

EFFECTS OF WATER WITHDRAWALS ON MACROINVERTEBRATE EMERGENCE:
UNEXPECTED RESULTS FOR THREE HOLOMETABOLOUS SPECIESP. D. BROWN,^{a*} D. WOOSTER,^b S. L. JOHNSON^c and S. J. DEBANO^b^a Department of Fisheries and Wildlife, Oregon State University, Corvallis, Oregon, USA^b Department of Fisheries and Wildlife, Hermiston Agricultural Research and Extension Center, Oregon State University, Hermiston Oregon, USA^c United States Forest Service, Pacific Northwest Research Station, Corvallis, Oregon, USA

ABSTRACT

Small, low-head diversion dams are capable of withdrawing much of the flow of a river, often resulting in elevated water temperatures. Accelerated growth and development of aquatic invertebrates has been demonstrated in warmer temperatures, suggesting that the timing of insect emergence and adult body size may be significantly altered by water withdrawals. To examine the influence of summer water withdrawals on aquatic invertebrate life histories, emergence timing and adult body mass of three holometabolous species were monitored continuously for 9–10 weeks on the Umatilla and Walla Walla Rivers in arid northeastern Oregon. On each river, multiple sample sites were located along gradients of decreasing discharge and increasing water temperatures caused by successive diversions.

Despite reductions in discharge of up to 93% and increases in average water temperature of up to 4.6°C from upstream to downstream, timing of median emergence was unaltered for *Helicopsyche borealis*, *Petrophila confusalis* and *Glossosoma triviatum*. However, in a laboratory experiment, higher temperatures led to earlier emergence for *H. borealis*. Water temperature in the field study was not significantly correlated with reduced adult body size of these species, though female *P. confusalis* were 31% smaller at the warmest sample site. Holometabolous life histories and high temperature tolerances are possible explanations for the observed resistance of these species to life history alteration. Copyright © 2010 John Wiley & Sons, Ltd.

KEY WORDS: life history; temperature; discharge; water abstraction; agriculture; *Helicopsyche*; *Petrophila*; *Glossosoma*

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INTRODUCTION

River systems worldwide are impacted by an array of human activities. Exploitation, water quality degradation, modified hydrology and physical habitat modification commonly degrade the biotic integrity of lotic systems (Malmqvist and Rundle, 2002; Dudgeon *et al.*, 2006). Water withdrawal for irrigated agriculture is one such widespread disturbance that has been increasing in severity as human populations expand throughout the world (Malmqvist and Rundle, 2002; Oki and Kanae, 2006). The impacts of large hydroelectric dams on the physical, chemical and ecological properties of rivers have garnered much attention in the literature, but the effects of low-head agricultural diversion dams on lotic ecology have received far less consideration. Large dams often dampen peak discharge, elevate summer base flow and decrease summer water temperatures (Allan, 1995; Poff and Allan, 1997; Vinson, 2001). Low-head diversion dams produce distinctly different effects by reducing summer base flow (Rader and Belish, 1999), which may increase water temperatures (Cazaubon and Giudicelli, 1999; Rader and Belish, 1999). Hydrologic and thermal impacts are absent or

minimized during winter and spring, when irrigation demands are low.

The growth, development and reproductive strategies of ectothermic organisms are controlled in large part by natural hydrologic events (Lytle, 2001; Lytle and Poff, 2004) and water temperatures (Gallepp, 1977; Sweeney and Vannote, 1978; Giberson and Rosenberg, 1992; Newbold *et al.*, 1994). If water withdrawals on a naturally perennial river are severe enough to create hydrologic and thermal regimes similar to those of seasonally intermittent streams, some of the specific life history challenges of intermittent streams (Poff and Ward, 1989) may be imposed upon an invertebrate community ill-adapted to handle them. Although such artificial reductions in discharge have been shown to alter aquatic invertebrate community composition and abundance (Rader and Belish, 1999; Dewson *et al.*, 2007; Miller *et al.*, 2007), the effect on life histories is less clear (e.g. Delucchi and Peckarsky, 1989).

Water temperature may have a significant effect on aquatic invertebrate life histories and reproductive success. Aquatic insects have been observed to grow and mature at a faster rate in warmer temperatures, but achieve smaller adult body sizes as a result (e.g. Giberson and Rosenberg, 1992; Hogg and Williams, 1996; McKee and Atkinson, 2000), although exceptions have been found (Gregory *et al.*, 2000;

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Cabanita and Atkinson, 2006). Aquatic invertebrates may thus be expected to emerge earlier and at a smaller body size in water of elevated temperatures. Given that aquatic invertebrate fecundity is directly related to adult body size (Sweeney *et al.*, 1995; Taylor *et al.*, 1998), and some taxa (e.g. Ephemeroptera) have brief adult life stages, changes in emergence timing and body size may have significant effects on reproductive success and competitive fitness. Sweeney and Vannote (1978) proposed that aquatic insects have a narrow temperature regime within which adult body size and fecundity are optimized, and hypothesized that changes of only 2 or 3°C could lead to local extinction at the margins of their geographic range.

The extent and character of water withdrawal impacts on aquatic invertebrate life histories remains largely hypothetical. Studies that have examined invertebrates below water diversions focused on community composition (e.g. Dudgeon, 1992; Castella *et al.*, 1995; Rader and Belish, 1999; Miller *et al.*, 2007) rather than life histories. Conversely, research on the roles of temperature and discharge on life histories has been confined to streams with natural flow and temperature regimes (e.g. Delucchi and Peckarsky, 1989; Harper *et al.*, 1995), systems modified by large dams (e.g. Ward, 1974; Vinson, 2001) and industrial thermal pollution (e.g. Tennessen and Miller, 1978; Coler and Kondratieff, 1989) or experiments in laboratory settings only (e.g. Nebeker, 1971; Giberson and Rosenberg, 1992; Cabanita and Atkinson, 2006). The intent of this study was to examine the effects that artificially depressed summer discharge and elevated water temperatures have on the life histories of aquatic invertebrates. Our study investigated the emergence timing and adult body mass for three holometabolous aquatic insect species in two arid-land rivers with multiple withdrawal points creating gradients of decreasing discharge and increasing water temperature. We expected the reduced discharge and higher water temperatures to (1) cause earlier summer emergence and (2) reduce the average adult body size of these three species from upstream to downstream.

SITE DESCRIPTION

The Umatilla and Walla Walla Rivers are 5th and 4th order tributaries of the Columbia River in northeastern Oregon. The rivers originate in the forested Blue Mountains and flow through the semi-arid plains of the Columbia Basin. Large dams are absent from the mainstem of each river, although multiple low-head irrigation diversion dams (<6 m) have been present since the early 1900s. Land use in the portion of the watershed surrounding the sample sites of each river is dominated by irrigated agriculture. The regional climate is arid with warm summers. Mean annual precipitation along the lower Umatilla River at Hermiston, Oregon is 22.7 cm, and mean maximum air temperatures range from 30.1°C in

summer to -3.2°C in winter (Western Regional Climate Center, 2007, site 353847). Mean annual precipitation along the Walla Walla River at Milton-Freewater, Oregon is 36.8 cm and mean maximum air temperatures range from 29.4°C in summer and -3.4°C in winter (Western Regional Climate Center, 2007, site 355593). The hydrology of the rivers is driven by snowmelt from the headwaters, with an average spring runoff (February–June) and baseflow (July–September) of 31.8 and 7.6 cubic metres *per second* (cms) for the Umatilla (United States Department of the Interior, Bureau of Reclamation, 2007a, site YOKO) and 25.7 and 3.1 cms for the Walla Walla at Touchet, WA (United States Department of the Interior, Geological Survey, 2007b, page 14018500).

A series of four irrigation diversion dams are present along the 31 km study reach of the lower Umatilla, and two diversion dams and a zone of high surface water loss to groundwater are located along the 7 km study reach of the Walla Walla (Figure 1). The diversion dams and the losing reach on the Walla Walla create longitudinal gradients of decreasing discharge and increasing water temperatures during the summer months (Table I). Umatilla River discharge was reduced sufficiently during the study period to produce extensive reaches of slack water between riffles throughout much of the study reach. No tributaries are present within the study reaches.

METHODS

Field sampling

Emergence of adult aquatic insects was monitored at a single selected riffle (sample site) above and below each diversion dam on both rivers and the losing reach on the Walla Walla during the summer of 2006. We chose the riffles nearest the diversion dams that did not bear any signs of influence from the dam structure or plunge pool immediately downstream. Thus, eight sample sites were located on the Umatilla, and six on the Walla Walla. At each sample site, four floating emergence traps were deployed randomly along a 50 m transect, with two of the traps placed mid channel and two placed along the bank to capture insects that crawl ashore to emerge (Paetzold and Tockner, 2005). If needed, traps placed along the bank were moved each week to track the receding water line. Emergence traps were pyramidal with a 0.25 m² basal area, panelled with 1 mm mesh-size screening, and tapered upwards to direct trapped insects into a sample bottle filled with 70% ethanol.

Emergence was monitored continuously and sampled weekly from 6 July to 1 September 2006 on the Umatilla and from 27 June to 30 August 2006 on the Walla Walla. Water temperature was continuously monitored at each sample site using Onset HOBO temperature loggers recording at 30 min intervals. River discharge at sites 54.7–27.4 km on the Umatilla was obtained from the United States Bureau of

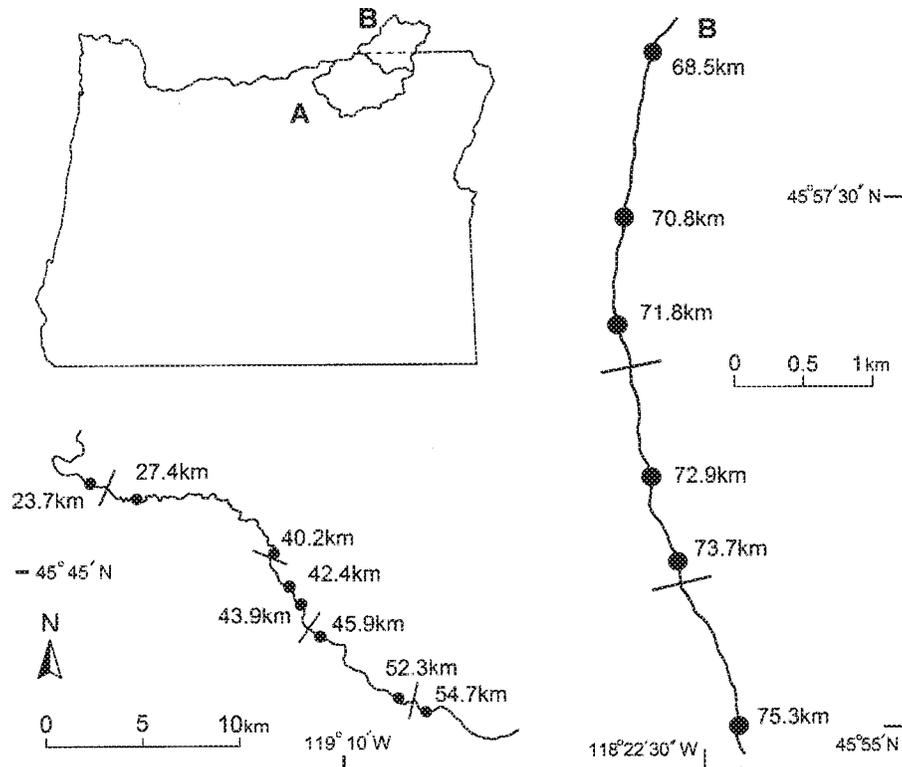


Figure 1. Delineated watersheds and relative location of study sites for the Umatilla River (A) and Walla Walla River (B). Lines perpendicular to each river represent the location of diversion structures. Surface water loss to groundwater occurs between sites 68.5 and 70.8 km.

Table I. Location, discharge and water temperatures of each study site

River kilometre ^a	Discharge (m ³ s ⁻¹)		Temperature (°C)	
	Average ^b	Min/Max ^c	Average ^b	Min/Max ^c
Umatilla River				
54.7	6.55	4.49/46.04	18.6	16.2/22.1
52.3	6.24	4.43/44.24	18.8	16.3/22.1
45.9	5.88	4.23/55.59	19.7	17.1/22.8
43.9	0.63	0.11/50.14	20.7	18.2/24.2
42.4	0.75	0.20/35.64	20.3	18.6/23.1
40.2	0.64	0.16/35.40	21.4	19.6/24.0
27.4	0.81	0.39/52.38	22.4	20.1/26.2
23.7	0.48	0.02/3.89	23.2	20.0/30.1
Walla Walla River				
75.3	3.23	2.78/4.10	15.5	13.8/17.8
73.7	1.12	0.65/1.25	16.3	14.4/18.8
72.9	1.09	0.99/1.24	16.0	13.9/18.5
71.8	0.77	0.73/0.83	16.7	14.9/19.1
70.8	0.74	0.44/0.86	16.9	15.0/19.5
68.5	0.40	0.26/0.55	17.9	15.5/21.0

Sites at 54.7 and 75.3 km are the most upstream sites.

^aRiver kilometre is distance from confluence with the Columbia River.

^bDischarge and temperature are averaged throughout the summer sampling period.

^cMinimum and maximum discharge and temperatures are daily averages.

Reclamation (<http://www.usbr.gov/pn/hydromet/>), and by monthly instantaneous measurements for site 23.7 km. Walla Walla discharge was determined from instantaneous measurements taken in mid-June, -July and -August, and did not appear to change discernibly between weekly sampling events from 5th July to the end of the sampling season. All instantaneous discharge measurements were made by measuring depth and water velocity (at six-tenths of depth) using a Marsh-McBirney digital flow velocity metre at a minimum of 20 points across the river. In addition to temperature and discharge, water depth at each trap and water velocity at the mid channel traps were recorded weekly.

Samples were collected from the emergence traps weekly and transported to the laboratory. The number of the snail-case caddisfly *Helicopsyche borealis* and aquatic moth *Petrophila confusalis* in each Umatilla sample and the number of *Glossosoma traviatum* in each Walla Walla sample was counted. These species were selected due to their presence at all or most sampling sites on their respective rivers and their discrete period of emergence towards the end of the sampling period, exposing the larvae to extended periods of altered temperature and discharge. Body length measurements were taken from randomly selected male and female insects from the three dates of highest emergence at each site. Body length from the front of the head to tip of the abdomen was measured to the nearest 0.1 mm with an ocular micrometre for all specimens. Length measurements were converted to mass using the regression equations in Sabo *et al.* (2002) for *P. confusalis* and Sample *et al.* (1993) for *H. borealis* and *G. traviatum*. Counts and body mass measurements from the four emergence trap samples at each site were composited for each sampling date due to the patchy distribution of these species within sites.

Data analysis

We examined if the date of median emergence and average individual male and female adult body mass at peak emergence were correlated with discharge, temperature, water velocity or water depth at each site using nonparametric multiplicative regression (NPMR) run with HYPERNICHE (version 1.0, Gleneden Beach, Oregon; McCune and Mefford, 2004). NPMR explores relationships between a single response variable and multiple explanatory variables, but unlike parametric techniques such as multiple linear regression, it does not force the data to fit a predetermined mathematical relationship (McCune, 2006). Rather, NPMR uses a local multiplicative smoothing function with a leave-one-out cross-validation, allowing the data itself to predict model shape (McCune, 2006). We chose NPMR for this analysis because we predicted complex nonlinear relationships between emergence timing and the environmental variables. We selected a local mean estimator and Gaussian

weighting function for the local model, and a minimum neighborhood size of 3 for calculating the weighted estimate. Model fit was judged using a cross-validated R^2 ($\times R^2$), which is more conservative than the traditional R^2 .

For species with both an early and late summer emergence period (*H. borealis* and *G. traviatum*), analysis was performed on the late period only, as the initiation of this emergence occurred during the sample period and the organisms emerging at this time would have been subjected to the summer discharge and temperature regimes for a longer period of time. The date of median emergence of a species (date at which 50% of individuals have emerged) was identified at each sample site using the cumulative emergence curve of that species for the site. For NPMR, we chose discharge and water temperature averaged over the entire sampling period as metrics of discharge and temperature, which resulted in significant gradients for these variables on both rivers. The average maximum daily temperature was considered for use in the analysis, but it was closely correlated with average daily temperature ($r^2 = 0.84$ and $p = 0.01$). Water velocity and depth were also averaged over time. Because the potential influence of predators on invertebrate life histories (Peckarsky *et al.*, 2001) must be separated from that of temperature and discharge, densities of predatory benthic invertebrates and fish taxa (Wooster *et al.* unpublished) from monthly surveys at the sample sites were included as variables in the analysis (Table II).

Laboratory experiment

Because increased temperature co-occurs with reduced discharge along the study reaches, we isolated the effect of

Table II. Average densities of predatory fish and invertebrate taxa from monthly surveys during June–August 2006

Site	Predatory fish density (CPUE) ^a	Predatory invertebrate density (No./m ⁻²)
Umatilla River		
54.7	7.7	290.1
52.3	15.9	480.2
45.9	9.5	467.1
43.9	5.4	895.1
42.4	12.8	522.2
40.2	24.0	1512.3
27.4	11.0	384.0
23.7	2.2	2198.8
Walla Walla River		
75.3	1.2	202.8
73.7	4.7	458.0
72.9	2.8	203.4
71.8	9.3	207.1
70.8	10.6	542.3
68.5	14.6	433.3

^aCatch per unit effort (CPUE) is number of fish captured per minute of electroshocking.

temperature on emergence timing of *H. borealis* using a controlled laboratory experiment during the summer of 2007. *H. borealis* was chosen for this experiment because *P. confusalis* proved intolerant of transport and laboratory conditions in preliminary experiments, and the field sites for *G. triviatum* were too distant from the laboratory to ensure transport survival. Five *H. borealis* larvae collected from the Umatilla River at river kilometre 23.7 were randomly placed into 8 cm × 8 cm microcosms within temperature-controlled chambers (Sheldon Manufacturing, Inc., model 2015-ZZMFG). Eight replicate microcosms were placed into each of four target temperature treatments (16, 19, 23 and 28°C). The treatments represent the range of water temperatures found at the Umatilla River study sites during the summer season, and are consistent with those found in the literature for this species (Williams *et al.*, 1983; Vaughn, 1985). Microcosms were filled with a 50% blend of Umatilla River and on-site well water and were aerated with aquarium air pumps. Water was changed biweekly to control water quality. Periphyton-coated cobbles and washed sand from the larval collection site were placed in each microcosm to provide a source of food and case-building materials. Water temperature was continuously monitored with an iButton temperature logger placed in a separate microcosm within each temperature chamber. Light cycles were set to follow the ambient day length. The average head length of individuals used in the experiment was 0.353 mm (standard deviation = 0.039). According to field observations, early to middle instars of the only cohort present in the river at the time were used in the experiment. Experiments were checked daily for emerged adults. Date of emergence was noted for each adult, and individuals were collected and preserved immediately in 70% ethanol.

Data analysis

Differences between the cumulative emergence curves for each temperature treatment were examined with Kolmogorov–Smirnov (K–S) tests using SYSTAT version 12. A K–S test is a goodness of fit test to detect significant differences between two distribution curves, where n is the number of days between initiation and cessation of emergence from the experiment. A high larval mortality rate prevented the use of microcosms as replicates to test for emergence timing among treatments. Because males and females must be measured separately due to differences in size, we had insufficient numbers to test for effects on adult body mass.

RESULTS

Emergence timing—field

Average discharge during the sampling period declined by 93% from upstream to downstream on the Umatilla River,

coinciding with a 4.6°C increase in average water temperature throughout the sampling period and a 6.8°C increase in average daily maximum temperature (Table I). Likewise, average discharge at the downstream site on the Walla Walla River was 88% lower than the upstream site, and the average temperature and average daily maximum temperature were 2.4 and 5.0°C higher, respectively. The pronounced longitudinal gradients in discharge and temperature existed throughout the entire sampling period because water abstraction had begun prior to emergence trap deployment.

Despite the large differences in discharge and temperature, the emergence periods for each of the three species were similar among sites (Figures 2 and 3). Initiation of *P. confusalis* emergence and peak emergence varied up to 14 days between sites (Figure 2), but cumulative emergence timing did not appear related to the gradients of discharge and temperature (Figure 4). Initiation of the late *H. borealis* and *G. triviatum* emergence periods varied up to 14–28 days between sites, and cumulative emergence curves suggest that emergence from this period may have occurred earlier at the lower sites for *H. borealis* only (Figure 4). NPMR analysis, however, indicates that date of median emergence was not significantly correlated with average discharge, water temperature, water velocity and depth or predatory invertebrate and fish densities for any of the three species ($\times R^2$ less than 0.1 for all variables). In addition, all three species emerged across a broad range of accumulated degree days, rather than the tight clustering around a narrow range that would be expected for temperature-driven emergence timing. The abundance of each species varied among sites (Table III).

Adult body mass—field

Average individual adult body mass of each species varied considerably between sites, but was not significantly related to average water temperature (Figure 5), average discharge or any measured habitat and predator density variable ($\times R^2$ less than 0.1 for all variables). However, average adult body mass of *P. confusalis* females was 31% lower at the warmest, lowermost Umatilla site than at the coolest, uppermost site, and this difference between means is highly significant (two-sample *t*-test, $p < 0.001$). Additionally, average adult female body mass at the warmest, lowermost site was 29% lower than the combined average from all other upstream sites (Figure 5), and this difference was also highly significant (two-sample *t*-test, $p < 0.001$), suggesting a possible threshold effect due to the high temperatures of this site. This pattern was not present for either *H. borealis* or *G. triviatum*.

Laboratory experiment

Water temperature within each treatment averaged 17.8, 19.4, 21.9 and 27.3°C, which differed slightly from the

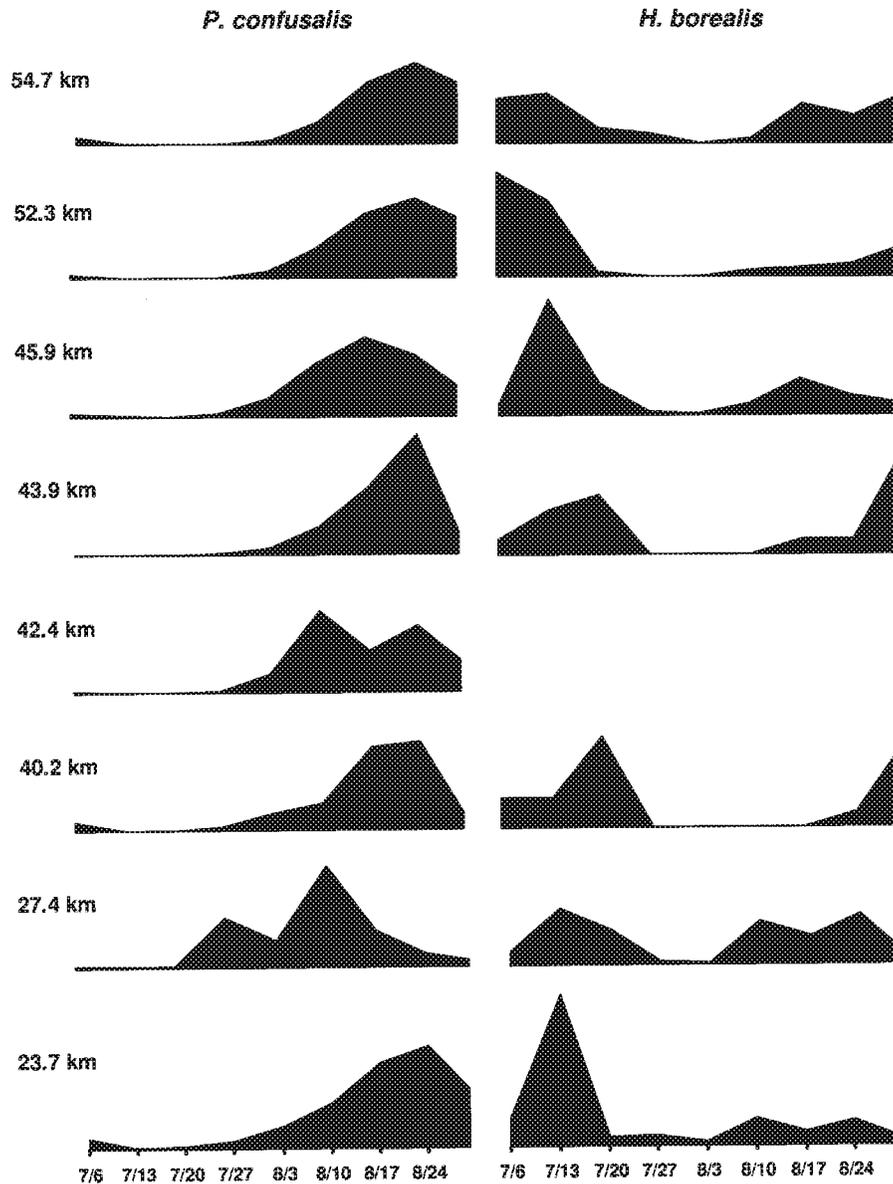


Figure 2. Emergence of *P. confusalis* and *H. borealis* from the Umatilla River sample sites (denoted by river kilometre) during the sample period. Vertical axes are standardized by the proportional emergence on each sample date. *H. borealis* at river kilometre 42.4 was excluded due to extremely low sample sizes.

target temperatures but provided clear separation between treatments. *H. borealis* emerged earlier in the warmer temperature treatments, with median emergence occurring 5 days sooner (Figure 6). Cumulative proportional emergence curves differed significantly between the coolest and warmest treatments (K-S test: 27.3°C vs. 17.8°C; $D = 0.56$, $n = 16$ and two-sided $p = 0.006$), and evidence of earlier emergence from the 21.9°C treatment compared to the coolest treatment is suggestive (K-S test: 21.9°C vs. 17.8°C; $D = 0.44$, $n = 16$ and two-sided $p = 0.065$). However, the two warmer treatments did not differ significantly

from each other (K-S test; 27.3°C vs. 21.9°C; $D = 0.31$, $n = 16$ and two-sided $p = 0.34$). Mortality rates over the course of the experiment increased with temperature (17.8°C = 75%, 21.9°C = 80% and 27.3°C = 83%), with the exception of 19.4°C (95%). Emerged adults from each temperature treatment were composited for analysis, as some microcosms had 100% mortality. The total number of adults emerged from each temperature treatment were 10 (17.8°C), 8 (21.9°C) and 7 (27.3°C). The sample size from the 19.4°C treatment was too small to include in the analysis.

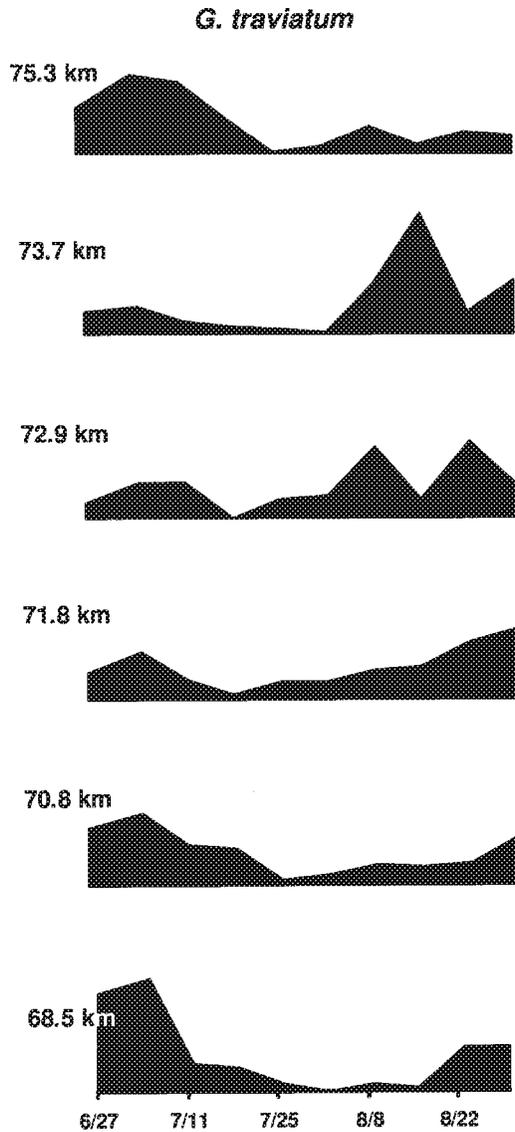


Figure 3. Emergence of *G. triviatum* from the Walla Walla River during the sample period. Vertical axes are standardized by the proportional emergence on each sample date.

DISCUSSION

Emergence timing

The similarity in emergence timing along the length of each river was unexpected given the magnitude of differences in temperature and discharge. The effect of water temperature on the metabolic rates of insects is well documented (Cummins and Klug, 1979; Ward and Stanford, 1982; Robinson *et al.*, 1983) and insects have been found to shape their life histories around discharge events (Lytle, 2001; Lytle and Poff, 2004), but elevated water temperatures and reduced discharge did not significantly influence the

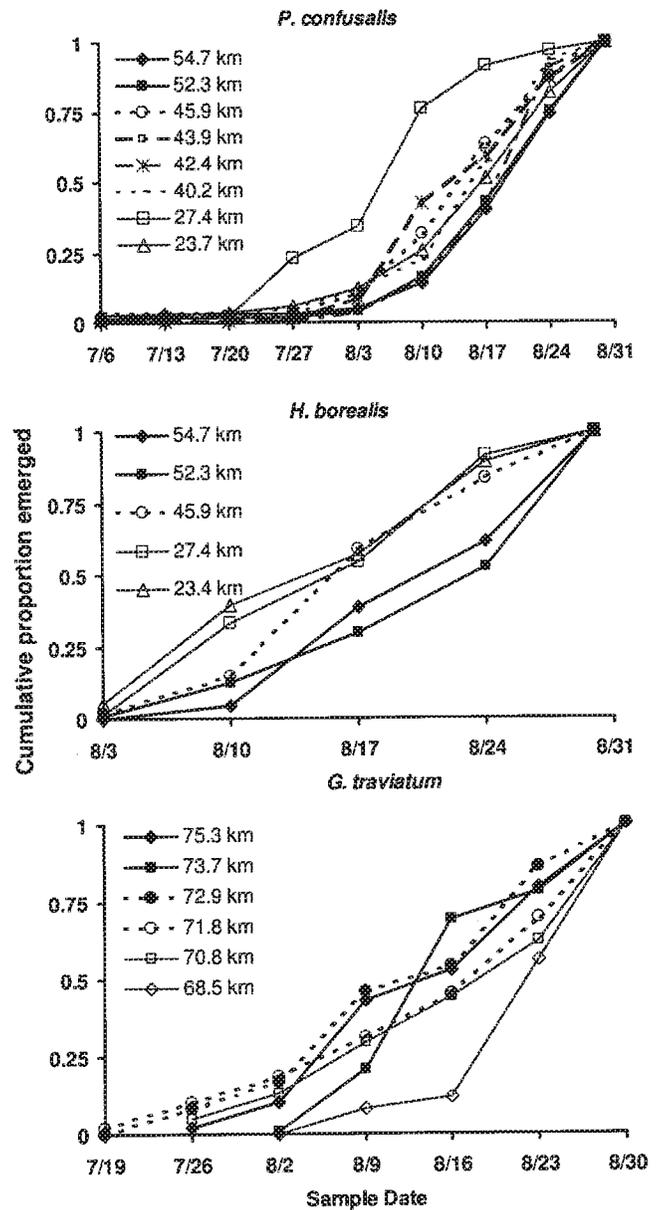


Figure 4. Cumulative proportional emergence of *P. confusalis* and the late summer peaks of *H. borealis* and *G. triviatum* at each sample site. *H. borealis* at river kilometres 43.9, 42.4 and 40.2 were excluded due to low sample sizes.

emergence timing of the species we observed at weekly sampling intervals.

The weekly sampling resolution may have been too coarse to detect small alterations in emergence timing, such as the 5 days difference observed during the *H. borealis* laboratory experiment. However, earlier emergence of aquatic invertebrates in warmer water has been demonstrated in studies with temperature differences similar to or smaller than those found in our study rivers. For instance, several mayfly

Table III. Total number of individuals collected during the entire sample period (*P. confusalis*) or the late season emergence period (*H. borealis* and *G. triviatum*), and number of males and females measured for adult body mass by sub-sampling

Site	<i>H. borealis</i> (no. of individuals)			<i>P. confusalis</i> (no. of individuals)			<i>G. triviatum</i> (no. of individuals)			
	Total emerged	Body mass		Total emerged	Body mass		Site	Total emerged	Body mass	
		Female	Male		Female	Male			Female	Male
54.7	91	20	56	586	89	127	75.3	48	23	5
52.3	482	97	111	927	88	121	73.7	100	49	24
45.9	60	14	23	208	75	90	72.9	100	31	20
43.9	8	—	—	170	47	63	71.8	145	54	45
42.4	7	—	—	148	55	54	70.8	58	21	17
40.2	6	—	—	177	66	43	68.5	25	17	6
27.4	624	115	71	294	60	87				
23.7	684	85	86	140	43	52				

Due to small sample sizes, *H. borealis* body mass was not measured at sites 40.2–43.9 km.

species initiated emergence 2–4 weeks earlier in mountain streams with average monthly temperatures a mere 1.2–1.6°C warmer year-round (Harper *et al.*, 1995), suggesting that any variation in emergence timing missed by the weekly sampling resolution in our study is comparatively small considering the gradients in temperature observed along our study rivers. Likewise, stoneflies (Harper and Pilon, 1970; Nebeker, 1971; Flannagan and Cobb, 1991; Gregory *et al.*, 2000) and a few caddisfly species (Nebeker, 1971; Hogg and Williams, 1996) emerged earlier in warmer temperature regimes, suggesting the effect of temperature may be geographically and taxonomically widespread. It also must be noted that we were unable to continue sampling beyond 1 September despite the continuing emergence of the studied taxa, and therefore the number of insects emerging after this date is unknown. We do however have confidence in our selected metric of emergence timing, as it encompasses a full 3–5 weeks of *H. borealis* and *G. triviatum* emergence, nearly captures the entire *P. confusalis* emergence peak, and is likely more representative than analysing the date of first emergence.

Scientific understanding of the mechanisms and processes behind the effects of temperature on growth and development is far from complete (Newbold *et al.*, 1994; Cabanita and Atkinson, 2006), and thus a number of factors may account for the similarity in emergence timing among sites. The three species in our study are holometabolous, while most published findings of emergence timing modified by temperature have examined hemimetabolous insect species. An important difference is that many caddisflies enter a diapause during the late larval or pupal stages (e.g. Hauer and Stanford, 1982; Martin and Barton, 1987), and this may act as a synchronizing mechanism for emergence (Otto, 1981; Hogue and Hawkins, 1991), a process unique to holometabolous life histories. If a pupal or pre-pupal

diapause of the three species in this study acted to synchronize emergence, the timing of emergence would remain unaltered among sites despite any difference in developmental rates of the larvae throughout the summer. Similar observations have been made for larval *Brachycentrus occidentalis* caddisflies along our study reach of the Umatilla River. Miller (2008) found that larval growth and development were more advanced at sites with warmer temperatures compared to sites with cooler temperatures during early and mid summer 2004 and 2005. By late summer, however, late instar growth and development had halted at the warmer sites, allowing the earlier instars at cooler sites to catch up in both developmental stage and size (Miller, 2008).

The short duration of the discharge and temperature alterations does not explain the similarity in emergence timing among sites. Discharge alteration occurred only during the summer months at our study sites, resulting in large differences in temperature in July and August only. The larvae of the studied species developed over a longer time period than the 2 months of severe temperature alteration, yet most growth occurs during the last 2–3 months of the larval stage for many aquatic insects (Hogue and Hawkins, 1991), indicating that year-round temperature alteration is not required to affect larval development or emergence timing. For instance, temperatures during the final few months of the larval stage of semivoltine stoneflies can highly influence emergence timing (Flannagan and Cobb, 1991; Gregory *et al.*, 2000), and changes in emergence timing with elevated temperatures during the final month for mayfly larvae has been documented (Harper and Peckarsky, 2006), suggesting the time period of highly divergent temperatures in our study is sufficient to alter development rates in many invertebrate species.

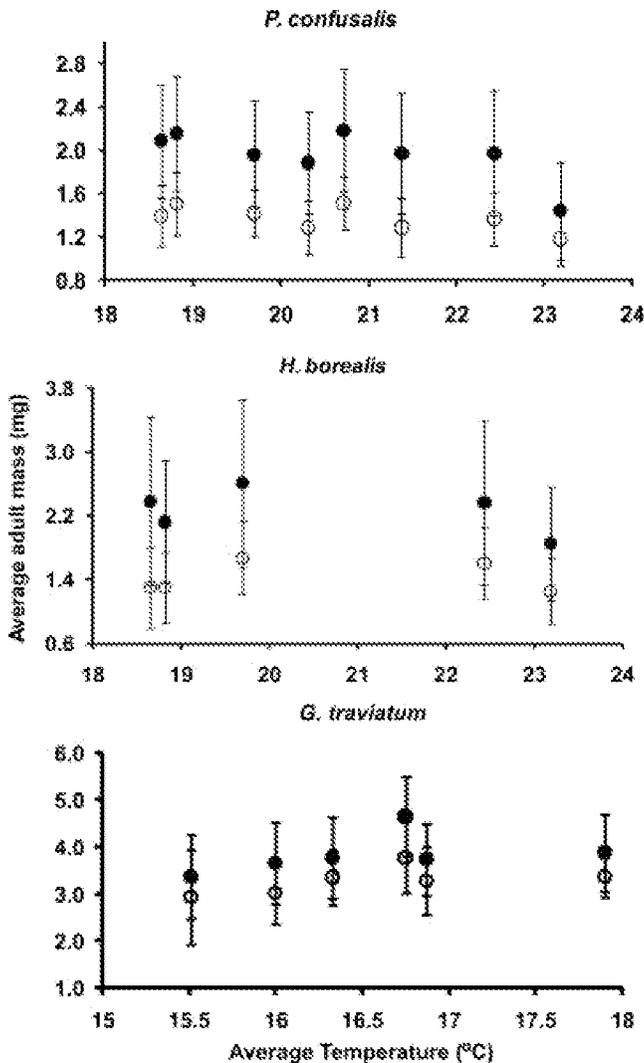


Figure 5. Average individual female (closed circles) and male (open circles) adult body mass at peak emergence at each sample site, denoted by the average water temperature of the site throughout the sampling period.

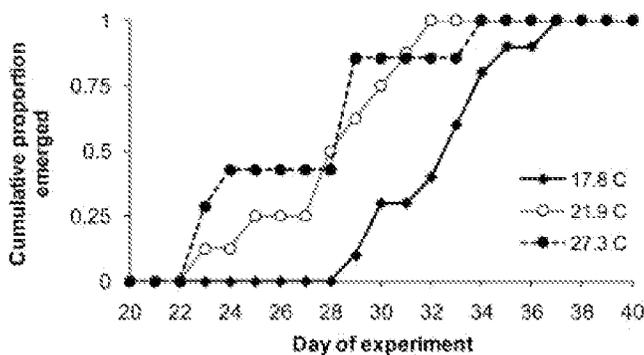


Figure 6. Cumulative proportional emergence of *H. borealis* from temperature treatments during the laboratory experiment.

Additional factors may constrain plasticity in emergence timing, including competition and emergence cues unrelated to temperature or discharge. The life histories of some aquatic insects are timed around temporal variability in food resources and the avoidance of competition (Cummins and Klug, 1979), which may limit the influence of temperature or discharge in determining the timing of emergence. However, we find this scenario unlikely, as temporal resource partitioning is common primarily in shredders rather than the grazers observed in this study (Cummins and Klug, 1979). Similarly, emergence may be influenced by additional synchronizing cues such as photoperiod (Lutz, 1968, 1974; Pritchard, 1989). However, emergence timing varied significantly in the controlled experiment despite consistent photoperiods for all temperature treatments, and photoperiod is considered secondary to temperature in governing development (Newbold *et al.*, 1994; Cabanita and Atkinson, 2006). Also, the density of predatory taxa such as trout and stoneflies has been shown to cause more rapid maturation and smaller body sizes of *Baetis* mayflies (Peckarsky *et al.*, 2001), but the densities of fish and predatory invertebrate taxa did not influence emergence timing or adult body mass in our study.

Laboratory experiment

The results of the controlled experiment indicate that temperature has an effect on the emergence timing of *H. borealis*. However, this effect was not observed in the field possibly because the weekly sampling resolution was too coarse, or because the effect of temperature was masked by environmental variables that were not measured. The effect of temperature on emergence has been observed in previous laboratory studies such as Giberson and Rosenberg (1992), who observed that the onset of emergence occurred 180 days sooner for *Hexagenia limbata* raised in water 5°C warmer. Similarly, emergence of *Baetis bicaudatus* was observed to occur significantly earlier for those larvae raised in water only 1.8°C warmer (Harper and Peckarsky, 2006). Growth has also frequently been observed to respond directly to temperature in laboratory experiments, but multiple physical and biological factors may cloud this relationship for invertebrates observed in the field (Hawkins, 1986).

The 4.1°C differences in temperature between the coolest (17.8°C) and earlier-emerging middle (21.9°C) temperature treatment was similar in magnitude to the 4.6°C range of average temperatures observed on the Umatilla River. However, the 5.4°C difference between the middle and the warmest (27.3°C) treatments yielded no further effect on emergence timing. These results suggest that the emergence of *H. borealis* responds differentially to temperature changes within the tested range, with a strong response to increasing

temperatures between approximately 18 and 22°C, and temperature increases above this reaching a physiological threshold and no longer triggering earlier emergence. If this is the case, it is curious that emergence timing did not vary in the field, where average site temperatures ranged from 18.6 to 23.2°C.

The observed pattern may be an artefact of comparing only three temperature treatments as opposed to a gradient of eight temperatures from sites on the Umatilla. The scope of inference for this experiment may also be limited, as the 17–25% survival rate is low enough to warrant caution when comparing the results to the large sample sizes collected in the field, although this mortality rate is similar to controlled experiments in other studies in which conclusions were made (e.g. Harper and Peckarsky, 2006).

Adult body size

The expected relationship between adult body mass and water temperature was found for only one species in this study, the pyralid lepidopteran *P. confusalis*. The average mass of female and male *P. confusalis* was 31 and 15% smaller, respectively, at the warmest Umatilla site (54.7 km) as compared to the coolest site (23.7 km). This decrease in body size may influence the reproductive capacity of the population at the warmest site. Fecundity of female insects is positively correlated with body size (Hinton, 1981) and larger males may be more successful at obtaining mates (Rantala *et al.*, 2001), though the effect may not be universal for all species (Taylor *et al.*, 1998). However, the emergence rate of *P. confusalis* at the impacted downstream sites is comparable to some of the less impacted upstream sites. This suggests that *P. confusalis* is capable of persisting at the impacted sites, and that the existing reproductive rate and downstream drift of insects during spring flows can mediate any loss of reproductive potential that may be due to reduced body mass.

Our results do not fully conform to common theories of how temperature influences the size of aquatic invertebrates. The temperature-size rule states that warmer water temperatures are correlated with smaller body sizes in ectotherms (Atkinson, 1994). The majority of studies on aquatic invertebrates support this concept (Atkinson, 1995), and factors such as seasonal time constraints on larval development have not explained the observed exceptions (Cabanita and Atkinson, 2006). The Thermal Equilibrium Hypothesis proposed by Vannote and Sweeney (1980) provides a mechanism for this temperature-size rule, proposing that increasing water temperatures may increase the energetic costs of respiration, thereby depressing growth rates and accelerating development. However, emergence timing remained unaltered for *P. confusalis* despite a

reduction in adult body mass at the most downstream site, and neither emergence timing nor body mass were altered for *H. borealis* and *G. triviatum*. Other studies have also found inconsistencies between the responses of emergence timing and body mass to increased temperatures; Hogg and Williams (1996) observed smaller adult body sizes for nemourid stoneflies in warmer water temperatures, but not for lepidostomatid caddisflies, despite earlier emergence of both. Hogg and Williams (1996) hypothesize that the response of body mass to temperature may be more common in hemimetabolous insects, but this is inconsistent with the markedly lower body size of the holometabolous *P. confusalis* at the site with the warmest temperatures in our study. Indeed, unlike the emergence timing results, adult body mass from our study cannot be explained by synchronized emergence through late instar or pupal diapause. While synchronized emergence will disrupt the temporal trend of decreasing body size throughout the flight season at a site, it cannot change any absolute differences in body sizes among sites (Hogue and Hawkins, 1991).

The three species in this study are present along the study reaches of their respective river and thus appear adapted to tolerate broad ranges of temperature and discharge and have life histories that are highly resistant to alteration by these two factors. Notably, *H. borealis* is tolerant of temperatures up to 36°C (Resh *et al.*, 1984) and low oxygen concentrations (Williams *et al.*, 1983), and *P. confusalis* has been found in waters up to 28°C (Tuskas, 1977). Changes in the life histories of these potentially resistant taxa may only be produced through changes in the temperature and discharge regimes more extreme than those observed in this study. Such a threshold may have been approached for *P. confusalis* at site 23.7 km, where a dramatic decrease in adult female body mass was observed.

Several additional factors may be masking the expected patterns in emergence timing and body size. Downstream drift of larvae cannot be ruled out on the Walla Walla River, but is unlikely on the Umatilla due to the long reaches of nearly still water separating the riffles downstream of river kilometre 45.9. It is possible that confounding effects resulting from the surrounding agricultural land use masked the impact of water temperatures. For example, nutrient inputs into river systems from agricultural land are common (Jarvie *et al.*, 2010). Nutrient inputs can increase the growth and development of macroinvertebrates (Cross *et al.*, 2005; Ramirez and Pringle, 2006), potentially masking the effects of other environmental variables on growth and development. However, this seems unlikely in our study systems. In both rivers agricultural lands were found throughout the study areas and thus agriculturally derived nutrient inputs should have been similar at all study sites within each river.

CONCLUSIONS

These results are novel in that we found no evidence of altered emergence timing at the weekly time scale for the three tested species and reduced body mass for only a single species, despite large gradients in discharge and water temperature from successive agricultural water withdrawals. We suspect that our results may be due to the synchronization of emergence caused by a possible diapause, and by the known tolerance of high temperatures by two of these species. Comparatively few studies have examined the role of temperature and discharge on the life histories of holometabolous species, focusing instead on hemimetabolous Ephemeroptera and Plecoptera. We submit that physiological differences between hemimetabolous and holometabolous species may prevent the relationship between emergence timing and temperature from occurring in the latter. Clearly more research is needed to elucidate any differential responses to temperature between these two life history strategies. Likewise, many studies have examined the effects of discharge and water temperature on relatively undisturbed stream systems or insects from such systems. Our results suggest that the three studied species are highly resistant to pronounced changes in discharge and temperature, and may be indicative of resistant invertebrate communities structured by decades of disturbance. It is important to note that the magnitude of discharge reduction and temperature elevation observed in our disturbed study rivers may have a much more pronounced impact on the life histories of invertebrates in small headwater streams or relatively undisturbed rivers.

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