

Trout reverse the effect of water temperature on the foraging of a mayfly

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Abstract Climate change is likely to increase the metabolisms of ectothermic animals living below their thermal optimum. While ectothermic top predators may compensate by increasing foraging, ectothermic prey may be unable to increase foraging because of increased predation risk from ectothermic predators. We examined how the diurnal drift behavior (i.e., the downstream movement associated with foraging) of the mayfly *Baetis*, an ectothermic herbivore, responds to changing temperature in the implied presence and absence of trout, an ectothermic predator. In an experiment replicated at the catchment scale, water temperature and trout presence strongly interacted to affect the diurnal drift of *Baetis* from artificial channels lacking periphyton over a water temperature range of 4.2–14.8 °C. In fishless streams, daytime drift increased with increasing water temperature, likely because of increased metabolic demand for food. However, in trout-bearing streams, daytime drift decreased with increasing water temperature. Our interpretation is that the perceived threat of trout rose with increasing water temperature, causing mayflies to reduce foraging despite heightened metabolic demand. These results

suggest that anticipated increases in stream temperature due to climate change may further escalate divergence in structure and process between fishless and trout-bearing streams. Similar dynamics may occur in other ecosystems with ectothermic predators and prey living below their thermal optima.

Keywords Invertebrate drift · Metabolic demand · Baetidae · Climate change · Invasive species · Foraging

Introduction

A growing challenge in ecology is to understand and predict how anthropogenic changes to the biotic and abiotic environment will alter animal behavior, and how those behavioral changes will affect ecosystem structure and processes. Air and water temperature are increasing due to anthropogenic forcing (Morrill et al. 2005; Pachauri et al. 2007), raising the body temperatures, and, therefore, metabolisms, of ectothermic animals living below their thermal optimum (Brown et al. 2004). Dell et al. (2011) showed that traits associated with predator avoidance exhibit optimal performance at colder temperatures than traits associated with prey capture. Therefore, ectothermic predators living below their thermal optima may become more dangerous to prey with climate change, both because of increased demand for food by predators and because prey capture traits will likely improve relative to predator avoidance traits (Dell et al. 2011). Here, we ask whether the presence of an ectothermic predator (trout) can prevent an ectothermic herbivore (mayfly) from increasing foraging in response to rising temperature.

We conducted our study in the Sierra Nevada across a series of catchments with and without trout. Historically,

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lakes and streams above 1,800 m in the Sierra Nevada were largely fishless (Knapp et al. 2001); however, following decades of stocking, many of these water bodies now contain trout (Knapp and Matthews 2000). Water temperatures vary annually from 0 to ~17 °C (Knapp et al. 2001), and are, therefore, generally below the temperature associated with peak feeding rate of regional trout species (~13–17 °C; Baldwin 1957; Grove et al. 1978; Ojanguren et al. 2001). Nevertheless, trout have altered lake (Knapp et al. 2001), terrestrial (Epanchin et al. 2010), and stream ecosystem structure (Herbst et al. 2009), and the downstream movement of invertebrates via the water column (i.e., invertebrate drift; Hammock et al. 2012). Trout are thought to affect invertebrate drift through their chemical and physical cues. For example, trout chemical cues cause mayflies (Ephemeroptera), the most well-studied organism that drifts, to restrict their drift behavior to the night (e.g., Douglas et al. 1994; Tikkanen et al. 1994). In the absence of benthic predators and disturbance, drift is predominantly a foraging behavior of mayflies (i.e., mayflies use stream current to ‘drift’ to new foraging sites; Kohler 1985; Hammock and Wetzel 2013).

We examined how the diurnal drift behavior of two species of *Baetis* (Ephemeroptera:Baetidae), are affected by water temperature in trout-bearing and fishless streams. In fishless streams, we expected that the diurnal drift of *Baetis* would increase with increasing temperature due to heightened metabolic demand for food (Brown et al. 2004). However, in streams with trout, rates of diurnal drift could increase with temperature due to increased metabolic demand, or decrease with increasing temperature because of increased predation threat from trout (Ojanguren et al. 2001; Dell et al. 2011), or changes in metabolic demand and predation threat might cancel, leading to no change in diurnal drift with temperature. To distinguish among these possibilities, we measured diurnal drift of *Baetis* at a low (4.2 °C) and moderate (14.8 °C) temperatures in eight trout-bearing and eight fishless catchments. We chose 14.8 °C as the upper temperature because it is within the range of summertime temperatures in the streams we visited and near the optimal feeding rate of trout species of the region (Baldwin 1957; Grove et al. 1978; Ojanguren et al. 2001). We used 4.2 °C because trout feeding rates are substantially slowed at this temperature, and it is within the range of water temperatures observed in the region (Knapp et al. 2001). In addition to the factorial experiment, we measured drift hourly for 24 consecutive hours in a trout-bearing stream (Convict Creek) nine times during a 9-month period (stream temperature range 0–17 °C). We used these data to determine whether the results of the factorial experiment, in which we manipulated temperature artificially, were similar to results from a trout-bearing stream in which temperature changed seasonally. Finally, because the seasonal data were correlative, we ran an experiment to isolate the

effect of temperature and dissolved oxygen on diurnal drift of *Baetis* in Convict Creek.

Methods

We tested whether the diurnal drift response of *Baetis* to water temperature depends on trout presence by running a 2 × 2 factorial experiment replicated at the catchment scale. The two factors were trout (present and absent) and water temperature (means of 4.2 and 14.8 °C). We conducted the experiment during daylight hours in the Sierra Nevada Mountains, USA from July to September 2011 at eight fishless streams and eight trout-bearing streams. Each stream drained a hydrologically independent catchment (site locations in electronic supplementary material, Table S1). We cooled water by diverting it from the stream through 30.5 m of coiled copper pipe (i.e., refrigerator tubing) that was immersed in a snow–water bath (pictured in electronic supplementary material, Fig. S1). We warmed water by diverting it through 15.25 m of the same copper pipe heated with a propane camp stove, although at four streams ambient temperature was already at the upper target temperature of ~15 °C. At these sites, we ran the water through the copper tubing but did not heat it. Mean stream temperature for the 16 streams was 11.0 °C (range 5.0–17.0 °C, measured at the beginning of each visit).

From the heat exchangers, water spilled into a simulated pool-run sequence that comprised the experimental arena. The pool consisted of a ‘three in. PVC Sanitary Tee’ that was cut in half and plugged to form a watertight cylindrical vessel (depth = 4 cm, diameter = 7.5 cm, volume = 0.2 L) with a half-pipe spillway on one side. Water flowed from this vessel through the spillway and down a PVC pipe cut length-wise to form a channel (160 cm long, 3.8 cm wide). This channel formed the ‘run’ section of the arena. A screened collection container captured drifting mayflies from the outflow so that they could be counted. The PVC vessel and half-pipe channel were roughened with a file to provide purchase for mayflies. We lined the experimental arena with exogenous gravel collected from beside each stream in order to limit food in the channels and thus stimulate mayflies to drift (Kohler 1985). Once water temperature was adjusted to approximately 4.2 or 14.8 °C, we introduced 30 *Baetis* to the simulated pool and counted the number that drifted from the arena after 30 min. We conducted one replicate at the low and moderate temperatures at each of the 16 sites. The starting time for the trials at each site ranged between 8:48 and 16:16. The order in which we visited trout-bearing and fishless streams was randomized, as was the order in which we ran the two temperature trials at each stream. At 12 streams (four of the trout-bearing streams and all eight fishless streams)

Table 1 Model comparison for the analysis of the factorial experiment

Factorial experiment models	df	Log (L)	AIC _c	ΔAIC _c	AIC _c wt
~T + F + T × F	5	-43.93	97.9	0	1
~T + F	4	-96.26	200.6	102.6	<0.001
~T	3	-99.72	205.5	107.5	<0.001
~F	3	-102.4	210.8	112.9	<0.001
Intercept only	2	-105.9	215.7	117.8	<0.001

All models have stream as a random effect, a binomial distribution of error, and predict the proportion of animals that drifted

T temperature, F presence/absence of fish, df degrees of freedom, Log (L) log-likelihood, AIC_c Akaike units corrected for small sample size, ΔAIC_c difference between model of interest and top-ranked model, AIC_c wt Akaike weight

we only observed *Baetis bicaudatus*, and, therefore, used *B. bicaudatus* in the experiment. However, at four of the trout-bearing streams, *Baetis tricaudatus* was the dominant or only baetid, so we used *B. tricaudatus* in the experiment at these sites. We were more interested in the response of *Baetis* to temperature than responses of individual species, so we did not differentiate between the two species in the analysis described in the main text. However, we also analyzed the species separately, and included the results in the electronic supplementary material (Factorial experiment).

To avoid the problems associated with null hypothesis significance testing (see Anderson et al. 2000), we analyzed the data using multi-model inference. We built five models that predicted the proportion of mayflies that drifted from the experimental arena. Each model included 'stream' as a random effect. Because the response variable was a proportion, each model had a binomial distribution of error and a logistic link function (Bolker et al. 2009). The models included an intercept (null) model, a linear temperature model, a linear trout model, a linear temperature and trout model, and the full model, which included both predictors and their interaction (Table 1). We included the temperature model because we expected metabolic demand for food, and, therefore, drift, to vary with temperature (Brown et al. 2004; Kohler 1985). We included the trout model because trout depress diurnal drift (e.g., Flecker 1992). The additive trout and temperature model was included because trout presence could suppress drift while not altering the effect of temperature. Finally, we included the full model because temperature could affect the predation threat posed by trout (e.g., Webb 1978; Ojanguren et al. 2001). We modeled trout as a categorical variable (present or absent), while temperature was modeled as a continuous variable because temperatures within the 'low' and 'moderate' treatments, though similar, were not equal. We conducted the analyses using R version 2.14.1, and models were fit using the

'glmer' function in the R statistical package 'lme4' (Bates et al. 2011; R Development Core Team 2011). Models were compared using Akaike Information Criterion, corrected for small sample size (AIC_c; Burnham and Anderson 2002).

To determine whether temperature correlates with drift in a natural ecosystem, we measured the drift of *B. tricaudatus* and stream temperature hourly during nine 24 h periods from Feb through Oct 2011 in Convict Creek (elevation 2,200 m). Both brown trout (*Salmo trutta*) and rainbow trout (*Oncorhynchus mykiss*) are present in Convict Creek (Jenkins et al. 1999). Drift data were collected for 24 consecutive hours beginning on the following dates in 2011: 7, 8, 11 Feb, 12 Mar, 13 Apr, 10 May, 10 Jun, 10 Aug, and 22 Oct. For each 24 h period, two drift nets (upstream aperture diameter 10.9 cm, mesh size 300 μm) were staked to the bottom of the stream in the same ~1 m riffle. Nets were removed from the stream hourly, contents were rinsed into sorting trays, and nets were replaced in the stream within 30 s of their removal. All *B. tricaudatus* estimated to be >1.5 mm in length were counted. We only counted individuals larger than 1.5 mm because the drift behaviors of larger baetids are more strongly affected by trout than smaller baetids (Allan 1978). At the conclusion of each 24 h sampling period, water velocity at the front of each drift net was measured using a Marsh McBirney Flo-Mate velocity meter.

To determine whether stream temperature predicted daytime drift rate, we summed all the diurnal measurements and all the nocturnal drift measurements for each 24 h period. We built three statistical models that predicted the proportion of *B. tricaudatus* that drifted diurnally out of total 24 h drift. We modeled the proportion of *B. tricaudatus* that drifted diurnally rather than the number that drifted diurnally to account for possible seasonal changes in 24 h drift of *B. tricaudatus* (due, for example, to changing population size). All models had beta-binomial distributions of error (to account for over-dispersion) and logistic link functions (Bolker 2008). They included an intercept (null) model, a model in which diurnal drift proportion varied linearly with mean daytime stream temperature, and a model in which diurnal drift proportion varied linearly with mean daytime stream temperature and day-length (Table 3). We included day-length (the ratio between the time from sunrise to sunset and the time from sunset to sunrise) because day-length varied substantially during the 9 months of observations, and, therefore, had the potential to explain variation in the proportion of *B. tricaudatus* drifting diurnally.

Of the nine 24 h periods during which we quantified drift in Convict Creek, three were in February and one was in August. We used these data to compare drift patterns between the coldest and warmest periods. Standard errors were calculated with each net as a replicate (i.e., $n = 6$ and $n = 2$ for each time point in February and August, respectively). To account for seasonal variation in discharge, we

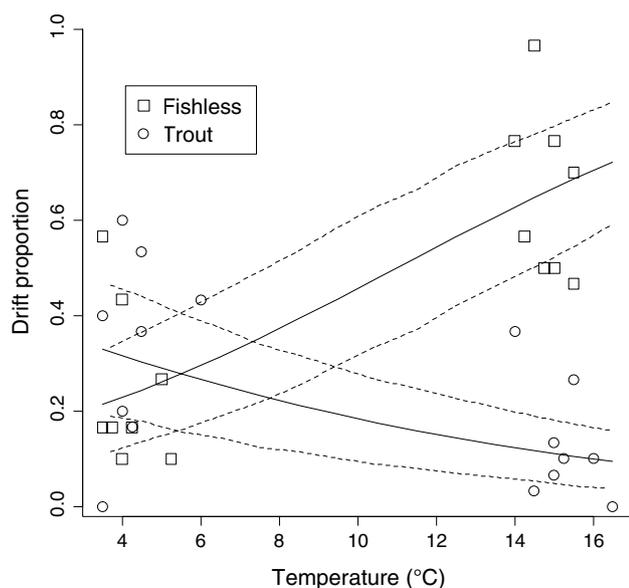


Fig. 1 Results of the factorial experiment. *Squares*: diurnal drift of *Baetis* in fishless streams ($n = 8$); *circles*: diurnal drift of *Baetis* in trout-bearing streams ($n = 8$). *Solid lines* show the mean predictions of the interaction model, and the *dashed lines* are the 95 % CI of the mean predictions. The line with a positive slope shows the mean predictions in fishless streams, the line with a negative slope in trout-bearing streams

expressed drift as a density (number/50 m³ water) following Flecker (1992). Because the relationship between temperature and drift for the seasonal Convict Creek data was correlative, we also measured drift across a range of temperatures (2.5–20.3 °C) in water piped from Convict Creek. We manipulated water temperature using two heat exchangers, and measured diurnal drift of *B. tricaudatus* from the same experimental arena used in the factorial experiment. Differences between the factorial and Convict Creek experiments were that: (1) 43 *Baetis*/channel were used per trial rather than 30; (2) each of the 33 trials lasted 1 h rather than 30 m; (3) we bubbled air into the water above 10 °C to loosen the correlation between dissolved oxygen and temperature; (4) we measured dissolved oxygen at the beginning of each trial; and (5) the experiment was run in a laboratory. We used the dissolved oxygen measurements to determine whether diurnal drift was better predicted with dissolved oxygen or temperature (additional methods in electronic supplementary material, Convict Creek experiment).

Results

Water temperature and trout presence strongly interacted to affect the diurnal drift of *Baetis* in the factorial experiment

Table 2 Parameter estimates and 95 % confidence intervals for the full GLMM of the factorial experiment

Parameter	Estimate	95 % CI
Intercept	-1.95	-2.68, -1.22
T	0.18	0.14, 0.22
F	1.65	0.62, 2.67
T × F	-0.30	-0.36, -0.24

All values on log-odds scale; intercept is log odds of drifting for fishless streams at 0 °C

T temperature, F presence/absence of fish

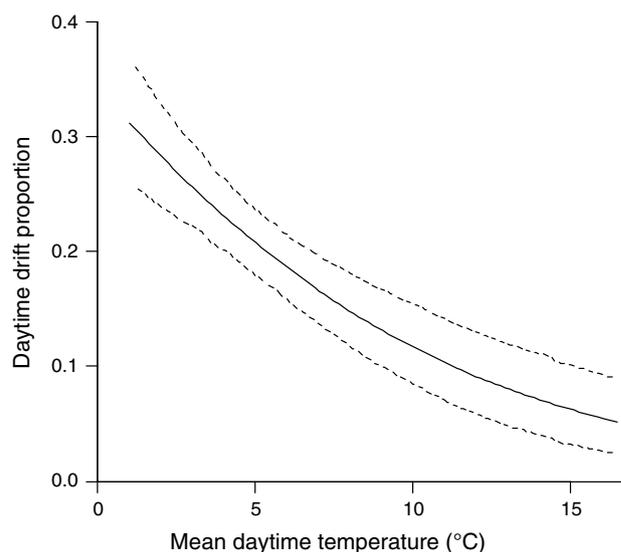


Fig. 2 The proportion of *B. tricaudatus* predicted to drift during the day as a function of mean daytime stream temperature in Convict Creek, a trout-bearing stream ($n = 9$). The *solid line* is the mean prediction for the top-ranked model, and the *broken lines* are the 95 % CI of the mean predictions. To make the predictions, the day-length parameter was held constant at 1, a 12 h day

Table 3 Model comparison for the analysis of the Convict Creek observational data

Convict Creek models	df	Log (L)	AIC _c	ΔAIC _c	AIC _c wt
~ST+DL	4	-34.1	76.3	0	0.819
~ST	3	-36.7	79.3	3.1	0.178
Intercept only	2	-41.8	87.5	11.2	0.003

The ST variable refers to mean daytime stream temperature. DL refers to the ratio of time from sunrise to sunset to sunrise for each 24 h sampling period. All models have beta-binomial distributions of error

df Degrees of freedom, Log (L) log-likelihood, AIC_c Akaike units corrected for small sample size, ΔAIC_c difference between model of interest and top-ranked model, AIC_c wt Akaike weight

Table 4 Parameter estimates and 95 % confidence intervals for the top-ranked model in the analysis of the Convict Creek observational data

Parameter	Estimate	95 % CI
Intercept	-1.75	-2.52, -0.99
ST	-0.14	-0.19, -0.08
DL	1.10	0.23, 1.97

The ST variable refers to mean daytime stream temperature. DL refers to the ratio of time from sunrise to sunset to sunset to sunrise for each 24 h sampling period

(AIC_c weight of full model = 1; Table 1; Fig. 1). The mean drift proportion increased from 0.25 to 0.65 in the fishless streams from low to moderate temperature, but decreased from 0.34 to 0.13 in the trout-bearing streams from low to moderate temperature. For the fishless streams, the odds of drifting increased by about 1.2× for each 1 °C increase in temperature, while they decreased by 0.89× for each 1 °C increase in trout bearing streams (parameter estimates in Table 2). Drift increased at all eight fishless streams with increasing temperature, and decreased in seven out of eight trout-bearing streams with increasing temperature (the drift proportions were zero at both the low and moderate temperature at one of the trout-bearing streams).

The proportion of drift of *B. tricaudatus* that occurred during the day increased almost eight-fold as mean daytime stream temperature declined from 16.5 to 1.0 °C over the 9-month sampling period in trout-bearing Convict Creek (Fig. 2). The cumulative AIC_c weight for the two models with a temperature parameter was 0.997, with the model that included both day-length and mean daytime stream temperature receiving substantially more AIC_c support than the other models (AIC_c weight = 0.819; Table 3). For the top-ranked model, the proportion of *B. tricaudatus* that drifted diurnally decreased predictably with rising stream temperature and increased predictably with increasing day-length (Table 4). We used this model to make predictions across the range in mean daytime temperature that we observed in Convict Creek holding the day-length variable constant at 1, a 12 h day (Fig. 2). For an increase in temperature of 1 °C the odds of drifting decreased by 0.87×. In Fig S2 we show the behavior of the model across the range in day-lengths during which we sampled drift.

In total, we counted 2,736 *B. tricaudatus* nymphs during the nine 24 h periods. Diurnal drift rates were substantially higher in winter than in summer (Fig. 3). In the Convict Creek experiment, we found that water temperature was a markedly better predictor of diurnal drift than dissolved oxygen (electronic supplementary material, Convict Creek experiment). Consistent with our other results, diurnal drift increased 1.9-fold as temperature decreased from 20.3 to 2.5 °C.

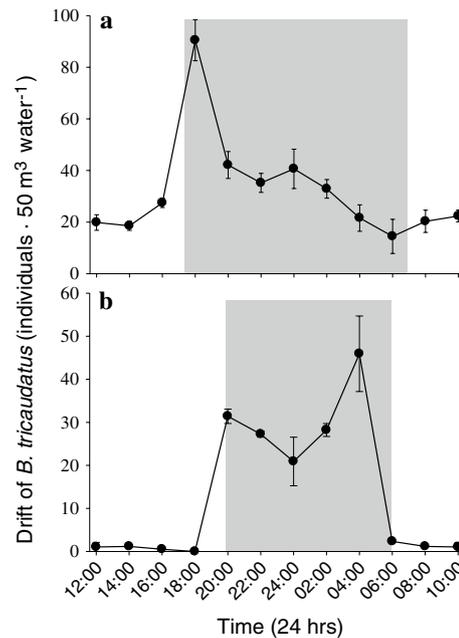


Fig. 3 24 h drift patterns of *B. tricaudatus* in Convict Creek, a trout-bearing stream. The shaded rectangles indicate times between sunset and sunrise and error bars indicate \pm SE. Panel a is the winter drift pattern and is averaged across three 24 h periods in winter (mean stream $T = 1.4$ °C; $n = 6$). Panel b shows drift measurements from a single 24 h period in Aug 2011 (mean stream $T = 15.7$ °C; $n = 2$). For further summertime drift data from the same location in Aug, see Fig. 1 in Hammock et al. (2012). Note that Convict Creek contains trout year-round (Maciolek and Needham 1952), and that the timing of drift in winter (a) is remarkably similar to the timing of drift in fishless streams of the region (Fig. 2, Hammock et al. 2012)

Discussion

Animals are thought to maximize fitness by minimizing their predation risk:foraging rate ratio in space, which they achieve by moving among patches (Gilliam and Fraser 1987). Following this theory, drift of mayflies decreases with increasing food, essentially ceasing when density of periphyton is high and benthic predators are absent (Kohler 1985; Hammock and Wetzel 2013). Therefore, our interpretation is that *Baetis* nymphs drifted from our experimental channels—which lacked benthic predators and periphyton—in search of food. Our results from the fishless streams are consistent with this interpretation, as drift increased 2.5-fold with increasing water temperature as hypothesized, likely because metabolic demand for food increased with increasing temperature (Fig. 1; Brown et al. 2004). However, increasing temperature had the opposite effect in the trout-bearing streams, where diurnal drift decreased 2.6-fold with increasing water temperature. The diurnal drift of *B. tricaudatus* also decreased with increasing temperature in the two data-sets from trout-bearing Convict Creek (Figs. 2, 3, Electronic supplementary

material, Convict Creek experiment). These results support the hypothesis that increasing water temperature increased the perceived predation threat of trout, overriding metabolic demand for food as a driver of drift behavior. Other interpretations are possible, as our experiments were limited in terms of the size and realism of the experimental arena and length of time for experimental trials. For example, individuals may have drifted in search of more optimal temperature and oxygen conditions. While drift was better predicted by temperature than dissolved oxygen in the Convict Creek experiment (Table S3), oxygen shortages at high temperatures occur mainly because oxygen requirements increase with increasing temperature, not because oxygen solubility decreases (Verberk et al. 2011). However, oxygen demand decreases with decreasing temperature (Verberk et al. 2011), so oxygen stress cannot easily explain why drift increased as temperature decreased in the trout-bearing streams. Thus, we consider food limitation to be the most likely cause of drift from our channels.

As they do spatially, animals are thought to maximize fitness temporally by foraging during periods that minimize their predation risk:foraging rate ratio (Metcalf et al. 1999). Therefore, drifting diurnally under conditions in which trout are less dangerous could improve fitness of *Baetis* in two ways. Individuals may consume more food when their drift behavior is not restricted to the nighttime, or drifting diurnally may reduce exposure to nocturnally active benthic predators, or both (Hammock et al. 2012). As theory would predict, baetids respond to the absence of trout cues by increasing diurnal drift (e.g., Douglas et al. 1994; Tikkanen et al. 1994). In addition, a study by Pekarsky and McIntosh (1998) links a decrease in a fitness proxy to altered foraging in the implied presence of trout. They demonstrated that when *B. bicaudatus* larvae are raised in the presence of trout chemical cues, larvae are smaller and, therefore, likely less fecund as adults (Pekarsky and McIntosh 1998). Finally, Flecker (1992) and McIntosh et al. (2002) found that baetids drift more diurnally in the absence of trout at the catchment scale, and Flecker (1992) suggested that drifting diurnally in the absence of trout improves mayfly fitness. Thus, we suggest that diurnal drift increased as temperature decreased in Convict Creek because drifting diurnally improved the predation risk:foraging rate ratio of *Baetis*.

We propose three reasons that the threat posed by trout should decrease with decreasing temperature, allowing the diurnal drift of *Baetis* to increase. First, the prey capture traits of trout may decline in efficacy with decreasing temperature more strongly than the predator avoidance traits of *Baetis*. Across a broad group of organisms, traits associated with predator avoidance perform optimally at colder temperatures than traits associated with prey capture (Dell et al. 2011). Dell et al. (2011) attribute this finding to a thermal

version of the life-dinner principle of Dawkins and Krebs (1979), suggesting that natural selection favors prey phenotypes that maintain evasion capability at cold temperatures more strongly than natural selection favors predator phenotypes that maintain attack capability. This hypothesis is consistent with our results. The increase in diurnal activity of *Baetis* in trout-bearing streams occurred over the same temperature range that the prey capture traits of regional trout species decline. For example, the swim acceleration of rainbow trout (*Oncorhynchus mykiss*) decreases with decreasing temperature from 15 to 5 °C (Webb 1978). Moreover, the swim acceleration of trout is most strongly reduced at low temperatures (Webb 1978), and thus mirrors the accelerating increase in diurnal drift proportion at low temperatures (Fig. 2). Second, trout likely became less dangerous during the day with decreasing temperature because salmonids become increasingly nocturnal as temperature decreases, beginning at ~10 °C (e.g., Fraser et al. 1993; Huusko et al. 2007). Finally, the food intake rates of trout decrease with decreasing temperature (e.g., Baldwin 1957; Grove et al. 1978; Ojanguren et al. 2001). Thus, trout may pose less risk to diurnally active *Baetis* as temperature decreases because the predator avoidance traits of *Baetis* may improve relative to the prey capture traits of trout, trout become less diurnally active, and trout consume less food.

Our results, in combination with the predictions of climatic models and previous studies on trophic cascades in streams, raise the possibility that continued atmospheric warming will increase divergence in community structure and process between streams with and without trout as a top-predator. There is extensive evidence linking reduced stream herbivore foraging due to trout presence to increased algal biomass in streams. For example, McIntosh and Townsend (1996) found higher densities of algae in the presence of trout, but similar grazer abundances, and argued that decreased grazer foraging caused by trout increased algal abundance. Pekarsky and McIntosh (1998) reported increased algal density and reduced mayfly foraging in an experimental treatment with trout odor. Herbst et al. (2009) found higher periphyton density and cover in streams invaded by trout, and suggests that trout presence reduced herbivore foraging in invaded streams, decreasing top-down control on algae. Finally, Kishi et al. (2005) found that trophic cascades caused by lotic fish were strongest at optimal temperatures for fish foraging. Stream temperature is expected to rise (Morrill et al. 2005), and we found that diurnal drift, a behavior baetids use to search for food, is more strongly reduced at higher temperatures. Thus, the diurnal drift of mayflies is likely to decrease in high elevation trout-bearing streams as temperature rises, potentially increasing algal biomass. Similar effects may be observed in other ecosystems with ectothermic predators and prey living below their thermal optima. For example,

Barton et al. (2009) found that the positive effect that spiders exert on primary producer biomass via grasshoppers was heightened as temperature increased. For ecosystems in which the ectothermic predators are invasive, like the trout in our study, we speculate that the top-down effects of those predators may be increased by climate change.

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