Ecology, 83(3), 2002, pp. 612–618
© 2002 by the Ecological Society of America

PREDATOR CHEMICALS INDUCE CHANGES IN MAYFLY LIFE HISTORY TRAITS: A WHOLE-STREAM MANIPULATION

BARBARA L. PECKARSKY,[1,2,6] ANGUS R. MCINTOSH,[2,3] BRAD W. TAYLOR,[2,4] AND JONAS DAHL[2,5]

[1]*Department of Entomology, Cornell University, Ithaca, New York 14853 USA*
[2]*Rocky Mountain Biological Laboratory, P.O. Box 519, Crested Butte, Colorado 81224 USA*
[3]*Department of Zoology, University of Canterbury, Christchurch, New Zealand*
[4]*Department of Zoology and Physiology, University of Wyoming, Laramie, Wyoming 82071 USA*
[5]*Department of Ecology, Lund University, Lund, Sweden*

Abstract. In high-elevation streams of western Colorado, mayflies (*Baetis bicaudatus*) develop faster, but mature at a smaller size where trout are present compared to streams where fish are absent. These life history traits reduce the time of larval exposure to trout predation, but cost reduced fecundity. We designed a field experiment involving manipulation of whole streams to determine whether these changes were caused by the presence of brook trout, and specifically, whether they could be triggered by trout chemical cues. In 1999 and 2000, we introduced water from containers with brook trout (*Salvelinus fontinalis*) into five naturally fishless streams, and fishless stream water into five adjacent control streams, to determine whether these cues alone could induce the mayfly life history traits we have observed in natural trout streams. As in previous small-scale experiments, the size at which mayflies matured declined significantly in streams with added trout chemicals but did not change in streams with fishless water only. Thus, life history traits similar to those observed in the field were induced within the natural variability inherent in streams. These results demonstrate the strength of this predator–prey interaction and indicate that brook trout are an important agent of natural selection on mayfly life history traits.

Key words: chemical induction; field experiment; life history traits; mayflies; nonconsumptive effects; predation; scale; size at emergence; streams; trout.

INTRODUCTION

Interesting patterns observed in nature are difficult to attribute definitively to specific mechanisms without the use of experiments. However, experiments are usually conducted in simplified environments at small scales, necessitated by the requirement of achieving control of all but the variables of interest (Carpenter 1996). Furthermore, observations made at small spatial and temporal scales in simple environments often cannot be extrapolated to scales relevant to the organisms or processes under investigation (Peckarsky et al. 1997, Petersen et al. 1999, Brönmark and Hansson 2000). The larger the scale of observation, the more difficult it is to manipulate the variables of interest. Therefore, ecologists often rely on making inferences from observations in nature to explain large-scale patterns (Power et al. 1998). However, the strength of these inferences can be substantially improved by innovative experiments carried out at relevant scales (e.g., Reznick et al. 1990, Carpenter et al. 1995, Wallace et al. 1999, Thrush et al. 2000).

We have observed a striking natural pattern in high-elevation streams of Western Colorado. Mayflies (*Baetis bicaudatus*) common in the diet of brook trout (*Salvelinus fontinalis*) (Allan 1981) matured at significantly smaller sizes in streams with trout compared to streams where trout were excluded by natural barriers to dispersal (Peckarsky et al. 2001). Also, the size at which *Baetis* metamorphosed declined over the emergence period, but only in streams that contained trout. These field patterns are consistent with the hypothesis that mayflies adaptively shifted their larval development in response to variable risk of predation (Peckarsky et al. 2001). Mayflies have relatively mobile larvae and terrestrial adults that may disperse from their natal streams to oviposit (Sweeney et al. 1986, Schmidt et al. 1995, Bunn and Hughes 1997, Peckarsky et al. 2000). Thus, they typically encounter a variety of environmental conditions within one generation, and should benefit by evolving flexible life history traits (Wilbur and Collins 1973, Newman 1989, Rowe and Ludwig 1991, Palmer and Poff 1997).

Using field observations of larval growth rates and development times (from egg to maturity) we determined that mayflies maturing in trout streams accelerated their larval development, which reduced their exposure time to predatory trout, thereby increasing their probability of survival in trout streams (Peckarsky et al. 2001). However, the cost of accelerating development was smaller body size at emergence, which reduced female fitness (lower fecundity; McPeek and Peckarsky 1998), but not male fitness. Previous work suggests that large males have no mating advantage over smaller males, and there is no size-assortative mat-

Manuscript received 21 June 2001; accepted 12 July 2001; final version received 27 August 2001.
[6] E-mail: BLP1@cornell.edu

ing in this species (B. L. Peckarsky, *personal observations*). In fishless streams, mayfly development was prolonged, enabling them to increase both size and fecundity. Thus, these nonconsumptive effects of trout have a large potential for affecting mayfly population growth (McPeek and Peckarsky 1998).

Controlled experiments carried out in mesocosms at small spatial and temporal scales have demonstrated that odor from brook trout can induce small *Baetis* size at emergence (Peckarsky and McIntosh 1998). However, mechanisms deduced from these small-scale experiments, which isolated only a few species from the community in simplified environments, may not accurately reflect life history traits of individuals living in complex, natural systems (Wilbur and Fauth 1990, Burks et al. 2000). Our challenge was to ascertain whether this striking pattern of variation in *Baetis* size at maturation could be induced within the natural variability inherent in streams. In this study we manipulated replicate natural fishless streams by introducing chemical cues from feeding brook trout to determine whether these cues alone could cause the life history traits we have observed in natural trout streams.

Methods

During summers 1999 and 2000, we placed 110-L plastic garbage bins near the headwaters of 10 naturally fishless tributaries of the East River that drain the steep eastern slope of Gothic Mountain at the Rocky Mountain Biological Laboratory in Western Colorado. We fashioned these bins with intake and outflow hoses so that fishless water from upstream was gravity-fed through them and then back into the stream at a rate of 2.5–3.0 L/min. We placed two brook trout (mean fork length $\pm$ 1 SE = 155 $\pm$ 6 mm in 1999; 169 $\pm$ 4 mm, mean mass $\pm$ 1 SE = 56 $\pm$ 4 g in 2000) in the bins flowing into five randomly allocated streams, and the outflow of fishless stream water drained into the other five streams serving as controls. We fed these brook trout a mixed diet of stream invertebrates (including *Baetis*) every other day throughout the experiments. During summer 1999, the experiment ran from 30 July to 9 September to measure the effect of fish chemical cues on the size at emergence of the short summer generation of this bivoltine mayfly (Peckarsky et al. 2001). In 2000, we ran the experiment from 29 June to 22 August to study the effect of fish chemicals on the size at emergence of the overwintering generation.

We delineated relatively low-gradient study sections of each stream from the outflow of the bins to 30 m downstream, which comprised about a third of the total length of each stream. In both experiments we collected mature *Baetis* larvae (with black wingpads: BWP) at weekly intervals, and measured their head capsule widths to the nearest 0.1 mm at 25$\times$ on a Wild dissecting microscope (Leitz Microsystems Incorporated, Bannockburn, Illinois) equipped with an ocular micrometer. We converted these linear measures to dry masses using regression equations for males and females (see Peckarsky et al. 2001:774), and analyzed treatment effects using dry masses. Mayflies with BWPs are within 24 h of emerging, have ceased feeding, growing, and have completed production of eggs (Peckarsky et al. 2001). Since adults do not feed, the size of BWP females is a good predictor of their fecundity (McPeek and Peckarsky 1998). We also measured sizes of BWP males, although large males do not have a mating advantage over smaller males (B. L. Peckarsky et al., *personal observations*).

We compared the size of mayflies that matured in fish–chemical treatment streams with those maturing in fishless control streams. In 1999, the summer generation began emerging 22 d after the start of the experiment, and we sampled individuals up to 43 d after the start of the experiment. Since the size of emerging summer generation *Baetis* remained constant over the emergence period in these and all streams previously studied (Peckarsky et al. 2001), we tested whether the mean size of BWP individuals differed among treatments. Due to low population densities (Peckarsky et al. 2001), and therefore small sample sizes of summer generation *Baetis*, we used individual mayflies as replicates in a two-way ANOVA to determine the effects of treatment (fish odor or control) and sex (male or female) on the size at maturation.

In contrast to the summer generation, we have previously observed significant temporal changes in the size of emerging winter generation *Baetis* (Peckarsky et al. 2001). Furthermore, higher population densities of this generation enabled us to collect sufficient numbers of mature individuals each week in 2000 to analyze effects of treatments on changes in *Baetis* size over time. In this analysis we used the mean size of individuals collected from each stream on each date as replicates, and time since the start of the experiment as a continuous variable. We tested for homogeneity of slopes of the relationship between time and mean size to determine whether the change in size of mature *Baetis* differed between streams that received trout chemicals and those that did not. We used maximum likelihood to compute all parameters including the variance components of a mixed model nested ANOVA (PROC MIXED; SAS 1989), with *Baetis*, sex, and fish odor treatment as fixed factors and stream nested within treatment as a random variable. Since mature individuals of both sexes were not obtained at every stream on every sampling date, we used a Satterthwaite correction for unbalanced designs to obtain the correct denominator degrees of freedom, which results in fractional df (see Table 2) (Searle 1987).

Smaller *Baetis* size at emergence and shorter development times in trout streams compared to fishless streams (Peckarsky et al. 2001) could be attributed to other differences between these two types of streams that we did not measure. Thus, we selected streams that

TABLE 1. Mean physicochemical conditions and invertebrate benthic densities measured before (depth, velocity, width, substrate, and benthic densities) and during (temperature, conductivity) the experiment in the five streams allocated to the fish chemical treatment (fish odor) and the five streams receiving fishless water (control).

Year and treatment	Mean water temperature (°C)	Degree days	Substrate index	Discharge (0.01 m^3/s)	Mean depth (cm)	Mean current velocity (cm/s)
1999						
Control	6.0 (0.5)	250 (19)	4.7 (0.1)	1.2 (0.2)	6.0 (0.8)	38 (5)
Fish odor	6.3 (0.7)	264 (31)	4.7 (0.1)	0.9 (0.2)	5.1 (0.6)	34 (3)
2000						
Control	7.1 (1.0)	384 (55)	4.8 (0.2)	0.5 (0.1)	6.2 (0.5)	19 (4)
Fish odor	6.4 (0.5)	344 (26)	4.7 (0.1)	0.6 (0.2)	6.5 (0.9)	24 (4)

Notes: Standard errors are given in parentheses. MANOVAs on physicochemical variables (mean temperature, substrate index, discharge, and conductivity) and benthic densities (*Baetis*, other grazers, and predatory invertebrates) indicated no significant differences between the odor and control streams. Univariate ANOVAs on these variables were also not significant, except for predatory invertebrates in 1999, where densities were higher in control streams ($F_{1,8} = 6.4$, $P = 0.04$). For 1999, the habitat MANOVA produced values of 0.568 for Wilks' lambda, with $F = 0.952$, df = 4, 5, $P = 0.51$; benthic density MANOVA, Wilks' lambda 0.539, $F = 1.712$, df = 3, 6, $P = 0.26$. For 2000, the habitat MANOVA produced values of 0.858 for Wilks' lambda, with $F = 0.207$, df = 4, 5, and $P = 0.92$; benthic density MANOVA, Wilks' lambda = 0.918, $F = 0.179$, df = 3, 6, $P = 0.91$.

were similar for both 1999 and 2000 experiments, and we measured attributes of the streams that could contribute to observed differences in size of mayflies at emergence (Table 1). Hobo data loggers (Onset Computer Corporation, Pocasset, Massachusetts) were used to continuously monitor water temperatures in each stream, and we determined cumulative degree-days over 0°C of control and fish-chemical treatment streams. We measured substrate particle sizes at 15 randomly chosen locations in each stream, and used a substrate index (Jowett et al. 1991) to summarize these data. We customized substrate categories for best resolution of variation among the streams as follows: bedrock, boulder >20 cm, large cobble = 12–20 cm, small cobble = 5–12 cm, coarse gravel = 2–5 cm, fine gravel = 2 mm–2 cm, and sand <2 cm. At each of these 15 locations, we also measured water depth, stream width, and current velocity, and estimated discharge at the beginning of each experiment. Finally, we measured conductivity in each stream using a YSI 30 meter (Yellow Springs Instruments, Yellow Springs, Ohio, USA).

To determine whether systematic habitat variation between streams allocated to different treatments could have confounded treatment effects, we conducted MANOVAs to test for differences between treatment and control streams in 1999 and 2000, including mean water temperature, discharge, substrate index, and conductivity. We also tested whether the treatment and control streams differed in algal biomass (food) and invertebrate densities (predators and competitors), since these variables have been shown experimentally to affect the development of mayflies (see citations in Peckarsky et al. [2001]).

Before starting the experiment, we estimated algal biomass (chlorophyll *a*) from 15 rocks in each stream, and used these data to demonstrate that resource levels did not vary systematically between streams allocated to the fish and fishless treatments (A. R. McIntosh and B. L. Peckarsky, *unpublished manuscript*). We also took benthic invertebrate samples in all streams before the experiments, using modified Hess samplers in 1999 and electrobugging in 2000 (Taylor et al. 2001) to reduce disturbance of the substrates. The benthos of all streams was dominated by grazing mayflies, including *Baetis* and *Cinygmula* (Heptageniidae), and predatory invertebrates (primarily stoneflies), the densities of which were highly variable (Table 1). We also used MANOVAs to determine whether densities of *Baetis*, other grazers, and predatory invertebrates differed among streams allocated to control and fish chemical treatments in 1999 or 2000.

RESULTS

1999, Summer generation Baetis

Summer generation *Baetis* emerging from the streams receiving odor from brook trout were ~20% smaller than those receiving fishless water (Fig. 1, two-way ANOVA odor treatment: $F_{1,15} = 4.468$, $P = 0.052$). Mean dry masses of females were significantly higher than males (two-way ANOVA sex treatment: $F_{1,15} = 11.488$, $P = 0.004$), which could be attributed to the mass of the developing eggs (Peckarsky et al. 1993). Size–fecundity regression equations (McPeek and Peckarsky 1998) estimate that trout chemicals reduced *Baetis* fecundity by 35% (Table 3). Since natural population densities of summer generation *Baetis* were too low to use streams as replicates in this analysis (see Peckarsky et al. 2001 for relative densities of summer and winter generations), we used individual mayflies as replicates. Thus, effects may disproportionately represent responses of mayflies from the streams with higher population densities. Nonetheless, this result was consistent with field patterns of differences in mean size at emergence of summer generation *Baetis* in natural fish and fishless streams (Peckarsky et al. 2001).

2000, Winter generation Baetis

In 2000 the size of overwintering individuals of both sexes emerging from streams that were allocated to the

TABLE 1. Extended.

Width (m)	Conductivity (μS/cm)	*Baetis* density (no./m²)	Other grazers (no./m²)	Predatory invertebrates (no./m²)
0.53 (0.05)	136 (8)	131 (44)	366 (42)	82 (37)
0.47 (0.05)	124 (5)	92 (64)	239 (60)	23 (6)
0.46 (0.05)	114 (6)	286 (158)	293 (53)	30 (5)
0.53 (0.04)	111 (4)	301 (136)	252 (90)	63 (36)

fish and fishless treatments was similar before the addition of fish odor (Fig. 2, day zero). However, a significant interaction between time from the start of the treatments and fish odor treatment indicated that the slopes of the relationship between mean size of mature *Baetis* and time differed between streams with and without fish odor over the period of the experiment (Table 2). Further analysis using linear regression demonstrated that the mean size of mature *Baetis* declined significantly over time in streams where trout odor was continuously added, but did not vary over time in streams with fishless water added (Fig. 2). This result was also consistent with patterns observed in natural streams where size of mature winter generation *Baetis* declined over time in streams containing trout, but not in fishless streams (Peckarsky et al. 2001). Interestingly, declining size at emergence of winter generation *Baetis* was not observed in 1995 and 1996 in two of the same channels we used for this experiment (Peckarsky et al. 2001), but was observed when fish chemicals were added to these same channels in 2000. In this experiment, trout chemicals caused ~13% reduction in mean *Baetis* size at emergence, which would result in about a 25% loss of fecundity (Table 3).

Alternative explanations for life history responses

MANOVAs on physicochemical conditions and invertebrate densities indicated that neither of these sets of factors differed significantly among treatments in 1999 or 2000 (Table 1). Thus, natural variation in habitat features, or densities of *Baetis* and other grazers did not contribute significantly to variation in *Baetis* size, as in field observations (Peckarsky et al. 2001). However, a univariate ANOVA showed that densities of predatory invertebrates were significantly higher in control streams than in odor treatment streams in 1999. High predatory stonefly densities can cause smaller *Baetis* in natural streams (Peckarsky et al. 2001) and small-scale experiments (Peckarsky et al. 1993, Peckarsky and McIntosh 1998). Thus, higher stonefly densities could have reduced the size of *Baetis* in control streams, which would have made it harder to observe the effect of trout chemicals in the treatment streams. Thus, there were no alternative systematic differences between the streams used for experiments in 1999 or 2000 that could explain the observed variation in *Baetis* life history traits in response to different fish odor treatments.

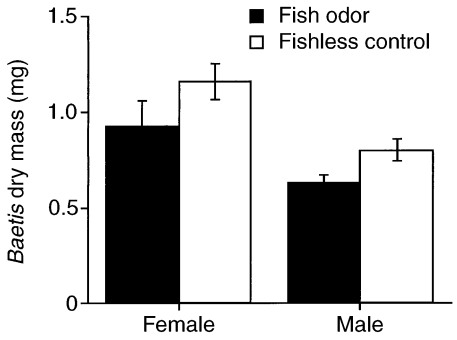

FIG. 1. Dry mass (mean ± 1 SE) of mature (black wingpad) female and male *Baetis* larvae was lower in streams with brook trout chemicals added (solid bars) compared to control streams with only fishless water added (open bars). Data are for the summer generation, 1999.

DISCUSSION

The results of these whole-stream experiments provide definitive evidence to support the hypothesis that chemical cues from brook trout caused alterations in mayfly life history traits within the backdrop of complexity and variability found in natural streams. Brook trout are one of the major predators of *Baetis* larvae (Allan 1981). Given that trout did not have access to mayflies in this experiment, we can completely rule out size-selective predation as the cause of observed reductions in *Baetis* size at emergence. Moreover, we can also rule out size-dependent predator-induced emigration (drift) as a possible mechanism explaining the results of these experiments. Large *Baetis* are less prone to drift when fish odor is present than are small *Baetis* (McIntosh et al. 1999), which would have produced the opposite effect (increased size of *Baetis* in streams with trout odor). Thus, this natural field experiment is the most dramatic example of the influence of predatory fish on *Baetis* life history traits that we also have observed at many different scales (Peckarsky and McIntosh 1998, Peckarsky et al. 2001). Taken together these studies support the hypothesis that *Baetis* larvae developing in trout streams sacrifice potential fecundity

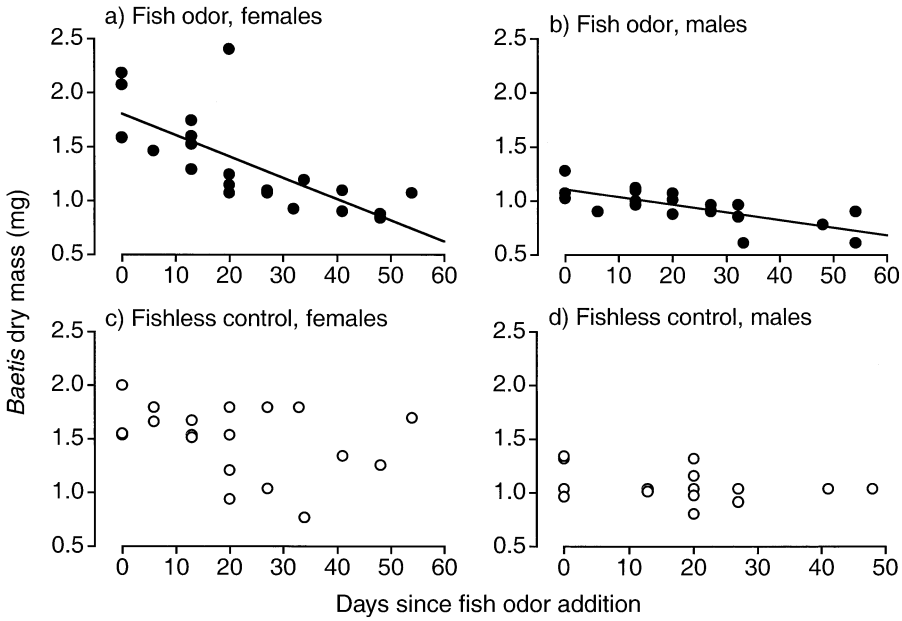

FIG. 2. Dry mass of mature (black wingpad) *Baetis* larvae decreased through time in streams with brook trout odor added (solid circles) but did not vary over time in control streams with only fishless water added (open circles). Fish odor was added continuously starting after day 0. Data points are means of all mature larvae collected per stream per day. Significant regressions were obtained between *Baetis* dry mass and days since the start of odor addition (d) for (a) females and (b) males in fish odor treatment streams only (females, $F_{1,20} = 22.02$, $P < 0.001$, $r^2 = 0.52$, dry mass $= -0.02d + 1.81$; males, $F_{1,18} = 19.42$, $P < 0.001$, $r^2 = 0.52$, dry mass $= -0.007d + 1.11$). No significant relationships were detected for (c) females or (d) males in control streams (females, $F_{1,18} = 2.08$, $P = 0.17$; males, $F_{1,13} = 1.51$, $P = 0.24$). Note that prior to odor addition (day 0), the dry masses of pre-emergent larvae were similar in streams allocated to the brook trout odor and control treatments.

by maturing at smaller sizes, so that they can reduce their exposure to a dangerous predator. Clearly, brook trout have the potential to significantly influence *Baetis* population dynamics through nonconsumptive effects on plastic life history traits (McPeek and Peckarsky 1998).

The consequences of nonconsumptive (or nontrophic) interactions between predators and prey mediated through chemical cues need careful consideration (Anholt 1997). A demographic analysis illustrated that by inducing mayflies to mature at smaller sizes, chemical cues from predators caused reductions in the rate of population growth of *Baetis* far exceeding the effects of direct consumption (McPeek and Peckarsky 1998). These nonconsumptive effects on prey population dynamics could also ramify to influence not only community dynamics (Werner 1991, Werner and Anholt 1996, Peacor and Werner 1997), but also ecosystem processes (e.g., phosphorus and carbon flows [Schindler et al. 1993, B. W. Taylor, *personal observations*]). Thus, it is conceivable that small size at emergence induced by trout chemical cues may cause reductions in *Baetis* biomass that could exceed those caused by direct consumption. Calculations based on data from previous studies suggest that the nontrophic effect of trout on *Baetis* biomass could be as much as two times greater than the trophic effect (McPeek and Peckarsky 1998). Here we estimate that chemicals from two fish caused a loss of ~65 mg dry mass of *Baetis* per day from a 30-m reach (Fig. 2), vs. an estimated 10 mg dry

TABLE 2. Nested homogeneity of slopes test on the mean dry mass of pre-emergent winter generation male and female (sex) *Baetis* larvae in streams with and without added brook trout chemicals (odor treatment) during the 2000 experiment.

Source	Numerator df	Denominator df	F	P
Odor	1	22.1	0.74	0.3998
Day	1	70.9	31.73	<0.0001
Day × odor	1	70.8	7.07	**0.0097**
Sex	1	68.3	61.72	<0.0001

Notes; Dry masses were ln(x) transformed, and days since the start of the experiment were used as the covariate (day). The stream (odor treatment) term was used as the denominator in the F ratio test of the odor term. The Satterthwaite approximation for unbalanced designs results in fractional degrees of freedom. A significant day × odor treatment interaction indicates that the slopes of the relationships between mayfly dry mass and day differed between treatments.

TABLE 3. Summary of mean dry masses of males and females and mean fecundity of females of the summer (1999) and winter (2000) generations of *Baetis* maturing in streams with (F) and without (N) fish odor added.

Generation	Sex	Dry mass (mg)		Size reduction (%)	Fecundity		Loss of fecundity (%)
		F	N		F	N	
Summer	M	0.632	0.802	21			
	F	0.927	1.161	20	357.9	547.6	35
Winter	M	0.896	1.104	14			
	F	1.259	1.455	13	638.1	838.9	24

Note: Comparisons between treatments provide an estimate of percentage reductions in size and fecundity caused by fish odor in the 1999 and 2000 experiments.

mass of *Baetis* consumed per capita per day averaged over three different size classes of brook trout (Allan 1978, 1981). The problem of comparing per capita consumptive effects to nontrophic effects of predators on prey biomass will be exceedingly challenging, because the larger spatial scales over which chemical cues operate may cause 1 or 2 fish to have the same effect as 10 or 20 fish. Nonetheless, we emphasize that ecologists need to incorporate nontrophic links into food web theory and empirical food webs.

We have previously observed that fish chemical cues induced *Baetis* to mature at smaller sizes in 0.8-m^2 mesocosms when all variables except for fish chemicals were controlled (Peckarsky and McIntosh 1998). It is most impressive that chemicals emitted from two brook trout held in a 110-L bin delivered at ~3 L/min caused an effect that was observed 30 m downstream of the source in stream. The identity of the chemicals inducing the effect is unknown, but they are associated with live, feeding brook trout and could be similar to kairomones that affect zooplankton in lakes (Von Elert and Loose 1996). Chemical signals are clearly a most effective cue for predator detection by *Baetis* because they are present day and night, do not necessitate encounters with predators, and signal a general risk of predation in the immediate environment (McIntosh and Peckarsky 1999, McIntosh et al. 1999). Other studies have demonstrated chemical induction of adaptive prey traits that reduce the risk of predation, and have nonconsumptive fitness consequences. For example, induced behaviors (see examples in Lima 1998), morphologies (see examples in Tollrian and Harvell 1999, Dahl and Peckarsky 2002), and life history traits (e.g., Newman 1989) often come at the cost of fecundity (see references in Agrawal 2000).

Despite broad agreement of the patterns observed at multiple scales and experimental types, there were subtle differences in the magnitude of effects between experiments and the natural variation in size of mature *Baetis* between fish and fishless streams (Peckarsky et al. 2001). In this whole-stream experiment brook trout odor induced summer *Baetis* to emerge ~20% smaller than those maturing in fishless treatments, compared to a 30–40% difference in mean size of summer generation *Baetis* maturing in natural fish and fishless streams (see Peckarsky et al. 2001: Fig. 3). Furthermore, the decline over time in the size of emerging winter generation female *Baetis* observed during the whole-stream experiment (−0.02 mg/d dry mass, Fig. 2) was not as rapid as that observed in natural trout streams (−0.13–−0.05 mg/d; Peckarsky et al. 2001). These differences in the magnitude of effects could be attributed to artifacts associated with making cross-scale or experiment–nature comparisons (Peckarsky et al. 1997, Sarnelle 1997, Cooper et al. 1998). Differences in the length of the experiments, the time at which the life history shift is triggered, concentration of the fish cues, and variation in the size of *Baetis* at the beginning of experiments could cause differences in the magnitude of effects observed in experiments vs. natural systems. These differences further illustrate the importance of considering scale in the design of experiments (Petersen et al. 1999).

In conclusion, we have observed the effects of chemical cues from predators on prey life history traits at multiple scales and levels of habitat complexity. It is most impressive that the induction of small size in both winter and summer generations of these mayflies could be observed in natural streams where physical, chemical and biological parameters were not controlled. This result attests to the strength of this interaction, and the importance of brook trout as an agent of natural selection on mayfly life histories.

ACKNOWLEDGMENTS

We thank Tracy Smith, Marge Penton, Chester Anderson, Bryan Horn, Alison Horn, Dewey Overholser, and Leanne O'Brian for help in the field and the lab. Don and Margaret Bailey kindly gave access to streams on their land. Suggestions from Emily Bernhardt, Andrea Encalada, Kate Macneale, Chris Caudill, Per Nyström, Mike Winterbourn, Jon Harding, and Dave Allan substantially improved the manuscript. This research was supported by National Science Foundation grant number DEB-9629404 to B. L. Peckarsky and A. R. McIntosh, travel funding from the University of Canterbury to A. R. McIntosh, and a Swedish Post Doctoral Fellowship to J. Dahl.

LITERATURE CITED

Agrawal, A. 2000. Benefits and costs of induced plant defense for *Lepidium virginicum* (Brassicaceae). Ecology **81**: 1804–1813.

Allan, J. D. 1978. Diet of brook trout (*Salvelinus fontinalis* Mitchill) and brown trout (*Salmo trutta* L.) in an alpine

stream. Internationale vereinigung für theoretische und engewandte Limnologie, Verhandlungen **20**:2045–2050.
Allan, J. D. 1981. Determinants of diet of brook trout (*Salvelinus fontinalis*) in a mountain stream. Canadian Journal of Fisheries and Aquatic Sciences **38**:184–192.
Anholt, B. R. 1997. How should we test for the role of behaviour in population dynamics? Evolutionary Ecology **11**: 633–640.
Bronmark, C., and L.-A. Hansson. 2000. Chemical communication in aquatic systems: an introduction. Oikos **88**: 103–110.
Bunn, S. E., and J. M. Hughes. 1997. Dispersal and recruitment in streams. Evidence from genetic studies. Journal of the North American Benthological Society **16**:338–346.
Burks, R. L., E. Jeppesen, and D. M. Lodge. 2000. Macrophyte and fish chemicals suppress *Daphnia* growth and later life-history traits. Oikos **88**:139–147.
Carpenter, S. R. 1996. Microcosm experiments have limited relevance for community and ecosystem ecology. Ecology **77**:667–680.
Carpenter, S. R., S. W. Chisholm, C. J. Krebs, D. W. Schindler, and R. F. Wright. 1995. Ecosystem experiments. Science **269**:324–327.
Cooper, S. D., S. Diehl, and O. Sarnelle. 1998. Implications of scale for patterns and processes in stream ecology. Australian Journal of Ecology **23**:27–40.
Dahl, J., and B. L. Peckarsky. 2002. Induced morphological defenses in the wild: predator effects on a mayfly, *Drunella coloradensis*. Ecology, *In press.*
Jowett, I. G., J. Richardson, B. J. Biggs, C. W. Hickey, and J. M. Quinn. 1991. Microhabitat preferences of benthic invertebrates and the development of generalized *Deleatidium* spp. habitat suitability curves, applied to four New Zealand rivers. New Zealand Journal of Marine and Freshwater Research **25**:187–199.
Lima, S. L. 1998. Nonlethal effects in the ecology of predator–prey interactions—what are the ecological effects of anti-predator decision making? BioScience **48**:25–34.
McIntosh, A. R., and B. L. Peckarsky. 1999. Criteria determining behavioural responses to multiple predators by a stream mayfly. Oikos **85**:554–564.
McIntosh, A. R., B. L. Peckarsky, and B. W. Taylor. 1999. Rapid size-specific changes in the drift of *Baetis bicaudatus* (Ephemeroptera) caused by alterations in fish odour concentration. Oecologia **118**:256–264.
McPeek, M. A., and B. L. Peckarsky. 1998. Life histories and the strengths of species interactions: combining mortality, growth, and fecundity effects. Ecology **79**:867–879.
Newman, R. A. 1989. Developmental plasticity of *Scaphiopus couchii* tadpoles in an unpredictable environment. Ecology **70**:1775–1787.
Palmer, M. A., and N. L. Poff. 1997. The influence of environmental heterogeneity on patterns and processes in streams. Journal of the North American Benthological Society **16**:169–173.
Peacor, S. D., and E. E. Werner. 1997. Trait-mediated indirect interactions in a simple aquatic food web. Ecology **78**: 1146–1156.
Peckarsky, B. L., S. D. Cooper, and A. R. McIntosh. 1997. Extrapolation from individual behavior to populations and communities in streams. Journal of the North American Benthological Society **16**:375–390.
Peckarsky, B. L., C. A. Cowan, M. A. Penton, and C. R. Anderson. 1993. Sublethal consequences of stream-dwelling predatory stoneflies on mayfly growth and fecundity. Ecology **74**:1836–1846.
Peckarsky, B. L., and A. R. McIntosh. 1998. Fitness and community consequences of avoiding multiple predators. Oecologia **113**:565–576.
Peckarsky, B. L., B. W. Taylor, and C. C. Caudill. 2000. Hydrologic and behavioral constraints on oviposition of stream insects: implications for dispersal. Oecologia **125**: 186–200.
Peckarsky, B. L., B. W. Taylor, A. R. McIntosh, M. A. McPeek, and D. A. Lytle. 2001. Variation in mayfly size at metamorphosis as a developmental response to risk of predation. Ecology **82**:740–757.
Petersen, J. E., J. C. Cornwell, and W. M. Kemp. 1999. Implicit scaling in the design of experimental aquatic ecosystems. Oikos **85**:3–18.
Power, M. E., W. E. Dietrich, and K. O. Sullivan. 1998. Experimentation, observation, and inference in river and watershed investigations. Pages 113–132 *in* W. J. Resetarits, Jr. and J. Bernardo, editors. Experimental ecology. Issues and perspectives. Oxford University Press, New York, New York, USA.
Reznick, D. N., H. Bryga, and J. A. Endler. 1990. Experimentally induced life-history evolution in a natural population. Nature **346**:357–359.
Rowe, L., and D. Ludwig. 1991. Size and timing of metamorphosis in complex life cycles: time constraints and variation. Ecology **72**:413–427.
Sarnelle, O. 1997. *Daphnia* effects on microzooplankton: comparisons of enclosure and whole-lake responses. Ecology **78**:913–928.
SAS. 1989. STAT user's guide, version 6. Fourth edition. Volumes 1 and 2. SAS Institute, Cary, Carolina, USA.
Schindler, D. E., J. F. Kitchell, X. He, S. R. Carpenter, J. R. Hodgson, and K. L. Cottingham. 1993. Food web structure and phosphorus cycling in lakes. Transactions of the American Fisheries Society **122**:756–772.
Schmidt, S. K., J. M. Hughes, and S. E. Bunn. 1995. Gene flow among conspecific populations of *Baetis* sp. (Ephemeroptera): adult flight and larval drift. Journal of the North American Benthological Society **14**:147–157.
Searle, S. R. 1987. Linear models for unbalanced data. Wiley, New York, New York, USA.
Sweeney, B. W., D. H. Funk, and R. L. Vannote. 1986. Population genetic structure of two mayflies (*Ephemerella subvaria, Eurylophella verisimilis*) in the Delaware River drainage basin. Journal of the North American Benthological Society **5**:253–262.
Taylor, B. W., A. R. McIntosh, and B. L. Peckarsky. 2001. Sampling stream invertebrates using electroshocking techniques: implications for basic and applied research. Canadian Journal of Fisheries and Aquatic Sciences **58**:1–9.
Thrush, S. F., J. E. Hewitt, V. J. Cummings, M. O. Green, G. A. Funnell, and M. R. Wilkinson. 2000. The generality of field experiments: interactions between local and broad-scale processes. Ecology **81**:399–415.
Tollrian, R., and C. D. Harvell. 1999. The ecology and evolution of inducible defenses. Princeton University Press, Princeton, New Jersey, USA.
Von Elert, E., and C. J. Loose. 1996. Predator-induced diel vertical migration in *Daphnia*: enrichment and preliminary chemical characterization of a kairomone exuded by fish. Journal of Chemical Ecology **22**:885–895.
Wallace, J. B., S. L. Eggert, J. L. Meyer, and J. R. Webster. 1999. Effects of resource limitation on a detrital-based ecosystem. Ecological Monographs **69**:409–442.
Werner, E. E. 1991. Nonlethal effects of a predator on competitive interactions between two anuran larvae. Ecology **72**:1709–1720.
Werner, E. E., and B. A. Anholt. 1996. Predator-induced behavioral indirect effects: consequences to competitive interactions in anuran larvae. Ecology **77**:157–169.
Wilbur, H. M., and J. P. Collins. 1973. Ecological aspects of amphibian metamorphosis. Science **182**:1305–1314.
Wilbur, H. M., and J. E. Fauth. 1990. Food webs with two predators and two prey: an experimental field study. American Naturalist **135**:176–204.