LIFE HISTORY AND SECONDARY PRODUCTION OF PREDACEOUS AQUATIC MACROINVERTEBRATES IN MANAGED EPHEMERAL PONDS.

THESIS

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By

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Dedicated to J. T. and Phillip Holmes who graced my life during the course of this project and whose smiles and laughter kept me going.

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ABSTRACT

Fish hatchery ponds are nutrient rich waters designed to support abundant phytoplankton and zooplankton populations to enhance fish fry production. Such enhanced waters can also secondarily lead to an increase in secondary production of predaceous aquatic insects. One objective of this study was to determine and compare the secondary production of predaceous aquatic insects found in fertilized and unfertilized lined fish hatchery ponds at the National Fish Hatchery and Technology Center, San Marcos, Hays County, Texas. Quantitative benthic dipnet and vacuum samples were collected from replicate fertilized and unfertilized ponds once a week, for sixteen weeks, beginning April 1st 1995. Organisms were sorted, identified to genus, headwidth and body length recorded, and dry weight (mg) measured. The secondary production of most predators was higher in fertilized ponds. However, the secondary production of *Pantala* (Libellulidae: Odonata) was an order of magnitude higher in unfertilized (0.31 g/m^2/year) than fertilized ponds (0.04 g/m^2/year). Whereas, production of the dominant predator *Berosus* (Hydrophilidae: Coleoptera) had higher production in fertilized ponds (0.53 g/m^2/year) than unfertilized ponds (0.02 g/m^2/year). Higher production of *Pantala* in the unfertilized ponds may have been a response to visual cues provided by unfertilized ponds to ovipositing females. Overall, production values are comparatively lower than in other studies and are the result of low standing stock biomass. The second objective was to determine the functional feeding response of the predators at different prey densities. Functional feeding responses were determined by placing predators of the same size-class/instar into individual replicated cubitainers with different prey densities. All predators increased consumption with increased prey density, but only *Pantala* showed a typical type-2 functional response. Species diversity was highest in the fertilized ponds. *Pantala* was dominant in the unfertilized ponds; whereas, *Berosus* was dominant in the fertilized ponds.

INTRODUCTION

Secondary production is the formation of heterotrophic biomass through time and is expressed as g/m²/year (Benke 1996). Secondary production measurements are important in understanding the transfer of energy and materials in natural ecosystems (Plante and Downing 1990). Thus, production analysis can provide insight into the role of insects in the functioning of aquatic ecosystems (Benke 1984).

Certain life history features are inherent in any secondary production study. Two important life history features that influence secondary production are length of aquatic life and voltinism (Waters 1979). The length of aquatic life is the time it takes for an insect to develop through its larval stages to adulthood. Voltinism is the frequency in which life cycles are completed. A population may be univoltine, bivoltine, trivoltine, or multivoltine depending on the number of life cycles a population can complete in one year. Data on voltinism are commonly used to correct production estimates by the size-frequency method (Butler 1984).

The larval stages account for the largest portion of the life cycle of aquatic insects (Butler 1984). Thus, the duration of the larval period is an important component in production estimates (Sweeney 1984). Two factors that affect the duration of the larval period are temperature and food quality and quantity (Anderson and Cummins 1979). At high temperatures, the duration of the larval period decreases and developmental time is significantly shorter (Sweeney

1984). The life cycle of certain species accelerates considerably when food levels are increased (Sweeney 1984) or food quality is higher (Ward and Cummins 1979).

There are several methods used to determine secondary production. These include the Allen curve, increment summation, removal-summation, instantaneous growth, and size-frequency (Benke 1984). The method chosen depends on whether cohorts can be distinguished from each other. Since cohorts of predaceous macroinvertebrates in this study were indistinguishable, the size-frequency method, a non-cohort technique, was used (Hynes and Coleman 1968, Hamilton 1969, and Benke 1979). Size-frequency estimates are usually made when complete life history data are unavailable or impossible to collect. Such occasions occur when successive cohorts are asynchronous and overlap considerably (Plante and Downing 1990).

The size frequency method, first introduced by Hynes and Coleman (1968), is a simple way to assess the production of benthic organisms in a stream. The method enabled an estimate of production of an entire invertebrate fauna through manipulation of size-frequency data (Hynes 1980). Two principle assumptions of the method are that all species are univoltine and all species grow to about the same length (Hynes and Coleman 1968). The Hynes-Coleman method was later modified by Hamilton (1969), who recognized that for multivoltine species, the Hynes production calculation must be multiplied by the number of generations per year. Also, to increase the accuracy of the Hynes

method, Hamilton (1969) showed the importance of treating data on a population rather than a community level. Benke (1979) further refined the size-frequency method by recognizing that it is the mean length of the aquatic stage relative to a full year, rather than voltinism per se, that is important in determining production estimates. The mean length of the aquatic stage is the cohort production interval (CPI). CPI is the mean developmental time from hatching to final size and refers to the interval during which growth and production occur (Benke 1979). All size frequency estimates of secondary production are corrected to annual production by multiplying the estimate by 365/CPI (Benke 1984).

A predator's functional feeding response is the way in which a predator will respond to changing abundance of prey (Colinvaux 1973). There are three types of functional responses and the type II response is typically exhibited by insects. In this response, predators consume more prey as prey become more common. This is because as prey density increases, finding prey becomes easier (Begon 1990).

Due to being nutrient enriched, fertilized hatchery ponds are productive ecosystems. Nutrients encourage the growth of phytoplankton, phytoplankton promote the growth of zooplankton, which in turn support the fish fry grown in fish hatchery ponds. Numbers of other prey species such as mayfly nymphs and chironomid larvae also should be abundant under such nutrient enriched conditions. Consequently, determining the functional feeding response provides insight into a predator's behavior at high prey densities and may provide a basis

for the magnitude of production observed. For example, the rate at which organisms consume food sets an upper limit to its productivity and the rate of feeding increases with increasing prey availability (Edmundson and Winberg 1971).

This study determines secondary production of predaceous aquatic macroinvertebrates without the presence of vertebrate predators or macrophytes in lined ephemeral hatchery ponds. The objectives of this study are: 1) to compare secondary production of predaceous aquatic macroinvertebrates in fertilized ponds to those in unfertilized ponds and; 2) to determine the functional feeding responses of predaceous aquatic macroinvertebrates.

METHODS

This study was conducted from April through July 1995 at the San Marcos National Fish Hatchery and Technology Center located in San Marcos, Hays County, Texas.

Pond set-up:

Four ponds lined with 40 mil polyethylene plastic were used. Each pond had a capacity to hold 431 m^3 of water and when filled had an area of 540 m^2. Ponds were filled with well water from the Edwards Aquifer. Water from the aquifer has an alkalinity of 270 $CaCO_3$ mg/l and hardness of 300 $CaCO_3$ mg/l and a pH near 7.0. Two ponds were unfertilized and two ponds were fertilized. The fertilization regime is one followed by fish hatcheries to encourage phytoplankton growth. The initial fertilization consisted of 9.0 kg alfalfa pellets, 0.66 kg urea, and 354 ml 75% phosphoric acid. This was followed by weekly additions of 4.6 kg alfalfa pellets, 0.33 kg urea, and 177 mL 75% phosphoric acid. Weekly fertilization with urea and phosphoric acid were discontinued when the pH reached 9.5 or higher.

Parameters:

Dissolved oxygen and temperature measurements were taken at 07:00 and 19:00 hours using an Orion 820 meter at a depth of one meter. 50 mL of water from each pond was sampled at 19:00 hours and taken to the lab for pH and relative fluorescence measurements. Relative fluorescence yields an

estimate of chlorophyll *a* concentrations, a measure of algal biomass in ponds. A Jenco model 6072 pH meter was used to measure pH and a Turner Fluorometer model 112 was used to determine relative fluorescence.

Zooplankton tows were taken daily for 2.5 weeks after the initial fertilization and then every other day for the next six weeks. To standardize samples, the plankton net (65 nm mesh and 24 cm diameter) was pulled 4 m through the water. The volume of water sampled by the net was 0.18 m^3.

Secondary production estimates

Ponds were sampled for predaceous aquatic macroinvertebrates one day prior to initial fertilization and at weekly intervals thereafter for a period of 16 weeks. Initially, all sample sites were randomly established and then these same sites were sampled throughout the rest of the study. To quantitatively sample the hard bottom of a lined fish hatchery pond, a modification to Wellnitz's (1991) continuous suction device was used (Figure 1). The sampler consisted of two main structures. One structure was a frame around which a wire screen with a mesh of 2.0 mm was attached. The bottom of the frame had an area of 0.12 m^2. The top of the frame was left open. A rope was attached to each side of the top of the frame. The second structure was a vacuum sampler comprised of three main components: 1)sampling wand, 2) a filter, and 3) a water pump. The sampling wand consisted of a PVC pipe 1 m in length and 5.6 cm in diameter. Attached to one end of this pipe was a swing check valve, which allowed the sampler to be primed and served as an opening through which organisms could

be collected. The second component was the filter, which was made from a PVC coupling with a diameter of 8.9 cm. A wire screen was attached across the opening. The filter was housed inside a canister made from a 10.2 cm PVC coupling, two 10.2 cm diameter PVC clean-out adaptors, and two 10.2 cm diameter PVC drain waste vent plugs. Tygon tubing attached the sampling wand to the canister. The canister was attached to the water pump by a standard garden hose. To vacuum sample a given site, the frame was dropped over the site and the primed sampler was then used to vacuum the area within the frame. A 21.1 L bucket was used to receive water exiting the pump. After vacuuming, the water from the bucket was poured through a 100 mesh sieve to collect organisms too small to be trapped in the filter. Those organisms trapped in the filter were also rinsed into the sieve. The sieve was then rinsed into a plastic bag. The bags were placed on ice in the field and later frozen when returned to the lab. Samples were kept frozen until processed. Weekly semi-quantitative dipnet samples also were taken.

The vacuum sample sites were chosen by a computer generated random coordinates. The coordinates entered into the computer were initially derived from the division of the width (x-axis) and the length (y-axis) of a pond into feet. The computer randomly paired the x and y values. The first four points generated were chosen as the vacuum sites (Figure 2). Vacuum site three was not processed, due to time constraints. The dipnet sites did not interfere with the vacuum sites located on the opposite side of the pond.

The dipnet was set at a distance of 1 m from the edge of the water and then was pulled back along the bottom to the shore. The area sampled by the dipnet was 0.30 m^2. The volume of water the dipnet pulled through was 0.14 m^3. Dipnet samples were processed in the same manner as vacuum samples.

Once sorted, macroinvertebrates were identified to genus, head width and body length measured, and dry weight determined. Invertebrate measurements were made using a calibrated ocular scale on a Nikon dissecting scope. Dry weights were determined by drying individuals in a Fisher Scientific Isotemp oven (model 655F) maintained at 60°C and later weighing (mg) individuals on a CAHN 29 Automatic Electrobalance. Prior to weighing, the balance was checked with calibrated weights.

To determine secondary production, four variables were obtained: size class, mean weight for each size class, developmental time, and density. Size class designations were made by associating size-frequency distributions with instars. Instars were determined from the literature or peaks in size-frequency distributions.

To determine average weight of each size class, a regression of the natural log weight versus the natural log headwidth or body length of each predator was determined (Smock 1980).

Developmental time for *Pantala* (Libellulidae: Odonata) was determined by measuring the length of time between occurrence of early instars and first emergence. Emergence was determined by daily records of the presence and

number of exuvia around the perimeter of the ponds. The developmental time for *Pelocoris* (Naucoridae: Hemiptera), *Notonecta* (Notonectidae: Hemiptera), *Buenoa* (Notonectidae: Hemiptera) and *Berosus* (Hydrophilidae: Coleoptera) were taken from the literature due to low abundance of these organisms.

Berosus has three larval instars and a developmental period of 66 d (Hilsenhoff 1995). In laboratory rearings, *Pelocoris femoratus* had five instars and a developmental period of 63 d when raised at a temperature of 27 °C. Under field conditions with temperatures ranging from 15 °C–22 °C, *Notonecta hoffmanni* exhibited five instars and a developmental period of 89 d. Therefore, developmental periods of 66 d for *Berosus*, 63 d for *Pelocoris*, and 89 d for *Notonecta* and *Buenoa* were used in the study to determine production.

Functional feeding response experiments:

Predators used in the functional feeding response experiments were collected from a non-study pond subjected to the same fertilization regime as the fertilized ponds. Functional feeding responses were determined for four different predators: *Pantala*, *Berosus*, *Pelocoris*, and *Buenoa*. The following procedure was performed for each set of experiments. Once collected, predators were taken to the lab and isolated into polystyrene specimen cups containing 100 ml of filtered pond water. All predators were starved for 48 h prior to the start of an experiment. A single predator was placed into 1 L sized cubitainers containing 600 ml of filtered pond water, with different numbers of prey placed into different cubitainers.

Immature size-class/instars used in the functional feeding response study for *Pantala*, *Buenoa*, and *Berosus* were 7th of 12 instars, 4th of 5 instars, and 2nd of 3 instars, respectively. Adult *Pelocoris* were used. *Pantala* were fed *Baetis* (Baetidae: Ephemeromptera), *Pelocoris* and *Berosus* were fed chironomid larvae, and *Buenoa* were fed *Chaoborus* (Chaoboridae: Diptera).

There were five prey densities: 1x, 2x, 4x, 8x, and 16x with two replicates per treatment. The cubitainers were placed into one end of a pond, in which they floated for 24 h. This length of time was chosen to allow for the diel rhythm exhibited by many animals and their prey in both feeding and activity (Edmundson and Winberg 1971). After 24 h, cubitainers were gathered from the pond, taken back to the lab and placed in the refrigerator to reduce activity. Cubitainers were then removed and rinsed three times with deionized water into a 200 mesh sieve. The predator from each cubitainer was placed into a vial of 80% EtOH and the remaining prey were rinsed into a glass bowl. Prey were counted and placed in the vial with the predator. Prey that were half or more consumed were considered eaten.

RESULTS

Physical Parameters

There were no differences in temperature of fertilized and unfertilized ponds (Figures 3 and 4). Temperature gradually increased in all ponds during the study with the onset of summer.

Morning dissolved oxygen concentrations in unfertilized ponds ranged from 6.7 to 12.1 mg/l and in fertilized ponds from 6.5 to 17.3 mg/l (Figure 5). In contrast, afternoon dissolved oxygen concentrations ranged from 8.9 to 13.9 mg/l in unfertilized ponds and from 9.1 to 28.2 mg/l in fertilized ponds (Figure 6). Dissolved oxygen was generally higher in fertilized than unfertilized ponds, especially at the beginning of the study. Fluctuations and variability in dissolved oxygen was much greater in fertilized than unfertilized ponds.

Relative fluorescence was generally higher and more variable in fertilized than unfertilized ponds, especially during the early stages of the study (Figure 7).

Throughout the study, the pH remained higher and more variable in fertilized ponds than in unfertilized ponds (Figure 8). The mean pH for the fertilized and unfertilized ponds was 9.6 and 8.8, respectively.

Life History

Developmental time for *Pantala* was determined to be 40 d in fertilized ponds and 30 d in the unfertilized ponds.

Several genera (*Berosus*, *Pelocoris*, *Buenoa*, and *Notonecta*) occurred in such low numbers that developmental times could not be determined. To calculate production values for these genera, I used developmental times from the literature. However, such values are likely to be conservative. The genera in this study were expected to have a shorter developmental times as a response to warm water temperatures and an abundance of available prey (Anderson and Cummins 1979, Lawton 1980).

Density/Biomass/Production

Pantala were more dense and had greater biomass in unfertilized ponds than in fertilized ponds (Figure 9), whereas, *Berosus* had greater densities and biomass in fertilized than in unfertilized ponds (Figure 10). No temporal patterns were evident and variability in experimental ponds was high.

Pelocoris, *Buenoa*, and *Notonecta* were more abundant, more variable and had greater biomass in fertilized ponds than in unfertilized ponds (Figures 11, 12, and 13). *Pelocoris* numbers were increasing when the study ended. *Buenoa* and *Notonecta* were most abundant during the middle stages of the study and no *Notonecta* were collected during the last month.

Pantala was the only species to have higher production in unfertilized ponds (Figure 14). The annual production for *Pantala* was 0.043 g/m^2/year in fertilized ponds and 0.31 g/m^2/year in unfertilized ponds. The highest production was by *Berosus* followed by *Notonecta* and *Buenoa* in fertilized ponds. The annual production for *Berosus* in the fertilized ponds was 0.53 g/m^2/year and

0.025 g/m²/year in the unfertilized ponds. *Pelocoris* had the lowest production of all species in both the fertilized and unfertilized ponds.

Functional Feeding Response Experiments

All predators increased consumption with increased prey density but only *Pantala* showed a typical type-2 functional response (Figures 15, 16, 17, and 18).

Species Diversity and Relative Abundance

Species diversity was highest in fertilized ponds with nine genera collected compared to six for unfertilized ponds (Figure 19). Six genera were common to both treatments. *Berosus* was the dominant predator in fertilized while *Pantala* was dominant in unfertilized ponds. Non-predaceous macroinvertebrates present were: *Ramphocorixa* (Corixidae: Hemiptera), *Baetis*, *Tricorythodes* (Tricorythidae: Ephemeroptera), *Oecetis* (Leptoceridae: Trichoptera), *Chaoborus*, chironomids, copepods, cladocerans, *Stenophysa* (Physidae: Gastropoda), and *Gyraulus* (Planorbidae: Gastropoda).

Colonization Patterns

Differences in colonization patterns were observed among predators in fertilized and unfertilized ponds. Generally, the insect predators colonized earlier and persisted longer in fertilized ponds (Figure 20).

DISCUSSION

Physical Parameters

The higher dissolved oxygen in the fertilized ponds was likely due to the greater abundance of phytoplankton and their photosynthetic activities (Boyd 1990) which led to diurnal supersaturation levels (Cole 1975 and Horne and Goldman 1994) during the first month of the study. Dissolved oxygen was never depleted in fertilized or unfertilized ponds. Availability of dissolved oxygen enhances secondary production of benthic organisms by allowing greater efficiency in metabolizing food (Downing and Rigler 1984).

Chlorophyll *a*, dissolved oxygen and pH of fertilized ponds were much more variable than for unfertilized ponds. This occurred in part, because the temporal dynamics of replicate fertilized ponds in response to fertilization, were not synchronous and of similar magnitude. For example, there was a pH discrepancy between replicate fertilized ponds. An algal bloom had occurred in one of the replicate fertilized ponds causing a higher pH (Figure 9). High pH commonly occurs when a decrease in carbon dioxide results from photosynthesis progressing more rapidly than respiration (Boyd 1990). Variablity in production ponds is common; two ponds treated in the same way will often differ in composition and density of populations of organisms that develop in them (Coker 1954).

Life History

Even though temperatures were similar, developmental times for *Pantala* in this study were nearly twice as fast as the 72 d reported by Begum *et al.* (1990) and comparable to larval development of *Palpopleura lucia lucia* (Libellulidae: Odonata) when fed large amounts of food (Hassan 1976).

Temperature, nutrition, and photoperiod are several factors which can affect the life histories and consequently the secondary production of aquatic insects (Sweeney 1984). The fertilized and unfertilized ponds remained warm throughout the study allowing shorter developmental times and expectations of high secondary production. Secondary production rates increase with increase in temperature by shortening developmental time and increasing feeding rates (Downing and Rigler 1984).

The effect of food quality and quantity on life histories and production of predaceous macroinvertebrates in this study was not clear. Nutrition in terms of food quality and quantity can affect life history by shortening developmental time, thus increasing voltinism and subsequently secondary production (Downing and Rigler 1984). For example, Ward and Cummins (1979) found that the growth of *Paratendipes albimanus* (Chironomidae: Diptera) may be slowed by poor food quality or alternately be accelerated to produce multiple generations if continuous supplies of high quality food are available. Food quality and quantity were high in this study. Chironomids and ephemeropterans were more abundant in fertilized

than unfertilized ponds (personal observation), and thus could potentially contribute to shorter developmental times of the predators.

The effect of photoperiod on the secondary production of predators in this study is not known. Photoperiod is probably the common cue for diapause induction, and the associated neurohormonal events frequently result in slower growth and up to twice the weight gain and fat storage (Scriber and Slansky 1981).

Density/Biomass/Production

Pantala was more abundant in unfertilized than fertilized ponds. Perhaps this preference was a result of a habitat selection mechanism by ovipositing females. Habitat selection is governed by the use of information from many physical and chemical variables by organisms when choosing their habitats (Meadows and Campbell 1972). For example, habitat selection in dragonflies is primarily visual and thus they tend to be attracted to reflective surfaces (Corbet 1962). Perhaps the surface reflective and visual properties of unfertilized ponds led to greater ovipositing rates by female dragonflies than in fertilized ponds.

Berosus densities had declined to near zero in the fertilized ponds by July 1st and *Pelocoris* densities were increasing at this time. *Pelocoris* feeds on small mollusks, dragonfly naiads, and other aquatic animals (McPherson *et al.* 1987). The decline of *Berosus* could be due to predation by *Pelocoris*. During *Pelocoris* population increases, exoskeletons of *Berosus* were found for the first time. Some authors suggest that predation leads to increased production, whereas

others suggest predation decreases production (see Downing and Rigler 1984). The effect of predation on production of *Berosus* in this study is not known.

Production values for *Pantala* in this study were much less than production of *Celithemis fasciata* (Libellulidae: Odonata), studied in Aiken, South Carolina by Benke (1976). Perhaps the high production determined in Benke's (1976) study was due to the presence of macrophytes. Macrophytes could increase the surface area of livable habitat and prey abundance for *C. fasciata*, thus ultimately increasing the production of this odonate. Edgar (1990) showed macrofaunal abundance, biomass and production were all much greater in vegetated than unvegetated habitats.

Runck and Blinn (1990) determined the production of the hemipteran *Ranatra*: (Nepidae) in Montezuma Well, Arizona, as 1.0 g/m^2/year. This value is higher than the production of hemipterans in this study. Again, this could be attributed to the presence of macrophytes in Montezuma Well.

The magnitude of production depends on standing stock biomass and the rate of biomass turnover (Benke 1984). For instance, high production can result from either high standing stock biomass alone, rapid rate of biomass turnover alone, or a combination of the two (Benke 1984). The production values in this study are comparatively lower than in other studies and are the result of low standing stock biomass.

Functional Feeding Response Experiments

The functional feeding response of predators showed that they consumed an increasing number of prey as prey densities increased. The hemipterans did not show a typical type-2 invertebrate curve as expected, since no asymptote in their feeding response was reached after 24h. Whereas, Fox (1978) showed that *Notonecta hoffmanni* had reached an asymptote after consuming eight mosquito larvae in a 3 h period.

The warm temperatures present throughout this study allowed for the magnitude of functional feeding responses observed. Temperature plays an important role in affecting the functional response of insects. For example, Thompson (1978) demonstrated that as temperature increases the number of prey consumed increases in *Ischnura elegans* (Coengrionidae: Odonata). Also, at higher predation rates, there will be secondary effects of increased growth (Murdoch 1971). For example, Benke (1976) showed that during periods of high odonate production, prey were consumed at such rates that prey biomass turned over once a week. Secondary production in this study was low despite the magnitude of the functional feeding responses observed.

Conclusions

Two sampling considerations may have affected density estimates. One involved the priming of the sampler. The priming of the sampler involved moving the sampling wand back and forth under water until water filled the sampler. Despite the sampler being primed 10 ft from each sample site, the disturbance

caused by the priming could have affected the number of predators collected. Predators such as *Pantala* and *Pelocoris* can move to escape disturbance. Also, they could have escaped before the frame sank to the bottom. The other potential sampling problem was due to the algal bloom in fertilized pond D9. The bloom clogged the plankton net and despite cleaning efforts, the net did not pull through the water as easily. Consequently, the number of notonectids collected after 29 May 1995 may have been underestimated.

Another consideration is related to estimation of generation times. The size-frequency method is highly dependent on an accurate estimate of generation time (Benke 1976), which was not possible for most of the organisms in this study. Benke *et al.* (1984) encountered similar problems and found the crudest production estimates in his study were for invertebrates in which he relied on literature values for larval developmental time.

Interest in this study began when the National Fish Hatchery and Technology Center (NFHTC) was in a black bass fry production operation mode and large numbers and size of coleopterans and notonectids were observed. Production losses of fry were as high as 30% and I hypothesized that a significant portion of this loss was due to predation by aquatic insect predators. This study was an attempt to determine production of aquatic insect predators in fertilized hatchery ponds and their potential role as predators in such managed aquatic systems. However, when this study began, the NFHTC had a change in mission objectives and no longer studied management practices to enhance fish

fry production. Consequently, fish fry were absent as a source of prey. Although production was generally much higher in fertilized than unfertilized ponds, I believe the presence of fish fry would have greatly enhanced insect predator densities, biomass, and turnover ratios. Further study is needed to address this question.

It is important to determine prey production as well as primary production in secondary production studies of predaceous aquatic insects. Although most secondary production studies consider the influence of prey, few secondary production studies simultaneously examine primary production (Minshall 1988).

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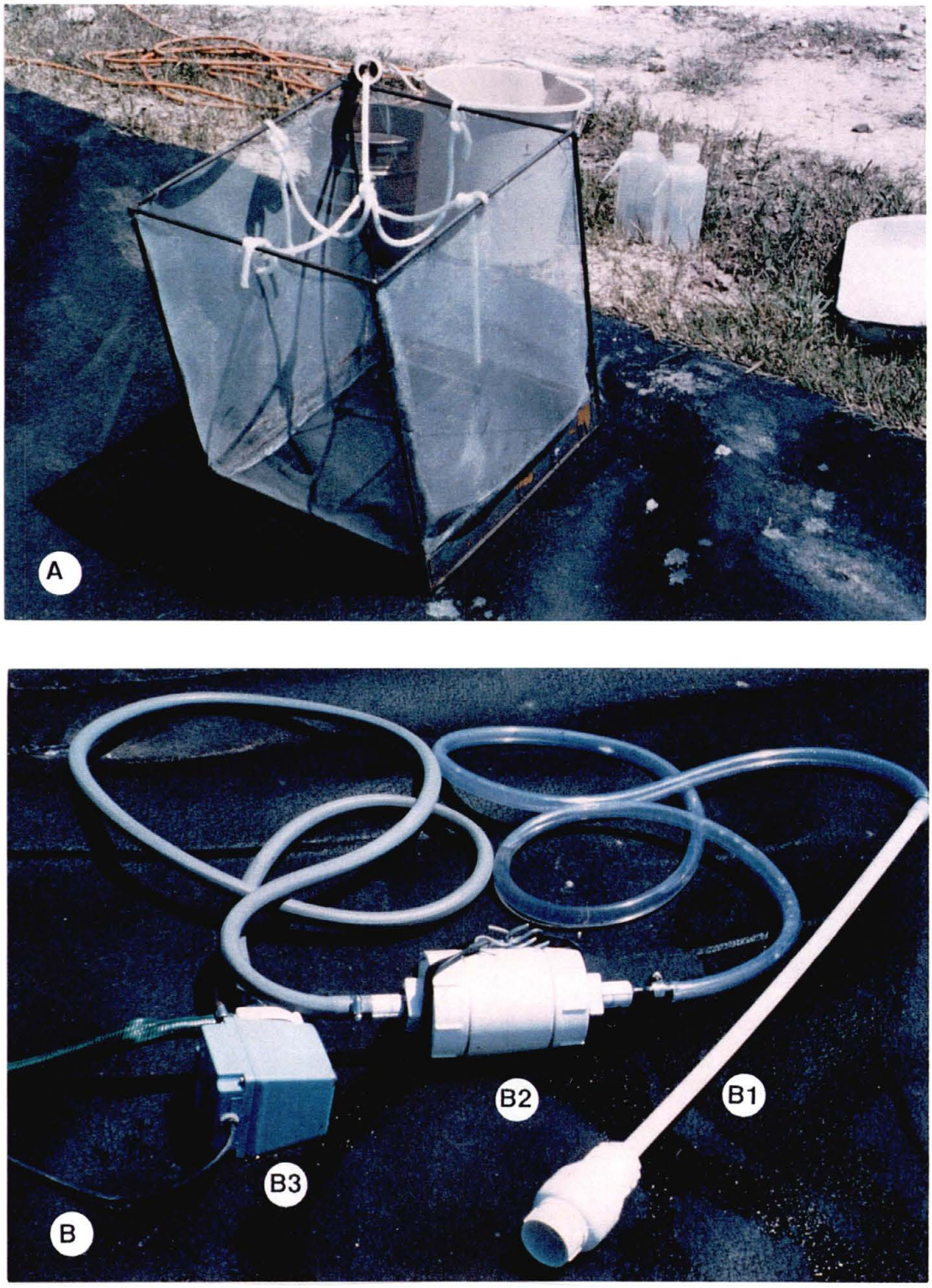

Figure 1. A modified Wellnitz (1991) continuous suction device, for sampling predaceous aquatic macroinvertebrates. A) frame and B) vacuum sampler. The vacuum sampler consisted of B1) sampling wand, B2) canister containing the filter, and B3) water pump.

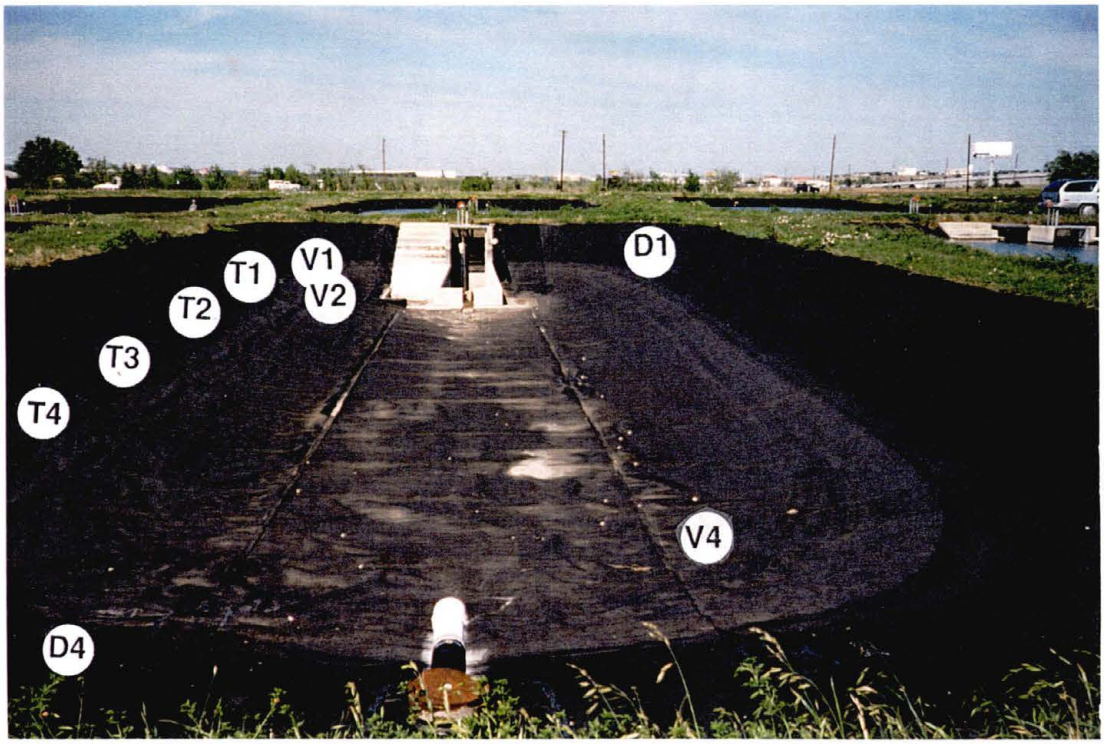

Figure 2. The location of the sampling sites in a lined ephemeral pond. Vacuum sites: V1, V2, and V4. Dipnet sites: D1 and D4. Zooplankton/macroinvertebrate tow sites: T1, T2. T3, and T4.

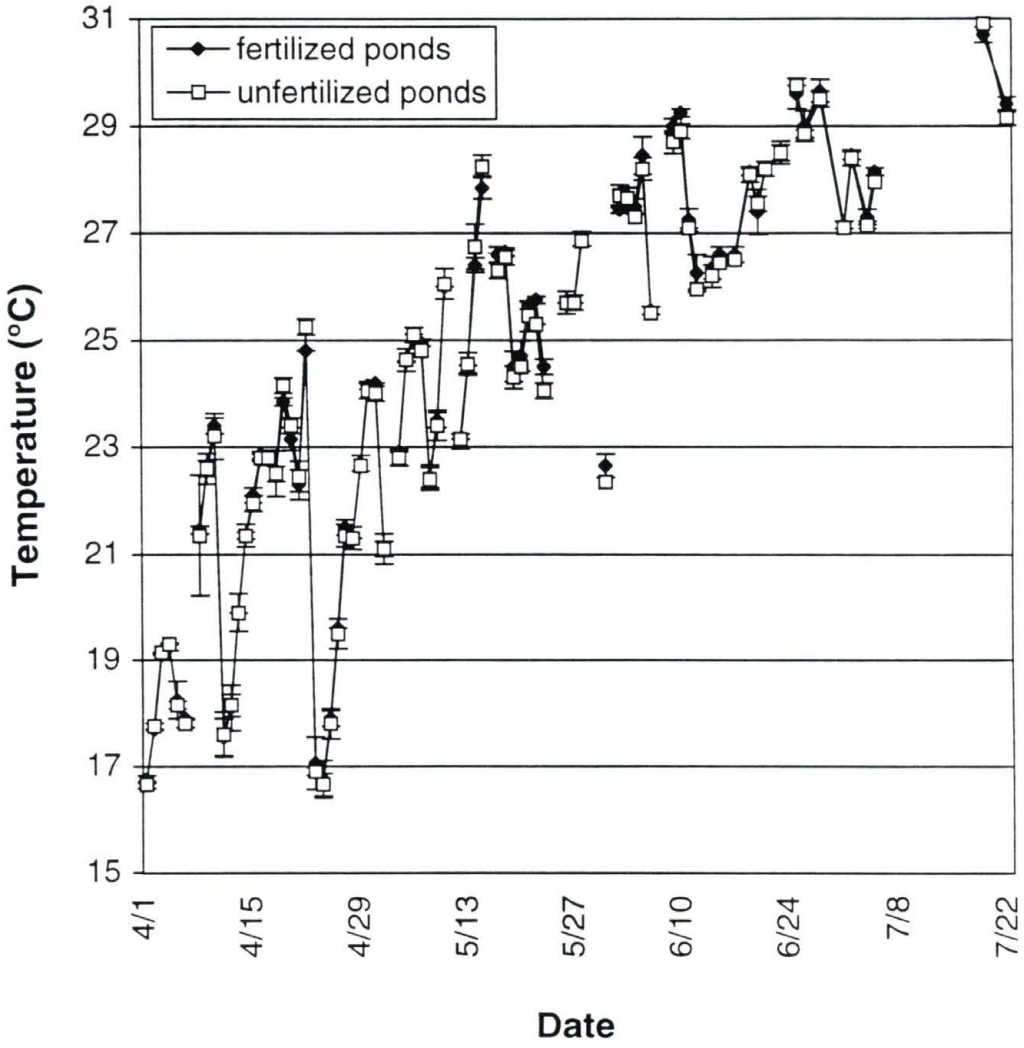

Figure 3. Mean (◆ or □) and standard deviation (vertical lines) of morning water temperatures in fertilized and unfertilized ponds.

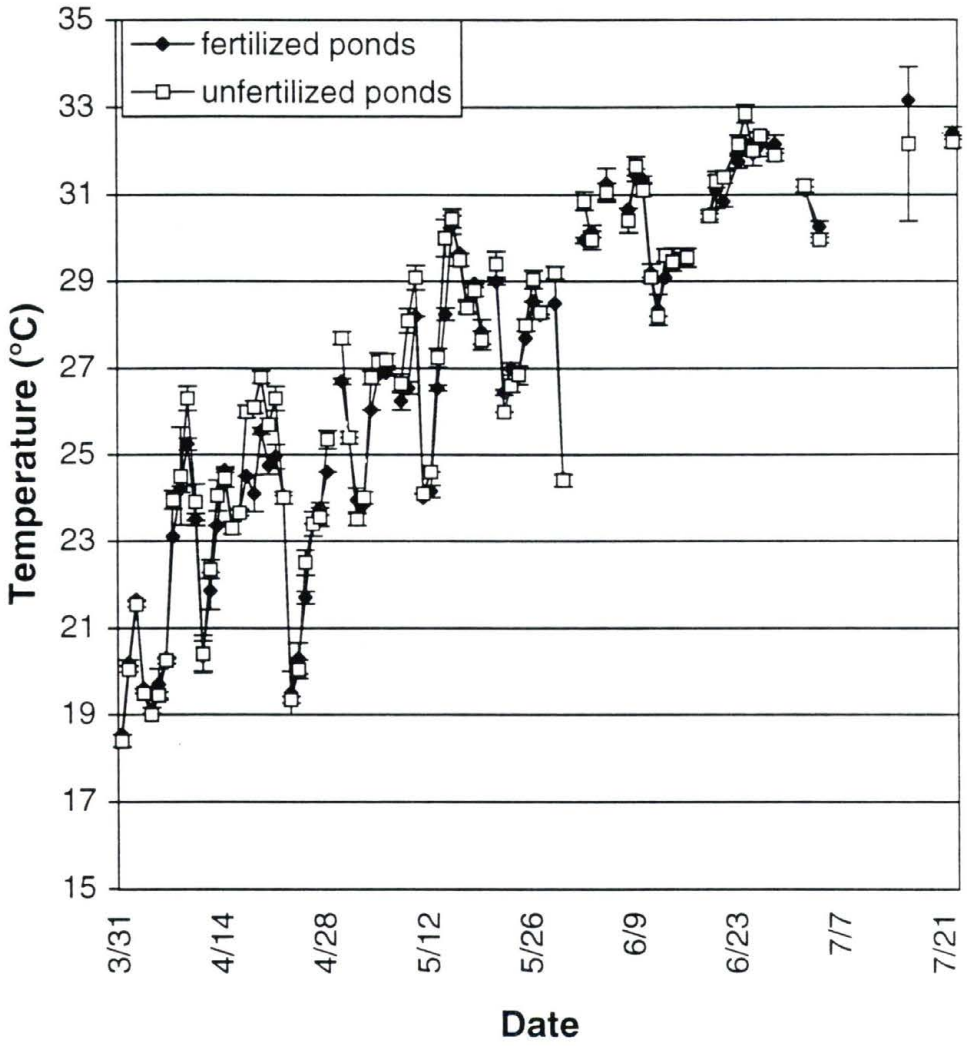

Figure 4. Mean (◆ or □) and standard deviation (vertical lines) of afternoon water temperatures in fertilized and unfertilized ponds.

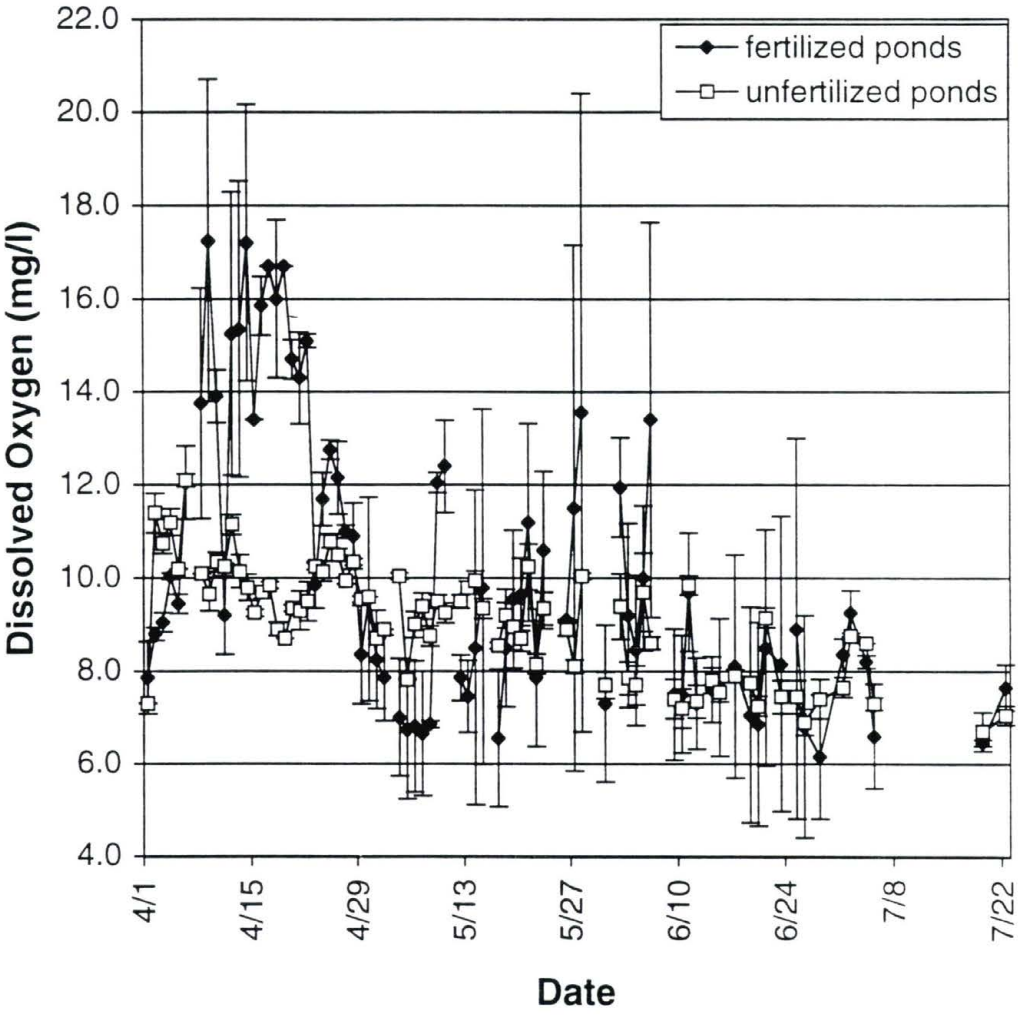

Figure 5. Mean (◆ or □) and standard deviation (vertical lines) of morning dissolved oxygen concentrations in fertilized and unfertilized ponds.

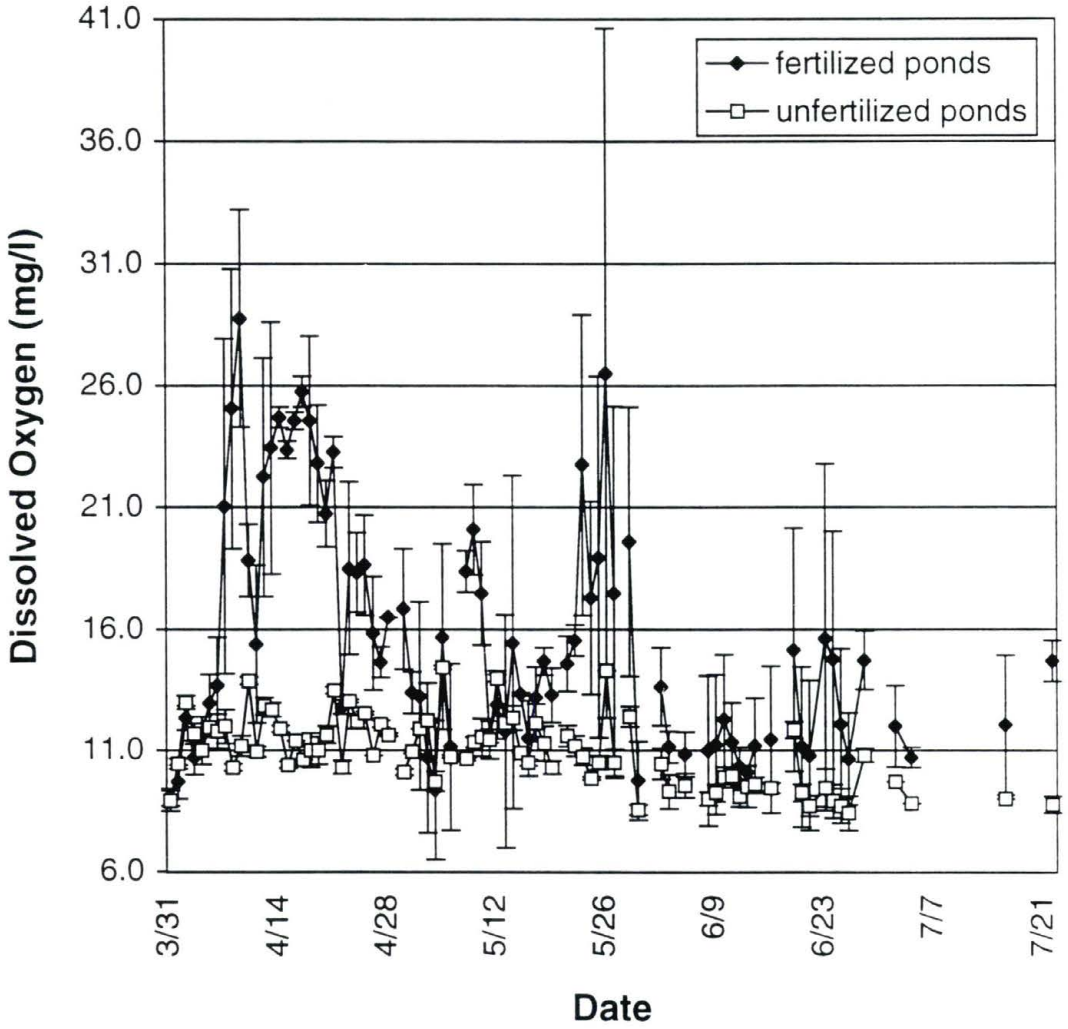

Figure 6. Mean (◆ or □) and standard deviation (vertical lines) of afternoon dissolved oxygen concentrations in fertilized and unfertilized ponds.

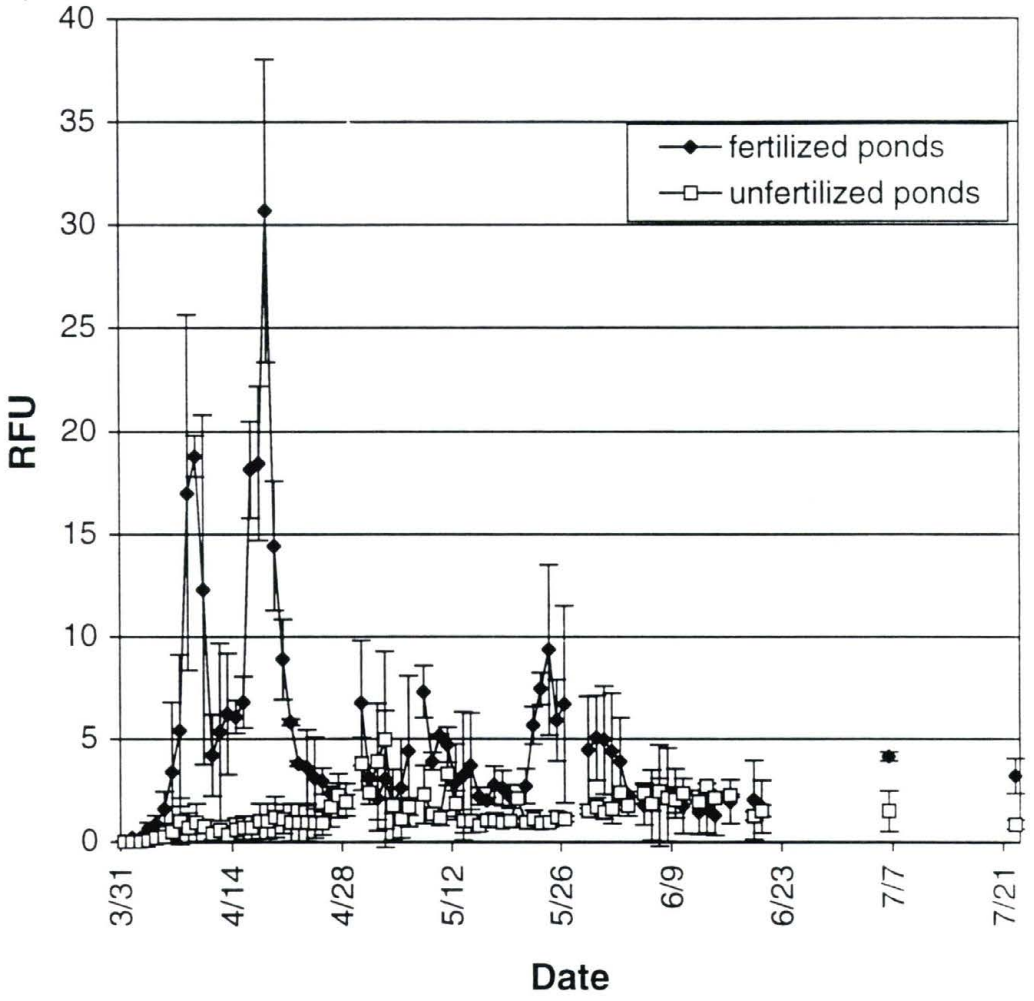

Figure 7. Mean (◆ or □) and standard deviation (vertical lines) of relative fluorescence units (RFU) in fertilized and unfertilized ponds.

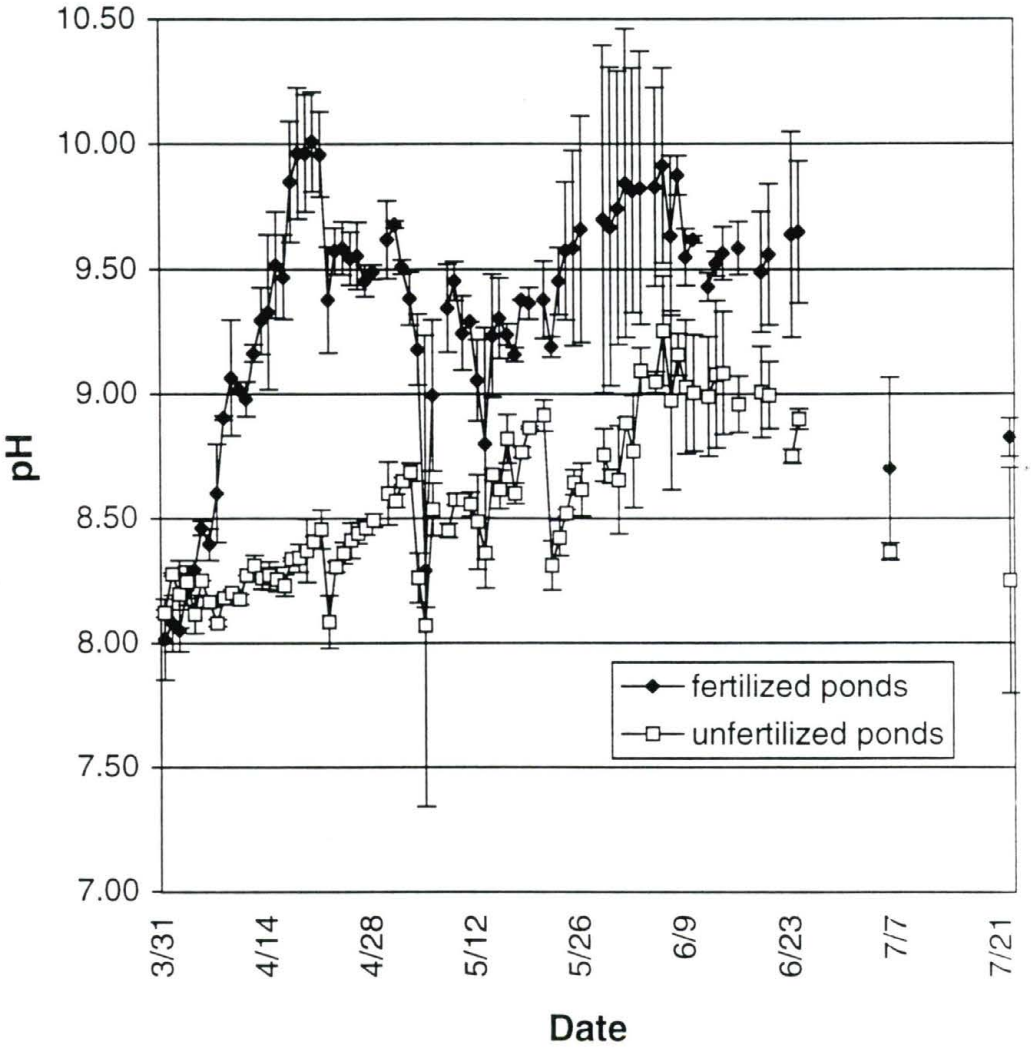

Figure 8. Mean (◆ or □) and standard deviation (vertical lines) of pH in fertilized and unfertilized ponds.

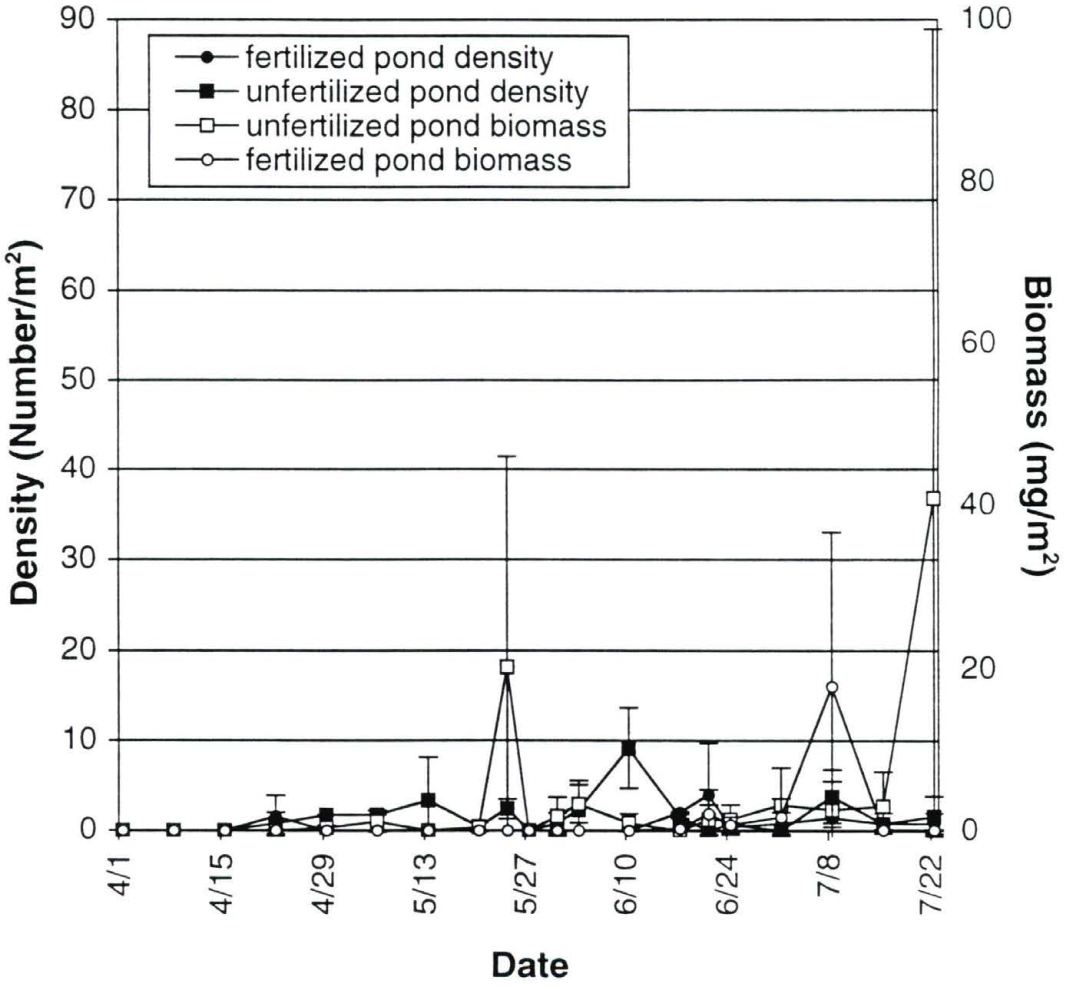

Figure 9. Mean (●, ■, □, or **o**) and standard deviation (vertical lines) of *Pantala* densities and biomass in fertilized and unfertilized ponds.

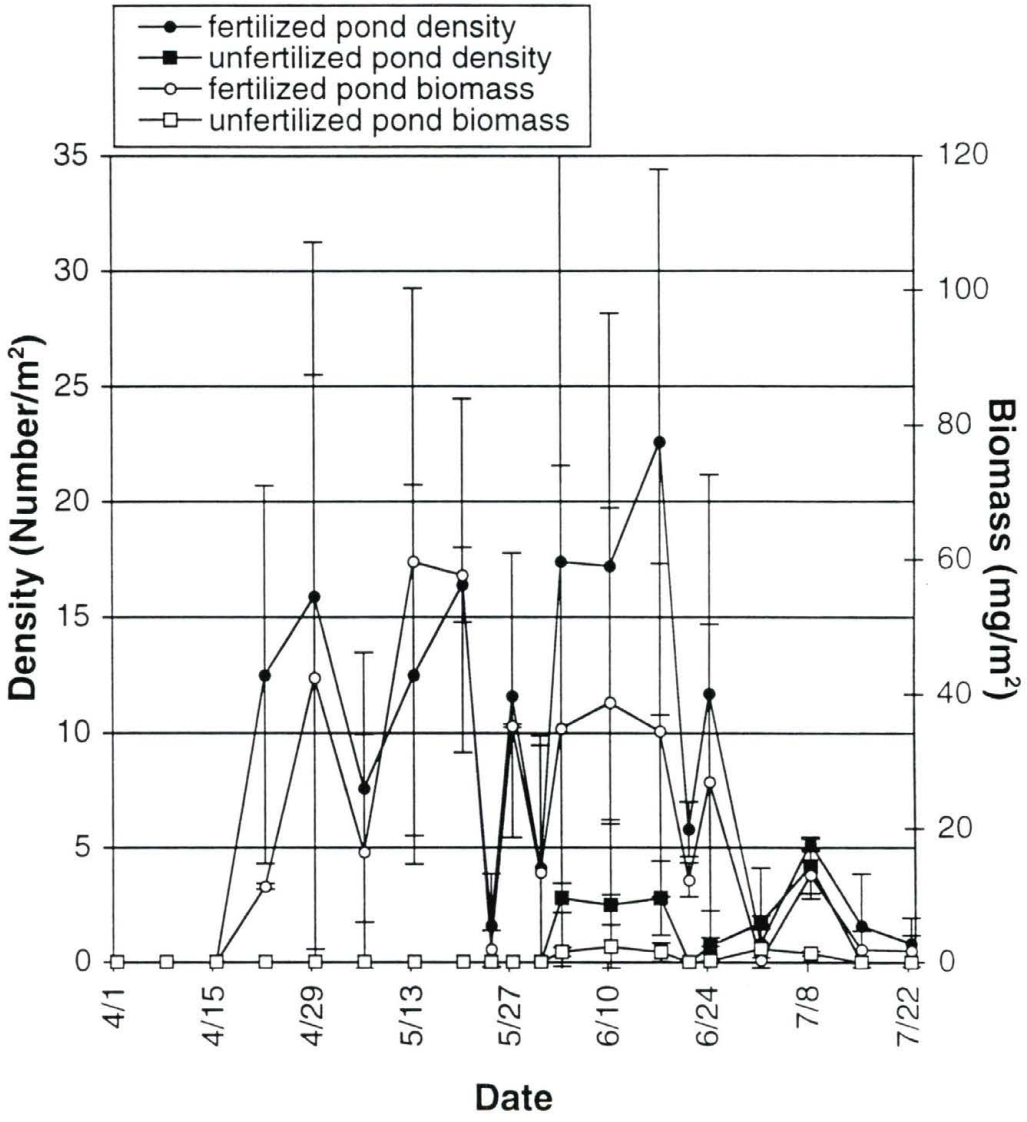

Figure 10. Mean (●, ■, □, or **o**) and standard deviation (vertical lines) of *Berosus* densities and biomass in fertilized and unfertilized ponds.

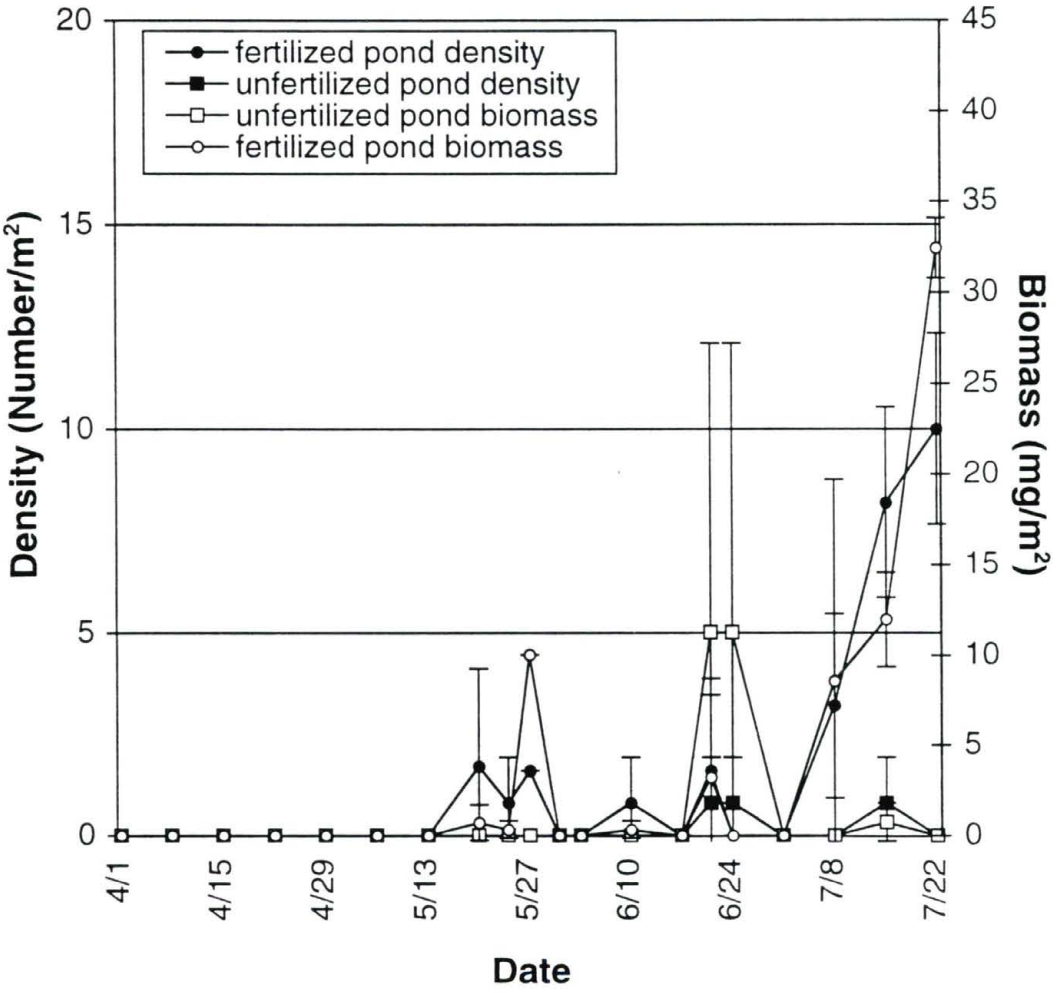

Figure 11. Mean (●, ■, □, or **o**) and standard deviation (vertical lines) of *Pelocoris* densities and biomass in fertilized and unfertilized ponds.

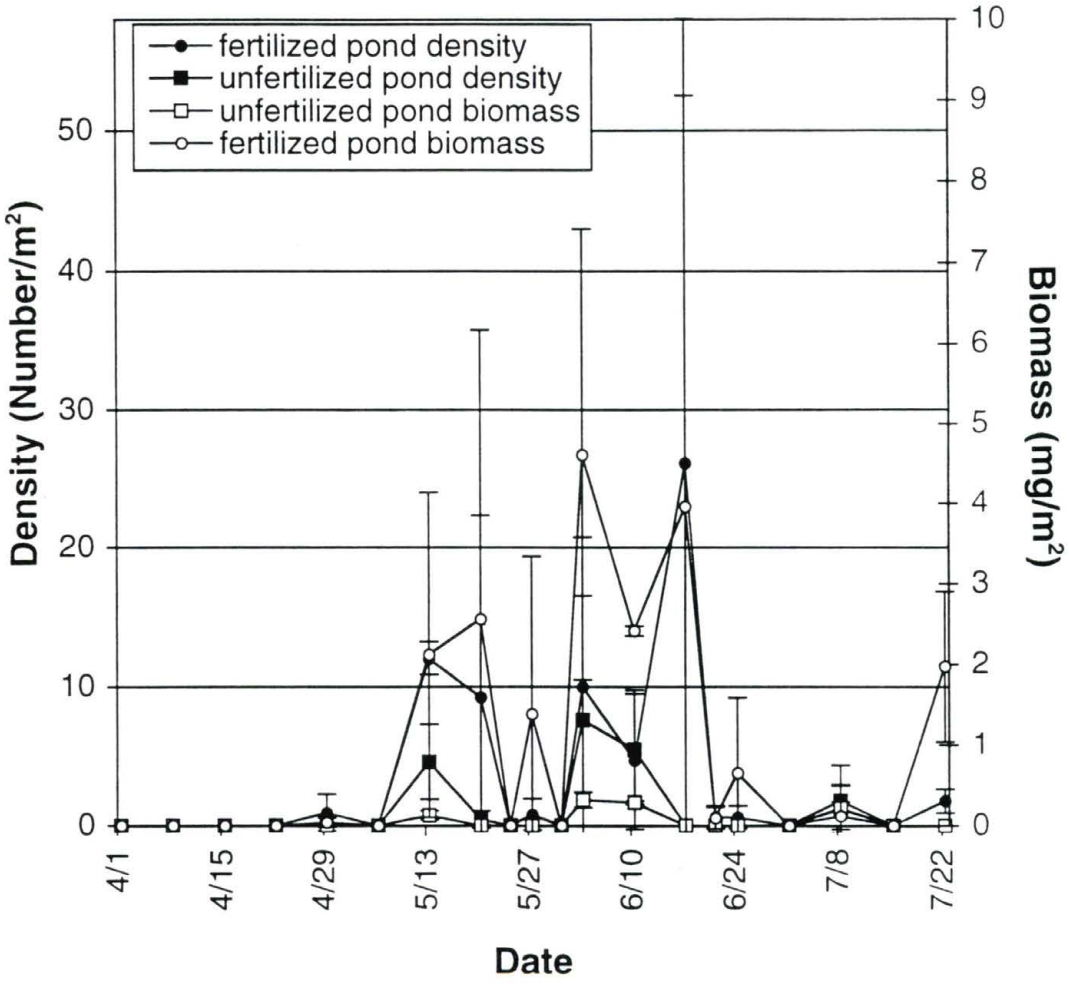

Figure 12. Mean (●, ■, □, or **o**) and standard deviation (vertical lines) of *Buenoa* densities and biomass in fertilized and unfertilized ponds.

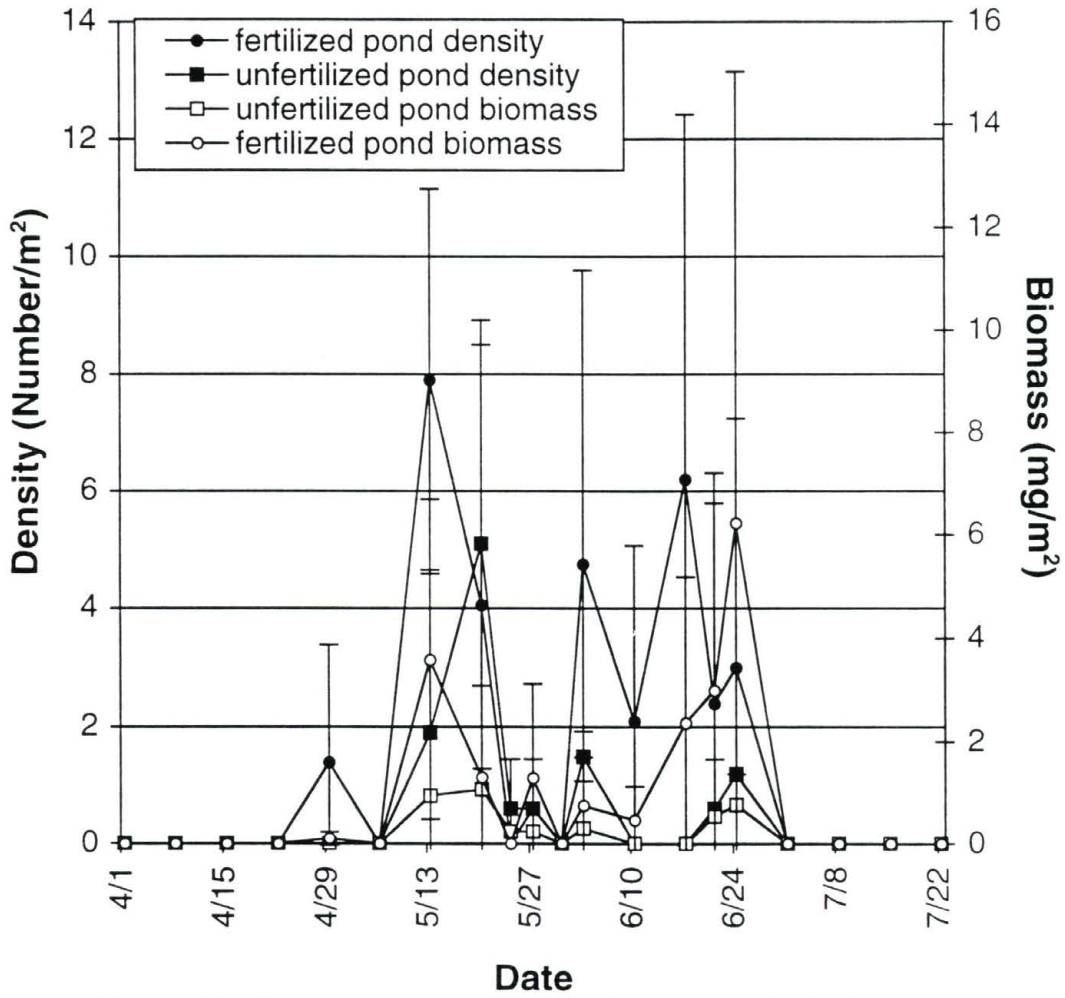

Figure 13. Mean (●, ■, □, or o) and standard deviation (vertical lines) of *Notonecta* densities and biomass in fertilized and unfertilized ponds.

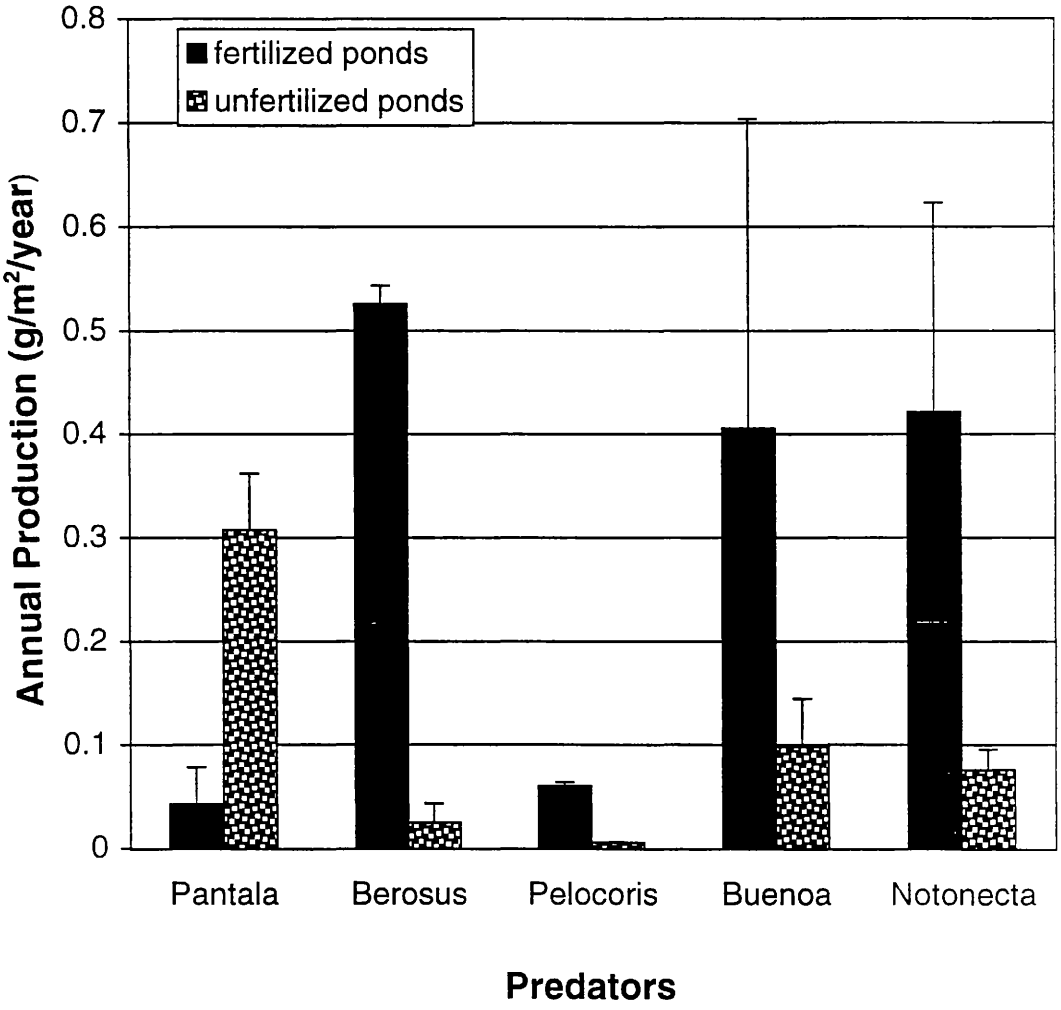

Figure 14. Mean annual production and standard deviation (vertical lines) of predaceous aquatic macroinvertebrates in fertilized and unfertilized ponds.

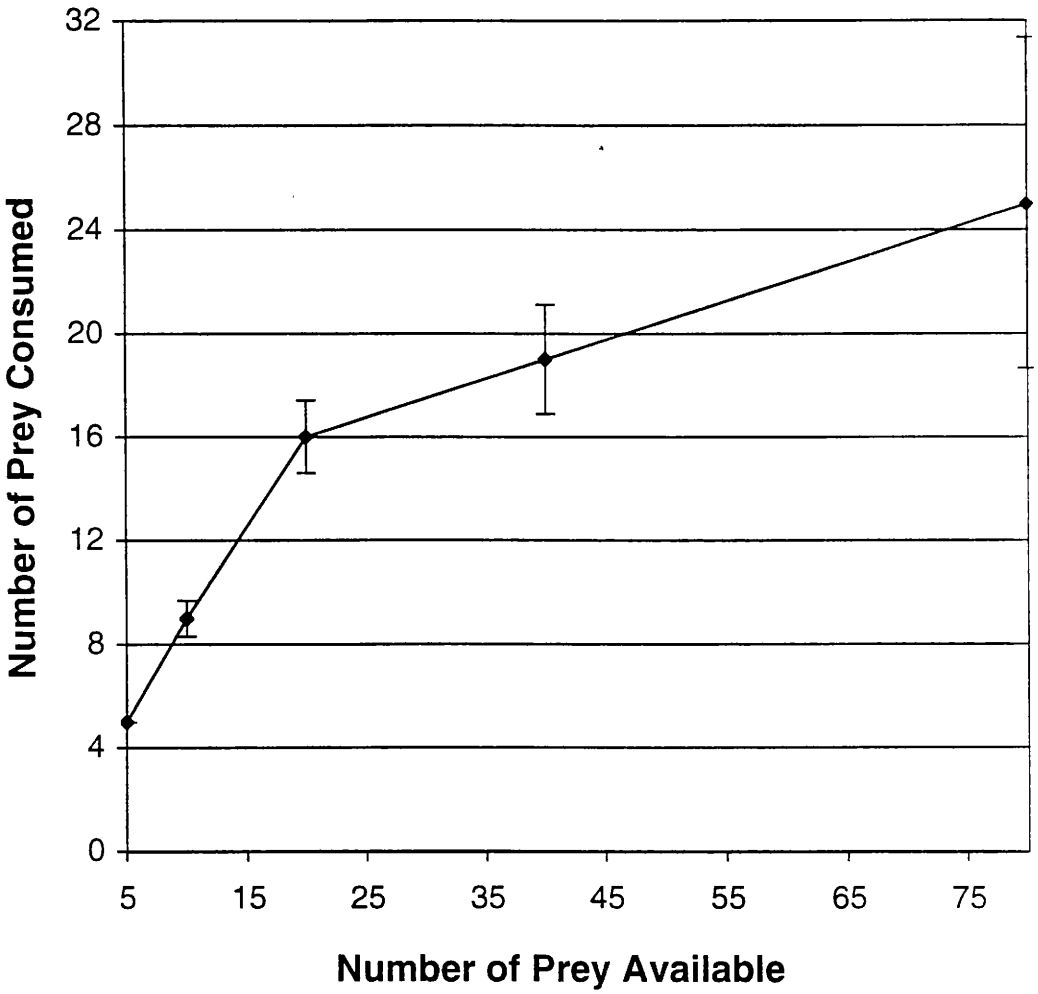

Figure 15. Functional feeding response, showing mean (◆) and standard deviation (vertical lines), for *Pantala* (6.4 mg dry weight) when fed *Baetis* (0.9 mg dry weight/individual) at different densities.

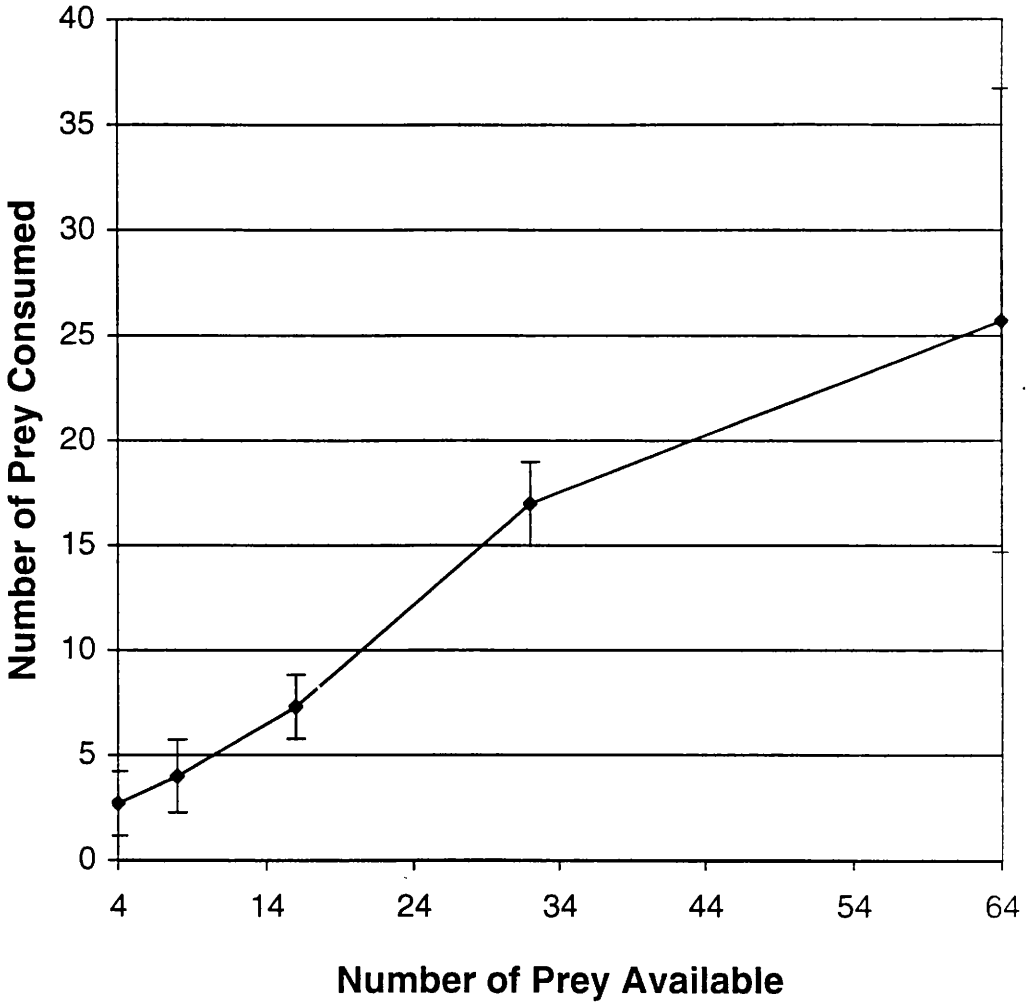

Figure 16. Functional feeding response, showing mean (◆) and standard deviation (vertical lines), for *Berosus* (2.1 mg dry weight) when fed chironomid larvae (0.2 mg dry weight/individual) at different densities.

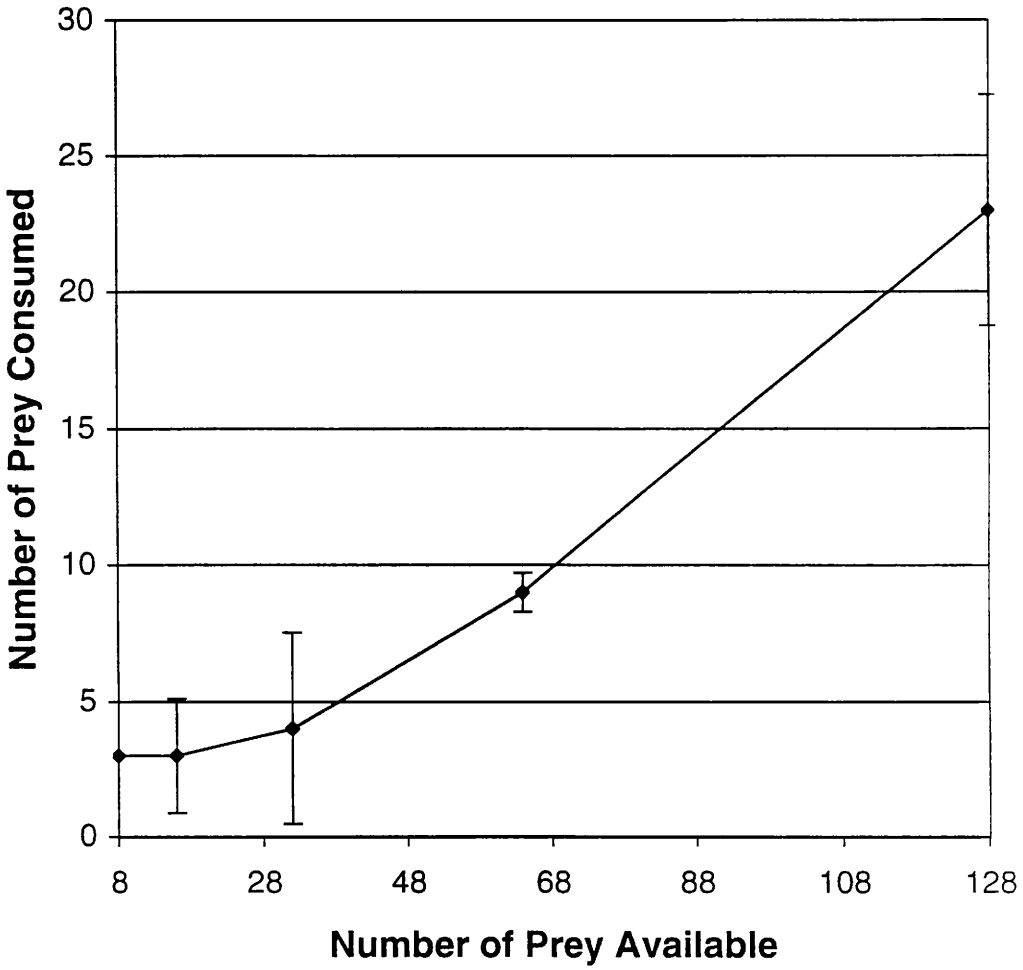

Figure 17. Functional feeding response, showing mean (◆) and standard deviation (vertical lines), for *Pelocoris* (18.5 mg) when fed chironomid larvae (1.3 mg dry weight /individual) at different densities.

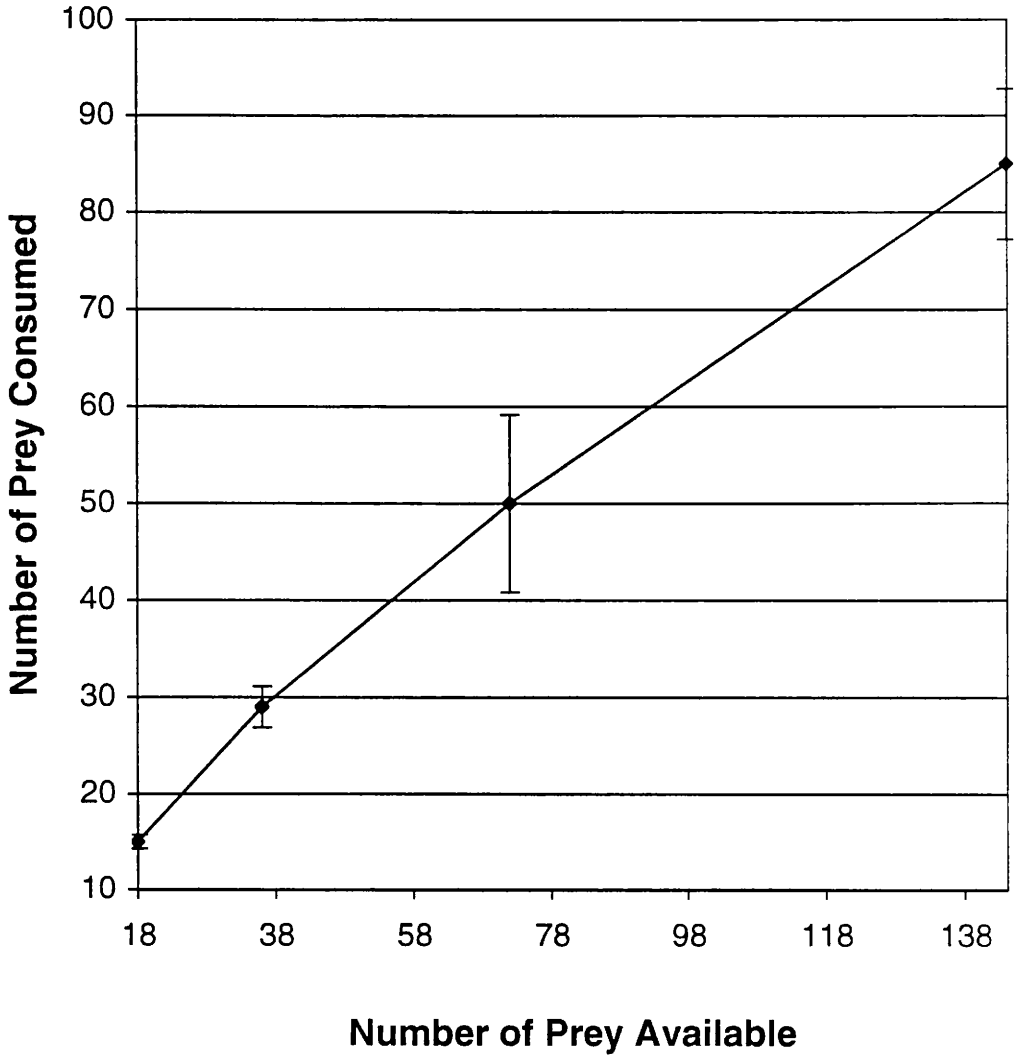

Figure 18. Functional feeding response, showing mean (◆) and standard deviation (vertical lines), for *Buenoa* (1.1 mg dry weight) when fed *Chaoborus* larvae (0.02 mg dry weight/individual) at different densities.

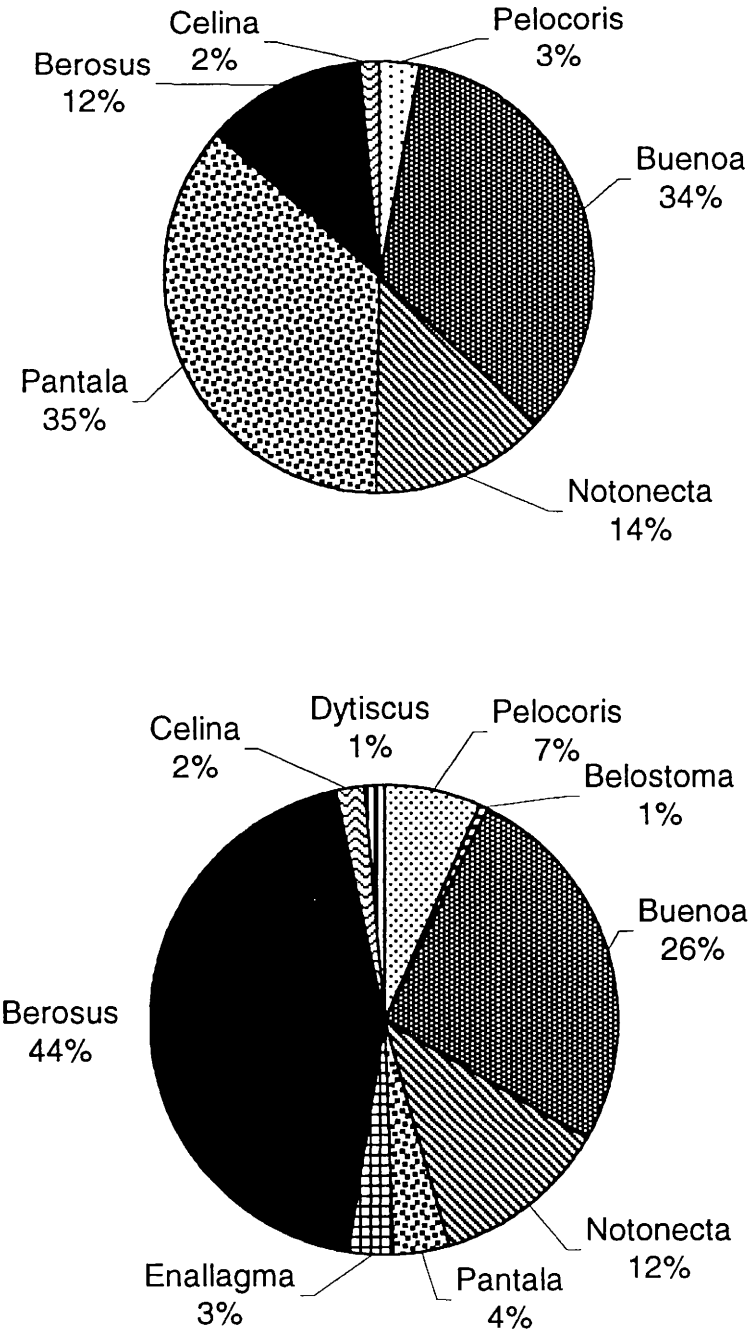

Figure 19. Relative abundance of predaceous aquatic macroinvertebrates collected in unfertilized (top) and fertilized (bottom) ponds. Total number of organisms collected was 678.

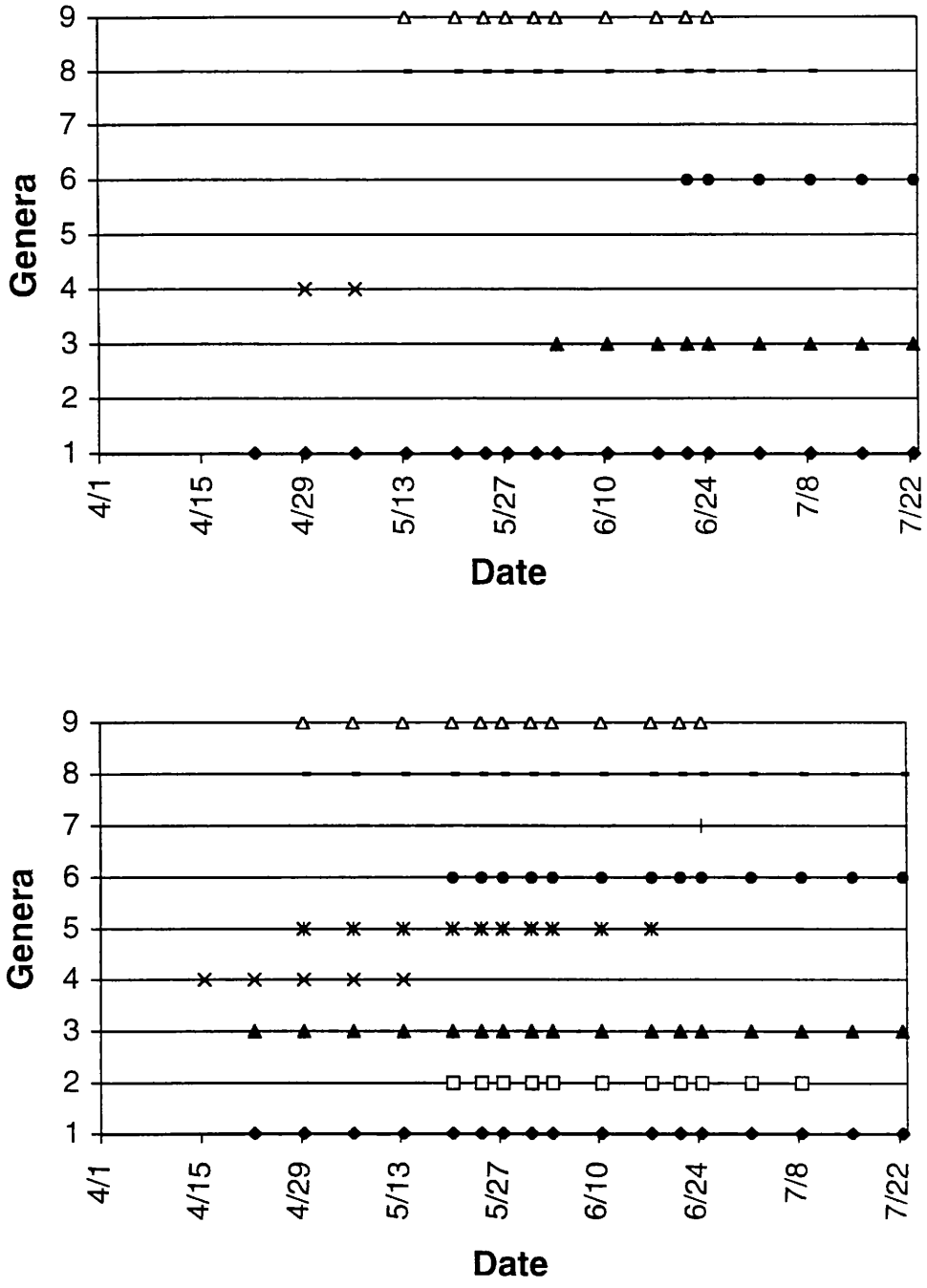

Figure 20. Patterns of predator colonization in unfertilized (top) and fertilized (bottom) ponds. Genera: (1) *Pantala*, (2) *Enallagma*, (3) *Berosus*, (4) *Celina*, (5) *Dytiscus*, (6) *Pelocoris*, (7) *Belostoma*, (8) *Buenoa*, and (9) *Notonecta*.

VITA

Anita Jeanette Holmes was born in Alice, Texas, on November 8, 1962, the daughter of Mary Melissa Byrn and James Edward Byrn. In 1970 she and her family moved to San Marcos, Texas. After completing her work at San Marcos High School, San Marcos, Texas, in 1981, she entered Southwest Texas State University. During the summer of 1986 she attended Texas A&M at Galveston, Texas. As an undergraduate Anita taught general science and botany labs. She received the degree of Bachelor of Science from Southwest Texas State University in August, 1987. During the Fall semester of that year she completed her requirements to become a certified science teacher. She taught chemistry and physics at Karnes City High School, Karnes City, Texas during the 1988 and 1989 school year. Also, she taught biology at the San Marcos Baptist Academy for three consecutive summers beginning in 1988. In July 1989 she was married to James Lincoln Holmes. The following year she enrolled as an intern at the Edwards Aquifer Research and Data Center, where she continued working until August 1996. She entered the Graduate School of Southwest Texas State University in September, 1991. Anita has given an oral presentation of her earlier work at the Texas Academy of Science and a poster presentation at the North American Benthological Society. She has two children; James Thomas Holmes who was born May 17, 1994 and Allan Phillip Holmes who was born October 17, 1997.

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