

9 *Understanding the Role of Predation in Open Systems*

THE VALUE OF PLACE-BASED RESEARCH

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Figure 9.0. (a) Experimental mesocosms on a slope above the East River. Mesocosms are being supplied with stream water that is circulated through a trout-occupied bin. (b) Experimental augmentation of trout odor in a natural trout stream with water from trout-occupied bins. Photographs by Angus R. McIntosh, 1995 (a) and 1996 (b).



Abstract

Studies of predation traditionally focus on how predators influence prey communities and prey population oscillations via mortality. Studies carried out for nearly 40 years in one place have enabled us to evaluate the generality of this focus. Early observations in one high-altitude, rocky-bottom stream in western Colorado fit the traditional model of negative correlation between predator and prey abundance, suggesting that predation by

salmonid fishes may explain spatial variation in the abundance of stream insects. In contrast, a large-scale experiment showed that predation did not explain variation in abundance of primary consumers (mayflies) or large insect predators (stoneflies). We describe a series of studies conducted in more streams over many years that forced traditional thinking to give way to a new appreciation for predator-induced changes in prey behavior and life history. Our research used a “follow your nose” approach, which allowed the place to motivate the questions and resulted in the evolution of a conceptual model to explain how the place works. Natural history observations, combined with many years of phenomenological and mechanistic experiments, have contributed to the following generalizations about the importance of nonconsumptive effects of predators. First, mechanisms of trophic cascades may be predominantly nonconsumptive. Second, the effects of predation may be obscured or exaggerated by prey immigration or emigration. Third, if top and intermediate predators have opposite effects on emigration of shared prey, counterintuitive patterns of prey abundance may result when both kinds of predators are present. Finally, predator-induced changes in prey behavior and development can reduce prey fecundity, which may affect rates of prey population growth more than predator-induced mortality. Thus, intuition gained from studying one set of organisms in one place supports a general conceptual model according to which in open systems with high levels of prey dispersal, the predominant influence of predators may be nonconsumptive.

Introduction

The science of ecology, generally defined as the study of factors influencing the distribution and abundance of organisms, involves a variety of approaches (e.g., Dodson et al. 1998), including intuition from natural history (Power 1998). Natural history has been integral to our own approach, motivating our questions and hypotheses, informing the interpretation of experiments, and enabling our understanding of a complex system to evolve. In this chapter we describe how implementing our approach in one place gradually revealed a lack of fit to the traditional model in which predators affect prey population dynamics via mortality. Continuously fueled by new findings, new conceptual models have thus evolved which emphasize the importance of nonconsumptive effects of predators that induce risk-sensitive behavioral and life-history responses of prey. We further recognized that a key feature of our system is the mobility of organisms: streams are open systems (Reiners and Driese 2001) characterized by high levels of dispersal. Under those conditions prey mobility can swamp direct effects of predation (Allan 1982a, Allan 1983, Cooper et al. 1990, Englund 1997), resulting in pat-

terns of predator and prey abundance that are inconsistent with traditional models of predator-prey dynamics.

Look Up, Look Down, Look All Around! Features of Our Place-Based Approach

Studying ecology in one place for a long time should not be equated with an overly narrow perspective or increasingly mechanistic approach, although those can be consequences. On the contrary, loyalty to one place has enabled us to develop a more comprehensive understanding of the system by extending our scope to larger spatial and temporal scales. Long-term observations over larger spatial scales have made it possible to identify unusual events (e.g., high-water years), generalize over generations of predators and prey, and incorporate spatial heterogeneity into our models. Our story thereby underscores the well-documented value of conducting long-term research (e.g., Strayer et al. 1986; Likens 1989; Magnuson 1990; Estes et al. 1998; Grant and Grant, chapter 6; Armitage, chapter 7; Estes, chapter 8).

Furthermore, our place-based research has fostered a team approach by attracting collaborators, graduate students, and undergraduate students. Those collaborators have contributed different perspectives and approaches, creating a multidisciplinary effort and diversifying the intellectual climate. To reap this benefit, pioneers of place-based research need to welcome new people to their places, not be overly possessive of ideas, embrace alternatives, and be willing to be wrong. Many other scholars have come to our place over the years attracted by the accumulated knowledge, and those people have enriched our story.

Our “place” includes high-altitude, rocky-bottom streams in western Colorado, near the Rocky Mountain Biological Laboratory (RMBL) and town of Mt. Crested Butte (figure 9.1). The smallest streams in this system arise from snowmelt, springs, or lake outlets. The confluence of small tributaries forms larger streams, many of which contain predatory fish that are excluded from some streams by waterfalls that prevent upstream dispersal. The structure of these drainage basins provides opportunities for studying replicate streams of varying size. Replication at small scale and in whole streams has strengthened our conclusions.

Our story follows a sequence of studies that implements a “follow your nose” approach and allows the place to motivate the research. We provide examples of patterns of distribution and abundance of organisms that were sometimes intuitive and sometimes not. We describe how our understanding of the mechanisms explaining those patterns evolved as we explored them at different temporal and spatial scales, diversified our approaches, and integrated across levels of organization. We present our work in the

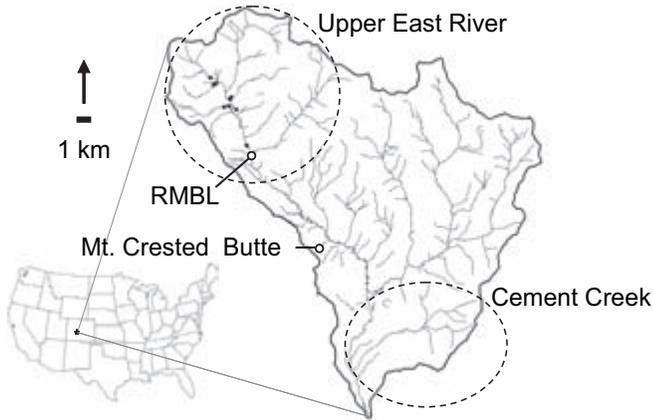


Figure 9.1. Map of the East River Drainage Basin—“the place”—indicating the Upper East River and Cement Creek sub-basins (circled) and specific sites (dots) in which we worked.

context of four generalizations that represent the current status (“the invisible present,” Magnuson 1990) of our conceptual model, along with the progression of evidence for the importance of nonconsumptive effects of predators. We describe the chronology of observations and experiments that produced each generalization, and suggest where continued research in this place should reduce uncertainties.

Four Generalizations

Generalization 1: Mechanisms of trophic cascades may be predominantly nonconsumptive

The food webs of our study system have four trophic levels: top predators (e.g., brook trout, *Salvelinus fontinalis*), predatory insects (e.g., stoneflies, Plecoptera), grazing insects (e.g., mayflies, Ephemeroptera), and attached algae (periphyton). Our first observational study (Allan 1975) compared the distribution and abundance of intermediate consumers along an elevation gradient of one stream, Cement Creek (figure 9.1). This study showed that trout-free headwaters had densities of stream insects several times higher than those of downstream reaches containing trout, suggesting that predation by salmonid fishes could explain spatial variation in the abundance of stream invertebrates. Those observations were broadly consistent with the traditional idea of top-down control by predators (Allen 1951; Allan 1981, 1983).

To test the hypotheses that were generated by our original observations, one of us subsequently implemented a challenging, large-scale field experi-

ment in Cement Creek over multiple years within the context of natural environmental variability. As an early indication of things to come, results of that experiment cast doubt on the traditional view. Experimental reduction of trout density in a 1.2 km reach of Cement Creek had no consistent effects on the abundance of primary consumers (primarily mayflies) or predatory stoneflies (Allan 1982a). Those results were unexpected, and they provided the first clue that a model of top-down control of prey abundance needed further scrutiny. Two hypotheses, highly speculative at the time, were that prey antipredator adaptations minimized predator effectiveness on intermediate consumers (the stoneflies), and that the continual renewal of mayfly prey due to downstream transport (by drift) obscured the effects of predation.

The inconsistency between that experiment and previous observations illustrates that underlying ecological processes may not be clearly detected by simply observing complex and dynamic ecological systems (Peckarsky et al. 1997). In those cases phenomenological experiments (mechanism-free experiments in which the system is modified to see what happens; Dunham and Beaupre 1998) may reveal cryptic processes that are obscured by other processes acting concurrently. We have repeatedly used phenomenological experiments as an effective means of generating explanatory hypotheses (Peckarsky 1998), despite initial obstacles.¹

To more fully develop the new conceptual model suggested by studies in Cement Creek, we subsequently expanded the spatial and temporal scales of observations to include multiple years and streams within the Upper East River drainage basin (figure 9.1). Those observations showed that large predatory stoneflies achieved high densities in some trout streams and were rare in some fishless streams (Peckarsky et al. 2001). We thus realized that the abundance patterns of stoneflies observed in Cement Creek could not be generalized to fish and fishless sections of other streams in the region (Peckarsky et al. 2008), and that predatory stonefly abundance is more likely controlled by physical variables related to bed disturbance (Peckarsky 1991) than by fish predation.

Although the results of both the fish density manipulation and the expansion of the scale of observations were consistent with the hypothesis that consumption by trout did not explain variation in the distribution and abundance of stream insects, neither approach provided a direct test of causation. Therefore, we implemented mechanistic experiments to explain and interpret results from phenomenological studies and fine-tune our new conceptual framework. In one type of experiment we estimated consumption rates by predators to test whether predation could explain abundance of prey or natural loss rates of prey in streams (Kerans et al. 1995, Peckarsky et al. 2008). The second type of experiment measured effects of predators on prey behavior as a test of the hypothesis that trophic cascades in these

streams were driven primarily by nonconsumptive mechanisms (Peckarsky and McIntosh 1998). Experiments were carried out in mesocosms (0.8 m²; see figure 9.0, top) using natural stream water. By preventing or allowing predators to consume prey, we could compare the behavioral and consumptive effects of predators on lower trophic levels.

In predation experiments, trout consumption of predatory stoneflies was negligible, consistent with the observed independence of stonefly abundance from the presence of fish (Peckarsky et al. 2008). However, both trout and stoneflies caused significant mayfly mortality in mesocosms, with trout consuming an order of magnitude more mayflies per predator than stoneflies (McPeck and Peckarsky 1998, Peckarsky et al. 2008). Note that estimates of annual prey consumption under natural conditions (three sites in Cement Creek) suggested that mayfly consumption by trout was roughly twice that of stoneflies in natural streams (Allan 1982b). Most interestingly, in predation experiments the effect of both predators foraging together was not additive: trout reduced the effects of stonefly predation in treatments with both predators (Peckarsky et al. 2008). Those results suggested a new hypothesis: Trout do not reduce stonefly abundance but instead modify stonefly foraging behavior, thereby reducing the impact of stoneflies on mayfly prey (a behavioral trophic cascade).

Observations in mesocosms showed that chemical cues from trout suppressed the movement behavior of stoneflies foraging on mayflies (McIntosh and Peckarsky 1999), which also cascaded to decrease the biomass of algae, the basal resource (Peckarsky and McIntosh 1998). Furthermore, stonefly predation rates on mayflies were negligible in the presence of fish (Kerans et al. 1995), but could be high enough to account for natural losses of the mayfly *Baetis bicaudatus* in streams without fish (Peckarsky et al. 2008). Results of both predation and behavioral experiments thus suggested that a traditional trophic cascade in which top predators reduce the density of intermediate predators by consumption, thereby releasing their prey from predation, was not operating.

Persistent inquiry in one place and experimental innovation reinforced a new conceptual model, indicating that we had to focus more on behavioral than on consumptive mechanisms. Furthermore, the combined effects of trout and stoneflies on mayfly mortality could not have been predicted from traditional models of predator-prey interactions, or from the individual effects of each predator. In this case, the top predator reduced predation rates of intermediate predators without affecting their densities. Interactions between the two types of predators reduced the rate of consumption of mayflies by the intermediate predator, even though trout predation on stoneflies was negligible.

Although those ideas were initially met with resistance, our commitment

to place prevented us from abandoning them. We conclude that behavioral interactions among multiple predators and shared prey may counteract or override the effects of consumption by predators in open systems where predators and prey are highly mobile. Future studies should compare estimates of predator impacts on prey mortality to predator impacts on prey emigration using a common currency, such as a standardized index of prey loss rate (e.g., Cooper et al. 1990). Such an approach will be challenging, but should allow effect sizes obtained in experiments to be used to explain patterns of abundance of multiple predators and shared prey in natural systems.

Generalization 2: Effects of predation may be obscured or exaggerated by prey immigration or emigration

The unexpected lack of a response of mayfly abundance to the large-scale trout reduction experiment in Cement Creek (Allan 1982a) forecast the surprising patterns obtained when we observed more streams in the upper East River drainage basin (Peckarsky et al. 2001). There we observed that drifting mayflies, the most important prey species for trout (Allan 1978a, 1981) were actually more abundant in trout streams than in fishless streams. Replication (rather than scale) of observations over space and time contributed most strongly to our ability to generalize, and further underscored the necessity for modifying existing models about the role of predators.

Mechanistic experiments carried out in semipermeable field enclosures supported Allan's (1982a) hypothesis that immigration of highly mobile prey swamped the effects of predation. Prey density was reduced in enclosures with stoneflies only when prey migration was not permitted (Peckarsky 1985, Cooper et al. 1990). This pioneering experimental approach demonstrated that prey behavior needed to be taken into account when measuring the effects of predators. Initial resistance to our unorthodox experimental methods has dissipated, because subsequent experiments have so clearly demonstrated that both trout and stoneflies can have profound effects on the behavior of their mayfly prey, particularly by affecting their emigration rates (drift in the water column).

Early studies in Cement Creek documented that large numbers of drifting invertebrates enter the water column during a 24-hour period (Allan 1982a), providing an important food source for trout, which feed on invertebrates from the drift more than from the benthos (stream bottom). Only a fraction of this potential resource is available to trout, however, because only a small percentage of total drift occurs during daylight hours (roughly 10 to 20% based on data in Allan 1978b). Moreover, drift-feeding trout are size-selective, and day-drifting individuals are mainly small taxa or instars (juvenile stages) that are less visible to these visual predators.

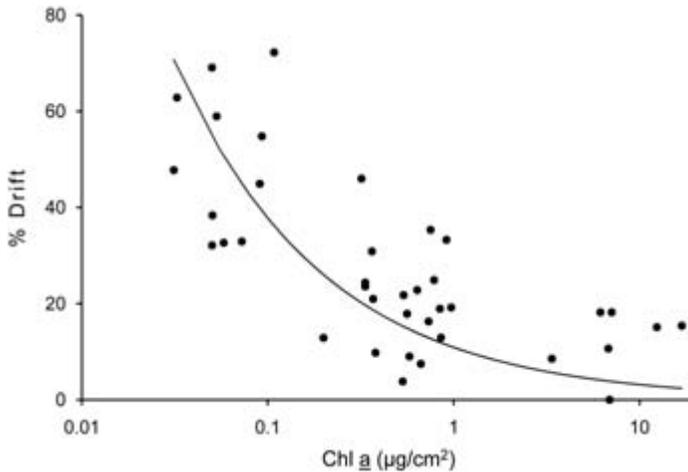


Figure 9.2. The percentage of *Baetis* individuals entering the drift in laboratory streams from stones containing different algal densities, measured as micrograms of chlorophyll a per square cm. Treatments were established during midday, and individuals did not drift until dusk, six to eight hours later. At very low food levels, more than half of all individuals drifted immediately after dusk, whereas few drifted from stones with abundant algae (J. D. Allan, unpublished data).

Unlike the first generalization, in which early observations in one stream were not representative, replicating observations of mayfly drift has yielded consistent results; natural patterns from many fish and fishless streams have shown clearly that mayfly drift is nocturnal in trout streams (Allan 1978b, Allan et al. 1986, Allan 1987, McIntosh et al. 1999), and aperiodic in fishless streams (McIntosh et al. 2002). Those observations might possibly be explained by (1) daytime consumption of drifting mayflies by trout, (2) induction of nocturnal foraging behavior of mayflies by trout (phenotypic plasticity), or (3) evolved responses (Flecker 1992).

Early mechanistic experiments in a laboratory stream were consistent with the third hypothesis, in that a highly mobile grazing mayfly common in the diets of trout (*Baetis*) delayed drifting until nightfall, but showed higher probabilities of emigrating from substrates with low algal biomass (figure 9.2). This response initially suggested hard-wired behaviors including avoidance of daytime foraging, saltatory search behavior during darkness, and more active foraging in response to food shortages. However, both the experimental water and the mayflies were obtained from streams with fish, and thus did not test for induced responses.

Subsequent mechanistic experiments carried out in microcosms (150 cm²) supported the second hypothesis—that *Baetis* activity is sensitive to the presence of trout—because *Baetis* in treatments using water from trout

streams showed nocturnal behavior, while individuals in fishless water were more aperiodic (Cowan and Peckarsky 1994). Similarly, experimental introduction of trout odor into stream-side mesocosms (figure 9.0, top) has consistently induced nocturnal drift periodicity and decreased the magnitude of nighttime drift for late-instar *Baetis* obtained from both fish and fishless streams (McIntosh and Peckarsky 1996, 1999; Peckarsky and McIntosh 1998). Furthermore, a phenomenological experiment introducing trout odor into naturally fishless streams caused mayflies to become nocturnal (McIntosh et al. 2004). Interestingly, the addition of high concentrations of trout odor into a natural trout stream (figure 9.0, bottom) reduced nighttime drift of large *Baetis*, but increased nocturnal drift of small *Baetis* larvae (McIntosh et al. 1999). In contrast, there were no effects of added trout odor on daytime drift of *Baetis*, which was low in all treatments in this trout stream.

Taken together, the results of our field and smaller-scale experiments demonstrated that responses of mayflies to trout chemical cues can be induced, and are prey size- and prey species-specific, both of which are potentially related to prey vulnerability. Allan (1978b) has shown that brook trout prefer large over small *Baetis* and consume markedly more *Baetis* than less mobile prey (e.g., *Cinygmula*, *Epeorus*; Allan 1981). Relative drift densities (scaled by benthic densities) of the mayfly prey species most common in trout diets (*Baetis*) are much higher than those of mayflies less common in trout diets (e.g., *Cinygmula*; Allan 1978a, 1983; Allan et al. 1986; Allan 1987) or stonefly diets (Allan 1982b, Peckarsky, 1985, Peckarsky et al. 1994) in both fish and fishless streams (McIntosh et al. 2002).

Highest drift rates for the most vulnerable mayfly species seemed counterintuitive at first, because we expected more risk-sensitive behavior from more vulnerable prey. However, high mobility of *Baetis* may be critical to its ecological dominance in many systems, providing benefits in both foraging and dispersal but exacting a cost in exposure to predation (Peckarsky 1996). Indeed, drift, which is a saltatory food search behavior, is most nocturnal in the size classes that are most vulnerable to trout predation (Allan 1978b, McIntosh et al. 2002). Likewise, mechanistic experiments in microcosms demonstrated that the magnitude of the response of mayflies to trout chemical cues (nocturnal drift) was greater for species with greater risk of predation (McIntosh et al. 2002). Furthermore, the activity of the most vulnerable prey species was most nocturnal when they were subjected to cues from the most effective predators (native cutthroat, *Oncorhynchus clarki*, versus non-native brook trout) (McIntosh and Peckarsky 2004).

In summary, the effects of predation in streams may not be detected by observing prey abundance because immigration of prey can counteract predation rates. Testing this hypothesis required us to present a cue indicating risk of predation while preventing actual consumption, which we did by

introducing “essence of brook trout” into experimental units as small as microcosms and as large as natural streams. This approach provided further support for the conceptual model that in open systems predator effects on prey behavior rather than on prey mortality may better explain the distribution and abundance of highly mobile organisms.

Generalization 3: If top and intermediate predators have opposite effects on emigration of shared prey, then counterintuitive patterns of prey abundance may result when both predators are present

Insights from studies of trout effects on stonefly and mayfly behavior suggested that the effectiveness of predatory stoneflies could also be altered by changes in the behavior of shared prey (mayflies) in the presence of trout. We have observed that while trout cause mayflies to decrease nocturnal drift rates, foraging stoneflies can cause mayflies to increase their nighttime drift in microcosms (Peckarsky 1996, McIntosh et al. 2002) and mesocosms (McIntosh and Peckarsky 1998, McIntosh and Peckarsky 1999) because they drift in response to encounters with stoneflies (Peckarsky 1980). While this behavior could increase mayfly susceptibility to drift-feeding trout, we have observed no evidence that the presence of stoneflies facilitates trout predation (Peckarsky et al. 2008), probably because stonefly-induced *Baetis* drift occurred primarily in the absence of trout and at night (Peckarsky and McIntosh 1998, McIntosh and Peckarsky 1999) when trout could not feed as effectively (McIntosh et al. 2002).

In our first mesocosm experiments we were able to induce the natural periodicity of *Baetis* drift and foraging only when we included stoneflies in both fish and fishless treatments (McIntosh and Peckarsky 1996). Although this interesting bit of natural history was not included in the published version of the study, it indicated that natural diel periodicity of these mayflies is a function of their responses to both predators: high nocturnal drift rates in the absence of fish are stimulated by foraging stoneflies, and low nocturnal drift rates in the presence of fish reflect both threat-sensitive behavior of mayflies and suppressed foraging by stoneflies.

Observations of behavioral responses of mayflies also stimulated our thinking about how nonconsumptive interactions between predators and prey might affect natural patterns of distribution and abundance (figure 9.3). For example, high rates of stonefly-induced mayfly drift (emigration) in fishless streams could reduce their natural abundance compared to that in streams with fish. In contrast, trout reduce mayfly drift (emigration), suppress stonefly consumption of mayflies, and decrease the effects of stoneflies on mayfly drift, all of which could increase mayfly abundance in fish streams.

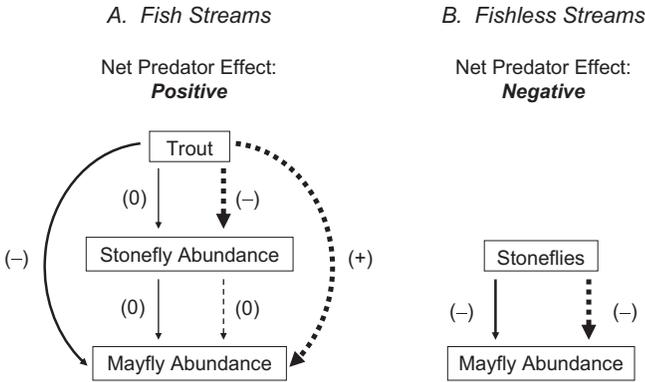
Net predator effect:

Figure 9.3. Conceptual model of consumptive (solid arrows) and behavioral (dashed arrows) effects of trout on stonefly and mayfly abundance, and of stoneflies on mayfly abundance. Thickness of arrows indicates hypothesized relative effect sizes, and (+), (-), or (o) respectively indicate positive, negative, or negligible effect on prey. (a) In fish streams, trout do not affect stonefly abundance via consumption (thin solid line), but do reduce their foraging activity (thick dashed line). Stoneflies have negligible consumptive (thin solid line) and behavioral effects (thin dashed line) on mayfly abundance. Consumption by trout decreases the abundance of mayflies (solid line), but trout suppress mayfly emigration (drift) and thereby increase their abundance (thick dashed line). Thus, the net effect of predators on mayfly abundance may be positive, depending on the magnitude of consumptive losses relative to positive direct and indirect behavioral effects. (b) In fishless streams, stoneflies are the top predator. Their consumption decreases mayfly abundance (solid line), and their foraging activity increases prey drift or emigration (dashed line). Both consumptive and nonconsumptive effects act in the same direction, resulting in a net negative effect of stoneflies on mayfly abundance.

In streams with both predators, positive behavioral effects may override the negative effects of consumption, providing a plausible mechanism to explain why mayfly abundance is higher in streams with fish than in fishless streams (Peckarsky et al. 2001, Peckarsky et al. 2008). Also, if the direct effect of trout on mayfly drift overrides stonefly-induced drift, trout streams will retain mayflies (Diehl et al. 2000). Consequently, the complex effects of interacting predators may obscure associations between stonefly densities and *Baetis* abundance in natural trout streams (Peckarsky 1991).

Tests of hypotheses involving the interactive consumptive and nonconsumptive effects of predators on prey abundance constitute a work in progress. Extrapolating drift densities observed in the field over 24 hours (from McIntosh et al. 2002) suggests that trout streams may be “sticky” (retaining individuals) and fishless streams may be “leaky” (losing individuals) because the foraging movements of mayflies are not constrained by any risk of

fish predation in fishless streams. However, preliminary studies measuring *Baetis* drift into and out of 45-m reaches of 12 different streams (Wilcox et al. 2008) suggest a more complex answer. While benthic density increased directly with the ratio of drift in to drift out (indicating “stickiness”) in fish streams, *Baetis* density was independent of this ratio in fishless stream reaches, suggesting that net migration could explain abundance patterns in streams with fish but not in fishless streams. Furthermore, fishless streams were not categorically more “leaky” than fish streams—that is, they did not have lower ratios of drift-in to drift-out.

In summary, although top and intermediate predators have opposite effects on emigration of shared prey, predator-induced prey emigration does not explain the counterintuitive patterns of prey abundance we observed (higher prey densities in fish streams). Even getting to this point was an extraordinary effort involving many intrepid field assistants and more all-nighters than occur in a college dormitory during final exams. And still we have no definitive answer. Nonetheless, we are convinced that we will eventually sort out the alternative hypotheses needed to understand the influence of predator-induced changes in prey movement on the distribution and abundance of mayflies relative to the effects of other factors.

Generalization 4: Predator-induced changes in prey behavior and development can reduce prey fecundity, which may have greater impact on rates of prey population growth than predator-induced mortality

In our earlier work we used observations and mechanistic experiments in microcosms to investigate the nonconsumptive effects of stoneflies on mayfly behavior, morphology, and life histories (Peckarsky et al. 1993, Peckarsky et al. 1994, Peckarsky 1996). We observed that interspecific trade-offs between prey mobility and the extent of morphological defense lead to a variety of prey antipredator strategies arranged along an axis of prey mobility. The most vulnerable mayfly species (*Baetis*) showed reduced feeding in the presence of stoneflies whose mouthparts were glued to prevent feeding (Peckarsky et al. 1993). Behavioral experiments further showed that the mechanism causing reduced *Baetis* feeding in the presence of stoneflies was energetically costly prey dispersal rather than microhabitat shifts (Peckarsky 1996). In longer-term experiments both male and female *Baetis* matured at smaller body sizes, and the fecundity of *Baetis* females was reduced in microcosms with glued stoneflies (Peckarsky et al. 1993). Smaller-bodied *Baetis* females produced fewer eggs; but we have found no disadvantage of small male body size in *Baetis* (Peckarsky et al. 2002a).

Peckarsky might have continued working only on stonefly-mayfly in-

teractions, thereby spinning into a mechanistic black hole, had it not been for inspiration from the perspectives of Allan, McIntosh, and Taylor to add more trophic levels and take a broader view of food webs in the East River system. Building on the classical work of Allan, we have now investigated the influence of salmonid fishes on prey population dynamics—revealing strong effects of brook trout on the behavior of their mayfly prey, especially the movement and foraging of *Baetis* on algal resources, and on the interactions of mayflies with predatory stoneflies (McIntosh and Peckarsky 1996, Peckarsky et al. 1997, McPeck and Peckarsky 1998, Peckarsky and McIntosh 1998, McIntosh and Peckarsky 1999, McIntosh et al. 1999, Dahl and Peckarsky 2002).

First, over multiple years and at multiple streams with and without fish in the upper East River drainage, we measured the size and fecundity of last-instar *Baetis* larvae, as well as other attributes (e.g., densities of predatory stoneflies, potential competitors, algal abundance, and stream physical-chemical characteristics) that could affect their growth or development rates. As a consequence of faster larval development times, the *Baetis* that emerge from trout streams are significantly smaller on average than those that develop in fishless streams (Peckarsky et al. 2001). Thus, *Baetis* reduce their exposure to mortality by emerging sooner from the risky larval environment, at the cost of reduced fecundity. A path analysis using structural equation modeling showed that size variation of *Baetis* that emerge from natural environments was best explained by predators (trout and stoneflies) rather than by variation in resources, resource-mediated competition, or other environmental variations such as temperature, stream size, or water chemistry (Peckarsky et al. 2001).

Field observations did not, however, rule out a consumptive mechanism for size differences in *Baetis* between streams with and without fish (e.g., size-selective predation). Therefore, we conducted mechanistic experiments in stream-side mesocosms to measure the impact of predator avoidance at medium spatial scales on the size and fecundity of *Baetis*. Trout odor and stoneflies (with mouthparts glued) reduced the size of male and female *Baetis* that emerged during the experiment, but only stoneflies delayed *Baetis* emergence, suggesting that stoneflies may have different nonconsumptive effects on *Baetis* life histories than do trout (Peckarsky and McIntosh 1998). We then increased the scale of our experiments, adding fish chemical cues to whole streams that were naturally fishless to test the influence of those cues on prey behavior, life history, and population dynamics as well as other community and ecosystem processes (Peckarsky et al. 2002b, McIntosh et al. 2004). Astoundingly, we were able to induce the development of smaller mayflies from 30-m reaches of fishless streams by introducing fish chemical

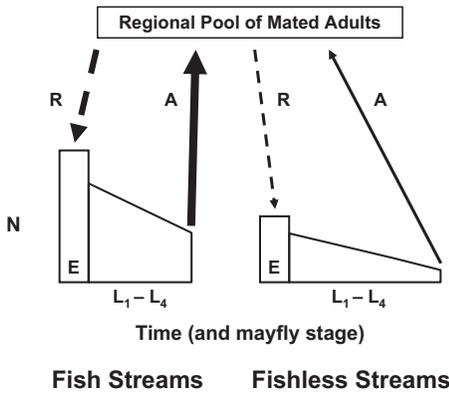


Figure 9.4. Demographic model of possible mechanisms for greater observed densities of *Baetis* in fish streams (left) than in fishless streams (right). Height of polygons indicates relative abundance (N) of eggs (E) and larval stages (L_1 to L_4). Eggs overwinter in diapause. Development from stages L_1 to L_4 is accelerated in fish streams; the relative time spent in each stage is unknown. Width of arrows indicates the relative number of eggs laid (dashed) or adults emerging (solid). More mayflies enter the regional pool of mated adults (A) from fish than fishless streams because they develop faster (shorter time from egg through larval developmental stages) and hence are exposed to risk for less time, despite having greater mortality rates. Therefore, demographic changes induced by cues from predatory fish increase the probability of survival in fish streams. Modified from Peckarsky et al. (2008).

cues, demonstrating definitively that observed variations in the life history attributes of *Baetis* in natural streams are indeed responses to predation risk, not to size-selective predation.

As a further test we compared the relative contributions of predator-induced mortality and predator-induced reduction of prey fecundity to the instantaneous rate of *Baetis* population growth. We estimated trout and stonefly predation rates on *Baetis* from mesocosm experiments (Kerans et al. 1995, McIntosh et al. 2002, Peckarsky et al. 2008), and effects of non-feeding predators on *Baetis* fecundity from microcosm and mesocosm experiments (Peckarsky et al. 1993, Peckarsky and McIntosh 1998). Integrating those approaches showed clearly that predation by trout and stoneflies contributed very little to reduction in rates of *Baetis* population growth compared to predator-induced reduction of fecundity (McPeck and Peckarsky 1998).

As “the invisible present” unfolds, we are in the process of modifying our conceptual model to incorporate recruitment as well as post-recruitment processes. Studies in collaboration with Andrea Encalada have demonstrated that regional-scale processes associated with variation in hydrology and geomorphology (independent of predation) can limit recruitment (oviposition) of *Baetis*, thereby having a major influence on their population dynamics (Encalada 2005). Thus, we have proposed a new demographic

model to explain the population dynamics of these mayflies (figure 9.4). To evaluate it, future research needs to focus on how recruitment (oviposition) interacts with post-recruitment processes such as trout and stonefly-induced changes in prey behavior, development, and mortality.

Discussion

The value of studying one place

Several key ingredients have contributed to the insights gained by our research group during nearly 40 years of studying one place. First, a long time-series of information on natural prey populations in one drainage basin has enabled us to establish a context for experimental evidence of the influence of predator-induced mortality on prey population dynamics. Second, our desire to understand and explain patterns observed in this system has necessitated the incorporation of processes spanning a wide range of levels of organization, from behavior of individuals to landscape configuration. Third, working in the same place has provided the circumstances for making discoveries. For example, detailed long-term knowledge of one system prepared us to recognize unusual or different patterns, such as the effects of unusually large snow pack and very high flow rates on prey population dynamics (Peckarsky et al. 2000). Fourth, focusing our studies in one place has also fostered the development of innovative methods, such as elaborate plumbing of micro- and mesocosms that use gravity and natural stream water, the presentation of predator cues while preventing prey consumption, whole-stream manipulation experiments (Allan 1982a, Peckarsky et al. 2002, McIntosh et al. 2004) and application of an electrofishing machine to sample invertebrates (Taylor et al. 2001, 2002). Finally, place-based research has fostered more persistence when we were faced with questions or approaches that led us astray or contradicted existing dogma.

Although we are tempted to argue that insights from place-based research can be extrapolated to other places (e.g., Flecker 1992), the validity of such extrapolation is debatable. Our data suggest that extensive prey dispersal in our open systems is what produces stronger nonconsumptive than consumptive predator effects. We have confirmed the logic of this speculation by collaborating with theoreticians to develop general models of the dynamics of prey populations in open systems (e.g., Abrams 2000, McPeck and Peckarsky 1998, Peckarsky et al. 2001). Nonetheless, we need to address whether more reliable generalizations can be made by thoroughly investigating one place than by comparing many systems.

Uncertainty regarding generalization to other systems raises a related question: What is the value of place-based research relative to that of a

comparative approach? Place-based research potentially leads to conclusions that may only be valid in one place, and may foster a particular way of thinking about ecology. At worst, long-term study at one site can potentially lead to false generalizations of how natural systems function or are structured on a more global scale. Frequently, more is learned when observations from one location do not agree with predictions derived from another. For example, the weak consumptive effects of trout observed in Rocky Mountain streams do not explain prey distribution and abundance in slower-moving streams with sessile grazers that are eaten by predatory invertebrates more susceptible to predatory fishes (Power 1990, Power et al. 1992). Furthermore, elaborate and innovative studies in another place have emphasized how predators can induce evolved life-history responses in guppies of Trinidad streams (e.g., Reznick et al. 1990) in contrast to our documentation of phenotypic plasticity. We have attempted to avoid potential place-based bias by involving new people in our research program who bring perspectives from other systems (e.g., streams in the Venezuelan piedmont, Sweden, Ecuador, Australia, New Zealand, and Spain), and by testing alternative hypotheses suggested by research on other systems (e.g., Peckarsky et al. 2004).

While it is indisputable that insights are gained from cumulative studies and weight of evidence, we contend that with many studies from many locations it is more tempting to explain away inconsistencies as simple idiosyncrasy. In contrast, place-based research embraces rather than denies the importance of contingency, thereby forcing us to resolve contradictions between observations and theory or across individual experiments and lines of evidence. Over time those resolutions have converged into a powerful body of evidence. In our combined work we have arrived at a number of conclusions that contrasted with initial expectations: that top-down numerical control was weak, which was explained partly by the open nature of the system with donor-controlled prey subsidies, and partly by a suite of risk-sensitive prey behaviors. We argue that this painstaking approach underscores the value of place-based research, and thereby maintain that our time-tested generalizations arising from Rocky Mountain streams are well worth testing in other systems.

Whether our place-based research on the ecology of streams has contributed to ecological theories outside the discipline warrants particular attention because stream ecology has been criticized by one of its most avid practitioners for not contributing to general theory (Fisher 1997). In fact, the lack of general laws in ecology has been a fundamental criticism of many ecologists (e.g., Peters 1991, Lawton 1999; see also Pulliam and Waser, chapter 4). That being said, we suggest that studies on prey exchange rates in

streams (Cooper et al. 1990), as well as larval and adult insect movement (Peckarsky et al. 2000, McIntosh et al. 2002) have been critical in shaping our understanding of other open systems (Speirs and Burney 2001, Anderson et al. 2005). Perhaps the most important contribution of our research is the realization that prey exchange rates and antipredator traits modulate consumptive effects of predators in open streams.

Long-term research without continuous monitoring

Another contentious issue related to place-based research is that of distinguishing its value from the well-established advantages of long-term environmental monitoring. Long-term studies are widely recognized as valuable (Strayer et al. 1986, Likens 1989, Cody and Smallwood 1996) and form an important component of the ecology of place because the sheer amount of information needed to understand complex ecological systems can only be accumulated over time. While many place-based research programs are built around continuous long-term monitoring, we argue that place-based research uses time to pursue a question, whereas long-term monitoring measures the effects of time on environmental parameters and interprets observed patterns with respect to historical measurements.

While our research on predator-prey interactions in Rocky Mountain streams has spanned almost four decades, our questions have evolved from the relationships among observations, experiments and ideas of many people rather than the continuous repeated sampling of organisms or processes by one or a few people that is more typical of long-term studies (e.g., Edmondson 1991). In our case, observations and experiments have continued to generate the fodder for future questions. Ironically, our approach has been viewed as an “intellectual weakness” which, according to a summary of a recent proposal funded by an National Science Foundation panel, is “an inductive boiling of hypotheses, with too little effort to place the work in a more general ecological context.” On the contrary, we believe that our long-term place-based research, an approach in which questions boil up out of the system, is not only intellectually sound but also has contributed significantly to general ecological understanding.

How we got here

What we have learned may be easier to articulate than how we got here. We think that insights arose partly from the place, and possibly even more from the community of people associated with the place. Clearly, our conceptual growth was motivated by natural history, repeating observations

in multiple streams, extracting system components and studying them in replicated arenas where interactions could be observed more directly. Nonetheless, we also attribute our progress to our open and sometimes heated discussions, which were very constructive in the evolution of new ideas and approaches. Ideas that initially seemed ridiculous or impossible (e.g., altering fish odor in whole streams) were tossed around until nonbelievers could be convinced rather than being quickly dismissed. Finally, many of our epiphanies came from being in the field—getting cold fingers pinched by heavy rocks, narrowly avoiding lightening strikes, and tolerating swarms of biting flies—where observations became new discoveries that would not have been possible by reading literature or solving equations. Thus, we got here by letting the place inform us of what was interesting and important, by sharing ideas, and by being open-minded and passionate about the work and the place.

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References

- Abrams, P. A. 2000. The impact of habitat selection on the spatial heterogeneity of resources in varying environments. *Ecology* 81:2902–13.

- Allan, J. D. The diversity and distributional ecology of benthic insects in Cement Creek, Colorado. *Ecology* 56:1040–53.
- . 1978a. Diet of brook trout (*Salvelinus fontinalis* Mitchell) and brown trout (*Salmo trutta* L.) in an alpine stream. *Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie* 20:2045–50.
- . 1978b. Trout predation and the size composition of stream drift. *Limnology and Oceanography* 23:1231–37.
- . 1981. Determinants of diet of brook trout (*Salvelinus fontinalis*) in a mountain stream. *Canadian Journal of Fisheries and Aquatic Sciences* 38:184–92.
- . 1982a. The effects of reduction in trout density on the invertebrate community of a mountain stream. *Ecology* 63:1444–55.
- . 1982b. Feeding habits and prey consumption of three predaceous stoneflies (Plecoptera) in a mountain stream. *Ecology* 63:26–34.
- . 1983. Food consumption by trout and stoneflies. Pages 371–390 in T.D. Fontaine III, and S. M. Bartell, eds. *Dynamics of Lotic Ecosystems*. Ann Arbor Science Publishers, Ann Arbor, Michigan.
- . 1987. Macroinvertebrate drift in a Rocky Mountain stream. *Hydrobiologia* 144:261–68.
- Allan, J. D., A. S. Flecker, and N. L. McClintock. 1986. Diel epibenthic activity of mayfly nymphs, and its non-concordance with behavioral drift. *Limnology and Oceanography* 31:1057–65.
- Allen, K. R. 1951. The Horokiwi Stream: A study of a trout population. *New Zealand Marine Department Fisheries Bulletin* 10.
- Anderson, K. E., R. M. Nisbet, S. Diehl, and S. D. Cooper. 2005. Scaling population responses to spatial environmental variability in advection-dominated systems. *Ecology Letters* 8:933–43.
- Brooks, J. L., and S. L. Dodson. 1965. Predation, body size, and composition of plankton. *Science* 150:28–35.
- Cody, M. L., and J. A. Smallwood. 1996. *Long-Term Studies of Vertebrate Communities*. Academic Press, New York.
- Cooper, S. D., S. J. Walde, and B. L. Peckarsky. 1990. Prey exchange rates and the impact of predators on prey populations in streams. *Ecology* 71:1503–14.
- Cowan, C. A., and B. L. Peckarsky. 1994. Diel feeding and positioning periodicity of a grazing mayfly in a trout stream and a fishless stream. *Canadian Journal of Fisheries and Aquatic Sciences* 51:450–59.
- Dahl, J., and B. L. Peckarsky. 2002. Induced morphological defenses in the wild: Predator effects on a mayfly, *Drunella coloradensis*. *Ecology* 83:1620–34.
- Diehl, S., S. D. Cooper, K. W. Kratz, R. M. Nisbet, S. K. Roll, S. W. Wiseman, and T. M. Jenkins Jr. 2000. Effects of multiple, predator-induced behaviors on short-term producer-grazer dynamics in open systems. *American Naturalist* 156:293–313.
- Dodson, S. I., T. F. H. Allen, S. R. Carpenter, A. R. Ives, R. L. Jeanne, J. F. Kitchell, N. E. Langston, and M.G. Turner. 1998. *Ecology*. Oxford University Press, New York.
- Dunham, A. E., and S. J. Beaupre. 1998. Ecological experiments: scale, phenomenology, mechanism, and the illusion of generality. Pages 27–49 in W. J. Reseratis Jr. and J. Bernardo, eds., *Experimental Ecology: Issues and Perspectives*. Oxford University Press, New York.
- Edmondson, W. T., ed. 1991. *The Uses of Ecology: Lake Washington and Beyond*. University of Washington Press, Seattle.
- Elton, C. S., and M. Nicholson. 1942. The ten-year cycle in numbers of the lynx in Canada. *Journal of Animal Ecology* 11: 215–44.

- Encalada, A. C. 2005. *Patterns and Mechanisms of Selective Oviposition of Baetis Bicaudatus (Ephemeroptera; Baetidae) and Its Consequences to Population Dynamics*. PhD dissertation, Cornell University, Ithaca, NY.
- Englund, G. 1997. Importance of spatial scale and prey movements in predator caging experiments. *Ecology* 78:2316–25.
- Estes, J. A., M. T. Tinker, T. M. Williams, and D. F. Doak. 1998. Killer whale predation on sea otters: Linking oceanic and nearshore processes. *Science* 282:473–76.
- Fisher, S. G. 1997. Creativity, idea generation, and the functional morphology of streams. *Journal of the North American Benthological Society* 16:305–18.
- Flecker, A. S. 1992. Fish predation and the evolution of invertebrate drift periodicity: Evidence from neotropical streams. *Ecology* 73:438–48.
- Kerans, B. L., B. L. Peckarsky, and C. R. Anderson. 1995. Estimates of mayfly mortality: Is stonefly predation a significant source? *Oikos* 74:315–23.
- Lawton, J. H. 1999. Are there general laws in ecology? *Oikos* 84:177–92.
- Likens, G. E. 1989. *Long-Term Studies in Ecology: Approaches and Alternatives*. Springer, New York.
- Magnuson, J. J. 1990. Long-term ecological research and the invisible present. *BioScience* 40:495–501.
- McIntosh, A. R., and B. L. Peckarsky. 1996. Differential behavioural responses of mayflies from streams with and without fish to trout odour. *Freshwater Biology* 35:141–48.
- . 1999. Criteria determining behavioural responses to multiple predators by a stream mayfly. *Oikos* 85:554–64.
- . 2004. Are mayfly anti-predator responses to fish odor proportional to risk? *Archiv für Hydrobiologie* 160:145–51.
- McIntosh, A. R., B. L. Peckarsky, and B. W. Taylor. 1999. Rapid size-specific changes in mayfly drift caused by alterations in fish odour. *Oecologia* 118:256–64.
- . 2002. The influence of predatory fish on mayfly drift: Extrapolating from experiments to nature. *Freshwater Biology* 47:1497–1513.
- . 2004. Predator-induced resource heterogeneity in a stream food web. *Ecology* 85:2279–90.
- McPeck, M. A., and B. L. Peckarsky. 1998. Life histories and the strengths of species interactions: Combining mortality, growth, and fecundity effects. *Ecology* 79:235–47.
- Mittelbach, G. G., A. M. Turner, D. J. Hall, J. E. Rettig, and C. W. Osenberg. 1995. Perturbation and resilience: A long-term whole-lake study of predator extinction and reintroduction. *Ecology* 76:2347–60.
- Paine, R. T. 1966. Foodweb complexity and species diversity. *American Naturalist* 100:65–75.
- Peckarsky, B. L. 1980. Predator-prey interactions between stoneflies and mayflies: Behavioral observations. *Ecology* 61:932–43.
- . 1985. Do predaceous stoneflies and siltation affect the structure of stream insect communities colonizing enclosures? *Canadian Journal of Zoology* 63:1519–30.
- . 1991. Habitat selection by stream-dwelling predatory stoneflies. *Canadian Journal of Fisheries and Aquatic Sciences* 48:1069–76.
- . 1996. Alternative predator avoidance syndromes in stream-dwelling mayflies. *Ecology* 77:1888–1905.
- . 1998. The dual role of experiments in complex and dynamic natural systems. Pages 311–423 in W. J. Resetaritis Jr. and J. Bernardo, eds., *Experimental Ecology: Issues and Perspectives*. Oxford University Press, New York.

- Peckarsky, B. L., C. A. Cowan, M. A. Penton, and C. Anderson. 1993. Sublethal consequences of stream-dwelling predatory stoneflies on mayfly growth and fecundity. *Ecology* 74:1836–46.
- Peckarsky, B. L., S. D. Cooper, and A. R. McIntosh. 1997. Extrapolating from individual behavior to populations and communities in streams. *Journal of the North American Benthological Society* 16:375–90.
- Peckarsky, B. L., C. A. Cowan, and C. Anderson. 1994. Consequences and plasticity of specialized predatory behavior of stream-dwelling stonefly larvae. *Ecology* 75:166–81.
- Peckarsky, B. L., J. M. Hughes, M. Hillyer, and A. C. Encalada. 2004. Are populations of mayflies living in adjacent fish and fishless streams genetically distinct? *Freshwater Biology* 50: 42–51.
- Peckarsky, B. L., B. L. Kerans, A. R. McIntosh, and B. W. Taylor. 2008. Predator effects on prey population dynamics in open systems. *Oecologia* 156:431–40.
- Peckarsky, B. L., and A. R. McIntosh. 1998. Fitness and community consequences of avoiding multiple predators. *Oecologia* 113:565–76.
- Peckarsky, B. L., A. R. McIntosh, C. C. Caudill, and J. Dahl. 2002a. Stabilizing selection on male body size of high altitude populations of *Baetis bicaudatus* (Ephemeroptera: Baetidae). *Behavioral Ecology and Sociobiology* 51:530–37.
- Peckarsky, B. L., A. R. McIntosh, B. W. Taylor and J. Dahl. 2002b. Predator chemicals induce changes in mayfly life history traits: A whole-stream manipulation. *Ecology* 83:612–18.
- Peckarsky, B. L., B. W. Taylor, and C. C. Caudill. 2000. Hydrologic and behavioral constraints on oviposition of stream insects: Implications for adult dispersal. *Oecologia* 125:186–200.
- Peckarsky, B. L., B. W. Taylor, A. R. McIntosh, M. A. McPeck, and D. A. Lytle. 2001. Variation in mayfly size at metamorphosis as a developmental response to risk of predation. *Ecology* 82:740–57.
- Peters, R. H. 1991. *A Critique for Ecology*. Cambridge University Press, Cambridge.
- Polis, G. A., and S. D. Hurd. 1996. Linking marine and terrestrial food webs: Allochthonous inputs from the ocean supports high secondary productivity on small islands and coastal land communities. *American Naturalist* 147:396–423.
- Power, M. E. 1990. Effects of fish in river food webs. *Science* 250:811–14.
- . 1998. Experimentation, observation, and inference in river and watershed investigations. Pages 113–32 in W. J. Resetarits, Jr. and J. Bernardo, eds., *Experimental Ecology: Issues and Perspectives*. Oxford University Press, New York.
- Power, M. E., J. C. Marks, and M. S. Parker. 1992. Variation in the vulnerability of prey to different predators: Community level consequences. *Ecology* 73:2218–23.
- Reiners, W. A., and K. L. Driese. 2001. The propagation of ecological influences through heterogeneous environmental space. *BioScience* 51:939–50.
- Reznick, D. N., H. Bryga, and J. A. Endler. 1990. Experimentally induced life-history evolution in a natural population. *Nature* 346:357–59.
- Roughgarden, J., S. D. Gaines, and S. Pacala. 1987. Supply side ecology: The role of physical transport processes. Pages 491–518 in P. Giller and J. Gee, eds., *Organization of Communities: Past and Present*. Blackwell Publishers, London.
- Speirs, D. C., and W. S. C. Gurney. 2001. Population persistence in rivers and estuaries. *Ecology* 82:1219–37.
- Stenseth, N. C., W. Falck, O. N. Bjørnstad, and C. J. Krebs. 1997. Population regulation in snowshoe hare and Canadian lynx: Asymmetric food web configurations between hare and lynx. *Proceedings of the National Academy of Sciences (USA)* 94:5147–52.
- Strayer, D., J. S. Glitzenstein, C. G. Jones, J. Kolasa, G. E. Likens, M. J. McDonnell, G. G. Parker, and S. T. A. Pickett. 1986. *Longterm Ecological Studies: An Illustrated Account of*

Their Design, Operation, and Importance to Ecology. Occasional Publication of the Institute of Ecosystem Studies, Millbrook, NY, no. 2, 38 pages.

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 Science* 58:1–9.

———. 2002. Large-scale invertebrate manipulations in stream ecosystems: Invertebrate removal, algal response, and opportunities for innovation. *Limnology and Oceanography* 47:893–99.

Wilcox, A. C, B. L. Peckarsky, B. W. Taylor, and A. C. Encalada. 2008. Hydraulic and geomorphic effects on mayfly drift in high-gradient streams at moderate discharges. *Ecohydrology* 1:176–86.

Note

1. Our approaches often met with resistance. For example, one anonymous reviewer of a proposal submitted by BLP to the National Science Foundation wrote: “At the outset, I confess that I’m not an enthusiastic believer in community organization studies involving manipulations (simplification) of community structure.”