	8.4	1.5	8

differences from expected species numbers, especially during summer months.

Coleman (1981) stated two assumptions of the RPH: homogeneity of environmental factors among sites and a lack of correlation in the locations of individuals. I addressed the assumption of environmental homogeneity in the previous chapter, concluding that the ponds were generally similar in environmental factors over the course of one year. Variation among ponds was temporary and inconsistent and I think the data support the assumption of environmental homogeneity.

I evaluated the assumption of a lack of correlation among individuals' locations by examining species-by-species partial correlations for species' presence/ absence data. Partial correlation coefficients measure the correlation between pairs of variables with other variables held constant. Of the 1830 correlation coefficients, only 160 (8.7%) were significant ($p \leq 0.05$). Also, significant correlations were scattered throughout the matrix, indicating that no one species (e.g., <u>Chaoborus</u>) had a strong, overall influence and that factors potentially affecting species occurrence were not affecting species similarly. I interpreted the result as indicating no overriding correlations among zooplankton species that might have affected the colonization curves.

I also examined Layton's (1989) data for distributions of benthic insects among ponds. Using the characterizations of taxa in Merritt and Cummins (1978), I identified 11 taxa as potential predators on zooplankton. Of these 11 taxa, 8 were found in all 12 ponds and the remaining 3 taxa were found in 11, 8, and 5 ponds. Not surprisingly, active-dispersing insects were evenly distributed among ponds. It does not seem likely that predaceous insects regulated the location of zooplankton species among ponds.

Equation 1 only requires information on $\mathbf{n_i}$ and **S** for the ponds since relative area was a constant. Characteristics of both factors apparently contributed to the difference between expected and observed species numbers in the ponds as discussed below.

Each species present contributes to **s(a)** in Equation 1 as an asymptotic function of $\mathbf{n_i}$ (Figure 4-4). Species with an $\mathbf{n_i} > 35$ have an adjusted contribution to **s(a)** of 0.95 or higher. Species with a lesser $\mathbf{n_i}$ contribute less to **s(a)**. Therefore, Equation 1 is especially sensitive to species with low overall abundances and **s(a)** is greater as species' $\mathbf{n_i}$'s tend to values of 35 or greater. The relationship between **s(a)**

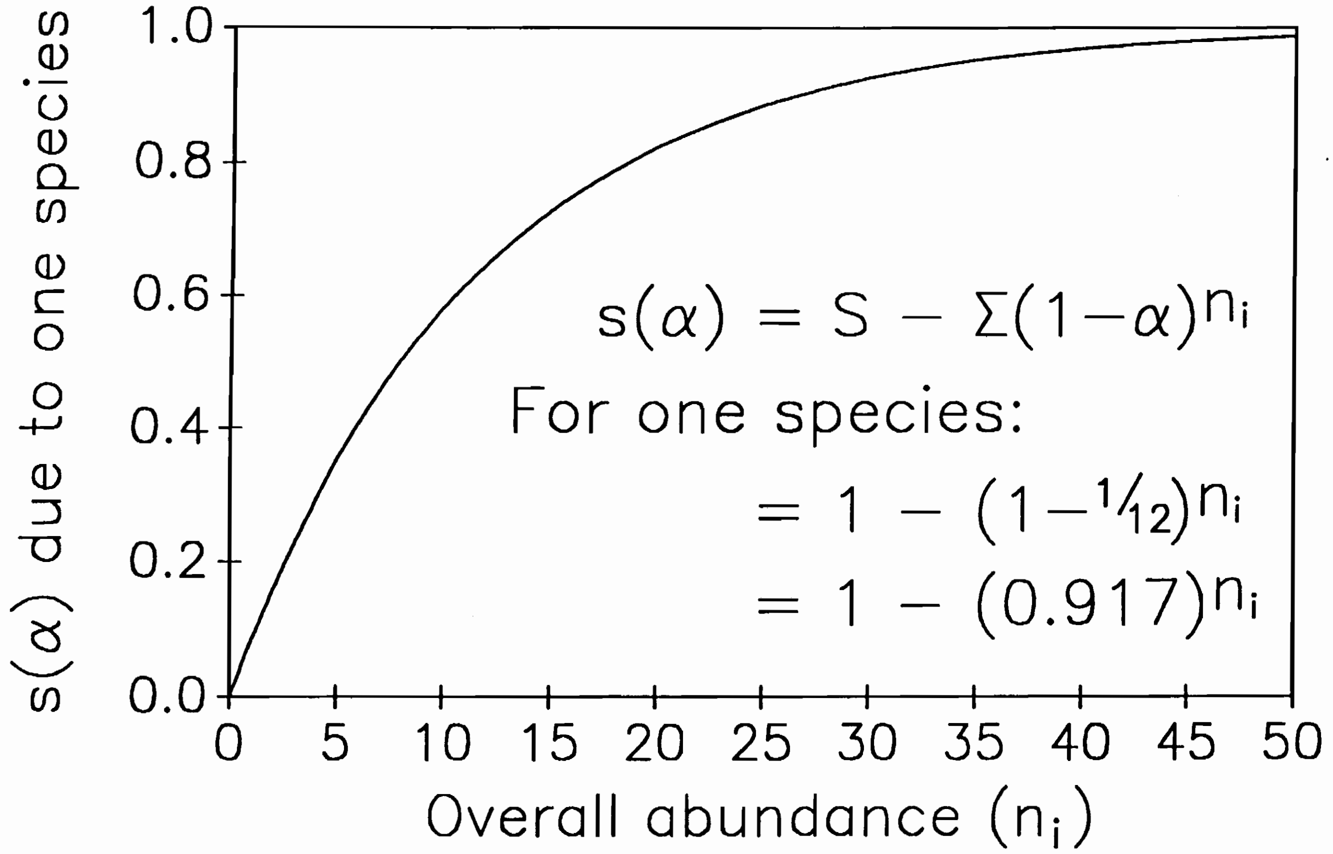


Figure 4-4. Relationship between species contribution to expected species number $s(\bar{\alpha})$ and overall abundance (n_i) of that species.

and $\mathbf{n_i}$ in Figure 4-4 would change for proportional areas different than $\mathbf{a} = 1/12$ for these ponds.

Table 4-2 lists the components of Equation 1 and the percentage of species' $\mathbf{n_i}$'s > 35 for each week of the study. Expected species numbers $\mathbf{s(a)}$ followed trends in $\mathbf{S}$, with adjustments made at different sample dates depending on $\mathbf{S}$ and $\mathbf{n_i}$ values. Proportions of species' $\mathbf{n_i}$'s > 35 were greatest at the times when $\mathbf{s(a)}$ exceeded observed species numbers (Table 4-1). The relationship between $\mathbf{n_i}$ and a species' contribution to $\mathbf{s(a)}$ helped elevate expected species numbers relative to observed values when overall species abundances ($\mathbf{n_i}$'s) were greatest.

The RPH (as stated by Coleman 1981 and Coleman et al. 1982) explicitly assumes no constraints on colonization success due to environmental heterogeneity or the presence of other organisms, leaving area as the only determinant of species number. An implicit assumption is that species' propagules are randomly distributed through space and at sufficient intensity (in space and/or time) for all islands to "collect" species solely as a function of area. For ponds of equal dimensions, this assumption would predict that (a) ponds should collect the same numbers of species given enough time, and (b) species would eventually occur in

Table 4-2. Components of expected species numbers (Eqn. 1) and percentage of ni's > 35.

Week	S	$(1-a)^{ni}$	s(a)	s.d.	% ni >35
1	5	2.76	2.24	0.45	40
3	4	3.06	0.94	0.54	0
5	5	4.05	0.95	0.81	0
7	6	4.97	1.03	0.75	0
9	7	4.67	2.33	0.84	0
11	5	2.50	2.50	0.63	20
13	6	3.71	2.29	0.47	33.3
15	15	8.19	6.81	1.04	26.7
17	17	7.45	9.55	1.13	35.3
19	17	6.74	10.26	1.28	35.3
21	16	5.07	10.93	1.08	37.5
23	19	6.89	12.11	1.40	42.1
25	20	4.66	15.35	1.22	60
27	25	8.75	16.25	1.29	40
29	24	7.82	16.18	1.44	41.7
31	29	13.35	15.65	1.36	41.4
33	27	10.04	16.96	1.59	40.7
35	30	13.67	16.33	1.68	33.3
37	26	13.49	12.51	1.54	30.8
39	24	12.77	11.23	1.63	25
42	24	11.12	12.88	1.73	29.2
44	22	10.88	11.12	1.54	31.8
46	15	6.79	8.21	1.20	33.3
48	21	9.64	11.36	1.61	28.6
50	26	15.43	10.57	1.72	19.2
52	21	10.69	10.31	1.57	19
54	17	8.64	8.36	1.55	17.6

all ponds (given that the explicit assumptions of RPH are valid).

I have already shown that ponds collected different numbers of species during their first year of existence (Figures 4-2, 4-3). There is no reason to expect one year to have been "enough time" for all ponds to accumulate the same number of species and ponds surely continued to accrue species the following year.

Data in Table 4-3 address the second prediction of species occurring in all ponds. Of the 61 species recorded, only 14 (23%) occurred in all twelve ponds at some time during the study. In addition, 29 (48%) occurred in $\leq$ 6 ponds. All species did not eventually occur in all ponds within the study period. Because both predictions were not supported, it appears that zooplankton colonization in the experimental ponds did not comply with the implicit assumption of the RPH (random dispersal in space and sufficient invasion intensities).

This assumption of dispersal affected differences between expected and observed species numbers at individual sample dates. For example, a species present in only one pond made the same contribution to **S** as a species present in all twelve ponds. According to Equation 1, the contribution to **s(a)** by a species was

Table 4–3. Ponds Colonized by Zooplankton Species.

Species	Ponds												Ponds/ Species
	1	2	3	4	5	6	7	8	9	10	11	12	
Anuraeopsis fissa	x	x	x	x	x	x	x	x	x	x	x	x	12
Brachionus urceolaris	x	x	x	x	x	x	x	x	x	x	x	x	12
Chaoborus americanus	x	x	x	x	x	x	x	x	x	x	x	x	12
Chaoborus punctipennis	x	x	x	x	x	x	x	x	x	x	x	x	12
Conochiloides dossuarius	x	x	x	x	x	x	x	x	x	x	x	x	12
Eucyclops agilis	x	x	x	x	x	x	x	x	x	x	x	x	12
Hexarthra mira	x	x	x	x	x	x	x	x	x	x	x	x	12
Keratella cochlearis	x	x	x	x	x	x	x	x	x	x	x	x	12
Keratella crassa	x	x	x	x	x	x	x	x	x	x	x	x	12
Keratella gracilenta	x	x	x	x	x	x	x	x	x	x	x	x	12
Lecane flexilis	x	x	x	x	x	x	x	x	x	x	x	x	12
Ostracod	x	x	x	x	x	x	x	x	x	x	x	x	12
Polyarthra vulgaris	x	x	x	x	x	x	x	x	x	x	x	x	12
Tropocyclops prasinus	x	x	x	x	x	x	x	x	x	x	x	x	12
Filinia terminalis		x	x	x	x	x	x	x	x	x	x	x	11
Monostyla quadridentata	x		x	x	x	x	x	x	x	x	x	x	11
Alona rustica	x	x		x	x	x	x	x	x		x	x	10
Bdelloid "X"	x	x	x		x		x	x	x	x	x	x	10
Bosmina longirostris	x	x	x	x	x	x	x		x		x	x	10
Lecane aeganea	x	x	x	x		x	x	x		x	x	x	10
Monostyla bulla	x		x	x	x	x	x	x	x	x	x		10
Monostyla lunaris	x	x	x	x	x	x	x	x			x	x	10
Kellicottia bostoniensis	x	x	x	x		x	x			x	x	x	9
Keratella quadrata			x	x	x		x	x	x	x	x	x	9
Monostyla elachis	x	x		x	x			x	x	x	x	x	9
Pleuroxus hamulatus	x	x	x	x	x		x			x	x	x	9
Trichocerca stylata	x	x	x	x			x	x		x	x	x	9
Monostyla pyriformis	x	x	x	x				x	x	x		x	8
Simocephalus serrulatus		x		x	x	x		x	x		x	x	8
Trichocerca similis	x		x	x	x		x		x	x	x		8
Chydorus sphaericus		x	x		x	x	x	x			x		7
Macrocyclops albidus		x		x	x		x	x	x	x			7
Ascomorpha ovalis	x	x	x			x	x					x	6
Cephalodella physalis	x		x		x				x	x		x	6
Bdelloid "Y"			x			x			x	x		x	5
Chaoborus flavicans								x	x	x	x		4
Conochilus hippocrepis	x	x		x	x								4
Lecane pusilla		x	x		x	x							4
Lepadella amphitropis			x			x	x	x					4
Trichocerca inermis	x			x		x				x			4
Brachionus angularis	x				x					x			3
Daphnia parvula	x		x							x			3
Lecane rhacois					x		x				x		3
Moina micrura									x	x	x		3
Trichocerca multicrinis				x					x			x	3
Cephalodella intuta				x			x						2
Euchlanis dilatata	x				x								2
Lecane hornemanni					x							x	2
Lecane sp. "X"					x	x							2
Lepadella acuminata					x					x			2
Trichocerca intermedia			x							x			2
Trichocerca pusilla			x	x									2
Trichocerca rattus			x		x								2
Ascomorpha saltans			x										1
Bdelloid "Z"												x	1
Colurella sp.							x						1
Keratella taurocephala										x			1
Keratella testudo					x								1
Lecane luna						x							1
Lecane tenuiseta							x						1
Monommatta sp.	x												1
Species per Pond	36	32	39	36	40	32	36	31	32	38	34	35	

adjusted for its $\mathbf{n_i}$ (as $1 - 0.91667^{\mathbf{ni}}$). If a low-dispersal species attained only a modest overall abundance its contribution to **s(a)** was still important (e.g., an $\mathbf{n_i}$=35 produces a contribution to **s(a)**=0.95). Therefore, low-dispersal species with only modest $\mathbf{n_i}$'s could contribute to expected species numbers while not contributing substantially to observed species numbers.

To test for the effect of low-dispersal species and $\mathbf{n_i}$'s, I counted the number of species at each sample date occurring in $\leq$ 6 ponds and having an $\mathbf{n_i} \geq 35$ (Table 4-4). After mid-May (Week 15), about 70% of the species present on any given sample date occurred in $\leq$ 6 ponds. No species in $\leq$ 6 ponds achieved $\mathbf{n_i} \geq 35$ prior to Week 15, but after Week 15 the proportion of species in $\leq$ 6 ponds and with $\mathbf{n_i} \geq 35$ ranged from 6 to 47% and exhibited a trend similar to that of expected species numbers ($r^2 = 0.69$, $p = 0.0001$). This analysis is conservative because my criteria for the category do not include all species that would have contributed to the effect of low-dispersion on **s(a)**.

I think this result, in conjunction with the effect of seasonal changes in $\mathbf{n_i}$ distributions, explains the difference between observed and expected zooplankton species numbers by the RPH. Expected species numbers exceeded observed values when overall abundances tended

Table 4-4. Number of Ponds Inhabited by Each Species at Each Sample Date.

	Weeks																									
Species	1	3	5	7	9	11	13	15	17	19	21	23	25	27	29	31	33	35	37	39	42	44	46	48	50	52	54
Filinia terminalis	10	3		2	2			1			1	2		7		2	3		1								
Keratella quadrata	8	1	2		2			3	1																		
Cyclopoid nauplii	4	5	7	11	10	10	10	11	12	12	12	12	12	12	12	12	12	12	12	12	12	11	9	11	5	8	10
Eucyclops agilis	2	6	7	9	10	11	11	11	10				1		4		12	4					1		1		4
Brachionus urceolaris	1			3	7	11	12	12	6	2	1																
Cephalodella physalis			1	2	1			2			1																
Cephalodella intuta			1	1																							
Euchlanis dilatata					1	1																					
Chaoborus punctipennis						10	9	12	12	12	12	12	12	12	12	12	12	12	11	10	2	1	1				
Chaoborus flavicans							3	1																			
Daphnia parvula							1	2	2	1															1		
Hexarthra mira								4	10	11	10	10	5	6	4	6	7	5		1					1		
Polyarthra vulgaris								3	7	7	8	11	11	11	11	12	10	8	5	2	3	2	1	1	1	1	1
Conochilus hippocrepis								3		1	1			1													
Kellicottia bostoniensis								1	2	3	2	3	6	3													
Keratella cochlearis								1	1	2	1	5	6	10	12	8	11	12	12	12	11	12	12	12	12	12	12
Moina micrura								1	3																		
Tropocyclops prasinus									3	12	12	12	12	12	12	12		12	12	12	12	12	12	12	10	11	11
Chaoborus americanus									2	2	10	8	6	4	1			1	1								
Anuraeopsis fissa									1	3	4	6	10	11	10	7	5	7	8	8	4	4					
Trichocerca inermis									1					1		1	1										
Keratella testudo									1																		
Lecane flexilis									1	4	3	3	6	3	1	1	5	9	7	2	2	1		4	4	5	4
Monostyla bulla										2		2	5	6	3	2		1	2		2						
Trichocerca intermedia										1				1													
Lecane aeganea										1		5	1			4	3	1	3		2						
Trichocerca stylata										1	2	6	5	4		1											
Bdelloid X											1	4	2	5	2	4	1	3	1	1	1	1		1	1		
Monostyla pyriformis												2	5	3		1	1		1								
Conochiloides dossuarius												2	4	6	7	10	4	3									
Monostyla lunaris												1	2	1	1			1	1	4	1	2		2	3	1	
Lepadella acuminata												1	1														1
Lepadella amphitropis													2							1					2		
Monostyla quadridentata														5	5	9	1										
Ostracod														2	4	8	6	6	6	9	9	8	5	9	8	11	10
Alona rustica														1		1	1	2	3	3	5	5	7	7	9	8	4
Ascomorpha ovalis														1		1	1	2		1					3	3	1
Pleuroxus hamulatus														1	2	2	3	2	3	2	7	6	2	8	5	4	4
Keratella gracilenta															4	8	9	11	10	8	10	10	10	9	9	6	5
Brachionus angularis															2	2											
Trichocerca similis															2	5	6	6	2			1					
Monostyla elachis															2		4	2	1	3	3						
Simocephalus serrulatus															1	1	1	1	3	3	2	4	5	6	4	4	6
Ascomorpha saltans															1												
Bdelloid Y															1	1		1						1		1	
Trichocerca pusilla																2		1									
Macrocyclops albidus																1		2	3	3	6	4	2	4	2	4	5
Bosmina longirostris																1	2	4	4	4	6	4	6	6	6	8	3
Keratella crassa																	5	10	12	11	10	12	12	8	10	6	8
Lecane luna																	1										
Trichocerca rattus																	1	2									
Chydorus sphaericus																			2	1	3	3	3	5	5	6	7
Keratella taurocephala																			1								
Lecane rhacois																				1	1	1			2		
Monommatta sp.																				1							
Lecane hornemanni																						1		1	1	1	
Trichocerca multicrinis																						1			2		
Lecane sp.																								1		1	
Lecane tenuiseta																									1		
Bdelloid Z																									1		
Colurella sp.																										1	
Lecane pusilla																										4	
% Spp. in < 6 ponds	60	100	60	67	57	20	33	73	71	71	63	74	75	72	71	66	74	69	69	67	64	68	60	58	73	71	65
% Spp. in < 6 ponds & with ni's > 35	0	0	0	0	0	0	0	27	8	17	20	29	47	17	24	26	25	15	11	6	21	20	22	18	16	7	9

to attain greater levels and when species with limited distributions among ponds reached at least modest overall abundances.

4.4 DISCUSSION

Zooplankton colonization curves differed among ponds in both temporal variability and general trends. Variability through time was probably related to both seasonality and the relatively brief life histories of most zooplankton species in the ponds. Many zooplankton species exhibited seasonal maxima in the ponds, as is typical of many zooplankton species in temperate waters (Hutchinson 1967). Some of these population cycles were brief, especially for some rotifers. Species numbers fluctuated most when several populations were roughly synchronous in a pond (e.g., Pond 7).

Seasons were an obvious influence on physico-chemical conditions in the ponds (Section 3.0) and apparently affected general trends of colonization curves in some (but not all) ponds. Some of the ponds exhibited general trends in species numbers roughly similar to the annual temperature cycle, but some ponds had no such similarity. Although quantititative comparisons of curves was not possible due to their variability, it is apparent that colonization curves were not similar for all ponds as predicted by the RPH.

Other long-term colonization studies have focused on terrestrial arthropods in less seasonal climates (Simberloff and Wilson 1969 and 1970, Rey 1981). Colonization curves in these studies were less variable through time than in my study, due to lesser effect of seasons on colonization and generally longer life cycles of the subject organisms. In addition, these studies were conducted on islands of different sizes for purposes of testing the Equilibrium Theory of MacArthur and Wilson (1967). Colonization curves were different due to different island sizes.

Species accrual trends were logistic in shape and differed among ponds in both their rates of increase and asymptotes. There are two possible reasons for logistic accrual curves. The first hypothesis (Seasonal) is that species accrual in the ponds was seasonal, being most frequent in summer months and less frequent in colder seasons. The second hypothesis (Normal) states that the logistic curves are cumulative results of normal distributions of species dispersal rates. A few fast dispersers colonize early, a few slow dispersers colonize late, and most species colonize at rates in between those extremes. This hypothesis assumes no effects of seasons.

I could not test these hypotheses with data from my study: seasons were an uncontrolled variable. However, I constructed species accrual curves for the data of Simberloff and Wilson (1969). Their study on defaunated islands was conducted in the Florida Keys and had minimal seasonal influence on colonization. If logistic accrual curves were not obtained in that study, there is little reason to expect the Normal Hypothesis to be appropriate under more complex conditions (seasons, potential "seed banks" of organisms in the soil). On the other hand, if logistic accrual curves were obtained by Simberloff and Wilson, the Normal Hypothesis would be supported and could also be applicable in other cases.

All six islands in the Appendix of Simberloff and Wilson (1969) had linear species accrual curves (lowest $r^2 = 0.95$, $p < 0.0001$). This result indicates that the colonization of defaunated islands in the sub-tropics was not a simple function of normally-distributed dispersal rates. If the Normal Hypothesis did not apply in Simberloff and Wilson's islands, it is very unlikely that ponds were colonized simply as a function of species dispersal rates. It is far more likely that seasons were also important in setting the shape of species accrual curves.

Observed species numbers did not closely coincide with expected species numbers according to the RPH. Differences between expected and observed species numbers were especially apparent during summer months, when observed values fell short of expected values (Table 4-1). My analyses indicate that these differences were related to the effects of a) greater overall abundances during summer months and b) restricted distributions of some abundant species among ponds.

Coleman et al. (1982) cautioned that the $\mathbf{n}_i$'s are considered as known quantities in Equations 1 and 2. They stated that if "only a probability distribution were specified for the list $\mathbf{n} = (\mathbf{n}_1, \mathbf{n}_2, \ldots, \mathbf{n}_s)$, the present results would be 'conditional upon $\mathbf{n}$', and replacement of each $\mathbf{n}_i$ in Eqs. [1] and [2] by its mean value $\mathbf{n}_i$ would not, in general, yield correct formulae for s(a) and o^2." Coleman et al. (1982) used "careful and repeated censuses" to obtain $\mathbf{n}_i$'s for their study of nesting birds.

Data from my study did not represent probability distributions of $\mathbf{n}$ but were the quantitative results of careful and repeated sampling within each pond. Values of $\mathbf{n}_i$ were summations of species densities and were not mean values. Nonetheless, expected species numbers did not fit observed data when $\mathbf{n_i}$'s tended to be large. This dependence on $\mathbf{n_i}$ was discernible in the ponds because all areas were the same and **s(a)** did not vary with both relative area and $\mathbf{n_i}$, as it may with islands of different sizes.

Because the Random Placement Hypothesis was not supported, alternate hypotheses can be considered (Connor and McCoy 1979, McGuinness 1984b). My study did not test other hypotheses, but I think some comment on their potential relevance is appropriate. The alternative hypotheses are the Equilibrium Theory (MacArthur and Wilson 1967), Habitat Diversity (Williams 1964), and Intermediate Disturbance (Connell 1978) Hypotheses.

Equilibrium Theory. The Equilibrium Theory does not seem to be appropriate for data of this study. According to the Equilibrium Theory, immigration curves should follow an exponential decline through time, colonization curves should follow a negative exponential shape and sites should attain an equilibrium species number (MacArthur and Wilson 1967). Immigration rates varied greatly through time but tended to be greatest during summer months, rather than at the beginning of the study, and were not a decreasing function of species numbers. Colonization curves did not conform to a negative exponential curve, and equilibrium species numbers were not apparent for zooplankton communities in the ponds. Extinction is another component of Equilibrium Theory but could not be estimated for zooplankton species due to their brief life cycles, production of resting stages, and ability to diapause. Finally, resident species are often distinguished from transient species in tests of Equilibrium Theory by sampling islands prior to defaunation (e.g., Simberloff and Wilson 1969, Rey 1981). This distinction could not be made because the ponds were newly constructed and for the same reasons that extinction rates could not be estimated.

Habitat Diversity. According to the data and conclusions of Section 3.0, it seems unlikely that habitat diversity among ponds contributed to different colonization and species accrual curves. Physico-chemical differences among ponds were generally ephemeral and inconsistent. Detectable differences among ponds in conductivity (related to addition of groundwater) were not reflected in species colonization or accrual curves. Based on the measured parameters, zooplankton habitat did not vary consistently or significantly enough to explain differences in colonization among ponds.

Intermediate Disturbance. According to this hypothesis, smaller areas are more susceptible to disturbances than larger areas, thus contributing to the differences in species numbers. This hypothesis also seems to have little explanatory power for the results in the same-sized ponds. Figures 4-1 and 4-2 display colonization and accrual plots, respectively, in the same configuration as the ponds were arranged at the site. Ponds were closely spaced and it seems reasonable to assume that weather events affected all ponds similarly. No patterns are evident in relation to prevailing wind direction or positions relative to the reservoir, surrounding road, nearby woods, elevation, etc. Ponds 5, 6, 8 and 9 received the greatest quantities of groundwater to maintain water levels, but no patterns emerge potentially related to this "disturbance." No other treatments were applied to ponds.

If none of these hypotheses seemed to account for the observed patterns, what other concepts might apply? Some ecologists have recently begun to examine the supply of organisms to a site as a regulating factor in community composition. This "supply-side ecology" has been largely overlooked in recent years, when many studies were conducted on competition and predation as regulators of community composition. The supply of organisms may be important, particularly when propagule availability varies among species and through time (Lewin 1986).

Focus on propagule supply is largely due to Underwood and Denley (1984). They argued that paradigms of competition and predation as regulating processes in intertidal zones may be premature and stated that "considerable variations in intensity and outcome of processes will occur because of the vagaries of larval settlement of the species in a system." Their work on Australian intertidal communities (e.g., Underwood et al. 1983) indicated that larval settlement, and not predation, was the main determinant of community composition.

Roughgarden et al. (1987) reviewed work on Californian intertidal barnacles and Caribbean lizards and concluded that the supply of propagules "is the rate-limiting step" for both communities. Roughgarden et al. (1987) stressed that all ecosystems are open systems, subject to large-scale physical transport processes, and that such processes need to be considered in ecological paradigms. Similarly, Ricklefs (1987) made the distinction between local (predation, competition, disease, etc.) and regional (speciation, geographical dispersal) processes controlling species richness.

Within the context of my study, it would appear that the regional process of zooplankton dispersal had a strong influence on community development in the ponds. Transport processes and propagule supply apparently varied among species and seasons. Species with relatively low dispersal were not necessarily less successful upon arrival, given that some of the species occurring in only a few ponds attained at least modest densities (Table 4-4). To borrow the terminology of research on intertidal zones, the "settlement" rate of zooplankton propagules in the ponds varied among species in intensity and timing.

Some zooplankton species were present before the ponds were filled. Some rotifer species were hatched from soils collected in November 1987, 2 months before ponds were filled with water (e.g., Brachionus urceolaris, two Cephalodella species; D. Jenkins, personal observation). Also collected on November 1987 were the cladoceran Moina micrura, present in about 15 cm of rain water in the bottom of Pond 3. Finally, adult female Eucyclops agilis, with egg sacs, were collected on the first sample date (5 February 1988) in a few ponds. It is possible that some zooplankton propagules lie dormant in terrestrial soils and were already present when the ponds were filled.

Some zooplankton species were observed only late in the study and/or in a few ponds (Table 4-4). Cladocerans were generally poor colonists and may be dispersed mostly by animals. Ponds were visited by deer, turkey, geese, ducks, heron, raccoon, rabbits, and at least one snapping turtle, as evidenced by sightings, feces, and tracks (D. Jenkins, personal observation). The patchy distributions of some zooplankton species among ponds and the uneven timings of some species may be related to animal transport.

Some other zooplankton, especially rotifers, probably disperse by windblown transport of resting eggs and cysts. It may be no small coincidence that many rotifer species colonized ponds during summer months, when water levels of other ponds in the region would be lowest and exposure of dry pond sediments to wind would be greatest.

Regardless of transport mechanisms, the RPH was not supported for zooplankton communities in these ponds because the implicit assumption of randomly dispersed propagules at sufficient "settlement" intensity was not met. Local processes such as competition and predation did not seem to regulate species richness during initial development of zooplankton communities in the ponds.

4.5 CONCLUSIONS

1. Zooplankton did not colonize experimental ponds similarly, as predicted by the Random Placement Hypothesis. Colonization curves were variable through time and appeared to differ among ponds. Species accrual curves also differed in both their estimated rates and asymptotes.
2. Seasons had a strong influence on colonization. This influence was probably due to effects on populations in the ponds (timing of diapause release, resource levels, population dynamics, etc.), but also may have been related to seasonality of zooplankton propagule dispersal.
3. Observed numbers of species did not correspond with expected numbers of species according to the Random Placement Hypothesis. Expected values exceeded observed when overall abundances tended to be high and when abundant species were distributed in only a few ponds. Explicit assumptions of the Random Placement Hypothesis appeared to be valid in the

ponds, but an implicit assumption of random dispersal at sufficiently high rates did not appear valid. This result indicates that supply of propagules was important in regulating species richness in these early zooplankton communities.

5.0 ZOOPLANKTON COMMUNITY STRUCTURE

5.1 INTRODUCTION

Experimental ponds (mesocosms) have been used in ecological research for a variety of both basic (Hall et al. 1970, Mittlebach 1986) and applied (e.g., Hurlbert et al. 1972, deNoyelles et al. 1982) purposes. Considerable attention is currently focused on using experimental ponds for ecological risk assessment of pesticides (Voshell 1989, Touart 1988).

Despite the variety and quantity of ecological research in experimental ponds, little research has been conducted on the initial colonization and development of these model ecosystems. Hubbard (1973) studied the colonization of two new experimental ponds for up to 86 days. Colonization curves appeared roughly similar and Hubbard claimed support for the MacArthur-Wilson colonization model (MacArthur and Wilson 1967), although data were very limited. I know of no other studies of initial colonization of experimental ponds.

A basic question, relevant from several perspectives, remains unanswered: do similar communities develop in similar ponds? This is essentially the same question asked by McCune and Allen (1985) of old-growth forests in Montana, where they found dissimilar forests on similar sites. They found historical factors (e.g., drought, seed dispersal events, herbivore densities, etc.) to be important in variation among sites and considered the successional climax concept inappropriate for their forest sites. Statistical evaluation of replicated treatments applied to ponds in experiments is predicated on the assumption that ponds are similar except for the effects of treatment. Substantial variation among ponds could either render results inconclusive or falsely contribute to significant differences among treatments. Both conditions should be of concern for applied experiments conducted as a basis of regulatory decisions on pesticides.

I concluded in Section 3.0 of this dissertation that ponds I studied were generally similar in their physico-chemistry over the course of one year. Also, the ponds shared a similar construction history. In Section 4.0, I concluded that ponds were not colonized by zooplankton similarly in the traditional terms of species numbers and did not conform to the Random Placement Hypothesis (RPH, Coleman 1981). One of my goals was to test the generality of the RPH to more complex measures of the zooplankton community structure, such as densities and biomass. Given that the RPH was not supported for simple species numbers, I expected that ponds would also differ in other community metrics.

This section addresses the question, "Do similar zooplankton communities develop in similar ponds?" by evaluating several measures of zooplankton community structure.

5.2 MATERIALS AND METHODS

Study Site

An experimental ponds facility was constructed during 1987-1988 at the Southern Piedmont Agricultural Experiment Station near Blackstone, Virginia. The site is in the Piedmont physiographic province ($77^{o}57'30"$W, $37^{o}5'30"$N) at an elevation 128 m above mean sea level. A complete description of the construction of the facility and its layout were provided in Section 3.0.

All twelve ponds were filled with water in late January 1988. Chlorinated tap water (source: Nottoway Reservoir) from a nearby fire hydrant was used. Water entered the ponds through underground pipes, so that all twelve ponds received water simultaneously. Ponds were filled over the course of 6 days, ending on 31 January 1988. Sampling started on 5 February 1988 and continued for one year, ending on 10 February 1989.

The only manipulation of the ponds was the addition of well water to maintain water levels. At no time was water transferred from one pond to another during this study, and no reservoir water was added to any ponds. No fish were stocked in the ponds and fish were never observed in any pond during the study.

Sampling Strategy

Sampling and analyses were conducted biweekly for one year, starting on 5 February 1988 and ending on 10 February 1989. One three-week interval occurred in November 1988 to avoid schedule conflicts. In addition, limited sampling was conducted during intervening weeks from March through October 1988. The criterion for initiating and ending these shorter sampling trips was an arbitrarily-chosen 10^{o} C water temperature.

All sampling was done according to a set of random sampling sequences prepared prior to the study. These random sequences ensured that no patterns would be established among ponds due to sampling activities. Each pond was sampled at three stations: always at the center (2.14 m depth) and at 2 of the 4 sides (1.07 m depth). The two sides were chosen each sampling trip by coin toss (East vs. West, North vs. South). Locations of sampling stations were consistent throughout the study with the use of the suspended ropes. The intersection of the ropes marked the center, and a position on the ropes at 1.07 m depth marked the side stations.

Sampling Procedures

Sampling procedures were consistent for all ponds at all sampling dates. Ponds were sampled from an inflatable raft. Upon entering the pond, sampling started at the center station, then proceeded to the two side stations. Two types of samples were collected at each station: tube and net samples.

Tube samples collected whole water for use in analyses of phytoplankton taxa, chlorophyll and water chemistry. Four liters of this water were also used to collect and preserve rotifers. Five tube samples were collected at each station. Tube samples were taken to 1.83 m depth at the center station and 0.91 m depth at side stations. Tube samples were collected with a 1.83 m long plexiglass tube (5 cm i.d.), fitted with a cable through the tube. A racquetball was attached to the bottom end of the cable. The ball fit in the end of the tube for a water-tight seal when the cable was pulled taut. The tube was lowered into the water, the cable pulled taut, and then the tube was lifted out of the water. The collected vertical "core" of water was then emptied into a bucket by releasing tension on the cable.

Two 20-L buckets were filled this way in each pond. The bucket contents were combined in a larger container upon exiting the pond. Four liters were subsampled and sieved through 35 um plankton netting. Collected organisms were rinsed from the sieve into a jar and preserved with about 4% formalin. Formalin was buffered with 5 % sodium acetate (Steedman 1976) and contained 5% sugar (Haney and Hall 1973).

Quantitative net samples were collected to estimate crustacean and Chaoborus densities. Net samples were collected at each station via vertical tows from the bottom with a Wisconsin-style plankton net, (80 um mesh: Wildlife Supply Co.). The net was gently placed on the bottom and allowed to lie there for about 2 min. before hauling up. This was done to obtain a representative sample of the whole water column, with minimal disturbance of bottom water. Two such net samples were collected at each station. Collected organisms were rinsed from the net into a second jar and preserved with 4 % formalin (as above).

Pond depth was recorded and used in calculations of water volume collected for quantitative estimates of zooplankton densities. Pond depth applied to calculations for net tows at the center station only: net tows at side stations were always in 1.07 m of water, regardless of pond depth.

Six of 648 samples were accidentally not preserved during the study. The average of preceding and subsequent samples were used to estimate densities for missing data points in analyses. If available (March - October), samples from intervening weekly trips were used in averaging. The following rules were used for assignment of species presence/absence to these missing samples:

Preceding Sample	Missing Sample	Subsequent Sample
Present	(Present)	Present
Present	(Absent)	Absent
Absent	(Absent)	Present
Absent	(Absent)	Absent

Densities in preceding and subsequent samples were averaged only in the case that a species was present on both dates.

Spatial heterogeneity and within-pond variance could not be evaluated because tube samples were pooled and subsampled and net samples were pooled for each pond. However, the purpose of this study was to compare colonization trends of ponds, with each pond serving as an experimental unit (Hurlbert 1984). Three sampling stations per each small pond and about 100 L of sampled water provided sufficiently representative data.

Sample Processing and Analyses

Preserved zooplankton were counted and identified with a Sedgwick-Rafter chamber and a Nikon binocular microscope at 40 X. Greater magnifications were used to aid identifications. Samples were examined before counting and sample volumes adjusted for the concentration of organisms. Entire samples were counted if densities were low, while dense samples were counted using at least three subsamples. Subsamples were obtained by mixing samples and transferring 1.0 mL to a Sedgwick-Rafter chamber using a calibrated autopipette. The autopipette tip was cut to have a 4 mm opening for representative subsampling of large organisms (Edmondson and Winberg 1971). Entire subsamples were counted. Original densities (organisms/L) were calculated using sample volumes, number of subsamples and volumes of water represented in net tows.

Using values or size-weight formulae from the literature, I calculated individual dry weights for zooplankton species. Estimated individual dry weights for Rotifera and size-weight regressions for other taxa are listed in Results. All organisms were measured with a Filar digital micrometer mounted on the microscope and calibrated with a stage micrometer. Average sizes were used for Rotifera dry weight estimates, while all counted individuals of all other taxa were measured.

I calculated a headwidth-dry-weight regression for Chaoborus punctipennis in the ponds, following procedures suggested by McCauley (1984). Individual organisms were rinsed with distilled water, measured with the the Filar micrometer, placed on tared aluminum pans, and dried at 60° C for 24 h. Organisms were then stored in a dessicator and weighed with a Cahn Electrobalance. Regression statistics are presented in Results.

Statistical analyses were conducted using SAS (SAS Institute 1985).

5.3 RESULTS

Taxa Densities

A total of 61 taxa were identified during the study, 47 of which were rotifer species. Ostracods were counted collectively without identification to species. Evaluation of this many individual taxa for all ponds was impractical and multivariate statistical analyses on species densities did not yield sufficiently summarize data. For example, the first principal component of species densities represented only 4% of total variation. I summed species densities for each of the following categories at each sampling date in each pond:

Rotifera, Copepoda, Cladocera, Chaoborus, and Ostracoda. Figure 5-1 presents results of these taxa densities. Ostracods are omitted from Figure 5-1 because densities were generally low. Ostracoda were included in statistical analyses.

Rotifers achieved densities an order of magnitude greater than the next most abundant taxon, Copepoda (Fig. 5-1). However, peak rotifer densities were brief, and some ponds never achieved rotifer densities exceeding about 1000 organisms/L. Population peaks were seasonal in that most occurred in mid-summer to early autumn. One pond (Pond 10) had high densities of Keratella during December 1988 - January 1989 while other ponds had relatively low rotifer densities.

Because Rotifera included 47 species while other taxa included far fewer (Copepoda: 3 species, Cladocera 7 species, Chaoborus: 3 species), I also examined eight major rotifer genera for trends among ponds. Rotifer genera in Figure 5-2 are usually considered to be littoral and/or benthic while genera in Figure 5-3 are planktonic (Ruttner-Kolisko 1974).

Four genera of benthic-littoral rotifers (Figure 5-2) represent 22 of the 61 zooplankton species recorded in the ponds but did not attain densities comparable to

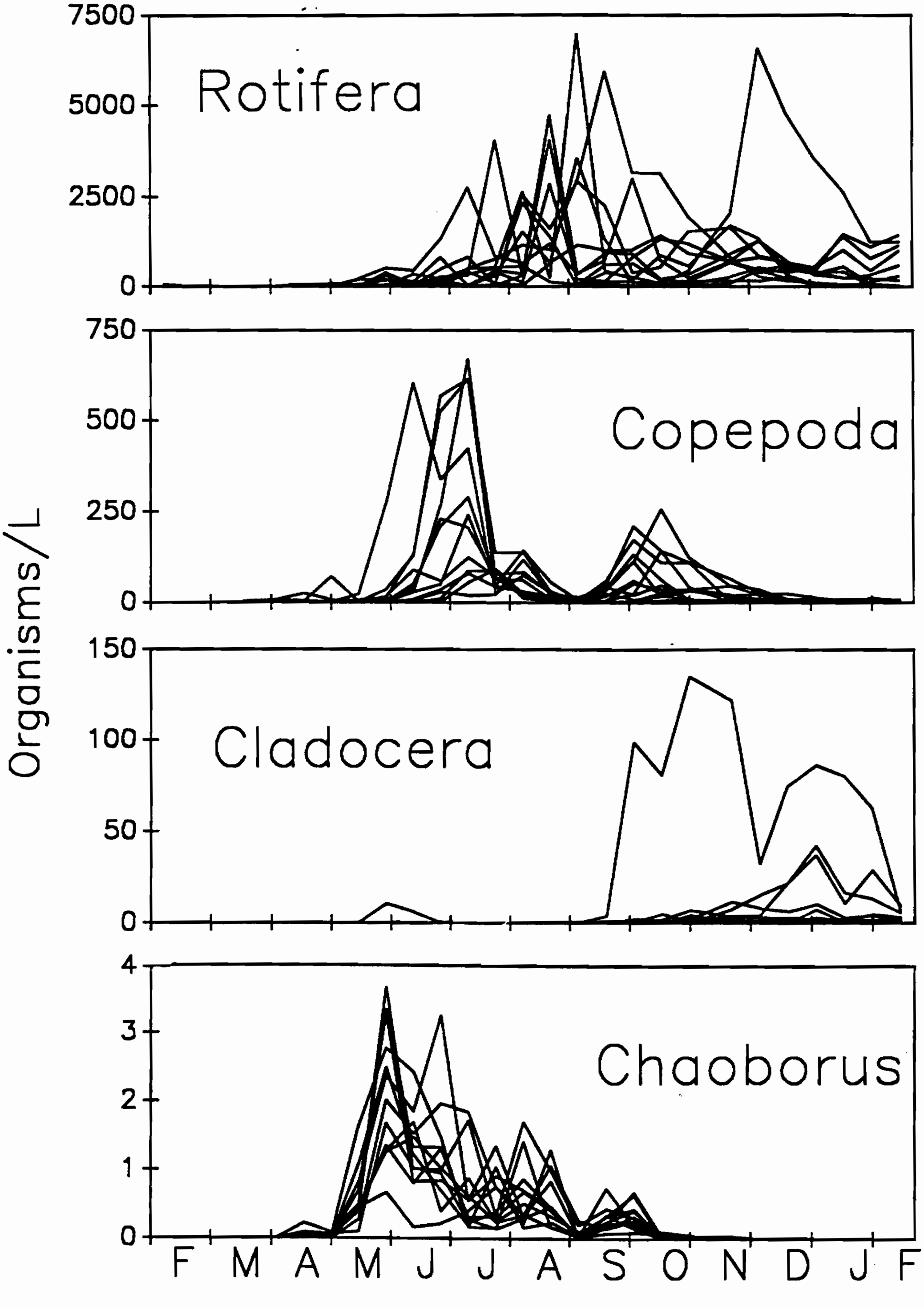


Figure 5-1. Zooplankton taxa density. Each line represents a pond.

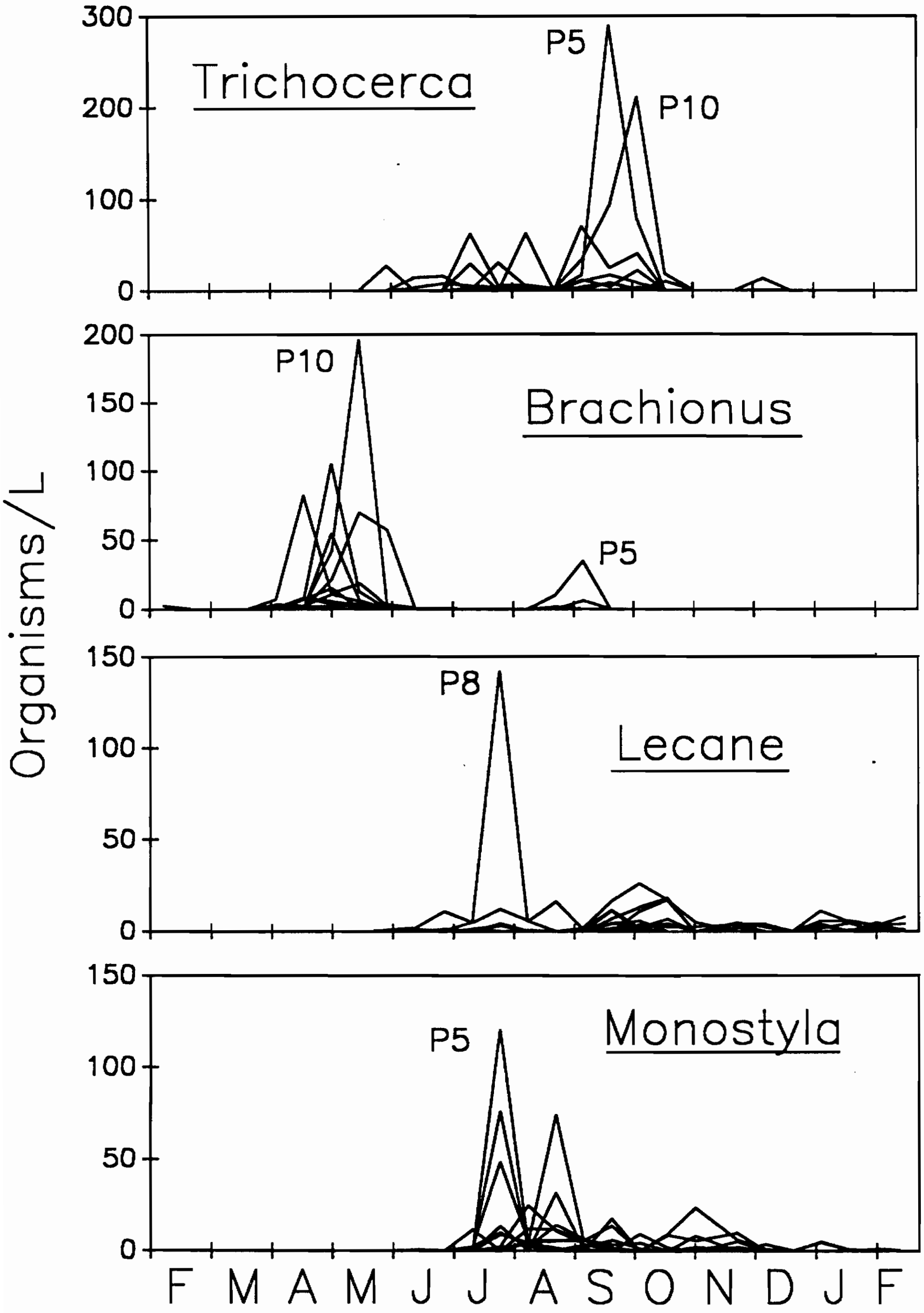


Figure 5-2. Dominant benthic-littoral rotifer genera.

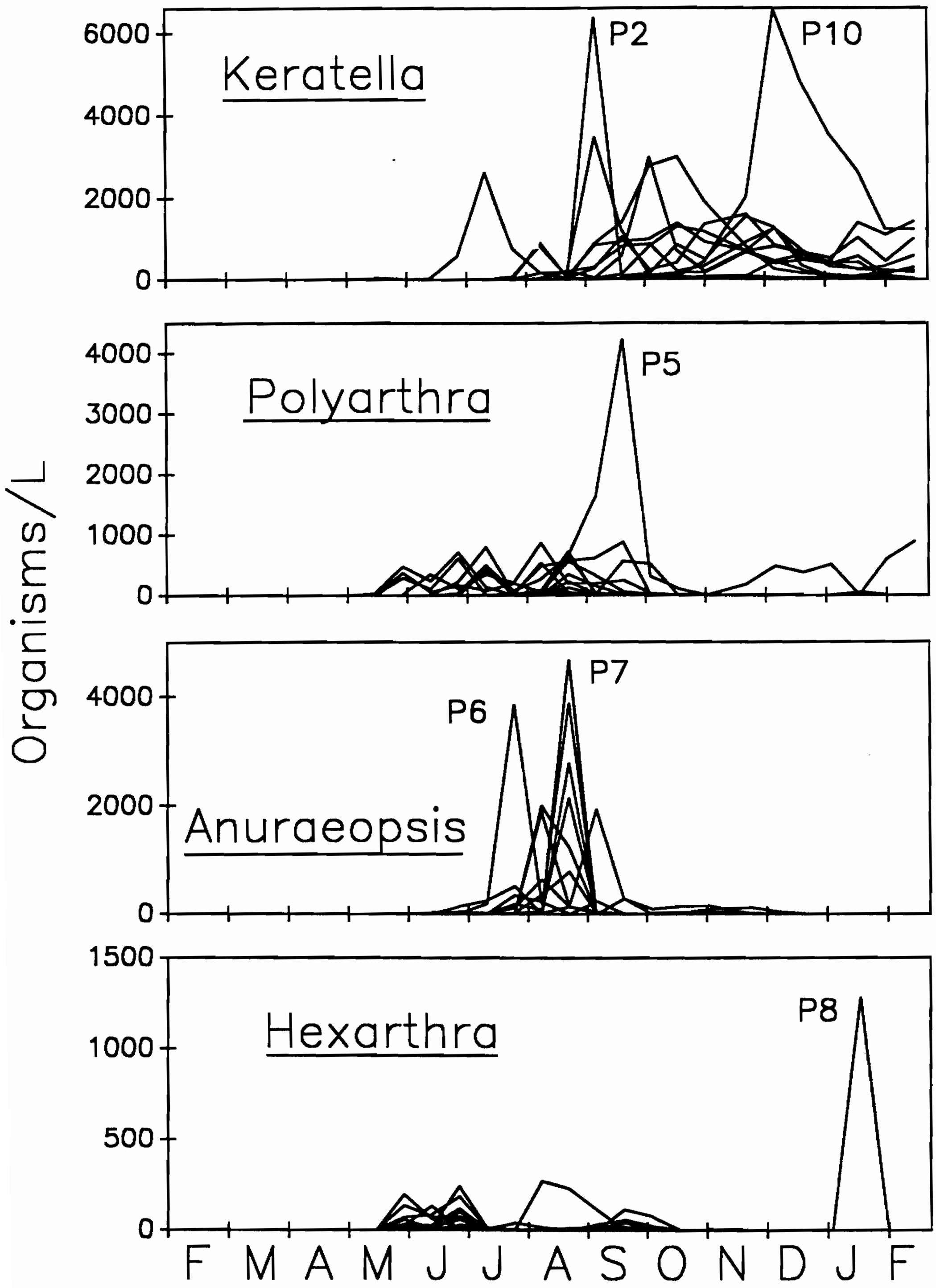


Figure 5-3. Dominant plankton rotifer genera.

some planktonic rotifers (Fig. 5-3). This may have been related to sampling technique. Whole-water samples collected with the tube sampler purposely did not include benthic sediments and may have excluded some benthic rotifers.

When large population peaks occurred for either benthic or planktonic species, peaks were often in one or a few ponds. Thus, a genus or species may have been present in all ponds but abundant in only one or a few ponds at any time. These population peaks were usually brief, with densities often returning to prior levels at the next sampling date.

Brachionus was the first rotifer genus to reach relatively high densities in the ponds, but many genera began to appear in May 1988. After May 1988, most population peaks occurred prior to October 1988, with two major exceptions. *Keratella* in Pond 10 exhibited very high densities during December 1988 and January 1989, and *Hexarthra* exhibited high densities in Pond 8 in January 1989.

Two copepod species, *Eucyclops agilis* and *Tropocyclops prasinus*, dominated Copepoda densities throughout the year. A third species, *Macrocyclops albidus*, was also observed at low densities in most ponds late in the study. *Eucyclops agilis* and

Tropocyclops prasinus are similar in size and could only be distinguished as adult females. However, the Spring 1988 peak in copepod densities (Figure 5-1) appears to be due to hatching of Eucyclops agilis nauplii, based on the timing of Eucyclops agilis adult females with egg sacs. Similarly, the lesser Autumn 1988 peak appears to be due to Tropocyclops prasinus nauplii. Thus, the two dominant copepod species seem to have been separated in timing of their cohorts, although their long life cycles meant temporal overlap in the presence of immatures and adults.

Peak copepod densities in five ponds during Spring 1988 exceeded peak values observed in Autumn 1988. However, all other Spring peak densities were similar to Autumn peak densities. A general depression in copepod densities occurred during early September 1988 following water temperatures of about 30° C and may indicate diapause of copepods.

Daphnia parvula and Moina micrura occurred briefly in a few ponds during Spring 1988, but Cladocera were not observed in most ponds until August 1988. In Autumn and Winter of 1988 and 1989, other cladocerans reached modest densities in a few ponds. However, no pond contained cladocerans at a level similar to Pond 9.

Bosmina longirostris maintained a dense population in Pond 9 from September 1988 through January 1989, while other ponds contained far fewer cladocerans.

Chaoborus punctipennis was the dominant species of Chaoborus: C. americanus and C. flavicans appeared in some samples. It is possible that Chaoborus densities were underestimated because Chaoborus reportedly sprawl on the substrate or burrow during the day and migrate to the surface at night to feed (Pennak 1978). However, comparisons among ponds should be valid because sampling methods were consistent among ponds. Chaoborus populations were roughly synchronous in ponds, exhibiting peak densities during May-June of 1988. Peak densities were due to early instars, and densities generally declined through the summer due to mortality and emergence.

As a measure of variability among ponds, I calculated coefficients of variation (CV) for log-transformed ($\log_{10}(x + 1)$) taxa densities among all twelve ponds at each sampling date (Table 5-1). I arbitrarily chose a criterion of 10% CV a priori as indicating replicable taxa densities among ponds at any sampling date. There was considerable variation among ponds in taxa densities throughout the study. No taxa densities at any sample date had a CV $\leq$ 10%, and, in

Table 5-1. Coefficients of Variation (CV's) among ponds for taxa densities.

Week	Rotifera	Copepoda	Cladocera	Chaoborus	Ostracoda
1	49.4%	248.2%	--	--	--
3	196.2%	131.2%	--	--	--
5	224.7%	150.2%	--	--	--
7	100.7%	99.8%	--	--	--
9	110.9%	109.2%	--	--	--
11	75.4%	117.1%	--	95.4%	--
13	49.8%	124.3%	331.7%	78.4%	--
15	56.1%	74.9%	273.9%	50.1%	--
17	39.2%	74.7%	235.4%	27.5%	--
19	28.7%	48.9%	331.7%	33.4%	--
21	32.2%	34.0%	--	42.7%	--
23	40.8%	20.1%	--	64.2%	--
25	21.7%	11.8%	--	56.9%	--
27	19.6%	21.3%	283.0%	56.5%	223.6%
29	15.2%	29.0%	241.0%	51.2%	177.0%
31	32.1%	38.1%	200.3%	98.5%	183.8%
33	17.8%	34.2%	208.3%	53.2%	168.4%
35	21.0%	32.7%	179.6%	50.9%	190.8%
37	25.5%	25.4%	147.2%	70.1%	168.1%
39	18.9%	30.6%	132.7%	87.0%	120.4%
42	13.6%	48.8%	111.2%	254.5%	91.5%
44	13.9%	50.8%	100.6%	331.7%	142.3%
46	13.0%	53.1%	104.3%	331.7%	173.7%
48	21.1%	48.5%	75.0%	--	123.3%
50	24.2%	72.0%	88.1%	--	107.2%
52	34.1%	56.1%	84.9%	--	102.2%
54	45.3%	66.6%	71.5%	--	128.8%

Coefficients of variation were calculated on log-transformed (log10(x+1)) taxa densities.

fact, only about one-third had CV < 50%.

I compared pond taxa densities (Rotifera, Copepoda, Cladocera, Chaoborus, Ostracoda) at all saample dates by cluster analysis, using Mahalanobis distances of log-transformed densities ($\log_{10}(x+1)$) and the centroid clustering algorithm (Digby and Kempton 1987, SAS Institute 1985). That cluster analysis (Figure 5-4) indicates that Ponds 8 and 9 were generally different from other ponds. Also, Ponds 2, 6, 4, and 5 were clustered separately from Ponds 1, 10, 11, 12, 3, and 7.

Taxa Biomasses

Biomass (dry weight) was calculated for each species according to the individual dry weight estimates (Tables 5-2 and 5-3). All formulae for calculating dry weights were taken from the literature except that for Chaoborus, which was calculated for animals of this study. Application of literature values for dry weights may introduce error for the organisms of this study in two ways: 1) reported formulae or individual weights may be different for organisms from different places; and 2) I applied formulae for species of similar dimensions to some species of this study lacking literature values. For example, I used a length-weight regression for Bosmina longirostris to estimate ostracod dry weights,

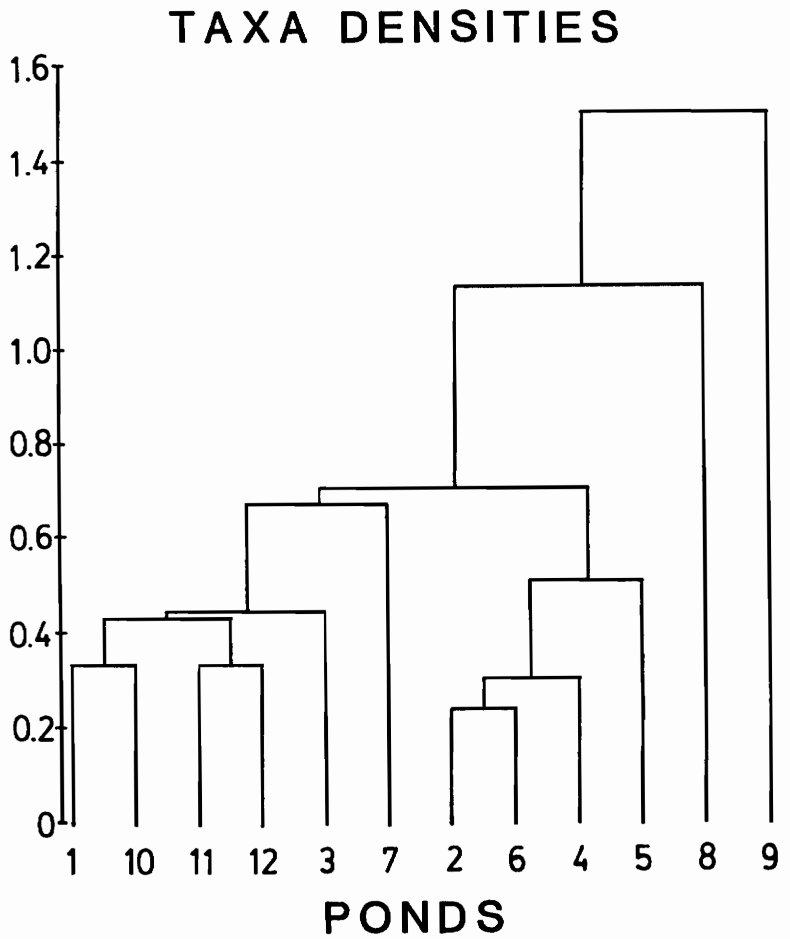


Figure 5-4. Cluster analysis of taxa density data. Vertical axis is distance between cluster centroids in multivariate space.

Table 5-2. Estimated Individual Rotifer Dry Weights.

Taxa	Estimated Dry Weights (ug)	Reference (b)
Anuraeopsis fissa	0.070	6
Ascomorpha ovalis	0.015	6
Ascomorpha saltans	0.015	6
Bdelloid X	0.200	6
Bdelloid Y	0.200	6
Bdelloid Z	0.200	6
Brachionus angularis	0.050	6
Brachionus urceolaris	0.160	4
Cephalodella intuta	0.016	5
Cephalodella physalis	0.031	6
Colurella sp.	0.016	5
Conochiloides dossuarius	0.015	6
Conochilus hippocrepis	0.015	6
Euchlanis dilatata	0.270	3
Filinia terminalis	0.053	3
Hexarthra mira	0.900	4
Kellicottia bostoniensis	0.066	2
Keratella cochlearis	0.070	2
Keratella crassa	0.070	2
Keratella gracilenta	0.070	6
Keratella quadrata	0.109	1
Keratella taurocephala	0.070	2
Keratella testudo	0.156	5
Lecane aeganea	0.200	6
Lecane flexilis	0.200	6
Lecane hornemanni	0.200	6
Lecane luna	0.200	6
Lecane pusilla	0.200	6
Lecane rhacois	0.200	6
Lecane sp.	0.200	6
Lecane tenuiseta	0.200	6
Lepadella acuminata	0.200	6
Lepadella amphitropis	0.200	6
Monommatta sp.	0.020	5
Monostyla bulla	0.200	6
Monostyla elachis	0.200	6
Monostyla lunaris	0.200	6
Monostyla pyriformis	0.200	6
Monostyla quadridentata	0.200	6
Polyarthra vulgaris	0.060	2
Trichocerca inermis	0.100	6
Trichocerca intermedia	0.030	5
Trichocerca multicrinis	0.039	5
Trichocerca pusilla	0.012	5
Trichocerca rattus	0.099	5
Trichocerca similis	0.036	5
Trichocerca stylata	0.012	5

(a) Estimates assumed specific gravity = 1.05 g/mL and dry wt. = 0.15 * wet wt.

(b) 1: Doohan and Rainbow (1971), 2: Makarewicz and Likens (1979), 3: Pace and Orcutt (1981), 4: Dumont et al. 1975), 5: Ruttner-Kolisko (1977), 6: Bottrell et al. (1976).

Table 5-3. Size-Weight Regressions Used to Estimate Crustacean and Insect Dry Weights.(a)

Taxa	Regressions
Cladocera	
Chydorus sphaericus	ln dry wt. (ug) = 4.543 + 3.636 * ln body-length (mm)
Daphnia parvula	ln dry wt. (ug) = 1.6026 + 3.632 * ln body-length (mm)
Moina micrura	ln dry wt. (ug) = 4.9344 + 4.849 * ln body-length (mm)
Pleuroxus hamulatus	ln dry wt. (ug) = 2.8713 + 3.079 * ln body-length (mm)
Simocephalus serrulatus	ln dry wt. (ug) = 1.4663 + 3.1932 * ln body-length (mm)
Bosmina longirostris	ln dry wt. (ug) = 4.9344 + 4.849 * ln body-length (mm)
Alona rustica	ln dry wt. (ug) = 2.8713 + 3.079 * ln body-length (mm)
Copepoda	ln dry wt. (ug) = 1.0866 + 1.5493 * ln body-length (mm)
Ostracoda	ln dry wt. (ug) = 4.9344 + 4.849 * ln body-length (mm)
Insecta	
Chaoborus punctipennis	ln dry wt. (ug) = 5.032498 + 1.97966 * ln head-width (mm)

(a) All regressions from McCauley (1984) except Chaoborus, which was calculated from this study: R = 0.88, N = 26.

assuming that similar dimensions of the organisms should yield similar size-weight relationships. Despite possible error in absolute dry weights, comparisons among ponds should be valid because dry weight calculations were applied identically to all ponds. Tables 5-2 and 5-3 list estimated dry weights for rotifers and size-weight regressions for other taxa, respectively.

As with taxa densities, I pooled individual biomasses into taxa biomasses (Figure 5-5). Trends in taxa biomasses were generally similar to taxa densities, with a few exceptions. Rotifer biomass in Pond 8 during January 1989 more than doubled peak values in any other pond during the year due to a moderately dense Hexarthra mira population. This rotifer is large and consequently contributed greatly to zooplankton community biomass. The extremely high cladoceran densities in Pond 9 during Autumn 1988 and Winter 1989 were due to Bosmina longirostris, a small cladoceran. Although this cladoceran had far greater densities at this time, its biomass was roughly comparable to the biomass of less numerous (but larger) cladocerans in other ponds.

Cluster analysis (as above) of taxa biomasses indicated Ponds 8 and 9 were different from the other ponds (Figure 5-6). Clustering of other ponds showed

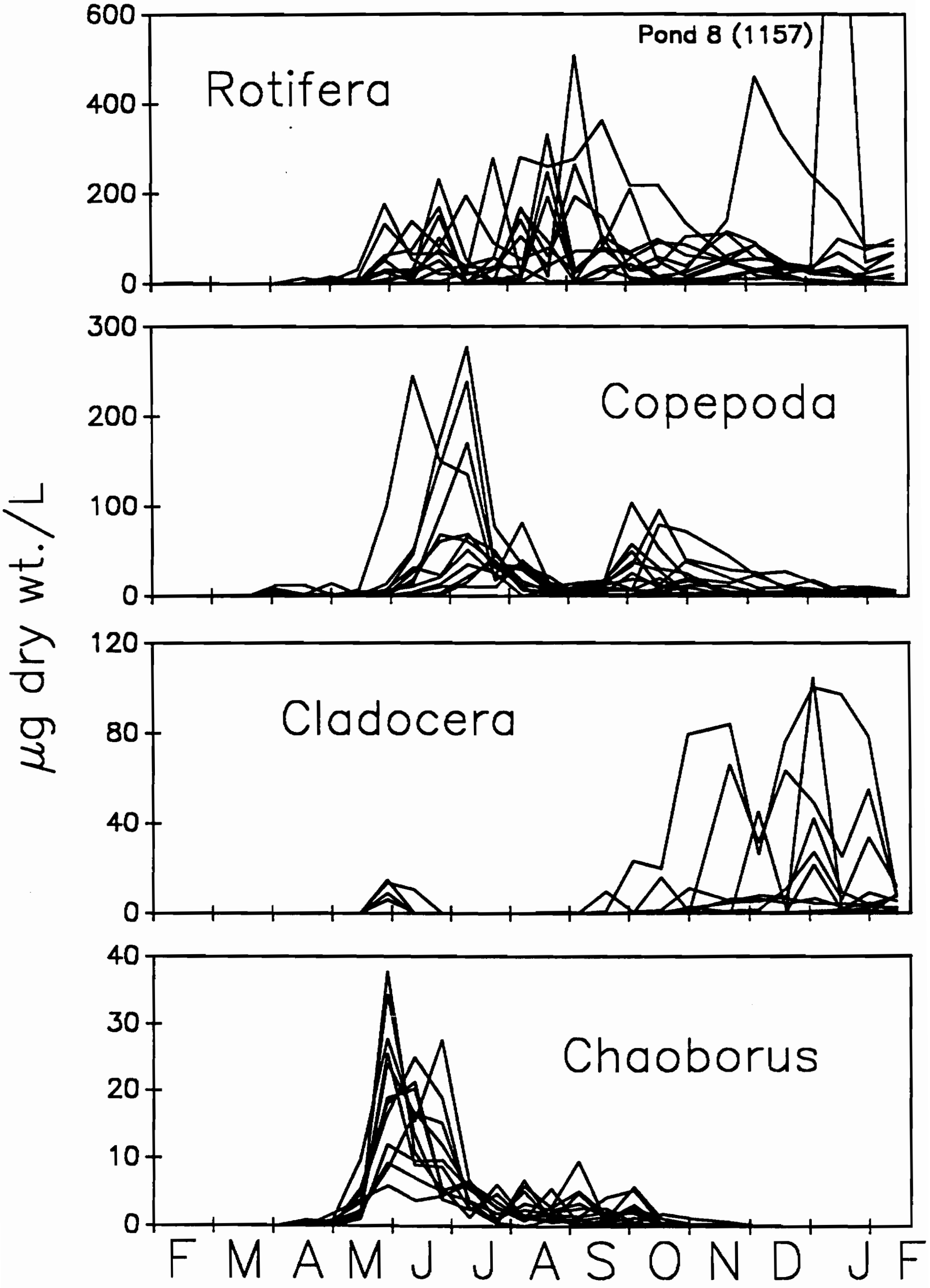


Figure 5-5. Zooplankton taxa biomass.Each line represents a pond.

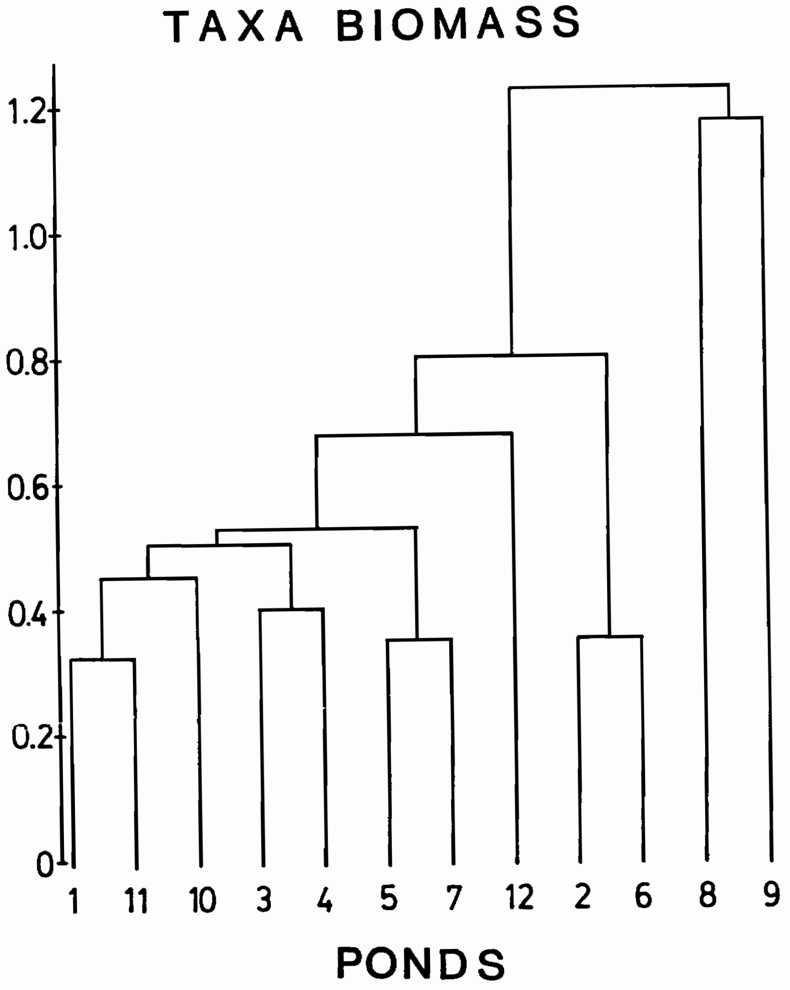


Figure 5-6. Cluster analysis of taxa biomass data. Vertical axis is distance between cluster centroids in multivariate space.

different patterns among ponds than for taxa densities. Ponds 2 and 6 were clustered together but separate from other ponds and Pond 12 was no longer grouped with other ponds.

Community Diversity

I calculated three measures of diversity for the zooplankton communities of all twelve ponds over the study. Tables 5-4, 5-5, and 5-6 list species richness (S), Shannon-Weiner diversity index (H′), and Pielou′s equitability index (J′), respectively.

Of the 3 indices, species richness appeared the least variable among ponds and over time. However, species richness did vary considerably (Table 5-4, Figure 4-1 in Section 4). Both H′ and J′ varied widely and frequently for most ponds during the study and provided little useful information for comparing ponds.

5.4 DISCUSSION

Timing and Densities

Zooplankton communities consist of populations with a range of life-histories. For example, some rotifers exhibit dense populations for very brief periods, while other species like copepods have almost annual life cycles (Hutchinson 1967, Wetzel 1983). This range of

Table 5-4. Species Richness (S).

	Pond													
Week	1	2	3	4	5	6	7	8	9	10	11	12	Avg.	S.D.	C.V.
1	2	3	3	3	3	1	2	2	2	0	2	2	2.1	0.9	41.4%
3	2	2	2	2	0	3	0	0	2	0	0	2	1.3	1.1	87.2%
5	2	2	2	4	0	2	0	0	2	1	0	3	1.5	1.3	83.9%
7	3	2	2	3	2	2	1	1	4	2	3	3	2.3	0.8	36.4%
9	3	2	4	3	3	3	1	3	3	2	3	3	2.8	0.7	26.2%
11	5	4	4	4	4	4	0	3	3	4	4	4	3.6	1.2	33.1%
13	4	4	5	3	3	3	1	5	5	5	4	4	3.8	1.1	29.8%
15	8	5	7	6	4	6	4	4	7	6	6	5	5.7	1.2	22.0%
17	8	5	7	7	5	7	5	5	7	7	6	6	6.3	1.0	16.2%
19	9	5	9	8	8	6	5	8	5	5	5	4	6.4	1.8	27.3%
21	7	8	7	9	8	8	5	7	5	5	7	5	6.8	1.4	20.2%
23	8	12	6	12	5	8	10	10	9	12	7	8	8.9	2.3	25.3%
25	9	10	10	12	8	6	10	13	9	8	10	9	9.5	1.8	18.5%
27	13	13	8	8	9	12	10	11	10	16	11	8	10.8	2.3	21.9%
29	10	9	10	9	9	9	6	11	11	14	11	7	9.7	2.0	20.4%
31	12	11	11	12	13	10	12	12	11	12	9	12	11.4	1.0	9.1%
33	12	12	9	13	10	11	11	11	11	8	10	10	10.7	1.3	12.3%
35	8	13	16	10	13	11	9	12	13	14	9	15	11.9	2.4	20.4%
37	10	9	8	9	12	10	9	12	11	15	14	8	10.6	2.2	20.6%
39	11	7	8	7	11	10	7	12	12	10	10	10	9.6	1.8	18.8%
42	6	9	8	9	12	10	13	13	7	8	12	8	9.6	2.3	23.9%
44	8	7	6	6	13	9	10	10	11	9	8	9	8.8	2.0	22.1%
46	7	7	7	8	9	6	8	10	6	6	7	7	7.3	1.2	16.1%
48	7	12	8	7	14	9	9	10	6	7	11	10	9.2	2.3	24.7%
50	8	8	7	9	13	9	15	10	4	6	9	11	9.1	2.8	31.3%
52	9	8	9	7	10	13	10	9	6	7	8	10	8.8	1.8	20.1%
54	6	8	5	8	11	9	10	8	8	7	8	8	8.0	1.5	19.1%

Table 5-5. Shannon-Weiner Diversity Index (H').

	Pond														
Week	1	2	3	4	5	6	7	8	9	10	11	12	Avg.	S.D.	C.V.
1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	--
3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	--
5	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	--
7	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	--
9	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	--
11	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	--
13	0.00	0.00	0.73	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.06	0.20	331.7%
15	0.65	0.06	1.10	0.30	0.00	1.52	0.47	0.00	1.11	0.00	0.00	0.96	0.51	0.52	101.2%
17	0.50	0.98	1.69	0.42	0.98	0.45	0.18	0.13	0.73	0.10	0.16	0.18	0.54	0.46	84.9%
19	1.74	0.61	2.24	1.18	0.54	1.24	0.32	0.16	1.01	1.00	0.56	0.96	0.96	0.57	59.0%
21	1.11	1.97	1.46	1.10	1.97	1.74	0.38	0.19	0.79	1.28	0.39	1.05	1.12	0.58	51.6%
23	0.37	1.89	0.34	2.78	0.57	1.90	1.99	0.58	0.28	1.66	1.06	0.42	1.15	0.81	70.6%
25	0.66	1.99	2.10	2.68	2.00	0.38	2.22	2.04	1.41	0.64	2.01	2.30	1.70	0.72	42.1%
27	1.98	2.16	1.33	1.21	2.16	1.62	1.85	2.14	1.19	0.81	2.71	0.83	1.67	0.57	34.3%
29	1.48	1.07	1.54	1.85	1.39	0.86	0.09	0.94	1.35	1.94	2.27	0.55	1.28	0.59	45.9%
31	0.85	0.57	1.28	1.34	1.89	0.90	2.24	1.14	1.27	2.30	0.24	2.44	1.37	0.68	49.4%
33	1.51	1.98	1.61	0.40	1.29	1.14	1.11	1.32	0.55	1.01	0.65	2.05	1.22	0.50	41.2%
35	0.71	2.17	2.29	0.27	0.90	0.23	0.40	1.94	1.71	1.69	0.69	2.16	1.26	0.77	60.9%
37	1.83	0.70	1.54	0.28	0.31	0.84	0.31	2.46	1.28	2.32	2.26	1.43	1.30	0.78	59.8%
39	1.02	0.84	0.64	0.14	0.12	1.68	0.09	0.55	1.36	0.87	2.05	1.57	0.91	0.62	68.3%
42	0.34	0.46	0.19	0.15	0.25	1.37	0.39	1.36	0.84	0.19	1.93	1.17	0.72	0.57	79.5%
44	0.96	0.23	0.15	0.14	0.39	1.08	0.36	0.60	0.83	0.06	0.46	0.83	0.51	0.33	65.5%
46	0.43	0.15	0.17	0.25	0.19	1.01	0.91	0.42	0.64	0.10	0.33	0.91	0.46	0.31	68.3%
48	0.62	0.59	0.29	0.24	0.96	0.76	1.63	0.80	0.72	0.05	0.30	1.60	0.71	0.48	66.9%
50	1.16	1.14	0.05	0.10	0.59	0.96	2.15	0.45	0.54	0.03	0.28	1.05	0.71	0.59	83.6%
52	0.58	1.93	0.12	1.05	0.29	0.48	1.49	0.92	1.04	0.03	0.02	1.59	0.79	0.62	77.9%
54	0.35	1.71	0.01	2.27	0.21	0.51	1.92	0.78	0.62	0.02	0.02	1.92	0.86	0.81	94.4%

Table 5-6. Pielou's Equitability Index (J').

	Pond														
Week	1	2	3	4	5	6	7	8	9	10	11	12	Avg.	S.D.	C.V.
1	--	--	--	--	--	--	--	--	--	--	--	--	0	0	--
3	--	--	--	--	--	--	--	--	--	--	--	--	0	0	--
5	--	--	--	--	--	--	--	--	--	--	--	--	0	0	--
7	--	--	--	--	--	--	--	--	--	--	--	--	0	0	--
9	--	--	--	--	--	--	--	--	--	--	--	--	0	0	--
11	--	--	--	--	--	--	--	--	--	--	--	--	0	0	--
13	--	--	0.73	--	--	--	--	--	--	--	--	--	0.06	0.20	331.7%
15	0.28	0.06	0.70	0.19	--	0.96	0.47	--	0.70	--	--	0.96	0.35	0.36	101.8%
17	0.19	0.62	0.85	0.18	0.98	0.19	0.18	0.08	0.46	0.06	0.10	0.11	0.33	0.30	90.6%
19	0.58	0.30	0.80	0.42	0.21	0.54	0.16	0.06	0.50	0.50	0.28	0.61	0.41	0.20	49.4%
21	0.43	0.70	0.57	0.37	0.76	0.62	0.19	0.08	0.39	0.64	0.15	0.53	0.45	0.21	47.1%
23	0.13	0.55	0.15	0.80	0.28	0.68	0.63	0.18	0.09	0.50	0.41	0.15	0.37	0.23	62.3%
25	0.22	0.66	0.70	0.77	0.71	0.16	0.70	0.59	0.47	0.25	0.63	0.77	0.55	0.21	38.6%
27	0.55	0.60	0.48	0.43	0.72	0.47	0.58	0.65	0.37	0.22	0.81	0.30	0.51	0.16	32.2%
29	0.47	0.36	0.55	0.62	0.46	0.29	0.04	0.31	0.43	0.52	0.72	0.24	0.41	0.17	42.0%
31	0.25	0.17	0.40	0.40	0.53	0.29	0.65	0.34	0.38	0.66	0.08	0.73	0.40	0.19	47.8%
33	0.45	0.60	0.62	0.11	0.43	0.38	0.35	0.44	0.17	0.39	0.22	0.68	0.40	0.16	41.7%
35	0.25	0.61	0.64	0.09	0.26	0.07	0.13	0.61	0.48	0.47	0.23	0.57	0.36	0.20	56.4%
37	0.58	0.25	0.55	0.09	0.09	0.28	0.10	0.78	0.38	0.63	0.61	0.51	0.40	0.22	56.0%
39	0.32	0.32	0.23	0.06	0.04	0.56	0.04	0.17	0.41	0.27	0.68	0.49	0.29	0.20	67.2%
42	0.15	0.15	0.07	0.05	0.08	0.49	0.11	0.41	0.33	0.07	0.61	0.42	0.24	0.18	76.6%
44	0.34	0.09	0.07	0.06	0.12	0.38	0.13	0.21	0.26	0.02	0.18	0.30	0.17	0.11	64.2%
46	0.17	0.06	0.07	0.09	0.06	0.51	0.35	0.16	0.28	0.04	0.13	0.39	0.19	0.14	76.6%
48	0.22	0.19	0.10	0.09	0.32	0.29	0.58	0.29	0.31	0.02	0.10	0.53	0.25	0.16	65.0%
50	0.39	0.38	0.02	0.03	0.21	0.34	0.62	0.16	0.27	0.01	0.10	0.35	0.24	0.17	73.8%
52	0.19	0.69	0.04	0.41	0.11	0.16	0.50	0.35	0.45	0.01	0.01	0.53	0.28	0.21	76.3%
54	0.14	0.66	0.00	0.81	0.08	0.20	0.64	0.34	0.27	0.01	0.01	0.83	0.33	0.30	91.9%

life-history strategies contributed to a seasonal series of population maxima and contributed to the temporal variation in zooplankton communities of the experimental ponds. For the ponds to have been truly similar in zooplankton community structure, temporal variations of species should have been both synchronous and of the same amplitude (in densities or biomass) for all ponds.

Synchrony of trends was roughly true for Copepoda and Chaoborus populations, indicating that timing of these populations was strongly controlled by seasonal changes such as daylength and temperature. Rotifera and Cladocera were also seasonal in presence with some notable exceptions. Many species were present in only a few ponds at any time, and some species were never collected in more than a few ponds. Thus, the timing among ponds was synchronous only on a very coarse scale (e.g., seasons) for many species and synchrony among ponds did not apply to the species that occurred in only a few ponds.

The timing of some species' presence in the ponds was probably a product of colonization timing and seasonal regulation of population growth. This is best illustrated by the Cladocera. Cladocerans often exhibit spring and autumn seasonal population maxima in established lakes and ponds, although the timing varies among lakes and regions (Wetzel 1983). In the new experimental ponds, two species (Daphnia parvula and Moina micrura) occurred in Spring 1988 and were present in only a few ponds. I collected Moina micrura from puddles of rainwater in the ponds during November 1987, prior to filling of the ponds. It is likely both species were already present in sediments when ponds filled with water, although not necessarily in all ponds. The other five cladoceran species did not appear in any of the ponds until Autumn 1988, and each of these five species occurred in only a few of the ponds. It seems likely that the timing of these cladoceran populations was also constrained by the timing of colonization since several of these species have been observed to have spring and summer maxima in other lakes (Hutchinson 1967).

Populations with synchronous timing among ponds often did not have similar densities (Fig.s 5-1, 5-3, Table 5-1). For example, Chaoborus punctipennis populations had similar timing among ponds, but the lowest coefficient of variation (CV) for population densities among ponds during the study was 27.5% (Table 5-1). At no time were density CVs lower than 10%. Also, variation in population densities was not a function of similar but out-of-phase population peaks among ponds. Many taxa exhibited marked peaks in one or a few ponds without similar peaks in other ponds.

No strong evidence was found to indicate that competition among zooplankton species regulated community structure in the experimental ponds. Major variation in zooplankton populations were due to ephemeral changes in densities, located in different ponds at different times. In laboratory experiments, Cladocera are competitively superior to several rotifers (Gilbert 1985), and it is unlikely that rotifer densities excluded Cladocera. In addition, rotifers select various food sizes and types (Edmondson 1965, Pourriot 1977), thereby reducing the potential for overlap in dietary requirements among rotifers. Finally, I found no evidence to suggest that resources in the ponds were limiting for zooplankton. If competition was important in controlling zooplankton community structure, its role was brief and not discernible from available data.

Predation surely had some impact on zooplankton population densities, especially during summer when potential invertebrate predators (e.g., some Diptera, Odonata, and Coleoptera) were most numerous. However, actively-dispersed predatory insects were well distributed among all ponds and had roughly the same timing and densities among ponds (Layton 1989: Appendix 2). As mentioned previously, fish were not stocked in the ponds and were never observed in any pond during the study. It does not seem likely that predation would have been responsible for observed differences among ponds in the timing and densities of zooplankton populations.

The presence of major population peaks in only a few ponds for many species indicates that those populations were responding favorably to factors other than daylength, temperature, etc. It is unlikely that zooplankton were responding to physico-chemical changes for two reasons: 1) most measured parameters did not vary dramatically between sample dates or among ponds; and 2) zooplankton are not known to be constrained by physico-chemistry within the range of values for the ponds (Hutchinson 1967). Evaluation of other potential factors, such as densities of phytoplankton size classes, etc. will require data not presently available.

A simpler and perhaps more likely reason for some of the observed trends in structure of zooplankton communities is chance. As discussed in Section 4.0, zooplankton species were not uniformly present in all ponds. It is also likely that propagule densities varied among ponds, either as resting eggs already present in sediments or as incoming cysts, etc. Chance availability of greater numbers of propagules may have contributed to differences among ponds in peak densities of zooplankton species. For example, peak Chaoborus densities in May-June 1988 and Copepoda densities in June-July 1988 (Figure 5-1) were primarily due to early instars. As shown in Figure 5-1, ponds varied considerably in early instar densities. Apparently, neonates were not uniformly available among all ponds.

If ponds contained different copepod and Chaoborus neonate densities and ponds were almost synchronous in these densities, then ponds probably varied in propagule densities of asynchronous species. Superimposed on the chance due to colonization are the added complexities of factors potentially affecting egg viability (sediment redox state, fungal infection, benthic macroinvertebrate predation on eggs and neonates, etc.). In reality, many processes potentially enter into what I have called chance.

Relative Importances of Zooplankton Taxa

Comparisons of taxa densities and biomasses show clearly that Rotifera were a large fraction of the zooplankton communities throughout the study, both numerically and in biomass. In addition, 47 of the 61 (77%) zooplankton taxa recorded in the experimental ponds were rotifers. This is not entirely surprising, given that others have found similar results in such different lakes as oligotrophic Mirror Lake in New Hampshire (Makarewicz and Likens 1979) and a eutrophic reservoir in Georgia (Pace and Orcutt 1981). Rotifers assumed a major proportion of zooplankton communities in experimental ponds within the first year. However, rotifers were not uniformly distributed among ponds. It is possible that dense, reproducing rotifer populations in some ponds would lead to continued heterogeneity among ponds via differential egg production.

Copepoda were present in some ponds at the first sampling date (one week after filling) and persisted throughout the study. A seasonal separation of the two dominant species (both herbivores) seemed to occur, with *Eucyclops agilis* occurring first, followed by *Tropocyclops prasinus*. However, juveniles of the two species could not be distinguished, preventing further evaluation of temporal differences. Adult *Macrocyclops* *albidus* were observed only rarely and late in the study in most ponds. *Macrocyclops albidus* is predatory and may assume an important role in the ponds in the future.

Cladocera never attained a dominant role in terms of density or biomass. Most Cladocera were not recorded until Autumn 1988 and were not well dispersed among the ponds during the first year.

Chaoborus were probably important predators on other zooplankton during summer months, as was probably true for a number of other insects in the ponds. I think it is unlikely, however, that invertebrate predation was so intense that it inhibited colonization of the ponds by zooplankton. *Chaoborus* may have been an important modifier of zooplankton densities during summer months, but *Chaoborus* larvae were well distributed among ponds and ponds contained roughly the same densities at any time.

Ostracods were enumerated collectively and biomass estimates were only approximate. Ostracods were not recorded in samples until Autumn 1988 and were never common. However, given the littoral habitat of the experimental ponds, it is likely that ostracods will gain in importance in zooplankton communities of the experimental ponds.

Multivariate Analyses and Diversity Indices

The large and sparse matrix of 61 taxa x 12 ponds x 27 sampling dates was not well represented by principal components analysis (PCA). Trends among species and ponds through time were too disparate to be graphically summarized and the first principal component represented only 4% of total variation. This failure of a powerful statistical technique to summarize data indicates that considerable variation existed within and among ponds. Rather than delete data to represent trends by several dominant species, I summarized the density and biomass by taxa (rotifers, copepods, cladocerans, *Chaoborus*, ostracods) as presented above. Because this reduced data to 5 variables, PCA on taxa provided essentially the same information as plots of taxa density or biomass. Cluster analyses on taxa density and biomass both indicated that Ponds 8 and 9 were very different from the other ponds over the course of the entire study. Other ponds differed as well, but to lesser degrees and in different patterns depending on whether density or biomass data were clustered.

Of three diversity indices I calculated, only species richness (S) had any value as a general indicator of zooplankton community diversity. However, ponds varied widely in S and average S was only a rough indicator of trends in diversity. Average values of H′ and J′ are not appropriate as a basis for discussion of zooplankton community trends in the ponds: values varied greatly within brief periods of time, and within and among ponds. Hurlbert (1971), Green (1979), and others have argued that diversity indices contribute little to an understanding of patterns in ecological communities. The results for zooplankton communities in the experimental ponds support this view.

Colonization Ecology

Given that ponds were environmentally similar for the parameters measured, it appears that historical factors, such as colonization timing and invasion intensities, were important in the structural variation of zooplankton communities among ponds. Some researchers have recently turned attention to the regional supply of individuals as a factor contributing to localized community structure (Ricklefs 1987, Roughgarden et al. 1987).

Very little information exists in the literature regarding zooplankton dispersal. Maguire (1963) studied dispersal of aquatic microorganisms around two lakes, but most of his data were on algal and protozoan species. However, during his 52-day study a few rotifer taxa, a cladoceran, copepod, ostracod, and Culex colonized his bottles around a pond. Obviously, proximity to a source of colonists affects colonization rates. Relatively greater distance of experimental ponds to source pools of colonists may have contributed to slower colonization rates in the experimental ponds than observed by Maguire (1963).

Experimental ponds were generally similar (Section 3.0) but did not develop structurally similar zooplankton communities (Section 4.0 and this section). This is essentially the same conclusion reached by McCune and Allen (1985) in their study of similar forest sites. Their forest sites and the experimental ponds of this study were insular, in that many species were not uniformly distributed among sites.

As discussed in Section 4.0, experimental ponds were not colonized similarly by zooplankton and the Random Placement Hypothesis (RPH) was not supported. Consequently, it was unreasonable to expect the RPH to extend to zooplankton community structure (densities, biomass) and my study did not test the generality of the RPH to zooplankton community structure. However, variation among ponds in zooplankton densities and biomass was greater than in species numbers during the study. This result indicates that it would be difficult to generalize the RPH to measures of communities more complex than species number.

Replicability

Results on zooplankton community structure indicate that zooplankton communities in experimental ponds develop differently if the ponds are colonized naturally. Other experimental ponds have also exhibited substantial heterogeneity after being left unmanipulated for two years (Hall et al. 1970). However, Hall et al. (1970) began their study after the ponds were two years old and presented no data for those two years. I am not aware of any other studies that have evaluated initial colonization and development of zooplankton community structure for the first year of a set of experimental ponds.

Because the timing of some species' occurrences was probably related to the timing of propagule availability in the experimental ponds, some taxa (e.g., Cladocera) may exhibit more typical (and therefore more predictable) seasonal periodicity in the future. Also, continued colonization of the ponds will eventually lead to more similar species lists among ponds, assuming a finite source pool of species in the region.

However, there is no indication from these results that ponds will develop similar densities of species. Species with histories of great abundance will also have produced large quantities of resting eggs. Those resting eggs will contribute to further large populations in some ponds. Thus, numeric heterogeneity among ponds may be self-perpetuating to some extent.

These results suggest that substantial natural variability through time and among ponds may persist for these zooplankton communities unless the ponds are actively managed. It is possible that a pond experiment conducted in the first year would be confounded by non-replicable timings and densities of zooplankton species and the ongoing colonization of new species. It is also likely that experiments conducted after one year of colonization would be subject to wide variability and lack of replication in the zooplankton communities.

At this time, it is not clear if draining and refilling the ponds with water from a common source (reservoir) will facilitate replicability of zooplankton communities among ponds. It is possible that replicable densities in the water column would be replaced by organisms from resting eggs in the sediments, thereby eroding any replicability. Potential management techniques for replicability might include inoculation with sediments or organisms collected from nearby ponds and lakes, repeated drain-refill cycles prior to treatments, and mixing of sediments and water among ponds would enhance replicability. Techniques such as these should be tested for inclusion in experimental protocols for pond systems.

6.0 ZOOPLANKTON COMMUNITY FUNCTION

6.1 INTRODUCTION

Colonization is, by definition, a phenomenon of community structure and has traditionally been considered in terms such as species richness and population density (e.g., Simberloff and Wilson 1969, Hubbard 1974, Barnes 1983, Rey 1984, Abele 1984, Ryti 1984, Enckell et al. 1987). Most studies of colonization have addressed species-area relationships by testing one of four species-area hypotheses: Random Placement (Arrhenius 1921, Coleman 1981), Habitat Diversity (Williams 1964), Equilibrium Theory (MacArthur and Wilson 1967), or Intermediate Disturbance (Connell 1978). All four hypotheses attempt to explain why larger areas contain more species and are appropriately considered in terms of the number of species present in the communities of interest.

However, ecosystems are also characterized by functional properties, related to energy flow and nutrient cycles (Odum 1971). O'Neill et al. (1986) presented the concept of ecosystems as dual hierarchies of structure and function. Structure and function have been studied in a variety of communities and ecosystems (e.g., Odum 1957, Golley 1965, Likens 1985), but to my knowledge, such a dual approach has not been applied to the study of colonization dynamics. Consequently, species-area hypotheses have not been evaluated for their generality to the early development of community or ecosystem function in parallel with structural development.

In this study I measured structure and function of zooplankton communities in twelve new experimental ponds and tested several predictions derived from the Random Placement Hypothesis (RPH; Coleman 1981). Previous dissertation sections have dealt with physico-chemistry, colonization dynamics and zooplankton community structure. This section addresses the prediction that developing zooplankton communities in the twelve ponds should have similar functional attributes, given that ponds of the same dimensions should be colonized similarly and that ponds were environmentally similar (according to the RPH).

As discussed in Sections 4.0 and 5.0, the experimental ponds were not colonized similarly by zooplankton. Ponds had different colonization and species accrual curves, species lists, and zooplankton community structure (densities and biomass). I did not find strong evidence to indicate explicit assumptions of the RPH were invalid (Sections 3.0 and 4.0), and I suggested that differences among zooplankton communities in the ponds may have been related to the availability and invasion intensities of zooplankton species in the area surrounding the ponds (Section 4.0).

Observed differences among ponds in zooplankton colonization and community structure might indicate that the prediction of functional similarity would be inappropriate. However, two characteristics of community function maintain the possibility of functional similarity. First, many species are functionally redundant, i.e., they perform essentially the same function in an ecosystem (O'Neill et al. 1986). Second, community function parameters summarize energy or nutrient processing rates irrespective of community structure. For example, secondary productivity is estimated per species, but zooplankton community productivity is the sum of species' productivity. As a result, function is usually not directly predictable from structure (O'Neill et al. 1986). Therefore, the prediction of functional similarity may still be appropriate, but only because community function is not clearly dependent on community structure.

The four functional parameters measured in this study were zooplankton community productivity, respiration rate, NH_3-N and PO_4-P regeneration rates. I chose productivity and respiration rates because they are related to major pathways of energy flow in aquatic ecosystems. I measured NH_3-N and PO_4-P regeneration rates because previous studies have shown that most of the N and P recycled by zooplankton is in the form of ammonia and soluble reactive phosphate (SRP) (Butler et al. 1969, Corner and Newell 1967, Peters and Lean 1973, Korstad 1983) and that this nutrient release can be a major source of N and P for phytoplankton (Hargrave and Geen 1968, Ganf and Blazka 1974, Lehman 1980).

5.2 MATERIALS AND METHODS

Study Site

This study was conducted at the new experimental ponds facility of the Southern Piedmont Agricultural Experiment Station near Blackstone, VA. Ponds were constructed during 1987-1988. A reservoir adjacent to the ponds was constructed during 1988 but was not included in the study. Ponds are square and have 405 m^2 surface area, 2.13 m depth and a 2.5:1 slope ratio. A complete description of the construction of the facility and its layout are provided in Section 3.0 (Comparative Physicochemistry).

All twelve experimental ponds were filled with water in late January 1988. Chlorinated tap water (source: Nottoway Reservoir) from a nearby fire hydrant was used. Water entered the ponds through the underground pipes, so that all twelve ponds received water simultaneously. Ponds were filled over the course of 6 days, ending on 31 January 1988. Sampling started on 5 February 1988 and continued for one year, ending on 10 February 1989.

The only manipulation of the ponds was the addition of well water to maintain water levels. At no time was water transferred from one pond to another during this study, and no reservoir water was added to any ponds. No fish were stocked in the ponds and fish were never observed in any pond during the study.

Sampling Strategy

Sampling and analyses were conducted biweekly for one year, starting on 5 February 1988 and ending on 10 February 1989. One three-week interval occurred in November 1988 to avoid schedule conflicts. In addition, limited sampling was conducted during intervening weeks from March through October 1988. The criterion for initiating and ending these shorter sampling trips was an arbitrarily-chosen 10^{o} C water temperature.

All sampling was done according to a set of random sampling sequences prepared prior to the study. These random sequences ensured that no patterns would be established among ponds due to sampling activities. Each pond was sampled at three stations: always at the center (2.14 m depth) and at 2 of the 4 sides (1.07 m depth). The two sides were chosen each sampling trip by coin toss (East vs. West, North vs. South). Sampling stations were consistent throughout the study with the use of the suspended ropes. The intersection of the ropes marked the center, and a position on the ropes at 1.07 m depth marked the side stations.

Field Procedures

I described zooplankton sampling procedures in detail in Section 5.0 (Zooplankton Community Structure). I will summarize general sampling procedures here and describe in detail only those procedures for functional measurements. Productivity estimates were derived from preserved zooplankton samples. Nutrient regeneration and respiration rate estimates were measured using live organisms.

Ponds were sampled from an inflatable raft, and two types of samples (tube and net) were collected at each of three stations per pond. Design of the tube sampler is described in Section 4.0. Tube samples collected whole water for analyses of rotifer populations and other analyses described in Section 4.0. Five tube samples were collected at each station and pooled for each pond.

I collected net samples at each station via vertical tows from the bottom with a Wisconsin-style plankton net (80 um mesh: Wildlife Supply Co.). I placed the net gently on the bottom and allowed it to lie there for about 2 min. before hauling up. This was done to obtain a representative sample of the whole water column, with minimal disturbance of bottom water. I made two such net tows at each station and rinsed collected organisms into a jar and preserved them with 4% formalin. Formalin was buffered with 5% sodium acetate (Steedman 1976) and contained 5 g/L sugar (Haney and Hall 1973).

Pond depth was recorded and used in calculations of water volume collected for quantitative estimates of zooplankton density. Pond depth applied to calculations for net tows at the center station only: net tows at side stations were always in 2.13 m of water, regardless of pond depth.

Upon exiting a pond, I sieved 4.0 L of water (collected with the tube sampler) through a 35 um Nitex sieve, rinsed collected organisms into a jar and added 4% formalin. Sieved water was collected in a bucket and used for procedures described below. Preserved organisms were stored until they could be enumerated as described under Laboratory Procedures.

The following procedures were used to concentrate live zooplankton for nutrient regeneration and respiration rate analyses. A set of 10 vertical net tows was made at each of the 3 stations per pond. Collected organisms were kept alive and rinsed into a bucket. These vertical tows were collected more rapidly than those for preserved organisms.

Of the 4 L of sieved water (above), 3.2 L were filtered through Whatman GF/D filters to remove phytoplankton and detritus. Water was filtered at $\leq$ 200 mm Hg negative pressure with a hand pump (Tarapchak et al. 1982).

Live zooplankton were concentrated by slowly pouring both the remaining tube-collected water (about 20 L) and the net-collected zooplankton through a 35 um sieve. This zooplankton concentrate was gently rinsed from the sieve into the 3.2 L of filtered water and was used to prepare nutrient regeneration and respiration rate assays.

Nutrient regeneration rates were estimated by comparing nutrient levels before and after enclosure of zooplankton in situ. Four subsamples of the zooplankton concentrate were placed in 300-mL B.O.D bottles. Bottled zooplankton were suspended in the pond at 1/2 Secchi depth for 2 - 5 hours. Upon retrieval, contents of each bottle were filtered through a tared Whatman GF/C filter and filtered water was transferred to a glass bottle. Filters were placed in vials, and both the water and filters weere stored on ice until laboratory analyses.

All glassware used in nutrient analyses was acid-washed (HCl), rinsed with distilled, deionized water and dried prior to use. Pre-enclosure nutrient levels were determined from analyses of whole water filtered through Whatman GF/C filters, as described in Section 3.0.

After placement of nutrient regeneration bottles in the appropriate pond, respiration rate assays were prepared by mixing the zooplankton concentrate again and removing four more subsamples (300 mL each). The subsamples were filtered onto a Whatman GF/D filter, placed in vials and stored on dry ice until return to the laboratory.

Laboratory Procedures

Productivity. Preserved zooplankton were counted and identified with a Sedgwick-Rafter chamber and a Nikon binocular microscope at 40 X. Entire samples were counted if depauperate, while dense samples were counted using at least three subsamples. Subsamples were obtained by mixing the sample and transferring one mL to the Sedgwick-Rafter chamber with a calibrated autopipette. The autopipette tip was cut to have a 4 mm opening tp prevent selective subsampling of large organisms (Edmondson and Winberg 1971). Entire subsamples were counted. Original densities (organisms/L) were calculated using sample volumes, number of subsamples and volumes of water represented in net tows.

Individual dry weights were calculated for zooplankton species using values or size-weight formulae from the literature. Estimated individual dry weights for Rotifera and size-weight regressions for other taxa are listed in Section 5.3. Organisms were measured with a Filar digital micrometer mounted on the microscope and calibrated with a stage micrometer. Average sizes were used to estimate rotifer dry weights.

I calculated a headwidth-dry weight regression for Chaoborus punctipennis in the ponds, following procedures suggested by McCauley (1984). Individual organisms were rinsed with distilled water, measured with the the Filar micrometer, placed on tared aluminum pans, and dried at 60° C for 24 h. Organisms were then stored in a dessicator and weighed on a Cahn Electrobalance. Regression statistics are presented in Section 5.3.

Crustacean and Chaoborus productivity was estimated by the increment-summation technique and using the CIPROD program prepared by A. Morin (1984). Productivity was not calculated for species collected on only one sampling date.

Rotifer productivity was also estimated by increment-summation, but using the modification for rotifers described by Rigler and Downing (1984). This modified method assumes rotifer growth after hatching is negligible and uses egg numbers in the calculations. Thus, rotifer productivity estimates were restricted to species that carry their eggs. Egg development time is also required for this modified method (Rigler and Downing 1984). Egg development time is a function of temperature and I used the general regression of Bottrell et al. (1976) to estimate rotifer egg development times.

Zooplankton community productivity at each sample date was calculated as the sum of species productivity estimates.

Nutrient Regeneration Rates. Pre- and post-enclosure water samples were analyzed for NH_3-N and SRP colorimetrically with a Gilford Response spectrophotometer and according to APHA (1985). The lowest value of standard curves for both nutrients was 0.02 mg/L. Samples with a calculated nutrient concentration $<$ 0.02 mg/L were entered in calculations of nutrient regeneration as having 0.00 mg/L of the nutrient.

Filters with zooplankton from the *in situ* enclosures were oven-dried at 60°C for $\geq$ 24 h and weighed on a Mettler analytical balance. I calculated zooplankton dry weights by subtracting filter tare weights from final weights. I calculated the quantity of either NH_3-N or SRP regenerated by the enclosed zooplankton during the enclosure period, expressed as ug nutrient/mg dry weight/h.

Respiration Rates. Respiration rate samples were processed and analyzed according to the method of Owens and King (1975). The method assays activity of the respiratory electron transport system (ETS) after extraction of the enzyme systems from cells. The ETS is a series of mitochondrial and microsomal dehydrogenase enzymes, flavoproteins, and cytochromes and is a key component in respiratory oxidation of energy. This assay measures activity of the entire enzyme system and is not an assay of one enzyme's activity.

I stored samples on dry ice until return to the lab, when I placed samples in a freezer at $\leq -20^{\circ}C$. Samples were processed within 3 days of return to the lab. Ahmed et al. (1976) showed that copepods frozen at $-20^{\circ}C$ for 7 days retained 100% of the ETS activity of fresh copepods.

Cell-free extracts were prepared by grinding filters in the presence of a phosphate buffer (ETS-B; Owens and King 1975). Samples were ground in a glass grinding tube with a Teflon pestle (A.H. Thomas Co.). The pestle was mounted in a variable-speed drill and samples were ground to a fine pulp with the grinding tube held in ice.

Sample-buffer slurries were measured and then centrifuged at top speed in a refrigerated centrifuge

(Beckman Model TJ-6) at $4^{o}C$ for 5 min. One mL of the resulting cell-free extract was incubated with 3 mL of substrate solution (containing NADH, NADPH, Triton X-100, pH = 8.5) and 1 mL 2-(p-iodophenyl)-3-(p-nitrophenyl)-5-phenyl tetrazolium chloride (INT) solution for 20 min (Owens and King 1975). Reactions by adding 1 mL quench solution (50% phosphoric acid, 50% formalin; Owens and King 1975).

INT turns red upon oxidation and is used here as an artificial terminal electron acceptor for the enzyme system. Absorbance at 490 nm was measured with a Dynatech MR600 Microplate Reader and 0.3 mL of samples in a microtiter plate. Two blanks were prepared for each pond's set of samples. One blank was for turbidity, the other for auto-oxidative color development. The color development of INT in this method has been shown to be directly related to the respiration rate of a variety of plankton species. I used the equation of Owens and King (1975) to express respiration rates as ug O_2/mg dry weight/h at in situ temperatures.

I used average zooplankton dry weights from the nutrient regeneration samples for dry weights in respiration rate calculations. Nutrient regeneration and respiration rate samples were subsampled identically from the zooplankton concentrate in the field.

Missing Samples. Some samples were missing for each of the functional measures at several sample dates. For all parameters, preceding and subsequent samples were averaged to represent missing samples in statistical analyses. As explained in Section 5.0, 6 zooplankton samples were accidentally left unpreserved. I used the same rules for productivity estimates as listed in Section 5.0 for estimation of species density and biomass. Respiration and nutrient regeneration samples were not collected on 16 December 1988 (Week 46) due to frozen filtration apparatus. Respiration rate samples for 13 May 1988 were accidentally permitted to thaw and were not analyzed. Again, nutrient regeneration and respiration rate samples were not collected on 10 February 1989 (Week 54) due to frozen filtration apparatus. Statistical analyses of functional parameters did not include that sample date and ended with 27 January 1989 (Week 52).

Statistical analyses were conducted using SAS (SAS Institute 1985).

6.3 RESULTS

Productivity

Zooplankton community productivity (ug dry wt./L/day) varied through time (Figure 6-1), with peaks in community productivity corresponding peak productivity by various species. Zooplankton community productivity peaked almost synchronously for all ponds on three occasions: late May, late June and early September (Figure 6-1). The general productivity peaks in late May and late June were due to the closely-timed *Chaoborus* and copepod populations in the ponds. Closely timed productivity peaks in early September were due to several rotifer taxa, especially *Anuraeopsis*, *Keratella*, and *Polyarthra*. At other times of the year, zooplankton community productivity stayed relatively low all ponds.

Although ponds had similar timing of productivity for several taxa, ponds varied considerably in amplitude of the productivity peaks (Figure 6-1). This variation among ponds is also reflected in total annual zooplankton community production (Table 6-1). Estimated total production ranged from 3825 ug dry weight/L (Pond 6) to 9702 ug dry weight/L (Pond 8). However, analysis of variance (ANOVA) with ponds and time as treatments showed no significant differences among ponds ($p=0.52$). Variations in productivity among ponds at a few points

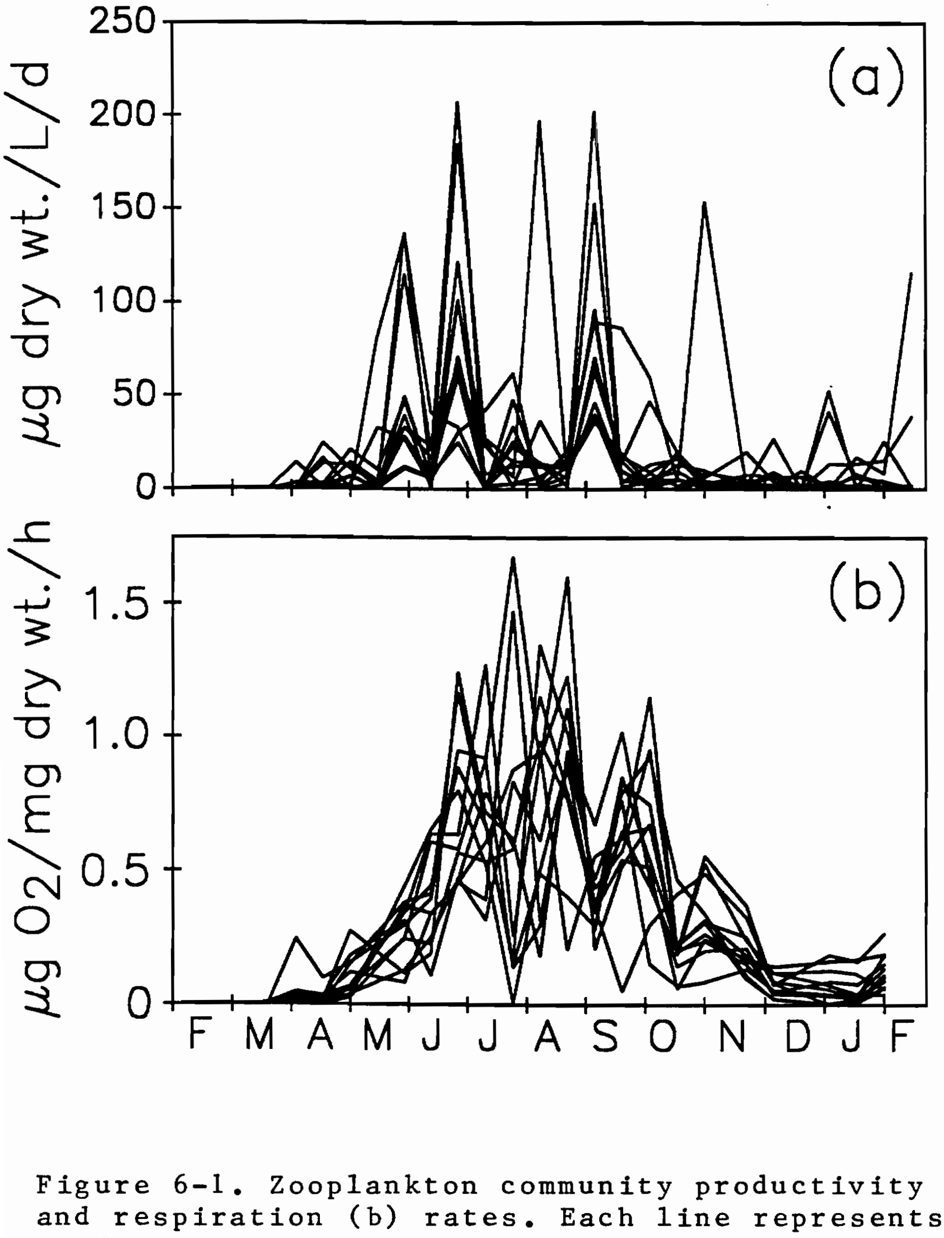


Figure 6-1. Zooplankton community productivity (a) and respiration (b) rates. Each line represents a pond.

Table 6-1. Zooplankton Taxa Annual Production (ug dry weight / L) and Percentage of Total Production (in parentheses).

Pond	Copepoda	Cladocera	Rotifera	*Chaoborus*	Total
1	680 (15.7)	44 (1.0)	1735 (40.1)	1863 (43.1)	4323
2	552 (11.6)	4 (0.1)	2076 (43.7)	2116 (44.6)	4748
3	964 (14.7)	23 (0.4)	1143 (17.4)	4441 (67.6)	6571
4	1548 (19.9)	27 (0.4)	1305 (16.8)	4904 (63.0)	7784
5	225 (2.5)	1488 (16.6)	4217 (47.1)	3014 (33.7)	8943
6	816 (21.3)	22 (0.6)	1274 (33.3)	1713 (44.8)	3825
7	414 (8.3)	176 (3.5)	1070 (21.5)	3306 (66.6)	4966
8	1052 (10.8)	4279 (44.1)	2209 (22.8)	2162 (22.3)	9702
9	1013 (18.6)	828 (15.2)	763 (14.0)	2830 (52.1)	5434
10	800 (11.4)	51 (0.7)	1170 (16.7)	4980 (71.1)	7000
11	1103 (25.4)	658 (15.2)	809 (18.6)	1772 (40.8)	4343
12	735 (13.0)	100 (1.8)	1131 (20.0)	3688 (65.2)	5654
Avg.	825	642	1575	3066	6108
S.D.	334	1181	907	1159	1828

in time were not sufficiently great and/or consistent to produce significant differences among ponds over the entire year.

Relative importance of zooplankton taxa in annual community production varied among ponds (Table 6-1). Of the four taxa listed in Table 6-1, Chaoborus was usually the greatest producer despite its relatively brief period of peak density. Chaoborus larvae attained far greater size and mass than most other zooplankton species, thus producing more biomass at low density than other more numerous species.

Rotifers were also important producers in the experimental ponds (Table 6-1). Annual rotifer production was comparable to or exceeded Chaoborus production in several ponds (e.g., Ponds 1, 2, 5, and 8). Rotifer production exceeded cladoceran production in all but 2 ponds (Ponds 8 and 9) and was greater than copepod production in all but 3 ponds (Ponds 4, 9, and 11).

Copepod production exceeded cladoceran production in all but two ponds (Ponds 5 and 8). Greater cladoceran production in these ponds, especially Pond 8, was due to persistent populations of the relatively large cladoceran, Simocephalus serrulatus, during Autumn

1988 and Winter 1989.

Respiration Rates

Zooplankton community respiration rates roughly followed an annual cycle (Figure 6-1). Respiration rates were adjusted for in situ temperature, so this seasonal effect on community respiration rates was not a direct effect of temperature.

Zooplankton community respiration rates were a function of zooplankton biomass (Table 6-2). Multiple regressions of respiration against taxa biomass were highly significant ($p=0.0001$) and had high r^2's (Table 6-2). Standard partial correlation coefficients (SPC's) indicate the rate of change (in standard deviation units) of community respiration rate per one standard deviation unit of change in a taxon's biomass, with all other taxa biomasses kept constant (Sokal and Rohlf 1981). Comparisons among taxa SPC's show that Copepoda, Chaoborus, and Rotifera biomass were most strongly related to community respiration rates for all ponds. Taxa SPC's were not the same for all ponds, but Copepoda, Chaoborus, and Rotifera were consistently more important to community respiration rates than Cladocera or Ostracoda. This result is consistent in general with zooplankton production results (Table 6-1).

Table 6–2. Standard partial regression coefficients of zooplankton taxa biomass to community respiration, NH3–N, and PO4–P regeneration rates. Multiple regressions were calculated on log–transformed (log10(x+1)) data. * indicates significant regression ($p < 0.05$).

	Taxa Biomass					Regression
Pond	Copepoda	Chaoborus	Rotifera	Cladocera	Ostracoda	R2
Respiration						
1	0.474	0.201	0.467	–0.208	–0.026	0.794 *
2	0.366	0.195	0.518	0.067	0.030	0.75 *
3	0.519	0.338	0.224	–0.059	0.048	0.756 *
4	0.572	0.445	0.246	0.209	0.089	0.776 *
5	0.125	0.378	0.703	–0.036	0.033	0.82 *
6	0.266	0.240	0.516	–0.097	0.078	0.725 *
7	0.422	0.424	0.321	0.301	0.018	0.783 *
8	0.484	0.349	0.373	0.065	0.118	0.784 *
9	0.582	0.131	0.364	0.076	0.141	0.784 *
10	0.522	0.227	0.412	0.075	–0.057	0.839 *
11	0.271	0.501	0.434	–0.126	0.105	0.812 *
12	0.489	0.434	0.090	–0.178	–0.001	0.712 *
NH3 Regeneration						
1	–0.151	–0.183	0.477	–0.052	–0.216	0.14
2	0.625	–0.403	0.406	–0.025	–0.110	0.631 *
3	0.533	–0.119	0.239	–0.094	–0.116	0.453 *
4	0.529	0.177	–0.079	–0.002	–0.036	0.286
5	1.029	–0.278	–0.247	–0.146	–0.029	0.673 *
6	0.358	–0.023	0.222	–0.001	0.094	0.325
7	0.356	0.063	–0.187	–0.348	–0.264	0.285
8	–0.101	0.517	0.012	0.931	–0.715	0.324
9	0.714	–0.196	–0.084	–0.123	–0.140	0.460 *
10	0.446	–0.074	–0.146	–0.172	0.474	0.389
11	0.580	–0.207	0.282	–0.566	–0.136	0.442 *
12	0.498	0.017	–0.098	–0.247	0.016	0.278
PO4 Regeneration						
1	0.421	0.205	–0.280	–0.265	0.042	0.151
2	–0.012	0.328	–0.150	–0.016	–0.054	0.118
3	–0.114	0.538	–0.395	–0.427	0.145	0.199
4	–0.239	–0.248	0.066	0.094	–0.054	0.141
5	0.547	0.253	–0.255	–0.016	0.037	0.357
6	0.181	0.556	–0.207	–0.021	–0.036	0.358
7	–0.263	0.442	–0.295	–0.153	–0.288	0.263
8	0.125	0.596	–0.517	0.194	0.147	0.475 *
9	0.001	0.013	–0.114	–0.205	–0.085	0.095
10	–0.226	0.054	0.006	–0.267	–0.024	0.109
11	–0.017	0.052	–0.036	0.017	1.005	0.988 *
12	–0.332	0.415	–0.196	0.005	0.028	0.183

Zooplankton community respiration rates were significantly different among ponds (ANOVA; p=0.0001). Annual mean respiration rates of ponds were separated into two widely overlapping groups (Tukey's HSD; p=0.05):

```
Pond    9   4   8   1   10   6   5   2   7   3   12   11
        AAAAAAAAAAAAAAAAAAAAAA
            BBBBBBBBBBBBBBBBBBBBBBBBBBBBBBBBBBBBBBBBBBBB
```

Ponds connected with the same letter were not significantly different. However, means separation tests such as Tukey's HSD do not permit this result to be interpreted as indicating Pond 9 was significantly different from Pond 11.

Ammonia Regeneration Rates

Zooplankton community NH_3-N regeneration rates were also variable among ponds (Figure 6-2). However, ponds were not significantly different by ANOVA over the entire year (p=0.168). Variations in NH_3 regeneration rates among ponds were not consistent through time.

Some ponds exhibited synchronous peaks in NH_3-N regeneration rates, but that synchrony appeared to be less uniform among ponds than common peaks in productivity and respiration rates (Figure 6-1). All ponds had low NH_3-N regeneration rates until June 1988, when most ponds exhibited increases in NH_3-N

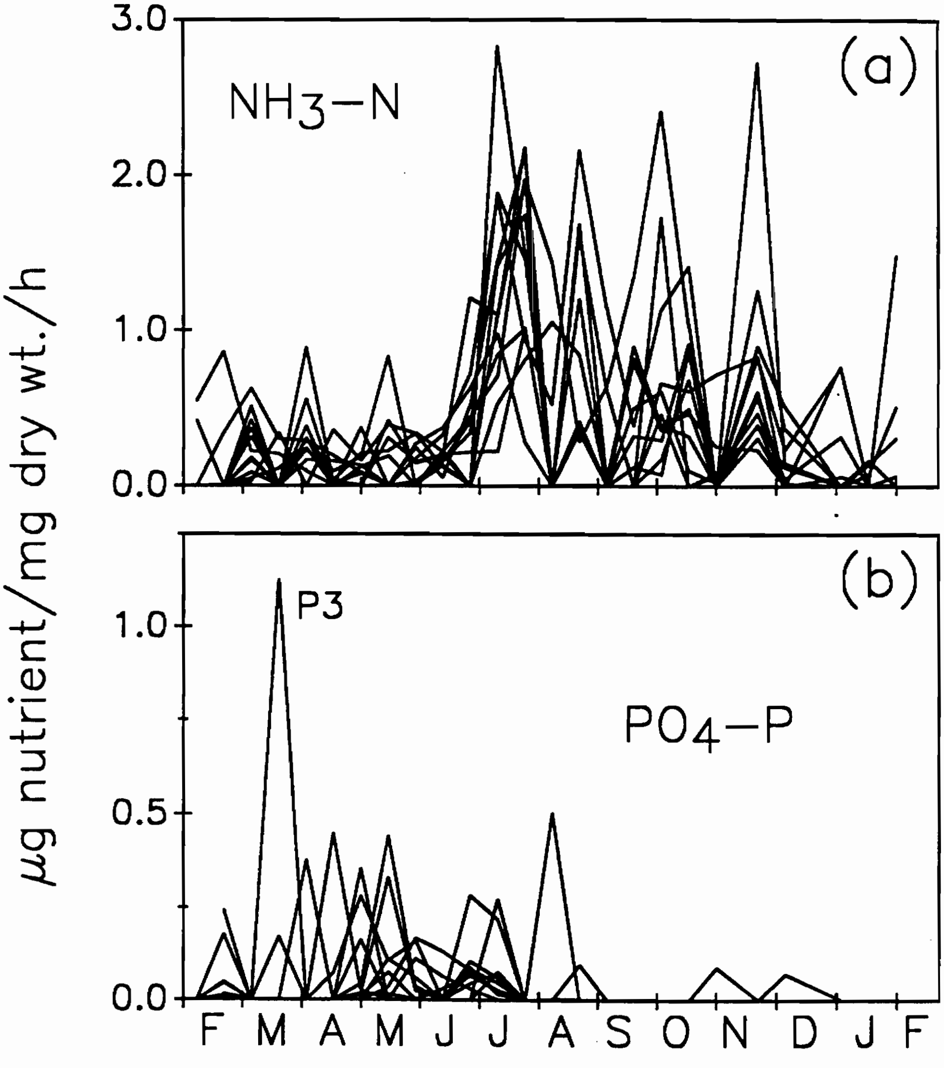


Figure 6-2. Zooplankton community nutrient regeneration rates. (a) ammonia-nitrogen and (b) soluble reactive phosphate.

regeneration. A few ponds shared similar timings during summer and most ponds again exhibited peaks in NH_3-N regeneration rates during November 1988. The June 1988 peaks in NH_3-N regeneration rates coincided with peak copepod densities. Other peaks during Summer and Autumn 1988 coincided with rotifer and/or cladoceran peaks in corresponding ponds. It is likely that peak densities of some organisms contributed to the peak NH_3-N regeneration rates.

Multiple regressions of zooplankton community NH_3-N regeneration rates and taxa biomasses were significant for only 5 of the 12 ponds (Table 6-2). Copepods were the most important taxa in those 5 regressions, based on standard partial correlation coefficients (SPC's) as explained above. No regression was particularly strong (highest $R^2 = 0.673$), and zooplankton taxa biomasses accounted for less variation in NH_3-N regeneration rates than they did for respiration rates.

Phosphate Regeneration Rates

Most detectable PO_4 regeneration rates occurred in the first half of the study year (Figure 6-2). Detectable PO_4 regeneration rates were recorded in only two samples after September 1988. Measured PO_4 regeneration rates generally coincided with ambient PO_4

concentrations, in that ambient soluble reactive phosphate levels also fell below detection limits (0.02 mg/L) after the first few months of the study (Section 3.0). Phosphate levels were low during most of the study and zooplankton regeneration did not produce sufficient quantities during in situ incubations to reach detectable levels. Ponds were not significantly different in PO_4 regeneration rates (ANOVA; p=0.30). Of the four functional variables measured, PO_4 regeneration was the least valuable.

Not surprisingly, multiple regressions of zooplankton biomass against PO_4 regeneration rates were insignificant for 10 of the 12 ponds. Pond 8 had a significant regression and Chaoborus had the greatest SPC in the regression (Table 6-2). Pond 11 also had a significant regression, due to a correlation between ostracod biomass and phosphate concentrations in water samples from Pond 11. This relationship is probably coincidental because ostracods were not also important in multiple regressions of respiration or NH_3 regeneration rates for Pond 11.

Multivariate Analyses

As in previous sections, I used two multivariate analyses to evaluate community function data: principal components analysis and cluster analysis, using the centroid clustering algorithm and Mahalanobis distances, were computed on log-transformed ($\log_{10}(x+1)$) data (SAS Institute 1985, Digby and Kempton 1987). Prior to these analyses, a multivariate analysis of variance (MANOVA) on the function data indicated a significant overall pond effect ($p=0.002$). This significant difference was apparently due to the difference among ponds in respiration data, since no significant differences were detected in other function data.

Figure 6-3 shows the first principal component for each pond plotted through time. The first principal component (PC 1) accounted for 44% of the total variation and was heavily weighted towards productivity, respiration, and NH_3-N regeneration rates (Table 6-3). The second principal component represented an additional 25% of the variance but was almost exclusively weighted by PO_4-P regeneration rates (Table 6-3). I will focus on PC 1 because a plot of PC 2 over time showed essentially the same trends as Figure 6-2b and PO_4-P regeneration rates provided the least information of functional variables measured.

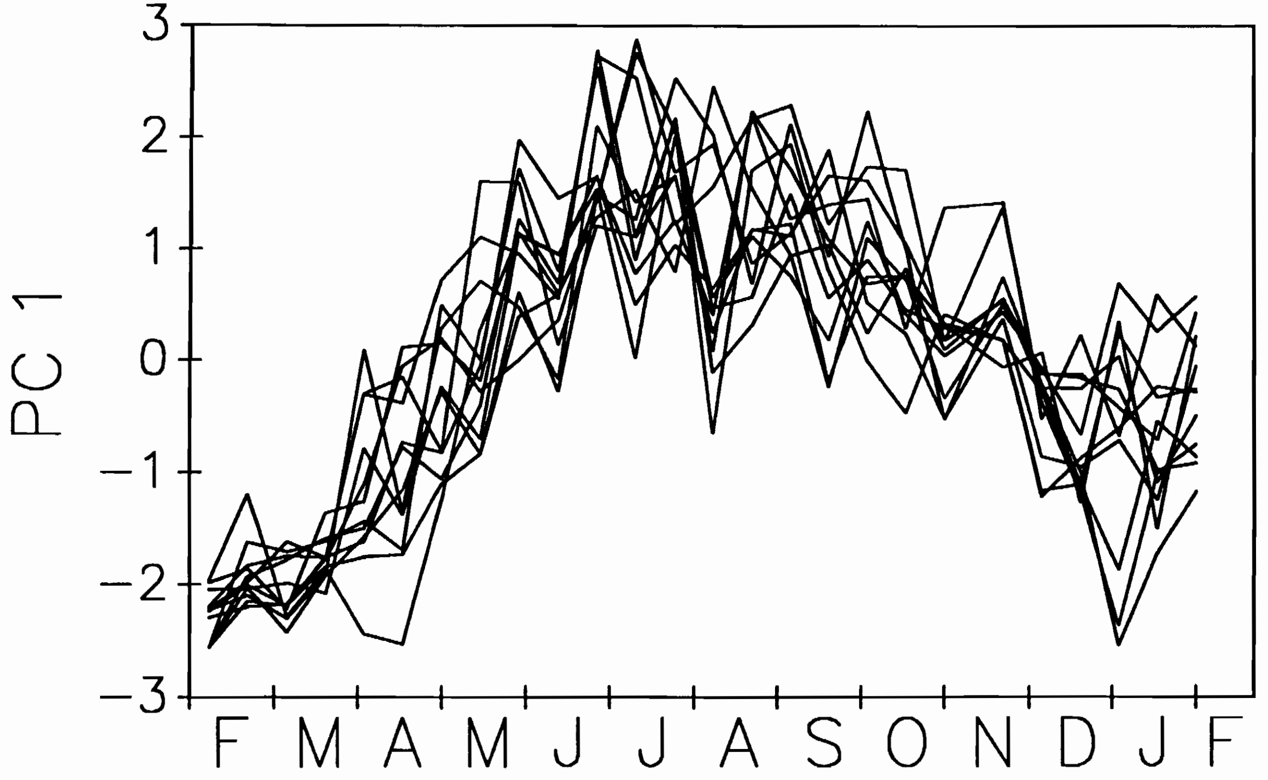


Figure6-3. Principal component analysis of zooplankton community function data. Principal component 1 represented community productivity, respiration, and NH_3 regeneration. See text for description of variable weights and variance accounted for.

Table 6-3. Multivariate Statistics for Zooplankton Community Function.
Log-transformed data (log10(x+1)) were used in analyses.

Correlations

Variables	Productivity	Respiration	NH3-N Regen.	PO4-P Regen.
Productivity	1.000			
Respiration	0.605	1.000		
NH3-N Regen.	0.149	0.353	1.000	
PO4-P Regen.	0.025	0.010	0.004	1.000

Principal Components Analysis

	PC 1	PC 2	PC 3	PC 4
Variables		Eigenvectors		
Productivity	0.6080	0.0271	-0.4823	0.6301
Respiration	0.6706	-0.0225	-0.1132	-0.7328
NH3-N Regen.	0.4240	-0.0732	0.8655	0.2565
PO4-P Regen.	0.0297	0.9967	0.0741	-0.0149
Eigenvalues	1.7725	1.0002	0.8712	0.3562
Proportion (%)	44.32	25.00	21.78	8.90
Cumulative %	44.32	69.32	91.10	100.00

Canonical Discriminant Analysis

Canonical Variable	Canonical Correlation	Eigenvalue	Approx. F	p *
CAN 1	0.2757	0.0823	0.8238	0.7875
CAN 2	0.1394	0.0198	0.4091	0.9981
CAN 3	0.1098	0.0122	0.3546	0.9941
CAN 4	0.0952	0.0092	0.3433	0.9484

* Tests of Ho: canonical correlation on current row and all that follow are zero.

Principal component 1 shows seasonal trends in community function of all ponds over time. It is no great surprise that zooplankton communities had the greatest metabolic activity during warmer months. The most interesting feature of Figure 6-3 is that all ponds followed about the same trajectory through time for PC 1. This result indicates that zooplankton communities in the ponds had similar trends in community respiration, productivity and NH_3-N regeneration rates. Clearly, ponds varied at any given time, but the summary view provided by principal components analysis indicates that the separate zooplankton communities developed similar functional processes and responded similarly to changes in seasons.

It is also interesting to compare PC 1 scores of the ponds at the start of the study to scores at the end of the study. Scores in January 1990 were greater than in February 1989 but also had a wider range (Figure 6-3). Since winter PC 1 scores probably represent a minimum of zooplankton community function for conditions at the time of the study, the shift in winter PC 1 scores may indicate successional development of zooplankton community function. The narrow range of initial PC 1 scores is a reflection of the paucity of zooplankton in all ponds at the start of the study. The range of PC 1 scores at the end of the study is similar to ranges at other times during the study and does not necessarily reflect increasing variation among ponds.

Cluster analyses were based on canonical discriminant analysis, which measured distances between ponds in multivariate space. Canonical discriminant analysis did not detect significant separations among ponds for zooplankton community function data ($p=0.79$; Table 6-3). This result indicates zooplankton communities in the ponds did not differ significantly in function, when considered over the entire year.

Results of the principal component and canonical discriminant analyses contrast with the MANOVA results. MANOVA was apparently more sensitive to the influence of respiration rate differences than the other analyses. As described above, differences among ponds in respiration rates provided no clear distinction between ponds or groups of ponds. This indistinct separation of ponds probably contributed to the similarities of ponds in principal component and canonical discriminant analyses.

Comparison of Structure and Function Variability

As a way to compare variability of structural and functional data among ponds, I listed coefficients of variation (CV's) for log-transformed ($\log_{10}(x+1)$) taxa density and functional parameters in Table 6-4. I also listed taxa density CV's in Section 5.0, where I used an arbitrary criterion of 10% CV as indicating major variation among ponds at any sample date. I use the same criterion here for functional data.

Two functional parameters, productivity and respiration rates, had CV's that were similar to or lower than structural CV's. Respiration rate CV's were especially low relative to other parameters for much of the study; 11 of 26 sample dates (42%) had CV's below 10%. Nutrient regeneration rate CV's were often more variable among ponds than structural parameter CV's and were only rarely similar to respiration rate CV's. The most variable of the functional parameters was PO_4-P regeneration rates. As shown in Table 6-3, PO_4-P regeneration rates did not correlate with other functional parameters and carried little weight in analyses.

Table 6–4. Coefficients of variation (as %) among ponds for zooplankton community structural and functional measures.

	Structure					Function			
Week	Copepoda Densities	Rotifera Densities	Chaoborus Densities	Cladocera Densities	Ostracoda Densities	Productivity	Respiration	NH3–N Regeneration	PO4–P Regeneration
1	248.2	49.4	—	—	—	—	97.4	225.2	—
3	131.2	196.2	—	—	—	149.4	13.4	234.6	161.5
5	150.2	224.7	—	—	—	221.4	61.3	72.4	—
7	99.8	100.7	—	—	—	305.8	19.5	152.4	275.3
9	109.2	110.9	—	—	—	146.1	63.9	72.1	331.7
11	117.1	75.4	95.4	—	—	76.0	46.7	138.9	278.6
13	124.3	49.8	78.4	331.7	—	75.7	16.7	81.0	148.5
15	74.9	56.1	50.1	273.9	—	91.8	6.6	117.6	143.2
17	74.7	39.2	27.5	235.4	—	20.6	9.4	87.7	130.4
19	48.9	28.7	33.4	331.7	—	40.1	8.8	38.7	203.9
21	34.0	32.2	42.7	—	—	14.8	5.4	85.7	97.3
23	20.1	40.8	64.2	—	—	76.3	5.6	38.7	113.9
25	11.8	21.7	56.9	—	—	36.5	23.5	31.1	—
27	21.3	19.6	56.5	283.0	223.6	55.2	9.2	182.5	329.7
29	29.0	15.2	51.2	241.0	177.0	26.0	7.6	73.4	331.7
31	38.1	32.1	98.5	200.3	183.8	12.0	5.0	171.1	—
33	34.2	17.8	53.2	208.3	168.4	57.1	11.6	90.8	—
35	32.7	21.0	50.9	179.6	190.8	56.7	8.4	68.6	—
37	25.4	25.5	70.1	147.2	168.1	41.7	10.8	65.0	—
39	30.6	18.9	87.0	132.7	120.4	69.6	8.4	197.6	331.7
42	48.8	13.6	254.5	111.2	91.5	42.3	7.5	54.1	—
44	50.8	13.9	331.7	100.6	142.3	61.7	14.6	129.0	331.7
46	53.1	13.0	331.7	104.3	173.7	82.7	52.1	173.3	—
48	48.5	21.1	—	75.0	123.3	92.6	24.2	181.9	—
50	72.0	24.2	—	88.1	107.2	67.4	11.5	190.8	—
52	56.1	34.1	—	84.9	102.2	81.7	52.4	210.5	—
54	66.6	45.3	—	71.5	128.8	122.9	—	—	—
Avg.	68.6	49.7	101.9	177.8	150.1	81.7	20.2	117.6	229.2

Coefficients of variation were calculated on log–transformed (log10(x+1)) data.

6.4 DISCUSSION

Zooplankton community function varied through time, but was not clearly different among ponds when considered over the entire study period. This result was partly due to the fact that most ponds exhibited marked changes in any given functional parameter at some point in time and many of the fluctuations through time were at least roughly synchronous among ponds for productivity, respiration and NH_3-N regeneration rates.

Both ANOVA and MANOVA detected significant differences among ponds in annual mean respiration rates, but those differences were due to two largely overlapping groups of ponds with no clear separation of ponds from each other. Likewise, Figure 6-1b shows the overlap of trends in respiration among ponds. This indistinct separation and the absence of differences for other functional parameters apparently contributed to the common trends of ponds in principal component analysis and the inability of canonical discriminant analysis to separate ponds.

The general similarity of zooplankton communities in their functional development supports the RPH-derived prediction of similarity among ponds, but not because the ponds were colonized similarly. I showed in Sections 4.0 and 5.0 that ponds differed in zooplankton colonization and community structure, contrary to predictions based on the RPH. Ponds contained functionally similar zooplankton communities because community function was insensitive to differences in community structure. Functional measurements reduced community structural differences to a common denominator (e.g., ug dry weight/L/d), and the functional redundancy of different species produced generally similar functional rates at the community level. Tables 6-1 and 6-2 indicate that zooplankton taxa varied among ponds in their contributions to community function. The summation of taxa functional contributions tended to minimize taxonomic differences among ponds and yielded greater similarity for zooplankton community function than was observed for community structure.

A number of studies have been conducted in experimental ponds (e.g., Hall et al. 1970, deNoyelles et al. 1982, Giddings et al. 1984, Crossland and Wolff 1985), but most studies focus on structural effects of pesticides. To my knowledge, only Hall et al. (1970) evaluated zooplankton community function (production) in multiple ponds. They estimated zooplankton production in ponds treated with nutrients and fish predation and presented zooplankton production estimates for 3 summers. My annual zooplankton production estimates are similar to those of Hall et al. (1970) in both range and variability. Little else can be compared between their data and mine for the purpose of examining variability among ponds.

Respiration rates were least variable among ponds of the four functional parameters and were significantly related to zooplankton taxa biomass (Table 6-2). In my opinion, respiration rates were the most valuable of the functional parameters measured. Sample collection and processing in the field was straight-forward, calculations include fewer and more substantiated assumptions than productivity estimates, and lab processing of samples took much less time than that required to obtain productivity estimates with preserved samples and a microscope. Based on the high correlations between respiration rates and taxa biomasses, it seems likely that this method would be valuable for use in other experimental pond studies.

Zooplankton community respiration rates in the ponds were generally lower than values obtained in laboratory studies of many of the same taxa (Lampert 1984). Lampert (1984) discusses a variety of exogenous factors that can affect respiration rates, including light, food, and physicochemistry. Because many zooplankters feed most actively at night (Hutchinson 1967) and samples were collected during the day, it is possible that diurnal differences in activity and respiration rates may have reduced <u>in</u> <u>situ</u> respiration rates relative to laboratory values. As Lampert (1984) indicates, potential factors affecting zooplankton respiration rates are not well known.

Nutrient regeneration rate estimates were more variable than productivity and respiration rate estimates. Both NH_3-N and PO_4 regeneration rates were within the ranges of values obtained by Korstad (1983). NH_3-N regeneration rates were generally greater than PO_4-P regeneration rates, again similar to the results of Korstad (1983). It is likely that measurable and reliable nutrient regeneration rates required both a critical mass of zooplankton in the incubated bottles and detectable background nutrient levels. If neither condition was met, as was probably the case for PO_4-P on most sample dates, any nutrient regenerated during incubations would have been too low to detect by my analytical methods. It is possible that other analytical techniques (e.g., organic extraction of PO_4-P, Autoanalyzer) may have yielded better PO_4-P regeneration results.

One more point arises from comparison of my data to other studies. Rotifers are usually considered minor contributors to zooplankton community structure and function in experimental ponds (e.g., Hall et al. 1970, deNoyelles et al. 1982). Results of my study indicate that rotifers were major components of zooplankton community structure (Section 5.0), production, respiration, and possibly nutrient regeneration (Tables 6-1 and 6-2). This discrepancy is probably due to sampling technique. Likens and Gilbert (1970) recommended the use of plankton nets with mesh $\leq$ 35 um for quantitative sampling of rotifers. Use of larger mesh nets has apparently led some researchers to underestimate rotifer populations, thereby underestimating their importance in zooplankton communities (e.g., Hall et al. 1970, deNoyelles et al. 1982). Other investigators have found rotifers to be important in systems ranging from Mirror Lake, New Hampshire (Makarewicz and Likens 1979) to a eutrophic reservoir in Georgia (Pace and Orcutt 1981). I recommend that efforts be made in future experimental pond studies to properly sample zooplankton communities for inclusion of rotifers, given their apparent importance in these zooplankton communities.

7.0 SUMMARY AND CONCLUSIONS

Colonization is usually discussed in terms of testing one of four species-area hypotheses. The Equilibrium Theory of MacArthur and Wilson (1967) has attracted the most research of the four hypotheses, but the Habitat Diversity (Williams 1943) and Intermediate Disturbance (Connell 1978) hypotheses have also been studied in various systems. These three hypotheses are alternate hypotheses to the Random Placement Hypothesis (RPH), generally attributed to Arrhenius (1921) and recently developed further by Coleman (1981). The RPH is the null hypothesis and should be tested prior to invoking other hypotheses (Connor and McCoy 1979, McGuinness 1984).

This dissertation tested four predictions derived from the Random Placement Hypothesis (RPH) with zooplankton communities of twelve new experimental ponds:

1. Ponds of the same dimensions will have similar colonization curves.
2. Observed colonization curves will closely match an expected colonization curve according to Coleman (1981).
3. Zooplankton communities in ponds will develop

similar structure (densities and biomass).

4. Zooplankton communities in ponds will develop similar function (community productivities, respiration and nutrient regeneration rates).

The RPH assumes all other factors are equal among sites (ponds) so that colonization is simply a function of the random placement of individuals. More specifically, Coleman (1981) stated two assumptions of the RPH - that sites (ponds) are environmentally homogeneous and that organisms are not correlated in their locations.

Assumptions

The assumption of environmental homogeneity was evaluated by measuring 11 physicochemical parameters in the ponds during the year-long study (Section 3.0). Some parameters, such as temperature and dissolved oxygen, exhibited little variation among ponds throughout the study. Other parameters, such as Secchi depth and NH_3-N, exhibited greater variation among ponds at any given sample date and showed significant differences among ponds in annual mean values.

When all parameters were considered in multivariate analyses, ponds were found to follow the same general course of seasonal and physicochemical changes. Some ponds differed in physicochemistry at any given sample date, but cluster analyses of seasonal data indicated that differences among ponds were transient from season to season. Although ponds were not absolutely homogeneous in their physicochemistry, ponds exhibited similar trends during the study period and were generally similar when considered for the entire year. In addition, variations among ponds in some physicochemical parameters probably had little influence on zooplankton, given that: a) zooplankton are not known to be limited by physicochemistry in the ranges measured (Hutchinson 1967), and b) herbivorous zooplankton are primarily size-selective grazers, feeding on a variety of phytoplankton species within a given size range (Wetzel 1983). This second point is relevant because those zooplankton are less sensitive to direct interactions between physicochemistry and phytoplankton species.

I evaluated the second assumption (no correlations among organisms' locations) by inspecting the matrix of partial correlation coefficients among species for presence/absence data (Section 4.0). Partial correlation coefficients measured the correlation between two species' presence or absence with the effects of all other species held constant. Of all the correlations among all possible pairs of species, only

8.7% were significant. I concluded from this result that correlations among species' locations was not an important factor in placement of species in the ponds.

Colonization Curves

Zooplankton colonization curves for the twelve ponds varied among ponds (Section 4.0). Colonization curves could not be statistically compared by analysis of covariance (ANACOVA) or dummy-variable regression analysis (DVRA) because of variability among curves and through time. Both ANACOVA and DVRA required that all ponds fit a curve, whether it be linear (ANACOVA) or curvilinear (DVRA), and no function could be fit to all twelve ponds for analysis. This inability to perform regression analyses of colonization curves is itself evidence of the differences among those colonization curves.

I analyzed species accrual curves as an alternative to colonization curves for the zooplankton communities (Section 4.0). Species accrual curves are cumulative records of the number of species that have been observed in ponds, ignoring the possibility of a species' extinction in a pond. Species accrual curves were sigmoidal and were fitted to the discrete logistic equation and analyzed by DVRA. Ponds had different rates and asymptotes of species accrual during the study period. The sigmoidal shape of accrual curves appeared to be due to greater immigration rates during summer months.

Both of the above analyses indicated that the first prediction (similar colonization curves) was not supported for zooplankton communities in the experimental ponds. To test the second prediction of observed and expected colonization curves, I applied the equations of Coleman (1981) to the data for the ponds, as described in Section 4.0.

The observed colonization curves for zooplankton communities of the ponds did not closely fit the expected curve (Section 4.0). Expected and observed species numbers were similar early in the study, when species numbers were low, but observed values did not attain expected values during summer months. Expected and observed species numbers became more similar again during the following autumn and winter. My analyses indicated that two factors contributed to the discrepancy between observed and expected species numbers during summer months. First, the number of species present over all ponds (S in the equations of Section 4.0) was greatest in summer months and elevated the expected species numbers. However, most of these species were not uniformly dispersed among ponds and did not contribute to a corresponding increase in observed species numbers. Secondly, some of the under-dispersed species attained sufficiently high densities to make a major contribution to expected species numbers (Section 4.0). The non-random distributions of some species contributed to the difference between expected and observed colonization curves.

If species did not colonize the ponds randomly and the RPH did not adequately predict colonization trends, were alternate hypotheses more appropriate? My study did not test other hypotheses, but results indicate that alternate hypotheses did not apply (Section 4.0). Colonization and immigration curves did not fit the predictions of Equilibrium Theory. Ponds were generally similar in physicochemical conditions and did not display Habitat Heterogeneity. Finally, any Disturbance (by storms, etc.) appeared to apply equally to all ponds. None of the alternate species-area hypotheses seemed appropriate.

The question of why ponds were different remains unanswered since the above hypotheses did not seem to apply. A possible answer is an approach recently coined "supply-side ecology" (Lewin 1986, Roughgarden et al. 1987, Ricklefs 1987). This perspective seeks to include the regional processes of organism dispersal in explanations of patterns in local community structure. In the same way that patterns in rocky intertidal communities are related to the availability of planktonic larvae (Roughgarden et al. 1987), the patterns in zooplankton communities among ponds may have been closely related to the availability of propagules (resting eggs, cysts, etc.). Some zooplankton species were uniformly present in all ponds (e.g., copepods) and were probably in all ponds as a result of high invasion intensities. Many other species (e.g., some cladocerans and rotifers) colonized only a few ponds and probably had relatively low invasion intensities. Limited dispersal of many zooplankton species probably contributed to differences among colonization curves of ponds and to the discrepancy between expected and observed species numbers.

Zooplankton Community Structure

The third prediction was that zooplankton communities in the ponds would develop similar structure (densities and biomass). In light of the differences in colonization discussed above, it is no great surprise that zooplankton communities also differed in densities and biomass (Section 5.0). Taxa that were well-dispersed, such as Copepoda and <u>Chaoborus</u>, exhibited similar timings among ponds in their population peaks, although amplitudes of peaks varied among ponds. Poorly-dispersed taxa (e.g., some Rotifera and Cladocera) exhibited wider variation among ponds in both timings and amplitudes of population peaks. Biomass trends were similar to trends in densities.

Multivariate analyses of species data indicated significant differences among ponds but patterns were not well summarized by principal components analysis. I pooled species data into five taxa - Rotifera, Cladocera, Copepoda, <u>Chaoborus</u> and Ostracoda (Section 5.0). Multivariate analyses of taxa densities and biomasses over the entire year indicated that Ponds 8 and 9 were most different from other ponds in community structure. Other ponds were grouped together in different patterns, depending on whether densities or biomasses were used.

Again, limited dispersal and incomplete colonization of ponds by some species contributed to differences in zooplankton community structure. Some under-dispersed species attained important roles in the zooplankton as measured by either densities or biomass.

Because these species did not colonize and develop similar populations in all ponds, zooplankton communities did not develop similarly in densities or biomass.

Zooplankton Community Function

The fourth prediction was that zooplankton community function would also be similar. Given the dissimilarities in colonization dynamics and community structure, it seemed doubtful that community function would be similar among ponds. However, the link between structure and function in ecological communities is not so predictable, in part due to functional redundancy of species in community energetics and nutrient cycling (O'Neill et al. 1986).

Of the four functional parameters (productivity, respiration, and NH_3-N and PO_4-P regeneration rates), only mean annual respiration rates were significantly different among ponds by ANOVA (Section 6.0). However, significant differences were between two broadly overlapping groups of ponds, with no clear separation of ponds from each other. Significant differences were also detected by MANOVA, apparently due to the influence of respiration rate differences on the multivariate data set. It is interesting to note that respiration rates generally had the lowest coefficients of variation among ponds of all functional parameters throughout the year. Significant differences among ponds occurred due to higher or lower values for some ponds within that relatively narrow range of variation.

Multivariate analyses indicated similar trends in zooplankton community function over the year-long study (Section 6.0). The significant separation of ponds in annual mean respiration rates was not sufficiently strong to permit clear separation of ponds using all variables collectively.

Based on these results, I concluded that zooplankton community function was generally similar among ponds when viewed over the entire year. As was true for physicochemical data, ponds varied at any given point in time, but overall they followed the same general trajectory in zooplankton community function.

This functional similarity was obviously not due to similar colonization dynamics or community structure, but in spite of differences in those measures. This conclusion supports the fourth prediction, but for different reasons than originally proposed. Zooplankton communities had similar functional processes because the community-level measurements were insensitive to variations at the population level. Community-level measures integrated structural variations, and functional redundancy of species contributed to similarities in function despite differences in structure.

Conclusions

1. The two explicit assumptions of the Random Placement Hypothesis were generally valid when considered over the entire year.

2. Ponds differed in zooplankton colonization and species acccrual curves, and the observed colonization curves did not closely correspond to an expected curve generated according to the Random Placement Hypothesis (Coleman 1981). Observed species numbers did not attain expected levels during summer months due to the combined effects of (a) poorly-dispersed species on overall species number and (b) moderate-to-high densities of some poorly-dispersed species in some ponds.

3. Although not tested in this study, other species-area hypotheses (Equilibrium Theory, Habitat Heterogeneity and Disturbance) did not seem to apply to the zooplankton communities of the experimental ponds. A possible reason for different colonization dynamics

among ponds is limited dispersal abilities of some zooplankton species.

4. Zooplankton community structure varied among ponds. Differences among ponds in structural measures (densities and biomasses) were partially related to differences in colonization, in that taxa densities were dependent on species within a taxon (e.g., Cladocera) being present.

5. Zooplankton community function was generally similar among ponds when considered over the entire study period. This was in spite of differences in colonization dynamics and community structure and was apparently due to functional redundancy of species and less sensitivity to population-level differences at the community-level of organization.

8.0 EPILOGUE

Results and conclusions of this study have implications for ecological risk assessment of pesticides in experimental ponds. As outlined in the Epilogue (Section 1.0), experimental pond studies are the ultimate test in the U.S. Environmental Protection Agency's (EPA's) series of studies required prior to registration of a pesticide. Experimental pond studies are conducted according to EPA guidelines (Touart 1988), and usually include replicated treatments at several levels. My discussion of implications for pesticide testing in ponds is based on the EPA guidelines (Touart 1988).

The first implication is that replicability of zooplankton community structure among naturally colonized ponds may be difficult to achieve without careful management. The experimental ponds of this study were not managed for replicability and zooplankton communities were allowed to develop independently. Replicability may be enhanced if water and sediments are circulated among ponds during pre-treatment periods. It is possible that draining ponds and refilling them from a common source will not have a lasting effect. Many zooplankton species produce resting eggs that reside in sediments until they hatch. Replacement of water in ponds will not replace these "seed banks" of zooplankters. Replicability of experimental ponds should not be assumed because ponds were untreated for a period of time. Experimental ponds will require careful monitoring and management to attain some degree of similarity prior to treatments. Research should be funded and conducted to determine management techniques that will bring about greatest similarity among experimental ponds.

Results of my study also imply that pond experiments should not be conducted for a short time period (e.g., $\leq$ six months). Zooplankton populations undergo marked changes over relatively brief periods and many species are seasonal. In addition, some populations considered important in the ecological risk assessment (e.g., cladocerans) were not synchronous among ponds. A pesticide test conducted for one month may be dependent on the species present in some ponds at that time. A longer study period (e.g., one year) may mitigate the dependence on seasonal species for interpretation of ecological effects of a pesticide.

It appears that more than a year is required for natural colonization of all twelve experimental ponds by many zooplankton species. This implies that pesticide tests should not be conducted within the first year of existence of naturally-colonized experimental ponds. Uneven colonization of ponds during a pesticide test could confuse results and lead to erroneous conclusions on ecological effects of pesticides. In addition, pesticide tests are intended to be conducted in ponds containing "representative" fauna. Zooplankton communities in the experimental ponds were not yet representative of the region because colonization was ongoing and an important factor in zooplankton community structure.

Finally, my study included structural and functional measures of zooplankton communities, whereas EPA guidelines for pond pesticide studies require measurements of dominant zooplankton species densities. My comparison of structural (densities) and functional measures (Table 6-4) indicated that zooplankton community respiration rates were usually less variable among ponds than taxa densities and other functional measures. Productivity estimates exhibited about the same variability among ponds as structural measures. Nutrient regeneration rates were as variable (or more so) among ponds, partially due to analytical restrictions on detectable nutrient levels. In the search for a most replicable and analytically reliable measure of zooplankton communities, respiration rates appear to be a strong candidate.

Zooplankton community respiration rates were valuable for another reason. Productivity estimates were taxonomically-based, and reflected community-level function only to the extent that summation of selected populations represents a community. Respiration rates, on the other hand, measured a physiological process common to all organisms in the zooplankton communities and were a more accurate measure of community-level function. If ecological effects of pesticides are to be evaluated in experimental ponds, parameters must be included that reflect changes above the population level of hierarchy. Community- or ecosystem-level effects of pesticides may best be measured by non-taxonomic methods. Zooplankton community respiration rates are one such measure.

9.0 LITERATURE CITED

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APPENDIX

All data collected in this dissertation are available on 5-1/4" diskettes (DS/DD). Data are stored as Lotus 1-2-3 .wk1 files, but can be obtained in ASCII format if requested. Data are organized as follows:

Disk 1: Physicochemical data.
Disk 2: Precipitation and air temperature data.
Disk 3: Net zooplankton density data I. Feb 1988 through Jul 1988.
Disk 4: Net zooplankton density data II. Aug 1988 through Feb 1989.
Disk 5: Rotifer density data.
Disk 6: Zooplankton productivity data.
Disk 7: Zooplankton respiration data.
Disk 8: Zooplankton ammonia regeneration data.
Disk 9: Zooplankton phosphate regeneration data.

Disks contain data for the entire study period (5 Feb 1988 thru 10 Feb 1989) unless stated otherwise. Data on the above disks are summary data. Raw data (e.g., individual zooplankton measurements) may also be obtained from David Jenkins on request.

Disks 1-9 may be obtained by sending an equivalent number of blank, formatted (DOS 2.1 or greater) disks, to:

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- Littoral-limnetic carbon and nutrient interactions
- Ecotoxicology

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