ECOLOGY OF CHIRONOMIDS ASSOCIATED WITH *Myruiohyllum spicatum* (L.) AND *Heteranthera dubia* (Jacq.) MacM.

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Macroinvertebrate communities inhabiting an exotic, *Myriophyllum spicatum*, and a native, *Heteranthera dubia* macrophyte were studied from March 1999 to June 2000 in experimental ponds. Although macrophyte architecture explained some variation in macroinvertebrate abundance between the two macrophytes, most variation was explained by the sampling months. Total number of macroinvertebrates was found to be positively correlated with epiphyton biomass which differed significantly between the two plant types and among sampling months. Taxa richness did not vary between the two plant types. Chironomid larvae were the most abundant organisms and dominated by *Apedilum elachistus* on both plant communities. Annual production of five chironomid species was estimated by the size-frequency method. Production estimates (P) in g dry wt m^{-2} yr^{-1} of plant surface area for the predator Tanypodinae larvae were: *Larsia decolarata*, P= 0.77 and 0.67, *Labrundinia virescens*, P= 0.59 and 0.35 on *M. spicatum* and *H. dubia*, respectively. Larvae of *Cricotopus sylvestris* and *Psectrocladius vernalis* were collected from *M. spicatum* from March to mid-June. Production of *C. sylvestris* was found to be 0.46 g dry wt m^{-2}, whereas it was 0.07 g dry wt m^{-2} for *P. vernalis* for this period. *Apedilum elachistus* exhibited the highest productivity: 9.9 g dry wt m^{-2} yr^{-1} of plant surface area on *M. spicatum*, and 8.5 g dry wt m^{-2} yr^{-1} on *H. dubia*. These production estimates are among the highest production values reported for a single species.

Additionally, post-ovipositing development times for five chironomid species collected from *Myriophyllum* and *Heteranthera* were determined. Three different temperatures (15°, 20° and 25°C) were chosen to rear eggs under 12L: 12D photoperiod. Egg development times ranged between 1-4 days. Larval development times ranged from 44 days at 20°C for *Tanypus neopunctipennis* to as few as 9 days at 20°C for *Larsia decolorata*.

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CHAPTER 1

EGG TO ADULT DEVELOPMENT TIMES OF FIVE SPECIES OF CHIRONOMIDS

Abstract

Development times were determined for five chironomid species collected from Eurasian milfoil, *Myriophyllum spicatum* L., a species introduced to North America and mixed-native macrophytes in experimental ponds, Denton, TX.

Keywords- Chironomid, development times, aquatic macrophytes.

Introduction

Numerous studies have revealed that chironomid larvae occur abundantly on many aquatic plants (Menzie 1981, Keast 1984, Pardue and Webb 1985, Peets et al. 1994). Chironomids are an important link in energy transfers in aquatic ecosystems and constitute a major food source for many juvenile and adult fish species and other macroinvertebrates (Gerking 1962, Engel 1988). However, little is known about the biology of most of the chironomid species. In order to provide the development data necessary for production studies on larval chironomids, chironomid egg masses collected from field were reared to adults in a controlled laboratory environment. These data provide critical development times needed to interpret the life cycle of chironomid taxa.

Materials and Methods

This study was conducted at the University of North Texas Water Research Field Station located in Denton, Texas. Constructed earthen ponds, often referred to as "mesocosms", were used for the field experiment (Kennedy et al. 1995). Each pond measures 30 m in length and 16 m in width and can be filled to a maximum depth of two meters. Water depth was maintained at approximately 50 cm during this study. Well water was used to compensate for evaporative losses during the study. In May 1998, five mesocosms were planted with the introduced macrophyte, Eurasian milfoil (*Myriophyllum spicatum* L.) and eight mesocoms were planted with the mixed-native macrophytes.

Two different methods were used to collect egg masses. Sweeps were made through the water with fine meshed nets (mesh size: 250μm). Debris collected in the nets was examined for egg masses. In addition to that, individual plants were collected and attached egg masses were removed in the laboratory for rearing. Collections were made, usually in the mornings between June and September 1999, from both native and Eurasian milfoil ponds. The collected eggs were placed in Petri dishes and reared in incubators at the constant temperatures of 15°, 20° and 25°C. All incubators had a 12L: 12D photoperiod. The chosen temperatures represented temperatures expected in the field. Egg masses were observed at least four times a day for hatching. First instars were transferred to mesh covered (mesh size: 600μm) plastic containers (12cm × 8cm), containing small rocks (4-6 cm diameter) and gravel (2-4 mm diameter) for substrate and

filled with 50 ml of dichlorinated water that was gently aerated with air stones. Chironominae larvae were fed daily 0.5 ml of Tetramin (Tetra) fish food (Menzie, 1981) solution (approximately 5g Tetramin/100 ml dechlorinated water). Predaceous Tanypodinae larvae were fed naidid oligochaetes, daily. Water was not changed but it was added to the containers in order to compensate evaporation loss. Excess food was not removed.

Rearing containers were checked daily for adults. When an adult was found, the container was examined carefully for the larval or pupal exuviae for taxonomic associations. Larvae representing each instar were collected with a Pasteur pipette and preserved in 70% ethanol for taxonomic references. Instar determination was made by measuring head capsule widths and lengths with an Olympus Series Cue-2 image analyzer (Olympus, Tokyo) and Olympus SZH dissecting microscope. Date of emergence was recorded for each adult.

Results and Discussion

Development times of five species are given in Table 1. As expected, for those species for which there are data from multiple rearing temperatures, generation times decreased at higher temperatures. *Apedilum elachistus* eggs collected in the field hatched within 2 days at 20° and 25 °C and in 4 days at 15°C. Larvae required an average of 23 days at 15°, 16 days at 20° and 11 days at 25 °C to complete its development from first instar to imago. The pupal stage lasted 3 days at 15 °C and within 1-2 days at 20° and 25°C. Based on the laboratory data one generation of *A. elachistus* could be completed in about 13 days at 25°, in 18 days at 20° and in 27 days at 15°C. The larval development rates for high temperatures (20-25°C) are similar to that (13 days, n=6, T=20-26°C) reported by Nolte (1995) for *A. elachistus* in South America.

Chironomus decorus completed a generation in 39 days at 15°, 27 days at 20° and 23 days at 25°C, whereas *Goeldichironomus holoprasinus* required 30 days at 20° and 22 days at 25° C to complete a generation. Eggs of *C. decorus* hatched in 4 days at 15°C and in 2 days at 20° and 25°C. The same egg development times were observed for *G. holoprasinus* at 20° and 25°C. Pupation took place within 3 days at 15 °C for *C. decorus* and within 1-2 days at 20° and 25 °C for both *C. decorus* and *G. holoprasinus*. The longer development times for *C. decorus* and *G. holoprasimus* compared to *A. elachistus* might reflect the large size of the species (Jackson and Sweeney, 1995).

Table 1. Development (egg to adult) times (in days) of chironomid taxa

Taxa	n (egg mass)	Mean ± SD	T (°C)
Apedilum elachistus Townes, 1945	5	27 ± 0.83	15 ± 0.5
	8	18 ± 0.88	20 ± 0.5
	8	13 ± 0.74	25 ± 0.5
Chironomus decorus Johannsen, 1905	4	39 ± 1.91	15 ± 0.5
	4	27 ± 1.70	20 ± 0.5
	5	23 ± 1.83	25 ± 0.5
Goeldichironomus holoprasinus Goeldi, 1905	4	30 ± 1.89	20 ± 0.5
	3	22 ± 0.81	25 ± 0.5
Larsia decolorata (Malloch, 1915)	2	12 ± 0.71	20 ± 0.5
Tanypus neopunctipennis Sublette, 1964	2	49 ± 0.70	20 ± 0.5
	1	45	25 ± 0.5

Predaceous Tanypodinae larvae, *Larsia decolarata* completed one generation in 12 days at 20°C. Egg masses incubated at 15° and 25 °C for this species were not successfully reared to the adult stage. Eggs of *L. decolorata* hatched in two days, and pupation took place within a day at 20°C. *Tanypus neopunctipennis* required 49 days at 20°C, and 45 days at 25°C to complete a generation. Eggs hatched within 2 days and

pupation occurred in 3 days at 20°C, whereas it took a day for egg hatching and 2 days for pupal development at 25°C.

Most studies estimated egg hatching within a few days to a few weeks after oviposition (Menzie 1981, Ladle et al. 1985, Jackson and Sweeney 1995). Although the exact oviposition times are not known for the collected egg masses of the five chironomid species examined in this study, the egg development time ranged from 1 to 4 days after they were brought to the lab. Temperature constitutes a major controlling factor in egg development (Tokeshi, 1995) and egg development time generally decreases as temperature increases (Jackson and Sweeney 1995). Longer egg development times (4 days) were observed at 15°C whereas eggs incubated at 20° and 25°C completed development within 2 days.

Short development times observed in this study are in general agreement with other laboratory growth studies of chironomids. For example, Mackey (1977) measured growth and development of several species of chironomids in the laboratory at temperatures of 10, 15, and 20°. Development time at 15 ° ranged between 5 days for a small Orthocladiinae, *Cricotopus coronata* to 60 days for larger Chironominae, *Chironomus plumosus*. Menzie (1981) reported that *Cricotopus sylvestris* completed larval development in 28 days at 15°C and 10 days at 22° and 29°C in a laboratory rearing experiment, while the developmental time took 21 days at 18°C and 14 days at 22°C for the same species (Konstantinov 1958). Stites and Benke (1989) and Hauer and Benke (1991) conducted a study that simulated natural conditions (food, light,

temperature) to obtain more realistic growth rates. They used specially designed growth chambers and reared early instar of chironomids. Their results tend to confirm the fast larval development rates observed in the laboratory in this study and several others (Mackey 1977, Menzie 1981, Gray 1981, Jackson and Sweeney 1995).

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CHAPTER 2

SECONDARY PRODUCTION OF *APEDILUM ELACHISTUS* TOWNES (DIPTERA: CHIRONOMIDAE) IN EXPERIMENTAL PONDS

Abstract

The chironomid fauna living on an exotic macrophyte, Eurasian milfoil (*Myriophyllum spicatum* L.) was studied quantitatively for a year in experimental ponds. A total of ten species, two of them Orthocladiinae, five Chironominae and three Tanypodinae, were recorded. Of these ten chironomid taxa, *Apedilum elachistus* comprised 79% of all chironomid species collected on the plants. Annual production of *A. elachistus* was estimated by the size-frequency method to be 9.9 g dry mass/m^2/yr for milfoil surface area. Annual production/biomass was 79/yr. Laboratory reared larvae required an average of 23 days at 15°, 16 days at 20° and 11 days at 25 °C to complete its development from first instar to imago.

Keywords- *Apedilum elachistus*, secondary production, eurasian milfoil, *Myriophyllum spicatum*, experimental ponds.

Introduction

Many studies have revealed that chironomid larvae form a significant portion of the insect fauna on many aquatic macrophytes (Menzie 1980, Keast 1984, Pardue and Webb 1985, Peets et al. 1994). Although the role of chironomids in the trophic dynamics of aquatic systems is well established (Bay 1974, Benke 1976, Dibble and Harrel 1997) there is a dearth of information present in the literature concerning the autoecology of individual species, which may hinder an understanding of their importance in energy flow in lentic ecosystems. Benke et al. (1988) also stated that accurate assessment of secondary production requires consideration of species-specific attributes.

Eurasian milfoil, *Myriophyllum spicatum*, is a submersed perennial plant with finely dissected leaves. It is native to Europe, Asia and Northern Africa (Weldon et al. 1977). Introduced into North America over 50 years ago, it is now widely distributed throughout the United States and portions of Canada (USGS 2000). Eurasian milfoil, often becomes a nuisance, producing dense canopies that shade-out native vegetation and impede recreational use of many lakes. In 1998, I initiated a study to investigate macroinvertebrate communities found on native and exotic macrophyte species. The chironomid *Apedilum elachistus* Townes, 1945 was the predominant macroinvertebrate living on the Eurasian milfoil in experimental ponds. It is also the dominant species of Chironomidae comprising 79% of all chironomid larvae living on the plants. Because of its abundance, *A. elachistus* could be an important food for invertebrates and fish. Larvae of *A. elachistus* were also collected among submersed vegetation from freshwater and

brackish ponds in Florida where the adults emerge all year round (Epler, 1988). Nolte (1995) recorded the same species from a tropical lowland river in central Brazil and provided information on its biology.

Apedilum elachistus has been recorded from North America where it seems to be widely distributed (Oliver et. al, 1990). Sublette (1960) assigned the genus to *Paralauterborniella*. The larva and pupa of *A. elachistus* (as *Paralauterborniella)* were briefly described by Beck and Beck (1970). Epler (1988) resurrects the generic status of *Apedilum* in distinguishing it from *Paralauterborniella* by giving detailed descriptions of larva, pupa, female and male imago.

The objectives of this study were to estimate the annual secondary production and to describe the life cycle of *Apedilum elachistus* inhabiting Eurasian milfoil.

Materials and Methods

Study Site and Design

This study was conducted at the University of North Texas Water Research Field Station located in Denton, Texas. Constructed earthen ponds often referred to as "mesocosms" were used for the field experiment. Each pond measures 30m in length and 16m in width and can be filled to a maximum depth of two meters. Water depth was maintained at approximately 50 cm during our study. Well water was used to compensate for evaporative losses during the study. Mean winter temperature was 11 °C

(range: 6-17°C), whereas the summer temperature ranged between 17-29 °C, with a mean of 24 °C (Fig. 1).

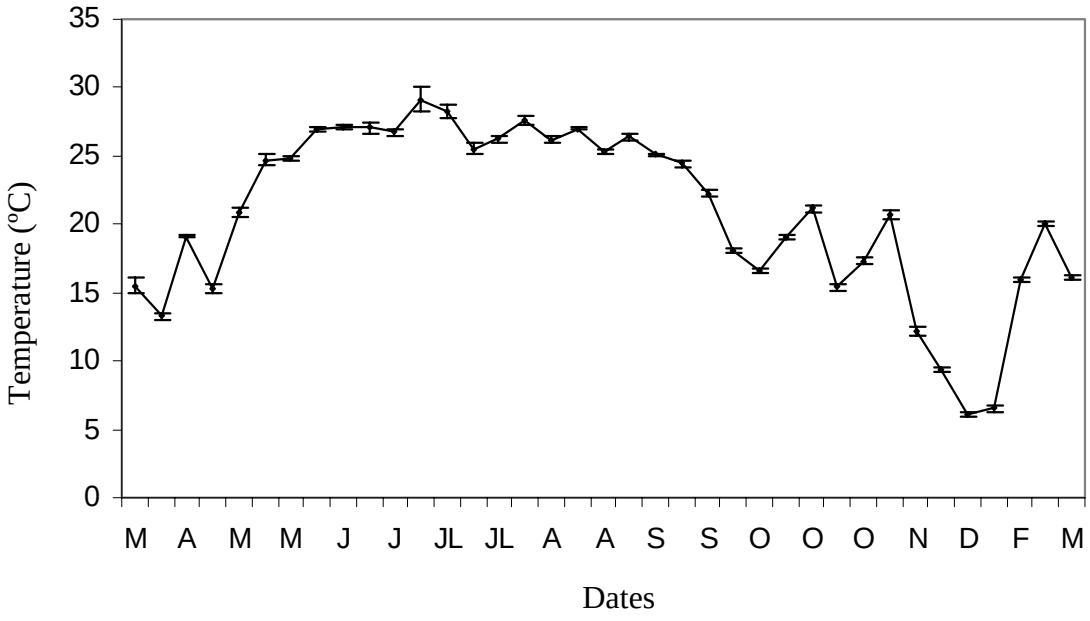

Fig. 1. Mean water surface temperatures ± standard deviation measured at experimental ponds during Mar 1999-Mar 2000.

Five mesocosms were planted with Eurasian milfoil in May 1998. Growth of milfoil was monitored by estimating its surface coverage in each pond. The three mesocosms with the greatest similarity in plant surface coverage were selected for use as replicates in this study.

Collection of Epiphytic Macroinvertebrates

A stratified random design was employed for the data collection. The mesocosms were divided into 12 regions within which random samples were collected. Nine plant samples were collected from the three ponds biweekly from March to June and from November to December 1999 and weekly from June to November 1999. Winter die-off of the plants was observed between late December and March. Plants were collected by cutting an approximately 25-30 cm portion of the leafy segments from the apical tips of plants *in situ*. During the preliminary sampling, prior to removal from the pond, plant sections were isolated by slipping a plexiglass tube, with one end covered by nylon net, over the plant. However, milfoil occurs in thick beds and placement of the tube caused disruption of the plants sufficient to dislodge the attached invertebrates. All collections after the first sampling period followed methods described by Beckett et al. (1991). In this method, the plant stem was cut and the plant was gently raised through the water column and placed in a sampling container. Samples were preserved in 10% formalin. In the laboratory, samples were transferred to petri dishes and all macroinvertebrates were removed from the milfoil under dissecting microscopes (model SZ30, Olympus Optical, Tokyo) at 40X magnification. Chironomids were sorted by taxon and counted. Larvae were mounted in CMC for identification. Instar determination was made by measuring head capsule widths and lengths with an Olympus Series Cue-2 image analyzer (Olympus, Tokyo) and Olympus SZH dissecting microscope.

Counts of macroinvertebrates were expressed in relation to the total surface area availability of Eurasian milfoil. I followed the methods described by Sher-Kaul et al.

(1995) to estimate the surface area of the finely dissected leaves of *M. spicatum*. Surface area per milfoil sample usually was between 80 and 140 cm^2. Animal densities were then converted to the number per square metre of habitat surface for each milfoil sample. The dry weight (biomass) of each sample of epiphyton was determined after washing off the epiphytes with water spray. The preservative in each bottle was also sieved to collect the epiphytes that had fallen off the milfoil. All the collected material were then dried at 105°C for 24 hours.

Adult emergence was monitored using floating emergence traps similar to those described by LeSage and Harrison (1979). The traps contained a collection bottle filled with alcohol that preserved emerging insects. Collection bottles were emptied each week. Water temperature was measured 10 cm below the surface and 10 cm off the bottom at each sampling zone on each sampling date using YSI model 57 dissolved oxygen meter and conductivity meter.

Immature life stages were associated with adults by rearing of fourth instar chironomids individually in 20ml glass vials (28x61mm) with approximately 5ml of dechlorinated water. Rearing chambers were held in an incubator at 20 °C. Sediment samples were also collected and reared in the laboratory during the winter months to find where the larvae were overwintering after the plant die-off.

Rearings of Eggs and Larvae

Egg masses of *Apedilum elachistus* were collected from the plant surface and reared to adults in the laboratory. Twenty- one egg masses were collected from June to

September 1999. The collected eggs were placed in Petri dishes and reared in incubators at the temperatures of 15°, 20° and 25 °C. All incubators had a 12L: 12D photoperiod. The chosen temperatures were selected to represent temperatures expected in the field. After egg hatching first instars were transferred to mesh covered (mesh size: 600μm) plastic containers (12cm × 8cm), containing small rocks and gravel for substrate and filled with 50 ml of dechlorinated water that was gently aerated with air stones. Larvae were fed Tetramin (Tetra) fish food (Menzie, 1981).

Rearing containers were checked daily for adults. Most of the larvae became adults within 1-4 days after the first pupae was seen. Date of emergence was recorded for each adult. Since all the adults did not emerge on the same day, median number of days from egg hatch to emergence was taken for emergence data. Observations were pooled for all egg masses examined at each temperature. Development data (egg to adult) were summarized with arithmetic means and standard deviations with the number of egg masses reared at each temperature.

Biomass and Secondary Production

Biomass (mg dry mass) of instars of *A.elachistus* larvae was estimated using fresh larvae dried at 105 °C for 24 h. Due to the small size of larval chironomids, individual dry weights were based on weights of 50-80 larvae, depending on instar. Dried larvae were weighed (±0.001 mg) on a Cahn C-13 microbalance (Cahn Instruments, Madison, WI).

Annual secondary production was estimated using the size-frequency method described by Hynes (1961) and Hynes and Coleman (1968), as modified by Hamilton (1969) and Benke (1979). The size-frequency method was used for species exhibiting asynchronous life histories with indistinguishable cohorts. Size-frequency histograms were constructed to determine whether cohort structure could be identified from the field samples taken throughout the sampling period. The cohort production interval (CPI), required to calculate annual secondary production, was estimated from laboratory rearing data at different temperatures since it was not possible to estimate the CPI from field data. Negative production values for the smallest size classes were excluded from the production estimates (Benke and Wallace, 1980).

Results

A total of ten species, two of them Orthocladiinae, five Chironominae and three Tanypodinae, were recorded (Table 1). Of these ten chironomid taxa, *Apedilum elachistus* comprised 79% of all chironomid specimens collected on the plants. *Apedilum elachistu*s appeared in late May and populations quickly increased through the summer and early fall, reaching peak densities of 9730 larvae per m^2 of milfoil surface in late August (Fig. 2).

Table 1: List of chironomid taxa recorded from *Myriophyllum spicatum* L. in the experimental ponds.

Subfamily Orthocladiinae
Cricotopus sylvestris (Fabricius, 1794)
Psectrocladius vernalis (Malloch, 1915)
Subfamily Chironominae
Apedilum elachistus Townes, 1945
Dicrotendipes nervosus (Staeger, 1839)
Chironomus decorus Johannsen, 1905
Pseudochironomus richardsoni Malloch, 1915
Tanytarsus spp. (Wulp, 1874)
Subfamily Tanypodinae
Ablabesmyia sp. (Johannsen, 1905)
Labrudinia virescens (Beck & Beck, 1966)
Larsia decolorata (Malloch, 1915)

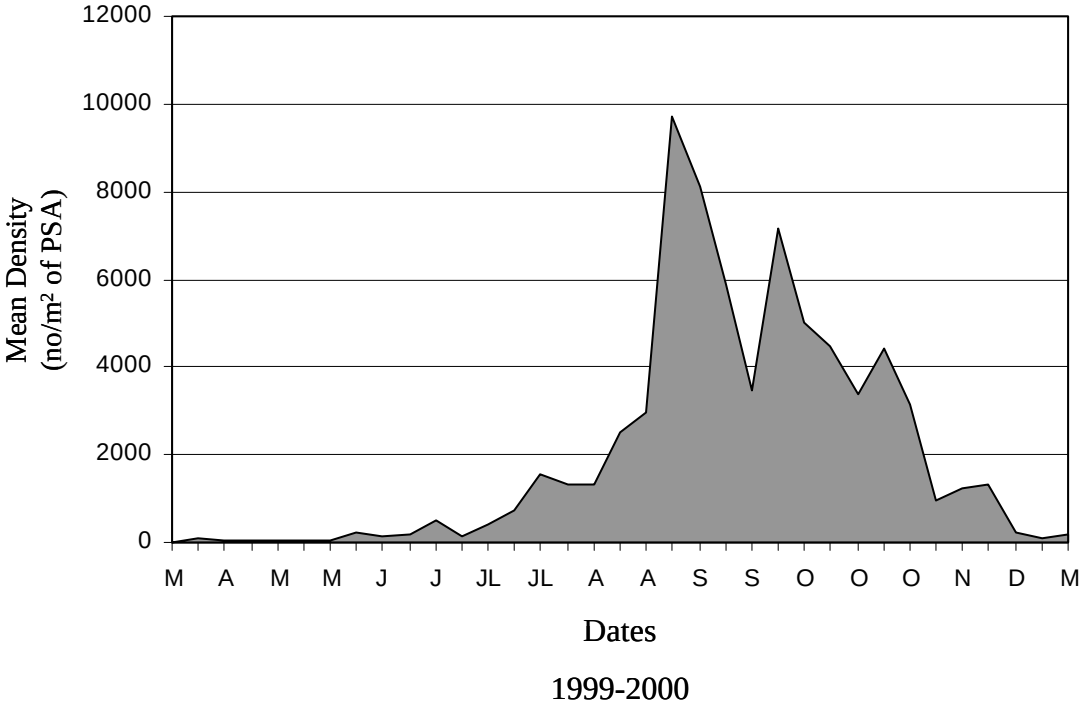

Fig. 2: Mean densities (numbers/m^2 of Plant Surface Area) of *A. elachistus* associated with *M. spicatum* in experimental ponds during sampling period.

Mean dry weights of epiphyton (g per m^2 of plant surface area) for each month are given in Table 2. Densities of *A. elachistus* were significantly correlated (Spearman rank correlation, r^2=0.63, p=0.0001) with the epiphytic growth on the plants.

Ranges of head capsule width and dry mass values for 4 instars of *A. elachistus* are given in Table 3. The following significant (r^2= 0.90, p=0.0001, n=40) simple linear regression was used to derive dry mass values for field preserved specimens: log dry mass = 0.185 + 2.598 (log head capsule width).

Table 2: Monthly mean biomass (g dry weight per m^2 of plant surface area) of epiphyton in experimental ponds, TX, March 1999-March 2000. Ranges are given in parenthesis.

Date	Biomass
Mar-99	0.033 (0.001-0.18)
Apr-99	0.107 (0.02-0.36)
May-99	0.192 (0.08-0.32)
Jun-99	0.117 (0.05-0.26)
Jul-99	0.618 (0.17-1.68)
Aug-99	0.823 (0.23-2.69)
Sep-99	1.186 (0.19-3.41)
Oct-99	0.810 (0.30-1.27)
Nov-99	0.476 (0.09-0.62)
Dec-99	0.205 (0.05-0.52)
Mar-00	0.230 (0.16-0.30)

Table 3: Observed arithmetic ranges of head capsule width and dry mass of the 4 instars of *A. elachistus* living on *M. spicatum,* in experimental ponds.

Instar	n	Head capsule width, mm	Dry mass, mg
1	357	0.062-0.083	0.001-0.002
2	1400	0.098-0.123	0.004-0.007
3	1481	0.147-0.193	0.011-0.021
4	898	0.228-0.295	0.033-0.064

A. elachistus had mixed size distributions on all dates that makes it hard to follow the cohort structure through time (Fig. 3). The major problem in calculating production for the Chironomidae is determining the CPI for each group (Benke et.al 1984). Because of the mixed size distribution of *A. elachistus*, I was unable to estimate CPI from the field data. Therefore, laboratory larval development times at three different temperatures were used to estimate the secondary production. The mean development time of *A. elachistus* from first instar to imago took 23 days at 15°C, 16 days at 20°C and 11 days at 25°C. Eggs collected in the field hatched within 2 days at 20 and 25°C and in 4 days at 15°C. Pupation took place within 3 days at 15°C and within 1-2 days at 20° and 25°C.

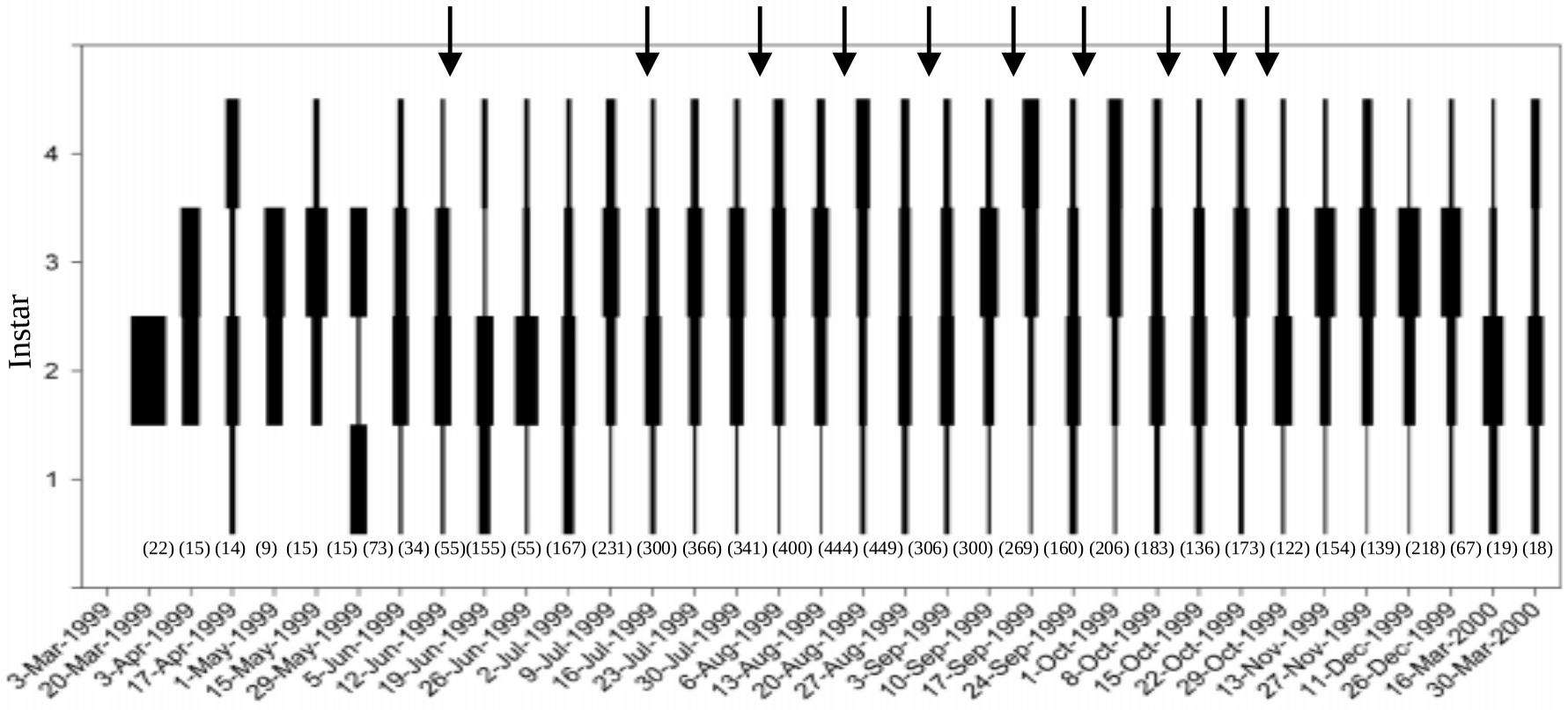

Fig. 3: Relative frequency distribution for *A. elachistus* instars by date in experimental ponds, Denton, TX, 1999-2000.

Arrows indicate the peak adult emergence. Numbers of individuals mounted per date are given in parentheses.

Based on the laboratory data one generation of *A. elachistus* could be completed in about 13 days at 25°, in 18 days at 20° and in 27 days at 15°C (Table 4). The larval development time (CPI) was estimated to be 20 days at 15 °C, 14 days at 20 °C and 10 days at 25 °C. The average CPI (15 days) was used in secondary production calculations.

Table 4: Development times (egg to adult) of *A.elachistus*

N (egg mass)	Days±SD	T (°C)
5	27 ± 0.83	15 ± 0.5
8	18 ± 0.88	20 ± 0.5
8	13 ± 0.74	25 ± 0.5

Annual production of *A. elachistus* was calculated to be 9,889.3 mg/m^2/yr (Table 5). Mean standing stock biomass was estimated 124.8 mg/m^2. The annual production/ biomass rate was calculated to be 79/yr for this population.

Table 5: Production calculations for *A. elachistus* living on Eurasian milfoil (*M. spicatum*) in experimental ponds, 1999-2000.

Instar	*n*, no/m^{2a}	DM,mg^{b}	B, mg^{c}	Δin n^{d}	DM at loss^{e}	Dm loss^{f}	×4, mg^{g}
1	737	0.001	1.11				
2	2321	0.005	11.61	-1584	0.003	-5.148	-20.59*
3	2535	0.017	43.10	-214	0.011	-2.354	-9.42*
4	1500	0.046	69.00	1035	0.032	32.603	130.41
				1500	0.046	69	276
Total			124.81				406.41

Total annual production= 406.41mg/m^2 (365d/15d) = 9889.31 mg/m^2

* negative values set to zero.

[a] Mean instar number present per square meter of milfoil surface area.

[b] Mean dry mass (in milligrams) of individuals of each instar.

[c] Total mean annual biomass for each instar.

[d] Change in number of individuals present between stadia.

[e] Mean dry mass of individuals of each instar when lost from the population (calculated as $DM^x + DM^{x+1}/2$)

[f] Total dry mass (milligrams) lost with each instar.

[g] dry mass loss × the number of instars gives mean annual production for each instar.

Discussion

In a review of the chironomid secondary production literature, few studies were found that examined insect secondary productivity on macrophytes (Table 6). Menzie (1981) reported an annual production of 5.8 g/m^2/yr for *Cricotopus slyvestris* associated with Eurasian milfoil (*M. spicatum*) in Hudson River Estuary. Mackey (1977a) conducted a 2-year study in the *Nuphar* habitat of the Thames River and estimated annual chironomid production for 11 species between 5.04-38.33 g/m^2 (dry weight) in two years. However, these figures are not strictly comparable to our results, since they were for a square meter of littoral zone bottom rather than the finely divided plant leaf surface area. Benson et al. (1980) conducted a study in a small pond (0.94 ha) in which the mean depth was 1.5 m, Denton, TX , and found an annual production value of 2.4 g/m^2/yr and 6.0 g/m^2/yr, for *Procladius* sp. and *Chironomus decorus*, respectively.

High productivity of *A. elachistus* (9.9 g/m^2/yr) from this study can be attributable to several factors. The high density of *A. elachistus* on milfoil habitat is primarily a function of the surface area availability and the spatial niches created by the dense interspersed stems and leaves of the milfoil. The abundance of *Apedilum elachistus* on submersed vegetation has also been noted by Epler (1988) in Florida and Darby (1962) in California rice fields. Several studies have also shown that *M. spicatum* support more invertebrates than other submersed macrophytes (Krecker 1939, Dvorak and Best 1982, Pardue and Webb 1985, Cyr and Downing 1988), whereas others present contradictory evidence (Krull 1970, Soszka 1975, Keast 1984).

Table 6: Comparison of annual production and P/B values of *A. elachistus* in experimental ponds with values reported in the literature from other stream and lake ecosystems

Aquatic ecosystem/ taxon	Annual production	Annual P/B	Reference
Pond, TX			
Procladius	2.4	19.8	Benson et al. 1980
Chironomus decorus	6.0	19.6	Benson et al. 1980
Littoral cove of Hudson River Estuary, NewYork			
Cricotopus slyvestris	5.8	21	Menzie, 1981
Lake Norman, USA			
Tanytarsus	6.8	135	Wilda, 1984
Cladotanytarsus	1.4	75	Wilda, 1984
Chironomus	2.2	66	Wilda, 1984
Laurel Creek Reservoir, Ontario			
Procladius bellus	0.10-0.17	13	Sephton & Paterson, 1986
Juday Creek, Indiana			
Polypedilum convictum	0.8	22	Berg& Hellenthal, 1991

Table 6 continued: Comparison of annual production and P/B values of *A. elachistus* in experimental ponds with values reported in the literature from other stream and lake ecosystems

Aquatic ecosystem/ taxon	Annual production	Annual P/B	Reference
Ogeechee River, SE USA			
Polypedilum	11.3	258	Benke, 1998
Rheotanytarsus	31.1	196	Benke, 1998
Rheocricotopus	9.8	158	Benke, 1998
Experimental ponds, TX	9.9	79	this study

All production values are in $g/m^2/yr$ (dry weight)

Dense plant stands may also provide protection from predators (Crowder and Cooper 1982) and a greater variety of food resources (Wright et al. 1983), both which may contribute to higher invertebrate density.

Coupled with high densities, short development times of *A. elachistus* contributed to high annual production. Accurate estimation of larval development times (CPI) is important in secondary production calculations. In this study, laboratory data were used in which the larvae completed its development in 20 days at 15°, 14 days at 20° and 10 days at 25 °C. These short larval development times are in general agreement with other studies. For example, Nolte (1995) reported that *A. elachistus* completed its development in 13 days at 20-26°C and 11 days at 26-31°C in the laboratory. She also observed that

the same species completed its development from egg to adult less than a week in the field experiment. Mackey (1977) measured growth and development of several species of chironomids at temperatures of 10, 15, and 20°C. Development time at 15° ranged between 5 days for a small Orthocladiinae, *Cricotopus coronata* to 60 days for larger Chironominae, *Chironomus plumosus*. Laboratory growth rates and development times were used in several studies to estimate production (Wilda 1984, Grzybkowska and Witczak 1990, Benke et. al 1984). However, some investigators question whether chironomid growth data obtained from laboratory cultures fed high nutrient content food reflect the growth rates in the field (Lindegaard and Mortensen 1988). Stites and Benke (1989) and Hauer and Benke (1991) conducted *in situ* experiments that simulated natural conditions (food, tempature, light) in order to obtain more realistic growth rates. Their study results confirmed the fast larval development rates observed in the laboratory.

Annual production/biomass for *A .elachistus* was 79/yr, moderate when compared to other values reported for Chironomidae (Table 6). Sephton and Paterson (1986) reported annual P/B rates of 13/yr for *Procladius bellus* in Laurel Creek reservoir, Ontario. An annual P/B of 19.8 and 19.6 were found for *Procladius* sp. and *Chironomus decorus*, respectively, in a shallow pond in North Texas (Benson et al. 1980). In Ogeechee River, in Coastal Plain of the southeastern USA, Benke (1998) reported P/B rates of 258, 196, and 158 for *Polypedilum*, *Rheotanytarsus* and *Rheocricotopus*, respectively, which can be attributed to short larval development times (<2 wk).

Benke (1998) pointed out the importance of quantity and quality of food on high chironomid biomass turnover and production. Tokeshi (1986) stated that the temporal

pattern in epiphytic chironomid community dynamics, especially in terms of production, was strongly influenced by epiphytic algae (predominantly diatoms). Although I did not analyze the gut contents of *A. elachistus* larvae, I found statistically significant positive correlations between *A. elachistus* densities and the amounts of epiphytic growth on the plants. Soszka (1975) reported that in general chironomidae species feed mainly on periphyton (periphytic algae and detritus) and the tissue of vascular plants only slightly contributes to the food. Lindegaard and Mortensen (1988) also reported that the development of a rich biofilm and larger concentration of particulate organic matter, the main sources of food for most chironomids, on macrophytes could cause higher chironomid production. Higher epiphyte biomass and production on *M. spicatum* than on other macrophytes have been noted by several studies (Kowalczewski 1975, Cattaneo and Kalff 1980).

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CHAPTER 3

COMPARISON OF CHIRONOMIDS AND OTHER MACROINVERTEBRATES ASSOCIATED WITH *MYRIOPHYLLUM SPICATUM* AND *HETERANTHERA DUBIA*

Abstract

Macroinvertebrate communities inhabiting exotic, *Myriophyllum spicatum* (L.), and native, *Heteranthera dubia* (Jacq.) MacM., macrophyte were studied from March 1999 to June 2000 in experimental ponds. Although macrophyte architecture explained some variation in macroinvertebrate abundance between the two macrophytes, most variation was explained by the sampling months. Total number of macroinvertebrates was found to be positively correlated with epiphyton biomass which differed significantly between the two plant types and among sampling months. Taxa richness did not vary between the two plant types. Chironomid larvae were the most abundant organisms and were dominated by *Apedilum elachistus* on both plant communities. Annual production of five chironomid species was estimated by the size-frequency method. *A. elachistus* exhibited the highest productivity, 9.9 g dry wt m^{-2} yr^{-1} of plant surface area on *Myriophyllum*, and 8.5 g dry wt m^{-2} yr^{-1} on *Heteranthera*. These production estimates are among the highest production values reported for a single species.

Keywords- Chironomids, secondary production, eurasian milfoil, *Myriophyllum spicatum*, water stargrass, *Heteranthera dubia*, experimental ponds.

Introduction

Submersed aquatic macrophytes are important components of aquatic ecosystems. Littoral zones of many lakes are often dominated by submersed macrophytes. These areas are important in regulating overall productivity of many lakes because of the presence of numerous invertebrates associated with submerged macrophytes, referred as "phytomacrofauna" by Gerking (1957). Aquatic macrophytes create a diversity of habitats for invertebrates requiring vegetative substrate for the attachment of eggs, pupae or larvae (Krull 1970, Keast 1984), provide protection for both predator and prey (Gerrish and Bristow 1979, Savino and Stein 1982) and supply food for many grazers that feed on attached algae (Gerrish and Bristow 1979).

The association of invertebrates with different plant communities has been studied by a variety of authors (Krull 1970, Keast 1984, Miller et. al 1989, Peets et al. 1994). Aquatic macrophytes have also been shown to support high macroinvertebrate densities (Gerking 1957, Soszka 1975, Engel 1988) and support more diverse taxa than adjacent open habitats (Pardue and Webb 1985, Thorp et al. 1997). However, these studies primarily focused on structural parameters, such as population densities, taxa richness and diversity, but functional parameters including secondary productivity have been generally ignored. Because ecosystems have both structure and function, to derive as much information as possible from ecosystem-level studies, both parameters should be studied in conjuction.

One objective of this study was to investigate the influence of different plant communities on macroinvertebrate abundance and community composition. Additionally, secondary productivity of chironomids, the major macrofauna associated with macrophytes was examined. Two aquatic macrophyte species with different leaf morphology were studied in this study: *Myriophyllum spicatum* L. (Eurasian milfoil) and *Heteranthera dubia* (Jacq.) MacM. (water stargrass). *M. spicatum* is a submersed perennial plant with finely dissected leaves. It is native to Europe, Asia and Northern Africa (Weldon et al. 1977). Introduced into North America over 50 years ago, it is now widely distributed throughout the United States and portions of Canada (USGS 1999). Eurasian milfoil often becomes a nuisance, producing dense canopies that shade-out native vegetation and impede recreational use of many lakes. *Heteranthera dubia* is a native plant that is widespread in middle and eastern United States (Muenscher 1944). The slender branching stems, ribbon-like leaves, and yellow flowers are distinctive characteristics of this species (Stutzenbaker, 1999).

Materials and Methods

Study Site and Design

This study was conducted at the University of North Texas Water Research Field Station in Denton, Texas. Constructed earthen ponds often referred to as "mesocosms" were used for the field experiment. Each pond measures 30m in length and 16m in width and can be filled to a maximum depth of two meters. Water depth was maintained at

approximately 50 cm during this study. Well water was used to compensate for evaporative losses during the study.

Five mesocosms were planted with Eurasian milfoil and eight mesocoms were planted with mixed-native macrophytes, including water stargrass, in May 1998. As it was hard to establish mixed-native macrophytes in ponds, additional planting was conducted during June and July 1998. Eurasian milfoil and mixed-native macrophyte growth was monitored by estimating surface coverage in each pond. The three mesocosms with the greatest similarity in plant surface coverage were selected for both mixed natives and Eurasian milfoil as replicates in this study.

Data Collection

A stratified random sampling design was used to sample macrophyte beds and epiphytic macroinvertebrates. The mesocosms were divided into 12 regions within which random samples were collected. Eurasian milfoil (n=9) was collected from the three ponds biweekly from March to June and from November to December 1999 and weekly from June to November 1999. Winter plant die-off was observed between late December and March. Plants were collected by cutting 25-30 cm of the leafy segments from the plants *in situ*. During preliminary sampling, prior to removal from the pond, plant sections were isolated by slipping a plexiglas tube, with one end covered by nylon net, over the plant. However, milfoil occurs in thick beds and placement of the tube distrupted the plants sufficiently to dislodge attached invertebrates. All collections after the first sampling period followed methods described by Beckett et al. (1991). In this

method, the plant stem was cut and the plant gently raised through the water column and placed in a sampling container.

Mixed-native species first appeared in late spring, and collections were began in June 1999. *Heteranthera dubia* (water stargrass) was the dominant native macrophyte. Water stargrass was collected by placing a plexiglass tube with one end covered with nylon net, over the plant. The plant stem was broken off at its base and the sampler brought to the surface with approximately 30-50 cm of plant inside. Nine replicates were collected from three mesocoms until mid-July. However, after this date water stargrass disappeared from two of the mesocosms. Three replicates were taken weekly until November 1999 and biweekly until mid-June 2000. Winter plant die-off was observed between December 1999 and mid-March 2000, and no samples were taken during this period. Milfoil and water stargrass samples were preserved in 10% formalin.

Adult emergence was monitored using floating emergence traps similar to those described by LeSage and Harrison (1979). The traps contained a collection bottle filled with alcohol that preserved emerging insects. Collection bottles were emptied each week.

Immature life stages were associated with adults by rearing fourth instar chironomids individually in 20ml glass vials (28x61mm) with approximately 5ml of dechlorinated water. Rearing chambers were held in an incubator at 20 °C. Egg masses of chironomids were collected from field and reared to adults in the laboratory (Balci and Kennedy, 2002).

Sample processing

In the laboratory, samples were transferred to petri dishes and macroinvertebrates were removed from the plants under dissecting microscopes (model SZ30, Olympus Optical, Tokyo) at 40X magnification. Chironomids were sorted by taxon and counted. Larvae were mounted in CMC for identification. Instar determination was made by measuring head capsule width and length with an Olympus Series Cue-2 image analyzer (Olympus, Tokyo) and Olympus SZH dissecting microscope. Biomass (mg dry mass) of *A. elachistus* larvae was estimated using fresh larvae dried at 105 ˚C for 24 h. Dried larvae were weighed (±0.001 mg) on a Cahn C-13 microbalance (Cahn Instruments, Madison, WI). Biomass for third and fourth instars of *L. decolarata* was also estimated using dried live larvae. Reared specimens preserved in 75% ethanol for 15 months were used to estimate biomass of first and second instar larvae of the same species. Preservation is known to cause weight loss in macroinvertebrates (Howmiller 1972). Berg (1989) showed that percentage weight loss of larval chironomids preserved in 80% ethanol over 48 months (y) could be described by the linear regression y= 5.8+15 log(x) (n=27, r^2=0.90), where x= months in preservative. Based on this regression our samples had a 23% reduction in biomass. This weight loss was checked by comparing late instars of live larvae and preserved larvae, and an average weight loss of 17% was found. I used 17% weight loss to correct the measured dry weight values for first and second instars of *L. decolarata*. Biomass values obtained for *L. decolarata* were used for the other Tanypodinae (*Labrundinia virescens*) to estimate production. Dry mass values reported by Menzie (1978) were used for *C. sylvestris.*

Macroinvertebrate counts were expressed in relation to total surface area availability of the macrophytes. Methods described by Sher-Kaul et al. (1995) were used to estimate the surface area of finely dissected leaves of *M. spicatum*. Leaves of *H. dubia* were considered as isosceles triangles with the bases attached to each other. The formula for a cylinder was used to estimate stem surface area of *H. dubia*. Leaf and stem surface areas were summed to obtain a total surface area for this species. Insect densities were converted to the number per square meter of habitat surface for each milfoil and water stargrass sample. Dry weight (biomass) of each epiphyton sample was determined after washing off the epiphytes with water spray. The preservative in each bottle was sieved to collect epiphytes that had fallen off the plants. All collected material was then dried at 105°C for 24 hours.

Secondary Production

Annual secondary production was estimated using the size-frequency method described by Hynes (1961) and Hynes and Coleman (1968), as modified by Hamilton (1969) and Benke (1979). The size-frequency method was used for species exhibiting asynchronous life histories with indistinguishable cohorts. Size-frequency histograms were constructed to determine whether cohort structure could be identified from field samples taken throughout the sampling period. The cohort production interval (CPI), required to calculate annual secondary production, was estimated from laboratory rearing data for *Apedilum elachistus* and *Larsia decolarata* since it was not possible to estimate the CPI from field data (Balci and Kennedy, 2002). CPI generated for *L. decolarata* was

used for *Labrundinia virescens*. Mackey's (1977) regression equation that predicts larval development time from temperature was used to estimate the CPI for *Cricotopus sylvestris*. CPI calculated for *C*. sylvestris was used for the other Orthocladiinae larvae, *Psectrocladius vernalis*. Negative production values for the smallest size classes were excluded from the production estimates (Benke and Wallace, 1980).

Data Analysis

Eurasian milfoil and water stargrass data were compared for eight months of the study. Sampling dates (n=26) were combined by month to evaluate changes in community structure through time. Total abundance and taxa richness were separately analyzed using two-way analysis of variance (ANOVA) with month (n=8) and plant type (n=2) as independent categorical variables in the SAS GLM procedure (SAS, 1999). Population densities of the dominant taxa and total number of organisms were log-transformed (x+1) prior to analysis to meet assumptions of normality. Pairwise comparisons among sample means were conducted using Student-Newman-Keuls (SNK) test. Independent t-test was used to compare total macroinvertebrate abundance and epiphyte biomass between plant types within the same month. Spearman rank correlation was used to assess the existence of significant relationships between macroinvertebrate abundance and epiphyte biomass (mg dry weight) for the two aquatic macrophytes examined. Epiphyte biomass was compared with date and plant type using two-way ANOVA on log transformed data.

Results

Macroinvertebrate Abundance

Invertebrate taxa observed on *M. spicatum* and *H. dubia* are given in Table 1. Total macrofaunal abundance was 25,274 organisms m^{-2} of plant surface area on *M. spicatum* and 20,898 organisms m^{-2} on *H. dubia*. Macroinvertebrate abundance was highest in August on *H. dubia* and in September on *M. spicatum*, reaching densities of 6720 and 6781 organisms m^{-2}, respectively (Fig. 1). Macroinvertebrates were not observed between late December and March due to macrophyte winter die-off. Chironomids were the most abundant taxa living on both macrophytes comprising 90% and 88% of all the macroinvertebrates on *Myriophyllum* and *Heteranthera*, respectively. *Apedilum elachistus* dominated the chironomids living on both macrophytes and reached densities of 9730 m^{-2} on *Myriophyllum* and 9913 m^{-2} on *Heteranthera* in late August (Fig. 2 and Fig. 3). Although there were shifts in abundance of other chironomid species living on the macrophytes, at no time were any species present in greater numbers than *A. elachistus*.

Table 1. List of macroinvertebrates collected from *M. spicatum* and *H. dubia* between March 1999-June 2000 in experimental ponds. * indicates the taxa found only on native macrophyte (*H. dubia*).

Odonata
Coenagrionidae
Enallagma Selys, 1875
Libellulidae
Libellula Linnaeus, 1758
Erythemis Hagen, 1861
Ephemeroptera
Baetidae
Callibaetis Eaton, 1815
Caenidae
Caenis latipennis Stephans, 1835
Coleoptera
Crysomelidae*
Hydrophilidae
Berosus Leach, 1817
Hemiptera
Notonectidae*
Buenoa Kirkaldy, 1904

Table 1 (continued).

	Mesoveliidae
	Mesovelia Mulsant & Rey, 1852
	Belastomatidae*
Diptera	
	Ceratopogonidae
	Ephydridae*
	Culicidae
	Culiseta Felt, 1904
	Stratiomyidae
	Odontomyia Meigen, 1803
	Chironomidae
	Ablabesmyia sp. (Johannsen, 1905)
	Larsia decolarata (Malloch, 1915)
	Labrundinia virescens (Beck and Beck, 1966)
	Cricotopus sylvestris (Fabricius, 1794)
	Psectrocladius vernalis (Malloch, 1915)
	Apedilum elachistus Townes, 1945
	Pseudochironomus richardsoni Malloch, 1915
	Chironomus decorus Johannsen, 1905
	Dicrotendipes nervosus (Staeger, 1839)

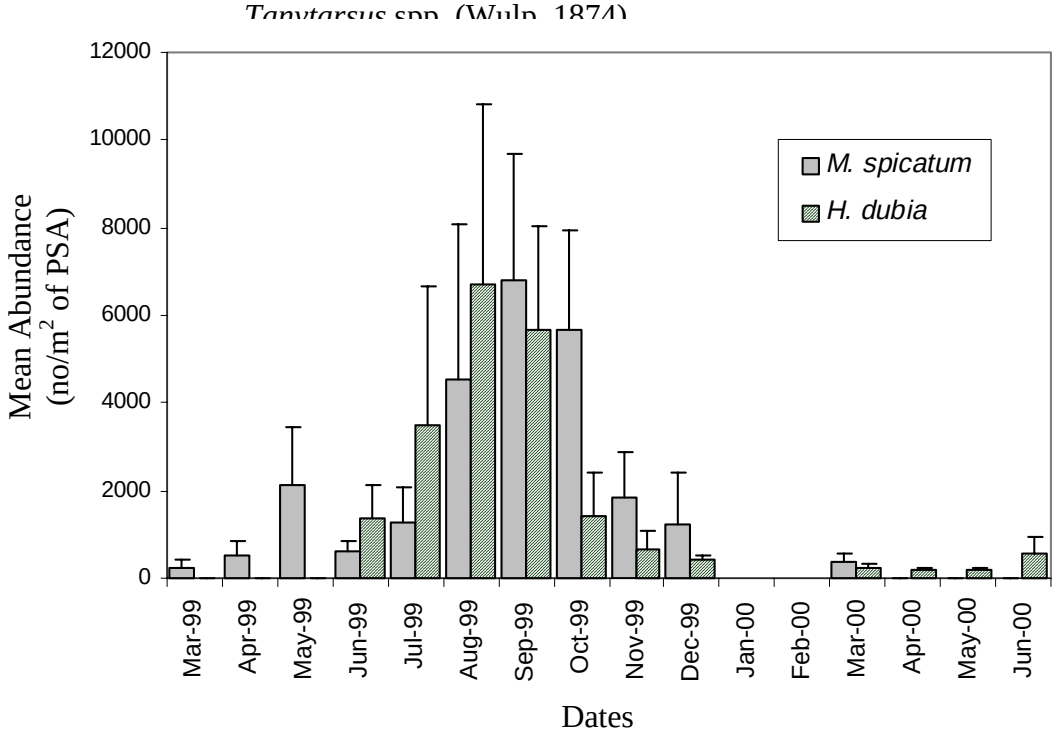

Fig. 1. Comparison of total abundances (no/m^2 of plant surface area) between *M. spicatum* and *H. dubia* in the experimental ponds, during 1999-2000.

The second most abundant chironomid species, *Cricotopus sylvestris*, reached a maximum abundance of 2920 m^{-2} in mid-May on *Myriophyllum* (Fig. 2), a small in comparison to that of *A. elachistus*. Populations of *C. sylvestris* declined sharply between late May and early June until their disappearance from *Myriophyllum* in mid-June. *Psectrocladius vernalis* larvae were also observed during spring on *Myriophyllum*, although with smaller densities. *C. sylvestris* and *P. vernalis* comprised 2.6% of all chironomids on *Heteranthera* and were collected infrequently between December and

mid May. *Larsia decolarata* and *Labrundinia virescens* were dominant Tanypodinae on the macrophytes. Larvae of *L. decolarata* reached their highest density (1270 m^{-2}) in late October on *Myriophyllum*, whereas density in early September was 540 m^{-2} on *Heteranthera* (Fig. 2 and Fig. 3). Larvae of *L. virescens* were less abundant than those of *L. decolarata*, reaching a peak abundance of 440 organisms m^{-2} in early October on *Myriophyllum* and 367 organisms m^{-2} in early September on *Heteranthera*. Coenagrionidae, Baetidae and Ceratopogonidae were dominant non-chironomid families, comprising 6% and 10% of total macroinvertebrate abundance on *Myriophyllum* and *Heteranthera*, respectively.

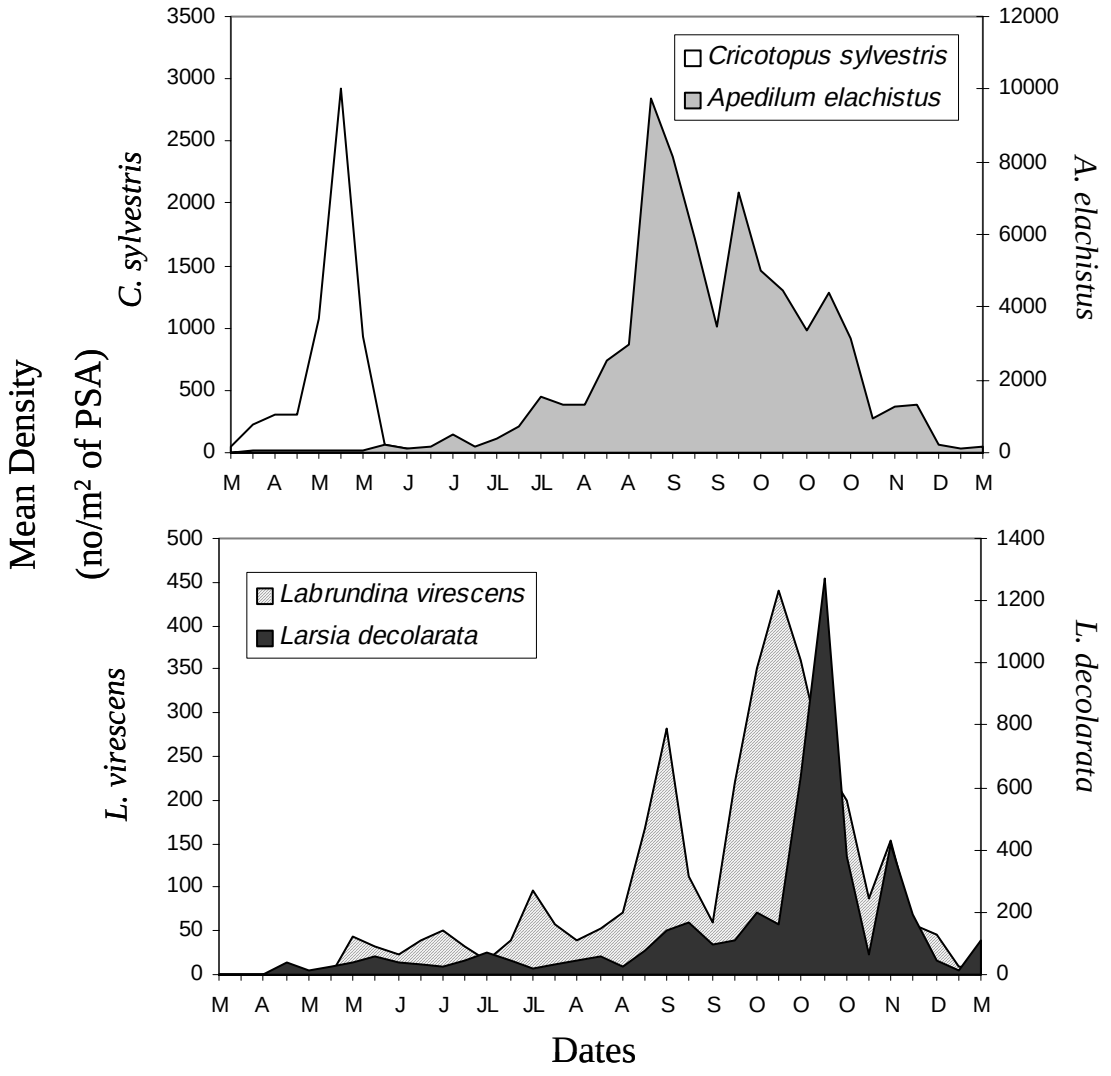

Fig. 2. Mean density (no/m^2 of plant surface area, PSA) of abundant chironomid taxa living on *Myriophyllum* in experimental ponds.

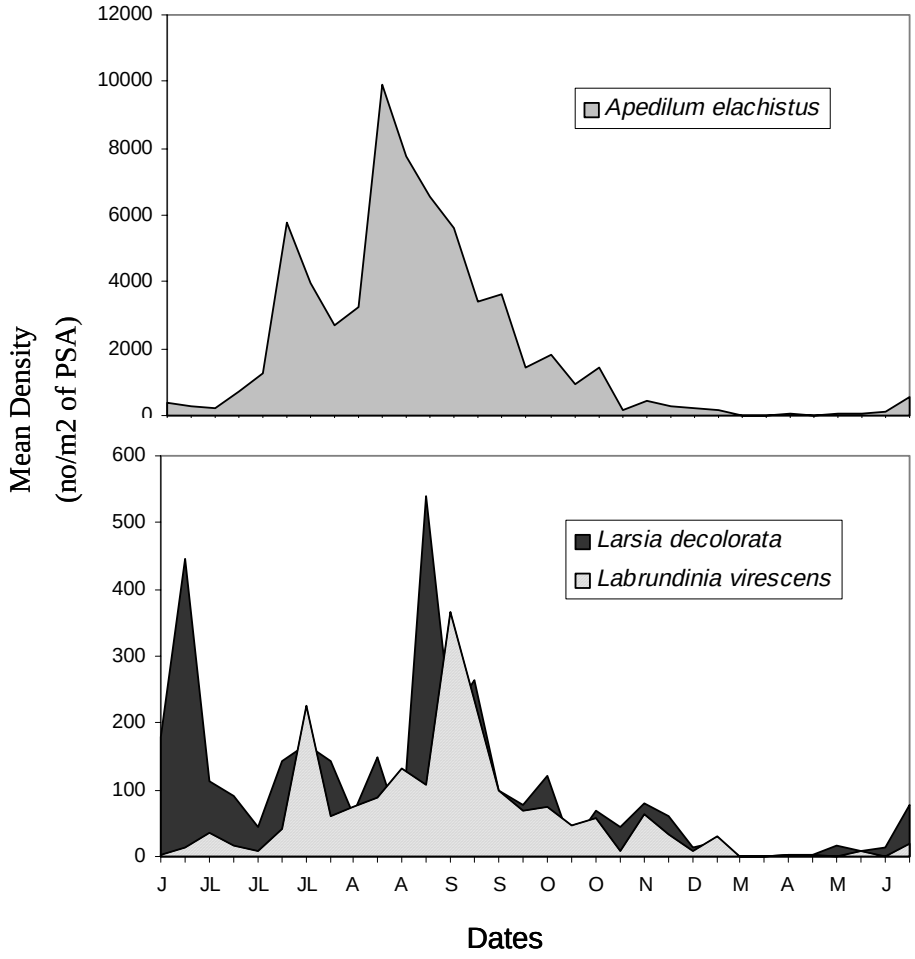

Fig. 3. Mean Density (no/m^2 of plant surface area, PSA) of abundant chironomid taxa living on *Heteranthera* in experimental ponds.

Significant differences for total abundance between *Myriophyllum* and *Heteranthera* were found with two-way ANOVA (Table 2). Although a majority of the variation appeared to be explained by month, interaction of month and plant type were also found to be significant for total abundance. SNK test was performed to identify which months differed significantly from others. Results of SNK showed four distinct groups (Table 3). Because the interaction of month and plant type was statistically significant, independent t-test was used to compare total macroinvertebrate abundance within each month. Total macroinvertebrate densities were significantly different between *Myriophyllum* and *Heteranthera* in June, July, October and November (independent t-test, $p \leq 0.03$, $p \leq 0.01$, $p \leq 0.0001$, $p \leq 0.03$, respectively). Densities were also significantly higher on *Heteranthera* in June and July and on *Myriophyllum* in October and November.

Table 2. Summary table of two-way analysis of variance (ANOVA) procedure comparing macroinvertebrate abundance between plant types (*Myriophyllum* vs. *Heteranthera*) and months in experimental ponds.

Source of Variation	SS	df	MS	*F*	*p*
Plant Type	0.35	1	0.35	4.16	0.043
Month	22.96	7	3.28	38.75	0.0001
Plant Type* Month	5.59	7	0.80	9.43	0.0001

Table 3. Results of Student- Newman- Keuls (SNK) (α= 0.05) procedure on macroinvertebrate total abundance data on two plant types (*M. spicatum* and *H. dubia*) for sampling months

SNK Grouping	Mean	*N*	Month
A	2.75	24	Sep-99
A			
A	2.64	24	Aug-99
B	2.37	30	Oct-99
B			
B	2.19	30	Jul-99
C	1.97	12	Nov-99
C			
C	1.95	12	June-99
C			
C	1.77	12	Dec-99
D	1.44	12	Mar-00

Both macrophytes hosted similar taxa. Macroinvertebrate richness was not significantly different between plant types but it was significantly different among months (Table 4). Number of taxa were significantly higher in June and July than the other sampling months included in the analysis. Two-way ANOVA also found significance in the interaction of month and plant type for taxa richness.

Table 4. Summary table of two-way analysis of variance (ANOVA) procedure comparing macroinvertebrate taxa richness between plant types (*Myriophyllum* vs. *Heteranthera*) and months in experimental ponds.

Source of Variation	SS	df	MS	*F*	*p*
Plant Type	0.78	1	0.78	0.24	0.626
Month	450.39	7	64.34	19.83	0.0001
Plant Type* Month	158.57	7	22.65	6.98	0.0001

Significant correlations were found between epiphyton biomass and total number of macroinvertebrates on both *M. spicatum* (r^2= 0.49, p≤ 0.0001) and *H. dubia* (r^2= 0.78, p≤ 0.0001). Epiphyte biomass reached the highest value of 1.09 g dry mass/m^2

on *H. dubia* in August and 1.19 g dry mass/m^2 on *M. spicatum* in September (Fig. 4). Significant differences were found for epiphyte biomass between *M. spicatum* and *H. dubia* ($p \leq 0.04$, $F=4.11$) and among months ($p \leq 0.0001$, $F=31.51$) using two-way ANOVA. Month and plant type interaction was also found to be highly significant ($p=0.0001$, $F= 9.47$). Significant differences in epiphyte biomass were measured between two plants in all months except August and September (Independent t-test). Epiphyte biomass was significantly different and higher on *H. dubia* in June and July ($p \leq 0.0008$, $p \leq 0.007$, respectively) and on *M. spicatum* in October, November, December and March-00 ($p \leq 0.03$, $p \leq 0.01$, $p \leq 0.008$, $p \leq 0.007$, respectively).

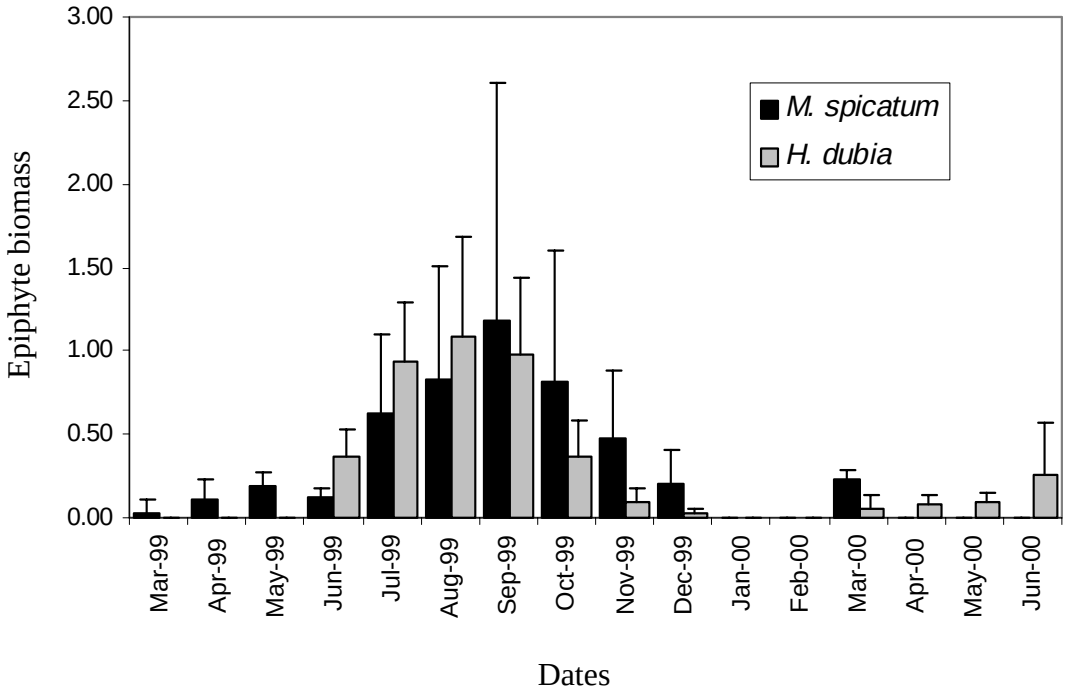

Fig. 4. Comparison of epiphyte biomass (g/m^2 of plant surface area) between *M. spicatum* and *H. dubia* in the experimental ponds, during 1999-2000. Bars indicate Standard Deviation.

Secondary Production of Chironomids

Annual production of *A. elachistus* was found to be 9.9 g dry wt m^{-2} yr^{-1} of plant surface area (Balci and Kennedy, 2001) on *M. spicatum* and 8.5 g dry wt m^{-2} yr^{-1} on *H. dubia* (Table 5). Production of the second most abundant chironomid on *M. spicatum*, *Cricotopus sylvestris* was estimated for the period (from March to mid-June) when the larvae were present on plants and found to be 0.46 g m^{-2} for 104 days. *Psectrocladius vernalis* larvae were present on *M. spicatum* during the same period and its production was calculated as 0.07 g m^{-2} for 111 days. Production estimates for the predator Tanypodinae larvae, *L. decolorata* and *L. virescens*, were found to be 0.77 g m^{-2} y^{-1} and 0.59 g m^{-2} y^{-1}, respectively, on *M. spicatum* whereas it was 0.67 g m^{-2} y^{-1} for *L. decolorata* and 0.35 g m^{-2} y^{-1} for *L. virescens* on *H. dubia*. Larvae of the remaining taxa were rare and collected too infrequently to assess secondary production.

Table 5. Annual production (g dry wt m^{-2} yr^{-1} of plant surface area), cohort and annual P:B ratios of dominant chironomids associated with *M. spicatum* and *H. dubia*.

Taxa	Habitat	P	Cohort P:B	Annual P:B
A. elachistus	*M. spicatum*	9.9	3.3	79
	H. dubia	8.5	3.1	76
C. sylvestris	*M. spicatum*	0.46*	5.0	40
P. vernalis	*M. spicatum*	0.07*	4.0	34
L. decolarata	*M. spicatum*	0.77	3.6	111
	H. dubia	0.67	3.1	95
L. virescens	*M. spicatum*	0.59	3.3	101
	H. dubia	0.35	3.6	110

* Values reported for the period the larvae were present on the plants (from March to mid-June).

Discussion

Macroinvertebrate Abundance and Composition

Jackson (1997) stated that plant morphology could influence epiphytic macroinvertebrate colonization and abundance. In this study, macrophyte morphology explained some of the variation in macroinvertebrate abundance. Plant species with highly dissected leaves are generally support larger macroinvertebrate populations than do plants with broader, undissected leaves (Krecker 1939, Gerrish and Bristow 1979, Dvorak and Best 1982, Jeffries 1993, Cheruvelil et. al 2000). It has been suggested that this pattern occurs because finely dissected leaves provide more habitat for colonization, epiphyton biomass for grazing macroinvertebrates or additional complexity which offers better refuge from predators. However, other studies did not report consistent differences in macroinvertebrate abundance with leaf dissection (Cyr and Downing 1988, Chilton 1990, Thorp et. al 1997). In this study, although some variation in macroinvertebrate abundance can be explained by macrophyte complexity or architecture, it is not the only factor in the observed differences. Significant interaction between plant type and sampling month indicates that factors varying through time were altering the mechanisms that produce a consistent plant-type effect. One of those factors might be the amount of attached epiphyton (Miller et. al 1989, Cattaneo et al. 1998). Significant correlation between epiphyton and macroinvertebrate abundance suggests a role for epiphyton as a food source for epiphytic fauna. The dominant taxon, *Apedilum elachistus*, consumes

organic detritus (Engel, 1988). Total macroinvertebrate abundance and epiphyte biomass were significantly higher on *H. dubia* in June and July-99 and on *M. spicatum* in October and November-99. Other factors such as variability in predation pressure (Dibble and Harrel 1997) and seasonal cycles of growth and decay of macrophytes (Smock and Stoneburner 1980, Beckett et al. 1992) can also be important regulators of macroinvertebrate densities.

Taxa richness between *H. dubia* and *M. spicatum* was not found to be statistically different. Chironomidae was the most dominant taxa on both plants. Other studies also showed chironomids being the most abundant taxa on macrophytes (Schramm et al. 1987).

Chironomid community composition changed through time within the same plant bed. *M. spicatum* was dominated by Orthocladiinae larvae, *C. sylvestris* and *P. vernalis*, during colder spring months, and they disappeared from the plant surfaces with the increasing temperature. The same taxa were observed on *H. dubia* from December-99 to mid May-00. *A. elachistus* dominated the warmer months in both plant communities. These results are similar to that observed by Armitage (1995). He stated that in temperate areas Orthocladiinae dominate the spring and autumn emergence, while Chironominae and Tanypodinae most commonly emerge during the summer months.

Secondary Production of Chironomids

Tokeshi (1995) reviewed the literature on chironomid production from both lentic and lotic systems and suggested that production values less than 2 g dry wt m^{-2} yr^{-1} as low productivity (oligotrophy) and 8-32 g m^{-2} y^{-1} as high productivity (eutrophy). The annual production estimates for *A. elachistus* associated with *M. spicatum* and *H. dubia* are in between the high production limits. High productivity of *A. elachistus* on both plants can be attributed to their high density, the amount of food resources and especially to their short larval development times (Balci and Kennedy 2001). Benke (1998) estimated annual production of 31.1, 11.3 and 9.8 g m^{-2} y^{-1} for snag surface area for *Rheotanytarsus*, *Polypedilum* and *Rheocricotopus*, respectively, found on the snag habitat of a Coastal Plain blackwater river. He reported those values are among the highest estimates reported for chironomids in freshwater systems because of short larval development times. In this study, production of *C. sylvestris* was estimated to be 0.46 g m^{-2} of plant surface for the period that the larvae were collected from the plants. In order to make comparisons with the literature production of *C. sylvestris* was recalculated for one year and found to be 1.6 g m^{-2} y^{-1}. According to Tokeshi (1995) this value is considered as low productivity. Menzie (1981) reported an annual production of 5.8 g m^{-2} y^{-1} for the same species associated with Eurasian milfoil (*M. spicatum*) in Hudson River Estuary, where *C. sylvestris* populations occur year round. Berg and Hellenthal (1991) found annual production estimates of 4.95, 13.4 and 2.88 g m^{-2} y^{-1} for *Cricotopus bicinctus*, *C. triannulatus* and *C. trifascia*, respectively, in a north temperate stream. The lowest production value was found for *Psectrocladius vernalis* (0.07 g m^{-2} from March to

mid- June and 0.23 g m^{-2} for one year) which may be due to the lower densities of the species on the plants. Smock et al. (1985) reported annual production values of 0.003 g m^{-2} y^{-1} and 0.015 g m^{-2} y^{-1} of *Sparganium* surface area for *Labrundinia pilosella* and *Larsia* sp., respectively, in a southeastern blackwater stream. In this study, production of *L. decolorata* and *L. virescens* were higher than those values reported. Tokeshi (1995) reported that species of Tanypodinae, except *Procladius*, have relatively low annual production, generally less than 1 g m^{-2} y^{-1} and more frequently below 0.1 g m^{-2} y^{-1}.

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CONCLUSIONS

Aquatic macrophytes are important components of aquatic ecosystems in several aspects. They occupy key interfaces in stream and lake ecosystems, controlling both productivity and biogeochemical cycles as well as structuring aquatic habitats (Carpenter and Lodge 1986). They also provide a substrate for epiphytic algae (Cattaneo and Kalff 1980) and for macroinvertebrates, which are important sources of food for fish (Mittelbach 1984, Killgore et al. 1989). The presence of aquatic macrophytes provides beneficial habitat for fish (Keast 1984), resulting in increased fish production (Moxley and Langford 1982), higher abundances, and greater species richness (Killgore et al. 1989). Hence, establishment of macrophyte communities in lentic ecosystems is usually a lake management goal. However, the presence of dense beds of submersed aquatic plants may interfere with recreational, ecological and other uses of resources. Several exotic species, including *M. spicatum*, often degrade water quality and deplete dissolved oxygen levels (Honnell et al. 1993). Populations of exotic species often form monocultures that cover large expanses and develop extensive canopies at the water surface, which contribute to degraded conditions (Honnell et al. 1993). Despite the problems non-native plants cause, distribution of many non-native species is increasing, especially in new reservoirs either intentionally by fishermen or unintentionally through transfer of plant fragments or reproductive structures on boats, other vehicles and by water currents (Aiken et al. 1979) or by natural means (ducks, etc.). As a long-term solution to the invasion of exotics in new reservoirs or open habitats of the reservoirs,

Doyle and Smart (1993) proposed the establishment of native plant species. Native plants rarely cause problems in lentic systems. Results of this study showed that taxa composition, density and productivity rates of invertebrates were similar between native and exotic plants. This suggests that the contribution of macroinvertebrates for fish consumption is similar in native and non-native plants. However, this experiment conducted in mesocosms is a small-scale study. Littoral habitats of lentic systems are certainly complex and studies are needed that include functional and structural parameters and different plant types to verify the results of this study.

Additionally, this study provided information on secondary production of chironomid taxa living on native and exotic plants. In most lentic systems, chironomid larvae form an important link between primary producers (phytoplankton and algae) and secondary consumers such as fish (Tokeshi 1995). Results of this study showed that chironomids could be energetically important components of lake ecosystems. Although chironomids are usually the most abundant taxa on aquatic plants, to my knowledge there are no studies present in the literature that compares the productivity of the chironomids on different aquatic plants. The information provided on production of chironomids can contribute to understanding energy dynamics of the littoral areas of many lentic systems.

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APPENDICES

APPENDIX A

Sampling date mean (± S. D.) for taxa associated with *Myriophyllum spicatum*.

Taxon	3-Mar-99		20-Mar-99		3-Apr-99		17-Apr-99		1-May-99	
Enallagma	0	(0)	0	(0)	20	(10)	6.7	(11.5)	13.3	(5.8)
Libellula	0	(0)	0	(0)	3.3	(5.8)	0	(0)	3.3	(5.8)
Erythemis	0	(0)	0	(0)	0	(0)	0	(0)	0	(0)
Callibaetis	0	(0)	0	(0)	3.3	(5.8)	3.3	(5.8)	30	(26.5)
Caenis	0	(0)	0	(0)	0	(0)	0	(0)	0	(0)
P. vernalis	20	(20)	100	(20)	106.7	(72.3)	126.7	(158.9)	90	(20)
C. sylvestris	50	(43.6)	216.7	(37.9)	310	(70)	313.3	(284.5)	1073.3	(64.3)
A. elachistus	0	(0)	73.3	(30.6)	46.7	(37.9)	46.7	(20.8)	33.3	(5.8)
P. richardsoni	0	(0)	0	(0)	13.3	(5.8)	43.3	(35.1)	110	(17.3)
Tanytarsus spp.	0	(0)	0	(0)	0	(0)	0	(0)	16.7	(20.8)
C. decorus	0	(0)	3.3	(5.8)	0	(0)	3.3	(5.8)	0	(0)
D. nervosus	0	(0)	0	(0)	0	(0)	13.3	(15.3)	10	(10)
L. decolarata	0	(0)	0	(0)	0	(0)	36.7	(32.1)	13.3	(11.5)
Ablabesmyia sp.	0	(0)	0	(0)	0	(0)	0	(0)	6.7	(11.5)
L. virescens	0	(0)	0	(0)	0	(0)	0	(0)	0	(0)
Chironomidae pupae	0	(0)	0	(0)	0	(0)	0	(0)	0	(0)
Culiseta	0	(0)	0	(0)	0	(0)	0	(0)	0	(0)
Ceratopogonidae	0	(0)	0	(0)	0	(0)	6.7	(11.5)	16.7	(20.8)
Stratiomyidae	0	(0)	0	(0)	0	(0)	0	(0)	0	(0)
Berosus	0	(0)	3.3	(5.8)	3.3	(5.8)	0	(0)	0	(0)
Mesovelia	0	(0)	0	(0)	0	(0)	0	(0)	0	(0)

Taxon	15-May-99		29-May-99		5-Jun-99		12-Jun-99		19-Jun-99	
Enallagma	23.3	(25.2)	96.7	(30.6)	90	(10)	46.7	(72.3)	30	(10)
Libellula	0	(0)	0	(0)	16.7	(15.3)	6.7	(5.8)	6.7	(5.8)
Erythemis	3.3	(5.8)	0	(0)	0	(0)	0	(0)	0	(0)
Callibaetis	93.3	(83.9)	140	(52.9)	20	(17.3)	40	(17.3)	160	(86.6)
Caenis	0	(0)	0	(0)	0	(0)	0	(0)	0	(0)
P. vernalis	263.3	(300.4)	6.7	(11.5)	26.7	(20.8)	16.7	(15.3)	36.7	(11.5)
C. sylvestris	2920	(1215.1)	926.7	(619.2)	73.3	(45.1)	40	(36.1)	0	(0)
A. elachistus	56.7	(20.8)	50	(60.8)	243.3	(23.1)	126.7	(70.9)	186.7	(46.2)
P. richardsoni	186.7	(83.3)	50	(30)	26.7	(5.8)	10	(10)	10	(10)
Tanytarsus spp.	36.7	(35.1)	16.7	(28.9)	63.3	(15.3)	30	(52)	56.7	(20.8)
C. decorus	0	(0)	0	(0)	0	(0)	0	(0)	0	(0)
D. nervosus	3.3	(5.8)	3.3	(5.8)	10	(10)	0	(0)	10	(10)
L. decolarata	26.7	(46.2)	36.7	(32.1)	56.7	(37.9)	36.7	(28.9)	30	(20)
Ablabesmyia sp.	13.3	(23.1)	0	(0)	0	(0)	3.3	(5.8)	6.7	(5.8)
L. virescens	0	(0)	43.3	(15.3)	33.3	(25.2)	23.3	(11.5)	40	(30)
Chironomidae pupae	0	(0)	0	(0)	0	(0)	0	(0)	0	(0)
Culiseta	0	(0)	0	(0)	0	(0)	0	(0)	0	(0)
Ceratopogonidae	16.7	(11.5)	6.7	(5.8)	16.7	(5.8)	10	(10)	36.7	(15.3)
Stratiomyidae	0	(0)	0	(0)	0	(0)	0	(0)	0	(0)
Berosus	0	(0)	0	(0)	0	(0)	0	(0)	0	(0)
Mesovelia	0	(0)	0	(0)	0	(0)	0	(0)	0	(0)

Taxon	26-Jun-99		2-Jul-99		9-Jul-99		16-Jul-99		23-Jul-99	
Enallagma	83.3	(32.1)	43.3	(15.3)	30	(10)	6.7	(11.5)	40	(10)
Libellula	3.3	(5.8)	13.3	(11.5)	0	(0)	16.7	(5.8)	16.7	(15.3)
Erythemis	0	(0)	0	(0)	0	(0)	0	(0)	0	(0)
Callibaetis	70	(10)	80	(17.3)	13.3	(15.3)	16.7	(5.8)	360	(360.6)
Caenis	0	(0)	0	(0)	0	(0)	0	(0)	0	(0)
P. vernalis	0	(0)	0	(0)	0	(0)	0	(0)	0	(0)
C. sylvestris	0	(0)	0	(0)	0	(0)	0	(0)	0	(0)
A. elachistus	496.7	(166.5)	146.7	(40.4)	393.3	(50.3)	740	(191.6)	1556.7	(570.7)
P. richardsoni	33.3	(11.5)	36.7	(5.8)	13.3	(5.8)	23.3	(20.8)	40	(36.1)
Tanytarsus spp.	60	(43.6)	33.3	(23.1)	70	(17.3)	30	(17.3)	203.3	(32.1)
C. decorus	0	(0)	0	(0)	0	(0)	0	(0)	0	(0)
D. nervosus	0	(0)	0	(0)	0	(0)	0	(0)	0	(0)
L. decolarata	23.3	(20.8)	46.7	(25.2)	73.3	(30.6)	46.7	(5.8)	20	(0)
Ablabesmyia sp.	6.7	(11.5)	30	(20)	13.3	(11.5)	20	(34.6)	6.7	(5.8)
L. virescens	50	(10)	33.3	(25.2)	16.7	(20.8)	40	(36.1)	96.7	(106.9)
Chironomidae pupae	0	(0)	0	(0)	0	(0)	3.3	(5.8)	6.7	(11.5)
Culiseta	0	(0)	0	(0)	0	(0)	10	(10)	0	(0)
Ceratopogonidae	23.3	(5.8)	23.3	(15.3)	20	(17.3)	10	(10)	43.3	(11.5)
Stratiomyidae	0	(0)	0	(0)	3.3	(5.8)	0	(0)	0	(0)
Berosus	0	(0)	0	(0)	0	(0)	0	(0)	3.3	(5.8)
Mesovelia	0	(0)	0	(0)	0	(0)	0	(0)	0	(0)

Taxon	30-Jul-99		6-Aug-99		13-Aug-99		20-Aug-99		27-Aug-99	
Enallagma	50	(30)	16.7	(15.3)	76.7	(15.3)	36.7	(15.3)	60	(26.5)
Libellula	30	(0)	10	(17.3)	30	(17.3)	3.3	(5.8)	33.3	(23.1)
Erythemis	0	(0)	0	(0)	6.7	(5.8)	0	(0)	0	(0)
Callibaetis	46.7	(5.8)	0	(0)	90	(17.3)	6.7	(5.8)	3.3	(5.8)
Caenis	0	(0)	0	(0)	0	(0)	0	(0)	0	(0)
P. vernalis	0	(0)	0	(0)	0	(0)	0	(0)	0	(0)
C. sylvestris	0	(0)	0	(0)	0	(0)	0	(0)	0	(0)
A. elachistus	1326.7	(260.8)	1326.7	(751.1)	2526.7	(1111)	2970	(1251.4)	9733.3	(1101.9)
P. richardsoni	50	(45.8)	0	(0)	0	(0)	20	(34.6)	0	(0)
Tanytarsus spp.	76.7	(15.3)	16.7	(20.8)	3.3	(5.8)	273.3	(197.3)	0	(0)
C. decorus	0	(0)	0	(0)	0	(0)	0	(0)	0	(0)
D. nervosus	0	(0)	0	(0)	0	(0)	0	(0)	0	(0)
L. decolarata	33.3	(25.2)	43.3	(11.5)	56.7	(56.9)	26.7	(15.3)	76.7	(20.8)
Ablabesmyia sp.	0	(0)	0	(0)	0	(0)	3.3	(5.8)	0	(0)
L. virescens	56.7	(72.3)	40	(17.3)	53.3	(40.4)	70	(60)	166.7	(58.6)
Chironomidae pupae	3.3	(5.8)	0	(0)	36.7	(15.3)	43.3	(28.9)	6.7	(11.5)
Culiseta	0	(0)	0	(0)	0	(0)	0	(0)	3.3	(5.8)
Ceratopogonidae	123.3	(65.1)	43.3	(15.3)	16.7	(11.5)	150	(65.6)	10	(17.3)
Stratiomyidae	0	(0)	0	(0)	0	(0)	0	(0)	0	(0)
Berosus	0	(0)	0	(0)	13.3	(11.5)	3.3	(5.8)	3.3	(5.8)
Mesovelia	0	(0)	0	(0)	0	(0)	13.3	(5.8)	3.3	(5.8)

Taxon	3-Sep-99		10-Sep-99		17-Sep-99		24-Sep-99		1-Oct-99	
Enallagma	100	(60.8)	36.7	(20.8)	30	(26.5)	23.3	(32.1)	66.7	(25.2)
Libellula	6.7	(5.8)	26.7	(20.8)	13.3	(15.3)	20	(0)	13.3	(11.5)
Erythemis	3.3	(5.8)	0	(0)	0	(0)	0	(0)	0	(0)
Callibaetis	73.3	(55.1)	6.7	(5.8)	0	(0)	16.7	(28.9)	13.3	(15.3)
Caenis	6.7	(5.8)	0	(0)	0	(0)	0	(0)	23.3	(40.4)
P. vernalis	0	(0)	0	(0)	0	(0)	0	(0)	0	(0)
C. sylvestris	0	(0)	0	(0)	0	(0)	0	(0)	0	(0)
A. elachistus	8133.3	(1500.5)	5906.7	(2683.6)	3460	(1585)	7156.7	(2763.2)	5033.3	(3629.9)
P. richardsoni	0	(0)	0	(0)	0	(0)	0	(0)	0	(0)
Tanytarsus spp.	0	(0)	0	(0)	0	(0)	246.7	(360.2)	30	(52)
C. decorus	0	(0)	0	(0)	0	(0)	0	(0)	0	(0)
D. nervosus	0	(0)	0	(0)	0	(0)	0	(0)	0	(0)
L. decolarata	140	(141.1)	166.7	(121)	96.7	(98.1)	110	(20)	200	(185.2)
Ablabesmyia sp.	16.7	(20.8)	0	(0)	0	(0)	0	(0)	0	(0)
L. virescens	283.3	(383.7)	113.3	(111.5)	60	(45.8)	220	(60)	350	190.5
Chironomidae pupae	6.7	(11.5)	0	(0)	23.3	(15.3)	46.7	(56.9)	66.7	(80.8)
Culiseta	0	(0)	0	(0)	0	(0)	0	(0)	0	(0)
Ceratopogonidae	26.7	(46.2)	106.7	(47.3)	160	(103.9)	186.7	(169.2)	236.7	(228.1)
Stratiomyidae	0	(0)	6.7	(11.5)	3.3	(5.8)	0	(0)	0	(0)
Berosus	20	(34.6)	0	(0)	0	(0)	20	(17.3)	0	(0)
Mesovelia	0	(0)	0	(0)	40	(43.6)	0	(0)	46.7	(72.3)

Taxon	8-Oct-99		15-Oct-99		22-Oct-99		29-Oct-99		13-Nov-99	
Enallagma	33.3	(40.4)	350	(79.4)	80	(52)	86.7	(40.4)	80	(43.6)
Libellula	93.3	(106.9)	36.7	(35.1)	103.3	(46.2)	16.7	(20.8)	23.3	(11.5)
Erythemis	0	(0)	0	(0)	0	(0)	0	(0)	0	(0)
Callibaetis	120	(130.8)	46.7	(20.8)	223.3	(105)	150	(210)	136.7	(168.6)
Caenis	0	(0)	0	(0)	0	(0)	0	(0)	0	(0)
P. vernalis	0	(0)	0	(0)	0	(0)	0	(0)	0	(0)
C. sylvestris	0	(0)	0	(0)	0	(0)	0	(0)	0	(0)
A. elachistus	4473.3	(1065)	3370	(1256.5)	4410	(1151.7)	3130	(2344.7)	963.3	(549.9)
P. richardsoni	0	(0)	0	(0)	0	(0)	0	(0)	0	(0)
Tanytarsus spp.	0	(0)	320	(121.7)	173.3	(242.1)	413.3	(217.3)	70	(55.7)
C. decorus	0	(0)	60	(103.9)	20	(34.6)	116.7	(63.5)	50	(86.6)
D. nervosus	0	(0)	0	(0)	0	(0)	0	(0)	0	(0)
L. decolarata	163.3	(45.1)	633.3	(238)	1270	(112.7)	376.7	(253.2)	63.3	(61.1)
Ablabesmyia sp.	0	(0)	0	(0)	0	(0)	0	(0)	0	(0)
L. virescens	440	(461.3)	360	(213.8)	240	(197)	200	(121.2)	86.7	(30.6)
Chironomidae pupae	26.7	(37.9)	6.7	(11.5)	20	(0)	10	(10)	3.3	(5.8)
Culiseta	3.3	(5.8)	0	(0)	0	(0)	0	(0)	0	(0)
Ceratopogonidae	150	(60.8)	123.3	(32.1)	180	(121.2)	103.3	(102.1)	0	(0)
Stratiomyidae	3.3	(5.8)	0	(0)	3.3	(5.8)	0	(0)	0	(0)
Berosus	3.3	(5.8)	0	(0)	0	(0)	0	(0)	0	(0)
Mesovelia	130	(216.6)	6.7	(11.5)	3.3	(5.8)	0	(0)	0	(0)

Taxon	27-Nov-99		11-Dec-99		25-Dec-99		16-Mar-00		30-Mar-00	
Enallagma	83.3	(30.6)	96.7	(63.5)	10	(10)	96.7	(66.6)	36.7	(40.4)
Libellula	10	(10)	30	(17.3)	0	(0)	0	(0)	0	(0)
Erythemis	0	(0)	0	(0)	0	(0)	0	(0)	0	(0)
Callibaetis	60	(20)	83.3	(25.2)	0	(0)	6.7	(11.5)	0	(0)
Caenis	0	(0)	26.7	(46.2)	0	(0)	0	(0)	0	(0)
P. vernalis	3.3	(5.8)	46.7	(35.1)	20	(10)	6.7	(11.5)	40	(45.8)
C. sylvestris	0	(0)	0	(0)	0	(0)	0	(0)	0	(0)
A. elachistus	1246.7	(740.4)	1333.3	(682.2)	223.3	(64.3)	86.7	(20.8)	170	(135.3)
P. richardsoni	0	(0)	96.7	(115.9)	0	(0)	0	(0)	0	(0)
Tanytarsus spp.	116.7	(83.3)	10	(17.3)	0	(0)	16.7	(28.9)	20	(17.3)
C. decorus	6.7	(11.5)	10	(17.3)	0	(0)	73.3	(102.1)	6.7	(11.5)
D. nervosus	10	(17.3)	0	(0)	0	(0)	0	(0)	0	(0)
L. decolarata	420	(355.5)	190	(60)	43.3	(15.3)	10	(17.3)	110	(127.7)
Ablabesmyia sp.	0	(0)	0	(0)	6.7	(11.5)	3.3	(5.8)	0	(0)
L. virescens	153.3	(127)	56.7	(37.9)	46.7	(20.8)	10	(17.3)	6.7	(11.5)
Chironomidae pupae	10	(10)	26.7	(46.2)	0	(0)	0	(0)	0	(0)
Culiseta	0	(0)	26.7	(46.2)	0	(0)	0	(0)	0	(0)
Ceratopogonidae	106.7	(83.9)	90	(26.5)	16.7	(11.5)	16.7	(20.8)	40	(45.8)
Stratiomyidae	0	(0)	0	(0)	0	(0)	0	(0)	0	(0)
Berosus	0	(0)	0	(0)	0	(0)	3.3	(5.8)	0	(0)
Mesovelia	0	(0)	0	(0)	0	(0)	0	(0)	0	(0)

APPENDIX B

Sampling date means (± S. D.) for taxa associated with *Heteranthera dubia*.

Taxon	19-Jun-99		26-Jun-99		2-Jul-99		9-Jul-99		16-Jul-99	
Enallagma	46.7	(28.9)	113.3	(127)	30	(17.3)	63.3	(30.6)	53.3	(11.6)
Libellula	0	(0)	40	(36.1)	3.3	(5.8)	10	(10)	16.7	(20.8)
Erythemis	0	(0)	10	(17.3)	0	(0)	0	(0)	0	(0)
Callibaetis	20	(20)	400	(275)	140	(10)	110	(78.1)	130	(130.8)
Caenis	0	(0)	0	(0)	3.3	(5.8)	16.7	(5.8)	6.7	(11.6)
P. vernalis	0	(0)	0	(0)	0	(0)	0	(0)	0	(0)
C. sylvestris	0	(0)	0	(0)	0	(0)	0	(0)	0	(0)
A. elachistus	380	(36.1)	266.7	(160.4)	233.3	(130.5)	726.7	(446.6)	1250	(340.4)
P. richardsoni	170	(95.4)	170	(53)	106.7	(81.4)	90	(52.9)	66.7	(20.8)
Tanytarsus spp.	40	(60.8)	30	(20)	0	(0)	6.7	(11.6)	0	(0)
C. decorus	6.7	(11.6)	0	(0)	0	(0)	0	(0)	0	(0)
L. decolarata	180	(88.9)	446.7	(209.8)	113.3	(55.1)	90	(43.6)	43.3	(20.8)
Ablabesmyia sp.	3.3	(5.8)	0	(0)	0	(0)	0	(0)	0	(0)
L. virescens	3.3	(5.8)	13.3	(23.1)	36.7	(28.9)	16.7	(28.9)	6.7	(5.8)
Chironomidae pupae	23.3	(32.2)	36.7	(37.9)	23.3	(25.2)	70	(62.4)	60	(36.1)
Culiseta	6.7	(5.8)	20	(10)	33.3	(25.2)	36.7	(25.2)	33.3	(20.8)
Ceratopogonidae	106.7	(106)	146.7	(158.9)	60	(55.7)	73.3	(15.3)	56.7	(5.8)
Ephyridae	0	(0)	6.7	(11.6)	10	(10)	3.3	(5.8)	6.7	(5.8)
Stratiomyidae	0	(0)	6.7	(5.8)	3.3	(5.8)	0	(0)	3.3	(5.8)
Crysomelidae	30	(20)	3.3	(5.8)	10	(10)	6.7	(5.8)	0	(0)
Berosus	0	(0)	3.3	(5.8)	3.3	(5.8)	0	(0)	3.3	(5.8)
Buenoa	0	(0)	3.3	(5.8)	0	(0)	13.3	(5.8)	0	(0)

Taxon	27-Aug-99		3-Sep-99		10-Sep-99		17-Sep-99		24-Sep-99	
Mesovelia	0	(0)	10	(17.3)	0	(0)	0	(0)	23.3	(15.3)
Belastomatidae	0	(0)	0	(0)	0	(0)	0	(0)	3.3	(5.8)
Enallagma	393.3	(257.8)	330	(60.8)	110	(60.8)	246.7	(263.1)	120	(40)
Libellula	13.3	(5.8)	20	(10)	6.7	(11.6)	3.3	(5.8)	0	(0)
Erythemis	0	(0)	0	(0)	0	(0)	0	(0)	0	(0)
Callibaetis	543.3	(215.5)	226.7	(212.2)	153.3	(64.3)	146.7	(96.1)	133.3	(56.9)
Caenis	0	(0)	3.3	(5.8)	0	(0)	0	(0)	3.3	(5.8)
P. vernalis	0	(0)	0	(0)	0	(0)	0	(0)	0	(0)
C. sylvestris	0	(0)	0	(0)	0	(0)	0	(0)	0	(0)
A. elachistus	5760	(1130.5)	3986.7	(832)	2686.7	(1631.8)	3256.7	(1397.3)	9913.3	(4810.1)
P. richardsoni	76.7	(75.1)	26.7	(46.2)	0	(0)	0	(0)	0	(0)
Tanytarsus spp.	0	(0)	13.3	(23.1)	0	(0)	0	(0)	0	(0)
C. decorus	0	(0)	0	(0)	0	(0)	0	(0)	0	(0)
L. decolarata	143.3	(45.1)	166.7	(83.3)	143.3	(64.3)	63.3	(32.2)	150	(165.2)
Ablabesmyia sp.	0	(0)	0	(0)	0	(0)	3.3	(5.8)	13.3	(23.1)
L. virescens	40	(26.5)	226.7	(66.6)	60	(34.6)	73.3	(46.2)	86.7	(66.6)
Chironomidae pupae	673.3	(332.9)	70	(26.5)	50	(36.1)	246.7	(90.7)	243.3	(106)
Culiseta	0	(0)	0	(0)	0	(0)	0	(0)	0	(0)
Ceratopogonidae	736.7	(452.4)	70	(26.5)	70	(112.1)	3.3	(5.8)	13.3	(5.8)
Ephyridae	23.3	(23.1)	3.3	(5.8)	0	(0)	3.3	(5.8)	0	(0)
Stratiomyidae	0	(0)	3.3	(5.8)	3.3	(5.8)	6.7	(11.6)	0	(0)
Crysomelidae	0	(0)	0	(0)	0	(0)	0	(0)	0	(0)
Berosus	13.3	(11.6)	3.3	(5.8)	10	(10)	40	(17.3)	23.3	(40.4)
Buenoa	3.3	(5.8)	0	(0)	0	(0)	6.7	(11.6)	10	(10)
Mesovelia	0	(0)	0	(0)	0	(0)	0	(0)	0	(0)
Belastomatidae	0	(0)	0	(0)	0	(0)	0	(0)	3.3	(5.8)

Taxon	27-Aug-99		3-Sep-99		10-Sep-99		17-Sep-99		24-Sep-99	
Enallagma	363.3	(176.2)	93.3	(66.6)	170	(20)	110	(52)	53.3	(35.1)
Libellula	10	(0)	0	(0)	3.3	(5.8)	20	(10)	6.7	(11.6)
Erythemis	0	(0)	0	(0)	0	(0)	0	(0)	0	(0)
Callibaetis	66.7	(37.9)	130	(40)	30	(34.6)	53.3	(25.2)	20	(17.3)
Caenis	3.3	(5.8)	3.3	(5.8)	3.3	(5.8)	20	(20)	6.7	(11.6)
P. vernalis	0	(0)	0	(0)	0	(0)	0	(0)	0	(0)
C. sylvestris	0	(0)	0	(0)	0	(0)	0	(0)	0	(0)
A. elachistus	7786.7	(703.2)	6546.7	(3035.4)	5636.7	(1523.3)	3393.3	(748.1)	3613.3	(575)
P. richardsoni	16.7	(28.9)	0	(0)	0	(0)	0	(0)	0	(0)
Tanytarsus spp.	0	(0)	76.7	(132.8)	0	(0)	0	(0)	10	(17.3)
C. decorus	0	(0)	0	(0)	0	(0)	0	(0)	0	(0)
L. decolarata	36.7	(25.2)	540	(325.1)	210	(140)	263.3	(40.4)	100	(79.4)
Ablabesmyia sp.	13.3	(15.3)	16.7	(15.3)	46.7	(35.1)	16.7	(15.3)	46.7	(25.2)
L. virescens	133.3	(97.1)	106.7	(71)	366.7	(125)	233.3	(25.2)	100	(36.1)
Chironomidae pupae	120	(34.6)	46.7	(37.9)	160	(70)	56.7	(5.8)	33.3	(11.6)
Culiseta	0	(0)	0	(0)	0	(0)	0	(0)	0	(0)
Ceratopogonidae	153.3	(230.9)	46.7	(37.9)	30	(17.3)	100	(138.6)	10	(10)
Ephyridae	0	(0)	0	(0)	0	(0)	0	(0)	0	(0)
Stratiomyidae	0	(0)	0	(0)	0	(0)	0	(0)	0	(0)
Crysomelidae	0	(0)	0	(0)	0	(0)	0	(0)	0	(0)
Berosus	36.7	(46.2)	0	(0)	6.7	(5.8)	0	(0)	0	(0)
Buenoa	10	(10)	10	(10)	10	(10)	6.7	(5.8)	0	(0)
Mesovelia	0	(0)	0	(0)	0	(0)	0	(0)	0	(0)
Belastomatidae	6.7	(11.6)	26.7	(30.6)	16.7	(15.3)	0	(0)	0	(0)

Taxon	1-Oct-99		8-Oct-99		15-Oct-99		22-Oct-99		29-Oct-99	
Enallagma	53.3	(35.1)	40	(26.5)	63.3	(61.1)	16.7	(5.8)	50	(10)
Libellula	6.7	(11.6)	6.7	(11.6)	13.3	(11.6)	3.3	(5.8)	3.33	(5.8)
Erythemis	0	(0)	0	(0)	0	(0)	0	(0)	0	(0)
Callibaetis	20	(17.3)	26.7	(30.6)	66.7	(72.3)	3.3	(5.8)	23.3	(32.1)
Caenis	6.7	(11.6)	0	(0)	6.7	(11.6)	3.3	(5.8)	0	(0)
P. vernalis	0	(0)	0	(0)	0	(0)	0	(0)	0	(0)
C. sylvestris	0	(0)	0	(0)	0	(0)	0	(0)	0	(0)
A. elachistus	3613.3	(575)	1433.3	(332.6)	1793.3	(1365.5)	946.7	(414.8)	1453.3	(616.6)
P. richardsoni	0	(0)	0	(0)	0	(0)	0	(0)	0	(0)
Tanytarsus spp.	10	(17.3)	6.7	(11.5)	0	(0)	0	(0)	3.33	(5.8)
C. decorus	0	(0)	0	(0)	0	(0)	6.7	(11.6)	0	(0)
L. decolarata	100	(79.4)	76.7	(15.3)	120	(148)	16.7	(15.3)	70	(26.5)
Ablabesmyia sp.	46.7	(25.2)	23.3	(40.4)	16.7	(15.3)	0	(0)	0	(0)
L. virescens	100	(36.1)	70	(30)	73.3	(61.1)	46.7	(50.3)	56.7	(49.3)
Chironomidae pupae	33.3	(11.6)	10	(17.3)	6.7	(11.6)	0	(0)	0	(0)
Culiseta	0	(0)	0	(0)	0	(0)	0	(0)	0	(0)
Ceratopogonidae	10	(10)	6.7	(5.8)	30	(10)	10	(0)	53.3	(40.4)
Ephyridae	0	(0)	0	(0)	0	(0)	0	(0)	0	(0)
Stratiomyidae	0	(0)	0	(0)	0	(0)	0	(0)	0	(0)
Crysomelidae	0	(0)	0	(0)	0	(0)	0	(0)	0	(0)
Berosus	0	(0)	10	(10)	10	(10)	10	(10)	3.3	(5.8)
Buenoa	0	(0)	0	(0)	0	(0)	0	(0)	0	(0)
Mesovelia	0	(0)	0	(0)	0	(0)	0	(0)	0	(0)
Belastomatidae	0	(0)	0	(0)	0	(0)	0	(0)	0	(0)

Taxon	13-Nov-99		27-Nov-99		11-Dec-99		25-Dec-99		16-Mar-00	
Enallagma	20	(0)	50	(36.1)	6.7	(5.8)	10	(10)	0	(0)
Libellula	6.7	(11.6)	0	(0)	0	(0)	0	(0)	0	(0)
Erythemis	0	(0)	0	(0)	0	(0)	0	(0)	0	(0)
Callibaetis	16.7	(20.8)	60	(87.2)	10	(17.3)	3.33	(5.8)	0	(0)
Caenis	0	(0)	13.3	(15.3)	0	(0)	0	(0)	0	(0)
P. vernalis	0	(0)	43.3	(5.8)	70	(45.8)	50	(17.3)	96.7	(28.9)
C. sylvestris	0	(0)	0	(0)	106.7	(66.6)	46.7	(5.8)	203.3	(56.9)
A. elachistus	443.3	(290.2)	283.3	(293.7)	240	(95.4)	176.7	(40.4)	0	(0)
P. richardsoni	0	(0)	0	(0)	0	(0)	0	(0)	0	(0)
Tanytarsus spp.	0	(0)	0	(0)	0	(0)	30	(10)	0	(0)
C. decorus	6.7	(11.6)	6.7	(11.6)	16.7	(15.3)	20	(26.5)	0	(0)
L. decolarata	80	(52)	60	(10)	13.3	(11.6)	23.3	(25.2)	0	(0)
Ablabesmyia sp.	0	(0)	73.3	(63.5)	0	(0)	0	(0)	0	(0)
L. virescens	63.3	(92.9)	33.3	(20.8)	6.7	(11.6)	30	(52)	0	(0)
Chironomidae pupae	0	(0)	0	(0)	0	(0)	0	(0)	0	(0)
Culiseta	0	(0)	0	(0)	0	(0)	0	(0)	0	(0)
Ceratopogonidae	16.7	(28.9)	23.3	(32.1)	6.7	(11.6)	0	(0)	0	(0)
Ephyridae	0	(0)	0	(0)	0	(0)	0	(0)	0	(0)
Stratiomyidae	0	(0)	0	(0)	0	(0)	0	(0)	0	(0)
Crysomelidae	0	(0)	0	(0)	0	(0)	0	(0)	0	(0)
Berosus	0	(0)	0	(0)	10	(10)	0	(0)	0	(0)
Buenoa	0	(0)	0	(0)	0	(0)	0	(0)	0	(0)
Mesovelia	0	(0)	0	(0)	0	(0)	0	(0)	0	(0)
Belastomatidae	0	(0)	0	(0)	0	(0)	0	(0)	0	(0)

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Taxon	30-Mar-00		14-Apr-00		29-Apr-00		12-May-00		26-May-00	
Enallagma	0	(0)	13.3	(11.6)	20	(10)	36.7	(23.1)	26.7	(15.3)
Libellula	0	(0)	3.3	(5.8)	0	(0)	0	(0)	0	(0)
Erythemis	0	(0)	0	(0)	0	(0)	0	(0)	0	(0)
Callibaetis	0	(0)	0	(0)	10	(10)	20	(20)	20	(0)
Caenis	0	(0)	0	(0)	0	(0)	0	(0)	0	(0)
P. vernalis	90	(36.1)	36.7	(15.3)	20	(17.3)	6.7	(11.6)	0	(0)
C. sylvestris	86.7	(15.3)	46.7	(25.2)	16.7	(5.8)	10	(10)	0	(0)
A. elachistus	0	(0)	33.3	(15.3)	26.7	(20.8)	30	(10)	40	(10)
P. richardsoni	0	(0)	0	(0)	3.3	(5.8)	13.3	(11.6)	33.3	(5.8)
Tanytarsus spp.	0	(0)	60	(52)	16.7	(11.6)	16.7	(5.8)	13.3	(5.8)
C. decorus	0	(0)	0	(0)	0	(0)	0	(0)	0	(0)
L. decolarata	0	(0)	3.3	(5.8)	3.3	(5.8)	16.7	(20.8)	6.7	(5.8)
Ablabesmyia sp.	0	(0)	0	(0)	0	(0)	0	(0)	6.7	(5.8)
L. virescens	0	(0)	3.3	(5.8)	3.3	(5.8)	0	(0)	6.7	(5.8)
Chironomidae pupae	0	(0)	0	(0)	0	(0)	0	(0)	0	(0)
Culiseta	0	(0)	0	(0)	0	(0)	0	(0)	0	(0)
Ceratopogonidae	0	(0)	0	(0)	10	(0)	16.7	(5.8)	50	(17.3)
Ephyridae	0	(0)	0	(0)	0	(0)	0	(0)	0	(0)
Stratiomyidae	0	(0)	0	(0)	0	(0)	0	(0)	6.7	(11.6)
Crysomelidae	0	(0)	0	(0)	0	(0)	0	(0)	0	(0)
Berosus	0	(0)	0	(0)	0	(0)	0	(0)	0	(0)
Buenoa	0	(0)	0	(0)	0	(0)	0	(0)	0	(0)
Mesovelia	0	(0)	0	(0)	0	(0)	0	(0)	0	(0)
Belastomatidae	0	(0)	0	(0)	0	(0)	0	(0)	0	(0)

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Taxon	3-Jun-00		16-Jun-00	
Enallagma	16.7	(15.3)	26.7	(28.9)
Libellula	0	(0)	3.3	(5.8)
Erythemis	0	(0)	0	(0)
Callibaetis	73.3	(15.3)	53.3	(40.4)
Caenis	0	(0)	0	(0)
P. vernalis	0	(0)	0	(0)
C. sylvestris	0	(0)	0	(0)
A. elachistus	103.3	(102.1)	530	(115.3)
P. richardsoni	16.7	(11.6)	100	(45.8)
Tanytarsus spp.	50	(26.5)	33.3	(30.6)
C. decorus	0	(0)	0	(0)
L. decolarata	13.3	(5.8)	76.7	(11.6)
Ablabesmyia sp.	0	(0)	0	(0)
L. virescens	0	(0)	20	(10)
Chironomidae pupae	0	(0)	3.3	(5.8)
Culiseta	0	(0)	0	(0)
Ceratopogonidae	0	(0)	46.7	(15.3)
Ephyridae	0	(0)	0	(0)
Stratiomyidae	0	(0)	6.7	(5.8)
Crysomelidae	0	(0)	0	(0)
Berosus	0	(0)	0	(0)
Buenoa	0	(0)	0	(0)
Mesovelia	0	(0)	0	(0)
Belastomatidae	0	(0)	0	(0)

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