COMMUNITY ECOLOGY - ORIGINAL PAPER

Predator effects on prey population dynamics in open systems

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Abstract Animal population dynamics in open systems are affected not only by agents of mortality and the influence of species interactions on behavior and life histories, but also by dispersal and recruitment. We used an extensive data set to compare natural loss rates of two mayfly species that co-occur in high-elevation streams varying in predation risk, and experience different abiotic conditions during larval development. Our goals were to generate hypotheses relating predation to variation in prey population dynamics and to evaluate alternative mechanisms to explain such variation. While neither loss rates nor abundance of the species that develops during snowmelt (*Baetis bicaudatus*) varied systematically with fish, loss rates of the species that develops during baseflow (*Baetis* B) were higher in streams containing brook trout than streams without fish; and surprisingly, larvae of this species were most abundant in trout streams. This counter-intuitive pattern could not be explained by a trophic cascade, because densities of intermediate predators (stoneflies) did not differ between fish and fishless streams and predation by trout on stoneflies was negligible. A statistical model estimated that higher recruitment and accelerated development enables *Baetis* B to maintain larger populations in trout streams despite higher mortality from predation. Experimental estimates suggested that predation by trout potentially accounts for natural losses of *Baetis* B, but not *Baetis bicaudatus*. Predation by stoneflies on *Baetis* is negligible in fish streams, but could make an important contribution to observed losses of both species in fishless streams. Non-predatory sources of loss were higher for *B. bicaudatus* in trout streams, and for *Baetis* B in fishless streams. We conclude that predation alone cannot explain variation in population dynamics of either species; and the relative importance of predation is species- and environment-specific compared to non-predatory losses, such as other agents of mortality and non-consumptive effects of predators.

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Introduction

Understanding the mechanisms underlying natural population fluctuations is a challenging problem, especially for organisms with complex life cycles living in open systems characterized by high levels of dispersal (Palmer et al.

1996; Schmidt et al. 1999). While predation has traditionally been considered an important process underlying patterns of prey population dynamics (e.g., Brooks and Dodson 1965; Mittelbach et al. 1995; Estes et al. 1998), other processes may overshadow effects of predation in some cases (Underwood and Fairweather 1989; Schmidt and Holbrook 1999; Wilson and Osenberg 2002). For example, processes affecting dispersal and recruitment may be independent of species interactions affecting local population abundance (Gadgil 1971; Holt and McPeek 1996). Thus, the influence of predation should be considered in the context of other factors affecting prey populations in open systems.

In addition to causing prey mortality, predators have the potential to affect prey population dynamics by modifying prey behavior, morphology or life history traits (Peacor and Werner 1997; Lima 1998). Increasing risk of predation often causes prey to trade off predator avoidance and habitat selection, foraging, mating or movement (Dill 1987; Sih and Wooster 1994). Consequently, adaptive traits for predator avoidance can have effects on prey population dynamics as or more important than predator-induced mortality (McNamara and Houston 1987; Abrams 1990; Anholt and Werner 1995; McPeek and Peckarsky 1998). Moreover, incorporating adaptive anti-predator prey behavior into predator–prey models changes the relationship between predator density and prey death rate (Abrams 1993). Under certain circumstances (generally involving adaptive prey behavior and indirect effects), one might even expect a positive association between predator and prey population densities (Abrams 1992). Such positive effects of predators on prey are difficult to detect experimentally (but see Peacor 2002), because most predation experiments are short term, use inflated predator densities, and are carried out at small scales under simplified conditions.

Ideally, studies of predator–prey interactions should be carried out at appropriate temporal and spatial scales, under conditions reflecting natural resource availability, associated density dependence and species interactions, and consider both consumptive and non-consumptive effects of predators on prey population dynamics (McNamara and Houston 1987; Nisbet et al. 1997; Peacor and Werner 2001). Furthermore, the role of predation in explaining prey population fluctuations should be placed in a larger context including recruitment and dispersal dynamics, which may be constrained by stochastic processes, such as disturbance, climate and environmental fluctuations (Kupferberg 1996; Butman 1987; Cottenie et al. 2003).

In reality, however, such an ideal study is very difficult to achieve. Consequently, the influence of predators on temporal and spatial variation in the abundance of stream insects that disperse in both larval and adult stages is not well understood. Often predictions from small-scale mechanistic studies are not consistent with observations (Peckarsky et al. 1997; Wiley et al. 1997), because multiple interacting factors obscure the effects of processes with weaker signals (Peckarsky et al. 2001). For example, predator removal or enclosure experiments have produced equivocal effects on invertebrate abundance in streams (Cooper et al. 1990; Dahl and Greenberg 1996). In fact, large-scale, long-term reduction of trout densities in one high-altitude stream had no detectable effects on the abundance of invertebrate prey (Allan 1982), probably because patchy prey distributions, high prey mobility and prey recruitment obscured consumption by predators (Cooper et al. 1990; Englund 1997). While demographic models imply that predators may be strong interactors in streams by affecting prey behavior and life history (McPeek and Peckarsky 1998), understanding the total effect of predators on prey population dynamics remains elusive (Diehl et al. 2000).

In this study we used a large-scale comparative approach and analyzed stage-specific mayfly abundance data acquired from streams with different predation regimes. We investigated the potential for predation, estimated experimentally, to explain natural loss rates of two mayfly species with different life histories and exposures to predators. For one species we were also able to estimate recruitment of early stage larvae and larval development times to evaluate a demographic hypothesis to explain a counter-intuitive pattern of variation in larval abundance among streams with different predation regimes. Our goal was to explore alternative hypotheses to explain spatial and temporal variation in mayfly population densities to place predation in the context of other potential explanatory factors.

Materials and methods

Study system

We studied two species of mayflies in the genus *Baetis* (Baetidae), which are common in a high-elevation catchment of western Colorado (upper East River, Gunnison County). Immature *Baetis* are more mobile (Forrester 1994; Peckarsky 1996) and more vulnerable to predation (Allan 1981, 1983; Peckarsky 1991; Forrester 1994) than other mayflies. Winged females oviposit under large rocks protruding from the water surface in high-velocity locations (Peckarsky et al. 2000; Encalada and Peckarsky 2006), providing the potential for regional-scale hydrologic processes such as snow accumulation, snow melt, summer rainfall, local geomorphology and channel structure to constrain their recruitment. Fish are completely absent from some streams in the catchment due to dispersal barriers (waterfalls), and brook trout (*Salvelinus fontinalis*) were the only fish present in other streams during the study (Peckarsky

et al. 2001). Previous multivariate analyses of nine environmental variables other than the presence of fish showed no systematic variation between fish and fishless streams (Peckarsky et al. 2001). However, an analysis of five dimensionless hydro-geomorphic variables indicated that fishless streams tended to be smaller than fish streams (A. Wilcox, B. L. Peckarsky, B. W. Taylor, and A. C. Encalada, unpublished manuscript).

The two *Baetis* species have contrasting life histories, subjecting them to different sources of mortality. Adults of *Baetis bicaudatus* (Dodds) emerge in early summer; females lay eggs that hatch in 2 weeks, and larvae overwinter as first instars ("winter *Baetis*" in previous studies). Larvae begin growing during the snowmelt period in late April or early May, and complete their development in June or early July coinciding with the descending limb of the annual hydrograph (Peckarsky et al. 2000). Thus, larval development occurs when the risk of trout predation is reduced by high and turbid flows (Sweka and Hartman 2001), but when high flow could constitute a stochastic risk of mortality. Due to overlapping phenologies, late-instar *B. bicaudatus* are vulnerable to predation by late instars of a large stonefly, *Megarcys signata* (Perlodidae) (Peckarsky and Cowan 1995).

A second undescribed species, *Baetis* B, which is difficult to distinguish from *B. bicaudatus* as early instars or adults, emerges and oviposits in late summer (August–September), and overwinters as eggs, possibly in diapause. Early-instar larvae appear in mid summer when *B. bicaudatus* adults emerge. The fast-growing larvae of *Baetis* B ("summer *Baetis*") complete their development during late July and August, a period of low flow and clear water associated with higher trout predation (Peckarsky et al. 2001). Larvae of *Baetis* B are also vulnerable to predation by a smaller perlodid stonefly (*Kogotus modestus*) and early instars of *M. signata* (Peckarsky and Cowan 1995).

Field estimates of mayfly dynamics in fish and fishless streams

We estimated loss rates from sequential samples of larvae of both species at multiple stream sites over 3 years. We sampled at 1-week (1994) and 2-week (1995, 1996) intervals during late-instar *B. bicaudatus* development, and over the entire larval period of *Baetis* B in 30-m reaches (16 sites with fish and 12 fishless sites; see Peckarsky et al. 2001). We considered site-years as independent in analyses because they were in unconnected channels, snowmelt floods cause physical and biotic conditions to "reset" in subsequent years at the same sites (Peckarsky et al. 2001), and females do not return to their natal streams to oviposit (Peckarsky et al. 2000). Nonetheless, we nested sites within stream types (fish, fishless) for analysis.

On each date we took five benthic samples using a fine-mesh (100 μm) D-net placed downstream of a single rock (10–20 cm diameter) and preserved invertebrates in 70% EtOH. We standardized mayfly densities per two-dimensional surface area from digitized tracings of rocks. This method may overestimate absolute densities of mayflies at the scale of stream reaches compared to other sampling techniques; but it accurately estimates stonefly densities (Taylor et al. 2001). Furthermore, it introduces no bias when used for comparisons of mayfly abundance over space and time.

To compare the larval dynamics between sites with and without fish we estimated natural loss rates (L) using analyses of covariance (PROC GLM, SAS 9.0) from slopes of linear regressions of time series of steadily declining larval densities (ln-transformed sum of five samples on each date) with site-years as replicates. Models included a fish effect (fish or fishless), site nested within stream-fish type, time (the regression effect) and all two-way interactions between the main effects (all factors fixed). Significant time × fish interactions indicated differences in the loss rates of *Baetis* between fish and fishless streams. Conservatively, we recognize that loss rates included both mortality and migration.

We classified mayfly larvae by developmental stage—no wing pads (I), wing pads shorter than wide (II), wing pads longer than wide (III), black wing pads (mature; IV)—but did not have sufficient data at all site-years to use stage-frequency data to estimate population sizes (e.g., Manly 1990). Instead, we compared peak densities of the relatively long-lived larval stage III among site-years. This parameter estimates the abundance of the stage when reproductive maturation occurs (Peckarsky et al. 1993, 2001), and is not confounded by losses to emergence, as is the short stage IV. We compared estimates of larval densities of each *Baetis* species between populations in fish and fishless streams using t-tests on $\ln(x + 1)$-transformed data with site-years as independent observations (PROC TTEST, SAS 9.0). Tests for equality of variances indicated that Satterthwaite corrections were not necessary.

Estimates of predation rates of trout and stoneflies

We extended methods developed by Kerans et al. (1995) to estimate predation rates on *Baetis* by trout and stoneflies from small- or medium-scale functional response and observational experiments. In July 1996 we conducted predation trials in 16 streamside oval flow-through mesocosms (see Peckarsky and McIntosh 1998) at a scale that accommodated feeding by trout (area = 0.82 m²). Flow was maintained by gravity-fed water from a fishless stream delivered through water jets to each mesocosm. We covered mesocosm floors with large cobbles (∼70 rocks, 7–25 cm widest dimension), which contributed to small-scale variation in

current velocities within mesocosms (10–60 cm^{-1}) typical of moderate to baseflow conditions in streams of the drainage basin. Water temperatures (4–14°C) reflected natural diel and seasonal variation of the source and were also typical of streams in the area (Peckarsky et al. 2001).

We repeated the same predation trial twice (23, 24 and 30, 31 July) and re-randomized the replicates of four treatments: fish (one brook trout = 1.2 m^{-2}) + 300 *Baetis* (365 m^{-2}), stoneflies (eight late-instar female *M. signata* = 10 m^{-2}) + 300 *Baetis*, fish + stoneflies + 300 *Baetis*, and controls (no predators + 300 *Baetis*). Data from the two trials were pooled for analysis to obtain replication of $n = 4$ for treatments with predators and $n = 2$ for controls. We tested for single and interactive effects of trout and stoneflies on *Baetis* mortality and effects of trout on stonefly mortality. We also measured trout predation at four prey densities (one brook trout + 50, 100, 300 or 500 *Baetis*) to test for variation in predation rates with prey density.

All organisms were collected from the East River (a trout stream). Prey were stage III *B. bicaudatus* (mean dry weight ± 1 SE = 0.968 mg ± 0.001, $n = 29$). Stonefly size (mean dry weight ± 1 SE, $n = 64$) was 36.31 mg ± 0.20, and mean wet weight (±1 SE, $n = 20$) of brook trout was (103 g ± 0.007). Predators were held without food in similar chambers for 24 h before trials, added to mesocosms at 1700 hours, and allowed to feed until 0900 hours the next morning (16 h including periods of active feeding by both types of predators: Peckarsky and Cowan 1995; McIntosh et al. 2002). At the end of each trial, we removed predators and counted all remaining prey to estimate the number of prey eaten correcting for numbers lost from controls.

We used data from those experiments to estimate predation rates by brook trout and *Megarcys* on *B. bicaudatus* and by brook trout on *Megarcys* as per capita mortality rate (M_P) per predator per day using the equation: $M_P = [\ln(N_I) - \ln(N_F)](P)^{-1}(d^{-1})$, where N_I = initial prey density, N_F = final prey density, P = predator density, and d = days of the feeding trial (as in Kerans et al. 1995). There was no significant effect of prey density on M_P over the range tested (60–600 m^{-2}; one-way ANOVA: $F_{3,12} = 1.78$, $P = 0.205$). Thus, the functional response was linear, which is a key assumption of the exponential decline model used to estimate losses of prey. Consequently, we used the mean mortality over all prey densities to estimate trout predation rates on *B. bicaudatus*. We also obtained independent estimates of prey-capture probabilities from video-taped observations of brook trout feeding on both species of *Baetis* in an experimental stream (McIntosh et al. 2002) as in McPeek and Peckarsky (1998).

We used a *t*-test to compare stonefly mortality in mesocosms with trout + stoneflies to stoneflies alone to test for predation by trout on stoneflies. We also tested for indirect effects of trout on rates of predation by stoneflies on

B. bicaudatus by examining the interaction term of an additive model using a two-way factorial ANOVA comparing overall mortality rates (M_T) {$M_T = [\ln(N_I) - \ln(N_F)](d^{-1})$} per mesocosm with eight stoneflies + 300 *Baetis*, one trout + 300 *Baetis*, or both predators + 300 *Baetis*.

To estimate predation rates by stoneflies on *Baetis* B we used M_P from previous functional response experiments (*Kogotus modestus*, Kerans et al. 1995; early-instar *Megarcys*, Peckarsky et al. 1994).

Comparison of predation rates to natural loss rates

Comparison of experimental estimates of predation rates to natural population dynamics is not trivial and involves accounting for interactions among predators and testing assumptions (e.g., predation rates, predator and prey sizes, and temperatures in experiments are representative of natural streams; the spatial variance and covariance between predator and prey density are the same in experiments and the field), many of which are unattainable even after years of work. Consequently, approaches using field manipulations of predators at various scales have been difficult to interpret (Allan 1982; Englund 1997). As an alternative approach, our spatially and temporally extensive data set provided a rare opportunity to generate hypotheses relating predation and other mechanisms to observed loss rates of prey as an initial step toward understanding the role of predation in natural systems.

As a first approximation, we scaled our experimental estimates of predation rates by densities of predators at each site-year ($M_P \times P$) and compared them to field estimates of prey loss rates [L from slopes of linear regressions of $\ln(x + 1)$ density versus time]. We estimated stonefly densities at each site-year using the benthic samples, and the abundance of brook trout by electrofishing (Peckarsky et al. 2001). We used average predator density for each site-year assuming that spatial and temporal variation in predator densities within streams was similar across streams. Thus, the error estimates in our analyses represent between-site variation. We assumed that losses of mayflies not accounted for by predation could be attributed to other sources (e.g., disease, disturbance, migration). Thus, we also evaluated the potential importance of non-predatory losses for each *Baetis* species in fish and fishless streams.

Demographic analyses

We were able to sample *Baetis* B over the entire larval cohort (summer), and thereby test hypotheses related to differences in additional demographic parameters between fish and fishless streams. We estimated the number of days for cohorts to develop from stages II–IV (D) by comparing dates of first observation of stage II to first observation of

stage IV in each site-year. We also estimated the probability of surviving the larval stage ($K = e^{-L \times D}$), assuming constant loss rate (L) during a relatively synchronous larval period of duration D. Estimates of D and K were compared between cohorts of *Baetis* B developing in fish and fishless streams using *t*-tests on ln-transformed data with site-years as independent observations (PROC TTEST, SAS 9.0). Tests for equality of variances indicated that Satterthwaite corrections were not necessary.

Finally, we used sequential abundance data to predict recruitment (I) of *Baetis* B into larval stage II by estimating the *y*-intercept (which represents the initial density of stage II) using analysis of covariance (PROC GLM, SAS 9.0) on ln-transformed densities. Models included a fish effect (fish or fishless), site nested within stream-fish type, time (the regression effect) and all two-way interactions between the main effects (all factors fixed). To backward extrapolate sequential samples to compare *y*-intercepts among site-years, we added the development time (D) to the number of days over which the regressions were calculated, which standardized estimates of *y*-intercepts for differences in development times of *Baetis* B among site-years. A significant fish effect indicates that the *y*-intercepts of regressions (recruitment into stage II) differ between fish and fishless streams (PROC GLM, SAS 9.0).

Results

Field estimates of mayfly dynamics in fish and fishless streams

The slopes of decline in ln abundance over time (loss rates) of *Baetis* B (Fig. 1) were significantly steeper in fish sites than fishless sites [significant time × fish interaction in the analysis of covariance model; $F_{1,31} = 8.67$, $P = 0.006$; See Electronic supplementary material (ESM) Appendix for full model]. While the loss rates of *B. bicaudatus*, which develops during high flow and low water clarity, were higher on average than those of *Baetis* B (Fig. 2), there was no significant difference between fish and fishless streams (time × fish interaction; $F_{1,29} = 0.65$, $P = 0.426$; See ESM Appendix for full model). Lack of significant differences between loss rates of *B. bicaudatus* between stream types could not be attributed to smaller sample sizes or to greater propagation of error for abundance estimates of this species than for *Baetis* B, for which significant differences were detected using similar sample sizes and levels of variation (See ESM Appendix).

Estimates of predation rates of trout and stoneflies

In predation experiments both trout and stoneflies caused significant daily per capita mortality of *B. bicaudatus*
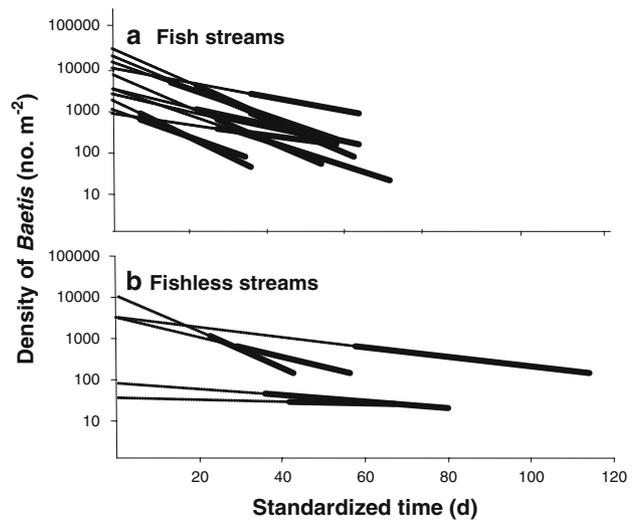

Fig. 1 Linear regressions of *Baetis* B density (ln number m^{-2}) over time of larval cohorts in **a** 11 fish and **b** five fishless sites sampled in 1994–1996 in the upper East River drainage basin. Slopes estimate loss rates (L), *y*-intercepts estimate recruitment into larval stage II (time 0), with estimated development times (*thin lines*) from stage II to IV (D) added to standardize estimates of intercepts. *Heights of lines* indicate relative abundance. *d* Days
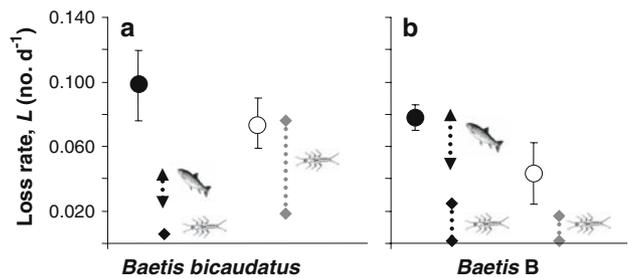

Fig. 2 Mean (±SE) L of both *Baetis* species estimated from slopes of ln(density + 1) regressed against time for **a** 16 fish (*filled circles*) and 12 fishless (*open circles*) sites (*Baetis bicaudatus*), and **b** 11 fish and five fishless sites for *Baetis* B. Sample sizes depended on availability of adequate time-series data to estimate slopes. Predation rates (M_P) on *Baetis* by trout (*triangles*) and stoneflies (*diamonds*) obtained from experiments, adjusted by predator densities (P) at each fish (*black symbols*, *black dash lines*) and fishless (*grey symbols*, *grey dashed lines*) site (±1 SEM $M_P \times P$)

(two-way ANOVA at one prey density (365 m^{-2}); stonefly effect, $F_{1,10} = 5.94$, $P = 0.035$, trout effect, $F_{1,10} = 25.08$, $P = 0.001$). Furthermore, a significant trout × stonefly interaction ($F_{1,10} = 9.04$, $P = 0.013$) indicated that effects of trout and stoneflies were not additive (Fig. 3a).

Consumption by trout of late-instar *Megarcys* was negligible in mesocosms. Trout consumed only one stonefly (Fig. 3b), whereas two stoneflies were missing from one control mesocosm ($t = 0.486$; $df = 6$; $P = 0.644$).

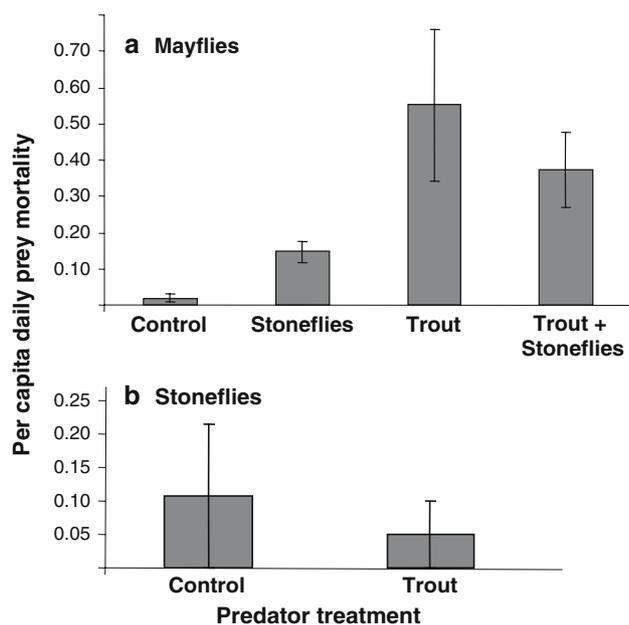Estimates of *B. bicaudatus* M_P from mesocosm experiments were 0.3563 ± 0.1195 per trout per day (mean ± SE)

Fig. 3 Predation rates (mean ± SE per capita daily prey mortality, per 0.823-m² mesocosm) during 16-h overnight trials in July 1996 on **a** 300 mayflies (*B. bicaudatus*) by no predator controls, eight stoneflies (late-instar female *Megarcys signata*), one brook trout or one brook trout + eight stoneflies, and on **b** eight stoneflies by no predator controls or one brook trout

and an order of magnitude lower (0.0138 ± 0.0035) per late-instar *Megarcys* per day. Capture probability for trout feeding on *B. bicaudatus* estimated from observational trials (0.3617 per trout per day, McIntosh et al. 2002) was very similar to M_P estimated from feeding trials in mesocosms. Capture probability of trout feeding on *Baetis* B in observational trials was 0.2288 per trout per day (McIntosh et al. 2002). Previous experiments showed that predation by late-instar *Kogotus* on *Baetis* B ($M_P = 0.010$, Kerans et al. 1995) was about an order of magnitude higher than predation by early-instar *Megarcys* ($M_P = 0.0039$ per predator per day) (Peckarsky et al. 1994), but lower than predation rates of late-instar *Megarcys* on *B. bicaudatus*.

Comparison of predation rates to natural loss rates

Our first approximations of M_P rates scaled by predator density in each site-year ($M_P \times P$) fell within the range of total losses of *Baetis* (*L*) observed in natural streams (juxtaposed on Fig. 2 for comparison). Those approximations were highly variable (depending on predator and prey species and variation in predator densities among site-years), suggesting that predation has the potential to cause substantial mortality of *Baetis* only under some circumstances. Specific comparisons of predation rates to natural loss rates generated the following hypotheses (Fig. 4):
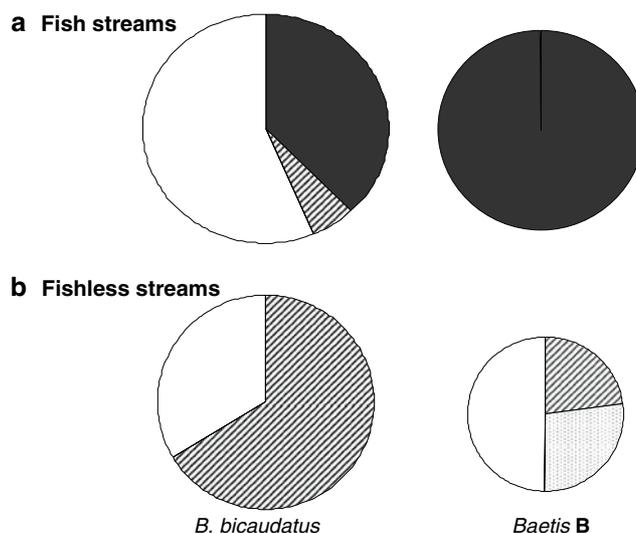
Fig. 4 Hypothesized relative contributions to losses of individuals for two *Baetis* species in **a** fish and **b** fishless streams. *Size of circles* indicates relative magnitude of average total losses estimated in multiple streams of each type over 3 years (see Fig. 2). *Pie slices* indicate proportion of those losses that could be attributed to predation by trout (*black*), *Megarcys* (*hatched*) or *Kogotus* (*stippled*) estimated from predation experiments. *White pie slices* indicate non-predatory losses (e.g., drift or mortality caused by disturbance or parasitism)

1. Consumption by trout has a greater potential to account for natural loss rates of the baseflow species (*Baetis* B) than the snowmelt species (*B. bicaudatus*), even though predation rates on *B. bicaudatus* were estimated at relatively low flows.
2. In fish streams, predation by stoneflies is negligible compared to trout predation and to natural loss rates of either *Baetis* species (as in Kerans et al. 1995).
3. In fishless streams, predation by late-instar *Megarcys* could make an important contribution to observed loss rates of *B. bicaudatus*, actually greater than that of trout predation in fish streams, because higher natural densities of stoneflies (Peckarsky et al. 2001) compensate in part for lower per capita stonefly predation rates than those of trout (Fig. 3a).
4. Combined predation by both stonefly species could account for a substantial proportion of the observed losses of *Baetis* B in fishless streams; but stoneflies are much less important predators on this species than trout in fish streams.
5. Non-predatory sources of mortality were higher for *B. bicaudatus* in trout streams, but higher for *Baetis* B in fishless streams.

Predators versus prey abundance

Densities of stage III larvae of the snowmelt species (*B. bicaudatus*) tended to be higher in fish sites (Fig. 5a),
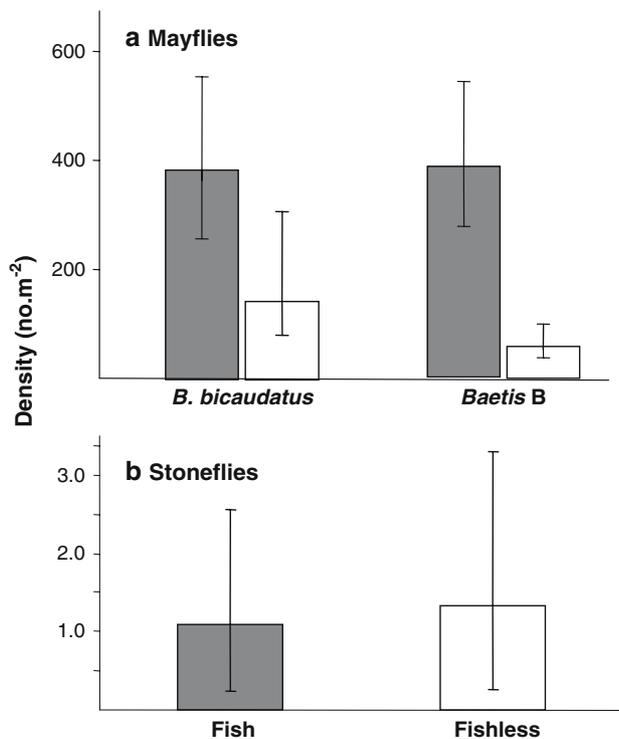
Fig. 5 Mean densities (number m^{-2}) of **a** peak stage III *B. bicaudatus* and *Baetis* B and **b** predatory stoneflies (Perlodidae) in 16 fish (*shaded bars*) and 12 fishless (*open bars*) sites in the East River drainage basin sampled summers 1994–1996 ± back-transformed upper and lower 95% confidence limits of ln(x + 1)-transformed densities

but were not significantly different than fishless sites due to high variation in densities within stream-fish types ($t = 1.26$, $df = 26$, $P = 0.220$). Consequently, power to detect significant differences was low (0.228), and the least significant number of sites was unattainable (70). Nonetheless, given similar effort, we were able to detect significantly higher densities of *Baetis* B in fish than fishless sites (Fig. 5a; $t = 3.01$, $df = 22$, $P = 0.007$). This observation is especially intriguing, because *Baetis* B develops during the baseflow, clear-water period, and has higher loss rates in fish sites than fishless sites (Figs. 1, 2). Furthermore, densities of predatory stoneflies did not differ between fish and fishless streams (Fig. 5b; $t = -0.29$, $df = 26$, $P = 0.777$). These results are not consistent with a consumptive trophic cascade hypothesis (Power 1990; Brönmark et al. 1992; Carpenter and Kitchell 1993), whereby a top predator reduces densities of an intermediate predator, indirectly increasing the abundance of primary consumers.

Demographic analyses

Further analyses of the sequential abundance samples of *Baetis* B showed that certain demographic parameters (mean ± SE) differed between fish and fishless streams. Shorter times to develop from stage II to IV in fish streams

(22.1 ± 3.0 days) than fishless streams (36.4 ± 6.0 days) ($t = -2.40$, $df = 14$, $P = 0.031$) compensated in part for higher loss rates in fish than fishless streams (Figs. 1, 2), resulting in similar probabilities of surviving from stage II to IV ($K = e^{-L \times D}$) between fish (0.26 ± 0.05) and fishless streams (0.36 ± 0.14) ($t = -0.83$, $df = 14$, $P = 0.422$). In addition, linear regression effects of the analysis of covariance models predicted that recruitment of *Baetis* B into stage II should be higher in fish than fishless streams (significant fish effects on intercepts; $F_{1,31} = 15.80$, $P = 0.0004$; Fig. 1; see ESM Appendix for full model).

Discussion

Understanding the relative contribution of predation to prey population dynamics is a fundamental issue in ecology. Our analyses of an extensive data set underscores the difficulty of quantifying the effects of predation on prey populations in ways that enable discrimination among alternative hypotheses to explain natural population dynamics. An even more difficult but important challenge is to devise methods to assess the total impact of predators (consumptive and non-consumptive) relative to other influences on population dynamics, especially for organisms with complex life cycles living in open systems (Hansson 1989; Hixon et al. 2002). Here a comparative approach generated results consistent with the hypothesis that variation in abundance of prey populations over space and time may be explained by predation in some cases, but in others, predation may be overshadowed by non-consumptive effects of predators on prey behavior and life history or by environmental factors.

Comparison of the two *Baetis* species in this study suggests that the relative importance of predator-induced mortality on prey population dynamics may depend on the environmental context (e.g., the disturbance regime) during periods of prey growth and development (Menge 1976; Peckarsky 1983; Walde 1986). For example, loss rates of *B. bicaudatus*, which develops during turbulent snowmelt periods in these high-elevation streams, were not only higher than those of its baseflow congener (*Baetis* B), but also not accounted for by trout predation (Fig. 4). A high proportion of non-predatory losses of this species in trout streams suggests that mortality or dislodgement caused by stochastic factors such as hydrologic disturbance may be more important to its dynamics. Such large-scale factors as hydrology, climate and geomorphology can thereby overshadow predation and contribute to mayfly dynamics not only by causing mortality directly, but also by constraining dispersal and recruitment. However, in fishless streams predation by stoneflies could account for a higher proportion of observed losses of *B. bicaudatus* than non-predatory

losses. We propose that hydrologic and geomorphic environments in fishless streams are more favorable to biotic interactions, even during snowmelt periods (A. Wilcox, B. L. Peckarsky, B. W. Taylor, and A. C. Encalada, unpublished manuscript), a hypothesis currently under investigation (A. R. McIntosh and B. L. Peckarsky, unpublished data).

In contrast, predators appear to have stronger effects on *Baetis* B, which develops during the baseflow period characterized by low disturbance regimes (Peckarsky et al. 2000). In fact, trout predation has the potential to explain the observed natural loss rates in fish streams, and stonefly predation could explain a high proportion of losses in fishless streams (Fig. 4). However, it is unlikely that non-predatory losses of *Baetis* B are caused by disturbance in fishless streams, especially if we assume systematically harsher disturbance regimes in fish streams. Another potential source of *Baetis* B mortality in fishless streams is mermithid parasitism, which increases in prevalence during baseflow periods in headwater streams (Vance and Peckarsky 1996).

Non-consumptive effects of predators on prey dispersal behavior could also contribute to losses of both *Baetis* species that are not explained by predation. Adaptive prey behavior can affect prey population dynamics if prey movement varies with risk of predation (Abrams 1990; Anholt and Werner 1995). For example, foraging by predatory stoneflies increases drift rates of many species of *Baetis* (Sih and Wooster 1994; Kratz 1996; Peckarsky 1996), an effect that becomes stronger in the absence of fish, which constrain stonefly foraging behavior (Peckarsky and McIntosh 1998). Consequently, adaptive drift may cause fishless streams to lose individuals if emigration is not compensated by immigration from upstream. Behavioral studies have also shown that brook trout cues reduce per capita *Baetis* drift rates (Peckarsky and McIntosh 1998). In a dynamical model patterned after a similar open stream system, Diehl et al. (2000) showed that predators cause increased mayfly densities if per capita prey emigration decreases in risky environments. Thus, non-consumptive effects of predators on prey behavior may explain in part why densities of *Baetis* B were higher in trout streams than fishless streams.

Evidence from previous work also shows that non-consumptive effects of predators on prey development are stronger for *Baetis* B (Peckarsky et al. 2001). Furthermore, demographic analyses in this study suggest that such effects could contribute to the counter-intuitive pattern of higher densities of this species in the more dangerous environment (Fig. 6). We hypothesize that faster development times of *Baetis* B in trout streams compared to fishless streams compensate in part for higher loss rates in trout streams, thereby increasing the probability of surviving the larval stage in the more dangerous environment, as has been shown in
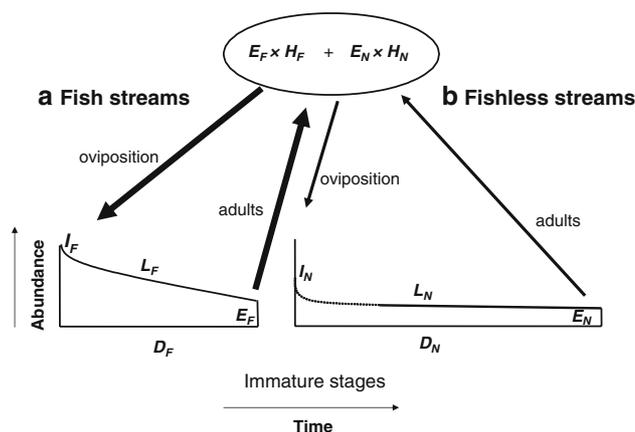

Fig. 6 A demographic hypothesis illustrating how differences between **a** fish (H_F) and **b** fishless streams (H_N) in recruitment ($I_F > I_N$), loss rates ($L_F > L_N$) and development times through immature stages ($D_N > D_F$) of *Baetis* B could contribute to higher numbers of individuals emerging from fish than fishless streams ($E_F > E_N$). Mated adult females enter a regional pool of adults (*circled*), and selectively oviposit in fish streams. See "Discussion" for further explanation

other systems (Reznick 1990). Such adaptive developmental responses to risk of predation have been induced experimentally (Peckarsky et al. 2002), and may explain why *Baetis* females do not avoid ovipositing in high-risk habitats, in contrast to other insect species (Resetarits 2001; Abjörnsson et al. 2002; Spencer et al. 2002).

In addition, higher recruitment in fish streams combined with faster development results in greater numbers of individuals emerging from risky habitats, despite higher loss rates (Fig. 6), consistent with the hypothesis that recruitment-limitation (Underwood and Fairweather 1989; Doherty and Fowler 1994) contributes to low abundance of *Baetis* B in fishless streams independently of predation risk. Previous work has shown that mated females are selective of oviposition sites that are more common in fish streams (large, protruding rocks in high-velocity locations), and that the probability of egg mass desiccation is higher in fishless streams, especially during baseflow conditions and in low water years (Encalada and Peckarsky 2006). Thus, fish streams may be "attractive sinks" (Delibes et al. 2001) attracting more oviposition despite having higher predation risks.

In summary, data from field studies, experiments and statistical models showed that spatial and temporal variation in the abundance of two *Baetis* species developing under different environmental conditions in western Colorado streams could not be explained simply in terms of predation. Clearly, models of predator effects on prey dynamics must consider the environmental context in which predators and prey interact. A more comprehensive conceptual framework is needed to better understand the importance of predators to dynamics of prey species with

complex life cycles living in open systems. Such a framework should include both direct and indirect effects, consumptive and non-consumptive effects (adaptive variation in prey behavior and development), and consider how the physical environment affects mortality as well as recruitment, which may be independent of predation risk.

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