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RELATIONSHIPS BETWEEN PRODUCTION AND ABUNDANCE OF RANID (*Rana pipiens*,
R. catesbeiana, and *R. clamitans*) TADPOLES AND THE EFFECTS OF TADPOLE
GRAZING ON ALGAL PRODUCTIVITY AND DIVERSITY AND ON PHOSPHORUS, NITROGEN,
AND ORGANIC CARBON

By

Diana L. Weigmann

A DISSERTATION

Submitted to
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Department of Fisheries and Wildlife

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ABSTRACT

RELATIONSHIPS BETWEEN PRODUCTION AND ABUNDANCE OF RANID (*Rana pipiens*, *R. catesbeiana*, and *R. clamitans*) TADPOLES AND THE EFFECTS OF TADPOLE GRAZING ON ALGAL PRODUCTIVITY AND DIVERSITY AND ON PHOSPHORUS, NITROGEN, AND ORGANIC CARBON

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The influence of stocking different densities and biomasses of tadpoles on their subsequent survival, growth, and production was assessed by culturing leopard frog (*R. pipiens*), bullfrog (*R. catesbeiana*), and green frog (*R. clamitans*) tadpoles at eutrophic Lake One and mesotrophic Lake Four of the Water Quality Management Project, Michigan State University and by rearing leopard frog tadpoles in the laboratory. In the laboratory, stocking density had no significant effects on individual growth rates of *R. pipiens*, which were stocked at five different densities but similar total biomasses. Survival and growth of all species were consistently higher in the more productive waters of Lake One. Stocking biomass was inversely related to daily production of monocultured *R. pipiens* at both lakes ($r = -0.91$ and $r = -0.85$ at Lakes One and Four, respectively). Monocultured tadpoles of bullfrogs exhibited higher productivity than those of green frogs; however, in mixed culture the production of *R. catesbeiana* was invariably lower than that of *R. clamitans*. Tadpole production was related to the supply of

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food/demand by tadpoles ($r = 0.93$) in laboratory and field experiments. Ecological, growth, and assimilation efficiencies were calculated for tadpoles and compared with efficiencies of other aquatic consumers.

The effects of tadpole grazing on nutrient cycling (phosphorus, nitrogen, and carbon) and on phytoplanktonic and periphytic algal communities (abundance, productivity, and diversity) were influenced by the trophic status of the lakes and the biomass of tadpoles stocked. All species of ranid tadpoles consumed periphyton primarily, as much as 87% of the periphytic carbon was daily diverted by tadpoles into respiration and tissue production or the accumulation of sestonic carbon. Grazing by tadpoles lowered the C-N ratio of the periphytic standing crop, elevated phytoplanktonic numbers and volumes, and altered the diversity of the phytoplanktonic assemblage. The feasibility of culturing ranid tadpoles and their potential impacts on nutrients and biotic communities in artificial environments and littoral zones of natural waters were evaluated.

ACKNOWLEDGEMENTS

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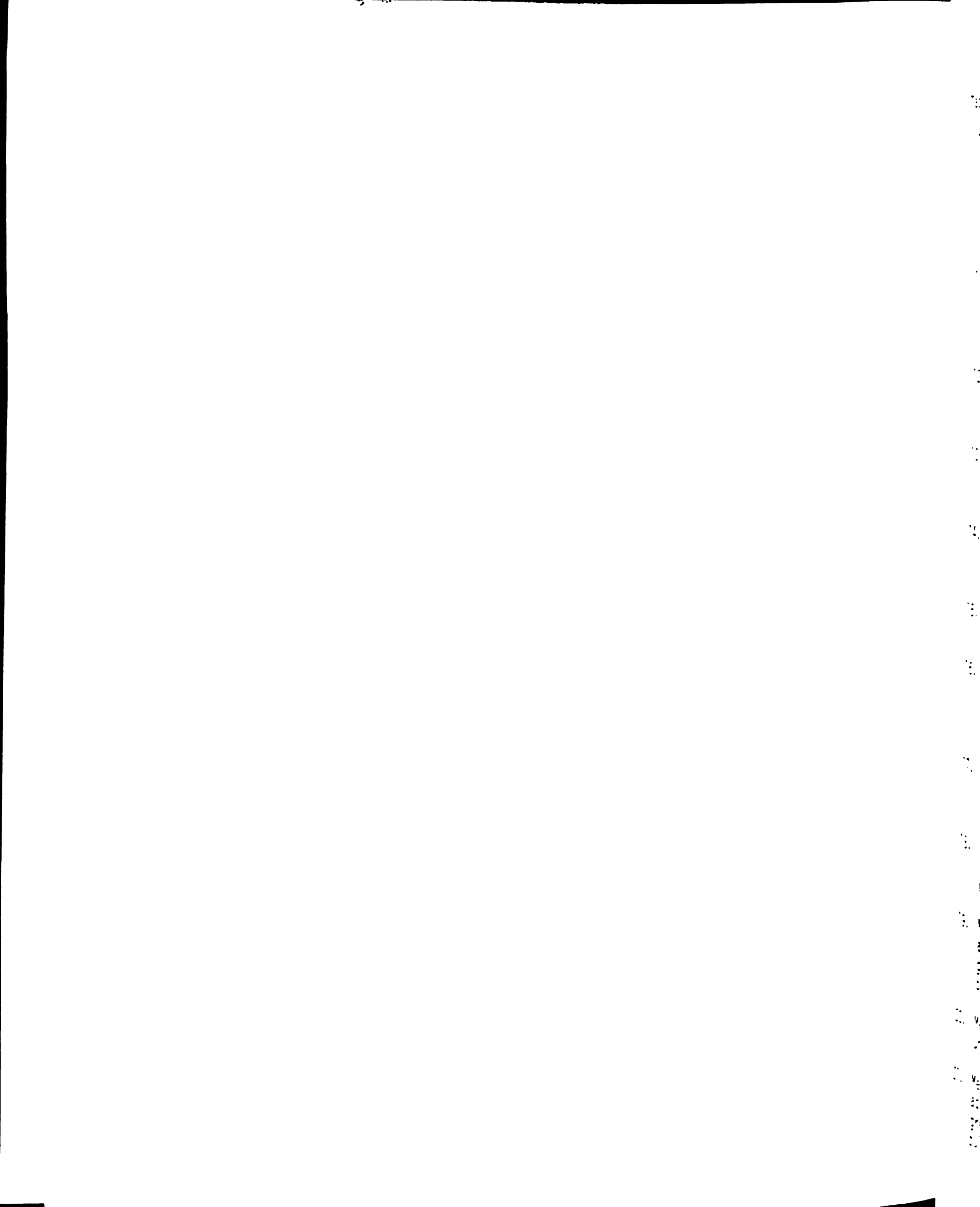


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INTRODUCTION

Laboratory and field experiments were designed to evaluate the potential role of ranid larvae in the biogeochemical dynamics of carbon, nitrogen, and phosphorus and the regulation of algal productivity. Field experiments with Rana pipiens, R. catesbeiana, and R. clamitans were conducted in water from two artificial lakes (part of the Water Quality Management Project, Michigan State University, East Lansing, Michigan) with different trophic characteristics. The relationships between density and biomass of tadpoles, their survival and growth, and production of the phytoplanktonic and periphytic communities were analyzed. In addition to density experiments designed to assess possible intraspecific interactions, evidence of interspecific interactions was examined between R. catesbeiana and R. clamitans. One aspect of this research concerned the affect of tadpoles (density, biomass, and species) on phytoplanktonic numbers and volumes, generic composition, and diversity (Shannon-Wiener). The results from this study provide information on the ecology of ranid tadpoles in natural systems and on the suitability of culturing these larvae in wastewater treatment systems.

Many of the problems associated with cultural eutrophication of aquatic systems concern changes in the pathways by which aquatic populations obtain energy and materials. Trophic pathways may be influenced by nutrient additions, temperature and oxygen changes, influxes of

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toxic substances, or other perturbations. The introduction of energy-rich materials may lead to major alterations in community structure and composition, which result in decreased or increased production of desirable animal protein or shifts to economically less important species. Therefore, one aspect of evaluating the effects of cultural eutrophication is to monitor the production of target populations in relation to the energy and material resources of the aquatic environment.

Studies of nutrient cycling, energy transfer, and species composition of communities in naturally occurring eutrophic waters provide information relevant for managing artificially-created ones, like wastewater treatment systems or aquacultural facilities. Such data may facilitate prevention of habitat degradation in natural systems and conversion of excess nutrients into useful production. Nutrient enrichment of natural systems does not necessarily result in habitat degradation and species depletion, if the systems can assimilate the nutrient influx. However, with continued high input of nutrients to aquatic systems, materials must be harvested and removed to maintain the system at the desired level of productivity. Otherwise, energy-rich substances accumulate in the sediments, unavailable for recycling to terrestrial systems and use by humans.

Most research on recycling materials has focused on wastewater fertilization of terrestrial crops or on growing vascular hydrophytes in wastewater. These hydrophytes are later harvested and fed to domestic animals to convert plant protein into animal protein for human consumption. Increases in the costs of fuel, harvesting, and transportation have made these approaches less attractive. An alternate

strategy of harvesting aquatic herbivores that graze the plants has been less comprehensively evaluated. Few aquatic herbivores in the temperate zone can be economically cultured and harvested for nutrient removal and animal protein. Common plant consumers, like zooplankton, are difficult to manage for high population abundances since they are influenced by biotic and abiotic controls. Oligochaetes, insects, molluscs, large crustaceans and certain herbivorous fish may be cultured and harvested more economically. Although certain species of these taxa may provide a form of protein attractive to the human market, most are specifically adapted to feed efficiently only on a fraction of the plant production. A desirable consumer for aquaculture in a wastewater treatment system should efficiently ingest and assimilate phytoplankton, periphyton, detritus, bacteria, and small animals; be relatively unaffected by density-dependent limiting factors; be able to survive in systems that are stressful, both chemically and physically; and be easily harvested by size-selective methods that maintain optimized size distributions in the cultured population. Anuran larvae or tadpoles possess characteristics that could allow them to function usefully in aquacultural or wastewater treatment systems.

In the north temperate zone, tadpoles of the genus Rana grow large and their complete development may take several years. Ranid tadpoles typically inhabit shallow, protected waters, like ponds or embayments of large lakes. Certain species, such as R. catesbeiana occur mainly in permanent waters, while others, like R. sylvatica or R. areolata are usually found in ephemeral waters. Many of the aquatic habitats occupied by tadpoles are eutrophic with abundant growths of algae or vascular hydrophytes. After analyzing the larvae of several

different anuran families, Wassersug (1975) proposed that tadpoles are generally adapted to exploit bursts of primary productivity in ephemeral ponds, where both the tadpoles and their food resources are temporary. These environments could be considered stressful because of fluctuating water levels, oxygen, temperature, and other chemical and physical factors. Heyer (1976) stressed that tadpoles are generally adapted to variable and unpredictable environments. Ranid tadpoles tolerate environmental fluctuations, but infrequently occur in turbulent waters or at depths of over a few meters, since they are not strong swimmers.

In several comparative morphological studies, the anatomy of feeding structures and mechanisms in Rana tadpoles were examined and shown to be similar (Savage 1952, deJongh 1968, Kenny 1969, Gradwell 1970, 1972a, b, Wassersug 1973). Kenny (1969) suggested four separate mechanisms are employed during feeding by tadpoles: a buccal rasp, a pharyngeal pump that drives the respiratory stream, gill filtration which removes food particles from the respiratory stream, and a mucus entanglement and transport mechanism that carries particles to the esophagus. Ranid tadpoles appear to be generalized, benthic feeders with buccal pumps designed for generating large suction at the oral orifice and small buccal displacement (Wassersug and Hoff 1979, Wassersug and Rosenberg 1979). These larvae are mainly adapted to graze substrates, but may filter seston from the water when densities of particulates are especially high. Tadpoles maintain an optimal density of particulates at gill filters by varying buccal pumping rates (Wassersug 1972) or buccal volumes (Seale and Wassersug 1979). Suspension feeding potential decreases as tadpoles develop because of larval growth patterns (Wassersug 1975). Although large tadpoles filter

greater volumes of water per unit time than small tadpoles, the small tadpoles filter more efficiently per unit of biomass. The feeding efficiency decreases as tadpoles grow, because growth is not allometric for filtering surfaces.

Ranid tadpoles have been described as non-selective, continuous feeders, since food is "involuntarily" extracted from water in the respiratory stream (Savage 1951, 1952, Jenssen 1967). The larvae are considered omnivorous, feeding mainly on living and dead plant material. Analyses of their intestinal contents have indicated that they also consume protozoa, small crustaceans, dead animal material, bacteria or other small particles less than one mm in diameter, as well as inorganic debris, like sand and clay. Farlowe (1928) found the algal species in the water and in the intestines of R. catesbeiana and R. clamitans to be qualitatively similar, 89.7% of the algal species identified from the pond were sampled in the tadpoles' guts. In another study, R. clamitans fed on diatoms, other algae, and minute quantities of small animals (Pope 1947). After examining food resources in pond habitats, Jenssen (1967) concluded that larvae of R. clamitans were fortuitous and indiscriminate feeders with no apparent food preferences. Algae were most prevalent in their intestines, especially diatoms, which were ingested in proportions similar to their availability in the ponds. However, entomostracans, decomposed higher plants, fungi, small microcrustaceans, unidentifiable debris, and sand were also consumed. Diatoms and green algae were important components in the diets of R. aurora and R. pretiosa (Licht 1974), while benthic algae and sediments were consumed by R. aurora from another locality (Calef 1973). Vegetable matter, algae and aquatic macrophytes, and animal

matter were necessary dietary items for R. tigrina (McCann 1933). Larvae of R. afghana, adapted to live in lotic environments, grazed the aufwuchs attached to rocks (Hora 1935). Kenny (1969) observed that R. temporaria used a buccal rasp to scrape material from substrates and generate suspensions of particulate material for filtration. He suggested this species was confined to habitats where the rasp operated effectively. Savage (1952, 1962) noted that R. temporaria fed mainly on algae, although protozoa were common in their intestines and small crustaceans were engulfed with debris. Higher plants were proposed to be useless as a food source, since R. temporaria exhibited little growth on macrophytes. Nathan and James (1972) found higher plants to provide a poor food resource for tadpoles and suggested that they fed on the microorganisms associated with the plants.

Some early investigators stated that tadpoles could derive nourishment from dissolved organic compounds (Krizenecky 1924, Podhradsky 1927, Gudvenatsch and Hoffman 1931, Krough 1931, Kratochwill 1933) and R. pretiosa have been reared to metamorphosis solely on a diet of bacteria (Burke 1933). Wassersug (1972) demonstrated that tadpoles of R. pipiens could potentially filter bacteria from the water, based on their ability to extract latex particles about $0.6\ \mu$ in diameter from suspensions. The clearance rates and buccal pumping activities intensified at 10^5 - 10^6 cells per cc, the upper range of ultraplanktonic densities in a naturally occurring eutrophic pond (Straskrabova and Legner 1969). Yeast cells (2 - $5\ \mu$) and carmine particles (0.5 - $5\ \mu$) were entangled in the mucus cords and concentrated in the respiratory stream of R. temporaria, indicating these tadpoles, which employ a buccal rasp, can ingest bacteria-size particles suspended in the water column.

Tadpoles reared in the laboratory ingest their feces and probably also do so in nature. Coprophagy enhanced the growth rates of R. pipiens, R. catesbeiana, and R. utricularia (Gromko et al. 1973, Steinwascher 1978a, b), but had no effect on the growth of R. clamitans (Steinwascher 1979a, b). Feces alone facilitated growth, while feces with bacteria caused additional growth in R. catesbeiana and R. utricularia (Steinwascher 1978a, b).

Certain ranid tadpoles may be predaceous, attacking other tadpoles and mosquito larvae (Smith 1916, Bhattacharya 1936). Heusser (1970, 1971a, b) noted intra- and interspecific predation of frog spawn by tadpoles. In a pond in Missouri, R. pipiens tadpoles which overwintered consumed egg clutches of R. pipiens that were deposited the following spring (Seale 1973).

All digestion and assimilation of ingested material occurs in the intestine, since the buccopharynx or "stomach" of tadpoles serves no digestive or storage function (Barrington 1946, Dodd 1950, Griffiths 1961, Ueck 1967). Tadpoles lack cellulase and seemingly whole algal cells are commonly found in the hind gut and feces (Li and Lin 1936, Costa and Balasubramanian 1965, Heyer 1973). Savage (1952) suggested algal cells are ruptured by labial teeth, osmotic swelling, or peristaltic action during digestion. Later authors proposed that the keratinized mouth parts generate the initial suspensions, but probably do not rupture cellulose walls of plants. The intestinal tract is poorly supplied with muscles, so peristalsis could be ruled out as contributing significantly to digestion (Wassersug 1975). Wassersug (1975) suggested that algal cells do not need to be ruptured, since the contents of the cells are extracted chemically. The great surface

area of their coiled gut assures that ingested material is in close contact with the gut lining for absorption.

Francis (1961) reported amylases from the pharynx of tadpoles. Although amylases do not function at this site, they are mixed with mucus and food particles so reactions proceed as soon as material enters the gut. Amylase, lipase, and pepsin activity have been demonstrated in the intestine of tadpoles (Barrington 1946, Ueck 1967, Altig et al. 1975). Altig et al. (1975) concluded that the presence of all these enzymes in ranid tadpoles substantiated their omnivory. Funkhouser (1976) found the ratio of pancreas weight to body weight decreased during the development of R. catesbeiana. She suggested tadpoles of this population were so strongly herbivorous that they would starve in the presence of raw or cooked meat or fish food. They would also not consume their own dead.

The length of the intestine in tadpoles is influenced by the types of foods consumed during larval development. Janes (1939) examined the effects of diet on the small intestine of R. sylvatica and found that tadpoles fed lettuce had the longest intestine and those fed liver had the shortest intestine. Tadpoles of R. sylvatica which consumed natural foods in ponds had guts of intermediate length. Tadpoles fed only lettuce during their development exhibited gross physical deformities. At metamorphosis, the lengths of the intestine were similar among all froglets, regardless of larval diet. Altig and Kelly (1974) used gut characteristics as indices of feeding types in anuran larvae. Ranid tadpoles had a high ratio of gut length to body length and the highest ratio of gut area to body length of any tadpoles examined, indicating that ranids consumed mainly plant

material. These tadpoles had a low ratio of inorganic material per unit weight of gut volume, although ranid tadpoles are characterized as bottom feeders.

Various investigators have measured the time required by tadpoles to evacuate their guts of food material and found gut clearance times to be rapid, compared to other animals (Savage 1952, Costa and Balasubramian 1965, Ueck 1967). Although data on the efficiency of digestion and assimilation by tadpoles on natural foods is limited, tadpoles are considered inefficient, based on the rapid rate at which food passes through their intestines, in combination with their lack of oral grinding structures and the enzyme, cellulase. Wassersug (1973) found the gut clearance times in ranids to vary with the developmental stage and food availability. At low food concentrations, gut clearance takes longer, indicating greater digestive and assimilative efficiency. Short gut clearance times were recorded for R. catesbeiana and R. heckscheri tadpoles fed fish meal (Altig and Kelly 1974, Altig and McDearman 1975). Gut clearance and digestive efficiency varied with temperature in R. catesbeiana; at 30 C, these tadpoles can clear their guts in about 30 minutes with an assimilation efficiency of 24.9%. At 22 C, their digestive efficiency was 7.8% and gut evacuation was faster than at 30 C. The 10 C rise in temperature increased the per cent assimilation by 3.2X, but decreased the gut clearance time by 2.5X. Efficiencies were higher for R. heckscheri; tadpoles of this species had an assimilation efficiency of 54% at 22 C. There was no apparent relationship between gut clearance times and per cent assimilation with gut length or body size.

Nagai, Nagai, and Nishikawa (1971) reared tadpoles on diets of artificial feed, tadpoles, fish meal, maize powder, an amino acid mixture, and no food. The conversion rates by tadpoles on all amino acids in the different diets were compared. Assimilation efficiencies of tadpoles were about 23% for lipids and 12-17% for proteins on diets of artificial feed and fish meal. The group that was fed other tadpoles had lower growth rates, but assimilation efficiencies were about 78% for lipids and 85% for proteins. Seale (1973) fed tadpoles a mixture of algae, predominantly Anabaena, and noted only 8% of the total nitrogen that was consumed by R. pipiens was released as ammonia, indicating complete metabolism of proteins.

Little is known about the assimilation efficiency of tadpoles on natural food sources like phytoplankton, periphyton or seston. Their rapid processing of food resources indicates that tadpoles can have a disproportionately large impact on food materials for their biomass by mobilizing inorganic and organic materials and contributing to the accumulation of detritus. Calef (1973) concluded that a low density of tadpoles ($3/\text{m}^2$) in an oligotrophic lake in British Columbia moved 10 kg/ha/day of dry sediments ($1 \text{ g}/\text{m}^2/\text{day}$). Wassersug (1975) suggested that tadpoles can influence nutrient cycling within aquatic habitats and between aquatic and terrestrial habitats through their metamorphosis. He cited information from studies on fish production in artificial ponds (Cross 1969, 1971), where incidental data on larval yields of R. catesbeiana were collected for two years. The range in yield of tadpoles was 106-1720 kg/ha with a mean value of 504 kg/ha. One tenth-acre pond produced 230 kg of tadpoles, which could have resulted in about 2.9 mg of phosphorus and 37.1 mg of nitrogen harvested

for every m^2 of bottom (Wassersug 1975).

Grazing by tadpoles can significantly alter the species composition and standing crop of periphyton. Dickman (1968) demonstrated that activities of R. aurora tadpoles reduced the standing crop of periphyton, especially filamentous green algae. In a study of two high altitude lakes in India, the primary factor cited for the reduction of plankton concentrations was intensive grazing by frog and fish larvae (Das et al. 1966). Seale (1980) and Seale and Beckvar (1980) have shown that blue-green algae are more damaged than other algal taxa after passage through tadpole guts. Anabaena are more effectively filtered and ingested than green algae like Chlorella (Seale and Wassersug 1979); placed in algal medium, Anabaena spp. in tadpole fecal pellets did not grow, whereas Chlorella began to grow within two days (Seale 1980). The effects of suspension feeding anuran larvae, predominantly ranid tadpoles, on limnological variables and community structure in a small pond in Missouri were examined by Seale (1973, 1980) and Seale, Rogers, and Borass (1975). The patterns of particulate organic nitrogen in the pond were related to amphibian population dynamics. The non-selective feeding activities of frog larvae altered the structure of the plankton community based on changes in the pigment ratio (D_{430}/D_{665}) and decreased the contribution of blue-green algae, especially Anabaena, to total algal volumes. Significant correlations were produced between tadpole biomass and certain limnological variables (particulate organic nitrogen, C^{14} , diel O_2 , D_{430}/D_{665} , and percentage of blue-green algae). Based on data from this small pond in Missouri, Seale (1980) proposed that tadpoles functioned as regulatory consumers and an appreciable amount

of total nutrients available to the ecosystem was channeled daily through the tadpoles.

Although numerous studies have cited the importance of algae in the diets of tadpoles, only limited data is available substantiating the affects of tadpoles on algal populations and nutrient dynamics (Dickman 1968, Seale 1973, 1980, Seale et al. 1975). The quality of algae as food for tadpoles is of primary importance, since algae are at the base of aquatic food chains and their composition and abundance can be altered by human activities and management practices. Certain algal qualities like chemical or caloric content, toxicity, or external structure affect whether or not particular taxa of algae are consumed. Grazers may significantly depress the abundance of algae in aquatic environments, but certain algal species, considered noxious, such as Aphanizomenon, Anabaena, and Sphaerocystis directly benefit from increased grazing (Porter 1977, Lynch 1980). Blue-green algae are of particular importance because their abundance in eutrophic waters suggest that they do not readily enter aquatic food chains (Porter 1977, Porter and Orcutt 1980).

Studies of natural anuran populations have revealed low survival from the egg to larval metamorphosis. Herreid and Kenny (1966) presented information on the Alaskan woodfrog (R. sylvatica), which indicated 96% of the population died before metamorphosis. They suggested that survival in larval anurans followed a Deevey (1947) Type III survival curve. Calef (1973) found similar numbers of eggs deposited and survivorship, only about 5% of the initial spawn survived to metamorphosis, for R. aurora in both years of a two year study in a permanent Canadian lake. He demonstrated that R. aurora

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tadpoles grew at the maximum rates permitted by temperature, since at all depths and at all times in the lake there was sufficient food. This lake could have supported 30 tadpoles/m² or about 100X the metamorphosing population. Predation, primarily by salamanders, regulated the population and maintained it at low levels. Licht (1974) considered predation and chance life history events kept survival to metamorphosis at about 10% of the original egg density in R. aurora and R. pretiosa. He, like Herreid and Kenny (1966) and Calef (1973), found the highest mortality shortly after hatching, when tadpoles were still grouped. Tadpoles were thought not to be food limited in any of the aquatic habitats they occupied. Without food, survival was high in the laboratory; in nature, they would be expected to move to a more productive area of the pond to procure food. Predation on all life history stages appeared to be the important regulatory factor for both anuran species.

Salamander larvae prey intensively on tadpoles in nature (Anderson 1968, Heusser 1972, Wilbur 1972, Calef 1973, Seale 1973, 1980), but rapidly growing tadpoles can outgrow certain newt and salamander predators (Avery 1968, Calef 1973, Cooke 1974). Many invertebrate predators, especially odonate naiads, feed indiscriminately on tadpoles (Savage 1961, Bragg 1965, Wagner 1965, Young 1967, Brockelman 1969, Heyer and Bellin 1973, Heyer et al. 1975, Heyer and Muedeking 1976), while fish prey selectively on eggs and larvae of different anuran taxa (Voris and Bacon 1966, Grubb 1972). The eggs and larvae of particular anuran families are unpalatable and toxic (Licht 1968, 1969) and these characteristics deter predation by vertebrates. Based on the likelihood of invertebrate or vertebrate

predation, an ecological model was proposed by Heyer, McDiarmid, and Weigmann (1975) which simulated probability of use by larval anurans of different types of aquatic habitats.

At high experimental densities in laboratory and pond enclosure studies, food limitation, not predation, has been proposed as an explanation for growth patterns and survivorship of anuran larvae. Both intra- and interspecific competition for limited nutrient resources have been invoked as the primary mechanisms determining anuran larval population dynamics. Based on data from enclosure experiments, Wilbur (1972) suggested that R. sylvatica were food limited and competed with zooplankton for this resource, although phyto- and zooplankton abundances were not measured. DeBenedictis (1974) was unable to demonstrate conclusively that intraspecific competition occurred between caged R. sylvatica and R. pipiens. In the first year of this field experiment, R. sylvatica and R. pipiens did not interact and survivorship of both species averaged 14%. DeBenedictis (1974) speculated that the carrying capacity of the pond was lower during the second year of his study, but no evidence was presented to substantiate this. Larvae of the two species acted like ecological equivalents with survivorship sensitive to food levels and nutrition. Brockelman (1969) found no evidence of intraspecific competition in an open pond with tadpole densities as high as $1000/m^2$; however, based on enclosure experiments in the same pond, he proposed intraspecific competition and food limitation regulated tadpole populations of Bufo americanus. Wilbur and Collins (1973) varied density of R. sylvatica tadpoles in enclosures and produced evidence of intraspecific competition. They thought food limitation explained

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Competition for food has been suggested as an important factor in the growth, survivorship, and metamorphosis of certain species that aggregate in nature, based on results from enclosure experiments (Brockelman 1969, Wilbur 1977). Others studying the same or similar species in natural situations have demonstrated that tadpoles actually benefit by aggregating at relatively high densities (Richmond 1947, Beiswenger 1975, 1977). Aggregating tadpoles more effectively exploit the food supply by collectively locating and mechanically stirring food from substrates (Beiswenger 1977).

Competition in nature is theoretically possible and competition apparently occurs in enclosures with unrealistically high densities of tadpoles. Natural densities of tadpoles are typically lower than those required to demonstrate competition experimentally. Heyer (1976) contrasted results from enclosure experiments of Wilbur and Collins (1973) with the highest estimated density of tadpoles reported for any natural pond (Turnipseed and Altig 1975). He concluded a density of 5208 tadpoles/m³ was required for intraspecific competition to be measurable in enclosures (Wilbur and Collins 1973), whereas the highest natural densities measured by Turnipseed and Altig (1975) were 3500 tadpoles/m³.

The proportion of tadpoles that successfully completed metamorphosis and body size at metamorphosis were highly correlated with initial density in field enclosure experiments (Brockelman 1969, Wilbur 1972, 1976, 1977, Wilbur and Collins 1973). The skewness of body sizes increased and the mean size of tadpoles decreased in dense populations of R. sylvatica, indicating only a few individuals would

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survive to metamorphosis (Wilbur 1976). The rest of the population of R. sylvatica was expected to succumb to predation or other sources of mortality before reaching the minimum size for metamorphosis. However, Wilbur (1976) found that less than 50% of the variation in larval and metamorphic sizes was caused by initial population density; the remainder of the variation was related to uninvestigated factors, such as genetic variation, environmental heterogeneity, and historical events that occurred within a population during the larval period.

After studying habitat partitioning by anuran larvae at sites in the temperate and tropical zones, Heyer (1973, 1974, 1976) proposed that "communities" of tadpoles represent only a collection of non-interactive species, co-occurring as larvae. The tadpole "community" is not an integrated whole, biological interactions are not important evolutionarily, and natural selection does not integrate or partition the "community". Habitat use by larvae and biological interactions involving predator-prey and species associations were different during each year of these studies. There was no partitioning of available food resources in aquatic habitats, instead tadpoles partitioned habitats by time and space. Other researchers have also found strong indications of temporal and spatial partitioning of aquatic habitats by tadpoles (Dixon and Heyer 1968, Weist 1974).

In laboratory experiments, tadpoles reared at high densities have slower growth and differentiation rates, sometimes reduced survivorship, and delayed metamorphosis (Yung 1878, 1885, Bilski 1921, Goetsch 1924, Adolph 1931a, b, Rugh 1934, Lynn and Edelman 1936, Rose 1959, 1960, Richards 1958, 1962, Rose and Rose 1965, Akin 1966, Gromko et al. 1973, John and Fenster 1975, Pourbagher 1968, 1969, Wilbur

1976, 1977, Steinwascher 1978a, b, 1979a, b, Dash and Hota 1980). Various hypotheses have been offered to explain these responses of tadpoles to crowding: (1) competition for food or other resources (exploitive competition), (2) allelopathic growth inhibitors or parasites (interference competition), or (3) social and behavioral interactions. Certain investigators suggested these density-dependent relationships were not caused by food limitation (Lynn and Edelman 1936, Richards 1958, 1962, Rose 1962, Gromko et al. 1973, John and Fenster 1975), while others thought limited food resources were important (Wilbur 1977, Steinwascher 1978a, b, 1979a, b). Steinwascher (1978a, b) proposed that the experimental results reported by Goetsch (1924), Adolph (1931), Rugh (1934), Lynn and Edelman (1936), Hodler (1958), Gromko et al. (1973), and John and Fenster (1975) could be explained by exploitive competition. All tadpoles were fed excess food and any initial differences in size and competitive abilities of larger tadpoles simply increased through time. The investigators cited by Steinwascher (1978a, b) stressed the importance of space or average volume occupied, shape of the holding container, volume of water tadpoles could move through unimpeded, or social interactions with other tadpoles as explanations for their experimental results. In other laboratory studies, growth retardation has been related to the presence of chemical inhibitory compounds, algal-like cells or parasites that reduce the growth of members of the same clutch, conspecifics, or individuals of wide phylogenetic difference (Rose 1959, 1960, Richards 1958, 1962, Steinwascher 1978b, 1979a). The consumption of feces was necessary to demonstrate chemical inhibition in certain investigations (Rose 1958, 1962), while coprophagy was

unnecessary to produce evidence of inhibition in other experiments (Akin 1966).

Boyd (1975) provided information which may affect the success of culturing tadpoles in a multispecies aquacultural system. He suggested the occurrence of R. catesbeiana tadpoles caused differences in the species composition of fish among apparently similar eutrophic ponds. A large, heat-labile molecule produced by these tadpoles was non-specific for fish and amphibians and markedly reduced reproduction in Poecilia reticularia. The inhibitory effectiveness of this proposed water-soluble substance was reduced by heating, sonification, ultraviolet light, freeze thawing, lowered pH, and charcoal filtration (Richards 1958, 1962, Pourbagher 1968).

Certain investigators have cited an "Allee effect", where growth of tadpoles reared at "low" (5000 tadpoles/m³) densities in the laboratory was greater than for tadpoles cultured singly (Wilbur 1977), but others have noted the lack of an "Allee effect" in low density stockings of tadpoles (Steinwascher 1979b).

Dash and Hota (1980) showed that crowded tadpoles grew slower than uncrowded tadpoles, but mortality of crowded tadpoles was independent of density. However, absolute mortality was related to initial density, since the larval period was longer and tadpoles metamorphosed at smaller sizes. Wilbur (1977) found food level and population density had significant effects on growth rates and body weights at metamorphosis, but no significant effect on the length of the larval period. The body weight of larvae and metamorphosing froglets was decreased by the addition of food to tadpoles reared at low densities (10-20 tadpoles/2.5 liters), whereas adding food increased body weights

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of tadpoles reared at high densities (80 tadpoles/2.5 liters). Wilbur (1977) thought the response of tadpoles to abundant food was caused by a "pollution effect". He used these results, obtained in the laboratory with tadpoles fed an artificial diet of Purina rabbit chow, to hypothesize a similar "pollution effect" which would be relevant to species that inhabited large eutrophic lakes or aquatic ecosystems with high nutrient loadings. Studies on the same species, R. sylvatica, in field enclosures (Wilbur 1972, 1976, Wilbur and Collins 1973, DeBenedictis 1974) produced no demonstrable "pollution effect" and were interpreted as evidence that food limitation is important in natural systems.

Based on results from laboratory studies, elaborate explanations and models have been devised for tadpole competition (especially Steinwascher 1978a, b, 1979a, b). However, the extremely high densities of tadpoles used, the unnatural foods (lettuce, spinach, rabbit chow, and rolled oats) employed, and the related importance of coprophagy for tadpoles fed these foods produce results that are not necessarily representative of situations in natural systems. Implied density-related effects are especially important when considering aquaculture of tadpoles at high densities. Although a large volume of literature is available on density effects in larval anurans, there is no consensus on the relevancy of these experimental studies to natural systems with indigenous food resources.

Studies of ranid tadpoles in natural systems indicate that these tadpoles satisfy several criteria of a desirable consumer for aquaculture in a wastewater treatment system. Their diets are catholic and they are adapted to unstable, stressful environments.

Depending on the goals of the management project, tadpoles may be easily harvested by size-selective methods or allowed to metamorphose, thereby recycling nutrients to the terrestrial environment. Stocking tadpoles in a multispecies aquacultural facility with predacious fish appears impractical unless tadpoles are provided with refugia. Presently, additional data on their efficiency of digestion and assimilation on different foods and the influence of density-dependent factors on the survival and growth of tadpoles are necessary before anuran larvae are selected for aquaculture. The results reported here provide information on the ecology of ranid tadpoles in natural systems and on the suitability of culturing these tadpoles in wastewater treatment systems.

MATERIALS AND METHODS

The Field Study

Description of the Site

The field site for this study was two lakes (One and Four) on the 200 ha Water Quality Management Project (WQMP), Michigan State University, East Lansing, Michigan. This facility receives wastewater from the East Lansing treatment plant, and includes a transmission line, four experimental lakes, three marshes, and a spray irrigation system (Figure 1). The primary objective of the WQMP, designed to study the recycling and reuse of municipal waste effluents, is to biologically remove nutrients from wastewater as it flows through the system by incorporating these nutrients into a harvestable biomass of aquatic and terrestrial plants and animals.

The East Lansing sewage treatment plant is a conventional, extended aeration, activated sludge facility, that was modified and enlarged in 1976 to process $56,770 \text{ m}^3/\text{day}$. Two types of effluent can be released from the treatment plant, one that has been treated chemically to remove phosphorus and one that has not been pretreated for partial phosphorus removal. Either the primary or secondary effluent can be pumped to the WQMP via a transmission line where it enters the first lake, then flows by gravity through each of the other three lakes. The four lakes have a total surface area of 16 ha with a maximum depth of 2.4 m at each outlet structure and a mean depth of 1.8 m. The

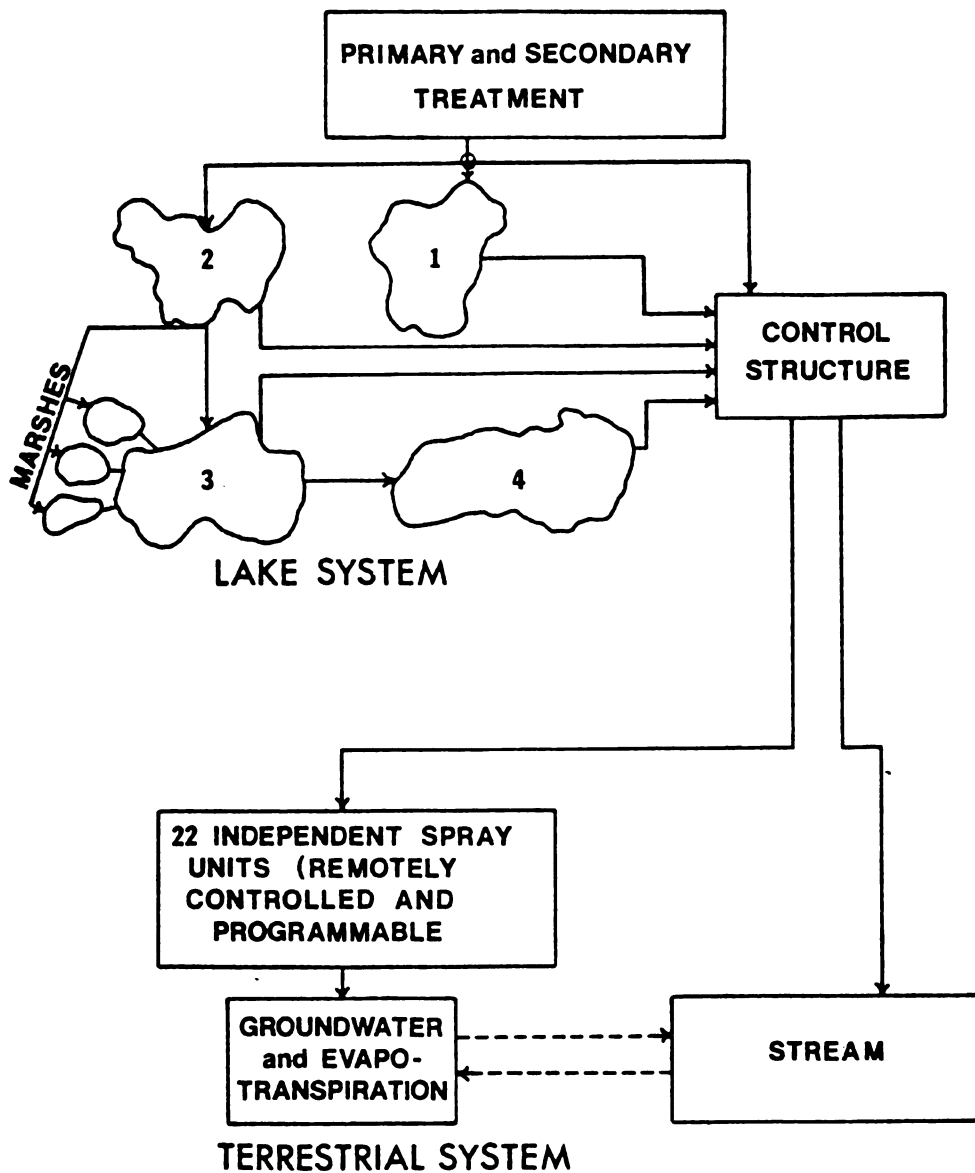


Figure 1. Diagram of the general facilities of the Water Quality Management Project, Michigan State University, East Lansing, Michigan.

system was described in detail by Burton et al. (1979).

Water from Lakes One and Four, representing two extremes in water quality and nutrient availability, was used in this study (Table 1). Lake One had a surface area of 3.2 ha and water elevation of 271.9 m. Emergent vegetation was comprised mainly of cattails (Typha) and willows (Salix); dense mats of Cladophora covered the surface of the lake during much of the summer and fall. Lake Four had a surface area of 4.98 ha and a water elevation of 268.2 m. Little emergent vegetation occurred around the perimeter of Lake Four, but a luxuriant growth of submerged Elodea covered most of the bottom.

Description of the Flow-through System

During the early spring of 1976, two sheds (2.44 m = length, 1.22 m = width, and 3.66 m = height at peak) were constructed on each of the two lakes to house nine, 20 gal (75.7 liter) aquaria and the flow-through apparatus (Figure 2). The roof was green plastic and the sides of the sheds were plywood with aluminum screening. Black plastic was secured over areas of screen on the sides and door to minimize variations of incoming light. These structures prevented disruption of the experimental system by predators, high winds and rain. The translucent roofs and black plastic coverings reduced illumination, so fluctuations in temperature and community metabolism were less extreme than would have occurred in systems not housed in sheds.

A schematic diagram of the experimental flow-through system located on Lakes One and Four is shown in Figure 3. Water inlet hoses from each lake were submerged at a depth of 0.5 m (maximum) and secured in place in the epilimnion with floats and weights. Lake water, drawn into the sheds with battery-operated pumps, passed through a 0.5 mm

Table 1. Physico-chemical characteristics of Lakes One and Four from May-October, 1976. Values represent the range of measurements (mg/l) on samples at lake outlets (Chemistry Laboratory of Michigan Institute of Water Research).

EXPERIMENTS:	ONE				TWO				THREE			
	1	4	1	4	1	4	1	4	1	4	1	4
LAKES:												
Total Alkalinity	171-196	53-65	147-231	60-75	150-163	89-106						
Total Carbon	39-75	17-30	-	-	-	-						
Dissolved Organic Carbon	6-7	4-6	-	-	-	-						
Total Organic Carbon	7-15	5-10	-	-	-	-						
Dissolved Oxygen	10.7-19.7	6.9-12.7	1.8-21.2	4.7-10.7	8.9-15.0	7.6-15.1						
Temperature (C)	17-24.5	16-26.5	20-23	19.5-22.5	6-17	4.5-16						
% Oxygen Saturation	110-240	70-155	17-235	50-121	91-121	67-138						
Ammonia - Nitrogen	0.02-1.82	0.03-0.20	0.02-5.25	<0.01-0.11	0.11-0.73	0.01-0.10						
Nitrate - Nitrogen	4.14-8.5	0.01-0.05	0.02-5.17	<0.01-0.01	3.51-7.91	<0.01-0.01						
Nitrite - Nitrogen	0.19-2.13	<0.01	0.07-0.64	0.01	0.15-1.18	<0.01-0.01						
Total Organic Nitrogen	0.81-2.60	0.46-0.78	0.45-5.99	0.66-1.21	0.79-1.85	0.64-0.97						
pH	9.1-10.2	9.2-10.7	8.4-10.6	9.05-10.8	8.3-9.6	8.6-10.7						
Total Phosphorus	0.70-1.39	0.03-0.052	0.49-5.00	0.012-0.065	1.83-3.30	0.041-0.100						
Hydro- (and) Ortho- Phosphorus	0.32-1.29	<0.01-0.02	0.26-4.81	0.046-0.040	0.89-2.70	0.030-0.087						
Ortho-Phosphorus	0.13-1.25	0.003-0.015	0.24-4.70	0.004-0.036	0.085-2.74	0.025-0.050						
Magnesium	25-35	18-19	26-28	19-70	24-27	22-25						

Table 1 (cont'd.).

EXPERIMENTS:	ONE				TWO				THREE			
	1	4	1	4	1	4	1	4	1	4	1	4
LAKES:												
Potassium	3.9-10	2.5-3.6	8.9-11	3.5-5.1	10-13	6.7-7.5						
Sodium	73-90	52-60	69-91	60-69	83-100	82-87						
Sulfate	114-132	80	-	-	-	-						
Manganese	0.05-0.06	<0.05-0.05	0.06-0.12	<0.05-0.07	<0.05-0.06	<0.05-0.06						
Zinc	0.04-0.05	<0.03-0.11	0.03-0.04	<0.03-0.03	<0.03-0.04	<0.03-0.03						
Iron	0.2	0.1-0.2	0.2	0.1-0.2	0.2-0.3	< 0.1-0.3						
Chloride	97-103	74-76	95-117	80-92	95-109	103-107						
Calcium	71-76	17-20	59-77	16-22	62-69	28-31						
Total Residue	586-640	304-378	578-618	495-570	518-720	378-560						
Total Filterable Residue	1-24	1-7	1-7	1-7	7-36	1-10						

- indicates not measured.

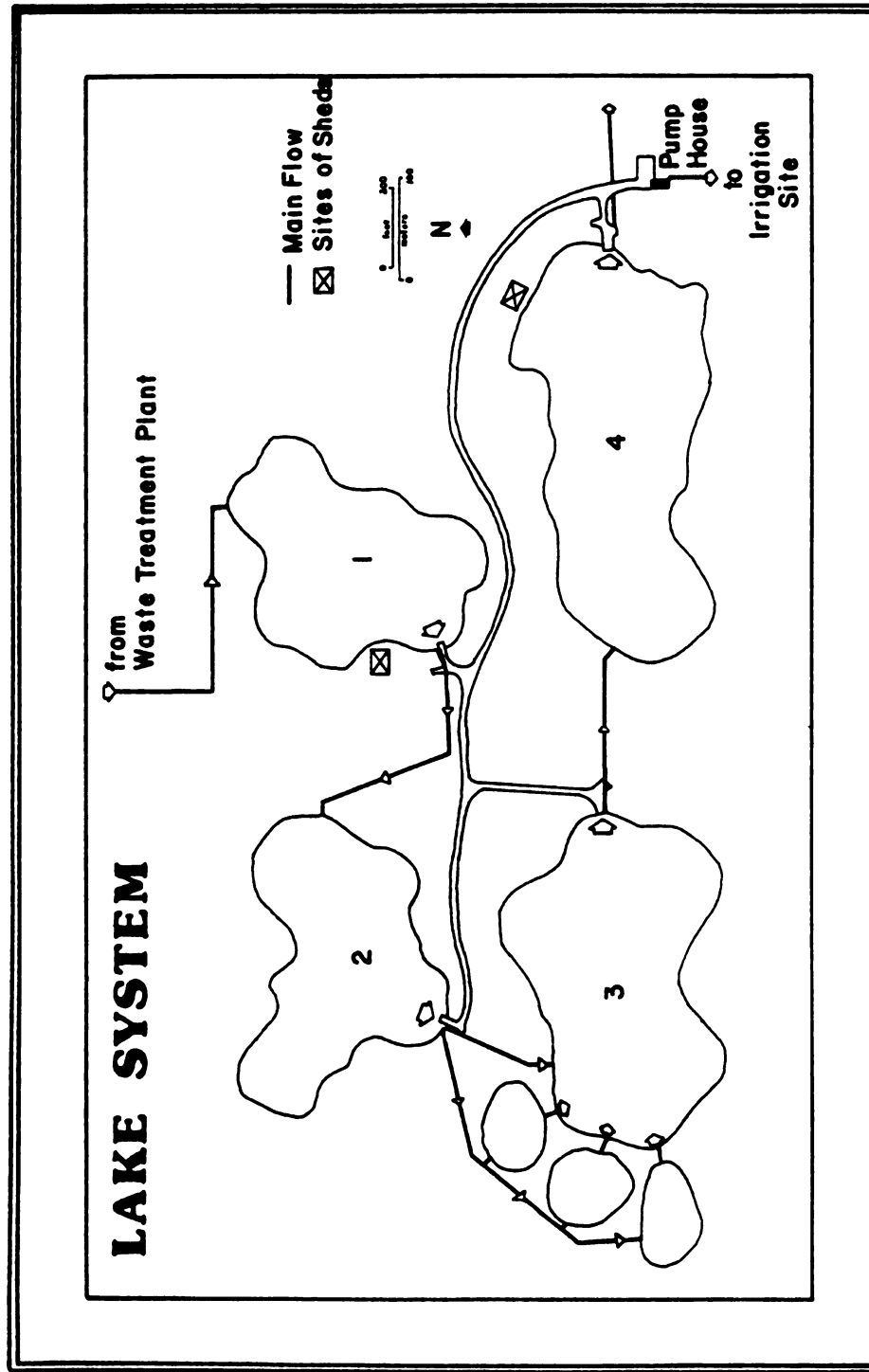


Figure 2. Map of the experimental lakes at the Water Quality Management Project and locations of sheds that housed flow-through systems at Lakes One and Four.

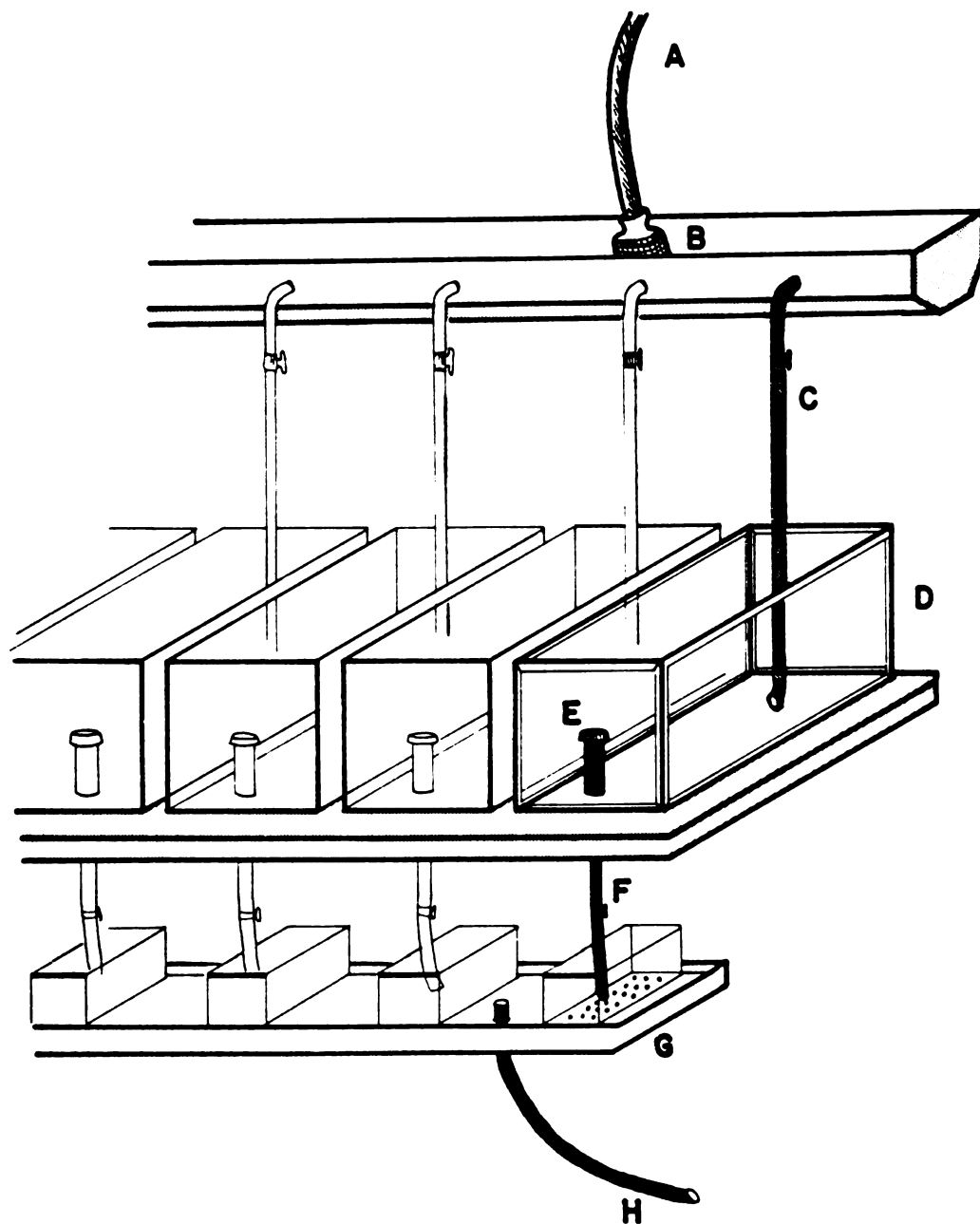


Figure 3. Diagram of flow-through system: A is an inflow hose for lake water, B is a trough with nine outlet hoses, C is a delivery hose to D (an aquarium, 75.5 liters), E is a screened, removeable standpipe, F is a drain pipe to G (catchment tray), and H returned water to the lake.

screen that eliminated macroinvertebrates and large filamentous algae. The water then flowed into a specially designed trough (1 x 0.5 x 0.5 m), fitted with nine outlet hoses (2.54 cm dia) with control valves to regulate the filling rates of the nine aquaria (30.5 x 73.7 x 31.7 cm). Each all-glass aquarium had one hole (2.45 cm) drilled in the bottom that was fitted with a PVC adapter and a removeable standpipe (15.24 cm = height). The standpipe maintained 42.8 liters of lake water in each aquarium. The screened standpipes allowed excess water to flow out, but prevented the escape of tadpoles. Tubing attached to each aquarium adapter returned water to a catchment basin then to the lake via an outlet hose.

Experimental Design

Three experiments were conducted during the spring, summer and fall of 1976. The first experiment started on 27 May, the second began on 16 July, and the third began on 13 September. The final dates were 19 June, 22 August, and 24 October, respectively. Experiments at both lakes followed a 4 x 3 block design with four treatments and three replicates/treatment. Lake water was sampled and characterized before introduction into the nine aquaria housed in each shed. In all experiments, these initial samples of lake water represented one of the four treatments. In the first two experiments, the nine aquaria provided for three treatments: three control aquaria contained no tadpoles, three aquaria stocked with a low density of tadpoles, and three aquaria stocked with a high density of tadpoles. One species, Rana pipiens, was used in the first two experiments. In Experiment Three, the treatments with three replicates were bullfrog (R. catesbeiana) tadpoles,

green frog (R. clamitans) tadpoles, and a combination of bullfrog and green frog tadpoles. The tadpoles were placed in the respective aquaria on 30 May in Experiment One, 28 July in Experiment Two, and 27 September in Experiment Three.

In the first two experiments, water from the lake was introduced and removed from aquaria daily (24 h), while in the third experiment, water remained in aquaria for 48 h before aquaria were drained and refilled. Each morning, prior to removing water that had been in aquaria for 24 h or 48 h, oxygen (mg/l) and temperature (C) readings were taken in each aquarium. Additional oxygen and temperature measurements were made immediately after aquaria had been filled with water from the lakes to determine if initial differences among aquaria existed. Oxygen concentrations were determined with a YSI (Yellowsprings Instrument Company) oxygen meter, calibrated daily with Winkler analyses. Daily extremes in temperature were obtained from minimum-maximum thermometers in aquaria.

Tadpole Procedure

Eggs of the northern leopard frog (Rana pipiens pipiens) were purchased from the Amphibian Facility, Ann Arbor, Michigan for Experiments One and Two. All clutches of eggs were thoroughly mixed, then placed in enamel pans and allowed to hatch at room temperature. Upon hatching, leopard frog tadpoles were redistributed and maintained in aquaria with aerated, dechlorinated water and fed TetraMin fish food (44.1% carbon, 7.7% nitrogen) until used in field experiments. Bullfrog and green frog tadpoles used as test animals in Experiment Three were collected from ponds at the Wolf Lake Fish Hatchery, near Grand Haven, Michigan. These larvae were kept in plastic pools (1.5 m) in

the laboratory and fed TetraMin fish food before they were tested in the field.

Prior to each experiment, individual tadpoles were measured (snout-vent length, mm), weighed wet to the nearest 0.01 mg, and their stage of development was recorded (Gosner 1960). Gravimetric determinations were made by quickly blotting individual larvae with filter paper to remove excess moisture, then transferring them to tared aluminum pans with water for weighing. This technique was chosen since it combined accuracy with a minimum of stress to the animals. Tadpole numbers were the same and biomasses similar within a particular treatment, experiment, and lake. Sorted tadpoles were held for about 12 h; dead animals were replaced. Tadpoles were acclimated to the field temperatures before being placed in the respective treatment units.

In all experiments, treatments with different densities and biomasses were used to assess the effects of grazing intensity on nutrient concentrations, community metabolism and algae. Stocking densities and biomasses of tadpoles, in conjunction with different water qualities, were also used to evaluate intra- and interspecific competition in tadpoles, as measured by survival, growth, and production. In Experiment One in both lakes, each low density treatment was stocked with 20 tadpoles/aquarium and each high density treatment had 40 tadpoles/aquarium (see Table 5 for biomass data). In Experiment Two, the low and high density treatments had dissimilar numbers and biomasses at the two lakes. At Lake One, there were 15 tadpoles/aquarium in the low density replicates and 45 tadpoles/aquarium in the high density. At Lake Four in Experiment Two, 5 tadpoles were stocked in each low density aquarium and 15 were stocked in each high density

treatment (biomass data in Table 5). In Experiment Three at Lake One, there were three replicates/treatment: bullfrogs at 10/aquarium, green frogs at 20/aquarium, and 5 bullfrogs plus 10 green frogs/aquarium. In the same experiment at Lake Four, there were 6 bullfrogs/aquarium, 12 green frogs/aquarium, and in the mixed treatment, 3 bullfrogs and 6 green frogs/aquarium (see Table 8 for biomass information).

At the conclusion of each experiment, length, weight and stage of development were determined and tadpoles were individually frozen for subsequent analyses. Linear regression analyses (log length-log wet weight) were applied on both the initial and final populations of tadpoles. Regressions were calculated for pooled samples and for individual replicates. The lengths of tadpoles that died during each experiment were put into appropriate initial and final regression equations; weight at time of death was estimated from these equations. Since dead tadpoles had been collected daily, weights could be adjusted to take into account the actual date that tadpoles died. A minimum and maximum value for dead biomass was calculated and used in estimating tadpole production.

Dry Weight and C-N Analysis of Tadpoles

A representative sample of 130 tadpoles, selected from the three experiments and the original TetraMin-fed laboratory animals, was oven-dried (60 C) according to the methods in Cummins and Wuycheck (1971). Tadpoles were defrosted and individually reweighed, since there were slight variations between frozen and prefrozen weights. Each larva was placed in a preweighed aluminum pan (previously ignited at 500 C for one h) and weighed to the nearest 0.01 mg. A series of

25 tadpoles were oven-dried for 24, 48, 72 and 96 h and weighed after each time interval to determine the appropriate drying time. Tadpoles were oven-dried for 48 h, then cooled in a desiccator with P_2O_5 for 24 h and weighed. This information was analyzed to determine the relationship between wet and dry weights of tadpoles. Regardless of species or treatment, there was a significant correlation ($r = 0.98$) between wet and dry weights (Figure 4).

Seventy-five oven-dried tadpoles, selected from the three experiments, were thoroughly ground with a mortar and pestle. Duplicate analyses of organic carbon and nitrogen content of individual tadpoles were conducted in a Perkin-Elmer Elemental Analyzer (Model 240). The variation in the carbon and nitrogen content of tadpoles within a treatment was not greater than that among treatments in both lakes within a particular experiment. Twenty-two tadpoles were analyzed from Experiment One, 20 from Experiment Two, and 33 from Experiment Three. Statistical comparisons (t tests) were performed on the mean carbon and nitrogen content in tadpoles from each of the three experiments. The percentages of carbon and nitrogen measured in samples of tadpoles from the three experiments are listed in Table 2. Although the ratio of carbon to nitrogen was similar in tadpoles from the three experiments, values for carbon and nitrogen were significantly different among all three experiments.

Limnological Assays

Dissolved oxygen and temperature: During each of the three experimental periods, four 24-h (or 48-h) measurements of dissolved oxygen and temperature were made at about weekly intervals. Dissolved

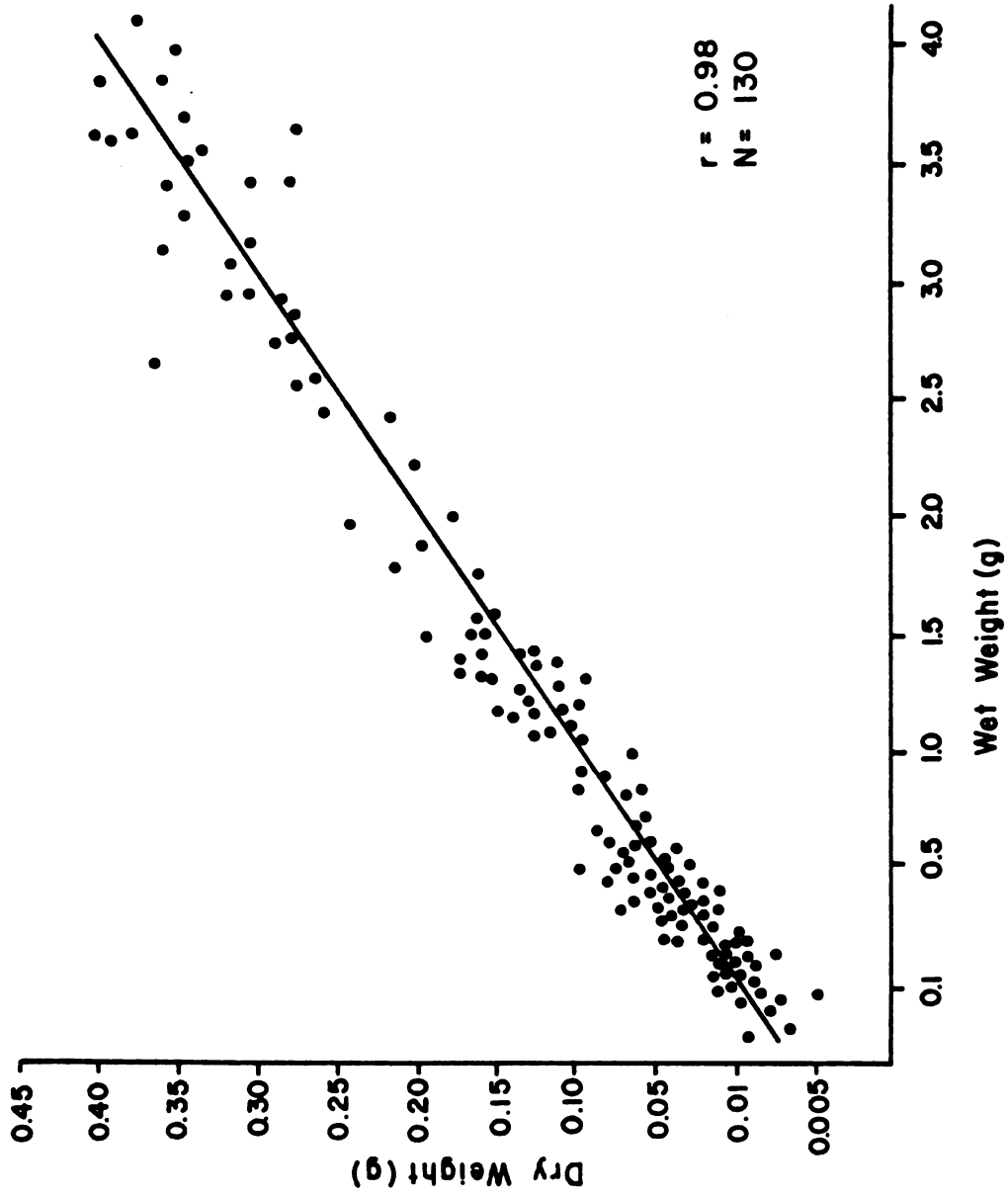


Figure 4. Wet-dry weight relationship for tadpoles of Rana pipiens, R. catesbeiana and R. clamitans.

Table 2. Concentrations of carbon and nitrogen ($\pm$ SD) measured in tadpoles after laboratory and field experiments.

EXPERIMENT	N	% CARBON	% NITROGEN	C:N
<u>Laboratory</u>				
(<u>Rana pipiens</u>)				
Phytoplankton	15	30.8 ($\pm$ 2.53)	6.1 ($\pm$ 1.05)	5.0:1
TetraMin	8	43.1 ($\pm$ 2.88)	8.8 ($\pm$ 0.28)	4.9:1
<u>Field</u>				
Experiment One (<u>R. pipiens</u>)	22	35.4 ($\pm$ 4.34)	8.7 ($\pm$ 1.97)	4.0:1
Experiment Two (<u>R. pipiens</u>)	20	39.0 ($\pm$ 2.52)	10.3 ($\pm$ 0.81)	3.8:1
Experiment Three (<u>R. catesbeiana</u> and <u>R. clamitans</u>)	33	42.3 ($\pm$ 2.69)	11.4 ($\pm$ 2.01)	3.7:1

oxygen and temperature were estimated hourly in each of the 18 aquaria and less frequently in the outlet areas of Lakes One and Four. Determinations made before tadpoles were stocked provided baseline information on dissolved oxygen and temperature.

Gross primary productivity and community respiration: Gross primary productivity and community respiration were calculated from diurnal oxygen and temperature curves (Odum 1956, Odum and Hoskin 1958, and Vollenweider 1974) with appropriate corrections for gaseous exchange with the atmosphere (Hart 1967) and respiratory uptake. Measurements of community metabolism in certain experiments were refined to correct for supersaturation of oxygen (Appendix A). Calculations of the amount of respiration contributed by tadpoles to the total community respiration were based on the biomass of tadpoles on each date, water temperature, and values reported by Parker (1976), Funkhouser and Foster (1970), and Sivula et al. (1972).

Nutrient and phytoplankton sampling: At the start of each 24-h (48-h) sampling period, triplicate lake-water samples were collected in one-liter, polyethylene, acid-washed bottles. These six samples were placed in a cooler with ice and transferred to the laboratory. Subsamples (500 ml) were removed and preserved with Lugol's solution for subsequent determinations of numbers and volumes of phytoplanktonic cells. A subsample (125 ml) from each lake was transferred to acid-washed bottles and stored in the refrigerator for analysis of total phosphorus, ammonia-nitrogen, nitrite-nitrogen, nitrate-nitrogen, Kjeldahl nitrogen, and organic carbon. An additional 125 ml was filtered through a 0.45 μ m millipore filter (filter was

rinsed by filtering 250 ml of double-distilled water and the filter apparatus was acid-washed). Filtered samples were refrigerated and later analyzed for dissolved Kjeldahl nitrogen, phosphorus, and organic carbon. The remaining water was refrigerated and kept for reference when identifying phytoplankton. At the end of each 24-h (48-h) monitoring period, the water in aquaria was mixed to resuspend any settled particulate matter and a one-liter water sample was taken from each experimental unit. Samples were placed in coolers, transported to the laboratory, and processed as described previously.

Phytoplankton methods: Phytoplankton were identified (Prescott 1962, 1970, Patrick and Reimer 1966) and enumerated by a membrane filter technique similar to that described by McNabb (1960) and Dozier and Richerson (1975). The volume of each aliquot filtered through a 0.45 μm millipore filter depended on the concentration of algal cells in the 500 ml samples. A series of subsamples were filtered and examined under the microscope to determine the appropriate volume for phytoplankton enumeration. Water from Lake Four had relatively low phytoplankton densities, so three to five times more water was filtered to obtain similar concentrations to Lake One. After filters were placed on glass slides (5.1 x 7.6 cm), cleared, and covered with a glass slip, they were examined with a dark phase microscope at 200X, 430X, and 900X magnification. Separate diatom mounts were made according to Hanna (1930) and Weber (1970), except a muffle furnace was used for ignition of organic material (540 C for 30 min.). This technique, in combination with wet mounts of living phytoplankton, facilitated the identification of filtered phytoplankton.

The numbers of algal cells in each genus were counted in 60 random fields by making duplicate counts at 900X magnification for each slide (1 field = area of Whipple micrometer). To test the effectiveness of counting phytoplankton at 900X, these counts were compared with those made at 200X and 430X magnification. By adjusting the volumes of water filtered, similar counts ($P > 0.05$) were obtained from all three magnifications. The results were converted and expressed as number of phytoplankton cells/ml.

Volumetric determinations were made by measuring the dimensions of algal cells (generally 20 individual cells in each size category) throughout the sampling period with a Whipple micrometer (Nalewajko 1966, Bellinger 1974). Formulae for geometric solids, most closely resembling shapes of phytoplankton, were used to determine the volume (μm^3) for individual cells, colonies, or filaments. The proportions of various cell sizes in each genus for each sampling date were determined and average generic volume was estimated. One-way and two-way ANOVAS were used to determine significant differences among treatments and Student-Newman-Keul's test was employed to separate the means for numbers and volumes of algal cells in each treatment.

Shannon-Wiener Diversity Index (H'), its variance ($\hat{\text{var}} H'$), and the evenness (J') (Pielou 1966a, b) were calculated with a FORTRAN computer program. Hierarchical diversity was estimated by splitting H' into components that were additive (Pielou 1974). By this method, the generic diversity within each algal class, the class diversity, phylum diversity, and total diversity were assessed for both numbers and volumes of phytoplankton. Measurements of hierarchical diversity were calculated for individual aquaria on each sampling date and on

pooled treatments for each date, experiment, and lake.

Carbon, nitrogen, phosphorus, and alkalinity analyses:

Nitrogen and phosphorus analyses were performed on a Technicon Auto-analyzer (USEPA 1974) by the Institute of Water Research's (IWR) chemistry laboratory. Determinations of total phosphorus, ammonia-nitrogen, nitrite-nitrogen, nitrate-nitrogen and total Kjeldahl nitrogen were made on unfiltered water samples; dissolved phosphorus and Kjeldahl nitrogen were analyzed in filtered samples. Total and dissolved organic carbon concentrations were measured on a Beckman Single-Channel Carbon Analyzer as described by USEPA (1974). All samples were stored in the refrigerator prior to analyses and examined within 72 h of collection. Concentrations of particulate phosphorus and particulate organic carbon were obtained by subtracting the dissolved fraction from the total phosphorus and organic carbon. Total inorganic nitrogen was calculated by adding the concentrations of ammonia-nitrogen, nitrate-nitrogen and nitrite-nitrogen. Ammonia-nitrogen was subtracted from Kjeldahl nitrogen for organic nitrogen determinations and dissolved organic nitrogen was subtracted from the total organic nitrogen to obtain the particulate organic nitrogen.

Hydrogen ion concentrations were measured with a Corning Glass electrode pH meter; carbonate, bicarbonate, and total alkalinity were determined by acid titration (APHA 1971).

Analysis of periphytic biomass and C-N content: A total surface area of $6,212.9 \text{ cm}^2$ was available in each aquarium for periphytic growth. To monitor the production of periphyton, nine glass slides (5.1 x 7.6 cm) were attached to plastic strips and hung

on each side of an aquarium and eight slides were fixed on plexiglass plates on the bottom of each aquarium. A total of 44 slides were placed in each aquarium at the beginning of an experimental period. During the experiment, eleven slides (426.4 cm^2) were removed for algal identification, oven-drying, ashing, and C-N analysis at the end of each 24-h (48-h) dissolved oxygen and temperature profile. At the end of each experiment, the plexiglass plates (232.3 cm^2) were collected and periphytic material was oven-dried and ashed. Slides for identification were stored in 10% buffered formalin, while slides used for determinations of periphytic biomass and C-N content were placed in plastic bags, air-dried, and stored in a desiccator with P_2O_5 . Periphytic material was scraped from the surface of slides and placed in preweighed, aluminum pans (previously ignited in a muffle furnace at 500°C for one h). Periphyton was oven-dried (60°C for 24 h), desiccated (P_2O_5) for 24 h, and weighed to the nearest 0.01 mg. This oven-dried material was ignited in a muffle furnace, moistened with distilled water, oven-dried to a constant weight, desiccated, and reweighed. The oven-drying and ashing procedures were similar to those described in APHA (1971), Cummins and Wuycheck (1971), and Vollenweider (1974). Periphyton used for carbon and nitrogen analyses was oven-dried, weighed, and thoroughly ground with a mortar and pestle. The organic carbon and nitrogen content was measured in a Perkin-Elmer Elemental Analyzer.

Estimates for accrual ($\text{mg}/\text{cm}^2/\text{d}$) of periphyton were corrected to account for more extensive growth on the bottom of aquaria. The sampling procedure resulted in the bottom representing 20% and each side representing 20% (4 sides = 80%) of the total periphyton on each

date. Actually, the sides comprised 64% and the bottom of the aquarium was 36% of the total surface area. Information on the periphytic material from the plexiglass plates was used as a correction factor.

Relative contributions of periphyton and phytoplankton to GPP

and R: To distinguish between the separate contributions of periphyton and phytoplankton to the total oxygen production (GPP) and community respiration (R) in aquaria, ancillary studies were conducted during the second and third experiments. On two different dates in Experiment Two and one date in Experiment Three, eight glass slides attached to plastic strips were placed on the bottom of each aquarium. The time allowed for periphytic growth on slides was 12 days in both separate tests in Experiment Two and 16 days in Experiment Three. At the end of each period allowed for periphytic growth, 18 wide-mouthed jars (0.95 liter) were filled with water from the appropriate lake. Glass slides were removed from each aquarium and one set of eight slides was placed in a jar filled with lake water (total of 18 jars with slides). These jars and jars with lake water only were capped; two jars, one with and one without slides, were placed in similar positions in each aquarium. Dissolved oxygen and temperature were measured in each jar (7-8 August, 21-22 August, and 22-24 October) concurrent with measurements on water in aquaria. The jars containing only lake water represented the contribution of phytoplankton (seston) to gross primary productivity and respiration, while the other jars with suspended glass slides were used to calculate the contribution of periphyton.

At the end of 24 (48) h, ten ml of formaldehyde were added to each jar. Attached material scraped from slides was returned to the jar. A known volume was filtered through a glass fiber filter and placed in an aluminum pan (both filter and pan were ignited in a muffle furnace and weighed). Sestonic material from lake water was filtered and all samples were oven-dried and ashed. Three replicates (300 ml) were filtered from jars with combined periphyton and phytoplankton. Calculations of gross primary productivity and total respiration, made on those jars containing seston only, were subtracted from the combined seston plus periphyton to determine the contribution of periphyton alone. Dry weight and ash-free weight of sestonic material were subtracted from combined measurements to obtain the dry and ash-free weight of periphyton. Sestonic values were corrected and converted to carbon, estimated as 50% of the ash-free dry weight (Vollenweider 1974). Amounts of carbon in periphyton were estimated from C-N analyses done previously.

The Laboratory Experiment

Natural Food Sources, Algae

Tadpole growth, survival, and efficiency of conversion and assimilation of algae (analyzed as particulate organic carbon and Kjeldahl nitrogen) were assessed for different-size tadpoles of Rana pipiens fed three different concentrations of natural food, phytoplankton. Fifteen aquaria, representing five treatments of tadpole density with three replicates per treatment, received similar total biomasses but different total numbers of tadpoles. Initially, the amount of food and space per total tadpole biomass was similar

in all aquaria. The effects of reducing food and space per individual tadpole, simulated by the density treatments (increasing the number of tadpoles per aquarium), was evaluated in this laboratory experiment.

Six weeks before the initiation of the feeding experiments, three containers (305 liters) were filled with equal portions of distilled water and tap water and enriched with modified Chu's Culture Medium (Chu 1942). Containers were stocked with either a mixture of phytoplankton from Lake One of the Water Quality Management Project, or Scenedesmus, or Pediastrum; pure strains of Scenedesmus and Pediastrum were obtained from the Indiana Culture Facility, Bloomington, Indiana. Cultures were illuminated 24 h/d and continually aerated. Phytoplankton were enumerated biweekly and Kjeldahl nitrogen, phosphorus, and organic carbon were measured weekly on filtered and unfiltered samples taken from the three cultures. Additional water and nutrient media were added three times per week to the cultures to maintain an abundance of phytoplanktonic growth.

Mixed clutches of Rana pipiens eggs (Amphibian Facility, Ann Arbor, Michigan) were held either at 20-21.5 C or 10 C. Each day, some of the eggs developing at the cooler temperature were removed and placed at room temperature (20-21.5 C) to obtain populations of different-sized tadpoles. Individual tadpoles were measured (snout-vent length, mm), weighed wet to the nearest 0.01 mg, and staged (Gosner 1960). The mean number of tadpoles in the 5 experimental densities was 9, 4, 3, 2, and 1 with a range of 701.0-714.4 mg for initial total biomass per aquarium.

All 18 aquaria (20.8 liters) were filled daily with 3.8 liters of aerated water, cleaned at the end of 24 h, and refilled

with aerated water. Tadpoles were supplied with different levels of algal food during the 24-day experiment. Initially, 500 ml of mixed algae were added to each aquarium and this level of feeding was continued for 14 days. The next higher addition of food material, 1000 ml of mixed algae per aquarium, was provided for 6 days. During the final 4 days of the experiment, tadpoles were fed 1,500 ml of mixed algae per day. The food mixture of algae was obtained by combining predetermined amounts from each of the three cultures. At the lowest feeding level, 250 ml were taken from each algal culture. These samples were thoroughly mixed, then 500 ml were added to each aquarium. At the higher feeding rate, 500 ml were removed from each algal culture; these samples were mixed and 1,000 ml were added to aquaria. The highest food concentration, 1,500 ml per aquarium per day, was achieved by removing 600 ml from each algal culture and combining these samples before adding the prescribed amount of material to aquaria. To determine initial concentrations and availability of nutrients provided at each feeding level, analyses of total and dissolved Kjeldahl nitrogen, organic carbon, phosphorus, and phytoplankton density were made on the remainders of the mixtures from the three algal cultures (Table 3).

Water in each aquarium was stirred and then sampled at the end of each 24-h feeding period. Water sampled from stocked aquaria was passed through a 0.5 mm screen to remove tadpole feces and concentrations of carbon, nitrogen, and phosphorus were analyzed. Unstocked aquaria were also sampled and the changes in phytoplankton, organic carbon, nitrogen, and phosphorus that occurred over the 24-h period were noted. All tadpoles were weighed individually every 48 h

Table 3. Average concentrations of nutrients (mg/d) and phytoplankton (cells/ml/d) at the three supply rates and their availability to tadpoles after dilution with 3.8 liters of water (largest CV for N, P, C, and algae were 12.4, 13.4, 9.2 and 19.8%, respectively).

Feeding Levels	Duration of Time	Kjeldahl Nitrogen Total	Phosphorus Particulate	Organic Carbon Total	Phytoplankton ¹			
I. 500 ml a) Total mg/ aq/day	14 d (280-296 degree d)	6.22	4.91	4.03	3.27	22.4	18.9	338,736
b) Availability/ aq/day		1.63	1.29	1.06	0.86	5.9	5.0	88,815
II. 1000 ml a) Total mg/ aq/day	6 d (120-127 degree d)	9.92	7.44	7.29	5.57	36.0	26.2	825,574
b) Availability/ aq/day		2.60	1.95	1.91	1.46	9.4	6.9	216,686
III. 1500 ml a) Total mg/ aq/day	4 d (80-85 degree d)	13.91	11.05	12.11	9.15	40.9	33.5	1,054,433
b) Availability/ aq/day		3.65	2.90	3.18	2.40	10.7	8.8	276,754

¹ Genera and average proportions of taxa encountered in aquaria: Green algae - Scenedesmus (16.9-29.8%), Pediculus (13.9-52.5%), other green algae (0.6%) - Ankistrodesmus, Actinastrium, Chlorella, Schroederia, coccoid green cell; Pennate diatoms (0.6-14.4%) - Navicula, Nitzschia, Diploneis, Fragilaria; Centric diatoms (0.6-4.9%) - Cymbella, Cyclotella.

during the 24-d experiment. At the conclusion of this experiment, tadpoles were individually frozen after being weighed, measured, and staged. Determinations of dry weight and carbon-nitrogen content were done subsequently as described in the field experiment section.

A Comparative Food, TetraMin

Ten leopard frog tadpoles, encompassing the range of tadpole sizes employed in the algal feeding experiments, were selected from the same laboratory population of tadpoles. Each tadpole was placed in a plastic container (11.2 x 11.2 x 5.1 cm) with 500 ml of aerated water. Tadpoles were fed TetraMin, a highly nutritious food, for 14 days, concurrent with the last part of the previous laboratory experiment. Containers were cleaned daily and resupplied with water and TetraMin. TetraMin was provided in excess to tadpole daily requirements to assure maximum individual growth on this food source. Tadpoles were weighed every 48 h at the same time as algal-fed tadpoles and at the end of the experiment were processed like algal-fed tadpoles. This ancillary experiment provided information on individual growth rates of tadpoles of different sizes and stages to contrast with results from the previous laboratory experiment when tadpoles were fed a natural food, algae.

RESULTS

Environmental Factors

Differential Effects

Tadpole exposure to the different physical and chemical characteristics of the lakes could have influenced the comparability of results among experiments. Environmental characteristics of Lake One and Lake Four are tabulated in Table 1 of the Materials and Methods section. These factors, along with temperature, oxygen, alkalinity, and pH measured in aquaria and described below, indicate the types and degrees of stress that tadpoles reared in water from the two lakes may have experienced.

Daily Measurements of Temperature and Oxygen

Within an experiment, temperatures usually varied less than 1 C among aquaria at both lakes (Figures 5 and 6). Therefore, tadpoles were exposed to similar thermal regimes within experiments at Lake One and Lake Four. The daily range in minimum-maximum temperature was 5-11 C in Experiment One and 4-15 C in Experiment Two. In the first experiment, the mean daily temperatures increased throughout the duration of the experiment in response to increasing day length and average air temperatures (Figures 5 and 6). In Experiment Two, summer storms and intermittent cloudiness caused erratic variation in water temperatures (Figure 5). Mean daily temperatures declined in late summer during the third experiment (Figure 6). The highest

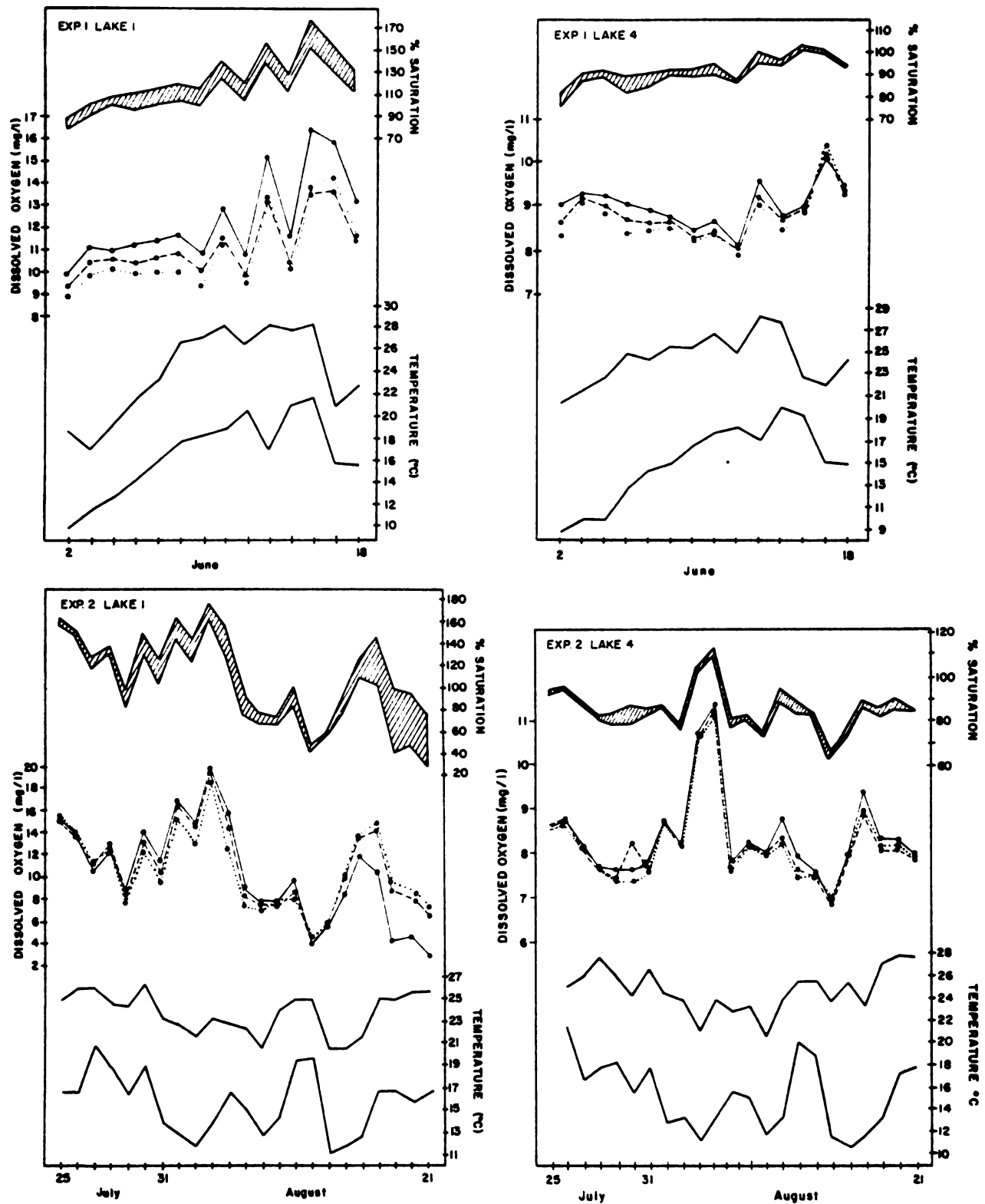


Figure 5. Range of relative oxygen saturation, mean dissolved oxygen, and temperature for Experiments One and Two at Lakes One and Four (for dissolved oxygen, unstocked aquaria = —, low density = ---, and high density = ···).

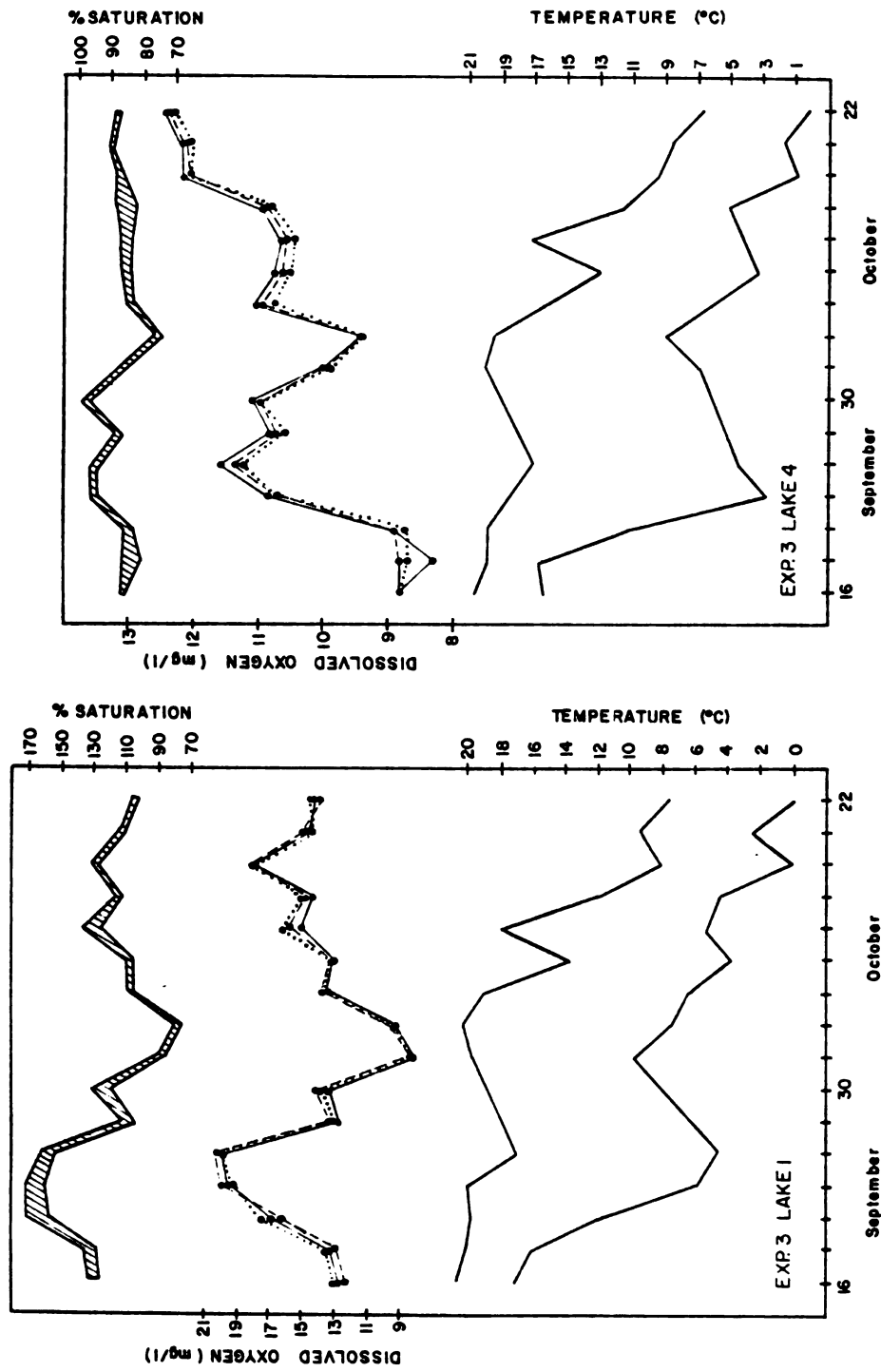


Figure 6. Range of relative oxygen saturation, mean dissolved oxygen, and temperature for Experiment Three at Lakes One and Four (for dissolved oxygen, bullfrogs = —, mixed-species = ---, and green frogs = ...). Measurements were made between 7-10 AM after water was in aquaria for 48 h; per cent saturation was calculated from lowest and highest O_2 readings.

temperatures for Experiments One, Two, and Three were 28, 27, and 21 C and the lowest temperatures were 10, 11 and 0 C, respectively. The mean daily temperature in Experiments One and Two was about 17 C, while in the third experiment, the temperature averaged 8 C.

As with temperature, similar patterns of daily fluctuations in oxygen concentrations occurred among aquaria at the two lakes (Figures 5 and 6). However, oxygen concentrations frequently differed among the three treatments at Lake One, presumably because of differences in community metabolism since reaeration coefficients should have been the same. In Experiment One at Lake One, the unstocked aquaria consistently had greater oxygen concentrations than aquaria with tadpoles, but oxygen was always above 8.8 mg/l in all aquaria (Figure 5). Throughout most of this experiment, the relative oxygen saturation exceeded 100%. Since oxygen was sampled early in the day, the peak concentrations were probably higher than measured and all aquaria were supersaturated with oxygen throughout the experiment. In Experiment Two, measurements of daily oxygen fluctuated, but all treatments remained within 1 mg/l of each other at Lake One until the final week in August (Figure 5). At this time, oxygen dropped sharply in unstocked aquaria to about 2 mg/l or 20-30% saturation. Oxygen levels also decreased in aquaria stocked with tadpoles, but remained at 60-80% saturation. In Experiment Three at Lake One, concentrations of dissolved oxygen were similar among treatments, invariably within 1 mg/l of each other (Figure 6). On only one date did oxygen decline slightly below 9 mg/l or 90% saturation.

At Lake Four, little variation occurred among treatment

aquaria within an experiment; oxygen levels were within 0.5 mg/l of each other (Figures 5 and 6). The changes in dissolved oxygen measured within an experimental period were considerably less than at Lake One. The lowest concentrations of oxygen recorded for Experiments One, Two, and Three were 8.0, 6.9, and 8.3 mg/l; only in Experiment Three did the highest oxygen level exceed 12 mg/l. Relative saturation of oxygen remained above 60% and was generally 80-100%.

Extremes of Dissolved Oxygen

Unlike temperature, diurnal extremes in oxygen concentrations and percent saturation in aquaria were different at Lakes One and Four. Minimum-maximum oxygen concentrations and percent saturation, based on 24-h and 48-h analyses on four representative dates during the three experiments at Lake One and Lake Four, are provided in Figures 7-9. Oxygen concentrations in all aquaria at a lake were similar on the first sampling date in each experiment, before tadpoles were introduced. In the first two experiments, particularly at Lake One, the diurnal variation and differences among treatments increased through time. The growth of periphytic communities and tadpole feeding activities most likely influenced this increase in diurnal variation. In Experiment Three, extremes in diurnal variation of oxygen decreased with time and may have been related to declining air temperatures. At Lake One, oxygen varied 7 mg/l in aquaria stocked with tadpoles in Experiment One, 14 mg/l in Experiment Two, and 9.5 mg/l in Experiment Three (Figures 7 and 9). In contrast, the maximum change in diurnal oxygen for stocked aquaria at Lake Four was only 2.3 mg/l in Experiment One, 2.4 mg/l in Experiment Two,

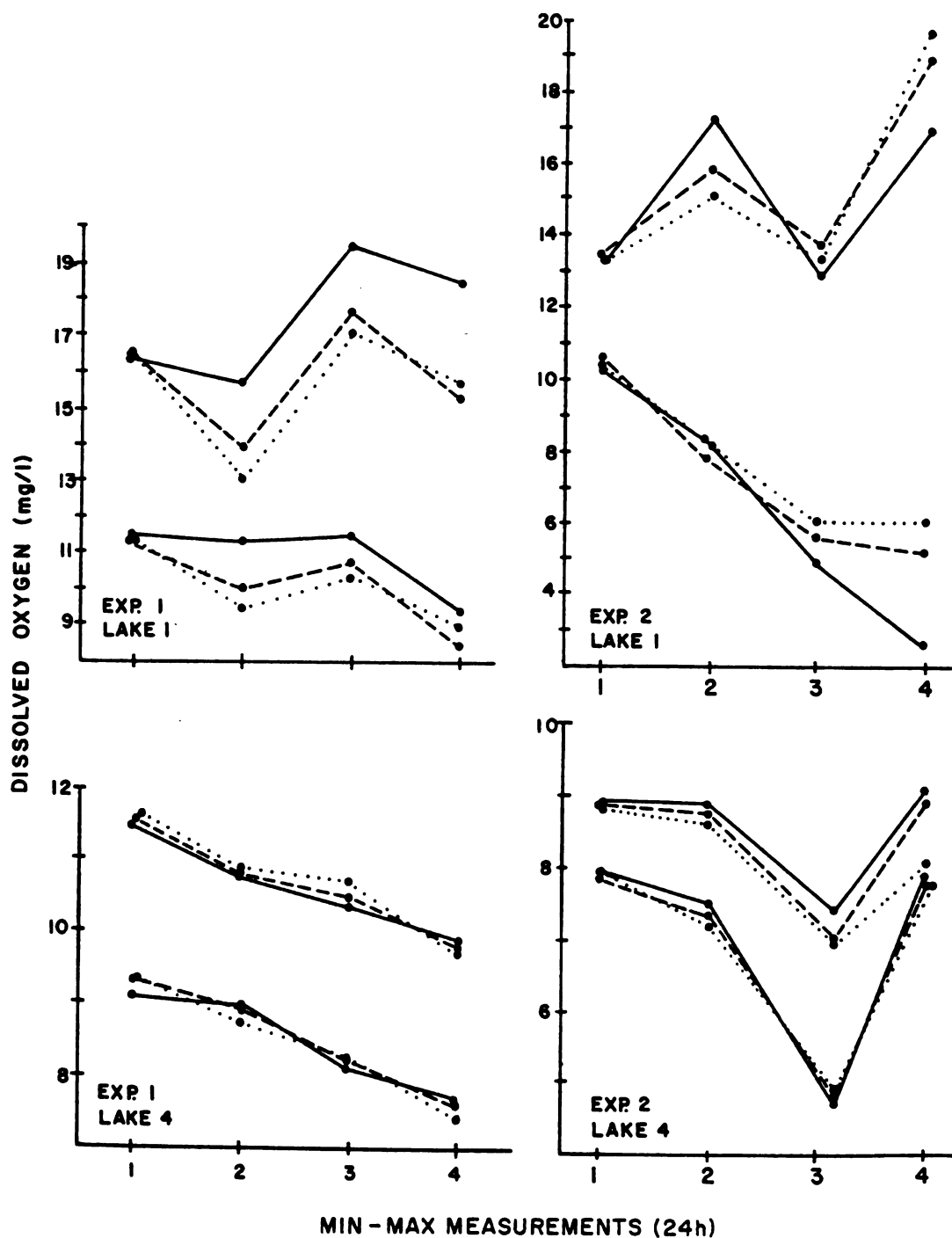


Figure 7. High and low concentrations of oxygen during four, 24-h periods in Experiments One and Two at Lakes One and Four (unstocked aquaria = —, low density = ---, and high density = ···).

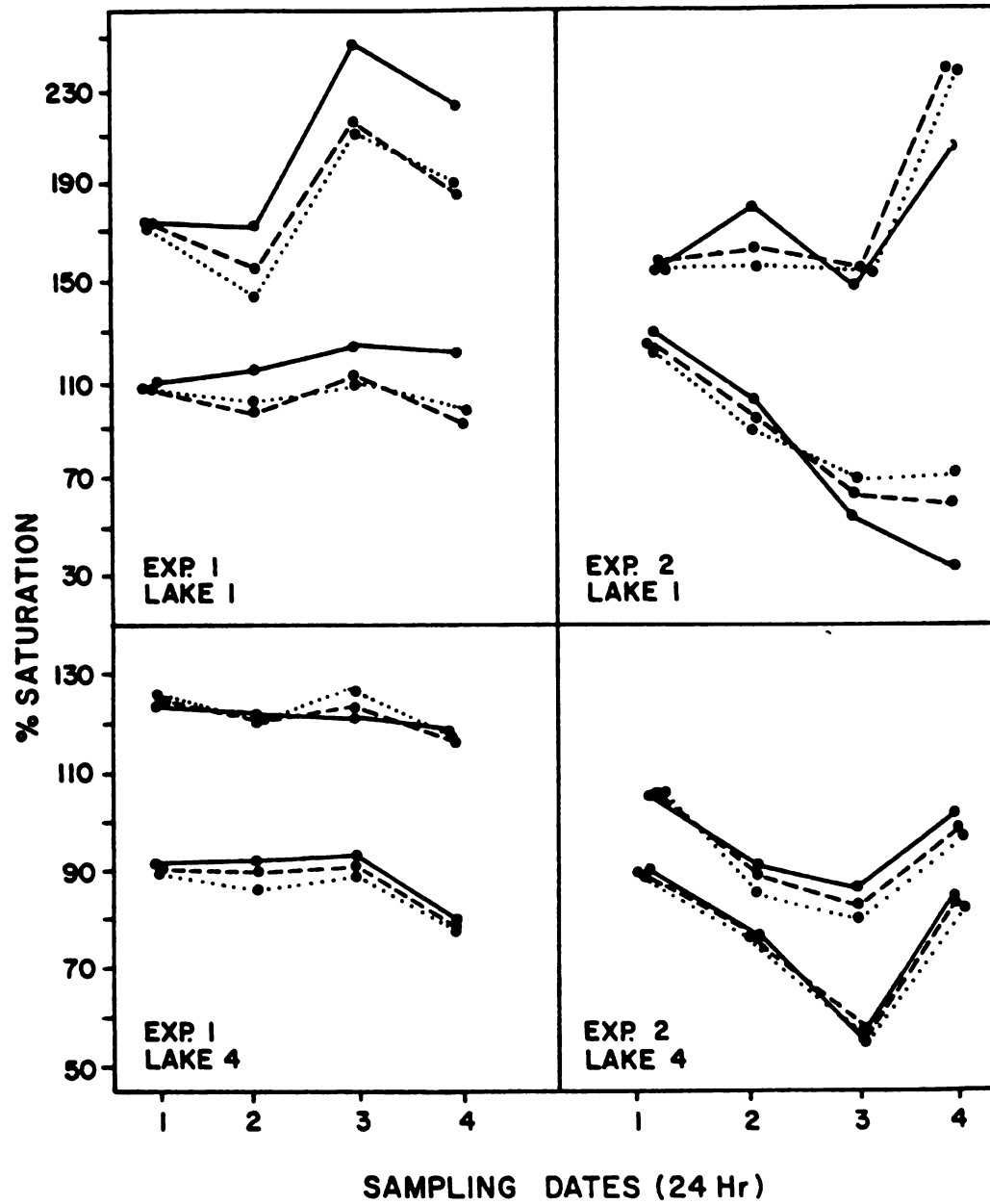


Figure 8. High and low relative saturations of oxygen during four, 24-h periods in Experiments One and Two at Lakes One and Four (unstocked aquaria = —, low density = ---, and high density = ...).

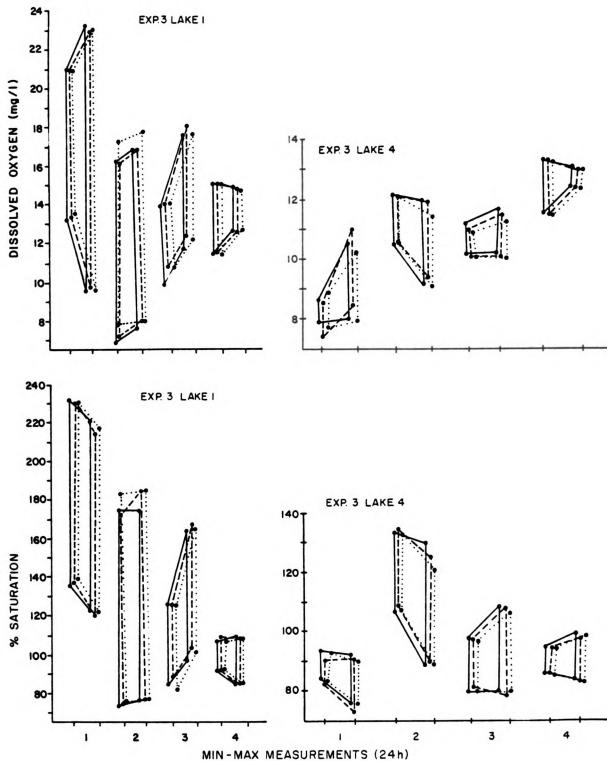


Figure 9. High and low concentrations and relative saturations of oxygen during four, 48-h periods in Experiment Three at Lakes One and Four (bullfrogs = —, mixed-species = ---, and green frogs = ···).

and 3.0 mg/l in Experiment Three (Figures 7 and 9).

The daily extremes in relative oxygen saturation also differed at the two lakes (Figures 8 and 9). At Lake One, the aquaria with tadpoles were always at least 90% saturated and peak saturation was greater than 200% in Experiment One (Figure 8). In Experiment Two at Lake One, daily extremes in oxygen saturation ranged from 60 to 240% in aquaria stocked with tadpoles, while in Experiment Three, the extreme range was 75 to 185% (Figure 9). At Lake Four, the maximum daily range in percent saturation was about 80-120% in Experiment One, 55-85% in Experiment Two, and 85-135% in Experiment Three. Only during the first experiment at Lake Four did relative saturation of oxygen remain above 100% for part of the day throughout the experimental period (Figure 8).

Alkalinity and pH

Throughout this study, both lakes were moderately alkaline (Table 1). In Experiment Three, the total alkalinity in aquaria at Lake Four averaged 68% of values at Lake One (Table 4). The pH range in aquaria at Lake One was 8.9 to 9.8, while at Lake Four the range was 9.3 to 10.0. Since measurements were made during morning hours when some carbon dioxide from nighttime respiratory activities may have remained in solution, the peak pH may not have been attained until after CO₂ was exhausted. The extent of diurnal change in pH caused by photosynthetic uptake of carbon dioxide was about one pH unit, based on the decline of oxygen fluctuations in Experiment Three. Some of the variation between lake and aquarium readings, especially at Lake Four, may have resulted from differences in sampling times.

Table 4. Alkalinity (mg/l) and pH measurements for Experiment Three at Lakes One and Four.

EXPERIMENT THREE	LAKE ONE				LAKE FOUR			
	Lake Readings	Bullfrogs	Mixed: Bullfrogs & Green Frogs	Green Frogs	Lake Readings	Bullfrogs	Mixed: Bullfrogs & Green Frogs	Green Frogs
1) Initial Readings 22-24 September 1976								
a) Carbonate	64.0	94.8	93.2	95.7	41.0	26.9	27.1	26.7
b) Bicarbonate	123.0	109.3	111.3	112.5	68.3	76.1	76.5	77.6
c) Total	187.0	204.1	204.1	208.2	109.3	103.0	103.5	104.3
d) pH	9.4	9.6	9.6	9.6	9.5	9.2	9.2	9.2
2) 3-5 October 1976								
a) Carbonate	48.4	48.3	52.5	48.7	59.6	50.3	52.1	49.2
b) Bicarbonate	128.4	129.7	127.2	129.4	60.8	67.5	66.2	67.7
c) Total	176.8	178.0	179.7	178.1	120.4	117.7	118.3	116.9
d) pH	9.1	9.1	9.1	9.1	9.9	9.3	9.4	9.3
3) 10-12 October 1976								
a) Carbonate	76.0	95.3	99.1	99.1	76.0	64.4	57.5	60.7
b) Bicarbonate	113.4	107.0	105.8	104.8	53.6	64.0	65.4	64.7
c) Total	189.4	202.3	204.9	203.9	129.6	128.4	122.9	125.4
d) pH	9.5	9.7	9.8	9.8	10.1	9.9	9.8	9.9
4) 22-24 October 1976								
a) Carbonate	23.2	25.5	25.1	25.5	80.4	65.2	70.7	73.7
b) Bicarbonate	144.4	140.8	138.8	145.5	53.4	63.5	59.9	58.7
c) Total	167.6	166.3	163.9	168.0	133.8	128.7	130.5	132.5
d) pH	8.8	8.9	8.9	8.9	10.1	10.0	10.0	10.0

Table 4 (cont'd.).

Mean of 3 Dates	Lake Readings	Bullfrogs	Mixed:	Green Frogs	Lake Readings	Bullfrogs	Mixed:	Green Frogs
a) Carbonate	49.2	56.4	58.9	57.7	72.0	60.0	60.0	61.2
b) Bicarbonate	128.7	125.8	123.9	125.6	59.9	65.0	63.8	63.7
c) Total	178.3	182.2	182.8	183.3	127.9	125.0	123.9	124.9
d) Range in pH	8.8-9.5	8.9-9.7	8.9-9.8	8.9-9.8	9.9-10.1	9.3-10.0	9.4-10.0	9.3-10.0

Tadpole Survival, Growth, and ProductionVarying Stocking Density and Biomass (Field Experiments One and Two)

Lake One: Survivorship and growth of leopard frog tadpoles in the low and high density treatments during Experiments One and Two are presented in Table 5. In both experiments, survivorship was greater for tadpoles reared at low densities than at high densities. In Experiment One, the survival of tadpoles stocked at low density (20 tadpoles/aquarium) was 90%; in the high density treatment (40 tadpoles/aquarium), survival was 76%. In the second experiment, 80% of the tadpoles in the low density treatment (15 tadpoles/aquarium) survived, while 53% of those stocked at high density (45 tadpoles/aquarium) survived. Initially, average biomass/aquarium in the first experiment was about four times greater than the second experiment for tadpoles stocked at low densities. In aquaria with high numbers of stocked tadpoles, average biomass/aquarium in Experiment One was initially twice as high as in Experiment Two.

While survivorship appeared to be density dependent within an experiment at Lake One, between experiments, survival was less influenced by stocking density than perhaps by initial developmental stages, individual sizes or random events. As mentioned, the R. pipiens initially stocked at a lower density and biomass in the second experiment had lower survival than tadpoles in Experiment One. In Experiment One, the tadpoles were larger and more developed (about stage 27 in Experiment One and stage 25 in Experiment Two). Since tadpoles in natural populations exhibit a Type III (Deevey 1947) survivorship curve, it was likely that tadpoles at the earlier developmental stage

Table 5. Densities, biomasses (wet weight, mg), and lengths (snout-vent, mm) of leopard frog tadpoles in Experiments One and Two at Lakes One and Four.

EXPERIMENTS	LAKE ONE				LAKE FOUR			
	Low Density		High Density		Low Density		High Density	
	Initial	Final	Initial	Final	Initial	Final	Initial	Final
<u>Experiment One</u>								
Total Biomass	28977 N ₀ = 60	30758 N ₁ = 54	50695* N ₀ = 120	38293 N ₁ = 91	24599 N ₀ = 60	11400 N ₁ = 29	50844 N ₀ = 120	21915 N ₁ = 59
Biomass/eq (range)	9659 (7463-11269)	10253 (9803-11055)	16898 (16370-17865)	12764 (11130-14293)	8200 (7829-8724)	3800 (2391-4537)	16948 (14959-20125)	7305 (5990-9103)
$\bar{x}$ Individual Wt. (range)	483.0 (373.5-517.5)	569.6 (490.2-614.2)	422.5 (409.2-444.6)	420.8 (402.2-433.1)	410.0 (391.4-436.2)	393.1 (319.4-504.1)	423.7 (374.0-503.1)	371.4 (352.3-395.8)
CV Wt.	42.3%	43.7%	29.8%	26.8%	41.6%	30.4%	37.7%	31.2%
$\bar{x}$ SV Length (range)	14.0 (12.9-15.0)	15.5 (14.8-15.8)	13.8 (13.2-14.2)	14.1 (13.9-14.3)	13.6 (13.4-13.8)	13.6 (13.0-14.0)	13.7 (13.1-14.2)	13.9 (13.2-14.3)
CV Length	11.1%	12.2%	7.1%	7.7%	9.5%	9.7%	8.4%	8.0%
<u>Experiment Two</u>								
Total Biomass	6498 N ₀ = 45	33846 N ₁ = 36	23108 N ₀ = 135	37508 N ₁ = 71	2243 N ₀ = 15	2348 N ₁ = 7	6321 N ₀ = 45	3256 N ₁ = 16
Biomass/eq (range)	2316 (2124-2440)	11282 (9849-13189)	7703 (7704-7651)	12503 (11525-13139)	748 (656-859)	783 (729-854)	2107 (1969-2176)	1085 (1032-1129)
$\bar{x}$ Individual Wt. (range)	154.5 (141.6-162.7)	940.2 (900.8-984.7)	171.2 (170.0-172.2)	528.3 (480.2-656.9)	149.6 (131.2-171.8)	335.4 (243.0-426.9)	140.5 (131.3-145.1)	203.5 (188.2-219.0)
CV Wt.	30.7%	53.9%	39.0%	63.5%	25.7%	26.9%	28.8%	31.4%
$\bar{x}$ SV Length (range)	10.5 (10.3-10.6)	18.8 (18.2-19.4)	10.5 (10.4-10.7)	15.3 (14.4-17.0)	10.2 (9.6-10.7)	13.3 (12.2-14.2)	9.9 (9.6-10.2)	11.1 (10.6-11.3)
CV Length	8.4%	15.8%	10.4%	16.6%	7.1%	7.3%	7.8%	8.9%

in Experiment Two had a slightly lower probability of survival than those in Experiment One. Environmental factors, measured during the two experiments, appeared similar so major influences by these factors could be discounted.

The information on tadpole mortality summarized in Table 6 indicated that dead tadpoles in both density treatments had larger average sizes than tadpoles which survived to the end of Experiment One (Table 5). In Experiment Two, the average weight of surviving tadpoles was higher than that for dead tadpoles, but the average weight of dead tadpoles exceeded the mean initial weight. In both experiments, the coefficients of variation of weight were larger among dead tadpoles than among initial or final weights of living tadpoles, indicating that no one size group died at a consistently higher rate. In the first experiment, both large and small tadpoles appeared to have a higher mortality than medium-size tadpoles, based on the weight distributions (Appendix B, Figures B1 and B2), R^2 values for length-weight regressions (Table 6), and average weights of dead tadpoles. The weights of tadpoles were more normally distributed among survivors than among those initially stocked (Appendix B, Figures B1 and B2). The relationship between length and weight (R^2) for tadpoles increased in both experiments, suggesting that misfits died or the condition factor increased similarly among survivors. In the second experiment, final weight distributions were more skewed than initially (Appendix B, Figures B3 and B4); however, the relationship between length and weight, indicated that smaller tadpoles were not thinner or in poorer condition than larger tadpoles. Overall, no consistent relationship emerged between tadpole size and survival, when the results from both

Table 6. Information (wet weight, mg and snout-vent length, mm) on tadpoles (*R. pipiens*) that died during Experiments One and Two.

EXPERIMENTS	LAKE ONE		LAKE FOUR	
	Low Density	High Density	Low Density	High Density
<u>Experiment One</u>				
Dead Biomass	3275.3 N = 6	14186.9 N = 29	13720.1 N = 31	25949.7 N = 61
$\bar{X}$ Wt. (range)	545.9 (241.9-1066.7)	489.2 (202.0-946.0)	442.5 (192.0-845.7)	425.4 (167.0-880.0)
CV Wt.	56.5%	53.4%	43.4%	40.2%
$\bar{X}$ Length (range)	14.4 (11.7-18.2)	14.2 (11.4-17.8)	14.1 (11.0-16.9)	13.7 (10.9-17.8)
CV Length	19.7%	15.1%	11.3%	11.2%
Initial Regression (Log Length - Log Weight)	$Y = 1.2541 + 0.3089X$	$Y = 1.2473 + 0.3403X$	$Y = 1.2449 + 0.2699X$	$Y = 1.2375 + 0.2589X$
R ²	0.92	0.70	0.82	0.81
CV Regression	1.6%	2.1%	2.0%	2.0%
Final Regression (Log Length - Log Weight)	$Y = 1.2805 + 0.3403X$	$Y = 1.2743 + 0.3297X$	$Y = 1.2640 + 0.3177X$	$Y = 1.2679 + 0.2855X$
R ²	0.95	0.79	0.78	0.69
CV Regression	1.3%	1.7%	2.4%	2.3%

Table 6 (cont'd.).

EXPERIMENTS	LAKE ONE		LAKE FOUR	
	Low Density	High Density	Low Density	High Density
<u>Experiment Two</u>				
Dead Biomass	3632.3 N = 9	18419.6 N = 64	1939.8 N = 8	6049.5 N = 29
$\bar{X}$ Wt. (range)	405.6 (157.8-1121.4)	287.8 (103.1-830.9)	266.4 (149.6-383.3)	191.3 (175.2-207.5)
CV Wt.	87.2%	69.9%	48.0%	42.1%
$\bar{X}$ Length (range)	13.1 (10.4-19.5)	11.1 (9.1-16.9)	10.8 (10.5-13.6)	10.4 (9.9-11.2)
CV Length	26.3%	15.8%	14.1%	15.0%
Initial Regression (Log Length - Log Weight)	$Y = 1.2746 + 0.3097X$	$Y = 1.2699 + 0.3150X$	$Y = 1.2363 + 0.2734X$	$Y = 1.2594 + 0.3058X$
R^2	0.79	0.83	0.66	0.76
CV Regression	2.1%	2.4%	2.5%	2.2%
Final Regression (Log Length - Log Weight)	$Y = 1.2962 + 0.3481X$	$Y = 1.2789 + 0.3163X$	$Y = 1.2760 + 0.3448X$	$Y = 1.2978 + 0.3626X$
R^2	0.96	0.88	0.82	0.81
CV Regression	1.4%	2.7%	2.5%	1.5%

experiments were compared.

In Experiment One, total tadpole production was almost three times greater in aquaria stocked with a low density of tadpoles than with a high density (Table 7). The ratio of production to biomass was about 24X greater for the low density treatment than for the high density. In the second experiment, total tadpole production per aquarium was slightly greater in the high density treatment, but production per unit of tadpole biomass was over three times greater for low density treatments. In Experiment Two, the production/aquarium/degree day was five times larger for tadpoles stocked at low density and almost 16 times larger in the high density stocking than values in Experiment One.

These data indicated an inverse relationship ($r = -0.91$) between initial stocking density and production per unit of tadpole biomass (TP/TB): 2,166 mg stocked, 4.4 (TP/TB); 7,702 mg stocked, 1.42 (TP/TB); 9,659 mg stocked, 0.775 (TP/TB); and 16,898 mg stocked, 0.032 (TP/TB) (Tables 5 and 7).

Lake Four: In the first experiment at Lake Four, leopard frog tadpoles were stocked at the same densities and biomasses as at Lake One (Table 5). Survivorship was similar in low and high density treatments, 48% for tadpoles stocked at low density and 49% for those stocked at high density. In the second experiment, lower densities and biomasses were tested than at Lake One; 36% of tadpoles stocked at low density (5 tadpoles/aquarium) survived and 47% survived in the high density treatment (15 tadpoles/aquarium). In Experiment Two, actual values for low and high densities of tadpoles were 25-38% and

Table 7: Total production (mg of wet weight, carbon, and nitrogen) and production per unit of biomass for leopard frog tadpoles in Experiment One (21 d, 361 degree d) and Two (25 d, 434 degree d).

EXPERIMENTS	LAKE ONE		LAKE FOUR	
	Low Density	High Density	Low Density	High Density
<u>Experiment One</u>				
Production/aq	1685.3	594.8	170.2	-992.9
Production/aq/d	80.3	28.3	8.1	-47.3
Production/aq/degree d	4.7	1.6	0.5	-2.7
Carbon Production/aq	59.0	20.8	5.9	-8.6
Nitrogen Production/aq	14.5	5.1	1.4	-34.8
P/B	0.775	0.032	0.021	-0.059
P/B/d	0.037	0.0015	0.001	-0.0028
<u>Experiment Two</u>				
Production/aq	10182.9	10939.8	614.3	828.1
Production/aq/d	407.3	437.6	24.6	33.1
Production/aq/degree d	23.5	25.2	1.4	1.9
Carbon Production/aq	393.6	422.8	23.7	32.0
Nitrogen Production/aq	104.1	111.9	6.3	8.4
P/B	4.40	1.42	0.32	0.39
P/B/d	0.176	0.057	0.033	0.016

biomasses were 9-12% of those in Experiment One at Lake Four. The initial abundance of tadpoles in the high density stocking at Lake Four in Experiment Two was like that stocked in the low density treatment at Lake One (Table 5). In both experiments at Lake Four, no discernable relationship was evident between survival and initial density or biomass. As at Lake One, tadpoles in the second experiment were at a younger stage of development and may have had a slightly lower probability of survival than those in Experiment One.

In the first experiment, average biomass/aquarium and mean individual weights of surviving tadpoles decreased (Table 6). The average weights of dead tadpoles were larger than those for survivors and coefficients of variability of weight for dead tadpoles were larger than initial coefficients (Table 5 and 6). In both density treatments of Experiment One, the range in the distributions of final weights was narrower than the initial range, mainly because the larger tadpoles died (Appendix B, Figures B5 and B6). This was particularly notable in the high density stocking. Average lengths of tadpoles remained the same or slightly decreased from the beginning to the end of Experiment One, while the mean weight of tadpoles declined. The relationship (R^2) between length and weight for tadpoles was lower at the end of the experiment than initially, indicating that some of the surviving tadpoles were thin and in poor condition. If the experiment had extended for a longer time period, survivorship would have decreased below recorded levels.

In Experiment Two, survivorship was low but surviving tadpoles grew. Average weights of dead tadpoles were lower than those for survivors, but larger than initial mean weights. The greater

variability in the coefficients of variation of weight for dead tadpoles showed that mortality was not specific for any one size group (Table 6). The smaller coefficients of variation of weight for surviving tadpoles and the range of final distributions of weight (Appendix B, Figure B7), depicted a narrower distribution of weights among survivors. The relationship between length and weight (R^2) was higher among surviving tadpoles than for the initially stocked population.

Total tadpole production and production per unit of tadpole biomass were more influenced by the initial biomass stocked than by the initial density stocked (Tables 5 and 7). Both measurements of tadpole production were considerably lower in the first experiment, when the starting biomasses were high. In both experiments, the production/aquarium was lower than that measured at Lake One (Table 7). An inverse relationship ($r = -0.85$) existed between stocking biomass and production per unit of biomass: 748 mg stocked, 0.82 (TP/TB); 2,107 mg stocked, 0.39 (TP/TB); 8,200 mg stocked, 0.21 (TP/TB); and 16,948 mg stocked, - 0.059 (this negative TP/TB demonstrated that tadpoles lost weight).

Comparisons of Lakes One and Four: Lake One had higher levels of primary productivity than Lake Four, as indicated by the larger oxygen fluctuations in aquaria at Lake One (four to five times greater than at Lake Four toward the end of each experiment). The trophic status of the aquatic environments influenced survival, growth, and production of leopard frog tadpoles. At Lake One, where food was more abundant, survival and production per unit of tadpole biomass appeared density dependent within an experiment. Overall, results

for both experiments at Lake One indicated these variables were not directly related to initial density. At Lake Four, where the food availability was lower, survival was independent of density in both experiments. However, production per unit of tadpole biomass was inversely related to stocking density and biomass in both experiments. Production per unit of biomass was inversely related to initial biomass at Lake One and Lake Four, while survival was not. The results for Lake One and Experiment Two at Lake Four indicated that food per unit area placed an upper limit on the final biomass of tadpoles. In both experiments at Lake One, despite the different starting biomasses, the final average biomass/aquarium was from 10.3 to 12.8 g. In Experiment Two at Lake Four, the low density accumulated biomass while the high density lost biomass, suggesting the two populations would have equilibrated at some intermediate biomass, perhaps 900 mg/aquarium. Since space was a constant factor, the differences observed between the lakes seemed to be related to food production. Aquaria with tadpoles stocked at low and high densities in Experiment One at Lake Four lost similar proportions of initial biomass, about 45%, indicating that final tadpole biomass/aquarium was related to factors other than food production per unit area. However, data presented subsequently demonstrates that the high density of tadpoles stimulated algal productivity more than the low density stocking. Food per unit area in this experiment at Lake Four also influenced the final biomass maintained in both density treatments.

While tadpoles are influenced by the trophic characteristics of aquatic habitats, the grazing and metabolic activities of tadpoles, in turn, effect changes in the aquatic community in proportion to

their density, biomass, and production. Daily tadpole production, rather than the tadpole biomass present, better predicts the influence of tadpole grazing, because production is a better index of tadpole feeding and metabolic rates. A feedback loop should exist between the feeding and metabolic rates of tadpoles and the productivity of the algal community. The activities of tadpoles stimulates or depresses the production of autotrophs; in turn, autotrophic production should regulate the grazing intensity and tadpole production. The suitability of a habitat for tadpoles depends on the levels of autochthonous primary productivity and the importation of allochthonous food materials. The sections that follow detail the interactions of tadpoles with algal diversity, algal abundance, and primary productivity.

Tadpole Species Composition (Field Experiment Three)

Experiment Three was designed to examine the survival, growth, and production of bullfrog and green frog tadpoles reared in monoculture and in mixed-species culture (Tables 8 and 9). Personal observations and suggestions of others indicated that in natural, mixed populations of the two species, bullfrog tadpoles appear larger and more robust than green frog tadpoles at the same stage of development. One anticipated outcome of this experiment was the quantification of competition or other measureable interactions between these two species. Bullfrogs were larger than green frogs in this study; density was adjusted so initial total biomasses were similar among all treatments. This resulted in green frogs being more abundant than bullfrogs in the single-species and mixed-species treatments (Table 8).

Table 8. *Necrotics, biomasses (wet weight, mg), and lengths (snout-vent, mm) for monocultured bullfrog tadpoles, monocultured green frog tadpoles, and the mixed-species culture (contribution of bullfrogs, [B] and green frogs, [G]) in Experiment Three.*

	Bullfrogs		Mixed: Bullfrogs & Green Frogs		Green Frogs	
	Initial	Final	Initial	Final	Initial	Final
<u>Lake One</u>						
Total Biomass	73539 N ₀ = 30	79695 N ₁ = 30	71760 N ₀ = 45 [B] 33330 [G] 38430 N ₀ = 15 N ₁ = 15 N ₀ = 30 N ₁ = 28	73214 N ₁ = 43 [B] 34838 [G] 38376 N ₁ = 15 N ₁ = 28	69756 N ₀ = 60	72679 N ₁ = 59
Biomass/aq (range)	24513 (23269-25881)	26565 (26102-27327)	23920 (22942-24438) [B] 11110 [G] 12810 (10875-11228) (12067-13210)	24405 (23881-24898) [B] 11612.7 [G] 12792 (10999-12486) (11948-13545)	23252 (22676-23636)	24226 (22134-25707)
$\bar{x}$ Individual Wt. (range)	2451.3 (2327-2588)	2656.5 (2610-2732)	1594.7 (1529-1629) [B] 2222 [G] 1281 (1207-1321)	1702.7 (1592-1778) [B] 2323 [G] 1371 (1228-1505)	1162.6 (1134-1882)	1231.8 (1165-1286)
CV Wt.	28.3%	33.8%	42.2% [B] 34.0% [G] 34.9%	43.4% [B] 29.0% [G] 30.0%	32.5%	31.1%
$\bar{x}$ SV Length (range)	25.2 (24.5-25.4)	26.0 (25.5-26.5)	- [B] 23.7 [G] 19.9 (19.4-20.2)	- [B] 24.5 [G] 20.6 (20.0-21.2)	19.7 (19.6-19.9)	21.5 (19.6-24.5)
CV Length	8.5%	8.7%	11.1% [B] 6.0% [G] 6.0%	10.1% [B] 7.4% [G] 7.4%	7.7%	7.3%

Table 8 (cont'd.).

	Bullfrogs		Mixed: Bullfrogs & Green Frogs				Green Frogs	
	Initial	Final	Initial	Final	Initial	Final	Initial	Final
<u>Lake Four</u>								
Total Biomass	41269 N ₀ = 18	38774 N ₁ = 17	45281 N ₀ = 27 [R] 20461 [G] 22120 N ₀ = 18	37678 N ₁ = 25 [B] 15617 [G] 22061 N ₀ = 18	40030 N ₀ = 36	36883 N ₁ = 34		
Biomass/eq (range)	13756 (13109-14697)	12925 (11852-14062)	14194 (13875-14667) [B] 6820 [G] 7374 (6734-6902) (6973-7933)	12560 (11719-14332) [B] 5206 [G] 7354 (7001-7689)	13343 (12384-14189)	12294 (11858-12807)		
$\bar{X}$ Individual Wt. (range)	2292.7 (2185-2450)	2280.8 (2143-2370)	14193.7 (13875-14667) [B] 2273.4 [G] 1229 (1162-1322)	13259.4 (11719-14332) [B] 2231 [G] 1226 (1167-1282)	1111.9 (1032-1182)	1084.9 (988-1164)		
CV Wt.	25.7%	28.1%	[B] 40.1% [G] 16.4% [G] 28.4%	[B] 39.4% [G] 20.0% [G] 27.0%	34.3%	34.2%		
$\bar{X}$ SV Length (range)	18.7 (18.1-19.4)	19.4 (18.7-20.0)	[B] 18.6 [G] 15.3 (14.9-15.7)	[B] 19.3 [G] 15.2 (15.1-15.7)	14.5 (14.3-14.7)	14.8 (14.3-15.2)		
CV Length	9.6%	10.6%	[B] 8.5% [G] 7.5%	[B] 6.2% [G] 8.5%	11.3%	10.2%		

Table 9. Tadpole production (mg of wet weight, carbon, and nitrogen) for single-species (bullfrog and green frog tadpoles) and mixed-species (contribution of bullfrogs, [B] and green frogs, [G]) cultures in Experiment Three (27 d, 20.6 degree d).

EXPERIMENT THREE				
Lake One	Bullfrogs	Mixed: Bullfrogs & Green Frogs	Green Frogs	
Production/aq	2052.2	1396.5 502.7 893.5	1047.4	
		[B] [G]		
Production/aq/d	76.0	51.7 18.6 33.6	38.8	
		[B] [G]		
Production/aq/degree d	9.9	6.7 2.4 4.3	5.1	
		[B] [G]		
Carbon Production/aq	85.9	58.5 21.1 37.4	43.7	
		[B] [G]		
Nitrogen Production/aq	23.2	15.8 5.7 10.1	11.8	
		[B] [G]		
P/B	0.034	0.058 0.045 0.069	0.045	
		[B] [G]		
Initial Regression (Log Length - Log Weight)	$Y = 1.2743 + 0.3336X$	$Y = 1.2528 + 0.3802X$ $Y = 1.2764 + 0.2369X$	$Y = 1.2788 + 0.3010X$	
R ²	0.895	0.96 0.71	0.83	
		[B] [G]		
CV Regression	1.47	0.9% 1.5%	1.4%	
		[B] [G]		

Table 9 (cont'd.).

	Bullfrogs	Mixed: Bullfrogs & Green Frogs	Green Frogs
Final Regression (Log Length - Log Weight)	$Y = 1.2700 + 0.3541X$	$\bar{Y} = 1.2703 + 0.3313X$ $[G] Y = 1.2760 + 0.3027X$	$Y = 1.2710 + 0.3336X$
R ²	0.92	$\bar{Y}$ 0.95 0.85	0.87
CV Regression	1.1%	$\bar{Y}$ 1.0% 1.3%	1.3%
<u>Lake Four</u>			
Production/aq	-28.2	-91.5 -72.0 -19.5	-286.1
Production/aq/d	-1.04	-3.39 -2.67 -0.72	-10.60
Production/aq/degree d	-0.14	-0.44 -0.35 -0.09	-1.38
Carbon Production/aq	-1.18	-3.83 -3.01 -0.82	-11.98
Nitrogen Production/aq	-0.32	-1.03 -0.81 -0.22	-3.23
P/B	-0.002	-0.014 -0.011 -0.003	-0.214
Initial Regression (Log Length - Log Weight)	$Y = 1.2585 + 0.3607X$	$\bar{Y} = 1.2070 + 0.5504X$ $[G] Y = 1.2773 + 0.2744X$	$Y = 1.2637 + 0.3322X$

Table 9 (cont'd.).

	Bullfrogs	Mixed: Bullfrogs & Green Frogs	Green Frogs
R ²	0.90	[B] [G] 0.93 0.92	0.90
CV Regression	1.0%	[B] [G] 0.7% 0.8%	1.2%
Final Regression (Log Length - Log Weight)	Y = 1.2795 + 0.3462X	[B] Y = 1.2910 + 0.3167X [G] Y = 1.2722 + 0.3171X	Y = 1.2766 + 0.2926X
R ²	0.77	[B] [G] 0.89 0.97	0.81
CV Regression	1.7%	[B] [G] 0.7% 0.6%	1.6%

At both lakes, survival was high in all aquaria, regardless of treatment. At Lake One, survivorship of bullfrogs was 100%, 98% of the green frogs survived, and in the mixture of the two species, 100% of the bullfrogs and 93% of the green frogs survived. At Lake Four, 94% of the bullfrogs, 94% of the green frogs, and in the mixed-species culture, 78% of the bullfrogs and 100% of the green frogs survived. The apparently lower survival of bullfrogs in the mixed culture at Lake Four probably reflected the smaller number present more than an interaction with green frogs, since only two individuals died.

At Lake One, biomass/aquarium and mean weight per individual increased in all treatments, despite the deaths that occurred (Table 8). The range in the distribution of weight classes for bullfrogs reared in single-species culture broadened, but appeared more normally distributed than initially (Appendix B, Figure B8). In mixed-species culture, the final weight distribution of green frogs reflected a general shift of individuals into weight classes greater than the mean (Appendix B, Figure B9). The weight distribution of smaller bullfrogs changed little in the mixed-species treatment, while the weights of larger bullfrogs were spread more than initially (Appendix B, Figure B9). Green frogs reared in monoculture exhibited more growth for small to medium-sized tadpoles than in the larger weight classes (Appendix B, Figure B10). Coefficients of variation based on final weights decreased below initial values for bullfrogs and green frogs in mixed-species culture and green frogs in single-species culture. This coefficient increased slightly for bullfrogs reared in monoculture. The final relationship (R^2) for length and weight of tadpoles was higher than that measured initially for green frogs in

single- and mixed-species treatments and for monocultured bullfrogs, indicating a higher, more similar condition factor among these tadpoles. Values for R^2 , based on initial and final length-weight relationships of bullfrogs in mixed-species culture, remained high and similar.

At Lake Four, the initial and final distributions of weight for monocultured bullfrog tadpoles were alike, except for one individual that grew significantly (Appendix B, Figure B11). In mixed-species culture, smaller bullfrog tadpoles appeared to be adversely affected by green frog tadpoles, as shown by their weight losses (Appendix B, Figure B12). The final distribution of weight classes for green frogs in mixed-species culture was similar to that measured initially (Appendix B, Figure B12). Only for green frogs in mixed-species culture was the initial and final average weight of individuals similar, in all other treatments the final weights of tadpoles decreased (Table 8). Also, the relationship between length and weight (R^2) decreased in all tests except for green frogs in mixed-species treatments (Table 9). In single-species treatment, a general shift of green frog tadpoles into smaller weight classes occurred, except for the increased growth of one tadpole (Appendix B, Figure B13).

At Lake One, productivity was highest for bullfrogs, intermediate in the mixture of the two species, and lowest for green frogs in monoculture. Values for tadpole production per unit of tadpole biomass (TP/TB) reaffirmed this sequence of results; bullfrogs had the highest TP/TB ratios (0.084), the mixed-species treatment was intermediate (0.058), and green frogs exhibited the lowest production per unit of biomass (0.045). The TP/TB for bullfrogs reared in

monoculture was twice that of green frogs in single-species treatments. In mixed-species culture, the TP/TB of bullfrogs decreased to about half the TP/TB measured for bullfrogs in single-species culture and was the same as that for green frogs in monoculture. The green frogs in mixed-species culture had higher TP/TB values than those in single-species culture, but not as high as monocultured bullfrogs. Apparently, an interaction occurred between bullfrog and green frog tadpoles that benefited green frogs.

At Lake Four, values for production/aquarium/day and production per unit of biomass were negative in all treatments, indicating tadpoles lost weight (Table 9). Although production estimates were negative, the trends were the same as those observed at Lake One. Monocultured bullfrogs were the most successful in that they lost the least weight, the mixed-species culture was intermediate in weight loss, and green frogs in monoculture lost the most weight. In mixed-species culture, bullfrogs lost more weight than when reared in monoculture. Green frogs from the mixed-species culture had similar TP/TB ratios to bullfrogs from single-species treatments. As at Lake One, green frog tadpoles reared with bullfrogs seemingly benefited from this association, while the production of bullfrogs was substantially lowered.

Reducing Food and Space per Individual (Laboratory Experiment)

Algal concentrations, TetraMin, and tadpole density: In field experiments at Lakes One and Four, both density and biomass were varied in Experiments One and Two, so determining the separate effects of these factors on tadpole growth and survival was difficult. Laboratory studies were designed to investigate the relationship

between the density of tadpoles and their growth when the food and space per unit of total tadpole biomass were initially the same. The largest initial difference in total biomass/aquarium among the five density stockings was 13.4 mg or 10% (Table 10). Since little variation occurred among the three replicates at each density (largest coefficient of variation = 4%), statistically significant differences were measured among the density treatments before the experiment began, even though actual differences in biomass were minor. The densities of tadpoles (9, 4, 3, 2, or 1 per aquarium), when converted to number per m^2 or m^3 , were moderately high (13 to 120 tadpoles/ m^2 or 263 to 2,638 tadpoles/ m^3) compared to densities estimated in natural systems, but similar to those employed in the field experiments at Lakes One and Four. Because tadpole biomass was held constant while density was varied, the mean size and stage of tadpoles at lower densities were greater than for tadpoles at higher densities (Table 10).

After each algal supply rate (500, 1,000, and 1,500 ml), statistically significant differences were found between the total biomass at the highest stocking density (nine tadpoles, A-1 in Table 10) and all other total biomasses of tadpoles at the lower densities. The lower total biomass (A-1) was partially caused by tadpole death early in the experiment, resulting in the average number of tadpoles in this treatment to be eight for the remainder of the experiment (Table 10). However, the average difference in total biomass (mg $\pm$ SD) between A-1 and the mean of all other density groups was 198.7 $\pm$ 30.8 mg at 500 ml, 255.7 $\pm$ 35.3 mg at 1,000 ml, and 450.7 $\pm$ 98.8 mg at 1,500 ml of algal food. The biomass of tadpoles in the A-1

Table 10. Daily changes in mean weight, biomass, and production per unit of biomass for leopard frog tadpoles (wet weight in mg, coefficient of variation of weight, body length in mm, and developmental stage) during the algal feeding experiment (* change in weight per unit of total weight per day).

	A-1	A-2	A-3	A-4	A-5
<u>Initial Conditions</u>					
N_0/aa	9	4	3	2	1
$\bar{X} \text{ Wt}$ ($\pm$ SD)	78.6 ($\pm$ 27.8)	176.5 ($\pm$ 25.0)	233.7 ($\pm$ 7.3)	357.2 ($\pm$ 58.5)	706.5 ($\pm$ 0.7)
CV	35.3%	14.2%	3.1%	16.4%	0.1%
B/aa ($\pm$ SD)	707.8 ($\pm$ 4.8)	706.0 ($\pm$ 3.3)	701.0 ($\pm$ 1.0)	714.4 ($\pm$ 1.2)	706.5 ($\pm$ 0.7)
BL	7.8	10.3	11.5	12.6	17.5
Stages (Range)	S-(24-25)	S-(25-26)	S-(25-27)	S-(27-29)	S-29
<u>@ 500 ml after 14 d</u>					
N_1/aa	8	4	3	2	1
$\bar{X} \text{ Wt}$ ($\pm$ SD)	156.5 ($\pm$ 58.3)	360.3 ($\pm$ 72.1)	494.4 ($\pm$ 58.3)	725.0 ($\pm$ 84.5)	1501.0 ($\pm$ 19.6)
CV	43.1%	20.0%	11.8%	11.7%	1.8%
B/aa ($\pm$ SD)	1268.0 ($\pm$ 1.2)	1443.0 ($\pm$ 10.4)	1493.3 ($\pm$ 5.0)	1450.0 ($\pm$ 23.5)	1501.0 ($\pm$ 19.6)
$\Delta \bar{X} \text{ Wt/d}$	5.7	12.4	18.1	25.3	56.7
$\Delta B/aa/d$	40.0	50.1	54.3	52.5	56.8
$P/B/d$	0.057 (0.073)*	0.076	0.080	0.074	0.080
<u>@ 1000 ml after 6 d</u>					
N_2/aa	8	4	3	2	1
$\bar{X} \text{ wt}$ ($\pm$ SD)	227.6 ($\pm$ 101.3)	513.9 ($\pm$ 110.0)	690.8 ($\pm$ 127.0)	1024.5 ($\pm$ 107.4)	2129.0 ($\pm$ 52.0)
CV	44.7%	21.4%	18.4%	10.5%	2.4%
B/aa ($\pm$ SD)	1820.8 ($\pm$ 9.8)	2055.7 ($\pm$ 7.3)	2072.3 ($\pm$ 1.7)	2049.0 ($\pm$ 8.1)	2129.0 ($\pm$ 52.0)
$\Delta \bar{X} \text{ wt/d}$	11.5	24.1	31.8	49.9	104.7
$\Delta B/aa/d$	92.3	96.3	95.4	99.8	104.7
$P/B/d$	0.073	0.077	0.066	0.069	0.070

Table 10 (cont'd.).

	A-1	A-2	A-3	A-4	A-5
<u>@ 1500 ml after 4 d</u>					
N ₃ /aq	3	4	3	2	1
$\bar{X}$ Wt ($\pm$ SD)	295.2 ($\pm$ 132.5)	683.0 ($\pm$ 149.4)	951.3 ($\pm$ 226.6)	1367.7 ($\pm$ 183.4)	2928.5 ($\pm$ 119.5)
CV	44.9%	21.9%	23.8%	13.4%	4.1%
B/aq ($\pm$ SD)	2361.8 ($\pm$ 30.6)	2732.1 ($\pm$ 36.7)	2853.9 ($\pm$ 65.3)	2735.5 ($\pm$ 57.2)	2928.5 ($\pm$ 119.5)
$\pm \bar{X}$ Wt/d	16.9	39.9	63.3	85.8	199.6
$\pm B$ /aq/d	135.2	159.5	189.9	171.6	199.6
P/B/d	0.074	0.082	0.094	0.084	0.094
SL	12.0	15.9	19.1	23.1	29.9
Stages (Range)	S-(26-29)	S-(28-30)	S-(29-31)	S-(30-32)	S-34

Total Biomass Comparisons ^a					
	A-3	A-2	A-5	A-1	A-4
1. Initial	<u>701.0</u>	<u>706.0</u>	706.5	<u>707.9</u>	714.4
2. @ 500 ml	A-1	A-2	A-4	A-3	A-5
	1268.0	<u>1443.0</u>	<u>1450.0</u>	1483.0	1501.0
3. @ 1000 ml	A-1	A-4	A-2	A-3	A-5
	1820.8	<u>2049.0</u>	<u>2055.7</u>	2072.3	<u>2129.0</u>
4. @ 1500 ml	A-1	A-2	A-3	A-4	A-5
	2361.8	<u>2732.1</u>	<u>2735.5</u>	2953.9	<u>2928.5</u>

^a $t_{.05(4)} = 2.776$.

treatment averaged 16, 14, and 19% lower than in the other density treatments at the three algal supply rates. The greatest difference in biomass should have occurred at the 500-ml supply level, since it was during this period that tadpoles died. Instead, the largest average in total biomass was measured during the final feeding period, 1,500 ml. This could indicate that intraspecific competition was beginning to exert an affect on tadpoles in A-1, resulting in slower growth of certain individuals.

The daily growth rates of individual tadpoles at each of the five densities were compared after each feeding level and over the total 24-d period. No significant differences occurred among the individual growth rates of tadpoles within each density treatment at any of the feeding intensities or over the whole experiment (Kruskal-Wallis nonparametric test, $H = 1.0$, $\chi^2_{.01(4)} = 13.277$). These results indicate that the density treatments had no identifiable effect on the growth rates of individual tadpoles exposed to the experimental conditions. The mean change in wet weight/d over the entire 24-d study (values for all three feeding intensities were incorporated) was A-1 = 11.5%, A-2 = 12.0%, A-3 = 12.8%, A-4 = 11.8%, and A-5 = 13.1%. If small, density-related effects occurred, they were relatively minor compared to other factors which influenced growth. In general, the largest tadpoles in each density treatment grew fastest, especially when individual growth rates were averaged over the 24-d study without regard for algal supply rates (Figure 10). However, the average weight gain of the smallest tadpole and of all tadpoles in the different density stockings was sometimes greater than or similar to that of the largest tadpole during certain feeding intervals. This

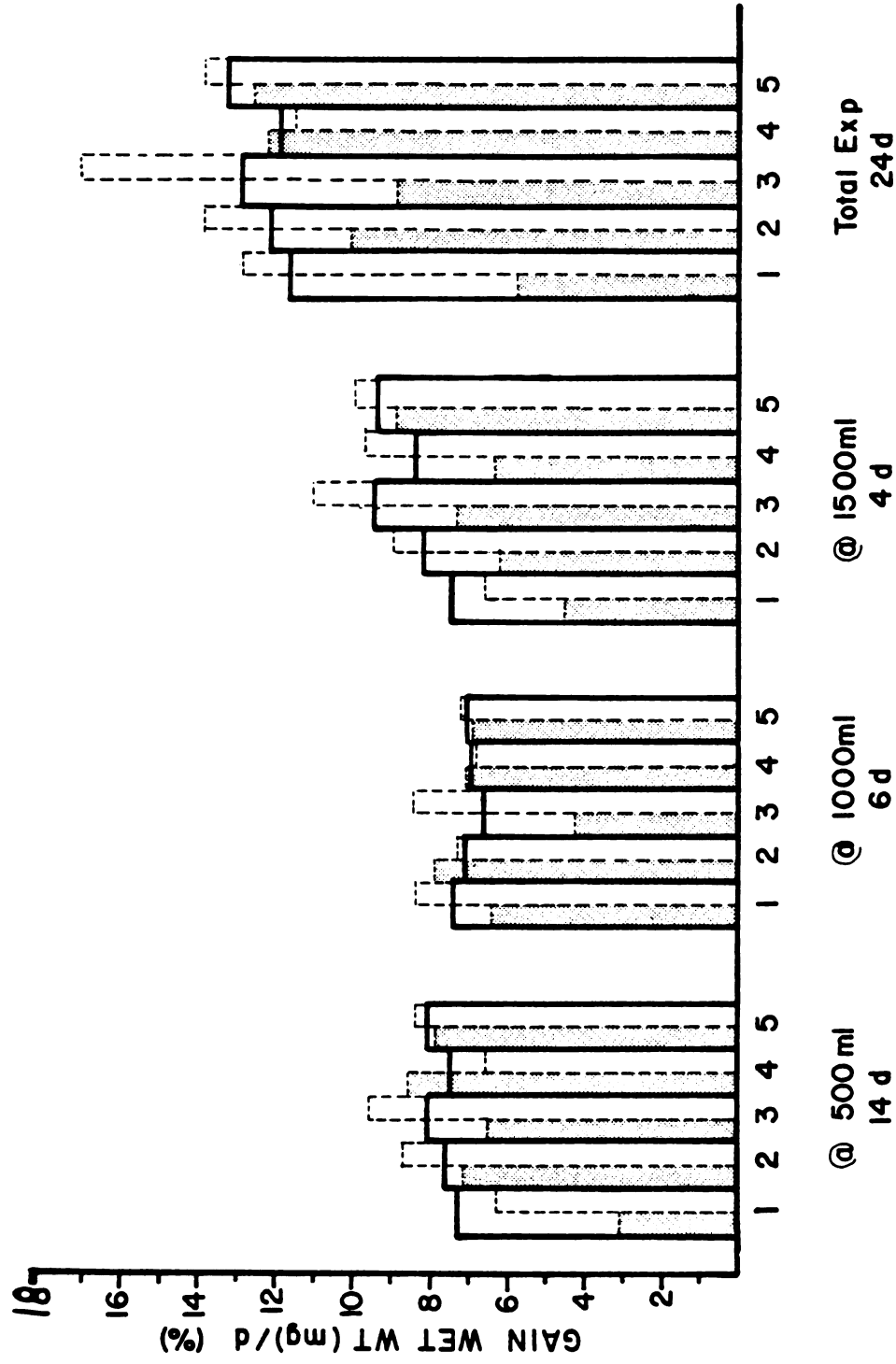


Figure 10. Average gain in weight of tadpoles (see Table 10 for numbers in density treatments A-1 through A-5) fed phytoplankton. Narrow, inner bars represent weight gain of smallest (shaded bar) and largest (unshaded bar) tadpole in each density stocking.

indicated that complete absence of growth or stunting did not consistently occur among the smaller tadpoles in the different density treatments.

Generally, the average change in weight/biomass/day was substantially higher for tadpoles fed TetraMin than for algal-fed tadpoles (Table 10 and Appendix B, Table B1). The two larger and better developed tadpoles, T(9) and T(10), exhibited average changes in weight like the algal-fed tadpoles. A relationship appeared to exist between the stage of development and the growth rates of tadpoles with younger, smaller tadpoles growing faster than older, larger tadpoles. The growth rates estimated for tadpoles fed TetraMin, a highly nutritious, digestible food, were higher than those measured for algal-fed tadpoles in the laboratory or for tadpoles in the field experiments at Lakes One and Four.

Ingestion and conversion efficiencies: The mean tadpole production/total biomass/day fluctuated during the periods when tadpoles were fed the three concentrations of algae (Table 10). At the first algal supply rate, the overall average TP/TB for all density treatments was 0.077. When food was increased to 1,000 ml, tadpole production averaged 0.070; at the final supply rate, 1,500 ml, mean daily tadpole production per unit of total biomass was 0.086. To some extent, these differences in tadpole production may have been influenced by variations in the supply of algae per unit of tadpole biomass in each stocking replicate. The concentrations of nutrients and phytoplankton varied over the duration of the study (Table 3). Although the amounts of algae provided to tadpoles increased through time, the actual

available food did not increase as anticipated (the second supply rate was designed to be 2X the first supply rate, and the third, 3X the first). The particulate carbon and nitrogen supplied in relation to the carbon and nitrogen measured in the tadpoles for A-1 (9 tadpoles) and A-5 (1 tadpole), the treatments with the extremes in tadpole density, are shown in Table 11.

In both density stockings, the average daily supply of carbon in relation to the growing biomass (carbon) of tadpoles decreased over the experimental period (Table 11). The ratio of the supply of nitrogen to tadpole biomass measured as nitrogen remained high at each supply level; the ratio (supply of nitrogen/tadpole nitrogen) was slightly lower at 1,000 ml of algae than at the 500- or 1,500-ml supply rate. However, the initial supply of carbon and nitrogen at the next supply rate was invariably higher than that at the previous feeding level (Table 11). The consumption of both carbon and nitrogen per unit of tadpole carbon and nitrogen decreased from the initial (500 ml) to the final (1,500 ml) supply level. Values for conversion (G/I) and assimilation (A/I) efficiencies indicated that tadpoles became increasingly more efficient at using the amounts of phytoplankton provided with the highest efficiencies estimated for tadpoles at the 1,500-ml supply rate (Table 12 and Appendix B, Table B2). The conversion of assimilated material into growth (G/A) was greatest for TetraMin-fed tadpoles (Table 12 and Appendix B, Table B2); the G/A estimated for TetraMin-fed tadpoles were similar to values for tadpoles fed 1,500 ml of cultured phytoplankton. The average carbon and nitrogen content of tadpoles fed TetraMin was significantly greater than for those fed algae ($P < 0.001$, Table 2), although the C-N ratios were similar

Table 11. Supply and consumption* of carbon and nitrogen in relation to the demand (measured as tadpole biomass in C and N) for the highest (A-1) and lowest (A-5) densities of leopard frog tadpoles.

	Supply of C,N/Biomass C,N		Consumption C,N/Biomass C,N	
	A-1	A-5	A-1	A-5
@ 500 ml				
1. Initial				
a) carbon (%)	87.6	87.7	70.4	70.6
b) nitrogen (%)	114.9	115.1	92.6	92.8
2. Final				
a) carbon (%)	48.9	41.3	39.3	33.2
b) nitrogen (%)	64.1	54.2	51.7	43.7
3. Average				
a) carbon (%)	68.2	64.5	54.8	51.9
b) nitrogen (%)	89.5	84.6	72.1	66.2
@ 1000 ml				
1. Initial				
a) carbon (%)	67.3	57.2	47.3	40.0
b) nitrogen (%)	97.2	82.1	85.5	72.3
2. Final				
a) carbon (%)	47.2	40.4	33.0	28.2
b) nitrogen (%)	67.7	57.9	59.6	50.9
3. Average				
a) carbon (%)	57.5	48.8	40.1	34.1
b) nitrogen (%)	82.4	70.0	72.5	61.6
@ 1500 ml				
1. Initial				
a) carbon (%)	60.2	51.5	40.9	35.0
b) nitrogen (%)	100.5	95.9	68.8	58.9
2. Final				
a) carbon (%)	46.4	37.5	31.5	25.4
b) nitrogen (%)	77.5	62.5	53.5	42.8
3. Average				
a) carbon (%)	53.3	44.5	36.2	30.2
b) nitrogen (%)	89.0	74.2	60.9	50.3

*Average tadpole consumption/d ($\pm$ SD):

@ 500 ml/d

- 1) 3.9 ($\pm$ 1.49) mg Particulate Kjeldahl N/aq
- 2) 15.2 ($\pm$ 2.01) mg Particulate Organic C/aq

@ 1000 mg/d

- 1) 6.55 ($\pm$ 2.14) mg Particulate Kjeldahl N/aq
- 2) 18.3 ($\pm$ 1.46) mg Particulate Organic C/aq

@ 1500 ml/d

- 1) 7.37 ($\pm$ 1.15) mg Particulate Kjeldahl N/aq
- 2) 22.7 ($\pm$ 2.58) mg Particulate Organic C/aq

Table 12. Growth (mg C), assimilation (mg C), and efficiencies (carbon) of tadpoles (*R. pipiens*) fed algae or TetraMin.

	Growth/d	Assimilation/d	Growth/ Assimilation (G/A%)	Conversion Efficiency (G/I%)	Assimilation Efficiency (A/I%)
PHYTOPLANKTON					
A-1					
$N_{t0} = 9, N_{t1-3} = 8$					
500 ml	1.22	3.17	38.5	3.0	20.9
1000 ml	2.91	6.04	46.7	15.4	33.0
1500 ml	4.13	8.13	50.8	18.2	35.3
A-2					
$N_{t0-3} = 4$					
500 ml	1.53	3.48	43.9	10.1	22.9
1000 ml	2.94	6.24	47.2	16.1	34.1
1500 ml	4.37	9.35	53.2	21.5	41.2
A-3					
$N_{t0-3} = 3$					
500 ml	1.56	3.59	45.0	10.9	24.3
1000 ml	2.91	6.22	46.9	15.9	34.0
1500 ml	5.80	10.37	55.9	25.5	45.7
A-4					
$N_{t0-3} = 2$					
500 ml	1.60	3.96	40.5	10.5	25.0
1000 ml	3.05	6.26	48.7	16.7	34.2
1500 ml	5.24	9.31	53.4	23.1	43.2
A-5					
$N_{t0-3} = 1$					
500 ml	1.73	3.84	45.1	11.4	25.3
1000 ml	3.20	6.67	47.9	17.5	36.4
1500 ml	6.09	10.95	55.7	25.8	48.2
TETRAMIN					
T(1)	1.55	1.41-2.88	72.3 (90.6-54.0)	-	-
T(2)	4.33	4.56-7.83	74.9 (94.6-55.3)	-	-
T(3)	6.85	7.17-12.31	75.5 (95.5-55.6)	-	-
T(4)	5.01	5.53-9.18	72.6 (90.6-54.6)	-	-
T(5)	7.68	9.46-14.14	72.5 (90.8-54.3)	-	-
T(6)	8.24	9.46-15.66	69.9 (87.1-52.5)	-	-
T(7)	9.19	11.05-17.98	67.1 (83.1-51.1)	-	-
T(8)	8.44	10.52-16.88	65.1 (80.2-50.0)	-	-
T(9)	7.02	10.55-15.34	65.4 (66.5-44.2)	-	-
T(10)	11.36	11.37-17.35	62.0 (75.8-48.0)	-	-

- indicates not measured.

in all tadpoles, regardless of the types of food ingested. Larger tadpoles fed TetraMin had slightly lower G/A and average daily weight gains than smaller tadpoles. Since tadpoles were fed excess TetraMin daily and density effects were excluded, this decrease in efficiency appeared related to developmental stage of the tadpoles.

Effects of Tadpoles on Organic Material and C, N, and P Dynamics

Tadpole Grazing Intensity and Periphyton (Experiments One and Two)

Lake One: Attached algae colonized all aquaria during the equilibration period before aquaria were stocked with tadpoles. The amount of organic material (oven-dried) averaged 1 g/aquarium in Experiments One and Two; no significant differences in amounts of periphytic algae and associated materials occurred in aquaria before tadpoles were introduced. After tadpoles were stocked in Experiment One, the daily accumulation of attached algae in stocked aquaria declined to about 30% of the accumulation rate in unstocked aquaria (Figure 11, Table 13 and Appendix B, Table B3). In Experiment Two, the tadpoles again significantly reduced the rates of periphytic accrual (Figure 11, Table 11 and Appendix B, Table B3). The daily accumulation of attached algae in aquaria with a high biomass of tadpoles declined to about 20% of that for unstocked aquaria. The aquaria with a low biomass stocking of tadpoles had accumulation rates about 30% of those measured for unstocked controls. In unstocked aquaria, mean rates of periphytic accumulation were slightly higher in the first experiment than in the second. In both experiments, periphytic carbon invariably comprised a major portion of the daily total amounts of organic carbon, regardless of treatment (Figure 11).

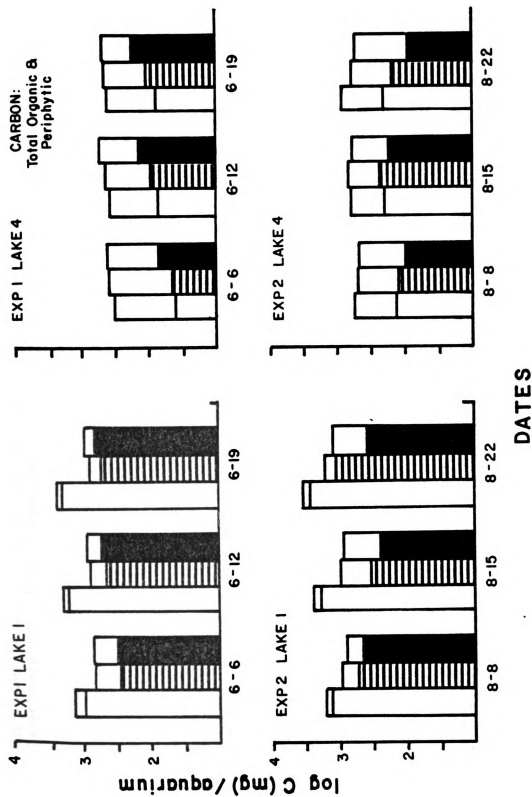


Figure 11. Total organic carbon and periphytic carbon (log C mg/aquarium) for Experiments One and Two at Lakes One and Four. Inner bars represent periphytic carbon (unstocked aquaria = unshaded bars, low biomass = horizontal bars and high biomass = shaded bars).

Table 13. Mean changes of organic carbon (mg C/42.8 liters/24 h) in unstocked and stocked (R. pipiens) aquaria for Experiments One and Two at Lake One.

CARBON	INITIAL IMPORT FROM LAKE	MEAN CHANGE OVER 24 H IN AQUARIA					
		UNSTOCKED		LOW STOCKING		HIGH STOCKING	
		GAIN	RESULT	GAIN	RESULT	GAIN	RESULT
<u>LAKE ONE -- EXPERIMENT ONE</u>							
(A) Dissolved organic	295.3	21.3	316.6	24.3	319.6	30.0	325.3
(B) Detrital	39.5	-29.2	10.3	-27.7	11.8	-25.3	14.2
(C) Phytoplanktonic	3.3	7.8	11.1	14.9	18.2	16.7	20.0
(D) Periphytic	0	95.5	95.5	25.8	25.8	28.0	28.0
(E) Tadpole	0	0	0	2.8	2.8	1.0	1.0
(F) Total organic	338.1	95.4	433.5	40.1	378.2	50.4	388.5
(G) Stored in aquaria: (D)+(E)	0	95.5	95.5	28.6	28.6	29.0	29.0
(H) Exported from aquaria: (A)+(B)+(C)	0	- 0.1	338.0	11.5	349.6	21.4	359.5
(I) (Storage) - (Export): (G)-(H)		95.6		17.1		8.0	
(J) Tadpole Effect: (Stocked) - (Unstocked)				-78.5		-87.6	

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Table 13 (cont'd.).

CARBON	LAKE ONE -- EXPERIMENT TWO	INITIAL IMPORT FROM LAKE	MEAN CHANGE OVER 24 H IN AQUARIA					
			UNSTOCKED		LOW STOCKING		HIGH STOCKING	
			GAIN	RESULT	GAIN	RESULT	GAIN	RESULT
(A)	Dissolved organic	393.4	-35.7	357.7	-10.5	382.9	-12.1	381.3
(B)	Detrital	82.1	13.9	96.0	-13.0	69.1	41.0	123.4
(C)	Phytoplanktonic	81.3	-48.9	32.4	3.7	85.0	25.2	106.5
(D)	Periphyton	0	89.8	89.8	28.0	28.0	12.1	12.1
(E)	Tadpole	0	0	0	15.7	15.7	16.9	16.9
(F)	Total organic	556.8	19.1	575.9	23.9	580.7	83.4	640.2
(G)	Stored in aquaria: (D)+(E)	0	89.8	89.8	43.7	43.7	29.0	29.0
(H)	Exported from aquaria: (A)+(B)+(C)	0	-70.7	486.1	-19.8	537.0	54.4	611.2
(I)	(Storage) - (Export): (G)-(H)		160.5		63.5		-25.4	
(J)	Tadpole Effect: (Stocked) - (Unstocked)				-97.0		-185.9	

During Experiment One, the high biomass of tadpoles had less impact than the low biomass on periphytic carbon, although differences between tadpole treatments were not statistically significant (Appendix B, Table B3). In Experiment Two, the high biomass stocking of tadpoles significantly depressed the periphytic biomass below levels in the aquaria with a low biomass of tadpoles (Appendix B, Table B3). The impacts of tadpoles on the periphytic biomass in the two experiments were not related simply to the biomass of tadpoles initially stocked. As a measure of differential grazing intensity in the two experiments, the initial and final tadpole biomass per aquarium were converted to carbon in mg. In Experiment One, the low stock of tadpoles initially contained 273.3 mg C and 358.1 mg C survived, whereas the high biomass treatment was initially 594.1 mg C and 446.7 mg C survived. In Experiment Two, 89.5 mg C were initially stocked and 436.0 mg C survived in the low biomass stocking of tadpoles and in the high biomass treatment, 297.7 mg C were stocked and 438.2 mg C survived. Tadpole production per unit of tadpole biomass per day was 24.7 times greater in the low biomass treatment in Experiment One and 3.1 times greater in Experiment Two than in the high biomass stocking. Although the stocked biomass of tadpoles was higher in Experiment One and tadpole production higher in Experiment Two, the average surviving biomass of tadpoles was similar in both experiments, 402.4 mg C in Experiment One and 409.4 mg C in Experiment Two. If grazing intensities were proportional to surviving biomasses of tadpoles, the estimated grazing intensities at the conclusion of the two experiments were similar. This may explain similarities in the response of the periphyton community to tadpoles. The similarity in rates of periphytic accumulation

in stocked aquaria for Experiments One and Two suggest that some critical amount of periphytic biomass was necessary to maintain algal production useful to tadpoles. Below that critical level, tadpoles had little additional impact on the rates of periphytic accumulation. But the net affect of tadpoles on periphyton may have been mediated by the availability of alternate food sources like phytoplankton and organic detritus.

Lake Four: At Lake Four, attached algae colonized aquaria during the equilibration period and aquaria were initially similar within an experiment. Amounts of organic material (oven-dried) averaged 94 mg/aquarium before tadpole introductions in the two experiments. Of the daily organic carbon present during the two experiments, about 25-35% was in the form of periphyton (Figure 11).

In Experiment One, tadpoles in both treatments appeared to stimulate periphytic accrual rates (Table 14). This response of the periphyton was associated with high biomasses of tadpoles stocked, high mortality, tadpole starvation, and low or even negative tadpole production. Less stimulation of periphytic growth occurred in treatments stocked with a low biomass of tadpoles, although tadpole production was greater than in the high biomass stocking of tadpoles. In Experiment Two, the high biomass of tadpoles depressed the attached algae while the periphytic biomass in aquaria with a low biomass of tadpoles was only slightly lower than in unstocked aquaria. At the conclusion of the second experiment, the abundance of periphyton in aquaria stocked with a high biomass of tadpoles was significantly lower than in unstocked aquaria (Appendix B, Table B3). In Experiment Two, the high

Table 14. Mean changes of organic carbon (mg C/42.4 liters/24 h) in unstocked and stocked (R. pipiens) aquaria for Experiments One and Two at Lake Four.

Table 14. Mean changes of organic carbon (mg C/42.4 liters/24 h) in unstocked and stocked (R. pipiens) aquaria for Experiments One and Two at Lake Four.

CARBON	INITIAL IMPORT FROM LAKE	MEAN CHANGE OVER 24 H IN AQUARIA					
		UNSTOCKED		LOW STOCKING		HIGH STOCKING	
		GAIN	RESULT	GAIN	RESULT	GAIN	RESULT
LAKE FOUR -- EXPERIMENT ONE							
(A) Dissolved organic	291.5	- 8.8	282.7	- 8.7	282.8	-13.3	278.2
(B) Detrital	29.0	- 4.8	24.2	- 6.4	22.6	- 0.2	28.8
(C) Phytoplanktonic	1.0	0.2	1.2	2.1	3.1	3.4	4.4
(D) Periphytic	0	3.5	3.5	4.5	4.5	6.8	6.8
(E) Tadpole	0	0	0	0.3	0.3	- 1.6	- 1.6
(F) Total organic	321.5	- 9.9	311.6	- 8.2	313.3	- 3.9	316.6
(G) Stored in aquaria: (D)+(E)	0	3.5	3.5	4.8	4.8	5.2	5.2
(H) Exported from aquaria: (A)+(B)+(C)	0	-13.4	308.1	-13.0	308.5	-10.1	311.4
(I) (Storage) - (Export): (G)-(H)		16.9		17.8		15.3	
(J) Tadpole Effect: (Stocked) - (Unstocked)				0.9		- 1.6	

Table 14 (cont'd.).

CARBON	INITIAL IMPORT FROM LAKE	MEAN CHANGE OVER 24 H IN AQUARIA					
		UNSTOCKED		LOW STOCKING		HIGH STOCKING	
		GAIN	RESULT	GAIN	RESULT	GAIN	RESULT
<u>LAKE FOUR -- EXPERIMENT TWO</u>							
(A) Dissolved organic	415.2	-34.9	380.3	-31.5	383.7	-42.4	372.8
(B) Detrital	21.3	25.7	47.0	5.6	26.9	1.1	22.4
(C) Phytoplanktonic	5.3	0.3	5.6	1.1	6.4	- 1.1	4.2
(D) Periphytic	0	4.1	4.1	4.0	4.0	2.6	2.6
(E) Tadpole	0	0	0	1.0	1.0	1.3	1.3
(F) Total organic	441.8	- 4.8	437.0	-19.8	422.0	-38.5	403.3
(G) Stored in aquaria: (D)+(E)	0	4.1	4.1	5.0	5.0	3.9	3.9
(H) Exported from aquaria: (A)+(B)+(C)	0	- 8.9	432.9	-24.8	417.0	-42.4	399.4
(I) (Storage) - (Export): (G)-(H)		13.0		29.8		46.2	
(J) Tadpole Effect: (Stocked) - (Unstocked)				16.8		33.2	

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biomass stock produced more tadpole biomass than any other initial stocking at Lake Four and the rate of periphytic accrual declined as tadpole productivity increased.

Grazing intensities were different in the two experiments at Lake Four. In Experiment One, the low biomass treatment was stocked with 287.0 mg C/aquarium and 133.9 mg C survived; the high biomass treatment was stocked with 593.1 mg C/aquarium and 255.6 mg C survived. In Experiment Two, tadpoles containing 28.9 mg C were stocked in each low biomass treatment and 30.2 mg C survived, while 81.4 mg C/aquarium was stocked in the high biomass treatment and 41.8 mg C survived.

Comparisons of Lakes One and Four: Overall, the average biomass of periphyton at Lake Four was about 4% of the amount at Lake One (Tables 13 and 14, Figure 11). In Experiment One, the similar stockings of tadpoles at the two lakes affected the periphyton differently. In contrast to Lake One where tadpole grazing consistently depressed periphyton, at Lake Four in Experiment One, tadpole activities stimulated periphytic growth. In the second experiment at Lake Four, the accumulation of periphyton was depressed by tadpoles, especially in aquaria with a high biomass stock. Apparently, the minimum periphytic production required by tadpoles was different at the two lakes, perhaps because of the dissimilarities in algal composition of the periphyton at Lakes One and Four.

The differences between the results of Experiment One at Lake Four and those of all other treatments in experiments at both lakes appeared related to the initial biomasses of tadpoles stocked and the daily accumulation rates of periphyton. The ratios of tadpole carbon stocked to periphytic carbon produced per day (unstocked aquaria

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provided an estimate of periphytic productivity without the influence of tadpoles) are presented in Table 15. The ratios calculated for

Table 15. Ratios of tadpole carbon (mg) initially stocked to periphytic carbon (mg/d) in unstocked aquaria.

	LOW BIOMASS	HIGH BIOMASS
<u>EXPERIMENT ONE</u>		
Lake One	5.05	8.84
Lake Four	117.00	242.00
<u>EXPERIMENT TWO</u>		
Lake One	1.29	4.29
Lake Four	9.12	25.70

Experiment One at Lake Four for tadpoles stocked at low and high biomass were 9-13 times greater than in any other treatment. The highest production of tadpoles occurred at Lake One in Experiment Two, when tadpole carbon stocked was 1.3-4.3 times the amount of periphytic carbon that accumulated per day.

Dissolved, Detrital, and Phytoplanktonic Organic Carbon (Experiments One and Two)

Lake One: The survival and production of tadpoles and their impact on the periphytic biomass were influenced by the availability of phytoplankton and detritus imported daily from the lakes into the aquaria. Tadpole activities, during the 24 h that the water remained in aquaria, affected the rates of flux between periphytic, particulate and dissolved organic carbon (Table 13). In this way, tadpoles influenced the total amount of organic carbon retained by aquaria or

exported from the system after 24 h. Carbon budgets that integrate the dynamic systems into average daily balances for the three treatments are presented in Table 13.

In the first and second experiments at Lake One, levels of dissolved organic carbon introduced into aquaria from the lake remained stable (Appendix B, Table B4). In Experiment One, dissolved organic carbon increased in both stocked and unstocked aquaria, while in Experiment Two, all aquaria exported this form of carbon (Table 13 and Appendix B, Table B4). However, in both experiments the dissolved carbon was always higher in water from aquaria stocked with tadpoles. In Experiments One and Two, most of the carbon that was imported and exported was dissolved (Table 13). Daily changes of dissolved organic carbon in aquaria were related to the rates that seston or periphyton generated dissolved carbon and decomposition rates of dissolved carbon. Dissolved carbon may have been generated by leakage of organics during algal productivity, lysis of dying algae, decomposition of imported detritus, or tadpole waste production. Tadpole-stocked aquaria in both experiments invariably had more dissolved carbon produced per day than unstocked aquaria. Although this may have been associated primarily with tadpole waste production, other tadpole affects on the autotrophic community or decomposers may have been involved.

Sestonic carbon introduced into aquaria from the lake remained stable during Experiment One and fluctuated in Experiment Two (Appendix B, Table B4 and Figure 12). In the first experiment, detritus comprised 92% of the seston in imported lake water, while in the second experiment, the seston was composed of similar proportions of detritus and phytoplankton (Table 13). In Experiment One, activities

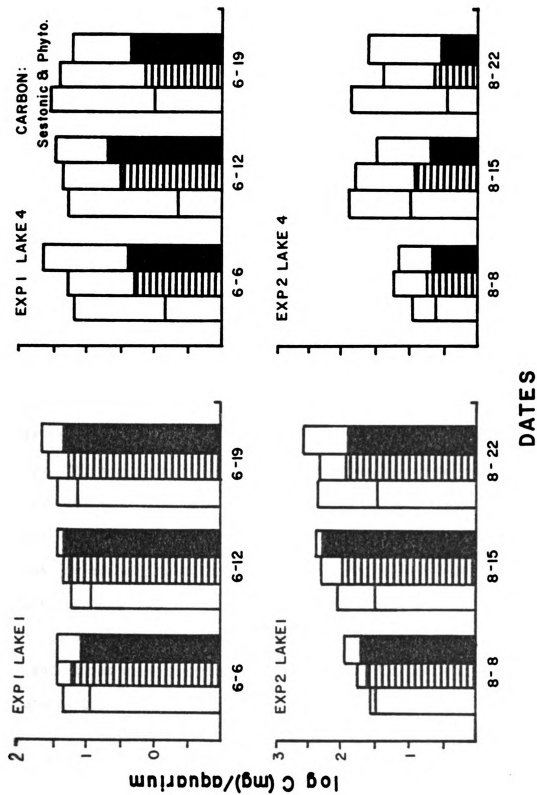


Figure 12. Sestonic and phytoplanktonic carbon ($\log C$ mg/aquarium/d) in aquaria during Experiments One and Two at Lakes One and Four. Inner bars represent phytoplanktonic carbon (unstocked aquaria - unshaded bars, low biomass = horizontal bars, and high biomass = shaded bars).

of tadpoles elevated the sestonic carbon above levels measured in the imported lake water and unstocked aquaria. In Experiment Two, the highest amounts of sestonic carbon in the water at the end of 24 h were sampled in aquaria with a high stock of tadpoles. Although both unstocked and low biomass stocked aquaria lost sestonic carbon over 24 h, the unstocked aquaria lost over four times more than aquaria with a low biomass of tadpoles.

Activities of tadpoles caused higher daily accumulations of phytoplankton than occurred in unstocked aquaria (Table 13, Figure 12). In Experiment One, mean phytoplanktonic biomass increased in all aquaria, but increased most in aquaria with tadpoles (39-44% higher than in unstocked aquaria). In Experiment Two, phytoplanktonic biomass declined in unstocked aquaria, but was maintained in tadpole-stocked aquaria, especially in those with a high biomass of tadpoles. If tadpoles consumed phytoplankton, the quantities consumed were lower than the amounts produced, otherwise the algal biomass would have declined or remained static. In Experiment One, phytoplankton were probably not an important food source, since tadpole production was low and phytoplankton increased dramatically. In Experiment Two, phytoplankton may have been consumed, along with periphyton, especially in aquaria with a low biomass of tadpoles. However, algal concentrations were elevated above those in imported lake water, unlike abundances in unstocked aquaria, which declined.

Compared to the amount of detritus imported from the lake, exported detritus was lower in all aquaria of Experiment One (Table 13 and Appendix B, Table B4). In Experiment Two, the amount of detritus decreased in aquaria with a low biomass of tadpoles, increased

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slightly in unstocked aquaria, and increased substantially in aquaria with a high biomass of tadpoles. Tadpoles apparently consumed or stimulated the decomposition of detritus in aquaria. In the high biomass treatment of Experiment Two, the depressive effects were outweighed by other tadpole activities that generated new detritus. Tadpoles were most productive in Experiment Two and had relatively high survival. Exceptionally active, healthy, and concentrated tadpoles could have increased turbulence, resuspended feces, and dislodged periphyton in excess of the amounts consumed or decomposed. Since live phytoplankton were abundant in aquaria with a high biomass of tadpoles, dying algae were probably not a major source of detritus.

In Experiment One, the overall impact of tadpoles on organic carbon was to increase the amount exported over that imported (Table 13). In Experiment Two, tadpoles stocked at a high biomass increased the export rates of organic carbon. In aquaria with a low biomass of tadpoles, export of organic carbon was much greater than that in unstocked aquaria. Tadpoles stocked at any biomass significantly depressed the amounts of carbon stored in periphyton in both experiments (Appendix B, Table B3 and Figure 11). In all cases, tadpoles reduced storage of organic carbon in aquaria, resulting in greater export than occurred in unstocked aquaria.

Lake Four: As at Lake One, tadpole survival, growth, and production were related to the amounts and kinds of seston imported daily from the lake, as well as periphytic production. Levels of total organic carbon were high in both experiments, but highest in the second experiment (Table 14 and Appendix B, Table B4). The dominant

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form of carbon in the imported lake water was dissolved organic carbon; it comprised 91-94% of the total organic carbon in the two experiments. The proportions of phytoplankton in the seston of the imported lake water differed in Experiments One and Two. Phytoplankton was about 3% of the seston in the first experiment and about 25% in the second experiment (Table 14 and Figure 12), so a major portion of the particulate organic carbon in both experiments was of detrital origin. Concentrations of dissolved and sestonic carbon fluctuated during both experiments at Lake Four (Appendix B, Table B4 and Figure 12).

In Experiment One, detrital and dissolved organic carbon were reduced in the water in stocked and unstocked aquaria, indicating that organic carbon was going to inorganic pools or being stored in the periphyton and tadpoles. The abundance of phytoplankton was higher in stocked aquaria than in the imported lake water or unstocked aquaria, this was especially notable in aquaria with a high biomass of tadpoles in Experiment One (Table 14 and Figure 12). The high stocking of tadpoles effected an increased export of detrital and phytoplanktonic carbon over levels in unstocked aquaria, but depressed dissolved organic carbon export. In Experiment One, all aquaria, regardless of treatment, had similar storage values of organic carbon, with the rates of import greater than those of export.

In Experiment Two, detrital carbon accumulated in the water in all aquaria, but stocked aquaria had much lower concentrations than unstocked controls. Tadpoles in Experiment Two apparently consumed a higher proportion of detrital organic carbon than in Experiment One. Phytoplanktonic carbon increased in aquaria with a low biomass of

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tadpoles and in unstocked aquaria over levels measured in imported lake water, but decreased in aquaria with a high biomass of tadpoles. In addition to detritus and periphyton, tadpoles in the high biomass treatment were evidently consuming phytoplankton. In the first experiment, no relationship occurred between tadpole treatments and the storage of organic carbon; in the second experiment, the storage of organic carbon was directly related to the presence and biomass of tadpoles.

Comparisons of Lakes One and Four: Concentrations of dissolved organic carbon were similar in Experiments One and Two at both lakes. Measurements of sestonic carbon at Lake Four were 70% of those at Lake One in Experiment One and 18% of Lake One values in Experiment Two (Tables 13 and 14). The ratio of phytoplankton to detritus at Lake Four was similar to that measured at Lake One in Experiment One. In Experiment Two at Lake Four, phytoplankton comprised a smaller portion of the seston than at Lake One, where living algae averaged half of the imported seston. The detrital carbon at Lake Four was apparently derived mainly from macrophytes, not phytoplankton.

At Lake One, concentrations of total organic carbon invariably increased in stocked and unstocked aquaria over the 24-h period, while at Lake Four, a decrease always occurred. The activities of tadpoles at Lake One caused considerably more organic carbon to be mobilized and exported from the system than in unstocked aquaria (see Tadpole Effects in Table 13). In Experiment One at Lake Four, the treatments had little influence on organic carbon, while in Experiment Two, tadpole stocking affected greater storage of organic carbon than in

unstocked aquaria (see Tadpole Effects in Table 14).

These data support the contention that as the fertility of a system is reduced, the total production exported from the system is reduced. Tadpoles in fertile waters increase the turnover rates and export of phytoplankton and periphyton, while deriving most of their nutrition from periphyton. Tadpoles in less productive environments, consume more imported detritus and are effective at retaining organic carbon in the system and reducing the proportion exported.

Impacts of Tadpole Composition on Phytoplankton and Periphyton (Experiment Three)

Comparisons of Lakes One and Four: The impacts on phytoplankton and periphyton by monocultured bullfrogs and green frogs were contrasted with those of a combination of the two species in Experiment Three (Table 16 and Figure 13). Although minor differences occurred among tadpole treatments, no major differences were consistently measured for phytoplankton and periphyton. The abundance of phytoplankton increased over levels in imported lake water in all aquaria during Experiment Three. Green frogs in single-species treatments increased the concentration of phytoplanktonic carbon over levels measured in aquaria with monocultures of bullfrogs at Lake One, but depressed phytoplanktonic biomass slightly more than single-species cultures of bullfrogs at Lake Four. Green frog tadpoles may have reduced periphyton slightly more than bullfrog tadpoles reared in single-species culture at Lake One (20% reduction of periphyton by green frogs below values for bullfrogs). The mixed-species culture consistently had intermediate affects on the periphyton at Lake One

Table 16. Mean changes in phytoplanktonic and periphytic carbon (mg C/42.8 liters) in aquaria with a single-species culture of bullfrog and green frog tadpoles and a mixed-species culture of bullfrogs and green frogs.

CARBON	INITIAL IMPORT FROM LAKE	MEAN CHANGE IN AQUARIA					
		BULLFROGS		MIXED: BULLFROGS AND GREEN FROGS		GREEN FROGS	
		GAIN	RESULT	GAIN	RESULT	GAIN	RESULT
<u>LAKE ONE -- EXPERIMENT THREE</u>							
Phytoplanktic (48 h)	47.9	6.7	54.6	10.6	58.5	8.3	56.2
Periphytic (24 h)		9.6		9.0		7.7	
Tadpole (24 h)		3.2		2.2		1.6	
<u>LAKE FOUR -- EXPERIMENT THREE</u>							
Phytoplanktic (48 h)	0.3	4.9	5.2	4.7	5.0	3.9	4.2
Periphytic (24 h)		5.4		4.8		4.8	
Tadpole (24 h)		-0.04		-0.14		-0.44	

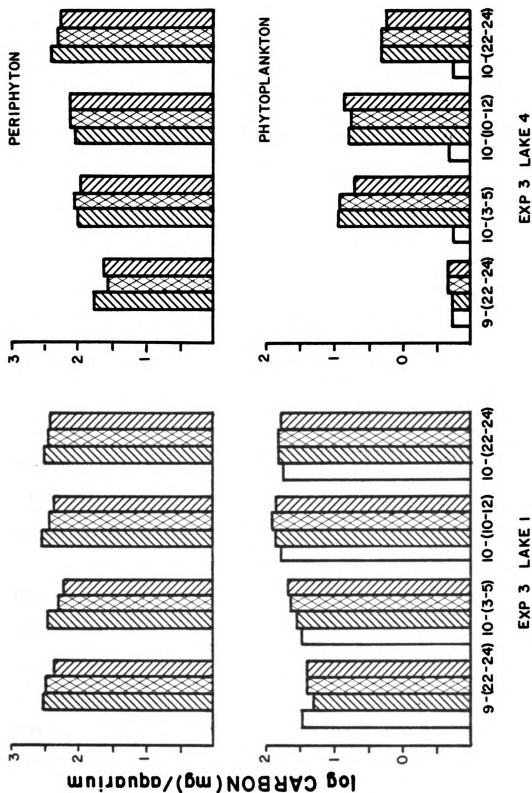


Figure 13. Periphytic and phytoplanktonic carbon in aquaria during Experiment Three at Lakes One and Four. Unshaded bars represent lake water and shaded bars represent bullfrogs, mixed-species and green frogs, respectively.

(Table 16, Figure 13). Comparisons of the average daily changes in periphytic carbon at Lake Four indicated that the mixed-species culture and green frogs reared in monoculture depressed periphyton the same amount, resulting in lower periphytic accrual than measured for bullfrogs in single-species treatments (Table 16). However, considerable variation occurred among sampling dates for the three tadpole treatments at Lake Four with no observable trend in total periphytic carbon among the tadpole groups tested.

Comparisons of Experiment Three with Experiments One and Two:

Results from Experiments One and Two with R. pipiens were compared with those of Experiment Three with R. catesbeiana and R. clamitans to determine if all species had similar effects upon primary producers. Relatively high biomasses of bullfrog and green frog tadpoles were stocked in Experiment Three, compared to stockings of leopard frog tadpoles in Experiments One and Two. At Lake One, the mean accrual of periphyton averaged somewhat less in Experiment Three than the mean accrual in Experiments One and Two, presumably because of the high stock of tadpoles and the shorter days with less light and cooler temperatures. At Lake Four, the mean daily accrual of periphyton in Experiment Three was similar to or slightly higher than that measured in Experiments One and Two. Periphyton declined more than anticipated in Experiment Three at Lake One and increased more than expected at Lake Four, based on results from Experiments One and Two.

Tadpole survival was higher in Experiment Three than in Experiments One and Two. At Lake One, tadpole production in Experiment Three was similar to production in Experiment One but lower than tadpole

production measured in Experiment Two. In summary, green frog and bullfrog tadpoles at Lake One produced more carbon than expected at the cooler temperatures and high biomasses of stocked tadpoles (see values for production/aquarium/degree d in Tables 7 and 9). Tadpoles at Lake Four in Experiment Three lost weight and may have died eventually of starvation as did leopard frog tadpoles in Experiment One. However, bullfrog and green frog tadpoles at Lake Four lost less weight than expected, based on results from R. pipiens treatments (see values for production/aquarium/degree d in Tables 7 and 9).

The phytoplanktonic carbon increased in all aquaria in Experiment Three over levels measured in the imported lake water as it did in tadpole-stocked aquaria in Experiments One and Two, except for the high biomass stocking of R. pipiens tadpoles in Experiment Two at Lake Four. In Experiment Three at Lake Four, the increase in the abundance of phytoplankton over values for imported lake water was proportionally greater than previous increases for any aquaria with tadpoles in Experiments One and Two. In summary, bullfrog, green frog and leopard frog tadpoles appeared to similarly affect the autotrophic communities in their respective aquaria. All three species consumed mainly periphyton and associated settled materials and usually stimulated the accumulation of phytoplankton in the water column.

Effects of Varying Tadpole Stocking Rates on Nitrogen (Experiments One and Two)

Lake One: Total inorganic nitrogen imported in lake water was over three times higher in Experiment One than in Experiment Two (Table 17 and Appendix B, Table B5). In the first experiment, nitrate

Table 17. Mean changes of nitrogen (mg N/42.8 liters/24 h) in unstocked and stocked (R. pipiens) aquaria for Experiments One and Two at Lake One.

NITROGEN	INITIAL IMPORT FROM LAKE	MEAN CHANGE OVER 24 H IN AQUARIA					
		UNSTOCKED		LOW STOCKING		HIGH STOCKING	
		STORED	EXPORTED	STORED	EXPORTED	STORED	EXPORTED
<u>LAKE ONE -- EXPERIMENT ONE</u>							
Inorganic (Total)	353.29	12.22	341.07	10.32	342.97	6.18	347.11
Nitrite	8.42	- 1.85	10.27	- 0.57	8.99	- 0.28	8.70
Nitrate	342.97	13.55	329.42	10.54	332.43	6.13	336.84
Ammonia	1.90	0.52	1.38	0.35	1.55	0.33	1.57
Organic (Total)	76.95	- 4.43	81.19	0.04	76.91	4.62	72.33
Dissolved	32.96	-25.33	58.29	-16.09	49.05	-26.66	59.62
Sestonic	43.99	21.19	22.80	16.13	27.86	31.28	12.71
Total Inorganic and Organic	430.24	7.98	422.26	10.39	419.88	10.82	419.44

Periphytic	0	8.18		3.54		3.50	
Tadpole	0	0		0.69		0.25	
Total Tadpole and Periphytic	0	8.18		4.23		3.75	

Nitrogen unaccounted for (after 24 h)			-0.20		6.16		7.05

Table 17 (cont'd.).

NITROGEN	INITIAL IMPORT FROM LAKE	MEAN CHANGE OVER 24 H IN AQUARIA					
		UNSTOCKED		LOW STOCKING		HIGH STOCKING	
		STORED	EXPORTED	STORED	EXPORTED	STORED	EXPORTED
<u>LAKE ONE -- EXPERIMENT TWO</u>							
Inorganic (Total)	113.89	+24.06	89.83	28.01	85.88	27.10	86.79
Nitrite	8.70	- 8.81	17.51	- 2.71	11.41	- 1.86	10.56
Nitrate	44.27	8.99	35.28	6.61	37.66	3.75	40.52
Ammonia	60.92	23.88	37.04	24.11	36.81	25.21	35.71
Organic (Total)	95.87	10.87	85.00	- 2.48	98.35	-16.74	112.61
Dissolved	42.20	-14.85	57.05	-13.70	55.90	-10.06	52.26
Sestonic	53.67	25.95	27.95	11.22	42.45	- 6.68	60.35
Total Inorganic and Organic	209.76	34.93	174.83	25.53	184.23	10.36	199.40
Periphytic	0	8.86		3.69		1.50	
Tadpole	0	0		4.17		4.48	
Total Tadpole and Periphytic	0	8.86		7.86		5.98	
Nitrogen unaccounted for (after 24 h)			26.07		17.67		4.38

comprised the largest proportion (97%) of the total inorganic nitrogen; in the second experiment, ammonia (53%) and nitrate (39%) predominated in the lake water. Proportions of dissolved and particulate organic nitrogen were similar in the two experiments, while total organic nitrogen was slightly higher in Experiment Two (20% higher) than in Experiment One.

Inorganic nitrogen was stored in all aquaria in both experiments, regardless of treatment (Table 17). In Experiment One, the unstocked aquaria stored the most inorganic nitrogen and in Experiment Two, the least inorganic nitrogen was stored in unstocked aquaria. The inorganic nitrogen imported into aquaria in Experiment One was mostly nitrate; in Experiment Two, particularly high concentrations of ammonia were imported with the nitrate. Ammonia concentrations declined in all aquaria in both experiments over the 24-h period. Some of the ammonia-nitrogen probably was absorbed by phytoplankton and the remainder escaped to the atmosphere as un-ionized ammonia formed at the high pH, temperature, and ammonia concentrations. In Experiment One, tadpoles appeared to accelerate the atmospheric loss of nitrogen and in Experiment Two, tadpoles retarded the escape of nitrogen to the atmosphere.

In Experiment One, organic nitrogen imported daily in lake water was stored by stocked aquaria (Table 17 and Appendix B, Table B5). Organic nitrogen was stored in unstocked aquaria and exported from stocked aquaria in Experiment Two. In both experiments, all aquaria exported dissolved organic nitrogen and aquaria without tadpoles generally lost the most. Tadpoles greatly elevated the export of sestonic nitrogen in the second experiment; aquaria with a high

stock of tadpoles lost more sestonic nitrogen from the system than was introduced in the lake water (Table 17 and Appendix B, Figure B14). In Experiment One, aquaria with a low biomass of tadpoles exported the most sestonic nitrogen and aquaria with a high stock exported the least (Table 17 and Appendix B, Figure B14). Tadpoles reduced the pool of total nitrogen stored in aquaria during both experiments by depressing the accumulation of periphytic nitrogen (Appendix B, Figure B15). Although tadpoles consistently lowered periphytic nitrogen, the amount of nitrogen relative to carbon (N:C ratio) in the periphyton was elevated in stocked aquaria.

As a consequence of their activities, tadpoles encouraged a net movement of nitrogen from periphyton into phytoplanktonic algae or themselves. In Experiment Two when tadpole production was highest, the decline in periphytic nitrogen was almost equivalent to storage in tadpole tissues, particularly in the low biomass stocking (Table 17). Although phytoplanktonic growth was stimulated in both experiments, the rate at which organic nitrogen was consumed or lost to the atmosphere in Experiment One exceeded its incorporation into phytoplankton. In Experiment Two, higher accumulations of phytoplankton resulted in a substantial export of organic nitrogen from stocked aquaria. This was particularly notable in aquaria with a high biomass of tadpoles in the second experiment, when little nitrogen was released to the atmosphere.

In summary, tadpoles in Experiment One slightly reduced the concentration of total nitrogen (non-gaseous) in the water which was later exported and in Experiment Two, tadpoles increased the export of total nitrogen (non-gaseous) in the water. In the first experiment,

tadpole activities elevated the amount of nitrogen that could not be accounted for by the nitrogen budget. This nitrogen probably escaped from stocked aquaria as ammonia or molecular nitrogen. Tadpoles depressed the release of nitrogen to the atmosphere in Experiment Two when more nitrogen escaped to the atmosphere from unstocked aquaria.

Lake Four: Organic nitrogen comprised over 95% of the total nitrogen during Experiments One and Two at Lake Four (Table 18 and Appendix B, Table B5). Most of the organic nitrogen was dissolved, only 11-12% was sestonic. The concentrations of inorganic nitrogen were particularly low, comprising less than 10% of the total nitrogen during both experiments at Lake Four. Total nitrogen concentrations varied less during the experiments at Lake Four than at Lake One (Appendix B, Figure B15 and Table B5). Average total nitrogen concentrations were much lower at Lake Four than at Lake One during the studies; dissolved organic nitrogen was the only component that was similar for the two lakes (Tables 17-18 and Appendix B, Figure B15).

In Experiment One, all aquaria exported nitrogen; aquaria with a high stocking of tadpoles exported the lowest amounts of total nitrogen, but the most total inorganic and dissolved organic nitrogen. In Experiment Two, all aquaria stored nitrogen, but unstocked aquaria stored the most, mainly because of the elevated storage of inorganic nitrogen (Table 18). Tadpoles generally caused nitrogen to be mobilized from detrital to dissolved organic nitrogen. In both experiments, aquaria stocked with a high biomass of tadpoles consistently exported the lowest amounts of sestonic nitrogen from the system (Table 18 and

Table 18. Mean changes of nitrogen (mg N/42.8 liters/24 h) in unstocked and stocked (R. pipiens) aquaria for Experiments One and Two at Lake Four.

NITROGEN	INITIAL IMPORT FROM LAKE	MEAN CHANGE OVER 24 H IN AQUARIA					
		UNSTOCKED		LOW STOCKING		HIGH STOCKING	
		STORED	EXPORTED	STORED	EXPORTED	STORED	EXPORTED
<u>LAKE FOUR -- EXPERIMENT ONE</u>							
Inorganic (Total)	1.28	-0.67	1.95	-0.81	2.09	-1.14	2.42
Nitrite	0.43	0	0.43	0	0.43	0	0.43
Nitrate	0.43	-0.58	1.01	-0.76	1.19	-0.95	1.38
Ammonia	0.43	-0.08	0.51	-0.04	0.47	-0.18	0.61
Organic (Total)	30.05	-2.14	32.19	-2.05	32.10	-1.28	31.33
Dissolved	26.28	-1.67	27.95	-1.20	27.48	-2.48	28.76
Sestonic	3.77	-0.47	4.24	-0.85	4.62	1.20	2.57
Total Inorganic and Organic	31.33	-2.81	34.14	-2.86	34.19	-2.42	33.75

Periphytic	0	0.53		0.70		1.05	
Tadpole	0	0		0.07		-1.41	
Total Tadpole and Periphytic	0	0.53		0.77		0.64	

Nitrogen unaccounted for (after 24 h)		-3.34		-3.63		-3.06	

Table 18 (cont'd.).

NITROGEN	INITIAL IMPORT FROM LAKE	MEAN CHANGE OVER 24 H IN AQUARIA					
		UNSTOCKED		LOW STOCKING		HIGH STOCKING	
		STORED	EXPORTED	STORED	EXPORTED	STORED	EXPORTED
<u>LAKE FOUR -- EXPERIMENT TWO</u>							
Inorganic (Total)	3.67	2.05	1.62	0.71	2.96	1.06	2.61
Nitrite	0.43	0	0.43	0	0.43	0	0.43
Nitrate	0.43	0	0.43	0	0.43	0	0.43
Ammonia	2.81	2.05	0.76	0.71	2.10	1.06	1.75
Organic (Total)	38.56	1.71	36.85	1.50	37.06	1.88	36.68
Dissolved	33.85	-0.95	34.80	-1.25	35.10	-1.50	35.35
Sestonic	4.71	2.66	2.06	2.74	1.96	3.38	1.33
Total Inorganic and Organic	42.23	3.76	38.47	2.21	40.02	2.94	39.29

Periphytic	0	0.64		0.61		0.41	
Tadpole	0	0		0.25		0.34	
Total Tadpole and Periphytic	0	0.64		0.86		0.75	

Nitrogen unaccounted for (after 24 h)			3.12		1.35		2.19

Appendix B, Figure B14). Aquaria with a low stocking of tadpoles effected the sestonic nitrogen differently in the two experiments; they increased the export in the first experiment and reduced it in the second. Periphytic nitrogen was stimulated in stocked aquaria in the first experiment; in Experiment Two, the accumulation of periphytic nitrogen was depressed in stocked aquaria below levels measured in unstocked aquaria (Table 18 and Appendix B, Figure B15). However, in the second experiment at Lake Four, more nitrogen was stored in periphyton and tadpoles than in the periphyton alone of unstocked aquaria.

Tadpoles in both experiments appeared to increase the levels of inorganic nitrogen in the water that was daily removed from aquaria. Elevated amounts of inorganic nitrogen in aquaria with tadpoles may have resulted from their ammonia excretion; this ammonia was later oxidized to nitrate. The concentrations of inorganic nitrogen were particularly low in Experiment One at Lake Four, probably low enough to encourage uptake of gaseous nitrogen by blue-green algae, causing a net gain of nitrogen in the aquaria by biological fixation. Levels of inorganic nitrogen exported from the system declined in all aquaria in Experiment Two. In this experiment, all aquaria lost nitrogen to the atmosphere, but stocked aquaria lost the least.

Carbon:Nitrogen ratios for organics: At Lake One, the C:N ratios in water of all aquaria tended to decline over the 24-h period, suggesting the amount of protein in the water increased (Appendix B, Table B6). The C:N ratio of dissolved organics was higher in stocked aquaria for both experiments at Lake One. In Experiment One, the carbon in seston was elevated in stocked aquaria; in Experiment Two,

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the amount of carbon relative to nitrogen in the seston was depressed in stocked aquaria below values estimated for unstocked aquaria. Tadpoles consistently depressed the C:N ratio of the periphyton, indicating they stimulated active growth of the remaining periphytic algae and removed unproductive material when feeding.

The C:N ratios of dissolved and sestonic materials in both experiments at Lake Four exceeded those estimated at Lake One, suggesting imported materials from Lake Four were less nutritious as food for tadpoles. The C:N ratio for dissolved organics decreased in all aquaria during the 24 h below values for the imported lake water, probably because of sestonic decomposition, leakage from photosynthesizing algae, or metabolic wastes from tadpoles. Sestonic C:N ratios were lower in unstocked aquaria and the low biomass stocking than in imported lake water during Experiment One. In all treatments in Experiment Two and the high stocking of tadpoles in Experiment One, the ratios of sestonic C:N were higher than originally measured in lake water.

The Effects of Tadpole Composition on Nitrogen (Experiment Three)

Lake One: Concentrations of nitrogen imported in the lake water in Experiment Three were similar to values in the two earlier experiments at Lake One (Tables 17 and 19 and Appendix B, Tables B5 and B7). All aquaria, whether stocked with bullfrogs, green frogs, or a combination of the two species, exported organic nitrogen (Table 19). Aquaria with a single-species culture of bullfrog or green frog tadpoles stored inorganic nitrogen, while aquaria representing the mixed-species treatment exported inorganic nitrogen. Inorganic nitrogen

Table 19. Mean changes of nitrogen (mg N/42.8 liters/48 h) in aquaria with a single-species culture of bullfrog and green frog tadpoles and a mixed-species culture of bullfrogs and green frogs.

Table 19. Mean changes of nitrogen (mg N/42.8 liters/48 h) in aquaria with a single-species culture of bullfrog and green frog tadpoles and a mixed-species culture of bullfrogs and green frogs.

NITROGEN	INITIAL IMPORT FROM LAKE	MEAN CHANGE OVER 24 H IN AQUARIA					
		BULLFROGS		MIXED SPECIES		GREEN FROGS	
		STORED	EXPORTED	STORED	EXPORTED	STORED	EXPORTED
<u>LAKE ONE -- EXPERIMENT THREE</u>							
Inorganic (Total)	308.15	4.26	303.89	- 3.09	311.24	+ 8.55	299.60
Nitrite	19.40	- 1.81	21.21	- 1.27	20.67	- 1.00	20.40
Nitrate	272.49	- 0.49	272.78	- 9.28	281.77	+ 0.85	271.64
Ammonia	16.26	6.36	9.90	7.46	8.80	8.70	7.56
Organic (Total)	88.17	-44.08	132.25	-35.09	123.26	-30.39	118.56
Dissolved	35.10	-26.26	61.63	-14.69	48.79	-11.98	47.08
Particulate	53.07	-17.55	70.62	-21.40	74.47	-18.41	71.48
Total Inorganic and Organic	396.62	-39.52	436.14	-37.88	434.50	-21.54	418.16

Periphytic	0	2.64		3.24		1.84	
Tadpole	0	1.72		1.16		0.88	
Total Periphytic and Tadpole	0	4.36		4.40		2.72	

Nitrogen unaccounted for (after 48 h)			-43.88		-42.28		-24.26

Table 19 (cont'd.).

NITROGEN	INITIAL IMPORT FROM LAKE	MEAN CHANGE OVER 24 H IN AQUARIA					
		BULLFROGS		MIXED SPECIES		GREEN FROGS	
		STORED	EXPORTED	STORED	EXPORTED	STORED	EXPORTED
<u>LAKE FOUR -- EXPERIMENT THREE</u>							
Inorganic (Total)	1.67	+ 0.14	1.53	0	1.67	0	1.67
Nitrite	0.43	0	0.43	0	0.43	0	0.43
Nitrate	0.43	0	0.43	0	0.43	0	0.43
Ammonia	0.81	+ 0.14	0.67	0	0.81	0	0.81
Organic (Total)	41.09	+ 3.00	38.09	+ 2.14	38.95	+ 4.28	36.81
Dissolved	24.40	- 7.27	31.67	+ 5.14	19.26	- 9.84	34.24
Particulate	16.69	+10.27	6.42	- 3.00	19.69	+14.12	2.57
Total Inorganic and Organic	42.76	+ 3.14	39.62	+ 2.14	40.62	+ 4.28	38.48

Periphytic	0	1.66		1.48		1.48	
Tadpole	0	- 0.02		- 0.08		- 0.24	
Total Periphytic and Tadpole	0	1.64		1.40		1.24	

Nitrogen unaccounted for (after 48 h)			1.50		0.74		3.04

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dynamics were influenced by ammonia concentrations; ammonia was always exported from aquaria at lower levels than was measured in the imported lake water (Table 19). Results from this study suggested that algae in all aquaria were fixing atmospheric nitrogen (Appendix B, Table B7 and Table 19). The maximum amount of nitrogen added by biological fixation was about 10% of the total nitrogen. This additional organic nitrogen was exported from aquaria as dissolved and sestonic nitrogen. Aquaria with a single-species culture of bullfrogs exported the most organic nitrogen and aquaria with monocultured green frogs exported the least. Bullfrog tadpoles in monoculture stored the most nitrogen in tadpole tissues; the elevated organic nitrogen and ammonia measured in these aquaria may have been related to tadpole waste production. Biological fixation of nitrogen at Lake One was difficult to interpret, since inorganic nitrogen was abundant and nitrogen-fixing blue-green algae were uncommon. Temporal variation occurred in the import of dissolved and sestonic organic nitrogen, indicating that the estimated increases in nitrogen may have been a sampling artifact (Appendix B, Figure B16 and Table B7). However, concentrations of organic nitrogen consistently increased during the 48-h periods on all sampling dates (Appendix B, Figure B16). Monocultured green frog tadpoles exhibited the lowest storage of nitrogen in tadpole tissues, but reduced the periphytic nitrogen more than the mixed-species treatment or single-species culture of bullfrogs (Table 19 and Appendix B, Figure B16). Generally, the affect of the mixed-species treatment on periphytic nitrogen was intermediate between that of monocultured bullfrogs and green frogs, so the impact of the combination of the two species was not

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substantially different from the average of the two single-species treatments.

Lake Four: Concentrations of nitrogen in the imported lake water resembled those measured in earlier studies at Lake Four, except for particulate nitrogen, which was higher in Experiment Three (Tables 18-19 and Appendix B, Tables B5 and B7). All treatments had little impact on inorganic nitrogen, the concentrations of inorganic nitrogen were low, similar to values measured in the first experiment. Estimates of exported organic nitrogen were lower than imported amounts in all aquaria, but lowest in aquaria with monocultured green frogs (Table 19). Green frogs in single-species culture accelerated the rates of transfer from sestonic to dissolved organic nitrogen. All tadpole treatments had a similar influence on periphytic nitrogen (Table 19 and Appendix B, Figure B16). Aquaria with a single-species culture of bullfrogs lost the most nitrogen from the system in the gaseous phase. The mixed-species treatment had the lowest amount of nitrogen leaving aquaria as ammonia or molecular nitrogen and the most exported in the water. Aquaria with monocultured green frogs stored the most organic nitrogen and the mixed-species treatment stored the least.

Effects of Tadpoles on Phosphorus (Experiments One, Two, and Three)

Concentrations of imported phosphorus were high and variable during Experiments One and Two at Lake One, but averaged higher in the second experiment (Table 20, Appendix B, Figure B17 and Table B8). In unstocked aquaria, a net movement of phosphorus out of seston and into the dissolved component occurred during both experiments (Table 20 and Appendix B, Figure B17). This dissolved phosphorus was used

Table 20. Mean changes of phosphorus (mg P/42.8 liters/24 h) in unstocked and stocked (R. piptens) aquaria.

Table 20. Mean changes of phosphorus (mg P/42.8 liters/24 h) in unstocked and stocked (R. pipiens) aquaria.

PHOSPHORUS	INITIAL IMPORT FROM LAKE	MEAN CHANGE OVER 24 H IN AQUARIA					
		UNSTOCKED		LOW STOCKING		HIGH STOCKING	
		STORED	EXPORTED	STORED	EXPORTED	STORED	EXPORTED
<u>LAKE ONE -- EXPERIMENT ONE</u>							
Total	28.68	+3.86	24.82	-0.85	29.53	0	28.68
Dissolved	23.54	+3.42	20.12	+3.42	20.12	+2.57	20.97
Particulate	5.14	+0.44	4.70	-4.27	9.41	-2.57	7.71
<u>LAKE ONE -- EXPERIMENT TWO</u>							
Total	63.77	+0.43	63.34	0	63.77	-2.14	65.91
Dissolved	48.79	-2.14	50.93	+0.85	47.94	+1.28	47.51
Particulate	14.98	+2.57	12.41	-0.85	15.83	-3.42	18.40
<u>LAKE FOUR -- EXPERIMENT ONE</u>							
Total	0.95	-0.21	1.16	-0.21	1.16	-0.46	1.41
Dissolved	0.56	-0.08	0.64	-0.17	0.73	-0.12	0.68
Particulate	0.39	-0.13	0.52	-0.04	0.43	-0.34	0.73

Table 20 (cont'd.).

PHOSPHORUS	INITIAL IMPORT FROM LAKE	MEAN CHANGE OVER 24 H IN AQUARIA					
		UNSTOCKED		LOW STOCKING		HIGH STOCKING	
		STORED	EXPORTED	STORED	EXPORTED	STORED	EXPORTED
		<u>LAKE FOUR -- EXPERIMENT TWO</u>					
Total	1.37	-0.04	1.41	-0.04	1.41	0	1.37
Dissolved	0.86	+0.43	0.43	+0.22	0.64	+0.26	0.60
Particulate	0.51	-0.47	0.98	-0.26	0.77	-0.26	0.77

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by periphyton or exported from unstocked aquaria. Tadpoles appeared to reverse this movement of phosphorus from sestonic to dissolved forms, so more phosphorus was exported from the system as particulates (Table 20 and Appendix B, Figure B17). Phytoplankton, which was daily exported from stocked aquaria in greater amounts than was exported from unstocked aquaria, evidently absorbed phosphorus and maintained it in particulate form.

Phosphorus concentrations in water imported from Lake Four were invariably lower than in water from Lake One; total phosphorus at Lake Four averaged only 2-3% of that at Lake One (Table 20, Appendix B, Figure B17 and Table B8). However, particulate phosphorus comprised a higher proportion of the total phosphorus in both experiments at Lake Four than at Lake One. As at Lake One, phosphorus concentrations were higher in the second experiment than in the first. In both experiments at Lake Four, all aquaria exported phosphorus from the system (Table 20). Aquaria with a high stock of tadpoles exported the most phosphorus in the first experiment, but 48% more phosphorus was exported from these aquaria than was measured in the imported lake water. During the second experiment, a movement of phosphorus out of sestonic into dissolved forms was observed in stocked aquaria (Table 20). Results from unstocked aquaria in Experiment Two depicted an increase in particulate phosphorus over values in imported lake water; this sestonic phosphorus was daily exported from unstocked aquaria.

In Experiment Three at both lakes, phosphorus concentrations were elevated above amounts measured in Experiments One and Two (Tables 20-21). At Lake One, the proportions of phosphorus in the particulate

Table 21. Mean changes of phosphorus (mg P/42.8 liters/48 h) in aquaria with a single-species culture of bullfrog and green frog tadpoles and a mixed-species culture of bullfrogs and green frogs.

PHOSPHORUS	INITIAL IMPORT FROM LAKE	MEAN CHANGE OVER 48 H IN AQUARIA					
		BULLFROGS		MIXED SPECIES		GREEN FROGS	
		STORED	EXPORTED	STORED	EXPORTED	STORED	EXPORTED
<u>LAKE ONE -- EXPERIMENT THREE</u>							
Total	111.28	+6.42	104.86	- 2.57	113.85	+ 3.43	107.85
Dissolved	87.31	+6.85	80.46	+ 9.41	77.90	+16.26	71.05
Particulate	23.97	-0.45	24.42	-11.98	35.95	-12.88	36.85
<u>LAKE FOUR -- EXPERIMENT THREE</u>							
Total	2.87	+0.17	2.70	+ 0.39	2.48	+ 0.43	2.44
Dissolved	2.40	+0.22	2.18	+ 0.26	2.14	+ 0.17	2.23
Particulate	0.47	-0.05	0.52	+ 0.12	0.34	+ 0.26	+ 0.21

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and dissolved forms were similar to those estimated in previous experiments (Appendix B, Tables B8-B9 and Figures B17-B18). In the third experiment at Lake Four, more of the phosphorus was dissolved than in the two earlier experiments (Tables 20-21 and Appendix B, Tables B7-B8).

The different species treatments appeared to effect phosphorus distributions at both lakes (Table 21 and Appendix B, Figure B18). At Lake One, green frog tadpoles reared in monoculture caused a net movement from the dissolved fraction into the particulate form of phosphorus. At Lake Four, single-species cultures of green frog tadpoles reversed this process and affected a higher rate of export of particulate phosphorus than occurred in monocultured bullfrogs or the mixed-species treatment. The mixed-species culture at both lakes generally had phosphorus concentrations which were intermediate between values for the two single-species treatments.

In summary, the net affect of tadpoles at Lake One, where phosphorus concentrations were high, was to maintain or increase the abundance of particulate phosphorus. Tadpoles at Lake Four generally depressed the movement of phosphorus from dissolved into particulate forms. Apparently, in the less productive waters of Lake Four, tadpoles accelerated the generation of dissolved phosphorus by their feeding and metabolic activities in excess of the phosphorus uptake rate by algae. In both lakes, the activities of tadpoles appeared to influence the phosphorus distribution and transferral of phosphorus between particulate and dissolved components.

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Phytoplanktonic Composition and Diversity

Overview

Ranid tadpoles potentially can influence the composition, diversity, and abundance of phytoplankton, since these tadpoles are among the larger suspension feeding vertebrates in aquatic environments of North America. The affect on the algal community may be direct, a result of their selection of particular algal taxa, or indirect, related to their influence on nutrient cycling or other physical and biological components. This portion of the field study was designed to elucidate the interactions between the phytoplanktonic community and different biomasses (densities) and species of tadpoles at Lakes One (hypereutrophic-eutrophic) and Four (mesotrophic-eutrophic).

In general, the same genera of algae were encountered at Lakes One and Four on particular sampling dates; however, abundances and proportions of phytoplankton in major algal groups differed substantially between the two lakes. Algal succession occurred at both lakes from May to October, so no particular algal taxon was dominant during any one experiment. The genera and volumes of phytoplankton sampled at Lakes One and Four during this study are presented in Appendix B, Table B10.

Experiment One (Lakes One and Four)

Imported lake water: In Experiment One, total algal numbers and volumes averaged two to three times higher at Lake One than at Lake Four (Appendix B, Tables B11-B12). Initially, diatoms were most

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numerous with lower concentrations of cryptophytes and green algae in water imported from Lake One (Appendix B, Table B12). During the experiment, diatoms decreased in abundance and green algae increased, which resulted in green algae comprising the largest proportion of algal numbers and volumes on the final sampling date in June. Algal succession also occurred at Lake Four, but blue-green algae numerically dominated the algal community at the conclusion of this study (Appendix B, Table B13). Diatoms were dominant volumetrically at Lake Four throughout the experiment; however, cryptophytes, green and blue-green algae were relatively important on particular sampling dates.

Tadpole effects: The major effects of tadpole feeding on the algal assemblages in Experiment One at Lake One are summarized in Table 22. In general, the activities of tadpoles stimulated phytoplanktonic growth; the highest total numbers and volumes of algae were invariably sampled in stocked aquaria (Table 22 and Appendix B, Table B11). The effects of grazing intensity, simulated by low or high densities (biomasses) of tadpoles, were usually not statistically separable. Although both tadpole treatments influenced the algal community similarly, the magnitude of the response was typically greater in aquaria stocked with a high abundance of tadpoles. On 6 June, after tadpoles had been in aquaria for six days, all algal groups (green algae, cryptophytes, diatoms, and blue-green algae) increased in abundance. In contrast, unstocked aquaria on this date had substantially lower concentrations of phytoplankton (Table 22 and Appendix B, Table B11). Among the major phyla of phytoplankton sampled, blue-green algae and diatoms were consistently elevated by

Table 22. Phytoplanktonic comparisons between unstocked (C for control) and tadpole-stocked (L for low and H for high stock of *R. pipiens*) aquaria in Experiment One at Lake One.

EXPERIMENT ONE--LAKE ONE				
	1. Numbers of Greens			
6 June	F = 19.3**	3607(C)	7068(H)	10539(L)
	2. Volumes of Greens			
6 June	F = 11.07**	301484(C)	496537(H)	842028(L)
	3. Numbers of Diatoms			
12 June	F = 4.41	7233(C)	19527(L)	26678(H)
19 June	F = 4.07	4046437(C)	5111234.7(L)	6754916.3(H)
Combined 3 Dates	F = 3.07**	9897(C)	18505(L)	20429(H)
	4. Volumes of Diatoms			
6 June	F = 4.88	3595389.7(C)	4534885.7(H)	5822352.3(L)
Combined 3 Dates	F = 1.43**	3475970(C)	5092362.3(L)	6695596.4(H)
	5. Number of Blue-greens			
6 June	F = 27.18***	62(C)	3505(L)	3544(H)
12 June	F = 4.93	2022(C)	7236(L)	9229(H)
19 June	F = 3.89	3896(C)	9408(L)	10179(H)
Combined 3 Dates	F = 7.94**	1993(C)	6716(L)	7651(H)
	6. Volumes of Blue-greens			
6 June	F = 30.42***	1030(C)	540020.7(L)	576726(H)
12 June	F = 6.70*	76405(C)	920241.7(L)	1246660.7(H)
19 June	F = 14.58**	91167.7(C)	909720.7(H)	1011011(L)
Combined 3 Dates	F = 19.77***	56201(C)	82357.8(L)	911035.9(H)
	7. Numbers of Cryptophytes			
6 June	F = 7.90*	860(C)	1592(L)	2059(H)
	8. Total Numbers of Algae			
6 June	F = 25.53**	15752(C)	26596(H)	32775(L)
12 June	F = 6.48*	25810(C)	48058(L)	62263(H)
Combined 3 Dates	F = 5.74**	26957(C)	43946(L)	48145(H)
	9. Total Volumes of Algae			
6 June	F = 8.65*	4264957(C)	5199578(H)	7733370(L)
12 June	F = 4.82	4382065.3(C)	9050150(L)	12223997.7(H)
Combined 3 Dates	F = 9.32***	5175412.4(C)	3505894.2(L)	3046361(H)
	10. Numerical Diversity of Diatoms			
19 June	F = 22.98**	0.3643(L)	0.3670(H)	1.000(C)

Table 22 (cont'd.).

EXPERIMENT ONE--LAKE ONE				
	11. Volume Diversity of Greens			
6 June	F = 8.18*	<u>0.9040(H)</u>	<u>0.9627(C)</u>	1.1533(L)
	12. Volume Diversity of Diatoms			
12 June	F = 8.16*	<u>0.4530(L)</u>	<u>0.5000(H)</u>	0.8267(C)
19 June	F = 27.99***	<u>0.3797(L)</u>	<u>0.4737(H)</u>	1.1650(C)
Combined 3 Dates	F = 3.09	<u>0.4276(L)</u>	<u>0.4401(H)</u>	<u>0.7259(C)</u>
	13. Volume Diversity of Blue-greens			
12 June	F = 11.66**	<u>0.0327(H)</u>	<u>0.1363(L)</u>	0.5507(C)
	14. Mean Sizes of Greens			
12 June	F = 4.39	<u>70.3(H)</u>	<u>79.3(L)</u>	<u>93.6(C)</u>
	15. Mean Sizes of Blue-greens			
6 June	F = 194.46***	16.6(C)	<u>154.1(L)</u>	<u>162.7(H)</u>
12 June	F = 25.49**	37.8(C)	<u>127.2(L)</u>	<u>135.1(H)</u>
19 June	F = 15.95**	23.4(C)	<u>39.4(H)</u>	<u>107.5(L)</u>
Combined 3 Dates	F = 15.22***	28.2(C)	<u>119.1(H)</u>	<u>122.7(L)</u>
	16. <u>Scenedesmus</u>			
Combined 3 Dates	F = 10.06**	<u>1178(H)</u>	<u>1648(L)</u>	5347(C)
	17. <u>Schroederia</u>			
Combined 3 Dates	F = 20.43***	677(C)	<u>4145(L)</u>	<u>5194(H)</u>
	18. <u>Dictyosphaerium</u>			
Combined 3 Dates	F = 7.07***	306(C)	<u>3306(L)</u>	<u>4090(H)</u>
	19. <u>Nitzschia</u>			
Combined 3 Dates	F = 7.13**	8472(C)	<u>17083(L)</u>	<u>19057(H)</u>
	20. Coccoid Blue-green Cell			
Combined 3 Dates	F = 20.76***	235(C)	<u>5106(L)</u>	<u>5546(H)</u>

*F_{.05} (2,6) = 5.14; F_{.05} (2,24) = 3.40

**F_{.01} (2,6) = 10.90; F_{.01} (2,24) = 5.61

***F_{.001} (2,6) = 27.00; F_{.001} (2,24) = 9.34

the activities of tadpoles (Table 22). This proportional increase in blue-green algae and diatoms in stocked aquaria was not related to the decreased abundances of green algae and cryptophytes, since values for these groups were similar to those in unstocked aquaria (Appendix B, Tables B11 and B13). Rather, the numerical proliferation of diatoms and blue-green algae in stocked aquaria decreased the relative contributions of green algae and cryptophytes to the total algal assemblage.

The mean size of blue-green algae was always greater in aquaria stocked with tadpoles, while green algae tended to be larger in unstocked controls (Table 22 and Appendix B, Table B11). The lowest numerical and volumetric diversity of diatoms, volumetric diversity of blue-green algae, and except on 6 June, the lowest total numerical and volumetric diversity and evenness were measured in stocked aquaria (Table 22 and Appendix B, Table B14). Green algae, Dictyosphaerium and Schroederia were significantly elevated and Scenedesmus was significantly depressed in stocked aquaria (Table 22 and Appendix B, Table B15). The diatom Nitzschia and a coccoid blue-green alga were more numerous in tadpole treatments than in unstocked controls (Table 22 and Appendix B, Table B15). Chlamydomonas and small Anabaena tended to decrease in aquaria stocked with tadpoles (Appendix B, Table B15). Concentrations of other algal genera varied among treatments and sampling dates with no distinctive patterns.

In Experiment One at Lake Four, tadpole grazing stimulated phytoplanktonic increases, resulting in greater total algal numbers, total algal volumes, and mean sizes of algae than occurred in unstocked aquaria (Table 23 and Appendix B, Table B12). The effects of grazing

Table 23. Phytoplanktonic comparisons between unstocked (C for control) and tadpole-stocked (L for low and H for high stock of *R. pipiens*) aquaria in Experiment One at Lake Four.

EXPERIMENT ONE--LAKE FOUR				
1. Number of Greens				
6 June	F = 5.40*	<u>2698(C)</u>	<u>3884(H)</u>	5069(L)
2. Volume of Greens				
6 June	F = 6.55*	<u>143516(C)</u>	<u>257266(H)</u>	371645.3(L)
3. Number of Diatoms				
6 June	F = 11.89**	<u>440(C)</u>	<u>918(L)</u>	1698(H)
12 June	F = 7.42*	245(C)	4960(L)	7580(H)
19 June	F = 13.35**	<u>1009(C)</u>	<u>2243(L)</u>	5102(H)
Combined 3 Dates	F = 8.92**	565(C)	2707(L)	4793(H)
4. Volume of Diatoms				
6 June	F = 6.62*	<u>145783.7(C)</u>	<u>292666.7(L)</u>	610393(H)
12 June	F = 7.36*	<u>75107(C)</u>	<u>1567038(L)</u>	2403114(H)
19 June	F = 18.29**	318844(C)	709482(L)	1612232(H)
Combined 3 Dates	F = 28.16***	179911.7(C)	356395.6(L)	1541913(H)
5. Volume of Blue-greens				
6 June	F = 7.91*	54980(C)	<u>193715(L)</u>	<u>219701.7(H)</u>
6. Total Number of Algae				
6 June	F = 17.02**	4413(C)	<u>7833(H)</u>	<u>8390(L)</u>
12 June	F = 6.68*	3669(C)	<u>5947(L)</u>	<u>11862(H)</u>
7. Total Volumes of Algae				
6 June	F = 15.77**	448847.7(C)	<u>933800(L)</u>	<u>1225962(H)</u>
12 June	F = 9.00*	215826(C)	1806356(L)	2639837(H)
19 June	F = 18.84**	<u>1105529(C)</u>	<u>1584649(L)</u>	2299105(H)
Combined 3 Dates	F = 12.63***	590494(C)	1441601.8(L)	2049387.1(H)
8. Numerical Diversity of Greens				
6 June	F = 17.93**	1.005(C)	<u>1.375(H)</u>	<u>1.458(L)</u>
Combined 3 Dates	F = 4.16*	1.070(C)	<u>1.290(L)</u>	<u>1.301(H)</u>
9. Volume Diversity of Blue-greens				
6 June	F = 5.45*	<u>0.094(H)</u>	<u>0.226(L)</u>	0.551(C)

Table 23 (cont'd.).

EXPERIMENT ONE--LAKE FOUR				
10. Total Volume Diversity of Algae				
12 June	F = 22.78**	<u>0.489(H)</u>	<u>0.625(L)</u>	1.685(C)
Combined				
3 Dates	F = 2.97	<u>1.051(H)</u>	<u>1.206(L)</u>	1.602(C)
11. Volume Evenness				
12 June	F = 20.68**	<u>0.202(H)</u>	<u>0.248(L)</u>	0.736(C)
Combined				
3 Dates	F = 6.92**	<u>0.419(H)</u>	<u>0.492(L)</u>	0.580(C)
12. Mean Sizes of Greens				
6 June	F = 6.36*	53.2(C)	<u>68.2(H)</u>	<u>73.3(L)</u>
13. Mean Sizes of Total Algae				
6 June	F = 5.38*	<u>101.7(C)</u>	<u>111.3(L)</u>	156.5(H)
12 June	F = 67.71***	58.2(C)	195.0(L)	222.5(H)
19 June	F = 14.81**	80.6(C)	93.2(L)	147.5(H)
Combined				
3 Dates	F = 18.35***	81.5(C)	122.4(L)	174.3(H)
14. <u>Scenedesmus</u>				
Combined				
3 Dates	F = 7.64**	75(C)	<u>508(H)</u>	<u>641(L)</u>
15. <u>Nitzschia</u>				
Combined				
3 Dates	F = 3.13**	553(C)	2699(L)	4773(H)
16. Coccoid Blue-green Cell				
Combined				
3 Dates	F = 4.51*	231(C)	<u>719(L)</u>	<u>779(H)</u>
17. Small <u>Anacystis</u>				
Combined				
3 Dates	F = 7.41**	61(H)	470(L)	739(C)

* $F_{.05}(2,6) = 5.14$; $F_{.05}(2,24) = 3.40$

** $F_{.01}(2,6) = 10.90$; $F_{.01}(2,24) = 5.61$

*** $F_{.001}(2,6) = 27.00$; $F_{.001}(2,24) = 9.34$

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intensity, simulated by low or high densities (biomasses) of tadpoles, influenced the algal community similarly, but the response was significantly greater in magnitude in aquaria with high numbers of tadpoles. Aquaria stocked with a low number (biomass) of tadpoles generally had algal abundances and volumes that were intermediate between those measured in unstocked aquaria and in aquaria with a high density (biomass) of tadpoles. The activities of tadpoles in both treatments elevated diatom numbers and volumes, total numbers of algae, and mean sizes of total algae over values in unstocked controls; however, these measurements were significantly higher in aquaria with a high stocking of tadpoles (Table 23 and Appendix B, Table B12). The greater numbers and volumes of diatoms sampled in stocked aquaria were related mainly to significant increases in Nitzschia (Table 23 and Appendix B, Table B15). The proportionately greater increases in numbers and volumes of diatoms in stocked aquaria lowered the relative contributions of all other algal groups, especially in aquaria with a high stock of tadpoles (Appendix B, Table B13).

Numbers and volumes of green algae tended to be greater in aquaria stocked with tadpoles than in unstocked aquaria (Appendix B, Table B12). In particular, one genus of green algae, Scenedesmus, was more numerous in aquaria with tadpoles (Table 23 and Appendix B, Table B15). Tadpole grazing also influenced the numerical diversity of green algae, resulting in higher diversity values than those estimated in aquaria without tadpoles (Table 23 and Appendix B, Table B16). After 6 June, the numbers and volumes of blue-green algae were lowest in aquaria with a high stocking of tadpoles. The total number of blue-green algae were typically lowest in unstocked

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aquaria, while the volumetric diversity of blue-green algae tended to be highest in aquaria without tadpoles (Table 23 and Appendix B, Table B16). Small Anacystis was least abundant in aquaria with tadpoles and a small coccoid blue-green alga was invariably elevated in stocked aquaria (Table 23 and Appendix B, Table B15). Throughout this experiment at Lake Four, activities of tadpoles decreased the volumetric diversity and evenness calculated for the total algal community (Table 23 and Appendix B, Table B16). As at Lake One, on 6 June, the first sampling date after tadpoles were stocked, significant increases were measured for many algal variables, including numbers, volumes, and mean sizes of green algae; volumes and volumetric diversity of blue-green algae; and total numbers, volumes and mean sizes of algae in stocked aquaria.

Experiment Two (Lakes One and Four)

Imported lake water: In July, when Experiment Two began, the total numbers, volumes, and mean sizes of algae were larger in the water imported from Lake Four than from Lake One (Appendix B, Tables B17-B18). During Experiment Two, algae bloomed at Lake One and afterwards, total algal numbers and volumes were much greater than at Lake Four, where no bloom occurred. Initially, the algal assemblage at Lake One was dominated numerically by green algae and volumetrically by diatoms (Appendix B, Table B19). Before the green and blue-green algal bloom in late August, cryptophytes, diatoms, and blue-green algae comprised a major proportion of total algal volumes and numbers on particular sampling dates. At Lake Four, the phytoplanktonic community changed from a blue-green algal assemblage to

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one dominated volumetrically and numerically by cryptophytes (Appendix B, Table B19).

Tadpole effects: Higher numbers of green algae, numbers and volumes of diatoms, and total algal numbers and volumes were consistently measured in stocked aquaria at Lake One in Experiment Two (Table 24 and Appendix B, Table B17). In general, diatoms comprised the highest percentage of total algae in stocked aquaria, except at the end of August, when a bloom of green and blue-green algae occurred (Appendix B, Table B19). At this time, numbers and volumes of diatoms were twice as high in stocked aquaria as in unstocked aquaria, but the proportionately greater increases in green and blue-green algae in stocked aquaria decreased the importance of the contribution by diatoms (Appendix B, Tables B17 and B19). The diatoms, Nitzschia and Navicula, were elevated by tadpole activities throughout the experimental period (Table 24 and Appendix B, Table B20). In Experiment Two, as in the first experiment at Lake One, the responses of the algal community to grazing intensity by tadpoles could not be separated statistically, except for differences in diatom volumes (Table 24). However, the magnitude of the responses of the algal community to tadpole grazing was typically greater when tadpoles were more abundant. On any particular sampling date in Experiment Two at Lake One, stocked aquaria had greater numbers, volumes and mean sizes of blue-green algae and volumes of green algae (Table 24 and Appendix B, Table B17). The volumetric diversity of green and blue-green algae tended to be higher in stocked aquaria, while total volumetric evenness and diversity were highest in unstocked aquaria on particular dates of

Table 24. Phytoplanktonic comparisons between unstocked (C for control) and tadpole-stocked (L for low and H for high stock of *R. pipiens* aquaria in Experiment Two at Lake One.

EXPERIMENT TWO--LAKE ONE				
1. Numbers of Greens				
8 August	F = 6.26*	<u>9976(C)</u>	<u>12184(L)</u>	15203(H)
15 August	F = 33.01***	<u>6412(C)</u>	<u>17104(L)</u>	<u>21551(H)</u>
22 August	F = 7.68*	<u>58862(C)</u>	<u>283697(L)</u>	<u>317121(H)</u>
2. Volumes of Greens				
15 August	F = 5.31*	<u>965732(C)</u>	<u>1920706.3(L)</u>	2181011.3(H)
3. Numbers of Diatoms				
8 August	F = 8.78*	<u>13815(C)</u>	<u>19432(L)</u>	29148(H)
15 August	F = 16.63**	<u>22553(C)</u>	<u>68633(L)</u>	123292(H)
Combined 3 Dates	F = 3.59*	<u>16129(C)</u>	<u>37827(L)</u>	58428(H)
4. Volumes of Diatoms				
8 August	F = 11.57**	<u>7212504(C)</u>	<u>7396200.3(L)</u>	14697000(H)
15 August	F = 24.02**	<u>13979000(C)</u>	<u>43388666(L)</u>	77581333(H)
Combined 3 Dates	F = 3.64*	<u>8906340(C)</u>	<u>21080046(L)</u>	34501262(H)
5. Numbers of Blue-greens				
22 August	F = 5.32*	<u>131470(C)</u>	<u>392257(H)</u>	412091(L)
6. Volumes of Blue-greens				
8 August	F = 12.54**	<u>10635.7(C)</u>	<u>23471(L)</u>	194477.7(H)
22 August	F = 5.42*	<u>1921038.3(C)</u>	<u>6078900.3(H)</u>	<u>6393489.3(L)</u>
7. Total Numbers of Algae				
8 August	F = 12.52**	<u>28442(C)</u>	<u>36885(L)</u>	51327(H)
15 August	F = 7.63*	<u>112839(C)</u>	<u>215541(L)</u>	284902(H)
22 August	F = 6.65*	<u>203103(C)</u>	<u>724599(L)</u>	<u>734295(H)</u>
8. Total Volumes of Algae				
8 August	F = 16.50**	<u>15507867.4(C)</u>	<u>19366893.3(L)</u>	26428475(H)
15 August	F = 27.68***	<u>16136822.3(C)</u>	<u>47343307.7(L)</u>	82248394(H)
22 August	F = 4.75	<u>13746452.3(C)</u>	<u>40147420.3(H)</u>	44538425.7(L)
Combined 3 Dates	F = 7.62**	<u>15130380.7(C)</u>	<u>37091329.7(L)</u>	<u>49004247.1(H)</u>
9. Numerical Diversity of Greens				
22 August	F = 5.12*	<u>1.032(L)</u>	<u>1.084(H)</u>	1.297(C)
10. Volume Diversity of Greens				
15 August	F = 12.00**	<u>1.328(C)</u>	<u>1.655(H)</u>	1.745(L)

Table 24 (cont'd.).

EXPERIMENT TWO--LAKE ONE				
	11. Volume Diversity of Blue-greens			
15 August	F = 8.35*	0.086(C)	<u>0.339(L)</u>	<u>0.461(H)</u>
	12. Total Volume Diversity			
15 August	F = 4.92	<u>0.799(H)</u>	<u>0.900(L)</u>	<u>1.034(C)</u>
	13. Volume Evenness			
15 August	F = 9.69*	<u>0.277(H)</u>	<u>0.308(L)</u>	<u>0.400(C)</u>
	14. Mean Sizes of Blue-greens			
3 August	F = 5.96*	7.9(C)	16.3(L)	83.3(H)
	15. <u>Nitzschia</u>			
Combined 3 Dates	F = 4.94*	7502(C)	<u>19914(L)</u>	<u>31337(H)</u>
	16. <u>Navicula</u>			
Combined 3 Dates	F = 4.86*	3137(C)	<u>17080(L)</u>	<u>25079(H)</u>

* F.05 (2,6) = 5.14; F.05 (2,24) = 3.40

** F.01 (2,6) = 10.90; F.01 (2,24) = 5.61

*** F.001 (2,6) = 27.00; F.001 (2,24) = 9.34

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the study (Table 24 and Appendix B, Table B21). Consistent trends in diversity and evenness components between stocked and unstocked aquaria were not obvious in Experiment Two at Lake One (Appendix B, Table B21). Concentrations of the green algae; Scenedesmus, a small coccoid green alga, Chlorella, Ankistrodesmus, and Actinastrum, and the blue-green algae; small Anacystis, small Anabaena, and a coccoid blue-green alga were typically elevated in aquaria stocked with tadpoles (Appendix B, Table B20).

Tadpole grazing in Experiment Two at Lake Four consistently increased abundances of Nitzschia and numbers and volumes of all genera of diatoms over values measured in unstocked aquaria (Table 25 and Appendix B, Table B18). Both the total number of diatoms and concentrations of Nitzschia were influenced by grazing intensity; aquaria with a high stocking of tadpoles elevated diatom numbers and concentrations of Nitzschia above levels measured in aquaria with a low stocking of tadpoles (Table 25 and Appendix B, Tables B18 and B20). Diatoms comprised the largest percentage of total algal volumes in stocked aquaria and blue-green algae contributed the highest proportion to total volumes in unstocked aquaria (Appendix B, Table B19). Different algal taxa were dominant in the three treatments on particular sampling dates; however, the average values for numerical composition of algae were similar in all aquaria in Experiment Two (Appendix B, Table B19).

The total number of algae was consistently lowest in aquaria with a high density (biomass) of tadpoles, while the mean size of all algae was lowest in unstocked aquaria (Appendix B, Table B18). On particular sampling dates in Experiment Two, stocked aquaria had

Table 25. Phytoplanktonic comparisons between unstocked (C for control) and tadpole-stocked (L for low and H for high stock of *R. pipiens*) aquaria in Experiment Two at Lake Four.

EXPERIMENT TWO--LAKE FOUR				
	1. Numbers of Greens			
15 August	F = 14.26**	<u>5444(H)</u>	<u>7979(L)</u>	13704(C)
	2. Volumes of Greens			
15 August	F = 9.95*	<u>479924.3(H)</u>	<u>568170(L)</u>	687225(C)
	3. Numbers of Diatoms			
8 August	F = 10.72*	<u>56(C)</u>	<u>133(L)</u>	266(H)
Combined				
3 Dates	F = 4.70*	<u>199(C)</u>	<u>436(L)</u>	575(H)
	4. Volumes of Diatoms			
8 August	F = 9.21*	<u>38243(C)</u>	<u>114279(L)</u>	221524(H)
22 August	F = 87.52***	172576(C)	548653.7(H)	742137(L)
Combined				
3 Dates	F = 5.66**	145416(C)	<u>432608.4(L)</u>	<u>472799.9(H)</u>
	5. Numbers of Blue-greens			
22 August	F = 12.60**	<u>15497(H)</u>	<u>16894(L)</u>	21446(C)
	6. Volumes of Blue-greens			
22 August	F = 20.97**	<u>282122.7(L)</u>	<u>296966.7(H)</u>	546721(C)
	7. Numbers of Cryptophytes			
8 August	F = 7.0*	<u>0(L)</u>	<u>9(C)</u>	28(H)
	8. Numerical Diversity of Diatoms			
22 August	F = 6.76*	0.5517(H)	<u>0.9913(L)</u>	<u>1.1550(C)</u>
	9. Numerical Diversity of Blue-greens			
15 August	F = 4.64	<u>0.6227(C)</u>	<u>0.6813(H)</u>	<u>0.9903(L)</u>
22 August	F = 9.33*	0.8953(L)	<u>1.1400(H)</u>	<u>1.2753(C)</u>
	10. Volume Diversity of Greens			
15 August	F = 12.41**	0.3324(C)	<u>0.7947(H)</u>	<u>0.8757(L)</u>
22 August	F = 6.59*	<u>1.1623(C)</u>	<u>1.2573(L)</u>	1.4970(H)
	11. Numerical Diversity of Total Algae			
15 August	F = 7.73*	1.1187(C)	<u>1.4700(H)</u>	<u>1.6310(L)</u>
	12. Numerical Evenness			
15 August	F = 3.98	<u>0.493(C)</u>	<u>0.685(L)</u>	0.685(H)

Table 25 (cont'd.).

EXPERIMENT TWO--LAKE FOUR				
	13. Volume Evenness			
22 August	F = 5.95*	<u>0.507(L)</u>	<u>0.649(C)</u>	0.695(H)
	14. Mean Sizes of Greens			
22 August	F = 6.10*	<u>56(H)</u>	<u>62.4(C)</u>	136.3(L)
Combined 3 Dates	F = 3.07	<u>65.6(C)</u>	<u>78(H)</u>	99.5(L)
	15. Mean Sizes of Diatoms			
Combined 3 Dates	F = 3.67	<u>730.7(C)</u>	<u>822.3(H)</u>	922.2(L)
	16. Mean Sizes of Blue-greens			
22 August	F = 7.41*	<u>16.7(L)</u>	<u>18.5(H)</u>	25.6(C)
	17. Mean Sizes of Total Algae			
22 August	F = 5.20*	<u>46.7(C)</u>	<u>70.0(H)</u>	88.5(L)
	18. <u>Nitzschia</u>			
Combined 3 Dates	F = 6.89**	128(C)	338(L)	481(H)

* F_{.05} (2,6) = 5.14; F_{.05} (2,24) = 3.40

** F_{.01} (2,6) = 10.90; F_{.01} (2,24) = 5.61

*** F_{.001} (2,6) = 27.00; F_{.001} (2,24) = 9.34

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greater numbers of cryptophytes, mean sizes and volumetric diversity of green algae, mean sizes and numerical diversity of total algae, and volumetric evenness of all algae (Table 25 and Appendix B, Tables B18 and B22). Also, aquaria stocked with tadpoles had lower numbers and volumes of green algae, numbers and volumes of blue-green algae, numerical diversity of green and blue-green algae, and mean sizes of blue-green algae during the sampling period (Table 25 and Appendix B, Tables B18 and B22). Concentrations of Ulothrix, a filamentous green alga, were lowest in stocked aquaria (Appendix B, Table B20). Abundances of large Anacystis and small Anabaena were depressed in aquaria with a high stocking of tadpoles (Appendix B, Table B20).

Experiment Three (Lakes One and Four)

Imported lake water: In Experiment Three at Lake Four, concentrations of phytoplankton were the lowest measured in any experiment at either lake. At Lake One, algal numbers were 30-40 times higher and volumes were about 20 times greater than at Lake Four (Appendix B, Tables B23-B24). Blue-green algae contributed the highest proportion to total numbers at both lakes; green algae at Lake One and diatoms at Lake Four comprised the highest percentage of total volumes (Appendix B, Table B25). A diverse green-algal assemblage was sampled at Lake One with Dictyosphaerium, Scenedesmus, Ankistrodesmus, Kirchneriella, and a large coccoid green alga present as major genera (Appendix B, Table B26). Chlamydomonas dominated the green-algal flora at Lake Four (Appendix B, Table B26). At both lakes, Nitzschia comprised the major portion of the diatoms and Rhodomonas dominated the genera of cryptophytes. The blue-green algae at both lakes were

were primarily Agmenellum and Anacystis, but small Anabaena were numerous at Lake One (Appendix B, Table B26). At Lake Four, the mean total size of phytoplankton was twice that measured at Lake One and mean sizes of diatoms were consistently greater at Lake Four (Appendix B, Tables B23-B24).

Tadpole effects: In Experiment Three at Lake One, comparisons among aquaria stocked with bullfrogs, green frogs, or a combination of the two species revealed no consistent trends that were statistically significant (Table 26). Total numbers and volumes of phytoplankton were invariably higher in the mixed-species culture than in single-species treatments (Appendix B, Table B23). In the mixed-species treatment, total numbers and volumes of blue-green algae were higher than other algal taxa in this treatment throughout the experiment (Appendix B, Tables B23 and B25). In aquaria with monocultured green frog or bullfrog tadpoles, total numbers and volumes fluctuated during the experiment with no discernible pattern (Appendix B, Tables B23 and B25). The lowest concentrations of Dictyosphaerium, a green alga, were measured in aquaria with a mixed culture of bullfrogs and green frogs (Appendix B, Table B26). The blue-green algae, Agmenellum and small Anacystis, and the green alga, Ankistrodesmus, were most abundant in the mixed-species treatment (Appendix B, Table B26). Aquaria stocked with a single-species culture of bullfrogs had the lowest concentrations of Scenedesmus and volumetric evenness of all algae (Appendix B, Tables B26-B27). The total numbers and volumes of diatoms and the numerical diversity calculated for all algae were highest in aquaria with monocultures of green frog tadpoles (Appendix

Table 26. Phytoplanktonic comparisons between aquaria with monocultured bullfrogs (B), mixed-species: bullfrogs and green frogs (M), and monocultured green frogs (G) in Experiment Three at Lake One.

EXPERIMENT THREE--LAKE ONE				
	1. Volumes of Diatoms			
5 October	F = 8.00*	<u>546158.7(B)</u>	<u>743654.3(M)</u>	987585.7(G)
	2. Numbers of Blue-greens			
12 October	F = 3.73	<u>259644(B)</u>	<u>275384(G)</u>	334297(M)
	3. Volumes of Blue-greens			
12 October	F = 3.52	<u>4231996(G)</u>	<u>4325810.7(B)</u>	5513913(M)
	4. Total Numbers of Algae			
12 October	F = 10.33*	<u>427685(B)</u>	<u>458322(G)</u>	516349(M)
	5. Numerical Diversity of Greens			
12 October	F = 4.07	<u>1.307(M)</u>	<u>1.355(G)</u>	1.399(B)
	6. Mean Sizes of Total Algae (Volume/Number)			
12 October	F = 9.79*	<u>65.2(M)</u>	<u>71.4(G)</u>	76.5(B)

* F_{.05} (2,6) = 5.14

B, Tables B23 and B27).

In Experiment Three at Lake Four, the treatments, species compositions of tadpoles, effected consistent differences in responses among the algal assemblage (Table 27). The highest numerical and volumetric diversity of all algae was measured in aquaria with monocultured green frog tadpoles (Table 27 and Appendix B, Table B28). Moreover, the average sizes of all algae tended to be lowest in single-species cultures of green frogs (Appendix B, Table B24). The relative proportions of algae in the different taxa were similar among all treatments, although blue-green algae contributed a greater proportion to the total algal assemblage in aquaria with monocultured green frogs (Appendix B, Table B25). Single-species cultures of bullfrog tadpoles generally had the lowest numerical and volumetric diversity of diatoms and abundances of Nitzschia estimated for any of the tadpole treatments (Appendix B, Tables B26 and B28).

Community Metabolism

Effects of Varying Tadpole Stocking Rates on Gross Primary Productivity (GPP) and GPP/Autotrophic Biomass (Experiments One and Two)

Lake One: Initial measurements of GPP were similar for all aquaria in Experiment One and Experiment Two before tadpoles were stocked (Figure 14 and Appendix B, Table B29). Tadpoles influenced the gross primary productivity in aquaria, but the response of the autotrophic community was small and not simply related to the intensity of grazing. In both experiments, average values of GPP/day fluctuated among sampling dates, apparently in response to factors other than tadpole grazing since unstocked and stocked aquaria responded

Table 27. Phytoplanktonic comparisons between aquaria with monocultured bullfrogs (B), mixed-species: bullfrogs and green frogs (M), and monocultured green frogs (G) in Experiment Three at Lake Four.

EXPERIMENT THREE--LAKE FOUR				
	1. Numbers of Greens			
12 October	F = 11.59**	<u>402(M)</u>	<u>554(G)</u>	722(B)
	2. Volumes of Greens			
12 October	F = 4.62	<u>44958.3(G)</u>	<u>47509.7(M)</u>	108518(B)
	3. Numbers of Diatoms			
5 October	F = 3.71	<u>7366(G)</u>	<u>11069(M)</u>	12527(B)
	4. Volumes of Diatoms			
5 October	F = 4.16	<u>1252566(G)</u>	<u>3115517(B)</u>	3185359.7(M)
	5. Volumes of Blue-greens			
5 October	F = 5.42*	<u>150110.3(G)</u>	<u>210561.7(M)</u>	359387.7(B)
	6. Total Volumes of Algae			
5 October	F = 4.44	<u>2090741.7(G)</u>	<u>3542571.4(M)</u>	3717774.7(B)
	7. Numerical Diversity of Diatoms			
5 October	F = 3.76	<u>0.056(M)</u>	<u>0.056(B)</u>	0.121(G)
24 October	F = 8.89*	<u>0.023(B)</u>	<u>0.053(M)</u>	0.097(G)
Combined 3 Dates	F = 7.21**	<u>0.029(B)</u>	<u>0.045(M)</u>	0.087(G)
	8. Volume Diversity of Diatoms			
5 October	F = 7.72*	<u>0.127(M)</u>	<u>0.130(B)</u>	0.229(G)
24 October	F = 6.76*	<u>0.053(B)</u>	<u>0.176(M)</u>	0.359(G)
Combined 3 Dates	F = 7.38**	<u>0.072(B)</u>	<u>0.132(M)</u>	0.241(G)
	9. Total Volume Diversity			
24 October	F = 4.05	<u>0.324(B)</u>	<u>0.485(M)</u>	0.624(G)
	10. Numerical Evenness			
5 October	F = 3.70	<u>0.428(M)</u>	<u>0.458(G)</u>	0.506(B)
	11. Volume Evenness			
5 October	F = 6.77*	<u>0.201(M)</u>	<u>0.267(G)</u>	0.303(B)
24 October	F = 7.95*	<u>0.113(M)</u>	<u>0.137(B)</u>	0.212(G)
Combined 3 Dates	F = 6.25**	<u>0.171(M)</u>	<u>0.195(B)</u>	0.254(G)
	12. Mean Sizes of Greens			
Combined 3 Dates	F = 3.36	<u>44.3(G)</u>	<u>93.9(M)</u>	162.2(B)

* $F_{.05}(2,6) = 5.14$; $F_{.05}(2,24) = 3.40$

** $F_{.01}(2,6) = 10.90$; $F_{.01}(2,24) = 5.61$

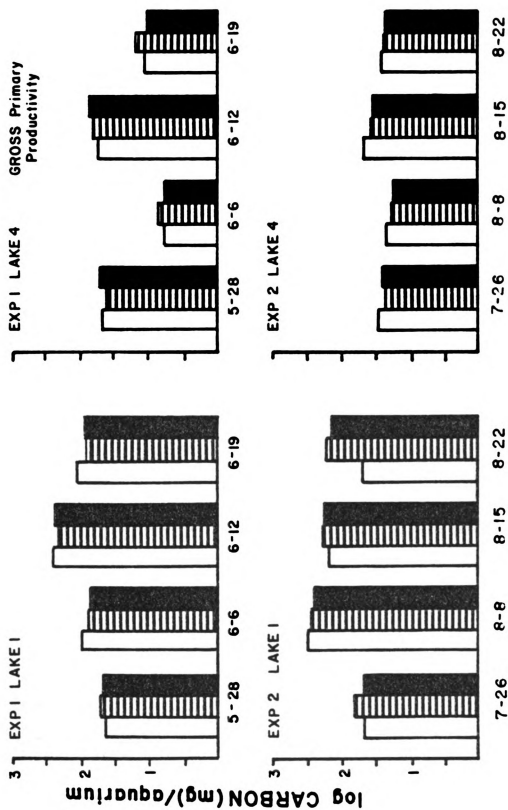


Figure 14. Measurements of GPP (log C (mg)/aquarium) for Experiments One and Two at Lakes One and Four (unstocked aquaria = unshaded bar, low stocking = bar with horizontal stripes, and high stocking = shaded bar).

similarly (Figure 14 and Appendix B, Table B29). In Experiment One, both biomasses of stocked tadpoles consistently depressed the GPP; the low biomass stocking reduced the total GPP by 20% and the high biomass stocking reduced it by 17%. In Experiment Two, the overall effect of tadpole grazing was to stimulate the GPP (Figure 14 and Appendix B, Table B29). The GPP in aquaria with a low stock of tadpoles averaged 21% higher than in unstocked aquaria, while in the high biomass stocking, GPP averaged 17% higher than in controls. A major temporal shift in primary production occurred toward the end of Experiment Two. If the experiment had not been terminated, GPP in unstocked aquaria may have continued to decline below levels of GPP in aquaria with tadpoles.

In both experiments, tadpoles increased the GPP/autotrophic (phytoplanktonic and periphytic) biomass (Figure 15). Although the total standing crop of periphyton was significantly lowered by tadpole grazing, a higher rate of primary production was maintained by the remaining periphyton and phytoplankton than occurred in unstocked aquaria. The feeding activities of tadpoles may have removed dying or less healthy plants and increased the availability of nutrients to autotrophs.

Lake Four: In Experiments One and Two, GPP measurements were similar among all aquaria before tadpoles were introduced (Figure 14 and Appendix B, Table B29). Within an experiment, levels of GPP varied among sampling dates in aquaria, regardless of treatment. Apparently, environmental factors influenced the primary productivity similarly in aquaria representing the different stockings, since trends in variation of GPP were alike in stocked and unstocked aquaria (Figure 14 and

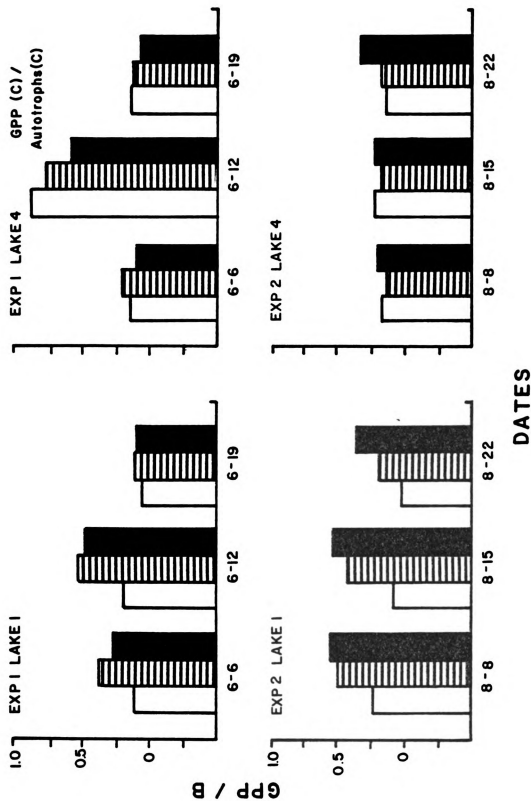


Figure 15. GPP/autotrophic biomass measured as carbon (mg/d) in Experiments One and Two at Lakes One and Four (unstocked aquaria = unshaded bar, low stock of leopard frog tadpoles = striped bar, and high stock = shaded bar).

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Appendix B, Table B29). In Experiment One, tadpoles increased the mean GPP by about 15% over the values measured in unstocked aquaria. On the third sampling date in Experiment One, the aquaria with a high biomass of tadpoles exhibited significantly higher GPP values than unstocked aquaria ($P < 0.05$). In Experiment Two, the tadpoles depressed the primary productivity (Figure 14 and Appendix B, Table B29). In stocked aquaria, the mean GPP declined about 23% below levels measured in unstocked aquaria.

Tadpoles did not have a consistent effect on the GPP/autotrophic biomass in Experiments One and Two at Lake Four (Figure 15). In Experiment One, the tadpoles, especially those stocked at a high biomass, elevated the GPP and the abundance of the autotrophic biomass. However, tadpole stocking increased the autotrophic biomass proportionately more than the GPP, so measurements of GPP/B were lower than in unstocked aquaria (Figure 15). In Experiment Two, tadpoles depressed the primary productivity and the autotrophic biomass, which resulted in an elevated GPP/autotrophic biomass at the conclusion of the experiment. Because tadpoles removed the less productive portions of the autotrophic biomass, the remaining autotrophs maintained a higher GPP/B than in unstocked aquaria.

Effects of Varying Tadpole Stocking Rates on Community Respiration (R), R/Autotrophic Biomass (R/B), and GPP/R (Experiments One and Two)

Lake One: Measurements of community respiration (R) were similar among aquaria at the initiation of Experiment One and Experiment Two (Figure 16 and Appendix B, Table B30). Values for community respiration fluctuated like GPP among sampling dates within an experiment and appeared to be influenced by environmental factors other than

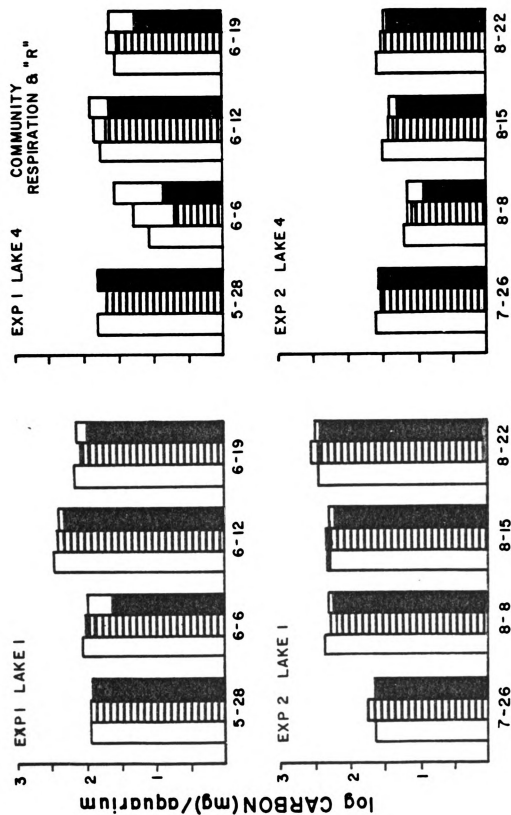


Figure 16. Community respiration (R) in Experiments One and Two at Lakes One and Four (inner bars represent R without tadpole respiration, unstocked aquaria are unshaded, low stock (R. pipiens) equals bar with stripes, and high stock is shaded).

tadpole grazing. Tadpole respiration was estimated to assess their contribution to community respiration in aquaria (Figure 16 and Appendix B, Table B31). In Experiment One, the low biomass of tadpoles contributed 12% and the high biomass stocking about 18% to the daily community respiration in their respective aquaria. In the second experiment, 8% of the total respiration was attributed to the low biomass and 11.4% to the high biomass of tadpoles (Figure 16, and Appendix B, Table B31).

One response of plants and decomposers to tadpole grazing was a measureable reduction in respiration. When respiration in unstocked and stocked aquaria was compared in Experiment One, the low biomass of tadpoles reduced the community respiration below that in unstocked aquaria by 22% and the high biomass stocking reduced it by 26% (Figure 16). In Experiment Two, respiration in aquaria with a low biomass of tadpoles averaged 3% lower and the high biomass stocking averaged 13% lower than values measured in unstocked aquaria.

The GPP/R ratios were less than one on several sampling dates in Experiments One and Two (Appendix B, Table B32). A GPP/R ratio less than unity indicated that heterotrophs, including tadpoles, consumed more organic matter than was produced by algae. Also, high respiratory demands by algae during daytime may have depressed the GPP/R ratio. Tadpoles slightly depressed GPP/R in Experiment One, but increased it in Experiment Two by stimulating primary productivity and depressing community respiration (Appendix B, Table B32). On the final sampling date in Experiment Two, GPP/R values in stocked aquaria were significantly higher ($P < 0.01$) than in unstocked aquaria. The values for GPP/"R" (where "R" equals community respiration minus tadpole respiration)

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were 2-11% higher in Experiment One and about 20% higher in Experiment Two than mean GPP/R in unstocked aquaria (Appendix B, Table B32). The highest values for respiration/autotrophic biomass (R/B) were consistently observed in stocked aquaria (Figure 17). Estimates of GPP/"R", R/B, and GPP/B indicated that tadpoles fed on dead and unproductive plant tissues, increasing the proportion of metabolically active plant material.

Lake Four: In Experiments One and Two, values for respiration within experiments were similar among all aquaria before tadpole stocking (Figure 16 and Appendix B, Table B30). Stocked aquaria had higher levels of community respiration than unstocked aquaria in the first experiment; average respiration was 30% greater in aquaria with a low biomass of tadpoles and 54.5% greater in aquaria with a high biomass of tadpoles. When respiration contributed by tadpoles was subtracted from community respiration, average respiration ("R") was 3% less in the low biomass stocking and 15% less in the high biomass stocking than respiration (R) in unstocked aquaria (Appendix B, Tables B30-B31). Therefore, in Experiment One, tadpoles accounted for about 25% of the respiration in aquaria with a low stocking and about 44.5% of R in aquaria with a high stocking. On the second and third sampling dates in Experiment One, aquaria with a high biomass of tadpoles had significantly higher community respiration measurements ($P < 0.05$) than unstocked aquaria. In Experiment Two, community respiration averaged 15% lower in aquaria with a low biomass of tadpoles and 17% less in those with a high biomass of tadpoles than community respiration values in unstocked aquaria (Figure 16 and Appnedix B, Table B30). When the estimated

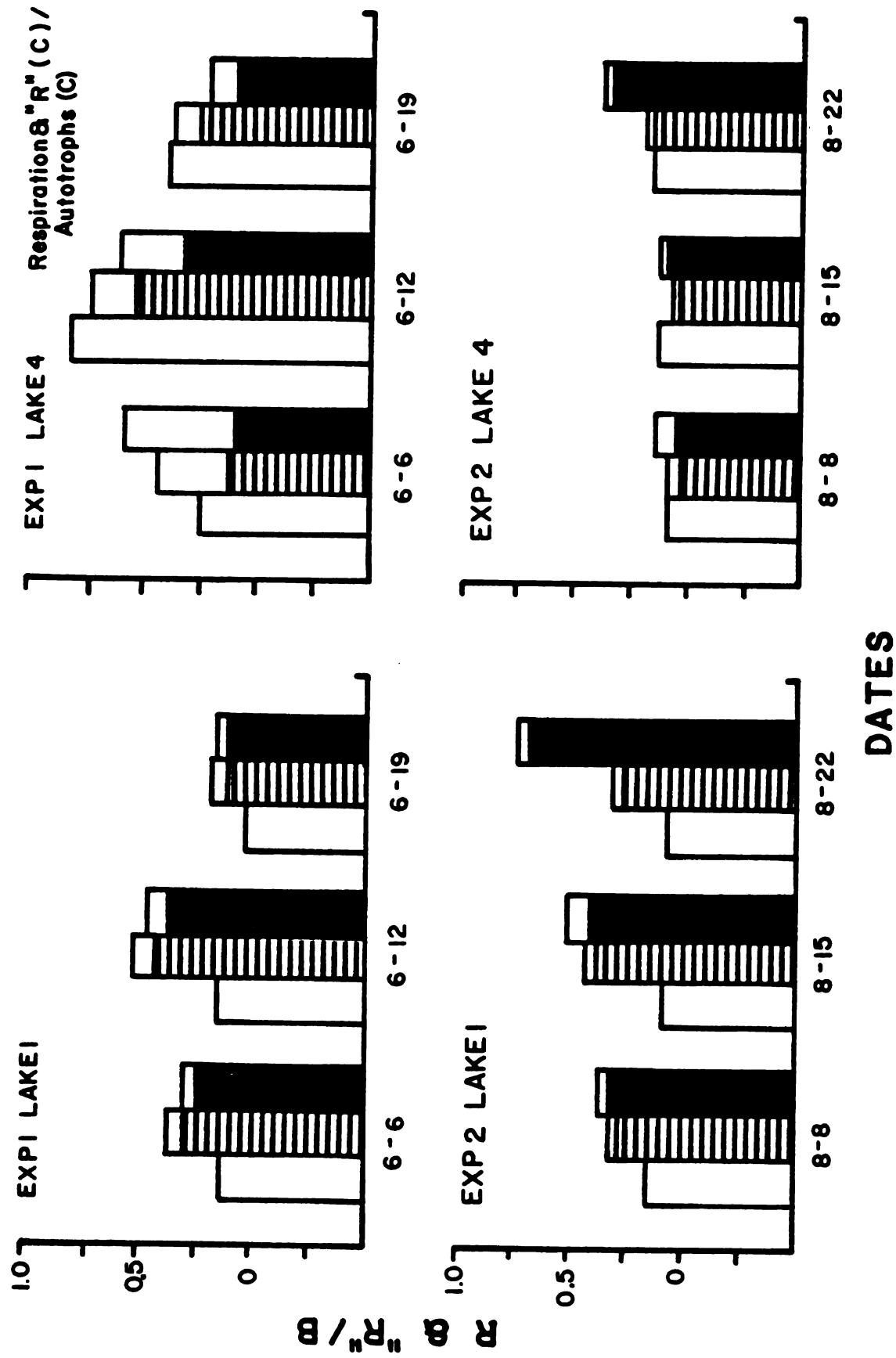


Figure 17. Community respiration (R) per unit of autotrophic biomass in Experiments One and Two at Lakes One and Four (R/B for unstocked aquaria = unshaded bar, " R "/ B for low stocking = inner striped bar and whole bar represents R/B , and " R "/ B for high stocking = shaded inner bar and whole bar represents R/B).

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contribution of tadpole respiration was deducted, "R" values averaged 19% and 29% lower in aquaria with a low biomass and high biomass of tadpoles than measurements of R in unstocked aquaria. About 6-14% of the total respiration was contributed by tadpoles in Experiment Two (Appendix B, Table B31).

In Experiment One, "R"/B was considerably lower in the tadpole-stocked aquaria than R/B in unstocked aquaria (Figure 17). Although tadpoles increased the GPP and depressed respiration, these changes were not proportional to the increased autotrophic accumulation. In Experiment Two, community respiration in stocked aquaria was depressed, but R/B and "R"/B were lower in stocked aquaria than R/B in unstocked aquaria. At the end of Experiment Two, these relationships altered and values for R, R/B, and "R"/B were higher in stocked aquaria, especially those with a high biomass of tadpoles, than in aquaria without tadpoles (Figures 16-17 and Appendix B, Table B30). The stocked biomasses of tadpoles were low in both treatments of Experiment Two, so the response of the autotrophic community to tadpole grazing may have been slower, not materializing until the end of the experiment. Tadpoles appeared to consume the less productive plant material, thereby increasing the metabolism per unit of autotrophic biomass.

Ratios of GPP/R fluctuated between sampling dates in all aquaria at Lake Four; mean GPP/R was less than unity in Experiment One and greater than one in Experiment Two for all treatments (Appendix B, Table B32). In the first experiment, GPP/R averaged 12-24% lower in stocked aquaria than estimates of GPP/R in unstocked aquaria. When tadpole respiration was deducted from the total respiration, the resulting ratios of GPP/"R" were 15-27% higher than GPP/R in unstocked aquaria.

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Average GPP/R values for treatments in Experiment Two were similar; unstocked estimates were only 3-7% higher than stocked. When the respiration attributed to tadpoles was subtracted from the total respiration, the resultant GPP/"R" values were 2-8% higher than GPP/R measurements in unstocked aquaria.

Partitioning the GPP and R of Phytoplankton and Periphyton (Ancillary Tests in Experiment Two)

Lake One: To distinguish between the individual contributions of periphyton and seston, which included detritus and phytoplankton, to total GPP and community respiration, ancillary tests were made on two separate dates in Experiment Two. Results from the first ancillary experiment at Lake One indicated that periphyton contributed the major proportion to the GPP and R (Figure 18 and Table 28). The ratios of GPP/autotrophic biomass and R/B were higher in jars simulating conditions in tadpole-stocked aquaria. The ratio of periphytic to sestonic carbon was almost twice as high in jars from unstocked aquaria as in jars from the low biomass stocking and almost three times higher than in jars from aquaria with a high biomass of tadpoles (Table 28). The GPP/R ratios in unstocked aquaria were about 10-20% lower than measured in stocked aquaria.

During the second ancillary test, the GPP in all jars was low, reflecting a situation similar to that monitored in the aquaria (Figure 18 and Table 28). No primary productivity was measured in jars from unstocked aquaria, where respiration by periphyton evidently consumed all of the oxygen generated by the phytoplankton. The ratios of periphytic to sestonic carbon were much higher in jars from unstocked

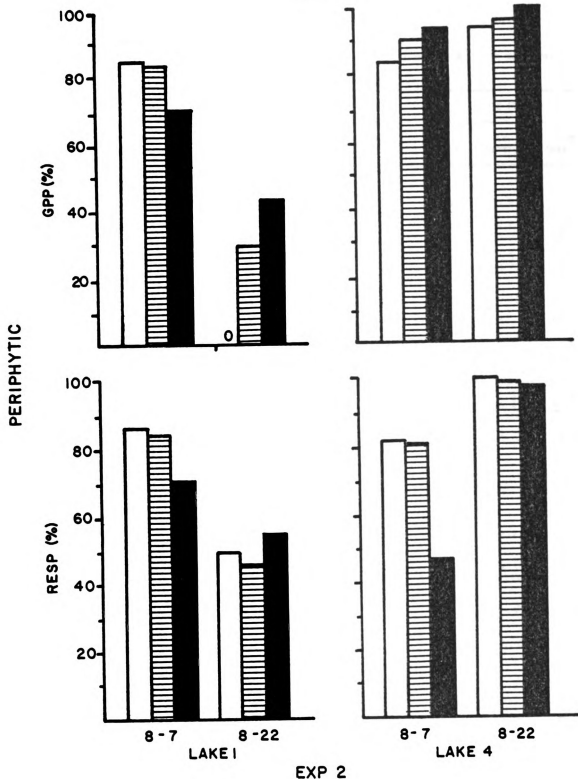


Figure 18. Percentages of GPP and R attributed to periphyton based on ancillary studies in Experiment Two at Lakes One and Four (jars in unstocked aquaria = unshaded bars, low biomass stocking of *R. pipiens* = striped bars, and high stocking = shaded bars).

Table 23. Contributions of periphyton and phytoplankton to the total GPP and R (O_2 in mg/l) based on ancillary studies during Experiment Two.

EXPERIMENT TWO	LAKE ONE			LAKE FOUR		
	Control	Low Density	High Density	Control	Low Density	High Density
A. 7-8 August						
1) Total GPP (O_2)	19.6	19.1	17.0	3.5	3.8	2.8
a) Phytoplankton	3.1 (± 0.08)	3.0 (± 0.32)	4.4 (± 0.98)	0.6 (± 0.17)	0.4 (± 0.30)	0.2 (± 0.10)
b) Periphyton	16.5 (± 3.2)	16.1 (± 2.6)	12.6 (± 2.8)	2.9 (± 0.5)	3.5 (± 0.7)	2.6 (± 0.5)
c) GPP in Carbon/ Autotrophic Biomass (C)	0.09	0.16	0.26	0.15	0.22	0.22
d) Periphytic % of GPP	84	84	74	83	90	93
2) Total RESP (O_2)	15.3	13.8	11.0	2.2	2.3	1.5
a) Phytoplankton	2.2 (± 0.24)	2.1 (± 0.32)	3.2 (± 0.98)	0.4 (± 0.06)	0.4 (± 0.07)	0.3 (± 0.03)
b) Periphyton	13.2 (± 2.4)	11.7 (± 0.7)	7.8 (± 1.5)	1.8 (± 0.2)	1.8 (± 0.5)	0.8 (± 0.3)
c) RESP in Carbon/ Autotrophic Biomass (C)	0.07	0.12	0.17	0.09	0.13	0.20
d) Periphytic % of RESP	86	85	71	82	81	47
3) Ratio--Periphytic (C): Phytoplanktonic (C)	32:1	19:1	11:1	95:1	69:1	50:1
B. 21-22 August						
1) Total GPP (O_2)	0 [-1.42]	14.4	18.2	3.3	5.2	3.9
a) Phytoplankton	9.5 (± 1.5)	10.4 (± 2.1)	10.8 (± 2.0)	0.3 (± 0.03)	0.3 (± 0.04)	0.2 (± 0.03)
b) Periphyton	0 [-10.9+5.2]	4.0 (± 2.0)	7.4 (± 1.4)	3.0 (± 1.1)	4.8 (± 0.1)	3.7 (± 0.2)
c) GPP in Carbon/ Autotrophic Biomass (C)	0	0.17	0.37	0.34	0.48	0.53
d) Periphytic % of GPP	0	28	41	91	92	95
2) Total RESP (O_2)	25.2	25.0	30.6	3.5	5.4	3.7
a) Phytoplankton	13.3 (± 1.2)	14.2 (± 1.3)	14.4 (± 1.4)	0.1 (± 0.03)	0.2 (± 0.06)	0.2 (± 0.05)
b) Periphyton	11.9 (± 2.4)	10.8 (± 5.4)	16.1 (± 3.9)	3.4 (± 1.2)	5.2 (± 0.1)	3.5 (± 0.2)
c) RESP in Carbon/ Autotrophic Biomass (C)	0.15	0.30	0.33	0.36	0.50	0.51
d) Periphytic % of RESP	47	43	53	97	96	95
3) Ratio--Periphytic (C): Phytoplanktonic (C)	9:1	4:1	2:1	17:1	21:1	15:1

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aquaria, 2.5 times that of the low biomass stocking and 4.5 times values for the high biomass stocking. The GPP/R ratios were zero in jars from unstocked aquaria and 0.58-0.59 in jars from stocked aquaria. The GPP/R estimates were similar to GPP/"R" measurements for aquaria after respiration contributed by tadpoles had been deducted. On this date, high concentrations of detritus, green and blue-green algae, about four times greater than recorded on earlier dates, were imported in the lake water. This abundance of seston in aquaria and jars apparently depressed periphytic production and elevated the relative contribution of phytoplanktonic production.

Tadpole stocking in ancillary experiments consistently elevated the GPP/R, GPP/B and R/B ratios over values in unstocked aquaria. A comparison of differences in periphyton and seston among the three treatments demonstrated that the low biomass stocking of tadpoles reduced the ratio of periphytic to sestonic material by 40-56% and the high biomass of tadpoles reduced the ratio by 75-80%.

Lake Four: Ancillary experiments at Lake Four revealed that periphyton, rather than seston and associated phytoplankton, contributed substantially (>80%) to the GPP in tests (Figure 18 and Table 28). The importance of periphytic production to the autotrophic community appeared proportionately greater at Lake Four than at Lake One. The jars from aquaria with a high biomass stocking of tadpoles invariably exhibited a lower ratio of periphyton to seston and a higher GPP/R ratio than those from unstocked aquaria. As at Lake One, GPP/B and R/B were highest in jars from tadpole-stocked aquaria in both ancillary tests. In all jar experiments at both lakes, tadpoles appeared to

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increase the ratio of community metabolism to autotrophic biomass, but the greatest effects were observed at Lake One.

Comparisons of Community Metabolism (Experiments One and Two)

In both experiments at Lakes One and Four, gross primary productivity and community respiration were related ($r = 0.74$, $P < 0.01$) in all aquaria, regardless of treatment (Figure 19). Measurements of GPP were higher at Lake One than at Lake Four; the mean GPP at Lake One was 5.9 times greater in Experiment One and 5.5 times greater in Experiment Two than at Lake Four (Appendix B, Table B29). In the first experiment, similar biomasses of tadpoles were stocked at Lakes One and Four. At Lake One, tadpoles depressed the GPP, while at Lake Four, the GPP was increased by tadpoles. In the second experiment, higher biomasses of tadpoles were stocked at Lake One than at Lake Four. Tadpoles elevated the mean GPP at Lake One and depressed the mean GPP at Lake Four.

In stocked aquaria, mean values of "R" (community respiration minus tadpole respiration) were lower in both experiments at Lakes One and Four than community respiration in unstocked aquaria (Figure 16, Appendix B, Tables B30-B31). Similarly, GPP/"R" ratios were higher in the two experiments at both lakes than GPP/R in unstocked aquaria (Appendix B, Table B32). On all sampling dates in both experiments at Lake One, measurements of GPP/autotrophic biomass were higher in tadpole-stocked aquaria than in unstocked aquaria (Figure 15). Values for R/B and "R"/B for aquaria with tadpoles were higher than estimates in unstocked aquaria on all sampling dates in Experiments One and Two at Lake One (Figure 17). These elevated values were a result of tadpoles influencing the autotrophic biomass proportionately more than metabolism.

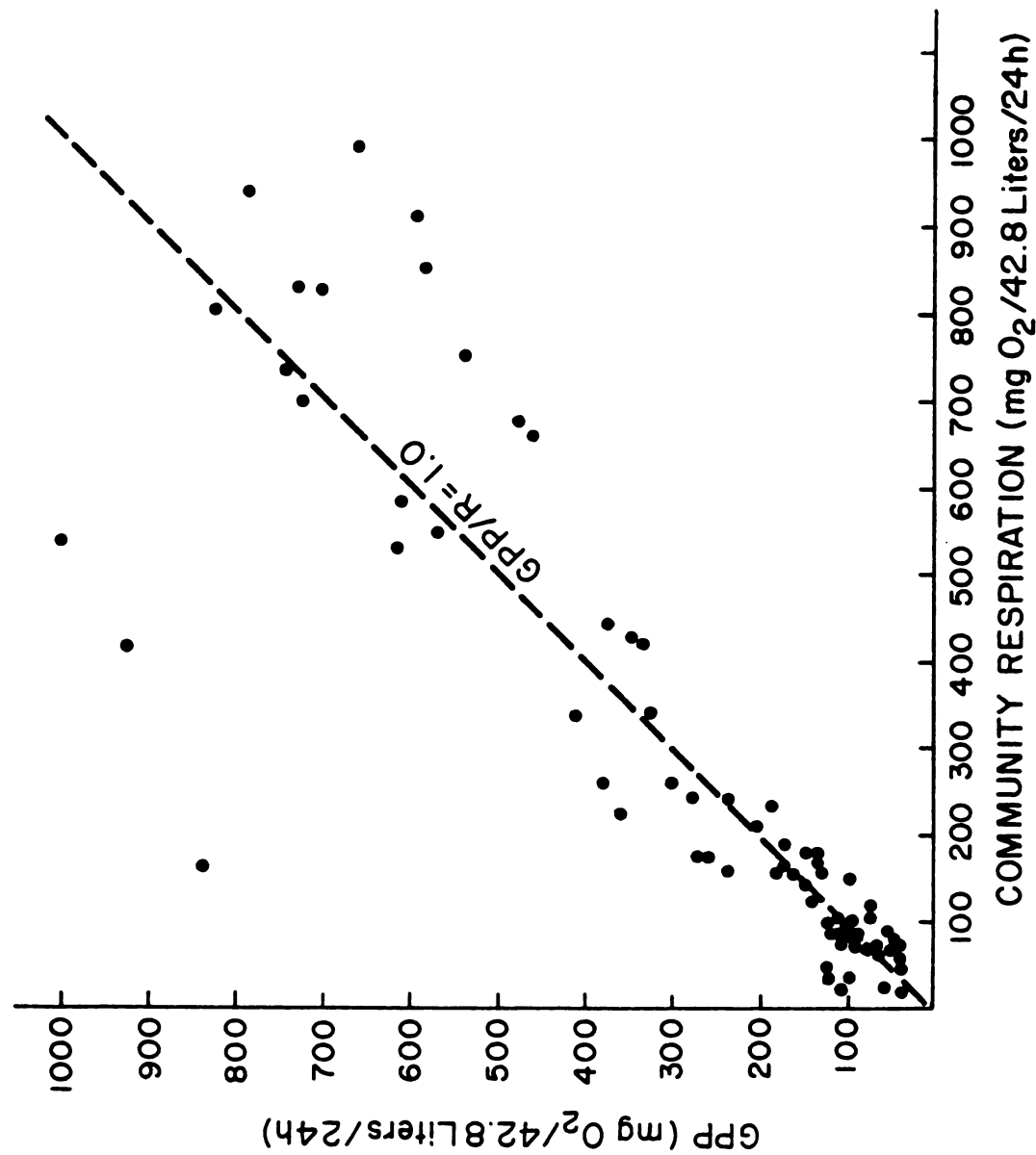


Figure 19. The relationship between GPP and R for all treatments in the three experiments at Lakes One and Four (correlation coefficient (r) equaled 0.74, $p < 0.01$).

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At Lake Four, GPP/B and R/B were more variable during both experiments than measurements at Lake One (Figures 15 and 17). In the first experiment at Lake Four, tadpoles decreased both the GPP/B and R/B below values measured in unstocked aquaria. In Experiment Two, stocked aquaria, especially those with a high biomass of tadpoles, increased the mean GPP/autotrophic biomass over values in unstocked aquaria. Measurements of "R"/B were lower than R/B for unstocked aquaria until the final sampling date in Experiment Two, when R/B declined in unstocked aquaria below R/B in tadpole-stocked aquaria.

Effects of Tadpole Composition on Community Metabolism (Experiment Three)

Lake One: The largest differences in gross primary productivity and community respiration occurred among aquaria before tadpoles were stocked (Figure 20 and Appendix B, Tables B33-B34). Measurements of GPP and R were positively correlated (Figure 19) and the magnitude of temporal variation for GPP and R was alike. Bullfrog tadpoles, green frog tadpoles, and the mixed culture of the two species affected the GPP and R similarly; tadpole activities appeared to dampen initial differences in GPP and R among aquaria (Figure 20 and Appendix B, Tables B33-B34). For the three groups of tadpoles, the difference in average GPP was 0.5-5%; for community respiration, the difference among treatments was 3-6%. Only minor differences were noted in GPP/R values among aquaria and GPP/R ratios always exceeded unity in Experiment Three (Appendix B, Table B35). Although monocultured green frogs reduced the periphytic biomass more than monocultured bullfrogs or the combination of the two species, values for GPP, R and GPP/R were similar among treatments (Appendix B, Tables B33-B35).

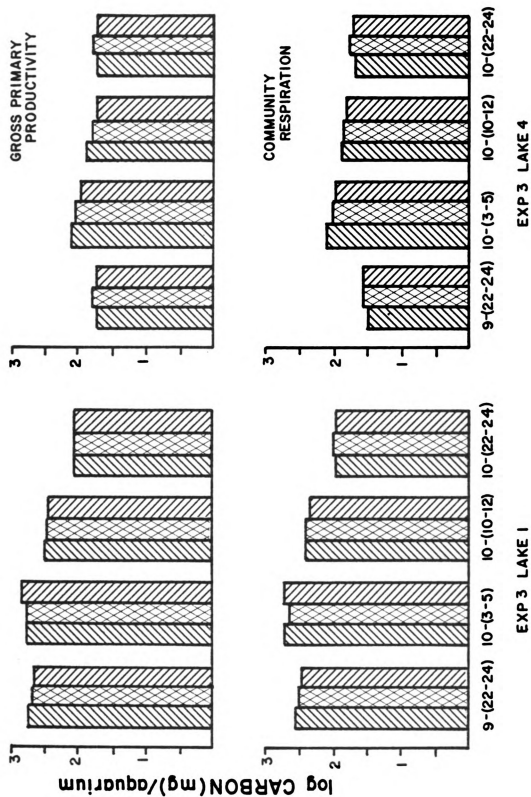


Figure 20. Gross primary productivity and community respiration in Experiment Three at Lakes One and Four (bars represent monocultured bullfrogs, mixed-species culture, and monocultured green frogs, respectively).

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Differences in GPP/autotrophic biomass and R/B were greatest among aquaria on the first sampling date after tadpoles were stocked (Figure 21). At the end of the third experiment, GPP/B and R/B were similar in aquaria with monocultures of bullfrogs or green frogs and in the mixed-species cultures. Although the differences were relatively minor, GPP/B and R/B were invariably highest in aquaria with monocultured green frog tadpoles and lowest in aquaria with single-species cultures of bullfrog tadpoles.

Lake Four: At Lake Four, measurements of gross primary productivity for Experiment Three averaged 5-6 times lower than at Lake One (Figure 20 and Appendix B, Tables B33-B34). The GPP and R were positively correlated (Figure 19) and varied similarly between sampling dates in all aquaria (Appendix B, Tables B33-B34). Measurements of GPP were consistently lowest in aquaria with monocultured green frogs, averaging 14% below values in aquaria with single-species cultures of bullfrogs. The lowest community respiration was also associated with green frogs in monoculture, averaging 10% lower than R values measured in single-species cultures of bullfrogs. Measurements of GPP and R were usually intermediate between the two single-species treatments (Figure 20 and Appendix B, Tables B33-B34). These trends in GPP and R were found throughout the experimental period, but differences among tadpole groups were small.

Single-species cultures of bullfrog tadpoles stimulated the primary productivity and accumulation of autotrophic biomass more than the mixed-species culture or monocultured bullfrogs. The GPP and R were elevated by the activities of monocultured bullfrogs to the extent

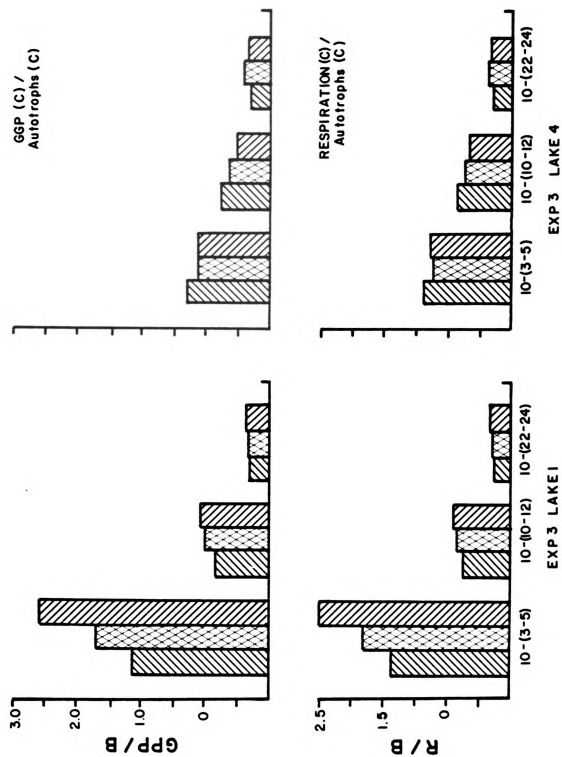


Figure 21. Ratios of GPP/B and R/B for Experiment Three at Lakes One and Four (bars represent monocultured bullfrogs, mixed-species culture, and monocultured green frogs, respectively).

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that GPP/B and R/B were highest in these aquaria, despite the increased autotrophic biomass (Figure 21). As at Lake One, ratios of GPP/B and R/B were similar for all tadpole groups at the end of the experiment. Bullfrog tadpoles in monoculture also maintained GPP/R ratios at slightly higher levels than were measured in the other treatments, but the increases in GPP/R were minor (6% was the largest difference among treatments). The lowest GPP/R ratios were estimated in aquaria with monocultured green frog tadpoles (Appendix B, Table B35).

Partitioning phytoplanktonic and periphytic GPP and R (ancillary test): To assess the relative contributions of periphyton and seston with associated phytoplankton to the gross primary productivity and community respiration, a 48-h ancillary experiment was conducted (Table 29 and Figure 22). At Lake One, the contribution of periphyton to the community respiration was similar for the three tadpole groupings, but the portion of the GPP attributed to periphyton fluctuated among treatments. Although the ratio of periphytic to sestonic carbon was lowest in jars simulating conditions in aquaria with monocultured green frogs, periphyton in this treatment generated the largest proportion of the GPP (Table 29 and Figure 22). Periphyton in jars from aquaria with monocultured bullfrogs contributed the least to the GPP and had the lowest GPP/R ratios. The highest respiration estimated for periphyton and phytoplankton (seston) occurred in jars simulating conditions in aquaria with a single-species culture of bullfrog tadpoles.

At Lake Four, the periphyton in jars accounted for all of the GPP and 89% or more of the respiration in all treatments (Table 29 and Figure 22). The highest GPP/R ratios were observed in jars from

Table 20. Contributions of periphyton and phytoplankton to the total GPP and R (O_2 in mg/l) based on an ancillary study during Experiment Three.

EXPERIMENT THREE	LAKE ONE			LAKE FOUR		
	Bullfrogs	Mixed: Bullfrogs & Green Frogs	Green Frogs	Bullfrogs	Mixed: Bullfrogs & Green Frogs	Green Frogs
A. 22-24 October						
1) Total GPP(O_2)	0.8	1.0	1.0	1.2	1.5	1.4
a) Phytoplankton	0.6 (+0.1)	0.5 (+0.2)	0.4 (+0.2)	0 [-0.1+0.08]	0 [-0.1+0.09]	0 [-0.1+0.04]
b) Periphyton	0.2 (+0.03)	0.5 (+0.1)	0.6 (+0.07)	1.3 (+0.06)	1.6 (+0.33)	1.5 (+0.21)
c) GPP in Carbon/ Autotrophic Biomass (C)	0.009	0.009	0.10	0.05	0.08	0.06
d) Periphytic % of GPP	24	47	60	100	100	100
2) Total RESP (O_2)	3.4	2.7	2.6	1.9	2.4	1.8
a) Phytoplankton	1.2 (+0.3)	0.7 (+0.3)	0.7 (+0.2)	0.1 (+0.06)	0.2 (+0.07)	0.2 (+0.02)
b) Periphyton	2.2 (+0.3)	2.0 (+0.6)	1.9 (+0.1)	1.8 (+0.1)	2.2 (+0.5)	1.6 (+0.1)
c) RESP in Carbon/ Autotrophic Biomass (C)	0.04	0.03	0.03	0.08	0.12	0.08
d) Periphytic % of RESP	64	74	72	95	92	89
3) Ratio--Periphytic (C): Phytoplanktonic (C)	15:1	19:1	14:1	123:1	129:1	143:1

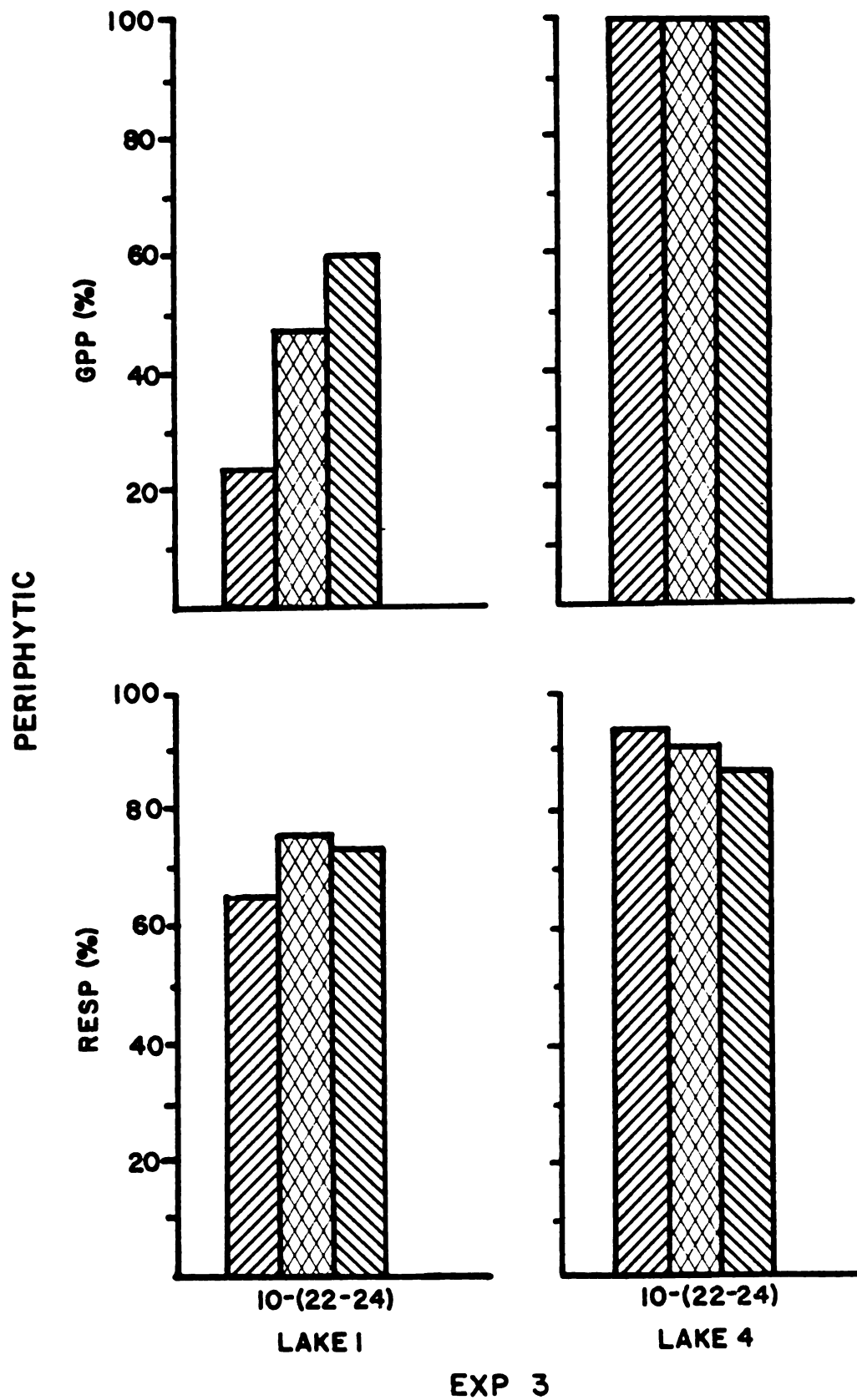


Figure 22. Percentages of GPP and R attributed to periphyton based on ancillary tests in Experiment Three at Lakes One and Four (bars represent monocultured bullfrogs, mixed-species culture, and monocultured green frogs, respectively).

aquaria with monocultured green frog tadpoles. This elevated GPP/R from aquaria with single-species cultures of green frogs resulted from lower respiration by autotrophs.

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DISCUSSION

Abiotic Environmental Effects

Since abiotic factors like temperature, light, and water quality can have major impacts on the production of algae and algal consumers, the potential influences of these factors on production were assessed. Water quality, as measured by the concentrations of nitrogen, phosphorus, and carbon, best explained the significantly higher primary productivity at Lake One. Extremes in certain abiotic factors like oxygen and ammonia were more prominent at Lake One; however, tadpole survival and growth were invariably higher at this lake. Apparently, food quality and availability had major impacts on the realized tadpole production at the two lakes and abiotic factors had few quantifiable effects.

Influences on Algal Communities in Aquaria

Temperature fluctuations in aquaria during single experiments at Lakes One and Four were similar and within ranges that commonly occur in shallow ponds. The average daily temperatures were alike in Experiments One and Two, about 17 C, whereas in Experiment Three, daily temperatures averaged 8 C. Differences in photoperiod and cloud cover also occurred among Experiments One, Two, and Three at both lakes. Despite the variations in these factors, gross primary productivity (mean values for all aquaria, whether stocked or unstocked) varied only 18% among the three experiments at Lake One and as little as 5% among those at Lake Four

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(Appendix B, Table 36B). Variations in community respiration among the three experiments at both lakes averaged 20 to 30% (Appendix B, Table 36B). Water quality, as indicated by concentrations of phosphorus, nitrogen, and organic carbon, differed widely among the three experiments at Lakes One and Four, but generally without significant impact on community metabolism.

Values for net primary productivity, phytoplanktonic biomass, total organic carbon, total nitrogen, and total phosphorus were compared with natural lakes of different trophic status (as summarized by Vollenweider 1970, Likens 1975, Wetzel 1975) in Table 30. Based on this classification, Lake One would be categorized as eutrophic for net primary productivity. Lake Four was less productive and values for primary productivity corresponded to those measured in oligotrophic waters. Since temperatures and light were similar in aquaria at the two lakes during each experimental period, the differences in the availability of nutrients must explain the disparate levels of primary productivity at the two lakes (Table 30).

Daily fluctuations of oxygen in aquaria were much greater at Lake One than at Lake Four and were caused by the higher photosynthesis and respiration of the algal standing crop. Algal productivity at Lake Four was about 14% of that at Lake One. Both lakes were moderately alkaline and the pH fluctuated little during the period from May to October.

Influences on Tadpoles

In general, the environments in aquaria at Lake One were more stressful than those at Lake Four; however, tadpole survival and growth

Table 30. Comparisons of Lakes One and Four with natural lakes of different trophic status (Vollenweider 1970, Likens 1975, and Wetzel 1975).

TROPHIC CATEGORY	MEAN NET PRIMARY PRODUCTION (mg C/m ² /d)	PHYTOPLANKTONIC BIOMASS (mg C/m ³ /d)	TOTAL ORGANIC CARBON (mg C/l)	TOTAL PHOSPHORUS (mg P/m ³)	TOTAL NITROGEN (mg N/m ³)
Ultra-oligotrophic	< 50	< 50	-	< 1-5	< 1-250
Oligotrophic	50-300	20-100	< 1-3	-	-
Oligo-mesotrophic	-	-	-	5-10	250-600
Mesotrophic	250-1,000	100-300	< 1-5	-	-
Meso-eutrophic	-	-	-	10-30	500-1,000
Eutrophic	> 1,000	> 300	5-30	-	-
Hypereutrophic	-	-	-	30->5,000	500->15,000
Lake One	971-1,300 ¹	182-934	7-15	490-2,599	560-10,050
Lake Four	120-200 ¹	28-131	5-10	12-70	500-1,004

¹ Based on estimates for unstocked aquaria

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were consistently higher at Lake One. Tadpoles at Lake One were subjected to extreme daily fluctuations in oxygen, especially in Experiment Two when oxygen ranged between 65 and 240% in relative saturation. The maximum range in relative saturation of oxygen (85 to 135%) at Lake Four occurred during Experiment Three. At both lakes, all aquaria had daily fluctuations in temperature and moderately high pH levels. Abiotic factors, such as oxygen, pH, and temperature, may have influenced tadpole survival, the efficiency of conversion of food material into tadpole tissues, or other variables measured for tadpoles in this study. Yet, many of the shallow aquatic systems inhabited by tadpoles are stressful with fluctuating water levels; diurnally variable oxygen, temperature, and pH levels; and dense populations of aquatic plants.

Variations in daily temperatures in aquaria during this study were similar to those measured in natural ponds inhabited by R. catesbeiana, R. pipiens sphenoccephala (18 to 36 C in June; Seale et al. 1975), and Bufo americanus (10.5 to 31.5 C in early July; Beisenger 1977). The influence of temperature in determining the growth rates of larval amphibians has been demonstrated in laboratory (Atlas 1935, Moore 1939, Ryan 1941a, b) and field studies (Calef 1973, Noland and Ultsch 1981). During single experiments at Lakes One and Four, temperature and photoperiod were alike at both lakes, so differences in growth and production exhibited by tadpoles were related to factors other than temperature and light. In the third experiment, average daily temperatures declined and the metabolism of tadpoles was probably lower than in the two earlier experiments. But values for growth per degree day, which should have minimized the temperature effects, were higher for individual

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tadpoles of R. pipiens in Experiments One and Two than those for R. catesbeiana and R. clamitans in Experiment Three.

Minimum concentrations of oxygen (50 to 70% in relative saturation) in stocked aquaria were higher than concentrations in most water bodies inhabited by tadpoles. For example, Cole and Fischer (1977) reported mean dawn concentrations of about 30% relative saturation with 6% saturation (0.6 mg/l) near bottom in a pond with large populations of R. clamitans and R. pretiosa. Tadpoles of R. pipiens (= R. utricularia) commonly inhabit swampy areas where waters are less than 50% saturated with oxygen (Noland and Ultsch 1981) and tadpoles of R. catesbeiana have been observed in littoral areas of ponds with daytime spatial variation in oxygen of 1 to 6 mg/l (Boyd 1975). In laboratory studies, critical oxygen tensions occurred at about 22% of relative saturation (1.7 to 1.8 mg O₂/l at 26 C) for unacclimated tadpoles of R. pipiens (Helff and Stubblefield 1931, Noland and Ultsch 1981).

Little information is available on diurnal oxygen fluctuations in ponds with tadpole populations, but limnological data for shallow, enriched systems suggest the oxygen variation in such habitats may be extreme (Wetzel 1975). These fluctuations may have a moderate effect on tadpole mortality since ranid tadpoles develop lungs early (Just et al. 1973) and gape or gulp surface air (Wassersug and Seibert 1975). Moreover, tadpoles can alter their behavior (Whitford and Massey 1970) and undergo metabolic and physicochemical reorganization at the tissue and cellular levels in response to changing oxygen conditions (Barbashova 1964, Brown 1967, Rose and Drotman 1967, Seibel 1970, Bennett 1978). Weigmann (1972) and Weigmann and Altig (1975a, b) assessed the ability of tadpoles to acclimate to various oxygen concentrations and to employ

anaerobic glycolysis during hypoxia. Larvae of R. pipiens were cultured successfully by Weigmann (1972) and Weigmann and Altig (1975a, b) under a cyclic oxygen regime with daily concentrations of oxygen ranging from 3 to 9 mg/l. In addition, leopard frogs were reared successfully from eggs into tadpoles at saturated (9 mg/l) and subsaturated (1.8 mg/l) oxygen levels.

No large differences in pH occurred between Lakes One and Four during this study and diurnal fluctuations in pH within each lake were small because the moderately high concentrations of bicarbonate dampened variations. Total ammonia concentrations at Lake One invariably exceeded those at Lake Four, creating a greater potential for higher concentrations of toxic un-ionized ammonia at Lake One. The adverse effects of high ammonia concentrations (38 mg/l) on tadpoles in experimental ponds have been reported by Champ et al. (1971), but concentrations of this magnitude were not measured at either lake (the highest concentration of ammonia-nitrogen at Lake One was 5 mg/l). If pH and ammonia levels had differential impacts at the two lakes, tadpoles should have been more stressed by conditions at Lake One.

Relationships Between Plant Production and Tadpole Production

Apparent Impact of Tadpoles on Algae and Nutrients

While nutrients were the key factors in determining the different levels of gross primary productivity at the two lakes, tadpoles played a major role in influencing the realized GPP in single experiments at each lake. The impact of ranid tadpoles on the aquatic environments in this study was a function of the trophic status of the lakes and the density and biomass of tadpoles stocked. This was obvious in the first

experiment when the same densities and biomasses of tadpoles were introduced at both lakes; the tadpoles at Lake One effected a maximum reduction of 34% in the GPP, whereas those at Lake Four promoted a maximum increase of 50% in the GPP (see Appendix A for amended values of community metabolism). During the second experiment, grazing pressure was initially lower at both lakes than in the first experiment, but lowest at Lake Four. In this experiment, tadpole grazing accounted for a maximum increase of 15% in the GPP at Lake One and a maximum decrease of 25% in the GPP at Lake Four. Community respiration was consistently lower in the stocked aquaria than in the unstocked aquaria at Lake One, despite the added contribution of tadpole respiration. Conversely, community respiration was invariably elevated, as much as 54% higher in aquaria with tadpoles than those without tadpoles at Lake Four.

Results from Lake One are similar to findings by Seale (1973, 1980) on tadpole populations in a small Missouri pond where tadpole grazing produced either a 10 to 30% increase or reduction in the gross primary productivity, depending on the biomass of tadpoles present. Changes in the ratio of gross primary productivity to tadpole biomass were non-linear; the growth rates of algae were enhanced by low levels and depressed by high levels of tadpole biomass (Seale 1973, 1980). Based on these findings, data from Lake Four, particularly from the first experiment when the high abundances of tadpoles stimulated the GPP, were difficult to interpret. Leopard frog tadpoles grew poorly in this experiment, many died, and survivors were thin. Apparently, foraging activities and metabolism of the numerous tadpoles promoted this increased production by algae, but the mechanisms were not clearly discernible.

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Studies of other aquatic consumers of algae report either stimulation of primary productivity (Porter 1972, 1973, 1975, 1976, 1978, Lehman 1980, Lynch 1980) or more typically depression of primary productivity (Wright 1965, Hargrave and Geen 1970, Haney 1971, 1973, Porter 1977); as much as 100% of the phytoplanktonic production can be cropped daily by zooplankton. Grazers reduce autotrophic production mainly by decreasing the overall abundance of algae; however, extensive data exist on the influence of grazers on phytoplanktonic composition and diversity by which they may also affect primary productivity (reviews by Porter 1977, Porter and Orcutt 1980). Similar data for tadpoles are scarce; only Dickman (1968) and Seale (1973, 1980) have reported on algal-tadpole interactions. Dickman (1968) observed that caged tadpoles reduced the abundance of filamentous green algae and promoted the growth of diatoms and bacteria. Seale (1973, 1980) analyzed changes in the ratio of chlorophyll α to phaeophytin during tadpole grazing and proposed that tadpoles altered the structure of the phytoplanktonic community by decreasing the contribution of blue-green algae. In this study at Lakes One and Four, total phytoplanktonic numbers and volumes in stocked aquaria were generally increased two to four times greater than the abundances measured in unstocked aquaria. This proliferation of phytoplankton occurred in stocked aquaria at both lakes, whether algal concentrations in the lakes were high or low. Growth of phytoplankton may not account solely for these phenomenal increases in stocked aquaria since algae that had been ingested by tadpoles on the previous day may have been deposited as feces during the sampling period. Thus, algal cells in feces may have been resuspended and enumerated as living phytoplankton. All algae which were counted

and measured were readily identifiable and had intracellular structures intact, so phytoplankton appeared viable even if they had passed through the guts of tadpoles.

Although large increases in most phytoplanktonic taxa occurred in stocked aquaria, certain taxa increased more than others in relative abundance. One consistent trend recorded at Lakes One and Four throughout the experimental periods was significant increases in diatom numbers and volumes in aquaria with tadpoles. This happened whether or not diatoms were, at that time, a major component of the algal community. In particular, diatoms of the genus, Nitzschia, and to a lesser extent, Navicula, increased in stocked aquaria. Assuming that specific growth rates of the different algal taxa did not account wholly for the observed results and all genera were grazed in proportion to their abundances or non-selectively, then some algae were more resistant than others to passage through tadpole guts. Increases in phytoplanktonic numbers and volumes partially may be explained by the accrual of algal cells from the previous day's feeding, but the significant increases in abundance of particular genera indicate that algae were differentially digested and certain taxa may survive and perhaps benefit from gut passage. Porter (1973, 1976) reported that colonies of gelatinous green algae, like Sphaerocystis and Elakothrix, not only survive passage through zooplanktonic guts but incorporate nutrients, such as phosphorus, into algal tissues during passage. More than 90% of these algal cells emerged from the grazers' guts intact and viable, resulting in a subsequent 63% elevation in the abundance of gelatinous green algae in the lake during the first 24 h after gut passage (Porter 1976). Laboratory studies by Seale and Beckvar (1980) indicate that certain algal

genera (Chlorella) are less damaged than others (Anabaena) after passage through tadpole guts and these taxa which are poorly digested will grow and reproduce when placed in algal nutrient media. Therefore, results of Porter (1973, 1976), Seale and Beckvar (1980), and those from this study suggest that certain taxa of algae gain a competitive advantage over others when grazers are present in aquatic systems.

Although most evidence does not substantiate selective grazing on algae by tadpoles (Farlowe 1928, Savage 1951, 1952, Jenssen 1967), leopard frog tadpoles in this study may have consumed proportionately more of certain algal genera than others. This could be attributed more to certain algal characteristics and tadpole feeding behavior than to the active selection of algae by tadpoles. For example, diatoms have been shown to sink more rapidly than other algal taxa (Lund 1965, Uhlmann 1971) and diatoms may have settled in high concentrations on the bottom of aquaria. Also, diatoms appeared to dominate the periphyton, adhering to the sides and bottoms of aquaria. Tadpoles in this study spent more time feeding on the sides and bottoms of aquaria than in the water column, thereby increasing the probability of their consuming more diatoms. If diatoms were poorly digested by tadpoles and even benefited from gut passage or tadpole metabolites, then they would be expected to increase in relative abundance. The mechanisms underlying the proliferation of certain algal taxa can only be postulated; however, the results are important because the composition of the phytoplanktonic community was altered by tadpole grazing.

The observed increases in overall phytoplanktonic abundances in aquaria with tadpoles can be explained partially by the tadpoles' foraging primarily on periphyton and their influence on nutrient

cycling. Concomitant with the elevation of total numbers and volumes of algae in stocked aquaria was a decrease in the numeric and volumetric diversity of all algae. Since tadpoles promoted the proliferation of certain algal taxa more than others, they effected a lower evenness value for algae than was measured in aquaria without tadpoles. In addition, the data suggest that in early spring when blue-green algae were rare, as in Experiment One at Lake One, activities of tadpoles can enhance the growth of blue-green algae, particularly that of larger blue-greens. Apparently, the mean sizes of all algae may increase significantly with high grazing pressure, as occurred in the first experiment at Lake Four with high-stocked biomasses of tadpoles.

Ranid tadpoles are typically categorized as suspension feeders; however, whether these suspensions are comprised of seston in the water column or are generated by materials scraped from substrates is influenced by characteristics of the aquatic habitat. Steinwascher (1978a, b, 1979a, b) proposed that the amount of time tadpoles spend scraping materials from substrates or filtering particles from the water depends on the quality and abundance of food. He investigated the effects of dispersed and concentrated food (Purina rabbit fodder) on the growth of three species of ranid tadpoles. Tadpoles exposed to clumped food resources spend more time scraping or rasping, whereas those exposed to less concentrated, dispersed food spend more time filtering. From these results, Steinwascher (1978a, b, 1979a, b) concluded that the energetic cost of scraping is greater than that of filtering for ranid tadpoles.

Studies designed to analyze the filtering ability of tadpoles have shown that algal concentrations required for maximal ingestion are

high, greater than $2.0 \times 10^7 \mu\text{m}^3/\text{ml}$ (Seale and Wassersug 1979, Seale and Beckvar 1980). The critical threshold or concentration of algae necessary for effective filtering by R. sylvatica is $1.0 \times 10^7 \mu\text{m}^3/\text{ml}$ and for R. catesbeiana, $1.0 \times 10^6 \mu\text{m}^3/\text{ml}$ (Seale and Wassersug 1979, Seale and Beckvar 1980). Assuming these critical thresholds for filtering and ingestion by ranid tadpoles determined in the laboratory apply to tadpoles in nature, then ranid tadpoles may infrequently filter phytoplankton since algal concentrations of this magnitude occur only during blooms in eutrophic waters.

In this study, algal concentrations in water from enriched Lake One were high, averaging 1.6×10^6 , 3.8×10^7 , and $2.2 \times 10^7 \mu\text{m}^3/\text{ml}$ in Experiments One, Two, and Three, respectively. Algal concentrations in water from Lake Four generally were lower (4.8×10^5 , 2.5×10^6 , and $1.2 \times 10^5 \mu\text{m}^3/\text{ml}$ in Experiments One, Two, and Three, respectively) than required for filtering efficacy of ranid tadpoles. Of the 21 eutrophic lakes cited by Vollenweider (1970), only five had maximal algal concentrations averaging or exceeding $1.0 \times 10^7 \mu\text{m}^3/\text{ml}$. For a given lake to be categorized as eutrophic, Vollenweider (1970) suggested algal volumes should approach or exceed $1.0 \times 10^5 \mu\text{m}^3/\text{ml}$. This concentration is much less than those proposed by Seale and Beckvar (1980) as critical thresholds for efficient filtering by ranid tadpoles. Few limnological studies have reported such high algal concentrations: maximum phytoplanktonic concentrations of $2.6 \times 10^7 \mu\text{m}^3/\text{ml}$ were reported by Baker and Baker (1976) in eutrophic Halstead Bay, Minnesota; in Lake Washington, enriched by sewage effluent, total algal volumes exceeded $1.0 \times 10^7 \mu\text{m}^3/\text{ml}$ during only one month of a three-year study (Parker 1977); and phytoplanktonic concentrations in western Lake Erie averaged

$1.4 \times 10^7 \mu\text{m}^3/\text{ml}$ annually (Marcus 1972, Wocjik 1978). Although filtering may be less energy demanding than scraping or rasping materials from substrates, aquatic habitats where tadpoles occur may have low concentrations of suspended particulates, below the critical thresholds required for efficient filtering.

In this study at Lakes One and Four, periphyton was the major food consumed by ranid tadpoles. Results on tadpole production at Lake One indicate that tadpoles may benefit energetically from feeding off substrates in shallow-water zones of enriched environments. The productivity of periphyton in aquaria with tadpoles averaged 30 mg organic matter/dm²/d at Lake One and at Lake Four, the periphytic accrual in unstocked aquaria averaged 1.3 mg organic matter/dm²/d. Estimates at Lake One approach the highest productivities recorded for many aquatic environments (the highest productivities reported by Wetzel (1975) were in rich warm springs which averaged 73 to 97 mg organic material/dm²/d). Measurements of daily periphytic growth at Lake Four are near the lowest productivities reported by Wetzel (1975); certain oligotrophic lakes had lower productivities, averaging 0.5 to 1.0 mg organic matter/dm²/d. So periphytic accumulation rates were over 25 times higher at Lake One than at Lake Four, but overall GPP for the three experiments was only about ten times greater at Lake One.

The tadpoles at Lake One greatly decreased the accrescence of periphyton and stimulated phytoplanktonic growth. At this lake, 78 to 87% of the periphytic carbon was diverted by tadpoles into tissue production or the accumulation of phytoplankton and detritus. A maximum of about 35% of the periphytic standing crop was converted daily into tadpole production and respiration. At Lake Four during the second

experiment, tadpoles reduced the periphytic standing crop by about 37% and more than 77% of the periphytic carbon was converted daily into tadpole biomass or respiration. In the first experiment at this lake, the biomass of periphyton in stocked aquaria increased as though it were unavailable as a food source. Certain algae, like the diatom Cocconeis, are largely unavailable to grazers because they secrete a jelly-like substance that cements them to the substrate (Patrick 1948, 1970, Marcus 1980). Tadpoles, weakened by poor nutrition in Experiment One at Lake Four, possibly could not rasp such closely adhering periphyton from the sides and bottoms of aquaria. Even in the second experiment at Lake Four, when tadpoles consumed attached algae, they removed a much lower proportion of the standing crop, but used it more efficiently than at Lake One.

In these experiments, the influence of tadpoles on the periphytic communities exceeded their cropping of algal production. Tadpoles also altered the carbon-nitrogen ratios of the periphyton. At Lake One, C:N ratios of periphyton averaged 11:1 in unstocked aquaria, whereas the C:N ratio averaged 7.5:1 in stocked aquaria. Decreases in the C:N ratio reflect increases in the protein fraction of the algal biomass, generally by decreases in the proportions of cellulose (Russell-Hunter 1970). Other grazers of the littoral zone, like snails, have also been observed to increase the ratio of nitrogen to carbon of the aufwuchs and grow more rapidly when feeding on periphyton with low C:N ratios (McMahon et al. 1974, Hunter 1975). Tadpoles at Lake One apparently removed the unproductive, senescent portions of the periphyton and maintained the remaining algae in a healthy, actively growing state. Aufwuchs communities with low C:N ratios are generally

dominated by diatoms, bacteria, and blue-green algae, whereas those with high C:N ratios tend to have single-celled and filamentous green algae as dominants (Russell-Hunter 1970, McMahon et al. 1974). My cursory examinations of glass slides colonized by periphyton indicated that more diatoms and blue-green algae were present among the periphyton in aquaria with tadpoles than in unstocked aquaria; green algae appeared to be more common on slides from unstocked aquaria.

Tadpoles and other consumers in the littoral zone of lakes and ponds may increase the rates of material cycling within this area, accelerate the transport of materials from the littoral to the pelagic zone, and increase the rates of transfer of materials to the sediments. These organisms appear capable of stimulating increased activity among autotrophs and heterotrophs at lower trophic levels, thus increasing the rate of decomposition processes and the metabolic activity of the system as a whole. Calef (1973) demonstrated that tadpoles of R. aurora could generate high turnover rates of sediments and epibenthic algae. When the oligotrophic lake studied by Calef (1973) supported 31 tadpoles/m² to metamorphosis, tadpoles at this density potentially could process 10 g/m²/d of dry sediments.

Rapid gut passage times are characteristic of tadpoles (Savage 1952, Ueck 1967, Altig and McDearman 1975, Wassersug 1975) and most invertebrates that feed on plants and debris (Berrie 1976). Large detrital particles may be broken down into finer detritus after passage through the alimentary canal of animal consumers, thereby accelerating a process that proceeds slowly by microbial activity. Surface sediments are reused by benthic feeders, so all sediments in aquatic systems may pass through the guts of indigenous populations several times

a year (Brinkhurst and Chua 1969, Appleby and Brinkhurst 1970, Calow 1973, Berrie 1976).

Both detrital and autotrophic pathways were influenced by the foraging and metabolic activities of tadpoles in this study at Lakes One and Four. Ranid tadpoles stimulated the accumulation of phytoplankton and detritus and depressed periphytic growth, partially as a consequence of their effects on nutrient cycling, measured as the mobilization and relocation of organic carbon, nitrogen, and phosphorus. Under the extreme eutrophy characteristic of Lake One, tadpoles appeared to facilitate the movement of total phosphorus, mainly as particulates, and organic carbon, both dissolved and sestonic, into the water (which was removed daily from aquaria). Activities of tadpoles in the less enriched waters of Lake Four promoted the release of higher concentrations of dissolved phosphorus and stimulated the storage of total organic carbon. Whether sestonic carbon decreased or increased in the water from aquaria at Lake Four depended on the extent to which it was consumed by tadpoles. Nitrogen dynamics were influenced by tadpoles at both lakes, but not in a consistent or predictable manner. Levels of inorganic and organic nitrogen measured in the water and the loss of nitrogen to the atmosphere either decreased or increased, depending on the abundances of tadpoles stocked and their subsequent production. In natural environments with similar grazing pressure simulated by the field experiments, tadpoles could consume over one-half of the periphytic standing crop daily. Nutrients not diverted into tissue elaboration and respiration by tadpoles could be exported to the pelagic zone as particulates and dissolved organics or recycled

within the littoral zone. Fecal material when sedimented would relocate nutrients to the benthic zone.

Seale (1973, 1980) proposed that tadpoles controlled the rate at which nitrogen was assimilated by phytoplankton. She found that when tadpole biomass was highest, the total nitrogen ingestion rates and ammonia excretion rates by tadpoles equaled the nitrogen demand by phytoplankton. Studies on other algal consumers, mainly crustacean zooplankton but also fish, have shown that nutrient regeneration by these organisms can have an immediate and substantial impact on overall nutrient budgets and on the nutrient demand of primary producers (Cushing and Nicholson 1963, Pomeroy et al. 1963, Marshall and Orr 1966, Hargrave and Geen 1968, Martin 1968, Butler et al. 1969a, b, Peterson and Lean 1973, Buechler and Dillon 1974, Ganf and Blazka 1974, Elwood and Goldstein 1975, Dugdale 1976, Jacobson and Comita 1976, Durbin et al. 1979). The population dynamics of algae and their patterns of species succession may depend just as much on the remineralization of nutrients as on algal mortality caused by grazers (Lehman 1980). For example, Lehman (1980) found that the epilimnetic zooplankton in Lake Washington supplied 10 times more P and 3 times more N to the surface-mixed layer during the summer months than entered the lake from all other sources. Algae in this lake were P limited (Edmondson 1970) and much of the calculated algal demand for P could be supplied by zooplanktonic populations during the summer (Devol 1979).

Relationships Between the Ratio of the Supply of Food/Demand by Tadpoles and Tadpole Production

At each lake, the biomass of leopard frog tadpoles stocked per aquarium was inversely related to their subsequent total production

($r = -0.91$ and -0.85 at Lakes One and Four, respectively); however, when data from the two lakes were pooled, the relationship between stocked biomass and total production of tadpoles was much lower ($r = -0.52$). The pooled data resulted in a poorer relationship between tadpole production and stocked biomass because patterns of tadpole survival and growth were different at the two lakes. Tadpoles survived and grew better at Lake One, despite the potentially more stressful conditions there than at Lake Four. Higher food production at Lake One appeared primarily responsible for the better performance of tadpoles.

If, as proposed, food availability was the major variable influencing tadpole performance at each lake, then the supply of food/demand by tadpoles, measured as GPP/TB, in relation to tadpole production should best explain the findings at both lakes. The ratio of supply to demand was highly correlated with total daily production by tadpoles ($r = 0.80$) and the daily growth of individual tadpoles ($r = 0.98$) at the different densities and biomasses tested in field experiments. Both total (TP/d) and individual (TP/TB/d) production by tadpoles were greatest when the ratio of supply to demand remained high throughout the experiment, as at Lake One in Experiment Two.

In order to examine the general applicability of this relationship between tadpole production and food supply/demand by tadpoles, results from laboratory studies were combined with those from the field experiments and reanalyzed. The values of TP/TB/degree d (A-1 and A-5, the two extremes of density) for R. pipiens reared in the laboratory on cultured phytoplankton and the TP/TB/degree d measured in field experiments in relation to the supply of food/demand by tadpoles were plotted in Figure 23. The correlation between the food supply, whether based

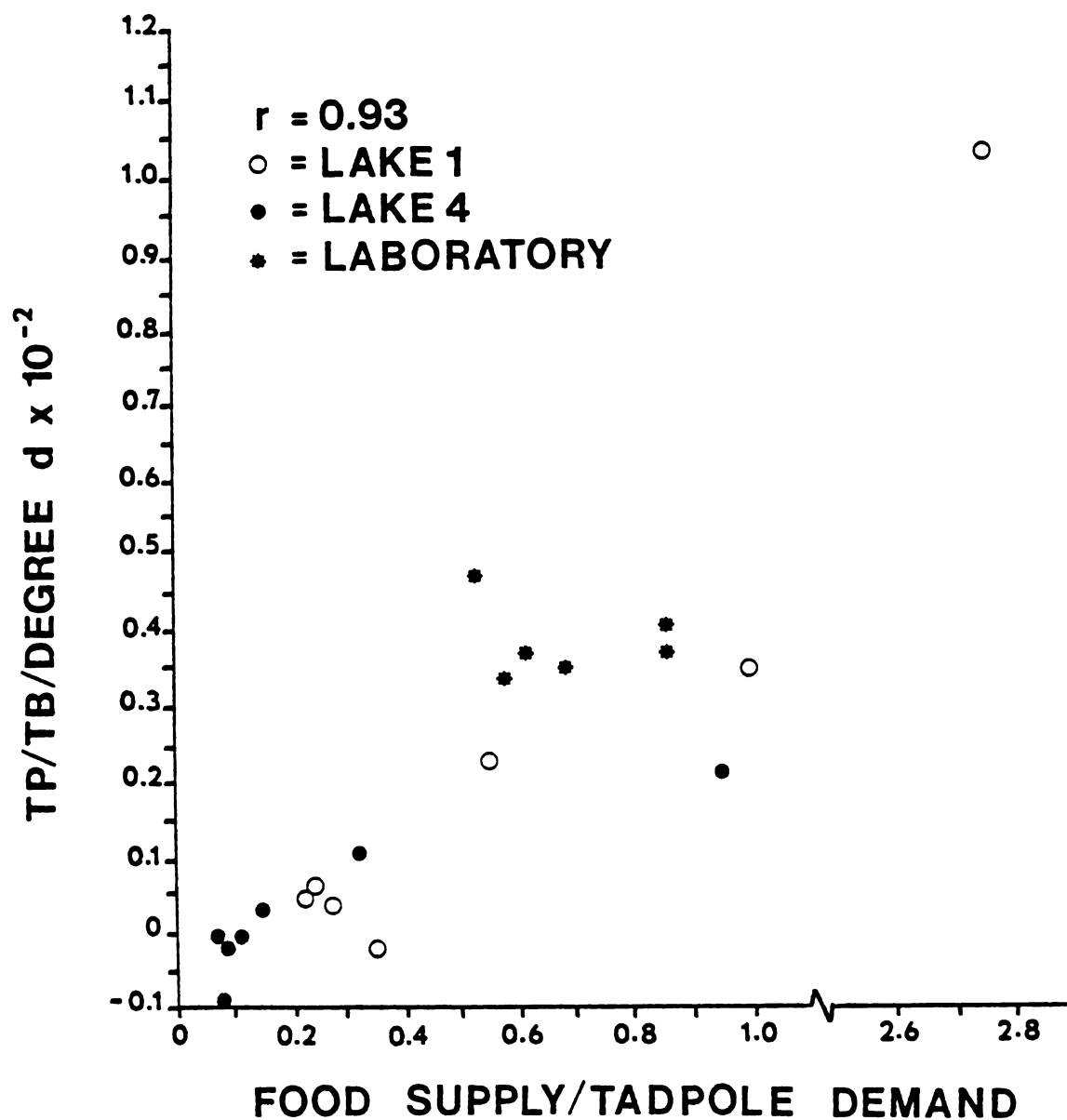


Figure 23. The relationship between tadpole production (mg C)/tadpole stocked biomass (mg C)/degree d and the supply of food (mg particulate organic C/d or GPP as mg C/d) per unit of stocked tadpole biomass (mg C) for all experiments at Lakes One and Four and the laboratory study (A-1 and A-5 at 500 ml, 1,000 ml, and 1,500 ml, respectively).

on particulate organic carbon measured in the laboratory or GPP in the field, per unit of demand (carbon biomass of tadpoles) and tadpole production remained high ($r = 0.93$), despite the different test conditions in the laboratory and field studies. Thus, tadpoles at the densities (laboratory, $13\text{--}120/\text{m}^2$ or $263\text{--}2368/\text{m}^3$ for R. pipiens; field, $22\text{--}220/\text{m}^2$ or $117\text{--}1051/\text{m}^3$ for R. pipiens, R. clamitans, and R. catesbeiana) and biomasses (wet weight, $9\text{--}36 \text{ g}/\text{m}^2$ or $186\text{--}770 \text{ g}/\text{m}^3$ in the laboratory and $3\text{--}109 \text{ g}/\text{m}^2$ or $54\text{--}573 \text{ g}/\text{m}^3$ in the field) stocked effectively divided the food resources among individuals. The main response of leopard frog tadpoles to crowding or high densities was slow growth caused by the lower food availability per individual. Low densities of tadpoles with abundant food grew fastest in contrast to findings reported by Wilbur (1977) of a "pollution effect" which reduced growth of tadpoles. Biomasses of leopard frog tadpoles stocked did not influence survival except, indirectly, by lowering the amount of food available per individual. Whether the surviving biomass or yield of tadpoles would exceed or be less than the initial biomass depended on the stocking intensity (TB/GPP), expressed as the ratio of biomass initially stocked to the average gross primary productivity (Table 31). At both lakes, low stocking intensities resulted in higher ratios of surviving biomass of R. pipiens to GPP than high stocking intensities. Neither exploitive competition, interference competition, nor social and behavioral interactions, as observed by other investigators (Rose 1965, Akin 1966, Pourbagher 1968, 1969, Wilbur 1977, Steinwascher 1978a, b, 1979a, b, Dash and Hota 1980), appeared to be operating consistently in Experiments One and Two and the laboratory study.

Table 31. Stocking intensities as₂ stocked tadpole biomass/initial GPP¹, stocked tadpole biomass/GPP², and surviving tadpole biomass/GPP² for the three experiments at Lakes One and Four. Values for tadpole biomass and GPP in carbon (mg).

EXPERIMENTS	LAKE ONE			LAKE FOUR		
	LOW STOCK	HIGH STOCK		LOW STOCK	HIGH STOCK	
<u>EXPERIMENT ONE</u>						
Stocked Tadpole Biomass/initial GPP	5.14	11.17		5.19		12.21
Stocked Tadpole Biomass/GPP	1.47	2.99		8.52		13.21
Surviving Tadpole Biomass/GPP	1.93	2.25		3.97		5.69
<u>EXPERIMENT TWO</u>						
Stocked Tadpole Biomass/initial GPP	1.49	4.96		1.00		2.82
Stocked Tadpole Biomass/GPP	0.37	1.03		1.07		3.22
Surviving Tadpole Biomass/GPP	1.79	1.52		1.12		1.65
<u>EXPERIMENT THREE</u>						
Stocked Tadpole Biomass/initial GPP	BULLFROG 4.65	MIXED 4.59	GREEN FROG 4.47	BULLFROG 22.78	MIXED 24.99	GREEN FROG 22.09
Stocked Tadpole Biomass/GPP	4.53	4.69	4.37	17.88	19.69	20.26
Surviving Tadpole Biomass/GPP	4.96	4.78	4.55	16.80	16.58	18.61

¹ initial GPP equals average GPP in all aquaria measured before tadpole stocking

² GPP refers to mean GPP for the three sampling dates per experiment after tadpole stocking

In the third experiment, the biomasses of surviving tadpoles of bullfrogs and green frogs/GPP were greater at both lakes than anticipated, based on results from the two earlier experiments on the effects of stocking intensity on leopard frog tadpoles (Table 31). Since GPP was not appreciably elevated in Experiment Three at either lake, the high biomasses of surviving tadpoles in the third experiment can best be explained by the cooler water temperatures and concomitant reduced metabolic rates of tadpoles, which promoted increased survival despite the high stocking intensities. Tadpole production for the monocultures of bullfrogs and green frogs in the third experiment was related to food availability as in earlier experiments with leopard frog tadpoles (Figure 23). In the mixed-species culture, pooled production values for tadpoles of the two species corresponded to the ratio of food supply/demand; however, when the growth of R. clamitans and R. catesbeiana was analyzed separately, green frog tadpoles performed better and bullfrog tadpoles performed poorer than expected, based on results from single-species cultures. Observations of tadpoles of these two species in natural habitats and information reported from laboratory studies have indicated that tadpoles of bullfrogs should grow better than those of green frogs when these species occur together. Steinwascher (1978a, b, 1979a, b) found that tadpoles of R. catesbeiana ingest their feces, especially during low abundances of particulate food. Large tadpoles more efficiently exploit the feces of small tadpoles and outcompete them for this food source. Tadpoles of R. clamitans are non-coprophagous and feed mainly on materials rasped from substrates, not particles in the water column as bullfrog tadpoles do (Steinwascher 1978a, b, 1979a, b).

In this study at Lakes One and Four, tadpoles of R. catesbeiana, because of their larger size, could have had a slight competitive advantage over those of R. clamitans (exploitive competition). As proposed by Steinwascher (1978a, b, 1979a, b), the clumped resource, represented by periphytic algae in this study, was reduced more by monocultured green frogs than bullfrogs; however, concentrations of particulate material, specifically phytoplankton, were not depressed more by bullfrog tadpoles. Tadpoles of bullfrogs and green frogs used the food resources similarly; when reared together, no measurable partitioning of food into suspended and attached components or differential resource utilization by tadpoles occurred in Experiment Three. Food, mainly periphyton and settled material, ingested by tadpoles of R. clamitans and R. catesbeiana was like that used by R. pipiens. Apparently, monocultured bullfrogs at both lakes used the available nutritional resources more efficiently than monocultured green frogs, since these tadpoles produced more biomass than those of green frogs. Data on algal production and nutrient concentrations from mixed-species cultures do not provide explanations for the higher production by green frog larvae. The smaller tadpoles of green frogs interfered with foraging and feeding by bullfrog tadpoles and the activities of bullfrogs increased the food available to green frogs. These results suggest that green frog tadpoles in natural environments may perform better in mixed-species populations with bullfrog tadpoles than in single-species populations. Bullfrog tadpoles, instead, may grow more rapidly when they occur in single-species populations. Tadpoles of bullfrogs and green frogs have not been reported to partition aquatic habitats by food, time, or space. Explanations for the different

performances of tadpoles of bullfrogs and green frogs singly and in combination will require additional investigations of these two species in natural habitats.

Ecological Efficiencies of Tadpoles

Net primary productivity (NPP), which is the excess of photosynthetic production remaining after respiration has taken place, is a better indicator of the availability of food to grazers, like tadpoles, than gross primary productivity (GPP). Although at least 90% of the GPP of algal salt marsh communities may appear as net production (Pomeroy 1959), crops and natural vegetation, including phytoplankton, more typically respire about 20 to 40 per cent of the gross primary productivity (Hargrave 1969, Whittaker 1970, Wetzel 1975, Cole and Fisher 1978, Moss 1980). Respiration can account for as much as 70% of the GPP in certain plant communities (Kira and Shidei 1967, Golley 1970, Whittaker 1970).

Accurately estimating net primary productivity of plants containing a few cells, which have a relatively short life span in aquatic environments, is difficult (Golley 1970, Barnes and Mann 1980, Moss 1980). In natural waters, estimates of algal respiration may be biased by the respiratory contributions of fungi, protozoa, microscopic zooplankton, and especially bacteria (Fogg 1980). At Lakes One and Four in this study, bacteria were not abundant in water samples or on membrane filters, so their respiration should not have exceeded about 20% of the total respiration. Leakage of organic compounds, like glycollate and peptides, can also influence estimates of net primary productivity. Fogg (1966, 1968, 1971, 1977) suggested that estimates

of NPP may have to be increased by as much as 40% to account for these extracellular compounds. However, the amount of organically combined carbon which is lost from algal cells relative to the amount of total carbon fixation is inconsequential in eutrophic waters, amounting to less than 1% (Fogg 1980).

Ecological efficiencies (TP/NPP) of ranid tadpoles feeding upon algae were calculated by assuming that NPP was 20, 60, and 100% of the GPP (Table 32). Based on the correlation between respiration and gross primary productivity for the three experiments at both lakes, realized net production by autotrophs at Lakes One and Four probably ranged between 20 to 60% of the GPP. At both lakes, the highest total production by tadpoles and ecological efficiencies of tadpoles feeding on algae were observed in Experiment Two (Table 32). Values for ecological efficiency during this experiment were 6 to 32%, assuming leopard frog tadpoles fed only on live algae and NPP was 20 to 60% of the GPP. Based on these same assumptions, in Experiment Three at Lake One, all groups of tadpoles, single-species cultures of bullfrogs and green frogs and mixed-species cultures, were more efficient in using algae than leopard frog tadpoles at both lakes during the first experiment. However, the efficiencies of bullfrog tadpoles were almost twice those of green frog tadpoles feeding on live algae (Table 32).

Ecological efficiencies for ranid tadpoles consuming algae are comparable to those of other grazers on primary productivity in aquatic systems. Energy transfers from primary productivity to secondary productivity for herbivorous benthos ranged from 1 to 14%; for herbivorous plankton, ecological efficiencies have been reported as 0.5 to 60%, but

Table 32. Ecological efficiencies of tadpoles (R. pipiens, R. clamitans, and R. catesbeiana), assuming NPP is 20, 60, or 100% of the GPP.

EXPERIMENTS	NPP/GPP X 100					
	LOW STOCK			HIGH STOCK		
	100%	60%	20%	100%	60%	20%
<u>EXPERIMENT ONE - LAKE ONE</u>						
Net primary productivity	185.2	111.1	37.0	196.6	118.0	39.3
Detrital import	39.5	39.5	39.5	39.5	39.5	39.5
Total food available	224.7	150.6	76.5	236.1	157.5	78.8
Total tadpole production	2.8	2.8	2.8	1.0	1.0	1.0
Efficiency % (total "food")	1.2	1.9	3.7	0.4	0.6	1.3
Efficiency % (no detritus)	1.5	2.5	7.6	0.5	0.8	2.5
<u>EXPERIMENT TWO - LAKE ONE</u>						
Net primary productivity	241.4	114.8	48.3	288.1	171.9	57.6
Detrital import	82.1	82.1	82.1	82.1	82.1	82.1
Total food available	323.5	196.9	130.4	370.2	255.0	139.7
Total tadpole production	15.7	15.7	15.7	16.9	16.9	16.9
Efficiency % (total "food")	4.9	8.0	12.0	4.9	6.6	12.1
Efficiency % (no detritus)	6.5	13.7	32.5	5.9	9.8	29.3

Table 32 (cont'd.).

EXPERIMENTS	NPP/GPP X 100					
	LOW STOCK			HIGH STOCK		
	100%	60%	20%	100%	60%	20%
<u>EXPERIMENT ONE - LAKE FOUR</u>						
Net primary productivity	33.8	20.3	6.8	46.5	27.9	9.3
Detrital import	29.0	29.0	29.0	29.0	29.0	29.0
Total food available	62.8	49.3	35.8	75.5	56.9	38.3
Total tadpole production	0.3	0.3	0.3	-1.6	-1.6	-1.6
Efficiency % (total "food")	0.5	0.6	0.8	-2.1	-2.8	-4.2
Efficiency % (no detritus)	0.9	1.5	4.4	-3.4	-5.7	-17.2
<u>EXPERIMENT TWO - LAKE FOUR</u>						
Net primary productivity	27.0	16.2	5.4	25.3	15.2	5.1
Detrital import	21.3	21.3	21.3	21.3	21.3	21.3
Total food available	48.3	37.5	26.7	46.6	36.5	26.4
Total tadpole production	1.0	1.0	1.0	1.3	1.3	1.3
Efficiency % (total "food")	2.1	2.7	3.7	2.8	3.6	4.9
Efficiency % (no detritus)	3.7	6.2	18.5	5.1	8.6	25.5

Table 32 (cont'd.).

EXPERIMENTS	NPP/GPP X 100									
	Monocultured bullfrogs			Mixed-species			Monocultured green frogs			
	100%	60%	20%	100%	60%	20%	100%	60%	20%	20%
<u>EXPERIMENT THREE - LAKE ONE</u>										
Net primary productivity	229.1	137.1	45.8	218.4	131.0	43.7	227.9	136.7	45.6	
Tadpole production	3.2	3.2	3.2	2.2	2.2	2.2	1.6	1.6	1.6	
Efficiency %	1.4	2.3	6.7	1.0	1.7	5.0	0.7	1.2	3.5	
<u>EXPERIMENT THREE - LAKE FOUR</u>										
Net primary productivity	32.9	19.8	6.6	32.4	19.4	6.5	28.3	17.0	5.7	
Tadpole production	-0.04	-0.04	-0.04	-0.14	-0.14	-0.14	-0.44	-0.44	-0.44	
Efficiency %	-0.1	-0.2	-0.6	-0.4	-0.7	-2.2	-1.6	-2.6	-7.7	

estimated efficiencies of 17 to 20% appear most reliable (Brylinsky and Mann 1973, Moriarty et al. 1973, Gulati 1975, Lam and Frost 1976, Lehman 1976, Pederson et al. 1976, Coveney et al. 1977, Makarewicz and Likens 1979, Hughes 1980, McCauley and Kalff 1981).

Values of ecological efficiency for planktivorous herbivores are influenced by the trophic status of the aquatic environment; ratios of herbivorous production to primary production are highest in oligotrophic waters and decrease with increasing eutrophy (Pederson et al. 1976, McCauley and Kalff 1981). The quality, which includes algal size and manageability, chemical composition and nutritional value, and toxicity among other attributes, as well as the quantity, expressed as dry matter, organic material, carbon or energy per unit area, of primary productivity determines its utilization within food webs of aquatic systems (Boyd 1970, 1971, Iverson 1974, Schroeder 1977, Onuf et al. 1977, McNeill and Southward 1978). In eutrophic waters, nanoplankton (10 to 50 μm ; Strickland 1960) are less abundant and many algal planktivores consume algae mainly in the nanoplanktonic range (Glicwicz 1967, 1977, Porter 1973, 1977, Nadin-Hurley and Duncan 1976). Because of their unmanageability and possible toxicity (toxin production varies among different strains of the same species; Carmichael and Gorham 1977, 1978), large filamentous blue-green algae, like Anabaena flos-aquae, are a low quality food for filter feeders, such as zooplankton (Porter 1973, 1977, Webster and Peters 1978, Lynch 1980, Porter and Orcutt 1980). Although these filaments are filtered and ingested at the lowest rates by zooplankton, they may be assimilated at rates and efficiencies comparable to other algae that are considered good food sources (Arnold 1971, Lampert 1977). Algal

macroconsumers, like brown bullhead catfish, non-selectively graze large quantities of filamentous algae (Cable 1929, Rubec 1975); however, the nutritional quality of different algal taxa affects the efficacy of digestion and assimilation by bullheads. For example, Gunn et al. (1977) have demonstrated that blue-greens (A. flos-aquae), which have a crude protein content of 48%, are assimilated more efficiently by brown bullheads than filamentous green algae like Spirogyra sp., with a crude protein content of 22% (A/I% for A. flos-aquae, 48 to 68%; and for Spirogyra sp., 24%).

Thus, using total NPP rather than ingested NPP may produce inaccurate estimates of ecological efficiency for consumers. In this study at Lakes One and Four, ecological efficiencies of ranid tadpoles were based on net autotrophic production of both phytoplankton and periphyton. Since tadpoles foraged predominantly on periphyton, the tadpoles' use of attached algae, representing only a portion of the NPP, may more accurately depict their ecological efficiency. Therefore, efficiencies of tadpoles calculated for total NPP may be underestimates.

Most suspension feeders and scrapers in aquatic systems are omnivorous, not strictly herbivorous, since they consume protozoa, detritus, and bacteria as well as living plants. Because both bacteria and detritus may be a major food source for consumers, estimates of NPP may not adequately represent energy availability and use. Even though the standing stock of bacterial biomass in an aquatic ecosystem may not be as great as that of phytoplankton, periphyton, and macrophytes, the bacterial contribution to secondary productivity can be substantial because the bacterial biomass may be replaced several times

each day under optimal conditions (Sieburth 1976, Watson et al. 1977). The production of microorganisms sometimes exceeds the production of phytoplankton, especially in shallow water-bodies, where most of the macrophytic production becomes detritus and a high input of allochthonous material occurs. Pomeroy (1980) cites studies that demonstrate as much as 90% of plant production goes to detritus in many aquatic systems. Detrital material rapidly loses proteinaceous compounds and becomes less nutritious to consumers (Berrie 1976). However, the microbial biomass associated with the decomposing detritus may increase the detrital protein or nitrogen content, making detritus an important energy source (Odum and de la Cruz 1967, Kaushik and Hynes 1968, 1971, Hynes et al. 1974, Heal and MacLean 1975). Microorganisms may fulfill a dual role by converting detritus into microbial tissues which are directly ingested and by catalyzing the partial degradation of refractory materials comprising detritus into substances that can be used by animal consumers (Bärlocker and Kendrick 1974, 1975a, b, Berrie 1976).

Because ranid tadpoles in natural habitats are omnivorous and may feed on bacteria and detritus, derived from plants, feces, or carcasses of other animals, ecological efficiencies were calculated for tadpoles consuming both algae and detritus ($TP/(NPP + \text{detrital carbon})$). Like TP/NPP , the highest ecological efficiency of ranid tadpoles on algae with detritus was measured in Experiment Two at Lakes One and Four (Table 32). Ecological efficiencies of tadpoles presumed feeding on algae and detritus were lower than efficiencies calculated for tadpoles consuming living algae at both lakes, but especially at Lake Four where detrital carbon comprised a large portion of the available food. This was obvious in Experiment Two when ecological efficiencies

($TP/(NPP + \text{detritus})$) at Lake Four (3 to 5%) were less than half of those at Lake One (7 to 12%). Detritus appeared to be less nutritious as a food than living algae at both lakes, but least nutritious at Lake Four. Ratios of C:N for detritus were high at Lake Four where much of the detrital material probably was derived from macrophytes, rather than algae as at Lake One. Macrophytic tissues have unfavorably high C:N ratios (average C:N greater than 17:1, Russell-Hunter 1970, McMahon et al. 1974) and resilient structural elements (van Soest and Wine 1967, Boyd and Goodyear 1971, Polisini and Boyd 1974) that make them less likely to be grazed than most algae (average C:N less than 6:1, Wetzel 1975). The correlation between ecological efficiency ($TP/(NPP + \text{detritus})$) and stocking intensity, denoted as the ratio of stocked tadpole biomass to NPP with detritus ($TB/(NPP + \text{detritus})$), was lower ($r = -0.75$) than the correlation obtained between stocking intensity and NPP without detritus ($r = -0.80$).

Although monitoring energy and material flow through producers and consumers will remain a major theme in ecology, present techniques for measuring energy transformations are oversimplifications of energy relationships in natural ecosystems (Steele 1970, Turner 1970, Edmondson and Winberg 1971, Slobodkin 1972, Grodzinski et al. 1975, van Dobben and Lowe-McConnell 1975, Wiegart 1976, Cooke 1977). For these reasons, Pomeroy (1980) has suggested that energy transfers between producers and consumers should be measured as gross growth efficiency (growth/ingestion) and consumers should not be strictly categorized as, for example, herbivores, detritivores, or carnivores.

Growth and Assimilation Efficiencies

Assessing energy flow in specific ecosystems by designating consumers as exclusively belonging to one of three categories--herbivores, omnivores, or carnivores--is misleading and inaccurate since many aquatic organisms are opportunists and more catholic in their dietary intake. However, this tripartite method of cataloging consumers as feeding primarily on plants, animals, or both has provided a conceptual framework for integrating anatomical structures and physiological processes in a diversity of taxa that feed on similar resources. For example, Welch (1968) reviewed reported values for growth and assimilation of aquatic herbivores, omnivores, and carnivores and observed that gross or ecological growth efficiencies (G/I or P/I) and assimilation efficiencies (A/I or P/I) were generally higher for carnivores than for herbivores. Tissue growth efficiency or net growth efficiency (G/A or P/A), in contrast, appeared to be slightly higher for herbivores. Welch (1968) suggested this evidence indicated an obvious nutritional difference between carnivores and herbivores. Carnivores digest and absorb more of their dietary intake at a high metabolic cost, whereas herbivores ingest larger quantities of less digestible foods. According to Welch (1968), omnivores occupy an intermediate position, possibly obtaining more of their protein requirements from animal tissues and their energy requirements from plant tissues. Recent data on aquatic consumers discussed below generally substantiates the relationships that Welch (1968) proposed between diet and efficiency.

In this study at Lakes One and Four and in the laboratory, ranid tadpoles under semi-natural conditions appeared to convert

primary productivity and organic carbon into tissues as efficiently as invertebrates and vertebrates feeding on similar foods. Ecological growth efficiencies (TP/ingestion) for leopard frog tadpoles measured in the laboratory, represented as G/I% since mortality was negligible, averaged 10.2%, 16.3%, and 23.0% at the 500 ml, 1,000 ml, and 1,500 ml algal supply rates, respectively. By assuming that leopard frog, bullfrog, and green frog tadpoles in field experiments ingested 20 to 60% of the GPP, similar ecological growth efficiencies can be estimated. At Lake One, leopard frog tadpoles stocked at low levels had efficiencies of 2.5 to 32.5% and those stocked at high levels had efficiencies of 0.8 to 29.3%. At Lake Four, tadpoles of R. pipiens in the low stocking had efficiencies of 1.5 to 18.5%, while those in the high stocking had ecological growth efficiencies that were negative to 25.5%. In the third experiment, gross growth efficiencies of bullfrog and green frog tadpoles averaged 1.2 to 6.7% at Lake One and were negative at Lake Four.

Assimilation efficiencies for leopard frog tadpoles fed algae in the laboratory were 23.8%, 34.4%, and 42.8% at the 500 ml, 1,000 ml, and 1,500 ml algal supply rates, respectively. In the laboratory, assimilation efficiencies were more than two times greater than growth efficiencies and perhaps would have shown a similar relationship in the field experiments. Tissue growth efficiencies (growth/assimilation) for leopard frog tadpoles supplied with phytoplankton were estimated as 42.6 to 53.9%, whereas those fed TetraMin had higher efficiencies, averaging 55.4 to 75.5%. The only data on tadpoles available for comparison are those of Altig and McDearman (1975) for assimilation efficiencies and Nagai et al. (1971) for ecological growth efficiencies.

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Assimilation efficiencies for R. catesbeiana ranged from 8 to 25% and those for R. heckscheri averaged 54% (Altig and McDearman 1975). Other tadpoles (Bufo woodhousei, Acris gryllus, and Gastrophryne carolinensis) tested by Altig and McDearman had higher efficiencies than the ranid tadpoles. Their efficiencies averaged 77 to 86% on a diet of Purina rabbit chow. Ecological growth efficiencies of 10 to 87% were estimated for Bufo vulgaris on different mixtures of grain, fish meal, amino acids, and dead tadpoles (Nagai et al. 1971).

Comparisons of data for ecological growth, assimilation, and tissue growth efficiencies of aquatic consumers reported in the literature are difficult, since efficiencies are influenced by the quantity and quality of the food supply, laboratory and field test conditions, age or stage of development of the organism, and many other abiotic and biotic factors. For example, rates of food passage through the guts of aquatic consumers like zooplankton and tadpoles are influenced by the quality and quantity of available food; organisms exposed to low levels of food process materials to feces less rapidly than those exposed to abundant food (Wassersug 1975, Porter 1978). Thus, consumers exposed to abundant food may feed superfluously and exhibit higher growth and assimilation efficiencies when foods of similar quality are less abundant (Corner 1966, Corner et al. 1967, Butler et al. 1970, Penderson et al. 1976, Porter 1977, Pomeroy 1980). Data from Lakes One and Four and the laboratory experiments indicate growth and assimilation efficiencies of tadpoles are influenced by the quality and quantity of food resources. When food was not highly concentrated as at Lake Four, ranid tadpoles appeared to utilize the available food, primarily attached algae, more efficiently than at Lake One.

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The efficiencies of invertebrates feeding on live plant material, detritus, bacteria, or a combination of these foods are highly variable; ecological growth efficiencies (G/I or P/I) were reported to range from 2 to 75% and tissue growth efficiencies (G/A or P/A) reportedly ranged between 6 and 99% (Richman 1958, Wright 1958, Corner 1961, 1972, Sorokin 1966, Hargrave 1970a, b, c, Winberg 1971, 1972, Ladle et al. 1972, Lasenby and Langford 1972, Monakov 1972, Saunders 1972, Edington and Hildrew 1973, Edmondson 1974, Nilsson 1974, Otto 1974, Anderson and Grafius 1975, McCollough et al. 1979, Benke and Wallace 1980). Values averaging 7 to 15% for ecological growth efficiency, 45 to 70% for tissue growth efficiency, and 7 to 50% for assimilation efficiency appear to be most common.

Gross ecological efficiencies of about 8% were measured for the common carp, Cyprinus carpio, feeding on detritus (Kevern 1966), whereas the grass carp (Ctenopharyngodon idellus) had gross efficiencies of 1.9% and net efficiencies of 14% when fed aquatic plants (Fisher 1970). Gross growth efficiencies for carnivorous fishes are higher than for omnivorous or herbivorous fishes, averaging 13 to 37% for salmonids (Warren and Davis 1967, Brett et al. 1969, LeBrasseur 1969, McCormick et al. 1972, Shelbourne et al. 1973, Brett and Shelbourne 1975, Biette and Green 1980) and 13 to 44% for other fresh-water and marine fishes (Ivlev 1945, Pandian 1967a, b, c, d, Birkett 1969, Edwards et al. 1970, Gerking 1971, Cowey and Sargent 1972, Klekowski et al. 1972, Wissing 1974, Nakashima and Leggett 1980). Assimilation efficiencies for carnivorous fishes ranged between 67 to 86% (Davies 1963, Wissing 1974) and the efficiency of protein assimilation is higher than 90% (Menzel 1960, Pandian 1967a, b, c, d, Birkett 1969). Fishes that are more

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omnivorous, like channel catfish, have assimilation efficiencies greater than 80% on plant protein and greater than 90% on animal protein (Hastings 1969). Other catfish, like brown bullheads, assimilate filamentous algae at efficiencies between 24 and 67%, depending on the protein content of the algal taxa ingested (Gunn et al. 1977). Tilapids (Sarotherodon mossambicus = Tilapia mossambica), which consume detrital material, have remarkably higher assimilation efficiencies, ranging from 37 to 46% (Bowen 1979). Tissue growth (net growth or production) efficiencies in carnivorous fishes range from 24 to 54% (Brett et al. 1969, Gerking 1971, Klekowski et al. 1972); average 91% in larval newts of Triturus helveticus and T. vulgaris (Avery 1971); and in the salamanders, Plethodon cinereus (Burton and Likens 1975) and Desmognathus ochrophaeus (Fitzpatrick 1973a, b), are 50 to 80% and 76 to 89%, respectively.

Gross or ecological growth efficiencies of ranid tadpoles assessed in this study were higher than those of most invertebrates and herbivorous or omnivorous fishes. In contrast to invertebrates, tadpoles are larger and can consume a broader size range of dietary items. More importantly, tadpoles are immature and do not reproduce, so the energy they ingest and assimilate goes toward tissue elaboration, not reproduction. Assimilation efficiencies of tadpoles are similar to those of invertebrates and higher than efficiencies of omnivorous fish like the common and grass carp. Tissue growth efficiencies of tadpoles feeding on algae are higher than those of carnivorous fishes and within the range of efficiencies of invertebrates. Tadpoles when fed a nutritious, easily digestible food like TetraMin have higher growth efficiencies than those of tadpoles feeding on

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algae; efficiencies for TetraMin resemble those of herbivorous or omnivorous invertebrates measured under optimal conditions. Based on these comparisons, ranid tadpoles in protected environments efficiently process materials and convert them into tadpole tissues.

Potential Roles of Tadpoles in Natural and Wastewater Treatment Systems

In aquatic systems, tadpoles frequently inhabit shallow, inshore areas with fringing plant communities, commonly designated as littoral zones. Although limnological investigations were initiated in Europe over 100 years ago (Elster 1974), these concentrated on the pelagic area and its associated phytoplankton; only more recently, in the last 15 years, have other plant associations like fringing plant communities in lakes and ponds been studied intensively. Results from these studies have demonstrated the importance of fringing plant communities comprised of macrophytes and microphytes to aquatic ecosystems in that they may (1) produce more carbon or calories annually than pelagic phytoplanktonic communities in the same water body (Straskaba 1963, Efford 1967, Hargrave 1969, Allen 1971, Pierczynska 1972, Dokulil 1973, Hutchison 1975, Talling 1975, Teal 1980); (2) serve as traps or sinks for nutrients during periods of the year, making certain nutrients largely unavailable to pelagic autotrophs (Chamberlain 1968, Confer 1972, Lee et al. 1975, Prentki et al. 1979, Teal 1980); (3) release high concentrations of dissolved organic materials and phosphorus by leakage during photosynthesis (McRoy et al. 1972, Wetzel and Manny 1972, Titus et al. 1975, Twilley et al. 1977, Smith 1978, Carpenter 1980, Teal 1980) or during decomposition (Solski

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1962, Nichols and Keeney 1973, Otsuki and Wetzel 1974, Carpenter and Adams 1978, 1979, Godschalk and Wetzel 1978a, b); and (4) inhibit growth of phytoplankters by reducing the availability of light through shading or by releasing allelopathic compounds (Strangeberg 1963, Goulder 1969, Brandl et al. 1970, Allen 1971, Dokulil 1973, Teal 1980). The influence of littoral zones on ecosystem metabolism extends beyond the primary and secondary production attributed to plants and animals of this area and may include contributions of nutrients and organic materials to augment production of phytoplankton, suspended bacteria, and pelagic and benthic consumers. Conversely, fringing plant communities, at least for certain periods of the year, may accumulate nutrients and organic material, thus potentially decreasing phytoplanktonic and microbial production in the open waters of lakes.

For tadpoles, littoral zones may serve as sources of abundant food with epibenthic and epiphytic communities comprised of algae, bacteria, protozoa, and associated detritus. Vascular macrophytes may be a major component of fringing plant communities, but these generally are not grazed directly by tadpoles or other aquatic consumers (Savage 1952, Odum 1957, Gajecskara 1969, McMahon et al. 1974, Hutchison 1975). Teal (1980) has reviewed data on productivity of fringing plant communities that shows the contribution of microphytes, specifically periphytic and epibenthic algae, can vary from insignificance to being considerably more important than macrophytic production. Although vascular macrophytes when reduced to detrital material are more likely to serve as food for aquatic consumers (Bärlocker and Kendrick 1975a, b, Berrie 1976), living macrophytes, as well as providing substrates for aufwuchs which are grazed, create a structurally complex habitat,

not found in the pelagic zone. Wiens (1970, 1972) has demonstrated that ranid tadpoles select particular habitats in the laboratory which are consistent with their ecological distributions in the field. These behavioral responses of tadpoles to habitat alternatives are genetically controlled, not a learned response (Wiens 1970, 1972).

The importance of structurally diverse environments in reducing the frequency of physical interactions among crowded leopard frog tadpoles has been investigated by John and Fenster (1975). They found that the growth of tadpoles reared at high densities was directly related to the frequency of physical encounters among tadpoles; however, growth rates were not determined simply by physical space but, rather, by "psychological space" not mediated by vision. Crowded tadpoles grown in aquaria with partitions simulating a structurally diverse environment did not exhibit the "crowding effect" that the same density of tadpoles exhibited in aquaria without partitions. The importance of social and behavioral factors in affecting the growth of tadpoles has been established by Goetsch (1924), Adolph (1931a, b), Rugh (1934), Lynn and Edelman (1936), Hodler (1958), Gromko et al. (1973), and Smith-Gill and Gill (1978). If, as suggested, social and behavioral factors limit tadpole production in the laboratory, these same factors may be relatively unimportant in natural habitats because of the structural complexity of littoral environments.

Ranid tadpoles grazing in fringing plant communities swim little and use the abundant filamentous algae and macrophytes as physical supports to maintain their position in the water column. Ranid tadpoles do not possess the morphological adaptations of certain open-water tadpoles like hylids and xenopids (Porter 1972), so the

energy required in swimming or maintaining a stationary position in the water should be higher for ranid tadpoles than for pelagic tadpoles specifically modified for filtering seston. In addition to support, littoral vegetation may provide refugia for tadpoles from predation by more accomplished swimmers like fish. Although quantitative data of fish predation on tadpoles in lakes and ponds are scarce, predation has been cited as the primary factor controlling tadpole populations in nature by Herreid and Kinney (1966), Calef (1973), Licht (1974), Heyer et al. (1975), and Heyer and Muedeking (1976). Shallow, inshore areas are characterized by warmer temperatures than are deeper waters and tadpoles have been observed to orient to thermal gradients, choosing temperatures within the optimal range for their growth and development (Beisenger 1977). Rapid growth of tadpoles to large sizes has been shown by Heyer, McDiarmid, and Weigmann (1975) to increase their probability of survival, since they may have outgrown certain vertebrate and invertebrate predators.

Results at Lake One from experiments which excluded grazing (unstocked aquaria) and simulated the effects of tadpole grazing in littoral zones with extensive standing crops of attached algae but without predation (stocked aquaria) were similar to those observed by Confer (1972). An open-water system comprised of 200-liter aquaria continuously supplied with water and radioactive phosphorus (^{32}P as H_3PO_4) was designed by Confer (1972) to represent phosphorus circulation in small lakes with extensive littoral zones during summer stratification. As in aquaria at Lake One, Confer's (1972) microecosystems approximated lakes with a large ratio of littoral area to open water and with abundant attached algae, without sediments or loss

of materials to the hypolimnion. In systems without grazers, both in Confer's (1972) aquaria and unstocked aquaria at Lake One, the net movement of phosphorus was out of the open-water phytoplanktonic community to the attached filamentous algae and associated organisms. Phosphorus was removed from the open water by incorporation into plant tissues of littoral algae, but more importantly, major amounts of phosphorus were trapped as particles by the attached algae associated with the sides and bottoms of aquaria. Trapping of particulate phosphorus by fringing plant communities was not an artifact of the micro-ecosystem design, since this occurs in natural aquatic habitats (Chandler 1937, 1939, Chamberlain 1968). Grazers, whether snails or ostracods introduced by Confer (1972) or tadpoles stocked in experiments at Lake One, reduced the standing crop of attached algae and promoted the increase of phosphorus, especially in particulate form, in the open water. Snails and ostracods, like tadpoles, significantly increased the proliferation of phytoplankton in the epilimnion.

Projections on the potential role of tadpoles in nutrient uptake and relocation in ecosystems with high standing crops of fringing plants can be made from observations at Lake One. In enriched systems where food is abundant and predators scarce, minimum densities of 100 tadpoles/m² appear reasonable. At this density, small tadpoles, averaging 200 mg (wet weight) per individual, could remove over 150 mg C/m²/d and about 4 mg P/m²/d. Larger tadpoles, averaging one gram, when present at the same density as small tadpoles, could ingest periphytic algae at the rate of 750 mg C/m²/d and 21 mg P/m²/d. Substantiation of these estimated rates of organic carbon and phosphorus removal by tadpoles is provided in laboratory studies by Seale (1973,

1980). She found that ranid tadpoles consumed filamentous algae (estimated C:N:P ratio of 40:7:1, Wetzel 1975) at the rate of 48 $\mu\text{g N/g}$ (wet weight of tadpoles)/h. Estimates presented by Seale (1973, 1980) when used to assess nutrient removal by tadpoles in nature indicated that at densities of $100/\text{m}^2$, ranid tadpoles averaging 200 mg could consume 144 mg $\text{C}/\text{m}^2/\text{d}$ and 3.4 mg $\text{P}/\text{m}^2/\text{d}$ and those averaging one gram could ingest 720 mg $\text{C}/\text{m}^2/\text{d}$ and 17 mg $\text{P}/\text{m}^2/\text{d}$.

Aquatic ecosystems with low primary production like Lake Four, where GPP averaged about 140 mg $\text{C}/\text{m}^2/\text{d}$ and standing crops of microphytic fringing plants were correspondingly low, could support about 10 to 25 ranid tadpoles/ m^2 . Nutrient removal by tadpoles stocked at these densities would be about 10 to 25% of those estimated for eutrophic waters like Lake One. In comparison to Lake Four, oligotrophic Marion Lake which purportedly could support 31 (*R. aurora*) tadpoles/ m^2 (Calef 1973) had mean annual values for primary productivity of 180 mg $\text{C}/\text{m}^2/\text{d}$ with epibenthic algal productivity averaging 109 mg $\text{C}/\text{m}^2/\text{d}$ (Efford 1967, Hargrave 1969, Gruedling 1971). Assuming differences in the biology of these two ranid species in Marion Lake and Lake Four were unimportant, the higher densities of tadpoles estimated in Marion Lake probably were related to the higher production by epibenthic algae, which averaged almost twice that of attached algae at Lake Four.

Expected yields, as wet weight, carbon, and phosphorus, of ranid tadpoles can be assessed for productive waters like Lake One and less productive waters like Lake Four. From eutrophic systems, about 127 g/ m^2 (5 g C/m^2 and 150 mg P/m^2 , assuming a C:P ratio of 35:1, Mackenthun 1969, Durbin et al. 1979) of live tadpoles could be harvested per month, if tadpoles (about 200 mg wet weight per

individual) were stocked at 20 g/m^2 and these grew at the maximum rates measured in field experiments (TP/TB/d of 0.176 in Experiment Two). In ecosystems like Lake Four with tadpole production as in Experiment Two (TP/TB/d of 0.033), 5.4 g/m^2 or 212.4 mg C/m^2 and 6.4 mg P/m^2 could be harvested monthly when 5 g/m^2 of tadpoles (averaging $200 \text{ mg/individual}$) were stocked initially. These potential rates of nutrient removal by tadpoles and harvest of tadpoles may not be realized in natural environments, whether eutrophic or oligotrophic, since they are based on extrapolations of data obtained from studies of tadpoles in protected environments. But the similarities in estimates of nutrient removal by tadpoles in these different studies indicate that ranids may serve as "harvestable" nutrient concentrators in wastewater treatment facilities where abiotic and biotic variables can be controlled to maintain an "optimal" (as yet undefined) environment for tadpoles. If as shown in experiments at Lakes One and Four that ranid tadpoles consume attached microphytes primarily, then more efficient systems for culturing tadpoles can be devised than those simulated by aquaria in this study. For example, shallow systems with high ratios of substrate-to-volume, like modified raceways, could enhance the growth and production of attached algae to be used as food for tadpoles.

Tadpoles are not the only consumers of algae and detritus in most water bodies; other organisms in the benthic, littoral, and pelagic zones may influence the quantity and quality of food available to tadpoles. Grazers like zooplankton which mainly filter seston in the pelagic area probably would not compete directly with populations of ranid tadpoles for food and, instead, may benefit from the activities of tadpoles. Evidence for this has been found in experimental systems

where higher survival and reproduction of cultured zooplankton occurred with the inclusion of tadpoles (Kurt Kearns, pers. comm.). An explanation for the better performance of zooplankton when cultured with tadpoles may be that grazing by tadpoles relocated nutrients to the open water and favored the accumulation of phytoplankton and detritus, making more seston available to filter-feeding zooplankters. Conversely, zooplanktonic grazing and metabolic by-products hypothetically may increase the availability of food to tadpoles, either, directly, by ameliorating growth of periphytic and epibenthic algae through increased water transparency and nutrient availability or, indirectly, by promoting the settling of high concentrations of seston, as algae or detritus and fecal pellets with associated microbes. Results from general studies on the ecology of pelagic zooplankton and ranid tadpoles indicate the two taxa interact in a mutually beneficial manner and can be successfully cultured together. However, this evidence is circumstantial and additional data are required from experiments specifically designed to elucidate the interrelationships between pelagic zooplankton and ranid tadpoles.

Other consumers in the littoral and benthic areas that graze substrates as their exclusive feeding mode could compete with tadpoles for limited food resources. Chydorid cladocerans (Meyers 1980), certain insects (Cummins 1975, Merritt and Cummins 1978), and other invertebrates like snails (McMahon et al. 1974, Hunter 1975) inhabit fringing plant communities and consume foods similar to those eaten by tadpoles. Also, settled seston and epibenthic algae are ingested by benthic infauna (Brinkhurst 1974), amphipods (Hargrave 1970a, b, c,

Mathias 1971), isopods (Johannes 1964, 1968, Prus 1971), and other organisms (Berrie 1976).

Tadpole interactions among conspecifics and congeners may be as important in the performance of tadpole populations as competition between tadpoles and various invertebrate taxa which utilize similar food and space resources. Despite a plethora of investigations on intraspecific and interspecific competition among tadpoles (reviews by Steinwascher 1978a, b, 1979a, b), none of the theories proposed have been universally accepted by researchers. Frequently the ecologists who design laboratory or field studies of ranid tadpoles are concerned with testing mathematical models of competition and know little about the ecology or life history of the species they employ. Thus, results and conclusions based on these experiments concerning the presence or absence of competition may not apply to tadpole populations in dynamic and structurally complex natural habitats.

Interpretations of findings from studies on the influence of intraspecific and interspecific competition on tadpole populations are further complicated by the conflicting results reported by different researchers testing the same species of anuran. For example, tadpoles of the wood frog (R. sylvatica) and leopard frog (R. pipiens) have been reared singly and in mixed-species cultures by Wilbur and Collins (1973), DeBenedictis (1974), and Smith-Gill and Gill (1978). Conclusions as to the importance of intraspecific and interspecific competition in these anuran taxa differ widely among the three studies. Smith-Gill and Gill (1978) after conducting laboratory investigations (densities of both species corresponded to 500 to 16,000 tadpoles/m³) proposed R. pipiens was more sensitive to densities of R. sylvatica

than conspecifics and the effects of R. pipiens on R. sylvatica were negligible. Similar studies by DeBenedictis (1974) in pond enclosures (tadpole densities of 165 to 1,600/m³) indicated that tadpoles of R. sylvatica exhibited lower growth and survival when cultured with R. pipiens, but tadpoles of R. sylvatica had no effect on the growth and survival of R. pipiens. Growth and survival by both wood frog and leopard frog tadpoles in the study by Smith-Gill and Gill (1978) were phenomenally high. At the highest densities of each species (8,000/m³) in mixed-species cultures, 84% of the leopard frog and 98% of the wood frog tadpoles metamorphosed. When species were reared singly at densities corresponding to 16,000/m³, 89% of the R. pipiens and 98% of the R. sylvatica metamorphosed (Smith-Gill and Gill 1978). DeBenedictis (1974) found tadpoles of both species grew and survived better in enclosures with conspecifics rather than with congenetics; however, maximum survival of either species in any density treatment was only 25% and typically was much lower.

Smith-Gill and Gill (1978) observed an "Allee effect" resulting in the highest growth of conspecific R. sylvatica at densities of 4,000 tadpoles/m³; growth at 500/m³ and 16,000/m³ was lower for tadpoles of this species. In contrast, enclosure experiments in ponds by Wilbur and Collins (1973) produced evidence of intraspecific competition and slower growth of R. sylvatica at densities (5,000/m³) similar to those where an "Allee effect" was observed by Smith-Gill and Gill (1978). Results from these studies (Wilbur and Collins 1973, DeBenedictis 1974, Smith-Gill and Gill 1978) and other studies reported in the literature (Steinwascher 1978a, b, 1979a, b) on ranid tadpoles indicate the difficulties encountered when attempting to apply

experimental findings to populations in nature. Discerning the effects of interactions among tadpoles is relevant to understanding the ecology of tadpoles in natural habitats and their potential performance in wastewater treatment systems. To achieve this, results and conclusions from previous studies must be reinterpreted and synthesized into hypotheses which, when tested, yield results applicable to tadpole populations in natural and managed environments.

In a recent review, Odum (1980) contrasted the efficacy of terrestrial and aquatic methods of harvesting and demonstrated that harvesting natural populations of aquatic plants and animals is more costly and energy-demanding than harvesting terrestrial organisms. As a means of improving aquatic harvests of natural populations of plants and animals to meet increasing food demands by human populations, Odum (1980) suggested the selective harvesting of organisms belonging to lower trophic levels and designing techniques to concentrate organisms more efficiently to approach a net energy balance (energy expended during harvesting/energy obtained from the harvest). Although these improved methods may yield more food at a lower cost, aquaculture was proposed by Odum (1980) as the most promising technique to create a significant food production and processing industry, analogous to agriculture, with reasonably predictable and controllable yields. Dramatic increases in current aquacultural yields may be achieved by (1) devoting more area to culture, (2) employing more herbivorous species, (3) farming several species with different trophic positions in the same enclosure (polyculture), (4) using greater densities of organisms, and (5) increasing the feeding and breeding efficiency through genetic selection. Organisms selected for aquaculture should

meet certain criteria, such as having simple life histories so they can be reared through all life stages in captivity; be hardy, resistant to diseases, and adaptable to crowding; and occupy a low trophic position, either a herbivore or detritivore, which produces a high biomass per unit area without expensive, (animal) protein-based feed (Odum 1980).

Results from this study at Lakes One and Four indicate that tissue production by ranid tadpoles in intensively managed wastewater treatment facilities may approach values reported for production of herbivorous fishes such as carp, tilapia, and milk fish, in fertilized ponds in Israel and the Far East (5,000 kg/ha/y, Bardach et al. 1972). However, the desirability of tadpole protein and monetary profits derived from the sale of tadpoles are likely not to be as high as that for fishes, since most humans would not accept tadpoles as suitable food. Indians in Mexico harvest and consume tadpoles, but ranid tadpoles, potentially grown at low cost in wastewater facilities, would be used primarily as a protein supplement for fish or livestock feeds. Evidence from Lake One demonstrates that tadpoles can be raised on natural crops of algae, are hardy, and adaptable to crowding. But ranids have complex life cycles and maintaining adults which require live animals or, at least, motile food (can be force-fed) is labor intensive and expensive (Culley and Gravois 1971, Culley and Meyers 1972, Culley 1973, Modzelewski and Culley 1974, Smalley 1978). Presently, a breeding program for bullfrogs is underway at Louisiana State University in indoor facilities where this species develops from eggs into frogs (227 g) in 10 to 12 months (Culley 1973). To insure that supplies of eggs are available when required for scheduled

stocking in wastewater treatment facilities, clutches of ranid eggs could be purchased from culture facilities (Nace 1968, Hirschfeld et al. 1970, Culley and Gravois 1971, Priddy and Culley 1971), collected from ponds and lakes when natural populations of ranid frogs are spawning, or obtained from adults previously captured in the field, which later were injected with pituitary extracts or hormones to induce egg and sperm production (Nace 1968).

Aquaculture, specifically polyculture, of organisms is a feasible technique for profitably employing the enriched "wastewaters" from treatment facilities. To achieve this, large-scale alterations of present facilities as well as modifications in the design of new treatment systems are necessary to incorporate the culture of desired plants and animals. Data from this study and others indicate that incorporating biological components into the design of wastewater treatment facilities is a cost-effective method to (1) produce protein for consumption by human populations or for supplements in the feeds of livestock, poultry, and fishes; and (2) remove excess nutrients from wastewaters, thereby reducing the potential impact of cultural eutrophication on natural waters.

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APPENDIX A

APPENDIX A

Refinement of Community Metabolism Measurements

Gross primary productivity and community respiration may have been underestimated in this study, influencing assessments of community metabolism. GPP can be underestimated when oxygen, produced by photosynthesis, supersaturated the water and resisted solution of additional oxygen generated by photosynthesis. Community respiration was estimated from changes in nighttime respiration, when no photorespiration occurred and temperatures were lowest for the day. Estimates for respiration could be refined by restricting calculations for respiration to the early hours of darkness, when temperatures were moderate; however, photorespiration could remain underestimated. Neither gross primary productivity or community respiration were likely to have been consistently measured inaccurately by the change-in-oxygen method, since instruments and techniques were properly applied.

When waters are supersaturated with oxygen, above 120%, small bubbles of oxygen may form and remain in algal mats, thereby not entering the pool of dissolved oxygen used for estimating community metabolism. The evolution of oxygen directly to the atmosphere would result in an underestimate of GPP. During all three experiments at Lake One, the highest daily oxygen concentrations in aquaria were between 150-230% (Figures 8-9), so the estimates of GPP for experiments at this lake were probably too low. At Lake Four, daily oxygen

concentrations exceeded 120% only in Experiment One (Figures 8-9). In the other experiments at Lake Four, oxygen remained below 120% of saturation concentration and GPP was accurately estimated.

Carbon budgets were recalculated for Experiments One and Two under the assumption that carbon import, storage, and export were correctly measured and either GPP or R were underestimated, depending on relative oxygen saturation (Table A1). When GPP was underestimated, as at Lake One, corrections were applied by assuming that organic carbon imported from the lake plus GPP minus community respiration should provide a reliable estimate of total organic carbon stored or exported. The impacts of tadpoles were amplified by these corrections. In general, the corrections for the two experiments at Lake One were proportional to the average daytime percentage saturations of oxygen, which were higher in Experiment Two. In Experiment One at Lake Four, relative saturation was above 120% and the corrected GPP was greater than the uncorrected GPP estimates in stocked aquaria (Table A1). In the second experiment at Lake Four, waters in aquaria were not supersaturated with oxygen; the difference between observed and expected export or storage of organic carbon was influenced by an underestimation of respiration. Community respiration may also have been underestimated in aquaria with supersaturated oxygen concentrations. If this occurred, corrected GPP would still underestimate actual GPP by that portion of the GPP lost to respiration. Therefore, the corrected measurements of GPP and R in Table A1 may still be underestimates.

Organic carbon was not analyzed in Experiment Three, so GPP could not be recalculated from organic carbon budgets. However, oxygen concentrations at Lake One were similar among the three experiments and

Table A1. Corrected carbon budget (mg C/42.8 liters/d) with estimated errors in GPP and community respiration (R).

	UNSTOCKED	LOW BIOMASS	HIGH BIOMASS
<u>EXPERIMENT ONE -- LAKE ONE</u>			
Initial organic carbon (total mg)	338.1	338.1	338.1
GPP/day	158.3	127.0	132.0
Respiration/day	-176.8	-148.5	-149.2
Expected balance	319.6	316.6	320.9
Actual balance	443.5	375.4	387.5
Apparent GPP underestimate	123.9	58.8	66.6
Apparent GPP	282.2	185.8	198.6
GPP/R	1.60	1.25	1.33
GPP/"R"	1.60	1.42	1.61

Table A1 (cont'd.).

	UNSTOCKED	LOW BIOMASS	HIGH BIOMASS
<u>EXPERIMENT TWO -- LAKE ONE</u>			
Initial organic carbon (total mg)	556.8	556.8	556.8
GPP/day	179.9	217.1	194.0
Respiration/day	-225.2	-235.6	-221.6
Expected balance	511.5	538.3	529.2
Actual balance	575.9	565.0	623.3
Apparent GPP underestimate	64.4	26.7	94.1
Apparent GPP	244.3	243.8	288.1
GPP/R	1.08	1.03	1.30
GPP/"R"	1.08	1.12	1.47

Table A1 (cont'd.).

	UNSTOCKED	LOW BIOMASS	HIGH BIOMASS
<u>EXPERIMENT ONE -- LAKE FOUR</u>			
Initial organic carbon (total mg)	321.5	321.5	321.5
GPP/day	26.7	30.6	31.5
Respiration/day	- 32.3	- 41.9	- 49.8
Expected balance	315.9	310.2	303.2
Actual balance	311.6	313.3	316.6
Apparent GPP underestimate	- 4.3	3.1	13.4
Apparent GPP	22.4	33.7	44.9
GPP/R	0.69	0.80	0.90
GPP/"R"	0.69	1.07	1.63

Table A1 (cont'd.).

	UNSTOCKED	LOW BIOMASS	HIGH BIOMASS
<u>EXPERIMENT TWO -- LAKE FOUR</u>			
Initial organic carbon (total mg)	441.8	441.8	441.8
GPP/day	32.7	27.0	25.3
Respiration/day	- 27.7	- 23.6	- 23.0
Expected balance	446.8	445.2	444.1
Actual balance	437.0	422.0	403.3
Apparent respiration underestimate	- 9.8	- 23.2	- 40.8
Apparent R	- 37.5	- 46.8	- 63.8
GPP/R	0.87	0.58	0.40
GPP/"R"	0.87	0.59	0.42

corrections were made based on average GPP values for all stocked aquaria. Uncorrected GPP values (mg C/42.8 liters/d) were 176.6 for monocultured bullfrogs, 168.4 for the mixed-species culture, and 175.5 for monocultured green frogs. Corrected GPP values (mg C/4.28 liters/d) were 229.1, 218.4, and 227.9 for the three tadpole groupings, respectively. At Lake Four during Experiment Three, oxygen concentrations were about 100% saturated and exceeded 120% only on one date, so original GPP estimates were considered accurate.

APPENDIX B

Table B1. Initial and final measurements of leopard frog tadpoles fed TetraMin (14 d, 280-296 degree d).

	Body Length (mm)		Wet Weight (mg)		Stage of Development		$\Delta Wt/d$	$\Delta Wt/Wt/d$
	IN	FI	IN	FI	IN	FI		
T(1)	7.5	16.9	70	578	24	29	36.4	0.518
T(2)	8.8	24.7	108	1528	25	33	101.4	0.939
T(3)	9.7	24.7	142	2387	26	34	160.4	1.129
T(4)	11.5	24.7	227	1817	26	33	117.4	0.517
T(5)	13.4	29.9	341	2817	27	34	179.9	0.519
T(6)	15.7	36.4	530	3232	28	34	193.0	0.364
T(7)	18.3	35.1	814	3827	29	36-37	215.2	0.264
T(8)	19.1	32.5	906	3674	29	35	197.7	0.218
T(9)	23.1	35.1	1540	3842	31	37	164.4	0.107
T(10)	23.7	39.0	1670	5593	31	37	280.2	0.168

Table B2. Growth and conversion efficiencies, expressed as nitrogen (mg/d), for algal-fed and TetraMin-fed tadpoles (R. pipiens).

	500 ml		1000 ml		1500 ml		TetraMin	
	Growth/d	(G/I)	Growth/d	(G/I)	Growth/d	(G/I)	Growth/d	
A-1	0.24	5.9%	0.54	8.3%	0.79	10.5%	T(1)	0.31
A-2	0.29	7.4%	0.57	8.7%	0.94	12.4%	T(2)	0.88
A-3	0.32	8.1%	0.56	8.6%	1.12	14.8%	T(3)	1.39
A-4	0.31	7.8%	0.59	9.0%	1.01	13.3%	T(4)	1.02
A-5	0.33	8.4%	0.62	9.4%	1.17	15.5%	T(5)	1.56
							T(6)	1.67
							T(7)	1.87
							T(8)	1.72
							T(9)	1.43
							T(10)	2.43

Table B3. Comparisons of periphytic carbon between unstocked (C for control) and tadpole-stocked (L for low and H for high biomass of *R. pipiens*) aquaria.

I. EXPERIMENT ONE--LAKE ONE				
A. Periphytic Carbon (mg/aq)				
6 June 1976	F = 54.12***	<u>243.1(L)</u>	<u>261.1(H)</u>	815.6(C)
12 June 1976	F = 30.53***	<u>403.4(L)</u>	<u>468.2(H)</u>	1422.8(C)
19 June 1976	F = 31.38***	<u>538.8(L)</u>	<u>618.4(H)</u>	2004.0(C)
B. Production (mg C/aq/d)				
$\bar{X}_3$ Dates	F = 11.14***	<u>25.8(L)</u>	<u>28.0(H)</u>	95.5(C)
II. EXPERIMENT ONE--LAKE FOUR				
A. Periphytic Carbon (mg/aq)				
12 June 1976	F = 4.69	<u>65.7(C)</u>	<u>82.5(L)</u>	120.0(H)
19 June 1976	F = 6.14*	<u>74.1(C)</u>	<u>107.7(L)</u>	169.2(H)
III. EXPERIMENT TWO--LAKE ONE				
A. Periphytic Carbon (mg/aq)				
8 August 1976	F = 20.53**	<u>435.1(H)</u>	<u>543.6(L)</u>	1294.2(C)
15 August 1976	F = 16.92**	<u>227.6(H)</u>	<u>324.1(L)</u>	1660.3(C)
22 August 1976	F = 12.52**	<u>302.4(H)</u>	<u>875.6(L)</u>	2372.0(C)
B. Production (mg C/aq/d)				
$\bar{X}_3$ Dates	F = 36.48***	<u>12.1(H)</u>	<u>28.0(L)</u>	89.8(C)
IV. EXPERIMENT TWO--LAKE FOUR				
A. Periphytic Carbon (mg/aq)				
22 August 1976	F = 5.85*	<u>76.0(H)</u>	<u>153.2(L)</u>	188.6(C)

*F._{.05}(2,6) = 5.14

**F._{.01}(2,6) = 10.90

***F._{.001}(2,6) = 27.00; F._{.001}(2,24) = 9.34

Table 84. Concentrations of dissolved and total organic carbon (mg/l $\pm$ SD) in imported lake water, unstocked (control) aquaria, and stocked (*R. pipiens*) aquaria during Experiments One and Two.

Sampling Dates	Lake Readings	Control	Low Density	High Density
LAKE ONE--EXPERIMENT ONE				
A. DISSOLVED ORGANIC CARBON				
6-(5-6)-1976	7.0 (± 0.06)	7.5 (± 0.23)	7.4 (± 0.14)	7.5 (± 0.31)
6-(11-12)-1976	6.8 (± 0.09)	7.1 (± 0.03)	7.5 (± 0.15)	7.8 (± 0.08)
6-(18-19)-1976	6.8 (± 0.05)	7.7 (± 0.13)	7.5 (± 0.20)	7.4 (± 0.17)
$\bar{X}_3$ Dates	6.9 (± 0.04)	7.4 (± 0.10)	7.5 (± 0.04)	7.6 (± 0.06)
B. TOTAL ORGANIC CARBON				
6-(5-6)-1976	7.9 (± 0.04)	8.0 (± 0.23)	8.1 (± 0.12)	8.2 (± 0.03)
6-(11-12)-1976	8.1 (± 0.07)	7.5 (± 0.26)	8.1 (± 0.08)	8.5 (± 0.06)
6-(18-19)-1976	7.8 (± 0.05)	8.3 (± 0.39)	8.3 (± 0.20)	8.4 (± 0.13)
$\bar{X}_3$ Dates	7.9 (± 0.06)	7.9 (± 0.12)	8.2 (± 0.06)	8.4 (± 0.06)
LAKE FOUR--EXPERIMENT ONE				
A. DISSOLVED ORGANIC CARBON				
6-(5-6)-1976	5.9 (± 0.15)	6.1 (± 0.19)	6.1 (± 0.15)	6.0 (± 0.23)
6-(11-12)-1976	6.6 (± 0.15)	6.6 (± 0.15)	6.9 (± 0.17)	6.8 (± 0.19)
6-(18-19)-1976	7.8 (± 0.25)	7.1 (± 0.16)	6.8 (± 0.00)	6.7 (± 0.06)
$\bar{X}_3$ Dates	6.8 (± 0.33)	6.6 (± 0.16)	6.6 (± 0.16)	6.5 (± 0.12)
B. TOTAL ORGANIC CARBON				
6-(5-6)-1976	7.7 (± 0.52)	6.5 (± 0.26)	5.6 (± 0.13)	7.0 (± 0.42)
6-(11-12)-1976	6.8 (± 0.20)	7.2 (± 0.29)	7.6 (± 0.36)	7.6 (± 0.64)
6-(18-19)-1976	8.0 (± 0.23)	7.9 (± 0.17)	7.4 (± 0.34)	7.2 (± 0.38)
$\bar{X}_3$ Dates	7.5 (± 0.36)	7.2 (± 0.24)	7.2 (± 0.18)	7.3 (± 0.10)

Table 84 (cont'd.).

Sampling Dates	Lake Readings	Control	Low Density	High Density
LAKE ONE--EXPERIMENT TWO				
A. DISSOLVED ORGANIC CARBON				
8-(7-8)-1976	9.2 (± 0.67)	7.8 (± 0.21)	8.3 (± 0.35)	8.1 (± 0.13)
8-(14-15)-1976	9.0 (± 0.48)	8.3 (± 0.08)	8.9 (± 0.33)	9.2 (± 0.82)
8-(21-22)-1976	9.4 (± 0.70)	8.9 (± 0.30)	9.6 (± 0.20)	9.5 (± 0.17)
$\bar{X}_3$ Dates	9.2 (± 0.07)	8.4 (± 0.18)	8.9 (± 0.22)	8.9 (± 0.24)
B. TOTAL ORGANIC CARBON				
8-(7-8)-1976	9.5 (± 0.78)	8.7 (± 0.15)	9.7 (± 0.30)	10.2 (± 0.37)
8-(14-15)-1976	11.0 (± 0.77)	10.9 (± 1.01)	13.1 (± 1.03)	14.9 (± 0.43)
8-(21-22)-1976	18.6 (± 1.48)	14.5 (± 1.12)	14.7 (± 1.54)	17.7 (± 1.02)
$\bar{X}_3$ Dates	13.0 (± 1.63)	11.4 (± 0.98)	12.5 (± 0.86)	14.3 (± 1.26)
LAKE FOUR--EXPERIMENT TWO				
A. DISSOLVED ORGANIC CARBON				
8-(7-8)-1976	8.3 (± 0.25)	8.0 (± 0.17)	7.8 (± 0.15)	7.7 (± 0.79)
8-(14-15)-1976	9.2 (± 0.10)	8.6 (± 0.40)	8.9 (± 0.47)	9.0 (± 0.74)
8-(21-22)-1976	11.6 (± 1.48)	10.1 (± 0.90)	10.1 (± 0.55)	9.4 (± 0.10)
$\bar{X}_3$ Dates	9.7 (± 0.57)	8.9 (± 0.36)	9.0 (± 0.38)	8.7 (± 0.28)
B. TOTAL ORGANIC CARBON				
8-(7-8)-1976	9.1 (± 0.47)	8.2 (± 0.08)	8.2 (± 0.15)	8.1 (± 0.86)
8-(14-15)-1976	10.1 (± 0.53)	10.4 (± 0.32)	10.4 (± 1.49)	9.6 (± 0.52)
8-(21-22)-1976	11.8 (± 1.49)	11.3 (± 1.47)	10.6 (± 0.52)	10.3 (± 0.10)
$\bar{X}_3$ Dates	10.3 (± 0.46)	10.1 (± 0.50)	9.7 (± 0.44)	9.3 (± 0.38)

Table B5. Concentrations of dissolved organic, total organic, and total inorganic nitrogen (mg/l $\pm$ SD) in imported lake water, unstocked (control) aquaria, and stocked (*R. pipiens*) aquaria during Experiments One and Two.

SAMPLING DATES	LAKE READINGS	CONTROL	LOW DENSITY	HIGH DENSITY
I. LAKE ONE--EXPERIMENT ONE				
A. Dissolved Organic Nitrogen				
6 June 1976	0.11 (± 0.01)	1.57 (± 0.02)	1.11 (± 0.003)	1.31 (± 0.13)
12 June 1976	1.21 (± 0.09)	1.47 (± 0.13)	1.65 (± 0.15)	1.78 (± 0.07)
19 June 1976	0.99 (± 0.03)	1.04 (± 0.14)	0.67 (± 0.17)	1.09 (± 0.04)
$\bar{X}_3$ Dates	0.77 (± 0.33)	1.36 (± 0.09)	1.14 (± 0.15)	1.39 (± 0.11)
B. Total Organic Nitrogen				
6 June 1976	7.44 (± 0.003)	7.51 (± 0.22)	7.16 (± 0.17)	7.44 (± 0.06)
12 June 1976	8.74 (± 0.003)	8.29 (± 0.12)	8.44 (± 0.11)	8.47 (± 0.03)
19 June 1976	8.58 (± 0.07)	8.31 (± 0.07)	8.43 (± 0.01)	8.43 (± 0.01)
$\bar{X}_3$ Dates	8.25 (± 0.40)	8.04 (± 0.15)	8.01 (± 0.66)	8.11 (± 0.51)

Table B5 (cont'd.).

SAMPLING DATES	LAKE READINGS	CONTROL	LOW DENSITY	HIGH DENSITY
C. Total Inorganic Nitrogen				
6 June 1976	1.57 (+0.02)	1.89 (+0.16)	1.73 (+0.14)	1.75 (+0.14)
12 June 1976	2.14 (+0.09)	2.09 (+0.11)	2.06 (+0.11)	1.92 (+0.03)
19 June 1976	1.69 (+0.09)	1.70 (+0.01)	1.60 (+0.15)	1.40 (+0.17)
$\bar{X}_3$ Dates	1.80 (+0.17)	1.90 (+0.08)	1.80 (+0.09)	1.69 (+0.10)
II. LAKE FOUR--EXPERIMENT ONE				
A. Dissolved Organic Nitrogen				
6 June 1976	0.56 (+0.02)	0.63 (+0.02)	0.60 (+0.01)	0.62 (+0.01)
12 June 1976	0.62 (+0.20)	0.67 (+0.03)	0.67 (+0.03)	0.71 (+0.04)
19 June 1976	0.66 (+0.02)	0.66 (+0.02)	0.66 (+0.01)	0.69 (+0.02)
$\bar{X}_3$ Dates	0.61 (+0.02)	0.65 (+0.01)	0.64 (+0.01)	0.67 (+0.02)

Table B5 (cont'd.).

SAMPLING DATES	LAKE READINGS	CONTROL	LOW DENSITY	HIGH DENSITY
B. Total Organic Nitrogen				
6 June 1976	0.62 (+0.01)	0.69 (+0.01)	0.64 (+0.03)	0.67 (+0.01)
12 June 1976	0.68 (+0.01)	0.78 (+0.02)	0.80 (+0.06)	0.76 (+0.05)
19 June 1976	0.81 (+0.06)	0.79 (+0.02)	0.81 (+0.02)	0.77 (+0.04)
$\bar{X}_3$ Dates	0.70 (+0.05)	0.75 (+0.02)	0.75 (+0.03)	0.73 (+0.02)
C. Total Inorganic Nitrogen				
6 June 1976	0.03 (+0.00)	0.03 (+0.00)	0.03 (+0.03)	0.04 (+0.04)
12 June 1976	0.03 (+0.00)	0.01 (+0.01)	0.02 (+0.01)	0.03 (+0.00)
19 June 1976	0.03 (+0.00)	0.09 (+0.01)	0.11 (+0.02)	0.07 (+0.03)
$\bar{X}_3$ Dates	0.03 (+0.00)	0.05 (+0.01)	0.05 (+0.01)	0.05 (+0.01)

Table B5 (cont'd.).

SAMPLING DATES	LAKE READINGS	CONTROL	LOW DENSITY	HIGH DENSITY
III. LAKE ONE--EXPERIMENT TWO				
A. Dissolved Organic Nitrogen				
8 August 1976	1.00 (± 0.02)	1.35 (± 0.05)	1.39 (± 0.01)	1.43 (± 0.04)
15 August 1976	1.07 (± 0.07)	1.20 (± 0.10)	1.07 (± 0.10)	1.12 (± 0.01)
22 August 1976	0.90 (± 0.13)	1.45 (± 0.20)	1.45 (± 0.12)	1.12 (± 0.09)
$\bar{X}_3$ Dates	0.99 (± 0.04)	1.33 (± 0.07)	1.31 (± 0.07)	1.22 (± 0.06)
B. Total Organic Nitrogen				
8 August 1976	1.44 (± 0.04)	1.96 (± 0.08)	2.08 (± 0.04)	2.23 (± 0.04)
15 August 1976	1.94 (± 0.10)	1.78 (± 0.03)	1.71 (± 0.28)	2.37 (± 0.40)
22 August 1976	3.34 (± 0.12)	2.22 (± 0.05)	3.10 (± 0.28)	3.29 (± 0.12)
$\bar{X}_3$ Dates	2.24 (± 0.56)	1.99 (± 0.07)	2.30 (± 0.23)	2.63 (± 0.20)

Table B5 (cont'd.).

SAMPLING DATES	LAKE READINGS	CONTROL	LOW DENSITY	HIGH DENSITY
C. Total Inorganic Nitrogen				
8 August 1976	3.40 (+0.02)	2.00 (+0.02)	2.11 (+0.07)	2.21 (+0.07)
15 August 1976	3.37 (+0.02)	2.80 (+0.06)	2.75 (+0.06)	2.73 (+0.06)
22 August 1976	1.18 (+0.02)	1.54 (+0.01)	1.14 (+0.11)	1.11 (+0.12)
$\bar{X}_3$ Dates	2.65 (+0.73)	2.12 (+0.18)	2.00 (+0.23)	2.027 (+0.24)
IV. LAKE FOUR--EXPERIMENT TWO				
A. Dissolved Organic Nitrogen				
8 August 1976	0.72 (+0.01)	0.80 (+0.02)	0.81 (+0.02)	0.80 (+0.01)
15 August 1976	0.82 (+0.02)	0.82 (+0.02)	0.76 (+0.02)	0.80 (+0.01)
22 August 1976	0.84 (+0.02)	0.82 (+0.01)	0.89 (+0.01)	0.87 (+0.01)
$\bar{X}_3$ Dates	0.79 (+0.03)	0.81 (+0.01)	0.82 (+0.02)	0.83 (+0.01)

Table B5 (cont'd.).

SAMPLING DATES	LAKE READINGS	CONTROL	LOW DENSITY	HIGH DENSITY
B. Total Organic Nitrogen				
8 August 1976	0.91 (+0.01)	0.86 (+0.01)	0.86 (+0.02)	0.84 (+0.01)
15 August 1976	0.86 (+0.01)	0.87 (+0.01)	0.83 (+0.04)	0.84 (+0.00)
22 August 1976	0.94 (+0.01)	0.85 (+0.00)	0.91 (+0.02)	0.89 (+0.01)
$\bar{X}_3$ Dates	0.90 (+0.02)	0.86 (+0.01)	0.87 (+0.01)	0.86 (+0.01)
C. Total Inorganic Nitrogen				
8 August 1976	0.17 (+0.01)	0.08 (+0.01)	0.12 (+0.01)	0.10 (+0.02)
15 August 1976	0.05 (+0.00)	0.04 (+0.01)	0.04 (+0.00)	0.04 (+0.00)
22 August 1976	0.04 (+0.00)	0.04 (+0.00)	0.05 (+0.00)	0.04 (+0.00)
$\bar{X}_3$ Dates	0.09 (+0.04)	0.05 (+0.01)	0.07 (+0.01)	0.06 (+0.01)

Table B6. Mean C:N ratios in organic material for Experiments One and Two at Lakes One and Four.

	LAKE IMPORT	UNSTOCKED AQUARIA	LOW STOCKING	HIGH STOCKING
LAKE ONE -- EXPERIMENT ONE				
Dissolved C:N	9.0	5.4	6.5	5.5
Sestonic C:N	1.0	0.9	1.1	2.7
Periphytic C:N	-	11.7	7.3	8.0
Tadpoles C:N	-	-	4.0	4.0
LAKE ONE -- EXPERIMENT TWO				
Dissolved C:N	9.3	6.3	6.9	7.3
Sestonic C:N	3.0	4.6	3.6	3.8
Periphytic C:N	-	10.1	7.6	8.1
Tadpole C:N	-	-	3.8	3.8
LAKE FOUR -- EXPERIMENT ONE				
Dissolved C:N	11.1	10.1	10.3	9.7
Sestonic C:N	8.0	6.0	5.6	12.9
Periphytic C:N	-	6.6	6.4	6.5
Tadpole C:N	-	-	4.0	4.0
LAKE FOUR -- EXPERIMENT TWO				
Dissolved C:N	12.3	10.9	10.9	10.6
Sestonic C:N	5.7	25.7	17.0	20.0
Periphytic C:N	-	6.4	6.6	6.3
Tadpole C:N	-	-	3.8	3.8

Table B7. Concentrations of dissolved organic, total organic, and total inorganic nitrogen (mg/l $\pm$ SD) in imported lake water and aquaria with monocultured bullfrogs, a mixed-species culture, or monocultured green frogs during Experiment Three.

SAMPLING DATES	LAKE READINGS	BULLFROGS	MIXED: BULLFROGS & GREEN FROGS	GREEN FROGS
I. LAKE ONE--EXPERIMENT THREE				
A. Dissolved Organic Nitrogen				
5 October 1976	0.46 (± 0.03)	1.34 (± 0.14)	0.90 (± 0.26)	1.30 (± 0.23)
12 October 1976	1.65 (± 0.03)	1.52 (± 0.24)	1.29 (± 0.13)	1.34 (± 0.12)
24 October 1976	0.36 (± 0.04)	1.46 (± 0.20)	1.23 (± 0.16)	0.67 (± 0.12)
$\bar{X}_3$ Dates	0.82 (± 0.41)	1.44 (± 0.10)	1.14 (± 0.11)	1.10 (± 0.13)
B. Total Organic Nitrogen				
5 October 1976	2.30 (± 0.05)	3.55 (± 0.42)	2.28 (± 0.12)	3.18 (± 0.33)
12 October 1976	2.77 (± 0.06)	3.87 (± 0.05)	3.65 (± 0.31)	3.46 (± 0.36)
24 October 1976	1.10 (± 0.01)	1.85 (± 0.24)	2.72 (± 0.11)	1.68 (± 0.18)
$\bar{X}_3$ Dates	2.06 (± 0.49)	3.09 (± 0.34)	2.88 (± 0.22)	2.77 (± 0.31)

Table B7 (cont'd.).

SAMPLING DATES	LAKE READINGS	BULLFROGS	MIXED	GREEN FROGS
C. Total Inorganic Nitrogen				
5 October 1976	7.73 (+0.05)	7.40 (+0.18)	7.47 (+0.16)	7.20 (+0.11)
12 October 1976	6.47 (+0.02)	6.06 (+0.11)	6.07 (+0.08)	6.20 (+0.08)
24 October 1976	7.37 (+0.01)	7.85 (+0.13)	8.28 (+0.11)	7.59 (+0.42)
$\bar{X}_3$ Dates	7.19 (+0.37)	7.10 (+0.27)	7.27 (+0.32)	7.00 (+0.24)
II. LAKE FOUR--EXPERIMENT THREE				
A. Dissolved Organic Nitrogen				
5 October 1976	0.50 (+0.13)	0.73 (+0.09)	0.12 (+0.01)	0.83 (+0.03)
12 October 1976	0.63 (+0.04)	0.79 (+0.02)	0.61 (+0.03)	0.81 (+0.03)
24 October 1976	0.60 (+0.01)	0.71 (+0.05)	0.63 (+0.02)	0.75 (+0.04)
$\bar{X}_3$ Dates	0.57 (+0.04)	0.74 (+0.03)	0.45 (+0.08)	0.80 (+0.02)

Table B7 (cont'd.).

SAMPLING DATES	LAKE READINGS	BULLFROGS	MIXED	GREEN FROGS
B. Total Organic Nitrogen				
5 October 1976	0.99 (+0.03)	0.87 (+0.05)	0.90 (+0.03)	0.88 (+0.03)
12 October 1976	1.01 (+0.02)	0.92 (+0.02)	0.90 (+0.03)	0.87 (+0.04)
24 October 1976	0.88 (+0.06)	0.87 (+0.04)	0.92 (+0.03)	0.84 (+0.02)
$\bar{X}_3$ Dates	0.96 (+0.04)	0.89 (+0.02)	0.91 (+0.01)	0.86 (+0.01)
C. Total Inorganic Nitrogen				
5 October 1976	0.04 (+0.00)	0.30 (+0.00)	0.04 (+0.00)	0.04 (+0.01)
12 October 1976	0.04 (+0.00)	0.03 (+0.00)	0.04 (+0.00)	0.04 (+0.00)
24 October 1976	0.04 (+0.00)	0.04 (+0.00)	0.04 (+0.00)	0.04 (+0.00)
$\bar{X}_3$ Dates	0.04 (+0.00)	0.04 (+0.00)	0.04 (+0.00)	0.04 (+0.01)

Table B8. Concentrations of dissolved and total phosphorus (mg/l $\pm$ SD) in imported lake water, unstocked (control) aquaria, and stocked (*R. pipiens*) aquaria during Experiments One and Two at Lakes One and Four.

SAMPLING DATES	LAKE READINGS	CONTROL	LOW DENSITY	HIGH DENSITY
I. LAKE ONE--EXPERIMENT ONE				
A. Dissolved Phosphorus				
6 June 1976	0.76 (± 0.02)	0.66 (± 0.08)	0.63 (± 0.08)	0.62 (± 0.05)
12 June 1976	0.48 (± 0.05)	0.40 (± 0.03)	0.37 (± 0.02)	0.43 (± 0.02)
19 June 1976	0.42 (± 0.05)	0.35 (± 0.04)	0.42 (± 0.14)	0.42 (± 0.07)
$\bar{X}_3$ Dates	0.55 (± 0.02)	0.47 (± 0.05)	0.47 (± 0.06)	0.49 (± 0.04)
B. Total Phosphorus				
6 June 1976	0.83 (± 0.02)	0.74 (± 0.07)	0.68 (± 0.08)	0.81 (± 0.05)
12 June 1976	0.61 (± 0.01)	0.54 (± 0.03)	0.68 (± 0.05)	0.67 (± 0.06)
19 June 1976	0.56 (± 0.08)	0.45 (± 0.06)	0.70 (± 0.14)	0.52 (± 0.04)
$\bar{X}_3$ Dates	0.67 (± 0.08)	0.58 (± 0.05)	0.69 (± 0.05)	0.67 (± 0.05)

Table B8 (cont'd.).

SAMPLING DATES	LAKE READINGS	CONTROL	LOW DENSITY	HIGH DENSITY
II. LAKE FOUR--EXPERIMENT ONE				
A. Dissolved Phosphorus				
6 June 1976	0.005 (+0.001)	0.012 (+0.002)	0.009 (+0.003)	0.014 (+0.001)
12 June 1976	0.015 (+0.002)	0.020 (+0.006)	0.023 (+0.012)	0.020 (+0.003)
19 June 1976	0.018 (+0.003)	0.017 (+0.002)	0.016 (+0.002)	0.015 (+0.004)
$\bar{X}_3$ Dates	0.013 (+0.004)	0.015 (+0.002)	0.017 (+0.004)	0.016 (+0.002)
B. Total Phosphorus				
6 June 1976	0.016 (+0.003)	0.023 (+0.003)	0.022 (+0.002)	0.033 (+0.009)
12 June 1976	0.024 (+0.005)	0.028 (+0.004)	0.029 (+0.005)	0.037 (+0.004)
19 June 1976	0.026 (+0.001)	0.029 (+0.005)	0.028 (+0.0003)	0.028 (+0.001)
$\bar{X}_3$ Dates	0.022 (+0.003)	0.027 (+0.002)	0.027 (+0.002)	0.033 (+0.003)

Table B8 (cont'd.).

SAMPLING DATES	LAKE READINGS	CONTROL	LOW DENSITY	HIGH DENSITY
III. LAKE ONE--EXPERIMENT TWO				
A. Dissolved Phosphorus				
8 August 1976	1.52 (+0.01)	1.26 (+0.07)	1.32 (+0.02)	1.38 (+0.03)
15 August 1976	1.66 (+0.03)	1.77 (+0.03)	1.69 (+0.06)	1.64 (+0.05)
22 August 1976	0.25 (+0.01)	0.54 (+0.05)	0.35 (+0.05)	0.29 (+0.02)
$\bar{X}_3$ Dates	1.14 (+0.45)	1.19 (+0.18)	1.12 (+0.20)	1.11 (+0.21)
B. Total Phosphorus				
8 August 1976	1.63 (+0.03)	1.41 (+0.04)	1.41 (+0.06)	1.60 (+0.13)
15 August 1976	1.94 (+0.08)	2.16 (+0.02)	2.04 (+0.12)	2.14 (+0.11)
22 August 1976	0.90 (+0.03)	0.86 (+0.03)	1.02 (+0.09)	0.87 (+0.01)
$\bar{X}_3$ Dates	1.49 (+0.31)	1.48 (+0.09)	1.49 (+0.16)	1.54 (+0.19)

Table B8 (cont'd.).

SAMPLING DATES	LAKE READINGS	CONTROL	LOW DENSITY	HIGH DENSITY
IV. LAKE FOUR--EXPERIMENT TWO				
A. Dissolved Phosphorus				
8 August 1976	0.026 (+0.004)	0.012 (+0.004)	0.020 (+0.004)	0.020 (+0.004)
15 August 1976	0.005 (+0.001)	0.005 (+0.002)	0.008 (+0.002)	0.009 (+0.004)
22 August 1976	0.028 (+0.005)	0.013 (+0.001)	0.017 (+0.002)	0.014 (+0.00)
$\bar{X}_3$ Dates	0.020 (+0.007)	0.010 (+0.001)	0.015 (+0.002)	0.014 (+0.002)
B. Total Phosphorus				
8 August 1976	0.033 (+0.002)	0.042 (+0.007)	0.035 (+0.003)	0.039 (+0.004)
15 August 1976	0.030 (+0.002)	0.028 (+0.006)	0.035 (+0.010)	0.030 (+0.009)
22 August 1976	0.032 (+0.005)	0.029 (+0.001)	0.030 (+0.005)	0.027 (+0.001)
$\bar{X}_3$ Dates	0.032 (+0.001)	0.033 (+0.004)	0.033 (+0.004)	0.032 (+0.003)

Table B9. Concentrations of dissolved and total phosphorus (mg/l $\pm$ SD) in imported lake water and aquaria with monocultured bullfrogs, a mixed-species culture, or monocultured green frogs during Experiment Three.

SAMPLINE DATES	LAKE READINGS	BULLFROGS	MIXED: BULLFROGS & GREEN FROGS	GREEN FROGS
I. LAKE ONE--EXPERIMENT THREE				
A. Dissolved Phosphorus				
5 October 1976	1.59 (± 0.02)	1.48 (± 0.18)	1.34 (± 0.10)	0.91 (± 0.03)
12 October 1976	2.05 (± 0.08)	1.71 (± 0.07)	1.66 (± 0.09)	1.68 (± 0.07)
24 October 1976	2.47 (± 0.03)	2.45 (± 0.02)	2.47 (± 0.01)	2.39 (± 0.06)
$\bar{X}_3$ Dates	2.04 (± 0.25)	1.88 (± 0.16)	1.82 (± 0.17)	1.66 (± 0.21)
B. Total Phosphorus				
5 October 1976	2.27 (± 0.02)	2.18 (± 0.07)	2.67 (± 0.31)	2.23 (± 0.07)
12 October 1976	2.68 (± 0.11)	2.37 (± 0.04)	2.36 (± 0.04)	2.36 (± 0.05)
24 October 1976	2.84 (± 0.05)	2.80 (± 0.12)	2.96 (± 0.08)	2.96 (± 0.07)
$\bar{X}_3$ Dates	2.60 (± 0.17)	2.45 (± 0.10)	2.66 (± 0.13)	2.52 (± 0.12)

Table B9 (cont'd.).

SAMPLING DATES	LAKE READINGS	BULLFROGS	MIXED:	GREEN FROGS
II. LAKE FOUR--EXPERIMENT THREE				
A. Dissolved Phosphorus				
5 October 1976	0.065 (± 0.001)	0.056 (± 0.001)	0.058 (± 0.003)	0.060 (± 0.003)
12 October 1976	0.042 (± 0.002)	0.034 (± 0.004)	0.035 (± 0.006)	0.037 (± 0.006)
24 October 1976	0.061 (± 0.001)	0.062 (± 0.002)	0.058 (± 0.003)	0.059 (± 0.001)
$\bar{X}_3$ Dates	0.056 (± 0.007)	0.051 (± 0.004)	0.050 (± 0.004)	0.052 (± 0.004)
B. Total Phosphorus				
5 October 1976	0.075 (± 0.004)	0.074 (± 0.004)	0.065 (± 0.001)	0.065 (± 0.002)
12 October 1976	0.053 (± 0.002)	0.052 (± 0.005)	0.044 (± 0.003)	0.044 (± 0.006)
24 October 1976	0.073 (± 0.002)	0.063 (± 0.002)	0.064 (± 0.002)	0.062 (± 0.001)
$\bar{X}_3$ Dates	0.067 (± 0.007)	0.063 (± 0.004)	0.058 (± 0.004)	0.057 (± 0.004)

Table B10. List of genera and mean volumes (μ^3) of phytoplankton at Lakes One and Four in Experiments One, Two, and Three.

PHYLA	Mean Cell
SUB-PHYLA	Volumes
Genera	
CHLOROPHYTA	
CHLOROPHYCEAE	
Actinastrum	61.8-185.7
Ankistrodesmus (1)	26.5
(2)	86.3
(3)	124.6
Chlamydomonas	105.0
Chlorella (1)	108.0
(2)	193.4
Cosmarium	4250.8
Crucigenia	283.5
Desmidium	16.1
Dictyosphaerium	28.7
Francia	60.1
Green Coccoid Cell (small)	5.3
Green Coccoid Cell (large)	220.8-1287.6
Hyalotheca	36.9
Kirchneriella	14.7-20.3
Langerheimia	33.0
Micratinium	65.4-104.7
Oocystis	269.7
Pediastrum	5.6-116.3
Quadrigula (cell)	4.4
(colony)	331.2
Scenedesmus (1)	85.1
(2)	48.3-53.1
Schroederia	23.4
Selenastrum	28.4-398.3
Small Kidney-shaped Cell	8.5
Staurastrum	58.8
Tetradismus	324.2
Tetraedon	66.0
Tetrastrum	25.1
Treubaria	48.2
Ulothrix	24.1
EUGLENOPHYTA	
Euglena	166.9
Trachelomonas	276.0

Table B10 (cont'd.).

PHYLA SUB-PHYLA Genera	Mean Cell Volumes
PYRRHOPHYTA	
Gymnodium	1976.1
CRYPTOPHYTA	
Cryptomonas	641.9-3255.6
Rhodomonas	74.1
CHRYSTOPHYTA XANTHOPHYCEAE	
Tribonema	767.1
BACILLARIOPHYCEAE	
Achnanthes	403.0
Amphora	571.0
Centric X	1657.5
Cocconeis	1615.1
Cocscinodiscus	3894.6
Cyclotella	425.6
Cymbella	405.0
Epithemia	1235.4
Eunotia	597.6
Fragilaria	165.4
Gomphonema	1057.5
Melosira	217.2
Navicula (1)	59.5-123.9
(2)	403.0
Nitzschia (1)	45.0-202.8
(2)	316.0-394.4
(3)	1094.4
Opephora	211.9
Pennate X	289.7
Pinnularia	488.8
Rhizosolenia	350.3
Stauroneis	8547.2-11499.8
Stephanodiscus	652.3
Surirella	2381.2
Synedra	2462.1-3836.9

Table B10 (cont'd.).

PHYLUM		Mean Cell Volumes
SUB-PHYLUM		
Genera		
CYANOPHYTA		
Anabaena	(1)	5.0
	(2)	68.9
Anacystis	(1)	17.1
	(2)	388.0
Agmenellum	(1)	22.2
	(2)	43.2
Coccoid Blue-green Cell		154.8
Lyngbya		16.1
Oscillatoria		273.2
Spirulina		246.8
Tetraspora		4.2

Table B11. Numbers and volumes of phytoplankton ($\mu\text{m}^3 \text{ ml}^{-1} \pm \text{SD}$) in imported lake water, unstocked (control) aquaria, and stocked (low and high stocks of leopard frog tadpoles) aquaria for Experiment One at Lake One.

EXPERIMENT ONE LAKE ONE	Greens	Diatoms	Blue-greens	Cryptophytes	Euglenoids	Totals
A. CONTROL						
1) Initial Readings 28 May 1976 X Number	2043 (± 106.3)	1231 (± 105.1)	0	5142 (± 176.4)	0	8416 (± 339.4)
X Volume	164502.3 (± 30753.2)	338242.7 (± 66891.4)	0	1104946.7 (± 222355.3)	0	1607691.7 (± 177859.9)
X Size	80.5	274.8	0	214.9	0	191.0 (± 15.3)
2) 6 June 1976 X Number	3607 (± 231.5)	11223 (± 1788.8)	62 (± 61.7)	860 (± 146.1)	0	15752 (± 1888.7)
X Volume	301484 (± 10480.3)	4495389.7 (± 557960.5)	1030 (± 1030)	367053.3 (± 104794.5)	0	4264957 (± 566636.3)
X Size	83.6	320.4	16.6	426.8	0	270.8 (± 4.4)
3) 12 June 1976 X Number	15899 (± 2282.3)	7233 (± 226.2)	2022 (± 1211.1)	637 (± 230.7)	19 (± 19)	25810 (± 3103.1)
X Volume	1241805 (± 177264.5)	2786084.7 (± 209178)	76405.3 (± 46034.2)	274124.3 (± 64479.5)	3646 (± 3650.3)	4382065.3 (± 244097.2)
X Size	78.1	385.2	37.8	430.3	191.9	169.8 (± 22.9)
4) 19 June 1976 X Number	22831 (± 3417.5)	11236 (± 2919.8)	3896 (± 1318.3)	1322 (± 1287)	24 (± 23.7)	39309 (± 5747.5)
X Volume	1870343 (± 284417.9)	4046437 (± 957561.3)	91167.7 (± 49967.1)	866724.7 (± 727169.1)	4541.7 (± 4547.0)	6879214.1 (± 1925053.7)
X Size	81.9	360.1	23.4	655.6	189.2	175.0 (± 21.5)

Table B11 (cont'd.).

	Greens	Diatoms	Blue-greens	Cryptophytes	Euglenoids	Totals
Mean of 3 Dates-						
$\bar{X}$ Number	14113 (+3051.3)	9897 (+1193.8)	1993 (+757.4)	940 (+393)	14 (+14)	26957 (+3936.6)
$\bar{X}$ Volume	1137877.3 (+247670.5)	3475970 (+374145.4)	56201 (+24073.3)	501634.1 (+1731929.4)	2729.2 (+2729.2)	5175412.4 (+722675.3)
$\bar{X}$ Size	80.6	351.2	28.2	534.7	194.9	192.0 (+20.9)
B. LOW DENSITY						
1) Initial Readings						
28 May 1976						
$\bar{X}$ Number	3002 (+362.5)	1218 (+298.7)	0	1,006 (+149.5)	0	9726 (+62.8)
$\bar{X}$ Volume	228615.3 (+30753.2)	431231 (+136998.2)	0	1751249 (+161482.2)	0	1914095 (+99612)
$\bar{X}$ Size	76.2	354.0	0	227.8	0	196.8 (+10.9)
2) 6 June 1976						
$\bar{X}$ Number	10539 (+1180.4)	17126 (+1568.7)	3505 (+385.4)	1191 (+155.1)	13 (+12.7)	32774 (+328.6)
$\bar{X}$ Volume	842028.3 (+140269.3)	5822352.3 (+205804.9)	540020.7 (+56634.3)	531538 (+145300)	2430.8 (+2433.5)	7738370 (+264253.5)
$\bar{X}$ Size	79.7	340.0	154.1	334.1	187.0	236.1 (+13.2)
3) 12 June 1976						
$\bar{X}$ Number	20302 (+3355.2)	19527 (+4600.7)	7236 (+2112.3)	959 (+190.8)	33 (+31.1)	48057 (+7510.7)
$\bar{X}$ Volume	1390800 (+169869.0)	6343500 (+1438114.1)	920241.7 (+369959.8)	389211.7 (+151956.3)	6397 (+6404.3)	9050150.4 (+1879359.1)
$\bar{X}$ Size	68.5	329.4	127.2	405.9	193.8	188.3 (+12.6)

Table B11 (cont'd.).

	Greens	Diatoms	Blue-greens	Cryptophytes	Euglenoids	Totals
4) 19 June 1976						
$\bar{X}$ Number	20740 (+782.9)	18862 (+2167.7)	9408 (+1147.4)	1901 (+1688.7)	95 (+63.0)	51006 (+1571.9)
$\bar{X}$ Volume	1334372.7 (+220448.2)	6111234.7 (+876149.3)	1011011.0 (+205591.5)	254313 (+73039.6)	18230.7 (+12090.9)	8729162.1 (+395258.4)
$\bar{X}$ Size	64.3	251.8	107.5	133.8	191.9	171.0 (+30.5)
Mean of 3 Dates-						
$\bar{X}$ Number	17194 (+1969)	18505 (+1577.5)	6716 (+1112)	1484 (+509.4)	47 (+24.7)	43946 (+3540.1)
$\bar{X}$ Volume	1189067 (+125250.2)	6092362.3 (+150916.7)	823757.8 (+142891.5)	391687.6 (+75862)	9019.5 (+4751.4)	8505894.2 (+395258.4)
$\bar{X}$ Size	69.2	329.2	122.7	263.9	191.9	193.5 (+13.7)
C. HIGH DENSITY						
1) Initial Readings 28 May 1976						
$\bar{X}$ Number	2280 (+456.9)	1352 (+439.1)	0	5637 (+537.8)	0	9269 (+1145.8)
$\bar{X}$ Volume	177020.7 (+32442.5)	339878.7 (+69896.6)	0	1149471 (+261274.8)	0	1666370.4 (+257226.5)
$\bar{X}$ Size	77.6	251.4	0	203.92	0	179.8 (+51.9)
2) 6 June 1976						
$\bar{X}$ Number	7067 (+645.4)	13921 (+1677.9)	3544 (+537.5)	2058 (+302.2)	5 (+4.7)	26595 (+2425.3)
$\bar{X}$ Volume	496536.7 (+16989.6)	4574885.7 (+643967.7)	576726.0 (+82492.2)	590534.3 (+126041.2)	895.7 (+896.7)	6199578.4 (+812152.8)
$\bar{X}$ Size	70.3	325.8	162.7	286.9	179.1	233.1 (+13.6)

Table B11 (cont'd.).

	Greens	Diatoms	Blue-greens	Cryptophytes	Euglenoids	Totals
3) 12 June 1976 X Number	25730 (+2572.9)	26678 (+1672.9)	9229 (+1578.8)	590 (+180.9)	36 (+20.5)	62263 (+9502.3)
X Volume	1647639 (+325837)	8791087.3 (+225260.1)	1246660.7 (+156006.6)	535766.3 (+49437.2)	6844 (+3937.9)	12223997.2 (+2468595.3)
X Size	63.9	329.5	135.1	908.1	190.1	196.3 (+19.6)
4) 19 June 1976 X Number	24637 (+5296.6)	20688 (+2305.9)	10179 (+2408.5)	71 (+41.3)	0	55575 (+7721.1)
X Volume	1870389.3 (+200450.3)	6754816.3 (+788837.5)	909720.7 (+87249.2)	80518 (+75437.8)	0	9615507.3 (+993844.3)
X Size	75.9	326.5	89.4	1134.9	0	173.0 (+9.6)
Mean of 3 Dates -						
X Number	19145 (+3694.4)	20429 (+2789.9)	7651 (+991.5)	906 (+317.6)	14 (+11.3)	48145 (+6506.3)
X Volume	1336855 (+239634.1)	6693596.4 (+1230497.8)	911035.8 (+173645.3)	402293.9 (+101441.1)	2579.9 (+1240)	9346361 (+1007071.4)
X Size	69.8	327.6	119.1	444.0	184.3	194.1 (+10.1)
D. LAKE READINGS						
1) Initial Readings 27 May 1976 X Number	1539	3249	0	2565	0	7153
X Volume	123023	1280550	0	734103	0	2137670
X Size	79.9	394.1	0	286.2	0	290.7

Table BII (cont'd.).

	Greens	Diatoms	Blue-greens	Cryptophytes	Euglenoids	Totals
2) 5 June 1976						
$\bar{X}$ Number	3207 (+326.6)	390 (+105)	0	1689 (+498.2)	0	5289 (+387.9)
$\bar{X}$ Volume	452564 (+63887.6)	312683.3 (+229101.9)	0	368034 (+91054.6)	0	1133281.3 (+264433.1)
$\bar{X}$ Size	141.2	801.8	0	217.9	0	214.3 (+34.5)
3) 11 June 1976						
$\bar{X}$ Number	10042 (+449.9)	313 (+100.2)	389 (+66.6)	3401 (+290.1)	0	14145 (+495.9)
$\bar{X}$ Volume	1279775.3 (+108376.6)	94705.3 (+29156.6)	21832.3 (+7822.4)	463078.3 (+73646.7)	0	1859391.2 (+176751.5)
$\bar{X}$ Size	127.4	302.6	56.1	136.2	0	131.5 (+7.9)
4) 18 June 1976						
$\bar{X}$ Number	14299 (+516.5)	351 (+162.4)	238 (+96.7)	665 (+309.4)	0	15343 (+499.9)
$\bar{X}$ Volume	1548302.3 (+46073.4)	129676.7 (+60827.7)	10820.3 (+3606.3)	139419 (+41430.4)	0	1826218 (+100331.6)
$\bar{X}$ Size	108.3	369.4	45.5	209.6	0	119.2 (+4.8)
Mean of 3 Dates -						
$\bar{X}$ Number	9183 (+1630.1)	351 (+63.8)	203 (+65.9)	1919 (+441.4)	0	11656 (+1670.1)
$\bar{X}$ Volume	1093547.2 (+169331.7)	179021.8 (+76707)	10884.2 (+4012.3)	323510.4 (+59909.9)	0	1606963.6 (+152612.1)
$\bar{X}$ Size	119.1	510.0	53.6	168.6	0	137.9 (+17.3)

Table B12. Numbers and volumes of phytoplankton (per ml $\pm$ SD) in imported lake water, unstocked (control) aquaria, and stocked (low and high stocks of leopard frog tadpoles) aquaria for Experiment One at Lake Four.

EXPERIMENT ONE LAKE FOUR	Greens	Diatoms	Blue-greens	Cryptophytes	Euglenoids	Totals
A. CONTROL						
1) Initial Readings 28 May 1976 $\bar{X}$ Number	5287 ($\pm$ 574)	1838 ($\pm$ 78)	0	133 ($\pm$ 106)	0	7257 ($\pm$ 462)
$\bar{X}$ Volume	363499 ($\pm$ 46644)	731409 ($\pm$ 128472)	0	8297 ($\pm$ 6304)	0	1103205 ($\pm$ 154791)
$\bar{X}$ Size	68.7	397.9	0	62.4	0	152 ($\pm$ 30.3)
2) 6 June 1976 $\bar{X}$ Number	2698 ($\pm$ 84.1)	440 ($\pm$ 60.2)	1228 ($\pm$ 444.7)	31 ($\pm$ 19.8)	15 ($\pm$ 15)	4413 ($\pm$ 394.6)
$\bar{X}$ Volume	143516 ($\pm$ 7299.8)	145783.7 ($\pm$ 7833.4)	54980 ($\pm$ 12459.9)	102009.3 ($\pm$ 64494.1)	2558.7 ($\pm$ 2558.7)	448847.7 ($\pm$ 74313.5)
$\bar{X}$ Size	53.2	104.1	44.8	3290.6	170.6	101.7 ($\pm$ 12.5)
3) 12 June 1976 $\bar{X}$ Number	1009 ($\pm$ 68.1)	245 ($\pm$ 73.2)	2410 ($\pm$ 704.1)	5 ($\pm$ 5.3)	0	3669 ($\pm$ 705.2)
$\bar{X}$ Volume	100750 ($\pm$ 30011.3)	75107 ($\pm$ 22491.5)	39574 ($\pm$ 15829.9)	395 ($\pm$ 395.3)	0	215826 ($\pm$ 23607.3)
$\bar{X}$ Size	99.8	306.6	16.4	79.0	0	58.8 ($\pm$ 9.4)
4) 18 June 1976 $\bar{X}$ Number	613 ($\pm$ 50.9)	1009 ($\pm$ 115.7)	11975 ($\pm$ 3091.9)	119 ($\pm$ 22.6)	0	13716 ($\pm$ 3023.6)
$\bar{X}$ Volume	67060 ($\pm$ 29743.4)	318844 ($\pm$ 36560.9)	710702 ($\pm$ 217996.4)	8843 ($\pm$ 1672.9)	0	1105529 ($\pm$ 184033.2)
$\bar{X}$ Size	109.4	316.0	59.4	74.3	0	80.6 ($\pm$ 10.4)
Mean of 3 Dates -						

Table B12 (cont'd.).

	Greens	Diatoms	Blue-greens	Cryptophytes	Euglenoids	Totals
$\bar{X}$ Number	1440 (+321.6)	565 (+122.4)	5204 (+1936.2)	52 (+19.4)	2 (+2)	7246 (+1856.3)
$\bar{X}$ Volume	103775.3 (+16600.4)	179911.7 (+38329)	268445.7 (+127388.5)	37082 (+24735.2)	1279.3 (+1279.3)	590494 (+149737.6)
$\bar{X}$ Size	72.1	318.4	51.6	713.1	639.7	81.5 (+10.8)
B. LOW DENSITY						
1) Initial Readings						
28 May 1976						
$\bar{X}$ Number	4385 (+601)	836 (+361)	0	570 (+371)	0	5790 (+892)
$\bar{X}$ Volume	337337 (+116345)	396429 (+151954)	0	284031 (+135776)	0	1017796 (+129947)
$\bar{X}$ Size	76.9	474.2	0	498.3	0	175.8 (+16.3)
2) 6 June 1978						
$\bar{X}$ Number	5069 (+785.9)	918 (+17)	2325 (+784.8)	78 (+78)	0	8390 (+642.7)
$\bar{X}$ Volume	371645.3 (+62144.3)	292666.7 (+7025.7)	193715 (+42277.3)	75773 (+75773)	0	933800 (+88075.3)
$\bar{X}$ Size	73.3	318.8	83.3	971.4	0	111.3 (+10.5)
3) 12 June 1976						
$\bar{X}$ Number	2547 (+566.2)	4960 (+470)	2293 (+429)	141 (+103.2)	5 (+5)	9947 (+1282.8)
$\bar{X}$ Volume	173720 (+28855.1)	1567038 (+149373.7)	54260 (+18738)	10448 (+7645.9)	890 (+890)	1806356 (+154215.3)
$\bar{X}$ Size	68.2	315.9	23.7	74.1	178.0	185.0 (+12.8)

Table B12 (cont'd.).

	Greens	Diatoms	Blue-greens	Cryptophytes	Euglenoids	Totals
4) 18 June 1976						
$\bar{X}$ Number	1024 (+311.6)	2243 (+543.8)	13641 (+1969.9)	91 (+37)	0	16999 (+1256.8)
$\bar{X}$ Volume	91112 (+25109.5)	709482 (+172480.8)	767743 (+201432.0)	16312 (+11564.4)	0	1584649 (+60662.4)
$\bar{X}$ Size	89.0	316.3	56.3	179.3	0	93.2 (+5.9)
Mean of 3 Dates -						
$\bar{X}$ Number	2890 (+658.9)	2707 (+630.1)	6087 (+1989.3)	103 (+40)	1 (+0.6)	11779 (+1434.3)
$\bar{X}$ Volume	212159.3 (+46643.9)	856395.6 (+198809.9)	338572.6 (+124403.7)	34177.7 (+24562.8)	296.7 (+296.7)	1441601.8 (+141685.6)
$\bar{X}$ Size	73.7	316.4	55.6	331.8	296.7	122.4 (+14.7)
C. HIGH DENSITY						
1) Initial Readings						
28 May 1976						
$\bar{X}$ Number	3525 (+309.3)	1045 (+444)	0	114 (+57)	0	4684 (+596)
$\bar{X}$ Volume	273455 (+52693)	608673 (+108944)	0	188757 (+106552)	0	1070885 (+343352)
$\bar{X}$ Size	77.6	582.5	0	1655.8	0	228.6 (+95.2)
2) 6 June 1976						
$\bar{X}$ Number	3884 (+394.6)	1698 (+312.6)	2179 (+326.9)	72 (+50.7)	0	7833 (+498.5)
$\bar{X}$ Volume	267266 (+45345.4)	610393 (+159553.2)	219701.7 (+32111.7)	128601.7 (+75730.5)	0	1225962 (+126617.3)
$\bar{X}$ Size	68.8	359.5	100.8	1786.1	0	156.5 (+14.7)

Table B12 (cont'd.).

	Greens	Diatoms	Blue-greens	Cryptophytes	Euglenoids	Totals
3) 12 June 1978						
$\bar{X}$ Number	2367 (+555.5)	7580 (+2315.2)	1867 (+468.1)	48 (+47.7)	0	11862 (+2510.9)
$\bar{X}$ Volume	156752 (+40872.2)	2403114 (+738914.3)	76439 (+44261.9)	3532 (+3532)	0	2639837 (+720079.9)
$\bar{X}$ Size	66.2	317.0	40.9	73.6	0	222.6 (+13.3)
4) 18 June 1978						
$\bar{X}$ Number	1317 (+367.6)	5102 (+641.5)	9054 (+1517.9)	108 (+60.4)	6 (+6)	15587 (+1345.4)
$\bar{X}$ Volume	93803 (+22299.8)	1612232 (+202728.9)	584035 (+116373.7)	7978 (+4482.1)	1057 (+1057)	2299105 (+141229.1)
$\bar{X}$ Size	71.2	316.0	64.5	73.9	176.2	147.5 (+18.8)
Mean of 3 Dates--						
$\bar{X}$ Number	2523 (+434.5)	4793 (+1102.7)	4367 (+1262.8)	76 (+28)	2 (+2.1)	11760 (+1396.6)
$\bar{X}$ Volume	172607 (+31538)	1541913 (+343962.4)	293392.1 (+84153.8)	50037 (+80073.5)	352 (+352)	2049387.1 (+304062.1)
$\bar{X}$ Size	68.4	321.7	67.2	658.4	176.0	174.3 (+13.1)
D. LAKE READINGS						
1) Initial Readings						
27 May 1976						
$\bar{X}$ Number	2337	1140	570	57	0	4684
$\bar{X}$ Volume	187512	379411	2394	4224	0	573541
$\bar{X}$ Size	80.2	332.8	4.2	74.1	0	139.8

Table B12 (cont'd.).

	Greens	Diatoms	Blue-greens	Cryptophytes	Euglenoids	Totals
2) 5 June 1976 X Number	2000 (+240.0)	147 (+26.3)	57 (+32.9)	190 (+17.2)	0	2394 (+172.0)
X Volume	155392 (+19396.2)	72200.3 (+9556.5)	15070.3 (+9014.8)	392702 (+60890.8)	0	635364.6 (+90060.5)
X Size	77.7	491.2	264.6	2066.9	0	265.4
3) 11 June 1976 X Number	1106 (+57.5)	245 (+65.8)	1061 (+241.9)	146 (+10.3)	5 (+5)	2563 (+300.5)
X Volume	83252 (+4443.5)	79095 (+19207.2)	19874 (+3512.9)	10794 (+761.9)	779 (+779)	193794 (+17038.5)
X Size	75.3	322.8	18.7	73.9	155.8	75.6
4) 18 June 1976 X Number	1019 (+58.2)	832 (+68.8)	3688 (+528.3)	366 (+13.8)	0	5875 (+688.6)
X Volume	101273 (+17476.6)	264067 (+36367.5)	158239 (+31822.0)	91734 (+18257.4)	0	615313 (+55117.4)
X Size	99.4	317.4	42.9	273.0	0	104.7
Mean of 3 Dates -						
X Number	1375 (+313.9)	408 (+214.1)	1602 (+625)	224 (+13.2)	2 (+1.8)	3611 (+654.3)
X Volume	113305.7 (+21702.4)	138454.1 (+62912.5)	64394.4 (+27102.4)	165076.7 (+67080.2)	259.7 (+259.7)	481490.5 (+83118.0)
X Size	82.4	339.3	40.2	736.9	130.0	133.3

Table B13. Composition (per cent) of phytoplanktonic algae by number and volume in imported lake waters, unstocked (control) aquaria and stocked (low and high stocks of leopard frog tadpoles) aquaria for Experiment One at Lakes One and Four.

EXPERIMENT ONE	LAKE ONE					LAKE FOUR				
	Control	Low Density	High Density	Lake Readings	Control	Low Density	High Density	Lake Readings	Control	Lake Readings
1) Initial Readings 27-28 May 1976										
a) Greens Number Volume	24.3 10.2	30.9 11.9	24.6 10.6	20.9 5.6	72.8 32.9	75.7 33.1	75.3 25.5	49.9 32.6		
b) Diatoms Number Volume	14.6 21.0	12.5 22.5	14.6 20.4	44.2 59.9	25.3 66.3	14.4 38.9	22.3 56.8	24.3 66.2		
c) Blue-greens Number Volume	0	0	0	0	0	0	0	12.2 0.4		
d) Cryptophytes Number Volume	61.1 73.3	56.6 65.5	60.8 69.0	34.9 34.3	1.8 0.7	9.8 27.9	2.4 17.6	1.2 0.7		
2) 5-6 June 1976										
a) Greens Number Volume	22.9 7.1	32.2 10.9	26.6 8.0	60.7 39.9	61.2 32.0	60.4 39.8	49.6 21.8	83.5 24.5		
b) Diatoms Number Volume	71.2 84.3	52.3 75.2	52.3 73.1	7.4 27.6	10.0 32.5	10.9 31.3	21.7 49.8	6.1 11.4		
c) Blue-greens Number Volume	0.4 0.2	10.7 6.9	13.3 9.3	0	27.8 12.2	27.7 20.7	27.8 17.9	2.4 2.4		
d) Cryptophytes Number Volume	5.5 8.6	4.9 6.9	7.7 9.5	31.9 32.5	0.7 22.7	0.9 8.1	0.9 10.5	7.9 61.8		

Table B13 (cont'd.).

	Control	Low Density	High Density	Lake Readings	Control	Low Density	High Density	Lake Readings
e) Euglenoids Number Volume	0	0.04 0.03	0.02 0.01	0	0.1 0.6	0	0	0
3) 11-12 June 1976								
a) Greens Number Volume	61.6 30.0	42.3 15.4	41.3 13.5	71.0 68.8	27.5 46.7	26.1 9.6	20.0 5.9	43.2 43.0
b) Diatoms Number Volume	28.0 67.4	40.6 70.1	42.8 71.9	2.2 5.1	6.7 34.8	50.8 86.8	63.9 91.0	9.6 40.8
c) Blue-greens Number Volume	7.8 1.8	15.1 10.2	14.8 10.2	2.7 1.2	65.7 18.3	23.5 3.0	15.7 2.9	41.4 10.3
d) Cryptophytes Number Volume	2.5 6.6	2.0 4.3	1.0 4.5	24.0 24.9	0.1 0.2	1.4 0.6	0.4 0.1	5.7 5.6
e) Euglenoids Number Volume	0.1 0.1	0.1 0.1	0.1 0.1	0	0	0.1 0.05	0	0.2 0.4
4) 18-19 June 1976								
a) Greens Number Volume	58.1 27.2	40.7 15.3	44.3 19.4	93.2 84.7	4.5 6.1	6.0 5.6	8.5 4.1	17.3 16.5
b) Diatoms Number Volume	28.6 58.8	37.0 70.0	37.2 70.3	2.3 7.1	7.4 28.8	13.2 44.8	32.7 70.1	14.2 42.9
c) Blue-greens Number Volume	9.9 1.3	18.4 11.6	18.3 9.5	1.6 0.6	87.3 64.3	80.2 48.4	58.1 25.4	62.8 25.7
d) Cryptophytes Number Volume	3.4 12.6	3.7 2.9	0.1 0.8	4.3 7.6	0.9 0.8	0.5 1.0	0.7 0.3	5.7 14.9

Table B13 (cont'd.).

	Control	Low Density	High Density	Lake Readings	Control	Low Density	High Density	Lake Readings
e) Euglenoids								
Number	0.1	0.2	0	0	0	0	0	0.03
Volume	0.1	0.2						0.05
Mean of 3 Dates								
a) Greens								
Number	52.4	39.1	39.8	78.8	19.9	24.4	21.4	38.1
Volume	22.0	14.0	14.3	68.1	17.6	14.7	8.4	25.5
b) Diatoms								
Number	36.7	42.9	42.4	3.0	7.8	23.0	40.8	11.3
Volume	67.2	71.6	71.6	11.1	30.5	59.4	75.2	28.8
c) Blue-greens								
Number	7.4	15.3	15.9	1.7	67.3	80.2	58.1	62.8
Volume	1.1	9.7	9.7	0.7	64.3	48.4	25.4	25.7
d) Cryptophytes								
Number	3.5	3.4	1.9	16.5	0.9	0.5	0.7	5.7
Volume	9.7	4.6	4.3	20.1	0.8	1.0	0.4	14.9
e) Euglenoids								
Number	0.05	0.1	0.03	0	0	0	0.04	0
Volume	0.05	0.1	0.03				0.05	

Table B14. Phytoplanktonic diversities (in hats) in imported lake water, unstocked (control) aquaria, and stocked (low and high stocks of leopard frog tadpoles) aquaria for Experiment One at Lake One.

EXPERIMENT ONE LAKE ONE	HIERARCHICAL DIVERSITY						Number of Genera (N _G)	Evenness (J')
	Greens	Diatoms	Blue-greens	Cryptophytes	Phyla	Total		
A. CONTROL								
1) Initial Readings								
28 May 1976								
a) Number Diversity								
X ₃	0.652	0.784	0	0.190		1.312	8	0.693
Pooled	0.671	0.967		0.154	0.651	0.774		0.372
b) Volume Diversity								
X ₃	0.355	0.641	0	0.631		1.420	8	0.750
Pooled	0.306	0.950		0.692	0.527	0.323		0.396
2) 6 June 1976								
a) Number Diversity								
X ₃	1.202	0.124	0	0.344		1.148	20	0.433
Pooled	1.115	0.154		0.141	0.641	0.776		0.256
b) Volume Diversity								
X ₃	0.963	0.189	0	0.454		3.309	20	0.305
Pooled	0.923	0.313		0.577	0.512	0.543		0.215
3) 12 June 1976								
a) Number Diversity								
X ₃	1.279	0.536	0.777	0.396		1.934		0.668
Pooled	1.472	0.763	0.820	0.693	0.752	1.251	25	0.389
b) Volume Diversity								
X ₃	1.137	0.827	0.551	0.399		1.764	25	0.608
Pooled	1.420	1.011	0.716	0.107	0.733	1.126		0.349
4) 19 June 1976								
a) Number Diversity								
X ₃	1.087	1.000	0.615	0		1.950	23	0.682
Pooled	1.183	0.843	0.424	0.090	0.870	1.310		0.418
b) Volume Diversity								
X ₃	1.027	1.165	0.656	0		1.885	23	0.659
Pooled	1.241	1.015	0.518	0.687	0.768	1.279		0.408
B. LOW DENSITY								
1) Initial Readings								
27 May 1976								
a) Number Diversity								
X ₃	0.956	1.171	0	0.245	1.056	1.858	11	0.775
b) Volume Diversity								
X ₃	0.623	1.390	0	0.553	0.336	1.398	11	0.791

Table B14 (cont'd.).

	Greens	Diatoms	Blue-greens	Cryptophytes	Phyla	Total	(Ng)	(J')
2) 5 June 1976								
a) Number Diversity								
$\bar{X}_3$	1.320	0.285	0.026	0.281		1.667	26	0.595
Pooled	1.500	0.360	0.100	0.466	0.718	0.954		0.293
b) Volume Diversity								
$\bar{X}_3$	1.153	0.450	0.004	0.552		1.315	26	0.465
Pooled	1.355	0.537	0.017	0.316	0.698	0.926		0.284
3) 11 June 1976								
a) Number Diversity								
$\bar{X}_3$	1.324	0.362	0.596	0.307		1.870	22	0.683
Pooled	1.300	0.541	0.351	0.451	0.729	1.070		0.346
b) Volume Diversity								
$\bar{X}_3$	1.142	0.453	0.136	0.214		1.405	22	0.512
Pooled	1.145	0.357	0.371	0.329	0.688	0.953		0.308
4) 18 June 1976								
a) Number Diversity								
$\bar{X}_3$	1.196	0.364	0.719	0.110		1.904	22	0.694
Pooled	1.270	0.409	1.249	0.071	0.371	1.208		0.391
b) Volume Diversity								
$\bar{X}_3$	0.991	0.380	0.209	0.151		1.345	22	0.491
Pooled	1.016	0.582	0.531	0.660	0.768	1.043		0.337
C. HIGH DENSITY								
1) Initial Readings								
28 May 1976								
a) Number Diversity								
$\bar{X}_3$	0.806	0.511	0	0.168		1.284	9	0.631
Pooled	1.036	0.670	0	0.180	0.693	0.971		0.396
b) Volume Diversity								
$\bar{X}_3$	0.410	0.562	0	0.599		1.402	9	0.688
Pooled	0.597	0.315	0	0.635	0.695	0.364		0.439
2) 6 June 1976								
a) Number Diversity								
$\bar{X}_3$	1.216	0.260	0.022	0.240		1.641	20	0.616
Pooled	1.275	0.269	0.074	0.257	0.694	0.324		0.309
b) Volume Diversity								
$\bar{X}_3$	0.904	0.347	0.001	0.559		1.259	20	0.470
Pooled	0.946	0.430	0.004	0.537	0.698	0.354		0.235
3) 12 June 1976								
a) Number Diversity								
$\bar{X}_3$	1.392	0.360	0.331	0.583		1.912	25	0.631
Pooled	1.481	0.448	0.610	0.693	0.627	0.546		0.263

Table B14 (cont'd.).

	Greens	Diatoms	Blue-greens	Cryptophytes	Phyla	Total	(N _G)	(J')
b) Volume Diversity								
$\bar{X}_3$	1.336	0.500	0.033	0.212		1.439		0.502
Pooled	1.497	0.639	0.074	0.107	0.585	0.761	25	0.236
4) 19 June 1976								
a) Number Diversity								
$\bar{X}_3$	1.080	0.367	0.918	0		1.831	24	0.666
Pooled	1.171	0.607	1.293		0.713	1.062		0.234
b) Volume Diversity								
$\bar{X}_3$	0.932	0.474	0.463	0		1.382	24	0.504
Pooled	1.164	0.335	0.638		0.672	0.959		0.302
D. LAKE READINGS								
1) Initial Readings								
23 May 1976								
a) Number Diversity								
$\bar{X}_3$	0.741	0.699	0	0.191		1.374	3	0.725
Pooled	0.973	0.924		0.203	0.638	0.879		0.423
b) Volume Diversity								
$\bar{X}_3$	0.436	0.617	0	0.619		1.440	3	0.761
Pooled	0.559	0.805		0.606	0.638	0.846		0.407
2) 6 June 1976								
a) Number Diversity								
$\bar{X}_3$	0.577	0.463	0	0.194		1.276	11	0.616
Pooled	0.699	0.889		0.142	0.738	0.916		0.382
b) Volume Diversity								
$\bar{X}_3$	0.709	0.316	0	0.606		1.584	11	0.764
Pooled	0.759	0.688		0.675	0.353	1.186		0.494
3) 12 June 1976								
a) Number Diversity								
$\bar{X}_3$	0.589	0.449	0.517	0.096		1.229	14	0.490
Pooled	0.531	0.792	0.231	0.042	0.525	0.750		0.284
b) Volume Diversity								
$\bar{X}_3$	0.693	0.369	0.296	0.637		1.452	14	0.579
Pooled	0.636	0.678	0.636	0.551	0.556	0.723		0.274
4) 19 June 1976								
a) Number Diversity								
$\bar{X}_3$	0.150	0.502	0.437	0.250		0.506	10	0.222
Pooled	0.231	1.745	0.327	0.115	0.516	0.602		0.217
b) Volume Diversity								
$\bar{X}_3$	0.236	0.628	0.223	0.251		0.308	10	0.351
Pooled	0.293	1.537	0.737	0.692	0.557	0.691		0.249

Table B15. Densities of dominant algal genera (cells/ml $\pm$ SD) in imported lake waters, unstocked (control) aquaria, and stocked (low and high stocks of leopard frog tadpoles) aquaria in Experiment One at Lakes One and Four.

EXPERIMENT ONE	LAKE ONE					LAKE FOUR				
	Control	Low Density	High Density	Lake Readings	Control	Low Density	High Density	Lake Readings	Control	Lake Readings
I. CHLOROPHYCEAE										
A. Chlamydomonas										
1) 27-28 May 1976	1397 (+60)	1881 (+272)	1482 (+261)	969	1254 (+119)	1117 (+102)	1064 (+442)	309		
2) 5-6 June 1976	2076 (+171)	4240 (+416)	3408 (+183)	2579 (+203)	535 (+62)	779 (+245)	775 (+273)	770 (+65)		
3) 11-12 June 1976	5494 (+710)	8381 (+1306)	8706 (+2146)	8380 (+187)	387 (+60)	763 (+190)	736 (+196)	624 (+19)		
4) 18-19 June 1976	8283 (+1559)	10667 (+620)	12663 (+350)	13891 (+461)	289 (+53)	470 (+30)	540 (+79)	724 (+51)		
B. Schroederia										
1) 27-28 May 1976	608 (+149)	855 (+114)	608 (+187)	399	570 (+371)	209 (+50)	266 (+19)	171		
2) 5-6 June 1976	756 (+73)	1667 (+370)	855 (+165)	43 (+7)	8 (+8)	93 (+12)	48 (+6)	24 (+17)		
3) 11-12 June 1976	779 (+221)	5602 (+2176)	7124 (+1208)	114 (+90)	0	20 (+9)	32 (+11)	0		
4) 18-19 June 1976	495 (+162)	5167 (+660)	7602 (+3815)	66 (+66)	16 (+12)	31 (+17)	28 (+25)	13 (+6)		
C. Scenedesmus										
1) 27-28 May 1976	0	0	0	0	57 (+57)	0	0	0		
2) 5-6 June 1976	1466 (+162)	766 (+196)	739 (+63)	38 (+5)	125 (+54)	1008 (+187)	591 (+160)	67 (+34)		
3) 11-12 June 1976	3189 (+1443)	2076 (+1142)	1525 (+345)	152 (+27)	63 (+2)	812 (+80)	660 (+234)	38 (+38)		
4) 18-19 June 1976	11387 (+2777)	2102 (+678)	1271 (+457)	28 (+14)	36 (+2)	103 (+72)	273 (+115)	124 (+15)		

Table B15 (cont'd.).

	Control	Low Density	High Density	Lake Readings	Control	Low Density	High Density	Lake Readings
D. Dictyosphaerium								
1) 27-28 May 1976	38 (+38)	266 (+266)	152 (+125)	114	2337 (+1000)	1634 (+591)	1188 (+310)	604
2) 5-6 June 1976	166 (+75)	3611 (+353)	1997 (+690)	0	1785 (+39)	1817 (+521)	1682 (+134)	784 (+402)
3) 11-12 June 1976	1112 (+210)	3670 (+614)	7495 (+1526)	171 (+15)	367 (+69)	783 (+308)	863 (+131)	380 (+104)
4) 18-19 June 1976	1141 (+573)	2637 (+434)	2779 (+1287)	57 (+21)	260 (+77)	326 (+202)	269 (+60)	146 (+22)
II. BACILLARIOPHYCEAE								
A. Nitzschia								
1) 27-28 May 1976	661 (+50)	741 (+87)	674 (+123)	1653	1705 (+61)	741 (+324)	836 (+393)	1083
2) 5-6 June 1976	10989 (+1769)	16188 (+1734)	13227 (+1610)	314 (+62)	417 (+61)	910 (+15)	1654 (+293)	138 (+24)
3) 11-12 June 1976	6254 (+220)	17784 (+3796)	24811 (+6417)	266 (+89)	234 (+70)	4950 (+467)	7564 (+2309)	241 (+70)
4) 18-19 June 1976	8172 (+2486)	17278 (+1959)	19084 (+2365)	275 (+130)	1009 (+116)	2237 (+538)	5102 (+642)	828 (+115)
B. Navicula								
1) 27-28 May 1976	494 (+237)	302 (+260)	675 (+675)	1026	0	19 (+19)	38 (+38)	0
2) 5-6 June 1976	148 (+64)	293 (+274)	306 (+136)	38 (+20)	15 (+15)	0	0	0
3) 11-12 June 1976	397 (+94)	1014 (+691)	756 (+152)	28 (+17)	10 (+3)	5 (+4)	3 (+3)	0
4) 18-19 June 1976	1097 (+65)	856 (+354)	499 (+130)	19 (+19)	0	0	0	2 (+2)

Table B15 (cont'd.)

	Control	Low Density	High Density	Lake Readings	Control	Low Density	High Density	Lake Readings	Control	Low Density	High Density	Lake Readings
III. CYANOPHYTA												
A. <i>Smalli</i> Anabaena												
1) 27-28 May 1976	0	0	0	0	0	0	0	0	0	0	0	0
2) 5-6 June 1976	62 (+62)	0	19 (+19)	0	255 (+227)	588 (+83)	782 (+361)	0				
3) 11-12 June 1976	565 (+95)	1223 (+220)	1129 (+576)	256 (+104)	1537 (+523)	1853 (+367)	1253 (+100)	825 (+127)				
4) 18-19 June 1976	1022 (+289)	2114 (+1299)	2423 (+1380)	95 (+53)	2634 (+2031)	3133 (+1266)	1164 (+587)	1501 (+186)				
B. <i>Smalli</i> Anacystis												
1) 27-28 May 1976	0	0	0	0	0	0	0	0				
2) 5-6 June 1976	0	19 (+19)	0	0	707 (+279)	570 (+571)	4 (+4)	0				
3) 11-12 June 1976	1109 (+993)	0	95 (+95)	0	547 (+359)	169 (+97)	151 (+84)	0				
4) 18-19 June 1976	2518 (+1267)	356 (+357)	1140 (+936)	86 (+86)	1113 (+715)	671 (+671)	28 (+15)	243 (+243)				
C. Coccoloid Blue-green Cell												
1) 27-28 May 1976	0	0	0	0	0	0	0	0				
2) 5-6 June 1976	0	3486 (+378)	3725 (+533)	0	266 (+62)	1164 (+235)	1393 (+213)	0				
3) 11-12 June 1976	348 (+183)	5752 (+2285)	8006 (+1700)	133 (+33)	33 (+10)	271 (+113)	414 (+253)	79 (+44)				
4) 18-19 June 1976	356 (+189)	6079 (+1033)	4906 (+864)	57 (+5)	394 (+198)	721 (+148)	529 (+127)	248 (+62)				
IV. CRYPTOPHYTA												
A. <i>Cryptomonas</i>												
1) 27-28 May 1976	228 (+53)	266 (+53)	230 (+89)	171	19 (+19)	76 (+38)	57 (+33)	0				

Table B15 (cont'd.).

	Control	Low Density	High Density	Lake Readings	Control	Low Density	High Density	Lake Readings
2) 5-6 June 1976	95 (+59)	130 (+85)	138 (+58)	76 (+26)	31 (+20)	22 (+22)	34 (+14)	119 (+20)
3) 11-12 June 1976	71 (+25)	100 (+53)	155 (+12)	66 (+26)	5 (+5)	144 (+40)	44 (+44)	146 (+9)
4) 18-19 June 1976	24 (+24)	36 (+21)	24 (+24)	28 (+17)	119 (+24)	88 (+37)	108 (+63)	315 (+21)
B. Rhodomonas								
1) 27-28 May 1976	4894 (+147)	5240 (+16)	5407 (+598)	2394	114 (+87)	494 (+355)	133 (+69)	57
2) 5-6 June 1976	765 (+283)	1461 (+350)	1921 (+479)	1613 (+859)	0	56 (+56)	38 (+38)	71 (+23)
3) 11-12 June 1976	565 (+260)	859 (+147)	435 (+179)	3335 (+317)	0	0	0	0
4) 18-19 June 1976	1299 (+1299)	1865 (+1791)	48 (+48)	637 (+336)	0	3 (+3)	0	32 (+15)

Table B16. Phytoplanktonic diversities (in nats) in imported lake water, unstocked (control) aquaria, and stocked (low and high stocks of leopard frog tadpoles) aquaria for Experiment One at Lake Four.

EXPERIMENT ONE LAKE FOUR	HIERARCHICAL DIVERSITY						Number of Genera (N _G)	Evenness (J')
	Greens	Diatoms	Blue-greens	Cryptophytes	Phyla	Total		
A. CONTROL								
1) Initial Readings								
28 May 1976								
a) Number								
Diversity								
X ₃	1.245	0.276	0	0.150		1.615	13	0.765
Pooled	1.555	0.485		0.451	0.475	1.983		0.422
b) Volume								
Diversity								
X ₃	1.154	0.486	0	0.110		1.445	13	0.633
Pooled	1.325	0.911	0	0.330	0.776	1.219		0.626
2) 6 June 1976								
a) Number								
Diversity								
X ₃	1.305	0.188	0.311	0		1.749	15	0.730
Pooled	0.992	0.473	1.046		0.779	1.150		0.424
b) Volume								
Diversity								
X ₃	1.285	0.244	0.551	0		1.827	15	0.765
Pooled	1.320	0.610	0.672		0.996	1.252		0.462
3) 12 June 1976								
a) Number								
Diversity								
X ₃	1.158	0.157	0.653	0		1.621	14	0.719
Pooled	1.302	0.301	1.003		0.668	1.213		0.460
b) Volume								
Diversity								
X ₃	1.097	0.068	0.897	0		1.685	14	0.736
Pooled	1.273	0.134	1.198		0.830	1.310		0.496
4) 19 June 1976								
a) Number								
Diversity								
X ₃	1.048	0	0.743	0		1.242	14	0.518
Pooled	1.389		1.017		0.514	0.901		0.341
b) Volume								
Diversity								
X ₃	0.884	0	0.583	0		1.294	14	0.538
Pooled	0.978		1.000		0.690	1.054		0.403
B. LOW DENSITY								
1) Initial Readings								
28 May 1976								
a) Number								
Diversity								
X ₃	1.386	0.392	0	0.311		1.560	11	0.736
Pooled	1.229	0.559		0.637	0.561	1.121		0.467
b) Volume								
Diversity								
X ₃	1.326	0.518	0	0.184		1.524	11	0.748
Pooled	0.912	0.356		0.179	0.913	1.301		0.543

Table B16 (cont'd.).

	Greens	Diatoms	Blue-greens	Cryptophytes	Phyla	Total	(N _G)	(J')
2) 6 June 1976								
a) Number Diversity								
$\bar{X}_3$	1.458	0.038	0.772	0.198		2.018	15	0.838
Pooled	1.524	0.113	1.017	0.595	0.928	1.173		0.433
b) Volume Diversity								
$\bar{X}_3$	1.414	0.066	0.206	0.071		1.794	15	0.742
Pooled	1.415	0.194	0.426	0.212	0.753	1.165		0.438
3) 12 June 1976								
a) Number Diversity								
$\bar{X}_3$	1.267	0.132	0.735	0		1.720	17	0.670
Pooled	1.515	0.036	0.247		0.753	0.875		0.309
b) Volume Diversity								
$\bar{X}_3$	1.244	0.010	0.649	0		0.626	17	0.242
Pooled	1.336	0.031	0.856		0.506	0.559		0.197
4) 19 June 1976								
a) Number Diversity								
$\bar{X}_3$	1.145	0.012	0.803	0.079		1.338	18	0.545
Pooled	1.730	0.072	0.711	0.252	0.553	0.356		0.297
b) Volume Diversity								
$\bar{X}_3$	1.045	0.015	0.611	0.198		1.195	18	0.495
Pooled	1.679	0.091	0.401	0.532	0.702	0.658		0.297
C. HIGH DENSITY								
1) Initial Readings								
28 May 1976								
a) Number Diversity								
$\bar{X}_3$	1.256	0.480	0	0.224		1.713	12	0.816
Pooled	1.346	0.799		0.500	0.715	1.227		0.494
b) Volume Diversity								
$\bar{X}_3$	1.140	0.395	0	0.048		1.473	12	0.714
Pooled	1.085	0.869		0.308	0.772	1.314		0.529
2) 6 June 1976								
a) Number Diversity								
$\bar{X}_3$	1.375	0.123	0.591	0.213		1.944	18	0.756
Pooled	1.396	0.222	0.490	0.434	0.756	1.021		0.353
b) Volume Diversity								
$\bar{X}_3$	1.442	0.363	0.094	0.204		1.769	18	0.626
Pooled	1.707	0.768	0.046	0.568	0.831	1.152		0.397
3) 12 June 1976								
a) Number Diversity								
$\bar{X}_3$	1.248	0.014	0.710	0		1.294	18	0.540
Pooled	1.312	0.031	0.976		0.715	0.658		0.297

Table 816 (cont'd.).

	Greens	Diatoms	Blue-greens	Cryptophytes	Phyla	Total	(Ng)	(J')
b) Volume Diversity $\bar{X}_3$ Pooled	1.219 1.345	0.025 0.065	0.585 1.011	0	0.470	0.489 0.535	18	0.202 0.185
4) June 1976								
a) Number Diversity $\bar{X}_3$ Pooled	1.281 1.770	0	0.674 0.799	0	0.665	1.379 0.337	16	0.554 0.302
b) Volume Diversity $\bar{X}_3$ Pooled	1.029 1.547	0	0.518 0.587	0	0.592	0.394 0.652	16	0.369 0.235
D. LAKE READINGS								
1) 27 May 1976								
a) Number Diversity $\bar{X}_3$	1.448	0.199	0	0	1.010	1.690	9	0.360
b) Volume Diversity $\bar{X}_3$	1.192	0.321	0	0	0.698	1.300	9	0.592
2) 5 June 1976								
a) Number Diversity $\bar{X}_3$ Pooled	1.209 1.331	0.200 0.633	0 0.637	0.622 0.655	0.615	1.670 1.211	17	0.714 0.427
b) Volume Diversity $\bar{X}_3$ Pooled	1.169 1.652	0.356 0.907	0 0.620	0.075 0.069	0.823	1.338 1.106	17	0.578 0.390
3) 11 June 1976								
a) Number Diversity $\bar{X}_3$ Pooled	0.928 1.326	0.124 0.177	0.476 0.787	0	0.839	1.710 1.225	13	0.331 0.478
b) Volume Diversity $\bar{X}_3$ Pooled	0.677 1.034	0.177 0.290	0.516 1.040	0	0.853	1.507 1.130	13	0.719 0.441
4) 18 June 1976								
a) Number Diversity $\bar{X}_3$ Pooled	0.882 0.848	0.029 0.071	1.069 1.350	0.210 0.278	0.780	1.925 1.222	16	0.752 0.441
b) Volume Diversity $\bar{X}_3$ Pooled	0.694 0.335	0.043 0.107	0.386 0.925	0.312 0.512	0.934	1.626 1.166	16	0.673 0.420

Table B17. Numbers and volumes of phytoplankton (per ml $\pm$ SD) in imported lake water, unstocked (control) aquaria, and stocked (low and high stocks of leopard frog tadpoles) aquaria for Experiment Two at Lake One.

EXPERIMENT TWO LAKE ONE	Greens	Diatoms	Blue-greens	Cryptophytes	Dinoflagellates	Euglenoids	Totals
A. CONTROL							
1) Initial Readings 26 July 1976							
$\bar{X}$ Number	7217 (± 403.1)	645 (± 165.8)	234 (± 51.8)	114 (± 19)	0	0	8210 (± 399.9)
$\bar{X}$ Volume	453651.3 (± 39091.1)	391463.7 (± 46991.5)	4955 (± 2237.2)	8447 (± 1407.7)	0	0	858517 (± 84001.3)
$\bar{X}$ Size	62.9	606.9	21.2	74.1	0	0	104.6
2) 8 August 1976							
$\bar{X}$ Number	9976 (± 1792.9)	13815 (± 1290.8)	1348 (± 648.1)	3303 (± 426.3)	0	0	28442 (± 3169.6)
$\bar{X}$ Volume	409915.7 (± 24138.7)	7212504 (± 757829)	10635.7 (± 3695.2)	7874812 (± 1016458.2)	0	0	15507867.4 (± 1499075.1)
$\bar{X}$ Size	41.1	522.1	7.9	2384.1	0	0	545.2
3) 15 August 1976							
$\bar{X}$ Number	6412 (± 901.4)	22558 (± 2943.3)	8386 (± 6874.9)	0	0	0	112839 (± 7015.7)
$\bar{X}$ Volume	865732 (± 94719.4)	13979000 (± 1960448.5)	1297090.3 (± 124027.5)	0	0	0	16136822.3 (± 2004769.2)
$\bar{X}$ Size	135.0	619.7	15.4	0	0	0	143.0
4) 22 August 1976							
$\bar{X}$ Number	58862 (± 10043.6)	12011 (± 4923.4)	131470 (± 46701)	152 (± 76)	608 (± 76.1)	0	203103 (± 57934.7)
$\bar{X}$ Volume	4884031.3 (± 1408544.2)	5527516 (± 2228913.7)	1921038.3 (± 746334.5)	362400 (± 181200)	1051466.7 (± 150444.8)	0	13746452.3 (± 3047033.4)
$\bar{X}$ Size	83.0	460.2	14.6	2384.2	1729.4	0	67.7
Mean of 3 Dates-							

Table B17 (cont'd.).

	Greens	Diatoms	Blue-greens	Cryptophytes	Dinoflagellates	Euglenoids	Totals
$\bar{X}$ Number	25084 (+18962.1)	16128 (+2352.1)	72229 (+23386.8)	1152 (+552.6)	203 (+117.0)	0	114795 (+30338.7)
$\bar{X}$ Volume	2053226.3 (+819328.3)	8906340 (+1567195.1)	1074588.1 (+355937.9)	2745737.3 (+1317491.6)	350488.9 (+202354.9)	0	15130380.7 (+1192400.1)
$\bar{X}$ Size	81.8	522.2	14.9	2383.4	1726.5	0	131.8 (+35)
B. LOW DENSITY							
1) Initial Readings							
26 July 1976							
$\bar{X}$ Number	7002 (+1208.3)	909 (+132.5)	557 (+177.9)	70 (+12.7)	0	0	8538 (+1497.6)
$\bar{X}$ Volume	409654.3 (+20995.9)	398947.3 (+67947.9)	11193 (+5852.5)	5163 (+938.7)	0	0	824957.6 (+76482.9)
$\bar{X}$ Size	58.5	438.9	20.1	74.1	0	0	96.6
2) 15 August 1976							
$\bar{X}$ Number	12184 (+235.6)	16432 (+4248.2)	1440 (+207.3)	4816 (+849.7)	0	13 (+7.7)	36885 (+4444.9)
$\bar{X}$ Volume	506188.7 (+110296.9)	7396200.3 (+1776423.5)	23471.0 (+9718.5)	11439753 (+3519577.7)	0	1279.3 (+1280.9)	19366093.3 (+1567321.9)
$\bar{X}$ Size	41.5	401.3	16.3	2375.4	0	98.4	525.1
3) 15 August 1976							
$\bar{X}$ Number	17104 (+2072.8)	68633 (+12591.8)	129804 (+29625.6)	0	0	0	215541 (+33443.4)
$\bar{X}$ Volume	1820706.3 (+390023.6)	43388666 (+7925859.4)	2133934.7 (+546999.5)	0	0	0	47343307.7 (+8285012.4)
$\bar{X}$ Size	106.4	632.2	16.3	0	0	0	219.6
4) 22 August 1976							
$\bar{X}$ Number	283697 (+65928.6)	26417 (+6962.7)	412091 (+84080)	0	1900 (+375.0)	494 (+297.1)	724599 (+151201.2)
$\bar{X}$ Volume	21887265 (+6695432.8)	12455272 (+279087.5)	6383489.3 (+1333946.9)	0	3753333.3 (+741386.7)	82428.7 (+49580.9)	44536425.7 (+9575022.5)

Table B17 (cont'd.).

	Greens	Diatoms	Blue-greens	Cryptophytes	Dinoflagellates	Euglenoids	Totals
$\bar{X}$ Size	77.1	471.5	15.5	0	1975.4	166.9	61.5
Mean of 3 Dates-							
$\bar{X}$ Number	104328 (+48722.8)	37827 (+4910.5)	18112 (+65878.8)	1605 (+839.4)	633 (+356.7)	169 (+93.8)	325673 (+112310.4)
$\bar{X}$ Volume	8071386.7 (+3964256.6)	21080046 (+6147212.6)	2846965 (+1023575.6)	3813251.2 (+1994822.4)	1251111.1 (+722329.3)	27902.7 (+15741.7)	37090662.7 (+5775366.7)
$\bar{X}$ Size	77.4	557.3	15.7	2375.9	1976.5	165.1	113.0 (+30.3)
C. HIGH DENSITY							
1) Initial Readings							
26 July 1976							
$\bar{X}$ Number	7177 (+1004.8)	752 (+116.3)	253 (+108.2)	82 (+16.8)	0	0	8264 (+1073.9)
$\bar{X}$ Volume	396645.3 (+40254.4)	462720 (+65629.4)	12208.3 (+6167.7)	6101 (+1241.4)	0	0	877674.6 (+96381.1)
$\bar{X}$ Size	55.3	615.3	48.3	74.4	0	0	106.2
2) 8 August 1976							
$\bar{X}$ Number	15203 (+164.9)	29148 (+1192.1)	2314 (+396.7)	4629 (+69.6)	0	13 (+7.7)	51327 (+1509.8)
$\bar{X}$ Volume	516052 (+27872.2)	14697000 (+998010.5)	19447.7 (+49110.4)	11019667 (+257274.8)	0	1279.3 (+1280.8)	26428475 (+933510.3)
$\bar{X}$ Size	33.9	504.2	83.3	2380.6	0	98.4	514.9
3) 15 August 1976							
$\bar{X}$ Number	21551 (+627.7)	123282 (+17068.7)	140069 (+53688.3)	0	0	0	284902 (+47188.8)
$\bar{X}$ Volume	2181011.3 (+316165.2)	77581333 (+7732057.4)	2486049.7 (+910197.5)	0	0	0	82248394 (+6773369.1)
$\bar{X}$ Size	84.5	629.3	17.7	0	0	0	288.7

Table B17 (cont'd.).

	Greens	Diatoms	Blue-greens	Cryptophytes	Dinoflagellates	Euglenoids	Totals
4) 22 August 1976							
$\bar{X}$ Number	317121 (+57123.2)	22854 (+2104.8)	392257 (+67711.4)	38 (+38)	1786 (+402.9)	228 (+174.3)	734285 (+124178.5)
$\bar{X}$ Volume	17459658.3 (+7219314.1)	11225453 (+707901)	6078940.3 (+1049715.9)	2815.7 (+2815.7)	3531000 (+796179.9)	38044 (+29091.0)	40147420.3 (+7128335.5)
$\bar{X}$ Size	55.1	491.2	15.5	74.1	1977.0	166.9	54.7
Mean of 3 Dates -							
$\bar{X}$ Number	117958 (+52458.7)	58428 (+16984.4)	178220 (+62295.7)	1556 (+768.7)	595 (+343.7)	80 (+42.7)	356856 (+107118.7)
$\bar{X}$ Volume	6718907.2 (+3406751.7)	34501262 (+11015951.2)	2919609.2 (+945625.6)	3674160.8 (+1836877.2)	1177000 (+679541.3)	13107 (+7201.6)	49004247.1 (+9027659.7)
$\bar{X}$ Size	57.0	590.5	16.4	2361.3	1978.1	163.8	137.3 (+29.2)
U. LAKE READINGS							
1) Initial Readings							
25 July 1976							
$\bar{X}$ Number	3545 (+321.9)	386 (+175.1)	717 (+241.9)	63 (+33.5)	0	0	4711 (+484.7)
$\bar{X}$ Volume	196421 (+29156.1)	178717.3 (+72856)	23632 (+9288.2)	4693 (+2486.2)	0	0	403463 (+57017.2)
$\bar{X}$ Size	55.4	463.0	33.0	74.5	0	0	85.6
2) 7 August 1976							
$\bar{X}$ Number	5942 (+303.7)	10545 (+839.0)	2046 (+1114.8)	5049 (+183.7)	0	11 (+6.9)	23593 (+553.5)
$\bar{X}$ Volume	405167.3 (+34358.5)	5238934 (+502023.7)	26057.3 (+6771.8)	8985819.7 (+944991.4)	0	1056.7 (+1057.9)	14657035 (+500300.4)
$\bar{X}$ Size	68.2	496.8	12.7	1779.7	0	96.1	621.2

Table B17 (cont'd.).

	Greens	Diatoms	Blue- greens	Cryptophytes	Dinoflagellates	Euglenoids	Totals
3) 14 August 1976							
$\bar{X}$ Number	25819 (+1664.4)	64744 (+3411.9)	87038 (+10335.7)	0	0	0	177601 (+6568.5)
$\bar{X}$ Volume	1598929 (+89607.9)	39986000 (+2267319.5)	1345031 (+165797.6)	0	0	0	42929960 (+2211102.6)
$\bar{X}$ Size	61.9	617.6	15.4	0	0	0	150.7
4) 21 August 1976							
$\bar{X}$ Number	429828 (+38572.9)	236119 (+2730.2)	548365 (+41804.1)	0	4219 (+748.4)	228 (+114.1)	1006329 (+73939.7)
$\bar{X}$ Volume	31371000 (+4134152.5)	8788974.3 (+1173150.8)	8144309.7 (+632001.3)	0	8337666.7 (+1479030.3)	38044 (+19044.5)	56679994.7 (+6040619.9)
$\bar{X}$ Size	73.0	371.0	14.8	0	1976.2	166.9	56.3
Mean of 3 Dates -							
$\bar{X}$ Number	153063 (+79733)	32993 (+9473.9)	212403 (+97990)	1683 (+971.7)	1406 (+811.9)	80 (+42.9)	402508 (+176187.9)
$\bar{X}$ Volume	11125032.1 (+5847893.1)	18004636.1 (+6372998.3)	3171799.3 (+1452175.3)	2995273.2 (+1729371.8)	2779222.2 (+1604584.7)	813033.6 (+7222)	38088996.5 (+7141883.3)
$\bar{X}$ Size	72.3	545.7	14.9	1779.7	1976.9	162.9	94.6

Table B18. Numbers and volumes of phytoplankton (per ml $\pm$ SD) in imported lake water, unstocked (control) aquaria, and stocked (low and high stocks of leopard frog tadpoles) aquaria for Experiment Two at Lake Four.

EXPERIMENT TWO LAKE FOUR	Greens	Diatoms	Blue-greens	Cryptophytes	Dinoflagellates	Euglenoids	Totals
A. CONTROL							
1) Initial Readings 26 July 1976 X Number	790 (+258.4)	92 (+27.1)	12235 (+214.2)	150 (+39.9)	0	0	13267 (+532.6)
X Volume	70910 (+27063.6)	79249 (+23390.6)	3907523.7 (+663129.1)	343818 (+81299)	0	0	4401500.7 (+698246)
X Size	89.8	861.4	319.4	2292.1	0	0	331.8
2) 8 August 1976 X Number	4085 (+1603)	56 (+16.5)	8704 (+4376.8)	9 (+9)	0	0	12854 (+3878.2)
X Volume	292470 (+76033)	38243 (+10093.5)	1643279 (+58065)	30385.7 (+30385.7)	0	0	2004377.7 (+524039)
X Size	71.6	682.9	188.8	3376.2	0	0	155.9
3) 15 August 1976 X Number	13704 (+1406.2)	275 (+90.8)	14241 (+7240.6)	70 (+23.4)	46 (+26.4)	0	28336 (+7014.5)
X Volume	887225 (+89441.6)	225428.7 (+75421.9)	3306751 (+2305019.2)	166111.3 (+55703.2)	90323.2 (+52249.9)	0	4704175.2 (+2277371.9)
X Size	64.7	819.7	232.2	2373.0	1963.5	0	166.0
4) 22 August 1976 X Number	4117 (+761.4)	266 (+58)	21446 (+861.4)	811 (+207.4)	0	0	26639 (+1458.9)
X Volume	256805 (+59804.6)	172576 (+30973.6)	548721 (+41113.4)	264900 (+113301.2)	0	0	1243002 (+204249.8)
X Size	62.4	648.8	25.6	327.0	0	0	46.7
Mean of 3 Dates							

Table B18 (cont'd.).

	Greens	Diatoms	Blue-greens	Cryptophytes	Dinoflagellates	Euglenoids	Totals
B. LOW DENSITY							
1) Initial Readings 26 July 1976							
$\bar{X}$ Number	7302 (+1674.7)	199 (+47.6)	14797 (+3070.7)	297 (+142.2)	14 (+10.5)	0	22608 (+3396.7)
$\bar{X}$ Volume	478833.1 (+109073.1)	145416 (+36586.0)	1832917 (+794806.7)	153799 (+50601.6)	28325.6 (+20668.9)	0	2639290.7 (+853522.9)
$\bar{X}$ Size	65.6	730.7	123.9	517.8	2023.3	0	116.7
2) 8 August 1976							
$\bar{X}$ Number	533 (+94.8)	95 (+29)	19196 (+5186.9)	82 (+6.2)	0	6 (+3.1)	19912 (+5321.1)
$\bar{X}$ Volume	52612 (+9612.4)	81833 (+25000.5)	5527627.7 (+236849.2)	196313 (+15101)	0	1056.7 (+1057.9)	5558385 (+247116.1)
$\bar{X}$ Size	98.7	861.4	272.3	2394.0	0	176.3	279.2
3) 15 August 1976							
$\bar{X}$ Number	3021 (+172.2)	133 (+9.3)	10452 (+2601.9)	0	0	0	13606 (+2689.6)
$\bar{X}$ Volume	230494 (+13458.9)	114278 (+8039.3)	2425288.7 (+741134)	0	0	0	2770060.7 (+746750.4)
$\bar{X}$ Size	76.3	859.2	232.0	0	0	0	203.6
4) 22 August 1976							
$\bar{X}$ Number	7079 (+1319.2)	532 (+137.3)	16077 (+2598.8)	57 (+19.6)	44 (+25.4)	0	23789 (+3042.9)
$\bar{X}$ Volume	568170 (+62563.4)	441409.7 (+118642.0)	2843782.7 (+1222176.7)	121277.7 (+49038.7)	86712.8 (+50123.0)	0	4061352.9 (+1234317.4)
$\bar{X}$ Size	80.3	829.7	176.9	2127.7	1970.7	0	170.7
5) 29 August 1976							
$\bar{X}$ Number	5595 (+909.4)	644 (+212.2)	16894 (+567.9)	1102 (+231.1)	22 (+12.7)	0	24257 (+435.2)
$\bar{X}$ Volume	762428 (+273719.3)	742137 (+34357.8)	282122.7 (+27146.3)	315782.7 (+60442.7)	43356.7 (+25032)	0	2145827.1 (+345393.8)

Table B1B (cont'd.).

	Greens	Diatoms	Blue-greens	Cryptophytes	Dinoflagellates	Euglenoids	Totals
$\bar{X}$ Size	136.3	1152.4	16.7	286.6	1970.8	0	88.5
Mean of 3 Dates-							
$\bar{X}$ Number	5232 (+793.5)	436 (+106.6)	14474 (+1475.9)	386 (+191.2)	13 (+12.7)	0	20541 (+2098)
$\bar{X}$ Volume	520363.8 (+112349.9)	432608.4 (+97438.3)	1850398 (+572431.4)	145686.7 (+51181.6)	25031.9 (+50123.0)	0	2974088.9 (+511065.3)
$\bar{X}$ Size	99.5	992.2	127.8	377.4	1925.5	0	144.8
C. HIGH DENSITY							
1) Initial Readings 26 July 1976							
$\bar{X}$ Number	905 (+422.5)	95 (+21.9)	12787 (+1739.9)	139 (+22.8)	0	0	13926 (+2000.6)
$\bar{X}$ Volume	91506 (+49740.1)	81833 (+18898.4)	3507037.3 (+970436.1)	332150.7 (+54397.9)	0	0	4012527 (+910395.2)
$\bar{X}$ Size	101.1	861.4	274.3	2389.6	0	0	288.1
2) 8 August 1976							
$\bar{X}$ Number	2641 (+679.2)	266 (+52.9)	6495 (+584.5)	28 (+0)	0	0	9430 (+1103.2)
$\bar{X}$ Volume	258792 (+102431)	221524 (+50932.7)	1618566.3 (+46786.6)	61211 (+29946)	0	0	2160113.2 (+137248.2)
$\bar{X}$ Size	98.0	832.8	249.2	2186.1	0	0	229.1
3) 15 August 1976							
$\bar{X}$ Number	5444 (+553.4)	799 (+183)	6154 (+1411.6)	48 (+10)	44 (+25.4)	0	12489 (+1912.9)
$\bar{X}$ Volume	479924.3 (+43876.6)	648022 (+139970.5)	928331 (+336557.5)	114451.3 (+23845.3)	86712.8 (+50063.7)	0	2257441.1 (+243642.8)
$\bar{X}$ Size	88.2	811.0	150.9	2384.4	1970.7	0	180.8

Table B1b (cont'd.).

	Greens	Diatoms	Blue-greens	Cryptophytes	Dinoflagellates	Euglenoids	Totals
4) 22 August 1976							
$\bar{X}$ Number	4892 (+482)	659 (+25.3)	15497 (+1113.4)	1343 (+67)	22 (+12.7)	0	22413 (+711.6)
$\bar{X}$ Volume	274129 (+76658.5)	548853.7 (+27122.3)	286966.7 (+30024)	415833.7 (+136090.4)	43356.7 (+25032)	0	1569139.8 (+101980.8)
$\bar{X}$ Size	56.0	832.9	18.5	309.6	1970.8	0	70.0
Mean of 3 Dates -							
$\bar{X}$ Number	4326 (+516.7)	575 (+97.1)	9381 (+1623.5)	473 (+218.3)	13 (+8.9)	0	14767 (+2070)
$\bar{X}$ Volume	337615.2 (+52873.8)	472799.9 (+77853.9)	944628 (+215996.9)	197165.3 (+68651.6)	25031.9 (+17760.2)	0	1977240 (+137203.7)
$\bar{X}$ Size	78.0	822.3	100.7	416.8	1925.5	0	133.9
D. LAKE READINGS							
1) Initial Readings 25 July 1976							
$\bar{X}$ Number	350 (+122.3)	18 (+6.1)	13453 (+869.9)	152 (+19)	0	0	13973 (+936)
$\bar{X}$ Volume	18173 (+9359.2)	15329 (+5406.3)	5087637 (+227224.0)	362424 (+45356.7)	0	0	5483563 (+246685.3)
$\bar{X}$ Size	51.9	851.6	378.2	2384.4	0	0	392.4
2) 7 August 1976							
$\bar{X}$ Number	1892 (+135.6)	46 (+18)	2007 (+124.7)	35 (+8.3)	0	0	3980 (+227.7)
$\bar{X}$ Volume	140672 (+8208.8)	29631 (+13771.4)	225439.7 (+48341.6)	82475 (+20643.4)	0	0	478217.7 (+57526.1)
$\bar{X}$ Size	74.3	644.1	112.3	2356.4	0	0	120.2

Table B18 (cont'd.).

	Greens	Diatoms	Blue-greens	Cryptophytes	Dinoflagellates	Euglenoids	Totals
3) 14 August 1976							
$\bar{X}$ Number	4783 (+706.3)	248 (+41.2)	10834 (+1015.7)	13 (+6.3)	11 (+6.3)	0	15889 (+713.3)
$\bar{X}$ Volume	291987 (+43634.6)	194198 (+25163.8)	1958255 (+793687.5)	30202 (+15118.9)	21678.3 (+12530.8)	0	2496320.3 (+748101.9)
$\bar{X}$ Size	61.0	783.1	180.8	2323.2	1970.8	0	157.1
4) 21 August 1976							
$\bar{X}$ Number	1711 (+104.4)	342 (+144.0)	3881 (+560)	4234 (+368.9)	38 (+22)	0	10206 (+254.1)
$\bar{X}$ Volume	413090 (+93001.1)	251868.7 (+69769.2)	298408.7 (+72786.9)	3442199 (+377050.5)	75095.5 (+43407.8)	0	4480661.9 (+235188.5)
$\bar{X}$ Size	241.4	736.5	76.9	813.0	1976.2	0	439.0
Mean of 3 Dates -							
$\bar{X}$ Number	2795 (+540)	212 (+61.7)	5574 (+1383.9)	1427 (+709.7)	15 (+9)	0	10023 (+1985.5)
$\bar{X}$ Volume	281916.1 (+49475.2)	158565.8 (+39766.8)	827367.8 (+364757.5)	1184958.7 (+574783.8)	29203.9 (+17452.6)	0	2482012.3 (+667081.9)
$\bar{X}$ Size	100.9	747.9	148.4	830.4	1946.9	0	247.6

Table B19. Composition (per cent) of phytoplanktonic algae by number and volume in imported lake waters, unstocked (control) aquaria and stocked (low and high stocks of leopard frog tadpoles) aquaria for Experiment Two at Lakes One and Four.

EXPERIMENT TWO	LAKE ONE				LAKE FOUR			
	Control	Low Density	High Density	Lake Readings	Control	Low Density	High Density	Lake Readings
1) Initial Readings 25-26 July 1976								
a) Greens Number	87.9	82.0	86.8	75.3	6.0	2.7	6.5	2.5
Volume	52.8	49.7	45.2	48.7	1.6	0.9	2.3	0.3
b) Diatoms Number	7.9	10.6	9.1	8.2	0.7	0.5	0.7	0.1
Volume	45.6	48.4	52.7	44.3	1.8	1.5	2.0	0.3
c) Blue-greens Number	2.8	6.5	3.1	15.2	92.2	96.4	91.9	96.3
Volume	0.6	1.4	1.4	5.9	88.8	94.1	87.4	92.8
d) Cryptophytes Number	1.4	0.8	1.0	1.3	1.1	1.1	1.0	1.1
Volume	1.0	0.6	0.7	1.2	6.6	7.8	8.3	6.6
2) 7-8 August 1976								
a) Greens Number	35.1	33.0	29.6	25.2	31.8	22.2	28.0	47.5
Volume	2.6	2.6	1.9	2.8	14.6	8.3	12.0	29.4
b) Diatoms Number	48.6	50.0	56.8	44.7	0.4	1.0	2.8	1.2
Volume	46.5	38.2	55.6	35.7	1.9	4.1	10.3	6.2
c) Blue-greens Number	4.7	3.9	4.5	8.7	67.7	76.8	68.9	50.4
Volume	0.1	0.1	0.8	0.2	82.0	87.6	74.9	47.1
d) Cryptophytes Number	11.6	13.1	9.0	21.4	0.1	0	0.3	0.9
Volume	50.8	59.1	41.7	61.3	1.5		2.8	17.3

Table B19 (cont'd.).

	Control	Low Density	High Density	Lake Readings	Control	Low Density	High Density	Lake Readings
e) Euglenoids Number Volume	0	0.04 0.01	0.02 0.01	0.05 0.01	0	0	0	0
3) 14-15 August 1976								
a) Greens Number Volume	5.7 5.4	8.0 3.8	7.6 2.7	14.5 3.7	48.4 18.9	29.8 14.0	43.6 21.3	30.1 11.7
b) Diatoms Number Volume	20.0 16.6	31.8 91.7	43.3 94.3	36.5 93.1	1.0 4.8	2.2 10.9	6.4 28.7	1.6 7.8
c) Blue-greens Number Volume	74.3 8.0	60.2 4.5	49.1 3.0	49.0 3.1	50.3 70.3	67.6 70.0	49.3 41.1	68.2 78.5
d) Cryptophytes Number Volume	0	0	0	0	0.2 3.5	0.2 3.0	0.4 5.1	0.1 1.2
e) Dinoflagellates Number Volume	0	0	0	0	0.2 1.9	0.2 2.1	0.4 3.8	0.1 0.9
4) 21-22 August 1976								
a) Greens Number Volume	30.0 35.5	39.2 49.1	43.2 43.5	42.7 55.3	15.5 20.7	23.1 35.5	21.8 17.5	16.8 9.2
b) Diatoms Number Volume	5.9 40.2	3.6 28.0	3.1 28.0	2.4 15.5	1.0 13.9	2.7 34.6	2.9 35.0	3.3 5.6
c) Blue-greens Number Volume	64.7 14.0	56.9 14.3	53.4 15.1	54.5 14.4	80.5 44.1	69.6 13.1	69.1 18.3	38.0 6.7
d) Cryptophytes Number Volume	0.1 2.6	0	0.01 0.01	0	3.0 21.3	4.5 14.7	6.0 26.5	41.5 76.8

Table B19 (cont'd.).

	Control	Low Density	High Density	Lake Readings	Control	Low Density	High Density	Lake Readings
e) Dinoflagellates								
Number	0.3	0.3	0.2	0.4	0.4	0.1	0.1	0.4
Volume	7.6	8.4	8.8	14.7	0	2.0	2.8	1.7
f) Euglenoids								
Number	0	0.1	0.03	0.02	0	0	0	0
Volume		0.2	0.1	0.1				
Mean of 3 Dates								
a) Greens								
Number	21.9	32.0	33.1	38.2	32.3	25.5	29.3	27.9
Volume	13.6	21.8	13.7	29.2	18.1	17.5	17.1	11.4
b) Diatoms								
Number	14.0	11.6	16.4	8.2	0.9	2.1	3.9	2.1
Volume	58.9	56.8	70.4	47.3	5.5	14.6	23.9	6.4
c) Blue-greens								
Number	62.9	55.6	49.9	52.8	65.4	70.5	65.5	55.6
Volume	7.1	7.7	6.0	8.3	69.4	62.2	47.8	33.4
d) Cryptophytes								
Number	1.0	0.5	0.4	0.4	1.3	1.9	3.2	14.2
Volume	18.1	10.3	7.5	7.9	5.8	4.9	10.0	47.7
e) Dinoflagellates								
Number	0.2	0.2	0.2	0.3	0.1	0.1	0.1	0.1
Volume	2.3	3.4	2.4	7.3	1.1	0.8	1.3	1.2
f) Euglenoids								
Number	0	0.05	0.02	0.02	0	0	0	0
Volume		0.1	0.03	0.03				

Table B20. Densities of dominant algal genera (cells/ml $\pm$ SD) in imported lake waters, unstocked (control) aquaria, and stocked (low and high stocks of leopard frog tadpoles) aquaria in Experiment Two at Lakes One and Four.

EXPERIMENT TWO	LAKE ONE				LAKE FOUR			
	Control	Low Density	High Density	Lake Readings	Control	Low Density	High Density	Lake Readings
I. CHLOROPHYCEAE								
A. Chlamydomonas								
1) 25-26 July 1976	2084 (± 127)	2077 (± 96)	2274 (± 154)	1387 (± 276)	545 (± 245)	451 (± 92)	727 (± 464)	217 (± 63)
2) 7-8 August 1976	278 (± 143)	180 (± 15)	99 (± 20)	375 (± 216)	1274 (± 525)	950 (± 458)	494 (± 83)	560 (± 67)
3) 14-15 August 1976	361 (± 190)	361 (± 67)	171 (± 119)	132 (± 132)	462 (± 60)	536 (± 333)	538 (± 216)	139 (± 128)
4) 21-22 August 1976	836 (± 266)	708 (± 132)	1330 (± 112)	3155 (± 1521)	481 (± 108)	986 (± 92)	697 (± 318)	405 (± 129)
B. Schroederia								
1) 25-26 July 1976	4110 (± 464)	4345 (± 940)	4378 (± 1078)	2019 (± 170)	30 (± 23)	0	13 (± 13)	13 (± 6)
2) 7-8 August 1976	86 (± 50)	172 (± 44)	144 (± 40)	190 (± 29)	9 (± 9)	0	0	0
3) 14-15 August 1976	142 (± 100)	608 (± 99)	589 (± 50)	964 (± 250)	15 (± 15)	0	8 (± 8)	0
4) 21-22 August 1976	228 (± 66)	266 (± 152)	494 (± 212)	874 (± 101)	0	0	0	0
C. Scenedesmus								
1) 25-26 July 1976	545 (± 276)	279 (± 116)	336 (± 167)	38 (± 22)	0	0	13 (± 13)	0
2) 7-8 August 1976	1814 (± 277)	3496 (± 542)	4173 (± 61)	3768 (± 397)	95 (± 50)	38 (± 19)	104 (± 53)	25 (± 13)
3) 14-15 August 1976	228 (± 228)	1806 (± 393)	2084 (± 181)	1198 (± 205)	284 (± 68)	182 (± 130)	28 (± 14)	263 (± 51)
4) 21-22 August 1976	1330 (± 553)	7906 (± 2076)	9312 (± 2550)	8765 (± 1570)	38 (± 18)	76 (± 44)	0	38 (± 22)

Table B20 (cont'd.).

	Control	Low Density	High Density	Lake Readings	Control	Low Density	High Density	Lake Readings
D. Small Coccoid								
Green Cell								
1) 25-26 July 1976	156 (+61)	142 (+86)	114 (+29)	95 (+44)	0	0	0	0
2) 7-8 August 1976	6225 (+1738)	7178 (+574)	9342 (+93)	659 (+659)	0	0	0	6 (+6)
3) 14-15 August 1976	475 (+475)	2300 (+2302)	4143 (+2143)	14558 (+1543)	175 (+99)	202 (+104)	134 (+77)	375 (+70)
4) 21-22 August 1976	28544 (+7302)	172799 (+36182)	182712 (+31856)	257899 (+19598)	594 (+53)	2736 (+84)	2364 (+110)	505 (+54)
E. Chlamydia								
1) 25-26 July 1976	19 (+19)	0	0	0	0	0	6 (+6)	22 (+8)
2) 7-8 August 1976	113 (+22)	110 (+37)	114 (+68)	82 (+56)	0	0	0	6 (+6)
3) 14-15 August 1976	1805 (+207)	2718 (+582)	3136 (+673)	3149 (+249)	0	15 (+15)	0	0
4) 21-22 August 1976	18822 (+6608)	85568 (+25620)	103509 (+21777)	138569 (+19035)	176 (+67)	445 (+85)	291 (+34)	268 (+64)
F. Actinostrodium								
1) 25-26 July 1976	0	0	6 (+6)	6 (+6)	0	0	0	0
2) 7-8 August 1976	312 (+95)	284 (+119)	243 (+114)	253 (+46)	9 (+9)	0	0	0
3) 14-15 August 1976	1501 (+349)	4371 (+1258)	5264 (+276)	2236 (+264)	0	38 (+38)	0	13 (+13)
4) 21-22 August 1976	1634 (+503)	5474 (+1446)	5322 (+840)	7336 (+1465)	0	0	0	0
G. Actinostrodium								
1) 25-26 July 1976	0	0	0	0	0	0	0	0

Table B70 (cont'd.).

	Control	Low Density	High Density	Lake Readings	Control	Low Density	High Density	Lake Readings
2) 7-8 August 1976	0	19 (+19)	0	0	0	0	0	0
3) 14-15 August 1976	76 (+76)	1273 (+1273)	779 (+779)	1622 (+1622)	0	0	0	0
4) 21-22 August 1976	3573 (+3573)	4067 (+4067)	5245 (+5245)	8704 (+8704)	0	38 (+38)	0	38 (+38)
H. <i>Ulothrix</i> 1) 25-26 July 1976	0	0	0	0	193 (+193)	82 (+82)	133 (+133)	82 (+82)
2) 7-8 August 1976	0	0	0	0	2014 (+2014)	1948 (+1948)	1725 (+1725)	1126 (+1126)
3) 14-15 August 1976	0	0	0	0	12760 (+12760)	6098 (+6098)	4707 (+4707)	4031 (+4031)
4) 21-22 August 1976	0	0	0	0	2337 (+2337)	773 (+773)	672 (+672)	165 (+165)
II. <i>BACILLARIOPHYCEAE</i> A. <i>Nitzschia</i> 1) 25-26 July 1976	366 (+366)	317 (+317)	455 (+455)	101 (+101)	92 (+92)	95 (+95)	95 (+95)	35 (+35)
2) 7-8 August 1976	5536 (+5536)	7954 (+7954)	10750 (+10750)	3705 (+3705)	19 (+19)	133 (+133)	252 (+252)	24 (+24)
3) 14-15 August 1976	13512 (+13512)	42665 (+42665)	75773 (+75773)	38588 (+38588)	248 (+248)	489 (+489)	659 (+659)	181 (+181)
4) 21-22 August 1976	3459 (+3459)	9123 (+9123)	7488 (+7488)	2091 (+2091)	127 (+127)	393 (+393)	532 (+532)	64 (+64)
B. <i>Navicula</i> 1) 25-26 July 1976	266 (+266)	586 (+586)	291 (+291)	266 (+266)	0	0	0	6 (+6)
2) 7-8 August 1976	7896 (+7896)	10031 (+10031)	17863 (+17863)	6504 (+6504)	19 (+19)	0	14 (+14)	4 (+4)

Table 6:0 (cont'd.).

	Control	Low Density	High Density	Lake Readings	Control	Low Density	High Density	Lake Readings
3) 14-15 August 1976	8495 (+1595)	24828 (+4623)	45741 (+12849)	24699 (+1212)	0	29 (+9)	0	22 (+14)
4) 21-22 August 1976	8020 (+3463)	16382 (+5956)	14634 (+2557)	20107 (+677)	13 (+13)	25 (+25)	13 (+13)	0
III. CYANOPHYTA								
A. Coccoid Blue-green Cell								
1) 25-26 July 1976	19 (+11)	22 (+8)	25 (+25)	108 (+62)	0 (+6)	0	6 (+6)	13 (+6)
2) 7-8 August 1976	14 (+7)	104 (+74)	1209 (+317)	25 (+25)	19 (+19)	0	109 (+56)	0
3) 14-15 August 1976	76 (+50)	475 (+201)	2375 (+537)	29 (+29)	6 (+6)	38 (+38)	0	19 (+11)
4) 21-22 August 1976	0	0	0	0	279 (+241)	279 (+165)	148 (+56)	241 (+108)
B. Small Anacyctis								
1) 25-26 July 1976	89 (+49)	22 (+18)	63 (+46)	95 (+11)	2011 (+1744)	5206 (+5213)	2977 (+2781)	0
2) 7-8 August 1976	165 (+69)	63 (+63)	152 (+77)	1362 (+653)	0	0	0	0
3) 14-15 August 1976	82025 (+8035)	124920 (+31062)	136439 (+53535)	86234 (+10748)	0	408 (+15)	0	0
4) 21-22 August 1976	110422 (+48883)	383569 (+83325)	365423 (+63711)	515720 (+39196)	4339 (+826)	1749 (+588)	2679 (+577)	1275 (+175)
C. Large Anacyctis								
1) 25-26 July 1976	0	0	0	0	9967 (+1778)	13161 (+642)	8062 (+2714)	13085 (+711)
2) 7-8 August 1976	0	0	0	0	4143 (+1433)	6148 (+1950)	3948 (+64)	510 (+129)
3) 14-15 August 1976	0	266 (+266)	0	0	8445 (+5935)	6894 (+3230)	2332 (+880)	4839 (+2107)
4) 21-22 August 1976	0	0	0	0	0	0	0	0

Table B20 (cont'd.).

	Control	Low Density	High Density	Lake Readings	Control	Low Density	High Density	Lake Readings
D. Small Anabaena								
1) 25-26 July 1976	127 (+23)	437 (+86)	63 (+46)	95 (+11)	152 (+76)	260 (+96)	443 (+328)	248 (+203)
2) 7-8 August 1976	1171 (+591)	1273 (+258)	973 (+112)	659 (+659)	4219 (+2789)	4019 (+2134)	1416 (+181)	1183 (+300)
3) 14-15 August 1976	1768 (+1220)	4143 (+1505)	1273 (+412)	775 (+394)	5790 (+136)	7030 (+1311)	3670 (+1254)	5507 (+896)
4) 21-22 August 1976	3155 (+1255)	9199 (+1022)	6462 (+764)	4789 (+656)	10410 (+425)	12032 (+193)	8968 (+758)	893 (+116)
E. Large Anabaena								
1) 25-26 July 1976	0	76 (+76)	101 (+52)	46 (+45)	108 (+73)	570 (+285)	880 (+797)	108 (+108)
2) 7-8 August 1976	0	0	0	0	19 (+19)	285 (+285)	808 (+583)	315 (+254)
3) 14-15 August 1976	0	0	0	0	0	234 (+234)	0	0
4) 21-22 August 1976	722 (+190)	874 (+166)	722 (+101)	526 (+265)	903 (+245)	127 (+25)	709 (+176)	408 (+79)
IV. CRYPTOPHYTA								
A. CRYPTOMONAS								
1) 25-26 July 1976	108 (+18)	70 (+13)	82 (+18)	63 (+35)	114 (+35)	89 (+7)	139 (+24)	152 (+20)
2) 7-8 August 1976	3303 (+447)	4797 (+895)	4622 (+165)	5019 (+208)	9 (+9)	0	19 (+10)	35 (+9)
3) 14-15 August 1976	0	0	0	0	70 (+24)	51 (+22)	48 (+10)	13 (+7)
4) 21-22 August 1976	152 (+80)	0	0	0	89 (+53)	101 (+35)	139 (+66)	1325 (+149)

Table 321. Phytoplanktonic diversities (in nats) in imported lake water, unstocked (control) aquaria, and stocked (low and high stocks of leopard frog tadpoles) aquaria for Experiment Two at Lake One.

EXPERIMENT TWO LAKE ONE	HIERARCHICAL DIVERSITY						Number of Genera (N _G)	Evenness (J')
	Greens	Diatoms	Blue-greens	Cryptophytes	Phyla	Total		
A. CONTROL								
1) Initial Readings								
26 July 1976								
a) Number								
Diversity								
X ₃	1.027	0.725	0.592			1.450		0.615
Pooled	1.309	0.852	0.992	0	0.540	0.981	15	0.362
b) Volume								
Diversity								
X ₃	1.208	0.572	0.557			1.672		0.710
Pooled	1.758	0.720	0.746	0	0.685	1.266	15	0.468
2) 8 August 1976								
a) Number								
Diversity								
X ₃	1.190	0.792	0.465			1.881		0.664
Pooled	1.248	0.360	0.465	0	0.814	1.164	22	0.377
b) Volume								
Diversity								
X ₃	1.632	0.751	0.530			1.047		0.420
Pooled	1.854	0.758	1.029	0	0.687	0.854	22	0.276
3) 15 August 1976								
a) Number								
Diversity								
X ₃	1.631	0.770	0.104			1.020		0.393
Pooled	2.050	0.970	0.074	0	0.592	0.708	19	0.241
b) Volume								
Diversity								
X ₃	1.328	0.541	0.086			1.034		0.400
Pooled	1.737	0.582	0.065	0	0.498	0.672	19	0.228
4) 22 August 1976								
a) Number								
Diversity								
X ₃	1.297	0.792	0.622			1.656		0.509
Pooled	1.216	1.003	0.593	0	0.433	0.577	25	0.179
b) Volume								
Diversity								
X ₃	1.048	0.348	0.508			1.662		0.627
Pooled	0.989	1.039	0.606	0	0.583	0.729	25	0.227
B. LOW DENSITY								
1) Initial Readings								
26 July 1976								
a) Number								
Diversity								
X ₃	0.324	0.673	0.473			1.479		0.605
Pooled	0.387	0.756	0.310	0	0.514	0.742	15	0.257
b) Volume								
Diversity								
X ₃	1.040	0.605	0.756			1.602		0.656
Pooled	1.142	0.799	0.602	0	0.625	0.943	15	0.348

Table B21 (cont'd.).

	Greens	Diatoms	Blue-greens	Cryptophytes	Phyla	Total	(N _G)	(J')
2) 8 August 1976								
a) Number Diversity								
$\bar{X}_3$	1.130	0.791	0.365	0.022		1.879		0.668
Pooled	1.396	0.776	0.397	0.051	0.814	1.151	22	0.372
b) Volume Diversity								
$\bar{X}_3$	1.545	0.757	0.651	0.001		1.078		0.385
Pooled	1.803	0.774	0.984	0.003	0.544	0.748	22	0.242
3) 15 August 1976								
a) Number Diversity								
$\bar{X}_3$	1.857	0.743	0.199	0		1.373		0.468
Pooled	2.086	0.759	0.090	0	0.629	0.855	23	0.273
b) Volume Diversity								
$\bar{X}_3$	1.745	0.514	0.339	0		0.900		0.308
Pooled	1.973	0.544	0.432	0	0.490	0.665	23	0.212
4) 22 August 1976								
a) Number Diversity								
$\bar{X}_3$	1.032	0.807	0.346	0		1.460		0.522
Pooled	1.047	0.803	0.285	0	0.723	0.983	28	0.295
b) Volume Diversity								
$\bar{X}_3$	0.754	0.739	0.314	0		1.800		0.574
Pooled	0.799	0.900	0.274	0	0.387	1.187	28	0.356
C. HIGH DENSITY								
1) Initial Readings								
26 July 1976								
a) Number Diversity								
$\bar{X}_3$	0.900	0.682	0.693	0		1.365		0.566
Pooled	1.093	0.797	1.287	0	0.505	0.791	15	0.282
b) Volume Diversity								
$\bar{X}_3$	0.932	0.512	0.447	0		1.493		0.620
Pooled	1.147	0.594	0.904	0	0.619	0.890	16	0.321
2) 8 August 1976								
a) Number Diversity								
$\bar{X}_3$	1.051	0.743	0.839	0.010		1.713		0.598
Pooled	1.117	0.773	0.870	0.032	0.635	0.355	22	0.277
b) Volume Diversity								
$\bar{X}_3$	1.311	0.741	0.198	0.0003		1.238		0.432
Pooled	1.333	0.724	0.163	0.002	0.651	0.312	22	0.263
3) 15 August 1976								
a) Number Diversity								
$\bar{X}_3$	1.312	0.726	0.159	0		1.417		0.487
Pooled	1.367	0.744	0.195	0	0.586	0.759	21	0.249

Table B21 (cont'd.).

	Greens	Diatoms	Blue-greens	Cryptophytes	Phyla	Total	(N _G)	(J')
b) Volume Diversity $\bar{X}_3$ Pooled	1.655 1.749	0.510 0.544	0.461 0.519	0	0.431	0.799 0.609	21	0.277 0.200
4) 22 August 1976								
a) Number Diversity $\bar{X}_3$ Pooled	1.084 1.209	0.791 1.056	0.322 0.354	0	0.528	1.492 0.697	30	0.476 0.205
b) Volume Diversity $\bar{X}_3$ Pooled	1.169 1.047	0.375 1.197	0.295 0.345	0	0.699	1.954 0.979	30	0.524 0.238
D. LAKE READINGS								
1) Initial Readings								
25 July 1975								
a) Number Diversity $\bar{X}_3$ Pooled	0.821 0.779	0.733 1.040	0.838 0.276	0	0.626	1.532 1.012	14	0.652 0.383
b) Volume Diversity $\bar{X}_3$ Pooled	0.651 0.638	0.830 1.220	0.833 1.202	0	0.700	1.552 1.018	14	0.657 0.326
2) 7 August 1976								
a) Number Diversity $\bar{X}_3$ Pooled	1.159 1.467	0.795 0.869	0.459 0.773	0.015 0.042	0.880	1.903 1.213	27	0.677 0.368
b) Volume Diversity $\bar{X}_3$ Pooled	1.185 1.423	0.803 0.907	0.185 0.794	0.001 0.002	0.631	1.092 0.738	27	0.389 0.224
3) 14 August 1976								
a) Number Diversity $\bar{X}_3$ Pooled	1.447 1.529	0.776 0.802	0.053 0.056	0	0.694	1.512 0.390	21	0.553 0.292
b) Volume Diversity $\bar{X}_3$ Pooled	1.607 1.673	0.542 0.550	0.036 0.084	0	0.468	0.863 0.583	21	0.314 0.224
4) 21 August 1976								
a) Number Diversity $\bar{X}_3$ Pooled	0.997 0.928	0.572 0.734	0.252 0.364	0	0.637	1.392 0.345	29	0.459 0.255
b) Volume Diversity $\bar{X}_3$ Pooled	0.681 0.681	0.355 1.058	0.101 0.193	0	0.696	1.700 0.363	28	0.550 0.259

Table B22. Phytoplanktonic diversities (in nats) in imported lake water, unstocked (control) aquaria, and stocked (low and high stocks of leopard frog tadpoles) aquaria for Experiment Two at Lake Four.

EXPERIMENT TWO LAKE FOUR	HIERARCHICAL DIVERSITY						Number of Genera (N _G)	Evenness (J')
	Greens	Diatoms	Blue-greens	Cryptophytes	Phyla	Total		
A. CONTROL								
1) Initial Readings								
26 July 1976								
a) Number								
Diversity								
X ₃	0.813	0	0.393	0.096		0.725	12	0.326
Pooled	0.903		0.814	0.385	0.476	0.745		0.300
b) Volume								
Diversity								
X ₃	0.576	0	0.070	0.006		0.516	12	0.322
Pooled	0.732		0.171	0.029	0.471	0.509		0.205
2) 3 August 1976								
a) Number								
Diversity								
X ₃	0.893	0.442	0.558	0		1.350	15	0.397
Pooled	1.254	0.693	0.709		0.581	0.898		0.332
b) Volume								
Diversity								
X ₃	0.948	0.334	0.093	0		0.823	15	0.632
Pooled	1.150	0.578	0.162		0.632	0.763		0.282
3) 15 August 1976								
a) Number								
Diversity								
X ₃	0.322	0.343	0.623	0		1.119	14	0.493
Pooled	0.384	0.948	0.703		0.447	0.537		0.204
b) Volume								
Diversity								
X ₃	0.333	0.277	0.085	0		1.149	14	0.570
Pooled	0.371	0.398	0.070		0.476	0.511		0.193
4) 22 August 1976								
a) Number								
Diversity								
X ₃	1.290	1.155	1.275	0.329		1.952	22	0.354
Pooled	1.566	1.346	1.235	0.257	0.538	0.933		0.302
b) Volume								
Diversity								
X ₃	1.162	0.966	1.567	0.520		2.431	22	0.649
Pooled	1.405	1.730	1.521	0.600	0.672	1.041		0.337
B. LOW DENSITY								
1) Initial Readings								
26 July 1976								
a) Number								
Diversity								
X ₃	0.353	0	0.429	0		0.610	9	0.194
Pooled	0.534		0.361		0.416	0.339		0.382
b) Volume								
Diversity								
X ₃	0.286	0	0.106	0		0.333	9	0.307
Pooled	0.425		0.250		0.453	0.533		0.242

Table 922 (cont'd.).

	Greens	Diatoms	Blue-greens	Cryptophytes	Phyla	Total	(N _G)	(J')
2) 8 August 1976								
a) Number Diversity								
$\bar{X}_3$	0.693	0	0.705	0		1.284	10	0.314
Pooled	0.845		0.922		0.471	0.650		0.282
b) Volume Diversity								
$\bar{X}_3$	0.676	0	0.110	0		0.647	10	0.633
Pooled	0.373		0.208		0.448	0.504		0.219
3) 15 August 1976								
a) Number Diversity								
$\bar{X}_3$	0.515	0.333	0.390	0.212		1.531	23	0.585
Pooled	1.339	0.521	0.987	0.637	0.588	0.329		0.296
b) Volume Diversity								
$\bar{X}_3$	0.976	0.215	0.458	0.026		1.367	23	0.507
Pooled	1.523	0.418	0.278	0.079	0.713	0.917		0.293
4) 22 August 1976								
a) Number Diversity								
$\bar{X}_3$	1.428	0.391	0.895	0.324		1.326	30	0.748
Pooled	1.712	1.759	1.048	0.117	0.668	1.072		0.315
b) Volume Diversity								
$\bar{X}_3$	1.267	0.563	1.577	0.511		2.251	30	0.607
Pooled	1.740	1.175	1.734	0.689	0.362	1.370		0.403
C. HIGH DENSITY								
1) Initial Readings								
26 July 1976								
a) Number Diversity								
$\bar{X}_3$	0.613	0	0.565	0		0.958	14	0.326
Pooled	1.389		0.662		0.429	0.596		0.226
b) Volume Diversity								
$\bar{X}_3$	0.599	0	0.232	0		0.718	14	0.435
Pooled	1.429		0.094		0.537	0.573		0.217
2) 3 August 1976								
a) Number Diversity								
$\bar{X}_3$	0.961	0.174	0.954	0		1.624	14	0.459
Pooled	1.305	0.333	1.102	0.593	0.554	0.968		0.329
b) Volume Diversity								
$\bar{X}_3$	0.964	0.108	0.232	0		1.058	14	0.705
Pooled	0.896	0.168	0.261	0.075	0.714	0.836		0.517
3) 15 August 1976								
a) Number Diversity								
$\bar{X}_3$	0.465	0.257	0.681	0		1.470	14	0.665
Pooled	0.693	0.672	0.666		0.767	1.047		0.397

Table 322 (cont'd.).

	Greens	Diatoms	Blue-greens	Cryptophytes	Phyla	Total	(N _G)	(J')
b) Volume Diversity								
$\bar{X}_3$	0.795	0.232	0.155	0		1.534	14	0.653
Pooled	1.037	0.562	0.334	0	0.857	1.068		0.405
4) 22 August 1976								
a) Number Diversity								
$\bar{X}_3$	1.388	0.552	1.140	0.315		1.992	24	0.784
Pooled	1.587	1.241	0.981	0.206	0.682	1.056		0.332
b) Volume Diversity								
$\bar{X}_3$	1.497	0.515	1.643	0.543		2.255	24	0.695
Pooled	1.742	1.241	1.621	0.653	0.979	1.332		0.419
D. LAKE READINGS								
1) Initial Readings								
25 July 1976								
a) Number Diversity								
$\bar{X}_3$	0.300	0.187	0.120	0		0.329	12	0.154
Pooled	1.047	0.575	0.287	0	0.456	0.576		0.232
b) Volume Diversity								
$\bar{X}_3$	0.710	0.114	0.145	0		0.331	12	0.151
Pooled	0.914	0.496	0.036	0	0.472	0.438		0.196
2) 7 August 1976								
a) Number Diversity								
$\bar{X}_3$	0.971	0.297	0.789	0		1.658	16	0.702
Pooled	1.183	1.289	0.381	0	0.555	1.019		0.368
b) Volume Diversity								
$\bar{X}_3$	0.939	0.221	0.395	0		1.441	16	0.705
Pooled	1.153	1.273	0.219	0	0.886	1.095		0.395
3) 14 August 1976								
a) Number Diversity								
$\bar{X}_3$	0.623	0.905	0.734	0		1.409	22	0.403
Pooled	0.624	1.421	0.792	0	0.555	0.826		0.267
b) Volume Diversity								
$\bar{X}_3$	0.486	0.704	0.269	0		1.063	22	0.532
Pooled	0.539	1.190	0.360	0	0.886	0.687		0.222
4) 21 August 1976								
a) Number Diversity								
$\bar{X}_3$	1.707	1.313	1.604	0.620		2.351	28	0.404
Pooled	1.958	1.777	1.523	0.603	0.770	1.156		0.347
b) Volume Diversity								
$\bar{X}_3$	1.158	1.075	1.133	0.235		1.232	28	0.769
Pooled	1.290	1.562	1.274	0.245	0.736	0.960		0.288

Table 323. Numbers and volumes of phytoplankton (per ml $\pm$ SD) in imported lake water and aquaria with monocultured bullfrogs, a mixed-species culture, or monocultured green frogs in Experiment Three at Lake One.

EXPERIMENT THREE LAKE ONE	Greens	Diatoms	Blue-greens	Cryptophytes	Totals
A. BULLFROGS					
1) Initial Readings 22 September 1976					
$\bar{X}$ Number	32606 (± 3964.7)	617 (± 34.3)	417341 (± 12313.1)	285 (± 87.1)	450850 (± 15422.7)
$\bar{X}$ Volume	2957362.3 (± 189512.7)	140246 (± 22424.9)	5875316 (± 2121011.3)	21118.3 (± 6451.9)	9004042.7 (± 2178492.5)
$\bar{X}$ Size	91.0	227.3	14.1	74.1	29.0
2) 5 October 1976					
$\bar{X}$ Number	153419 (± 18182.1)	1900 (± 462.3)	273235 (± 98979.2)	342 (± 57)	429896 (± 24413.9)
$\bar{X}$ Volume	10750000.3 (± 1655691.3)	546158.7 (± 127950.8)	4424416.7 (± 1586406.2)	25342.7 (± 4223.7)	15695319.4 (± 428191.9)
$\bar{X}$ Size	69.7	287.5	16.2	74.1	36.6
3) 12 October 1976					
$\bar{X}$ Number	159355 (± 6266.9)	7070 (± 853.7)	259644 (± 18543.1)	1615 (± 214.4)	427635 (± 15476.3)
$\bar{X}$ Volume	25663000 (± 845780.2)	2581742.7 (± 292698.4)	4328810.7 (± 252761.5)	138024 (± 9280)	32711577.4 (± 552384.9)
$\bar{X}$ Size	161.0	365.2	16.7	35.5	76.5
4) 24 October 1976					
$\bar{X}$ Number	103746 (± 1878.8)	2622 (± 457.4)	296841 (± 54824.9)	2052 (± 230.4)	395261 (± 52392.4)
$\bar{X}$ Volume	24432333 (± 994630.9)	698518.2 (± 129705.9)	2929048.7 (± 1031661.3)	152053.3 (± 17069.8)	28110953.2 (± 346657.6)
$\bar{X}$ Size	235.5	266.4	9.9	74.1	71.1
Mean of 3 Dates-					
$\bar{X}$ Number	138840 (± 24303.2)	3864 (± 865.6)	273240 (± 33330.9)	1336 (± 272.6)	417291 (± 18250.9)
$\bar{X}$ Volume	20265111.1 (± 2768817.3)	1275473.2 (± 342072.9)	3860425.4 (± 608723.8)	105140 (± 20880.1)	25506149.7 (± 2933937.7)
$\bar{X}$ Size	146.0	330.1	14.1	78.7	61.1
B. MIXED: BULLFROGS AND GREEN FROGS					
1) Initial Readings 22 September 1976					
$\bar{X}$ Number	32351 (± 1684.4)	684 (± 197.5)	433487 (± 7503.5)	342 (± 55.9)	466864 (± 9125.5)
$\bar{X}$ Volume	3314108 (± 246207.3)	174179 (± 55304)	3115125 (± 114867.9)	25342.3 (± 4877.2)	11623755.3 (± 270635.1)
$\bar{X}$ Size	102.4	254.6	18.7	74.1	24.9
2) 5 October 1976					
$\bar{X}$ Number	38561 (± 10259.2)	3040 (± 219.1)	194624 (± 50257.1)	364 (± 70.9)	586589 (± 60479.7)

Table 823 (cont'd.).

	Greens	Diatoms	Blue-greens	Cryptophytes	Totals
$\bar{X}$ Volume	10455418 (+1704324.9)	743654.3 (+23893.9)	8291817.7 (+1193209.5)	25997.3 (+5250.6)	19517887.3 (+2882996.2)
$\bar{X}$ Size	113.1	244.6	16.8	74.2	33.3
3) 12 October 1976					
$\bar{X}$ Number	174038 (+14391)	6975 (+785.5)	334297 (+27843.7)	1539 (+65.8)	516849 (+16833.6)
$\bar{X}$ Volume	25569666 (+990466.7)	2497942 (+284175.3)	5513913 (+573087.3)	114040 (+4876.9)	33695561 (+1047712.5)
$\bar{X}$ Size	146.9	358.1	16.5	74.1	65.2
4) 24 October 1976					
$\bar{X}$ Number	100816 (+3097.6)	2869 (+18.3)	315387 (+41653.8)	2623 (+352.5)	421695 (+41405.2)
$\bar{X}$ Volume	24355000 (+1530646.7)	230710.3 (+25504.3)	3393669 (+762385.9)	194339.7 (+26129.9)	23773719 (+946104.5)
$\bar{X}$ Size	241.6	289.5	10.8	74.1	68.2
Mean of 3 Dates-					
$\bar{X}$ Number	121138 (+14315.1)	4295 (+710.6)	381436 (+35084)	1509 (+343)	508378 (+32293.8)
$\bar{X}$ Volume	20125694.7 (+2520103.3)	1357435.8 (+297132.4)	5733133.2 (+336234.6)	111792.3 (+25418.2)	27329055.8 (+2275210.2)
$\bar{X}$ Size	166.1	316.0	15.0	74.1	53.3
C. GREEN FROGS					
1) Initial Readings 22 September 1976					
$\bar{X}$ Number	33537 (+2156)	494 (+133)	412557 (+5907.3)	323 (+76)	446912 (+7843.6)
$\bar{X}$ Volume	3082443 (+335453)	116113 (+21431.8)	7775900.3 (+85789.1)	23934.3 (+5631.7)	10998391 (+391077.3)
$\bar{X}$ Size	91.9	254.6	18.3	74.1	24.6
2) 5 October 1976					
$\bar{X}$ Number	102316 (+12073.2)	3753 (+33.7)	442892 (+66120.7)	494 (+190)	549455 (+68150.3)
$\bar{X}$ Volume	11746213 (+1657183.9)	987585.7 (+36990.5)	751765.7 (+1445961.1)	36605 (+13924.6)	20342169.4 (+2982996.2)
$\bar{X}$ Size	114.3	263.1	17.1	74.1	37.0
3) 12 October 1976					
$\bar{X}$ Number	173983 (+4535.6)	7298 (+717.4)	275384 (+11349.4)	1657 (+204.4)	458322 (+8556.5)
$\bar{X}$ Volume	25749000 (+792610.2)	2640554 (+93528.1)	4221996 (+191668.8)	122303.3 (+15142.3)	32744353.3 (+741694.7)
$\bar{X}$ Size	148.0	361.3	15.4	74.1	71.4

Table B23 (cont'd.).

	Greens	Diatoms	Blue-greens	Cryptophytes	Totals
4) 24 October 1976					
$\bar{X}$ Number	98562 (+5794.3)	2812 (+193.2)	223004 (+5227.1)	2223 (+228.3)	325601 (+2712.5)
$\bar{X}$ Volume	23114666 (+935769.3)	768789.7 (+86274.4)	1598511.7 (+16462.9)	164749.3 (+16745.8)	25646716.7 (+1294052.4)
$\bar{X}$ Size	234.5	273.4	7.2	74.1	78.5
Mean of 3 Dates-					
$\bar{X}$ Number	124954 (+12930.3)	4621 (+788.5)	313750 (+38427.3)	1458 (+275)	444793 (+33271.7)
$\bar{X}$ Volume	20203293 (+2221259.3)	1465643.1 (+297890.8)	4467424.5 (+961306.5)	108054.2 (+21777.9)	25244414.8 (+2052022.8)
$\bar{X}$ Size	161.7	317.2	14.2	74.1	36.3
D. LAKE READINGS					
1) Initial Readings 22 September 1976					
$\bar{X}$ Number	47710 (+1196.9)	2468 (+285.0)	423251 (+39966.3)	380 (+81.9)	473809 (+13472.6)
$\bar{X}$ Volume	3939445.7 (+32445.8)	495902 (+19137.2)	9573054.7 (+221894.1)	28158 (+6073.3)	14036560.4 (+121606.6)
$\bar{X}$ Size	82.6	200.9	22.6	74.1	29.6
2) 3 October 1976					
$\bar{X}$ Number	84077 (+15308.5)	2831 (+114.7)	313336 (+21376.9)	513 (+117.4)	400757 (+11926.6)
$\bar{X}$ Volume	8890906 (+1155834.1)	727341.3 (+67264.2)	4798083.3 (+466872.9)	38013.3 (+8702.1)	14454343 (+764018.9)
$\bar{X}$ Size	105.7	256.9	15.3	74.1	36.1
3) 10 October 1976					
$\bar{X}$ Number	149263 (+6380.6)	6347 (+104.6)	281748 (+30431.1)	1852 (+199.3)	439220 (+28556.6)
$\bar{X}$ Volume	20105000 (+661634.9)	2417436.3 (+87217.7)	4737256 (+554308.5)	137999 (+14765.7)	27397691.3 (+483753.7)
$\bar{X}$ Size	134.7	380.9	16.8	75.5	62.4
4) 22 October 1976					
$\bar{X}$ Number	98891 (+4946.6)	7244 (+512.1)	238468 (+19450.9)	2927 (+183.1)	347530 (+22212)
$\bar{X}$ Volume	20763333 (+295603.3)	2145517.3 (+254536.1)	2197810 (+101766.4)	198563.7 (+27356.2)	25305224.3 (+642000.1)
$\bar{X}$ Size	210.0	296.2	9.2	67.8	72.8
Mean of 3 Dates-					
$\bar{X}$ Number	110744 (+11390.4)	5474 (+777.5)	277351 (+12528.5)	1757 (+403.3)	395826 (+1395.2)
$\bar{X}$ Volume	16516968.7 (+2224209.5)	1763431.6 (+302507.5)	3911049.9 (+494673.5)	124858.7 (+27025.9)	22335732.9 (+2301721.5)
$\bar{X}$ Size	149.1	322.1	14.1	70.7	56.5

Table 924. Numbers and volumes of phytoplankton (per ml $\pm$ SD) in imported lake water and aquaria with monocultured bullfrogs, a mixed-species culture, or monocultured green frogs in Experiment Three at Lake Four.

EXPERIMENT THREE LAKE FOUR	Greens	Diatoms	Blue-greens	Cryptophytes	Totals
A. BULLFROGS					
1) Initial Readings 22 September 1976					
$\bar{X}$ Number	462 (± 126.2)	89 (± 51.8)	3052 (± 377)	133 (± 29)	3736 (± 471.2)
$\bar{X}$ Volume	26797 (± 7089.3)	21747 (± 12714.9)	64002.3 (± 8309.4)	9855.3 (± 2150.5)	122401.6 (± 17940.7)
$\bar{X}$ Size	58.0	244.3	21.0	74.1	32.9
2) 5 October 1976					
$\bar{X}$ Number	1330 (± 307.7)	12527 (± 1931.3)	11862 (± 3086.4)	152 (± 50.3)	25871 (± 5208.9)
$\bar{X}$ Volume	230506.7 (± 81046.3)	3116517 (± 454449.2)	359387.7 (± 14169.3)	11263.3 (± 3724.9)	3717774.7 (± 500404.6)
$\bar{X}$ Size	173.4	248.8	30.3	74.1	143.7
3) 12 October 1976					
$\bar{X}$ Number	722 (± 37.7)	10143 (± 701.3)	1380 (± 1214.5)	63 (± 6.3)	12308 (± 1436.5)
$\bar{X}$ Volume	108518 (± 23338.8)	2500411.7 (± 169134.1)	42140.7 (± 24892.4)	4693 (± 469.3)	2655763.7 (± 215006.7)
$\bar{X}$ Size	150.3	246.5	30.5	74.5	215.8
4) 24 October 1976					
$\bar{X}$ Number	139 (± 27.6)	3496 (± 142.6)	823 (± 130.9)	6 (± 6.3)	4465 (± 237.6)
$\bar{X}$ Volume	16001.7 (± 6336.9)	887072 (± 57957.9)	31452.3 (± 7041.7)	469.3 (± 469.3)	934995.3 (± 65021.6)
$\bar{X}$ Size	115.1	253.7	38.2	78.2	209.4
Mean of 3 Dates-					
$\bar{X}$ Number	630 (± 193.9)	9722 (± 1476.2)	4688 (± 2014.7)	74 (± 25.8)	14214 (± 3494.5)
$\bar{X}$ Volume	113375.5 (± 39518)	2168000.2 (± 361013.5)	144326.9 (± 54457.1)	5475.3 (± 1912.7)	2436177.9 (± 435219.2)
$\bar{X}$ Size	162.2	248.6	30.8	74.0	171.4
B. MIXED: BULLFROGS AND GREEN FROGS					
1) Initial Readings 22 September 1976					
$\bar{X}$ Number	918 (± 299.8)	70 (± 22.8)	2705 (± 297.7)	133 (± 47.3)	3326 (± 552.5)
$\bar{X}$ Volume	40817 (± 4087)	17086.7 (± 5600.6)	54810.7 (± 5005)	10794 (± 4009.7)	123508.4 (± 5679.7)
$\bar{X}$ Size	44.5	244.1	20.3	31.2	32.3
2) 5 October 1976					
$\bar{X}$ Number	968 (± 112)	11069 (± 574.1)	5865 (± 2457.5)	152 (± 68.5)	17954 (± 3116.9)

Table B24 (cont'd.).

	Greens	Diatoms	Blue-greens	Cryptophytes	Totals
$\bar{X}$ Volume	79777.7 (+5940.9)	3185959.7 (+333852.1)	210661.7 (+52743.4)	66172.3 (+56543.2)	3542571.4 (+357099.6)
$\bar{X}$ Size	91.9	287.8	35.9	435.3	197.3
3) 12 October 1976					
$\bar{X}$ Number	402 (+41.6)	9787 (+1605.3)	361 (+159)	38 (+21.9)	10588 (+1536.4)
$\bar{X}$ Volume	47509.7 (+15093.3)	2444106.3 (+416593.9)	24687.3 (+12715.5)	2816 (+1625.9)	2519119.3 (+422263.4)
$\bar{X}$ Size	118.2	249.7	68.4	74.1	237.9
4) 24 October 1976					
$\bar{X}$ Number	361 (+24.6)	3439 (+456.4)	374 (+437.1)	0	4674 (+958.9)
$\bar{X}$ Volume	25676.7 (+10465.9)	974948.3 (+122218)	25364 (+9846.8)	0	925991 (+130393.1)
$\bar{X}$ Size	71.1	254.4	29.0	0	198.1
Mean of 3 Dates-					
$\bar{X}$ Number	543 (+97.7)	8098 (+1234.8)	2367 (+1136.6)	63 (+30.9)	11071 (+2184.4)
$\bar{X}$ Volume	50989 (+9311.1)	2168338.1 (+375519.0)	86904 (+34794.1)	22996.1 (+20062.6)	2329227.2 (+414477.2)
$\bar{X}$ Size	93.9	267.3	36.7	365.0	210.4
C. GREEN FROGS					
1) Initial Readings 22 September 1976					
$\bar{X}$ Number	679 (+119.4)	114 (+32.9)	2951 (+233.6)	146 (+35.3)	3890 (+396.1)
$\bar{X}$ Volume	45054 (+6350.3)	27960.3 (+8071.6)	58148 (+5495.9)	9447.7 (+2915.7)	139610 (+21646.1)
$\bar{X}$ Size	56.4	245.3	19.7	57.9	35.9
2) 5 October 1976					
$\bar{X}$ Number	2464 (+1382.9)	7366 (+1289.5)	6293 (+2546.9)	133 (+47.9)	16246 (+3361)
$\bar{X}$ Volume	78209.7 (+42173.7)	1852566.3 (+297150.1)	150110.3 (+51772.6)	9855.3 (+3543.1)	2090741.6 (+401528.9)
$\bar{X}$ Size	31.7	251.5	23.9	74.1	129.7
3) 12 October 1976					
$\bar{X}$ Number	554 (+59)	3771 (+855.4)	5902 (+4908.2)	63 (+10.9)	16290 (+4902.3)
$\bar{X}$ Volume	44958.3 (+3305.9)	2200153.3 (+204200.3)	301316.7 (+780572.4)	4693 (+2045.5)	3051121.3 (+799171.9)
$\bar{X}$ Size	81.1	250.8	135.3	74.5	169.5

Table B24 (cont'd.).

	Greens	Diatoms	Blue-greens	Cryptophytes	Totals
4) 24 October 1976					
$\bar{X}$ Number	177 (± 60.4)	3293 (± 591.8)	937 (± 472.1)	0	4407 (± 1068.6)
$\bar{X}$ Volume	19927.3 (± 11032.2)	767491.7 (± 236796.3)	25472.3 (± 9371.1)	0	812891.3 (± 257043.6)
$\bar{X}$ Size	112.6	233.1	27.2	.0	184.5
Mean of 3 Dates-					
$\bar{X}$ Number	1065 (± 534)	6477 (± 950.3)	4374 (± 1818.8)	65 (± 25)	11981 (± 2577.3)
$\bar{X}$ Volume	47698.4 (± 15341)	1606737.1 (± 249085.4)	325633.1 (± 256057.7)	4349 (± 1849.3)	1984917.6 (± 419414.9)
$\bar{X}$ Size	44.8	248.1	74.5	74.6	165.7
0. LAKE READINGS					
1) Initial Readings 20 September 1976					
$\bar{X}$ Number	177 (± 38.1)	38 (± 21.7)	3827 (± 113.7)	51 (± 16.6)	4093 (± 292)
$\bar{X}$ Volume	13481.4 (± 1962.9)	35355 (± 20202.9)	96737.7 (± 1483.5)	3754.7 (± 1228.9)	139329 (± 12816.9)
$\bar{X}$ Size	76.2	930.4	22.7	73.6	34.0
2) 3 October 1976					
$\bar{X}$ Number	101 (± 43.9)	70 (± 39.8)	1564 (± 335.9)	25 (± 16.6)	1760 (± 314.3)
$\bar{X}$ Volume	24159.7 (± 11051.8)	62541.3 (± 1113.4)	24921.7 (± 58.1)	1377.3 (± 1228.9)	113500 (± 21130.8)
$\bar{X}$ Size	239.2	893.4	15.9	75.1	64.5
3) 10 October 1976					
$\bar{X}$ Number	95 (± 18.8)	120 (± 34.9)	546 (± 238.1)	70 (± 16.6)	931 (± 207.3)
$\bar{X}$ Volume	7319.3 (± 1350.5)	107618.7 (± 73401.3)	11292 (± 3769.5)	5162 (± 1229)	131382 (± 71048.4)
$\bar{X}$ Size	77.0	896.8	17.5	73.7	141.1
4) 22 October 1976					
$\bar{X}$ Number	146 (± 45.2)	101 (± 12.5)	564 (± 215.3)	25 (± 12.5)	833 (± 232.6)
$\bar{X}$ Volume	16264.3 (± 10391.4)	92742.7 (± 24562.2)	3103.2 (± 1799.6)	1877 (± 929)	118987.7 (± 22413)
$\bar{X}$ Size	111.4	918.2	14.4	75.1	142.5
Mean of 3 Dates-					
$\bar{X}$ Number	114 (± 15.9)	97 (± 14.4)	325 (± 209.9)	40 (± 10.7)	1176 (± 169.3)
$\bar{X}$ Volume	15914.4 (± 4814.7)	87634.3 (± 13125)	14769 (± 3562.9)	2972.4 (± 793.3)	101290.1 (± 3064.4)
$\bar{X}$ Size	139.6	903.4	16.0	74.3	103.1

Table B25. Composition (per cent) of phytoplanktonic algae by number and volume in imported lake waters and aquaria with monocultured bullfrogs, a mixed-species culture, or monocultured green frogs in Experiment Three at Lakes One and Four.

EXPERIMENT THREE	LAKE ONE				LAKE FOUR			
	Bullfrogs	Mixed: Bullfrogs & Green Frogs	Green Frogs	Lake Readings	Bullfrogs	Mixed: Bullfrogs & Green Frogs	Green Frogs	Lake Readings
1) Initial Readings 22-24 September 1976								
a) Greens								
Number	7.2	6.9	7.5	10.1	12.4	24.0	17.5	4.3
Volume	33.0	28.5	28.0	28.1	21.9	33.0	32.3	9.7
b) Diatoms								
Number	0.1	0.2	0.1	0.5	2.4	1.8	2.9	0.9
Volume	0.4	1.5	1.1	3.5	17.8	13.8	20.0	25.4
c) Blue-greens								
Number	92.6	92.9	92.3	83.3	81.7	70.7	75.9	93.5
Volume	65.3	69.8	70.7	68.2	52.3	44.4	41.6	62.2
d) Cryptophytes								
Number	0.1	0.1	0.1	0.1	3.6	3.5	3.7	1.3
Volume	0.2	0.2	0.2	0.2	8.0	8.7	6.0	2.7
2) 3-5 October 1976								
a) Greens								
Number	35.8	15.1	18.6	21.0	5.1	4.8	15.2	5.7
Volume	68.2	53.6	57.7	61.5	6.2	2.2	3.7	21.3
b) Diatoms								
Number	0.4	0.5	0.7	0.7	48.4	61.6	45.3	4.0
Volume	3.5	3.8	4.8	0.5	83.8	89.9	88.6	55.1
c) Blue-greens								
Number	63.7	84.3	80.6	78.2	48.8	32.7	38.6	88.9
Volume	28.2	42.5	37.2	33.2	9.7	6.0	7.2	22.0
d) Cryptophytes								
Number	0.1	0.1	0.1	0.1	0.6	0.9	0.8	1.4
Volume	0.2	0.1	0.2	0.3	0.3	1.9	0.5	1.6
3) 10-12 October 1976								
a) Greens								
Number	37.3	33.7	38.0	34.0	5.9	3.8	3.6	10.2
Volume	78.4	75.9	78.6	73.4	4.1	1.9	1.5	5.6

Table B25 (cont'd.).

	Bullfrogs	Mixed:	Green Frogs	Lake Readings	Bullfrogs	Mixed:	Green Frogs	Lake Readings
b) Diatoms Number Volume	1.7 7.9	1.3 7.4	1.6 8.1	1.4 8.8	82.4 94.1	92.4 97.0	57.4 72.1	12.9 81.9
c) Blue-greens Number Volume	60.7 13.2	64.7 11.2	60.1 12.9	64.1 17.3	11.2 1.6	3.4 1.0	38.6 26.3	69.4 8.6
d) Cryptophytes Number Volume	0.4 0.4	0.3 0.3	0.3 0.04	0.4 0.5	0.5 0.2	0.4 0.1	0.4 0.1	7.5 3.9
4) 22-24 October 1976								
a) Greens Number Volume	26.2 86.9	23.9 84.6	30.2 90.1	28.5 82.0	3.1 1.7	7.7 2.8	4.0 2.4	9.7 13.1
b) Diatoms Number Volume	0.7 2.5	0.7 2.9	0.9 3.0	2.1 8.5	78.3 94.9	74.7 94.5	74.7 94.4	8.2 72.2
c) Blue-greens Number Volume	72.6 10.1	74.8 11.8	68.3 6.2	68.6 8.9	18.4 3.4	18.7 2.7	21.3 3.1	78.7 12.2
d) Cryptophytes Number Volume	0.5 0.5	0.6 0.7	0.7 0.6	0.8 0.8	0.1 0.05	0	0	3.4 2.5
Mean of 3 Dates								
a) Greens Number Volume	33.3 79.4	23.8 73.6	28.1 77.0	28.0 73.8	5.1 4.9	4.9 2.2	8.9 2.4	9.7 13.1
b) Diatoms Number Volume	0.9 5.0	0.8 5.0	1.0 5.6	1.4 7.9	61.4 89.0	73.1 93.1	54.1 80.9	8.2 72.2
c) Blue-greens Number Volume	65.5 15.1	75.0 21.0	70.5 17.0	70.2 17.5	33.0 5.9	21.4 3.7	36.5 16.4	78.7 12.2
d) Cryptophytes Number Volume	0.3 0.4	0.4 0.4	0.4 0.4	0.4 0.8	0.5 0.2	0.6 1.0	0.5 0.3	3.4 2.5

Table IV. Descriptions of dominant algal species (cell/cul. $\pm$ SD) in imported lake waters, and aquaria with monocultures of bullfrog and green frog tadpoles, and a mixed species culture in Experiment Three at Lakes One and Four.

EXPERIMENT THREE	LAKE ONE					LAKE FOUR				
	Bullfrogs	Mixed: Bullfrogs & Green Frogs	Green Frogs	Lake Readings	Bullfrogs	Mixed: Bullfrogs & Green Frogs	Green Frogs	Lake Readings	Bullfrogs	Lake Readings
1. CHLOROPHYCEAE										
A. <i>Chlamydomonas</i>										
1) 20-22 September 1976	646 (± 250)	817 (± 393)	722 (± 153)	988 (± 83)	171 (± 50)	320 (± 32)	337 (± 43)	108 (± 13)		
2) 3-5 October 1976	171 (± 66)	456 (± 119)	209 (± 68)	380 (± 169)	266 (± 143)	190 (± 95)	304 (± 76)	51 (± 16)		
3) 10-12 October 1976	570 (± 171)	399 (± 65)	333 (± 90)	295 (± 65)	386 (± 83)	278 (± 58)	275 (± 10)	44 (± 6)		
4) 22-24 October 1976	665 (± 338)	608 (± 214)	589 (± 133)	703 (± 133)	32 (± 13)	57 (± 22)	51 (± 32)	38 (± 22)		
B. <i>Schroederia</i>										
1) 20-22 October 1976	0	19 (± 19)	409 (± 301)	304 (± 276)	6 (± 6)	19 (± 11)	32 (± 12)	13 (± 6)		
2) 3-5 October 1976	0	76 (± 76)	0	0	13 (± 6)	44 (± 35)	32 (± 23)	0		
3) 10-12 October 1976	0	0	0	0	73 (± 11)	63 (± 6)	47 (± 16)	19 (± 10)		
4) 22-24 October 1976	38 (± 19)	38 (± 38)	57 (± 59)	38 (± 38)	13 (± 6)	13 (± 12)	0	0		
C. <i>Dictyosphaerium</i>										
1) 20-22 September 1976	4860 (± 1809)	2344 (± 61)	5834 (± 1075)	1674 (± 220)	227 (± 127)	541 (± 211)	310 (± 24)	51 (± 27)		
2) 3-5 October 1976	10382 (± 8378)	23899 (± 6422)	29363 (± 10056)	36471 (± 14774)	190 (± 162)	44 (± 27)	127 (± 83)	0		
3) 10-12 October 1976	2262 (± 5947)	14500 (± 5312)	27787 (± 5241)	35463 (± 2275)	0	0	0	0		
4) 22-24 October 1976	3373 (± 543)	29571 (± 5825)	35536 (± 1071)	31244 (± 5944)	38 (± 38)	184 (± 131)	32 (± 31)	70 (± 16)		

Table B26 (cont'd.).

	Bullfrogs	Mixed: Bullfrogs & Green Frogs	Green Frogs	Lake Readings	Bullfrogs	Mixed: Bullfrogs & Green Frogs	Green Frogs	Lake Readings
D. Scenedesmus								
1) 20-22 September 1976	23205 (+1852)	25313 (+1660)	23129 (+1809)	39416 (+1567)	0	25 (+25)	0	6 (+6)
2) 3-5 October 1976	35463 (+1532)	47987 (+2392)	55907 (+9707)	34019 (+1682)	538 (+175)	279 (+89)	298 (+194)	25 (+25)
3) 10-12 October 1976	85959 (+1813)	93295 (+1434)	96982 (+3711)	77046 (+1138)	136 (+59)	41 (+8)	146 (+6)	25 (+25)
4) 22-24 October 1976	26474 (+247)	28389 (+1907)	27234 (+2590)	25551 (+457)	38 (+22)	76 (+22)	82 (+41)	25 (+12)
E. Ankiistrodesmus								
1) 20-22 September 1976	1349 (+468)	1558 (+68)	1463 (+384)	2546 (+124)	0	0	0	0
2) 3-5 October 1976	3877 (+287)	5321 (+704)	5550 (+956)	3953 (+249)	6 (+6)	13 (+6)	19 (+19)	0
3) 10-10 October 1976	9616 (+977)	10130 (+330)	9632 (+381)	7735 (+333)	44 (+23)	28 (+24)	13 (+12)	6 (+6)
4) 22-24 October 1976	1976 (+152)	3022 (+198)	2166 (+420)	2547 (+287)	6 (+6)	0	0	6 (+6)
F. Actinastrum								
1) 20-22 September 1976	855 (+257)	456 (+0)	323 (+95)	634 (+112)	0	6 (+6)	0	0
2) 3-5 October 1976	703 (+342)	361 (+162)	779 (+338)	665 (+105)	51 (+50)	0	13 (+12)	0
3) 10-12 October 1976	3516 (+336)	4029 (+813)	2439 (+414)	2831 (+631)	0	0	0	0
4) 22-24 October 1976	5283 (+719)	5017 (+356)	3592 (+571)	371 (+214)	0	0	0	0
G. Selenastrum								
1) 20-22 September 1976	988 (+242)	1064 (+628)	798 (+200)	507 (+293)	0	6 (+6)	0	0

Table 826 (cont'd.).

	Bullfrogs	Mixed: Bullfrogs & Green Frogs	Green Frogs	Lake Readings	Bullfrogs	Mixed: Bullfrogs & Green Frogs	Green Frogs	Lake Readings	Bullfrogs	Mixed: Bullfrogs & Green Frogs	Green Frogs	Lake Readings
2) 3-5 October 1976	912 (+131)	760 (+298)	1064 (+330)	798 (+143)	6 (+6)	6 (+6)	6 (+6)	0	0	6 (+6)	6 (+6)	0
3) 10-12 October 1976	1368 (+65)	1368 (+237)	1349 (+283)	266 (+19)	6 (+6)	0	6 (+6)	0	0	6 (+6)	6 (+6)	0
4) 22-24 October 1976	19 (+19)	152 (+50)	43 (+42)	114 (+87)	0	0	0	0	0	0	0	0
H. Kirschmiller												
1) 20-22 September 1976	114 (+87)	76 (+76)	57 (+57)	323 (+95)	0	0	0	0	0	0	0	0
2) 3-5 October 1976	4884 (+468)	5777 (+731)	4542 (+1259)	4048 (+820)	0	0	0	0	0	0	0	0
3) 10-12 October 1976	21628 (+2180)	20400 (+4254)	23468 (+1219)	15413 (+857)	0	0	0	0	0	3 (+2)	3 (+2)	0
4) 22-24 October 1976	19556 (+906)	17361 (+2306)	17902 (+734)	21380 (+2976)	0	0	0	0	0	0	0	0
I. Large Coccoid Green Cell												
1) 20-22 September 1976	589 (+95)	703 (+100)	722 (+181)	309 (+87)	0	0	0	0	0	0	0	0
2) 3-5 October 1976	366 (+437)	3034 (+571)	4846 (+1455)	3706 (+560)	114 (+54)	19 (+0)	13 (+12)	13 (+6)	13 (+12)	13 (+12)	13 (+6)	13 (+6)
3) 10-12 October 1976	1379 (+480)	13284 (+465)	11913 (+640)	9673 (+560)	19 (+19)	13 (+12)	0	0	0	0	0	0
4) 22-24 October 1976	15679 (+661)	15261 (+189)	14196 (+727)	12752 (+591)	6 (+6)	19 (+19)	6 (+6)	6 (+6)	6 (+16)	6 (+16)	6 (+6)	6 (+6)
II. BACILLARIOPHYCEAE												
A. Nitzschia												
1) 20-22 September 1976	266 (+16)	418 (+137)	228 (+87)	1064 (+100)	89 (+52)	70 (+23)	114 (+32)	19 (+11)	19 (+11)	114 (+32)	114 (+32)	19 (+11)
2) 3-5 October 1976	950 (+402)	1501 (+124)	1710 (+164)	1539 (+119)	12407 (+1889)	10969 (+552)	7182 (+1204)	32 (+23)	32 (+23)	7182 (+1204)	7182 (+1204)	32 (+23)

Table B26 (cont'd.).

	Bullfrogs	Mixed: Bullfrogs & Green Frogs	Green Frogs	Lake Readings	Bullfrogs	Mixed: Bullfrogs & Green Frogs	Green Frogs	Lake Readings
B. Small Anacystis								
1) 20-22 September 1976	177790 (+11934)	192190 (+6783)	170860 (+5374)	296539 (+14879)	553 (+12)	777 (+210)	735 (+187)	101 (+55)
2) 3-5 October 1976	211944 (+95298)	379149 (+18010)	314229 (+16650)	279260 (+16918)	7505 (+3703)	4066 (+2528)	5535 (+2149)	1463 (+252)
3) 10-12 October 1976	190240 (+22221)	231196 (+24691)	182075 (+11718)	209397 (+25264)	396 (+256)	98 (+67)	450 (+376)	456 (+218)
4) 22-24 October 1976	14234 (+987)	19955 (+257)	16895 (+3505)	19451 (+3108)	171 (+182)	127 (+62)	374 (+317)	25 (+21)
C. Small Anabaena								
1) 20-22 September 1976	11473 (+538)	12980 (+1569)	13638 (+854)	12089 (+1507)	0	0	0	0
2) 3-5 October 1976	13740 (+2336)	10605 (+3566)	9940 (+4516)	17009 (+6301)	475 (+439)	228 (+150)	253 (+253)	0
3) 10-12 October 1976	13518 (+5013)	20734 (+7355)	20802 (+6074)	8818 (+890)	203 (+38)	66 (+66)	184 (+139)	0
4) 22-24 October 1976	206394 (+11694)	203467 (+24097)	198982 (+652)	180642 (+20930)	95 (+76)	190 (+87)	120 (+49)	247 (+30)
D. Coccolid Blue-green Cell								
1) 20-22 September 1976	544 (+402)	266 (+238)	498 (+93)	285 (+87)	0	0	0	19 (+19)
2) 3-5 October 1976	114 (+65)	266 (+187)	133 (+76)	38 (+38)	1165 (+368)	855 (+208)	393 (+182)	0
3) 10-12 October 1976	33 (+19)	57 (+57)	0	0	133 (+76)	139 (+78)	85 (+45)	0
4) 22-24 October 1976	622 (+306)	209 (+100)	266 (+105)	380 (+50)	120 (+38)	76 (+47)	70 (+16)	0

Table B26 (cont'd.).

	Bullfrogs	Mixed: Bullfrogs & Green Frogs	Green Frogs	Lake Readings	Bullfrogs	Mixed: Bullfrogs & Green Frogs	Green Frogs	Lake Readings
IV. CRYPTOPHYTA								
A. Rhodomonas								
1) 20-22 September 1976	285 (+75)	342 (+57)	323 (+59)	380 (+76)	133 (+28)	146 (+54)	146 (+35)	51 (+16)
2) 3-5 October 1976	342 (+44)	364 (+71)	494 (+190)	513 (+119)	152 (+43)	152 (+59)	133 (+41)	25 (+14)
3) 10-12 October 1976	1615 (+214)	1539 (+65)	1657 (+204)	1862 (+201)	63 (+5)	38 (+19)	63 (+24)	70 (+16)
4) 22-24 October 1976	2052 (+230)	2623 (+356)	2223 (+228)	2680 (+380)	6 (+6)	0	0	25 (+15)

Table B27. Phytoplanktonic diversities (in nats) in imported lake water and aquaria with monocultured bullfrogs, a mixed-species culture, or monocultured green frogs in Experiment Three at Lake One.

EXPERIMENT THREE LAKE ONE	HIERARCHICAL DIVERSITY				Number of Genera (N _G)	Evenness (J')
	Greens	Diatoms	Blue-greens	Total		
A. BULLFROGS						
1) Initial Readings						
22 September 1976						
a) Number	0.992	0.944	0.791	1.080	16	0.402
b) Volume	1.314	0.756	0.689	1.516		0.565
2) 5 October 1976						
a) Number	1.053	1.025	0.717	1.170	19	0.416
b) Volume	1.179	0.941	0.569	1.586		0.601
3) 12 October 1976						
a) Number	1.399	0.977	0.703	1.724	22	0.590
b) Volume	0.990	0.374	0.733	1.523		0.557
4) 24 October 1976						
a) Number	1.412	0.474	0.625	1.541	22	0.537
b) Volume	0.728	0.615	0.969	1.200		0.478
Mean of 3 Dates-						
a) Number	1.288	0.925	0.682	1.478	21	0.514
b) Volume	0.969	0.810	0.790	1.505		0.525
B. MIXED: BULLFROGS AND GREEN FROGS						
1) Initial Readings						
22 September 1976						
a) Number	0.984	0.684	0.304	1.077	13	0.402
b) Volume	1.217	0.711	0.707	1.533		0.573
2) 5 October 1976						
a) Number	1.264	1.016	0.551	1.240	19	0.365
b) Volume	1.151	1.097	0.563	1.731		0.616
3) 12 October 1976						
a) Number	1.307	0.935	0.747	1.666	20	0.584
b) Volume	1.013	0.784	0.703	1.555		0.580
4) 24 October 1976						
a) Number	1.613	0.778	0.798	1.523	22	0.558
b) Volume	0.777	0.920	0.946	1.318		0.454
Mean of 3 Dates-						
a) Number	1.395	0.910	0.699	1.509	20	0.502
b) Volume	0.980	0.934	0.737	1.568		0.550
C. GREEN FROGS						
1) Initial Readings						
22 September 1976						
a) Number	1.046	0.987	0.305	1.103	13	0.404
b) Volume	1.284	0.955	0.668	1.515		0.556
2) 5 October 1976						
a) Number	1.195	1.145	0.637	1.274	21	0.441
b) Volume	1.164	1.180	0.648	1.319		0.630

Table 827 (cont'd.).

	Greens	Diatoms	Blue-greens	Total	(Mg)	(J')
3) 12 October 1976						
a) Number	1.349	1.039	0.784	1.777	23	0.592
b) Volume	1.075	0.981	0.793	1.704		0.567
4) 24 October 1976						
a) Number	1.563	0.849	0.515	1.524	19	0.538
b) Volume	0.836	0.876	1.006	1.246		0.440
Mean of 3 Dates-						
a) Number	1.369	1.011	0.645	1.525	21	0.524
b) Volume	1.025	1.012	0.816	1.590		0.546
D. LAKE READINGS						
1) Initial Readings						
20 September 1976						
a) Number	0.770	0.978	0.517	1.025	19	0.362
b) Volume	1.113	1.065	0.732	1.598		0.564
2) 3 October 1976						
a) Number	1.208	1.075	0.381	1.115	21	0.391
b) Volume	1.242	1.243	0.318	1.760		0.671
3) 10 October 1976						
a) Number	1.355	1.177	0.555	1.532	23	0.545
b) Volume	1.072	1.226	0.684	1.781		0.595
4) 22 October 1976						
a) Number	1.595	0.708	0.723	1.702	25	0.575
b) Volume	0.334	0.946	1.109	0.992		0.499
Mean of 3 Dates-						
a) Number	1.386	0.987	0.586	1.483	23	0.504
b) Volume	1.049	1.138	0.704	1.511		0.570

Table 828. Phytoplanktonic diversities (in hats) in imported lake water and aquaria with mono-cultured bullfrogs, a mixed-species culture, or monocultured green frogs in Experiment Three at Lake Four.

EXPERIMENT THREE LAKE FOUR	HIERARCHICAL DIVERSITY				Number of Genera (N _G)	Evenness (J')
	Greens	Diatoms	Blue-greens	Total		
A. BULLFROGS						
1) Initial Readings 22 September 1976						
a) Number	0.711	0	0.460	1.091	8	0.581
b) Volume	0.688		0.399	1.446		0.767
2) 5 October 1976						
a) Number	1.406	0.056	0.341	1.360	21	0.506
b) Volume	1.165	0.130	0.371	0.311		0.303
3) 12 October 1976						
a) Number	1.235	0.007	0.764	0.723	16	0.297
b) Volume	0.399	0.035	0.755	0.335		0.137
4) 24 October 1976						
a) Number	1.127	0.023	1.036	0.775	15	0.384
b) Volume	0.829	0.053	0.926	0.324		0.144
Mean of 3 Dates-						
a) Number	1.256	0.029	0.380	0.953	17	0.396
b) Volume	0.364	0.072	0.357	0.490		0.195
B. MIXED: BULLFROGS AND GREEN FROGS						
1) Initial Readings 22 September 1976						
a) Number	0.851	0	0.582	1.373	10	0.676
b) Volume	0.319		0.510	1.695		0.834
2) 5 October 1976						
a) Number	1.381	0.058	0.924	1.169	20	0.428
b) Volume	1.406	0.127	0.768	0.549		0.201
3) 12 October 1976						
a) Number	1.232	0.027	0.792	0.449	16	0.188
b) Volume	0.720	0.912	0.496	0.266		0.113
4) 24 October 1976						
a) Number	1.013	0.053	0.984	0.342	14	0.412
b) Volume	0.946	0.176	0.320	0.458		0.199
Mean of 3 Dates-						
a) Number	1.209	0.045	0.367	0.353	17	0.343
b) Volume	1.044	0.132	0.695	0.421		0.171
C. GREEN FROGS						
1) Initial Readings 22 September 1976						
a) Number	0.333	0	0.559	1.298	7	0.653
b) Volume	0.564		0.392	1.572		0.803
2) 5 October 1976						
a) Number	1.422	0.121	0.363	1.194	20	0.458
b) Volume	1.145	0.229	0.697	0.699		0.267

Table B28 (cont'd.).

	Greens	Diatoms	Blue-greens	Total	(N _G)	(J')
3) 12 October 1976						
a) Number	1.242	0.042	0.582	0.736	17	0.319
b) Volume	0.995	0.134	0.593	0.519		0.212
4) 24 October 1976						
a) Number	0.846	0.097	1.074	0.949	11	0.432
b) Volume	0.708	0.359	1.002	0.624		0.284
Mean of 3 Dates-						
a) Number	1.170	0.087	0.673	0.977	16	0.403
b) Volume	0.949	0.241	0.764	0.514		0.254
D. LAKE READINGS						
1) Initial Readings						
20 September 1976						
a) Number	0.762	0.462	0.136	0.460	10	0.237
b) Volume	0.441	0.260	0.189	1.055		0.534
2) 3 October 1976						
a) Number	0.659	0.656	0.135	0.664	11	0.357
b) Volume	0.534	0.457	0.161	1.430		0.736
3) 10 October 1976						
a) Number	0.737	0.333	0.168	0.259	9	0.631
b) Volume	0.506	0.273	0.194	1.167		0.630
4) 22 October 1976						
a) Number	0.952	0.631	0.695	1.668	12	0.790
b) Volume	0.904	0.390	0.638	1.109		0.519
Mean of 3 Dates-						
a) Number	0.723	0.540	0.333	0.864	11	0.609
b) Volume	0.581	0.373	0.351	1.235		0.645

Table B29. Gross primary productivity as mg O₂/42.8 liters/24 h ($\pm$ SD) during Experiments One and Two at Lakes One and Four.

SAMPLING DATES	UNSTOCKED CONTROL		LOW BIOMASS		HIGH BIOMASS	
<u>Lake One--Experiment One</u>						
5-28-1976	167.5	(+10.6)	172.1	(+12.3)	158.9	(+19.2)
6-6-1976	341.8	(+34.7)	261.7	(+15.5)	246.1	(+38.1)
6-12-1976	804.9	(+56.1)	697.3	(+74.4)	729.6	(+54.2)
6-19-1976	337.9	(+74.3)	232.0	(+16.8)	261.4	(+14.4)
$\bar{X}_3$ Dates	494.7	(+94.2)	397.0	(+78.9)	412.4	(+81.7)
<u>Lake Four--Experiment One</u>						
5-28-1976	159.8	(+35.3)	132.8	(+5.9)	162.8	(+31.5)
6-6-1976	20.6	(+4.4)	23.9	(+2.5)	19.1	(+8.1)
6-12-1976	191.4	(+2.5)	211.4	(+10.0)	240.1	(+13.9)
6-19-1976	38.3	(+12.0)	51.4	(+11.5)	36.0	(+13.3)
$\bar{X}_3$ Dates	83.5	(+27.3)	95.6	(+29.5)	98.4	(+71.1)
<u>Lake One--Experiment Two</u>						
7-26-1976	154.7	(+12.7)	234.3	(+62.4)	173.8	(+63.1)
8-8-1976	990.7	(+57.1)	913.7	(+88.8)	854.5	(+110.9)
8-15-1976	532.4	(+34.5)	585.7	(+51.7)	547.8	(+51.7)
8-22-1976	163.4	(+38.6)	536.2	(+62.1)	416.7	(+75.6)
$\bar{X}_3$ Dates	562.2	(+121.7)	678.50	(+68.6)	606.3	(+77.0)
<u>Lake Four--Experiment Two</u>						
7-26-1976	102.8	(+17.7)	80.0	(+7.1)	87.6	(+9.0)
8-8-1976	68.8	(+9.1)	57.6	(+2.8)	52.7	(+2.9)
8-15-1976	150.3	(+19.8)	114.6	(+13.2)	108.4	(+14.6)
8-22-1976	87.8	(+8.2)	80.9	(+9.7)	76.0	(+3.5)
$\bar{X}_3$ Dates	102.3	(+14.0)	84.4	(+9.5)	79.1	(+9.2)

Table B30. Community respiration as mg O₂/42.8 liters/24 h ($\pm$ SD) during Experiments One and Two at Lakes One and Four.

SAMPLING DATES	UNSTOCKED CONTROL		LOW BIOMASS		HIGH BIOMASS	
<u>Lake One--Experiment One</u>						
5-28-1976	263.5	(+11.7)	264.6	(+22.5)	235.5	(+35.0)
6-6-1976	332.7	(+40.9)	304.4	(+26.8)	277.4	(+12.9)
6-12-1976	821.7	(+67.3)	727.2	(+72.8)	741.0	(+46.7)
6-19-1976	413.2	(+89.3)	360.0	(+6.6)	379.9	(+15.0)
$\bar{X}_3$ Dates	552.5	(+96.0)	464.0	(+70.0)	466.1	(+71.8)
<u>Lake Four--Experiment One</u>						
5-28-1976	177.8	(+40.5)	134.2	(+8.8)	177.3	(+39.6)
6-6-1976	32.6	(+2.7)	57.0	(+14.7)	106.8	(+14.0)
6-12-1976	171.8	(+7.1)	203.8	(+13.0)	237.8	(+17.5)
6-19-1976	98.5	(+21.7)	132.6	(+20.5)	122.0	(+10.8)
$\bar{X}_3$ Dates	101.0	(+21.1)	131.1	(+22.7)	155.5	(+21.9)
<u>Lake One--Experiment Two</u>						
7-26-1976	131.4	(+50.5)	181.0	(+65.7)	135.8	(+64.4)
8-8-1976	658.7	(+12.5)	595.6	(+93.7)	588.8	(+60.1)
8-15-1976	615.4	(+26.1)	611.8	(+33.5)	568.0	(+21.5)
8-22-1976	837.1	(+51.8)	1001.7	(+20.2)	921.1	(+50.4)
$\bar{X}_3$ Dates	703.8	(+67.9)	736.4	(+72.5)	692.6	(+61.8)
<u>Lake Four--Experiment Two</u>						
7-26-1976	119.0	(+9.7)	101.6	(+9.8)	112.7	(+11.9)
8-8-1976	47.0	(+7.3)	42.3	(+5.3)	42.6	(+5.8)
8-15-1976	97.0	(+16.3)	77.1	(+7.0)	76.4	(+11.0)
8-22-1976	115.4	(+6.6)	102.2	(+12.8)	97.1	(+3.4)
$\bar{X}_3$ Dates	86.5	(+11.6)	73.9	(+9.7)	72.0	(+8.7)

Table B31. Community respiration (R) in unstocked aquaria and corrected respiration ("R" without tadpole respiration) in stocked aquaria as mg O₂/42.8 liters/24 h during Experiments One and Two at Lakes One and Four.

SAMPLING DATES	UNSTOCKED CONTROL		LOW BIOMASS		HIGH BIOMASS	
<u>Lake One--Experiment One</u>						
5-28-1976	263.5	(+11.7)	264.6	(+22.5)	235.5	(+35.0)
6-6-1976	332.7	(+40.9)	251.7	(+18.7)	189.2	(+5.4)
6-12-1976	821.7	(+67.3)	672.0	(+63.4)	661.1	(+37.9)
6-19-1976	413.2	(+189.3)	301.5	(+4.8)	311.0	(+10.2)
$\bar{X}_3$ Dates	522.5	(+151.5)	408.4	(+132.6)	387.1	(+143.5)
<u>Lake Four--Experiment One</u>						
5-28-1976	177.8	(+40.5)	134.2	(+8.8)	177.3	(+39.6)
6-6-1976	32.6	(+2.7)	14.4	(+4.0)	18.0	(+2.5)
6-12-1976	171.8	(+7.1)	167.5	(+9.4)	161.4	(+9.0)
6-19-1976	98.5	(+21.7)	112.1	(+15.0)	79.2	(+4.7)
$\bar{X}_3$ Dates	101.0	(+21.1)	98.0	(+49.7)	86.2	(+51.4)
<u>Lake One--Experiment Two</u>						
7-26-1976	131.4	(+50.5)	181.0	(+65.7)	135.8	(+64.4)
8-8-1976	658.7	(+12.5)	558.6	(+90.2)	526.5	(+57.8)
8-15-1976	615.4	(+26.1)	557.3	(+30.0)	489.9	(+17.9)
8-22-1976	837.1	(+51.8)	927.3	(+18.0)	825.0	(+43.9)
$\bar{X}_3$ Dates	703.8	(+67.9)	681.1	(+111.8)	613.8	(+98.3)
<u>Lake Four--Experiment One</u>						
7-26-1976	119.0	(+9.7)	101.6	(+9.8)	112.7	(+11.9)
8-8-1976	47.0	(+7.3)	38.3	(+4.4)	30.0	(+3.0)
8-15-1976	97.0	(+16.3)	73.0	(+6.4)	73.5	(+8.8)
8-22-1976	115.4	(+6.6)	98.1	(+11.9)	82.0	(+3.0)
$\bar{X}_3$ Dates	86.5	(+11.6)	69.8	(+17.3)	61.8	(+18.7)

Table B32. Ratios of GPP/R and GPP/"R" (in parentheses) for Experiments One and Two at Lakes One and Four.

SAMPLING DATES	LAKE ONE			LAKE FOUR		
	UNSTOCKED	LOW STOCK	HIGH STOCK	UNSTOCKED	LOW STOCK	HIGH STOCK
<u>EXPERIMENT ONE</u>						
28 May	0.64	0.65	0.67	0.90	0.99	0.92
6 June	1.03	0.86 (1.04)	0.89 (1.30)	0.63	0.42 (1.66)	0.19 (1.06)
12 June	0.98	0.96 (1.04)	0.98 (1.10)	1.06	1.06 (1.26)	1.01 (1.49)
14 June	0.82	0.64 (0.77)	0.69 (0.84)	0.39	0.39 (0.46)	0.30 (0.45)
Mean of 3 dates	0.95	0.86 (0.97)	0.88 (1.07)	0.83	0.73 (0.98)	0.63 (1.14)
<u>EXPERIMENT TWO</u>						
26 July	1.18	1.29	1.28	0.86	0.79	0.78
8 August	1.50	1.53 (1.64)	1.45 (1.62)	1.46	1.36 (1.50)	1.24 (1.76)
15 August	0.86	0.96 (1.05)	0.96 (1.12)	1.55	1.49 (1.57)	1.42 (1.47)
22 August	0.19	0.53 (0.58)	0.45 (0.51)	0.76	0.79 (0.82)	0.78 (0.93)
Mean of 3 dates	0.80	0.92 (1.00)	0.88 (0.99)	1.18	1.14 (1.21)	1.10 (1.28)

Table B33. Gross primary productivity as $\text{mg O}_2/42.8 \text{ liters}/48 \text{ h}$ ($\pm \text{SD}$) during Experiment Three at Lakes One and Four.

EXPERIMENT THREE						
Sampling Dates	Bullfrogs		Mixed: Bullfrogs & Green Frogs		Green Frogs	
LAKE ONE						
9-24-1976	1504.6	(<u>+25.4</u>)	1350.3	(<u>+90.8</u>)	1323.0	(<u>+26.5</u>)
10-5-1976	1661.7	(<u>+249.6</u>)	1650.9	(<u>+116.0</u>)	1882.4	(<u>+335.5</u>)
10-12-1976	887.8	(<u>+61.6</u>)	850.7	(<u>+46.3</u>)	843.0	(<u>+68.9</u>)
10-24-1976	359.3	(<u>+25.6</u>)	357.5	(<u>+35.1</u>)	344.2	(<u>+16.8</u>)
$\bar{X}_3$ Dates	1103.6	(<u>+298.9</u>)	1052.4	(<u>+284.3</u>)	1098.2	(<u>+329.0</u>)
LAKE FOUR						
9-24-1976	152.8	(<u>+26.5</u>)	178.0	(<u>+25.8</u>)	153.1	(<u>+53.2</u>)
10-5-1976	314.1	(<u>+21.1</u>)	288.0	(<u>+8.7</u>)	253.9	(<u>+4.5</u>)
10-12-1976	208.0	(<u>+34.7</u>)	184.0	(<u>+11.3</u>)	153.3	(<u>+10.1</u>)
10-24-1976	148.3	(<u>+13.0</u>)	160.3	(<u>+2.5</u>)	146.6	(<u>+5.2</u>)
$\bar{X}_3$ Dates	205.8	(<u>+38.5</u>)	202.6	(<u>+28.9</u>)	176.7	(<u>+25.7</u>)

Table B34. Community respiration as $\text{mg O}_2/42.8 \text{ liters}/48 \text{ h}$ ($\pm$ SD) during Experiment Three at Lakes One and Four.

EXPERIMENT THREE						
Sampling Dates	Bullfrogs		Mixed: Bullfrogs & Green Frogs		Green Frogs	
LAKE ONE						
9-24-1976	1079.6	(<u>+18.1</u>)	957.0	(<u>+112.8</u>)	927.7	(<u>+159.6</u>)
10-5-1976	1455.4	(<u>+174.7</u>)	1399.0	(<u>+97.7</u>)	1573.3	(<u>+212.8</u>)
10-12-1976	753.0	(<u>+29.3</u>)	696.8	(<u>+22.9</u>)	679.4	(<u>+43.3</u>)
10-24-1976	284.6	(<u>+29.6</u>)	295.3	(<u>+25.1</u>)	276.8	(<u>+13.7</u>)
$\bar{X}_3$ Dates	893.1	(<u>+248.4</u>)	837.0	(<u>+231.5</u>)	864.3	(<u>+271.7</u>)
LAKE FOUR						
9-24-1976	85.4	(<u>+14.9</u>)	106.4	(<u>+30.7</u>)	96.2	(<u>+37.5</u>)
10-5-1976	326.2	(<u>+17.6</u>)	301.9	(<u>+6.7</u>)	280.2	(<u>+9.9</u>)
10-12-1976	226.9	(<u>+24.8</u>)	206.9	(<u>+10.6</u>)	182.9	(<u>+12.8</u>)
10-24-1976	134.1	(<u>+6.5</u>)	152.5	(<u>+5.7</u>)	137.8	(<u>+4.9</u>)
$\bar{X}_3$ Dates	193.2	(<u>+53.1</u>)	191.9	(<u>+42.0</u>)	174.3	(<u>+39.5</u>)

Table B35. Ratios of GPP/R in aquaria with monocultured bullfrogs, a mixed-species culture, and monocultured green frogs during Experiment Three at Lakes One and Four.

SAMPLING DATES	EXPERIMENT THREE		
	BULLFROGS	MIXED: BULLFROGS AND GREEN FROGS	GREEN FROGS
<u>LAKE ONE</u>			
19 September	1.39	1.41	1.43
2 October	1.14	1.18	1.20
10 October	1.18	1.22	1.24
19 October	1.26	1.21	1.24
Mean of 3 dates	1.24	1.26	1.27
<u>LAKE FOUR</u>			
19 September	1.79	1.67	1.59
2 October	0.96	0.95	0.91
10 October	0.92	0.89	0.84
19 October	1.11	1.05	1.06
Mean of 3 dates	1.07	1.06	1.01

Table B36. Average gross primary productivity, community respiration (mg O₂/42.8 liters/d), and GPP/R for all aquaria, regardless of treatment, in the three experiments at Lakes One and Four ("R" without tadpole respiration).

	EXPERIMENT ONE	EXPERIMENT TWO	EXPERIMENT THREE	VARIATION FOR 3 EXPERIMENTS
<u>$\bar{X}$ Gross Primary Productivity</u>				
Lake One	434.7	615.7	542.1	$\pm 18\% \bar{X}$ GPP
Lake Four	92.5	88.6	97.5	$\pm 5\% \bar{X}$ GPP
<u>$\bar{X}$ Community Respiration ($\bar{X}$ Corrected Respiration)</u>				
Lake One	494.2 (439.2)	710.9 (666.2)	432.4	$\pm 30\% \bar{X}$ R $\pm 21\% \bar{X}$ "R"
Lake Four	129.2 (95.1)	77.5 (72.7)	93.2	$\pm 29\% \bar{X}$ R $\pm 23\% \bar{X}$ "R"
<u>$\bar{X}$ Ratio of GPP/R ($\bar{X}$ GPP/"R")</u>				
Lake One	0.88 (0.99)	0.87 (0.92)	1.25	
Lake Four	0.72 (0.97)	1.14 (1.22)	1.05	

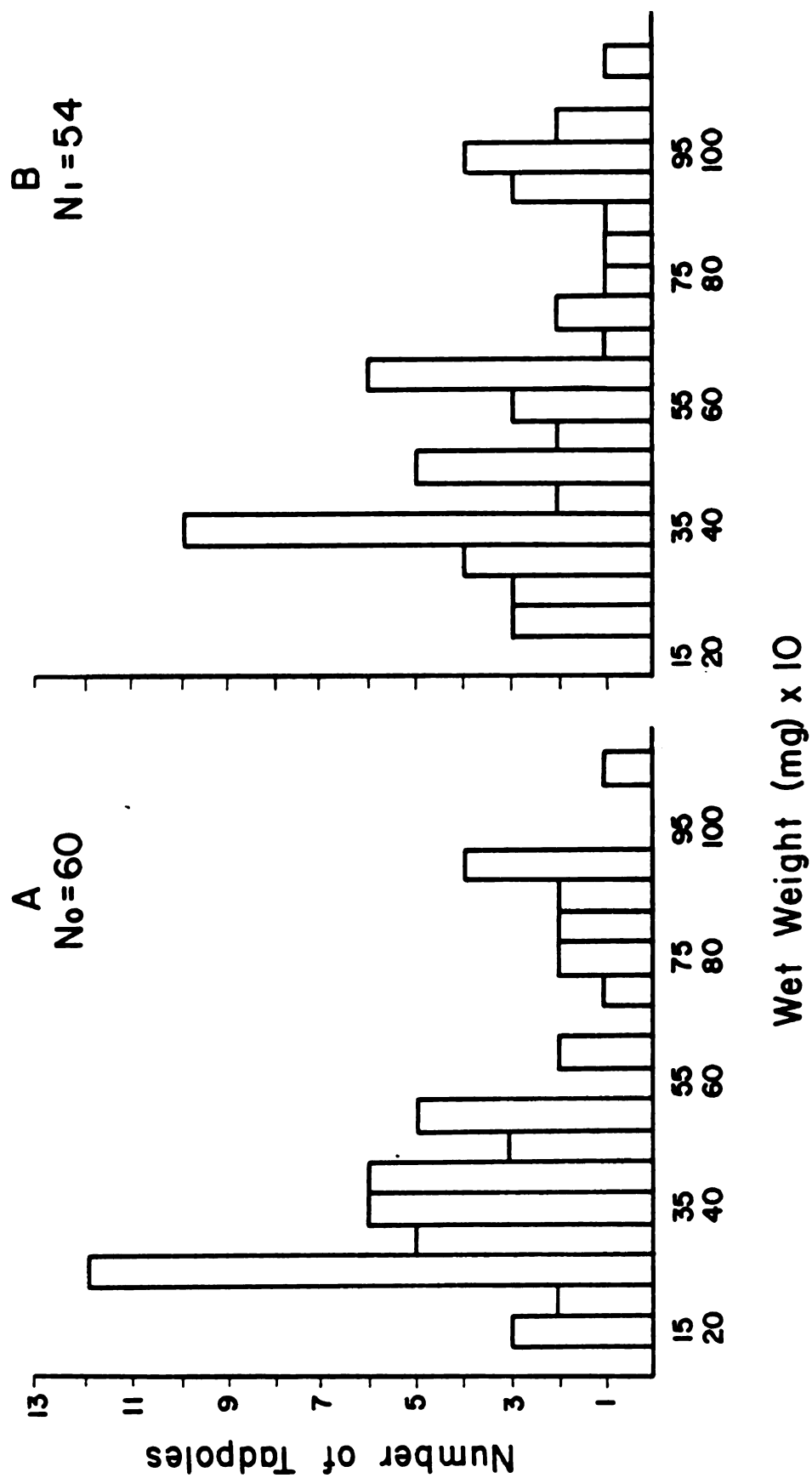


Figure B1. Weight distributions (A = initial, B = final) for tadpoles (R. pipiens) at low density in Experiment One at Lake One.

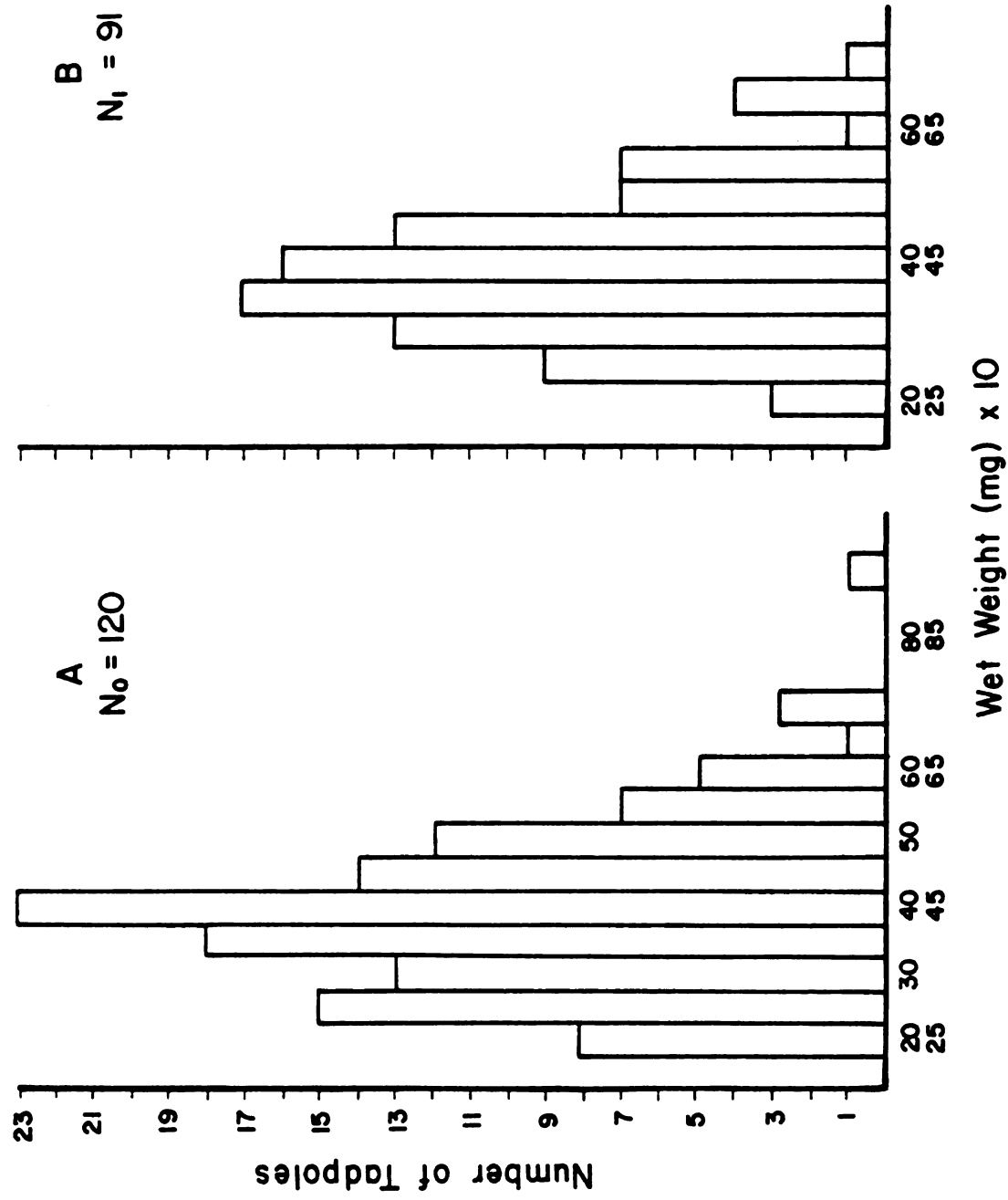


Figure B2. Weight distributions (A = initial, B = final) for tadpoles (*R. pipiens*) at high density in Experiment One at Lake One.

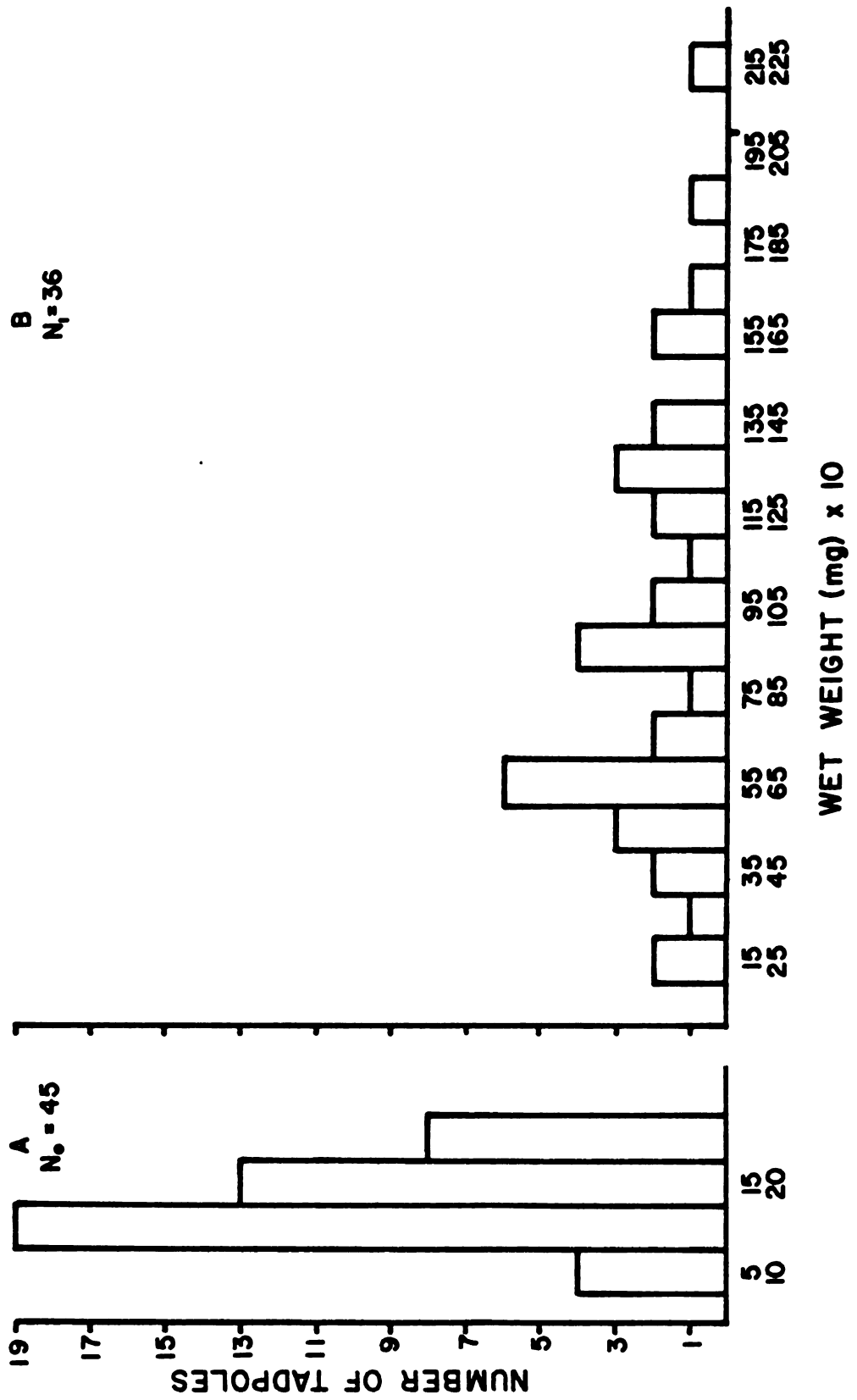


Figure B3. Weight distributions (A = initial, B = final) for tadpoles (*R. pipiens*) at low density in Experiment Two at Lake One.

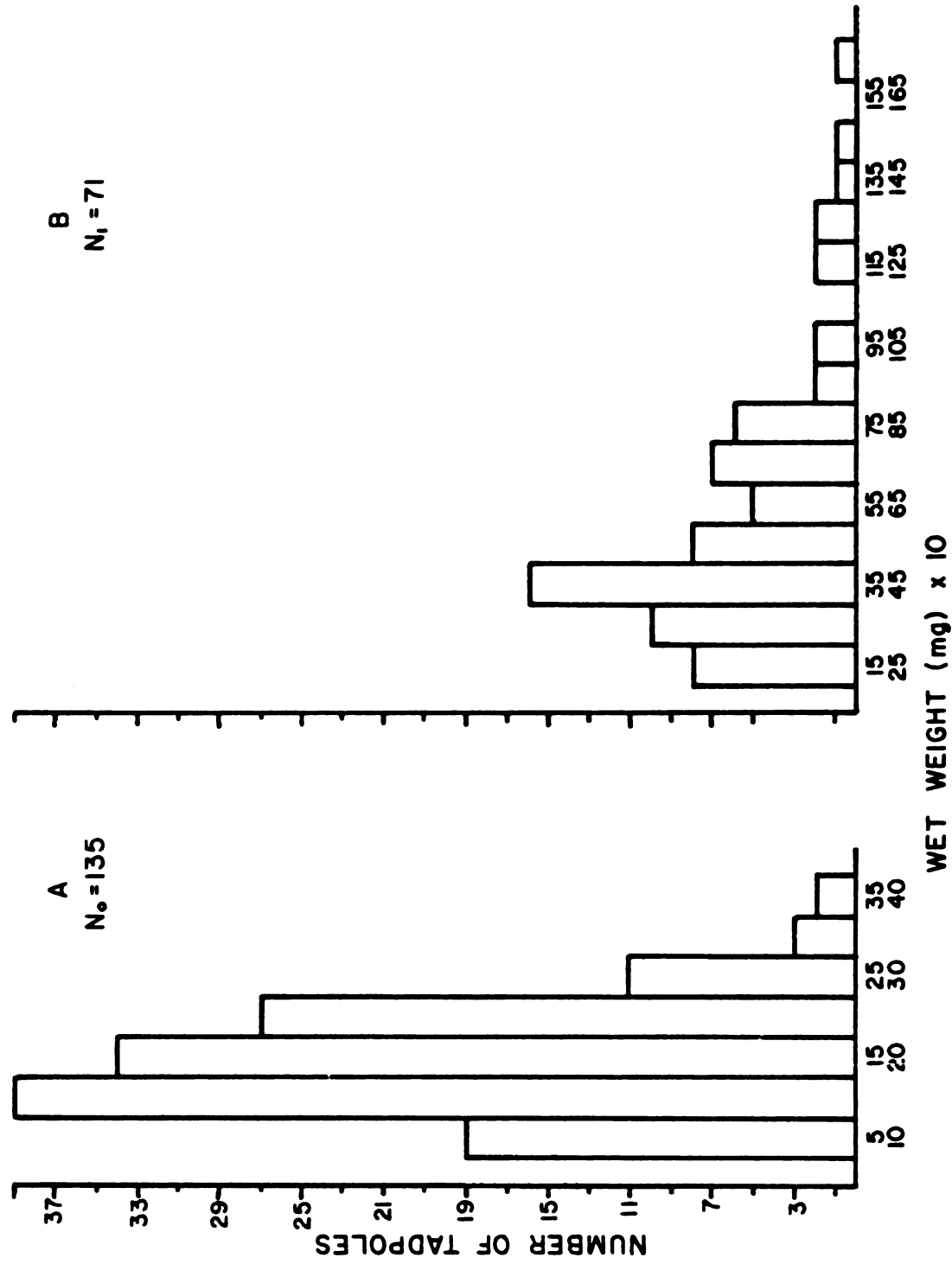


Figure B4. Weights (A = initial, B = final) for R. pipiens at high density in Experiment Two, Lake One.

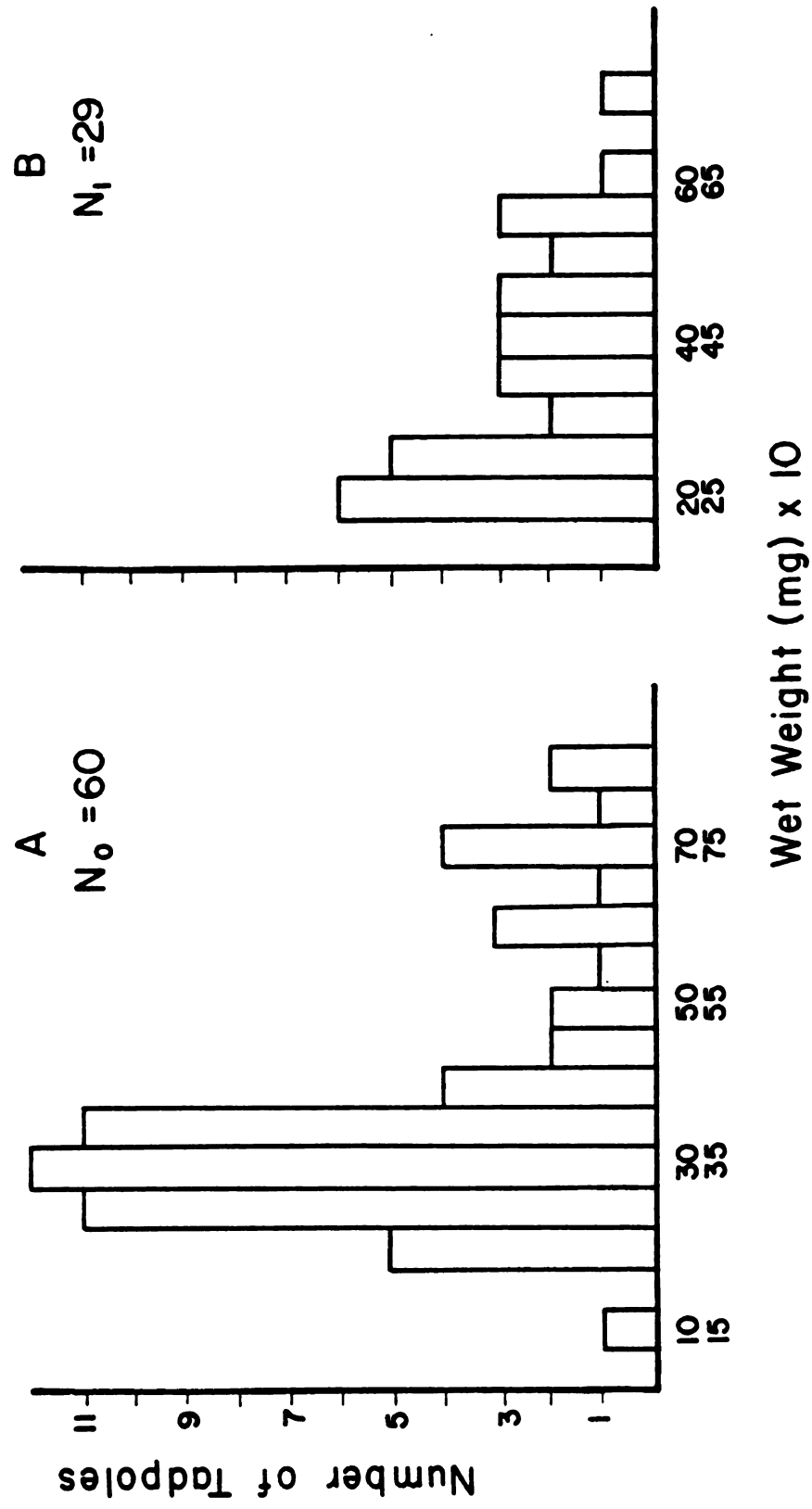


Figure B5. Weight distributions (A = initial, B = final) for tadpoles (*R. pipiens*) at low density in Experiment One at Lake Four.

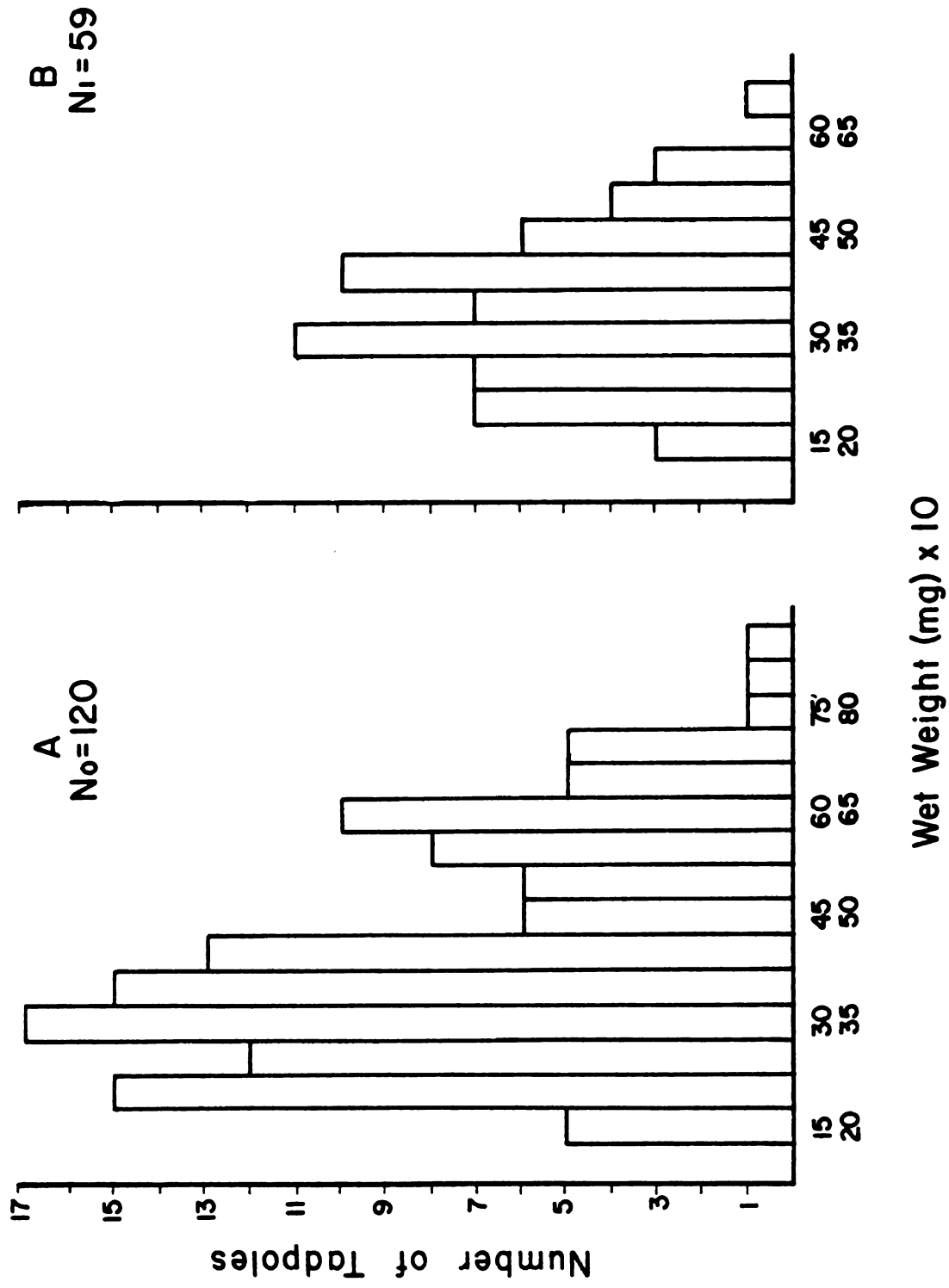


Figure B6. Weight distributions (A = initial, B = final) for tadpoles (*R. pipiens*) at high density in Experiment One at Lake Four.

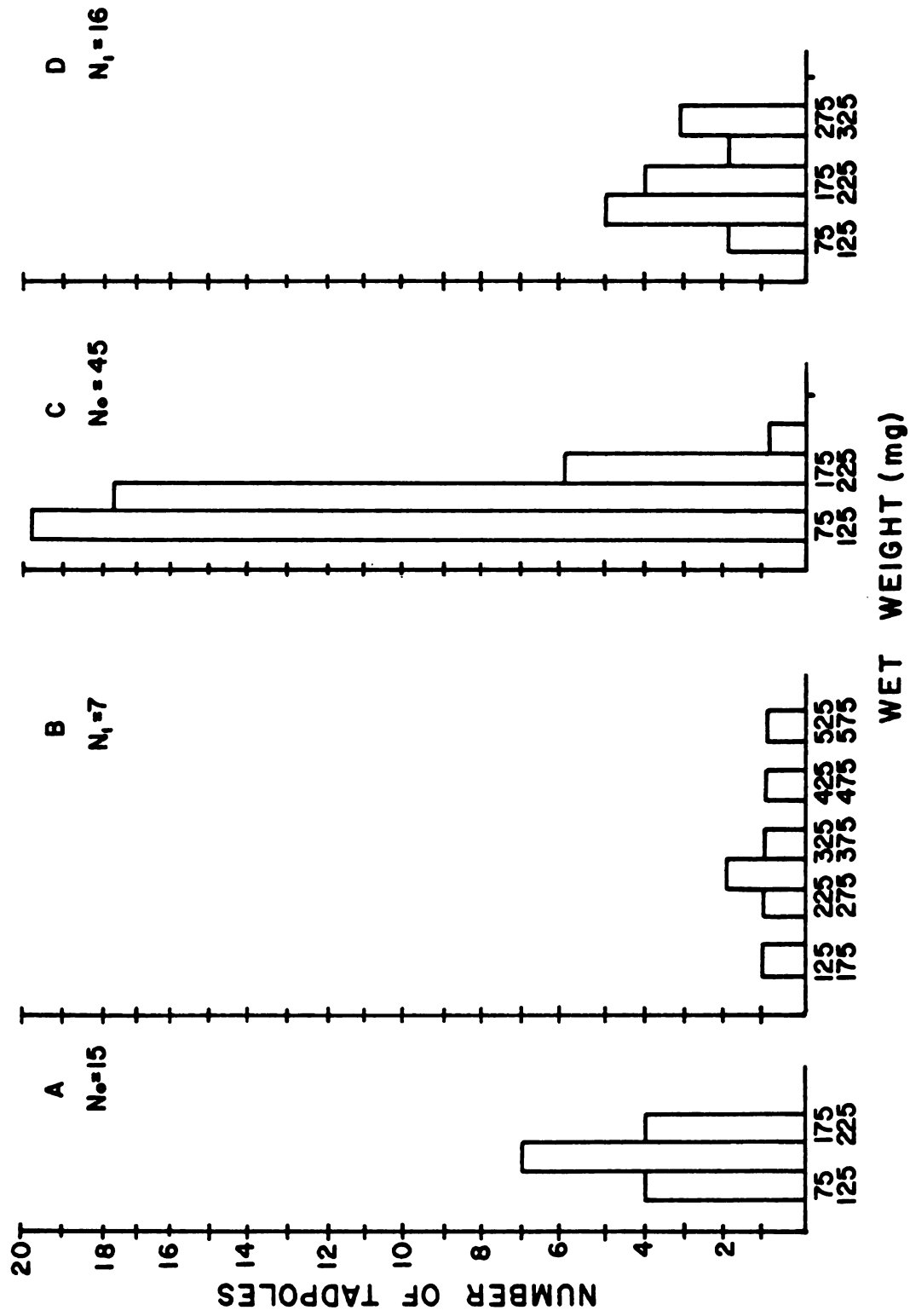


Figure B7. Distributions of weights (R. pipiens) in Experiment Two at Lake Four for low density (A = initial, B = final) and high density (C = initial, D = final) treatments.

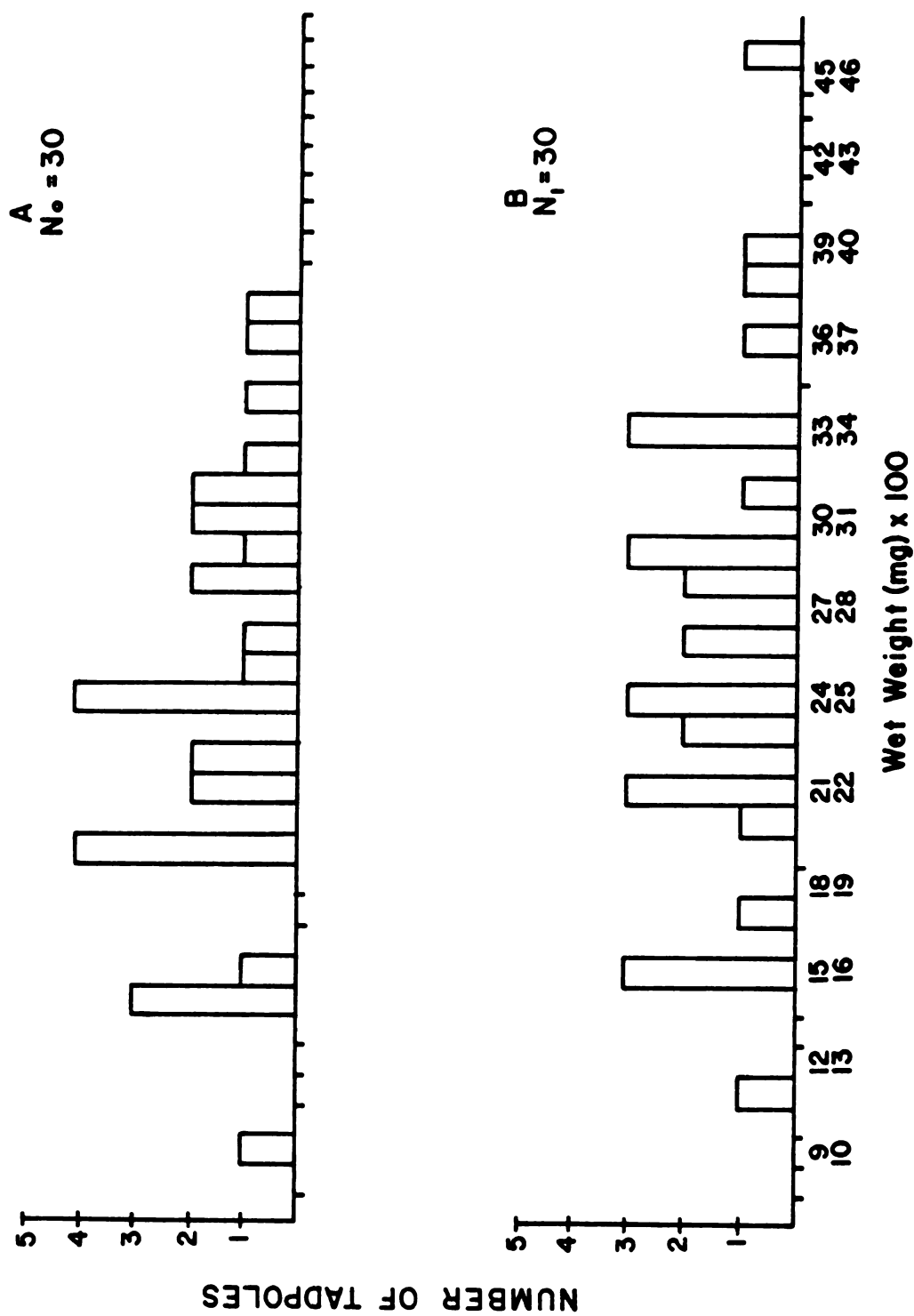


Figure B8. Weight distributions (A = initial, B = final) for tadpoles (R. catesbeiana) in single-species culture in Experiment Three at Lake One.

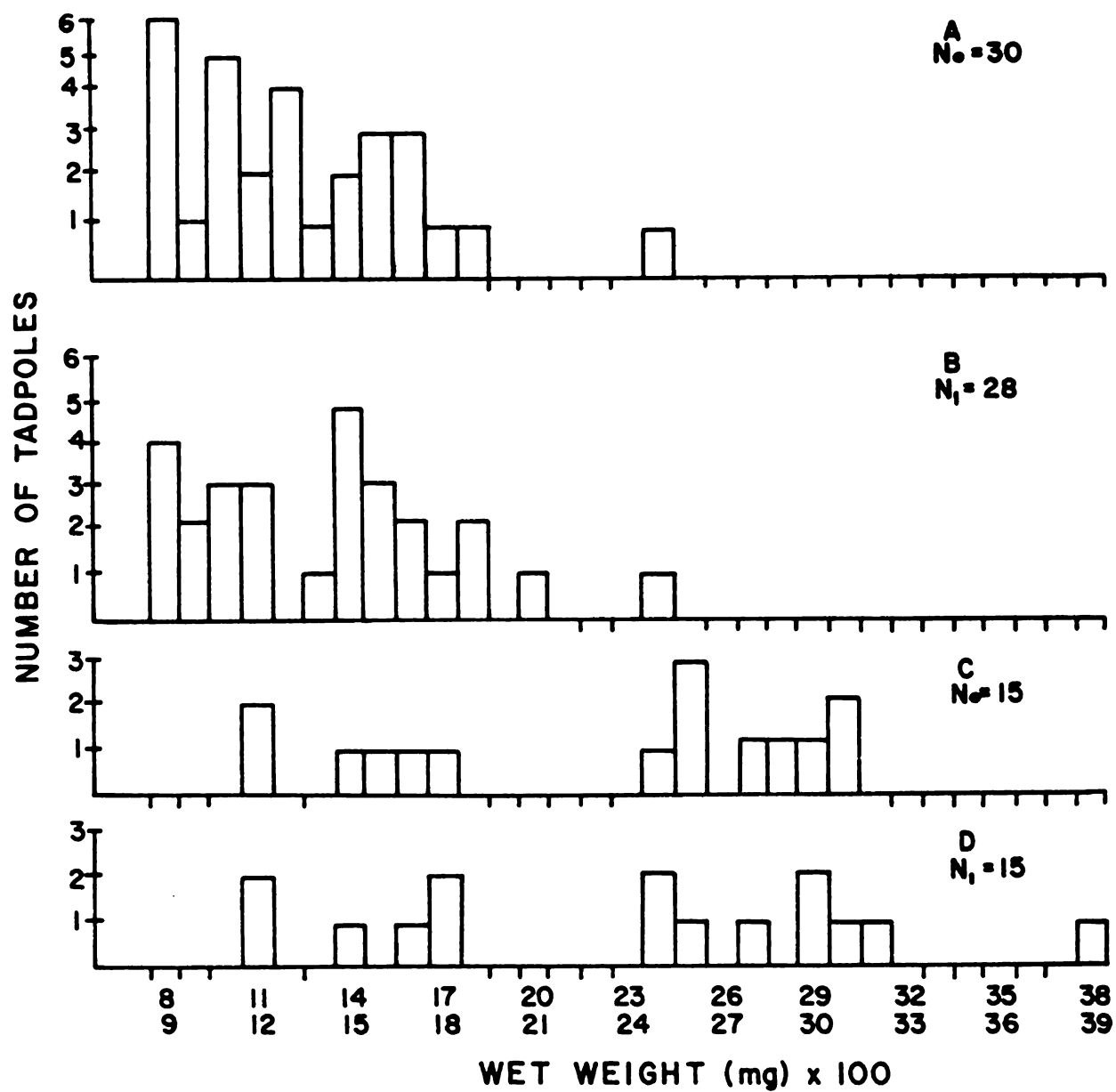


Figure B9. Distributions of weights for green frog tadpoles (A = initial, B = final) and bullfrog tadpoles (C = initial, D = final) in the mixed-species treatment in Experiment Three at Lake One.

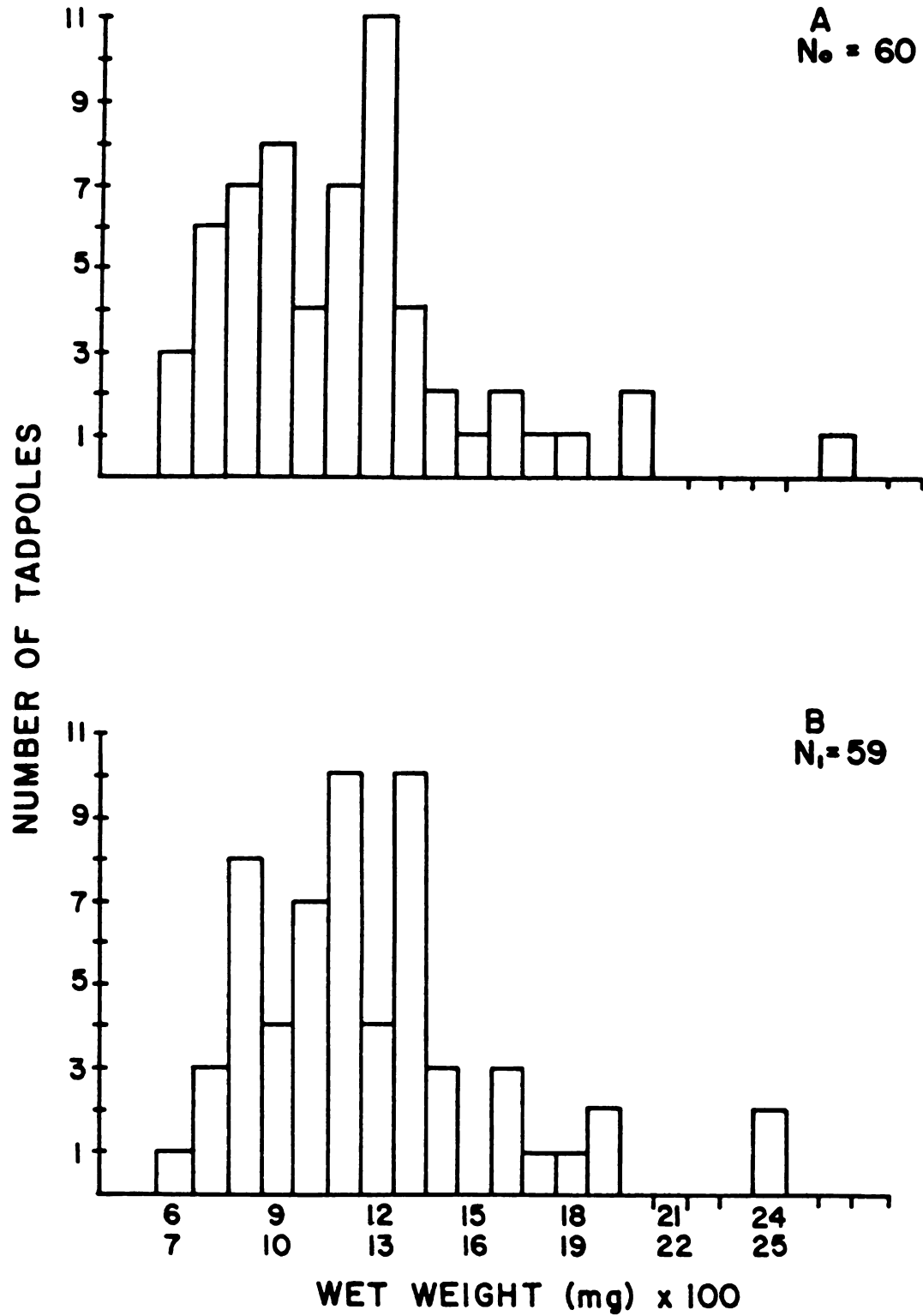


Figure B10. Weight distributions (A = initial, B = final) for mono-cultured tadpoles (R. clamitans) in Experiment Three at Lake One.

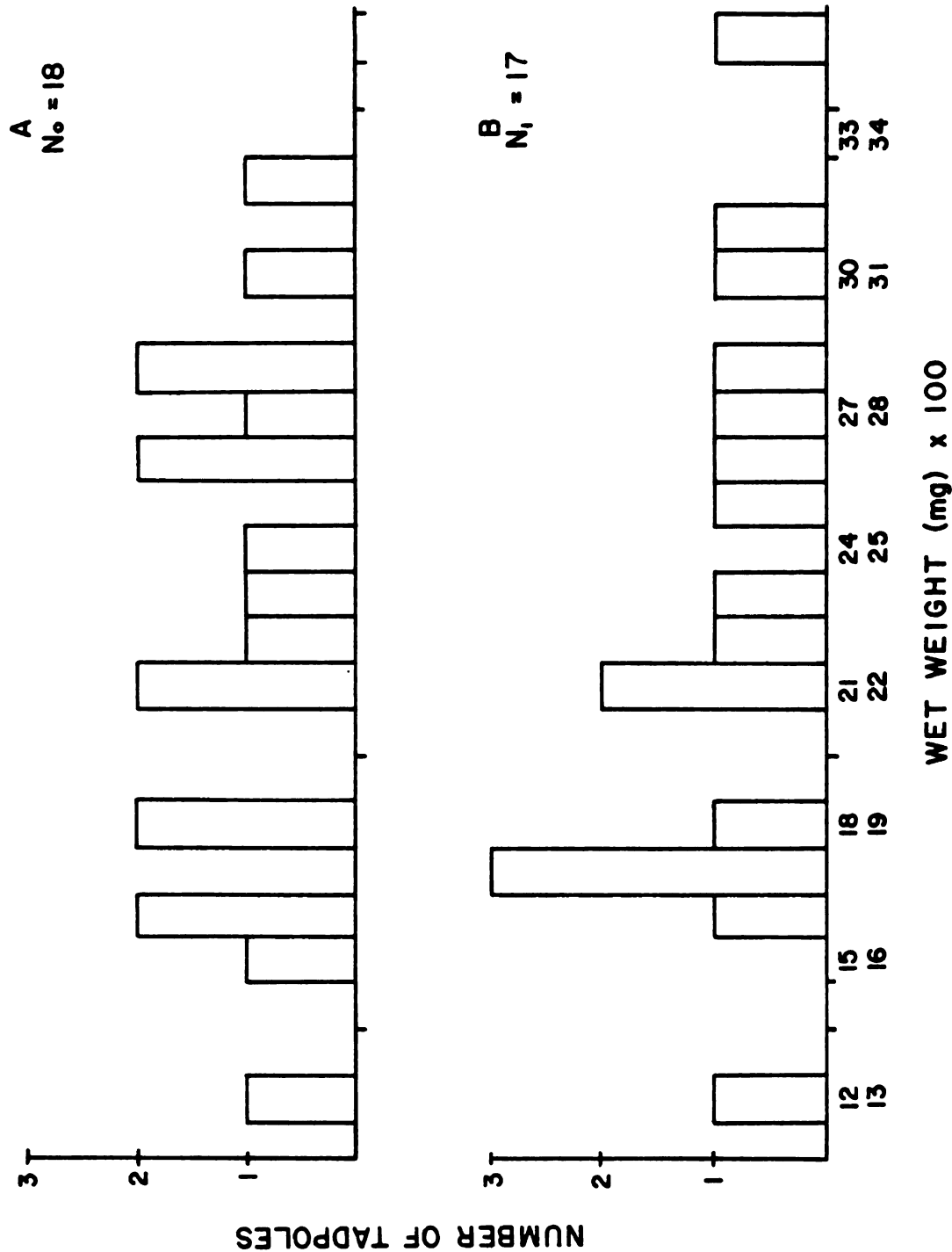


Figure B11. Initial (A) and final (B) distributions of weights for monocultured bullfrog tadpoles in Experiment Three at Lake Four.

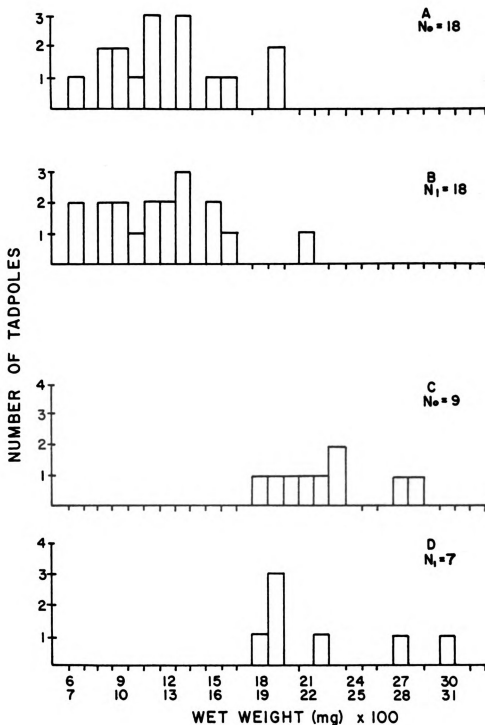


Figure B12. Distributions of weights for green frog (A = initial, B = final) and bullfrog (C = initial, D = final) tadpoles in mixed-species culture in Experiment Three at Lake Four.

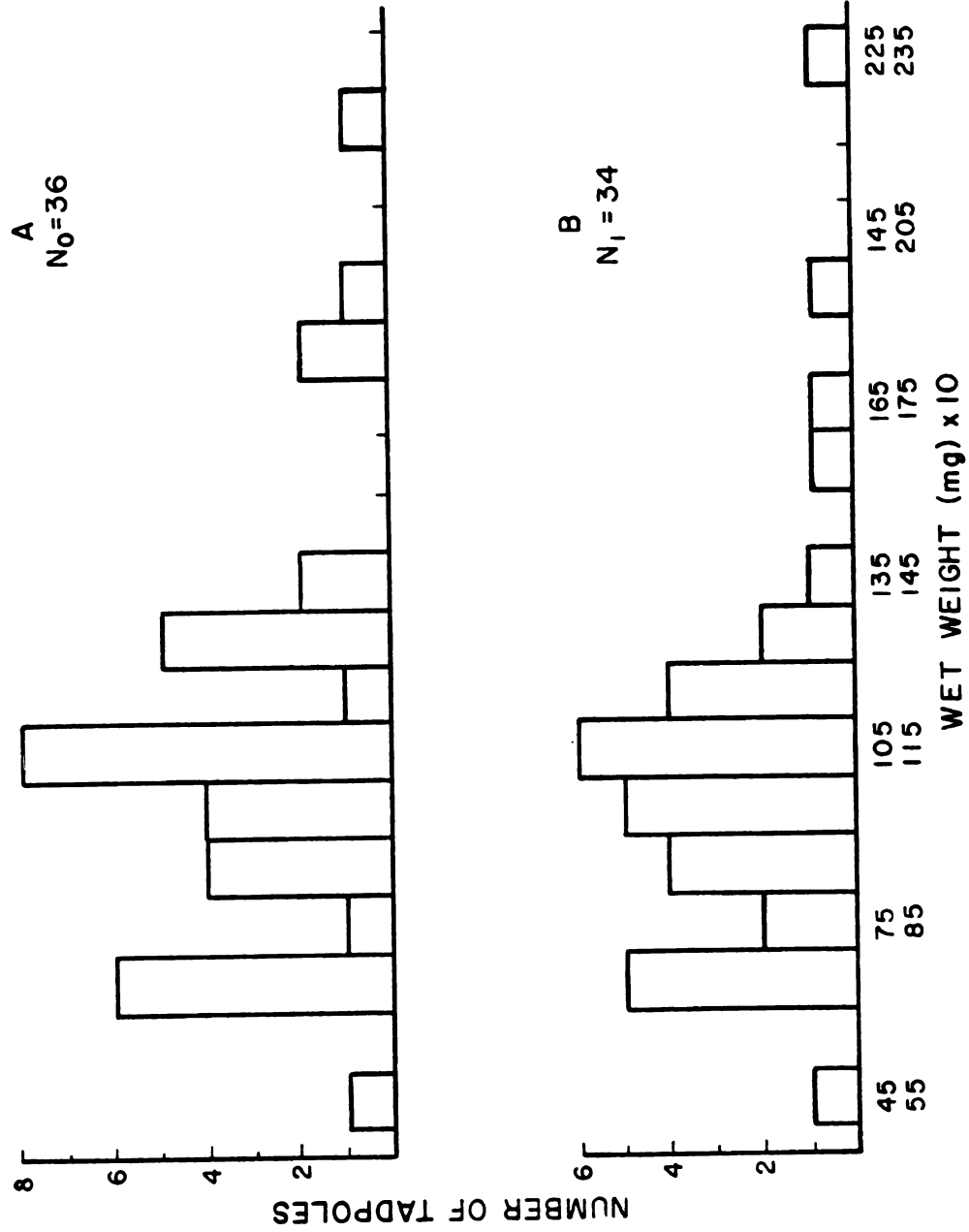


Figure B13. Weight distributions (A = initial, B = final) for tadpoles (*R. clamitans*) in single-species culture in Experiment Three at Lake Four.

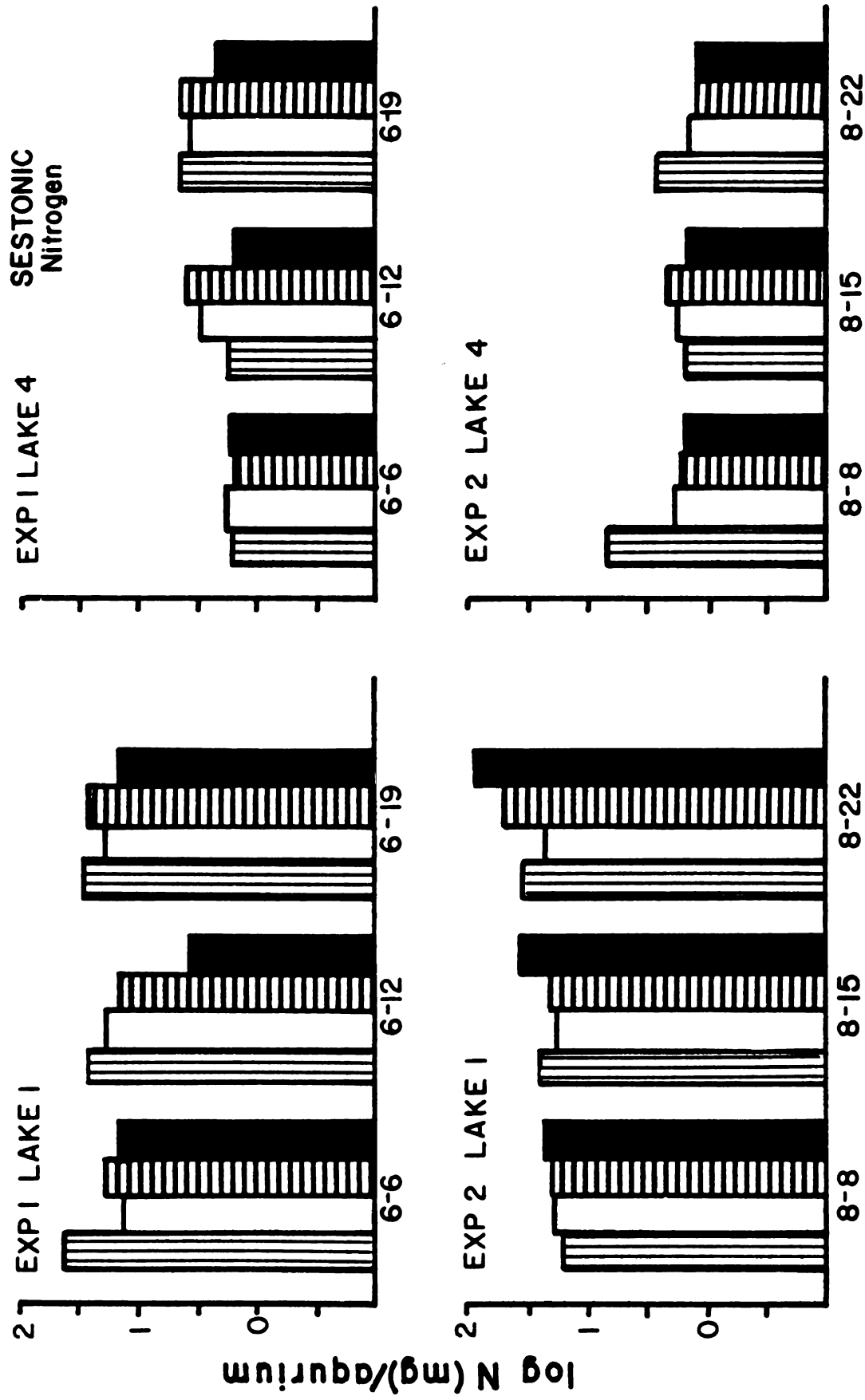


Figure B14. Sestonic nitrogen (log mg N/aquarium/d) in Experiments One and Two at Lakes One and Four (bar with vertical lines = imported lake water, unshaded bar = unstocked aquaria, bar with horizontal lines = low stock of leopard frog tadpoles and shaded bar = high stock).

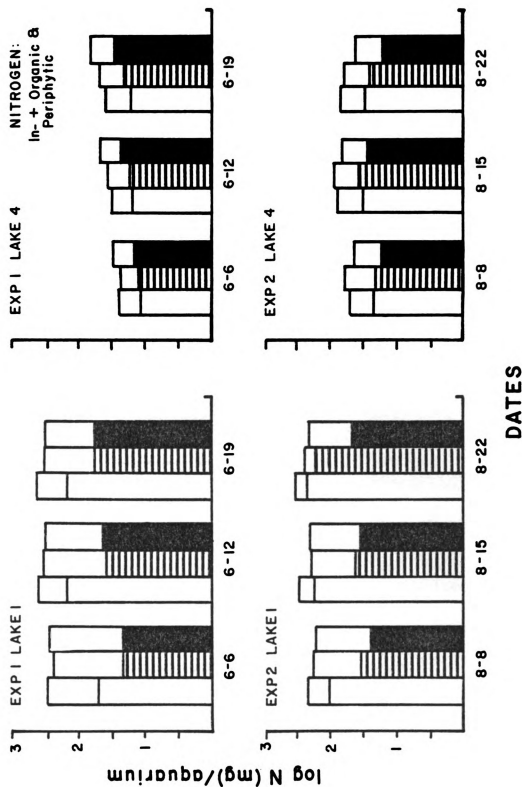


Figure B15. Total and periphytic nitrogen in Experiments One and Two at Lakes One and Four (inner bars represent periphytic nitrogen with unstocked aquaria = unshaded, low stocking of leopard frog tadpoles = horizontal bars, and high stocking = shaded).

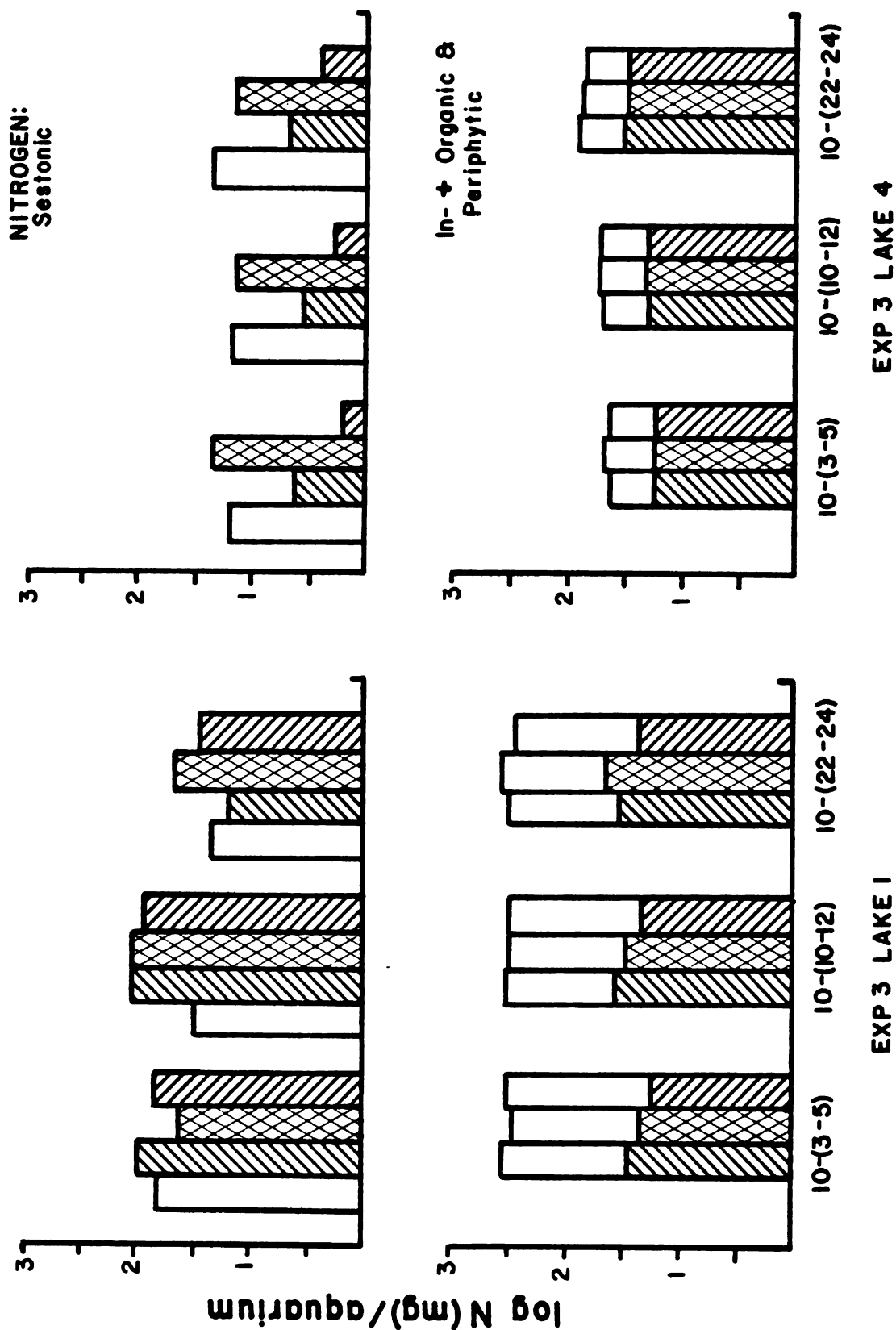


Figure B16. Sestonic, total and periphytic nitrogen for Experiment Three at Lakes One and Four (for sestonic N: unshaded bar = imported lake water and shaded bars represent, respectively, bullfrogs, mixed-species and green frogs. Shaded bars represent these same treatments for periphytic N).

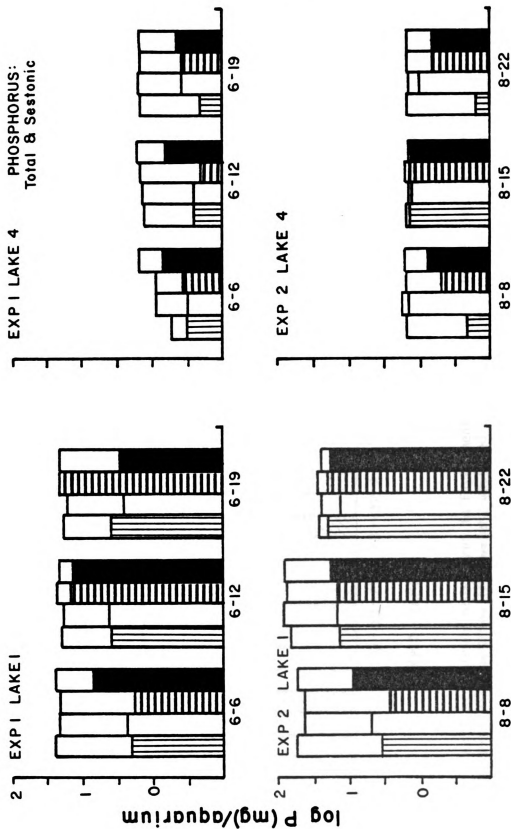


Figure B17. Total and sestonic phosphorus for Experiments One and Four (inner bars represent sestonic phosphorus with imported lake water = vertical stripes, unstocked aquaria = unshaded, low stocking of *R. pipiens* = horizontal stripes, and high stocking = shaded).

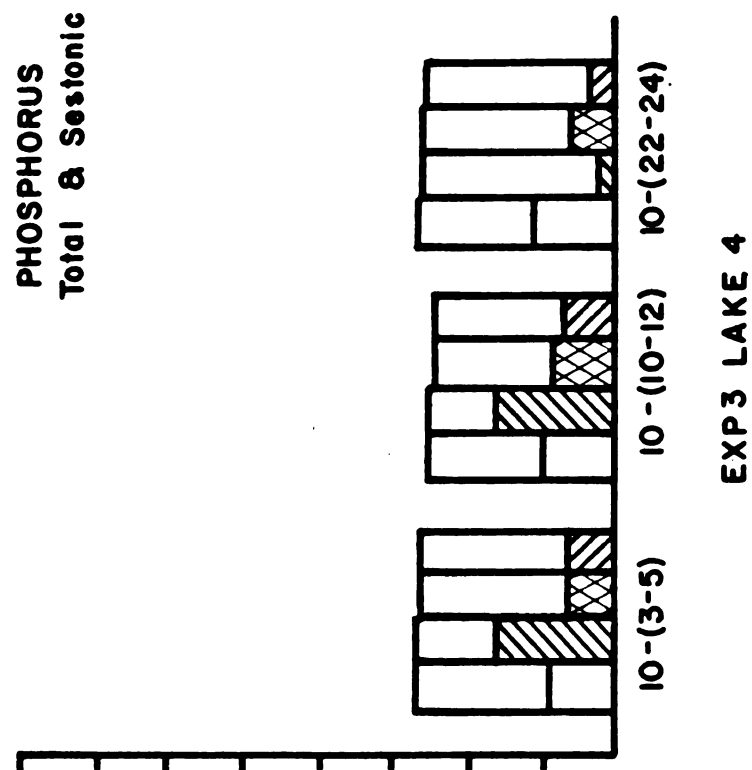
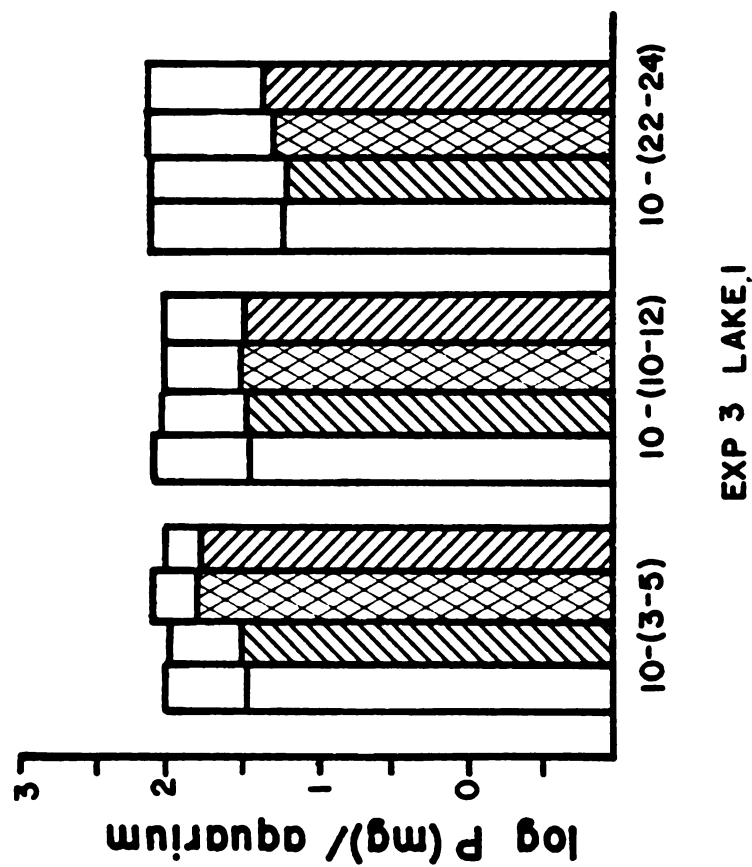


Figure B18. Total and sestonic phosphorus in Experiment Three at Lakes One and Four (inner bars represent sestonic phosphorus with imported lake water, unshaded and shaded bars represent, respectively, bullfrog tadpoles, mixed-species, and green frog tadpoles).