# How does water temperature affect the development and growth of various mayfly species?

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## Abstract

Previous research has shown that mayflies (Order: Ephemeroptera) exhibit high life-history plasticity (Peckarsky, 2001). In order to better understand the effects of increasing global temperatures, it is important to seek a better understanding of the variations in plasticity, and the effects of that variance within aquatic ecosystems. However, the potential adverse effects of developmental plasticity, such as smaller average size, shorter lifecycles, and altering of niche partitioning, is understudied. This project aims to provide a better understanding of developmental differences between mayfly species in streams of varying temperatures. Harper and Peckarsky (2006) examined the development and emergence of *Baetis bicaudatus* in relation to stream flow and temperature. Other studies show that Baetidae growth remains unaffected by stream temperature (Sweeney et al., 2018), but that average size lessens due to less time spent as a nymph. However, the study only examined one species of mayfly (*Baetis bicaudatus*), and concentrated only on the relationships between temperature, emergence, and development. This study seeks to further the understanding of mayfly growth and development in relation to stream temperature, across a variety of mayfly species. By sampling six streams across a 4°C temperature gradient, in two river systems, this study widens the understanding of mayfly growth and development, and examines the potential effects of climate change on the species.


## Introduction and General Plan of Study

River and watershed management is a debated topic in the American West. While some watersheds might accumulate more water in the future, others will be faced with a net loss of water (Trenbert, 2011). Recent changes in climate and precipitation have endangered this necessary resource for both humans and nature (Pitt et al., 2000; Yang et al., 2020). Shifts in precipitation are accompanying rising global temperatures (Trenberth, 2011), which in turn further alter hydrologic regimes (Barnett et al., 2008). Already, the West is feeling the effects of decreased precipitation, causing ecological and social stress (Anderson and Woosley, 2005). During low-snow years, streams and water ways which typically run full with snowpack from the previous winter may rely on groundwater to fill their banks (Carol et al., 2023). The implications of climatic regime shifts in global temperature and precipitation are disputed, but the effects of these changes are tangible.

A decrease in precipitation, particularly in the form of snow, in the Mountain West, specifically the Rocky Mountains, has serious and cascading effects on its aquatic and terrestrial systems. In addition to warming temperatures, decreased hydrologic discharge may lead to exponential warming of streams due to less energy being needed to heat the water (Isaak et al., 2017). Warmer water temperatures will affect mountain river biomes from the bottom of the food

chain to the top (Johnson, 2024). Warmer temperatures, to an extent, may also increase algal growth (MacDougall, 2024; Butterwick et al., 2005), causing varying effects for each species. Altered temperatures also affect patterns of growth and development in aquatic invertebrates. For example, Harper and Peckarsky (2006) displayed that *Baetis bicaudatus* emergence times occur earlier in warmer streams, showing how temperature directly and significantly affects the phenology and timing of life histories of aquatic invertebrates in the Rocky Mountains. While mayflies are a phenologically flexible order (Peckarsky, 2001), not all organisms have this same biological adaptability. Vertebrates, for example trout, also have shown behavioral and metabolic changes in streams with higher temperatures (Hodge, 2017; Clarke, 2004). Higher temperatures also result in water being less able to store dissolved oxygen (Calvert, 1933), meaning that in warmer streams the altered chemistry of the water may lead to adverse effects on the biota.

Biological and chemical changes, related to warming temperatures, can have particularly strong effects on invertebrate success and life history. Warmer temperatures also can cause shifts in emergence times, having potentially significant effects on trophic patterns and energy convergence throughout stream systems (Harper and Peckarsky, 2006). Earlier mayfly emergence times may  mismatches in timing between predators and prey (Peckarsky et al, 2002), and lower growth compared to mayflies developing in colder streams (Vannote and Sweeney, 1980). Size and developmental changes in mayflies may also affect predator populations, as predators would need to consume greater numbers of mayflies to receive the same energy payoff. A decrease in mayfly body size or population, coupled with predators' increased metabolism, may inhibit a predator's ability to match its metabolic needs (Dodrill et al., 2016). This change in predator-prey interaction may lead to a shift in the population size of both predators and prey. Additionally, mayfly size is a large indicator of fecundity in female mayflies within a particular population (Brittian, 1982). Smaller females produce fewer eggs, thereby reducing future mayfly populations (McPeek and Peckarsky, 1998). Possible implications of warmer streams include decreased growth rates of various species, changes in emergence times and the overall timing of species, nutrient availability, predator-prey dynamics, and in the flow of energy through the trophic pyramid.

The objective of this research is to better understand how different species of mayflies respond to varying stream temperatures. Previous studies (Harper and Peckarsky, 2006) have shown that warmer stream temperatures increase the developmental rates of *Baetis bicaudatus* (Harper and Peckarsky, 2006). The effects of temperature on the families Baetidae and Ephemeridae have also been tested. In both, the body size of both males and females were found to decrease in warmer streams (Sweeney et al., 2018; Giberson and Rosenberg, 1992). Conversely, other studies show that in some streams, temperature can be used to predict mayfly growth and fecundity (Rader and Ward, 1990). Warmer systems speed up metabolic processes of poikilotherms, possibly accelerating mayflies' growth and metabolism (Clarke and Fraser, 2004). It is important to understand how the same phenomena— rising average stream temperature— may affect growth and development of mayfly species differently and to different extents.

In this study, I test whether and how the growth rates and development of different mayfly species respond to warmer water temperatures. I predict that the growth rates of all species of mayflies studied will not be affected by stream temperature. Similarly, I also predict, in agreement with Harper and Peckarsky's study (2006), that though the mayflies will grow faster in warmer water, their average size will be smaller than those in colder streams. Understanding the variation in growth and developmental rates is important for understanding energy and population dynamics within streams, and how these dynamics might change in a future, warmer climate.

## Specific Methodologies

### *Study sites*

Throughout the 2026 summer season, mayfly samples were collected from six sites in and around the Rocky Mountain Biological Laboratory (RMBL). RMBL is located in Gothic, Colorado, at approximately 2,900m in elevation. Of the six sites, three are located on the East River (Avery, Levi, and Oregon Road), and three on Copper Creek (Second Crossing, Judd Falls, and Bridge). Each of these sites vary both in average temperature and elevation. The sites were chosen due to the available long-term data, which provided background information on the temperatures and mayfly species composition at each site. Based on data collected during the summers of 2011-2026, and using HOBO loggers, the historical mean summer temperature at Levi was 11°C, and at Oregon Rd, the coldest site, was 6.9°C. This represented a temperature gradient of ~4°C. Mayflies were collected from each site every 7 to 15 days, where the same protocol was repeated each time. The focal species collected included *Baetis bicaudatus, Baetis billybarrii, Epeorus longimanus, Epeorus deceptivus, Drunella coloradensis, Drunella doddsi*, and *Cinygmula (spp)*. In addition to these species, other mayflies were also collected and measured. This broader collection method allowed for more complete data regarding the overall growth and development patterns of all mayflies present in the East River and Copper Creek.

| Stream | Site | Mean Historical Temperature (C) | Summer Mean Temperature (C) | Average Difference (C) |
|---|---|---|---|---|
| Copper Creek | Second Crossing | 7.3 | 8.66 | + 1.36 |
| Copper Creek | Judd Falls | 7.6 | 9.36 | + 1.76 |
| Copper Creek | Copper Bridge | 8.2 | 9.95 | + 1.75 |
| East River | Levi | 11 | 13.6 | + 2.6 |
| East River | Avery | 10.1 | 12.35 | + 2.25 |
| East River | Oregon Rd | 6.9 | 7.65 | + 0.75 |

*Table 1. Includes site descriptions such as stream, mean historical temperature (since 2011-2025, based on HOBO logger data). The mean stream temperature for this summer is recorded in a separate column (recorded with HOBO loggers). The average temperature difference between all sites was + 1.745°C.*

***Field Protocol***

At each site, water temperature was collected continuously throughout the summer using Hobo data loggers, installed at each site on its first visit. A D-net was used at each site to collect qualitative samples by putting the net in the water and turning over rocks to release mayflies into the net. The net was then emptied into a 20 L liter bucket, filled partially with water. The bucket was then elutriated to separate the organic matter from the inorganic material. The organic material was poured into a 1 mm mesh soil sieve. The contents of the filter were then transferred to a shallow tray where the samples were further examined. This preliminary examination aimed to identify that the quantity and diversity of the samples were enough to provide an accurate picture of the stream, not to actively identify the samples for data. Once the sample size was deemed to provide an adequate number of individuals and species, the contents of the tray was then transferred back into the filter. The sample was washed from the filter into a Whirl-Pack and preserved, using a 70% ethanol solution. The Whirl-Pack was filled with ethanol until it covered the sample. This was done to preserve the contents of the sample for later identification in the lab. Each Whirl-Pack contained a label which had the initials of the collector, and the date and site at which the sample was collected.

***Lab Protocol***

In the lab, the samples were emptied from the Whirl-Pack into a shallow tray, partially filled with water. Forceps were used to pick the mayflies from the tray into a clear glass vial, marked with a label stating the location of the sample, the collector, and the date. The vial was filled partially with a fresh 70% ethanol solution to preserve the samples. The vial then was sealed and put away for storage until time for sorting and measuring the mayflies.

The mayflies collected at each site were identified to the species or genus level using dichotomous keys specific to the RMBL area. From each site, a minimum of 1- individuals and a maximum of 25 individuals were collected and measured of each species from every date. The mayfly's body length was measured to the nearest millimeter, not including the tails. Using this body length, the individual's body mass will be calculated using previously published length-mass relationships (Benke et al. 1999). In addition to measuring size and growth, the developmental stages of the mayflies were tracked based on the development of the wingpads. Mayflies were assigned to one of four developmental stages (Clifford et al., 1979): Stage 1) No wingpads visible; Stage 2) Wingpads visible, and wider than long; Stage 3) Wingpads visible, and longer than wide; or Stage 4) Wingpads totally black. Stage 4 represents mayflies that would have flown from the stream within 24 hours. The main measure of development used was Date of Onset Maturation, which represents the first date Stage 4 individuals were found present at the site. The data collected were used to determine mayfly growth rates, by tracking body length and mass throughout the season. The development of the mayflies was tracked by observing their

wingpad stages, indicating developmental speed, to better understand the relationship between growth and development in streams of differing temperatures.

By collecting growth and developmental data over the course of the summer, I aimed to answer questions pertaining to developmental rates in relation to stream temperature. The winter of 2025-26 was a record low snow year, and the mean water temperature across all streams was 1.75°C warmer than the historical mean (B.L. Peckarsky, unpublished; L.M. Demi, unpublished).

***Analysis***

After data collection and entry was complete, it was entered and combined with the stream temperature data collected using HOBO loggers. The HOBO loggers collected stream temperature data continuously from June 23rd until July 24th. The developmental data collected was primarily used to identify Stage 4 individuals and what the Date of Maturation was for each individual. This allowed data from 2026 to be compared to previous data, and understand the phenologic differences in timing from this year to previous years.

The length (mm) data collected was used to estimate the average body mass of each individual on each sampling date. The body mass (mg) measurements were then imputed into a linear regression model, displayed below, which estimated the mean Instantaneous Growth Rate of each individual between each sampling date (Anthony et al., 2018).

$$\text{IGR} = \ln(\text{final mass}/\text{initial mass})/\text{days}$$

Because there were four sampling dates, there were three sampling interval periods in total. For each plot, a minimum number of individuals at a site were required in order to be included in the figure. This minimum number ranged from 5 to 6 on each date. This was to ensure that the sample size was statistically substantial enough to ensure the presence of a certain individual or trait was not a random effect.

Because I had initially thought that average growth rates could only increase, in the IGR equation, at first I only included positive outcomes, assuming that any negative values were errors (Figure 1). However, to ensure that I was not purposefully ignoring any data, a second graph was made (Figure 2) which took into account the negative growth rates as well, and which included all species recorded instead of only the study species.

**Results**

At all six sites the mean stream temperature during 2026 was warmer than historical averages (Table 1). The minimum change in temperature, from the historic average, was a 0.75 degrees Celsius increase in East River Oregon, while the maximum change in temperature was 2.25 degrees Celsius in East River Avery. The mean stream temperature increase for all streams was 1.75 degrees Celsius.

Stream temperature had no observable relationship to mayfly growth for any species (Figure 1, Figure 2). There was no significant relationship between temperature and growth

across all taxa when negative growth rates were excluded (Figure 1, Table 2). Additionally there was no relationship between growth and temperature across all taxa when negative growth rates were included (Figure 2, Table 3). No significant fluctuation in Body Mass (mg) of mature individuals was found across sites, despite the temperature gradient (Figure 3, Table 4). The lack of correlation between body mass and temperature mirrors the lack of correlation between IGR and temperature discussed previously.

The relationship between Interval Temperature and Date of Maturation is shown for three of the study species (*Baetis bicaudatus*, *Drunella doddsi*, and *Epeorus deceptivus*) (Figure 4, Table 5). For only one of those species, *Epeorus deceptivus*, the relationship between water temperature and date of maturation is negative and statistically significant (Table 5), with temperature accounting for 81% of the variation in maturation. *Baetis bicaudatus*, matured earlier than all other species collected in this study (Figure 5). Despite the shifts in temperature, the Date of Maturation that *Baetis bicaudatus* was first recorded as fully matured in 2026 follows the same line of best fit as the dates observed by Harper and Peckarsky (2006) (Figure 5).

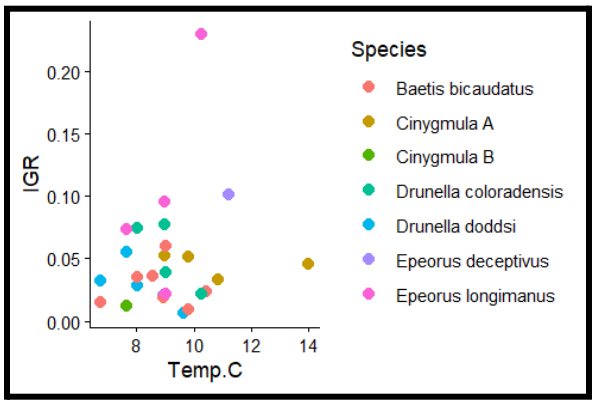


*Figure 1. Species specific Instantaneous Growth Rate (IGR) in relation to Temperature(C) between each sampling date. Individual study species represented by color. Each point represents a sampling date in which at least four individuals were identified. Fewer points means that the species was not found as consistently, or in enough numbers to be represented. Most species occupied a relatively similar portion of the graph. For significance values see Table 2.*

| Species | Intercept | Slope | R^2 | p value |
|---|---|---|---|---|
| Baetis bicaudatus | 0.0305 (0.0663) | -0.0003 (0.0074) | 0.000303 | 0.9705 |
| Cinygmula A | 0.0408 (0.0233) | 0.00027 (0.0023) | 0.004812 | 0.9117 |
| Drunella coloradensis | 0.27060 (0.10868) | -0.02396 (0.01192) | 0.669 | 0.1821 |
| Global | 0.003696 (0.044154) | 0.004909 (0.004634) | 0.0399 | 0.2989 |

*Table 2. Regression equation outputs regarding Instantaneous Growth Rates of study species. Only using positive values, minimum individuals required to be counted (n > 5).*

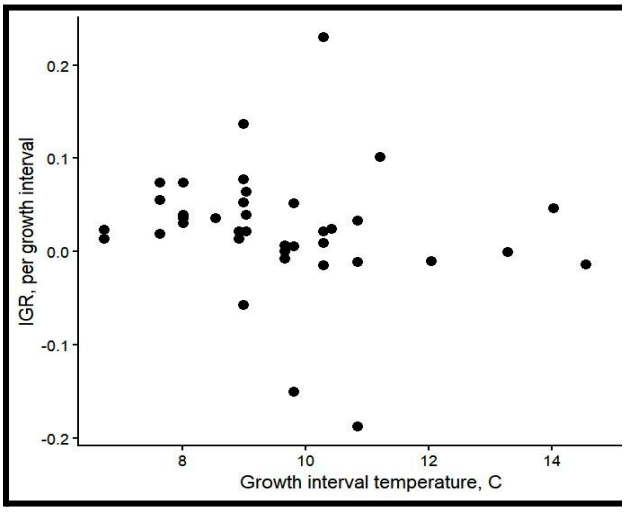


*Figure 2. Global Instantaneous Growth Rate (IGR) across all species in regards to stream temperature. This graph includes negative values (in which using the Body Mass regression equation, mass was found to have been lost as the summer progressed). For significance values see Table 3.*

| Species | Intercept | Slope | R^2 | p value |
|---|---|---|---|---|
| Baetis bicaudatus | 0.072177 (0.095180) | -0.006695 (0.010452) | 0.04879 | 0.5397 |
| Cinygmula A | 0.075167 (0.041245) | -0.003582 (0.003733) | 0.1871 | 0.3916 |
| Drunella doddsi | 0.099525 (0.049977) | -0.008821 (0.005830) | 0.4328 | 0.2275 |
| Epeorus deceptivus | 0.172640 (0.115108) | -0.014291 (0.009443) | 0.3641 | 0.2047 |
| Epeorus longimanus | 0.004758 (0.750667) | 0.006269 (0.081602) | 0.001963 | 0.9436 |
| Global | 0.078678 (0.051421) | -0.005684 (0.005075) | 0.03196 | 0.2697 |

*Table 3. Regression equation outputs regarding Instantaneous Growth Rate of all species recorded. Not separated by species, including negative values, minimum individuals required to be counted (n > 5).*

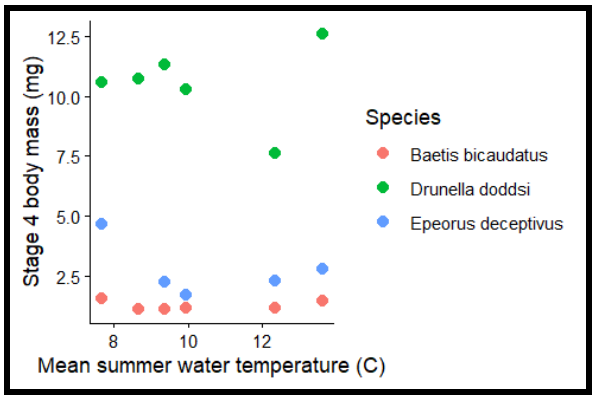


*Figure 3. Species which reached the final stage of development (Stage 4), by the mean temperature of the stream throughout the whole summer, in which that occurred. Minimum number of individuals recorded at Stage 4 to be included was n > 3. Only Baetis bicaudatus, Drunella doddsi, and Epeorus deceptivus met this criterion. (Baetis bicaudatus, p = 0.3437; Drunella doddsi, p = 0.8767; Epeorus deceptivus, p = 0.4158)*

| Species | Intercept | Slope | R^2 | p value |
|---|---|---|---|---|
| Baetis bicaudatus | 2.04248 (0.38191) | -0.03913 (0.03647) | 0.2235 | 0.3437 |
| Drunella doddsi | 11.27059 (3.87183) | -0.6112 (0.36972) | 0.0067897 | 0.8767 |
| Epeorus deceptivus | 5.2203 (2.6718) | -0.2330 (0.2475) | 0.2281 | 0.4158 |

*Table 4. Stage 4 body mass (mg) in relation to stream temperature. Only study species which were observed at > 4 sites represented. Species represented by color.*

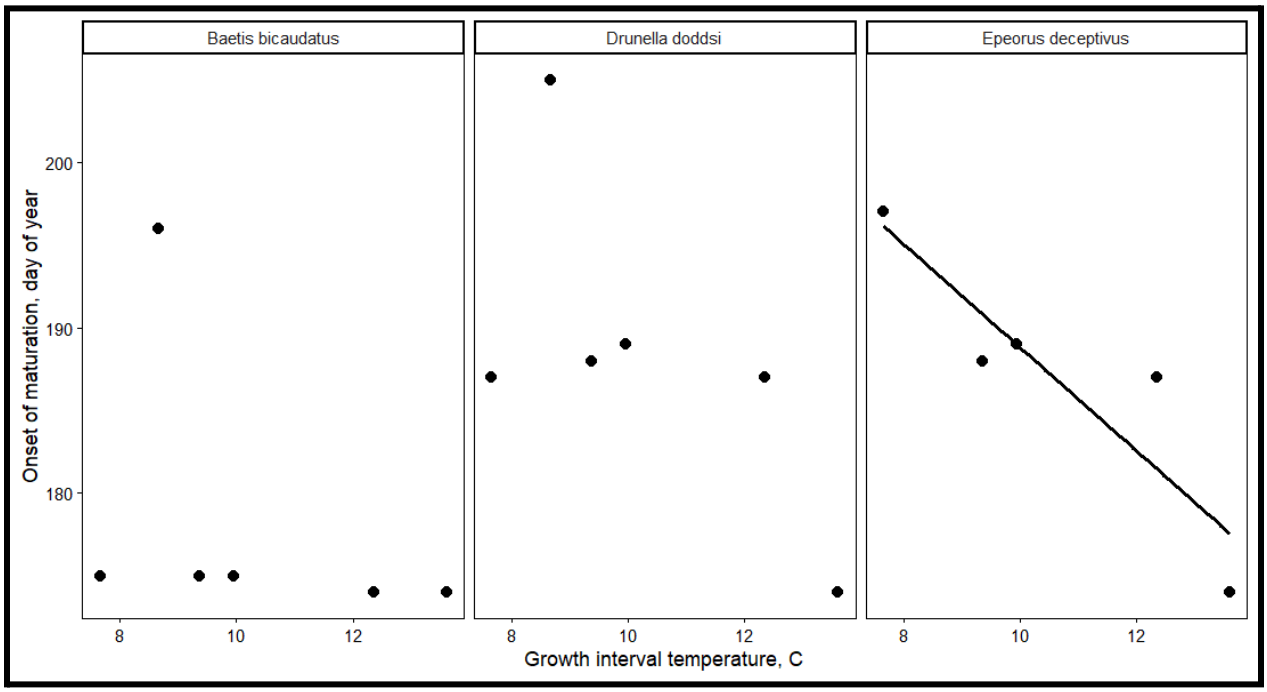

*Figure 4. Date in which site was first recorded as having the minimum number of Stage 4 individuals. Minimum number of individuals to be recorded was n > 4. Three species met this criterion. The DOY of first occurrence is plotted in relation to the mean stream temperature between each sampling interval. (Baetis bicaudatus, p = 0.4412 , $R^2$ = 0.1543; Drunella doddsi, p = 0.4328 , $R^2$ = 0.1556; Epeorus deceptivus, p = 0.03716 , $R^2$ = 0.8107)*

| Species | Intercept | Slope | R^2 | p value |
|---|---|---|---|---|
| Drunella doddsi | 217.690 (17.145) | -2.860 (1.637) | 0.4328 | 0.1556 |
| Epeorus deceptivus | 220.1027 (9.4192) | -3.1273 (0.8723) | 0.8107 | 0.03716 |
| Baetis bicaudatus | 193.701 (18.555) | -1.513 (1.772) | 0.1543 | 0.4412 |

*Table 5. Date of Onset Maturation of study species which were observed at >4 sites. Temperature represents mean stream temperature between sampling intervals.*

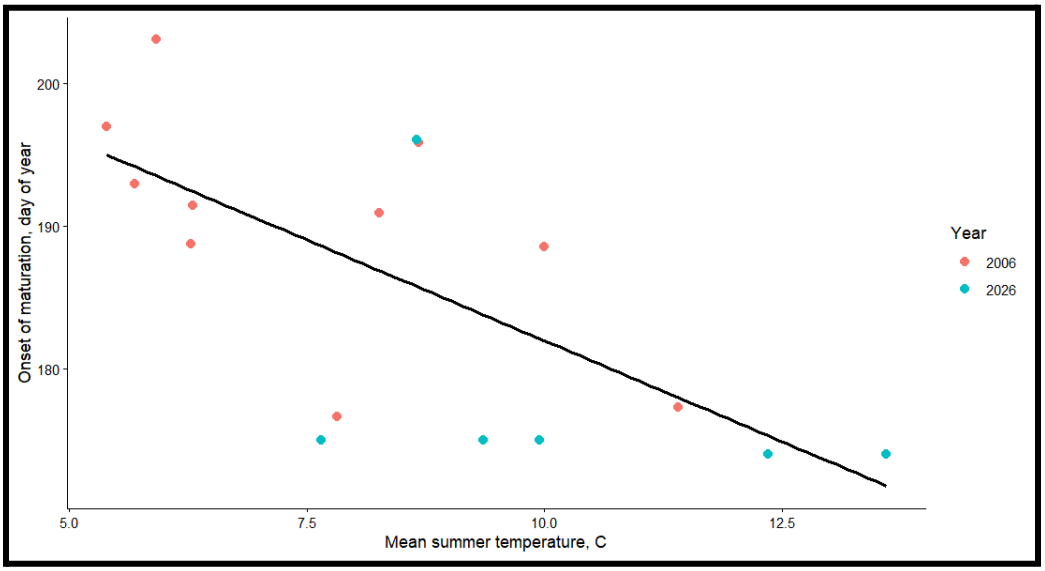


*Figure 5. This graph shows the data from Harper and Peckarsky (2006) overlaid with the data collected from this summer (2026), of Baetis bicaudatus only. 2006 data in red, 2026 data in blue. Notice similarities in temperature patterns despite having 20 years of separation between the sampling. (p = 0.002839)*

## Discussion

This research tested the relationship between mayfly growth and development, and stream temperature, and sought to understand what, if any, relationship existed between the factors. I specifically tested two hypotheses: whether water temperature affected growth or development independently.

The first hypothesis predicted that the growth rates of all taxa of mayfly would not be significantly affected by stream temperature. There was no significant relationship between growth and temperature in any of the study species (Figure 1). This corroborates the findings of Harper and Peckarsky (2006), in which *Baetis bicaudatus* growth was found to have no relationship with temperature. This result remains consistent even as temperatures rise to above the 2006 average. One possible explanation for the non-significant results is that metabolism was sped up by the temperature, but the mayfly populations were able to compensate for this by consuming more food, and their growth and body mass was left relatively unchanged, so that the increased metabolism had no effect (Brittian, 1982).

Temperature being found to have no relationship with growth may be due to highly regulated metabolic processes across stream temperatures. Brittian (1982) discusses the regulation of oxygen consumption and respiration, as a measure of metabolism, and points out that stream flow as opposed to stream temperature might be a better predictor of metabolism. In this case, development could be predicted by temperature, and growth could be predicted by flow. A study by Rader and Ward (1990) found that in *Drunella grandis* and *Ephemerella infrequens*, two species present in this study, growth was continuous between 2°C and 10°C, but growth slowed or stopped when it exceeded that maximum. This may explain a lack of growth in certain streams which exceeded 10°C. It is also possible that these mayflies are adapted to grow best within a different range of temperatures, perhaps explaining why temperature had no effect even within that temperature range. A longer sampling period, or a more in depth study focusing on growth, could help to clarify some of these lingering questions as to what determines mayfly growth rates.

The second hypothesis focused specifically on mayfly development in relation to stream temperature. For the species *Baetis bicaudatus,* temperature was previously shown to have a significant relationship with development , with individuals maturing faster in warmer water(Harper and Peckarsky, 2006). However, I sought to better understand if this relationship would be observed across multiple species, and whether the magnitude of the effect changed depending on the species. Figure 5 shows the relationship between mean stream temperature, between sampling intervals, to the Date of Onset Maturation. These species included *Baetis bicaudatus*, *Drunella doddsi,* and *Epeorus deceptivus*. A significant relationship was found regarding *Epeorus deceptivus* development and stream temperature. *Epeorus deceptivus* were found to exhibit a similar relationship to *Baetis bicaudatus* emergence, with their Dates of Maturation being earliest in warmer streams and latest in colder streams. This result is consistent with results from Harper and Peckarsky (2006). *Drunella doddsi* also displayed similar patterns to *Epeorus deceptivus*, although the relationship was not significant. Had the sampling season been longer, or the sampling intervals more frequent, it is possible that this relationship too would have been significant.

In all figures in which *Baetis bicaudatus* were identified to species (Figures 1, 4, 5) *Baetis* were found at Stage 4 at all sites simultaneously. Based on the trends published in Harper and Peckarsky (2006), and echoed in *Drunella doddsi* and *Epeorus deceptivus*, the pattern of

*Baetis* is likely not due to a biological reason, but an error in sampling due to warming streams. At the warmest site, such as Levi, *Baetis bicaudatus* had already emerged and were flying, so were largely missing from the site by the time of first sampling. For the coldest sites, such as Oregon and Second Crossing, the *Baetis* had not yet left the streams totally, though they were already beginning to mature. Because of the warmer stream temperatures this summer that *Baetis bicaudatus* emerged earlier than we were able to record. The points plotted on Figures 4 and 5 represent the first date of emergence for the specified species. However, in the case of *Baetis bicaudatus*, it is more likely that the data recorded represented the end of the maturation of the *Baetis* nymphs.

Figures 1 and 7 further suggest that *Baetis bicaudatus* emerged too early to be accurately recorded this year. The same grouping of points is found at the bottom of Figure 5 as is found in the *Baetis bicaudatus* panel in Figure 2 and Figure 5. Had the true DOY of first maturation of *Baetis bicaudatus* been recorded, the line of best fit likely would have had a more negative slope, showing the adjustment of the species to the warmer stream temperatures of this year. The changes in water temperature illustrated in Table 1 could affect mayfly development in a number of ways. Firstly, mayfly competitiveness may decrease due to a smaller average body size in mature mayflies. While mayflies develop faster in warmer temperatures, there is no evidence provided to suggest a corresponding increase in growth rate; for this reason, mayflies will be fully matured at smaller sizes. Smaller body size may impact their fitness in evading predators. Female mayfly body size is strongly and positively related to their fecundity (McPeek & Peckarsky, 1998), it may still alter their fitness and ability to compete for common resources or escape predators (Peckarsky et al., 2001).

Secondly, increased average water temperature may cause a phenological mismatch between stream predators and their prey (Leathers et al., 2024). Earlier mayfly emergence among certain species, and not others, may cause certain mismatches in community timing. Certain niches therefore may become unfulfilled, leaving certain ecosystem functions unfulfilled, or cause increased competition in other niches. Other than *Baetis bicaudatus* and *Epeorus deceptivus*, this study was not able to conclude the specific differences as to the extent in which each species' development is affected by temperature. Different mayfly species may be impacted by temperature at different degrees, which has the potential to alter community diversity, timing, and cause unforeseen downstream ecological changes.

Water and aquatic ecosystems management is extremely important, especially in the American Mountain West, where the availability of water as a resource becomes increasingly scarce. The management of these systems is then all the more important for law-makers and citizens alike to value and prioritize. Because mayflies typically need clean and clear water to thrive at the community level, they can generally be considered an indicator species of stream health (Brittian, 1982; Tzilkowski and Stauffer, 2011). Their ecological successes and difficulties should be understood and utilized as a way to better understand complex stream systems. Mayflies are also important prey for trout and other fish (Tippets and Moyle, 1978); these

predators attract economic income by way of outdoor recreation fees and permits. Protecting and understanding mayfly phenology has economic benefits too, then, as well as ecologic ones.

In summary, water temperature significantly influences nymphal development across multiple mayfly species. The rapid warming of stream temperatures is contributed to by a lack of winter snowpack and snowmelt, a lack of summer rain, and increased climatic temperatures, and may worsen in the future, thus further impacting mayfly fitness and timing. Mayfly growth does not show any significant effect based on water temperature according to the data collected. This mismatch in temperature influence may cause a decrease in mayfly fitness, as well as alter community and predator-prey dynamics, as stream temperatures are predicted to rise in the future.

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