MULTIPLE PREDATOR EFFECTS: PREDICTING COMBINED FUNCTIONAL RESPONSE OF STREAM FISH AND INVERTEBRATE PREDATORS[1]

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Abstract. The effects of different types of predators may combine in complex ways to impact prey populations. In a series of microcosm experiments I empirically derived the functional response curves for two common types of stream predators, sculpins (*Cottus bairdi*) and stonefly larvae (*Agnetina capitata*), on two behaviorally and morphologically distinct types of mayfly prey (*Baetis tricaudatus* and *Ephemerella subvaria*). Data from these separate trials were combined using simple additive models to generate predicted combined functional responses for both types of predator.

For both types of prey, actual combined functional response curves (both types of predators together in a treatment) differed significantly from predicted combined functional response for some ranges of prey densities. When *Baetis* was used as prey, significant departures from the predicted values occurred at moderate and high prey densities and were in a negative direction (interference between predators). When *Ephemerella* was the prey, significant departures occurred at low and moderate densities and were in a positive direction (facilitation between predators). Additive models for predicting combined predator effects cannot account for non-linearities in combined functional response introduced by non-trophic (behavioral) interactions that occur between fish and stoneflies, and between these predators and their prey. Other aquatic and terrestrial food webs contain similar linkages between vertebrate and invertebrate predators and their prey. Inclusion of behavioral interaction terms seems likely to be a necessary part of any general model predicting combined effects of predators on prey populations in these systems.

Key words: behavioral flexibility and predator effects models; behavioral indirect effects; benthic community structure; Ephemeroptera; facilitation; interference; non-additive interactions; Plecoptera; predator–prey interactions; prey density vs. predator interaction; sculpin; trophic web complexity.

INTRODUCTION

Very few organisms are the exclusive prey of only one type of predator. In natural communities, prey species usually face a number of potential predators that may use a variety of search and capture strategies. Despite this, studies of predator–prey interactions commonly evaluate the effect of one type of predator on prey abundance and behavior in isolation from the effects of other predators (e.g., Peckarsky and Dodson 1980, Allan 1982, Wilbur et al. 1983, Sih et al. 1985, Lima and Dill 1990). This approach is adequate as long as the effects of multiple predators on prey populations or communities can be viewed simply as an additive outcome of individual pairwise interactions between predators and prey. However, such a simple

relationship seems increasingly improbable given the potential non-linearities introduced by the indirect effects of predation and competition within natural communities (e.g., Neill 1974, Abrams 1983, 1987, Morin 1986, Yodzis 1988, Wilbur and Fauth 1990). A mechanistic understanding of how predation acts to structure communities and accurate predictions of the impact of predators on particular prey populations both require knowledge of how the effects of different predators combine to yield an overall effect on prey.

Despite the importance of understanding how predator effects combine to impact prey populations and communities, there are few experiments that directly assess combined predator effects on prey populations, and these few have yielded conflicting results. Van Buskirk (1988) reports experimental results from pond communities indicating that the predatory impacts of larvae of different odonate species are additive on populations of their anuran prey. Wilbur and Fauth (1990) report similar findings with respect to the combined effects of predatory newts and odonate larvae on anuran tadpoles. Alternatively, Soluk and Collins (1988*a*)

in freshwater stream communities, and Martin et al. (1989) in marine eel-grass communities, found that the combined effects of fish and invertebrate predators were not simply additive and that their combined impact on prey populations could be more, or less, than would be anticipated from what the predators did separately.

The contradictory conclusions of these experimental studies suggest that it may not be possible to develop simple generalizations about the way predator effects combine. However, one important shortcoming of these studies is that they were conducted at single initial prey densities. Perhaps measured additivity or non-additivity are not consistent features of interactions between the various types of predators, but rather are transitional outcomes determined by initial prey density. For example, interference between two predators will, by definition, lower their overall impact on prey populations, tending to make the combined effects of such predators non-additive. Increasing prey density, however, may lessen measurable interference between predators and allow combined predator effects to converge on an additive model.

Within stream communities the diets of small benthivorous fishes and invertebrate predators such as stoneflies overlap extensively, and thus the combined effects of these predators is a potentially important influence on prey distribution and abundance. Previous studies of the combined effects of fish and stonefly larvae on particular prey populations (Soluk and Collins 1988*a, b, c*) have indicated that the combined effects of these predators are non-additive, with predators either taking more or less of a particular mayfly prey than would be expected if their effects were additive. When allowed to prey upon *Ephemerella* larvae, sculpins and stoneflies together captured more prey than expected, and thus the net interaction between predators was positive (facilitation) for this prey type. However, when preying upon *Baetis* larvae fewer prey were taken, and the net interaction between predators was negative (interference). Risk of a mayfly being consumed is lowered by interference and increased by facilitation between predators.

The dependence of direction and magnitude of interactions among predators on prey type, as reported by Soluk and Collins (1988*a*) and Martin et al. (1989), does not necessarily confound our ability to predict the combined impact of predators on prey populations. Prey-specific variance in interactions between predators could be incorporated into models, as long as it is a predictable feature of interactions between particular types of predators when they are preying on particular types of prey. In this study, under conditions that simulate the natural heterogeneity of riffle environments in streams, I explored whether combined effects of fish and stonefly predators on particular prey are predictable over a range of prey densities, both in terms of simple additivity vs. nonadditivity, and in terms of direction of deviation from model predictions.

METHODS

Design of experiments

Four species (two predator and two prey species) collected from the east fork of the Credit River in southern Ontario, Canada, were used in this study. The predators were a small benthic fish (mottled sculpin, *Cottus bairdi*) and larvae of the perlid stonefly *Agnetina captitata*. The prey species were both mayfly larvae (Ephemeroptera); however, they differ in morphology and behavior, with *Ephemerella subvaria* being a slow-moving heavily cuticularized species and *Baetis tricaudatus* being a relatively thinly cuticularized species that usually flees predators by swimming rapidly into the water column (Peckarsky 1980, Williams 1987). This assemblage of species is generally representative of similar assemblages associated with riffle areas in small rivers and streams throughout the nearctic region.

Experiments were carried out in air-powered, recirculating stream tanks (see Soluk and Collins 1988*a*) with a mean current speed of 20 cm/s and a bottom area of 0.19 m². Substrate in each tank was 18 stones (5.3–11.0 cm in diameter) collected from the east fork of the Credit River, Ontario, Canada. After removal of all visible benthic invertebrates the stones (with intact periphyton) were arranged in a single layer covering most of the bottom of each tank. This arrangement of substrates simulated the top layer of stones in a riffle and provided a structurally and hydrodynamically heterogenous environment with food and potential refuges for prey and predators. Lighting was provided on a 12:12 L:D light cycle using full-spectrum fluorescent lighting.

Prey densities were set to values that span a range of abundances similar to those reported in studies of *Baetis* and *Ephemerella* spp. larvae in the holarctic region (e.g., Waters and Crawford 1973, Clifford 1979). Density limits were set recognizing that benthic organisms typically exhibit a clumped dispersion pattern and that most studies report benthic densities on large spatial scales (whole riffle or whole stream sections); thus they tend to underestimate prey and predator abundance within favorable habitat patches.

For each type of prey and each density (37, 75, 150, and 225 larvae/tank for *Ephemerella,* and 37, 75, 150, and 300 for *Baetis*) separate, replicated experiments compared the number of prey consumed in three different treatments. Data for 75 *Ephemerella* larvae/tank and for 150 *Baetis* larvae/tank were partially extracted from Soluk and Collins (1988*a*), but more replicates were added in each case. Expressed on an areal basis, prey densities in the separate experiments were 198, 396, 792, and 1188 larvae/m² for *E. subvaria* and 198, 396, 792, and 1584 larvae/m² for *B. tricaudatus.*

Experimental treatments run in separate tanks were: (1) stoneflies with prey, (2) fish with prey, and (3) fish and stoneflies with prey. For each succeeding replicate,
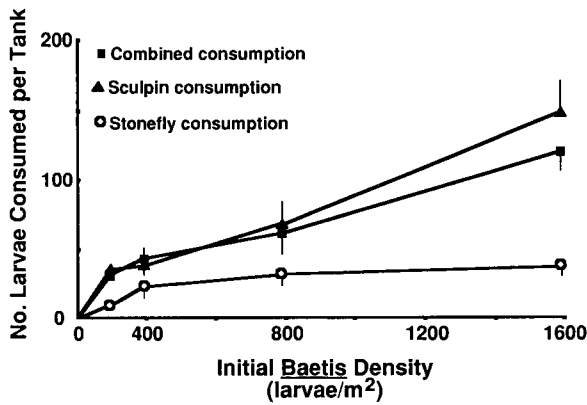
FIG. 1. Number of *Baetis tricaudatus* larvae (means ± 1 SE) consumed in separate simulated-stream laboratory trials by mottled sculpins, larvae of the stonefly *Agnetina*, and both of these predators together, as a function of initial *Baetis* density.

treatments were alternated among stream tanks. The total number of replicates varied among different densities and prey type. From lowest to highest densities the number of replicates were: 9, 9, 7, and 6 for *Ephemerella*, and 5, 6, 6, and 5 for *Baetis* trials. In all cases prey were introduced first and predators added 24 h later to minimize any effects of disturbance on prey susceptibility. Predators fed undisturbed for 24 h and then were removed. Stones were then removed from the tanks and all remaining prey (both living and intact dead larvae) were collected and counted. Controls (prey alone) were not run since error due to miscounts or failure to remove all individuals had been previously found to be insignificant (Soluk and Collins 1988*a*). Replicates in which the sculpin had consumed one or more stoneflies were rejected. To avoid any possible effects of selection or preconditioning, prey removed from treatments were not reused in subsequent trials.

For treatments using fish, one *Cottus bairdi* (73–90 mm total length) was selected at random from a holding tank and added to each stream tank. For treatments using stoneflies, 5 *Agnetina* larvae/stream (15–21 mm in body length) were added. Both predators were starved for a 24-h period before being introduced.

Predicting combined effects of predators

Consumption of prey as a function of initial prey density defines a functional response for a predator on a particular prey. When added together for either *Ephemerella* or *Baetis* separately, the values used to derive the functional response curves for sculpins and stoneflies provide an estimate of the combined impact of these predators on that particular prey. Consideration of the addition theorem of probability (see Mendenhall 1979) suggests two models with which separate effects of predators on prey populations can be combined to yield an expected combined consumption:

$$C_{\mathrm{fs}} = N_p(P_f + P_s) \qquad (1)$$

$$C_{\mathrm{fs}} = N_p(P_f + P_s - P_f P_s) \qquad (2)$$

where for both models, C_{fs} is predicted combined consumption for a particular initial prey density (N_p), and P_f and P_s are the probabilities of being consumed by sculpin or stoneflies, respectively, over a 24-h period of exposure. The primary difference between the models is that Eq. 1 assumes capture probabilities are independent (no effect of capture by one predator on probability of capture by the other predator) whereas Eq. 2 assumes finite populations and lack of independence in capture probabilities (capture of prey by either predator lowers capture probability by the other). Wilbur and Fauth (1990) discuss the relative merits of combining predator effects using models of this general type, which they refer to, respectively, as additive and multiplicative risk models. Model (Eq.) 2 (multiplicative model) has the advantage that predicted combined consumption (C_{fs}) cannot exceed total number of prey introduced (combined capture probability cannot exceed 1.0). In this experiment, comparison of actual consumption with either additive or multiplicative risk models yielded qualitatively similar results except at one density of *Baetis* (see *Results*); thus only comparisons with model (Eq.) 2 are presented below.

Because previous experiments (Soluk and Collins 1988*a*) gave an a priori expectation of positive interactions (facilitation) between predators when *Ephemerella* larvae were prey, and negative interactions (interference) when *Baetis* larvae were prey, one-tailed paired *t* tests (Zar 1984) based on these expectations were used for each prey type to evaluate whether actual combined consumption of predators deviated in a consistent manner from model predictions over the range of prey densities.

RESULTS

Consumption of *Baetis* by stoneflies as a function of *Baetis* larval density (Fig. 1) reached a maximum of ≈30–35 larvae per tank at prey densities >792 larvae/m² (150 larvae/tank). Functional response of sculpins on *Baetis* (Fig. 1) showed no such asymptote and increased throughout the range of prey densities used in the experiments.

Functional response of stoneflies on *Ephemerella* (Fig. 2) is linear, with no tendency toward an asymptote. At all prey densities stoneflies took a surprisingly consistent proportion (5–7%) of *Ephemerella* larvae. The number of *Ephemerella* larvae taken by sculpins, although higher than that taken by stoneflies, showed a very similar pattern over the range of *Ephemerella* densities used.

The predicted combined functional response of sculpins and stoneflies on *Baetis* showed a similar pattern to the actual combined functional response of these predators (Fig. 3), although actual values were consistently lower. The actual mean number of prey taken
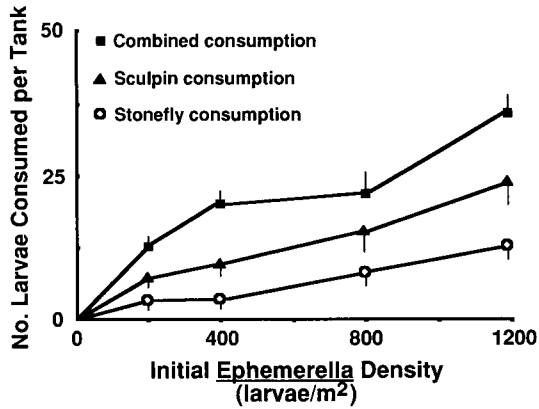
FIG. 2. Number of *Ephemerella subvaria* larvae (means ± 1 SE) consumed in separate simulated-stream laboratory trials by mottled sculpins, larvae of the stonefly *Agnetina,* and both of these predators together, as a function of initial *Ephemerella* density.

by both predators was not significantly lower than that predicted by Eq. 2 for the 198 *Baetis* larvae/m² density ($P = .192$); however, it was significantly lower than predicted by Eq. 1 ($P = .03$). The actual combined number of prey taken was significantly less than Eq. 2 predictions for all higher *Baetis* densities (for 396, 792, and 1584 larvae/m², $P = .046, .012,$ and $.025$, respectively). If highly conservative Bonferroni adjustments for simultaneous inferences (Rice 1989) are applied to these results (with concomitant loss of statistical power), then the actual mean consumption was significantly lower than expected at only the 792 prey/m² density.

The predicted combined functional response of sculpins and stoneflies on *Ephemerella* (Fig. 4) differed from actual combined response primarily in that actual number of prey consumed for the densities of 198 and 396 larvae/m² were significantly higher ($P = .0013$ and $.00004$, respectively). For higher densities, actual consumption was not significantly greater than predicted by the model ($P = .46$ and $.55$ for 792 and 1188 *Ephemerella* larvae/m², respectively). Sequential Bonferroni adjustments do not modify interpretation of these results.

Comparison of the proportional magnitudes of the interaction between sculpins and stoneflies when these predators are feeding on *Baetis* and *Ephemerella* (Fig. 5) indicate that not only does the sign of the interaction differ, but also the shape of the underlying function. Over the range of densities used in this experiment, interactions between sculpins and stoneflies were relatively linear when *Baetis* was the prey, but were dramatically non-linear when *Ephemerella* was the prey. The magnitude of the negative interaction between predators when *Baetis* was the prey appears to increase steadily with increasing prey density approaching 30% less than expected from model predictions.

DISUSSION

Additivity vs. non-additivity

Although assumptions about additive predator effects are not a necessary precondition for modelling multispecies predator–prey systems, the presence of additivity greatly simplifies the construction of predictive models (Van Buskirk 1988, Wilbur and Fauth 1990). This is primarily because simple additivity decreases the need for detailed a priori knowledge about all the interactions (both direct and indirect) that can occur between species in such a predator–prey system. This study provides little support for the hopeful view that simple additive models, using information derived from studies of pairwise trophic interactions, will generally describe the impact of multiple predators on prey populations.

Given the apparent inadequacy of simple additive models based on direct trophic linkages, it is important to consider what factors drive the combined impact of predators away from predicted values. Such factors could include both indirect trophic and non-trophic (behavioral) responses between predators, between prey and predators, and/or interactions among prey. The set of species used in my study is especially appropriate for such analysis since there are a number of previous studies of trophic and behavioral interactions among these species in particular (Soluk and Collins 1988*a, b, c,* Soluk 1990) and among fish, stoneflies, and mayfly larvae in general (e.g., Peckarsky 1980, Peckarsky and Dodson 1980, Williams 1986, Allan et al. 1987, Allan and Flecker 1988).

Interference

The net interaction between fish and stoneflies was negative for all but the lowest density of *Baetis* larvae to which the predators were exposed, and it increased in magnitude as prey density increased. The persistence
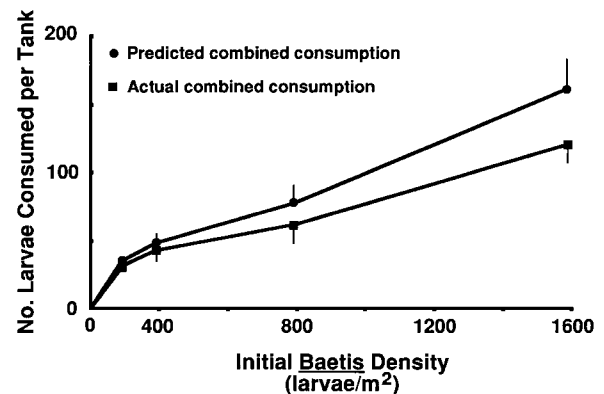

FIG. 3. Actual and predicted combined consumption (means ± 1 SE) of *Baetis* larvae by mottled sculpins and larvae of the stonefly *Agnetina* as a function of initial *Baetis* density, in simulated-stream laboratory trials. Predicted combined values were generated by substituting data from the separate predators (Fig. 1) into Eq. 2.
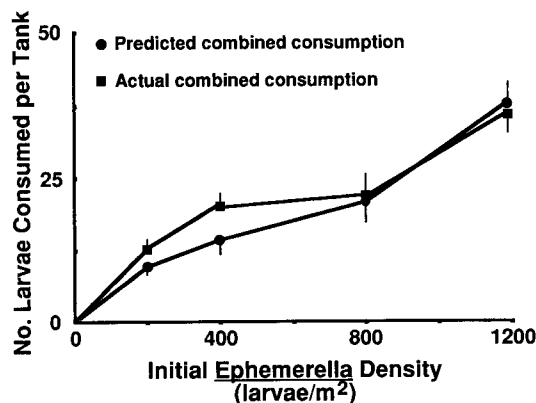
FIG. 4. Actual and predicted combined consumption (means ± 1 SE) of *Ephemerella* larvae by mottled sculpins and larvae of the stonefly *Agnetina* as a function of initial *Ephemerella* density, in simulated-stream laboratory trials. Predicted combined values were generated by substituting data from separate predators (Fig. 2) into Eq. 2.

of a negative interaction between two species over a wide range in abundance of a commonly exploited resource provides indirect evidence of interference between species. However, for fish and stoneflies there is also direct evidence of strong interference between these predators.

Fish have strong effects on the behavior of larval stoneflies (e.g., Feltmate et al. 1986, Williams 1986, Soluk 1988, Soluk and Collins 1988*a, c*). Such responses are expected, given that fish are not only potential competitors with stoneflies for various types of invertebrate prey, but are also potential predators on stoneflies. *Agnetina* larvae, in the presence of sculpins, seldom leave the undersurface of stones, and dramatically reduce movements in general (Soluk and Collins 1988*c*). This response, coupled with the fact that *Baetis* larvae avoid stoneflies by swimming away (Peckarsky 1980, Williams 1987), or by moving to the upper surfaces of stones (Soluk and Collins 1988*b*), reduces the ability of stoneflies to obtain *Baetis* in the presence of sculpins. This was true even when the sculpins themselves could not feed because their mouths had been sewn shut (Soluk and Collins 1988*a*).

From prey-choice experiments, *Baetis* larvae are known to be favored prey items of stoneflies (Molles and Pietruzska 1983, 1987, Allan and Flecker 1988). Sculpins are certainly able to capture *Baetis* larvae, and this suggests that sculpins should have a negative impact on *Baetis* populations. However, this study indicates that *Baetis* larvae also benefit from the presence of sculpins in that risk of predation from stonefly larvae was significantly reduced by the presence of these fish.

Facilitation

Facilitation between predators, although once viewed as an oddity (e.g., Dayton 1973), is increasingly recognized as an important interaction influencing the

structure of communities (Vandermeer et al. 1985). At low to moderate densities of *Ephemerella* there was a significant positive interaction between sculpins and stoneflies. The main beneficiary of this positive interaction appears to be the fish, since there is no evidence of increased prey capture by stoneflies in the presence of sculpins (Soluk and Collins 1988*a*).

Facilitation between stoneflies and sculpins may be driven by differences in the way *Ephemerella* larvae respond to the two types of predators. *Ephemerella* larvae respond to the close proximity of stonefly larvae by exhibiting a characteristic "defensive" posturing behavior (scorpion posturing) or by crawling away (Peckarsky 1980, Williams 1987, Peckarsky and Penton 1988), behaviors that are likely to make them more conspicuous to fish predators. In addition, *Agnetina* is known to cause movement of *Ephemerella* larvae from the underside of stones, whereas sculpins had no effect on the distribution of *Ephemerella* (Soluk and Collins 1988*c*). Failure by *Ephemerella* to effectively balance the risk of predation from sculpins when responding to stonefly larvae provides a probable mechanism for the increased rate of prey capture by sculpins in the presence of *Agnetina*.

At higher prey densities (Fig. 4) there was no evidence of significant facilitation between predators. Convergence on an additive model for these densities would occur if enough *Ephemerella* were available on exposed surfaces of stones (either by chance or perhaps because of interactions between *Ephemerella* larvae) so that sculpins no longer required them to be forced to exposed surfaces by the presence of stoneflies.

Whatever the specific mechanisms for the absence of facilitation at higher *Ephemerella* densities, facilitation at low densities may have important consequences for benthivorous fish such as sculpins. Interseasonal fluctuations in the density of invertebrate prey species are a common feature of benthic communities in streams. In the heterogeneous environment of streams it may be very difficult to obtain larger cryptic prey when the density of these animals is relatively low. Although we do not know how extensive facilitative interactions are between fish and stoneflies, on-
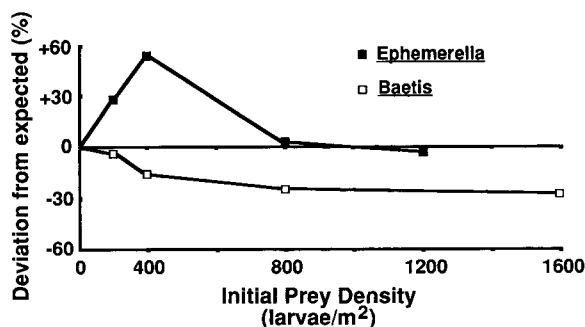

FIG. 5. Mean deviation of actual combined consumption of sculpins and stoneflies from predictions of Eq. 2 for both *Ephemerella* and *Baetis* prey types.

going studies indicate that fish growth rates in the field are enhanced by the activities of invertebrate predators (D. A. Soluk and J. S. Richardson, *unpublished data*).

Non-trophic influences

Assumptions about static food webs and fixed pairwise interaction terms within community matrices may facilitate mathematical analyses; however, a vast body of literature challenges the utility of using such simple descriptors to predict the future states of any reasonably complex community (e.g., Neill 1974, Brown 1981, 1984, Rigler 1982, Bradley 1983, Kerfoot and Sih 1987, Paine 1988, Yodzis 1988). In a similar way, using simple trophic models to describe interactions among species that have the ability to adjust their activities in response to the presence of potential competitors or predators, may also fail to predict the way even simple communities will respond to the removal of species (e.g., Abrams 1987, Sih 1987). Within the simple model community studied here, complexity does not result from direct or indirect trophic interactions among species, but rather is a consequence of behavioral responses of prey to predators, and of predators to each other.

Responses of one species to another that are mediated by behavioral responses to the presence of a third species have been termed "behavioral indirect effects" (Miller and Kerfoot 1987). Many studies have proposed or have actually found important behavioral indirect effects (see Miller and Kerfoot 1987); however, their general importance in structuring communities, relative to direct and indirect trophic effects, is still poorly understood. Clearly, all of these forces must act to some extent in communities containing species that can alter their behavior to minimize the negative impacts of interactions with other species.

Although behavioral flexibility in responses to predators and competitors may add complexity to how we define interactions between populations, its ultimate importance may be to stabilize the structure of communities in which populations of both predators and prey vary unpredictably. Soluk and Collins (1988a, c) suggested that because stonefly larvae are able to adjust their behavior and feed more effectively in the absence of fish, they may tend to buffer benthic invertebrate communities from the effects of variation in fish abundance. My finding that significant interference occurs between fish and stonefly predators over a wide range of prey densities supports this suggestion, at least with respect to prey such as *Baetis,* which occupy the upper surfaces of stones.

Although interference between predators may help to stabilize communities, it is not clear that this is true for facilitation. The presence of facilitation between fish and stoneflies at low *Ephemerella* densities suggests the possibility that stoneflies enhance food supply for fish (see *Facilitation,* above) and thus help to stabilize fish populations. Such facilitation is unlikely to have a stabilizing effect on populations of prey, like *Ephemerella,* that depend on crypsis or seek refuges on the underside of stones. Such species will still be subject to fish predation even at low densities when there is an apparent abundance of places in which they would be inaccessible to fish.

A limitation of this study is that it focuses upon a relatively small subset of the species that occupy riffle areas of high-gradient streams. Although it seems very unlikely, given theoretical analyses of complex food webs (Yodzis 1988), it is possible that different combinations of predators and prey, and/or the addition of more prey species, could generate results more consistent with predictions derived from an understanding of trophic interactions alone. Even given this possible limitation, this study still strongly indicates that caution be exercised in extrapolating additive effects of predators over a range of prey densities. Even if there is good experimental evidence of additivity at any one particular density, extrapolating combined predator effects will be a dubious activity whenever there is little direct knowledge of behavioral interactions among the species concerned.

Acquisition of detailed knowledge of behavioral interactions among all species in any complex community seems an unrealistic goal. Such complete knowledge may be necessary; however, it may also be possible to develop generalizations for particular taxa or categories of predators (e.g., vertebrate vs. invertebrate, visual vs. tactile, active vs. sedentary). There is already a rich body of knowledge on the responses of animals to the presence of potential predators (Dill 1987, Sih 1987, Lima and Dill 1990). Unfortunately, most of these studies focus primarily on the adaptive function of predator avoidance behavior, and little is known on ecologically relevant time scales about the implications of predator avoidance behavior for either populations or communities (Sih 1987). Integrating such behavioral information into trophic models may seem to make the daunting task of elucidating the structure and function of communities even more difficult. However, such an approach is worth exploring, given the need to develop a more refined mechanistic understanding of how communities operate, or will operate, in the presence of widespread anthropogenic manipulation of natural systems.

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