Larval Life History of the Small Minnow Mayfly (*Baetis tricaudatus*)
in the Russian River Watershed

Carolyn Lam

ABSTRACT

Evaluating the life history of aquatic insects is fundamental because it leads to a greater understanding to the overall biology of these organisms, and their role in the ecosystem. *Baetis tricaudatus*, a small minnow mayfly, is one of the most common grazers in the lotic food web in western North America. I studied the larval life history of *B. tricaudatus*, in two northern California locations -- a tributary (Austin Creek) and a river (Russian River mainstem) -- in the Russian River watershed. By measuring body lengths and head widths, I calculated morphological differences to determine emergence and voltinism at each sampling site. In body length, the largest larva measured 7.4mm, and the smallest measured 1.5mm. Moreover, in head width, the largest larva measured 1.0mm, and the smallest measured 0.1mm. Final instars indicated emergence patterns. Austin Creek and the Russian River mainstem larvae were at least bivoltine. Austin Creek larvae emerged between (1) July and August; (2) and September and October. Russian River mainstem larvae emerged between (1) August and September; (2) October and November; and (3) December and January. In addition, the abundances of *B. tricaudatus* varied throughout the sampling period in the sites. Their emergence periods occurred in different months during the sampling period, suggesting habitat differences are likely influencing the life history of this species.

KEYWORDS

growth patterns, emergence, voltinism, habitat differences, benthic macroinvertebrates

INTRODUCTION

Biological monitoring of aquatic habitats, such as streams, can be useful in determining the health of an aquatic ecosystem (Meyer 1997). Environmental factors, such as water quality and seasonality, and human disturbances, such as land-use change and agricultural run-off, influence the organisms that inhabit the ecosystem (Karr 1993, Robinson et al. 1992, Moore and Palmer 2005, Schulz and Liess 1999). Benthic macroinvertebrates are influenced by these factors such as impaired habitats and water quality, which is indicated by decreases in benthic macroinvertebrate taxa richness (Robinson et al. 1992, Karr 1993, Resh and Jackson 1993). One powerful way to biologically monitor water quality is to analyze the life history of benthic macroinvertebrates (Elliot 1967, Winterbourn 1974, Verberk et al. 2008). However, the number of life history research of benthic biology has declined over time because this area of study has moved from descriptive to more experimental research (Resh and Rosenberg 2010).

Examining life history of aquatic insects is essential in biological monitoring of freshwater habitats because it leads to a greater understanding to the behavior and habitat of that organism, and their role in the ecosystem (Merritt et al. 2008, Resh and Rosenberg 2010, Johnson et al. 2012). In particular, changes in benthic macroinvertebrate life history may be influenced by changes in their habitat, such as seasonality, flow regime (Robinson et al. 1992, Bêche et al. 2006), or temperature (Barton 1980, Dobrin and Giberson 2003). Several aquatic insects exhibit life history variability in habitats with different characteristics (Barton 1980, Dobrin and Giberson 2003, Mendez and Resh 2008). For example, a stone fly species such as *Hastaperla brevis* grows slowly through autumn and winter, but grows rapidly in spring within streams in Alberta, Canada, a subarctic climate, but not in Quebec and Massachusetts. This variability is likely resulting from differences in climate (Barton 1980). Likewise, species in the minnow mayflies of the genus *Baetis* exhibit a range in their life histories related to biotic and abiotic factors (Brittain 1982, Clifford 1969). Overall, some *Baetis* species (e.g. *Baetis ephippiatus* and *Baetis intercalaris*) have extensive multivoltinism, or multiple generations per year, which is largely because of mean annual temperatures increase within the environment (Jacobi and Benke 1991). However, some *Baetis* species are not well-studied, such as *Baetis tricaudatus.*

Baetis tricaudatus is one of the most common and abundant grazers in the lotic (flowing water) food chain in western North America, and it is sensitive to a variety of disturbances (Irving

et al. 2003, Scrimgeour et al. 1994) making it a good candidate for life history studies. *Baetis tricaudatus* has variation in life history resulting from habitat differences, such as flow regime which influences temperature (Robinson et al. 1992, Ciborowski and Clifford 1983, Dobrin and Giberson 2003). After flooding, an abundance of *B. tricaudatus* occurs because *B. tricaudatus* are commonly found in riffle habitats that have fast moving water (Ciborowski and Clifford 1983). Increased inconsistent flow regime to a stream imparts more natural environmental variation to *B. tricaudatus*, rather than a disturbance (Robinson et al. 1992). Despite the ubiquity of *B. tricaudatus*, there are few studies that examine their life history in streams with differing habitat characteristics, particularly in northern California, which makes their life history relatively unknown (Rader and Ward 1989, Robinson et al. 1992, Dobrin and Giberson 2003).

The objective of this study was to (1) examine the larval life history of *B. tricaudatus* in two sites in a Mediterranean climate in the Russian River watershed in northern California, and (2) relate habitat differences in the two locations to the pattern of growth over time. I evaluated *B. tricaudatus* larvae from benthic macroinvertebrate samples collected monthly for seven months within the Russian River watershed.

METHODS

Study site

The source of the Russian River watershed is in Central Mendocino County in northern California and drains 1,485 square miles (1,846 square kilometers) through Mendocino and Sonoma Counties and empties into the Pacific Ocean at Jenner, CA. The Russian River is 110 miles (177 km) long with five main tributaries. The three collection sites of riffle (shallow areas with fast waters) habitats are within the Russian River watershed: (1) Austin Creek (AC, N 38°28.639', W 123°02.807'); and (2) the Russian River mainstem at Sunset Park (RR, N 38°30.151', W 122°56.041') (Figure 1). These sites are representative of typical habitats, which includes riparian vegetation (e.g. trees and brush) and varying substrate sizes (e.g. cobble stones and pebble stones) of the Russian River. The sites have visual differences in flow, substrate, and canopy cover (Figure 2).
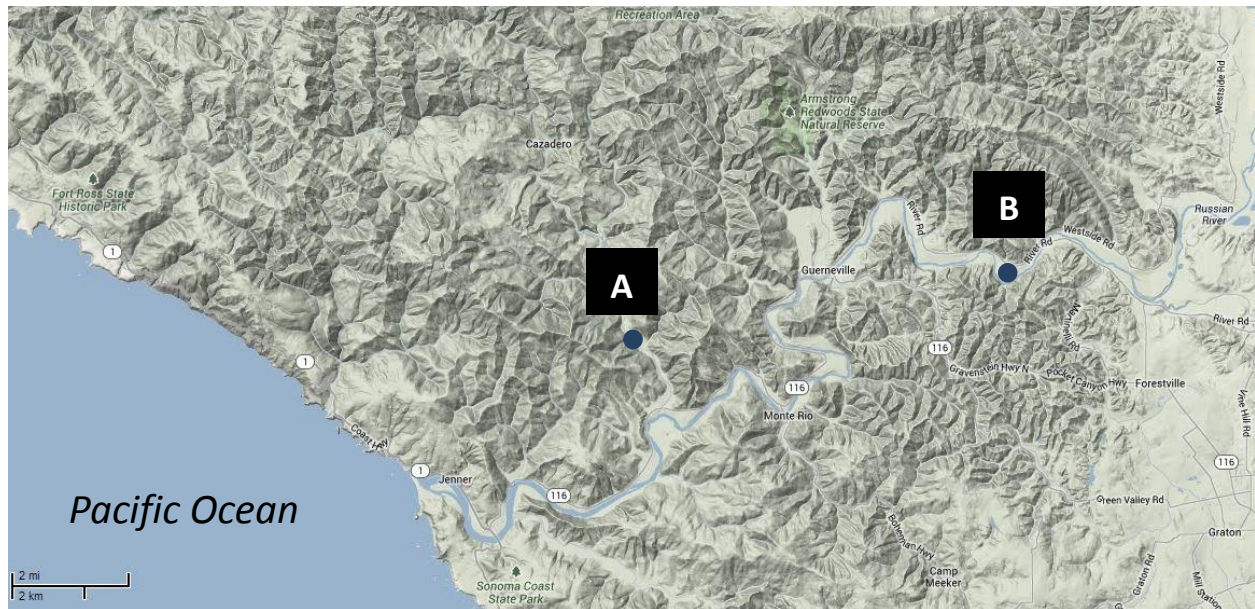
Figure 1. Collection sites in northern California. (A) Austin Creek; (B) Russian River mainstem at Sunset Park. The Russian River debauches at Jenner, CA into the Pacific Ocean.

Figure 2. Canopy cover and substrate size. (A) Canopy cover of Austin Creek. (B) Substrate size of Austin Creek had 25% large cobble stones and 75% pebble stones. (C) Canopy cover of Russian River mainstem at Sunset Park. (D) Substrate size of Russian River mainstem at Sunset Park had 10% cobble stones and 90% pebble stones.

Study organism

Baetis tricaudatus is one of the most commonly collected minnow mayflies in North America, and is found in riffle habitats (fast-moving waters) (Ciborowski and Clifford 1983). They are identifiable by their notched labium, long antenna, and their dark bilobed markings on their pronotum (Jacobus and Randolph 2005). As larvae, they feed on diatoms, filamentous algae, and detritus (Rader and Ward 1989). They can grow to approximately 5.4mm in length as mature larvae (Scrimgeour et al. 1994). Many studies examine voltinism (number of generations per year) and have found that *B. tricaudatus* is multivoltine (Ciborowski and Clifford 1983, Robinson et al. 1992, Dobrin and Giberson 2003). *Baetis tricaudatus* has been found to have at least two generations per year (Dobrin and Giberson 2003). In a Canadian study, *B. tricaudatus* had three

generations per year (Ciborowski and Clifford 1983). Furthermore, *B. tricaudatus* tend to have asynchronous cohorts, meaning they do not grow at the same rate (Rader and Ward 1989, Dobrin and Giberson 2003).

Data collection and sampling

I studied *B. tricaudatus* from benthic macroinvertebrate samples collected monthly from June 2013 – December 2013 by my mentor, Natalie Stauffer (University of California, Berkeley, Resh Aquatic Ecology Lab). To collect benthic macroinvertebrates, she used a 0.5 mm mesh D-frame kicknet and collected three kick samples of benthic macroinvertebrates within a 100 m reach at each site. At each site, all three kick samples were composited into one general sample. In this study, I used 14 individual samples, which derived from seven months with one sample from each site.

For each sample, Stauffer followed the guidelines from the U.S. EPA's Rapid Bioassessment Protocol (Barbour et al. 1999). First, she placed the D-frame net in the riffle. Then, she disturbed the rocks upstream of the net with her hands and feet for one minute, which loosened macroinvertebrates on the rocks and into the stationary net. After, she preserved the macroinvertebrates in a Ziploc bag with enough 95% ethanol to cover the sample.

To account for other environmental variables, temperature and conductivity were measured with a handheld meter (YSI 550A) at each site. Stauffer measured pH with two sets of pH indicator strips; one with a pH range 4-10 (Johnson® Test Papers, catalogue number: 106.3C), and the second with a pH range 6-7.7 (Machery-Nagel, catalogue number: 48PNS67). In addition, data from USGS (United States Geological Survey) was observed for discharge. For the month of December 2013, I measured canopy cover using a spherical densiometer (Forestry Suppliers Inc., model A).

To process the samples, Stauffer took the samples to the Resh Aquatic Ecology Lab (UC Berkeley) where Stauffer and URAP (Undergraduate Research Apprenticeship Program) students (including myself) sorted and identified benthic macroinvertebrates to the family level. For each sample, I transferred the contents of the Ziploc bag to a tray. I sorted the benthic macroinvertebrates by eye, and identified them to family under a dissecting microscope at 63x magnification. After, I picked out mayfly larvae in the family *Baetidae*, and identified them to the

genus level using a taxonomic key by Merritt et al. (2008). Then, I identified the mayfly larva from the family *Baetidae* to the species level with the same dissecting microscope at 63x magnification using a taxonomic key by Jacobus and Randolph (2005).

I measured interocular distance (distance between the eyes) (Figure 3) and the body length (excluding the cerci) using a metric mini scale (Figure 4) (Metric Mini Scale #3, catalogue number: 62135-03) to the nearest tenth millimeter. Head width and body length have been used as measurements in a number of life history studies (Ciborowski and Clifford 1983, Jacobi and Benke 1991, Robinson et al. 1992, Becker et al. 2009). Because the body shape of *B. tricaudatus* are often curved upon preservation in ethyl alcohol, I measured the body length by measuring the curved parts and the straight parts separately. Then, I added the curved and straight parts together to obtain the final body length measurement.
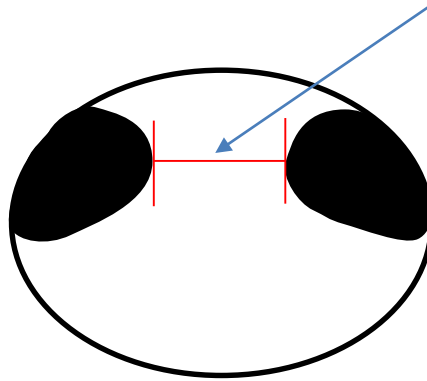

Figure 3. *Baetis* head only showing the eyes and the interocular distance.

Figure 4. *Baetis tricaudatus* **against the metric mini scale**. The ruler is 1 cm in length.

Data analysis

To identify instars, I plotted the measurements of interocular distance against body length. In an ideal situation, a cluster of data points indicated a group of individuals that were a single instar group. However, I was not able to identify individual instars; instead, I divided the lengths into size classes. To assess for life history differences in *B. tricaudatus*, I compared the relative abundance for each size class of one site to the other to determine if the frequency of each instar is similar for all sites for each month. I also plotted monthly size-frequency histograms and compared them among sampling dates. Additionally, I used final instars (mature *B. tricaudatus* indicated by black wing pads) as signals of emergence (life stage when they become their winged counterparts) and voltinism.

RESULTS

General discharge of the Russian River

Discharge data from USGS was measured by a hydrologic unit (N 38°30′, W 122°55′), which indicated peaks in discharge in late June and early September (Figure 5). There was also a gradual increase in discharge in November (Figure 5).
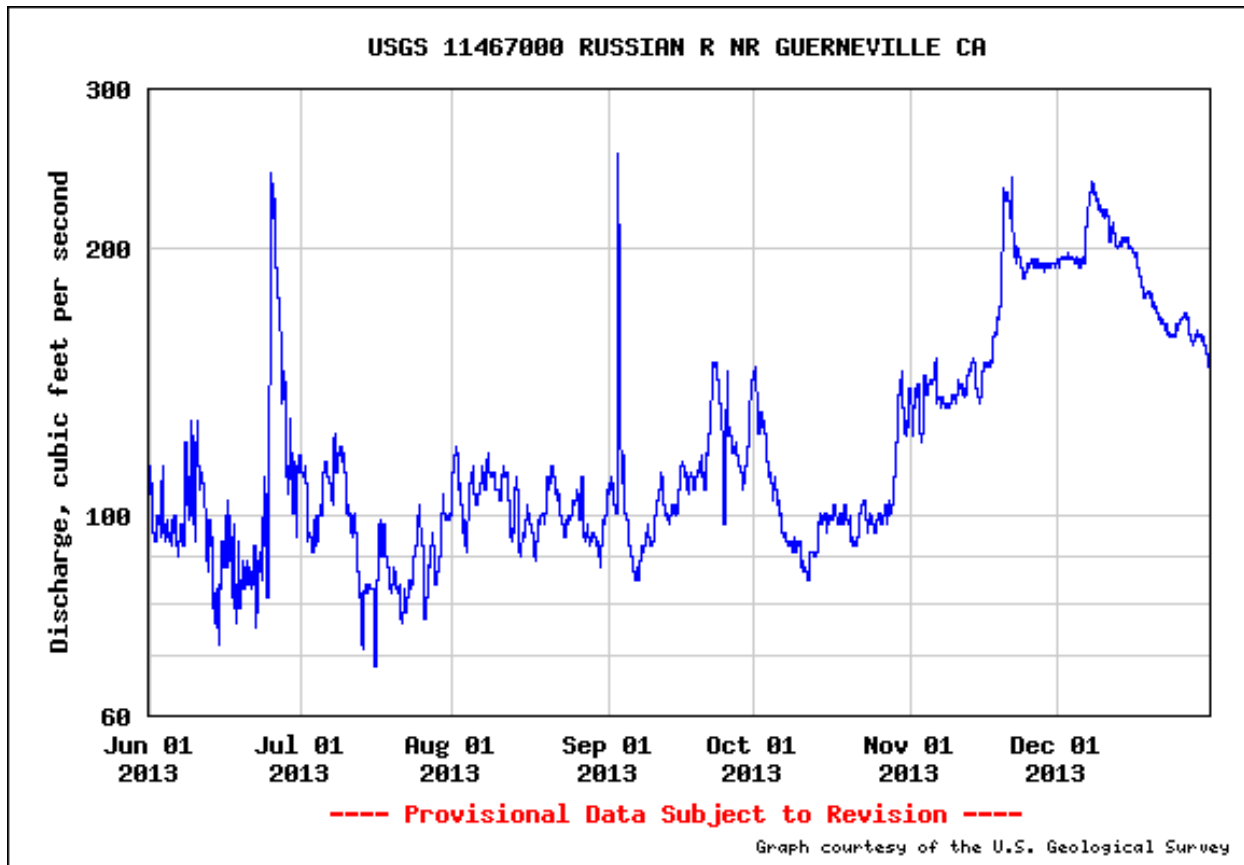

Figure 5. USGS discharge of the Russian River in June 2013 – December 2013. (Source: United States Geological Survey, downloaded 1 May 2014).

Physical differences in the sites

In December, AC and RR differed in water depth, flow, and canopy cover with AC having lower stream depth than the others (0.09m) compared to RR (0.30m) (Table 1).

Table 1. Summary of measured environmental factors in December 18, 2013 from the two sites. These environmental factors were collected during sampling.

	Austin Creek	Russian River mainstem
Stream depth (m)	0.09	0.30
Discharge (m^3/s)	0.09	3.3
Canopy cover	90.1	76.0

pH, and conductivity were similar for the two sites during the sampling period (Table 2), but RR temperatures were considerably higher during the sampling period (Figure 6).

Table 2. **Monthly means and standard deviations of water parameters of September 2012– July 2013 from the three sites**. *****pH were not measured in October and November because pH strips were not available.

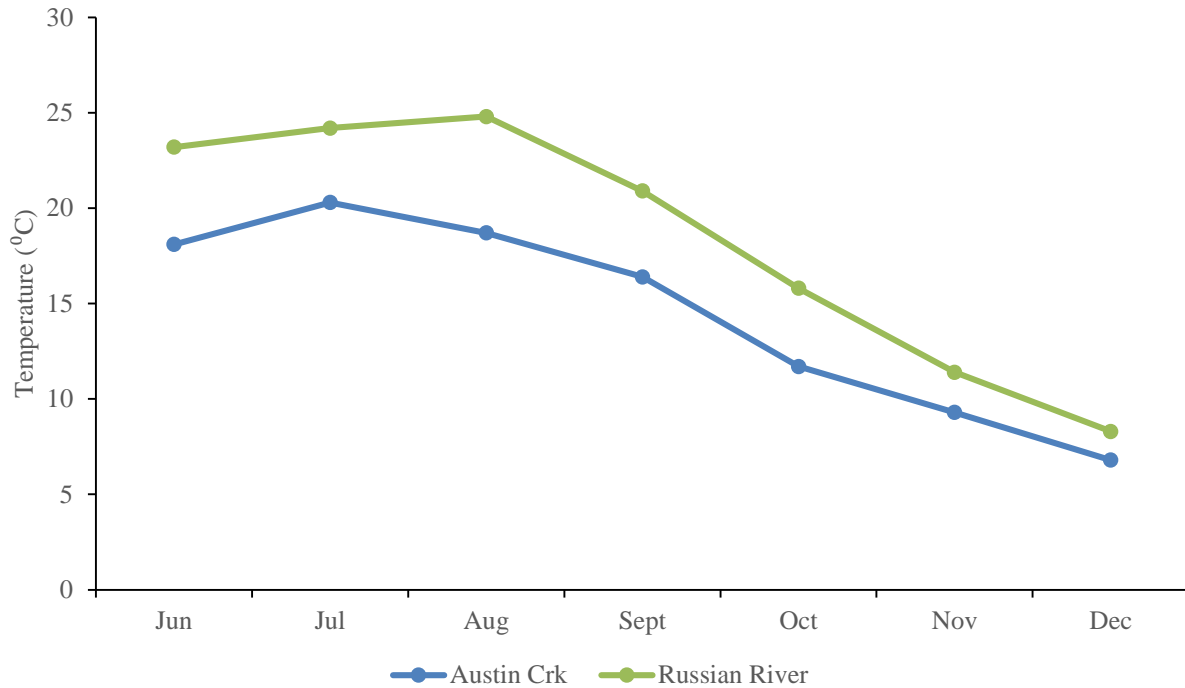| Parameter	Austin Creek	Russian River mainstem
pH	6.3 ± 0.26*	6.3 ± 0.26*
Conductivity (ppt)	0.2 ± 3.0E-17	0.2 ± 3.0E-17
Temperature (^{0}C)	14.5 ± 5.2	18.4 ± 6.6

Figure 6. Monthly water temperatures of June 2013 – December 2013 from the two sites.

Abundance and larval growth patterns

The abundance of *B. tricaudatus* varied between the sites and throughout the sampling period with the July sample having the fewest number of individuals with a total of seven individuals for all two locations (Figure 7). September had the most number of individuals with 217 in RR. *Baetis tricaudatus* was sometimes present in one site, but absent in the other (Figure 7). June, August, September, and December had specimens at all two sites.
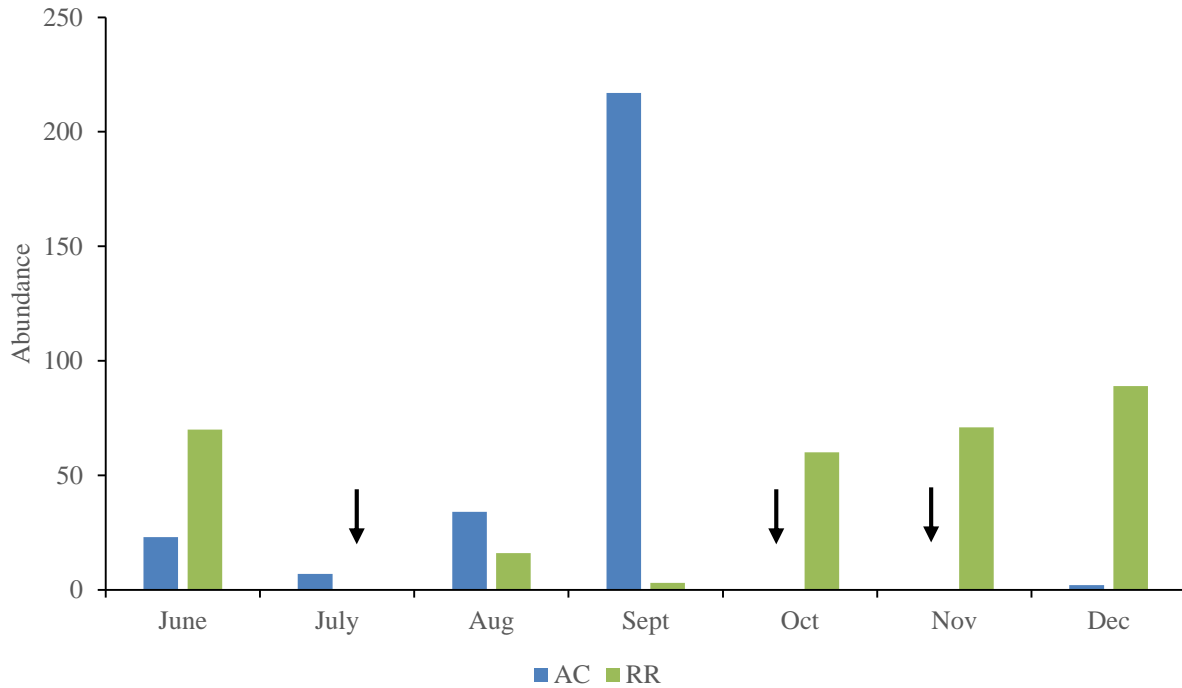
Figure 7. Abundance of *B. tricaudatus* for each site, June 2013 - December 2013. Arrows indicate 0 larvae present in the months at the sites.

   I was unable to identify distinct instars from the distribution of interocular distance against body length because there were no clear breaks that may indicate the instars. However, the majority of the measurements were in the smaller size ranges (< 4.0mm in body length and < 0.4mm in interocular distance) (Figure 8). The points shown in Figure 8 are jittered to better show density. Jittered points were calculated in Excel using the function, RANDBETWEEN(-100/100)/1000. I added that number to the measured number to obtain the jittered point. This was completed for both body length and interocular distance measurements. The size frequencies of body length varied from a range of 1.0mm to 7.9mm, however, most measured between 3.0-3.5mm (Figure 9). Interocular distance size frequencies were most commonly measured in the range of 0.3mm to 0.39mm (Figure 10).
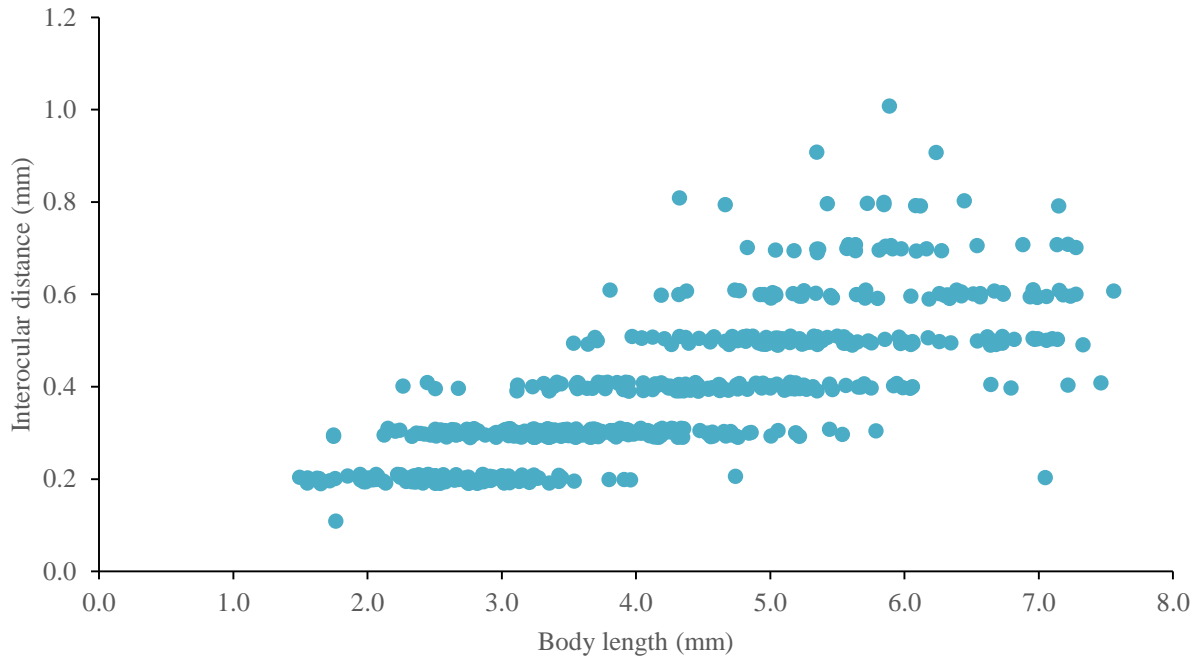
Figure 8. Body length and interocular distance plotted against each other in the sites, June 2013 – December 2013. Points are jittered to better show density.
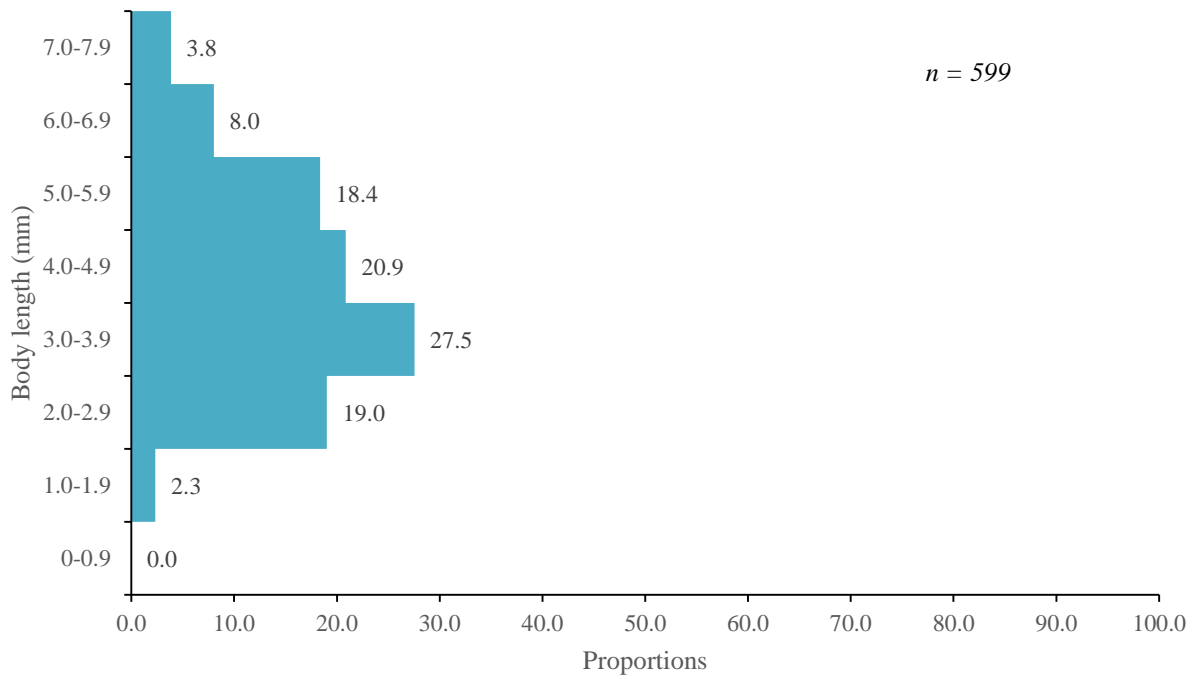

Figure 9. Proportion distributions of larval body length sampled monthly in the sites, June 2013 – December 2013.
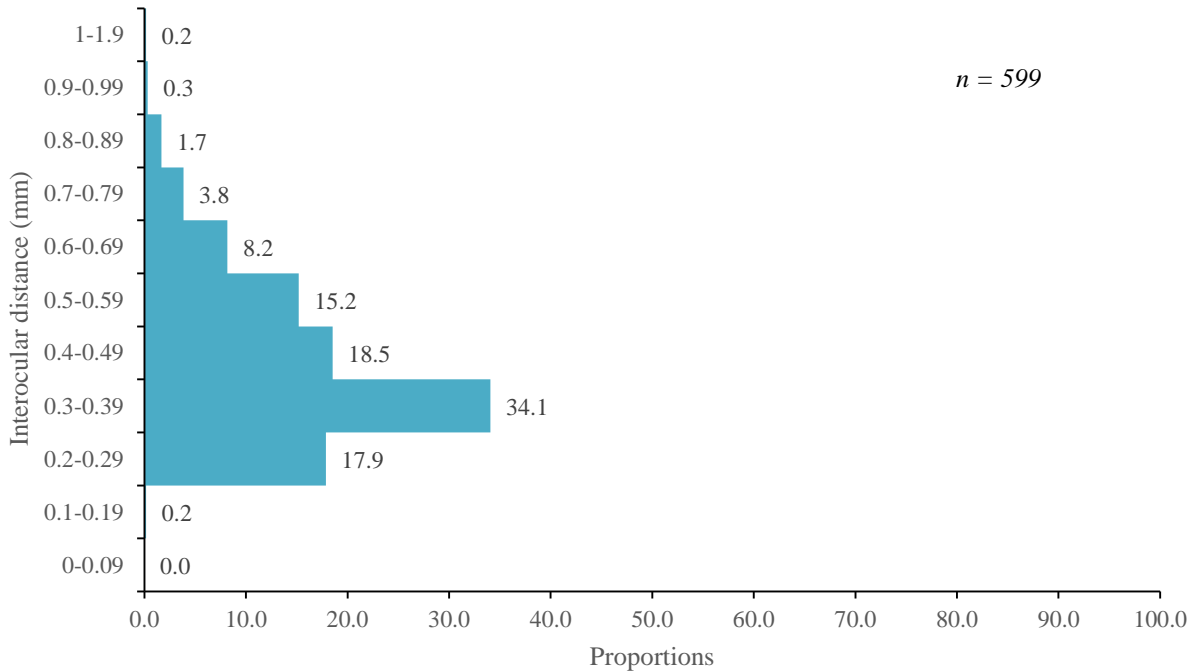
Figure 10. Proportion distribution of interocular distance of larvae sampled monthly in the sites, June 2013 – December 2013.

Monthly phenology and larval growth patterns

Body length

The size proportions in body length varied among the months for the two locations. In AC, larvae were present in all months, except October, and November. There was a larger body length size range in September and August (1.0-7.9mm, n = 217; and 1.0-6.9mm, n = 35, respectively) than in July (2.0-6.9mm, n = 7) (Figure 11). In RR, larvae were present in all months, except July. All months, except July, had a larger range in sizes compared to September (Figure 12).

Interocular distance

Similar to the size distribution of body lengths, size proportions in interocular distance varied among the months between the two locations. In AC, the range of measurements increased from July to September, each gaining a category of 0.1mm each month (Figure 13). In RR, the

range of measurements were similar in August and September (0.3-0.79mm, n = 15; and 0.3-0.69mm, n = 4, respectively), but there was larger range in October, November, and December (0.2-1.9mm, n = 60; 0.2-0.89mm, n = 71; and 0.2-0.89mm, n = 89, respectively) (Figure 14).
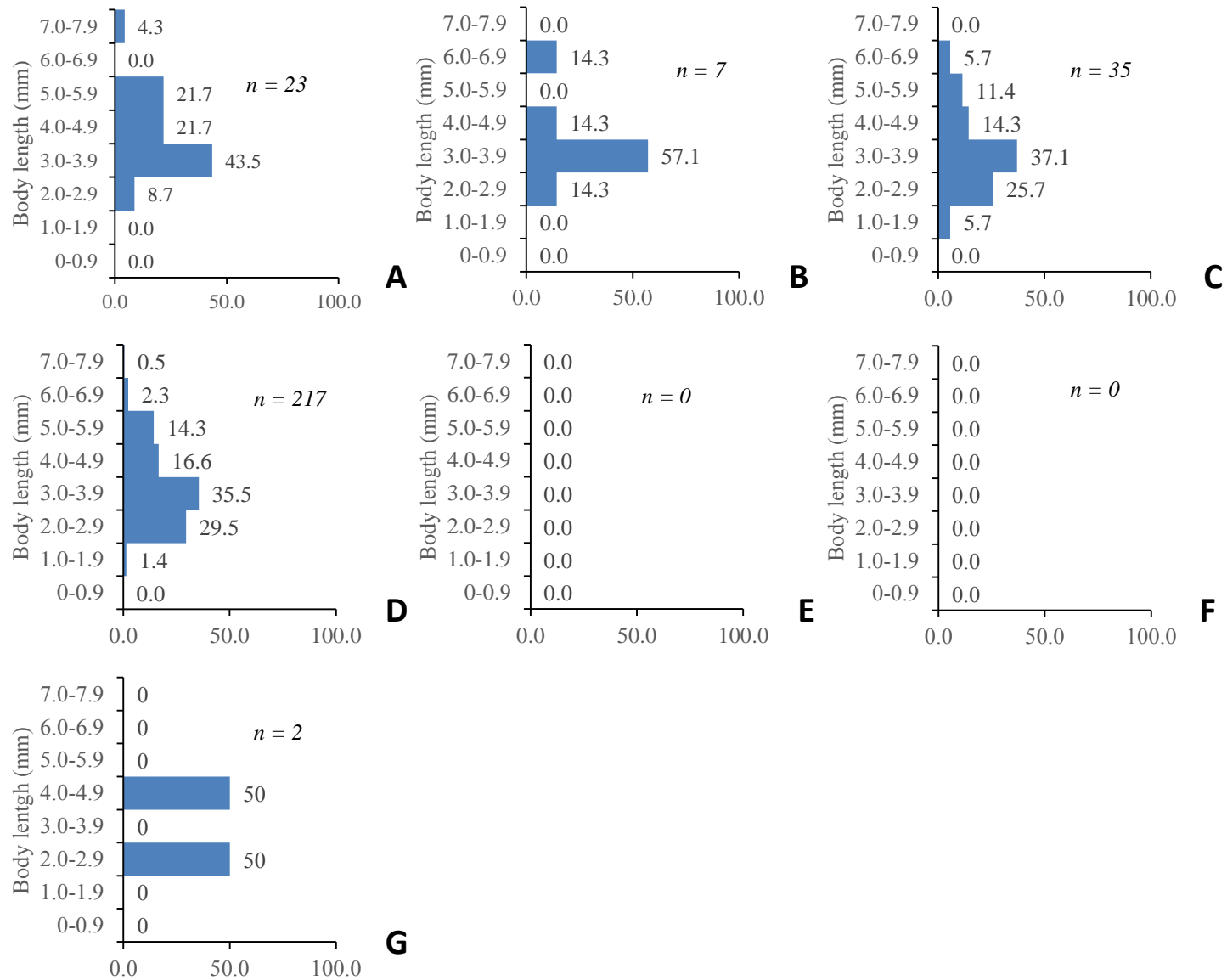
Figure 11. Size proportion distributions of body length of *B. tricaudatus* from June 2013 – December 2013 in Austin Creek. (A) June, (B) July, (C) August, (D) September, (E) October, (F) November, and (G) December.
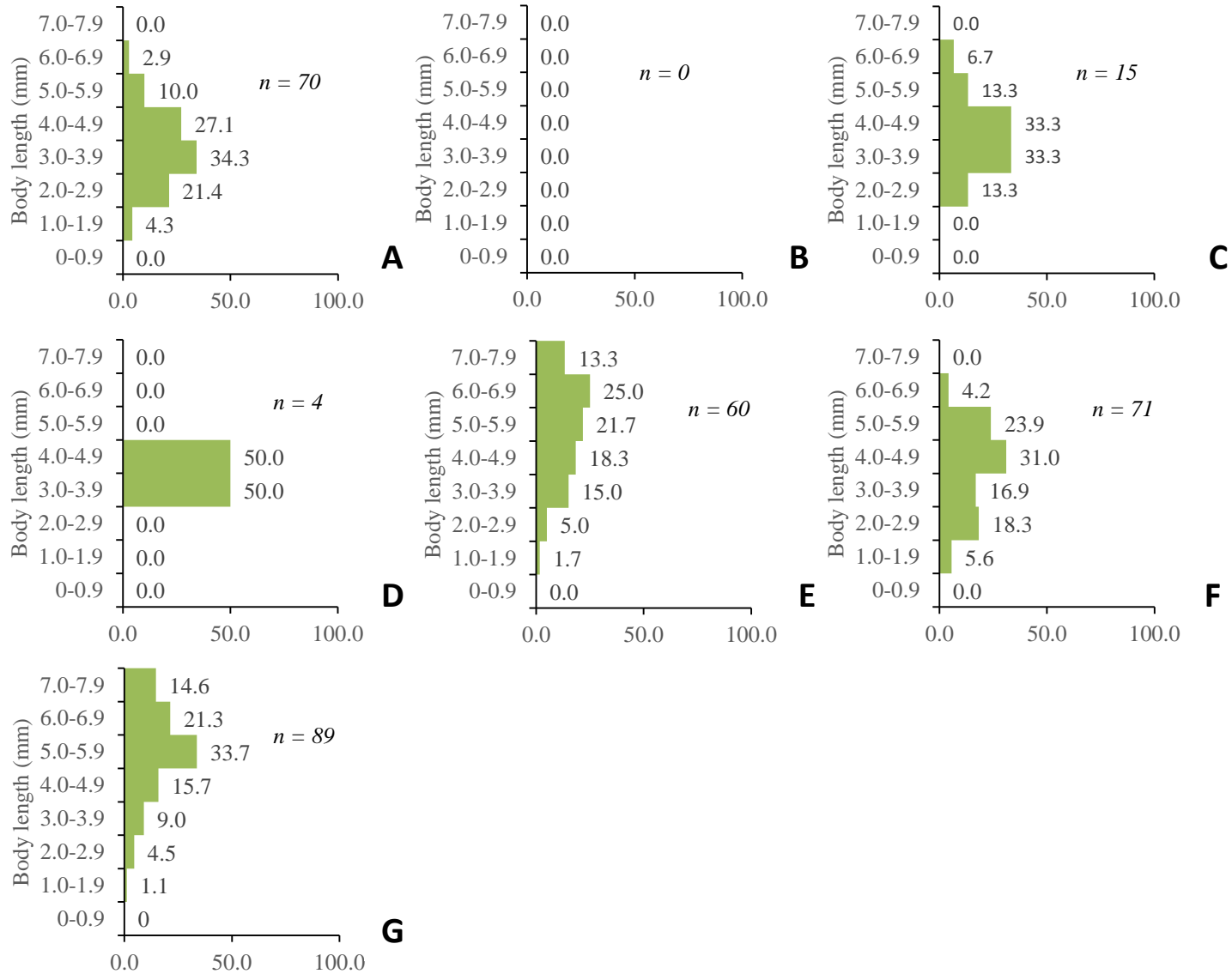
Figure 12. Size proportion distributions of body length of *B. tricaudatus* from June 2013 – December 2013 in Russian River mainstem. (A) June, (B) July, (C) August, (D) September, (E) October, (F) November, and (G) December.
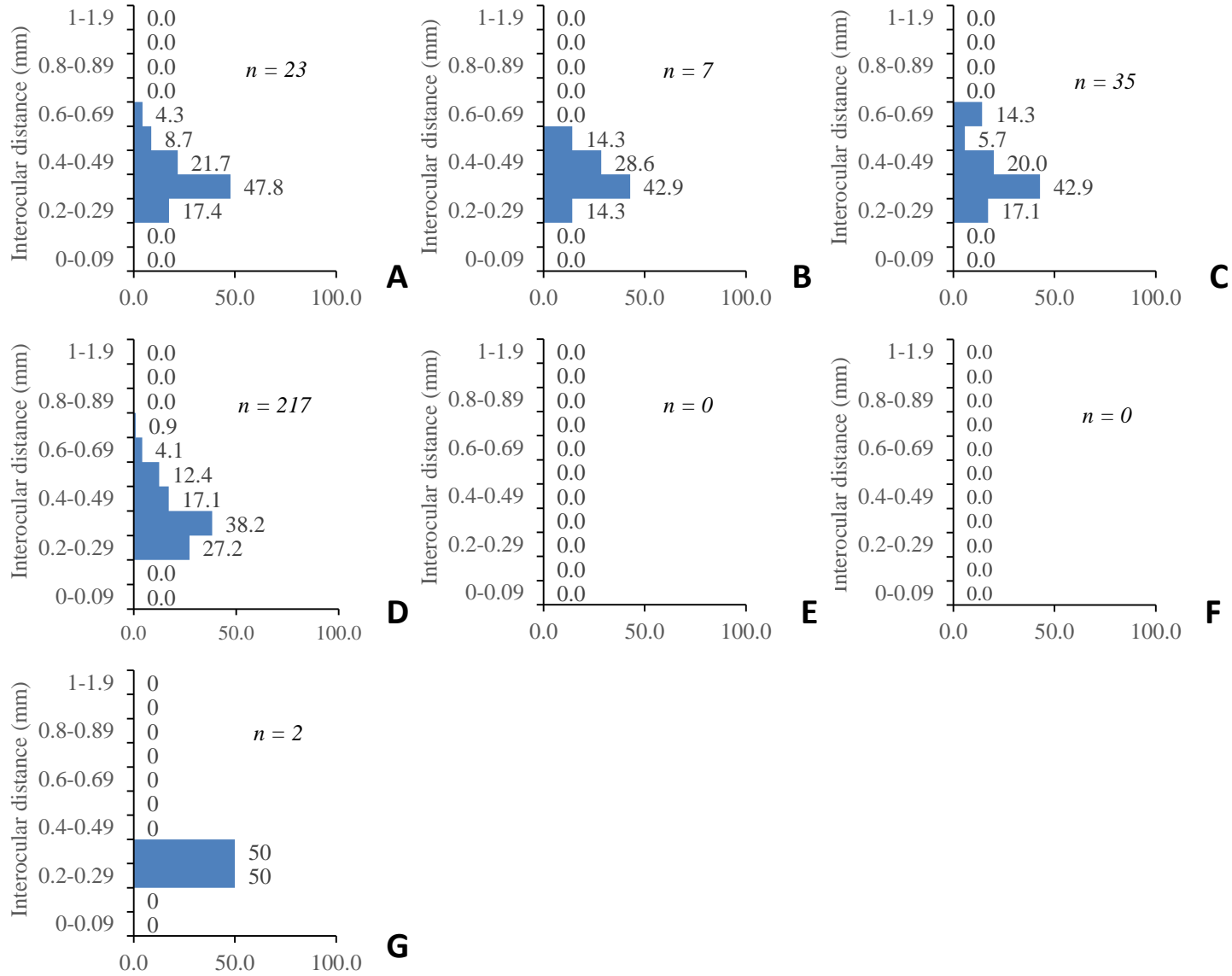
Figure 13. Size proportion distributions in interocular distance of *B. tricaudatus* from June 2013 – December 2013 in Austin Creek. (A) June, (B) July, (C) August, (D) September, (E) October, (F) November, and (G) December.
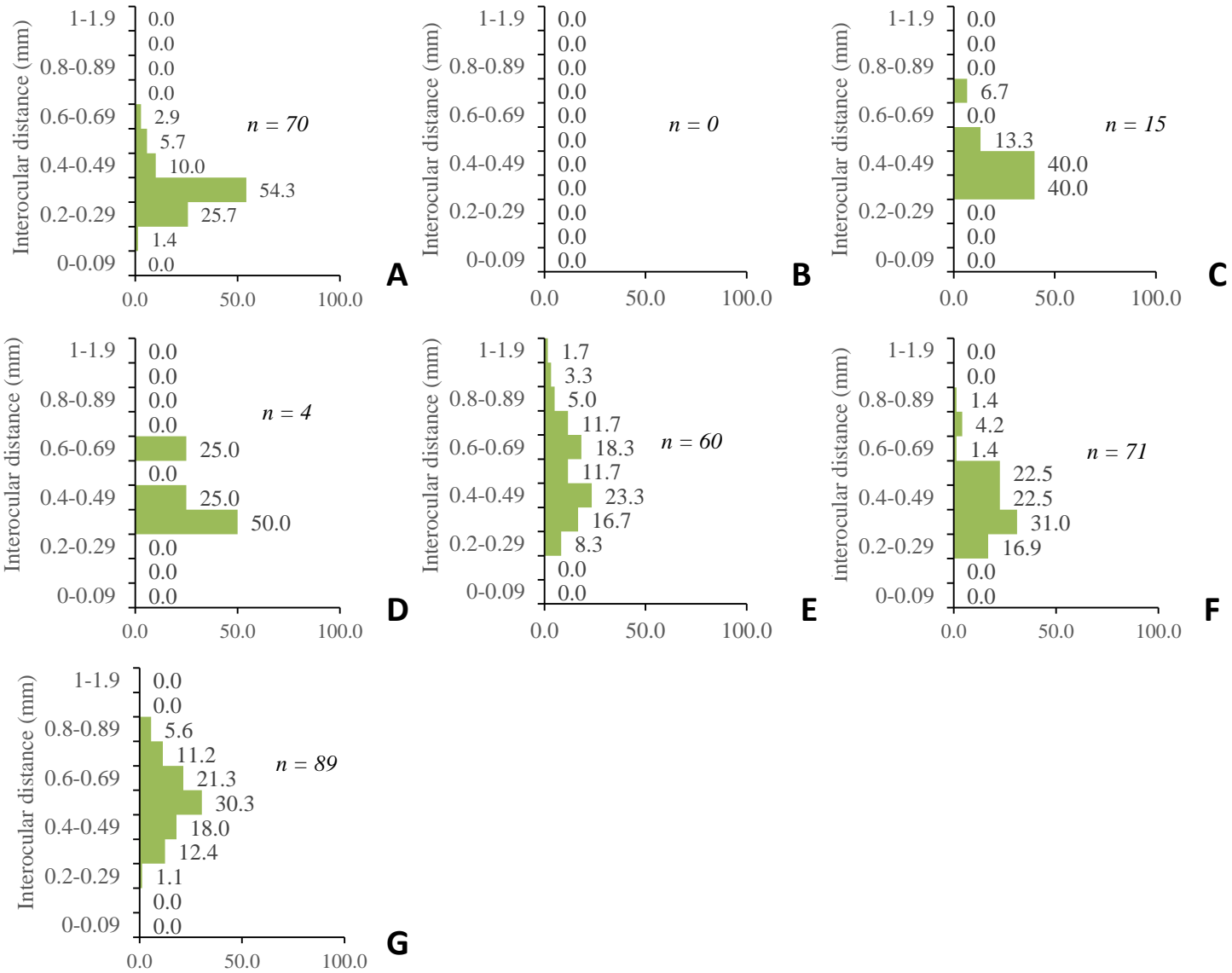
Figure 14. Size proportion distributions in interocular distance of *B. tricaudatus* from June 2013 – December 2013 in Russian River mainstem. (A) June, (B) July, (C) August, (D) September, (E) October, (F) November, and (G) December.

Final instars

AC had final instars in two out of the seven months (July and September), whereas RR had final instars in three out of the seven months (August, October, and December) (Table 3).

Table 3. Abundance of final instars for each site, June 2013 – December 2013. The total abundance of *B. tricaudatus* was also indicated for each site.

Sampling month	AC	Total abundance	RR	Total abundance
June	0	23	0	70
July	1	7	0	0
August	0	34	2	16
September	2	217	0	3
October	0	0	4	60
November	0	0	0	71
December	0	2	12	89

DISCUSSION

Understanding the life history of aquatic insects is critical to successful biomonitoring programs because it leads to the greater understanding of the organisms' behavior and habitat (Resh and Rosenberg 2010, Johnson et al. 2012). The main goal of this study was to distinguish larval life history differences in *B. tricaudatus* between two sites in Mediterranean climate freshwater ecosytems in California. The results indicated differences between sites in growth and larval growth patterns. Although the separation of instars was not apparent using size frequency histograms, I identified *B. tricaudatus'* final instars to inform voltinism and emergence period. Their presence and growth patterns suggest at least bivoltinism. Other studies analyzed *B. tricaudatus* and their life history, but none so far in a Mediterranean climate in California. My study fills in this gap in the literature.

General larval growth patterns within sites

Baetis tricaudatus showed multiple emergences at each sampling site but had overlapping size classes and/or increasing size classes coupled with the presence of final instars, indicating *B. tricaudatus* was multivoltine (Figure 15). Neither sampling sites had mature larvae in each month in the sampling period, which indicated periodic emergence periods (Figure 15). AC did not have clear signals of increasing size classes to show emergence, but rather, AC had overlapping dominant size classes in two months and had final instars in those months as well (Figure 15). RR showed increasing dominate size classes throughout the sampling period along with overlapping size classes and the presence of final instars (Figure 15). Final instars has been used as estimates in emergence patterns in *Baetis* studies (Ciborowski and Clifford 1983, Rader and Ward 1989). Within both sampling sites, final instars were present in different months and *B. tricaudatus* had different abundances in sizes classes, indicating there may be differences in growth patterns.

In AC, final instars of *B. tricaudatus* were present in July and September, suggesting *B. tricaudatus* was at least bivoltine in the sampling period and emerged between: (1) July and August; and (2) September and October. *Baetis tricaudatus* showed two peaks of abundances in June and September with the length of most (>0.50) of the individuals in the range of 3.0-3.9mm and 2.0-3.9mm, respectively (Figure 15). In August, the dominant size class was the same as September, 2.0-3.9mm (Figure 15). Because September had the most individuals that were small larvae and the sample also included late instars, these results may indicate fast growth and another emergence period, or could possibly be interpreted as a cohort growth within a generation. A Canadian study also found *B. tricaudatus* bivoltine in a stream, however, this study was conducted over a two-year period (Clifford 1969). In a Hong Kong study conducted over a two-year period, a species of *Baetis* was found multivoltine, complete with at least eight generations (Salas and Dudgeon 2003).

In RR, final instars of *B. tricaudatus* were present in August, October, and December, suggesting *B. tricaudatus* was most likely multivoltine in the sampling period, but could possibly be interpreted as univoltine. These growth patterns indicated that *B. tricaudatus* emerged between: (1) August and September; (2) October and November; and (3) possibly* December and January. (*Note: January was not part of the sampling period.) *Baetis tricaudatus* showed four peaks of abundances in June, October, November, and December with gradually increasing size classes: (1)

June: 3.0-4.9mm; (2) October: 5.0-6.9mm; (3) November: 4.0-5.9mm; and (4) December: 5.0-6.9mm (Figure 15). The increasing length size class indicated a single generation. However, because there were final instars in August, October and December, where multiple cohorts may have emerged asynchronously within this one generation. Studies of *B. tricaudatus* are not generally reported as univoltine, but other species of *Baetis* are univoltine (Fisher and Gray 1983). These univoltine phenologies are most likely because the study was located in a desert stream with low flow (Fisher and Gray 1983). In contrast, in a Canadian river, *B. tricaudatus* was multivoltine, producing three generations in one year (Ciborowski and Clifford 1983). Other studies have also reported other species of *Baetis* as multivoltine in rivers in Georgia and Canada (Jacobi and Benke 1991, Giberson et al. 2007), suggesting that multivoltinism is the primary life history phenology for this group.

Emergence

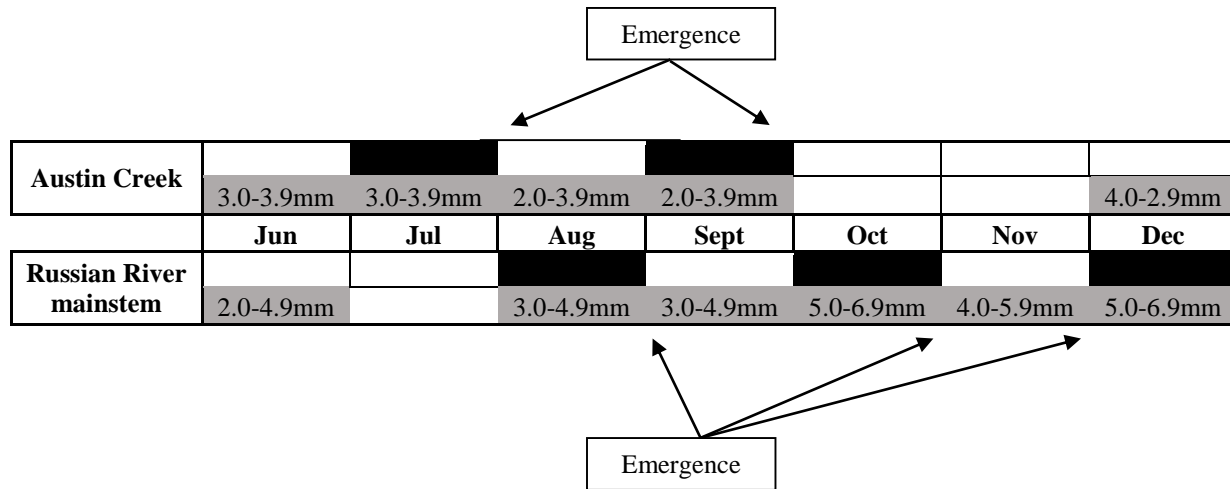|	Jun	Jul	Aug	Sept	Oct	Nov	Dec
Austin Creek	3.0-3.9mm	3.0-3.9mm	2.0-3.9mm	2.0-3.9mm			4.0-2.9mm
Russian River mainstem	2.0-4.9mm		3.0-4.9mm	3.0-4.9mm	5.0-6.9mm	4.0-5.9mm	5.0-6.9mm

Emergence

Figure 15. Generalized life history showing voltinism, emergence, and the dominant size classes of *B. tricaudatus* in Austin Creek and the Russian River mainstem. Black areas indicate final instars present. Gray areas indicate general larvae present. White areas indicate no larvae present. Arrows indicate emergence.

Differences in overall growth patterns between sites

Baetis tricaudatus emerged at different times in AC compared to RR, indicating their larval growth patterns differed between the sampling sites. In addition, voltinism differed between the sites. This suggests habitat differences may be the cause. One of the key habitat differences was the RR sampling site was located on a river's mainstem, whereas AC was a tributary with significantly lower flow. Studies in rivers mostly found *B. tricaudatus* and other *Baetis* species multivoltine (Ciborowski and Clifford 1983, Jacobi and Benke 1991, Giberson et al. 2007). Studies

in streams also found *B. tricaudatus* multivoltine (Clifford 1969). Furthermore, water depth and discharge varied between the sites. According to December's measurements, RR was 0.21m deeper than AC, and had a faster discharge of 3.3m^3/s compared to AC of 0.09m^3/s. RR had larvae present in more sampling months, and had an overall faster discharge. Many studies are consistent with this finding in that species of *Baetis*, including *B. tricaudatus*, are commonly found in riffles (Ciborowski and Clifford 1983, Rader and Ward 1989, Giberson et al. 2007). Moreover, monthly mean temperatures were higher in RR, which may explain the multiple emergence periods or cohort growths within a generation. Temperature affects growth; generally more mayflies emerge as temperature rises (Clifford 1969, Robinson et al. 1992). Overall, *B. tricaudatus* is recognized as a mayfly species that is highly adaptable to environmental variances (Robinson et al. 1992), which explains why different growth patterns were observed between the two sampling sites.

Challenges in life history of *Baetis*

       An important challenge in constructing a life history within *Baetis* is identifying instars, which indicates a gap in these studies (Ciborowski and Clifford 1983, Jacobi and Benke 1991, Robinson et al. 1992). Present research struggles to understand life stages because of this difficulty. Generally, mayflies are expected to have between 15 and 22 instars (Brittain 1982). However, the number of instars may not be constant for a particular species. The number of instars is affected by environmental conditions (Brittain 1982). More often than not, *Baetis* life history studies do not indicate the instar number (Ciborowski and Clifford 1983, Jacobi and Benke 1991, Robinson et al. 1992). Consequently, to determine voltinism, life history studies include emergence and presence of final instars (Clifford 1969, Barton 1980). Ultimately, in my study, determining the number of instars using measurements taken at 63x magnification was difficult. To gain a general sense of variability in measuring interocular distance, I assumed a bivoltine emergence period, a maximum interocular distance of 1.0mm, and a projected number of 20 instars. Each measurement increment between instars is 0.05mm:

$$\frac{1.0mm}{20\ instars} = 0.05mm\ of\ growth\ to\ next\ instar$$

This is below the accuracy of my measurement instrument, where I was able to measure to the closest tenth millimeter.

In addition, assuming a bivoltine emergence period where one generation emerges after six months (128 days) and a projected number of instars of 20, a new instar would occur every 8.4 days:

$$\frac{168 \ days}{20 \ instars} = 8.4 \ days \ until \ next \ instar$$

This indicates that sampling should occur every week to capture every instar in order to have a better understanding of the larval life cycle.

Limitations and future directions

Measuring individual mayfly features was a challenge because there were not enough individuals in the samples. Additionally, there were inaccuracies in measuring body length with the ruler because some mayflies were curved. Measuring to the nearest tenth millimeter can be difficult because they can be curved in different ways, requiring different measuring methods. Moreover, measuring interocular distance is not very common (Becker et al. 2009). Many studies measure general head width of mayflies (Ciborowski and Clifford 1983, Rader and Ward 1989, Jacobi and Benke 1991, Vásquez et al. 2009).

To reduce error in measuring curved body lengths, a more precise measurement system should be used to measure body length to, including digital methods. Measuring another straight scleritized area of the mayfly's bodies, such as the tibia, would decrease measurement inaccuracies as well. Additionally, measuring the head width with an ocular micrometer would also help give a more precise measurement.

To increase the number of individuals in samples, more frequent sampling events and a longer sampling period, such as an entire year, would increase the chances of having mature nymphs to better determine voltinism. Ideally, with more individuals in the samples, I would have a more accurate resolution in understanding their larval life stages. Furthermore, because there was size overlap across months within the sites, lab rearing (catching specimen alive and observing their emergence to an adult mayfly) or light collection catching (catching adult mayflies) to

determine emergence events may provide a more precise estimate of maturity (Ciborowski and Clifford 1983, Dobrin and Giberson 2003).

Broader implications

In conclusion, there may be differences in larval life history of *B. tricaudatus* between the two sites in relation to emergence period and voltinism. Although preliminary, this study is a promising start in understanding their larval life history in this California Mediterranean climate. Moreover, if temperature and climate are key factors in life history, it is necessary to understand baseline information, such as the instar number, voltinism, and emergence, because the California Mediterranean climate is highly variable. Finally, *B. tricaudatus* is one of the benthic macroinvertebrates species that is commonly used for biological monitoring because the species is ubiquitous and it has an important role in the lotic food chain. This study helps further understand their life history and their phenology, which is essential in bioassessment studies.

my workgroup, Wet N' Wild (Zane Rankin, Kristen Chen, Rachel Phoa, and Annie Lu) for giving feedback on my drafts and being each other's eyes and ears when we practiced presenting for our symposium. I could not ask for a better group to write this thesis.

REFERENCES

Barbour, M. T., J. Gerritsen, B. D. Snyder, and J. B. Stribling. 1999. Rapid bioassessment protocols for use in streams and wadeable rivers: periphyton, benthic macroinvertebrates and fish, Second Edition. EPA 841-B-99-002. U.S. Environmental Protection Agency, Office of Water, Washington, D.C., USA.

Barton, D. R. 1980. Observations on the life histories and biology of Ephemeroptera and Plecoptera in northeastern Alberta Canada. Aquatic Insects 2:97–111.

Becker, B., M. Moretti, and M. Callisto. 2009. Length-dry mass relationships for a typical shredder in Brazilian streams (Trichoptera: Calamoceratidae). Aquatic Insects 31:227–234.

Bêche, L. A., E. P. McElravy, and V. H. Resh. 2006. Long-term seasonal variation in the biological traits of benthic-macroinvertebrates in two Mediterranean-climate streams in California, USA. Freshwater Biology 51:56–75.

Brittain, J. 1982. Biology of mayflies. Annual Review of Entomology 27:119–147.

Ciborowski, J., and H. Clifford. 1983. Life histories, microdistribution and drift of 2 mayfly (Ephemeroptera) species in the Pembina River, Alberta, Canada. Holarctic Ecology 6:3–10.

Clifford, H. 1969. Limnological features of a northern brown-water stream, with special reference to life histories of aquatic insects. American Midland Naturalist 82:578–&.

Dobrin, M., and D. J. Giberson. 2003. Life history and production of mayflies, stoneflies, and caddisflies (Ephemeroptera, Plecoptera, and Trichoptera) in a spring-fed stream in Prince Edward Island, Canada: evidence for population asynchrony in spring habitats? Canadian Journal of Zoology-Revue Canadienne De Zoologie 81:1083–1095.

Elliott, J. 1967. Life Histories and Drifting of Plecoptera and Ephemeroptera in a Dartmoor Stream. Journal of Animal Ecology 36:343–&.

Fisher, S., and L. Gray. 1983. Secondary production and organic-matter processing by collector macroinvertebrates in a desert stream. Ecology 64:1217–1224.

Giberson, D. J., S. K. Burian, and M. Shouldice. 2007. Life history of the northern mayfly *Baetis*

bundyae in Rankin Inlet, Nunavut, Canada, with updates to the list of mayflies of Nunavut. Canadian Entomologist 139:628–642.

Irving, E. C., D. J. Baird, and J. M. Culp. 2003. Ecotoxicological responses of the mayfly *Baetis tricaudatus* to dietary and waterborne cadmium: Implications for toxicity testing. Environmental Toxicology and Chemistry 22:1058–1064.

Jacobi, D., and A. Benke. 1991. Life histories and abundance patterns of snag-dwelling mayflies in a blackwater coastal-plain river. Journal of the North American Benthological Society 10:372–387.

Jacobus, L., and P. Randolph. 2005. Mayflies in Moscow: northwest Emphemeroptera nymphs. Moscow, Idaho, University of Idaho.

Johnson, R. C., M. M. Carreiro, H.-S. Jin, and J. D. Jack. 2012. Within-year temporal variation and life-cycle seasonality affect stream macroinvertebrate community structure and biotic metrics. Ecological Indicators 13:206–214.

Karr, J. R. 1993. Defining and assessing ecological integrity: beyond water quality. Environmental Toxicology and Chemistry 12:1521–1531.

Mendez, P. K., and V. H. Resh. 2008. Life history of *Neophylax rickeri* (Trichoptera: Uenoidae) in two northern California streams. Annals of the Entomological Society of America 101:573–584.

Merritt R. W., K. W. Cummins, and M. B. Berg. 2008. An introduction to the aquatic insects of North America. Kendall/Hunt Publishing Company, Dubuque, Iowa, USA.

Meyer, J. L. 1997. Stream health: incorporating the human dimension to advance stream ecology. Journal of the North American Benthological Society 16:439–447.

Moore, A. A., and M. A. Palmer. 2005. Invertebrate biodiversity in agricultural and urban headwater streams: implications for conservation and management. Ecological Applications 15:1169–1177.

Rader, R., and J. Ward. 1989. Influence of impoundments on mayfly diets, life histories, and production. Journal of the North American Benthological Society 8:64–73.

Resh V. H. and J. K. Jackson. 1993. Rapid assessment approaches to biomonitoring using benthic macroinvertebrates. Pages 195-223 *in* D.M. Rosenberg and V.H. Resh, editors. Freshwater biomonitoring and benthic macroinvertebrates. Chapman and Hall, New York, New York, USA.

Resh, V. H., and D. M. Rosenberg. 2010. Recent trends in life-history research on benthic macroinvertebrates. Journal of the North American Benthological Society 29:207–219.

Robinson, C., L. Reed, and G. Minshall. 1992. Influence of flow regime on life-history, production, and genetic-structure of *Baetis-tricaudatus* (Ephemeroptera) and *Hesperoperla-pacifica* (Plecoptera). Journal of the North American Benthological Society 11:278–289.

Salas, M., and D. Dudgeon. 2003. Life histories, production dynamics and resource utilisation of mayflies (Ephemeroptera) in two tropical Asian forest streams. Freshwater Biology 48:485–499.

Schulz, R., and M. Liess. 1999. A field study of the effects of agriculturally derived insecticide input on stream macroinvertebrate dynamics. Aquatic Toxicology 46:155–176.

Scrimgeour, G., J. Culp, and F. Wrona. 1994. Feeding while avoiding predators - evidence for a size-specific trade-off by a lotic mayfly. Journal of the North American Benthological Society 13:368–378.

Vásquez, D., R. W. Flowers, and M. Springer. 2009. Life history of five small minnow mayflies (Ephemeroptera: Baetidae) in a small tropical stream on the Caribbean slope of Costa Rica. Aquatic Insects 31:319–332

Verberk, W. C. E. P., H. Siepel, and H. Esselink. 2008. Applying life-history strategies for freshwater macroinvertebrates to lentic waters. Freshwater Biology 53:1739–1753.

Winterbourn, M. 1974. Life histories, trophic relations and production of *Stenoperla-prasina* (Plecoptera) and *Deleatidium* sp (Ephemeroptera) in a New-Zealand river. Freshwater Biology 4:507–524.