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Three responses to small changes in stream temperature by autumn-emerging aquatic insects

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Abstract. In this experimental study, conducted in coastal Oregon USA, we examined how small increases in summer water temperatures affected aquatic insect growth and autumn emergence. We maintained naturally fluctuating temperatures from 2 nearby streams and a 3rd regime, naturally fluctuating temperatures warmed by 3–5°C, in flow-through troughs from mid-summer until autumn. We added selected abundant Ephemeroptera, Plecoptera, and Trichoptera species to the 3 treatments in late July and observed emergence until early December. We described the taxon-specific responses of the caddisfly *Psychoglypha bella* and the mayfly *Paraleptophlebia bicornuta*, both of which survived well in the troughs (67–86%), and the stonefly *Mesocapnia projecta*, which we did not collect in mid-summer but had colonized all experimental troughs by October. We observed primarily phenological rather than morphological responses to higher water temperatures. The most synchronous emergence of male and female *P. bella* and *P. bicornuta* occurred in the trough with the coolest temperatures. Only *P. bella* emerged asynchronously from the trough with the warmest temperatures. The decreases in synchrony were largely the result of earlier emergence of males. *Paraleptophlebia bicornuta* were larger and tended towards asynchrony in the trough with water (and temperatures) from their natal stream. Individuals in the trough with the warmest temperature were smaller than individuals in other troughs, but did not emerge earlier. *Mesocapnia projecta* showed greater synchrony in emergence, which occurred over a shorter interval, than the other species. When exposed to increased water temperatures, autumn-emergent taxa may be most vulnerable to trade-offs between asynchronous emergence and the probabilities for finding mates in unpredictable weather conditions.

Key words: emergence, stream temperature, phenology, *Paraleptophlebia*, *Psychoglypha*, *Mesocapnia*, hyporheos.

Insects adjust to annual variations in climate, hydrology, and temperature with remarkable phenotypic plasticity. Typical responses to water-temperature increases include altered patterns of growth and changes in life-history phenologies (Brittain 1982, Sweeney 1984, Hogg and Williams 1996, Watanabe et al. 1999, Harper and Peckarsky 2006). These 2 responses are interconnected because rates of growth and sexual maturation affect the timing and duration

of developmental stages. Phenotypes expressed by a particular species are a complex mixture influenced by basic developmental patterns (e.g., voltinism) (Mendez and Resh 2008), resource availability (Gregory et al. 2000, Griffiths and Northcote 2006), and other stressors, such as predation and parasitism (Nylin and Gotthard 1998, Peckarsky et al. 2001, Mendez and Resh 2008). Because insect phenotypic plasticity is sensitive to this wide array of factors, an experiment isolating singular influences on development could help us better understand underlying mechanisms. We focused on one critical driver, temperature, and how it affected aquatic insects at a

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crucial stage in their life history, emergence into the adult imago.

Higher water temperatures might arise because of human disturbances (Ward and Stanford 1982) that include removal of riparian shading through timber harvest (Johnson and Jones 2000), agricultural activities or urbanization (Miller et al. 2007, Brown et al. 2010), and climate change (Hogg and Williams 1996, Durance and Ormerod 2007). Warmer temperatures cause some aquatic insects to mature more quickly and at smaller sizes (Sweeney and Vannote 1978, Hogg and Williams 1996). Smaller size at emergence at higher temperatures implies that growth rate does not necessarily change in response to the increase in temperature. Thus, earlier emergence can result in smaller size. Larger size tends to confer greater fecundity to female insects (Hogg and Williams 1996, Taylor et al. 1998, Peckarsky et al. 2001) and probably confers greater mobility to males, which improves their ability to find mates (Nylín and Gotthard 1998). Thus, an earlier emergence strategy can create a trade-off between quicker development and reduced reproductive potential (Ward and Stanford 1982). However, the caddisfly *Allogamus uncutus* maintained a large body size with shorter development time, a result suggesting possible physiological compensations under varying conditions (Shama and Robinson 2006). Similarly, male *Pteronarcys* spp. emerged earlier and larger in warmed stream conditions (Perry et al. 1987, Gregory et al. 2000). In another study, *Glossosoma traviatum* and *Petrophila confusalis* showed no shift in emergence at higher temperatures (Brown et al. 2010). Therefore, morphological responses of specific taxa to increasing temperatures are not entirely predictable.

Reproductive asynchrony, occurrence of reproductively active individuals at different times within the reproductive period of the larger population (Calabrese and Fagan 2004), is sometimes associated with unstable or unpredictable environmental conditions. This kind of asymmetry ensures that at least some individuals will be able to reproduce at key favorable, if unpredictable, times (Courtney 1991, Peckarsky et al. 2001). In some species, asynchrony spans across seasons, resulting in dispersed emergence (Harper et al. 1995) or bimodal pulses within a year (Mendez and Resh 2008). With this bet-hedging strategy, a population may be choosing between spreading their risk of survival in an unpredictable environment and maintaining temporal overlap to ensure reproductive success (Waldbauer 1978). A particular kind of reproductive asynchrony, protandry, occurs when emergence of sexes has little overlap at a site during the reproductive season. Thus, phenological respons-

es to temperature may include varying the onset of emergence (Ward and Stanford 1982), its duration, or its temporal synchrony, particularly between sexes (Calabrese and Fagan 2004).

Numerous studies have been done on spring-emerging insects, but less is known about those that emerge in autumn (Anderson and Wold 1972, Brittain and Mutch 1984, Kondratieff and Lechleitner 2002). During spring and early summer, gradually increasing temperatures may be proximal cues that are seasonally correlated with upcoming periods of lower discharge and greater food availability in many streams (Durance and Ormerod 2007). These changes in resources are thought to cue larval growth (Corbet 1957) or maturation of adult tissues (Sweeney and Vannote 1981). Declining temperatures that naturally occur during autumn probably affect insect development differently than temperatures in early summer (Hogue and Hawkins 1991, Newbold et al. 1994). Moreover, risks for emerging in late autumn may be substantially different from emergence in other seasons of the year. We expected life-history patterns for autumn-emerging insects to reflect the progression of seasonal constraints encountered as they mature. In contrast to responses of spring emergents, autumn-emerging aquatic insects must be adapted to more-variable conditions of flow, decreasing daylight, and increased allochthonous and decreased autochthonous resources (Griffiths and Northcote 2006).

To explore the influence of temperature, we designed an experiment using autumn-emerging species with fundamentally different developmental characteristics (i.e., hemimetabolous and holometabolous). Because related taxa in previous studies responded to higher temperatures in the last larval instars (Giberson and Rosenberg 1994), we maximized exposure time in temperature treatments by collecting early instars of study organisms in mid-summer. We experimentally controlled for other factors and asked the following questions: 1) What is the effect of small changes in stream temperature on the timing of autumn emergence? 2) How does a small change in stream temperature affect the body size of adult autumn emergents? 3) How do altered temperatures affect the emergence timing of males and females?

Methods

Experimental troughs

We conducted the experiments from July through December 2007 at the Oregon Hatchery Research Center, Lincoln County, Oregon. We modified experimental flow-through troughs, originally constructed for hatching salmon eggs and raising trout fry, to rear

larval benthic insects. We established 3 temperature regimes (Fig. 1A) using ambient stream water from 2 adjacent streams, Carnes Creek and Fall Creek, and water from Carnes Creek that was heated with a heat exchanger (Advantage Engineering, Greenwood, Indiana). Stream temperatures in the troughs fluctuated daily and captured natural differences in temperature regimes during the study.

Fall Creek is a 3rd-order stream that flows next to the laboratory, and Carnes Creek is a 1st-order tributary that joins Fall Creek 200 m downstream of the laboratory. These streams are high-gradient and cobble-lined with riparian vegetation composed of red alder (*Alnus rubra*), big leaf maple (*Acer macrophyllum*), and Douglas-fir (*Pseudotsuga menziesii*). During summer low flows, stream temperatures were 2–3°C cooler in Carnes Creek and in the Carnes Creek troughs than in Fall Creek and Fall Creek troughs. Diurnal variations in temperature also were less in Carnes Creek than in Fall Creek. Water chemistry in the 2 streams was similar, except for higher NO₃-N in Carnes Creek (0.82 vs 0.36 mg/L NO₃-N + NO₂-N). The water intakes in Carnes and Fall Creeks were each ~500 m from the laboratory, and stream water flowed through underground pipes before entering the laboratory.

The experimental troughs were 5.4 m long × 0.4 m wide with water depth of 0.2 m. Stream water flowed constantly through the troughs at a rate of ~12 L/min. We placed temperature sensors (Stowaway Temperature Loggers; Onset Corporation, Bourne, Massachusetts) at the inlet and outlet of each trough to compare temperature among treatments and to detect if temperature variations occurred over the length of each trough. Temperatures were measured every ½ h. Full-spectrum lights in the laboratory provided light regimes standardized for 12 h on and off.

We added appropriate food resources for macroinvertebrates to all troughs. Before the experiment began, we grew algae on unglazed ceramic tiles in a separate laboratory flow-through trough with Fall Creek water. An observable film of diatoms and other algae was present after 2 wk. We collected dry fallen leaves from red alder (*Alnus rubra*) riparian vegetation and air-dried it to prevent accidental introductions of aquatic insects with the leaves. After drying, we conditioned leaves in filtered Fall Creek water for a week before placing them in experimental baskets and chambers in each trough as food for shredders and collectors.

Study taxa

The taxa we used were abundant in Carnes and Fall Creeks. Members of the mayfly genus *Paraleptophlebia* are shredders (Dietrich and Anderson 1995). Conge-

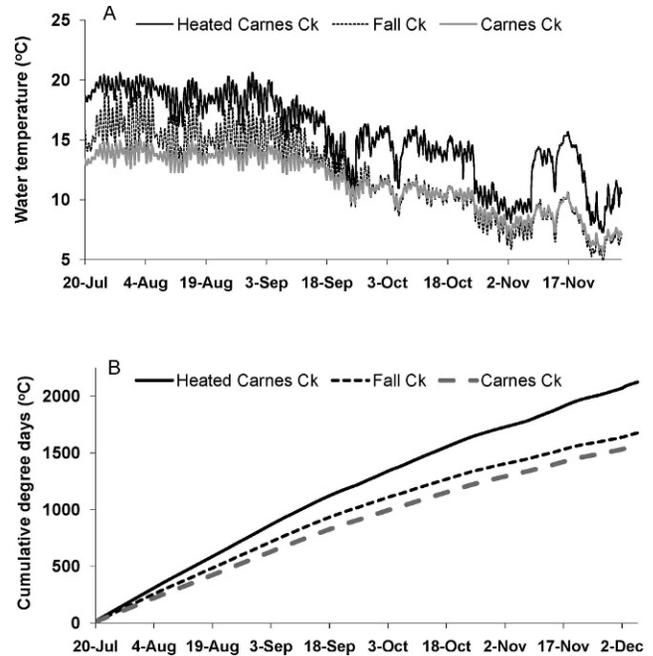


FIG. 1. Water temperatures in 3 indoor treatment troughs during the experiment. A.—Daily maxima and minima throughout the experiment. B.—Cumulative degree days using daily average temperatures through the experiment.

ners in western Oregon display a wide array of emergence patterns from spring through autumn, but a few species emerge entirely in autumn (Harper et al. 1995). *Paraleptophlebia bicornuta* used in our experiment are univoltine, tusked mayflies commonly found along the edges of slow-moving streams and rivers under silty stones (Lehmkuhl and Anderson 1971). Members of the caddisfly genus *Psychoglypha* also are shredders as larvae (Anderson 1976). Most species in this genus are cold-adapted, and adults occur in late autumn through early spring (Denning 1970). *Psychoglypha bella* collected for our experiment came from a headwater stream, but collection records for this species range widely from ditches to larger streams and lakes (Anderson 1976). Information about the capniid stonefly *Mesocapnia projecta* is limited, but it is assumed they, like other members of the genus, develop in the hyporheos and collect detrital material for food (Stark et al. 1998).

We collected *P. bella* on 11 July 2007 from Carnes Creek, transported them by bucket to the laboratory, and placed them immediately in metal baskets (2-mm mesh) submerged in each of the 3 troughs. We placed tiles with algae and a handful of incubated leaves, small gravel, and twigs in each basket and covered the baskets with an inverted mesh basket to contain emerging individuals. Each trough contained 6

submerged baskets with 11 individuals in each basket. Thus, 66 *P. bella* were introduced to each of 3 treatments.

We collected *P. bicornuta* from Fall Creek on 19 July 2007 and placed them in small chambers in each of the 3 troughs. We constructed the small chambers of 10-cm-diameter, white, polyvinyl chloride tubes with 64- μ m mesh on each end. The chambers were 21 cm long. We placed them in the troughs so that each chamber contained several cm of air as headspace for adults to emerge. We positioned chambers above the bottom of the trough so that stream water could flow through. This style of rearing chamber had been used successfully in these troughs for hatching fish eggs, so we were confident about O₂ levels and flow-through capabilities. To maximize flow, we checked the mesh screens regularly for clogging. We placed small tiles with algae and a few alder leaves in each chamber with 15 *P. bicornuta* individuals. We separated individuals by body size (small, medium, and large) into 3 chambers that were placed in each trough for a total of 45 *P. bicornuta* per treatment.

We checked baskets and chambers twice a week and collected adults and any dead individuals. We added or replaced conditioned leaves and tiles with algae twice a month. We froze emergent adults for later length and weight measurements. After each adult was defrosted, it was sexed, measured for body length (excluding antennae and cerci), dried for 24 h at 65°C, and weighed.

We did not find *M. projecta* stoneflies in Carnes or Fall Creeks during July when the other 2 taxa were collected. However, they began emerging from experimental troughs and were captured in the inverted baskets containing *P. bella* in mid-October. After they appeared in the baskets, we began collecting *M. projecta* twice a week and handled them in the same manner as other emerging adults. Because they emerged from all treatments, *M. projecta* must have been transported into the troughs with both Carnes and Fall Creek water. We do not know how long they were in the troughs, but they would have been exposed to the natural variation in temperatures between the 2 streams in situ.

Analysis

We calculated average degree days for each temperature treatment as the cumulative total of daily average temperature beginning 20 July (Fig. 1B). Within each treatment, we calculated time to emergence as the number of days from the beginning of the experiment to the date of emergence. For each species, we calculated the total emergence interval as the total

number of days over which emergence occurred for each treatment.

To compare timing of emergence among temperature treatments, we used a Kolmogorov–Smirnov test, a nonparametric test for examining differences in probability distributions. To test for differences in length and mass of emerging adults of each taxon, we used 2-way analysis of variance (ANOVA) (SigmaStat, version 2.03; Aspire Software International, Ashburn, Virginia) with temperature treatment (trough) and sex as the 2 factors. Mass of *P. bella* and *P. bicornuta* failed tests for normal distributions, so we $\ln(x)$ -transformed values for statistical testing. When the trough effect was significant in the ANOVA tests ($p < 0.05$), we made pairwise comparisons among troughs with Tukey tests.

Results

Temperature patterns

Temperatures were most different among the 3 troughs from the start of the experiment on 20 July to mid-September (Fig. 1A, B). The ambient Carnes Creek trough was the coolest (average of 13.7°C), and experienced the smallest diurnal variation (Fig. 1A) with temperatures generally ranging between 12.5 and 14.5°C during the late summer period. The Fall Creek trough had warmer maximum and minimum temperatures and the broadest range of diurnal fluctuations, with an average temperature of 15.3°C in late summer (Fig. 1A). The heated Carnes Creek trough was 5°C warmer than the ambient Carnes Creek trough with similar 2°C diurnal fluctuations and an average temperature during this summer period of 18.6°C. Temperatures did not differ >0.1°C between the inlet and outlet of the troughs within a treatment.

Concurrent with seasonal changes and the beginning of autumn precipitation, temperatures of the Fall and ambient Carnes Creek troughs converged at the end of September, but the heated Carnes Creek trough continued to be 3–4°C warmer than the other 2 troughs. Mean temperatures between 28 September and 30 November for the heated Carnes Creek trough were 12.8°C. During that interval, mean temperatures in the Fall and ambient Carnes Creek troughs were 9.6°C, and the Fall Creek trough continued to have wider diurnal fluctuations. Between 25 October and 8 November, temperatures in the heated Carnes Creek trough were only 2°C warmer than in the other temperature treatments because of a malfunction in the water heating system. During the ~4 mo of the study, the heated Carnes Creek trough accumulated 448 more degree days than did the Fall Creek trough

TABLE 1. Number of male and female *Psychoglypha bella*, *Paraleptophlebia bicornuta*, and *Mesocapnia projecta* surviving to adulthood and emerging in the 3 experimental troughs. *n* is the number of juveniles introduced to each treatment. The sex of juveniles was not known. Total includes emerging individuals whose sex was not determined.

Species	Male	Female	Total emerged	% survival	Emergence interval (d)
<i>Psychoglypha bella</i>					
Heated Carnes (<i>n</i> = 66)	35	17	57	86	45
Fall Creek (<i>n</i> = 66)	34	22	56	85	26
Carnes Creek (<i>n</i> = 66)	31	20	52	79	38
<i>Paraleptophlebia bicornuta</i>					
Heated Carnes (<i>n</i> = 45)	11	13	24	53	53
Fall Creek (<i>n</i> = 45)	6	14	21	47	70
Carnes Creek (<i>n</i> = 45)	15	15	30	67	35
<i>Mesocapnia projecta</i>					
Heated Carnes	16	21	37	–	22
Fall Creek	18	12	30	–	28
Carnes Creek	27	15	43	–	36

(1676 degree days) and 554 more degree days than did the ambient Carnes Creek trough (1569 degree days). The Fall Creek trough accumulated only 106 degree days more than the ambient Carnes Creek trough (Fig. 1B).

Insect responses to temperature

Survival to emergence varied greatly among species. *Psychoglypha bella* had the highest survival rates, and 79–86% of the individuals in the experimental troughs emerged successfully (Table 1). More male than female *P. bella* emerged in all troughs. *Paraleptophlebia bicornuta* had moderate to high survival (range: 47–67%). These mayflies originated in Fall Creek, but their greatest survival was in the ambient Carnes Creek trough (Table 1).

Comparisons between species showed differences in sexual dimorphisms among *P. bella* and *M. projecta*, regardless of trough. Female *P. bella* were, on average, 5.1 mg heavier (ANOVA, *p* < 0.001) and 0.5 mm longer than males (*p* < 0.05) (Table 2). The same dimorphism occurred in *M. projecta*. Females were, on average, 0.13 mg heavier (*p* < 0.001) and 0.8 mm longer than males (*p* < 0.001) (Table 2). Male and female *P. bicornuta* were similar in mass and length (Table 2).

No significant differences in mass were associated with trough for *P. bella* or *M. projecta*, nor did adult length differ significantly among treatments for any taxon. The only difference in body size associated with troughs was observed for *P. bicornuta*. *Paraleptophlebia bicornuta* mass was greater in the Fall Creek (their natal stream) trough (mean = 1.40 mg)

than in the heated Carnes Creek trough (mean = 0.97 mg) (*F* = 3.72, *p* < 0.05) regardless of sex.

Emergence patterns

Cumulative emergence patterns (Fig. 2A–C, Table 3) and differences in emergence intervals (Figs 3A–C, 4A–C, 5A–C) suggested taxon-specific developmental responses to increased temperature. In general, *P. bicornuta* emerged earliest, beginning 13 August, before most *P. bella* or *M. projecta* emergence began (Fig. 2A–C). The total emergence interval for *P. bicornuta* was 70 d (Fig. 2B), but most *P. bella* larvae pupated by early October, and these caddisflies began

TABLE 2. Mean (SD) individual dry mass and length for female and male *Psychoglypha bella*, *Paraleptophlebia bicornuta*, and *Mesocapnia projecta* at emergence. *F*-values are from 2-way analyses of variance for differences in mass and length between sexes, and *p*-values are included when significant.

Species	Dry mass (mg)	Length (mm)
<i>Psychoglypha bella</i>		
Females	30.0 (4.21)	17.4 (1.01)
Males	24.9 (4.58)	16.9 (1.23)
<i>F</i> -value	46.86, <i>p</i> < 0.001	4.36, <i>p</i> < 0.05
<i>Paraleptophlebia bicornuta</i>		
Females	1.2 (0.63)	8.2 (0.88)
Males	1.1 (0.36)	8.3 (0.74)
<i>F</i> -value	0.11	0.27
<i>Mesocapnia projecta</i>		
Females	0.38 (0.15)	6.8 (0.64)
Males	0.25 (0.08)	6.0 (0.45)
<i>F</i> -value	22.87, <i>p</i> < 0.001	57.75, <i>p</i> < 0.001

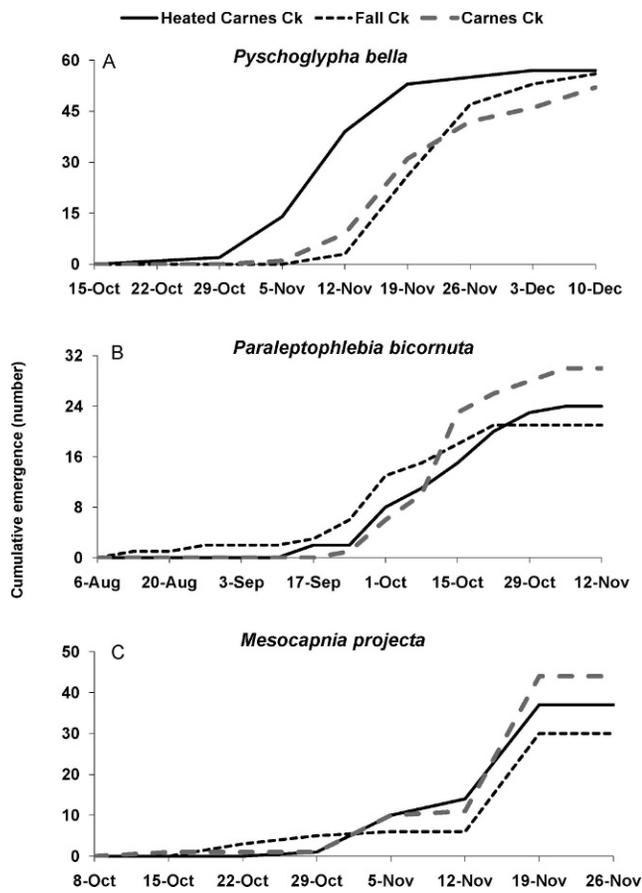


FIG. 2. Cumulative emergences of *Psychoglypha bella* (A), *Paraleptophlebia bicornuta* (B), and *Mesocapnia projecta* (C) from experimental troughs.

emerging on 12 October, with a shorter total emergence interval of 56 d (Fig. 2A). The shortest emergence interval occurred for *M. projecta*, whose emergence began on 11 October in the Fall Creek

trough and ended on 16 November, for a total emergence interval of only 36 d (Fig. 2C).

Psychoglypha bella emerged significantly earlier in the heated Carnes Creek trough than in either the Fall Creek or ambient Carnes Creek troughs (Table 4). The median number of days to emergence in the heated Carnes Creek trough was 121 d and 126 d for males and females, respectively. At cooler temperatures, the median number of days to emergence for *P. bella* was 131 to 133 d (Table 3). Protandry was pronounced in the heated Carnes Creek trough (Fig. 3A). Male *P. bella* began emerging on 19 October, 23 d earlier than the first females. In contrast, female *P. bella* emergence extended until 3 December, 14 d beyond the last male emergence. Carnes Creek was the natal stream for *P. bella*. In the ambient Carnes Creek trough, females emerged during the entire emergence interval, whereas males emerged during only 68% of the interval (Fig. 3C). In the Fall Creek trough, which averaged only 2°C higher than the Carnes Creek trough in summer and was essentially the same temperature as the Carnes Creek trough in autumn, female *P. bella* also emerged throughout the emergence interval, and male emergence overlapped female emergence for 93% of the interval (Fig. 3B).

Emergence of *P. bicornuta* occurred significantly earlier in the Fall Creek trough (its natal stream) than in the Carnes Creek trough (Table 4, Fig. 4A–C). Whereas >½ of the *P. bicornuta* males in Fall Creek trough had emerged by 27 September and females by 4 October, median emergence in the ambient Carnes Creek trough, the coldest treatment, and the heated Carnes Creek trough, the warmest treatment, did not occur until after 11 October (Table 3). Thus, *P. bicornuta* emerged earlier and heavier in the trough corresponding to its natal stream.

In addition, reduced overlap between the emergence intervals of female and male *P. bicornuta* in the Fall

TABLE 3. Median date of male and female adult emergence from temperature treatments, calculated as the number of days since the beginning of the experiment at which ½ of the successful emergents appeared. Cumulative degree days for water temperature and number of days of exposure to temperature treatment were calculated for the median date.

Species	Median emergence date		Cumulative degree days		Number of days in treatment	
	Male	Female	Male	Female	Male	Female
<i>Psychoglypha bella</i>						
Heated Carnes	9 Nov	14 Nov	1799	1866	121	126
Fall Creek	20 Nov	21 Nov	1558	1566	132	133
Carnes Creek	19 Nov	19 Nov	1440	1440	131	131
<i>Paraleptophlebia bicornuta</i>						
Heated Carnes	18 Oct	11 Oct	1552	1453	91	84
Fall Creek	27 Sept	4 Oct	1028	1109	70	77
Carnes Creek	11 Oct	11 Oct	1079	1079	84	84

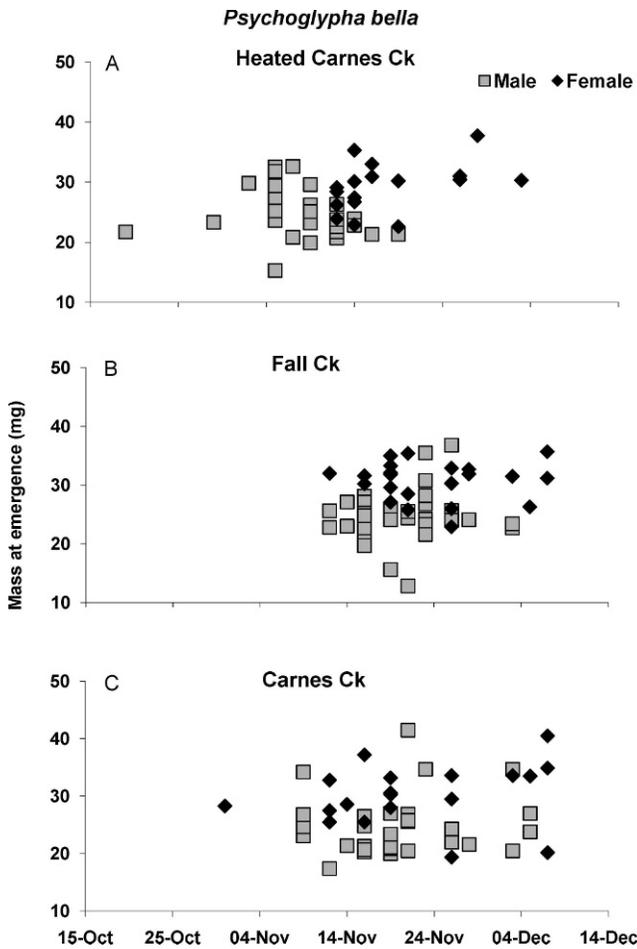


FIG. 3. Mass of individual male and female *Psychoglypha bella* by date of emergence from heated Carnes Creek (A), Fall Creek (B), and ambient Carnes Creek (C) troughs. Some symbols are obscured because sizes of individuals were similar.

Creek trough (75%; Fig. 4B) suggested a tendency toward protandry. Six of the 14 females that emerged from the trough emerged between 11 and 19 October. Thus, 40% of the females emerged after the last male, which emerged on 8 October (Fig. 4B). Low numbers of emerging males (Table 1) may have skewed this observation in the Fall Creek trough. However, males emerging from the heated Carnes Creek trough ($n = 11$) clearly overlapped with emerging females (Fig. 4A). At the beginning of the experiment, *P. bicornuta* were separated by size class in each trough because of slight differences in sizes of collected individuals, but no significant differences in timing were related to size. Medium-sized individuals at the beginning of the experiment were actually the first to emerge.

Mesocapnia projecta probably colonized the streams late in the season, so these stoneflies probably did not experience the greater temperature differences among

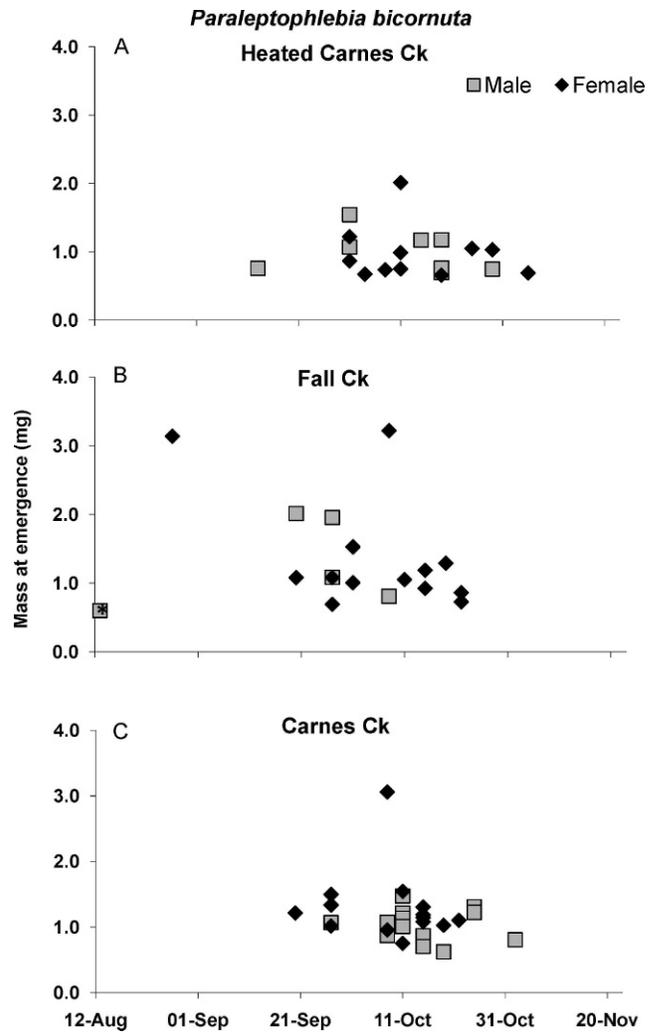


FIG. 4. Mass of individual male and female *Paraleptophlebia bicornuta* by date of emergence from the heated Carnes Creek (A), Fall Creek (B), and ambient Carnes Creek (C) troughs. Some symbols are obscured because sizes of individuals were similar. * denotes approximated mass of an individual.

troughs in the July–August period (compared to the September–November period) (Fig. 1A). Within their short total emergence interval, males emerged progressively later with warmer temperatures: 11 October in the ambient Carnes Creek trough, 19 October in the Fall Creek trough, and 25 October in the heated Carnes Creek trough. Males were present when females were emerging in all troughs (Fig. 5A–C). With the exception of singular males that emerged earlier, synchrony between sexes was strong in all troughs (Fig. 5A–C). The emergence interval for *M. projecta* was shortest in the heated Carnes Creek trough (22 d, 25 October to 16 November; Fig. 5A–C, Table 1).

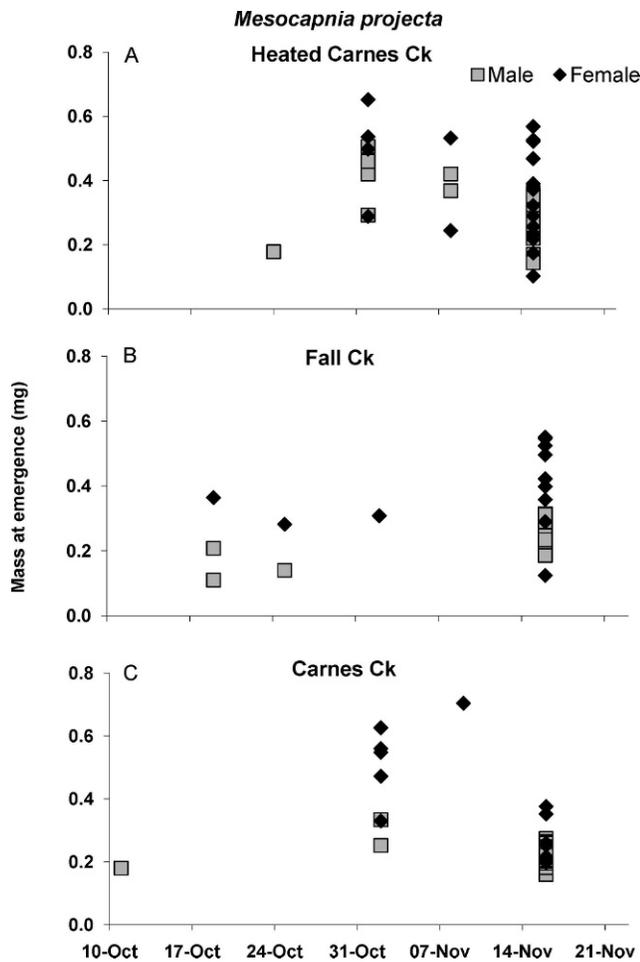


FIG. 5. Mass of individual male and female *Mesocapnia projecta* by date of emergence from heated Carnes Creek (A), Fall Creek (B), and ambient Carnes Creek (C) troughs. Some symbols are obscured because sizes of individuals were similar.

Discussion

Temperature manipulations in our study were modest and incorporated the natural temperature differences within each stream. Such modifications are similar to those associated with climate change (Durance and Ormerod 2007), but less than increases commonly observed with anthropogenic effects (Johnson and Jones 2000, Miller et al. 2007). Alterations to natal temperature regimes in laboratory troughs for >4 mo generated taxon-specific responses by *P. bella*, *P. bicornuta*, and *M. projecta*. Their varied responses, which were primarily phenological rather than morphological, illustrated the diverse strategies that autumn-emergent insects can exhibit when adjusting to warmer temperatures.

In the trough corresponding to its cooler natal stream (Carnes Creek), where diel fluctuations during

TABLE 4. Results of Kolmogorov–Smirnov 2-way comparisons of cumulative emergence between temperature treatments for the 3 study taxa.

Species	Heated Carnes vs Carnes	Heated Carnes vs Fall	Carnes vs Fall
<i>Psychoglypha bella</i>			
<i>D</i>	0.594	0.735	0.142
<i>p</i> -value	<0.001	<0.001	0.619
<i>Paraleptophlebia bicornuta</i>			
<i>D</i>	0.175	0.351	0.419
<i>p</i> -value	0.768	0.098	0.018
<i>Mesocapnia projecta</i>			
<i>D</i>	0.123	0.178	0.143
<i>p</i> -value	0.908	0.623	0.831

the summer months were small, and in the ambient Fall Creek trough, where the temperature averaged 2°C warmer, most *P. bella* emergence occurred during synchronous time intervals. Temperature increases of 5°C that persisted through pupation induced significantly earlier emergence of *P. bella* and resulted in a longer emergence interval. This result is contrary to other studies in which patterns suggested that pupal stages in holometabolous insects could act as buffers to minimize early emergence (Hogue and Hawkins 1991, Nylin and Gotthard 1998). The clearly protandrous response observed in our study may have required a threshold of cumulative degree days.

Reproductive asynchrony and protandry are risky strategies hypothesized to be responses to unpredictable disturbances (Moreira and Peckarsky 1994, Mendez and Resh 2008). In models based on reproductive strategies of different taxa, Calabrese and Fagan (2004) obtained results suggesting that reproductive asynchrony can reduce reproductive potential by: 1) reducing the average overlap in emergence between sexes while 2) increasing probabilistic failure of males before they find a mate, and 3) at low densities, stranding some females as mateless because of isolation in time. We think some of these risks would be lower in species with longer adult life spans. If *P. bella* are similar to other autumn-emerging limnephilid caddisflies in the region (Li and Gregory 1989), they probably survive in the terrestrial environment for several weeks. Total overlap between sexes may not be critical as long as enough males survive to mate with females.

Male and female insect growth rates can differ in response to environmental factors (Dietrich and Anderson 1995, Nylin and Gotthard 1998, Shama and Robinson 2009). Earlier-emerging male insects are often smaller than later-emerging females (Newbold

et al. 1994, Mendez and Resh 2008). In all troughs in our study, male *P. bella* were consistently smaller than females, and male size was not affected by temperature. The early emergence of *P. bella* males and potential protandrous tendencies in other species suggest that identifying the gender of emerging individuals is important for understanding emergence patterns. If the gender of individuals is not identified, lower biomass might be incorrectly interpreted as a temperature-specific response by a species instead of as a shift to earlier emergence by males.

Psychoglypha bella males showed phenotypic plasticity that included both earlier emergence and faster developmental times to retain body size. In a manipulative study of stream temperature in Canada, *Lepidostoma vernale* emerged 1 to 2 wk earlier when exposed to annual temperature increases of 2.1 to 2.4°C but were not reduced in size (Hogg and Williams 1996). Our results suggest that no size consequences accompanied earlier emergence for *P. bella*. Therefore, potential risks of an earlier-emergence strategy might be associated primarily with asynchrony rather than with loss in reproductive potential associated with size.

Autumn-emergent mayflies in the Cascade Range of Oregon exhibit synchronous emergence patterns (Harper et al. 1995), but in the Fall Creek trough of our study, *P. bicornuta* females emerged somewhat asynchronously. *Paraleptophlebia bicornuta* are regarded as having life histories that are essentially the same as those of *P. debilis* (Lehmkuhl and Anderson 1971) in which males survive to swarm for only 1 d. With such a short adult life span, a long emergence interval and tendency towards asynchrony probably would reduce the likelihood of finding mates (Calabrese and Fagan 2004). After examining *Baetis bicaudatus* emergence from multiple sites, Harper and Peckarsky (2006) cautioned that a difference of 4 d in the timing of emergence was a significant time interval for adult mayflies. In support of that idea, the models of Calabrese and Fagan (2004) indicated that minimal levels of protandry, only 2 d difference in emergence time, could increase the risk of extinction. Thus, the short adult lives of *P. bicornuta* would place them at high risk when asynchrony occurs, and persistence of the population may depend on high densities to overcome the reduced probability of mating encounters (Calabrese and Fagan 2004).

Mesocapnia projecta, like other *Mesocapnia* spp. (Brittain and Mutch 1984), differ from most other Capniidae in that they emerge in autumn rather than in winter. Little is known about these stoneflies (Stark et al. 1998), and our study indicates that their short, late-season emergence period and residence in hy-

porheic substrates probably contributes to the difficulty of locating them. In comparison to other taxa, *M. projecta* had the shortest emergence intervals and strong synchrony between sexes. Synchronization maximizes the opportunity for finding mates, especially in short-lived species (Brittain 1982, Dietrich and Anderson 1995). Some models suggest that organisms in stable environments may exhibit dispersed, rather than synchronous emergence (Nylin and Gotthard 1998). We assume that hyporheic habitats are stable, but *M. projecta* emergence is notably synchronous and concentrated. Developing in the constant hyporheic environment, moving into unpredictable surface waters, and emerging into the terrestrial environment probably result in a unique life-history pattern that requires more study. At present, we do not know whether this synchrony is an adaptation to autumn seasonal conditions or is characteristic of hyporheic populations in general.

The adaptive significance of *P. bella*, *P. bicornuta*, and *M. projecta* responses to increases in temperature are best understood in the context of the autumn season when they must survive to reproduce and lay eggs. In the Pacific Northwest (USA), insects emerging in autumn must be able to survive cooling air temperatures and increasing fluctuations in climatic and hydrologic conditions. In previous studies of aquatic insect responses to temperature changes, aquatic insects responded to warmer stream temperatures by emerging earlier and smaller (Sweeney and Vannote 1978, Hogg and Williams 1996). That strategy resulted in a trade-off between faster development and lower fecundity associated with smaller size. Phenotypic changes in our study were less likely to include changes in size because only *P. bicornuta* adults were smaller in the warmest trough than in the coolest trough. Instead, these autumn-emergent taxa may be more vulnerable to the trade-off between asynchronous emergence and a reduced probability for reproductive success at the onset of winter. Ultimately, the adaptive value of these phenotypic plasticities will depend on whether individuals survive the risks of autumn weather to find spatially or temporally dispersed mates.

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