

The role of stoneflies in enhancing growth of trout: a test of the importance of predator-predator facilitation within a stream community

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Soluk, D. A. and Richardson, J. S. 1997. The role of stoneflies in enhancing growth of trout: a test of the importance of predator-predator facilitation within a stream community. – *Oikos* 80: 214–219.

Failure to understand subtle behavioral mechanisms can lead to mischaracterization of interactions within food webs. Laboratory studies indicating increased prey capture by fish when predatory invertebrates are present suggested a field experiment to evaluate the effect of stonefly removal on growth rate of fish. Individually marked juvenile cutthroat trout (*Oncorhynchus clarki*) were introduced into replicate experimental stream channels beside a coastal Pacific rainforest stream. In stream channels with large perlid stoneflies (*Doroneuria* and *Calineuria* sp.) trout gained mass, whereas in channels without stoneflies trout lost body mass. There was no significant effect of stoneflies on trout mortality over the month-long experiments. Although total predator number and biomass were higher in channels with stoneflies (trout and stonefly biomass combined), trout apparently gained more from the way prey behavior was altered by the presence of stoneflies, than they lost from any effects of competition for common prey resources. The presence of significant facilitation amongst predators complicates our view of trophic structuring in stream communities, requiring that such non-intuitive interactions be more explicitly considered both by modelers and experimentalists seeking to evaluate the role of predators in these and in other communities.

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Direct and indirect trophic interactions within food webs can modify the structure of natural communities in a number of complex ways (e.g. Paine 1980, Kerfoot 1987, Yodzis 1988, Schoener 1989, Power 1990, Winemiller and Polis 1996). Consideration of trophic interactions alone, however, only hints at the complex dynamics possible within natural communities where behavioral interactions also influence populations both directly and indirectly (e.g. Chesson and Rosenzweig 1991, Werner 1992, Werner and Anholt 1993). For example, although behavioral interactions such as suc-

cessful predator-avoidance behaviors and interspecific aggression are not directly expressible as trophic exchanges, they may have strong impacts both directly on the populations involved and indirectly on other populations within a community (e.g. Werner et al. 1983, Power et al. 1985, Gilliam et al. 1989, Persson 1991, Werner 1992, Abrams 1993). In some situations the direct and indirect effects of behavioral interactions may even overwhelm trophic effects, structuring the community and generating dynamics not predictable from knowledge of energy flows (Abrams 1984, 1993,

Accepted 11 March 1997

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ISSN 0030-1299

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Mittelbach and Chesson 1987). In this study we report how, because of complex behavioral interactions between predators and their prey, stream fish may benefit from the presence of predatory invertebrates, even though they must share an apparently limited prey resource.

The juveniles and adults of many species of stream fish feed on a spectrum of benthic invertebrate species similar to that exploited by larger invertebrate predators such as the larvae of stoneflies (Plecoptera) or dragonflies (Odonata). Predatory invertebrates are known to show strong behavioral responses to the presence of fish, which lower their ability to capture prey (Wellborn and Robinson 1987, Soluk and Collins 1988a); however, the effect of predatory invertebrates on fish has rarely been examined. Laboratory studies of interactions between fish and stonefly larvae (Soluk and Collins 1988a, Soluk 1993) have indicated that fish and predatory invertebrates affect each other in complex ways that vary as a function of both prey type and prey density. For example, although the rate at which stonefly larvae captured a slow-moving and cryptically colored prey (larvae of the mayfly *Ephemerella*) was unaffected by the presence of fish (mottled sculpins, *Cottus bairdi*), the capture rate of a fast-moving and highly favored prey (larvae of the mayfly *Baetis*) was greatly reduced when sculpins were present (Soluk and Collins 1988a). In contrast, although the rate at which sculpins captured *Baetis* was unaffected by the presence of stoneflies, their capture rate for *Ephemerella* was greatly enhanced when stoneflies were present. This enhanced ability to capture cryptic prey was a consequence of behavioral responses to stoneflies which make *Ephemerella* more accessible and detectable by benthic fish (Soluk and Collins 1988b). Because many species of stream invertebrates exhibit cryptic coloration or avoid fish predation by hiding on the undersides of stones, it is reasonable to hypothesize that whereas stonefly larvae might be negatively affected overall by the presence of fish (because their ability to capture some types of prey is reduced), fish may be positively affected overall by the presence of stoneflies (because their ability to capture cryptic prey is increased).

Many stream fish appear to be limited by the availability and/or abundance of prey at least on a seasonal basis (Warren et al. 1964, Ensign et al. 1990, Johnston et al. 1990, Richardson 1993). Facilitation driven by the presence of predatory invertebrates thus has potentially important consequences for the growth and persistence of fish populations in streams. This will be especially true if the net indirect benefit that accrues from the presence of predatory invertebrates over the long term is larger than the negative effects that derive from increased direct competition for common prey resources.

Materials and methods

To quantitatively test whether predatory stoneflies have a net positive effect on fish populations we conducted a field experiment to evaluate the growth response of juvenile coastal cutthroat trout (*Oncorhynchus clarki clarki*) to manipulation of stonefly abundance. Growth is defined here as percentage change in mass from initial mass. Growth was used as the response variable rather than diet, since growth integrates diet and other short-term dynamics over time and thus more clearly represents the net ecological interaction between species.

Coastal cutthroat trout were used in this study because they are an important game species that occurs widely along the Pacific coast of North America. Coastal cutthroat trout exhibit a heterogeneous mix of life history patterns including anadromous (sea-run), potamodromous (lake- and stream-run), and non-migratory forms. The non-migratory form typically inhabits small, high-gradient headwater streams and exhibits much lower rates of growth and much smaller size at maturity than either of the other forms (Trotter 1989), suggesting the presence of severe resource limitation (probably food) for these populations.

Experiments were conducted in a series of six replicated streamside channels located in the University of British Columbia Research Forest (49°16'N, 122°34'W) near Haney in southwestern British Columbia, Canada. The channels were flow-through systems (each 15 m long by 0.35 m wide) fed by water diverted from Mayfly Creek, a small high-gradient headwater tributary of the North Allouette River, that drains an area of second-growth coastal rainforest. Channels allowed prey migration to and from source populations in the stream; however, netting on the inlets and outlets of the channels (3.0 and 5.0 mm, respectively) prevented immigration or emigration of fish and large stonefly larvae. Bottoms of the channels were lined with natural mineral substrates formed into a sequence of pool and riffle areas. To promote prey colonization, streamside channels were allowed to run freely for at least one month before the experiments began. Previous studies have indicated that the channels are rapidly colonized by benthic invertebrates and that they support an assemblage of species dominated by chironomids, mayflies, stoneflies and caddisflies, similar to that found in Mayfly Creek (Richardson 1991, Richardson and Neill 1991). Discharge from each channel was one to two l/s over the course of the experiment.

Experiments tested the facilitation hypothesis by comparing mass changes of individually marked juvenile cutthroat trout (1.2–5.1 g bodymass) in channels where large stonefly larvae (17.0–22.0 mm bodylength, *Doroneuria baumanni* and *Calineuria californica*) had been removed, with those in channels with large stoneflies present. The small size of the trout meant that

although they fed on prey sizes similar to those consumed by stoneflies, they were too small to eat the large stoneflies. Each individual trout was uniquely marked by loosely sewing small colored beads onto their back anterior to the dorsal fin. The trout were then individually weighed and placed into a holding bucket prior to addition into the channels. Fish showing ill effects of handling were replaced.

Ten days prior to addition of fish, stoneflies were removed from all channels and the channels were netted off to prevent recolonization of stoneflies. Removal was accomplished by first turning off flow in the stream channel, then meticulously searching and removing stonefly larvae from each channel. Efficiency of removal was high (only one larva was ever found in the removal treatments during post-experiment searches) because under low flow condition the larvae of stoneflies become quite active, probably in an attempt to find more suitable flow environments. After stonefly larvae had been removed from all the channels they were then reintroduced into every second channel at a density of 18 larvae/channel (3.4 larvae/m²), a density which approximated that found in parts of Mayfly Creek (J. S. Richardson pers. obs.). After the trout were introduced, the experiment was allowed to run for 4 weeks relatively undisturbed except for routine cleaning of nets and monitoring for fish mortality twice a week. At the end of the experiment the marked fish were retrieved from the channels and reweighed. Two fish (one from each treatment group) showed obvious signs of disease (fungus) and were excluded from the growth analysis. The experiment was first conducted in September-October 1990 with six fish initially introduced into each channel and then was repeated in May-June 1991, with four fish in each channel. The initial trout densities were set to values that lay between biomass and abundance values reported for trout in small coastal rain-forest streams (e.g. Murphy and Hall 1981, Moore and Gregory 1988).

Results

Trout in the presence of stoneflies exhibited higher mean rates of growth than those in channels with stoneflies removed (Fig. 1), which actually exhibited a net loss in mean bodymass. Two-way analysis of variance (Table 1), using the mean growth rate per stream as the response variable, date and treatment as main effects and mean initial bodymass as a covariate, indicated a significant effect of stonefly presence on fish growth ($p = 0.009$, one tailed) but no significant effect of season ($p = 0.14$), and no significant season \times treatment interaction ($p = 0.19$). The one-tailed p value reported for the stonefly effect is justified since the study was designed to evaluate the a priori prediction of

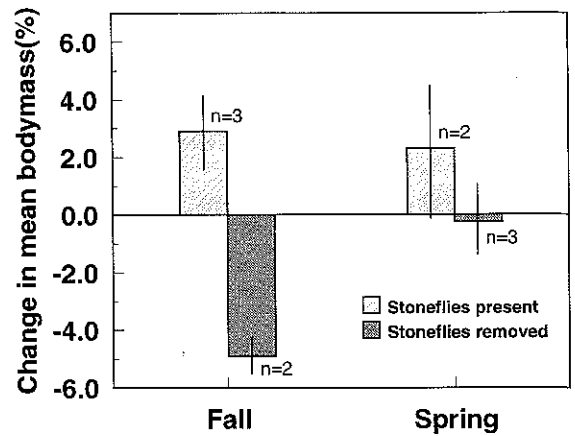


Fig. 1. Comparison of mean mass gain/loss for cutthroat trout in channels with stoneflies (*Calineuria* and *Doroneuria*) and where stoneflies had been removed, for both (fall and spring) runs of the experiment. Vertical bars indicate the standard error of the channel means, "n" is the number of channels from which mean masses were obtained.

growth enhancement and no predictions were made about seasonal effects or survivorship (see below). For both dates combined, mean growth over four weeks was +2.4% for treatments with stoneflies and -2.6% for those in which stoneflies had been removed.

Mean survivorship ranged from 35 to 100% across treatment groups; however, there were no statistically significant differences in gross survivorship among groups (Fig. 2). Two-way ANOVA (Table 2), with percent mortality as the response variable and mean initial bodymass as a covariate, indicated no significant effect of season ($p = 0.246$) or stonefly presence ($p = 0.11$) and no significant season \times treatment interaction ($p = 0.66$). Apparent differences in Fig. 2 are largely a result of all the fish being lost from one of the "with stonefly" replicates (0 survivorship) in the spring run. If this replicate is removed from the analysis, then effect of season moves close to the critical value ($p = 0.062$); however, p values for both stonefly presence and stonefly \times season interaction increase ($p = 0.20$ and $p = 0.82$, respectively). Actual source of mortality in this experiment is unclear, although the streams were checked twice a week only 1 dead fish was actually observed. Predation by either birds or mammals may have been the primary source of mortality.

Table 1. Results of a two-way ANOVA of growth data.

Source	SS	DF	MS	F-ratio	p
Season	14.26	1	14.26	2.41	0.181
Stonefly	69.22	1	69.22	11.72	0.009*
Mean initial wt.	10.14	1	10.14	1.72	0.247
Stonefly \times Season	13.62	1	13.62	2.31	0.189
Error	29.53	5	5.90		

* One-tailed p value used because of a priori expectation of growth enhancement.

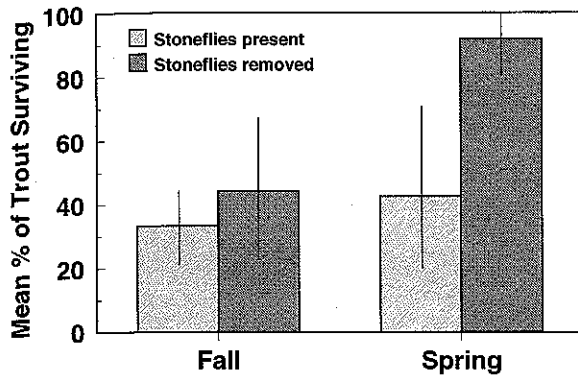


Fig. 2. Comparison of mean survivorship for cutthroat trout in channels with and without stoneflies present, for both fall and spring runs of the experiment. Vertical bars indicate the standard error, $n = 3$ for both treatments in both runs of the experiment.

The results of this experiment are consistent with the hypothesis of prey-mediated indirect facilitation between stoneflies and trout. However, differences in growth rate could also be explained if there were systematic differences in pattern of survivorship among treatments. For example, if significantly more individuals were to die, or if smaller slower growing trout were to be eliminated as a function of stonefly presence, then remaining individuals might appear to do better on average. In a sense, this would still be growth facilitation attributable to the presence of stoneflies, but through "thinning" rather than through enhancement of foraging success. Although this would be an intriguing observation, there is no evidence either of selective mortality ($p = 0.11$, see above) or a correlation between trout size and proportional growth rate in this study ($r^2 = 0.05$). The results of this study thus are seen to support our prediction that predatory stoneflies exert a net positive effect on fish growth rates, and not the alternative hypothesis that growth facilitation occurred as a result of selective mortality amongst trout.

Discussion

For many fish and invertebrates, growth rate is a good predictor of both the fitness of individuals and the potential numerical growth rate of populations. For juvenile salmonids and many other fish, size is posi-

Table 2. Results of a two-way ANOVA of percent mortality data.

Source	SS	DF	MS	F-ratio	p
Season	1399.64	1	1399.64	1.60	0.25
Stonefly	2908.27	1	2908.27	3.34	0.11
Mean initial wt.	188.01	1	188.01	0.21	0.66
Stonefly \times Season	745.68	1	745.68	0.86	0.39
Error	6103.47	7	871.93		

tively correlated with overall survivorship (e.g. Peterman 1982, Adams and DeAngelis 1987). Amongst juvenile salmonids relative size has often been found to be an extremely important predictor of ability to survive over the winter season (e.g. Mason 1976, Holtby 1988, Smith and Griffith 1994). For stream-dwelling coastal cutthroat populations (which generally exhibit extremely slow growth rates) even small differences in growth of juvenile fish could have substantial effects on size at maturity or overwintering mortality. The difference in mean growth rate observed between trout in the two treatment groups in this study was relatively small (5.0% overall); however, this experiment was only one month in duration. If growth differences are cumulative over the growing season then larger differences might be expected in an extended experiment. In addition, trout in streams where stoneflies had been removed were losing bodymass suggesting ominous consequences for these individuals if the duration of the experiments had been extended. It thus seems reasonable to suggest that indirect facilitation between fish and stoneflies may have significant consequences not only at the level of individual fish, but also for cutthroat trout populations as well.

Although anecdotal accounts of indirect facilitation between predators are common, the quantitative impacts of such interactions for the predator or prey populations involved have received little attention (Vandermeer et al. 1985, Kotler et al. 1992, Soluk 1993). Facilitation between species at all levels has generally received little attention from either theoretical or experimental ecologists who have traditionally focused on elucidating the roles of competition and predation in regulating populations and communities. One probable reason for the lack of interest in indirect facilitation between predators is that such positive feedback mechanisms are typically assumed to be destabilizing influences on population dynamics (May 1981). For example, one might assume that although very short-term foraging studies may suggest increases in rates of prey capture (on the order of hours or days), such an unstable situation would not persist in the long term (over weeks or months) because prey resources would tend to diminish in treatments with larger numbers of predators. In headwater streams, one feature mitigating this anticipated diminishment of prey resources may be the highly asymmetrical nature of interactions between fish and stoneflies. Although growth rates of stoneflies were not determined in this study, other studies suggest that stoneflies forage less effectively and as a consequence grow more slowly in the presence of fish predators (Soluk and Collins 1988a, Feltmate and Williams 1991, Soluk 1993). If what fish gain is sufficiently compensated for by what stoneflies lose in the interaction, then the net effect of the observed facilitation on prey abundance as a whole may be minimized, although individual prey species may be differentially

impacted. Ultimately, whatever intuitive prediction we make about long-term instability, the observation of significant facilitation after a month indicates that short-term gains for fish foraging in the presence of stoneflies can be translated into significant growth enhancement.

The indirect facilitation observed between fish and stoneflies in streams may reflect both the way prey respond differentially to the two types of predators, and the structural complexity of benthic environments in streams. The interstices between the gravel and cobbles that form the bed of high-gradient streams offer prey an abundance of refuges from foraging fish that are in close proximity to sources of algae and detritus. Predatory stoneflies can forage both in the interstices and on the exposed surface of stones; however, when fish are present stoneflies reduce time spent on exposed surfaces where they might themselves be consumed by fish (Soluk and Collins 1988c). Thus, prey can best escape stoneflies by moving onto the exposed upper surfaces of stones or by swimming into the water column, where they are then susceptible to fish. Many studies have described specific behavioral responses of mayflies, caddisflies, and other stream invertebrates to avoid either fish or stoneflies (Peckarsky 1980, Williams 1987, Kohler and McPeck 1989, Culp et al. 1991). However, it is unclear what decision rules are used by prey to resolve the dilemma they face when both types of predators are present. For the assemblage of species present in this study, the dilemma faced by prey seems to be resolved in favor of taking their chances with trout, a finding consistent with lab studies indicating a higher responsiveness of prey species to stoneflies than to fish predators (Soluk and Collins 1988b).

The importance of fish as a major force in structuring stream communities remains a matter of vigorous debate amongst aquatic ecologists (Allan 1983, Power 1990, Flecker 1992). If facilitation between fish and predatory invertebrates such as was observed in this study is widespread in streams, then perhaps we have to redefine the parameters of this debate and develop a more complicated model of stream communities than has been used for other systems. Perhaps simple trophic or energetic models are a necessary, but not a sufficient condition for understanding the dynamics of either headwater stream communities in general or stream fish populations in particular. This study clearly suggests that there remains much to be understood about the more subtle ways fish interact within stream communities and about the importance of behavioral interactions in general in shaping the structure of natural communities.

Acknowledgements - We would like to acknowledge the support and facilities provided by Larry Dill and Bernie Roitberg. Special thanks to Bill Neill for use of the stream channels. Thanks to Guy Martell and Alex Fraser for helpful hints on sewing beads onto fish. Helpful comments which greatly improved the manuscript were provided by Mary Power, Bobbi Peckarsky, and Steve Kohler. This research was supported by

funds provided to D. A. Soluk by the Dept of Biological Sciences, Simon Fraser Univ.

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