INFLUENCE OF TEMPERATURE ON GROWTH AND TIMING OF EMERGENCE OF FOUR MAYFLY SPECIES

By

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ABSTRACT

TEMPERATURE INFLUENCE ON MAYFLY GROWTH AND EMERGENCE ON THE AU SABLE RIVER

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Individual growth rates and timing of emergence of four species of *Ephemerellid* mayflies were examined in relation to temperature among six sites on the Au Sable River near Grayling, Michigan. All species showed definite reductions in specific growth rates at lower temperatures, but incremental growth in mean length was continuous until emergence. These results indicate the degree-day concept is a useful tool in relating insect growth to thermal regime at intermediate temperatures, but is less accurate at temperatures approaching upper and lower development thresholds. Mean larval size and growth rates varied unpredictably among taxa and across sites, and could not be explained by variations in temperature at different sites. Other habitat variables not estimated in this study clearly influenced patterns in growth and timing of emergence of these species.

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INTRODUCTION

Aquatic invertebrates are critical components of freshwater ecosystems. They are ubiquitous in nearly every habitat from small vernal pools to large lakes, and can even inhabit extreme environments such as the open ocean or hot springs (Bouchard 2004). Aquatic invertebrates play an integral role in the processing and cycling of nutrients in aquatic systems (Covich et al. 1999, Malmqvist 2002, Wallace and Webster 1996). Allochthonous carbon inputs, particularly riparian leaf-litter, are a major food resource for stream invertebrates (Boling et al. 1974, Cummins et al. 1973, Hynes 1970). Riparian leaf-litter processing by stream invertebrates provides essential ecosystem services by accelerating the rate of detrital decomposition, thereby releasing otherwise inaccessible nutrients and energy to other aquatic flora and fauna (Wallace and Webster 1996). Microbial and plant productivity is greatly enhanced by the uptake of dissolved nutrients by primary producers in aquatic systems (Cummins et al. 1995, Pelegri and Blackburn 1996, van de Bund et al. 1994, Wallace et al. 1997). It has been estimated that 20-73% of riparian leaf-litter inputs in headwater streams are processed by benthic invertebrates (Covich et al. 1999). Invertebrates are also important prey for other invertebrates and fish. Jenkins and Keeley (2010) found that trout habitat quality is directly related to the availability of invertebrate food sources. Anglers continually seek information regarding aquatic insects; both as fish food to be imitated and for better understanding of invertebrate emergence schedules to advance their angling pursuits. Additionally, adult insect emergence constitutes a significant terrestrial prey subsidy for riparian birds, beetles, bats, spiders, lizards, and amphibians (Baxter et al. 2005). Invertebrates are also useful indicators of water quality and have long been used in

biomonitoring of freshwater habitats (Bartsch and Ingram 1966, Cairns and Pratt 1993, Kuehne 1962, Rosenberg and Resh 1993, Warren 1971, Wilhm and Dorris 1968).

Mayflies are among the most widely distributed aquatic invertebrates, and are particularly abundant in coldwater lotic habitats. Mayflies belong to a very diverse and widespread order of aquatic invertebrates, represented by over 3,000 described species in 42 families (Barber-James et al. 2008). They spend most of their life cycle in an aquatic nymphal stage, existing briefly as terrestrial adults for a short period at the end of their life cycle. Eggs are generally deposited on the water surface and settle into the bottom sediments, although some species drop eggs from the air and others crawl beneath the water (e.g., Baetis) to lay eggs directly on the substrate (Brittain 1982, Elliot 1972, Waltz and Burian 2008). Embryonic development generally occurs within a few weeks, however delayed hatching as a result of egg diapause has been observed in several species (Brittain 1982, Ward and Stanford 1982). Annual and seasonal thermal regimes appear to play a significant role in determining the length of embryonic diapauses (Brittain 1982, Sweeney 1984). Mayfly larvae undergo several molts, termed instars, during their life cycle. The number of instars and length of nymphal life varies regionally and altitudinally both within and across species, but most mayflies have 15-25 instars (Brittain 1982, Jacobsen et al. 1997). The number of instars can vary within species and this variability has been correlated with local environmental conditions such as food quality and temperature (Brittain 1982). Average nymphal life-stage length can be as short as 10-14 days in small species inhabiting warm environments, or as long as two years in the large mayfly *Hexagenia limbata* inhabiting cold habitats (Brittain 1982, Waltz and Burian 2008).

Mayfly larvae are generally omnivorous and consume a variety of foods throughout their life cycle (Hawkins 1985, Schwiebert 2007). Diatoms and detritus are the most commonly

consumed food items, particularly among early instars. Larger larvae may become carnivorous during the later stages of development, preying on other developing aquatic insect larvae (Schwiebert 2007). Hawkins (1985) compared the gut contents of 20 species of ephemerellid larvae and observed that several species also consumed significant proportions of moss. Feeding habits appear to be highly facultative and vary temporally with seasonal availability of food items and spatially from site to site and among different habitats within a particular species (Hawkins 1985).

Mayflies are the only live order of insects that have two winged-instars, the subimago and the imago. Subimagos are generally sexually immature and are covered in dense hydrofuge hairs which presumably reduce the risk of being trapped in the air-water interphase. This unique life stage can last anywhere from a few minutes to a few days and is suggested to be the result of significant evolutionary pressure acting on mayflies during emergence when they are most vulnerable. Adult mayflies of most species live two hours to three days, although some live less than 90 minutes (Leonard and Leonard 1962, Miller 2011).

There are approximately 80 species of Ephemerellidae recognized in North America (Hawkins 1985), at least 10 of which occur in Michigan streams (Miller 2011). Species in this family are ubiquitous and abundant taxon found in abundance in most northern temperate stream ecosystems (Allen 1980, Leonard and Leonard 1962). Further, the taxonomy of this family in North America has been well documented (Allen 1965, Funk et al. 2008, Jacobus and McCafferty 2003, 2008). Four species of ephemerellid mayflies occupy the Au Sable River near Grayling, Michigan and are the subject of this research: *Ephemerella subvaria*, *E. invaria*, *E. dorothea*, and *Drunella lata*. Their prolific hatches, commonly referred to as the Hendricksons, Sulphurs or Light Hendricksons, Little Sulphurs, and Slate Wing Olives, respectively, are among

the most important and well known for both fish and fisherman (Leonard and Leonard 1962, Schwiebert 2007).

Factors affecting aquatic invertebrate growth

Individual life-history strategies of aquatic insects represent the intersection of ecological and evolutionary responses to abiotic and biotic factors. For a given species, spatial variability of specific life history parameters is driven by a complex relationship among local environmental conditions. For example, aquatic invertebrate growth may be influenced by competition (Rosillon 1988, Sweeney and Vannote 1981), predation (Peckarsky and McIntosh 1998), nutrition (Anderson and Cummins 1979, Sweeney and Vannote 1981, 1986, Webb and Merritt 1987), or temperature (Brittain 1976, Fahy 1973, Hawkins 1986, Humpesch 1981, Ward and Stanford 1982, Wise 1980). Among these factors it appears that the annual temperature regime and the quantity and quality of available food resources are the two most important factors affecting growth and timing of emergence of aquatic invertebrates (Anderson and Cummins 1979, Fuller and Mackay 1981, Giberson and Rosenberg 1992, Sweeney 1984, Sweeney and Vannote 1986, Vannote and Sweeney 1980, Webb and Merritt 1987). Complex interactions in nature make it difficult to partition the relative importance of each factor, however. For example, temperature directly influences metabolic rates (Sweeney 1984), as well as food quality and quantity (Anderson and Cummins 1979, Cummins and Klug 1979).

The influence of food on aquatic invertebrate development has been clearly demonstrated in laboratory studies (e.g., Anderson and Cummins 1979, Bird and Kaushik 1984, Ward and Cummins 1979, Webb and Merritt 1987), however temperature has been observed to be more closely correlated to larval growth than diet (Brittain 1976, Giberson and Rosenberg 1992, Hawkins 1986, Mackey 1977, Rosillon 1988, Sweeney 1984, Sweeney and Vannote 1981,

1986). For example, Sweeney and Vannote (1986) noted that although diet exerts some influence on larval growth rates, temperature was more closely correlated to larval growth in their study of a stream stonefly. Merritt et al. (1982) also observed temperature to exert greater influence than diet on larval growth of three species of black flies. Hawkins (1986) found little evidence to implicate diet as a cause for observed differences in growth rates of six western *ephemerellid* mayfly species.

Several empirical studies of aquatic invertebrates strongly suggest temperature is the single most important factor affecting growth rates (Breitenmoser-Wursten and Sartori 1995, Brittain 1976, Hawkins 1986, Humpesch 1979, 1981, Mackey 1977, Markarian 1980, Nebeker 1971 a, b, Sweeney 1978, 1984, Sweeney and Vannote 1978, 1981, Vannote and Sweeney 1980, Ward and Stanford 1982). For example, the timing of adult emergence varies predictably with temperature during years with atypical weather conditions (Langford 1975) and warmer temperatures associated with lower latitudes and/or altitudes also induce earlier emergence (Nebeker 1971b, Ward and Stanford 1982).

Temperature variability in lotic habitats

Aquatic invertebrates in lotic habitats are subject to thermal regimes that vary seasonally and diurnally, as well as spatially within a stream reach. Localized water temperatures are the consequence of altitudinal, latitudinal, hydrological, geological and meteorological influences (Smith and Lavis 1975) which interact to produce significant thermal variability within lotic systems. Although water temperatures are highly variable, the spatial and temporal heterogeneity of temperatures produce observable and predictable patterns for a stream of a given order, altitude, and latitude (Vannote and Sweeney 1980). In their study using 10 years of temperature data, Vannote and Sweeney (1980) observed that water temperatures in White Clay Creek

showed summer and winter temperatures characterized by a high degree of constancy (temporal uniformity) and fall and spring temperatures characterized by a high degree of contingency (sequential temporal variability). The predictability of thermal heterogeneity is an important feature of natural streams influencing the density, distribution and life history of aquatic invertebrates.

Localized groundwater discharge zones also subject aquatic invertebrates to thermal heterogeneities on a much smaller scale within a single reach (Brunke and Gosner 1997). Differential mixing of surface and groundwater sources create spatially diverse thermal patterns vertically and laterally within and along a stream channel (Ebersole et al. 2003, Brunke and Gonser (1997) and is suggested to be a function of channel morphology (Poole and Berman 2001). For example, White et al. (1987) observed longitudinal differences in streambed temperature patterns along a short pool-riffle-pool sequence in a northern Michigan river. Brunke and Gonser (1997) also observed warmer temperatures as depth decreased in down welling zones toward the end of pool habitats and cooler temperatures as depth increased in upwelling zones toward the end of riffle habitats. The diversity of thermal habitats within a short distance can provide a refuge for stenothermal insects (Ebersole et al. 2003) as well as enhance species diversity by temporally segregating species with different thermal responses (Ward and Stanford 1982).

The relationship between temperature and growth can be used to predict the timing of adult emergence by calculating the accumulation of heat in degree-days (DD) above a minimum threshold necessary to complete adult maturation (Anderson 1969, Higley et al. 1986, Sweeney 1984). Degree-day models have been used for several decades to understand insect phenology with important applications in plant sciences, pest management, and insect ecology (Higley et al.

1986, Yazdani and Agarwal 1997). Several studies have observed that the growth of aquatic invertebrates is directly proportional to the number of degree-days experienced by a population (Anderson 1969, Fahy 1973, Markarian 1980, Sweeney 1984, Thorup 1973). Few studies, however, have evaluated the extent to which a DD model applies to field studies of northern populations of mayflies.

Research goals

This research seeks to evaluate the relative influence of temperature on the growth of several closely related species of *ephemerellid* mayfies. In comparing spatial variations in mayfly growth relative to temperature variability, my objectives are to 1) determine the relative influence of temperature on growth across sites (i.e., how much of the variance in annual growth can be explained by concurrent variations in temperature) and 2) evaluate the validity of applying a cumulative degree-day model to predict the timing of emergence for *ephemerellid* mayflies in northern Michigan. I hypothesize that site-specific variations in water temperature will be the major factor influencing aquatic insect growth and emergence.

METHODS

Study Site

This research was conducted in the Au Sable River watershed near Grayling, Michigan (Figure 1). The watershed is characterized by low topographical relief with sandy soils and permeable outwash plains which contribute to a sustained groundwater flow (Hendrickson 1966). The topography, climate, and geology of the region moderate the temperature and flow regimes resulting in smaller temperature fluctuations and stable flow patterns relative to streams with less groundwater dominance. The Au Sable River is designated a blue ribbon trout stream by the Michigan Department of Natural Resources, and is the birthplace of Trout Unlimited. It is a valuable natural resource asset which attracts anglers nationwide to fish in the highly productive streams and tributaries. The Au Sable River has played an important role in the development of current trout management philosophy through great public interest as well as intensive scientific research. Located in a region with relatively little development, the Au Sable River is minimally disturbed. Additionally, the Au Sable is readily accessible from several locations, and supports diverse macroinvertebrate fauna.

Six sites along the Au Sable River near Grayling, Michigan were selected for study based on similarities in stream order, size, accessibility and degree of recreational use. Sites were selected with the anticipation that they would represent a thermal gradient that would provide variation in mayfly growth and emergence, but that would not cause total exclusion of species from certain areas of the stream. These sites include: Old Dam Road, Burton's Landing, Thendara Road, Stephan Bridge, and Wakely Bridge on the main stem and Kellog Bridge on the North Branch.

Temperature

Hobo Water Temp Pro ® sensors were deployed at each site to monitor water temperature continuously throughout the study period. Temperature was recorded once per hour with an accuracy of ±0.2°C at 25°C. Two sensors were deployed at each site to minimize the potential for loss of sensors and placed in locations where potential interference by recreational users was minimal.

Temperature data were used to calculate day-degrees Celsius (D°C) with the formula: D°C = T_{ave} – threshold temperature (°C) (Gage and Haynes 1973). Accumulation of day-degrees above a minimum threshold for growth began with the initial appearance of first instars for each species and were used to estimate physiological time necessary to complete larval development, with the exception of *E. subvaria* and *E. invaria* because temperature data was not available during early instar growth of these species. Minimum critical temperature for growth was approximated by plotting the mean water temperature between two consecutive sampling dates against growth rate between those dates. For a particular species, a cluster of points was identified where growth rate was either very slow or nonexistent. The highest temperature indicated by the cluster was considered the minimal growth level temperature.

Benthic Samples

Individuals in the benthic phase were qualitatively sampled monthly during September through May, and bi-weekly May to August using a seine with a 0.5 mm mesh size. The size distribution of mayflies captured suggested that this gear was effective for sampling individuals greater than 3.0 mm in length. Samples were preserved in the field in 70% ethanol. Body length (front of head to end of last abdominal segment) was measured to the nearest .05mm and average length determined for each sampling date. Incremental growth was calculated as: $(L_{t+1} – L_t)/\Delta t$, where L_t= mean initial length, L_{t+1}= mean final length, and Δt = the time interval in days. This

method of calculating growth is sensitive to error because only two data points were used, thus, growth was also estimated by regression analysis to evaluate site-specific differences in growth rates. For each species, only data points that exhibited nearly linear growth were used to calculate growth by regression.

Adult Emergence

Emerging adult insects were sampled using emergence traps. Light-weight, transportable emergence traps shaped like small tents were constructed using polyvinyl chloride (PVC) pipe and white fine-mesh netting. The traps covered 0.33 m^2 of the stream surface, allowing them to maintain efficiency with minimal flow interference. White no-see-um netting (mesh size: ~0.5mm) was used because it blocked less light than other colors to simulate more natural conditions for emergence. Each trap was deployed using two pieces of rebar on the upstream edge to hold it in place and Styrofoam floats to allow for continuous sampling while water levels rose or fell. Two traps were placed near benthos sampling locations at each site, and where potential interference by recreational stream users was minimized. Insects were removed from the traps every 3-4 days from June through August.

Analysis

Preliminary analyses exploring differences among sites and dates using a General Linear Model (GLM) with an interaction term to explore potential differences in temporal patterns among sites indicated a statistically significant ($p<0.0001$) but minor interaction between site and date. Further, animals were not captured at every site on every day, which prevented estimation of least square mean lengths for sites or dates. Thus, a reduced model without the interaction term was used to determine differences in mean sizes among sites. Estimation of growth by regression allowed statistical comparison by analysis of variance for site to site differences.

RESULTS

Temperature

Mean water temperatures across Burton's Landing, Old Dam, and Kellog Bridge differed by less than 1°C for the entire study period, with the exception of a few days in the spring There was very little variability in temperature across Burton's Landing, Old Dam, and Kellog Bridge, although some general patterns are apparent (Figure 2). Overall, Old Dam was the coldest site and Kellog Bridge the warmest during the winter and spring, while Kellog Bridge was coldest and Burton's Landing warmest during the summer, however the difference between the warmest and coldest sites each day was less than 1°C throughout the entire study period, with the exception of a few days during spring. Diel temperature fluctuations were much more pronounced during the summer at all three sites.

The pattern in water temperature at Stephan Bridge and Wa Wa Sum was significantly different from Burton's Landing, Kellog Bridge, and Old Dam (Figure 2). Temperatures were notably warmer at Wa Wa Sum and Stephan Bridge during the winter, and colder during the summer. Temperatures at Stephan Bridge and Wa Wa Sum were similar during the winter, but Stephan Bridge was substantially warmer than Wa Wa Sum during the summer. The unusual temperature patterns observed at Stephan Bridge and Wa Wa Sum suggest sensors were influenced by close proximity to groundwater inflows and may not accurately represent general thermal conditions at these sites. Sensors were not recovered from the Wakely Bridge site.

Temperature data collected at Stephan Bridge and Wakely from October 2011 through March 2012 by the Hydrogeology Lab at Michigan State University using Odyssy Data Loggers indicate the Stephan Bridge is less than 3°C cooler on average than Wakely Bridge.

Larval Growth and Adult Emergence

For all species, growth was nearly linear until emergence when average length reached an asymptote or declined (Figure 3). *Ephemerella subvaria* was the first species to emerge in the spring at the largest average size, followed by *E. invaria*, then *E. dorothea*, and *D. lata* was the last species to emerge in the summer. A progressive decrease in average size was observed between earlier and later emerging species, with the exception of *D. lata* which emerged last at a size similar to *E. dorothea*. The mesh size of our net was not fine enough to capture early instars, therefore estimates of average size are probably biased toward larger larvae, particularly during early life stages. Individual lengths of *D. lata* were much more variable than the other three species (Figure 4). For all species, specific growth rates were reduced at all sites when water temperatures were lowest but did not cease at even the lowest average temperatures (Figure 5). Because no critical minimum temperature could be determined, degree-days greater than 0°C were summed from the date of first appearance in samples.

Emergence data was limited by the location of emergence traps in the stream. *Ephemerellid* mayflies tend to emerge from riffles and areas closer to the middle of the stream; however heavy canoe traffic prevented traps from being placed in optimal emergence zones. Emergence data for *E. subvaria* and *E. invaria* are particularly limited because traps were only checked once a week during their emergence period and may not accurately represent true emergence patterns.

Ephemerella subvaria

For *E. subvaria*, there were significant differences in mean length among sites over time (R^2=.79, $p<0.0001$). In general, mean length was greatest at Wakely Bridge, followed by Old Dam, then Burton's Landing, Wa Wa Sum, and Kellog Bridge, with the smallest mean length at Stephan Bridge (Table 1). Early instars were first captured at all sites on 9 November, and the

last individuals were sampled from 30 April to 13 May. Across sites, mean length over time generally increased until 21 March, when mean length decreased at all sites except Burton's Landing and Old Dam, where mean length continued to increase until 30 April and then declined (Figure 6).

There were significant differences ($p<0.0001$) in *E. subvaria* growth rates across sites and throughout the study period (Table 2). There was no clear pattern in the timing of maximum growth rates of *E. subvaria* larvae. Maximum growth rates occurred from 21 March to 30 April at Burton's Landing, from 4 February to 21 March at Kellog Bridge, Old Dam, and Stephan Bridge, and from 9 November to 27 December at Wa Wa Sum and Wakely Bridge (Figure 7). *E. subvaria* required between 512 and 538 degree days above 0°C to complete growth.

Very few *E. subvaria* adults were observed in emergence traps. Most (77.8%) were observed in traps from 9 May through 16 May, although few (22.2%) were observed from 17 May to 23 May. *E. subvaria* adults were only observed in traps at Burton's Landing and Kellog Bridge (Table 3).

Ephemerella invaria

For *E. invaria*, there were significant differences in mean length among sites over time ($R^2=.83$, $p<0.0001$). In general, mean length increased nearly linearly until 26 May when it either reached an asymptote or decreased, suggesting emergence (Figure 8). Mean length was greatest at Burton's Landing, followed by Wa Wa Sum, then Wakely Bridge, Stephan Bridge, and Kellog Bridge, with the smallest mean length at Old Dam (Table 1). Across sites, first capture of early instars ranged from 9 November to 27 December, and the last individuals were sampled 5 June to 11 June.

There were significant differences ($p<0.0001$) in *E. invaria* growth rates across sites and over time (Table 2). In general, growth rates were relatively stable until 30 April when growth rates increased rapidly until 18 May; maximum growth rates occurred between 30 April and 18 May (Figure 9). Growth rates were significantly higher at Stephan Bridge, Wa Wa Sum, and Burton's Landing during this period and then declined rapidly at all sites after 18 May. *E. invaria* required between 650 and 693 degree days above 0°C to complete growth.

E. invaria adults were first observed in traps at Burton's Landing, Old Dam, Stephan Bridge, and Wa Wa Sum during the last week of May. The majority of adults from all sites were observed in traps from 24 May to 8 June, although some were observed in traps through 16 June (Figure 10). Of all adults observed, most were obtained from traps at Stephan Bridge, Burton's Landing, and Wa Wa Sum; very few adults were collected from Old Dam and Wakely Bridge (Table 3). No adults were observed in traps at Kellog Bridge.

Ephemerella dorothea

For *E. dorothea*, there were significant differences in mean length over time among sites ($R^2=.78$, $p<0.0001$). In general, the mean length was greatest at Burton's Landing, followed by Old Dam, then Wa Wa Sum, Stephan Bridge, and Wakely Bridge, with the smallest mean length at Kellog Bridge (Table 1). Across sites, first capture of early instars ranged from 2 February to 21 March, and the last individuals were sampled from 17 June to 25 June. Across all sites, mean length over time generally increased until 1 June, when mean length either reached an asymptote or decreased, suggesting adult emergence (Figure 11).

There were significant differences ($p<0.0001$) in *E. dorothea* growth rates across sites and over time (Table 2). In general, growth rates were steady through the winter and increased rapidly after 13 May at Wakely Bridge, Wa Wa Sum, Burton's Landing, and Stephan Bridge,

and after 27 May at Kellog Bridge and Old Dam (Figure 12). Maximum growth rates occurred from 13 May to 18 May at Wakely Bridge, Wa Wa Sum, and Stephan Bridge, and from 26 May to 1 June at Kellog and Old Dam. Lowest growth rates were consistently observed at Burton's Landing throughout the study period. *E. dorothea* required between 729 and 875 degree days above 0°C to complete growth.

E. dorothea adults were first observed in traps at Kellog Bridge, Old Dam, Stephan Bridge, and Wa Wa Sum the first week of June and at Wakely Bridge during the second week of June. All adults (100%) were observed in traps from 1-23 June (Figure 13). Of all adults observed, most were collected from traps at Stephan Bridge and Wa Wa Sum; few were collected at Kellog Bridge, Old Dam, and Wakely Bridge (Table 3). No adults were observed in traps at Burton's Landing.

Drunella lata

For *D. lata*, there were significant differences in mean length over time among sites (R^2= .85, $p<0.0001$). In general, mean length was greatest at Stephan Bridge, followed by Wakely Bridge, then Burton's Landing and Kellog Bridge, with the smallest mean lengths observed at Wa Wa Sum and Old Dam (Table 1). Across sites, first capture of early instars ranged from 13 May to 26 May, and the last individuals were sampled 22 July to 28 July. Across all sites, mean length over time generally increased until 8 July when mean length either reached an asymptote or decreased, suggesting emergence (Figure 14).

There were significant differences ($p<0.0001$) in *D. lata* growth rates across sites over time (Table 2). Maximum growth rates occurred from 11 June to 17 June at Wakely Bridge, Kellog Bridge, Stephan Bridge, and Wa Wa Sum, and from 25 June to 1 July at Old Dam and Burton's Landing (Figure 15). The greatest observed difference in growth rate occurred between

Old Dam and Stephan Bridge from 25 June to 1 July; however this difference was no longer apparent by 15 July. *D. lata* required between 630 and 760 degree days above 0°C to complete growth.

Adult *D. lata* individuals were first observed in emergence traps at Burton's Landing on 22 June and were present in traps at all sites by 30 June (Figure 16). Approximately 85% (84.3%) of *Drunella* adults emerged from all sites between 24 June and 23 July. Of all adults observed in traps, most were obtained at Stephan Bridge and Wa Wa Sum; relatively few adult individuals were obtained from traps at Burton's Landing, Kellog Bridge, Old Dam, and Wakely Bridge (Table 3).

DISCUSSION

Degree Day Models

A major underlying assumption of the degree-day model is that development is directly related to temperature and is therefore calculated as a linear relationship. For these species, the relationship between temperature and growth rate was better represented by a sigmoid curve (Figure 5), with slower growth rates at low temperatures and an approximately linear increase across intermediate temperatures. Interestingly, the response of increasing temperature on specific growth rate was similar for all species (Figure 5). The relationship for D. lata was less clear because this species completes most of its larval growth during periods of higher average temperatures, limiting our understanding of growth at lower temperature. The parabolic relationship between temperature and growth rate observed for *D. lata* may be an indication of an upper development threshold temperature which was not apparent in the other three species which emerge earlier in the spring and early summer. A curvilinear relationship between temperature and growth rate has been observed in studies of other poikilothermic organisms (Higley et al. 1986, Ostrovosky 1995, Wagner et al. 1984) where growth is slowed or ceases at lower and upper development threshold temperatures, but proceeds at a constant rate at intermediate temperatures. Previous lab studies have suggested that there are minimum and maximum threshold temperatures where growth approaches zero or is even negative (Higley et al. 1986, Logan et al. 1976, Wagner et al. 1984). In field studies such as this, it is difficult to determine these thresholds empirically; however, my data suggests that although reduced at lower temperatures, growth was positive across the full range of temperatures observed in the Au Sable River. Furthermore, threshold temperatures frequently vary with the age or life stage of the organism (Higley et al. 1986, Sanborn et al. 1982), thereby confounding analyses of field data.

Therefore, degree-day models may underestimate development time at lower threshold temperatures and overestimate at upper threshold temperatures.

Other implicit assumptions in degree-day models are that the organism cannot regulate its own temperature and the temperature data used for analysis represent the same temperatures experienced by the organism. The first assumption is violated by many aquatic insects which employ behavioral mechanisms to regulate their temperature, such as seeking thermally favorable microhabitats (Brittain and Eikeland 1988, May 1979). Such behavior produces uncertainty in regard to the second assumption, that temperature data for calculations reflect actual temperatures experienced by the organism. Although subject to many limitations and approximations, degree-day models are still a useful and widely used tool in interpreting relationships between growth and temperature, provided analyses are interpreted as estimates of development time and the underlying assumptions of the approach are acknowledged. For these species, accumulation of degree-days over 0°C provided a reasonable estimate of mean length when considered over intermediate temperatures (Figure 17).

Growth and Temperature

Site to site variations in mean length were significant but minor relative to day of year as a predictor of mean length for all species. These results are not surprising; all development depends on time and growth is not instantaneous. It was interesting, however, that each species to respond differently to habitat variables other than temperature across sites in terms of mean length and growth rate. For example, mean lengths of *E. subvaria* and *E. dorothea* were among the largest at Old Dam, but *E. invaria* and *D. lata* were the smallest at this site. At Stephan Bridge, the smallest *E. subvaria* and largest *D. lata* larvae were collected, although both species' growth rates were among the greatest at this site. Mean lengths were smaller at Kellog Bridge for

all species, even though *D. lata* exhibited the highest average growth rate at this site. Although temperature has been attributed a major role driving life history patterns of aquatic insects (e.g., Brittain 1976, Breitenmoser and Sartori 1995, Elliot 1978, Fahy 1973, Hawkins 1986, 1990, Humpesch 1979, Markarian 1979, Sweeney 1978, 1984, Sweeney and Vannote 1981, Ward and Stanford 1982, among others), these results indicate that the observed spatial variations in mean length and growth of these species cannot be generalized as a solely as a function of temperature. The difficulty discerning the relative influence of temperature from other physical factors such as habitat or food resources in natural populations has been documented elsewhere (e.g., Anderson and Cummins 1979, Clifford 1970, Hawkins 1986, Sweeney and Vannote 1986).

Interpretation is further confounded because the relative influence of individual factors depends on the scale at which the effect is evaluated and may vary simultaneously among sites with different biotic and geophysical properties and along a longitudinal gradient in stream ecosystems (Hawkins 1990, Hynes 1970, Vannote et al. 1980). For example, temperature has a direct effect on individual metabolism and larval development (Nebeker 1971, Sweeney 1984, Vannote 1978, Vannote and Sweeney 1980, Ward and Stanford 1982), but also indirectly influences the quality and quantity of available food and habitat as well as processing and production rates at the population and community levels (Anderson and Cummins 1979, Rempel and Carter 1986, Rosillon 1988, Vannote and Sweeney 1980, Wallace and Merritt 1980, Ward and Stanford 1982, Webb and Merritt 1987).

Care must be taken in interpreting growth from population growth curves; rates are accurate only if average length adequately represents the response of a single individual. Thorup (1973) cautioned against using population growth curves to estimate growth rate because of the potential effect of differential immigration and emigration of animals of different size.

Additionally, growth rates based on population means may underestimate true individual rates if extended hatching of eggs occurs. The observed variability in size and timing of growth among individuals within a subpopulation confound growth estimates, but may manifest as an artifact of thermal heterogeneity within a given stretch resulting in subpopulations whose individuals are subject to very different temperature conditions, making it difficult to evaluate thermal effects on populations. The difficulty in using field data for growth studies has been documented for other mayfly species as well as other aquatic insects (Anderson and Cummins 1979, Clifford 1970, Hawkins 1986, Markarian 1980, Thorup 1973). Despite these concerns, I feel that my data accurately represents the mean length and growth rate of for the majority of the development time of these species. However, it was apparent that reductions in mean length during periods of emergence lead to non-representative estimates, and as such, these data were excluded from this part of the life history.

Emergence

Emergence was generally synchronous (>90% emerging with a 3-week period) for all species except *D. lata*, which exhibited a prolonged emergence across 7 weeks. Emergence trap data are supplemented by emergence literature from several different sources (Table 4). Despite limited adult emergence data, particularly for *E. subvaria* and *E. invaria*, these data are in general agreement with the literature.

Synchronous emergence of several species of mayflies has been observed consistently year after year (Sweeney and Vannote 1981, 1982, Watanabe et al. 1999, Watanabe and Ohkita 2000). Several theories exist to explain the adaptive processes favoring synchronous emergence. For example, synchronous emergence of adults may increase the potential for reproductive success (Macan 1958), which would suggest early or late-emerging individuals are subject to

heavy selective pressure. However, this does not appear to be the case because extended emergence has been observed year after year, indicating either natural selection is not more severe on early or late-emerging individuals, or these individuals are not always offspring of late-emerging adults of the previous generation. Some variability in timing of emergence can be expected as a result of differential environmental conditions throughout development, or even genetic differences among subpopulations. A more likely explanation for population synchrony is to reduce the risk of predation as a result of predator satiation (Peckarsky et al. 2001, Sweeney and Vannote 1981, 1982). Vannote (1978) also suggests that synchronous growth of larvae may be adaptive because selective processes favor individuals whose growth is proportional to seasonal changes in temperature.

Sweeney and Vannote (1981) suggest a model for *E. subvaria* to explain the observed synchronous emergence despite high variability in larval sizes throughout the growth period. In their study, *E. subvaria* larvae were sorted into four different size classes and reared in a laboratory and observed that the largest larvae emerged first and were the largest adults, while the smallest larvae emerged at the end of the emergence period at a reduced size. They propose that adult tissue development is stimulated in all larvae at the same time by temperatures above a threshold, regardless of larval size. The differential size of adults throughout emergence suggests that the rate of adult tissue synthesis may be size dependent as larger individuals tend to reach metamorphosis more rapidly than smaller larvae (Sweeney and Vannote 1981). They concluded that the ultimate size depends on the size of larvae at the onset of adult tissue development and the decrease in size throughout emergence appears to be the result of the sequential emergence of smaller larvae.

In addition to an extended emergence period, *D. lata* also exhibited the greatest variability in larval sizes. Both phenomena may result from microhabitat or thermal differences within a particular site, or differences in the timing of egg hatch. If ovipositing patterns are influenced by a species' emergence schedule, then species with longer, extended emergence periods (e.g. *Drunella lata*) should be reflected by a wider larval size distribution; more synchronous emergence (e.g. *Ephemerella subvaria, E. invaria, and E. dorothea*) should be reflected by less larval size variability, which is consistent with my observations of the coefficient of variation among species (Figure 4).

The observed decline in larval size throughout the emergence period has been observed in studies of other mayfly species (Harker 1952, Langford 1975, Macan 1957, Sweeney 1978, Sweeney and Vannote 1978, Vannote and Sweeney 1980). An additional explanation for this size reduction may be the result of delayed egg hatching, which has been observed in field studies of several mayfly species (Clifford et al. 1979, Gledhill 1960, Sweeney and Vannote 1981). Clifford (1982) identified 15 species with at least four months of egg dormancy during the summer, five of which were *Ephemerella* genera. Hawkins (1986) noted that there was no apparent trend in the onset of growth relative to temperature in a Western *Ephemerella* species complex and observed the initiation of growth differed up to 4 months within a species, even among sites with similar temperature regimes.

Implications

Mayflies of the family Ephemerellidae are widely distributed and abundant in most temperate stream ecosystems. Higher growth rates at warmer temperatures and slowed growth at lower temperatures clearly demonstrate the significance of temperature on life history patterns of aquatic invertebrates. Many anthropogenic factors drive large and small-scale changes in thermal

regimes in freshwater ecosystems. Some examples from a long list include climate change, impoundments, discharge of heated effluent, land use practices, or water withdrawals for municipal or agricultural use. Although the relative influence of these factors on temperature depends on the scale at which the effect is evaluated, the general trend has been to cause warmer thermal regimes. The results of this study suggest that individuals in these populations will likely grow more rapidly at higher temperatures, however it is more difficult to indicate whether this will equate to earlier emergence. Degree-day estimates suggest earlier emergence patterns are likely, but the lack of significant site-to-site variations in temperature make it difficult to discern the effect of temperature on timing of emergence. Although these data support increased growth in warmer thermal regimes, sustained temperatures exceeding an upper development threshold for growth may reduce fecundity, increase larval mortality or exclude thermally sensitive species altogether, leading to overall population reductions. Aquatic invertebrates serve an important role in maintaining ecosystem function and energy flow in for both terrestrial and aquatic food webs such that the loss of one or a few species may significantly alter food web dynamics. As a primary consumer and important energy source for fish, this type of a perturbation may result in detrimental losses of valuable ecosystem services as well as significantly impact sport fishing economies. Therefore, effective fisheries management must account for fish-invertebrate linkages in the context of a human-altered landscape and climate.

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APPENDIX

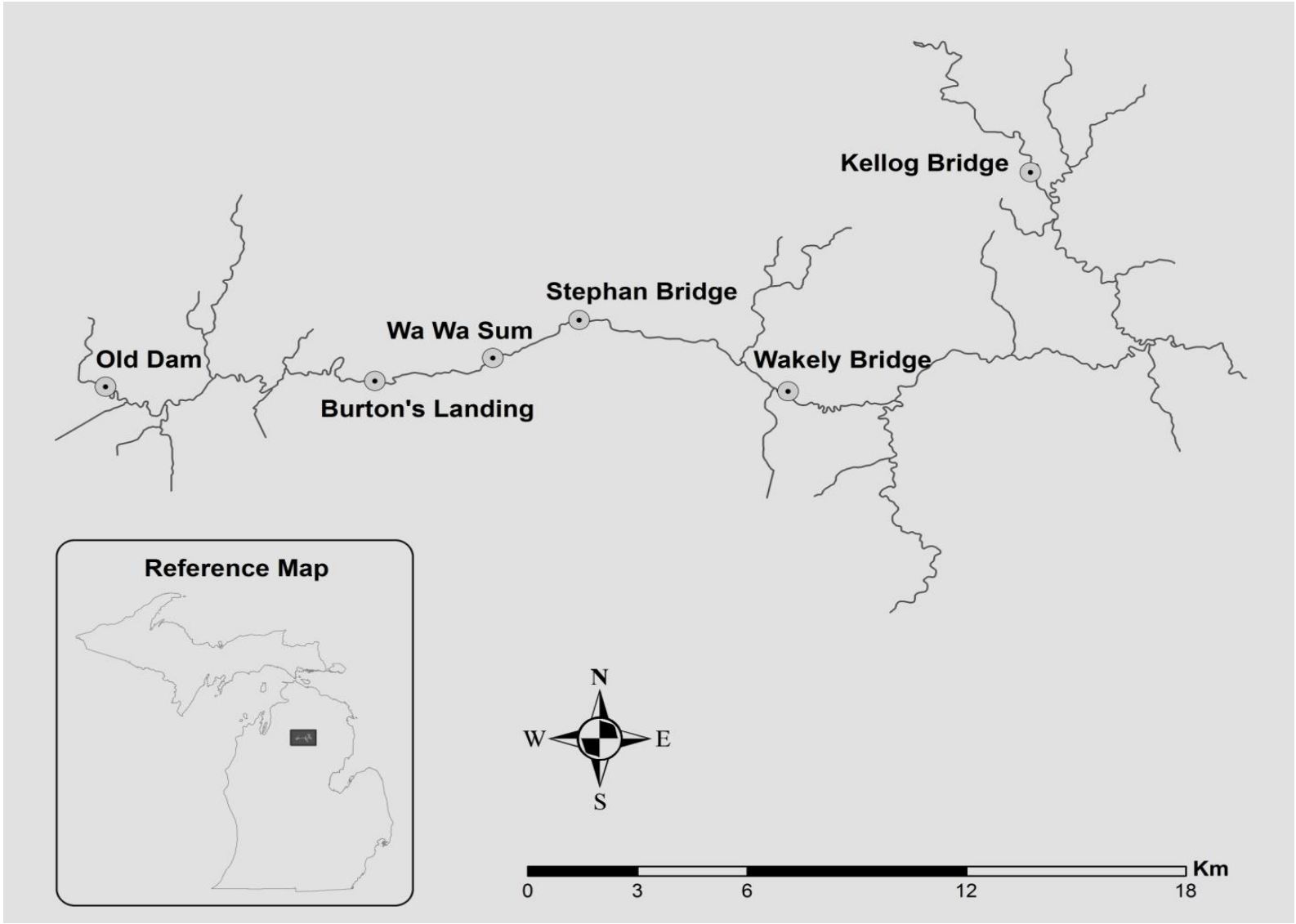

Figure 1. Location of the study sites on the Au Sable River near Grayling, Michigan. Inset map shows location of study area in Michigan's Lower Peninsula.

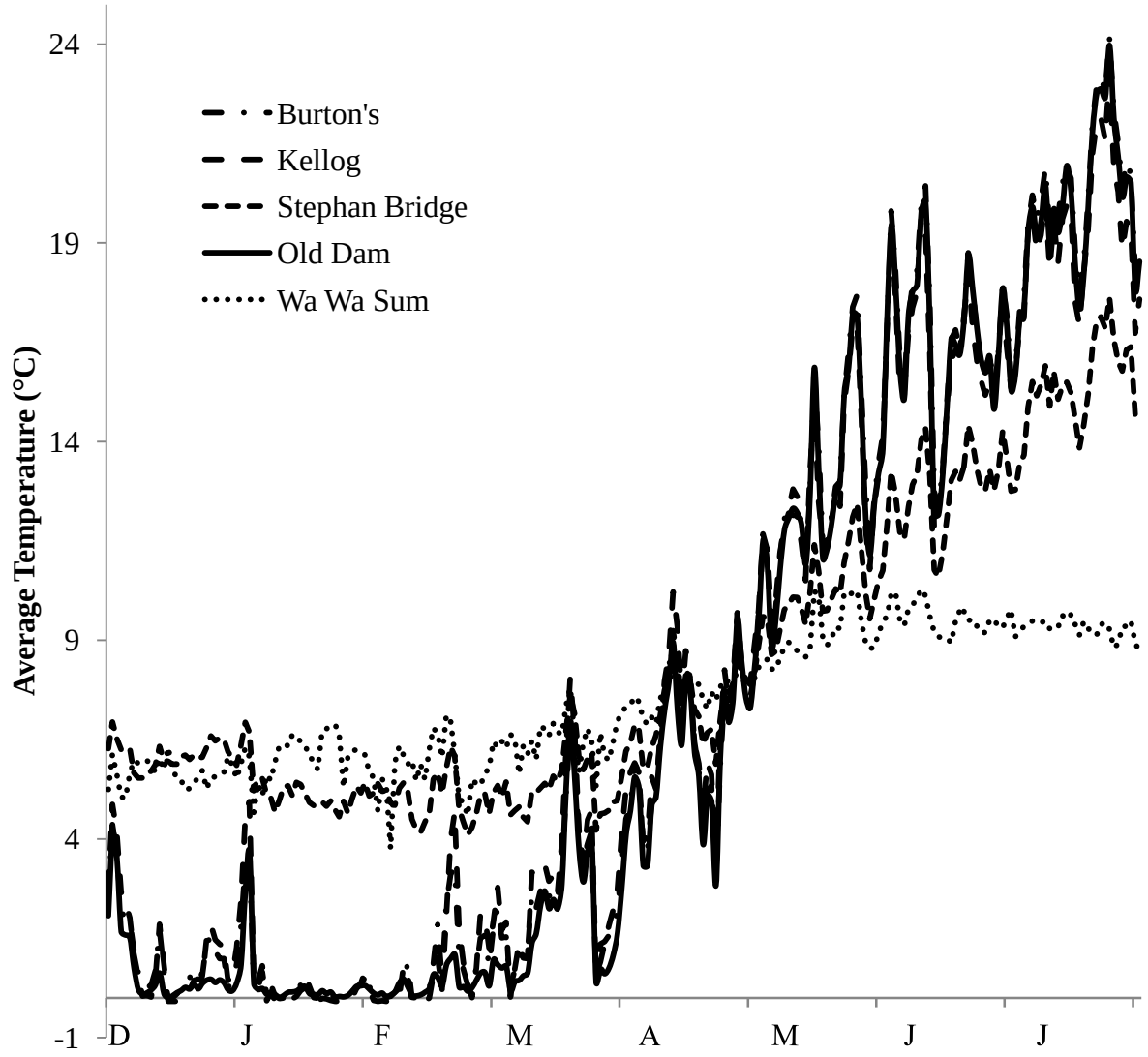

Figure 2. Average daily stream temperature at Burton's Landing, Kellog Bridge, Stephan Bridge, Wa Wa Sum, and Old Dam on the Au Sable River near Grayling, Michigan November 2010 – July 2011**.**

Table 1. Least square mean lengths (mm) across all species and sites and General Linear Model analysis results. Standard errors are in parentheses.

	Species			
Site	*E. subvaria*	*E. invaria*	*E. dorothea*	*D. lata*
Old Dam	8.98 (.106)	6.53 (.039)	6.56 (.054)	5.13 (.061)
Burton's Landing	8.95 (.123)	7.14 (.047)	6.87 (.060)	5.37 (.056)
Wa Wa Sum	8.92 (.107)	7.11 (.038)	6.42 (.048)	5.15 (.064)
Stephan Bridge	8.08 (.101	6.69 (.043)	6.23 (.053)	5.65 (.061)
Wakely Bridge	9.22 (.123)	6.98 (.039)	6.22 (.050)	5.40 (.064)
Kellog Bridge	8.26 (.115)	6.64 (.040)	5.98 (.051)	5.19 (.062)
ANOVA	$P<0.0001$	$P<0.0001$	$P<0.0001$	$P<0.0001$
	$r^2=.79$	$r^2=.83$	$r^2=.78$	$r^2=.85$
MS Day	86.81	26.12	16.47	93.27
MS Site	9.03	7.08	6.27	3.76

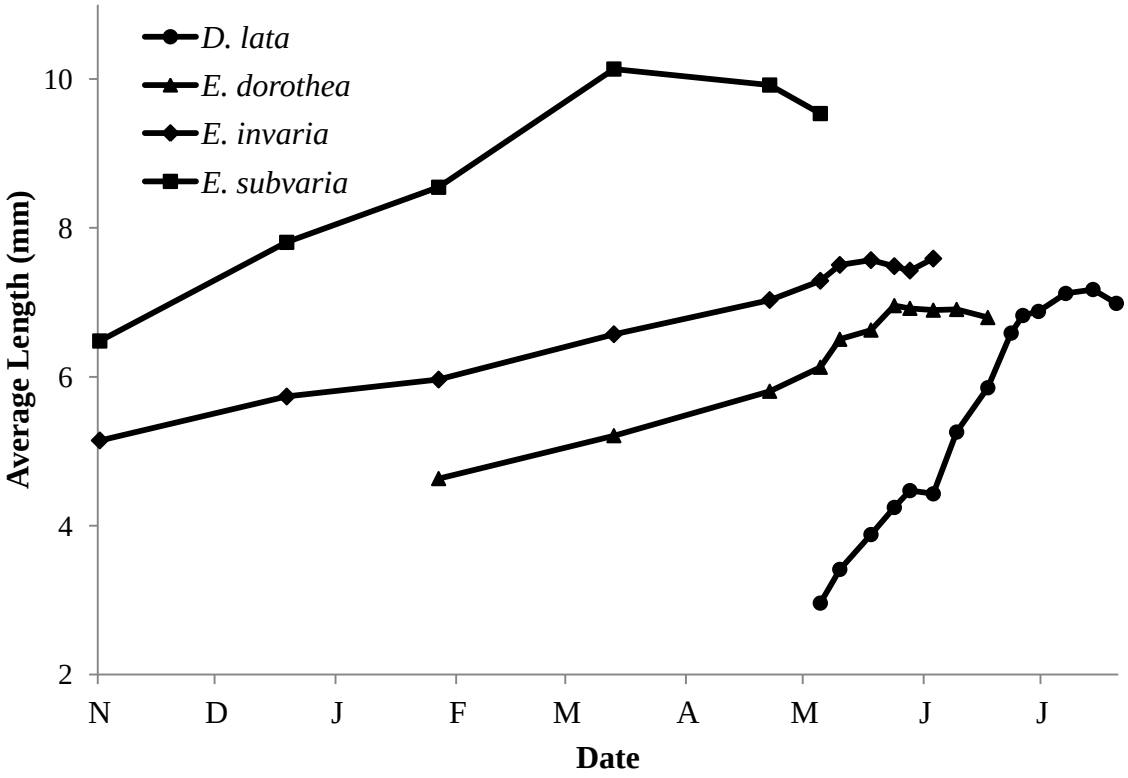

Figure 3. Mean length of *Ephemerellid* larvae averaged across all sites November 2010 – July 2011.

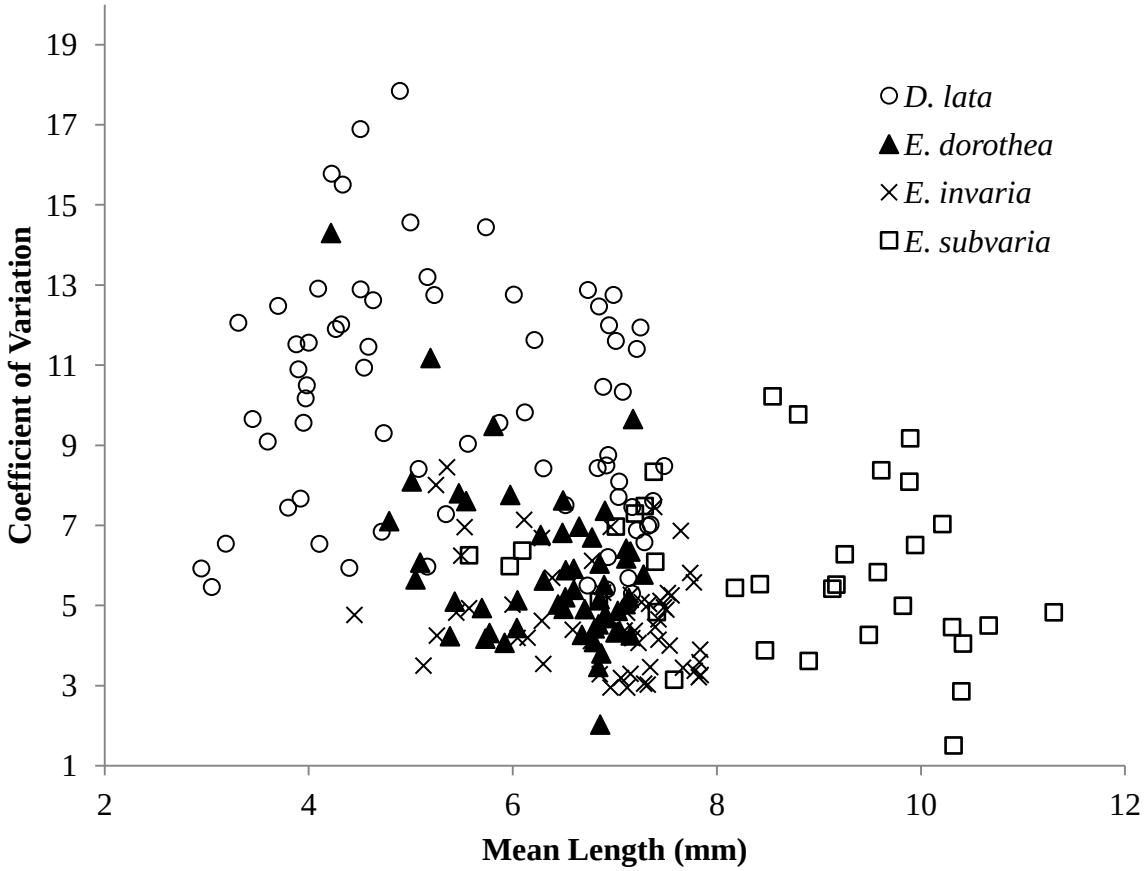

Figure 4. Coefficient of variation (CV) as a function of mean length for all species.

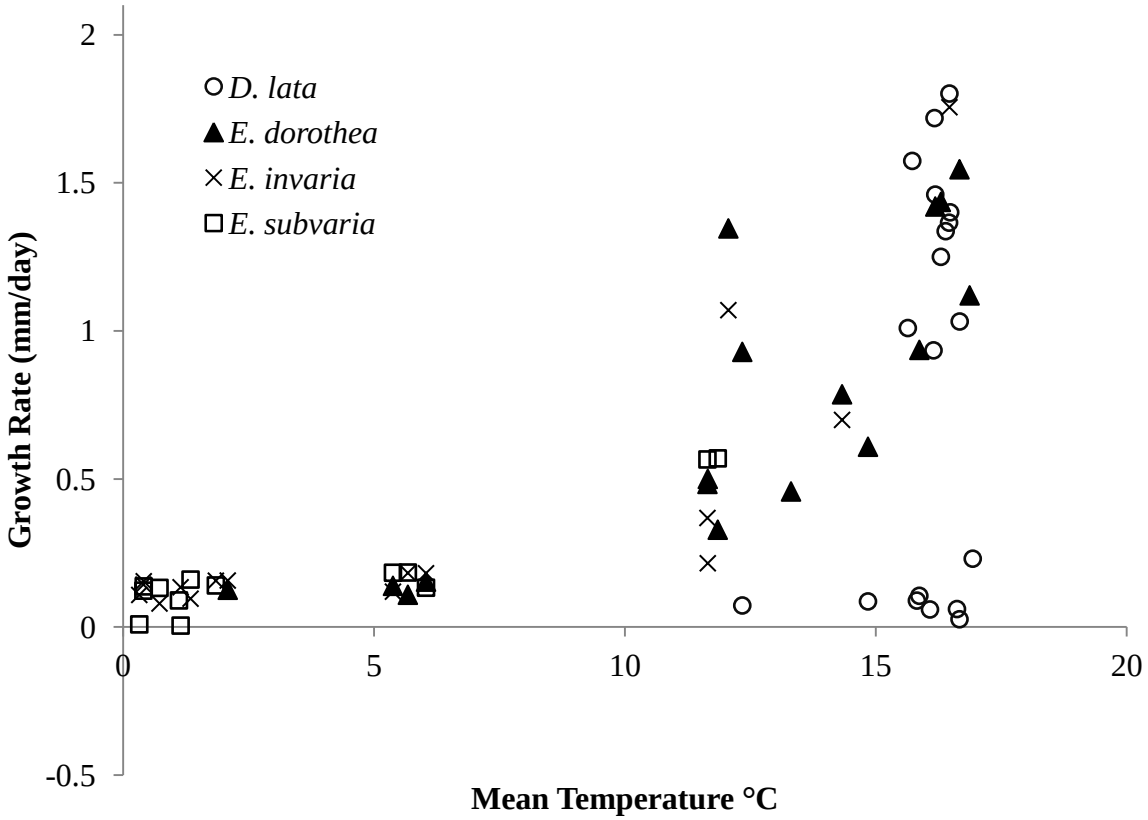

Figure 5. Plot for estimating the critical minimum growth temperature for all species.

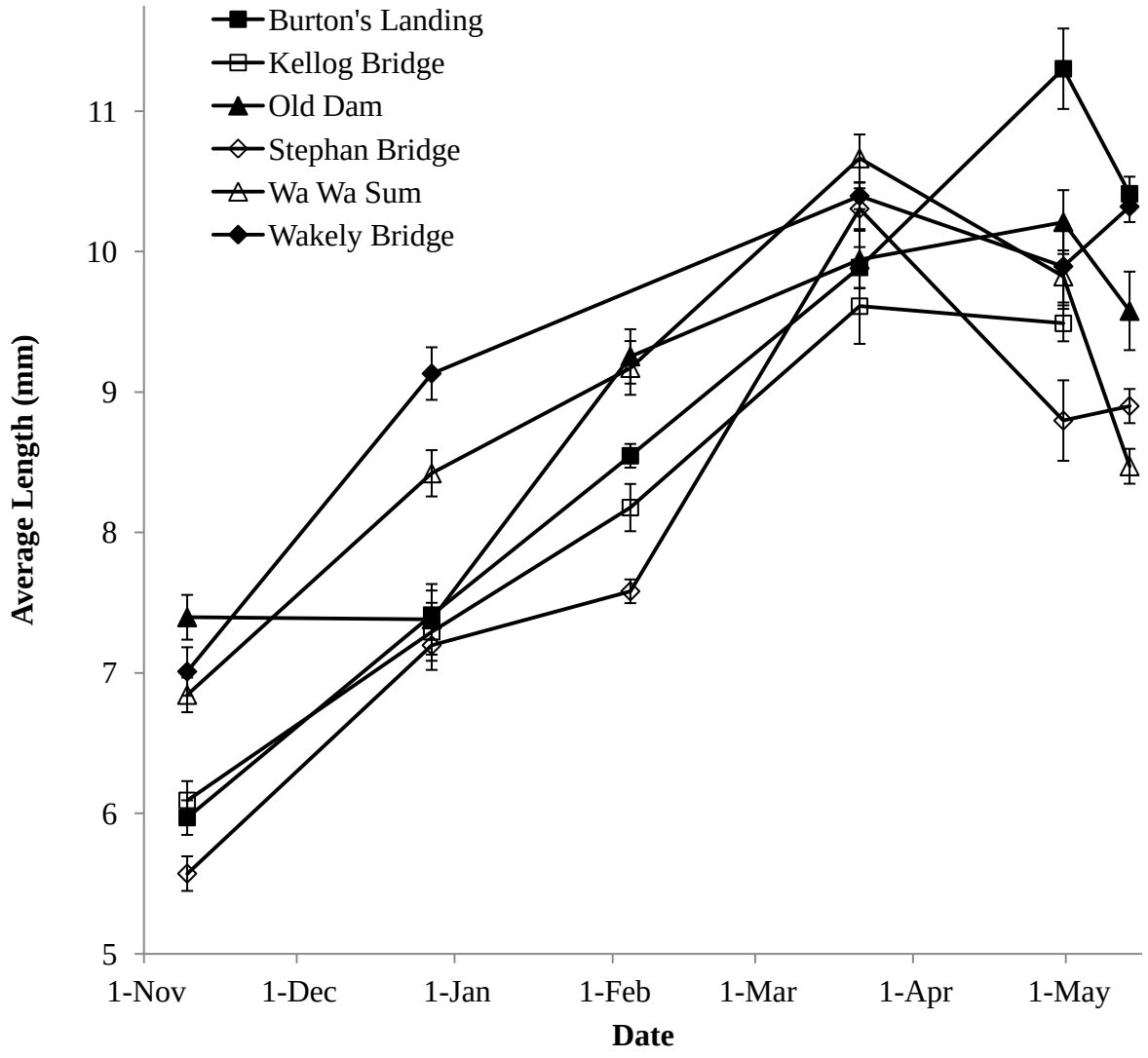

Figure 6. Mean length (±1 standard error) of *E. subvaria* larvae at all sites November 2010 – May 2011.

Table 2. Growth statistics for four species of Ephemerellidae. Specific growth rate (G) as estimated by linear regression analysis is provided for each site with number of data points (n) used to calculate G. The coefficient of determination (r^2) describes the fit of data to the linear model.

	E. subvaria			*E. invaria*			*E. dorothea*			*D. lata*		
Site	*G*	*n*	r^2	*G*	*n*	r^2	*G*	*n*	r^2	*G*	*n*	r^2
Old Dam	.019	43	.73	.015	80	.90	.022	59	.63	.073	79	.76
Burton's Landing	.031	28	.91	.013	64	.74	.020	50	.61	.069	83	.78
Wa Wa Sum	.020	38	.74	.011	75	.80	.018	62	.70	.057	74	.77
Stephan Bridge	.023	44	.66	.016	65	.86	.030	58	.71	.078	83	.83
Wakely Bridge	.017	34	.65	.010	71	.81	.026	56	.76	.073	78	.73
Kellog Bridge	.021	41	.82	.010	76	.83	.017	65	.72	.086	76	.83
ANOVA	$F = 67.42$			$F = 212.79$			$F = 94.98$			$F = 158.50$		
	$P < 0.0001$			$P < 0.0001$			$P < 0.0001$			$P < 0.0001$		
	$r^2 = .77$			$r^2 = .85$			$r^2 = .76$			$r^2 = .79$		

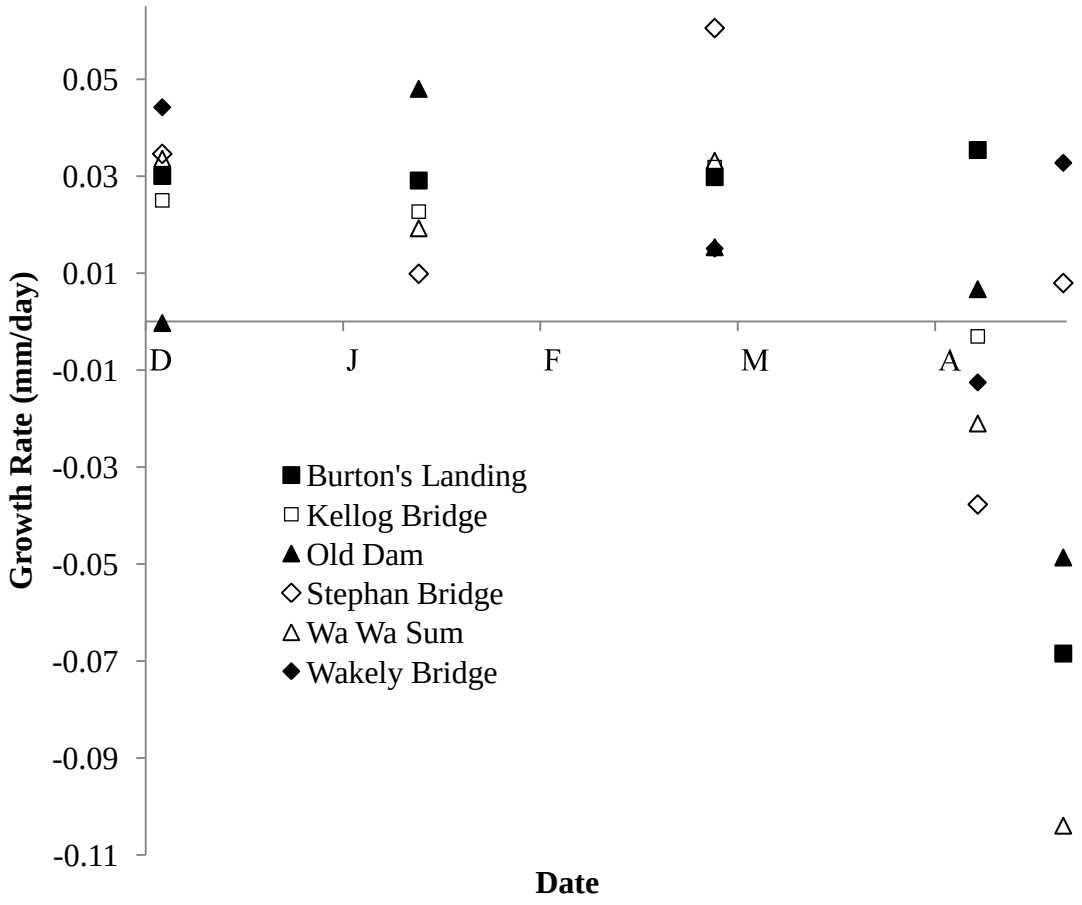

Figure 7. Specific growth rate (mm/day) of *E. subvaria* larvae at all sites December 2010 – May 2011.

Table 3. Total number of adults observed in emergence traps at all sites across all dates.

	Species			
Site	*E. subvaria*	*E. invaria*	*E. dorothea*	*D. lata*
Burton's Landing	6	9	-	17
Kellog Bridge	3	-	3	9
Old Dam	-	3	3	5
Stephan Bridge	-	17	9	79
Wa Wa Sum	-	9	6	36
Wakely Bridge	-	1	2	7

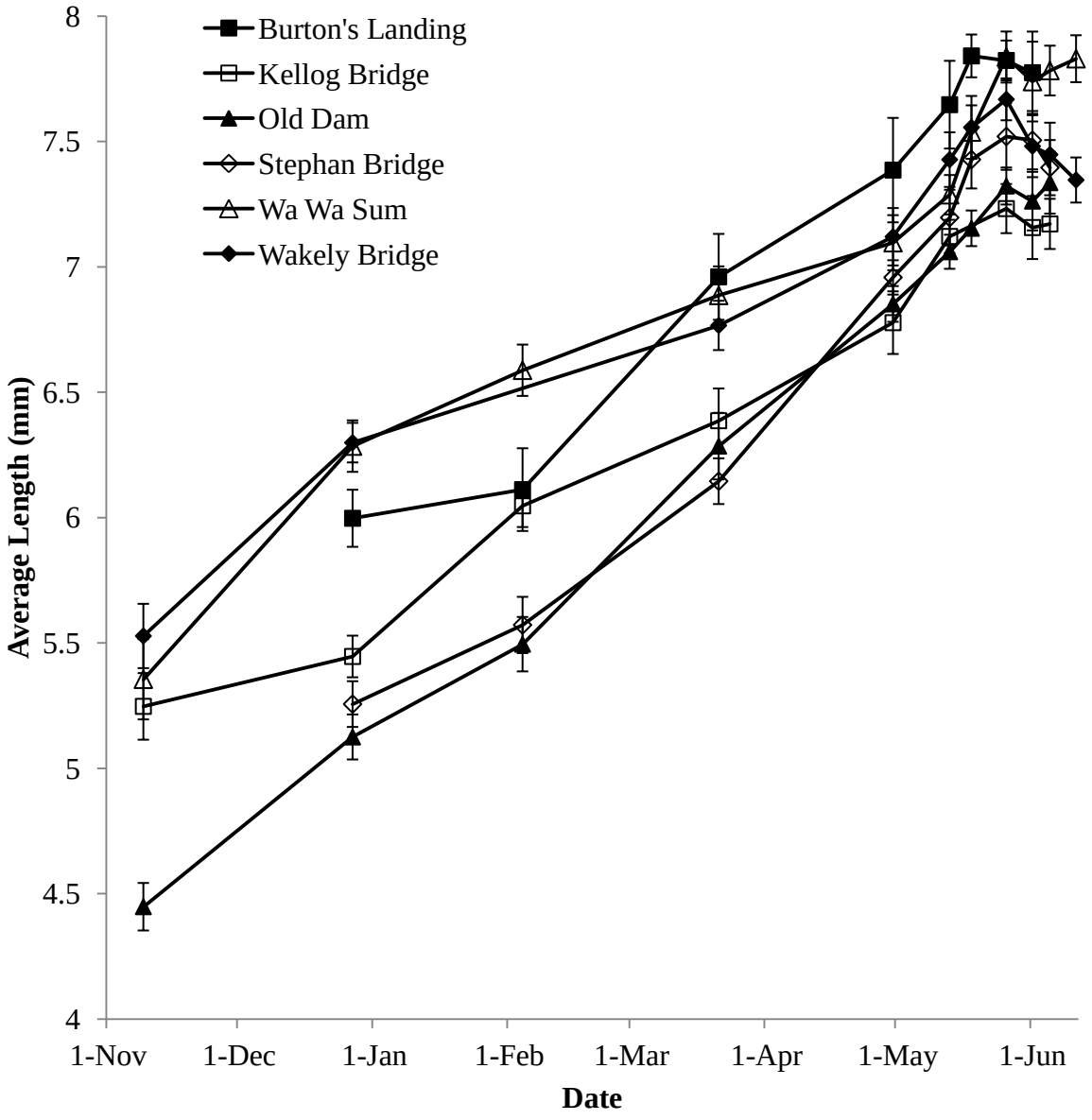

Figure 8. Mean length (±1 standard error) of *E. invaria* larvae at all sites November 2010 – May 2011.

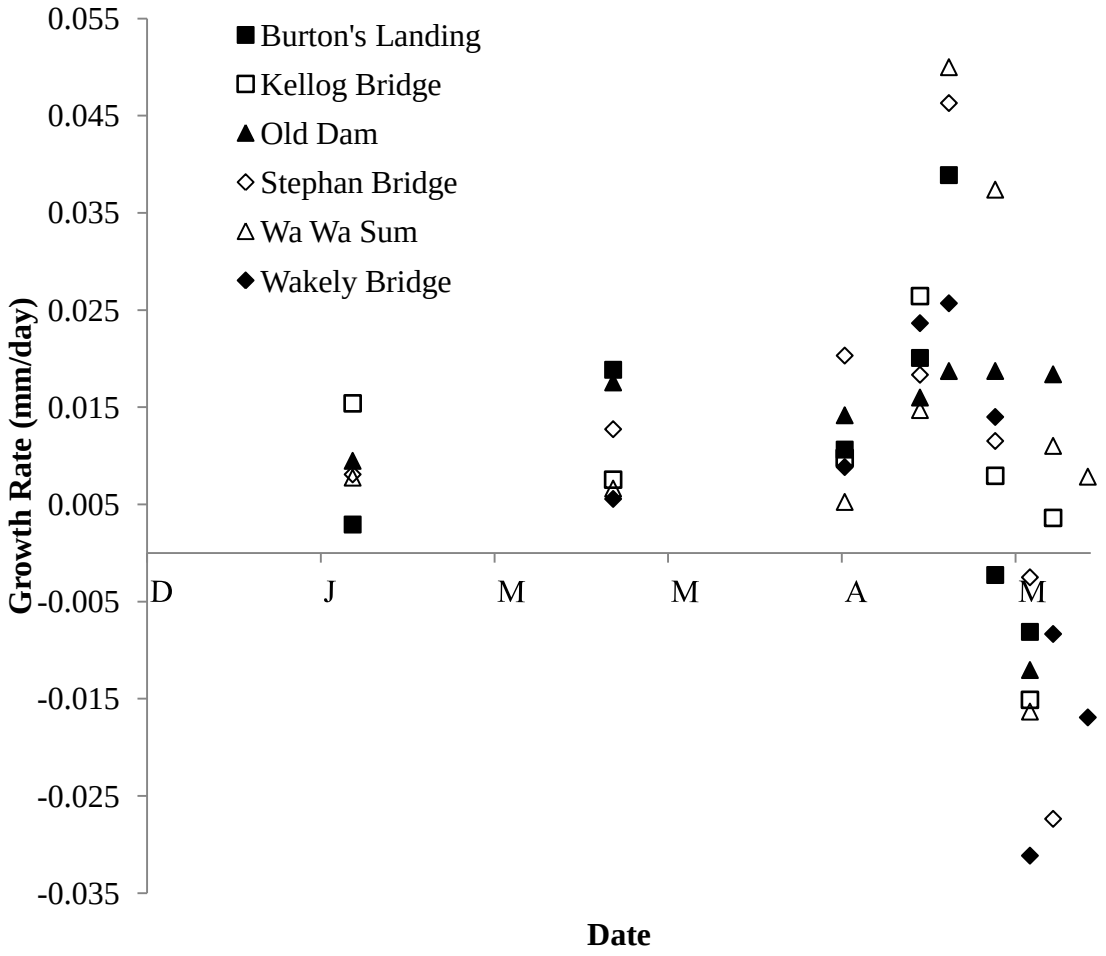

Figure 9. Specific growth rate (mm/day) of *E. invaria* larvae at all sites December 2010 – May 2011.

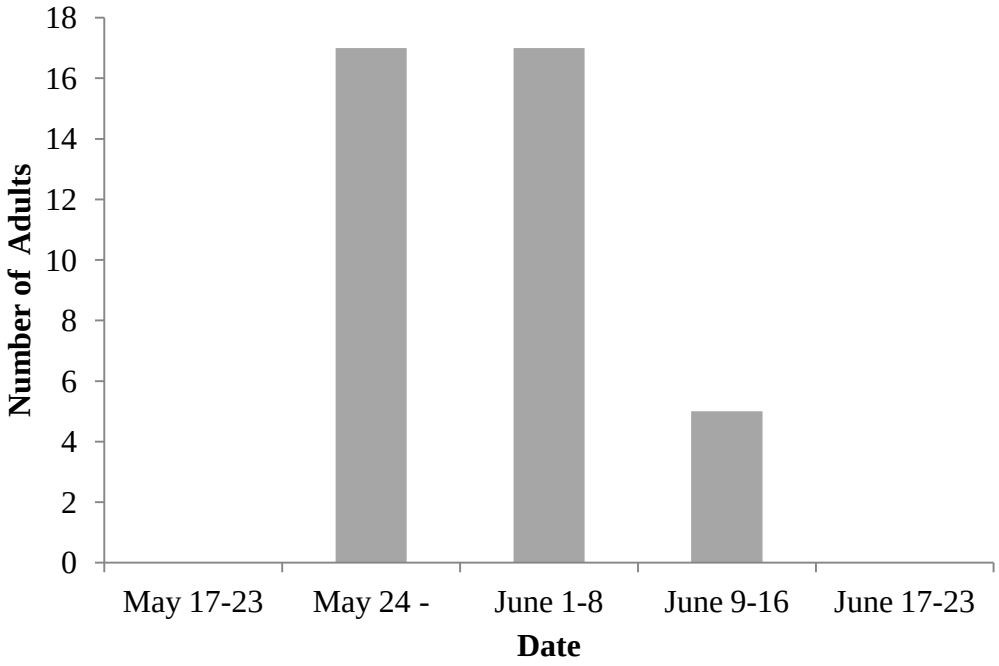

Figure 10. Total number of adult *E. invaria* observed in traps across all six sites on the Au Sable River near Grayling, Michigan.

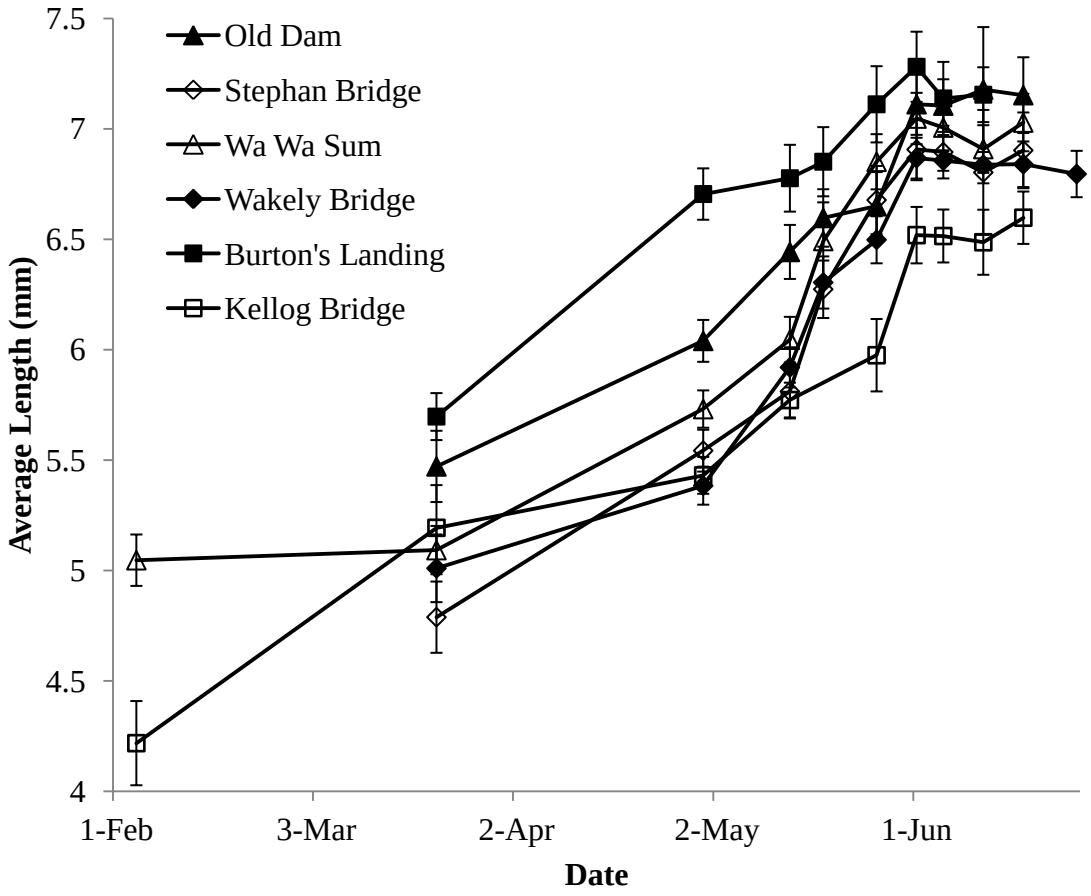

Figure 11. Mean length (±1 standard error) of *E. dorothea* larvae at all sites November 2010 – May 2011.

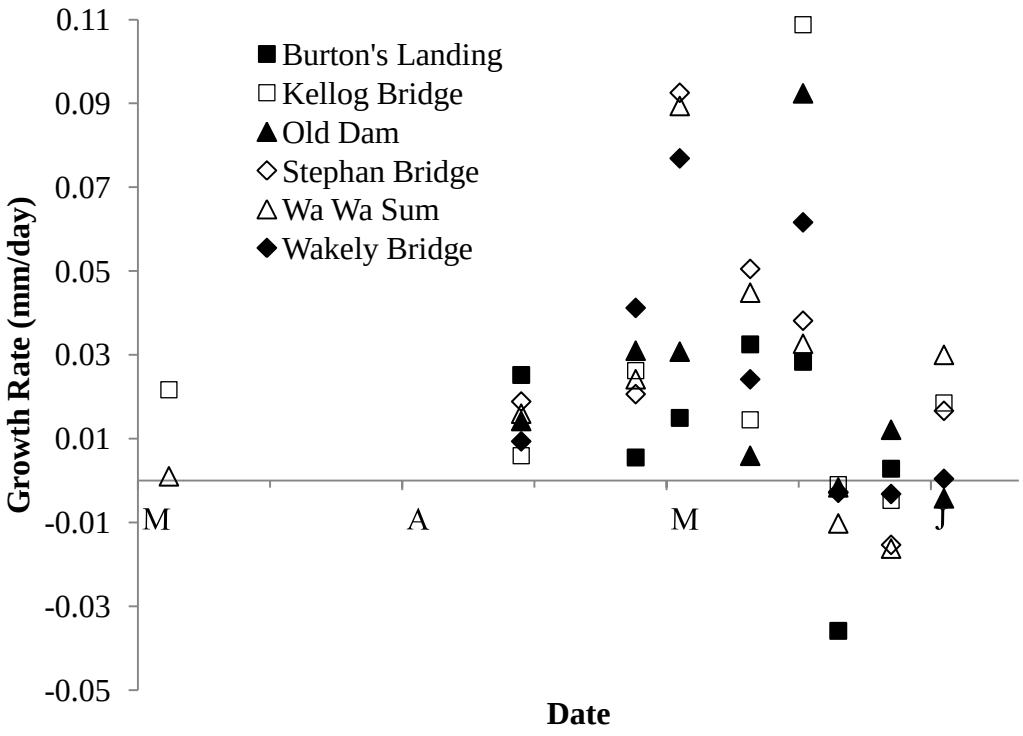

Figure 12. Specific growth rate (mm/day) of *E. dorothea* larvae at all sites March 2011 – June 2011.

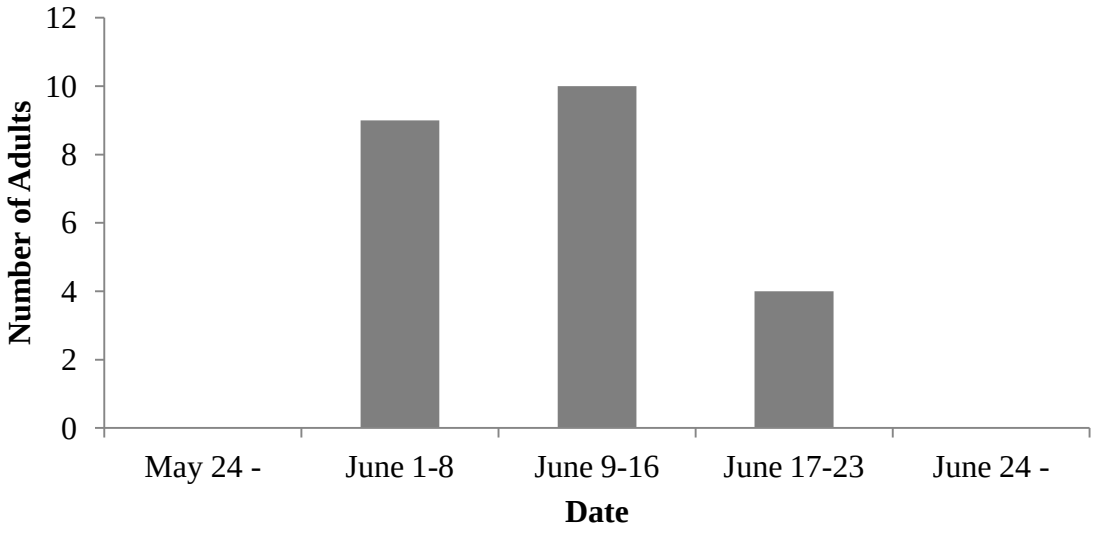

Figure 13. Total number of adult *E. dorothea* observed in traps across all six sites on the Au Sable River near Grayling, Michigan.

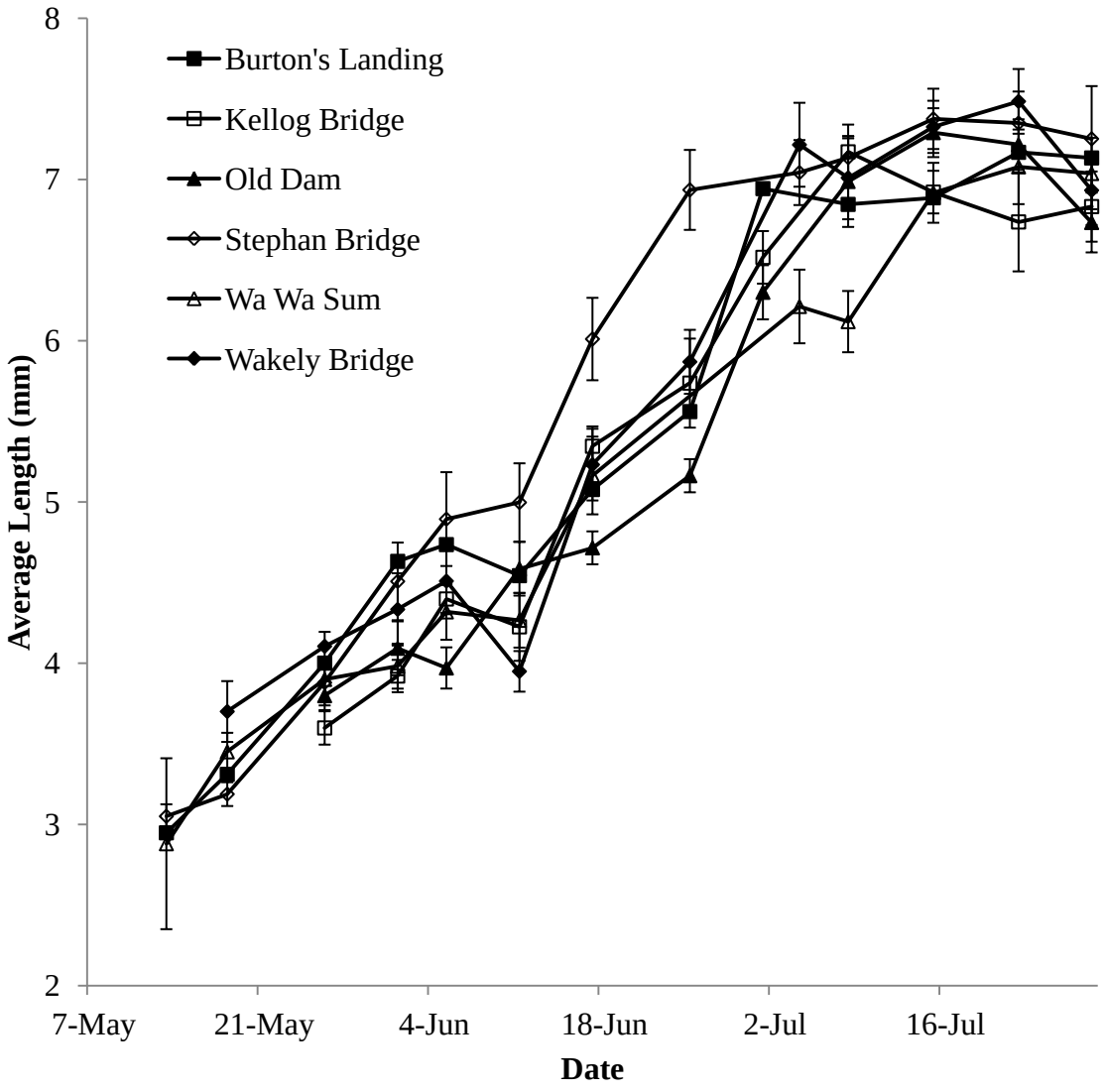

Figure 14. Mean length (±1 standard error) of *D. lata* larvae at all sites May 2011 – July 2011.

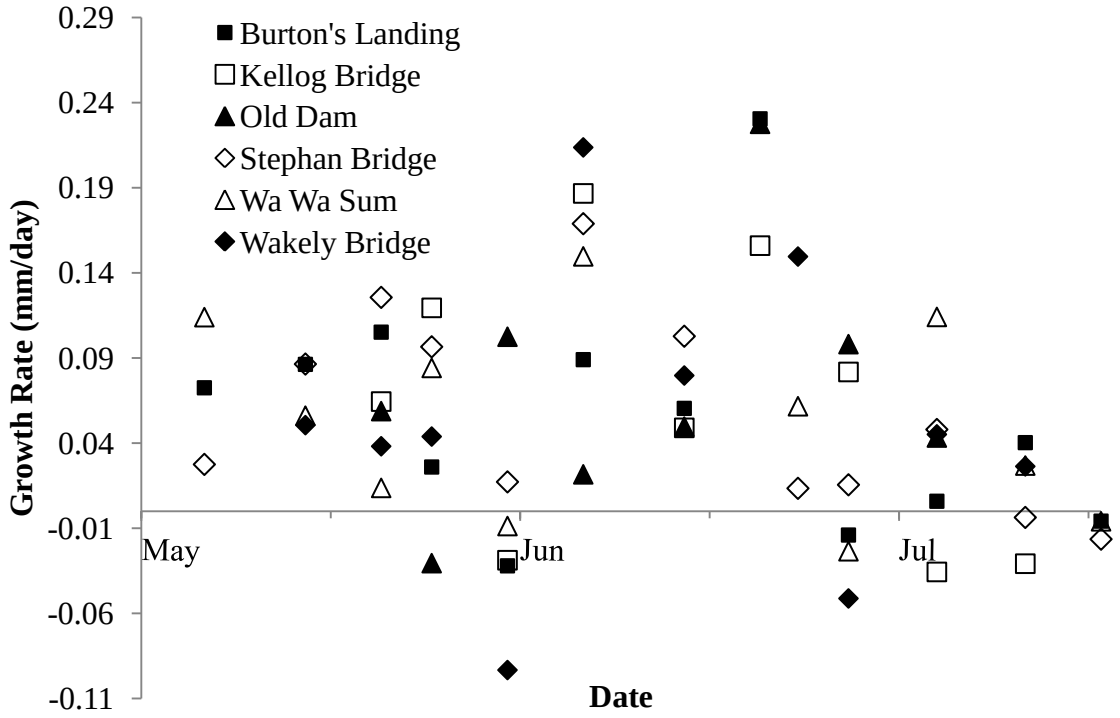

Figure 15. Specific growth rate (mm/day) of *D. lata* larvae at all sites May 2011 – July 2011.

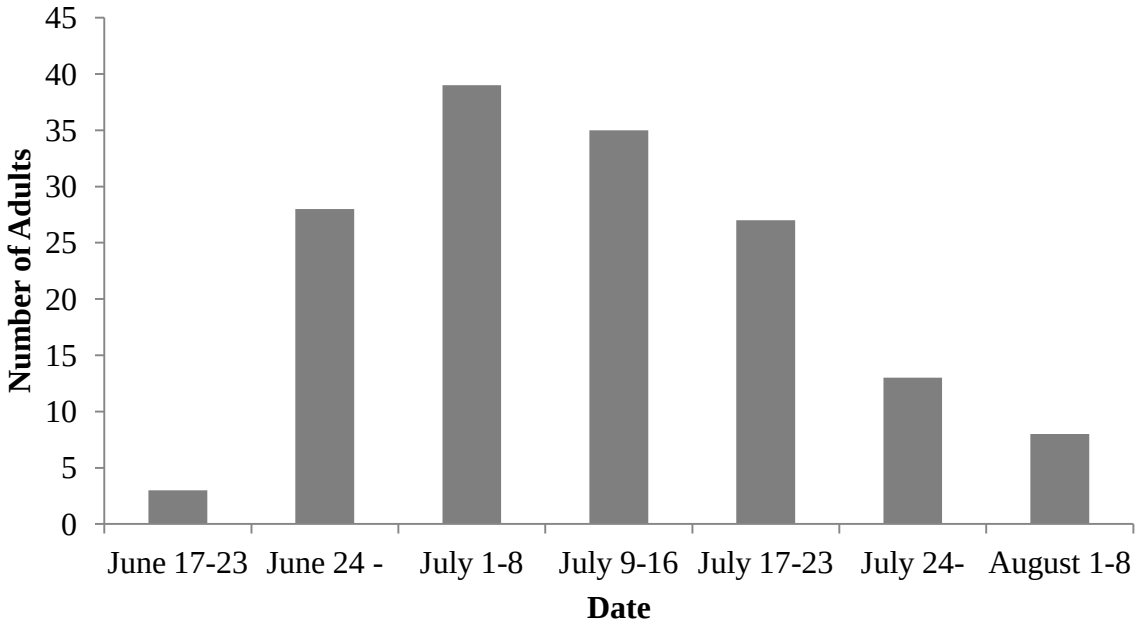

Figure 16. Total number of adult *D. lata* observed in traps across all six sites on the Au Sable River near Grayling, Michigan.

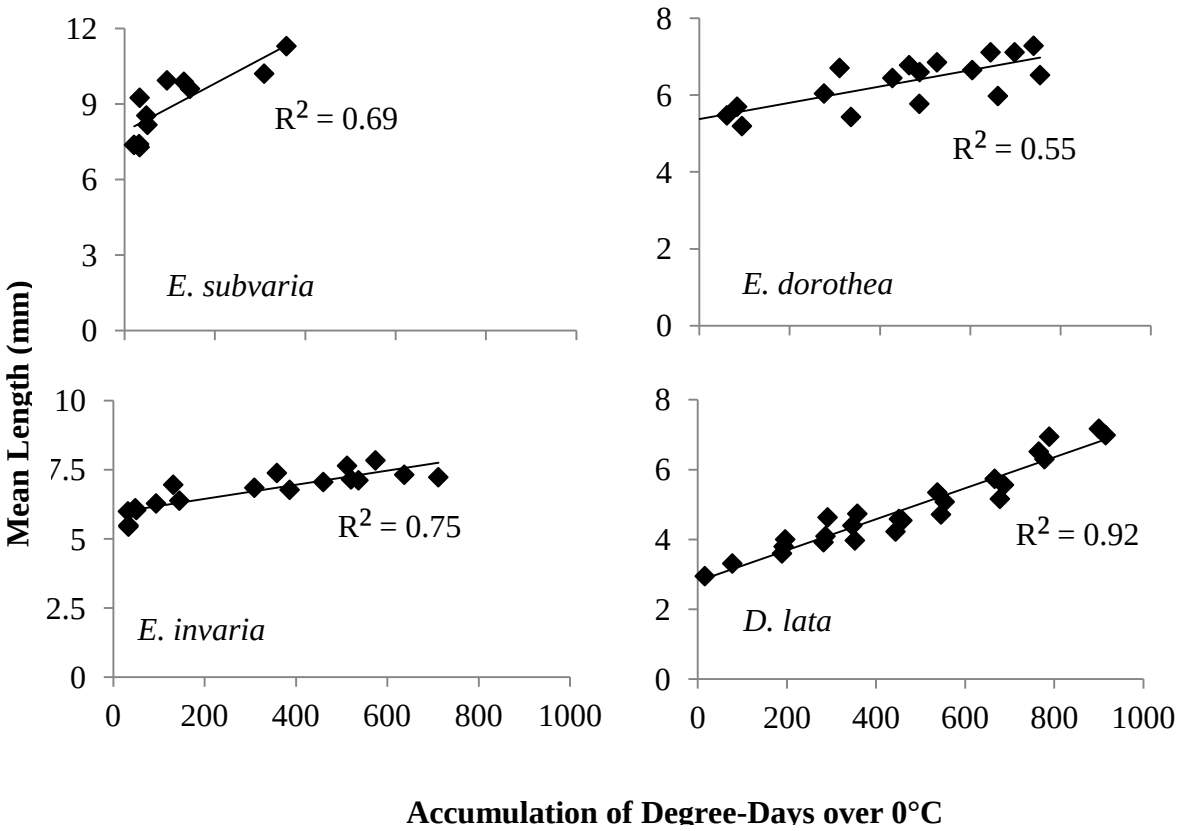

Figure 17. Relationship between mean length for a particular sample event and the summed degree-days over 0°C prior to that sampling date for all species.

Table 4. Literature comparison of emergence schedules.

[1]Pobst 1990, [2]Stochastic Anglers, [3]Leonard and Leonard 1962, [4]Caucci and Nastasi 1975, [5]Lofland 2000, [6]Miller 2011

	E. subvaria	***E. invaria***	***E. dorothea***	***E. lata***
Personal data	??-May 18	May 24-June 11	May 26-June 25	June 22-August 7
Trout Stream Insects[1]	Late April-May	May -June	Late May-June	Mid July-mid August
Midwest Emergence Calendar[2]	April 24-May 28	May 15-June 1	May 26-June 21	July 1-August 10
Mayflies of Michigan Trout Streams[3]	April 25-June 16	May 3-July 28	May 12-July 3	June 25-August 13
Hatches II[4]	April 21-May 16	May 15-June 14	May 21-July 7	July 1-August 14
Trout Flies for the Michigan Emergence Schedule[5]	April 25-May 21	Mid May-early June	May 10-July 15	Late June-mid August
Hatch Guide for Upper Midwest Streams[6]	Mid-April-May	May-June	Late May-early July	Late June-mid August

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