

Spatiotemporal patterns of emergence phenology reveal complex species-specific responses to temperature in aquatic insects

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Funding information

Division of Environmental Biology, Grant/Award Number: DEB-1440409

Editor: Amanda Bates

Abstract

Aim: Climate change is broadly affecting phenology, but species-specific phenological response to temperature is not well understood. In streams, insect emergence has important ecosystem-level consequences because emergent adults link aquatic and terrestrial food webs. We quantified emergence timing and duration (within-population synchronicity) of insects among streams along a spatiotemporal gradient of mean water temperature in a montane basin to assess the sensitivity of these phenological traits to heat accumulation from mid-winter through spring emergence periods.

Location: Six headwater streams in the Lookout Creek basin, H.J. Andrews Experimental Forest, Oregon, USA.

Methods: We collected emerging adults of four abundant insect species twice weekly throughout spring for 6 consecutive years. We fit Gaussian models to the empirical temporal distributions to characterize peak emergence timing (mean) and duration (days between 5th and 95th percentiles) for each species/stream/year combination. We then quantified relationships between degree-day accumulation and phenological response.

Results: Only one of the four species (a caddisfly) showed a simple response of earlier emergence timing in both warmer streams and years. One stonefly had lengthy emergence periods resulting in substantial phenological overlap between warmer and cooler streams/years. Interestingly, two species (a mayfly and a stonefly) responded strongly to temporal (interannual) temperature differences but minimally to spatial differences, indicating that emergence was nearly synchronous among streams, within years. These two species had among-stream differences approaching 500 degree-days from mid-winter to peak emergence. Conversely, duration of emergence was more strongly associated with spatial than temporal differences, with longer duration in lower-elevation (warmer) streams.

Main conclusions: Emergence phenology has species-specific responses to temperature likely driven by complex cues for diapause or quiescence periods during preceding

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life cycle stages. We hypothesize a trade-off between complex phenological response that synchronizes emergence among heterogeneous sites and other traits such as adult longevity and dispersal capacity.

KEYWORDS

aquatic insects, headwater streams, life history traits, phenology, temperature

1 | INTRODUCTION

The consistent warming trend currently affecting natural systems has stimulated strong research interest in understanding thermal controls on life history traits, including the timing (phenology) and duration of life cycle events within and among populations (Parmesan & Yohe, 2003; Schwartz et al., 2012). At the population level, phenological concerns include the possibility of shifts in life history events to suboptimal timing for resource availability (Thackeray et al., 2016; Van Dyck et al., 2015), in addition to the more extreme possibility that increasing temperatures push metabolic rates and/or by-products beyond tolerable ranges (e.g. Chou et al., 2018; Galen & Stanton, 1991; Shah et al., 2017). Consequences may also occur at community and ecosystem levels, including development of temporal mismatches between trophic groups in food webs (Edwards & Richardson, 2004; Renner & Zohner, 2018; van Asch & Visser, 2007) or between plants and pollinators (Forrest & Thomson, 2011; Hegland et al., 2009).

Climate-associated phenological shifts are strong possibilities for ectotherms, plants, and other organisms whose biological rates are directly influenced by ambient temperature (Cohen et al., 2018; Van Dyck et al., 2015). For example, simple measures of accumulated "heat units," typically measured as degree-days, from the onset of growing seasons in the temperate zone are often broadly predictive of the timing of insect life cycle events such as pupation and emergence (Bartomeus et al., 2011), salmon fry emergence (Kaylor et al., 2021), and budbreak and flowering in plants (Ward et al., 2018). However, many ectotherms and plants also have periods of diapause or quiescence, during which the biological clock associated with accumulation of heat units is temporarily paused. During such periods, growth and development stop or slow substantially regardless of temperature, making thermal effects on life cycle phenology more difficult to predict. Animals for which we currently have the best physiological understanding of the interplay of thermal regime, diapause and phenological traits are mostly terrestrial insects of economic importance, typically pests or pollinators. Common environmental cues for both initiating and ending periods of diapause in insects include temperature thresholds (high or low) and photoperiod (Bean et al., 2007; Bentz et al., 2014; Forrest, 2016). Hence, the combination of degree-day accumulation rate during periods of growth and activity, and the timing and length of diapause, together are major variables useful for predicting phenological response to changes in temperature. Cues and responses can vary substantially among species, however, such that an understanding of phenological

response to temperature in one species often does not translate to another (Li et al., 2011; Marshall et al., 2020).

In aquatic insects, the timing and duration of life cycle events such as adult emergence have well-studied ecological upshots including trophic subsidies from aquatic to terrestrial systems (Anderson et al., 2019; Nakano & Murakami, 2001; Schindler & Smits, 2017). Although emergence phenology has widely appreciated consequences at the ecosystem level, the underlying physiology associated with phenological response to temperature is not well understood in aquatic insects (Woods et al., 2021). General patterns of faster development rates and earlier emergence timing with warmer conditions have been documented either in natural systems within a limited spatial extent (e.g. Baranov et al., 2020; DeWalt & Stewart, 1995; Finn & Poff, 2008; Peckarsky et al., 2000) or in controlled experiments in simplified systems (e.g. Harper & Peckarsky, 2006; Li et al., 2011; Sweeney et al., 2018). As such, general predictions associated with warming in aquatic ecosystems typically assume a simple and direct link between warmer conditions and earlier timing of life cycle events (Durance & Ormerod, 2007; Finn et al., 2014; Larsen et al., 2016; McCulloch & Waters, 2018).

However, as noted for the better studied terrestrial insects, aquatic insect phenological response to thermal regime is likely not so simple. For example, Newbold et al. (1994) used a model to show that both high- and low-temperature diapause thresholds were necessary to explain the maintenance of univoltine life cycles and nearly synchronous emergence in several mayflies along a lengthy thermal gradient in streams spanning 16° latitude. Although this model was able to explain phenological outcomes with temperature patterns as the sole input, thermal regime probably interacts with photoperiod or other environmental cues to affect phenological traits in some stream insects (Cabanita & Atkinson, 2006; Mendez & Resh, 2008). Even in some mayfly species modelled by Newbold et al. (1994), a high-temperature diapause could not be induced under laboratory-controlled thermal regimes (Funk et al., 2019). Funk et al. (2019) suggested that photoperiod likely interacts with water temperature to cue high-temperature diapause in natural streams.

Thermal regime might also influence the duration of emergence periods of some aquatic insects, with longer emergence periods associated with populations experiencing warmer conditions during growth and development (Richardson & Clifford, 1986; Li et al., 2011; Cheney et al., 2019; but see DeWalt & Stewart, 1995). A longer emergence period at the population level indicates increasing life cycle asynchrony and may be a response to unstable environments (Calabrese & Fagan, 2004; Li et al., 2011; Lytle, 2001). Alternatively,

in early-emerging insects, longer emergence periods may be an adaptive response that extends adult activity periods in years when a longer growing season is likely (Buckley et al., 2015).

We still have limited understanding of the direct impact of thermal regime on phenological traits in aquatic insects, but streams are ideal systems for detailed investigation. Stream networks are natural mosaics of habitat conditions, including temperature (Ebersole et al., 2003; Johnson, 2004; Uno & Power, 2015; Ward & Stanford, 1982). Mountain stream networks in particular contain a mosaic of local, reach-scale thermal environments thanks to elevational gradients, shading, substrate, and heterogeneity of hydrological sources to headwaters (Hotaling et al., 2017; Rupp et al., 2020; Ward, 1994). Furthermore, the topographical complexity of mountain landscapes coupled with interannual heterogeneity of weather results in thermal conditions in one year that are rarely predictive of thermal conditions in the next (Bales et al., 2006; Reiter et al., 2020). As such, mountain stream networks should be useful settings for documenting phenological response along thermal gradients, both spatially and temporally, while controlling for photoperiod and other local/regional-scale environmental cues.

Here, we documented emergence timing and duration of four spring-emerging aquatic insect species from six headwater streams within a fifth-order stream network of the Cascade Range, USA, for 6 consecutive years. High spatial and temporal variability in thermal conditions allowed us to address the overarching question: Is

emergence phenology of common stream insects predictable based strictly on differences in heat accumulation from mid-winter, across both space and time? We focused efforts on spring-emerging insects because environmental conditions in the study region are predicted to be highly responsive to changing climate during this season (Cook et al., 2012; Safeeq et al., 2013; Wu et al., 2012). Additionally, spring-emerging insects are likely to be directly responsive to thermal influences during the transition between winter (when diapause or quiescence is most likely to occur) and the peak growing season. This study was conducted in coordination with other research into spring phenological events across trophic levels in the same basin, including plant budbreak (Ward et al., 2018), terrestrial insect activity (Schmidt, 2019), and bird arrival and dispersal (Frey, Hadley, and Betts, 2016).

Because we had minimal understanding of the potential physiological drivers of emergence phenology for our study taxa, for each species we tested two basic and plausible hypotheses addressing the influence of water temperature on (1) *timing* of emergence and (2) *duration* of the emergence period (Figure 1). H1: Adult emergence timing responds directly to water temperature, such that warmer streams in the network and warmer years yield predictably earlier emergence. H2: Duration of emergence period is longer in warmer streams in the network and in warmer years. For both hypotheses, we quantified “warmth” as heat accumulation in degree-days (DD) from a mid-winter period of reduced ecosystem-scale metabolic rates through the early summer growing season.

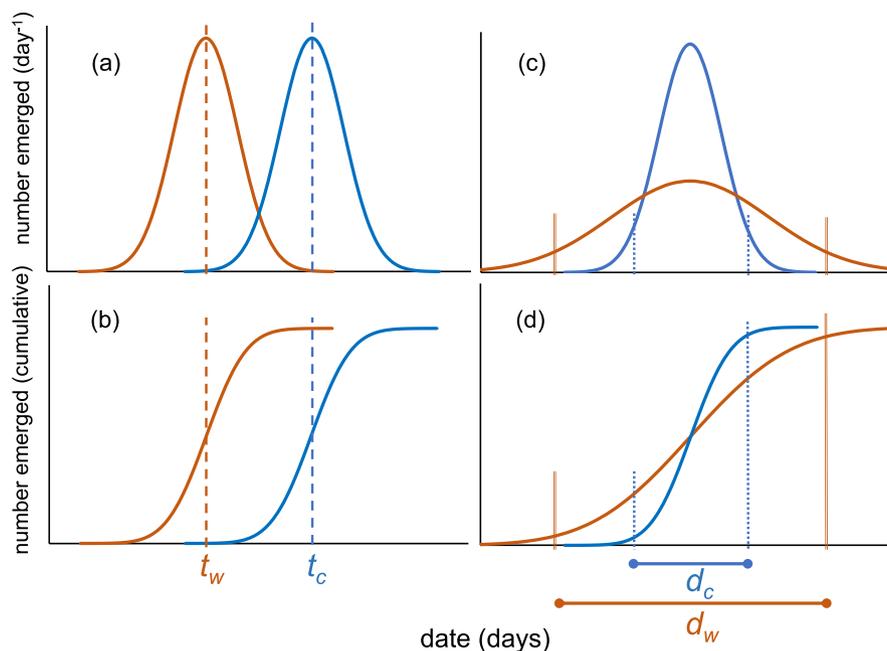


FIGURE 1 Hypotheses and our definitions of two traits: peak emergence *timing* (t) and *duration* (d) of emergence period. Blue curves and variables indicate cooler (c) streams or years; orange curves and variables indicate warmer (w) streams or years. Panels (a) and (b) represent Hypothesis 1 with distributions presented in two ways: (a) absolute, and (b) cumulative emergence through time. Vertical broken lines illustrate our definition of “peak” emergence timing as the mean ordinal date from fitted Gaussian curves. Panels (c) and (d) represent Hypothesis 2, again with distributions presented as absolute (c) and cumulative (d) emergence. Here, both curves in each panel have the same peak emergence timing, but emergence duration as the number of days between the 5th and 95th percentiles of the Gaussian models is longer in the warmer than in the cooler stream or year. Vertical dotted lines represent 5th and 95th percentiles for the cool stream/year; vertical double-lines represent 5th and 95th percentiles for the warm stream/year

2 | METHODS

2.1 | Study sites

This study took place in six headwater streams of the Lookout Creek basin in the H.J Andrews Experimental Forest (Oregon, USA; Figure 2). Dominant overstorey vegetation is Douglas fir (*Pseudotsuga menziesii*), with riparian woody vegetation of Douglas fir, western red cedar (*Thuja plicata*), red alder (*Alnus rubra*) and big leaf maple (*Acer macrophyllum*) (Frady et al., 2007). Each of the six focal streams was first or second order at the 1:24,000 scale, and streams spanned a range of elevations (457–1010 m) and two major categories of surrounding forest age (Table 1). Annual precipitation in the Lookout Creek basin averages 2285 mm, with the majority occurring as winter rainfall (October through April). Higher-elevation locations in the basin experience winter snowfall that typically melts during the season, and lower elevations experience winter snow only sporadically. Thermal regimes vary among streams with differences in basin area, elevation and hydrology. The six study streams spanned a wide range of environmental conditions in the basin (Table 1), including one with spring-fed base flow generating stable, cold temperature and flow year-round (Stream E, “Cold Creek,” Figure 3) and one with a small basin area and bedrock substrate, often drying down to disconnected pools by late summer (Stream F, “South Creek”). We collected data from 30-m reaches at each of the study streams and will henceforth refer to these locations as “streams,” which are coded alphabetically (A–F) in order of increasing elevation (Table 1).

2.2 | Focal species

We selected the four most abundant, spring-emerging species from the orders Ephemeroptera, Plecoptera, and Trichoptera (“EPT”) across the six study streams. Prior studies in the region have shown spring–summer adult emergence phenology for each. *Neoleptophlebia temporalis* (McDunnough, 1926; Ephemeroptera: Leptophlebiidae) populations have emergence periods ranging from April to June at lower elevations (Lehmkuhl & Anderson, 1971) and May to July at higher elevations in the study region (Farrand, 2004; Harper et al., 1995). *Alloperla fraterna* Frison, 1935 (Plecoptera: Chloroperlidae), emergence timing also appears to vary with elevation and latitude, with April–June emergence documented at low elevations in Northern California and Oregon (Bottorff & Bottorff, 2007; Kerst & Anderson, 1974), emergence extending to mid-July at an intermediate elevation in Lookout Creek (Farrand, 2004), and May–August emergence at higher elevations on Mt. Rainier in Washington state (Kondratieff & Lechleitner, 2002). A second stonefly *Moselia infuscata* (Claassen, 1923) (Plecoptera: Leuctridae) has longer emergence periods, from February through May in three western Oregon basins (Progar & Moldenke, 2009) and March–August across multiple streams around Mt. Rainier (Kondratieff & Lechleitner, 2002). The caddisfly *Dolophilodes dorca* (Ross, 1938) (Trichoptera: Philopotamidae) in the western Oregon Cascades

emerges in May/June through August (Anderson et al., 1984; Farrand, 2004), and a few emergent *D. dorca* were also documented at Mt. Rainier in July and August (Ruiter et al., 2005).

We assumed all four species to be univoltine because each had single narrow or broad annual emergence periods in other studies from western Oregon (Anderson et al., 1984; Harper et al., 1995; Kerst & Anderson, 1974; Progar & Moldenke, 2009). However, just one of the four species (the mayfly *Neoleptophlebia temporalis*) has been confirmed to be univoltine (Lehmkuhl & Anderson, 1971). *Moselia infuscata* has also been considered univoltine (Banks et al., 2007; Muchow & Richardson, 2000), but no published life cycle information is available to confirm. Diapause has not been evaluated for any of our focal species but is common in Plecoptera in egg or nymph stages (Bogan, 2017; DeWalt & Kondratieff, 2019), and some Trichoptera diapause in egg, larval or adult stages (Holzenthal et al., 2015). Ephemeroptera are not known to diapause as nymphs or adults, but egg diapause has been documented in a few species (Sartori & Brittain, 2015). Henceforth, we refer to the four focal species by their generic names.

2.3 | Data collection

Temperature dataloggers (HOBO Pro V2 U22-001, accuracy 0.2°C, Onset Computer Corporation) were programmed to record instantaneous temperature at half-hour intervals, placed in protective flow-through housings, and secured in each of the six study streams. All data were downloaded twice yearly, archived, and compiled at the end of the study into a single file for each stream. Following the statistical procedure detailed by Frey, Hadley, Johnson, et al. (2016), we quality checked all data from 1 January 2009 through 31 July 2014 to flag any outliers and gaps. Unflagged half-hourly data were then averaged to an hourly time step, and linear regression relationships among all six streams were quantified. We also calculated regressions with hourly water temperature data from eight other nearby streamflow gauges in the Lookout Creek basin (<https://doi.org/10.6073/pasta/9437d1603044f5b92189110dd8343763>; Gregory & Johnson, 2019). Data flagged as anomalous or missing from our six study streams for the 6-year duration of the study (<2% of all values) were then replaced or filled according to the resulting best-fit regressions (see Appendix S2 for an example). We then converted the hourly temperatures to daily means to calculate degree-days (as described below). All final hourly temperatures are publicly available (<https://doi.org/10.6073/pasta/7dc5e1f888281081de71818082bd0c78>; Johnson, 2017).

We collected emergent insects in each stream/year throughout the spring and early summer season with four emergence traps deployed per stream (Frady et al., 2007). Each trap covered 0.3 m² of stream surface and consisted of a pyramidal PVC frame draped with no-see-um netting. At the top of each trap frame, we suspended an insect collection cup containing propylene glycol with a few drops of unscented biodegradable soap. Traps remained in place from a mean start date of 18 April to a mean stop

H.J Andrews Experimental Forest

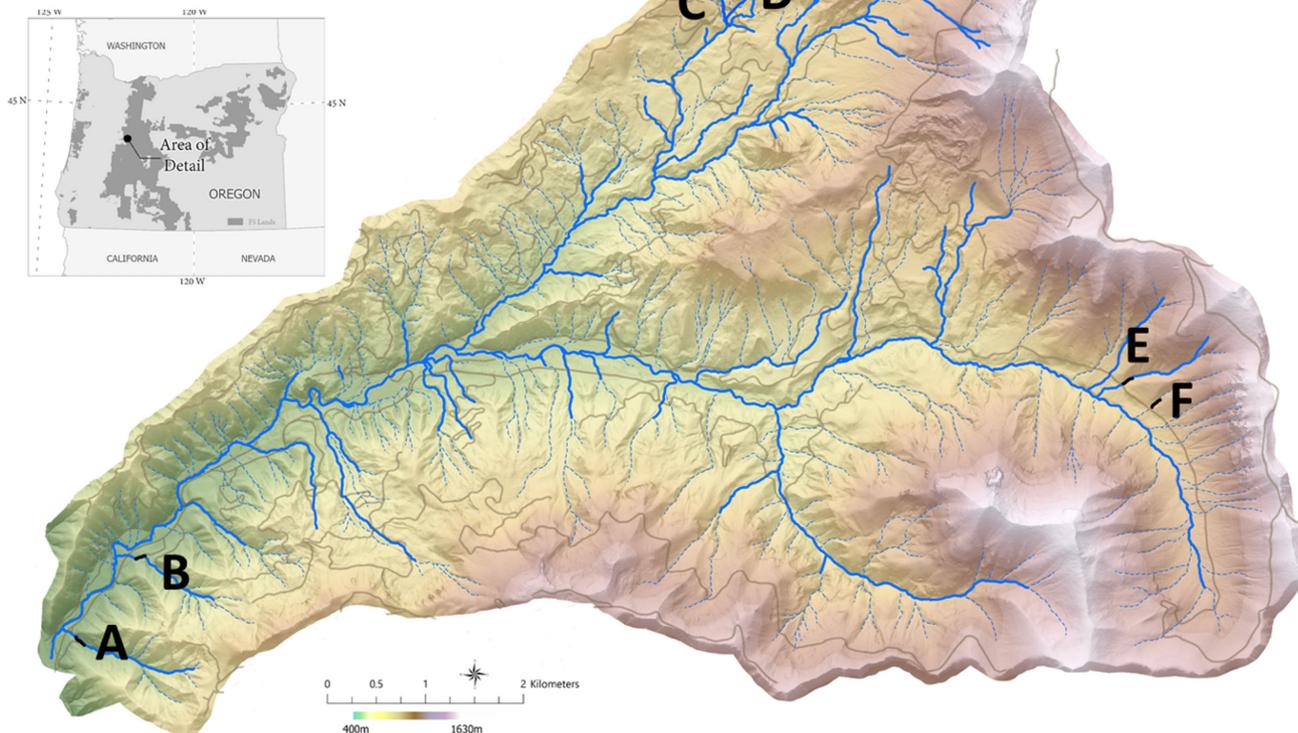


FIGURE 2 Map of the stream network in the Lookout Creek basin with six focal headwater stream reaches (Streams A–F) marked. Broken line for Stream F indicates surface water is usually reduced to disconnected pools by late summer. See [Table 1](#) for additional information about study streams

date of 1 July (Appendix S1) in each of the six years (2009–2014), with collections typically retrieved every 3–4 days for the duration of the study period. Annual start date was delayed at the two highest-elevation streams in some years when late-season snow prevented access, particularly in the coldest year of study (2011, [Table 1](#)). On each retrieval date, we used a 250- μm sieve to filter insects from the preservative and aspirated any additional individuals remaining in the trap mesh. Specimens were then preserved in 95% ethanol and transported to the laboratory for identification and enumeration.

2.4 | Data analysis

We used mean daily water temperature for each stream throughout the study period to calculate cumulative degree-days (DD) from ordinal date 1 (1 January) to 189 (8 July in nonleap years). Cumulative DD to ordinal date 189 represented how warm each stream/year was, in terms of heat-unit accumulation, from mid-winter throughout the observed spring emergence period. We also calculated the

total DD accumulated to peak emergence date (described in the following paragraph) for each species/stream/year combination.

Many insects have emergence patterns that can be described by a normal (Gaussian) distribution of abundance of emergent adults through time (e.g. Harper & Peckarsky, 2006; Li et al., 2011). For each of the four focal species at each stream/year, we used a maximum likelihood routine in MATLAB (MathWorks, Inc.) to fit a parametric model to our empirical observations of numbers of emergent adults through time. Code for the model is available from Warren et al. (2012). From each fitted model, we used the mean ordinal date to represent the “peak” emergence timing for each species/stream/year, and we extracted the 5th and 95th percentiles of each distribution to represent endpoints for describing a standardized duration, in days, of emergence period for each species/stream/year ([Figure 1](#)). Data were discarded for any individual species/stream/year combination that did not fit the model, typically due to low sample size (too few emergent adults collected). If peak emergence timing modelled for a particular species/stream/year fell later than the final date of empirical field sampling, we also removed that data point from further analysis. This latter issue was primarily faced during the coolest

TABLE 1 Site description and mean annual water temperatures (°C) of the six study streams

Stream	HJA ^a name	Elevation (m.a.s.l.)	Drainage area (ha)	Forest relative age	Mean annual temperature range (°C) ^b	2009 (°C)	2010 (°C)	2011 (°C)	2012 (°C)	2013 (°C)	2014 (°C)
Stream A	WS1	457	90	Young	2.8–14.9	7.5	7.6	7.0	7.3	7.8	8.2
Stream B	WS2	487	85	Old	3.8–12.8	7.2	7.1	6.4	7.2	7.5	7.8
Stream C	WS7	940	15	Young	3.2–12.9	6.0	6.2	5.5	5.7	6.1	6.9
Stream D	WS8	964	21	Old	1.8–14.8	5.2	5.3	4.3	4.9	5.4	6.2
Stream E	Cold Creek	1,005	70	Old	0.8–9.1	4.1	4.5	3.5	3.9	4.1	4.9
Stream F	South Creek	1,010	19	Old	0.9–14.1	4.4	4.4	3.5	4.0	4.6	5.4

Note: Forest relative age is at the basin scale, with old-growth forests ("Old") 450–550 years old and young-growth forests ("Young") 40–50 years following forest harvest. Cross-site mean temperature values (°C) per year 2009–2014 were 5.7, 5.9, 5.0, 5.5, 5.9 and 6.6 respectively. Cross-year mean temperature values (°C) by stream were 7.6 (Stream A), 7.2 (Stream B), 6.1 (Stream C), 5.2 (Stream D), 4.2 (Stream E) and 4.4 (Stream F).

^aHJA—H.J. Andrews Experimental Forest. HJA name refers to alternative names of the basins used in prior studies (WS—"watershed")

^bCalculated using full years of data 2009–2013.

sample year (2011) for the stonefly *Moselia* (which exhibits a relatively long emergence period, Table 2).

We used analysis of variance (ANOVA) with each of the four focal species to summarize and address whether overall patterns of three phenological traits varied consistently among the six streams in the Lookout Creek basin. The first set of ANOVAs used the modelled ordinal date of peak emergence as the response variable (*timing*). The second set of analyses addressed whether *duration* of the emergence period varied, and the third asked if DD accumulated from ordinal date 1 through the peak emergence timing varied among streams, for each species. In each of these ANOVAs, replicates were sample years within streams. We assessed significance at $\alpha = 0.05$.

We then used Analysis of Covariance (ANCOVA), with ordinal date of peak emergence for each species/stream/year as the phenological response variable to ask if there were consistent negative relationships between peak emergence timing and temperature. In a first set of ANCOVA, we used stream as the categorical independent variable and DD accumulated through ordinal date 189 as the covariate, for each of the four focal species. If slopes of the relationships were significant and negative, we interpreted this as evidence in support of H1 (earlier emergence in warmer conditions). Under the same hypothesis, we also expected a similar species-specific response among streams; therefore, we did not expect ANCOVA intercepts to be different. If slopes of the relationships between DD accumulation and ordinal date of emergence were not statistically different from zero (tested with 95% confidence intervals around slope values), we could not reject the null hypothesis and could infer that temperature alone was not strongly predictive of emergence timing.

Following an unexpected observation of significant slopes within streams but significantly different intercepts among streams for two of the four focal species (*Alloperla* and *Neoleptophlebia*), we ran a second set of ANCOVA in which we again used ordinal date of peak emergence for each species/stream/year as the response variable and DD accumulated through ordinal date 189 as the covariate, but with year instead of stream as the categorical independent variable. Under H1, we expected slopes of the relationships between DD accumulation and ordinal date of emergence to be significantly negative both within sample years (among streams of different temperature) and within streams (as above, among years with different temperature). Between the two ANCOVAs, if just one of the two sets of slopes was significant, this result would indicate that temperature influenced emergence timing but in a more complex manner than stated in H1.

3 | RESULTS

In spring and early summer seasons of years 2009–2014, we collected a total of 8888 emergent adults of the four focal species across the six headwater streams in the Lookout Creek basin. Across all streams and years, the most abundant of the emergent EPT species was *Alloperla* (46% of all individuals of the four species), second most abundant *Moselia* (28%), third most abundant *Neoleptophlebia*

(19%) and fourth most abundant was *Dolophilodes* (7%) (Appendix S1). Emergent *Dolophilodes* were rarely trapped at the two highest-elevation streams but were collected in sufficient numbers at the remaining four streams to be included in the statistical analyses.

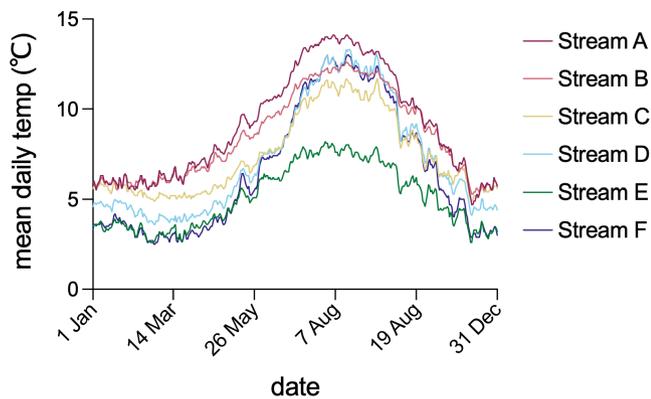


FIGURE 3 Mean daily water temperature for each of the six streams across the 6 years of the study period. Note: mean daily values for dates 1 Aug to 31 Dec are based on 5 years of data (2009–2013) because the study ended after July 2014 (the 6th year of study)

Based on differences in elevation, hydrology and forest age, the six study streams ranked approximately as expected according to overall mean water temperatures (lowest at the spring-fed Stream E and highest at the lowest-elevation Stream A with young forest) and annual temperature range (lowest at spring-fed Stream E and highest at the summer-drying Stream F; Table 1; Figure 3). Temperature patterns also varied among the 6 years of the study, with 2011 the coolest year and 2014 the warmest (Table 1).

Gaussian models fitted 87% (125) of the 144 possible species/stream/year emergence datasets. These models allowed us to extract ordinal dates of peak emergence and duration of emergence (Table 2) to be used as response variables in further analysis. Most of the problems with model fitting were due to small sample size, particularly of *Dolophilodes* from the two highest-elevation streams. In a few cases, species/stream/year combinations were removed from analysis due to modelled peaks occurring later than the empirical sampling period (primarily 2011 data for *Moselia*).

For three of the four focal species, mean ordinal date of peak emergence did not vary strongly among the six streams, despite the spatial differences in temperature (Figure 4a). The exception was the caddisfly *Dolophilodes*, which showed significant ($p = .0009$)

TABLE 2 Ordinal dates of peak emergence timing and duration of emergence for each stream and year

Species	Year	Stream A	Stream B	Stream C	Stream D	Stream E	Stream F
<i>Dolophilodes</i>	2009	158 (142–174)	165 (153–178)		174 (173–175)		
	2010	154 (135–172)	168 (155–182)	178 (175–181)	177 (174–181)		
	2011	172 (151–193)	173 (158–187)	185 (184–187)	187 (184–190)		
	2012	163 (143–184)	169 (157–182)	177 (171–183)			
	2013	150 (128–172)	158 (147–169)	171 (164–177)	175 (167–182)		
	2014	154 (121–187)	158 (126–190)	167 (155–178)	170 (161–178)		173 (165–181)
<i>Moselia</i>	2009	132 (97–168)		146 (113–178)	144 (118–170)	156 (143–169)	153 (134–170)
	2010	135 (77–193)	110 (96–125)	159 (94–224)	123 (104–142)	128 (117–140)	127 (117–136)
	2011	119 (71–168)	129 (85–174)				
	2012	117 (100–134)	120 (87–152)	120 (98–143)	126 (110–142)	130 (114–146)	140 (124–156)
	2013	104 (90–119)	108 (97–120)	120 (110–129)	124 (112–136)	120 (106–133)	135 (104–166)
	2014	103 (90–115)	104 (88–119)	136 (84–189)	126 (91–161)	119 (97–141)	137 (98–175)
<i>Alloperla</i>	2009	155 (140–169)	156 (147–166)	162 (154–169)	166 (158–173)	167 (160–174)	164 (157–172)
	2010	172 (154–190)	166 (152–179)	170 (155–184)	173 (161–184)	172 (165–179)	177 (171–184)
	2011	176 (155–197)	168 (154–182)	179 (169–189)	182 (174–189)	179 (169–189)	184 (178–189)
	2012	176 (150–203)	164 (150–178)	178 (167–189)	178 (168–189)	173 (163–184)	179 (167–191)
	2013	159 (141–177)	158 (142–174)	169 (157–181)	173 (159–187)	170 (152–188)	167 (154–179)
	2014	151 (130–172)	151 (132–170)	160 (148–171)	162 (151–174)	164 (153–175)	162 (151–174)
<i>Neoleptophlebia</i>	2009	159 (129–188)	160 (144–177)	159 (141–177)	161 (147–175)		177 (161–193)
	2010	160 (120–200)	163 (143–183)	165 (145–186)	172 (157–186)	172 (159–186)	179 (172–186)
	2011	183 (136–230)	168 (155–181)	173 (159–187)	185 (167–204)	179 (164–194)	183 (177–189)
	2012	170 (129–212)	159 (142–176)	172 (154–190)	179 (156–201)	172 (162–182)	180 (172–188)
	2013	151 (124–177)	161 (141–182)	163 (144–181)	167 (153–182)	163 (155–171)	168 (157–179)
	2014	151 (112–190)	161 (122–201)	157 (140–173)	162 (138–186)	161 (151–171)	165 (150–179)

Note: In parentheses are ordinal dates of 5th and 95th percentiles of the emergence distributions. Blank cells indicate models that could not be fit due to low sample size or models discarded due to estimated emergence peaks falling after empirical sampling was terminated for that year.

differences in emergence timing among sites with a pattern of earlier emergence in warmer (lower elevation) streams. Across all streams, peak emergence timing occurred between ordinal dates 150–187 for *Dolophilodes*, *Alloperla* and *Neoleptophlebia*. The stonefly *Moselia* on average showed an earlier peak emergence than the other three species, although there was substantially more variation around the modelled peak timing for *Moselia* owing to the longer duration of its emergence period.

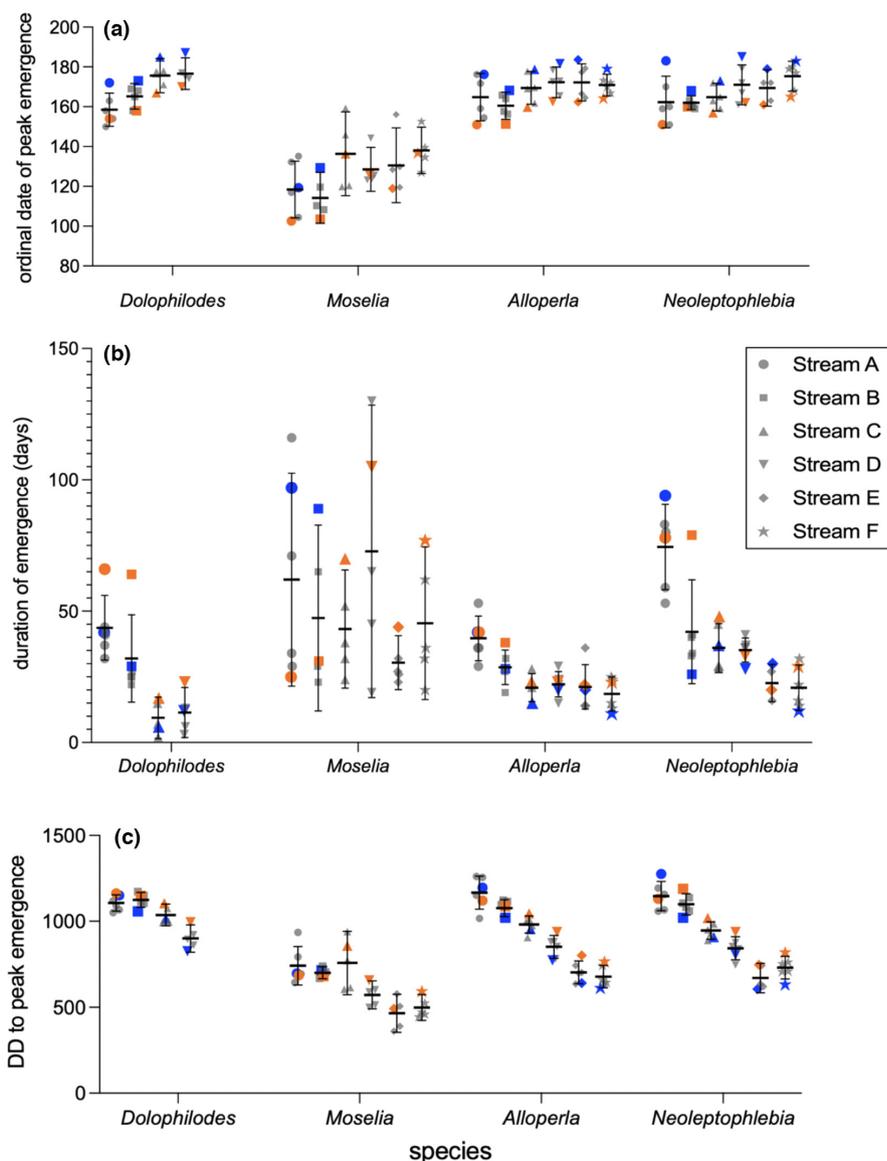
Of the four species, *Moselia* had the longest emergence duration (mean 50.6 days between the 5th and 95th percentiles of the distributions; Table 2, Figure 4b). *Dolophilodes* (25.0 days) and *Alloperla* (25.2 days) had the shortest emergence duration, with *Neoleptophlebia* of intermediate mean duration (39.0 days). In contrast to the results for peak emergence timing, the duration of emergence periods varied significantly among streams for *Dolophilodes*, *Alloperla* and *Neoleptophlebia*, with an overall pattern of longer emergence duration at lower-elevation streams (Figure 4b). For *Moselia*, duration of emergence exhibited greater variability around

the means for individual streams than did those for the other three species, and there were no discernible differences among streams, but the coldest stream (E) had substantially lower variation around the mean than the other five streams.

For all four species, cumulative degree-days from ordinal date 1 to peak emergence timing varied significantly among streams, with populations occupying colder streams requiring substantially fewer DD for development to the adult stage than populations occupying warmer streams (Figure 4c). Mean DD to peak emergence ranged 900–1107 for *Dolophilodes* (across just the four lowest-elevation streams); and 465–758 for *Moselia*, 678–1167 for *Alloperla*, and 670–1147 for *Neoleptophlebia* across all six streams.

Across all streams and years of data collection, there was an overall trend of earlier timing of peak emergence with more accumulated heat (cumulative degree-days through ordinal date 189, henceforth “temperature”) for each of the four species (Figure 5, Table 3 “DDrate” effect). However, ANCOVAs revealed three unique, species-specific patterns based on the relationship

FIGURE 4 (a) Timing of peak emergence varied among species but did not vary strongly among streams. For each of the four species, peak emergence timing is grouped by stream, and points within streams represent different years. (b) Duration of emergence periods calculated as number of days between 5th and 95th percentiles of Gaussian models for each stream/year and for each of the four species. For each species, emergence durations are grouped by study stream, and points within streams represent different years. (c) Degree-days (DD) accumulated to peak emergence date varied spatially, with higher-elevation streams on average requiring significantly fewer DD, especially in the “Pattern 3” species (*Alloperla* and *Neoleptophlebia*). In each panel, horizontal lines for each species/stream are means; error bars are 95% confidence intervals. Points marked in orange are from the warmest sample year (2014); points in blue are from the coolest sample year (2011). Points only plotted for species/stream/year with fitted normal distributions. *Moselia* was missing 2011 data for streams C–F because modelled peak emergence occurred later than the empirical collection period in the coolest year, and those data were discarded



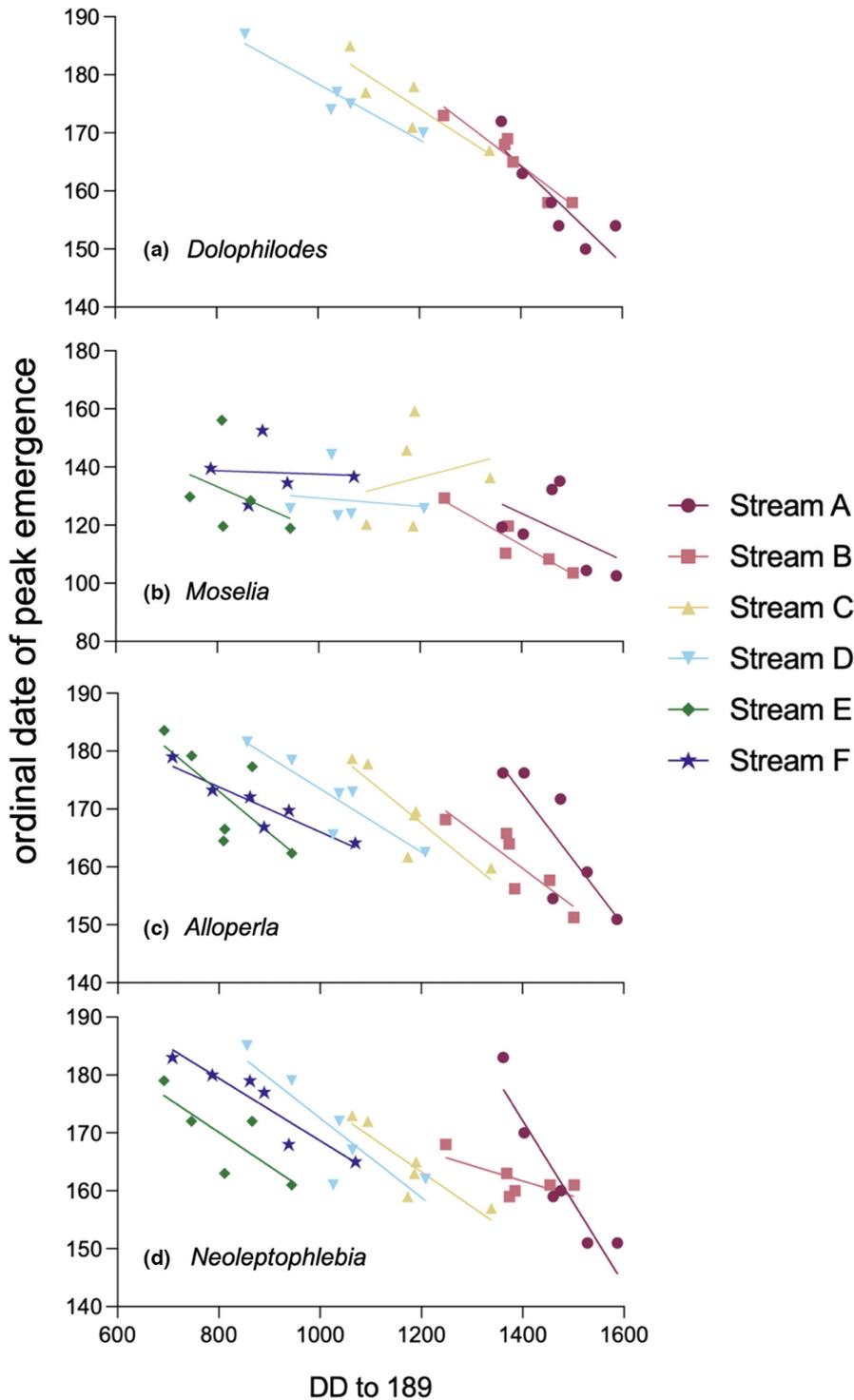


FIGURE 5 Plots of ordinal date of peak emergence versus temperature as cumulative degree-days (DD) through mid-year (ordinal date 189) for all stream/year combinations for which Gaussian models could be fit. (a) *Dolophilodes dorca*; (b) *Moselia infuscata*; (c) *Alloperla fraterna*; (d) *Neoleptophlebia temporalis*. Note difference in Y-axis scale for earlier-emerging *Moselia*. Lines are best-fit linear regressions for each stream. See Tables 3 and 5 for statistical results

between temperature and peak emergence timing. The caddisfly *Dolophilodes* exhibited an overall significant negative relationship between temperature and emergence timing temporally (year-to-year) and spatially among streams in the basin; that is, *Dolophilodes* emerged predictably earlier both in warmer years and within years in warmer streams (Figure 5a). The second observed pattern was for the stonefly *Moselia*, which showed a weak but significant overall negative relationship between temperature and emergence timing but no clear effects either within streams or within years due to substantial scatter of the data around the stream- or year-specific

lines of best fit (Figure 5b, Table 3). Pattern 2 might be applicable to any species with lengthy emergence periods that have naturally high variation around the peak timing.

The third and final species-specific pattern was a strong response to interannual (temporal) variation in temperature but limited spatial response among streams within years. Pattern 3 was observed for both the stonefly *Alloperla* and the mayfly *Neoleptophlebia* (Figure 5c,d). The strong effect of stream but negligible significance of the interaction terms in ANCOVA (Table 3) for these two species indicated that emergence timing was nearly synchronous among

TABLE 3 Results of Analysis of Covariance with stream as categorical variable and ordinal date of peak emergence as response variable

Species	Factor	MS	F	p	Significance level
<i>Dolophilodes</i>	M1: DDrate ^a	1772.4	152.3	<.001	***
	M1: stream ^a	45.1	3.9	.033	*
	M1: DDrate*stream ^a	10.1	0.87	.480	NS
	M2: DDrate ^b	1772.4	156	<.001	***
	M2: stream ^b	45.1	4	.026	*
<i>Moselia</i>	M1: DDrate ^a	1654.1	9.6	.006	**
	M1: stream ^a	198.1	1.15	.370	NS
	M1: DDrate*stream ^a	104.3	0.61	.700	NS
	M2: DDrate ^b	1654.1	10.5	.004	**
	M2: stream ^b	198.1	1.25	.320	NS
<i>Alloperla</i>	M1: DDrate ^a	1099.1	44.4	<.001	***
	M1: stream ^a	157.7	6.4	<.001	***
	M1: DDrate*stream ^a	29.1	1.2	.350	NS
	M2: DDrate ^b	1099.1	43.1	<.001	***
	M2: stream ^b	157.7	6.2	<.001	***
<i>Neoleptophlebia</i>	M1: DDrate ^a	1358.9	76	<.001	***
	M1: stream ^a	154.3	8.6	<.001	***
	M1: DDrate*stream ^a	52.6	2.9	.034	*
	M2: DDrate ^b	1358.9	56.5	<.001	***
	M2: stream ^b	154.3	6.4	<.001	***

Note: DDrate—heat accumulation through ordinal date 189.

Statistical significance denoted by ***=.001, **=.01, *=.05. Interaction terms are associated with the null hypothesis that slopes were not different among streams. Results plotted in Figure 5.

Abbreviation: NS, not significant.

^aModel 1: Includes interaction between stream and DDrate.

^bModel 2: Does not include interaction between stream and DDrate.

streams within years but that among years, emergence across all streams was earlier in warmer years. The second ANCOVA on these two species with year as categorical variable showed that intercepts were different (a year effect, Table 4), but simple linear regression applied to each single year of data revealed only two of six slopes to be significantly nonzero for *Alloperla* and just one of six slopes as nonzero for *Neoleptophlebia* (Table 5). Furthermore, the magnitudes of slopes were substantially lower within years than within streams (the first ANCOVA).

4 | DISCUSSION

Contrary to an expectation of a simple relationship of earlier emergence timing with warmer stream conditions (hypothesis H1), we observed three distinct phenological patterns among the four aquatic insect species in our study. Of the three patterns conceptualized in Figure 6, Pattern 1 (Figure 6a) depicts emergence timing responding to water temperature differences across both space and time and supports H1. We observed this pattern in just one of our four focal species, the caddisfly *Dolophilodes dorca*. Overall, our observations

suggest that temporal (interannual) variation in temperature, more so than spatial variation, influences emergence timing. However, emergence duration appears to be more tightly associated with spatial than temporal variation in temperature, such that populations in warmer streams have longer emergence periods (supporting H2; Figure 6). Perhaps surprisingly, the answer to the general question of whether emergence phenology of spring-emerging aquatic insects is predictable based solely on differences in heat accumulation is a resounding “no.”

4.1 | Timing of emergence

All four species showed some evidence of earlier emergence timing with warmer conditions (Figure 6a-c), but two of the four exhibited the intriguing Pattern 3, which implicates a stronger phenological response to temporal than spatial differences in water temperature (Figure 6c). Describing a spatially near-synchronized response to interannual temperature differences, Pattern 3 reflects minimal phenological response to among-stream thermal differences despite relatively strong interannual variation. To our knowledge,

TABLE 4 Results of Analysis of Covariance with sample year as categorical variable and ordinal date of peak emergence as response variable

Species	Factor	MS	F	p	Significance level
<i>Dolophilodes</i>	M1: DDrate ^a	1772.4	133.2	<.001	***
	M1: year ^a	30.2	2.3	.13	NS
	M1: DDrate*year ^a	8.9	0.67	.66	NS
	M2: DDrate ^b	1772.4	149.9	<.001	***
	M2: year ^b	30.2	2.6	.07	NS
<i>Moselia</i>	M1: DDrate ^a	1640.8	13.2	.002	**
	M1: year ^a	508.5	4.1	.010	*
	M1: DDrate*year ^a	83.5	0.67	.620	NS
	M2: DDrate ^b	1640.8	14	.001	**
	M2: year ^b	508.5	4.4	.009	**
<i>Alloperla</i>	M1: DDrate ^a	1099.1	74	<.001	***
	M1: year ^a	227.2	15.3	<.001	***
	M1: DDrate*year ^a	7.1	0.48	.790	NS
	M2: DDrate ^b	1099.1	81.4	<.001	***
	M2: year ^b	227.2	16.8	<.001	***
<i>Neoleptophlebia</i>	M1: DDrate ^a	1358.9	51.6	<.001	***
	M1: year ^a	155.1	5.9	.001	**
	M1: DDrate*year ^a	12.9	0.49	.780	NS
	M2: DDrate ^b	1358.9	56.8	<.001	***
	M2: year ^b	155.1	6.5	<.001	***

Note: DDrate—heat accumulation through ordinal date 189.

Statistical significance denoted by ***=.001, **=.01, *=.05, NS, not significant. Interaction terms are associated with the null hypothesis that slopes are not different among years.

^aModel 1: Includes interaction between year and DDrate.

^bModel 2: Does not include interaction between year and DDrate.

this pattern has never been documented nor hypothesized for any aquatic insect. It is particularly noteworthy because the among-stream range of mean water temperature (3.4°C between coldest and warmest streams) was more than double the interannual range (1.6°C between coldest and warmest years of study; Table 1). Among-stream differences in heat accumulation required to reach peak emergence for the Pattern 3 stonefly *Alloperla fraterna* and mayfly *Neoleptophlebia temporalis* approached 500 degree-days between the coolest and warmest streams. These differences allowed the near-synchronous emergence timing observed across heterogeneous streams in the Lookout Creek basin within years. In some insects, photoperiod cues drive spatially coordinated response (e.g. Bean et al., 2007), but our Pattern 3 species differed in peak emergence timing by nearly a month between the coolest and warmest years of observation. These interannual differences rule out photoperiod cues and point instead to a strong role of diapause or quiescence periods induced by common environmental variables experienced similarly in streams throughout the Lookout Creek basin.

Diapause and quiescence are different types of dormancy in the life cycle, during which development is paused and metabolic activity drastically slowed, leading to similar phenological responses

(Diniz et al., 2017). Diapause is under genetically determined hormonal control, whereas quiescence is a plastic response to environmental cues and can therefore be “switched on and off” much more quickly than diapause. Most databases for aquatic insect traits (e.g. Poff et al., 2006; Tachet et al., 2010) include diapause but not quiescence, possibly because the capacity for quiescence is ubiquitous in insects and typically initiated in response to temperature extremes (e.g. Newbold et al., 1994). For example, diapause at any life stage is rare in mayflies, but most Ephemeroptera probably have minimum and/or maximum temperature thresholds for nymphal growth and development (Newbold et al., 1994; Tokeshi, 1985; Ward & Stanford, 1982). Importantly, combinations of high- and/or low-temperature thresholds to dormancy can allow escape from extreme environmental conditions and synchronize population life cycles across heterogeneous environments. In insects, such synchronization has mainly been recognized along latitudinal gradients (Bentz et al., 2014; Newbold et al., 1994). Our results now suggest that similar drivers might synchronize life cycle events across much smaller spatial extents.

Conditions affecting dormancy response during preceding winters might play a role in synchronizing some spring-emerging

species among Lookout Creek headwater streams. Winter conditions have rarely been considered in studies of insect emergence phenology, but it is becoming apparent that winter dormancy may be as important in some insect life histories as in temperate plants, many of which require winter dormancy (Forrest, 2016; Marshall et al., 2020). Winter temperatures can influence both the timing and depth of dormancy periods in complex and sometimes counterintuitive ways. For example, many terrestrial insects require low temperatures, known as the “chill factor,” to induce a deep diapause, after which spring development can then proceed more rapidly than if winter temperatures remained warm enough to forego diapause (Forrest & Thomson, 2011; Stålhandske et al., 2017). Furthermore, temperature thresholds to induce cold-temperature dormancy can vary among instars within populations (Bentz et al., 2014; Logan & Bentz, 1999), a mechanism that helps synchronize population phenology. More research on the effects of both summer (Sweeney et al., 1992) and winter thermal regimes on complex phenological responses in aquatic insects is strongly needed.

4.2 | Duration of the emergence period

In support of H2, populations in warmer streams tended to have longer emergence periods. In contrast to emergence timing, emergence duration was more responsive to spatial variation than to temporal variation. Our measures of emergence duration can be translated directly as the degree of synchrony among individuals completing the life cycle transition to the adult stage within a population. Mechanistic drivers of intraspecific differences in emergence duration/synchrony are not well understood but are hypothesized to be influenced by environmental stability at the scale of the local habitat (Corkum et al., 2006; Li et al., 2011). In our study, the observation of longer emergence duration (decreased local synchrony) at lower-elevation streams suggests that water temperature is a cue. Other variables thought to affect emergence period duration, including predation pressure (Peckarsky et al., 2000), flow disturbance (Lytle, 2001), and quality of conditions for adult activity (Schultheis et al., 2008) are unlikely to vary consistently with elevation within the limited spatial extent of Lookout Creek or among its trophically similar headwaters (Zatkos et al., 2021). Although the mechanism is unclear for how water temperature influences emergence period duration, the pattern has been observed elsewhere (e.g. Cheney et al., 2019; Li et al., 2011; Richardson & Clifford, 1986) and merits further investigation. As with thermal drivers of emergence timing, responses are likely complex and variable among species. For example, the “chill factor” required in some terrestrial insects to induce deep diapause has also been linked to greater emergence synchrony in spring-emerging species (Forrest, 2016). It is also possible in some species that extended duration of emergence period following warmer winters confers a selective advantage in anticipation of longer breeding seasons, such as in spring-emerging montane grasshoppers (Buckley et al., 2015).

4.3 | Climate change implications

Among-year differences in peak emergence timing of nearly 1 month associated with differences in mean water temperature of $<2.0^{\circ}\text{C}$ in our Pattern 3 species is a cause for concern associated with climate change. Both earlier emergence timing and increasing duration of emergence periods have been documented in a European stream that warmed during a 42-year study period by 1.9°C (Baranov et al., 2020), and similar patterns are expected in other regions. Lookout Creek has experienced a recent trend of decreasing late-summer streamflow (Kaylor et al., 2019), but despite overall warming of air temperature, multi-decadal trends in water temperature appear to be highly variable among streams of the topographically and hydrologically complex basin (Arismendi et al., 2012). We argue here that thermal heterogeneity within and among streams in a naturally complex basin, interactions of other species-specific biological traits with phenological traits, and the potential for phenological traits to adapt to changing conditions might each contribute to ecosystem-scale resilience in the face of ongoing climate change.

A value of our study in comparison to multi-year studies at single locations (e.g. Baranov et al., 2020; Finn & Poff, 2008; Harper & Peckarsky, 2006) is that we incorporated the natural mosaicism of thermal conditions among streams in a topographically complex basin. Concurrent with our study, terrestrial investigations in the Lookout Creek basin also demonstrated spatially heterogeneous microclimates associated with air temperature (Ward et al., 2018), and habitat use by birds (Frey, Hadley, & Betts, 2016) and terrestrial insect flight patterns (Schmidt, 2019) were linked to microhabitat-scale thermal regimes, which shifted spatially from year to year. Like these terrestrial taxa, most emergent aquatic insects fly and can therefore respond behaviourally to environmental heterogeneity across streams in a basin by dispersing among tributaries. Similarly, thermal heterogeneity typically exists at the local scale within streams (Johnson, 2004; Kaylor et al., 2021), to which immature stages of aquatic insects can also respond behaviourally (Uno & Power, 2015), particularly when a hyporheic zone is present and accessible (Dorff & Finn, 2020). For example, *Moselia infusata* likely occupies the cooler and more thermally stable hyporheic zone for at least part of its nymphal development period (Gill et al., 2015), which could help explain the highly variable patterns of emergence timing and duration we observed in this species. If individuals move between the hyporheic and benthic zones, nymphal development is affected by water temperature in both these contrasting locations. *Moselia* had a lengthy emergence duration on average, but it was shortest and least variable in the coldest, spring-fed Stream E, possibly because hyporheic and benthic temperatures were more similar there than in other streams with warmer surface water. Overall, thermal habitat heterogeneity from basin to local scales will likely increase resilience in the face of broader-scale climate change.

Phenological traits like emergence timing and synchronicity probably interact with additional species-specific traits such as flight ability and adult longevity in ways that could temper the ecosystem effects of climate change at the basin scale. For example,

TABLE 5 Slope values from simple linear regression between heat accumulation to ordinal date 189 (in degree-days) and ordinal date of peak emergence for the stonefly *Alloperla* and the mayfly *Neoleptophlebia* (the two “Pattern 3” species). Stream is the categorical variable (with sample years as replicates) for the first two columns; year is the categorical variable (with streams as replicates) in the final two columns. The relationship between temperature and timing of emergence was overall stronger within streams (among years) than within years (among streams) for these two species

Species	Stream	Slope (date of peak emergence/ cumulative degree-days)	Year	Slope (date of peak emergence/ cumulative degree-days)
<i>Alloperla</i>	Stream A	-0.11	2009	-0.01
	Stream B	-0.07	2010	NS
	Stream C	-0.07	2011	NS
	Stream D	-0.05	2012	NS
	Stream E	NS	2013	NS
	Stream F	-0.04	2014	-0.02
<i>Neoleptophlebia</i>	Stream A	-0.14	2009	NS
	Stream B	NS	2010	-0.02
	Stream C	-0.06	2011	NS
	Stream D	-0.07	2012	NS
	Stream E	NS	2013	NS
	Stream F	-0.05	2014	NS

Note: NS—slope value not significant

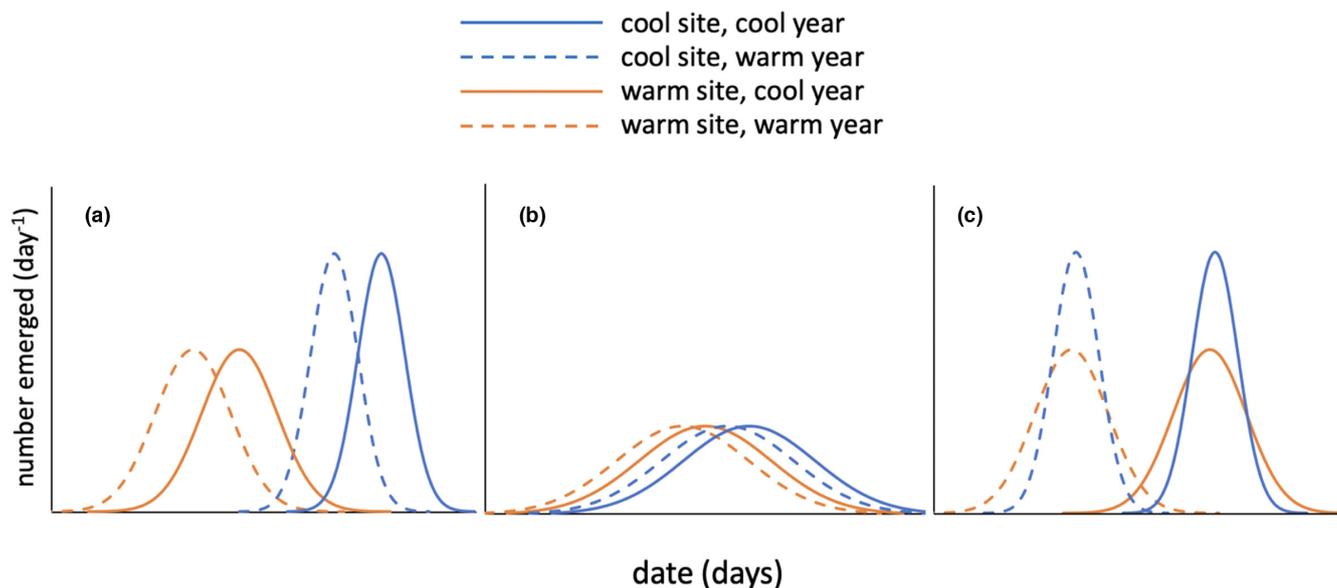


FIGURE 6 Conceptual diagrams representing three major patterns of emergence timing and duration observed in this study. (a) Pattern 1: relatively consistent spatial and temporal response of emergence timing to temperature, and longer duration of emergence period in warmer years and at warmer streams (*Dolophilodes*); (b) Pattern 2: some evidence for response to heat accumulation rate but overall lengthy emergence periods make patterns difficult to distinguish among streams and years (*Moselia*); (c) Pattern 3: temporal (among-year) response to temperature but spatial near-synchrony of emergence timing across cooler and warmer streams within years, with longer emergence period in warmer years (*Alloperla* and *Neoleptophlebia*)

duration of the emergence period varied widely among individual streams in our study, but combined duration at the basin scale is much longer. A lengthy duration of emergence at the basin scale should ameliorate some of the potential for trophic mismatch and other hypothesized ecosystem-level consequences, particularly in species with longer-lived adults and/or stronger flight ability. The

caddisfly *Dolophilodes dorca*, for example, exhibited the most sensitive response of emergence timing to local water temperature (Pattern 1), so emergence was not synchronized among streams. But caddisfly adults are relatively long lived (on the order of weeks) and typically are strong flyers. The combination of asynchronous emergence among streams with relatively long-lived and

strong-flying adults is likely what explains the approximately 4-month flight period of this single species reported at the basin scale in Lookout Creek (May–August; Anderson et al., 1984). Indeed, the sensitivity of *D. dorca* to local thermal regime, combined with our termination of data collection in early July, probably explains the dearth of data from the two highest-elevation streams. For stronger dispersing species that can more readily shift spatial distribution in response to changing conditions, complex and fine-tuned phenological responses to temperature (e.g. to increase spatial synchrony) may not be selectively advantageous.

Mayflies like *Neoleptophlebia temporalis*, by contrast, have extremely short adult life spans, usually a maximum of 24 h, and relatively weak flight. Hence, complex responses to water temperature that synchronize emergence along spatial gradients (as in Pattern 3) should be more selectively advantageous for mayflies, particularly for finding mates (Calabrese & Fagan, 2004; Corkum et al., 2006). As such, we hypothesize a trade-off between traits of adult longevity and/or strong flight and complex phenological response associated with synchronized emergence, such that Pattern 3 might be expected in shorter-lived species with weaker flight ability. Our other Pattern 3 species was the stonefly *Alloperla fraterna*, for which biological traits have not been well studied. However, most stoneflies in the Systellognatha group are functionally comparable to mayflies in that adults have reduced or nonfunctional mouthparts, and necessarily short adult life spans (<2 weeks for most species; DeWalt & Kondratieff, 2019). Moreover, stonefly flight ability is generally weak to intermediate.

Overall, the phenological responses we quantified in this study were highly variable among species and among populations within species. There was no evidence that phylogenetically more closely related species shared similar phenological traits, an observation that suggests a high degree of evolutionary lability (“flexibility”) to adapt relatively quickly to changing conditions (Poff et al., 2006). Although greater lability implies that these traits are difficult to predict and must be measured on a species-by-species basis, it also presumably confers greater potential for adaptation to relatively rapid environmental change. Evidence for rapid evolution of phenological traits exists for some terrestrial insects, including pine beetles that have intraspecific genetic differences associated with dormancy cues along latitudinal gradients (e.g. Bentz et al., 2014). Overall, both high levels of plasticity in some traits (e.g. duration of emergence) and the potential for relatively rapid evolution of others might allow flexibility of phenological response into the future and contribute to ecosystem-scale resilience with climate change.

5 | CONCLUSIONS

Aquatic ecology has a rich heritage of mechanistically linking thermal regimes to distributions and habitat associations of invertebrates (e.g. Vannote & Sweeney, 1980; Ward & Stanford,

1982), but the physiological mechanisms associated with phenological response to specific thermal cues remain little understood (Woods et al., 2021). Our detailed spatial and temporal observations among thermally different headwater streams shed new light on the complexity of phenological responses of aquatic insects to water temperature. Among just four species, we observed three distinct patterns of emergence timing associated with temperature. The intriguing Pattern 3 suggests complex physiological response to thermal cues generating near-synchronous emergence from thermally distinct streams despite strong differences in peak timing among years. Variability in peak emergence timing by up to a month between years with <2°C mean temperature difference can help explain interannual variation in taxa present in benthic communities sampled at the same time each year (e.g. Frady et al., 2007). Another practical implication is that because many insects likely respond to winter thermal conditions, it is important to rear individuals throughout the life span for studies measuring phenological response to experimental treatments (e.g. Funk et al., 2019; Li et al., 2011).

The sensitive and variable responses documented among species underscore the importance of mechanistic explanations linking phenological traits to water temperature and improved predictive ability associated with climate change in aquatic ecosystems. For aquatic ectotherms in general, we recommend closer collaboration between physiologists and ecologists (Chmura et al., 2019) and more attention to the terrestrial insect literature for promising research angles, particularly associated with dormancy cues and the potential role of winter chill factors. It will also be important to improve our understanding of other biological traits that could interact with phenological traits (Forrest, 2016; Nelson et al., 2020; Thomas & Bacher, 2018). We hypothesized a trade-off between complex response mechanisms associated with phenological synchronization and traits such as adult longevity and/or dispersal ability. Studies designed to test this hypothesis might identify predictable “syndromes” of strongly associated traits that can improve community- and ecosystem-level prediction of phenological response to climate change in aquatic ecosystems.

ACKNOWLEDGEMENTS

This research was conducted at the HJ Andrews Experimental Forest, which is administered cooperatively by the USDA Forest Service Pacific Northwest Research Station, Oregon State University and the Willamette National Forest. The research was primarily funded through the Long Term Ecological Research (LTER) grant from National Science Foundation, DEB-1440409. We thank Chrissy Murphy, Denis Newbold, Mark Schulze, Jay Sexton and Bern Sweeney for discussions at various stages of this project, and Mark Schulze, Jay Sexton, Ari DeMarco, Sarah Ward, Sarah Perez-Sanz, Jessica Celis and Alex Martin for help with field collections. Liz Baker and Charlie Chamberlain assisted with sorting and identification. Bob Wisseman consulted on identification of Trichoptera.

CONFLICT OF INTERESTS

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The stream temperature data that support the findings of this study are openly available from the EDI data portal at <https://doi.org/10.6073/pasta/7dc5e1f888281081de71818082bd0c78>. All insect emergence data are provided in supplementary material and in Table 2 of the paper.

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BIOSKETCH

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Author Contribution: SLJ and JLL conceived of and designed the study. DSF led data analysis, interpretation, writing, and revising of the manuscript with active participation of all coauthors (SLJ, WJG, IA, JLL) throughout the process. All authors are accountable for the accuracy and integrity of this work.

SUPPORTING INFORMATION

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How to cite this article: Finn, D. S., Johnson, S. L., Gerth, W. J., Arismendi, I., & Li, J. L. (2022). Spatiotemporal patterns of emergence phenology reveal complex species-specific responses to temperature in aquatic insects. *Diversity and Distributions*, 28, 1524–1541. <https://doi.org/10.1111/ddi.13472>