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VARIATION IN MAYFLY SIZE AT METAMORPHOSIS AS A DEVELOPMENTAL RESPONSE TO RISK OF PREDATION

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Abstract. Animals with complex life cycles often show large variation in the size and timing of metamorphosis in response to environmental variability. If fecundity increases with body size and large individuals are more vulnerable to predation, then organisms may not be able to optimize simultaneously size and timing of metamorphosis. The goals of this study were to measure and explain large-scale spatial and temporal patterns of phenotypic variation in size at metamorphosis of the mayfly, *Baetis bicaudatus* (Baetidae), from habitats with variable levels of predation risk. Within a single high-elevation watershed in western Colorado, USA, from 1994 to 1996 we measured dry masses of mature larvae of the overwintering and summer generations of *Baetis* at 28 site-years in streams with and without predatory fish (trout). We also estimated larval growth rates and development times at 16 site-years. Patterns of spatial variation in mayfly size could not be explained by resource (algae) standing stock, competitor densities, or physical–chemical variables. However, size at metamorphosis of males and females of summer generation *Baetis* was smaller in fish streams than in fishless streams and decreased as densities of predatory stoneflies increased. Furthermore, overwintering individuals matured at larger sizes than summer generation *Baetis*, and the size of emerging *Baetis* declined over the summer, but predominantly in trout streams. Theoretical consideration of the effect of predation risk on size and timing of metamorphosis accurately predicted the observed temporal variation in size and timing of mayflies at emergence in fish and fishless streams. *Baetis* populations had similar growth rates but followed different developmental trajectories in high and low risk environments. In risky environments larval development was accelerated, resulting in metamorphosis of younger and smaller individuals, minimizing exposure of larvae to risk of mortality from trout predation, but at the cost of future reproduction. In safe environments, larvae extended their development, resulting in larger, more fecund adults. Thus, we propose that large-scale patterns of variation in size and timing of metamorphosis represent adaptive phenotypic plasticity, whereby mayflies respond to variation in risk of predation, thereby maximizing their fitness in variable environments.

Key words: adaptive phenotypic plasticity; development; fecundity; growth; mayflies; metamorphosis, size and timing; path analysis; predation; streams; structural equation modeling; trout; water temperature.

INTRODUCTION

Body size can have important consequences for the fitness of individuals by affecting both mortality rates and reproductive success (Werner 1988). Larger individuals may be better competitors (Van Buskirk and Yurewicz 1998), less vulnerable to predation (Werner 1986, Crowl and Covich 1990, Wissinger 1992), have greater longevity (Bradshaw and Holzapfel 1992, Neems et al. 1998), or higher probabilities of surviving harsh abiotic conditions (Calow and Townsend 1981). Furthermore, large females of many species are more fecund (Wickman and Karlsson 1989, Honek 1993), and larger males often have greater reproductive success through male–male competition or female choice (Blum and Blum 1979, Bateson 1983, Thornhill and Alcock 1983). However, large size can also be a liability in environments where predators selectively consume large individuals of a prey population (Brooks and Dodson 1965, Allan 1978, Lynch 1980, Reznick 1982, Wellborn 1994).

The costs and benefits of large body size may be reflected in life history traits of organisms that can mature and reproduce at different sizes (Wilbur 1980, Dill 1987, Werner 1988). For example, variation in environmental risk factors may affect the timing and size of individuals at metamorphosis (Wilbur and Collins 1973, Werner 1986, Abrams et al. 1996, Twombly 1996). The timing and body size of individuals at metamorphosis often varies with the risk of predation in the larval environment (Abrams and Rowe 1996), espe-

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cially for organisms in which fecundity increases with body size (Forrest 1987, Lardner 1998, Laurila et al. 1998, McPeek and Peckarsky 1998). If large individuals are more fecund and more vulnerable to predation, then there should be a trade-off between maximizing body size and completing development faster to avoid predation (Werner and Anholt 1993, Abrams et al. 1996). This trade-off constrains simultaneous optimization of age and size at metamorphosis (Hensley 1993). However, animals can maximize fitness by adjusting life history traits thereby attaining the lowest possible ratio of mortality to fecundity (Calow and Townsend 1981, Gilliam et al. 1989, Schluter et al. 1991, Werner and Anholt 1993, Nylin and Gotthard 1998).

Although theory on this topic is well developed (Abrams 1991, Abrams and Rowe 1996, Abrams et al. 1996, McPeek and Peckarsky 1998), more large-scale empirical studies of life history trade-offs between size and timing of metamorphosis in natural systems are needed (e.g., Crowl and Covich 1990, Reznick 1990). Furthermore, tests of mechanisms responsible for predator-induced life history variation have rarely been conducted using large-scale experiments (Hairston and Walton 1986). Proposed mechanisms often involve mixtures of adaptations and constraints and may be reversible or irreversible during development (Alford and Harris 1988, Stearns 1989, Kirkpatrick and Lofsvold 1992, Morgan and Christy 1994). Constraints on growth and development may be imposed by environmental variation in temperature (Bradshaw 1973, Vannote and Sweeney 1980, Taylor 1981, Kindleman and Dixon 1992, Berrigan and Charnov 1994, Newbold et al. 1994), timing of food availability during development (Wilbur and Collins 1973, Nijhout 1975, Alford and Harris 1988, Hensley 1993, Bradshaw and Johnson 1995, Twombly 1996), density of competitors (Travis 1984, Hawley 1985, Simmonds and Blaney 1986, So and Dudgeon 1989, Goodbrod and Goff 1990, Peckarsky and Cowan 1991, Bradshaw and Holzapfel 1992, Scott 1994), predator avoidance (Skelly and Werner 1990, Peckarsky et al. 1993, Ball and Baker 1996, Belk 1998, Peckarsky and McIntosh 1998), or complex combinations of environmental variation (e.g., Skelly 1992, Babbitt and Tanner 1998). Observational data obtained in natural systems can be used not only to examine large-scale patterns of life history variation, but also, in combination with small-scale experiments and theory, to provide strong inference to evaluate alternative mechanistic hypotheses to explain those patterns (Power et al. 1998, Werner 1998).

Size variation among populations may have a genetic component (Kurzava and Morin 1994, Klingenberg and Spence 1997, Svensson 1997) often caused by size-selective predation (Reznick et al. 1990, Spitze 1991, 1992, Wellborn 1994, Hechtel and Juliano 1997, Rodd and Reznick 1997, Rodd et al. 1997). Alternatively, life history variation may result from phenotypically plastic responses of populations containing individuals with the genetic capability to respond directly to changes in the environment (Crowl and Covich 1990, Gotthard and Nylin 1995, Abrams et al. 1996, DeWitt 1998, Nijhout 1999). Phenotypic plasticity in life history traits, as opposed to fixed patterns of life history adapted to different environments, will be favored when some mortality agent is variable and can be anticipated (DeWitt et al. 1998). Thus, individuals that can modulate life history parameters through behavioral or developmental plasticity should have a fitness advantage in variable environments (Bradshaw 1973, Newman 1992).

Adaptive plasticity in life history responses is commonly observed in organisms operating under time constraints to metamorphose before a predictable unfavorable environmental change occurs (Wilbur and Collins 1973, Semlitch and Gibbons 1985, Newman 1989, Ludwig and Rowe 1990, Rowe and Ludwig 1991, Juliano and Stoffregen 1994, Twombly 1996, Denver et al. 1998). For species with short-lived adults, size variation may also result from selection to mature at the same time as the majority of a cohort (Sweeney et al. 1995). Finally, developmental plasticity may be driven by time constraints on metamorphosis in environments where predation pressure varies spatially or temporally throughout the larval period (Werner 1986, Abrams et al. 1996, Arnqvist and Johannson 1998, McPeek and Peckarsky 1998).

Since biotic and abiotic risk factors are highly variable in the larval habitat of stream insects (Flecker 1997, Palmer and Poff 1997), the ability of stream organisms to alter their life histories to respond to environmental variation should be particularly important. Furthermore, in hemimetabolous aquatic insects the trade-off between body size and timing of metamorphosis often involves an ontogenetic niche shift featuring rapid transformation from an aquatic larval stage to a terrestrial adult stage. In some insect orders with extremely brief adult stages (e.g., Ephemeroptera), processes that normally occur in the adult (reproductive maturation) are completed in the larval stage. In these organisms, potential reproductive success depends strongly on interactions that influence larval mortality, growth rate, duration, and the developmental pathways taken by individuals (Werner and Gilliam 1984, Werner 1986, Lima and Dill 1990, Ludwig and Rowe 1990, Werner and Anholt 1993, 1996, Ball and Baker 1996, McPeek and Peckarsky 1998). Thus, phenotypic plasticity in larval development results in delayed costs or benefits as realized reproductive potential of adults (Bradshaw and Holzapfel 1992).

The goals of this study were to measure and explain phenotypic variation in size and timing of metamorphosis in populations of the swimming mayfly larvae, *Baetis bicaudatus* (Baetidae), which live in high-altitude streams in western Colorado. These fluctuating environments not only affect insect development di-

rectly, but also contribute indirectly to temporal and spatial variability of predation risk. For example, some streams have trout and others are completely fishless due to dispersal barriers (waterfalls that drop >1 m). Stream discharge varies annually, seasonally, and daily depending on the winter snow pack and summer air temperatures, which affect snow melting rates, water clarity, and water temperatures. Foraging activity and digestion rates of salmonid fish decline with decreasing temperature (Elliott 1972, Nicieza et al. 1994); some salmonids cease feeding when water temperatures drop below 4°–6°C, and others become nocturnal in winter, reducing their ability to capture prey (Cunjak and Power 1986, Fraser et al. 1993, Heggenes et al. 1993, Fraser and Metcalfe 1997, Nicieza and Metcalfe 1997, Valdimarsson et al. 1997). Also, the reaction distances of salmonids may be substantially reduced during spring runoff when snow melt decreases water clarity (Berg and Northcote 1985, Wilzbach et al. 1986, Gregory and Northcote 1993).

Despite this environmental variability, *Baetis* larvae are relatively abundant in these and similar habitats and interact with many other species in stream food webs. They are eaten by both predatory stoneflies and trout. While rates of consumption by stoneflies are minimal (Kerans et al. 1995), fitness costs (smaller size and reduced fecundity) of fleeing to avoid stonefly predation may be substantial (Peckarsky et al. 1993, McPeek and Peckarsky 1998, Peckarsky and McIntosh 1998). *Baetis* larvae are also common prey of visually oriented, drift-feeding trout (Elliott 1973, Ware 1973, Allan 1978, 1981, Angradi and Griffith 1990); but likewise, demographic models demonstrate that mortality due to predation by trout, while greater than to stoneflies, may be small compared to the population consequences of fitness costs associated with minimizing trout predation (McPeek and Peckarsky 1998). *Baetis* larvae are also susceptible to infection by mermithid parasites, which cause significant mortality of early instars or castration of late instars (Vance and Peckarsky 1996).

The survival and fecundity of *Baetis* are both related to body size. Larger females are more fecund (Clifford 1970, Benech 1972, Peckarsky et al. 1993, Scrimgeour and Culp 1994), and larger males may obtain more matings, as has been shown in other mayflies (Flecker et al. 1988). Large stoneflies prey selectively on large *Baetis,* but smaller predatory stoneflies prefer small *Baetis* (Allan et al. 1987, Allan and Flecker 1988). Stoneflies are nocturnal predators (Peckarsky and McIntosh 1998) and both large and small stoneflies are continuously present in the larval microhabitat (Taylor et al. 1998). Therefore, *Baetis* has neither a spatial, a temporal, nor a size refuge from stonefly predation. Although large *Baetis* are more vulnerable to predation by trout (Allan 1978, 1981), experimental removal of neither trout (Allan 1982) nor stoneflies (Peckarsky 1985) from *Baetis* habitats affects their size distribution in the field. However, in trout streams large *Baetis* individuals are more constrained to nocturnal movement (Allan 1978, Malmqvist 1988, Flecker 1992, McIntosh et al. 1999) and nocturnal feeding on diatoms on the substrate surface (Culp et al. 1991, Cowan and Peckarsky 1994).

TABLE 1. Expected size at metamorphosis, growth rate, and development time of *Baetis bicaudatus* in fish streams compared to fishless streams in Western Colorado, USA, under three alternative mechanistic hypotheses to explain observed size variation.

Hypotheses	Size at metamorphosis	Growth rate	Development time
Lost feeding time due to predator avoidance	small	slow	long
Adaptive developmental response to predators	small	fast	short
Size-selective predation	small	same	same

Our previous measures of the consequences of predator avoidance on *Baetis* size at metamorphosis have been obtained from experiments carried out in streamside, circular, flow-through chambers (Peckarsky et al. 1993, Peckarsky and McIntosh 1998). Those experiments were relatively short-term (~3 wk), using the overwintering generation of *Baetis,* covering the period of development when females matured their eggs and both sexes developed wing pads (Stages III–IV, Delucchi and Peckarsky 1989). The present study was designed to determine whether the small body size induced by high predation risk observed in experimental chambers could be detected under natural field conditions.

Size differences among *Baetis* individuals emerging from high and low predation-risk environments could be caused by three potential mechanisms (Table 1). First, predator-avoidance behavior could reduce *Baetis* foraging time, resulting in slower growth rates and/or longer development times in trout streams. Second, small size at metamorphosis from trout streams could result from accelerated larval growth and/or development in the high-risk environment. In this case, *Baetis* individuals should have different developmental trajectories in fish and fishless environments, developing quickly and emerging at a minimum size in fish streams, and delaying maturation, thereby increasing size and fecundity in fishless streams. Observed life-history differences between *Baetis* emerging from fish and fishless streams could be the result of adaptive phenotypic plasticity or genetic differences between populations in the two environments (Nijhout 1999). However, previous studies suggest that *Baetis* larvae in fish and fishless streams are derived from ovipositing females that have dispersed from multiple source populations (Peckarsky et al. 2000). Extensive dispersal should promote gene flow among streams and counter fish-mediated selection on *Baetis* larval development.

TABLE 2. Summary of data used in structural equation models and path analysis.

Site	Year	Black wing pad sample sizes: Winter Male	Winter Female	Summer Male	Summer Female	Fish (no./m²)†	Stoneflies (no./m²)†	*Baetis* (no./m²)†	Grazers (no./m²)†	Diatoms (mm³/cm²)†	Degree days per day	Length of study reach (m)
Fish streams (n = 16)												
AV	1994	2	⋯	24	17	⋯	474	4220	901	0.15	9.3	30
AV	1995	8	6	28	30	⋯	164	618	141	0.01	7.7	30
AV	1996	5	2	12	10	0.91	232	7927	295	0.29	10.0	30
CO	1994	48	36	8	14	⋯	267	1652	2580	0.18	7.1	10
(CO)	(1995)	18	33	⋯	⋯	⋯	(34)	(374)	(905)	(0.14)	(5.7)	10
CO	1996	27	29	28	28	0.05	195	3601	1217	0.15	6.3	10
ER	1994	19	31	13	9	⋯	146	1176	906	0.12	10.2	10
ER	1995	19	35	19	25	⋯	14	769	1232	0.17	6.8	10
ER	1996	38	50	25	37	0.07	200	930	907	0.63	8.3	10
(LQ)	(1995)	25	26	⋯	⋯	⋯	(77)	(834)	(759)	(0.01)	⋯	15
LR	1995	17	14	23	21	⋯	56	561	542	0.02	⋯	15
LR	1996	37	49	14	9	0.20	216	1093	817	0.39	8.7	15
RU	1994	36	24	14	18	⋯	417	3068	2041	0.18	5.6	10
(RU)	(1995)	9	23	⋯	⋯	⋯	(54)	(308)	(816)	(0.13)	(3.4)	10
RU	1996	18	27	12	17	0.06	208	2459	1049	0.32	6.3	10
(UQ)	(1995)	24	34	⋯	⋯	⋯	(133)	(1405)	(1155)	(0.31)	⋯	15
Fishless streams (n = 12)												
BB	1995	7	2	1	⋯	0	8	39	146	0.24	⋯	30
BB	1996	3	3	5	7	0	55	73	65	0.48	5.9	30
LB	1994	13	10	3	5	0	825	1632	690	0.56	12.4	15
LB	1995	25	40	8	7	0	195	249	475	0.09	5.3	15
LB	1996	25	45	2	2	0	290	481	62	0.24	7.8	15
SG	1996	17	13	2	⋯	0	54	348	295	0.48	11.4	30
(UB)	(1995)	6	14	⋯	⋯	0	(106)	(391)	(1003)	(0.07)	⋯	30
UB	1996	25	30	1	1	0	121	632	204	0.19	5.4	30
UR	1994	43	28	7	⋯	0	501	1702	1393	0.09	7.5	10
UR	1995	8	13	⋯	3	0	21	1002	551	0.02	3.4	10
UR	1996	43	33	17	10	0	202	3000	959	0.14	5.7	10
(VR)	(1995)	12	19	⋯	⋯	0	(15)	(27)	(78)	(0.00)	⋯	20

Notes: Site codes are as follows. Fish streams: AV = Avery Creek, CO = Copper Creek, ER = East River, LQ = Lower Quigley Creek, LR = Lower Rock Creek, RU = Rustler's Gulch Creek, UQ = Upper Quigley Creek. Fishless streams: BB = billy's brook, LB = Lower Benthette Brook, SG = Snodgrass Creek, UB = Upper Benthette Brook, UR = Upper Rock Creek, VR = Virginia Creek. Ellipses (⋯) indicate no data; parentheses indicate streams that did not produce a*Baetis* summer generation and were not included in the path analysis.

† Data are means.

Finally, size-selective predation by trout could remove larger individuals from trout streams. If size differences between *Baetis* emerging from fish and fishless streams are caused by size-selective predation, we would not expect to observe differences between growth rates and development times of *Baetis* emerging from fish and fishless streams. This third mechanism is a density-mediated effect, whereas the first two mechanisms would be trait-mediated effects (Peacor and Werner 1997).

We took three different approaches using observational data to test the hypothesis that temporal and spatial variation in size of *Baetis* at metamorphosis resulted from a life history response to risk of predation by trout. First, we estimated larval growth rates and development times (from egg to mature larvae) of summer generation *Baetis* to distinguish between the three potential mechanisms whereby variation in risk of predation could cause observed patterns of *Baetis* size at metamorphosis. Second, we compared observed patterns of temporal variation in size and timing of metamorphosis to theoretical predictions of the effects of variable risk of predation by trout on mayfly life history strategies. Third, we applied path analysis to our field data to evaluate alternative hypotheses that could explain spatial variation in *Baetis* size at metamorphosis.

METHODS

Describing patterns of size variation

To describe the spatial and temporal patterns of variation in size of *Baetis bicaudatus* at metamorphosis we conducted a field survey of 28 site-years in streams of the East River drainage basin near the Rocky Mountain Biological Laboratory in western Colorado, USA, during summers in 1994, 1995, and 1996 (Table 2). Sites were 0.5–10.2 m wide and 10–30 m long with lengths adjusted to standardize areas of stream reach sampled (Tables 2, 3). Some sites contained reproductive populations of brook trout (*Salvelinus fontinalis*), and others were completely fishless (Table 2), as a result of barriers to fish dispersal (waterfalls >1 m high). Sites also varied with respect to other physical–chemical variables (Table 3).

TABLE 3. Summary of data used in principal components analysis, obtained in September 1996.

Site	Elevation (m)	Width (m)	Discharge (m^3/s)	Conductivity ($\mu S/cm$)	Degree-days	SRP ($\mu g/L$)	TDP ($\mu g/L$)	NO_3 ($\mu g/L$)	TDN ($\mu g/L$)
Fish streams ($n = 5$)									
AV	2940	1.36	0.044	196	830	1.427	2.77	45.89	254.1
CO	2860	8.65	1.202	190	367	0.941	1.15	109.5	242.2
ER	2890	8.30	1.101	155	407	1.184	1.50	82.74	182.2
LR	2930	3.33	0.044	181	561	1.427	2.19	35.49	194.2
RU	2950	10.20	0.435	270	367	4.223	11.69	147.5	266.1
Fishless streams ($n = 5$)									
BB	2920	1.43	0.003	151	588	0.576	0.80	93.39	266.1
LB	2910	1.57	0.025	130	777	1.306	2.08	51.12	242.2
SG	2940	1.79	0.016	150	764	2.548	3.59	70.26	268.3
UB	2930	0.50	0.020	126	223	1.063	0.33	120.3	242.2
UR	2990	3.30	0.048	187	233	1.306	2.77	30.26	194.2

Notes: Abbreviations are: SRP = soluble reactive phosphorus, TDP = total dissolved phosphorus, NO_3 = nitrate, TDN = total dissolved nitrogen. See Table 1 for meaning of site codes.

At weekly intervals we collected and measured the dry mass (DM) of mature larvae with black wing-pads (BWP = Stage IV; Delucchi and Peckarsky 1989) that have ceased feeding and will metamorphose within 24 h. This protocol enabled us to examine the temporal variation in size at metamorphosis within sites and the spatial variation the sizes of *Baetis* emerging from different sites. While we tried to obtain at least 15 males and 15 females per site, low population densities at some sites in some years limited the numbers of individuals we could collect (Table 2). At 22 site-years *Baetis* was bivoltine, having both summer and overwintering generations, which enabled us to follow the development of an entire cohort (summer generation) from the egg to BWP stage. While we also measured size at metamorphosis of overwintering *Baetis* at all 28 site-years for comparison to the summer cohort, we analyzed the conditions affecting growth and development of only the summer generation. Water temperatures, standing stock of algal resource, densities of *Baetis* and other grazers, and predator densities all differed between years even at the same sites (Table 2), because these conditions ''reset'' each year after floods associated with snow melt each spring. Therefore, we treated sites sampled in multiple years as replicates (site-years), but nested sites within treatments (stream type) in our analyses.

We preserved mature *Baetis* larvae in 70% ethyl alcohol and measured head capsule widths (HCW) using an ocular micrometer on a dissecting microscope. Each individual was dried at 60°C for 24 h and weighed on a Cahn microbalance. We analyzed males and females separately, because females were ~25% larger (DM) than males, mostly due to egg mass (Peckarsky et al. 1993). Although the DM data reported in this paper are from direct measurements, we also used these data to construct standard regression equations so that we could estimate DM of mature *Baetis* males and females from HCW in future studies. Those regression equations are: male DM = $0.7994 \times HCW^{3.3053}$, $r^2 = 0.89$, $N = 580$; female DM = $1.5304 \times HCW^{3.9816}$, $r^2 = 0.90$, $N = 648$. We ran one-way ANOVAs on male and female *Baetis* of summer and winter generations to compare DM between fish and fishless sites. In these and all other analysis we included site as a random factor nested within stream type (fish or fishless), and main treatment effects (here = stream type) were always tested using site (type) as the error term.

Estimating growth rates and development times

Development times were determined by monitoring oviposition (Peckarsky et al. 2000) and maturation of summer generation *Baetis* at each site on a weekly basis. Number of weeks from egg (= developmental zero) to metamorphosis was estimated as the difference between the date of first observation of egg masses to the date of first summer BWPs. Although the summer cohorts at each site were not tightly synchronous, we assumed that development time did not change over the larval period within sites, because the oviposition and emergence periods were of similar duration and had similar temporal distributions (Peckarsky et al. 2000). We estimated *Baetis* growth rates (in milligrams per day, DM) for each site by comparing the mean final size (BWP) of larvae at that site with the size of hatchlings, divided by development time for that site (as in McPeek and Peckarsky 1998). We obtained *Baetis* growth rates and development times from all streams in 1995 and 1996, but recorded oviposition times in only one stream (East River) in 1994.

We tested whether *Baetis* growth rates or development times differed between fish and fishless streams using separate one-way MANOVAs on males and females with site as a random factor nested within stream type. If MANOVAs were significant, we conducted univariate ANOVAs on growth rates and development times separately to determine the sources of significant variation between stream types. We rejected null hy-

potheses at $\alpha = 0.025$, since significant differences in either growth or development time between fish and fishless streams could explain patterns of size distributions.

Comparing observed to predicted seasonal size variation under variable risk of predation by trout

To determine whether size of mature *Baetis* changed over the flight period (each summer separately) in fish and fishless streams, we used a homogeneity of slopes test of an analysis of covariance model. This analysis compared the slopes of regressions of *Baetis* DM (males and females separately) over day of year between fish and fishless streams (with site as a random factor nested within stream type). The date × stream type interaction tests the null hypothesis that the slopes of the relationship between date and *Baetis* size do not significantly differ between fish and fishless streams. Thus, this analysis enables us to ask whether the size of mature *Baetis* showed the same or different seasonal pattern between fish and fishless streams each year.

The life history theory developed by Ludwig and Rowe (1990) and Rowe and Ludwig (1991) extended the classic work of Wilbur and Collins (1973), providing a framework for predicting the effects of predation risk from trout on *Baetis* body size and timing of emergence. Rowe and Ludwig's (1991) model combines information about an organism's growth rate, fecundity, and sources of mortality to predict the optimal body size (M) and time (T) for metamorphosis into the adult stage in environments where the end of the season constrains reproduction. The model generates a mechanistic explanation, based on fundamental life history parameters, for the seasonal decline in body size observed in many organisms (Atkinson 1994). By incorporating a function for *Baetis* mortality due to predation by trout into this model, while retaining end of the season constraints, theoretical predictions of M and T could be estimated for fish and fishless streams and compared with actual data. Following Lytle (2000), predation regime was modeled as a time-dependent mortality function:

$$\mu(T) = \lambda\left(\frac{1}{1 + e^{-c(T-p_d)}\left(\frac{1}{p_b} - 1\right)}\right) \quad (1)$$

where T is time (in days), p_b is the background level of fish activity, p_d is the delay in the onset of fish activity (in days), c is a rate parameter that controls the steepness of the curve, and λ is a scaling factor that represents the efficiency of trout as predators. Eq. 1 gives fish predation a logistic form in which predation stays at a low background level during the winter and early spring, increases according to the rate parameter c, and reaches an asymptotic maximum at 1 (Fig. 1, shaded regions).

As parameters in the model we set $c = 0.1$ for fish streams and allowed fish activity to increase to near-maximum over ~10 wk, at a rate reflecting the rate of change in stream discharge, water temperature, and water clarity over the emergence period of *Baetis*. Since fish activity in these streams is low in the winter (Allan 1983), we set $p_b = 0.01$. We set $p_d = 0$ wk in 1994 and 1996, and $p_d = 8$ wk in 1995, because the hydrologic regime resulting from extremely high snow pack delayed the onset of fish activity by this amount of time. Although risk of predation by trout declines at the end of the season (Allan 1981; A. R. McIntosh and B. W. Taylor, *personal observations*), the rate and precise timing of this decline are unknown. Therefore, we used a simple increasing predation function that can be elaborated with supporting data in the future.

Evaluating alternative hypotheses

We used two different analyses to test alternative hypotheses that might explain spatial variation in *Baetis* size at metamorphosis. First, in September 1996 we measured nine biologically relevant physical and chemical variables in five fish and five fishless streams to determine whether there were any consistent environmental differences between fish and fishless streams other than the presence of fish (Table 3). Elevation was obtained from topographic maps. Stream width, depth, and current velocity were measured at three transects to estimate stream discharge. Conductivity was measured in the field using a conductivity meter, and water samples were analyzed in the laboratory to determine nutrient chemistry (soluble reactive phosphorus [SRP], total dissolved phosphorus [TDP], nitrate [NO_3], and total dissolved nitrogen [TDN]). We conducted a discriminant function analysis (DFA) using SAS (1989) to determine whether a linear combination of environmental variables separated streams with and without fish (Table 3). In addition we compared the environmental data to a null model, using a one-way MANOVA to test statistically whether fish and fishless streams differed with respect to any of the measured variables.

Second, throughout the larval period of summer generation *Baetis* in all three years, we measured other biotic and abiotic factors that could influence growth and development rates of mayflies, and thereby account for variation in size at metamorphosis. During 1994 and 1995 we noted presence or absence of brook trout, and in 1996 we estimated brook trout density by making three passes of each stream reach with an electroshocker (Table 2). Unpublished trout density estimates for 1997, 1998, and 1999 indicate that while fish presence or absence has remained consistent for six summers, trout densities have changed from year to year. Therefore, we used presence or absence of trout as a categorical variable in the analysis.

We estimated densities of predatory stoneflies and competitors (conspecifics and other algal grazers) from five random benthic samples of individual rocks once

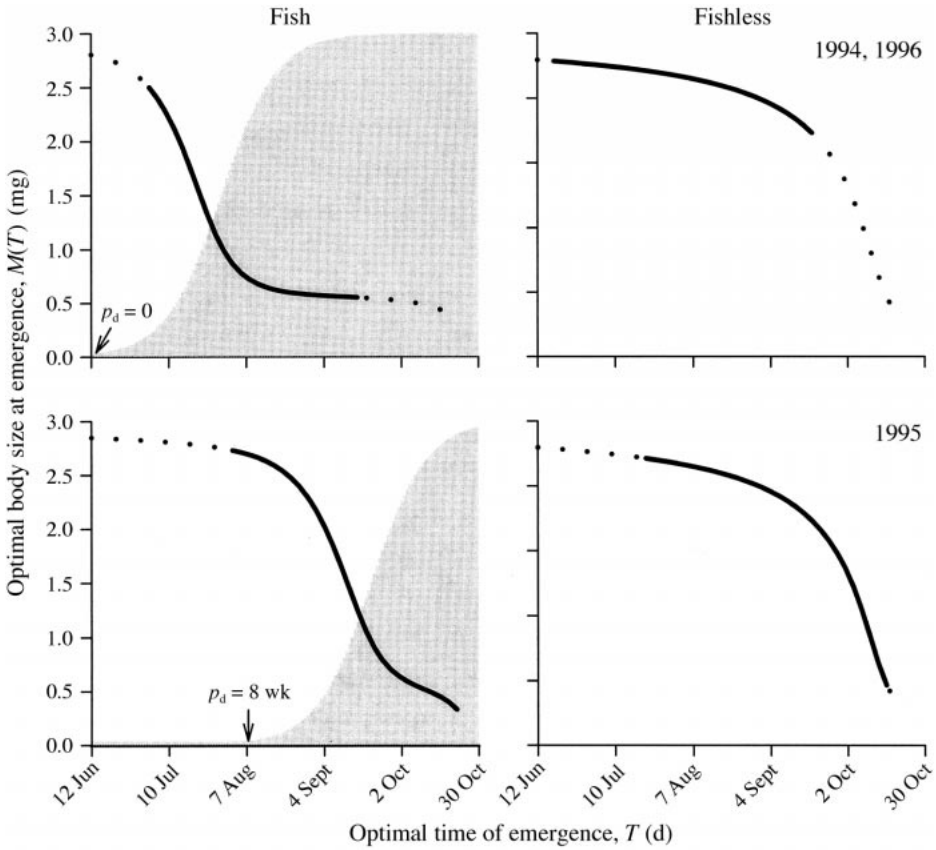

FIG. 1. Theoretical predictions (Eq. 1) of the effect of trout predation on *Baetis bicaudatus* size (M) and timing (T) of emergence. Bold lines indicate observed emergence periods of *Baetis* during the three years of the study. Dotted lines indicate predicted size if emergence periods had been extended. Shaded regions represent risk of trout predation ($\mu(T)$, scaled from 0 to 1). Onset of trout predation (p_d) was delayed by 8 wk in 1995. Sources of model parameters (see Rowe and Ludwig [1991] for elaboration of definitions): factor scaling size at emergence to fecundity, $\beta = 1.8$ (from McPeek and Peckarsky 1998); end of the emergence season, $T_C = 16$ October (from Fig. 5); factor scaling oviposition timing to fitness, $\alpha = 2$; maximum body size, $k = 3.0$ (from Fig. 5); minimum body size, $M_c = 0.3$ (from Fig. 5); minimum trout activity, $p_b = 0.01$; rate parameter of the trout activity curve, $c = 0.1$; efficiency of trout predation, $\lambda = 0.425$ (from McPeek and Peckarsky 1998); growth rate in fish streams, $r = 0.1481$; and in fishless streams, $r = 0.0910$ (calculated from data shown in Fig. 4).

per week (1994) or once every two weeks (1995, 1996). Total algal and diatom biovolumes were estimated at each site from three random rock samples taken once per week (1994) or once every two weeks (1995, 1996). Rock sizes were estimated by digitizing top surface areas traced on acetate sheets to estimate the amount of two-dimensional surface of stream bottom occupied. Water temperatures were monitored throughout the larval period using Onset Stowaway data loggers (Onset Computer, Pocasset, Massachusetts, USA). Temperature data were converted to cumulative degree-days per day for the period of development of the summer generation (from egg stage to BWP) to standardize for differences in total days among sites.

We used path analysis with structural equation modeling (SEM) (Mitchell 1992, Grace and Pugesek 1998) to estimate the proportion of observed variation in size of *Baetis* at metamorphosis that could be attributed to presence/absence of trout, density of predatory stoneflies, density of competitors (intra- and interspecific), food (diatom biovolume), and cumulative degree-days. We obtained path coefficients for the effects of each variable on size of male and female *Baetis* separately from data shown in Table 2 using LISREL on the Dartmouth College mainframe computer. SEM includes all the information provided by standard path analysis using multiple regression (Li 1981, Boelin 1989, Wootton 1994, Shipley 1997, Smith et al. 1997, 1998), such as total effects, path coefficients, and measures of variance. The advantage of SEM is that it allows tests of multivariate causation to be made from observational data (Shipley 1999). Furthermore, SEM uses exact variables rather than standardizing variables to a mean of zero and standard deviation of one and allows determination of the overall agreement between the path diagram (model) and the data, thereby facilitating comparisons of competing models of the same system. SEM also incorporates estimates of measurement error, cir-

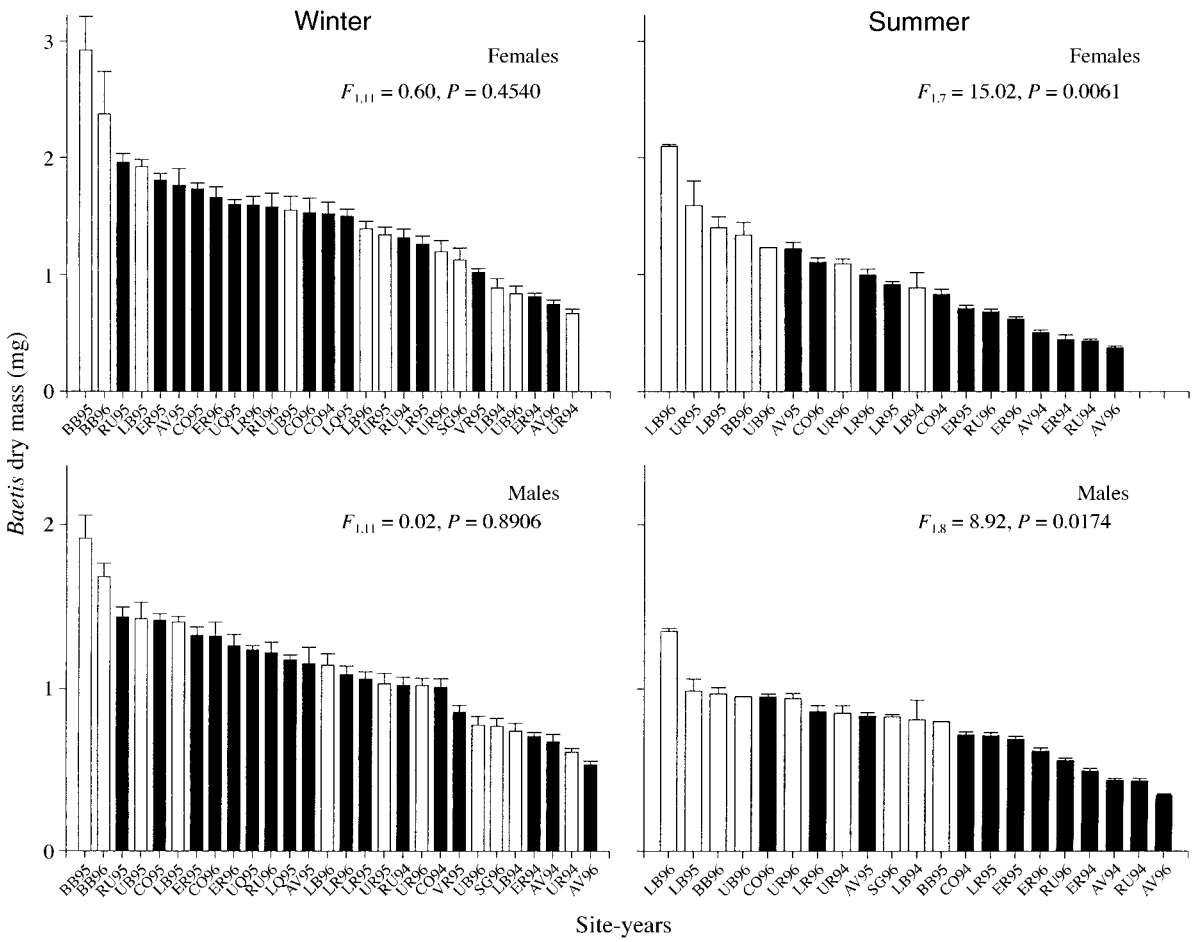

FIG. 2. Dry mass of mature larvae (black wing pad stage) of *Baetis bicaudatus* females and males of the overwintering and summer generations from fish (solid bars) and fishless (open bars) stream sites in the East River watershed, western Colorado, USA, during 1994, 1995, and 1996 (means + 1 SE). Site codes are as follows. Fish streams: AV = Avery Creek, CO = Copper Creek, ER = East River, LQ = Lower Quigley Creek, LR = Lower Rock Creek, RU = Rustler's Gulch Creek, UQ = Upper Quigley Creek. Fishless streams: BB = billy's brook, LB = Lower Benthette Brook, SG = Snodgrass Creek, UB = Upper Benthette Brook, UR = Upper Rock Creek, VR = Virginia Creek. F_{df} and P values are given for ANOVAs testing for effects of stream type (fish or fishless) on *Baetis* size at emergence.

cumvents problems with multicolinearity and indicates areas where the model fit is especially poor (Mitchell 1992).

RESULTS

Patterns of size variation

We observed large variation in *Baetis bicaudatus* size at emergence over space and time in the East River catchment, with greater than six-fold differences in mean DM from streams with the largest to the smallest individuals (Fig. 2). Size of mature *Baetis* varied among years even at the same sites, resulting in different ranking of sites from year to year (Fig. 2). Results of ANOVA showed that both male and female *Baetis* maturing in fishless streams were significantly larger than those maturing in fish streams, but only for the summer generation (Fig. 2). Mean size of mature individuals of the overwintering generation of *Baetis* was slightly but not significantly larger in fish streams than fishless streams (Figs. 2 and 3). These results are consistent with the hypothesis that risk of trout predation affected *Baetis* size at metamorphosis of only the summer generation, which grew and developed entirely during the snow- and ice-free season when trout were feeding most actively.

Growth rates and development times

We used observational data on *Baetis* growth rates and development times to evaluate three hypotheses for the mechanism explaining variation in size of *Baetis* maturing in fish and fishless streams (Table 1). Growth rates of both male and female *Baetis* were slightly but not significantly faster in fish streams than in fishless streams (Fig. 4). However, development times (duration of the larval period from egg to BWP) were significantly shorter for both males and females in trout

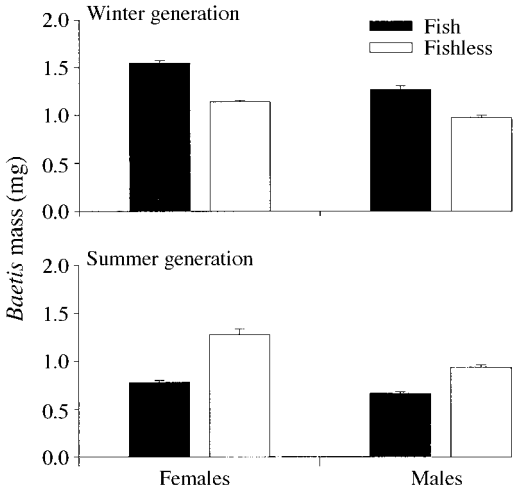

FIG. 3. Dry mass of winter and summer generation *Baetis bicaudatus* in fish ($N = 9$) and fishless ($N = 8$) streams (means + 1 SE). Replicates = site means shown in Fig. 2. Differences between fish and fishless streams were significant for males and females of summer generation *Baetis* only (see Fig. 2).

streams than in fishless streams. The observed acceleration of maturation in trout streams was no small effect, since larval development took an average of 3 wk longer in fishless than in fish streams (Fig. 4). Thus, neither size-selective predation nor lost feeding opportunities could explain the observed differences in *Baetis* growth and development between fish and fishless streams (Table 1). Instead our data are consistent with the hypothesis that accelerated larval development with similar growth rates resulted in smaller mayflies emerging from fish streams than fishless streams. This mechanism of an adaptive developmental plasticity in response to risk of predation by trout could also explain the larger size of winter vs. summer *Baetis* in trout streams (Figs. 2 and 3).

Comparing observed to predicted seasonal size variation under variable risk of predation by trout

Differences between sizes of winter and summer generation *Baetis* were also reflected in a seasonal decline in size of *Baetis* emerging from fish streams over the flight season (Fig. 5), which could also be explained by adaptive developmental plasticity in response to increasing risk of predation by trout. The largest mayflies were females that overwintered and matured early in the summer. Over time in fish streams, both males and females became smaller, with the latest winter individuals maturing at the same small size as the summer generation *Baetis*. The homogeneity of slopes test (Fig. 5, inset in fish plots) showed that seasonal patterns of size at emergence differed between fish and fishless streams during some years.

In 1994 and 1996 the water levels receded and temperatures rose early in the summer, and there was a concomitant early risk of predation in fish streams. A significant fish × date interaction for males in 1994 and both sexes in 1996 showed that a seasonal decline in size of mature *Baetis* occurred only in fish streams and not in fishless streams in these low-flow summers (1994, 1996; Fig. 5, upper and center panels). These observed patterns of temporal variation are consistent with theoretical predictions of the effects of increasing risk of predation by trout on *Baetis* size at emergence when the onset of predation occurs early in the emergence period (Fig. 1, upper panels).

In 1995, the water levels receded and temperatures rose later in the summer, and there was a concomitant delayed risk of predation in fish streams. In this year there was no significant fish × date interaction (Fig. 5, lower panels), indicating that size of mature *Baetis* declined similarly in fish and fishless streams (significant date effect for females: $F_{1,9} = 10.48$, $P = 0.0102$, but not males: $F_{1,7} = 4.84$, $P = 0.0637$). Furthermore, mature *Baetis* in summer 1995 were larger on average than those during the low-water summers of 1994 and 1996 (Figs. 2 and 5). These patterns of seasonal variation in size at metamorphosis are also consistent with model predictions of effects of hydrologically induced delayed onset of trout predation on the size and timing of emergence (Fig. 1, lower panels). Furthermore, delayed maturation due to high water levels in 1995 correctly predicted the gradual seasonal decline in *Baetis* body size in fishless streams (Fig. 5, lower panels).

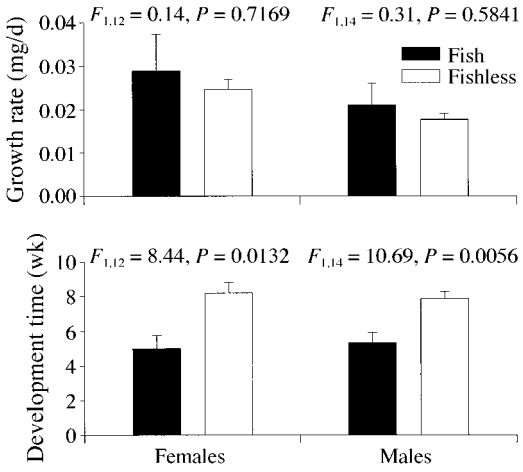

FIG. 4. Growth rate and development time from egg to black wing pad stage of summer generation *Baetis* females and males from fish ($N = 9$) and fishless ($N = 8$) streams (means + 1 SE). Replicates = same streams as in Fig. 3. MANOVA: Wilks' λ for females = 0.491, $F_{2,11} = 5.68$, $P = 0.0202$; Wilks' λ for males = 0.447, $F_{2,13} = 8.02$, $P = 0.0054$. F and P values are from ANOVA of effects of stream type (nested within site) on growth rates and development times for females and males. Growth rates were not significantly different between fish and fishless streams, but development times were significantly faster for both male and female *Baetis* in fish streams than in fishless streams ($P < 0.025$).

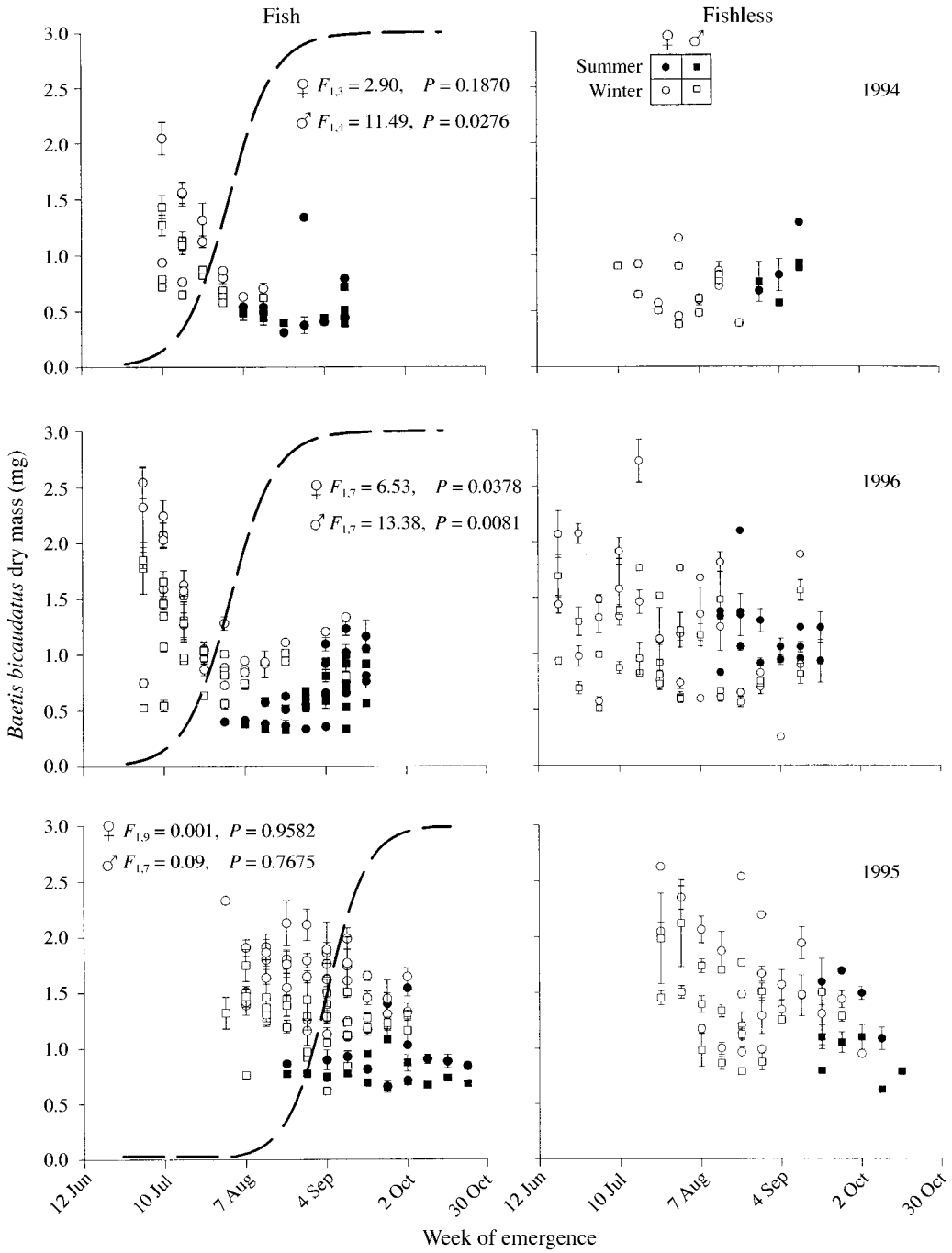

FIG. 5. Dry mass of mature larvae (black wing pad stage) of *Baetis bicaudatus* females and males of the overwintering and summer generations over the emergence periods in low water (1994 and 1996) and high water (1995) years in fish and fishless streams. Points and error bars represent means ± 1 SE for all individuals collected at each site on each date. Note that the first mature larvae were collected on 6 July in 1994, 19 June in 1996, and 26 July in 1995. Dashed lines represent increasing risk of trout predation in fish streams (see Fig. 1). *F* and *P* values are given for males and females for the homogeneity of slopes test of a nested ANCOVA model for the effect of stream type (fish or fishless) on *Baetis* size at metamorphosis over the emergence period. $P < 0.05$ indicates significant time × stream type interactions (using site(type) as the error term). Seasonal patterns of change of *Baetis* size over time differed between fish vs. fishless streams in low water years (1994 and 1996), but not when emergence was delayed by high water (1995). Tests of main effects (stream type and date) are given in the text for 1995 when interaction terms were not significant.

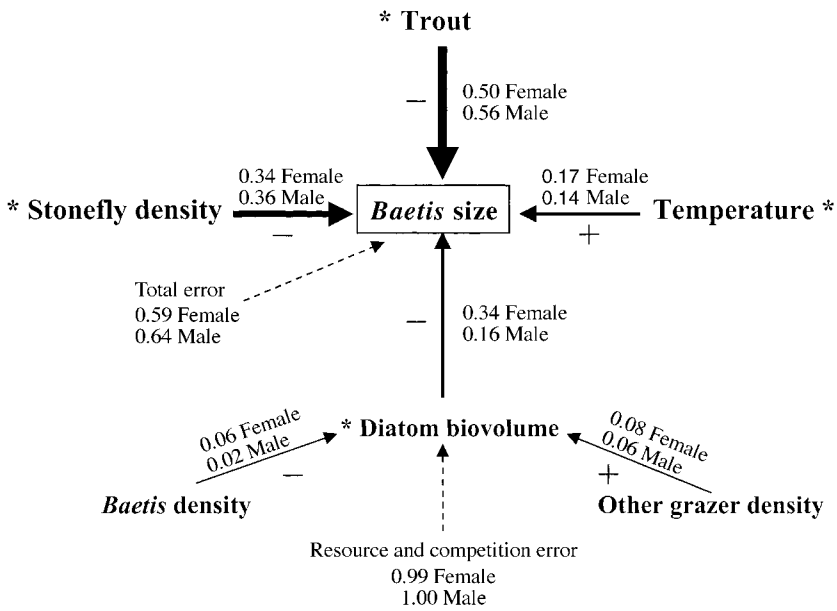

FIG. 6. Path diagram illustrating the effects of the presence of trout, predatory stonefly density, water temperature (degree-days per day), diatom biovolume (food), and density of potential competitors (conspecifics and other grazers) on size of summer generation *Baetis bicaudatus* males and females at metamorphosis. Path coefficients and direction of effects (positive or negative) are given for males and females. Error coefficients (dashed lines) may be squared to estimate the proportion of variation not explained by the path model. Error coefficients are given for the entire path model (left) and for the indirect food-mediated pathways (bottom). Asterisks indicate path coefficients significantly different from 0 (coefficients >0.14 are significant at $\alpha = 0.05$, 13 df).

Alternative hypotheses to explain variation in Baetis *size at emergence*

We evaluated the alternative hypothesis that systematic environmental variation (other than presence of trout) could explain spatial variation in *Baetis* size at metamorphosis. Based on a linear combination of nine environmental variables (Table 3: elevation, stream width, stream discharge, conductivity, degree-days, SRP, TDP, NO_3, and TDN), the discriminate function analysis (DFA) classified 40% of the fish streams as fish streams and the remaining 60% were misclassified. The one-way MANOVA showed no significant differences between the environmental variables measured in fish and fishless streams (Wilks' $\lambda = 0.057$, $F_{1,8} = 2.07$, $P = 0.493$; $P > 0.05$ for all individual ANOVAs). Thus, these analyses fail to support the alternative hypothesis that systematic environmental variation among streams explains the observed differences in size at metamorphosis of *Baetis* from fish and fishless streams.

Additionally, we used path analysis with structural equation modeling (SEM) to evaluate alternative hypotheses that other biological factors that influence mayfly growth and development could explain natural patterns of variation in size at metamorphosis of summer generation *Baetis*. We derived specific hypotheses from our previous experiments suggesting that predatory stonefly densities, diatom biovolume (food), and densities of competitors (inter- and intraspecific) may explain some of the observed variance in size of mature *Baetis*. We also included water temperature as a variable in the path analysis, because it has been clearly linked to rates of aquatic insect growth and development (Sweeney and Vannote 1978). Our path model represents a set of expectations derived from underlying mechanistic hypotheses relating to how the system's components influence each other (Fig. 6). If paths do not explain significant amounts of variation in *Baetis* size at emergence, then they can be rejected as alternative hypotheses. However, a significant fit of data with the model can only be suggestive of cause, since we cannot rule out untested alternative hypotheses.

The value of path analysis depends on how well investigators understand relationships among variables, thereby specifying the order of dependence among them. We have used the most basic path model including indirect pathways only if they have been demonstrated by previous experimental evidence. For example, we did not include a direct competitive interaction between *Baetis* or other grazer densities and *Baetis* size in the path model, because previous data showed that competitive interactions among grazers affect *Baetis* size indirectly, mediated through exploitation of resources (Kohler and McPeek 1989, Kohler 1992; J. D. Allan and A. S. Flecker, *unpublished data*; P. R. Ode, *unpublished data*). Similarly, we excluded indirect predator–prey pathways (trout → stonefly density, trout → *Baetis* density, trout → other grazer den-

sity, stoneflies → *Baetis* density, or stoneflies → other grazer density), because these predators do not reduce prey densities in this or other similar streams (Table 2; Allan 1982, Kerans et al. 1995, McPeek and Peckarsky 1998).

Presence/absence of trout explained the largest proportion of the variance in male and female *Baetis* size at metamorphosis (Fig. 6). Significant negative path coefficients indicated that smaller *Baetis* emerged from sites with trout. Similarly, streams with high densities of stoneflies had smaller mayflies (as in Peckarsky et al. 1993, Peckarsky and McIntosh 1998). The water temperature path coefficients were marginally significant but positive, indicating that larger *Baetis* emerged from warmer streams, contrary to most other studies (Sweeney 1978, Sweeney and Vannote 1978, 1984, 1986, Rowe and Berrill 1989, Atkinson 1994, Berrigan and Charnov 1994, Atkinson and Sibley 1997) and to the notion of a universal physiological mechanism explaining body size–temperature interactions in ectotherms (Atkinson 1994, Sweeney et al. 1995). Also surprising were the negative path coefficients (significant for females and marginal for males) between diatom biovolume and *Baetis* size, indicating that smaller

variability and responding adaptively with flexible development.

The observed developmental response of *Baetis* to increasing predation risk is similar to responses shown by other insects to increasing competitor density in the laboratory (Simmonds and Blaney 1986, So and Dudgeon 1989, Goodbrod and Goff 1990) and by amphibians to threat of predation in the field (Wilbur and Fauth 1990). Organisms from a wide variety of taxa with complex life cycles have also shown developmental responses to time constraints imposed by mortality agents such as habitat drying, flooding, or the imminent onset of winter (Wilbur and Collins 1973, Roff 1980, Werner 1986, Wilbur 1987, Newman 1989, Ludwig and Rowe 1990, Rowe and Ludwig 1991, Abrams et al. 1996, Twombly 1996, Klingenberg and Spence 1997, Johansson and Rowe 1999, Plaistow and Siva-Jothy 1999). In high-elevation streams, the onset of winter also imposes a time constraint that should influence the optimal size and timing of metamorphosis. However, during years of low stream flow, *Baetis* completed the emergence period well before the onset of winter, and predation risk more strongly influenced size at emergence (Figs. 1 and 5). In the high water year (1995) when the emergence period was delayed (Fig. 5), we observed a seasonal decline in *Baetis* body size at emergence in both high and low predation risk environments, as predicted by the models that focused on abiotic mortality risks (Wilbur 1987, Rowe and Ludwig 1991). Thus, *Baetis* may accelerate development in response to unfavorable biotic and abiotic conditions.

We expect that differences in development between mayflies from fish and fishless streams are due to phenotypic plasticity rather than genetic differentiation among fish and fishless *Baetis* populations (Nijhout 1999). Extensive dispersal of larvae and ovipositing adults should facilitate genetic mixing of populations derived from fish and fishless streams, countering fish-mediated selection on development times (Peckarsky et al. 2000). Phenotypic plasticity in larval behavior and 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, McPeek and Peckarsky 1998). *Baetis* larvae from both fish and fishless streams in the East River Valley show flexible behavior and size at maturation when exposed experimentally to chemicals emitted by trout (Cowan and Peckarsky 1984, McIntosh and Peckarsky 1996, 1999, Peckarsky and McIntosh 1998), Thus, we suspect that the chemical environment associated with actively feeding trout triggers accelerated development of summer generation *Baetis* and of the later emerging winter generation individuals. Many other aquatic invertebrates (e.g., Crowl and Covich 1990, Dodson et al. 1994, Arnqvist and Johansson 1998) have been shown to alter their behavior, morphology, or life histories in response to chemical cues from predators.

We would also argue that differences in size at metamorphosis of the two cohorts of the same *Baetis* population are a function of differences in the environmental conditions under which they develop (Forrest 1987, Gislason and Johansson 1991, Johannson and Rowe 1999). The overwintering generation of *Baetis* grows very slowly through the winter when stream temperatures, resources, and predator activity are very low (Allan 1983). Individuals that have attained large size early in the summer and emerge before predation by trout becomes intense have a distinct fitness advantage over those whose growth lags behind. Daytime feeding activity of salmonids increases with water temperature (up to $\sim$20°C), and reaction distance increases with water clarity (Elliott 1972, Dunbrack and Dill 1984, Fraser and Metcalfe 1997, Metcalfe et al. 1997). This seasonally increasing mortality risk should exert strong selection for overwintering *Baetis* larvae to have flexible development and to emerge at smaller sizes as predation pressure intensifies. Thus, our data suggest that increasing predation risk (Wilbur and Fauth 1990) explains seasonal declines in *Baetis* body size at metamorphosis, rather than water temperature or food as has been observed in other populations of ectotherms (Wilbur and Collins 1973, Humpesch 1979, Sweeney and Vannote 1986, Rowe and Ludwig 1991, Atkinson 1994, Berrigan and Charnov 1994, Huryn 1996).

In contrast, size at metamorphosis of the short summer generation was relatively constant over the emergence period and similar to that of the smallest, late-maturing individuals of the winter cohort. This pattern suggests that although mayflies can mature and reproduce at a wide range of sizes, there may be a minimum threshold size for reproductive maturation (Nijhout 1975, Blakley and Goodner 1978, Bradshaw and Johnson 1995, Twombly 1996, Moehrlin and Juliano 1998) at which an organism could replace itself in the population ($\lambda > 1$) given its expected survivorship and fecundity (Lewontin 1965). Thus, we argue that selection pressure to avoid predation by trout induces the sum-

and experimental conditions (Peckarsky et al. 1993, 1997, Peckarsky and McIntosh 1998). In contrast, effects of food and competition that have been observed at small scales over a subset of the larval stage did not extrapolate to larger spatial and longer temporal scales. By blending theory with observational and experimental approaches at multiple temporal and spatial scales, we can evaluate the relative strengths of interactions in natural systems (Bernardo 1998, Lodge et al. 1998, Peckarsky 1998, Polis et al. 1998, Power et al. 1998, Werner 1998). Thus we conclude that risk of predation rather than resource limitation determines the life history traits of mayflies in this system.

From 20 yr of data of this stream system, we assert that the effects of predators on prey populations are extremely important, but mediated more strongly through plastic behavioral and developmental responses of prey rather than through prey mortality (McPeek and Peckarsky 1998). This assertion may explain the equivocal results of studies measuring density-mediated effects of predators on patterns of prey population abundance in stream communities (e.g., Table 2; Allan 1982, Flecker and Allan 1984, Bowlby and Roff 1986, Culp 1986, Bechara et al. 1993, Harvey 1993, Wooster

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