ABSTRACT

SECONDARY PRODUCTION OF CHIRONOMIDAE
IN A LARGE EUTROPHIC LAKE

By Timothy J. Anderson

To date the majority of food web research in lentic systems has focused on pelagic primary (phytoplankton) and secondary (zooplankton) production as the primary energy sources for higher trophic level production. Recently research has provided evidence that benthic secondary production of primary consumers can impact pelagic fish production and food web structure in lakes. I calculated secondary production of chironomids in Lake Winnebago Wisconsin where previous research has shown that lake sturgeon (*Acipenser fulvescens*) rely heavily on the benthos (chironomids) as a food source. I also calculated lake sturgeon annual production from literature-derived data using the instantaneous growth method in order to determine if there is sufficient chironomid production to support the current lake sturgeon population in Lake Winnebago. Benthic samples were collected with an Ekman dredge at four profundal sites on eleven dates from spring 2008 through spring 2009. Instantaneous growth rates for seven chironomid length-classes at five thermal regimes were measured in the laboratory. Mean annual production of Chironomidae using the instantaneous growth rate method was 7.59 g dry mass (DM) m^{-2} yr^{-1}. The subfamily Chironominae accounted for 5.56 g DM m^{-2} yr^{-1} and Tanypodinae production was 2.04 g DM m^{-2} yr^{-1}. Lake sturgeon annual production was estimated at 0.044 g dry mass (DM) m^{-2} yr^{-1}. Mean annual density of Chironomidae was 2714 m^{-2} and mean biomass was 2.75 g DM m^{-2}. In 2008-2009 there was sufficient chironomid secondary production to support the lake sturgeon population in Lake Winnebago. The annual production estimates for chironomids are higher than many other chironomid production rates from lakes in North America, presumably due the eutrophic conditions of Lake Winnebago.

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IN A LARGE EUTROPHIC LAKE

by

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CHAPTER I

INTRODUCTION

The understanding of energy pathways in aquatic ecosystems became an area of intense research after Lindeman (1942) emphasized that in order to understand how an aquatic ecosystem functions, we need to understand the energy pathways, and energy flow (Odum 1971), through ecosystems. Since then the energy budgets of lakes and streams have been determined for different trophic (feeding) levels. Ecological efficiency is used to describe how much energy, defined as biomass, is transferred through each trophic level. Defining an organism's trophic position attempts to determine from what trophic level(s) energy is obtained. Much of the energy produced from photosynthesis that is available to the next trophic level is lost because energy is passed through basal trophic levels inefficiently. Research has shown that about 4-16% of the available energy (as biomass) from basal trophic levels will be passed on to the next trophic level (Wolff 1994, Manickchand-Heileman et al. 1998, Manickchand-Heileman et al. 2004, Chen et al. 2006, Villanueva et al. 2008). Therefore, understanding the amount of biomass produced by basal trophic levels is important when researchers and resource managers want to determine how population densities are maintained for diverse communities in ecosystems.

Secondary production is defined as the amount of biomass produced by consumers. Secondary production is expressed in units of mass (grams) or energy (joules) that are produced by consumers per unit area, per unit time (Benke 1984). There are several different methods researchers use to calculate secondary production based primarily on whether or not researchers can detect generations (cohorts) of invertebrates (Benke and Huryn 2006). When cohorts are easily discernable, researchers calculate production by inferring growth from changes in population size and biomass. When cohorts cannot be followed over time, growth must be

measured either in the field or the laboratory. Measures of secondary production of invertebrates in aquatic ecosystems are useful because invertebrates are prey for secondary consumers (e.g. fishes) which, aside from their importance from an energy flow standpoint to higher trophic levels, are economically important.

Invertebrates in aquatic ecosystems are an important energy source for higher trophic positions. Secondary production studies in aquatic ecosystems can yield information on population and community dynamics such as density, biomass, growth rate, development time, and survivorship (Benke and Huryn 2006). Once researchers have an understanding on the life-history traits of aquatic organisms they can use to that information to determine to what extent organisms function in an ecosystem. It is important from a research perspective, and a resource management (economic) perspective, to learn how much energy is available to higher trophic positions. Predation upon basal trophic positions (predator-prey interactions) is an important biological interaction that shapes the food web and food chain length in an ecosystem (Morin 1999). When secondary production of prey is limited, there can be significant declines in predator abundance and biomass (Wallace et al. 1997). Secondary production is a useful measure of energy flow and of ecosystem function, especially if researchers want to assess trophic-level dynamics in aquatic ecosystems (Benke 2010).

Lake Winnebago is a large, shallow, eutrophic lake in east-central Wisconsin that supports a large fish community. Primary consumers in Lake Winnebago probably obtain considerable energy from phytoplankton production. Phytoplankton is likely an important food source for the benthic invertebratesin Lake Winnebago. One of the most common invertebrates found in the benthos of Lake Winnebago is the Chironomidae (non-biting midges). During the late 1950s and early 1960s the biology and ecology of the Lake Winnebago chironomid community were studied by Hilsenhoff (1966, 1967) in order to determine if there was an

effective way to manage the "nuisance" insects. This research consequently led to a greater understanding of the Lake Winnebago chironomid community. Hilsenhoff's studies of the chironomid community concluded that there was not an effective way to manage the insects. Research has provided evidence that the chironomids support one of North America's largest lake sturgeon populations (+40,000 individuals) (Probst and Cooper 1955, Hilsenhoff 1967, Bruch 1999, Stelzer et al. 2008) and most likely support other animal populations that reside in and around Lake Winnebago.

Research has been published on the population and community dynamics of the chironomid community in Lake Winnebago (Hilsenhoff 1966, 1967, Koehnke 1997). However, there have been no previous measurements of chironomid production in the lake. Therefore, to gain a greater understanding of the trophic interactions occurring in Lake Winnebago, my objectives are (1) to determine the annual secondary production of Chironomidae (Tanypodinae and Chironominae separately) in Lake Winnebago, (2) to determine length and temperature-specific instantaneous growth rates for chironomids in Lake Winnebago, (3) to determine if the chironomid community composition have changed based on comparisons to the studies by Hilsenhoff (1967) and Koehnke (1997), and (4) to calculate an estimate potential annual production of lake sturgeon to determine if there is sufficient chironomid production to support the lake sturgeon population in Lake Winnebago.

CHAPTER II

Secondary production of Chironomidae in a large eutrophic lake

Introduction

Production estimates of organisms at various trophic levels provide a framework which researchers can use to better understand how energy flows through an ecosystem (Odum 1957). Secondary production estimates are often used to better understand population, community, and ecosystem dynamics of aquatic invertebrates (Huryn and Wallace 1986, Babler et al. 2008.) Secondary production of primary consumers can limit the production of higher consumers, and when both estimates are available energetic efficiencies can be estimated. Researchers can also use secondary production estimates, dietary information, and assimilation efficiencies to determine the trophic basis of production which provides information about food web linkages and the trophic position of various organisms (Benke and Wallace 1980, Benke and Wallace 1997, Benke and Huryn 2010). Several recent studies have highlighted the importance of benthic invertebrates in lake food webs in the context of benthic-pelagic linkages (Vadeboncoeur et al. 2002, Vander Zanden and Vadeboncoeur 2002). Investigators have addressed the importance of benthic production to fishes in streams (Huryn 1996, Poff and Huryn 1998), and in lakes (Vander Zanden and Vadeboncoeur 2002). However, studies that directly compare the production of benthic primary consumers and secondary consumers (fishes) in aquatic ecosystems are uncommon.

Chironomids (Diptera: Chironomidae) are the dominant macroinvertebrate group in many benthic habitats, including those in lenthic systems, where chironomid production can account for up to 87% of the total benthic production (Potter and Learner 1974, Dermott et al. 1977, Lindegaard and Jonasson 1979, Butler and Anderson 1990, Lindegaard 1994). Globally,

chironomids are the most widely distributed and often the most abundant holometabolous insect group (Cranston 1995). Most chironomid species are collector/gatherers (Grzybkowska and Witczak 1990, Lindegaard 1994) as larvae, but some are predaceous. Chironomid populations typically have overlapping cohorts and exist in diverse community assemblages. Chironomids are often not included in secondary production estimates due to difficulties with identification and production quantification (Hauer and Benke 1991, Berg and Hellenthal 1991), or production estimates are restricted to taxa that are easily identifiable (Menzie 1981, Johnson et al. 1989, Balci et al. 2005). Many predaceous genera, particularly members of the subfamily Tanypodinae, are not included in the majority of secondary production estimates (Huryn 1990, Reynolds and Benke 2005) due to difficulties in determining accurate growth rates (Benke et al. 1999).

I measured secondary production of Chironomidae in Lake Winnebago, the largest inland lake in Wisconsin. Lake Winnebago contains one of the largest self sustaining populations of lake sturgeon (*Aciperser fulvescens* Rafinesque) in North America (over 40,000 adults) (Bruch 1999) in addition to 76 other fish species including walleye (*Sander vitreus* (Mitchill)) and yellow perch (*Perca flavescens* (Mitchill)) (Becker 1964, Priegel 1967). Previous research has shown that chironomids contribute about half of the carbon assimilated by lake sturgeon in Lake Winnebago (Stelzer et al. 2008). Many other fishes in the lake, including yellow perch and freshwater drum (*Aplodinotus grunniens* Rafinesque), may also rely on chironomids as a food source (Hilsenhoff 1967). Although there are previous estimates of chironomid density from Lake Winnebago extending to the 1960s (Hilsenhoff 1967, Koehnke 1997), my estimates of chironomid secondary production are the first for this lake. The objectives of my study were: (1) to determine the annual secondary production of Chironomidae (Tanypodinae and Chironominae separately) in Lake Winnebago, (2) to determine length and temperature-specific instantaneous growth rates for chironomids in Lake Winnebago, (3) to determine if the chironomid community

composition has changed based on comparisons to the studies by Hilsenhoff (1967) and Koehnke (1997), and (4) to estimate potential annual production of lake sturgeon to determine if there is sufficient chironomid production to support the lake sturgeon population in Lake Winnebago.

Methods

Lake Winnebago system

Lake Winnebago is a large (55,766 hectares), shallow, eutrophic lake in east-central Wisconsin with a mean depth of 4.7 m (Figure 1) (Stelzer et. al 2008). More than 80% of Lake Winnebago is greater than 5 m deep (Hilsenhoff 1966). The profundal bottom consists of fine organic sediment except for the southern $1/10^{th}$ of the lake which is comprised of sand (Hilsenhoff 1966, Stelzer et. al 2008). The Chironomidae inhabit the organic-sediment (mud) basin of Lake Winnebago where some genera construct u-shaped burrows in the substrate. The subfamily Tanypodinae is represented by numerous species in Lake Winnebago including predatory *Procladius* species and the predatory *Coelotanypus concinnus* (Coquillett) (Hilsenhoff 1967). The Tanypodinae are described as free living and motile throughout their larval life cycle (Hilsenhoff 1966). The Chironominae (mostly collector/gatherers) are motile as first instars but become sedentary and create burrows as second instars in which they reside through the fourth instar stage (Hilsenhoff 1966). Four genera belonging to Chironominae were encountered. Hilsenhoff (1966, 1967) and Koehnke (1997) determined that *Chironomus* species (*Chironomus plumosus* (Linnaeus) and *Chironomus entis* Schobanov) are typically the most abundant chironomids in the lake and feed as collector/gathers on the surface of the lake sediment. The *Chironomus* spp. are responsible for the large adult mass-emergence which Hilsenhoff researched in the late 1950s and early 1960s (Hilsenhoff 1966, 1967). Other genera of collector/gatherer Chironominae present in the lake include *Dicrotendipes* and *Tanytarsus* (Hilsenhoff 1967).

These two genera and the predatory *Cryptochironomus digitatus* Malloch are far less frequently encountered (Hilsenhoff 1967, Koehnke 1997).

Sampling and sample processing

I sampled chironomids from four sites at approximately the same locations sampled by Hilsenhoff (1966, 1967). Sediment samples were taken approximately biweekly from 27 April 2008 to 13 October 2008 at the four sample sites. A final set of samples was taken on 29 April 2009 to estimate annual secondary production of Chironomidae. At each of the four sites, two

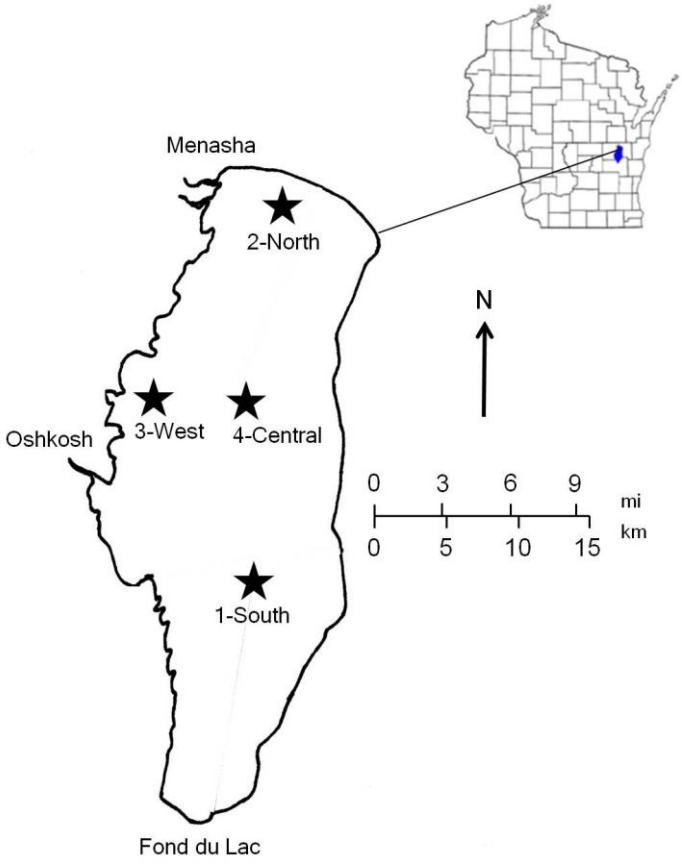

Figure 1. Map of Lake Winnebago, Wisconsin depicting the locations of the four sampling sites and some of the major cities near the lake.

replicate samples were collected using a 523 cm^2 Ekman Dredge. The sediment samples were processed in the laboratory by sieving the sediment through a 250 μm U.S.A. standard test sieve. The material trapped on the sieve was preserved in ~95% ethanol (EtOH). All Chironomidae were separated from the remaining material captured in the sieve at 6.3x magnification with a Leica dissecting microscope and stored in 70% EtOH. The Chironomidae were then sorted by subfamily (Tanypodinae or Chironominae) into 1-mm length classes. Larvae ranging from <1mm to 1.9 mm were grouped into the 1-mm length class. Larvae ranging from 2.0 mm to 2.9 mm were grouped together in the 2-mm length class. All subsequent larval length classes were assigned according to this grouping rule. There were a total of 29 length classes. Surface water temperature, sediment temperature, sample site depth and Secchi Disk measurements for water transparency were recorded for each sampling site on each sampling date when the sediment samples were collected (Table 1). A boat-mounted Lowrance Global Positioning System (GPS) fish-finder sonar receiver (model no. LMS350A) was used to locate sampling sites and to measure sample site water depth and temperature. Sediment temperatures at each site were measured using a Fisher Science digital thermometer. Water transparency was assessed using a Secchi Disk. Bruch (1999) and Stelzer et al. (2008) provide more information about the physical and chemical properties of Lake Winnebago.

Table 1. Sample site locations, mean (and standard deviation) surface water temperature, sediment temperature, depth, and Secchi disk readings for each sample site during the study period.

Site	Coordinates	Surface Water (°C)	Sediment (°C)	Depth (m)	Secchi Disk (m)
1-South	(N43°55’36”, W088°24’31”)	17.3 (5.2)	16.9 (5.5)	5.1 (0.59)	0.95 (0.39)
2-North	(N44°10’20”, W088°21’53”)	18.6 (5.7)	17.0 (5.7)	5.4 (0.48)	1.12 (1.1)
3-West	(N44°03’88”, W088°29’55”)	18.3 (5.6)	16.9 (5.4)	5.0 (0.26)	1.09 (0.72)
4-Central	(N44°03’22”, W088°25’42”)	17.4 (5.2)	16.5 (5.5)	6.0 (0.27)	1.04 (0.76)

Length-weight regression

Chironomid larvae of various lengths (2.0 to 29.4 mm) were collected from sites 1-South, 2-North, and 4-Central on 30 June 2009 to develop a length-weight regression for determining the mass of individuals in a given length class. The total length of each freshly frozen larva was measured to the nearest 0.1 mm with a Leica dissecting microscope and mass was determined to 0.001 mg using a Mettler Toledo MX5 microbalance. The larvae were dried at 60 °C for 24 hours and weighed to determine dry mass. Dry mass was regressed on larval length to convert length classes into dry mass classes for the biomass calculations described below.

Growth experiment

Laboratory experiments were conducted in the summer of 2008 and 2009 to determine length- and temperature-specific somatic growth rates of Chironomidae using the methods of Huryn and Wallace (1986). Chironomid larvae were grouped in a community assemblage in the mesocosms because it is believed that changes in weight of mixed taxa can be used to estimate mean growth rates reflective of an entire community (Huryn and Wallace 1986, Huryn 1990). Chironomid larvae were collected from the four sampling sites and grouped into seven length classes (1-4, 5-8, 9-12, 13-16, 17-20, 21-24, and $\geq$ 25 mm). Larval length was measured to the nearest millimeter using 6.3x magnification with a Leica dissecting microscope and wet mass was measured on a Mettler Toledo MX5 microbalance to 0.01 mg. Ten to fifteen chironomid larvae of each length-class were placed in microcosms (1276 mL plastic containers) separated by length-class. Each microcosm received 250 mL of Lake Winnebago sediment,forced through a 500 μm U.S.A. standard test sieve to remove macroinvertebrates, and 500 mL of unfiltered water

collected from Miller's Bay in Lake Winnebago. Microcosms were placed in incubators set at 4, 8, 13, 18, and 23°C, which span the range of sediment temperatures observed for most of the year in Lake Winnebago. The instantaneous growth rate (IGR) equation was used to estimate daily growth rates

$$g = (\ln(w_f)-\ln(w_i))/t \quad (1)$$

where w_f = final mean wet weight, w_i = initial mean wet weight, t = time in days. The mean IGR for each length class was regressed against temperature to determine the temperature-specific IGR for each length class. The number of replicate microcosms per length-class and temperature varied, largely due to the availability of chironomids at particular length classes during the experiments (Table 2). The containers were aerated to prevent anoxia. The water in each

Table 2. The number of replicate microcosms for each length-class and temperatures for the growth experiments.

	Length (mm)						
	1-4	5-8	9-12	13-16	17-20	21-24	+25
Temperature (°C)							
4	-	3	-	-	1	3	-
8	2	4	2	2	2	3	1
13	2	4	2	2	2	3	2
18	1	7	7	1	2	3	2
23	1	3	1	-	2	4	1
Total	6	21	12	5	9	16	6

microcosm was changed every three days with water collected from Miller's Bay. Final larval mass (mean weight) and total length was measured after 15 days of incubation. We assumed that the calculated growth rates for a given length class did not differ between subfamilies.

Modeled growth

The empirically-determined relationships between IGR and water temperature from the growth experiments were used in conjunction with daily water temperature data for Lake Winnebago to estimate length-specific IGR of chironomids in the lake throughout the study period. Daily water temperature data were obtained from the intake of the Appleton Water Treatment Facility in Menasha, Wisconsin. The intake water temperature was similar to the ambient temperature of the Lake Winnebago sediment at the sample sites (the former was 1 C° warmer on average).

Chironomid density, biomass, and production estimations

Chironomid density was determined at each study site for each sample date by averaging abundance data from the two replicate sediment samples. Chironomid biomass was determined by multiplying the density of each length class by the estimated dry mass of an individual in the length class based on the length-weight regressions described previously. Interval biomass was determined by calculating the mean biomass for two consecutive sampling dates. Secondary production (P) for each length class during each sample interval was calculated using the following equation:

$$P = BGd \qquad (2)$$

where B = interval biomass, G =daily instantaneous growth rate, and d = days in interval. Annual production at a particular study site was determined by summing all interval production estimations within and among length classes for that site. I estimated chironomid production at

the whole-lake scale by calculating the mean production estimates across the four sampling sites. Production to biomass ratios (P/B) were calculated for each sampling site and for the whole lake.

Lake sturgeon production estimation

Lake Sturgeon annual production was estimated using the instantaneous growth method (equation 2) and based on historical published lake sturgeon data in Lake Winnebago. Instantaneous growth rate was estimated based on the average size of adult sturgeon (using 1995 data) (Bruch 1999) and average weights in two consecutive years (Probst and Cooper 1955). Adult lake sturgeon abundance data for 2006 and 2007 (40,475 and 38,988 individuals respectively) in Lake Winnebago were taken from Bruch (2008) and converted into mean density. Bruch (1999) states the mean length range of male lake sturgeon from 1954 to 1997 was 132-138 cm and females ranged 160-164 cm during the same time frame. I estimated the mean length of all adult lake sturgeon in Lake Winnebago at 149 cm using the range of length data published by Bruch (1999). Density was used to determine biomass by converting the mean length of an adult lake sturgeon in the Lake Winnebago population into mean weight based on a length-weight conversion determined from by data in Probst and Cooper (1955). I multiplied the mean weight of an adult sturgeon by the density in Lake Winnebago to estimate sturgeon biomass. Annual production of lake sturgeon for 2006-2007 was calculated by multiplying the 2006-2007 interval biomass, the IGR of the average adult lake sturgeon and the production interval (365 days). I converted sturgeon wet mass to dry mass based on data in Beamish et al. (1996). There were some assumptions that I made in order to estimate lake sturgeon production in Lake Winnebago. I assumed that the lake sturgeon length and weight data I used from Probst and Cooper (1955), and the density data from Bruch (1999, 2008) were an accurate representation of the population

of adult lake sturgeon in Lake Winnebago from 2007 to 2008. Additionally, I assumed that the growth rate data I calculated was representative of the current lake sturgeon population.

Statistical analysis

Growth models were used to predict larval chironomid dry mass from length. Least-square linear regressions of instantaneous growth rate on incubation temperature for each length-class were used to predict chironomid growth rate from temperature. Temperature-specific instantaneous growth rates were linearly regressed against the midpoint length of each length-class to determine if instantaneous growth rate changed with increasing chironomid length. A logarithmic regression model provided by Probst and Cooper (1955) was used to predict lake sturgeon wet weight from length. An inverse regression model was used to predict lake sturgeon instantaneous growth from the weight data provided by Probst and Cooper (1955). One-way ANOVAs were used to determine if mean chironomid density, biomass, and secondary production differed among the four sampling sites. Tukey-Kramer post hoc tests were conducted to determine which means differed from each other in the ANOVAs. All statistical analyses and assessments for normality and homogeneity of variances were performed with SPSS (v.16.0/2007, IBM, Chicago). Data were log-transformed as necessary to increase homogeneity of variance among groups.

Results

Physical data

The mean sediment temperature was 16.9 °C and the mean surface water temperature was 17.9 °C. There were no differences in sediment temperatures (ANOVA: $F = 0.019$, $P = 0.996$, $n = 48$) or surface water temperatures (ANOVA: $F = 0.153$, $P = 0.927$, $n = 46$) among sites (Table 1). The range in sample-site depth was 5.1-6.0 m (Table 1). Sample site 4-Central was deeper than the other sites (ANOVA: $F = 125.582$, $P < 0.001$, $n = 45$). Mean Secchi Disk transparency did not differ among the four sites (ANOVA: $F = 0.111$, $P = 0.953$, $n = 48$) (Table 1).

Length-mass conversions

The length-classes of the measured Tanypodinae larvae (range = 4.0-12.0 mm) were converted to dry mass-classes using the following growth model: $M = e^{(-3.764 + (0.323L)}$ ($r^2 = 0.92$, $P < 0.001$, $n = 28$) where M is larval mass (mg) and L is total length (mm). Chironominae length-classes (range = 2.0-29.0 mm) were converted to dry-mass classes using the growth model: $M = e^{(-4.017 + (0.224L)}$ ($r^2 = 0.98$, $P < 0.001$, $n = 43$).

Growth experiments

An average of 67% of chironomid larvae were recovered from the microcosms at the end of the experiments (range 25-100% recovery). Some microcosms contained in various combinations pupae, pupal exuviae, or adults at the end of the growth incubations which accounts for some of the loss of larvae. Dead larvae were also found in some of the microcosms. No other types of macroinvertebrates were recovered at the end of the growth experiments. Instantaneous growth rates (IGR) for 1-4, 5-8, 17-20, and 21-24 mm larvae increased significantly with

increased temperature (Table 3). The 9-12, 13-16, and 25-29 mm larvae did not respond significantly to increased incubation temperature.

Table 3. Parameters for least-square linear regressions of instantaneous growth rate of chironomid larvae on temperature from the growth experiments.

Length Class (mm)	Slope	Intercept	r^2	P-Value
1-4	0.007	-0.068	0.91	0.044
5-8	0.003	-0.020	0.88	0.018
9-12	0.004	-0.013	0.73	0.145
13-16	0.001	0.014	0.41	0.557
17-20	0.001	-0.002	0.98	0.002
21-24	0.0002	0.001	0.84	0.028
25-29	-0.0004	0.006	0.85	0.076

The regression parameters for the 1-4, 5-8, 17-20, and 21-24 mm larvae were used to estimate instantaneous growth rate. The regression parameters (Table 3) were also used for the 9-12 and 25-29 mm larvae because growth changed with temperature albeit not significantly (Figure 2). Since growth of the 13-16 mm larvae did not respond to temperature the mean growth rate (0.0243 d^{-1}) of this group was used in place of the IGR for all temperatures. Length-class did not influence IGR at 4 °C ($r^2 = 0.775$, $P = 0.315$), 8 °C ($r^2 = 0.002$, $P = 0.922$), or 13 °C ($r^2 = 0.057$, $P = 0.606$). Smaller larvae grew at faster rates than larger larvae at 18 °C ($r^2 = 0.896$, $P < 0.001$) and at 23 °C ($r^2 = 0.880$, $P = 0.01$) (Figure 2).

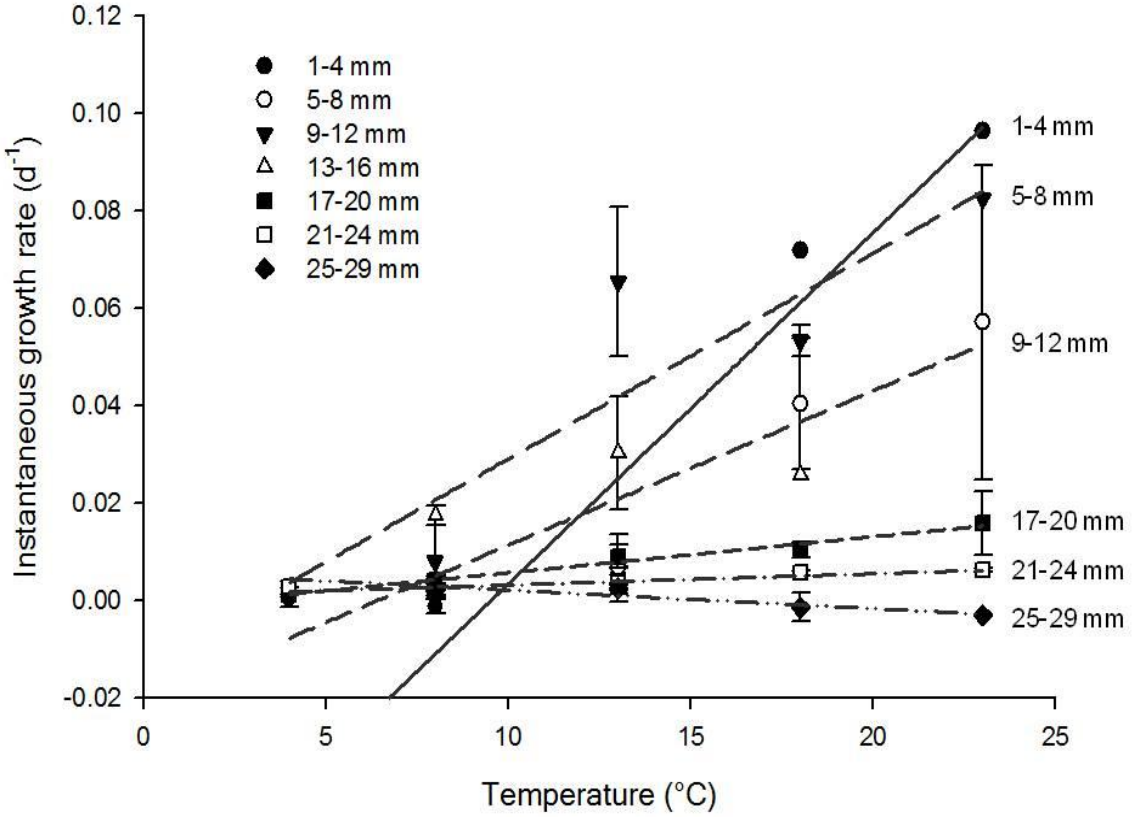

Figure 2. The relationship between instantaneous growth rate (IGR) and temperature for six chironomid length-classes used in the growth experiments. Trend lines are graphical representations of the least squares linear regression parameters used to predict IGR from temperature provided in Table 3. Mean IGR for 13-16 mm larvae at various temperatures are provided but since the regression was not significant a trend line was not determined.

Modeled growth

Chironomids of most length-classes had positive growth rates in Lake Winnebago throughout the study except for the 1-4, 5-8, 9-12, and 17-20 mm larvae during winter months and 25-29 mm larvae during the summer months (Figure 3). Smaller larvae grew at faster rates than larger larvae except in late October 2008 and through the winter months when the modeled growth rates of smaller larvae decreased. The negative growth rates were designated as zero growth for the purpose of estimating chironomid secondary production.

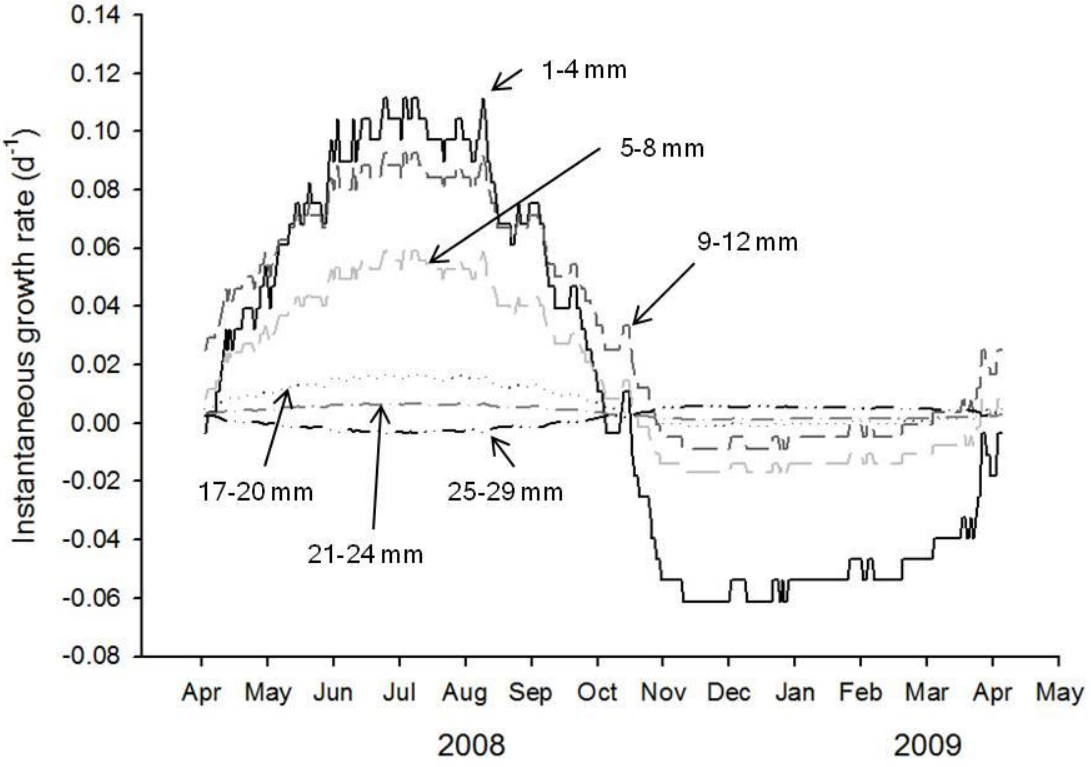

Figure 3. Modeled instantaneous growth rates of Chrionomidae larvae by length-class in Lake Winnebago throughout the study period.

Chironomid abundance

Mean Chironomidae density was 2714 larvae m^{-2} (Table 4). Mean Chironominae and Tanypodinae densities in Lake Winnebago were 1488 larvae m^{-2} and 1226 larvae m^{-2}, respectively (Table 4). Mean Chironomidae density differed among sample sites (ANOVA: F = 3.212, P = 0.019, n = 48). The mean density of Chironomidae at sample site 2-North was higher than at sites 3-West (Tukey: P = 0.031) and 4-Central (Tukey: P = 0.027) but not site 1-South. There were significantly more Chironominae than Tanypodinae at site 4-Central (student's t-test: P = 0.023). Chironominae density did not differ significantly among sample sites (ANOVA: F =

0.182, P = 0.908, n = 48). Tanypodinae density differed significantly among the sample sites (ANOVA: F = 5.347, P < 0.001, n = 48). Sample site 2-North had a higher density of Tanypodinae (Tukey: P = 0.04) compared to the other sampling sites (Table 4).

Table 4. Mean density, biomass, annual production, and production:biomass (P/B) for Chironomidae and the subfamilies Tanypodinae and Chironominae from 29 April 2008 through 27 April 2009 at each sample site. Density and biomass values are presented with standard error. Biomass and production are presented as dry mass.

Taxon	Site	Density (no. m^{-2})	Biomass (mg m^{-2})	Production (mg m^{-2} yr^{-1})	P/B
Tanypodinae					
	1-South	1102 (205)	180 (17)	1860	10.3
	2-North	1938 (265)	304 (29)	3038	10.0
	3-West	1154 (140)	179 (14)	1834	10.2
	4-Central	710 (175)	143 (20)	1406	9.8
	Grand Mean	1226 (151)	201 (13)	2035	10.1
Chironominae					
	1-South	1261 (212)	2701 (581)	5619	2.1
	2-North	2383 (1012)	2809 (556)	6728	2.4
	3-West	949 (190)	2046 (393)	4076	2.0
	4-Central	1357 (199)	2633 (536)	5803	2.2
	Grand Mean	1488 (307)	2547 (484)	5556	2.2
Chironomidae					
	1-South	2363 (362)	2881 (578)	7479	2.6
	2-North	4321 (968)	3113 (550)	9766	3.1
	3-West	2103 (295)	2225 (386)	5910	2.7
	4-Central	2067 (305)	2776 (546)	7209	2.6
	Grand Mean	2714 (335)	2748 (482)	7591	2.8

There were significant differences in Chironomidae density among sample dates (ANOVA: F = 4.776, P < 0.001, n = 48). The general trend, as illustrated in Figure 4, shows that Chironomidae density increased in the spring of 2008. Chironomidae density was low at the beginning of the study in late April 2008 and early May 2008 and remained low before increasing after a mass emergence in the middle of May 2008 (Figure 4). Chironomid density remained

significantly higher throughout the remainder of this study from June 2008 through April 2009 (Figure 4) (Tukey: $P < 0.003$).

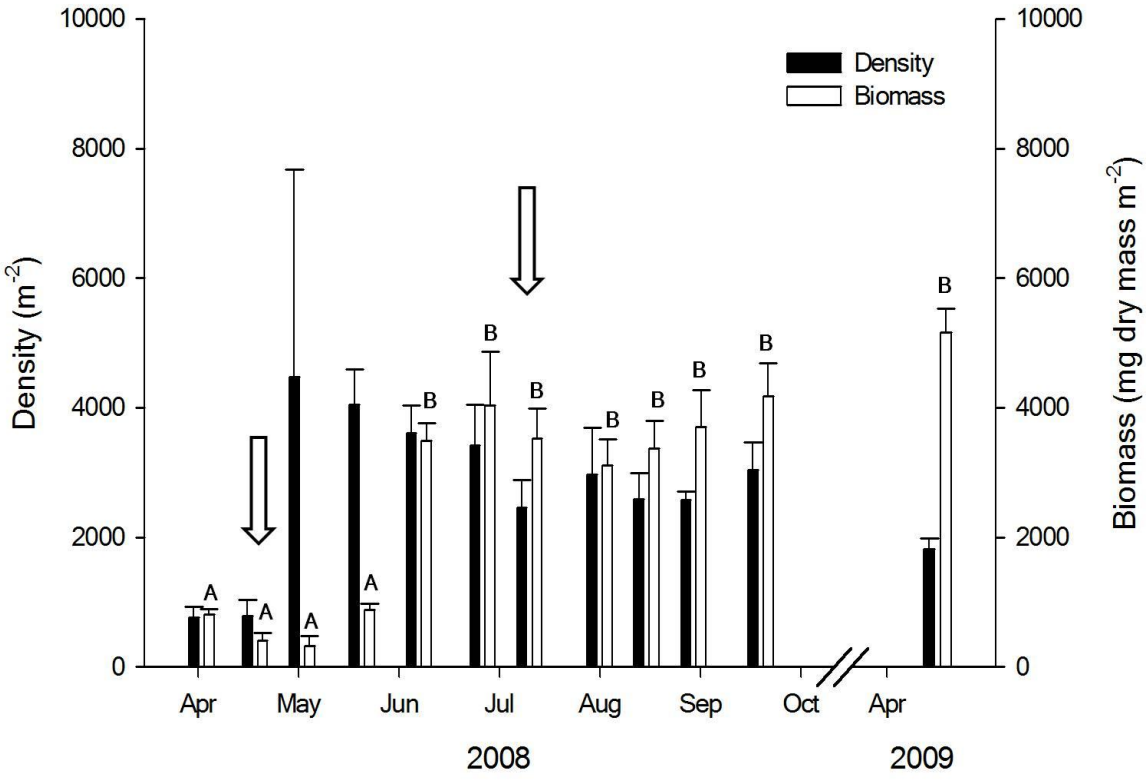

Figure 4. Temporal patterns in mean (+ standard error) larval chironomid density and biomass in Lake Winnebago. Letters indicate significant ($P < 0.05$) differences in mean biomass among sample dates. Arrows indicate mass emergence events of adult *Chironomus* spp. in early May and late July.

Chironomid biomass

Mean Chironomidae biomass was 2748 mg m^{-2}. Mean Chironominae and Tanypodinae biomass were 2547 mg m^{-2} and 201 mg m^{-2} respectively (Table 4). There were no significant differences in mean Chironomidae biomass among sites (ANOVA: $F = 0.523$, $P = 0.669$, $n = 48$). There was significantly more Chironominae biomass than Tanypodinae biomass at all four sites (student's t-test: $P < 0.001$) mostly due to the larger overall size of the Chironominae (0.023 to 12.0 mg dry mass per individual) compared to the Tanypodinae (0.032 to 2.1 mg dry mass per individual). There were no significant differences in mean Chironominae biomass among sites (ANOVA: $F = 0.429$, $P = 0.733$, $n = 48$). Mean Tanypodinae biomass exhibited significant variation among the sample sites (ANOVA: $F = 9.193$, $P < 0.001$, $n = 48$). There was significantly more Tanypodinae biomass at sample site 2-North compared to the other three sampling sites (Tukey: $P \leq 0.012$).

Chironomidae biomass in Lake Winnebago increased significantly throughout the study (ANOVA: $F = 15.801$, $P < 0.001$, $n = 48$, Figure 4). Mean Chironomidae biomass in the sediments of Lake Winnebago was low in April 2008 (Figure 4). Biomass decreased slightly through late May 2008 after the first mass emergence of adult chironomids in early May. In June 2008 chironomid biomass started to increase following chironomid oviposition in the lake and subsequent growth of early instar larvae. Chironomid biomass reached a peak in July 2008 which was significantly higher than the chironomid biomass in late April through June of 2008 (Tukey: $P < 0.027$, Figure 4). Chironomid biomass showed a decreasing nonsignificant trend from late July 2008 to August 2008 which coincided with a second emergence of adult chironomids from Lake Winnebago.

Chironomid secondary production

Mean Chironomidae production was 7591 mg dry mass m^{-2} yr^{-1} (Table 4). Means for Chrionominae and Tanypodinae production in Lake Winnebago were 5556 mg DM m^{-2} yr^{-1} and 2035 mg DM m^{-2} yr^{-1} respectively (Table 4). Mean Chironomidae production did not differ among sample sites (ANOVA: F = 0.385, P = 0.764, n = 44). Chironominae accounted for 73% of the family-level production at all sample sites (Figure 5). The distribution of Chironominae production from individual length classes was skewed towards larger length-classes. The 21-24 mm Chironominae larvae and the 25-29 mm Chironominae larvae were the greatest contributors to family (Chironomidae) production (Figure 5). Tanypodinae larvae of 9-12 mm length class contributed the greatest portion of Tanypodinae production to Chironomidae production.

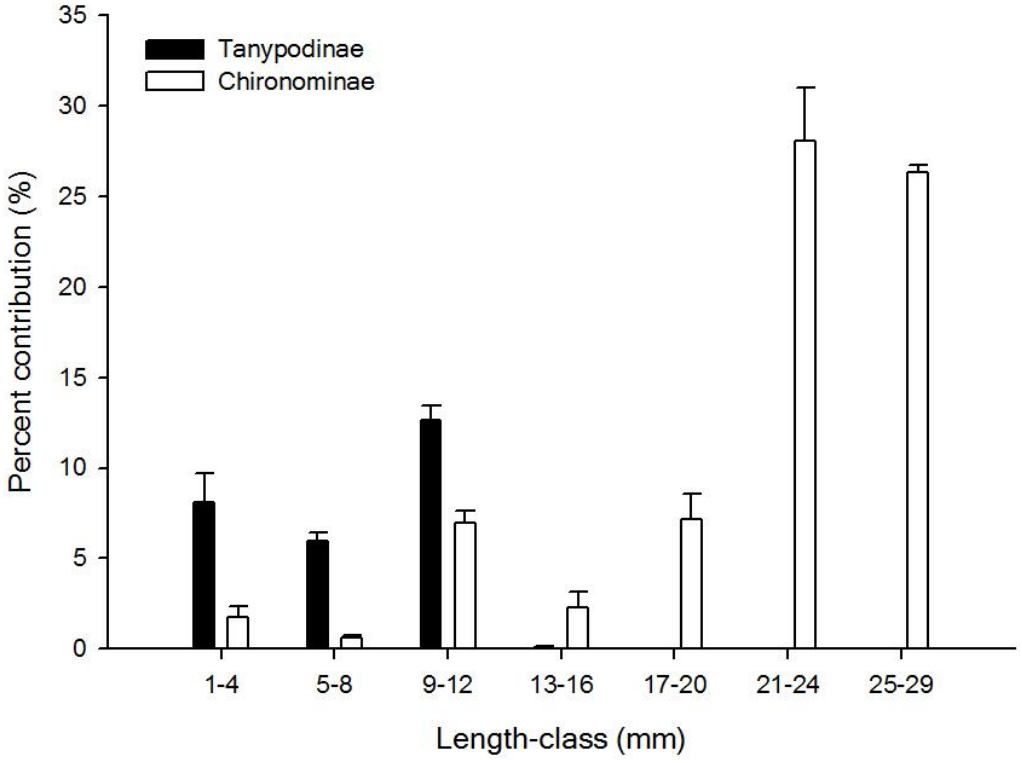

Figure 5. Percent contributions by length-class of each subfamily to total secondary production of Chironomidae in Lake Winnebago.

Chironominae production did not differ significantly among sample sites (ANOVA: F = 0.175, P = 0.912, n = 44). Tanypodinae production differed significantly among the sampling sites (ANOVA: F = 8.095, P < 0.001, n = 44). Sample site 2-North had more Tanypodinae production than at any other site (Tukey: P = 0.008).

Daily Chironomidae production in Lake Winnebago varied significantly throughout the study period (ANOVA: F = 7.686, P < 0.001, n = 44). Daily chironomid production was relatively low from late April 2008 through May 2008. Chironomid production increased in June and peaked in early July 2008 (Figure 6). The increase in production was associated with chironomid recruitment after the large mass emergence event in May.

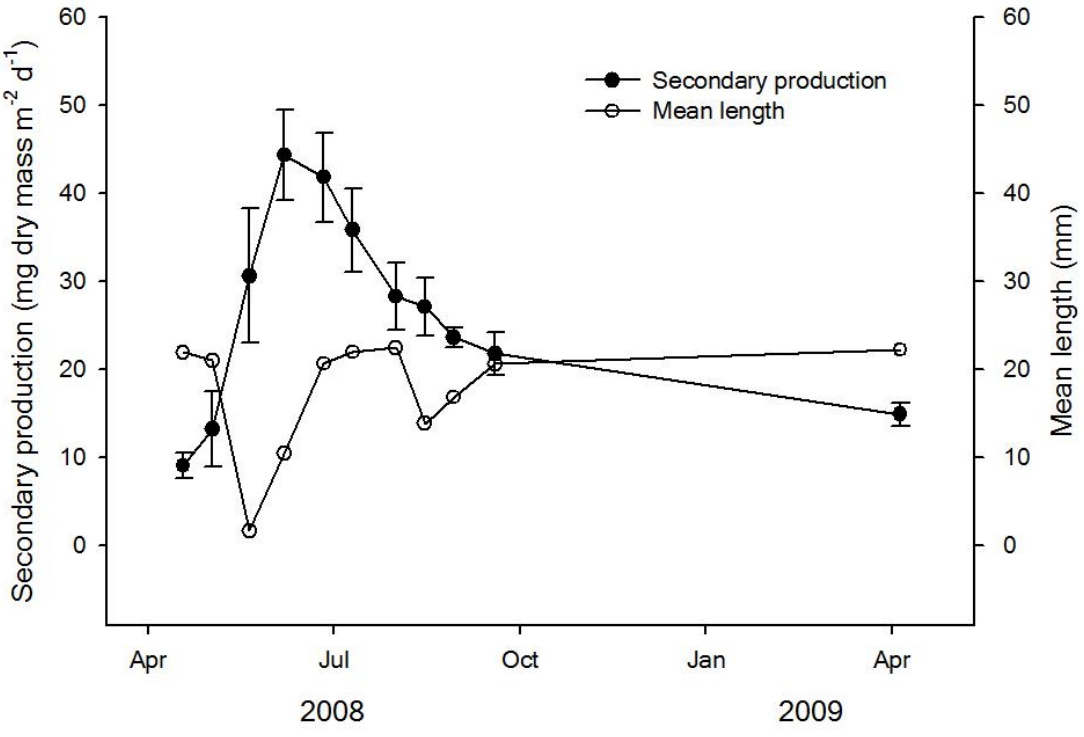

Figure 6. Secondary production and mean length of Chironomidae (mean +/- standard error) in Lake Winnebago plotted against time. These data points are inferring secondary production and mean length between sampling periods.

P/B ratios

The mean Chironomidae P/B ratio was 2.8 with the highest ratio occurring at sample site 2-North (Table 4). Chironominae P/B ratios were much lower at each sample site compared to Tanypodinae. The P/B ratios suggest that there are multiple generations of Tanypodinae per year and that Tanypodinae are turning over biomass more frequently than Chironominae.

Lake Sturgeon Instantaneous Growth Rate, Biomass, and Production

Lake sturgeon instantaneous growth rate (IGR) in Lake Winnebago was best described using the following inverse model: IGR = 0.000304 + (0.000165 / weight) ($r^2 = 0.81$, $P < 0.001$, $n = 41$). The mean biomass of the adult lake sturgeon in Lake Winnebago from 2006 through 2007 was estimated at 862,454.5 kg wet mass for the entire lake and on a per area basis, 1.5 g wet mass and 0.38 g dry mass m^{-2}. Lake sturgeon annual production was estimated at 0.18 g wet mass m^{-2} yr^{-1} and 0.044 g dry mass m^{-2} yr^{-1}.

Discussion

Chironomidae produced on average 7.59 g dry mass (DM) m^{-2} yr^{-1} in the benthic zone of Lake Winnebago in 2008. Chironominae was the greatest contributor (73%) to family level production. Chironominae averaged 13x more biomass in Lake Winnebago than Tanypodinae biomass, yet the average densities of the two subfamilies were similar (Table 4). For most length-classes instantaneous growth of chironomid larvae was a positive function of water temperature for the temperatures encounteredin Lake Winnebago. Smaller larvae grew at faster

rates in warmer water temperatures than larger larvae. Chironomid annual production in Lake Winnebago was two orders of magnitude greater than lake sturgeon annual production which suggests that there is sufficient chironomid production in 2008-2009 to support the lake sturgeon population.

Mean Chironomidae secondary production did not vary among sample sites in Lake Winnebago. A study by Babler et at. (2008) on Crampton Lake showed that area-specific rates of chironomid production remained constant across depths. The lack of spatial variation in annual production at the family-level can be explained by the similarities in Chironominae density among sample sites. The Tanypodinae had a higher rate of biomass turnover than Chironominae. The Tanypodinae in Lake Winnebago most likely have multiple generations per year but larval size-frequency plots were unable to detect discrete cohorts (data not shown). Frank (1982) showed that the density of *Chironomus plumosus* larvae in Lake Federsee, a highly eutrophic lake in south-western Germany, also had an even distribution. Chrionomidae density varied among sample sites in Lake Winnebago due to the significantly higher density of Tanypodinae at site 2-North in comparison to the other sites. Tanypodinae production was also significantly higher at site 2-North while the other three sites had similar annual production estimates. Generally, there were more chironomids present in the lake sediment at site 2-North than at the other sites. Stelzer et al. (2008) determined that there was more chlorophyll *a* in the water column at site 2-North in 2005. Tanypodid larvae may be more productive at the northern end of Lake Winnebago because there are more food sources available for herbivores that are consumed by predaceous tanypodid larvae.

Chironomid secondary production in Lake Winnebago varied considerably through 2008 and into 2009. Chironomid secondary production was very low in late April 2008 as a result of low chironomid densities and the overall size structure of the chironomid community. The

Chironominae present in the April 2008 samples were large fourth instar larvae that were nearing pupation. Because of their large size the chironomid larvae probably did not feed as much, as suggested by the results of the growth experiments using large larvae. This may explain why secondary production was low in April 2008. There was a significant increase in chironomid secondary production from late May to late June 2008 following a mass emergence of adult *Chironomus* spp. which suggests that rapid growth of early instar larvae that had recruited to the population drove the increase in production. There was not a significant increase in chironomid secondary production following the second, smaller emergence of *Chironomus* spp. that occurred in August 2008 although there was recruitment of new larvae. Lake Winnebago may have a smaller second emergence of chironomids due to food resources that limit the pupation of the larvae generated from the spring emergence. Hilsenhoff (1966 & 1967) emphasized that a feeding stimulus (diatoms) was necessary to promote pupation and without this stimulus the larvae would remain in the sediment as large 4th instar larvae until a food source became present in sufficient quantities on the sediment surface. Trabeau et al. (2004) observed that the *Daphnia pulicaria* population in Lake Winnebago increased in the spring and then decreased rapidly in abundance during late June and early July each year of their study. They suggested that an increase of cyanobacteria abundance (up to 10-fold) in Lake Winnebago resulted in unfavorable conditions for the *Daphnia*. The second smaller *Chironomus* spp. emergence that is observed in late July to early August each year from Lake Winnebago may be a result of poor food quality that limits adult emergence.

Temporal patterns of chironomid density and biomass in Lake Winnebago can be explained in part by the emergence of adults. Mean chironomid density and biomass displayed a similar pattern to mean chironomid production --low at the beginning of the study and then an increase following the mass spring emergence of adult *Chironomus* spp. (Figure 4). An important

difference between temporal chironomid production and biomass in this study is that biomass increased and remained high relative to the beginning of the study and production decreased as time progressed. Modeled production decreased through time because the growth rate of larvae decreased as the larvae increased in length, as indicated by the growth experiments. Chironomid biomass remained high through time because density increased following the first mass spring emergence of *Chironomus* spp. and remained high throughout the rest of the study. It is not clear why there were so few chironomid larvae in the lake sediment in late April and early May 2008. Population fluctuations in larval chironomids, as I observed between spring 2008 to spring 2009 have been documented in the past in Lake Winnnebago (Hilsenhoff 1967, Koehnke 1997).

Two chironomid functional feeding groups were present in the benthos of Lake Winnebago. The collector-gatherer Chironominae contributed the majority of family-level secondary production. The predatory taxa in Lake Winnebago contributed about 27% of the Chironomidae secondary production in this study. Strayer and Likens (1986) concluded that predatory macrozoobenthic taxa contribute about 20% of the total secondary production in Mirror Lake, NH. My results are consistent with other research that has shown chironomid collector-gatherer taxa contribute a larger percentage to secondary production than predatory chironomid taxa (Potter and Learner 1974, Dermott et al. 1977, Mason 1977, Lindegaard 1994).

The previous research on the temporal population dynamics of the chironomid community in Lake Winnebago by Hilsenhoff (1967) and Koehnke (1997) allow for comparisons of chironomid density among the studies which may represent one of the longest, although not continuous, lentic chironomid community composition records. The density of *Chironomus* spp. 18-28 millimeters in length in Lake Winnebago in 2008-2009 were higher than the estimates by Koehnke (1997) in 1995 and 1996 and is similar to the reported densities of Hilsenhoff (1967) described from 1961 through 1964 (Table 5). In contrast, Tanypodinae (*Procladius* spp. and

Coelotanypus concinnus) density is lower than what was reported by Hilsenhoff (1967) and Koehnke (1997). Changes in chironomid abundance in Lake Winnebago between the mid-1990s

Table 5. A comparison between the chironomid density in this study and the chironomid densities from previous studies in Lake Winnebago. All *Chironomus* spp. density estimates are larvae ranging 18-28 millimeters in length as determined by Hilsenhoff (1966). The Tanypodinae density estimates are either larvae ranging 9-12 millimeters in length (Hilsenhoff 1967, this study) or larvae with a head capsule width greater than 0.6 mm (Koehnke 1997).

Taxa	Density (number m^{-2})	Year	Study
Chironomus spp.	1406	1961	Hilsenhoff (1967)
	467	1962	Hilsenhoff (1967)
	581	1963	Hilsenhoff (1967)
	861	1964	Hilsenhoff (1967)
	414	1995	Koehnke (1997)
	251	1996	Koehnke (1997)
	759	2008	This Study
Tanypodinae	434	1961	Hilsenhoff (1967)
	560	1962	Hilsenhoff (1967)
	434	1963	Hilsenhoff (1967)
	333	1964	Hilsenhoff (1967)
	512	1995	Koehnke (1997)
	763	1996	Koehnke (1997)
	174	2008	This Study

and 2008 may have been partly driven by changes in the Lake Winnebago invertebrate community. In 1998 zebra mussels (*Dreissena polymorpha* (Pallas)) colonized Lake Winnebago and became established in the lake within a few years (Bruch 2008). Johannsson et al. (2000) concluded that zebra mussels did not directly affect the biomass of other benthic invertebrate populations in the eastern and western basin of Lake Erie, but there was a change in community structure in the eastern basin. If the conditions observed by Johannsson et al. (2000) in Lake Erie could be applied to Lake Winnebago then it is possible that zebra mussels, (which likely yet indirectly compete for the same food source) along with other factors such as disease and

parasitism (Hilsenhoff 1967), may be influencing the chironomid community dynamics in Lake Winnebago.

Generally, chironomid instantaneous growth rate increased with increasing temperature. Other factors, such as food quality and/or quantity or chironomid community composition in the mesocosms, may have influenced larval growth in the experiments (Hauer and Benke 1991, Benke 1998, Reynolds and Benke 2005). Although the result was marginally non-significant, the 25-29 mm length class responded negatively to temperature. This may have occurred due to the physiological changes that were occurring in preparation for pupation (Huryn and Wallace 1986). As the larvae were maturing and nearing pupation, it is possible that they began to feed less often and their biomass decreased as metabolism changed in preparation for pupation. These changes might lead to a reduction in IGR that was detected in this study. A higher mesocosm temperature (23°C verses 8°C) may have amplified the rate of change in metabolism associated with pupation which also could have lead to more rapid weight loss thereby altering the instantaneous growth rate.

My chironomid annual production estimates are similar to many other values of chironomid production from lentic systems in North America but lower than most values from lentic systems in Europe (Table 6). Research has shown that many Chironominae consume phytoplankton in lentic systems (McLachlan 1977, Johnson et al. 1989). The high amount of annual primary phytoplankton production in Lake Winnebago, which is eutrophic (Lueschow et al. 1970, Sloey and Blum 1972), may be why the annual production of the chironomid community is at least comparable to that in other North American lentic ecosystems at lower latitudes, which probably have higher annual water temperatures. Many estimates of chironomid annual production higher than we calculated for Lake Winnebago are based on smaller species than *C. plumosus* and *C. entis*, the primary contributors to secondary production in Lake

Winnebago (Charles et al 1974, Potter and Learner 1974, Lindegaard and Jonasson 1979, Wilda 1984, Lindegaard 1994, Balci and Kenedy 2002). Smaller chironomid taxa tend to have shorter generation times and, therefore, have high production to biomass ratios compared to larger chironomid species (Waters 1977, Benke 1984, Wilda 1984, Butler and Anderson 1990). Mean chironomid biomass in Lake Winnebago is higher than many of the studies presented in Table 6 because of the high standing stock biomass of the large *C. plumosus* and *C. entis* larvae. The relatively low production to biomass ratios calculated for the chironomids in Lake Winnebago were unexpected given the high production values (Table 4). The low P/B values for the Chironominae (range 2.1-2.4) are some of the lowest reported in the literature. Generally, P/B ratios for *Chironomus* spp. have a range of 3.0-4.0 (Butler 1982), but P/B ratios similar to Lake Winnebago were recorded by Frank (1982) for *C. plumosus* in Lake Federsee, Germany (1.3-3.2). Mason (1977) reported that *C. plumosus* had a P/B ratio ranging 1.6-1.9 in Alderfen Broad, a shallow lake in Norwich, England. The predatory subfamily Tanypodinae had much higher P/B ratios in Lake Winnebago in this study (range 9.8-10.3) than the collector-gatherers of the Chironominae. The Tanypodinae in Lake Winnebago are probably multivoltine which would account for the high turnover rates. The P/B ratio for Tanypodinae in Lake Winnebago is at the higher end of published values for Tanypodinae and is similar to the values reported in Terek and Losos 1979, Benson et al. 1980, and Sephton and Patterson 1986 (range 9.1-19.8). The P/B ratios for Chironomidae in Lake Winnebago largely reflect the high standing stock biomass of the subfamily Chironominae.

By comparing the secondary production of Chironomidae and the production of lake sturgeon in Lake Winnebago I can assess if chironomid production is sufficient to maintain the sturgeon population. . Assuming a 4-16% value for trophic efficiency (Wolff 1994, Manickchand-Heileman et al. 1998, Manickchand-Heileman et al. 2004, Chen et al. 2006,

Villanueva et al. 2008), chironomids could support 0.044 g dry mass m^{-2} yr^{-1} of sturgeon production. My estimate of sturgeon production for Lake Winnebago suggests that there likely was sufficient chironomid secondary production in 2008-2009 to support the lake sturgeon population. However, during years of low chironomid abundance, chironomid secondary production levels could conceivably fall to levels that may be insufficient for lake sturgeon. In this vein, Bruch (2008) showed that the condition factor of lake sturgeon in Lake Winnebago was associated with the densities of prey items (especially chironomids and dead fishes) available to lake sturgeon.

Secondary production of Chironomidae in Lake Winnebago is relatively high and past work suggest chironomids are an important source of energy to higher trophic positions. Recent studies have provided evidence that pelagic fishes in lakes rely on benthic secondary production as a source of energy (Blumenshine et al. 1997, Vadeboncoeur et al. 2002, Vander Zanden and Vadeboncoeur 2002). In light of the growing body of evidence that benthic production can play a major role in supporting whole lake food webs, more studies of benthic secondary production are needed to assess the flux of energy available to higher trophic levels. Comparing my estimate of larval chironomid secondary production in Lake Winnebago to estimated lake sturgeon production provides researchers and fisheries managers with baseline data that can be used to more accurately infer ecological processes that can impact the sustainability of an important fish species.

Table 6. Chironomid annual production estimates (dry mass = DM) (g m^{-2} yr^{-1}), mean biomass (g DM m^{-2}) and annual production:biomass (P/B) ratios from lentic systems. Some values were calculated to dry mass using the conversion: 1g dry mass = 0.9g ash-free dry mass = 20.95 kJ (Waters 1977).

Taxa	System	DM (g)	Biomass	P/B	Reference
Chironomus anthracinus	L. Esrom, Sweden	12.9	-	3.8	Jonasson (1972)
Chironomus anthracinus	Loch Leven, Scotland	25.7	6.5	3.9	Charles et al. (1974)
Chironomidae	Eglwys Nunydd Res., Wales	19.8	3.4	3.2-7.6	Potter and Learner (1974)
Procladius denticulatus	L. Memphremagog, Quebec-Vermont	0.1-0.9	0.05-0.3	-	Dermott (1977)
Chironomus anthracinus	L. Memphremagog, Quebec-Vermont	1.3-3.4	0.4-1.1	-	Dermott (1977)
Procladius islandicus	L. Myvatn, Iceland	0.56[b]	-	-	Lindegaard and Jonasson (1979)
Tanytarsus gracilentus	L. Myvatn, Iceland	21.2[b]	-	7.5	Lindegaard and Jonasson (1979)
Chironomus islandicus	L. Myvatn, Iceland	7.4[b]	-	2.0	Lindegaard and Jonasson (1979)
Procladius sp.	A Texas pond, Texas	2.4	-	19.8	Benson et al. (1980)
Chironomus decorus	A Texas pond, Texas	6.0	-	19.6	Benson et al. (1980)
Cricotopus sylvestris	Estuarine Cove, New York	5.8	0.28	21.0	Menzie (1981)
Chironomidae	L. Tjeukemeer, Netherlands	0.4-3.7	-	-	Beattie (1982)
Chironomus spp.	Tundra Pond, Alaska	4.1	8.4	0.49	Butler (1982)
Chironomus plumosus	L. Federsee, Germany	6.8-11.0	3.0-8.5	1.29-3.23	Frank (1982)
Chironomus spp.	L. Hayes, New Zealand	29.2	1.6	18.5	Graham and Burns (1983)
Cricotopus ornatus	Waldsea Lake, Saskatchewan	0.07-0.1	-	5.4-6.8	Swanson and Hammer (1983)
Tanytarsus spp.	L. Norman, North Carolina	0.7-8.8	-	66-176	Wilda (1984)
Cladotanytarsus spp.	L. Norman, North Carolina	0.07-2.4	-	69-100	Wilda (1984)
Chironomus sp.	L. Norman, North Carolina	0.2-7.3	-	50-70	Wilda (1984)
Cryptochironomus spp.	L. Norman, North Carolina	0.1-0.4	-	71-221	Wilda (1984)
Procladius bellus	Laurel Creek Res., Ontario	0.10-0.18	0.008-0.013	13.0-13.5	Sephton and Paterson (1986)
Chironomus plumosus	L. Vallentunasjon, Sweden	1.67[b]	-	-	Johnson et al. (1989)
Chironomus tenuistylus	Crystal Bog, Wisconsin	4-5	4.1	1.05	Butler and Anderson (1990)
Chironomidae	L. Thingvallavatn, Iceland	1.4[a]	-	3.7	Lindegaard (1992)
Chironomidae	L. Myvatn, Iceland	41.9[a]	-	-	Lindegaard (1994)
Chironomidae	Hjarbaek Fjord, Denmark	52.2[a]	-	-	Lindegaard (1994)
Chironomidae	Rainbow Bay, South Carolina	1.07-7.22	0.1-0.5	-	Leper and Taylor (1998)
Chironomidae	Cypress-Gum Swamps, Georgia	0.67-2.2[b]	-	4.2-12.7	Entrekin et al. (2001)
Chironomidae	Grass-Sedge Marshes, Georgia	0.62-5.4[b]	-	7.9-8.4	Entrekin et al. (2001)
Apedilum elachistum	Simulated Res. Wetland, Texas	9.9	0.13	79	Balci and Kennedy (2002)
Chironomus major	Kentucky Lake, Kentucky	1.5	0.4	3.4	Balci et al. (2005)
Procladius spp.	Crampton Lake, Wisconsin	4.0	0.85	3.34-5.23	Babler et al. (2008)
Chironomus spp.	Crampton Lake, Wisconsin	2.8	0.52	4.55-4.83	Babler et al. (2008)
Tanypodinae	L. Winnebago, Wisconsin	2.0	0.2	10.1	This Study
Chironominae	L. Winnebago, Wisconsin	5.6	2.5	2.2	This Study

[a] Converted from kJ m^{-2} yr^{-1}

[b] Converted from AFDM m^{-2} yr^{-1}

CHAPTER III

CONCLUSIONS

Mean annual Chironomidae production in Lake Winnebago was 7.59 g DM m^{-2} yr^{-1}. Mean Chrionominae production in Lake Winnebago was 5.56 g DM m^{-2} yr^{-1}. Mean Tanypodinae production in Lake Winnebago was 2.04 g DM m^{-2} yr^{-1}. Chironomidae production did not show significant variation among sample sites. Chironominae accounted for 73% of the family level production at all sample sites. Sample site 2-North had more Tanypodinae production than at any other site. Daily Chironomidae production in Lake Winnebago varied significantly throughout this study showing an increase in production through the summer of 2008.

Generally, the instantaneous growth rates developed from the laboratory growth experiments could be used to predict the temperature-specific growth rates of chironomid larvae in Lake Winnebago. The instantaneous growth rates of the intermediate length classes used in the experiments did not respond to changes in water temperature possibly indicating that some other factor is stimulating growth and/or experimental error associated with the experimental design. The largest length class showed a trend of decreasing growth rate with increasing temperature which may indicate that the physiology of the insects may be changing before they pupate leading to a lack of growth. All larvae ranging from 1-29 mm in length grew at a similar rate statistically at temperatures at or below 13°C but smaller larvae grew at significantly faster rates than larger larvae above 13°C.

The densities of the large-bodied *Chironomus* spp. that occur in Lake Winnebago seem to have rebounded from the low reports by Koehnke (1997) back to levels as observed by Hilsenhoff (1967). In contrast, Tanypodinae community densities have decreased compared to what Hilsenhoff (1967) and Koehnke (1997) reported. There is not a clear answer as to why there

is so much density variation in the chironomid community among studies but the ecological impacts of the recent colonization (1998) of the zebra mussel (*Dreissena polymorpha*) and interactions between parasites and viruses (Hilsenhoff 1967) likely influence the temporal density dynamics.

The estimate for lake sturgeon production is the first known production estimate for a wild lake sturgeon population, and the first comparison between the secondary production of a food source (non-biting midges) with the annual production of this large and long-lived fish species. Although the estimates of lake sturgeon production are approximate, they provide knowledge on how much energy is required to support the large lake sturgeon population. The conservative value of 0.044 g dry mass m^{-2} yr^{-1} for the lake sturgeon population falls below 4-16% of the annual Chironomidae production estimate (4-16% = 0.30-1.2 g DM m^{-2} yr^{-1}) indicating that there was enough chironomid biomass produced in 2008 to support the lake sturgeon population and other animal populations relying on chironomids as a food source.

The importance of understanding invertebrate production is critical to understanding how an ecosystem functions. Energy pathways determine how energy flows through different trophic levels. Secondary production estimates the amount of biomass or energy produced by primary consumers that will be available for consumption by the next trophic level. Food chain length is restricted by the amount of energy that is available from basal trophic levels. Research on fish production in lakes has been focused on pelagic derived energy pathways. The benthic invertebrate community in lakes represents a less understood pathway through which energy is transferred to fish production. This research provides the first estimate of chironomid secondary production in Lake Winnebago, Wisconsin where previous research has shown that the large lake sturgeon population of Lake Winnebago relies on chironomids for somatic growth. My estimates of chironomid annual production and mean biomass are higher than many other lentic chironomid

production estimates from North America but lower than most values from some highly productive lakes in Europe. Based on my research there was sufficient chironomid production in Lake Winnebago to support the current population of lake sturgeon and possibly other animals that rely on chironomids as a food source.

APPENDIX A

Sample Date Chironomid Length-Class Density Profiles

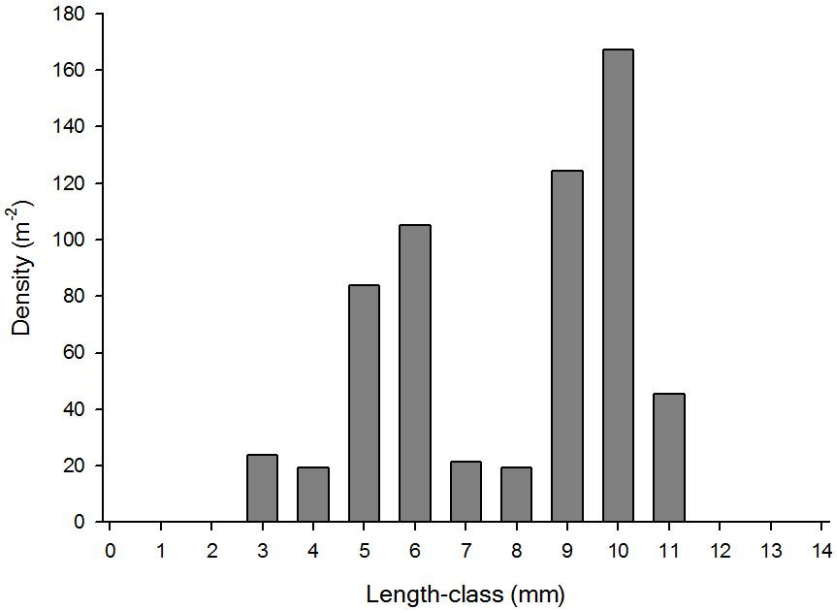

Figure A-1. Mean density of Tanypodinae length-classes on 29 April 2008.

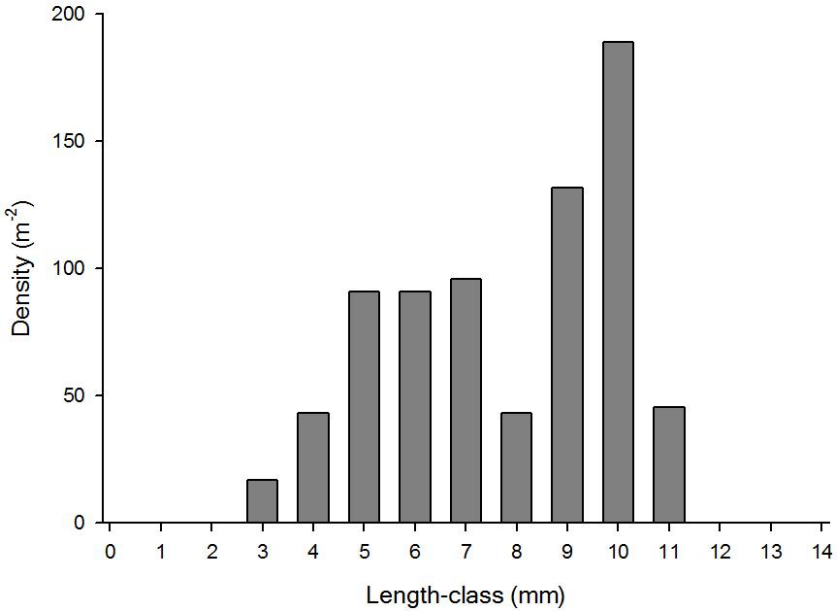

Figure A-2. Mean density of Tanypodinae length-classes on 15 May 2008.

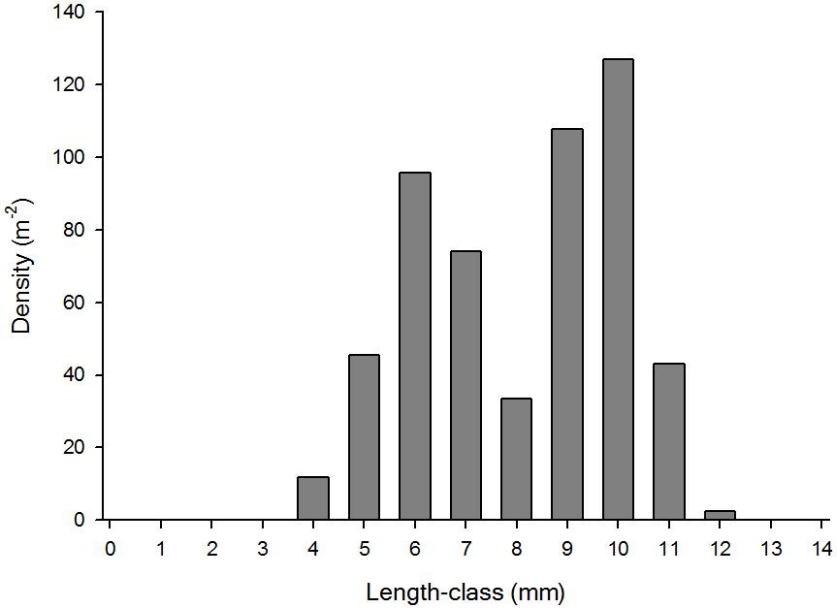

Figure A-3. Mean density of Tanypodinae length-classes on 29 May 2008.

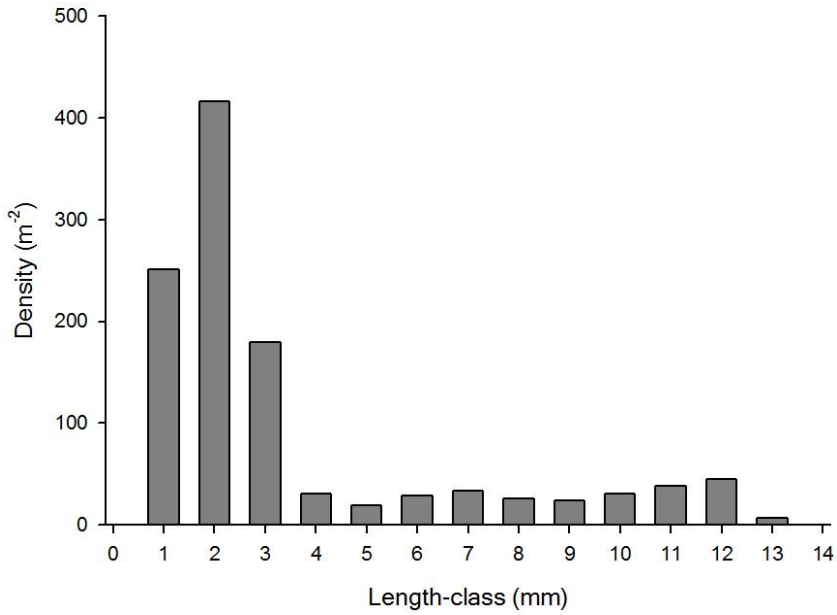

Figure A-4. Mean density of Tanypodinae length-classes on 16 June 2008.

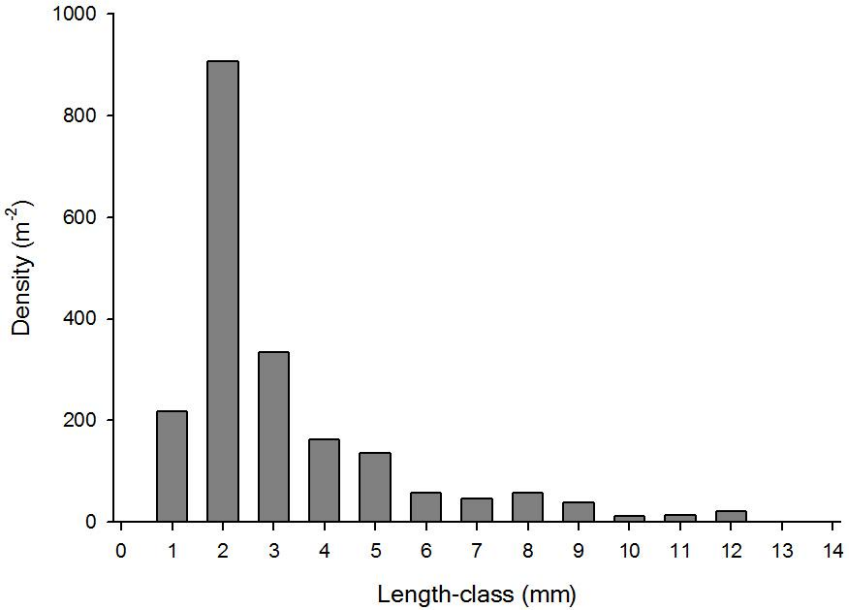

Figure A-5. Mean density of Tanypodinae length-classes on 3 July 2008.

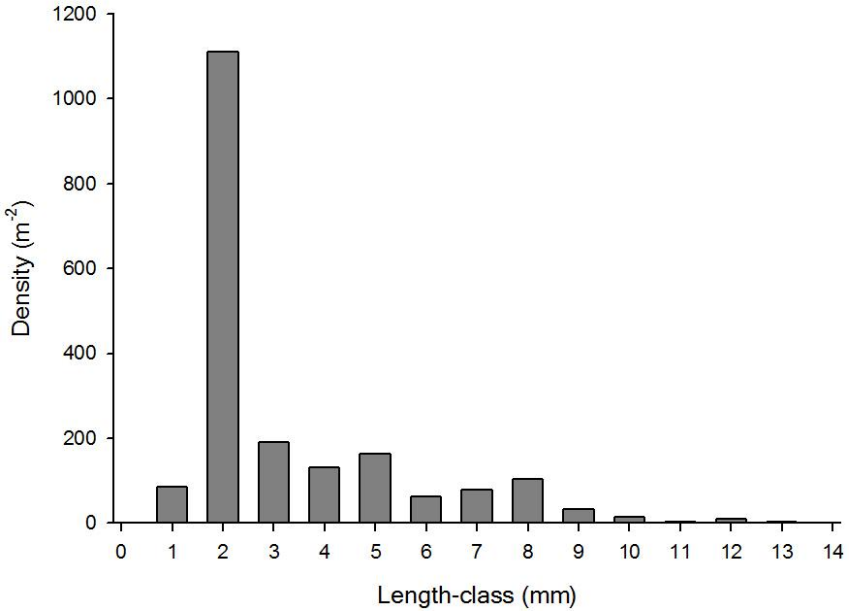

Figure A-6. Mean density of Tanypodinae length-classes on 22 July 2008.

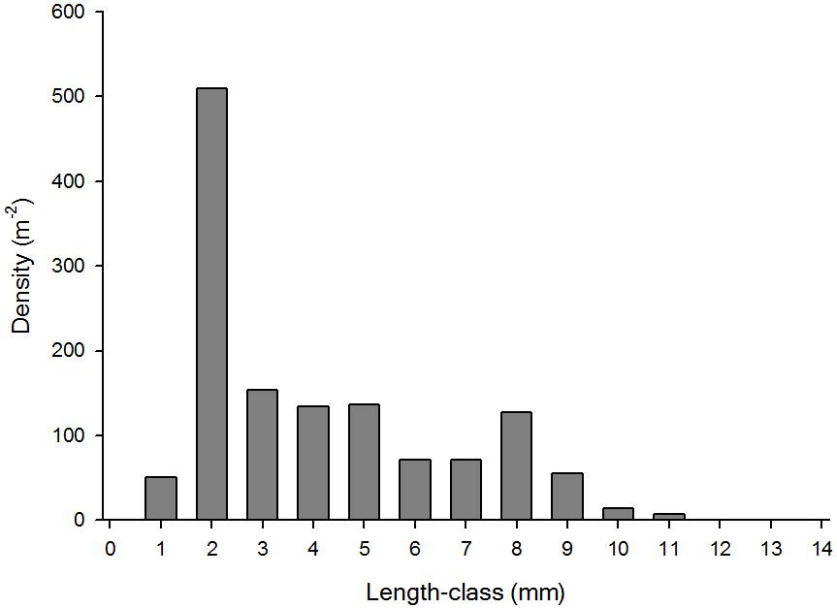

Figure A-7. Mean density of Tanypodinae length-classes on 5 August 2008.

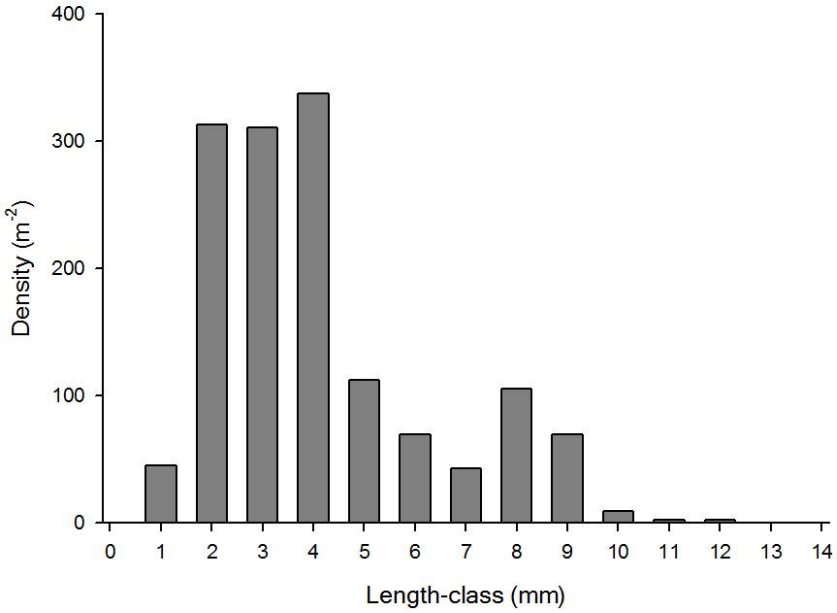

Figure A-8. Mean density of Tanypodinae length-classes on 26 August 2008.

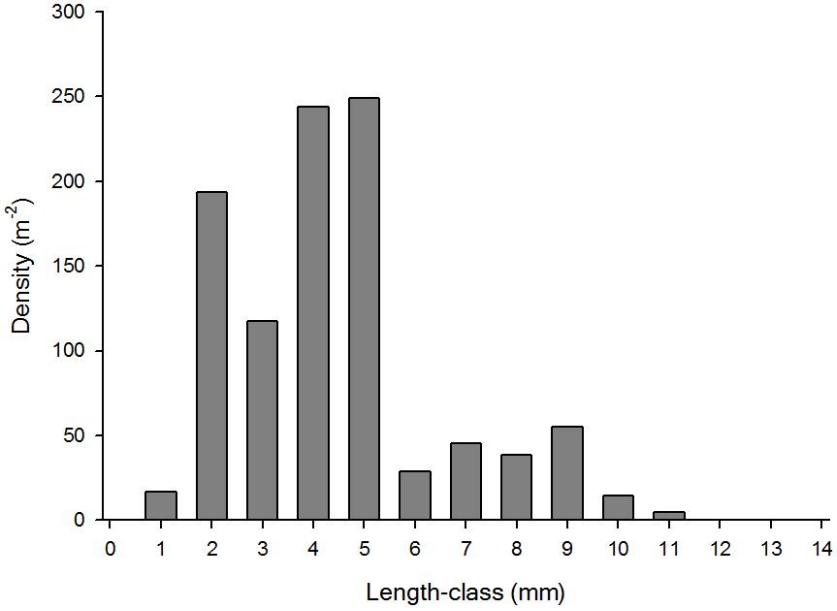

Figure A-9. Mean density of Tanypodinae length-classes on 9 September 2008.

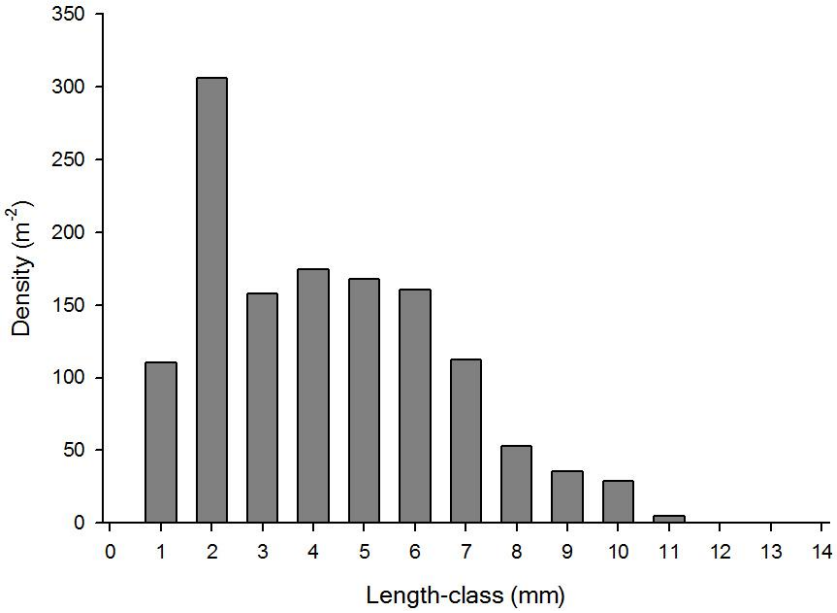

Figure A-10. Mean density of Tanypodinae length-classes on 23 September 2008.

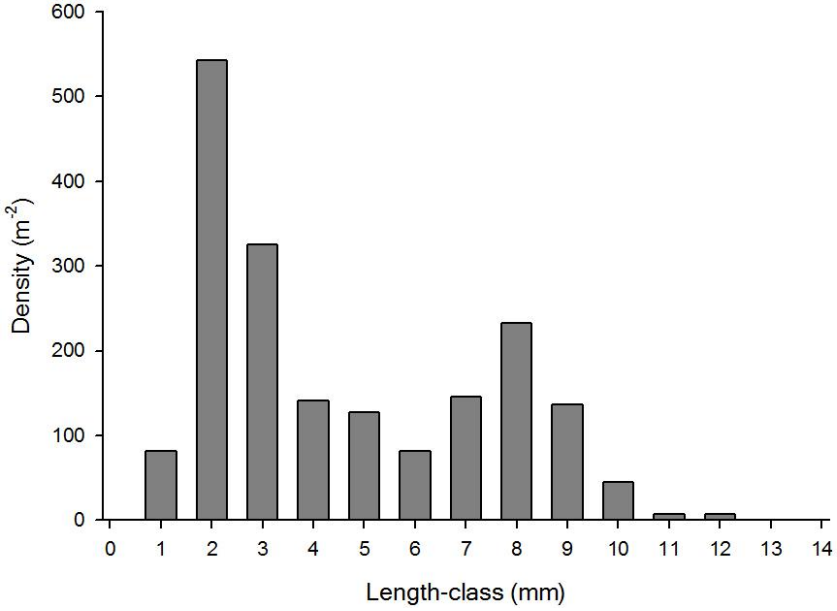

Figure A-11. Mean density of Tanypodinae length-classes on 9/13 October 2008.

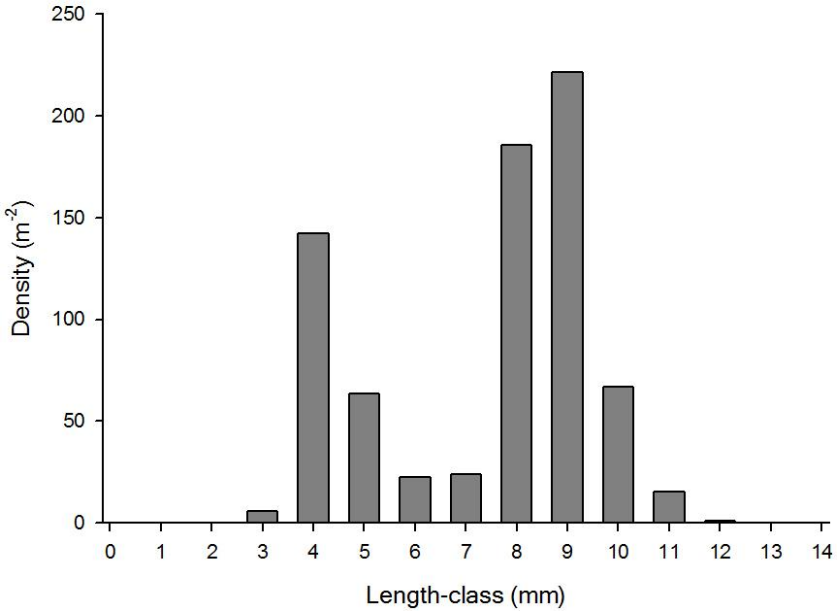

Figure A-12. Mean density of Tanypodinae length-classes on 27 April 2009.

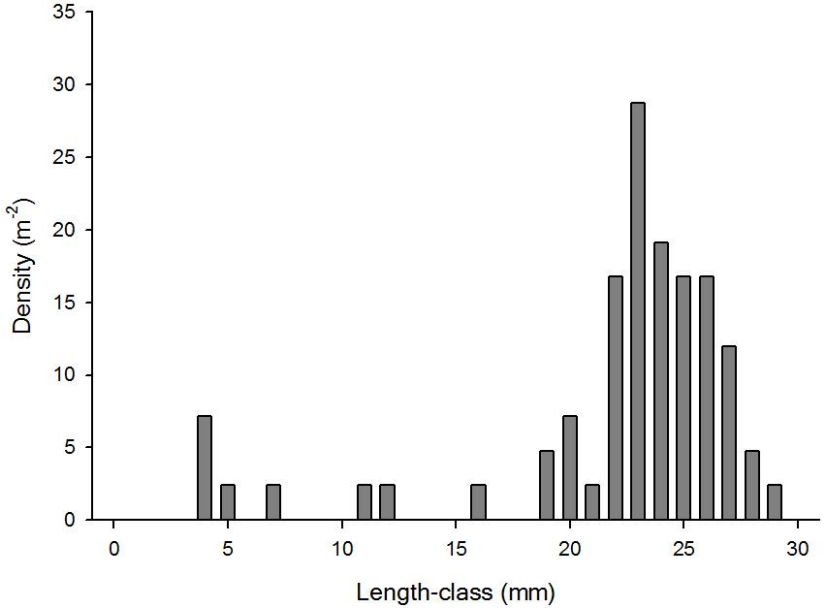

Figure A-13. Mean density of Chironomidae length-classes on 29 April 2008.

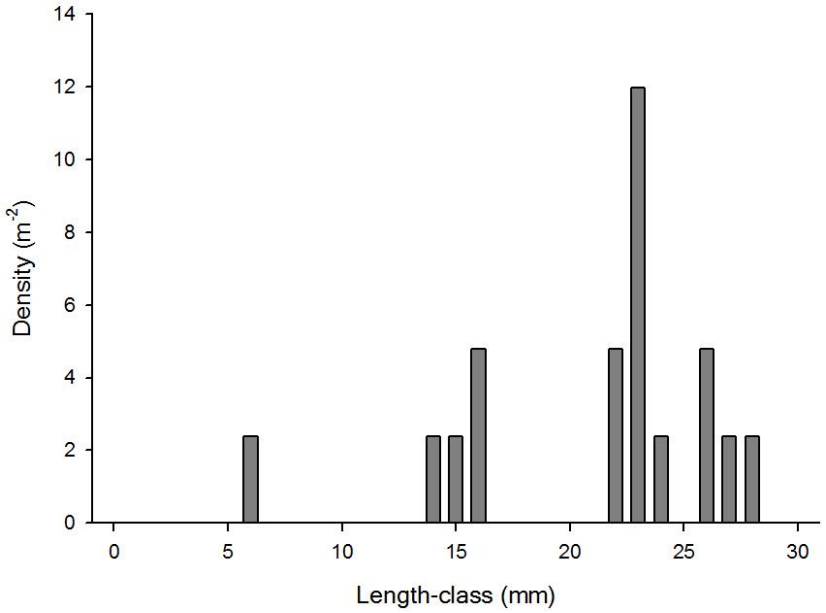

Figure A-14. Mean density of Chironomidae length-classes on 15 May 2008.

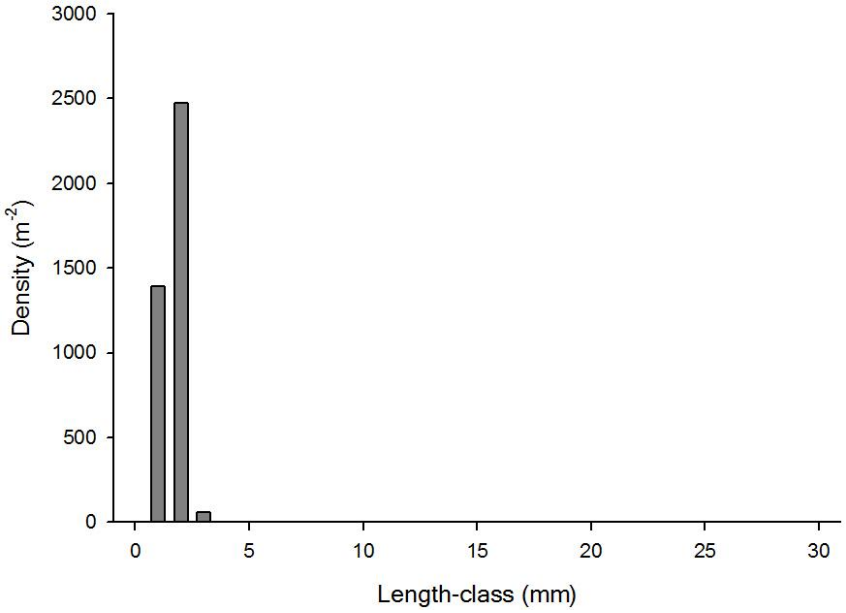

Figure A-15. Mean density of Chironomidae length-classes on 29 May 2008.

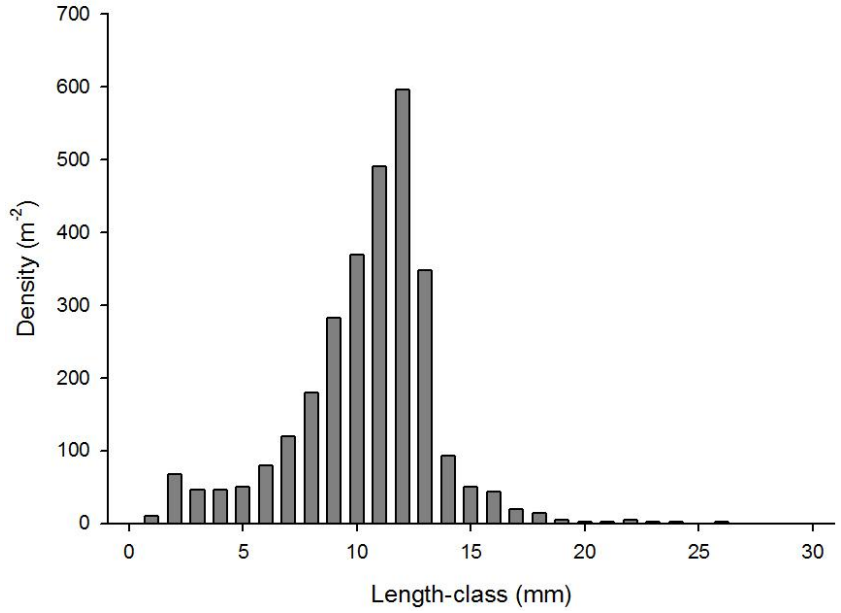

Figure A-16. Mean density of Chironomidae length-classes on 16 June 2008.

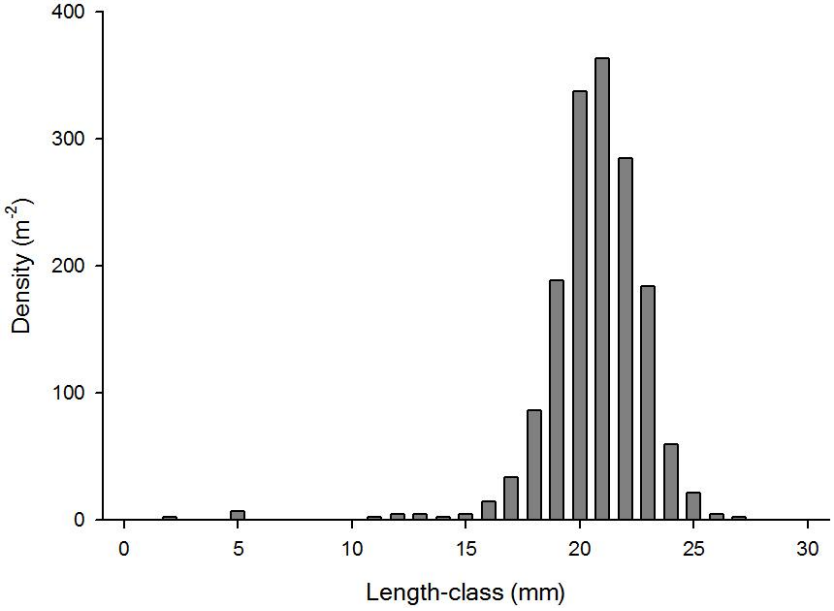

Figure A-17. Mean density of Chironomidae length-classes on 3 July 2008.

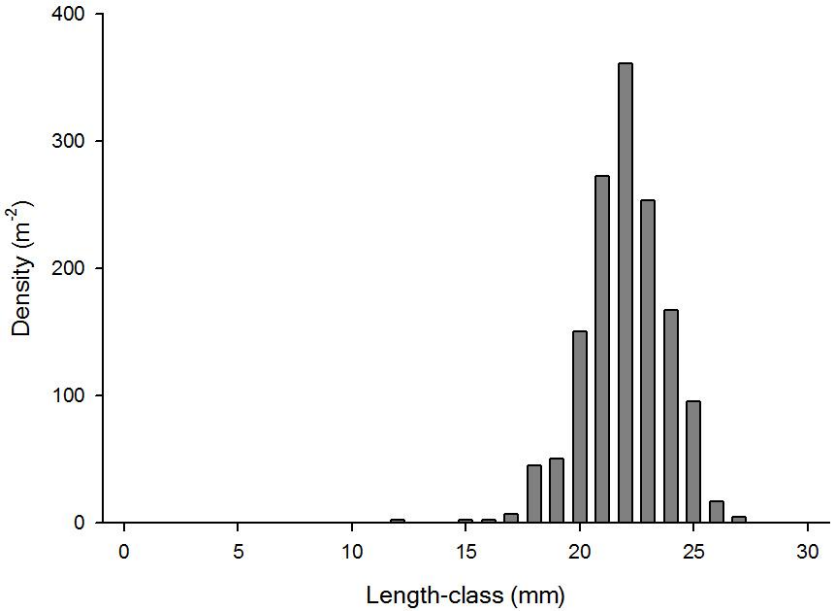

Figure A-18. Mean density of Chironomidae length-classes on 22 July 2008.

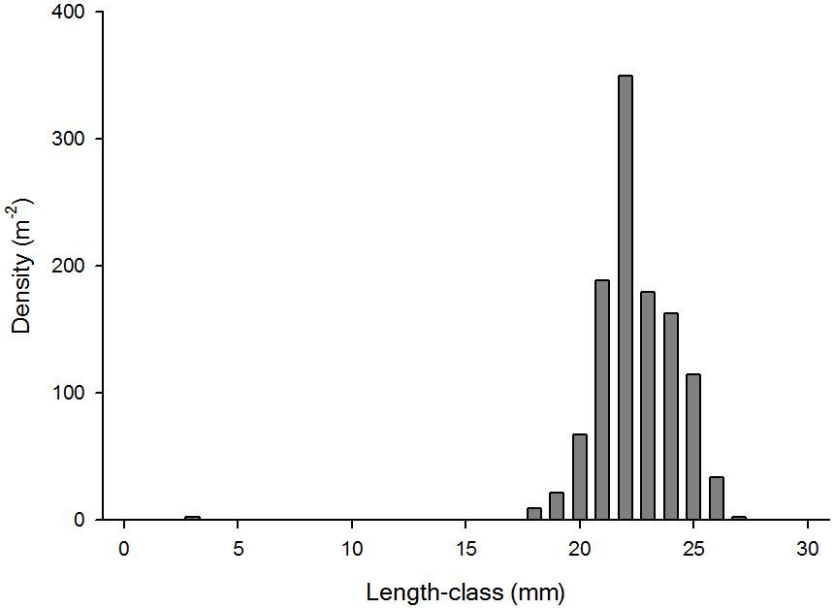

Figure A-19. Mean density of Chironomidae length-classes on 5 August 2008.

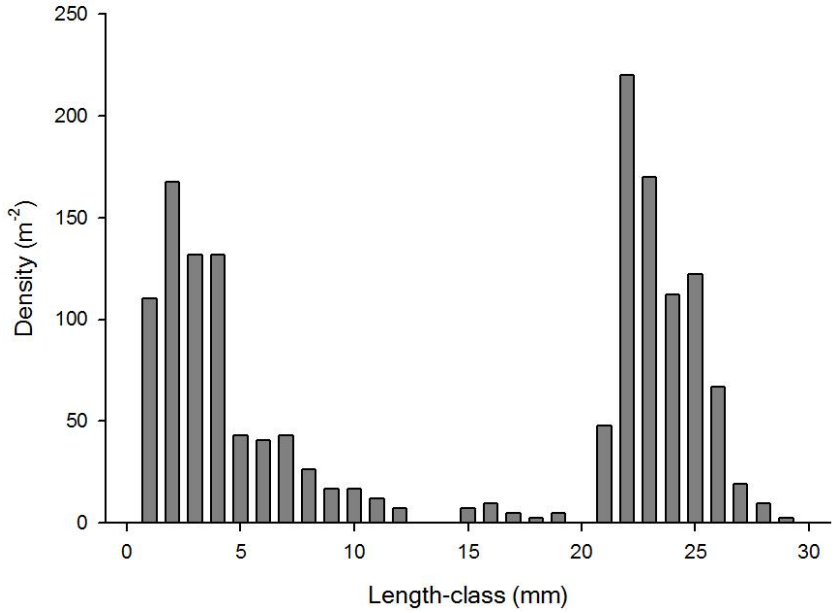

Figure A-20. Mean density of Chironomidae length-classes on 26 August 2008.

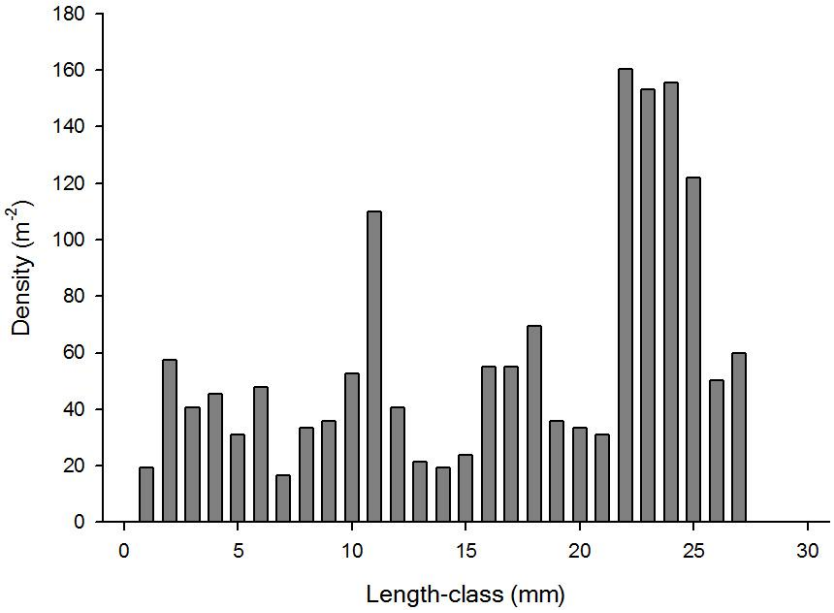

Figure A-21. Mean density of Chironomidae length-classes on 9 September 2008.

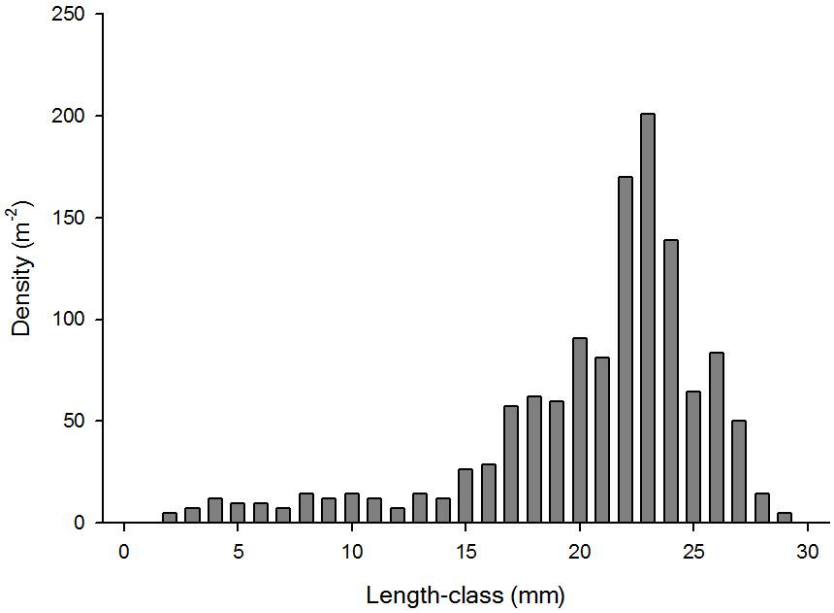

Figure A-22. Mean density of Chironomidae length-classes on 23 September 2008.

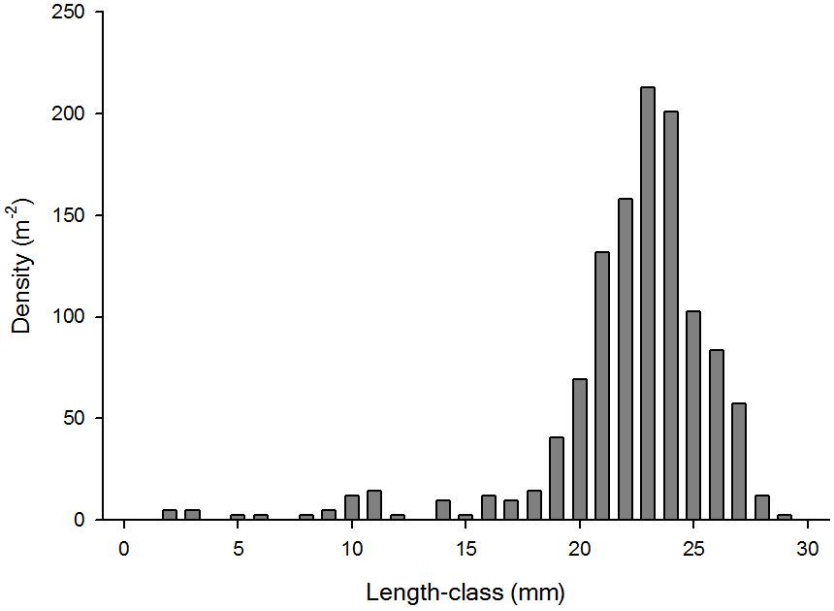

Figure A-23. Mean density of Chironomidae length-classes on 9/13 October 2008.

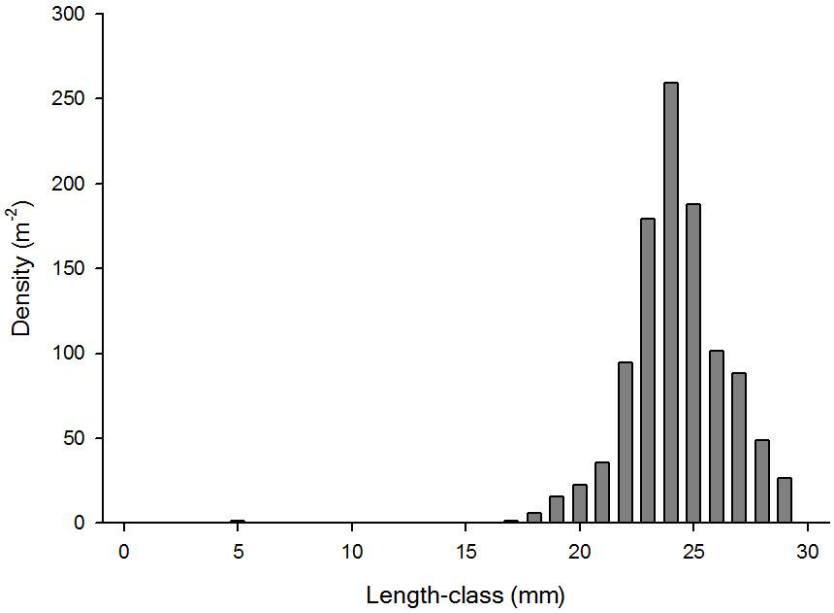

Figure A-24. Mean density of Chironomidae length-classes on 27 April 2009.

APPENDIX B

Sample Date Chironomid Length-Class Biomass Profiles

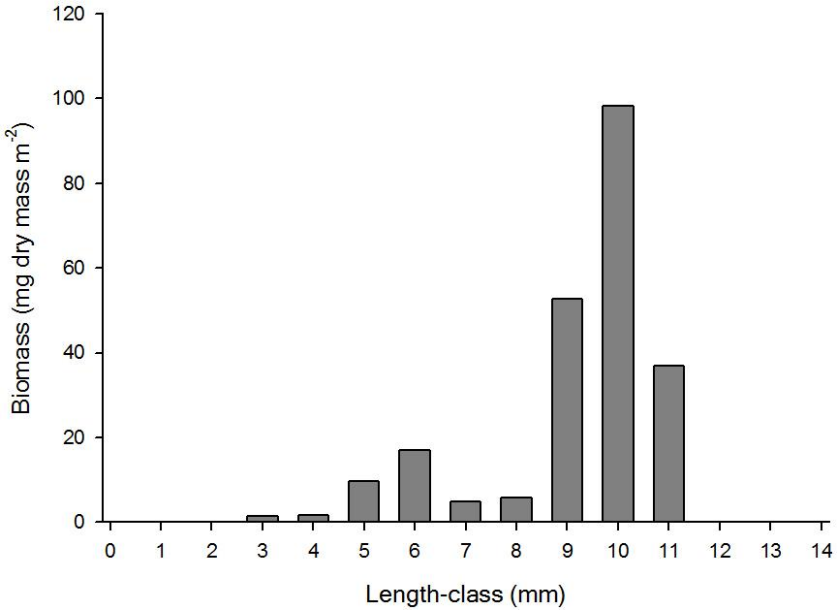

Figure B-1. Mean biomass of Tanypodinae length-classes on 29 April 2008.

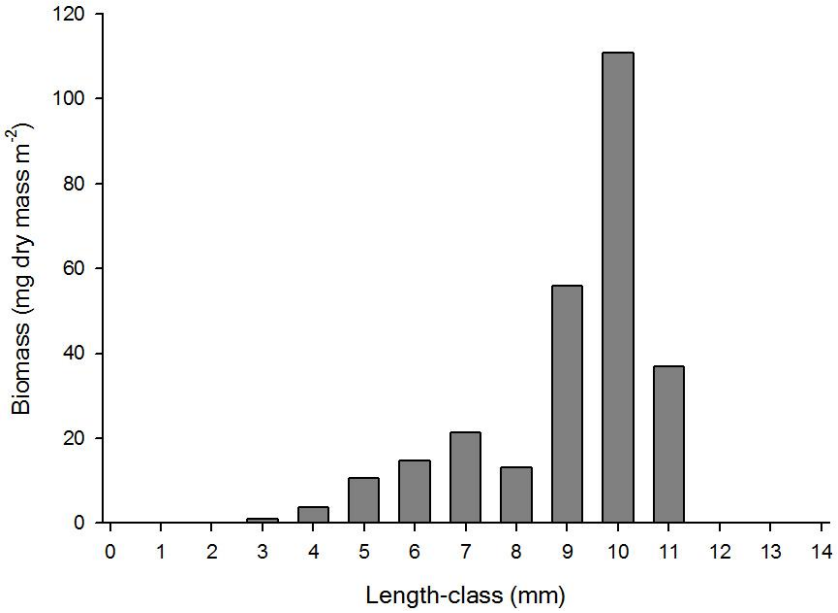

Figure B-2. Mean biomass of Tanypodinae length-classes on 15 May 2008.

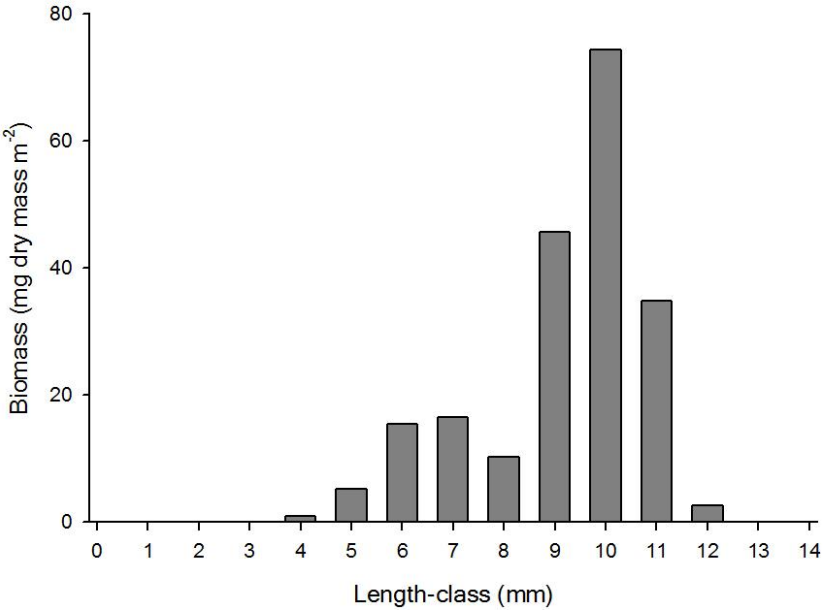

Figure B-3. Mean biomass of Tanypodinae length-classes on 29 May 2008.

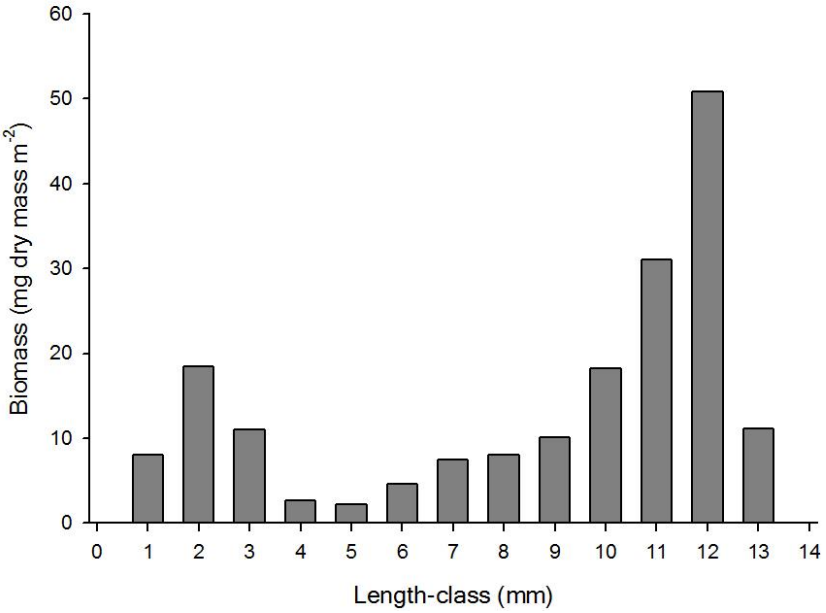

Figure B-4. Mean biomass of Tanypodinae length-classes on 16 June 2008.

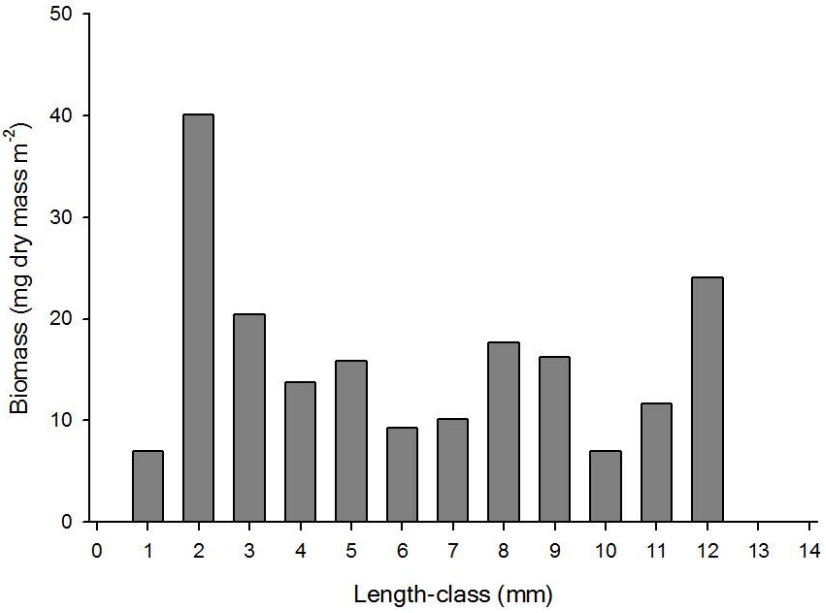

Figure B-5. Mean biomass of Tanypodinae length-classes on 3 July 2008.

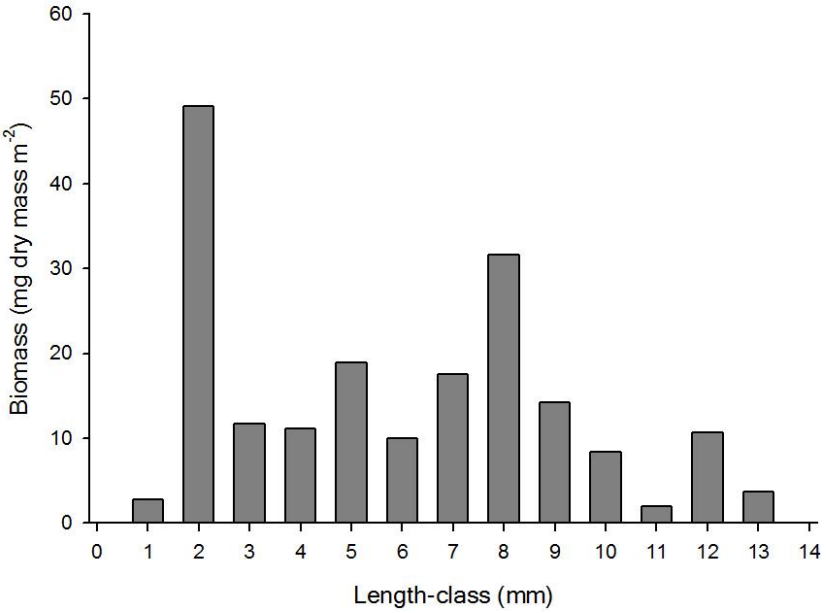

Figure B-6. Mean biomass of Tanypodinae length-classes on 22 July 2008.

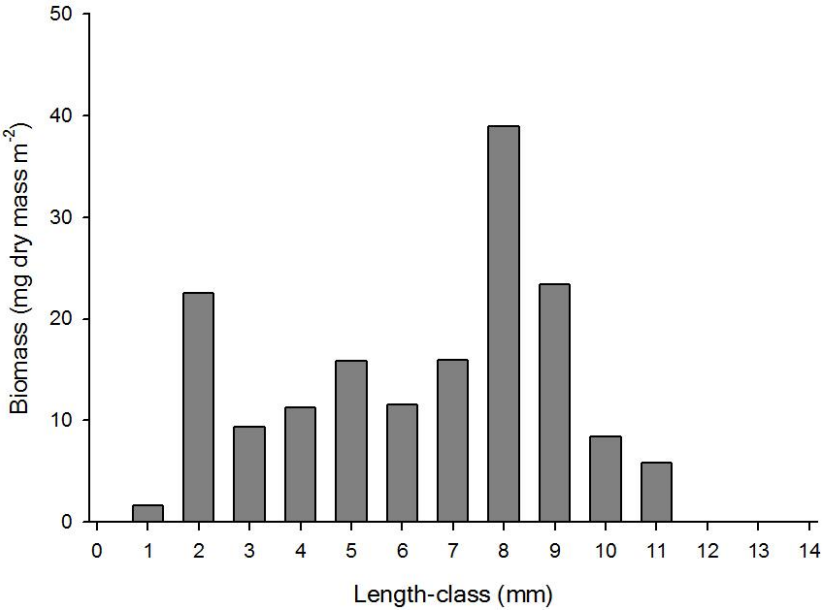

Figure B-7. Mean biomass of Tanypodinae length-classes on 5 August 2008.

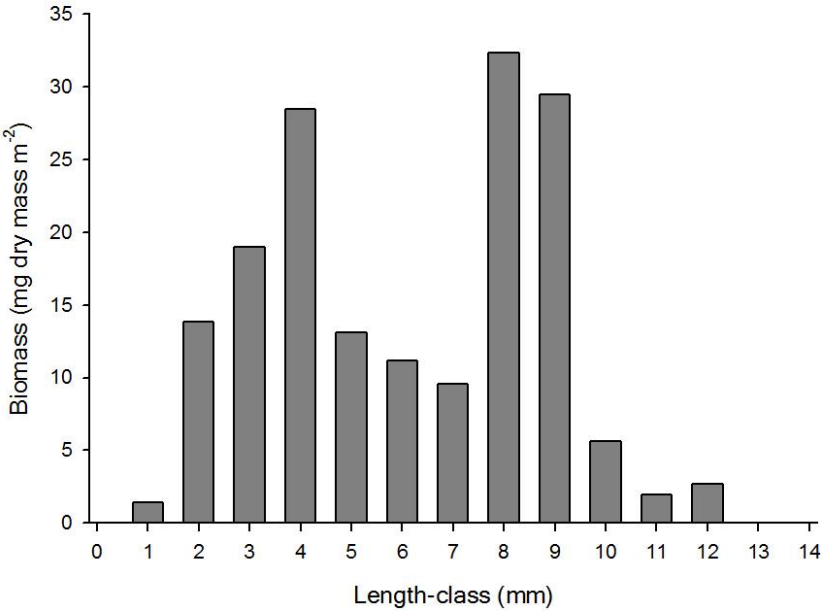

Figure B-8. Mean biomass of Tanypodinae length-classes on 26 August 2008.

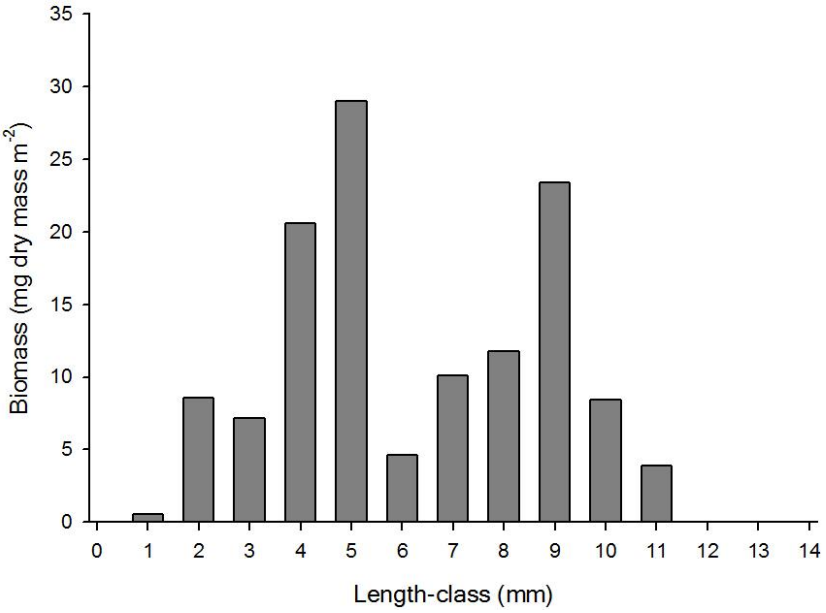

Figure B-9. Mean biomass of Tanypodinae length-classes on 9 September 2008.

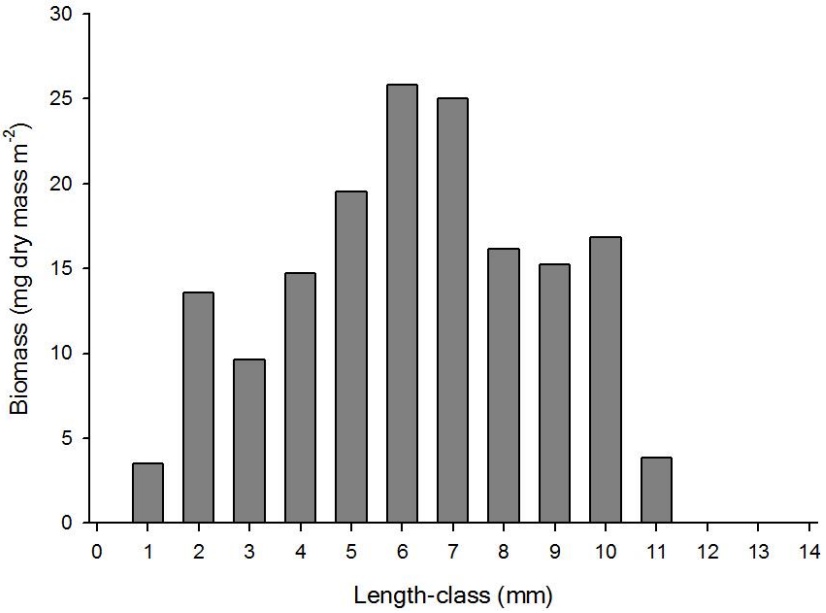

Figure B-10. Mean biomass of Tanypodinae length-classes on 23 September 2008.

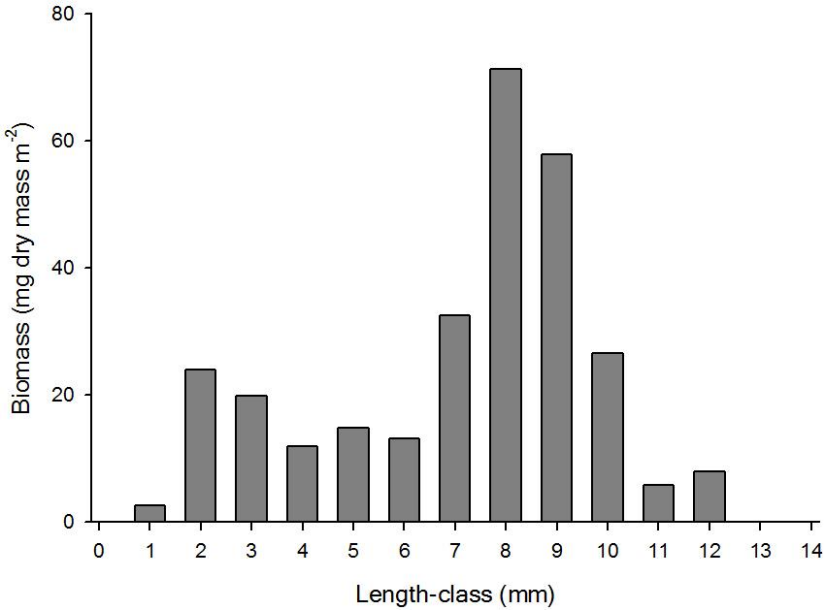

Figure B-11. Mean biomass of Tanypodinae length-classes on 9/13 October 2008.

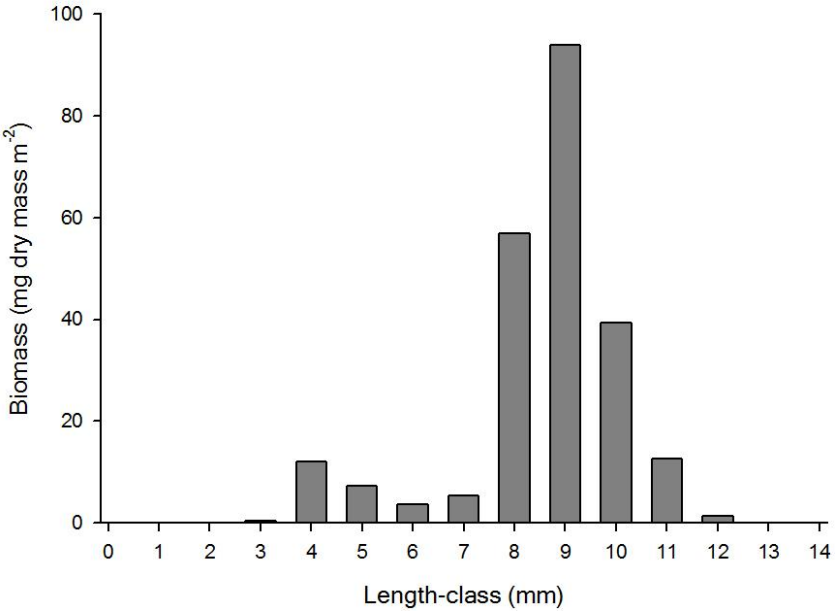

Figure B-12. Mean biomass of Tanypodinae length-classes on 27 April 2009.

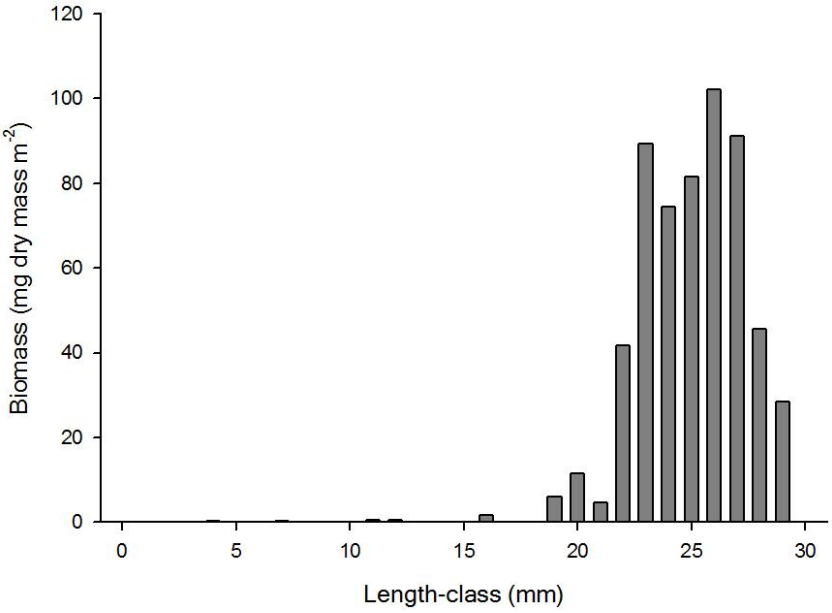

Figure B-13. Mean biomass of Chironominae length-classes on 29 April 2008.

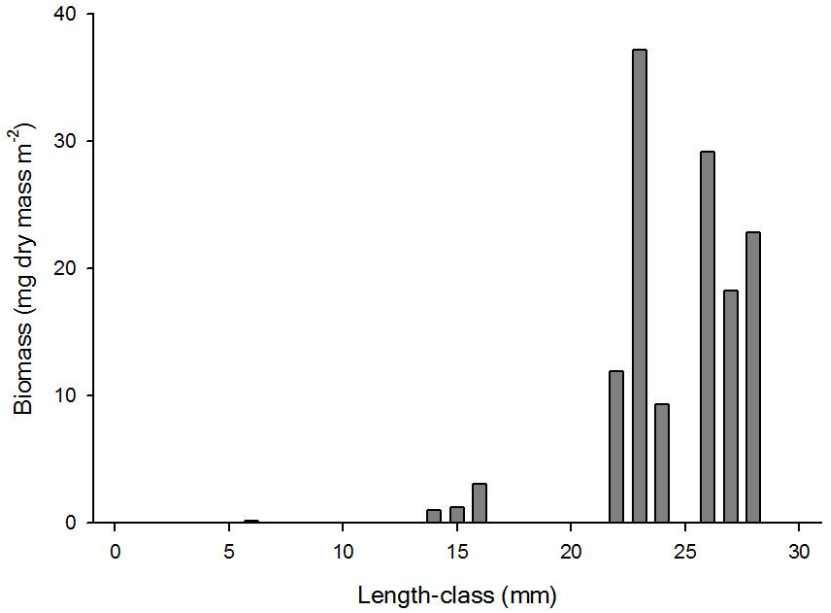

Figure B-14. Mean biomass of Chironominae length-classes on 15 May 2008.

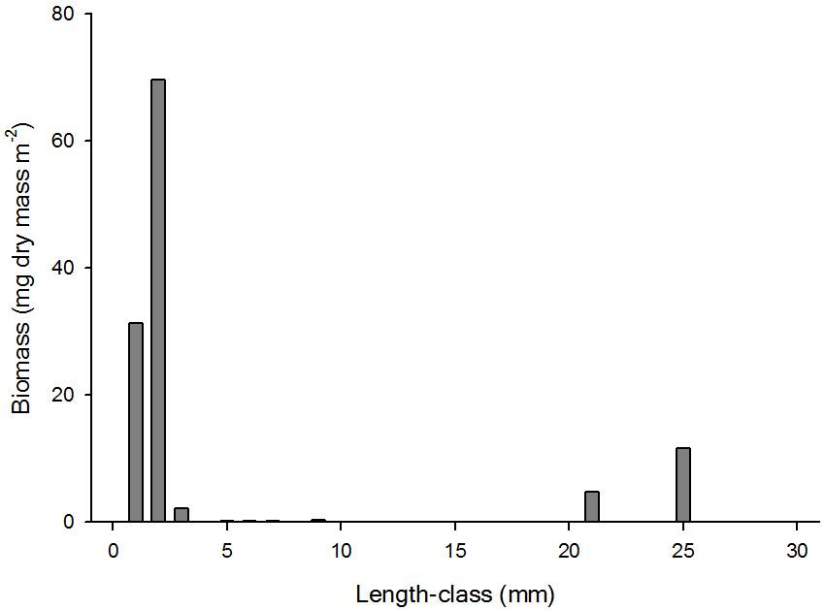

Figure B-15. Mean biomass of Chironominae length-classes on 29 May 2008.

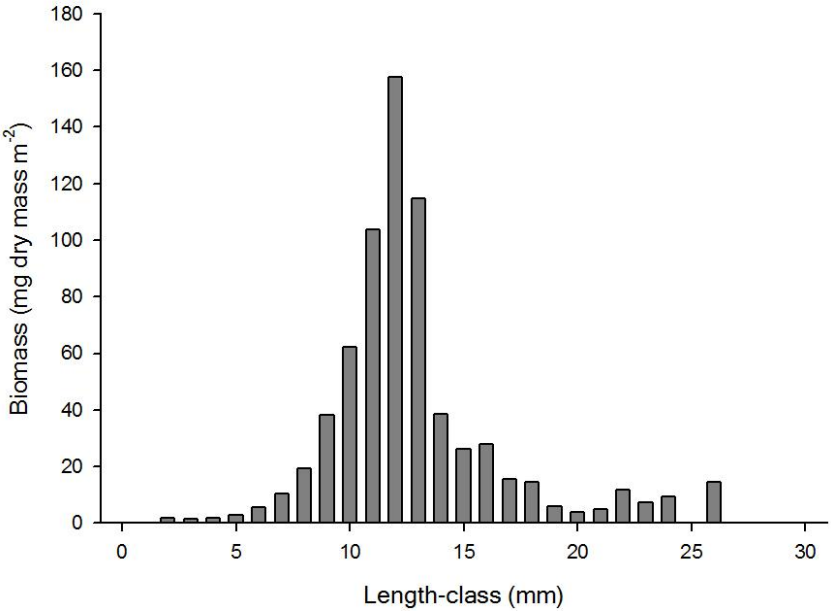

Figure B-16. Mean biomass of Chironominae length-classes on 16 June 2008.

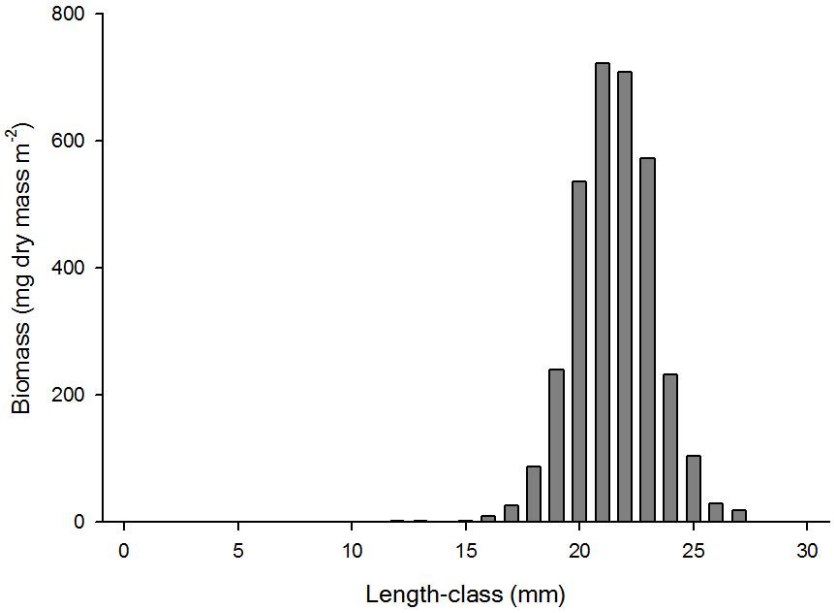

Figure B-17. Mean biomass of Chironominae length-classes on 3 July 2008.

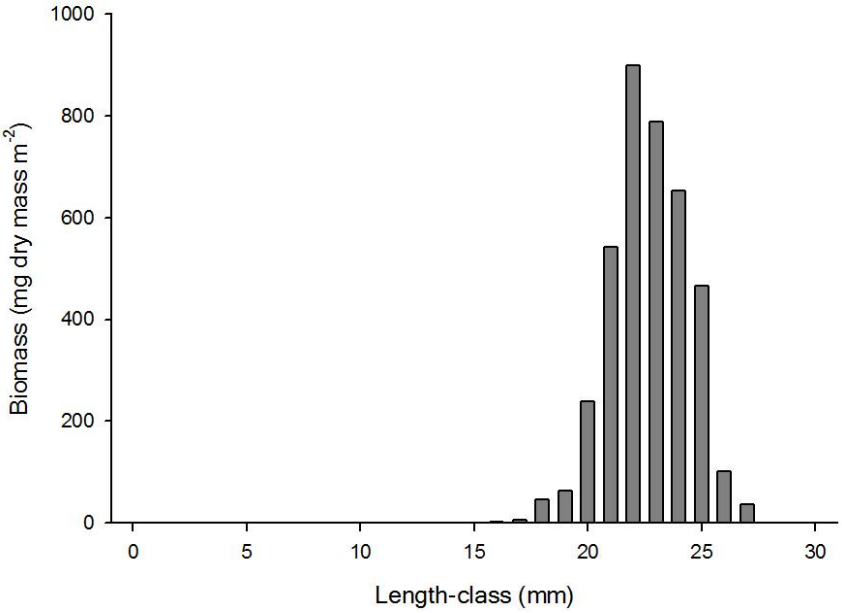

Figure B-18. Mean biomass of Chironominae length-classes on 22 July 2008.

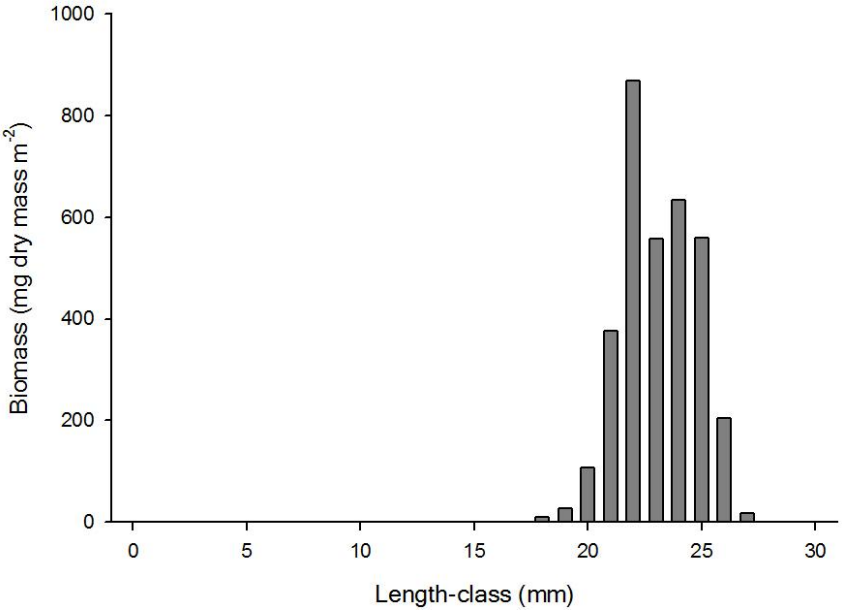

Figure B-19. Mean biomass of Chironominae length-classes on 5 August 2008.

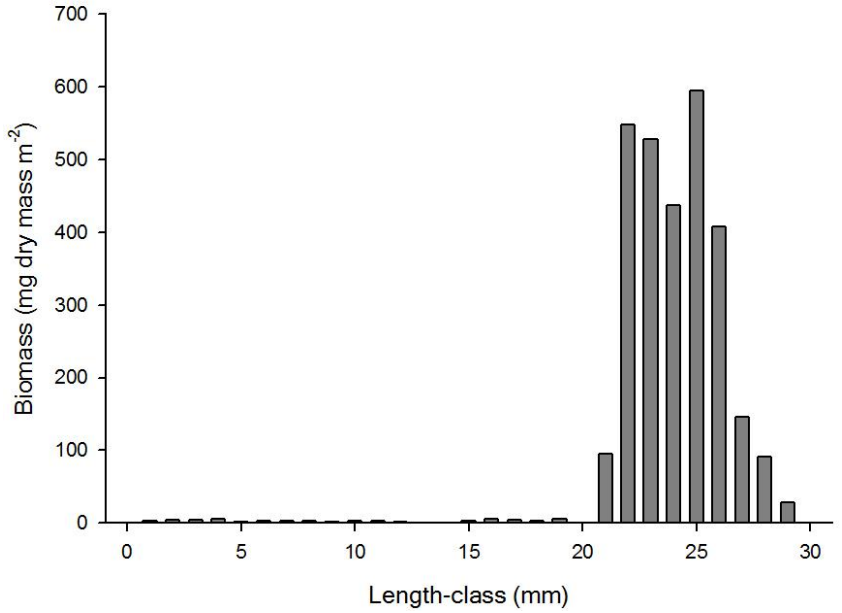

Figure B-20. Mean biomass of Chironominae length-classes on 26 August 2008.

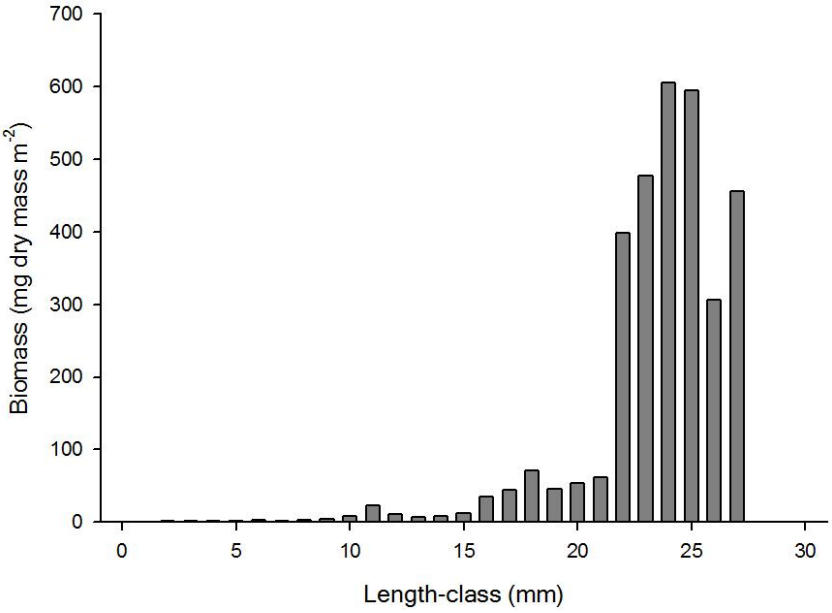

Figure B-21. Mean biomass of Chironominae length-classes on 9 September 2008.

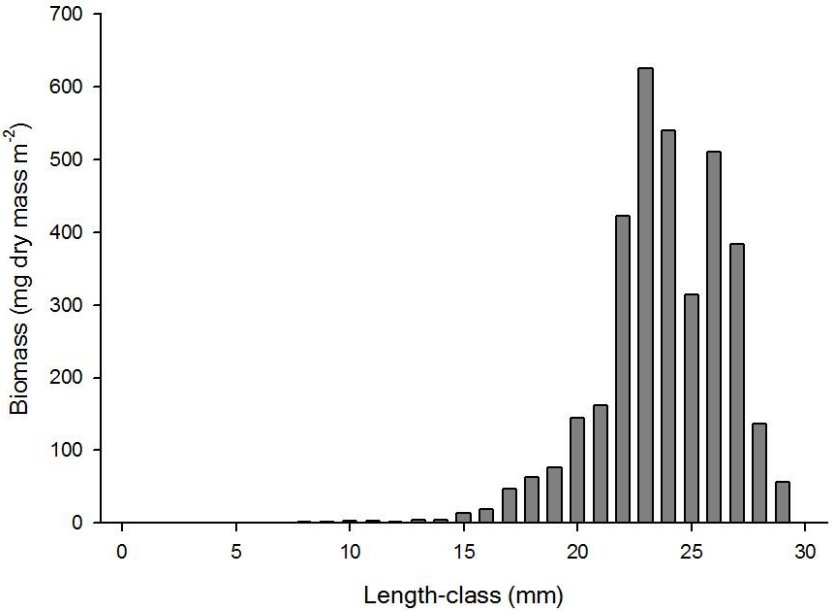

Figure B-22. Mean biomass of Chironominae length-classes on 23 September 2008.

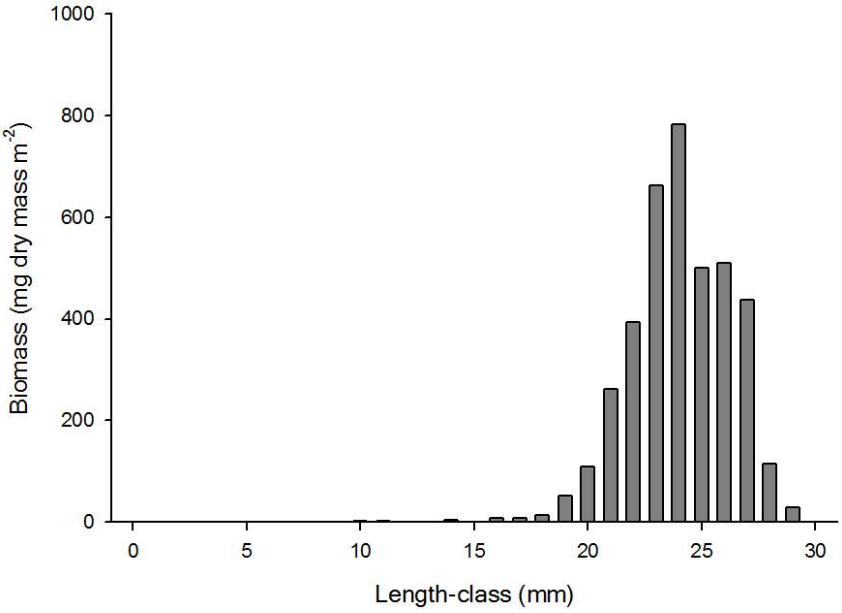

Figure B-23. Mean biomass of Chironominae length-classes on 9/13 October 2008.

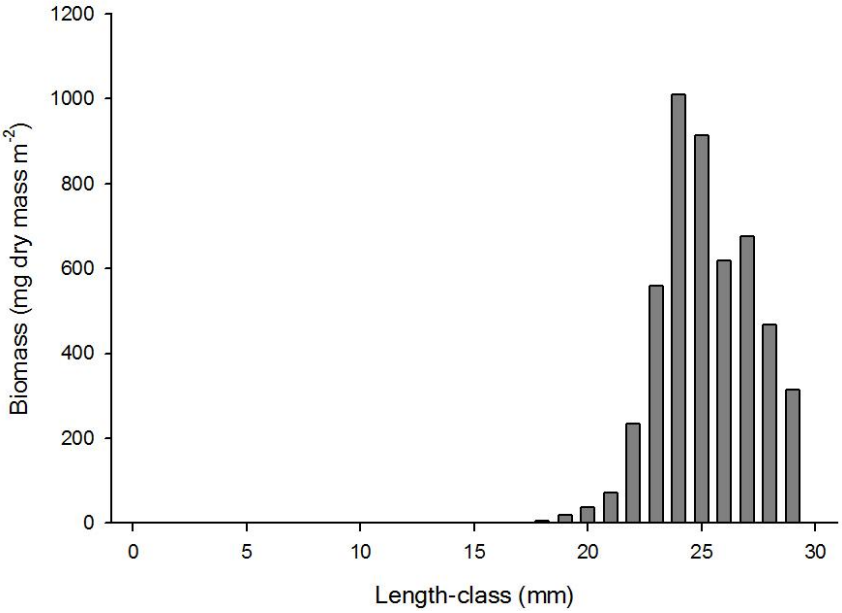

Figure B-24. Mean biomass of Chironominae length-classes on 27 April 2009.

APPENDIX C

Length-Weight Regressions

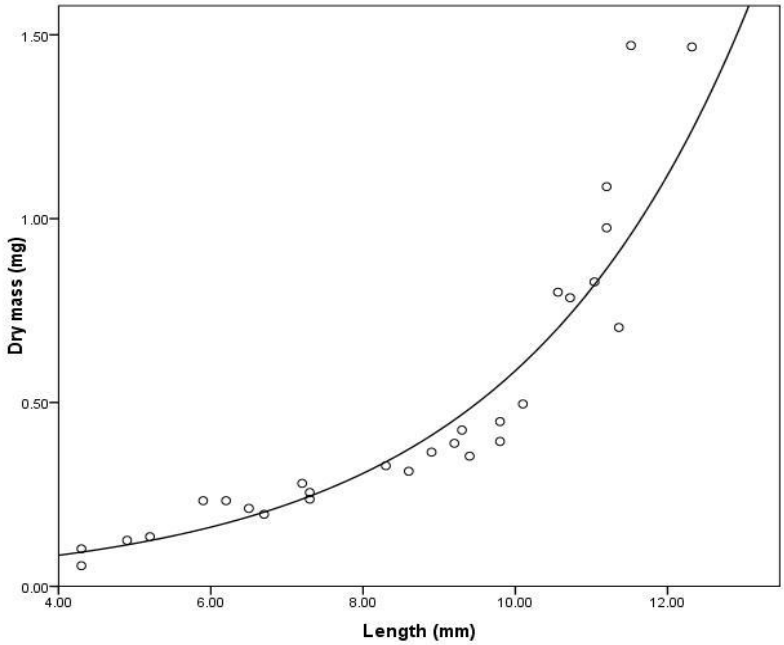

Figure C-1. Tanypodinae length-weight dry mass regression.

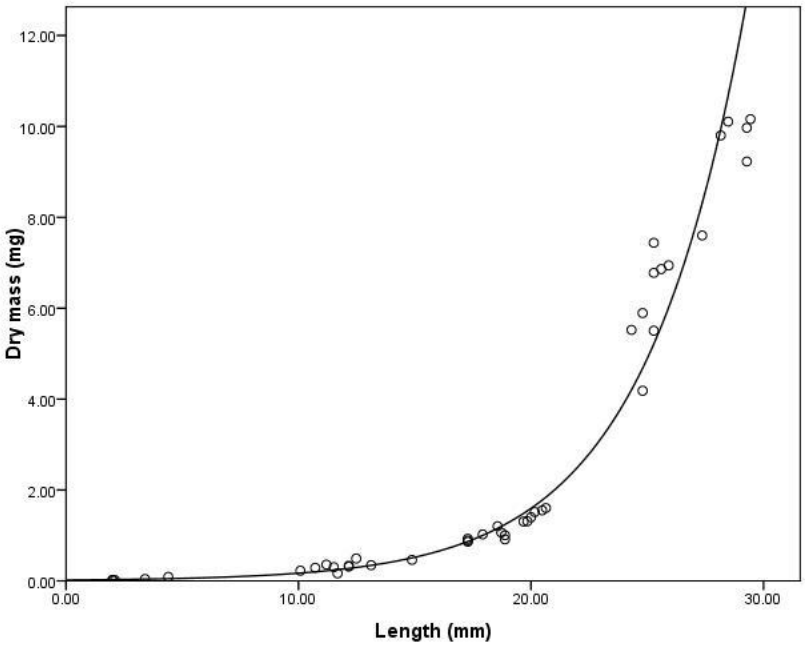

Figure C-2. Chironominae length-weight dry mass regression.

APPENDIX D

Mean Instantaneous Growth Rates for Each Length-Class at Each Temperature Regime

Table 1-D. Experimentally derived mean instantaneous growth rates (IGR) for each length-class at each temperature regime that were used to model larval chironomid growth in Lake Winnebago, Wisconsin.

Length-Class (mm)	Temperature Regime (°C)	IGR (d^{-1})
1-4	23	0.0964
5-8	23	0.0571
9-12	23	0.0824
17-20	23	0.0159
21-24	23	0.00623
25-29	23	-0.00293
1-4	18	0.0719
5-8	18	0.0405
9-12	18	0.0533
17-20	18	0.0104
21-24	18	0.00565
25-29	18	-0.0013
1-4	13	0.00521
5-8	13	0.00681
9-12	13	0.0656
17-20	13	0.00898
21-24	13	0.00368
25-29	13	0.00252
1-4	8	-0.00124
5-8	8	0.00275
9-12	8	0.00799
17-20	8	0.00418
21-24	8	0.00272
25-29	8	0.00211
5-8	4	0.000704
17-20	4	0.00418
21-24	4	0.00272

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