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Life histories and production of three Rocky Mountain aquatic insects along an elevation-driven temperature gradient

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Abstract   Although temperature is known to influence individual traits such as growth, body size, and fecundity, few studies have examined how these relationships influence population-level secondary production in natural settings. We quantified life history traits and production of three dominant aquatic insects (Ephemeroptera: *Ephemerella infrequens*; *Drunella doddsii*; Trichoptera: *Hydropsyche cockerelli*) along an elevation-driven thermal gradient in the northern Rockies. We predicted that production would be highest at sites where temperature regimes lead to the largest terminal body size, individual fecundity, and reproductive potential (i.e., eggs per female x abundance of mature nymphs or larvae). In general, we found that temperature had idiosyncratic effects on life history traits of the study taxa, with no consistent effect of temperature on production. Although growth rates were generally highest during the warm months, growth did not consistently covary with temperature among sites along the elevation gradient. Terminal body size also differed among sites and was inconsistently related to mean temperature and reproductive potential. One of three taxa, *D. doddsii*, showed patterns entirely consistent with predictions, including smallest body size, reproductive potential, and secondary production at the warmest, low-elevation sites. Our findings suggest that connections among temperature regime, life history characteristics, and secondary production may not be straightforward, and are likely influenced by characteristics unmeasured in our study, including factors that influence survivorship throughout the larval phase, as well as adult mating or oviposition success. Such additional information will enrich our understanding of thermal effects on aquatic insects, and may contribute to predicting how these taxa may respond to ongoing changes in climate.

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Introduction

Temperature is an important environmental variable that influences the ecology and evolution of aquatic insects (e.g., Vannote & Sweeney, 1980; Ward & Stanford, 1982; Ward, 1992). Stream and river temperature regimes vary widely across latitudinal and elevation gradients (Webb, 1996), and anthropogenic factors such as greenhouse gas emissions and land-use change are modifying these patterns globally (Kaushal et al., 2010; IPCC 2013). These natural and novel thermal gradients have the potential to drive variation in species life history traits, population dynamics, and ecosystem-level productivity (Angilletta & Angilletta, 2009; Nelson et al., 2017a), and thus provide a useful context for understanding how ongoing changes in temperature shape aquatic insect communities (e.g., Jacobsen et al., 1997).

Within heterogeneous thermal landscapes, the distribution of insect taxa may be defined by physiological performance attributes, which broadly influence the geographic range where species may survive and persist (Sinclair et al., 2012). Although geographic distributions of many stream insect taxa are relatively large, sometimes spanning entire continental regions (e.g., Allen & Edmunds, 1965; Vinson & Hawkins, 2003), thermal variation within these ranges can lead to plasticity in life history attributes that may influence population abundance. For instance, responses of growth, respiration, and development time to thermal variation can all lead to shifts in adult body size and individual fecundity (Sweeney, 1978, 1984; Vannote & Sweeney, 1980). Yet, how such differences translate to population-level characteristics such as abundance and secondary production is rarely assessed.

A few general hypotheses have been proposed for understanding the influence of temperature on the life histories of insects. The 'Thermal Equilibrium Hypothesis' (TEH), originally proposed for aquatic insects, predicts that species have 'optimum' thermal regimes, above and below which population density should decline (Sweeney & Vannote, 1978; Vannote & Sweeney, 1980). At super-optimal temperatures, where thermal energy (i.e., growing degree-days) accumulates rapidly, a large amount of energy is required for maintenance components of metabolism and therefore diverted away from growth and reproduction (Sweeney & Vannote, 1978; Sweeney et al.,

2018). Under this scenario, individuals are predicted to reach maturity rapidly and emerge at a smaller size with lower fecundity (Stearns, 1992; Honěk, 1993). In contrast, at sub-optimal temperatures less energy is allocated to respiration, growth rates are reduced, and development time is protracted. Under these conditions, adults are predicted to achieve intermediate body sizes, but energy allocated to reproduction is reduced and the extended maturation time may limit the number of generations possible during the growing period (Vannote & Sweeney, 1980). Thus, based on the TEH, natural selection should favor life history strategies between these two extremes—those with intermediate generation times, large terminal body sizes, and high fecundity to offset any losses to mortality.

A complementary hypothesis, the Temperature Size Rule (TSR; Atkinson, 1994; Atkinson & Sibly, 1996; also referred to as 'Bergmann's Rule' in natural environments), predicts that body size, and therefore other measures of success such as fecundity and population density (Buckley et al., 2008), should be maximized at the cold end of the species' thermal tolerance range instead of an intermediate optimum temperature (Sweeney et al., 2018). Theoretical and empirical work suggest that this pattern should manifest if the rate of development (i.e., maturation of adult tissue) increases faster than the rate of growth with warmer temperatures (Forster & Hirst 2012; Sweeney et al., 2018). Although there is considerable support for this hypothesis, a general explanation for what causes these temperature-size patterns is still somewhat elusive (Angilletta & Dunham, 2003; Angilletta et al., 2004). In addition, regardless of whether life history attributes of aquatic insects match predictions of the TSR—or the TEH—it is still unclear whether landscape-scale variation in individual body size at maturity and fecundity translate into spatial differences in population abundance or secondary production.

Climate change is influencing freshwater ecosystems globally (Woodward et al., 2010b), with significant effects on water temperature (Adrian et al., 2009; Kaushal et al., 2010; Isaak et al., 2012). Streams in the North American Rocky Mountains are warming faster than most and are expected to warm by ~1 °C per decade in the coming century (Isaak et al., 2012; Whitlock et al., 2017). Even small increases in temperature (~1–3 °C) are ecologically relevant and have

been shown to influence aquatic insect growth rates, respiration, body size, lifespan, and gender ratios (Sweeney et al., 1986, 1992; Cogo et al., 2020), with the potential for large effects on fecundity (Sweeney et al., 2018). Consequently, warming is likely to influence the composition and productivity of stream invertebrate communities (Durance & Ormerod 2007; Hering et al., 2009) by modifying some of these life history traits. Detailed observations of populations across natural thermal gradients can provide a valuable approach for understanding how populations and communities may respond to subtle changes in temperature (e.g., Jacobsen et al., 1997; Shah et al., 2017). Such studies also complement the much larger laboratory-based literature that benefits from control and replication, but lacks ecological realism.

Here, we examined how natural variation in stream temperature, driven by elevation, influenced the life history and ecology of three common and abundant Rocky Mountain aquatic insect taxa. We asked: (1) how does the thermal regime vary along a natural elevation gradient; (2) how does this variation influence body size phenology, growth rates, terminal body size, and reproductive potential?; and (3) does variation in terminal body size or reproductive potential translate to differences in population-level abundance, biomass, and secondary production? We further qualitatively assessed whether study taxa maximized their terminal body size, reproductive potential, and secondary production at intermediate temperatures (in alignment with the TEH) or at colder temperatures within their thermal range (in alignment with the TSR).

Methods

Study area

Our study was conducted over a full annual cycle from March 2017 to March 2018 at multiple sites along the west fork of the Gallatin River in southwest Montana, U.S.A (Fig. 1). The Gallatin River Watershed has a catchment area of 3,480 km^2 and ranges in elevation from 1,225 m to 3,440 m (Gustafson, 1990). The river originates in Wyoming in the northwest corner of Yellowstone National Park, flows to the north, and culminates at the headwaters of the Missouri River near Three Forks, Montana.

This watershed experiences four distinct seasons. Maximum snowpack occurs during winter and melts through the spring, typically leading to peak stream-flow during June. Following snowmelt, the watershed experiences a relatively dry summer and autumn (Farnes & Shafer, 1972), with low flows persisting through the winter. Boulders, cobble, and gravel are the dominant substrate types. Bryophytes are common in the tributaries and the upper Gallatin River, but not farther downstream where bed movement and scouring are more frequent (Gustafson, 1990).

Most of the landscape upstream of the Gallatin River valley contains montane coniferous forest. The upper Gallatin, near the western entrance of Yellowstone National Park, meanders through an open valley lined by exposed cliffs on the east side, and forested hills to the west. The river then flows through the relatively narrow Gallatin Canyon where it is shaded by vegetation and steep hillslopes, and then emerges into an open alluvial valley near the town of Gallatin Gateway. Here, cottonwoods and other deciduous vegetation dominate the riparian zone, and a greater amount of incident light reaches the river. Land cover in the valley is a mixture of suburban/urban development, grasslands, and agricultural lands. Although the Gallatin River is unregulated, significant irrigated agriculture and water withdrawals lead to reduced stream flows and warming in the summer (Poole & Berman, 2001; Whitlock et al., 2017).

Five sampling locations were established nearly equidistant from one another along the elevation gradient, beginning near the western boundary of Yellowstone National Park (site 1) and terminating downstream near Manhattan, Montana (Fig. 1; site 5). Sites 2 and 3 were located in the narrow section of Gallatin Canyon and site 4 was located in the alluvial valley. The difference in elevation between the highest and the lowest site was 730 m, and the elevation difference between sites averaged ~ 180 m (Table 1). Sites were chosen to encompass most of the variation in thermal regime along the mainstem of the Gallatin River continuum.

Stream temperature

We quantified temperature at a two-hour timestep throughout the study by deploying a pair of precision-checked ONSET HOBO temperature loggers at each site. These loggers were fixed to large boulders,

Fig. 1 (**A**) Map of project study sites along the mainstem of the Gallatin River in Gallatin County, Montana, and drawings (credit: J. McCarty) of the study taxa: *Ephemerella infequens* (**B**), *Drunella doddsii* (**C**), and *Hydropsyche cockerelli* (**D**). The river flows from south to north; site 1 is the highest elevation site (2017 m) and site 5 is the lowest elevation site (1287 m)
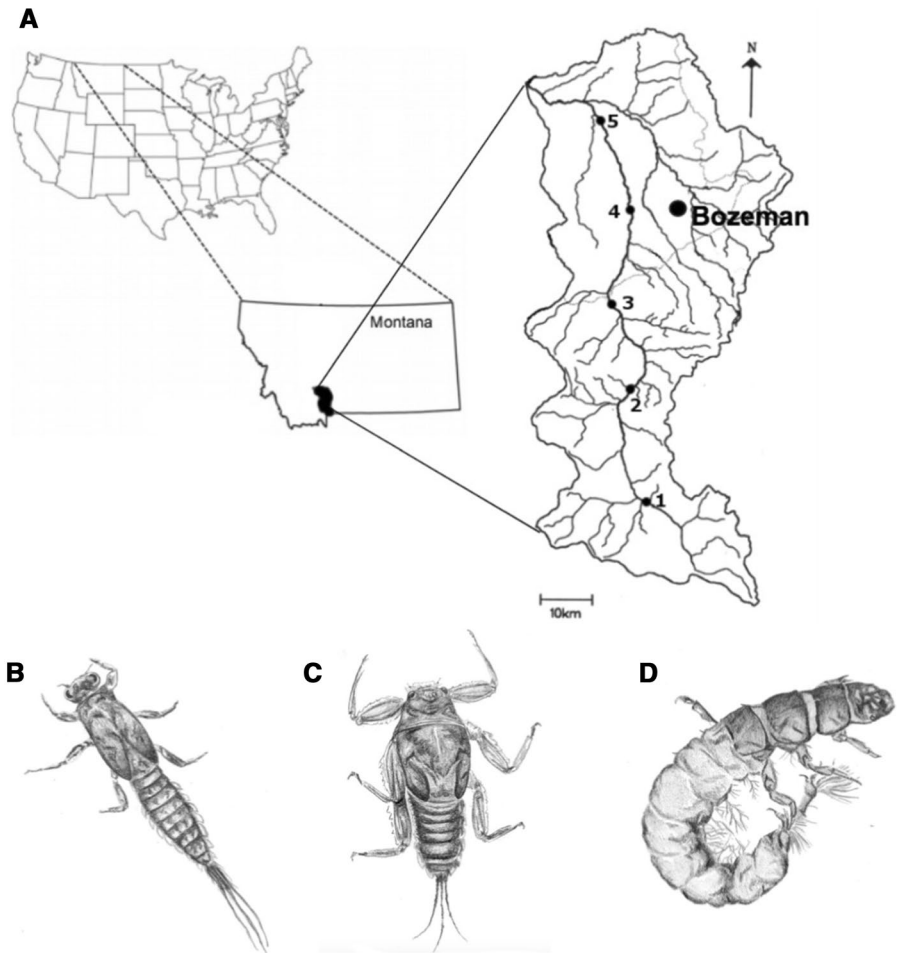
bedrock, or submerged bridge pilings near the thalweg using climbing bolt hangers and protective casing made of PVC (Fogg et al., 2020). Thermal patterns recorded by the two loggers at each site were nearly identical and therefore averaged. To examine seasonal temperature patterns and difference in these patterns among sites, annual thermographs were binned into winter, spring–summer, and summer-autumn periods. These periods have been applied in previous studies (e.g., Rader & Ward, 1990) and were chosen to correspond to three major life-cycle periods for the study taxa: (1) winter: slow development and growth between November 1 and March 19 when temperatures remain near or below 5 °C at all sites; (2) spring–summer: rapid growth and development between mid-March and July 20 that occurs prior to the emergence of adults; and (3) summer-autumn: growth of newly hatched early instars between July

21 and October 31 that represents changes in phenology prior to the winter period of reduced metabolism. Growing degree-days were calculated for all study species as both the annual and seasonal cumulative heat above 0 °C, which we considered the common developmental threshold (Ephemeroptera: Clifford et al., 1973; Trichoptera: Ross, 1967; Wiggins, 1996).

Study taxa

Lifehistory traits and population characteristics of three species (Ephemeroptera: *Ephemerella infrequens, Drunella doddsii;* Trichoptera: *Hydropsyche cockerelli*; Fig. 1) were quantified at each of the five sites for the one-year study period. These species were chosen because of their high relative abundance across the thermal gradient (see Gustafson, 1990). In addition, these species are univoltine

Table 1 Location, elevation, growing degree-days (GDD), and mean daily temperature (°C) at study sites. Tukey's HSD results, as lower-case letters, show differences among sites within each column

Site	Latitude	Longitude	Elevation (m)	Total annual GDD	°C	Summer–Autumn GDD	°C	Winter GDD	°C	Spring–Summer GDD	°C
1	45.06506	− 111.18245	2,017	2,220 a	5.7 a	1,194 a	9.0 a	343 a	2.9 a	682 a,b	7.2 a,b
2	45.28152	− 111.22528	1,816	2,507 b	6.5 b	1,386 b	10.5 b	391 b	3.2 b	726 b,c	7.8 b,c
3	45.47722	− 111.26953	1,585	2,291 a	6.2 a	1,376 b	9.7 b	157 c	1.4 c	758 c	8.2 c
4	45.67308	− 111.21047	1,430	2,590 b	6.6 b	1,560 c	12.0 c	151 c	1.4 c	879 d	9.4 d
5	45.86015	− 111.29751	1,287	2,939 d	8.7 d	1,784 d	13.6 d	142 d	1.3 d	1,013 e	10.8 e

and have relatively synchronous cohorts, enabling us to characterize temporal life history patterns using monthly field sampling (e.g., Hauer and Stanford 1982). Although these species do not clearly group into functional feeding groups (e.g., Hawkins 1985), *E. infrequens* is typically categorized as a collector/gatherer, *D. doddsii* an omnivore, and *H. cockerelli* a collector/filter feeder (Gustafson, 1990; Merritt et al., 2019).

Benthic sampling

The benthic invertebrate community was sampled quantitatively once per month with five oversized Surber samples (0.75 m X 0.75 m; 250 micron mesh) from a single riffle at each site, representing a total of 2.81 m^2 of sampled benthic habitat. Individual samples were selected to encompass variation in local microhabitat, pooled, and preserved in ethanol (70%) to provide a single representative sample on each date. Samples from each site-date combination were pooled to reduce the time necessary to remove invertebrates in the laboratory. Sample pooling precluded any estimate of spatial variability within a given sampling date and limited our ability to statistically compare population-level metrics (density, biomass, production) among sites. On a few dates and sites (May 2017: sites 3 and 4; December 2017: all sites; June 2018: sites 3–5), high stream flows or ice cover did not allow for safe sample collection, but missing samples represented less than 7% of the total. It should be noted that our annual sampling schedule encompassed the end of one population cohort (March– June 2017) and the beginning of another (July 2017–March 2018) for all three species; although we examine general phenological and life history patterns below, the transition from June to July 2017 represents a change from one generation to the next.

In the laboratory, benthic samples were separated into fine (0.25–1 mm) and coarse (> 1.0 mm) fractions with stacked metal sieves. Focal taxa were removed from these samples in the laboratory with a dissecting microscope at 10X- 40X magnification. Smaller samples were picked completely, while others were typically subsampled to 1/8th with a Folsom Plankton Splitter until at least 100 individuals per sample were enumerated. Density (number/m^2) and biomass (mg ash-free dry mass [AFDM]/m^2) were quantified for each taxon, though not all

taxa were present at all sites during each collection month. Lengths of individuals were measured to the nearest 1 mm, and individual mass (mg AFDM) of each mm size class was estimated using previously established length-mass equations (Benke et al., 1999). Biomass of each taxon on a given date was quantified by multiplying density in each 1-mm size category by individual mass, and summing across size categories.

Lengths of specimens were measured to the nearest 0.1 mm with an ocular micrometer. Ephemerellids were measured from the anterior end of the head to posterior of the abdomen, and hydropsychids were measured from the anterior end of the head to the beginning of the anal proleg. The unpicked sample portion was further examined to augment the number of individuals included in size frequency distributions, aiming for at least 50 individuals per date. Additional individuals were also removed to augment our estimates of terminal body size (see below).

Growth rates and secondary production

Mean daily growth rates (g, d^{-1}) were calculated between each sampling date and for each season using differences in body size distributions between start and end dates as: $g = (ln(M_f)-ln(M_i))/d$, where M_f is average final body mass of the cohort, M_i is average initial body mass of the cohort, and d is the number of days in the time interval. Mass measurements were ln-transformed because individuals typically grow exponentially. It was not possible to calculate growth rates in instances when individuals were not found in start- or end-date samples.

Population-level secondary production was estimated for each species at each site using the instantaneous growth method (Benke, 1984; Benke & Huryn, 2017). Secondary production between sampling dates (i.e., interval production (P_{int}; mg AFDM m^{-2} interval^{-1}) was estimated as $P_{int} = \Sigma_i$ ($[B_i(t+1)+B_i(t)]/2$) x g x d, where i = number of 1-mm size classes, $B_i(t+1)$ = mean larval biomass at sampling interval $t+1$, $B_i(t)$ = mean larval biomass at sampling interval t, g = instantaneous growth rate (d^{-1}) calculated from size-frequency data, and d = number of days in the interval. Annual secondary production for each population was estimated as the sum of all interval production values.

Terminal body size and reproductive potential

We sought to quantify the influence of stream temperature on terminal body size and reproductive potential of *E. infrequens* and *D. doddsii*. We did not do so for *H. cockerelli* because of difficulty quantifying egg numbers from late-stage larvae or pupae. Terminal body size was measured as the mass of individuals at the black wing-pad stage of the last larval instar just prior to emergence. Total length of these individuals was measured and converted to mass (AFDM) using length-mass relationships described above (Benke et al., 1999). To calculate reproductive potential, black wing-pad stage nymphs of *E. infrequens* and *D. doddsii* were separated from benthic samples or collected at each site just prior to or during the emergence periods (twice weekly: June–July 2017, Gustafson 1990), measured, and stored in 70% ethanol. Although *D. doddsii* were collected intermittently at Site 4, no black wing-pad stage nymphs were found. Eggs were quantified by dissecting gravid females and carefully flushing eggs onto a petri dish. Eggs were then dispersed across the petri dish to avoid overlap, digitally imaged at 40X magnification, and counted using ImageJ processing software (Abramoff et al., 2004). Female body lengths were converted to AFDM using length-mass relationships described above (Benke et al., 1999), and mass was plotted against the number of eggs to provide species-specific general linear models relating body size to egg number (Supplementary Fig. 3). We then estimated reproductive potential during the emergence phase by multiplying half of June larval densities (assuming a 1:1 male to female ratio; Sweeney et al., 2018) by the predicted number of eggs (based on mass-egg number relationships; Supplementary Fig. 3) for each species at each site. Our estimate of reproductive potential should be interpreted with caution because (a) there is significant error in the body size-egg number relationships, (b) density sampled in June is a rough proxy for the final number of adult females emerging, and (c) body size of emerging adults may change throughout the emergence period (Peckarsky et al. 2001). Despite these limitations, our estimates of reproductive potential provided a relative metric that could be compared among sites.

Food quantity and quality

Differences in food quantity or quality, along with temperature, have the potential to influence invertebrate life history traits and population-level metrics (Sweeney et al., 1986; Johnson et al., 2003; Cross et al., 2005). We thus quantified aspects of seston and benthic biofilm quarterly during routine benthic sampling. Seston concentrations were measured by submerging a seston net (80 μm mesh size; 12.7 cm diameter) near the upstream boundary of the benthic sampling area for a known time interval (typically five to ten minutes). Flow velocity was measured directly upstream of the net with a Marsh McBirney electromagnetic flow meter following sample collection, and these values were multiplied by the net area to calculate seston flux on a per-liter basis (Hauer & Lamberti, 2017). A volumetric subsample of the seston was then collected onto a glass microfiber filter (Whatman GF/F, 0.7 μm pore size) in the field, and chlorophyll *a* content was subsequently ethanol-extracted in the laboratory and quantified using the Welschmeyer non-acidification method on a Turner Trilogy fluorometer (Turner Designs, San Jose, California). The remainder of the sample was dried, weighed, incinerated at 450 °C, and reweighed in the laboratory to quantify total organic matter (as mg AFDM m^3). These values were used to estimate the quantity (AFDM) and quality of food resources (using AFDM:chlorophyll *a* ratios as a proxy; Biggs and Close 1989, Feio et al., 2010) for drift-feeding hydropsychids. High values of AFDM:chlorophyll *a* of seston were interpreted as relatively low-quality seston with a high contribution of detritus.

To estimate food quantity and quality for the collector-gatherer and omnivorous ephemerellid species, epilithic biofilm was scraped quarterly from benthic cobbles (10 cm^2 area; n = 10 per site) and pooled, totaling 100 cm^2 of rock surface area sampled at each site on each date. Samples were returned to the laboratory and analyzed in a similar fashion as above to examine inter-site variation in food quantity (AFDM) and quality (AFDM:chlorophyll *a*).

Statistical analysis

To examine among-site differences in temperature, we used a repeated-measures mixed effects ANOVA (rmANOVA), accounting for the fixed effect of season, and the random effect of mean daily temperature. If substantial effects were detected (i.e., $P < 0.05$), *post-hoc* Tukey's Honestly Significant Difference (HSD) multiple comparisons were used to determine differences among sites, as well as differences within sites among seasons (Gotelli & Ellison, 2012).

Variation associated with seasonal growth rates was estimated using a bootstrapping approach (Huryn, 1996). Body size distributions at each site were randomly resampled 1,000 times between sampling intervals and used to calculate 1,000 estimates of instantaneous growth rate. These estimates were then used to calculate median growth rates, interquartile ranges (IQR, range defined by the 25th and 75th percentiles), and 95% confidence intervals. Differences in growth rate among sites were assessed by comparing overlap of the interquartile range. Among-site differences in body size of mature nymphs or larvae (hereafter 'terminal body size') were assessed using one-way ANOVA on all individuals from each site, followed by a *post-hoc* Tukey's HSD. Ordinary least squares regression was used to quantify relationships between female terminal body size and number of eggs per individual. One-way ANOVA was used to examine differences in reproductive potential among sites. To achieve normality, body size data were square-root or log$_{10}$-transformed where necessary prior to analysis. Inter-site differences in mean annual density, biomass, secondary production, and production to biomass ratios (P:B) were compared qualitatively due to pooling of samples for each site-date combination. Among-site variation in biofilm, seston, and autotrophic index were examined across quarterly collections using one-way ANOVA and post-hoc Tukey's HSD (Gotelli & Ellison, 2012). Pearson correlation coefficients were used to examine relationships between reproductive potential and production, body size, and average number of eggs per female. All statistical analyses were performed in R 3.5.1 (R Core Team, 2018).

Results

Discharge and temperature

Discharge and temperature regimes of the Gallatin River followed a pattern expected for Rocky

Mountain rivers, with peak discharge occurring in the spring-early summer during snowmelt, and peak temperatures following snowmelt in the summer months (Fig. 2). Temperatures were warmest in summer and at or near freezing in the winter months, with daily mean temperature generally decreasing in the autumn

Fig. 2 **A** Discharge (m³/s) measured by USGS near site 4 (Gage 10109000). **B** Mean daily temperature at the study sites. Vertical dashed lines delimit seasons. **C** Summarized daily temperatures among sites and seasons. Boxes show the median and 25th-to 75th-percentile range. Whiskers extend to the 2.5th and 97.5th percentile, dots represent data outside of this range
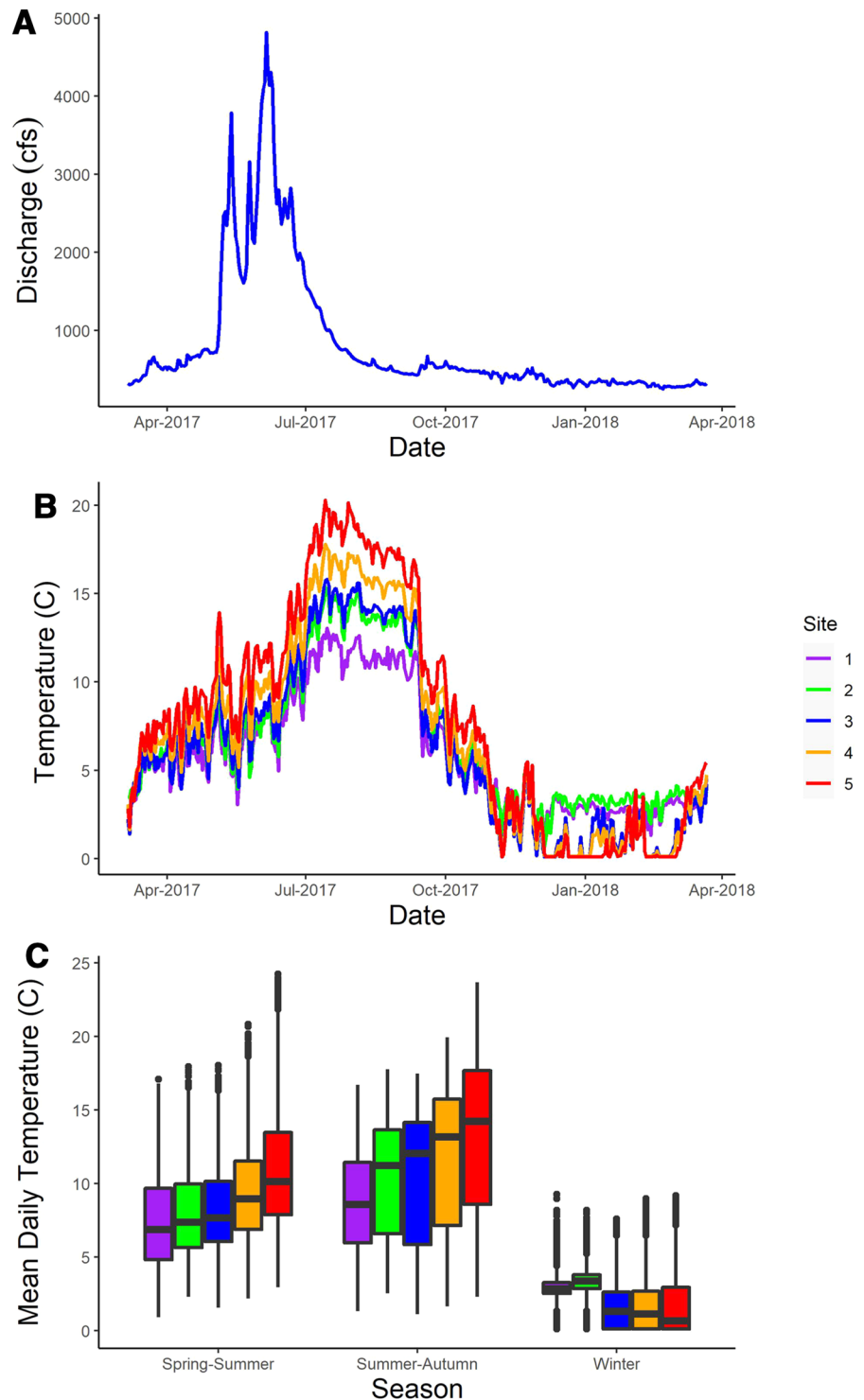
and increasing in the spring at all sites (Fig. 2B). Mean temperature differed by at least 3 °C between the highest and lowest elevation sites (Sites 1 and 5, respectively; Fig. 2B, Table 1) and increased progressively from upstream to downstream, with the exception of the mid-elevation site within Gallatin Canyon (site 3), which was slightly cooler than sites directly upstream or downstream (Table 1). Mean annual temperature was significantly different among sites (repeated measures [rm] ANOVA, $F_{(1,4)} = 741.98$, $P < 0.0001$), but sites 1 and 3, and sites 2 and 4 were similar at this annual scale (Table 1; Tukey HSD).

Mean daily temperatures differed among seasons (rmANOVA, $F_{(1,4)} = 324.57$, $P < 0.001$) and among sites within each season (rmANOVA, $F_{(1,4)} = 118.61$, $P < 0.001$). Temperatures at each site were highest in the summer-autumn and lowest in winter (Fig. 2C; Tukey HSD: $P < 0.05$). Spring–summer temperatures

were also warmer than winter, but cooler than summer-autumn (Fig. 2C; Table 1; Tukey HSD: $P < 0.05$). Mean daily temperature generally decreased with increasing elevation in summer-autumn and spring–summer, but opposite was true in winter, when mean daily temperatures were greatest at the highest elevation sites and near freezing at the lowest elevation sites (Fig. 2C). Among-site variation in mean daily temperature was greatest in the summer-autumn (up to 4.7 **°C**) and lowest in the winter (up to 1.9 **°C**; Fig. 2C).

Differences in temperature among sites were reflected in patterns of growing degree-day accumulation over time. Annual growing degree-days followed mean annual temperature trends (Fig. 3A; rmANOVA, $F_{(1,4)} = 2,450.14$, $P < 0.0001$), with the lowest elevation site (site 5) accumulating the greatest number of growing degree-days (2,939), and the

Fig. 3 A Mean daily growing degree-days (base 0 °C) throughout the year, representing mean daily temperature in degrees Celsius. **B** Accumulation of degree-days over time, with a break between population cohorts. Note that individuals in 2017 would have already accumulated degree-days from the period between July 2016 and March 2017, which was outside the sampling period
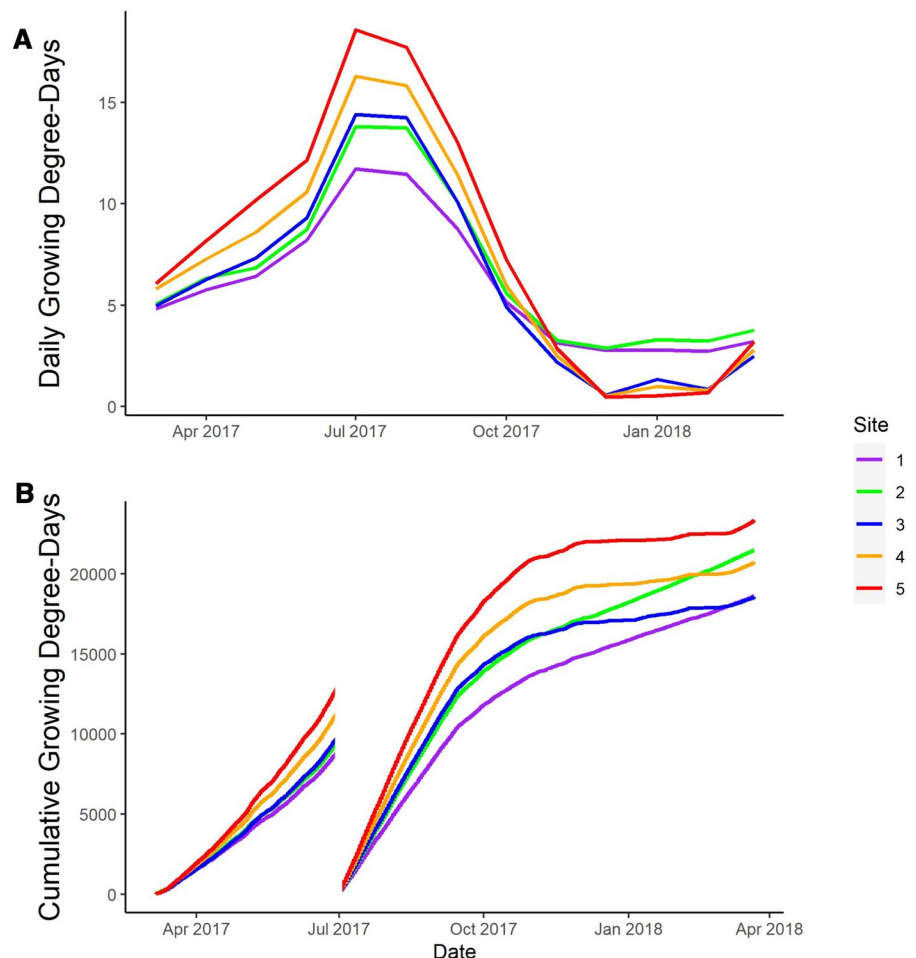
highest elevation site (site 1) accumulating the fewest (2,220; Fig. 3A; Table 1; Tukey HSD: $P < 0.05$). Significant seasonal differences in the accumulation of growing degree-days were apparent for all sites (rmANOVA, $F_{(1,4)} = 613.14$, $P < 0.0001$), with more heat accumulated in the summer-autumn than in other seasons, and in the spring–summer versus winter (Fig. 3A). Average daily growing degree-days increased with elevation in the winter, but decreased with elevation during the other seasons (Fig. 3A; Table 1; ANOVA, $F_{(1,4)} = 101.6$, $P < 0.0001$; Tukey HSD; $P < 0.05$). In the winter, lower elevation sites (sites 3–5) accumulated ~ 1 growing degree-day per day, while high-elevation sites (sites 1 and 2) accumulated more than twice this amount (2.83 per day; Fig. 3A). This disparity was evident in the slopes of cumulative degree-day distributions in winter months (Fig. 3B); sites 3–5 had slopes near zero, whereas slopes at sites 1 and 2 remained positive, highlighting the large apparent differences in winter heat accumulation between high- and low-elevation sites.

Food quantity and quality

Measures of food quantity and quality showed a high degree of variability, and no significant or systematic differences were detected among sites, with the exception that biofilm AFDM to chlorophyll *a* ratios were higher at Site 4 than the other sites [ANOVA, $F_{(1,4)} = 101.6$, $P = 0.01$; Tukey HSD, $P < 0.05$; Supplemental Fig. 1].

Body size phenology

Temporal and spatial variation in body size phenology was observed for each of the focal species, but patterns were not consistently related to differences in temperature. In general, body sizes of both ephemerellid species (*E. infrequens* and *D. doddsii*) increased slowly through summer-autumn and winter, with a rapid increase in size during spring–summer prior to emergence (Fig. 4A and 4B). In late autumn and winter, *E. infrequens* achieved the largest body size at high-elevation sites (sites 1 and 2; Fig. 4A) where growing degree-days continued to accumulate (Fig. 3A), but these differences were not apparent in the final life stages of the previous cohort (Feb–May 2017). Body size phenology of *D. doddsii* was relatively similar among sites during the initial part of the
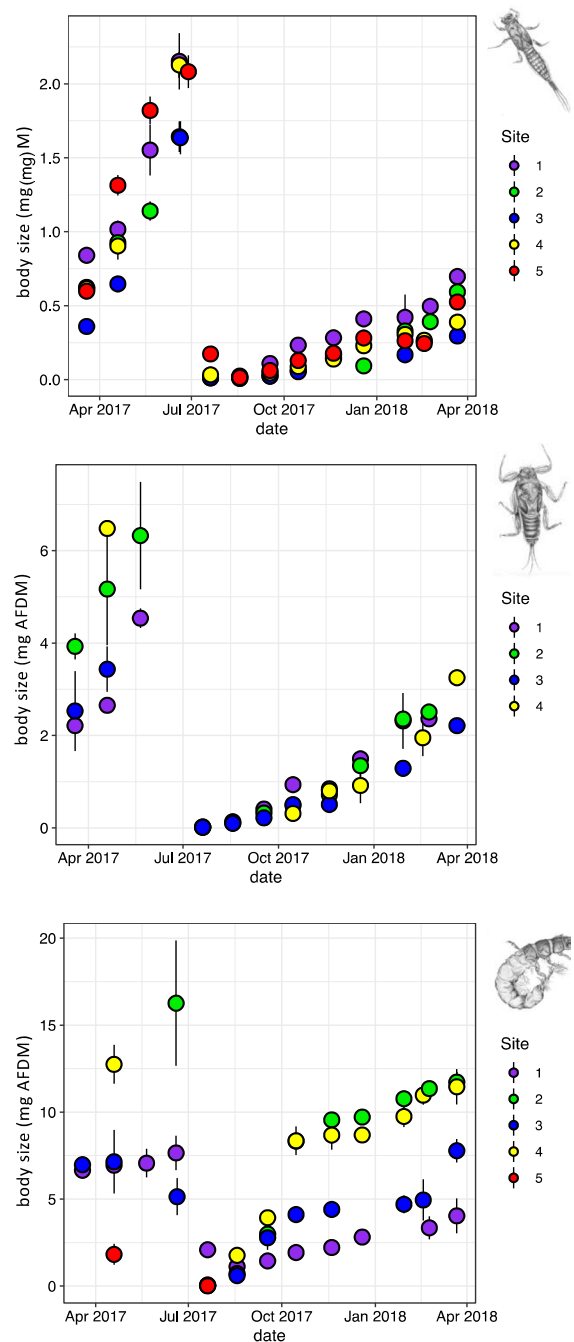

Fig. 4 Temporal patterns of individual body size ([mg AFDM] median ± 95%CI) for immature *Ephemerella infrequens* (**A**), *Drunella doddsii* (**B**), and *Hydropsyche cockerelli* (**C**). Missing points indicate that the species was either not detected at the site or, less commonly, that the site was not sampled due to high flows or ice

life cycle in summer, but individuals attained somewhat larger body size at upstream sites (sites 1 and 2) during the winter months when these locations were warmer (Fig. 4B and Table 1). In the spring–summer of 2017, *D. doddsii* individuals were larger at sites 2 and 4 relative to sites 1 and 3, consistent with differences in mean annual temperatures, but not differences in temperature during the spring–summer (Table 1). *Drunella doddsii* was not found at site 4 during two months of the spring–summer period, and was absent from samples at site 5 during all spring–summer dates. Body size of *H. cockerelli* increased rapidly in the autumn at sites 2 and 4, while changes in body size were much smaller at the slightly cooler sites (sites 1 and 3) during this time (Fig. 4C). By the end of summer-autumn, average body size of *H. cockerelli* was > 100% larger at sites 2 and 4 (average: 8.3 mg AFDM) than sites 1 and 3 (average: 3.0 mg AFDM), and these differences were also apparent in the spring–summer cohort of 2017. Body size of *H. cockerelli* at the warmest site (site 5) was consistently small suggesting that individuals at this site did not complete development.

Daily growth rates

Although daily growth rates of all species decreased with body size (Supplementary Fig. 2 and Supplementary Table 1), there were still detectable differences among seasons and sites that were not clearly related to temperature. Growth rates were generally fastest during the summer-autumn for all sites and species (Fig. 5), corresponding to the presence of early-instar life stages and warm temperatures. Daily growth rates slowed during winter and then increased slightly in spring–summer, though not to the magnitude observed in summer-autumn (Fig. 5). In the summer-autumn, growth rates of *E. infrequens* were highest at the cooler sites (sites 1–3), while growth rates of *H. cockerelli* were highest at sites 2 and 4 (non-overlapping IQRs), likely driving the rapid changes in body size described above (Fig. 5C). In winter, there was a general trend toward faster median growth rates at warmer high-elevation sites, but this pattern was somewhat idiosyncratic and the IQRs typically overlapped among sites. Apparent inter-site differences in growth during the spring–summer were difficult to assess because growth rates of *D. doddsii*

and *H. cockerelli* could not be estimated at all sites (Fig. 5B and C).

Terminal body size and reproductive potential

Terminal body size varied among sites for each species (Fig. 6 and Table 2) but was not consistently related to mean annual temperature. Average terminal body size of *E. infrequens* was larger at sites 1, 4, and 5 than sites 2 and 3 (Fig. 6A), and did not reflect patterns of mean annual temperature. Terminal body size of *D. doddsii* decreased significantly at lower elevations, consistent with increases in mean annual temperature [Fig. 6B; ANOVA, $F_{(1,3)} = 5.82$ $P = 0.02$; Tukey HSD] *Hydropsyche cockerelli* achieved largest terminal body size at sites 2 and 4 where mean annual temperatures were intermediate (Fig. 6C; ANOVA, $F_{(1,3)} = 5.02$, $P = 0.03$; Tukey HSD).

Terminal body size explained relatively little variation in the number of eggs produced by mature ephemerellid females, but these relationships showed a positive trend for both taxa consistent with other investigations (e.g., Honěk 1993; Supplementary Fig. 3; *E. infrequens*: $r^2 = 0.26$, $P < 0.001$; *D. doddsii*: $r^2 = 0.04$, $P = 0.10$). Reproductive potential decreased at lower elevations for both ephemerellid taxa (Fig. 7, Table 2, ANOVA, $P < 0.01$;Tukey HSD) and was correlated with terminal body size for *D. doddsii* ($r = 0.52$, $P < 0.001$) but only marginally so for *E. infrequens* ($r = 0.24$, $P = 0.10$).

Density, biomass, and secondary production

Mean annual population density and biomass varied by species and site (Table 3), and was inconsistently related to variation in temperature, terminal body size, and reproductive potential. For *E. infrequens*, there was no consistent pattern in mean annual density or biomass among sites, but abundance and biomass were highest at sites with the highest reproductive potential (sites 1 and 5). Density and biomass of *D. doddsii* declined at lower elevations and increasing temperatures (Table 3), but correlations between these metrics and other life history traits were not significant. *Hydropsyche cockerelli* densities and biomass were highest at sites with intermediate annual mean temperatures (i.e., sites 2 and 4); in this case, both density ($r = 0.77$, $P < 0.0001$) and biomass

Fig. 5 Instantaneous growth rates of immature *Ephemerella infrequens* (**A**), *Drunella doddsii* (**B**), and *Hydropsyche cockerelli* (**C**) among sites and seasons. Boxes show the median and 25th- to 75th-percentile range. Whiskers extend to the 95th percentile. 'ND' indicates insufficient data
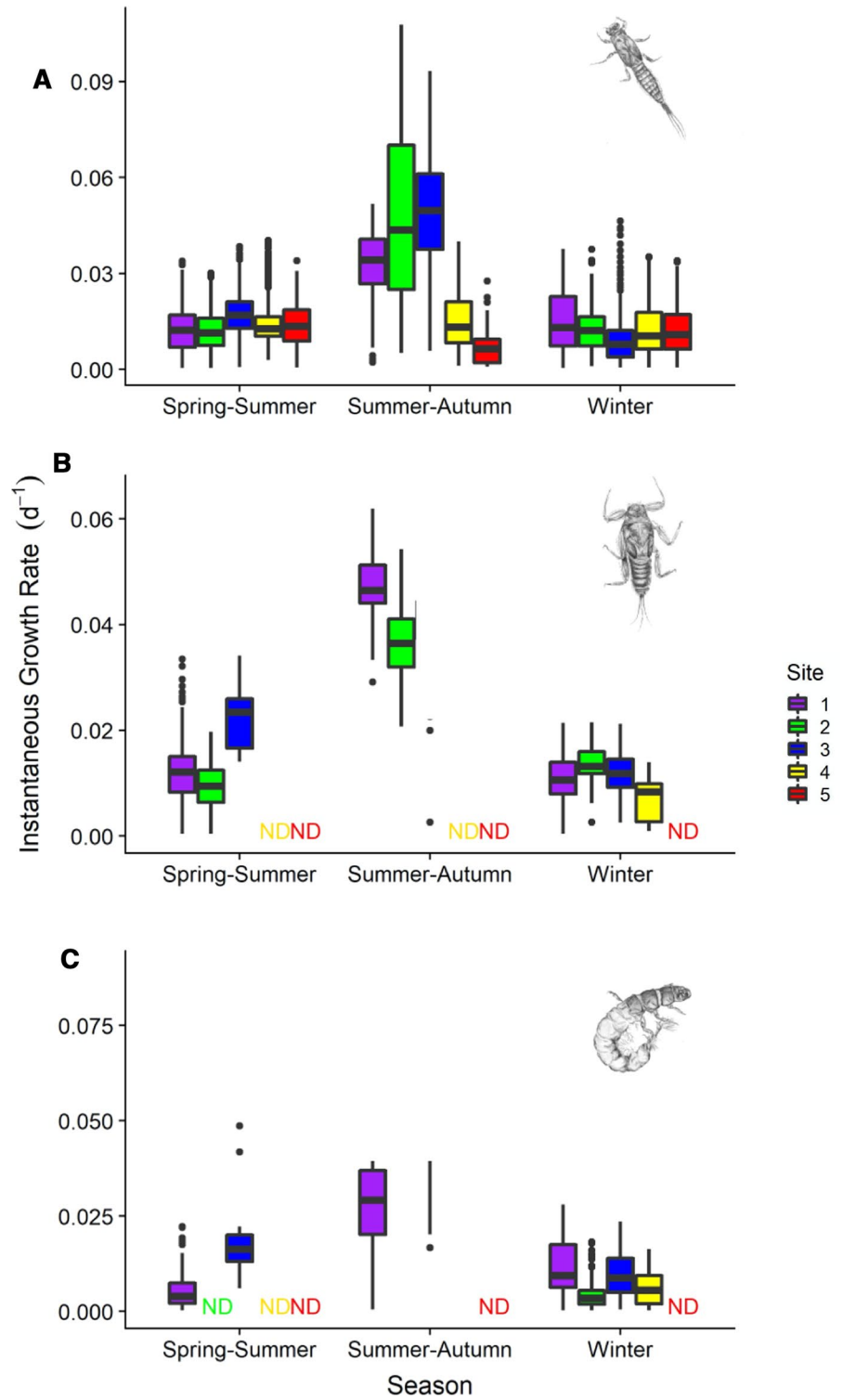
Fig. 6 Terminal body size (mg AFDM) of immature *Ephemerella infrequens* (**A**), *Drunella doddsii* (**B**), and *Hydropsyche cockerelli* (**C**) among sites. Columns show mean terminal body size ± 1SE
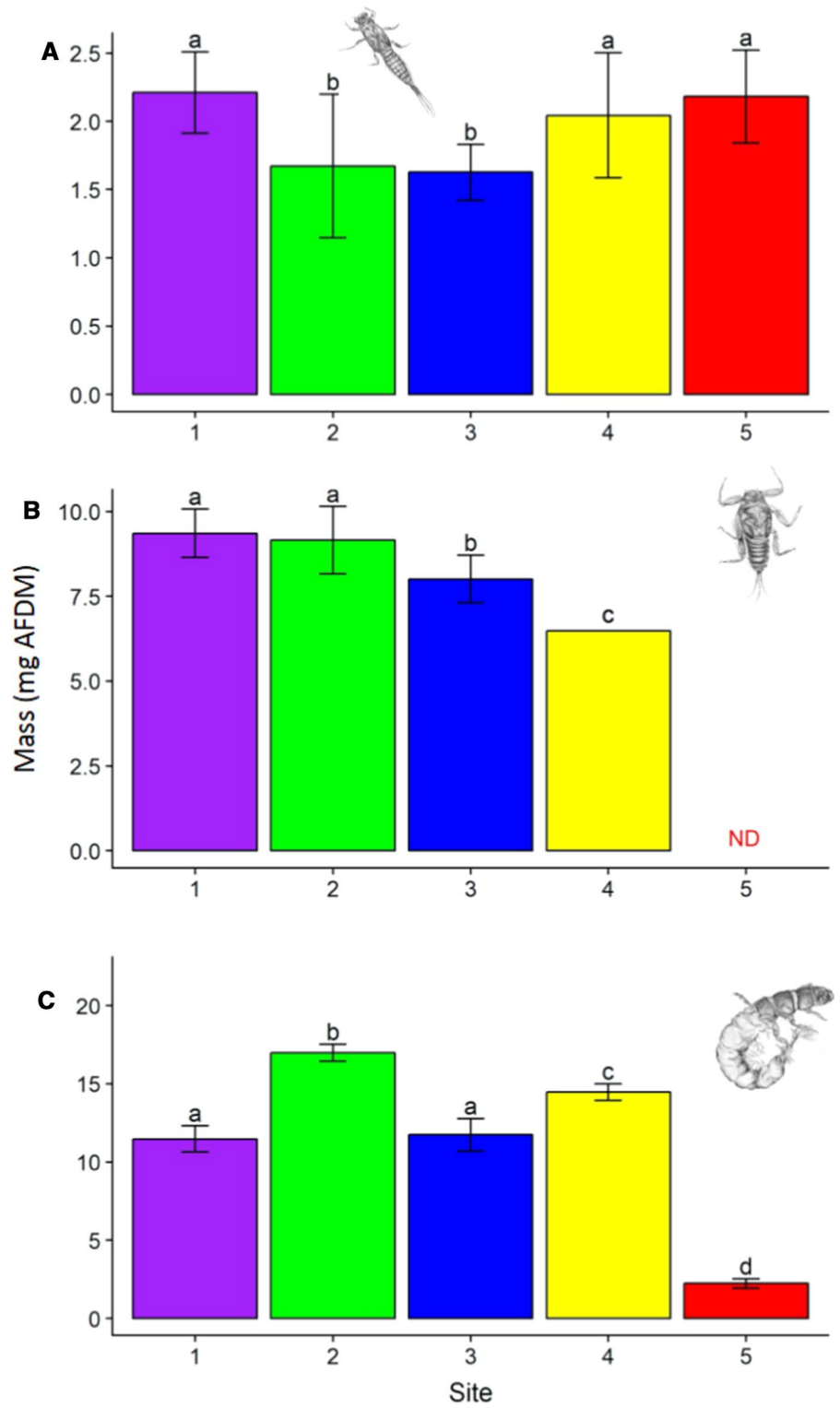
Table 2 One-way ANOVA comparing terminal body size and reproductive potential among sites for each species

Species	Measurement	Degrees of Freedom	F value	P <
E. infrequens	Terminal body size	1,4	1.41	0.05
	Reproductive potential	1,4	42.31	0.0001
D. doddsii	Terminal body size	1,3	5.82	0.05
	Reproductive potential	1,2	640.10	0.0001
H. cockerelli	Terminal body size	1,4	5.02	0.05

Fig. 7 Reproductive potential of *Ephemerella infrequens* (**A**) and *Drunella doddsii* (**B**) estimated as the total number of eggs m^{-2} at each site. Boxes show the median and 25th- to 75th-percentile range; whiskers extend to the 95th percentile and points fall outside of this range
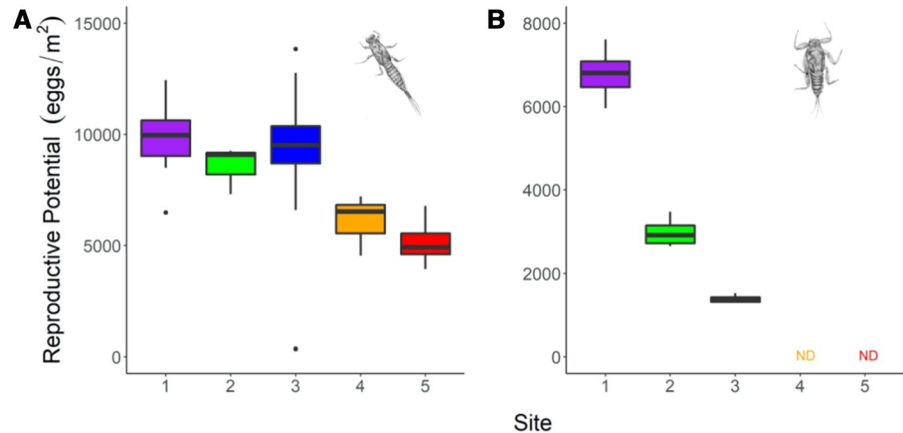
Table 3 Average annual density, biomass, secondary production and annual P:B ratio of each study species at each site

Species	Site	Density (individuals m^{-2})	Biomass (mg AFDM m^{-2})	Production (mg AFDM m^{-2} year^{-1})	P:B (year^{-1})
E. infrequens	1	179.7	108.3	439.7	4.1
	2	67.4	28.0	101.5	3.6
	3	541.1	55.8	321.8	5.8
	4	79.7	17.0	77.2	4.6
	5	401.9	97.5	449.6	4.6
D. doddsii	1	31.0	50.9	292.7	5.8
	2	12.3	13.3	52.4	3.9
	3	14.3	9.3	36.1	3.9
	4	1.5	2.7	8.2	3.1
H. cockerelli	1	29.7	110.7	164.1	1.5
	2	60.9	561.9	1073.8	1.9
	3	36.2	106.6	329.0	3.1
	4	40.8	216.2	1211.1	5.6

($r = 0.72$, $P < 0.0001$) were positively correlated with terminal body size.

Annual secondary production also varied by species and site (Table 3), and was inconsistently related to temperature and other life history traits. Secondary production of *E. infrequens* was highest at the coolest and warmest sites (sites 1 and 5) and was not related to mean annual temperature, terminal body size, or reproductive potential (Pearson's *r*; all $P > 0.1$). Secondary production of *D. doddsii* declined with increasing mean annual temperature and was positively correlated with terminal body size ($r = 0.60$,

$P < 0.0001$) and reproductive potential ($r = 0.63$, $P < 0.001$). Production of *H. cockerelli* was highest at sites 2 and 4 (Table 3), was not related to mean annual temperature, and was positively correlated with terminal body size ($r = 0.57$, $P < 0.0001$). No distinct longitudinal pattern in annual P:B was observed for *E. infrequens* (Table 3). Annual P:B of *D. doddsii* decreased at lower elevations and increasing mean annual temperature, and P:B of *H. cockerelli* was not associated with elevation or temperature.

Discussion

We examined how variation in temperature regime along an elevation gradient influenced body size, reproductive potential, and population-level production of three common Rocky Mountain aquatic insect taxa. We found that growth varied with season and site, leading to significant variation in the phenology of growth and terminal body size. Yet, these patterns were not clearly related to temperature. We also found that reproductive potential of the mayfly taxa was negatively associated with mean annual temperature (i.e., reproductive potential declined with elevation), but was not correlated with terminal body size. Population-level characteristics including density, biomass, and secondary production generally reflected differences in terminal body size for *D. doddsii* and *H. cockerelli*; however, this outcome was not the case for *E. infrequens*. Our findings suggest that relationships between temperature, life history characteristics, and secondary production are complex, and may not follow the general expectation that production is greatest where females are largest and most fecund.

Vannote and Sweeney (1980) predicted that fecundity in ectotherms is positively correlated with female body size and should therefore be greatest at temperatures that produce low weight-specific respiration and intermediate generation times (which were not measured in this study). Furthermore, they predicted that reproductive success and local population abundance will depend on the number and fecundity of emerging females. In our study, we estimated reproductive potential by multiplying the average number of eggs per female by densities at each site prior to emergence. We found that while the number of eggs per female was positively correlated with body size (Supplementary Fig. 3), our estimate of reproductive

potential was only correlated with body size for *D. doddsii*. Further, we found that reproductive potential was most related to annual differences in temperature, with a consistent reduction from cooler high-elevation sites to warmer low-elevation sites (Fig. 7). In our case, the decoupling of terminal body size and reproductive potential can be attributed to lower densities of fecund females at downstream sites just prior to the time of emergence. The specific mechanism for reduced densities is unknown, but could be driven by increased mortality with elevated temperatures. At low-elevation sites, daytime temperatures reached ~ 20 °C, which may have a negative effect on performance and survival (Ward & Stanford, 1982). In addition, warm temperatures could accelerate predation by invertebrate or fish predators (Kishi et al., 2005), thus reducing densities at these downstream sites. Although fecundity (i.e., eggs per female) is likely a critical factor determining success of subsequent generations in aquatic insects (Buckley et al., 2008; but see Bovill et al., 2018), factors that influence pre-emergence population densities may be equally or even more important (Stanley & Short 1988; Rader & Ward, 1990).

Vannote and Sweeney (1980) also predicted that maximum body size and fecundity at a species' thermal optimum would translate into highest local abundance and secondary production. They further suggested that highest local abundance should occur near the center of a species' geographic range. We simultaneously measured life history characteristics and average annual density, biomass, and production to test this prediction. Importantly, our elevation gradient captured most of the thermal range experienced by the study species across their broad geographic distributions (Fischer, 1960; Allen & Edmunds, 1965; Allen 1980). For *D. doddsii* and *H. cockerelli*, variation in secondary production generally reflected spatial patterns of terminal body size, which is consistent with the original TEH predictions. For *H. cockerelli*, highest production occurred in the middle of the temperature range (i.e., sites 2 and 4), suggesting their optimum thermal regime may indeed exist near the center of their geographic distribution (Rasmussen & Morse, 2020). In contrast, *D. doddsii* was most abundant and productive at the coldest site where body size, fecundity, and reproductive potential were highest. Thus, in contrast to the TEH predictions, it appears that *D. doddsii* may be most successful at the

coldest end of their geographic range and near their lower thermal limit. Patterns of *E. infequens* body size were not correlated with abundance or secondary production, suggesting other factors prior to, or after emergence, may be more important. Clearly, additional research is needed to identify whether or under what circumstances terminal body size and individual fecundity may predict local population-level abundance or secondary production.

A recent laboratory study by Sweeney et al. (2018) sheds considerable light on how temperature influences life history characteristics of the mayfly *Cloen dipterum*, providing new insights that expand and revise the original TEH (Vannote & Sweeney, 1980). Most relevant to our study, Sweeney et al. (2018) found that maximum body size occurred at the coldest temperatures, consistent with the TSR and not the TEH, and was driven by differences in development rate versus growth rate that led to earlier adult maturation at warming temperatures (also see Forster & Hirst, 2012). Although we were not able to quantify development rate in our study, it is possible that this mechanism contributed to variation in terminal body size patterns in our study. In addition, Sweeney et al. (2018) found that maximum population growth rate of *Cleon dipterum*, as measured by fecundity and survivorship in laboratory containers, was greatest near the upper end of their thermal range or thermal 'acclimation zone'. Although adult females were smaller and less fecund at these warmer temperatures, survivorship was still relatively high and development time sufficiently low to produce maximum per capita rates of population increase at relatively warm temperatures (Sweeney et al., 2018). Assuming these patterns are relevant to field populations, these results suggest that population abundance and production may be highest near the upper thermal range, at least for some mayfly taxa; however, our study does not support this hypothesis. Given the many factors that may combine or interact to influence local secondary production, additional studies are needed to predict thermal effects on aquatic insect populations in natural settings. This includes the need for more information about factors that influence survivorship, as well as the influence of adult-stage life history characteristics including reproductive and oviposition success (Bovill et al., 2019; Miller et al., 2020).

Although our field study allowed us to examine thermal effects on the study taxa under ecologically realistic conditions, there are obvious tradeoffs associated with *in-situ* studies versus controlled laboratory experiments (e.g., Sweeney et al., 2018; Uno & Stillman, 2020). For instance, although we selected sites in an effort to isolate the effects of temperature, human activities including water withdrawals for agriculture, siltation, and nutrient enrichment at the lower elevation sites may have influenced life history traits examined in this study and obscured the direct effects of temperature. In addition, it is possible that drift and longitudinal movement of insects occurred among sites (Waters, 1972; Lancaster et al., 2020), influencing the range of temperatures experienced by individuals collected at a given site. Further, we did not consider spatial differences in community structure, and the potential for species interactions such as competition or predation to influence growth and survivorship. However, such factors are difficult to quantify without comprehensive food web or community-level studies. Finally, we were not able to separate individuals by sex, and it is likely that sexual dimorphism led to significant variation in our estimates of growth and body size (Fischer & Fiedler, 2002; Karl & Fischer, 2008; Sweeney et al., 2018). Despite these limitations, our study provides an important in situ study that can serve as a foundation for future investigation of the thermal ecology of aquatic insects.

Global stream temperatures are changing at unprecedented rates (Woodward et al., 2010b; IPCC 2013), and Rocky Mountain streams are warming more quickly than many other regions of the U.S. due to changes in climate, urbanization, and decreasing snowpack (Keleher & Rahel, 1996; Isaak et al., 2016; Whitlock et al., 2017). Such changes are important, as mountain streams can provide refugia for cold-adapted species in larger landscapes (Ross, 1963; Isaak et al., 2016). In response to warming stream temperatures, cold-adapted species will likely experience increased respiration at the cost of growth, reduced body sizes, and the potential for reduced fecundity (Sweeney & Vannote, 1978; Sweeney et al., 2018). Yet changes in survivorship may play a larger role in driving shifts in population-level biomass and secondary production, as well as wholesale changes in community structure (Gonzalez et al., 2003; Huryn & Wallace, 2000). Such predictions have been corroborated by several studies demonstrating that warming can lead to shifts in stream communities (Hogg & Williams, 1996; Durance & Ormerod,

2007; Woodward et al., 2010a; Nelson et al., 2017b). Anecdotally, such changes might already be occurring in our study system. For instance, *D. doddsii* and *H. cockerelli* had low abundance at site 4 and were not observed at the warmest low-elevation site with the greatest anthropogenic influence (site 5). Yet these taxa were relatively abundant at these sites just 30 years prior (Gustafson, 1990). Such results underscore how rapidly changes to stream thermal regime or other human-related factors may influence insect populations and community composition.

Quantifying patterns of aquatic insect life history and production along natural thermal gradients may help to better predict how aquatic insects may respond to a changing climate (Harper & Peckarsky, 2006; Sweeney et al., 2018; Junker et al., 2020). The TEH and TSR provide useful frameworks for conceptualizing how insect physiological and life history traits may vary across thermal gradients. However, our results suggests that additional studies are needed, particularly in natural field settings, to refine our understanding of how responses to variation in temperature scale to influence the local success of populations. In particular, robust tests of conceptual frameworks such as the TEH or TSR, as well as their connection to population-level secondary production, will need to consider a more rigorous sampling design that includes stream-level replication of thermal variation, as well as more careful accounting of how fecundity translates to population success. Although there is still much learn, progress on this front will be invaluable in efforts to forecast shifts in species distributions and changes to the structure and function of stream ecosystems in a changing climate.

Declarations

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