

Jonas Dahl · Barbara L. Peckarsky

Developmental responses to predation risk in morphologically defended mayflies

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Abstract Densities and species composition of predators could affect morphological defences, larval development and the timing of emergence of their prey. To address this issue we studied the morphology and life history of an ephemereid mayfly, *Ephemerella invaria*, from two streams in a deciduous forested drainage basin in central New York. Both streams contained predatory fish, but densities and species composition of fish differed. A field survey provided evidence that *Ephemerella* inhabiting a stream with ≥ 10 fish species and high relative densities of fish emerged several weeks earlier and at smaller sizes than *Ephemerella* inhabiting a nearby tributary with ~ 2 fish species and low relative densities of fish. However, the two populations of mayflies showed no differences in defensive morphology or growth rates. In laboratory rearing experiments, we exposed *Ephemerella* larvae from these two locations to fish chemical cues or control water (no fish) over 2 months to test whether differences in life histories could be attributed to fish. Fish cues induced faster larval development, but also smaller size of mature *Ephemerella* individuals from both high and low predator locations. Although shorter development times in more dangerous environments could increase larval survival, smaller size of females results in a fecundity cost associated with this life history shift. Consistent with the field studies, laboratory rearing experiments revealed

no effects of fish cues on *Ephemerella*'s morphological defences. These data suggest that variation in the density or species composition of predators may favour the evolution of developmental plasticity to reduce mortality in the larval environment.

Keywords Life history traits · Mayflies · Morphological defences · Predation · Streams

Introduction

Organisms living in environments with spatial and temporal variation face a fundamental problem, in that the phenotype with maximum fitness often changes with the environment. Thus, it may not be possible for organisms to evolve a single optimal phenotype in variable environments. One important source of environmental heterogeneity is the distribution of predators. Predation generally exerts strong selection pressure on prey populations, favouring individuals with effective anti-predator defences (Sih et al. 1985; Endler 1986; Harvell 1990; Lima and Dill 1990; Brönmark and Miner 1992). While many defensive characters are constitutive, i.e. fixed, a number of studies have demonstrated the importance of environmentally induced defences (Dodson 1984; Harvell 1984; Lively 1986; Appleton and Palmer 1988).

Prey species can evolve many different forms of phenotypic plasticity that function to defend individuals against predation. For example, high predation risk frequently induces defensive prey morphology (Brönmark and Miner 1992; Reimer and Tedengren 1996; Arnqvist and Johansson 1998), and antipredatory behaviour (Petranka et al. 1987; Skelly and Werner 1990). Predators might also induce plasticity in life history strategies. Prey have been shown to increase or decrease development rates when exposed to predators (Semlitsch et al. 1988; Scott 1994; Bradshaw and Johnsson 1995; Arnqvist and Johansson 1998).

J. Dahl (✉)

Laboratory of Streamwater Ecology,
National Board of Fisheries,
Brobacken, 81494 Älvkarleby, Sweden
e-mail: Jonas.dahl@Fiskeriverket.se

B. L. Peckarsky

Department of Entomology, Cornell University,
Comstock Hall, Ithaca, NY 14853, USA

Present address:

J. Dahl, Rocky Mountain Biological Laboratory,
Crested Butte, CO 81224, USA

Present address:

B. L. Peckarsky, Rocky Mountain Biological Laboratory,
Crested Butte, CO 81224, USA

Mayfly larvae possess a range of defences against vertebrate and invertebrate predators. Some species decrease or increase levels of activity to reduce their exposure to predators (Kohler and McPeck 1989; Douglas et al. 1994; Forrester 1994; Diehl et al. 2000). Peckarsky et al. (2001, 2002a) found that the presence of brook trout caused life history shifts in mayflies (*Baetis bicaudatus*) in high altitude streams in western Colorado. With trout present, *Baetis* increased their development rates and emerged at smaller sizes compared to *Baetis* inhabiting fishless streams. Other mayflies have morphological defences including thick exoskeletons, abdominal spines and long caudal filaments, which decrease predation rates (Peckarsky 1987; Peckarsky and Penton 1988; Soluk 1990; Dahl and Peckarsky 2002). Dahl and Peckarsky (2002) found that larvae of *Drunella coloradensis* from a high altitude drainage basin in western Colorado had longer caudal filaments and heavier exoskeletons in streams with brook trout compared to larvae developing in fishless streams. These morphological defences were induced experimentally by exposing larvae to chemical cues from brook trout. Dahl and Peckarsky (2002) also found that individuals with longer caudal filaments had significantly higher survival rates in predation experiments than individuals with shorter caudal filaments. However, trout had no effect on *Drunella* life history traits.

In this study, we were interested in whether species composition and densities of fish predators affected development rates, timing of metamorphosis and morphological defence characters of *Ephemerella invaria* (a mayfly from the same family as *Drunella*). Larvae of *E. invaria* are common in woodland streams in the north-eastern United States, which are rarely fishless, but vary in density and species composition of predatory fish (e.g. darters, dace, cyprinids, salmonids and suckers), and have a diverse predatory stonefly fauna (Peckarsky 1985). *Ephemerella* emerges to the adult stage and reproduces in April and May, and most of their larval growth occurs from January to March. We studied the development of *Ephemerella* larvae in two streams in the Cascadilla Creek watershed: Cascadilla Creek (third order); and a second-order tributary, Hunt Hill Creek, Tompkins County, N.Y. Since the field survey was unreplicated, we also conducted laboratory experiments, in which we exposed individuals of one cohort from both locations to fish chemical cues or control water (no fish) for the last two months of their larval period.

Materials and methods

Field survey

We conducted a field survey of two streams in the Cascadilla Creek drainage basin near Ithaca, N.Y., USA from January to May 1999. In this area, we were unable to locate any fishless streams with adequate flow to support populations of *Ephemerella*. Thus, we contrasted two streams with different densities and assemblages of predatory fish. One third-order stream (Cascadilla Creek) contained

a diverse fish community, including creek chubs (*Semotilus atromaculatus*), white suckers (*Catostomus commersoni*), bluntnose minnows (*Pimephales notatus*), fantail darters (*Etheostoma flabellare*), cutlips minnows (*Exoglossum maxillingua*), blacknose dace (*Rhinichthys atratulus*), fallfish (*Semotilus corporalis*), mottled sculpins (*Cottus bairdi*), longnose dace (*Rhinichthys cataractae*), brook trout (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*). The other stream (Hunt Hill Creek) is a second-order tributary of Cascadilla Creek that often dries during summers to a series of small pools (Delucchi and Peckarsky 1989). Fantail darters and blacknose dace are common in this stream, but creek chubs and brook trout also occur occasionally (B.L. Peckarsky and students, unpublished data). We electroshocked these two streams, once in March and once in May, to determine the densities and community structure of their fish populations. On each date we used a three-pass removal method to estimate the fish populations in two different 50-m-long sections within each stream (Bohlin 1984). Densities of fish were an order of magnitude higher in Cascadilla Creek (ranging from 1.4 to 1.6 individuals m⁻²) than in Hunt Hill Creek (range = 0.10–0.15 individuals m⁻²).

To obtain measures of the defensive morphology of *Ephemerella* at these two sites, larvae were collected weekly from January to May, preserved in 70% ETOH and brought to the laboratory for morphometric analysis, accomplished within a few days after preservation to minimise weight loss in ETOH. The invertebrates were collected using travelling kick samples with a D-net with an equal sampling effort in the two streams on each date. We estimated the size of individuals at emergence from these two streams by weighing larvae with black wing-pads. When mayflies develop black wing-pads (BWP = stage IV) they have ceased feeding and growing and will metamorphose within 24 h (Delucchi and Peckarsky 1989; Peckarsky et al. 2001; Dahl and Peckarsky 2002). We also estimated mean growth rates of *Ephemerella* larvae at each site as $(w_f - w_i)/d$, where w_i = the mean weight of 20 individuals collected on the first sampling date, w_f = the mean final weight of 20 BWP individuals, and d = the number of days between the collections of the initial and the BWP individuals. Since all larvae were members of the same cohort of these univoltine populations, this method enabled us to estimate the mean rate of growth of individuals within each population from January to May.

Water temperatures were measured each time mayflies were sampled, and were similar at these two sites throughout the sampling period, ranging from 3°C to 13°C. The mean water temperatures were 6.5°C and 6.6°C in Cascadilla Creek and Hunt Hill Creek, respectively. Delucchi (1988) also found that the diel and annual temperature ranges in these two streams were similar.

Rearing experiment

Experiments were carried out in 15-cm-diameter cylindrical plastic flow-through chambers [similar in design to those illustrated in Peckarsky et al. (1993)] housed in the Schwardt Laboratory at Cornell University in Ithaca, N.Y. Well water was delivered to each chamber by a separate valve and drained out of a central standpipe. Each chamber received natural substrate consisting of gravel and five stones of 5 cm diameter. Water temperatures varied little and were between 5°C and 8°C throughout the experiment. Current velocity in the chambers ranged from 5 to 20 cm/s, which was within the range observed in the natural habitat. We used mixed species of conditioned detritus (leaves + epiphytic biofilm) collected from both Hunt Hill Creek and Cascadilla Creek as a food source for *Ephemerella* larvae. These leaves were changed each week to keep food sources as natural as possible. Waterborne fish cues originated from three plastic holding tanks (100 l), which contained longnose dace and fantail darters (one of each species). Water was piped from each holding tank, divided and distributed (dripped) into the chambers allocated to the fish-cue treatments for the entire experiment. Fish in containers were fed every other day a mixed invertebrate diet, including *Ephemerella* larvae.

Each chamber contained five *Ephemerella* larvae collected from either Cascadilla Creek (high fish density and diversity) or Hunt

Hill Creek (lower fish density and diversity), and received waterborne fish cues or control water from holding tanks with no fish present (four treatments: Cascadilla or Hunt Hill *Ephemera* × fish or fishless water, with eight replicates per treatment). Means of response variables of the five individuals per chamber were used as the unit of replication for statistical analyses. The experiment started on 3 March and was terminated 20 May 1999 after the last *Ephemera* developed black wing pads. A subsample of the population of individuals that were used for the experiment (all collected on the same day from each stream) were measured to estimate the starting size of individuals used in the experiment. The initial mass did not differ among streams (Cascadilla Creek: 0.68 ± 0.12 mg; Hunt Hill Creek: 0.63 ± 0.10 mg) and mortality rates were similar among treatments (0–20%; i.e. most individuals survived but one individual died in some containers). Growth rates of *Ephemera* larvae were then determined as in the field study, by comparing the mean weight of BWP individuals from each chamber to the mean initial weight of a subsample of 20 individuals collected from each site at the beginning of the experiment.

Morphometric analyses

For field-collected and experimental animals, morphometric measurements were made using a binocular dissecting microscope equipped with an ocular micrometer. We measured head width, body length, caudal filament length (the middle filament) and the length of the lateral spines on abdominal segments VIII and IX. Body weights were obtained by drying individuals at 60°C for 3 days, and weighing them to the nearest 0.01 mg on a Cahn microbalance.

Statistical analyses

Emergence dates and sizes of individuals at emergence of *Ephemera* were compared between sites using the non-parametric Kolmogorov-Smirnov two-sample test, which tests for differences between the two size- or time-frequency distributions (Julian date) between sites. For the laboratory experiment we tested the effects of fish cues (treatment) and origin of larvae (site) on emergence date, weight at emergence and growth rates using a two-way MANOVA (site × treatment).

We used analyses of covariance to characterise the variation in allometry of abdominal spine and caudal filament lengths between the two natural populations of *Ephemera*, with larval body length as the covariate. We first tested the assumption of homogeneity of slopes of the relationship between body length (the covariate) and each morphological defensive character for each mayfly population (field study), treatment (experiment) and site (experiment). If the slopes of these relationships did not differ between treatments or sites, further analyses of main effects of treatments on defensive characters were conducted using MANCOVA, followed by separate ANCOVAs on each response variable when MANCOVAs were significant. Field data were analysed with one-way MANCOVA (site), and experimental data were analysed using two-way MANCOVAs (fish treatment × site).

Estimates of measurement error for each linear variable were obtained by repeating 20 measurements of each parameter on 20 different individuals and calculating their deviation from the original measurements. These deviations were then divided by the original measurements and averaged to determine a percentage error.

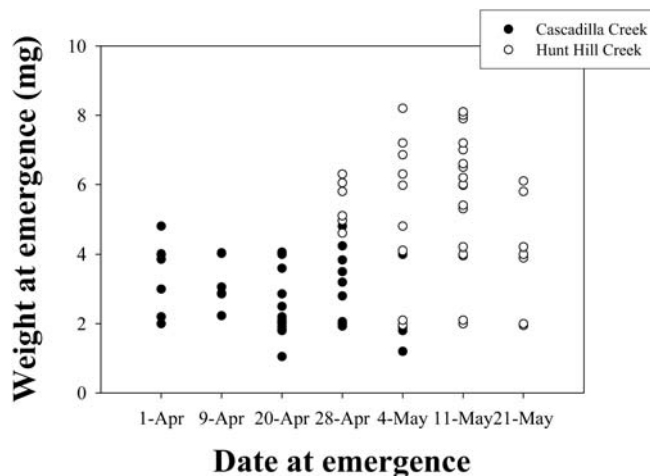


Fig. 1 Date and size of emergence of *Ephemera* individuals from Cascadilla Creek and Hunt Hill Creek. Each point represents one individual

Results

Field study

Individuals from Cascadilla Creek began emerging several weeks before individuals from Hunt Hill Creek (Fig. 1). The first individuals in the BWP stage were found on 1 April 1999 in Cascadilla Creek, whereas the first BWP individuals in Hunt Hill Creek were found on 1 May 1999. The time-frequency distribution of *Ephemera* emergence was significantly different between the two sites (Kolmogorov-Smirnov two-sample test, $P < 0.001$), with very little overlap between the last individuals to emerge from Cascadilla Creek and the first to emerge from Hunt Hill Creek (Fig. 1).

Weights of mature (BWP) *Ephemera* individuals from Cascadilla Creek were significantly lower than those maturing in Hunt Hill Creek (Kolmogorov-Smirnov two-sample test, $P < 0.001$; Fig. 1). However, we found no difference in growth rates between these two populations (mean growth rate \pm SE Hunt Hill Creek: 0.025 ± 0.024 mg day⁻¹; Cascadilla Creek: 0.022 ± 0.025 mg day⁻¹), indicating that earlier emergence at a smaller size from Cascadilla Creek was caused by accelerated larval development rather than by differences in growth rates between populations in these two streams.

The slopes of the relationships between body length and defensive characters did not differ between streams (caudal filament length: $F_{1,8} = 0.20$, $P = 0.65$; lateral IX spines: $F_{1,8} = 1.10$, $P = 0.33$; lateral VIII spines: $F_{1,8} = 1.18$, $P = 0.25$). The MANCOVA showed that there were no differences between sites in the relative length of abdominal spines or caudal filaments ($F_{3,10} = 0.19$, $P = 0.90$, Wilks' lambda = 0.946, caudal filament length illustrated in Fig. 2). Error estimates for these measurements ranged from 1.0 to 1.5%, demonstrating that measurement error was not a significant source of variability in this study.

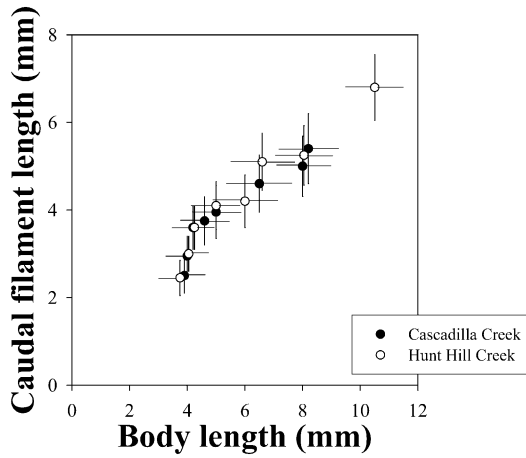


Fig. 2 The allometric relationship between body length and caudal filament length in natural *Ephemerella* populations sampled in Cascadilla Creek and Hunt Hill Creek. Each point (replicate) represents the mean of individuals collected on each date at each site. The x-axis (body length) roughly approximates time

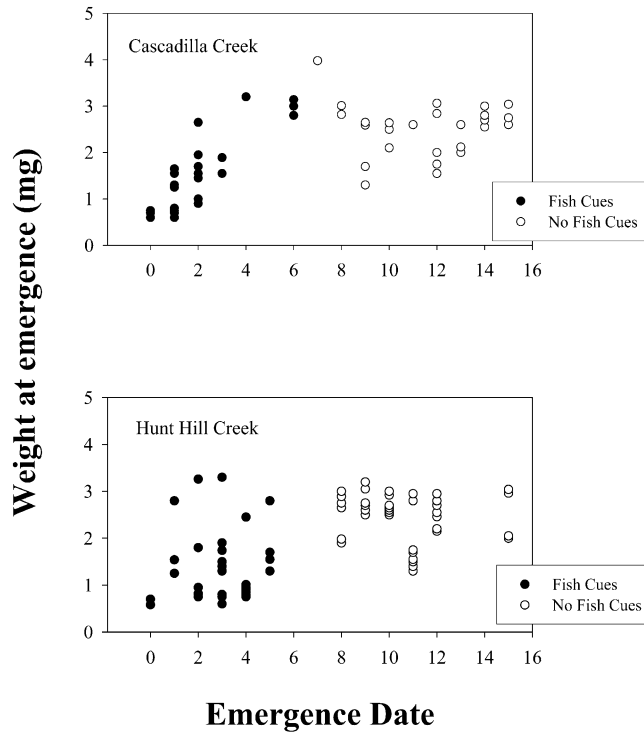


Fig. 3 Dry weight at emergence for *Ephemerella* individuals collected from either Cascadilla Creek or Hunt Hill Creek and reared with either control water or waterborne fish cues. The x-axis indicates the temporal pattern, with 0 = date of observation of the first BWP individuals

Laboratory experiment

Individuals originating from both Cascadilla Creek and Hunt Hill Creek emerged earlier and at a smaller size in chambers receiving fish cues than in ones with no fish cues (Fig. 3). Fish effects on date and size at emergence

Table 1 MANOVA for effects of predator treatment (presence versus absence of fish cues) and site (Cascadilla Creek versus Hunt Hill Creek) on date of emergence, weight at emergence and growth rates of *Ephemerella* individuals in the 1999 laboratory experiment

	<i>df</i>	Wilks' lambda	<i>F</i>	<i>P</i>
Fish	3,26	0.14	54.8	<0.001
Site	3,26	0.96	0.35	0.79
Fish × site	3,26	0.96	1.10	0.36

Table 2 ANOVA for effects of predator treatment (presence versus absence of fish cues) and site (Cascadilla Creek versus Hunt Hill Creek) on date of emergence, weight at emergence and growth rates of *Ephemerella* individuals in the 1999 laboratory experiment

	<i>df</i>	<i>F</i>	<i>P</i>
Date of emergence			
Fish	1,28	156.20	<0.001
Site	1,28	0.95	0.34
Fish × site	1,28	0.21	0.93
Weight at emergence			
Fish	1,28	10.46	0.003
Site	1,28	0.19	0.67
Fish × site	1,28	0.04	0.84
Growth			
Fish	1,28	2.81	0.11
Site	1,28	0.02	0.88
Fish × site	1,28	0.21	0.65

were significant, but there were no significant site effects or interactions between fish treatment and site (Tables 1, 2). Similar to the field data, there were no treatment or site effects on growth rates of *Ephemerella* in the experiment (Tables 1, 2). The average growth rate range was 0.012–0.013 mg day⁻¹ (mean growth rates Cascadilla Creek: 0.012±0.012 mg day⁻¹; Hunt Hill Creek: 0.012±0.011 mg day⁻¹). These growth rates were only half those measured for field populations, possibly due to experimental artefacts that reduced mayfly growth. Sizes of mature mayflies were also smaller after rearing in experimental chambers compared to field populations (Fig. 1 vs Fig. 3), as previously reported for other mayflies (Peckarsky et al. 1993).

Finally, we found no evidence that fish cues induced any differences in relative caudal filament or abdominal spine lengths in individuals from Cascadilla Creek or Hunt Hill Creek populations (Fig. 4). The slopes of the relationship between body length and defensive characters did not differ among treatments or sites (fish cues: caudal filaments, IX lateral and VIII lateral spines: $F_{1,38} < 1.66$, $P > 0.20$). Two-way MANCOVAs of the effects of the fish treatment and site on caudal filament length and abdominal spine length detected no treatment or site effects on any of the morphological characters, and no significant interactions between treatment and site (fish: $F_{3,26} = 0.48$, $P = 0.7$, Wilks' lambda = 0.98; site: $F_{3,26} = 0.65$, $P = 0.56$, Wilks' lambda = 0.97; fish × site: $F_{3,26} = 0.15$, $P = 0.93$, Wilks' lambda = 0.99).

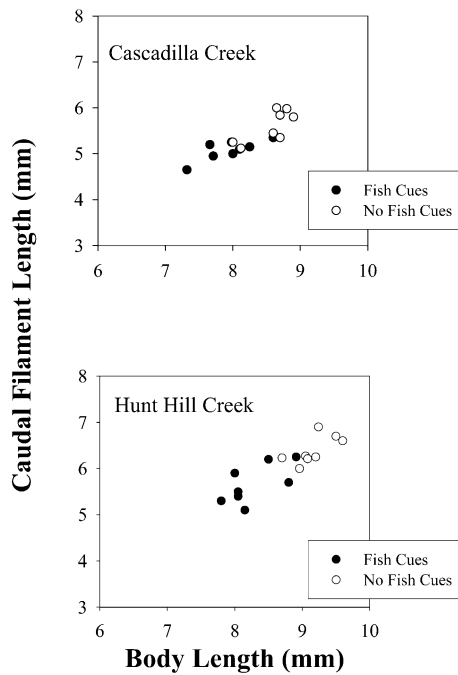


Fig. 4 The allometric relationship between body length and caudal filament length for *Ephemera* originating from Cascadilla Creek or Hunt Hill Creek, reared with either control water or waterborne fish cues. Each point (replicate) represents the mean of all individuals per tank

Discussion

Phenotypic plasticity and specialisation are two means by which organisms can adapt to environmental heterogeneity. If the environment is spatially, but not temporally, variable, specialists with fixed phenotypes may evolve if a single phenotype consistently has the highest fitness (Levins 1962, 1968). However, if environments vary temporally, or animals are mobile such that individuals experience a range of habitats, selection should favour phenotypic plasticity (Lively 1986; Harvell 1990; Pettersson 1999). Plasticity is only effective if reliable cues exist by which organisms can assess environmental conditions (Tollrian and Harvell 1999), because flexible individuals can then match their phenotype to specific environments.

In this study, we found evidence for plasticity of development rates and size at maturity associated with graded differences between high and low risk environments. Individuals from a stream with higher density and diversity of predatory fish emerged several weeks earlier than individuals from a nearby stream with fewer fish species and lower fish densities. Laboratory experiments corroborated that accelerated development could be induced by chemical cues from fish in populations of *Ephemera* derived from both the high and low predator streams. Similar developmental plasticity has been observed in other species in response to increasing risks of competition or predation (Simmonds and Blaney 1986; So

and Dudgeon 1989; Goodbrod and Goff 1990; Wilbur and Fauth 1990; Peckarsky et al. 2001).

We suspect that differences in rates of development between mayflies from high and low predator streams were due to phenotypic plasticity rather than genetic differentiation between individuals from different streams (Nijhout 1999). These two stream sites were only ~2 km apart and were connected at their confluence. Dispersal of larvae and winged adults should facilitate genetic mixing of populations derived from the different streams, countering fish-mediated selection on development times. We suspect that the chemical environment associated with actively feeding fish triggered accelerated development of *Ephemera* larvae, as suggested by the laboratory experiment. A few other aquatic invertebrates have been shown to alter their life histories in response to chemical cues from actively feeding predators (Crowl and Covitch 1990; Peckarsky et al. 2001, 2002a). Phenotypic plasticity in larval development can balance the conflicting demands of feeding and predator avoidance ultimately to increase fitness of organisms whose size at metamorphosis influences adult fecundity (Forrest 1987; McPeck and Peckarsky 1998).

Observed differences in larval development time between streams could not be explained by predator-induced decreased growth rates. Growth rates of mayflies were similar between treatments in the laboratory experiment and between the natural streams, suggesting that fish cues induced early development, but did not affect growth rates (as in Peckarsky et al. 2001). Alternatively, differences in development times and size at emergence of mayflies in high and low predator streams could be explained by other differences between the two streams, such as water temperature and food. In this case, the temperature regime did not differ between streams (see also Delucchi 1988; Delucchi and Peckarsky 1989). While we did not measure other attributes of the two streams that could influence mayfly development rates, the laboratory rearing experiment carried out under the same food and temperature conditions for all treatments supports the hypothesis that fish cues induced early development in this mayfly species.

This study also suggests that predator-induced accelerated development had an associated cost to mayfly fitness. As adult mayflies do not feed and larger females are more fecund (Sweeney and Vannote 1981; Peckarsky et al. 1993; Dahl and Peckarsky 2002), size at metamorphosis determines the potential contribution of individuals to the next generation. *Ephemera* emerging from the high-predator stream emerged earlier, but were smaller than mayflies emerging from the low-predator stream. Similarly, another mayfly (*Baetis bicaudatus*) developing in trout streams had faster development times, but emerged smaller than individuals developing in fishless streams in western Colorado (Peckarsky et al. 2001). Thus, the cost of faster development to reduce exposure to predators in the more dangerous habitats was a reduction in fecundity of females. It is unclear whether there is a cost of small size for males of this species of mayflies, as

has been shown for some species (Flecker et al. 1988), but not others (Peckarsky et al. 2002b).

Developmental plasticity enables mayflies to adopt different life history trajectories in habitats or at times when predation pressure intensifies, minimising their exposure to predation in the most dangerous habitats. The mechanism by which mayflies achieve this plasticity is unknown, but could be related to the large number of larval moults commonly observed for mayflies (between 10 and 50; Brittain 1982). Furthermore, many mayflies have been shown to have an indeterminate number of instars (Brittain 1982), which could also enable them to vary the length of their larval stage in response to environmental cues.

In contrast to *Drunella coloradensis* (Dahl and Peckarsky 2002) we did not find any evidence for induced morphological defences in *Ephemerella*. Abdominal spine and caudal filament lengths showed the same allometric relationship to body size in populations of mayflies from high- and low-predator streams. Furthermore, removal or addition of fish cues in the laboratory rearing experiment had no effect on these defensive structures.

It is interesting to note that these two related mayfly species responded to variation in predator risk in different ways. *Drunella* had inducible morphological defences, but similar development, in fish and fishless streams (Dahl and Peckarsky 2002). In contrast, *Ephemerella* had fixed morphological defences, but inducible plasticity in rates of development. Perhaps differences between these two species can be explained on the basis of the extent of investment in behavioural, developmental and morphological plasticity, and whether these responses to predation risk are reversible.

Firstly, behaviour is the most plastic aspect of phenotype that requires relatively little investment, and is often reversible. Thus, we would expect to observe behavioural responses to predators most widely (Lima and Dill 1990). In mayflies, predator-induced plasticity in behaviour has been reported in streams all over the world (Bechara et al. 1993; Douglas et al. 1994; Forrester 1994; McIntosh and Townsend 1994; Dahl 1998a, 1998b), as long as these species have evolved in habitats with predators. Interestingly, nocturnal activity periodicity in *B. bicaudatus* was not reversible, possibly because once an individual mayfly is exposed to fish cues, there is very little chance it will experience a fishless environment again (trout streams are downstream from fishless streams; Peckarsky and McIntosh 1998; McIntosh and Peckarsky 1999). Potentially, changing morphology or development could require more investment than changing behaviour, and induced morphologies or physiological developmental trajectories may not be easily reversed.

Comparison of the induction of defensive responses in these two species of ephemereids shows that even closely related species with similar behaviours, morphologies and life histories may have different defence strategies (Lardner 2000). This variation among closely related species suggests that the relative profitability of

different defence strategies is a function of the selection pressures experienced in different habitats. We suspect that *Ephemerella* larvae experience some level of fish predation throughout their range in eastern North American streams. Thus, they may invest in a fixed morphological defence, but vary their development as a graded response to the relative risk of predation. In contrast, *Drunella* larvae develop in both fish and fishless streams, which may enable them to invest in defensive morphology only in the presence of fish (Dahl and Peckarsky 2002). We need a better resolution of the differences between the perception of variation in the environment to understand the factors involved in the evolution and maintenance of defensive traits.

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