

Invading rainbow trout usurp a terrestrial prey subsidy from native charr and reduce their growth and abundance

Colden V. Baxter · Kurt D. Fausch ·
Masashi Murakami · Phillip L. Chapman

Received: 6 March 2007 / Accepted: 26 March 2007 / Published online: 26 May 2007
© Springer-Verlag 2007

Abstract Movements of prey organisms across ecosystem boundaries often subsidize consumer populations in adjacent habitats. Human disturbances such as habitat degradation or non-native species invasions may alter the characteristics or fate of these prey subsidies, but few studies have measured the direct effects of this disruption on the growth and local abundance of predators in recipient habitats. Here we present evidence, obtained from a combined experimental and comparative study in northern Japan, that an invading stream fish usurped the flux of allochthonous prey to a native fish, consequently altering the diet and reducing the growth and abundance of the native species. A large-scale field experiment showed that excluding terrestrial

invertebrates that fell into the stream with a mesh greenhouse reduced terrestrial prey in diets of native Dolly Varden charr (*Salvelinus malma*) by 46–70%, and reduced their growth by 25% over six weeks. However, when nonnative rainbow trout (*Oncorhynchus mykiss*) were introduced, they monopolized these prey and caused an even greater reduction of terrestrial prey in charr diets of 82–93%, and reduced charr growth by 31% over the same period. Adding both greenhouse and rainbow trout treatments together produced similar results to adding either alone. Results from a comparative field study of six other stream sites in the region corroborated the experimental findings, showing that at invaded sites rainbow trout usurped the terrestrial prey subsidy, causing a more than 75% decrease in the biomass of terrestrial invertebrates in Dolly Varden diets and forcing them to shift their foraging to insects on the stream bottom. Moreover, at sites with even low densities of rainbow trout, biomass of Dolly Varden was more than 75% lower than at sites without rainbow trout. Disruption of resource fluxes between habitats may be a common, but unidentified, consequence of invasions, and an additional mechanism contributing to the loss of native species

Communicated by Pete Peterson.

Electronic supplementary material The online version of this article (doi:10.1007/s00442-007-0743-x) contains supplementary material, which is available to authorized users.

C. V. Baxter · K. D. Fausch
Graduate Degree Program in Ecology, and Department of Fish,
Wildlife, and Conservation Biology, Colorado State University,
Fort Collins, CO 80523, USA

M. Murakami
Field Science Center for the Northern Biosphere,
Tomakomai Research Station, Hokkaido University,
Tomakomai, 053-0035, Japan

P. L. Chapman
Department of Statistics, Colorado State University,
Fort Collins, CO 80523, USA

C. V. Baxter (✉)
Department of Biological Sciences, Idaho State University,
Pocatello, ID 83209, USA
e-mail: baxtcold@isu.edu

Keywords Hokkaido · Japan · Invasion ecology ·
Oncorhynchus mykiss · Resource subsidies ·
Salvelinus malma

Introduction

Ecologists have recently focused research on the movement of prey, materials, and energy across habitat boundaries in order to understand the importance of landscape physiognomy and connectivity to population and ecosystem

processes (Polis et al. 1997, 2004; Power and Rainey 2000; Nakano and Murakami 2001). In particular, subsidies of prey from donor to recipient habitats may support an increased abundance of predators, which in turn depresses local prey populations and results in cascading indirect effects on the recipient communities. Indeed, these indirect effects have received a great deal of attention from researchers (Nakano et al. 1999c; Murakami and Nakano 2002; Sabo and Power 2002b). In contrast, considerably less attention has been given to studying the direct effects of prey subsidies on the behavior, growth, and abundance of recipient predators themselves (but see Duggins et al. 1989; Sabo and Power 2002a; Kawaguchi et al. 2003), despite the importance of understanding these linkages for predicting population responses to human-caused disturbances of landscapes.

Habitat degradation and introductions of non-native species are two important human disturbances that may alter these prey subsidies. Evidence obtained from experiments on linked stream-forest ecosystems indicates that either type of disturbance can trigger complicated indirect effects in the recipient food webs (Nakano et al. 1999c; Sabo and Power 2002b; see Baxter et al. 2005 for a review). For example, we recently reported results from a field experiment which showed that an invading stream fish dominated a terrestrial invertebrate prey subsidy and caused a trophic cascade within the stream community, but it also had indirect effects that reduced a reciprocal subsidy of emerging insects back to the forest and caused riparian spiders to decline as a result (Baxter et al. 2004). In contrast, to date there have been no focused studies of the direct effects of non-native species invasions on native consumers by altering the fate or characteristics of prey subsidies. Moreover, knowledge of the individual and population-level responses of consumers that precipitate the indirect effects is often a key to understanding higher-order effects in communities and ecosystems (Werner 1992; Peacor and Werner 1997; Trussell et al. 2003).

A second issue is that although experiments on these food web subsidies have all been conducted in the field, and at relatively large scales, most have been relatively short term, raising concern about whether they can be generalized to real populations in complex landscapes (Peckarsky et al. 1997; Englund and Cooper 2003). A useful strategy for addressing these concerns is to conduct both controlled field experiments and comparative field studies (Diamond 1986; Polis et al. 1998; Power et al. 1998), which allows a more sophisticated understanding of the extent to which the experimental results can be “scaled up” to the landscape level and generalized to longer time periods. Such complementary approaches are relatively rare in ecology, but they are essential because they provide both experimental evidence for mechanisms of ecological processes and empirical

evidence for their generality in real systems (Reseratis and Bernardo 1998). Here we report new results from our large-scale field experiment that show the direct effects of an invading stream fish on the diet and growth of the native fish species. We couple this with findings from a complementary, comparative field study, aimed at (1) testing whether the effects on diet that we found in our experiment in one stream could be demonstrated in a set of other similar streams (i.e., expanding the spatial scale), and (2) evaluating the long-term consequences of this invasion for the abundance of the native species (extending the temporal scale).

Materials and methods

We chose a study system in which terrestrial invertebrate prey are an important subsidy for a native stream fish, but which is simultaneously being invaded by a non-native fish that may disrupt this subsidy. Native Dolly Varden charr (*Salvelinus malma*; S1 of Supplementary Material) inhabit streams of Hokkaido Island, northern Japan, and derive about 50% of their annual energy from terrestrial invertebrates (Nakano et al. 1999c; Kawaguchi and Nakano 2001; Nakano and Murakami 2001; Kawaguchi et al. 2003), but the effect of altering this subsidy on charr growth is unknown. Non-native rainbow trout (*Oncorhynchus mykiss*) are rapidly invading Hokkaido streams (Takami and Aoyama 1999; Fausch et al. 2001) and this species also forages preferentially on terrestrial invertebrates (Nakano et al. 1999b). Therefore, if the non-native fish usurps the subsidy of terrestrial prey, we predicted that this would have direct negative effects on the diet, growth, and abundance of the charr.

Field experiment

We conducted a large-scale field experiment aimed at measuring the effects of the non-native trout invader on the subsidy of terrestrial prey and, consequently, on the diet and growth of the charr. These effects were compared to those from an experimental manipulation that reduced the subsidy directly. The experiment was conducted in Horonai Stream, a small spring stream draining an undisturbed watershed in the Hokkaido University Tomakomai Experimental Forest (described in detail in Nakano et al. 1999c). Terrestrial prey input and rainbow trout were manipulated in a 2 × 2 factorial design, which has been described previously in Baxter et al. (2004). The four treatments were: (1) control (Dolly Varden at natural density); (2) wild rainbow trout added at natural densities; (3) a mesh greenhouse that reduced the input of terrestrial prey (Nakano et al. 1999c); (4) both rainbow trout and the mesh greenhouse added. We used a randomized complete block design in which 16

fenced reaches [length 27.5 ± 0.7 m (mean ± 1 SE), 100-m^2 surface area] were divided into four blocks, from upstream to downstream, and four replicates of each treatment were randomly assigned within each block. After removing all salmonids, native wild Dolly Varden [134.1 ± 0.9 mm (mean \pm SE) fork length (FL)] were added to each reach to achieve densities similar to those previously measured in undisturbed Hokkaido streams ($0.4/\text{m}^2$; Fausch et al. 1994; Nakano et al. 1999a). Likewise, wild rainbow trout of similar sizes (144.9 ± 2.3 mm) were added to half the reaches at the density previously estimated for Horonai Stream ($0.2/\text{m}^2$; Nakano et al. 1999b). This additive design has been recommended for measuring effects of non-native fishes because it mimics the initial stages of invasion (Fausch 1998; Peterson and Fausch 2003). Greenhouses constructed of transparent 1-mm nylon mesh supported by aluminum frames (see Baxter et al. 2004; Fig. 2) were used to cover half of the reaches to exclude the input of terrestrial prey, and extended 25 m upstream to reduce the amount of prey drifting into reaches. The mesh was pinned along the stream banks to exclude falling input from all but a very narrow strip of vegetation (<0.5 m wide), and both ends were blocked to prevent flying insects from entering. Roof windows were cut at each end to allow emerging aquatic insects to escape (Nakano et al. 1999c). The greenhouses had minimal effects on light and water temperature beneath the closed deciduous forest canopy (Baxter et al. 2004).

The experiment was conducted for 6 weeks, from 11 June to 22 July 2002, which is a time period when terrestrial prey input to the stream is normally relatively high (Nakano and Murakami 2001). In each reach we measured the biomass of falling and drifting terrestrial invertebrates and the diets and growth of fish. Methods for measuring these components have been described in detail in Baxter et al. (2004) and generally followed those used in previous research (Nakano et al. 1999c; Kawaguchi and Nakano 2001; Nakano and Murakami 2001). The biomass of terrestrial invertebrates falling into each reach was measured four times during the experimental period for 3-day intervals using pan traps, and the biomass drifting into each reach was measured twice for 20-min intervals using drift nets set at dusk. To estimate the terrestrial and aquatic prey in the fish diets, we recaptured fish from each reach at the middle and end of the experiment by two-pass electrofishing. Ten to fifteen of the recaptured fish per species from each reach were then anesthetized and the diet contents collected using a pipette to flush prey items from the stomachs (Giles 1980). Diet data for the second half of the experiment have been reported in Baxter et al. (2004), but these are included here for completeness to allow comparisons. To measure growth, we marked all fish before the experiment with a fluorescent elastomer dye (red, yellow, pink, and orange;

Northwest Marine Technology, Shaw Island, Wash.). Each fish received a unique combination of two marks, arrayed among fin rays, adipose tissue behind the eyes, and the ventral surface of the lower jaw. All marked fish that were recaptured in each sample were measured (nearest 1 mm FL), and the body mass was determined using an electronic balance (nearest 0.1 g). After recovery, the fish were returned to their reach.

Data from the experiment were analyzed using a two-way ANOVA for randomized complete-block designs with repeated measures (SAS 1999). The greenhouse and rainbow trout treatments were both fixed factors. In one reach with the rainbow trout treatment, the fish suffered heavy predation by mink (*Mustela vison*), which resulted in an ineffective treatment. This treatment was subsequently excluded from the data analysis. Fish growth data were transformed using logarithms to stabilize variance. We used plots of residuals versus predicted values to evaluate the heterogeneity of variances and skewness, but none were detected. When two- or three-way interactions between main effects were detected, treatment means were compared individually for each time period using least significant difference (LSD) comparisons. When interactions among main effects were not detected, the effect of a factor was examined by averaging over one or more of the other factors.

Comparative field study

To determine how well the results from our experiment in one stream “scale up,” we conducted a comparative study from mid-June to mid-July 2003 to measure fish diets and fish density and size structure in six similar Hokkaido streams. We selected approximately 100-m reaches [length 100.6 ± 5.6 m (mean ± 1 SE)] of small spring streams similar to Horonai Stream (Supplementary Material, S1 and S2) that emerge from the flanks of Yoteizan, a large volcano in southwestern Hokkaido ($42^{\circ}49'N$, $140^{\circ}48'E$). The reaches were chosen based on a broad survey of fishes using single-pass electrofishing at 20 sites throughout this region of the Shiribetsu River basin. Two of the six reaches chosen had only native Dolly Varden in allopatry, and four had both rainbow trout and Dolly Varden in sympatry. Because we anticipated the effects of rainbow trout on charr might vary with invader abundance, we selected two sympatric sites with low relative abundance of rainbow trout and two with a higher abundance.

To estimate the amount of terrestrial and aquatic prey in the fish diets, fish were captured by electrofishing during the afternoon on one date in mid-June at each site, and the stomach contents were collected from 10–20 fish (minimum FL = 85 mm) per species using stomach lavage (Giles 1980). Species abundance and size structure was estimated on one date during mid-July at each site by three-pass

removal electrofishing after blocking the ends of each site with 4-mm-mesh seines (Riley and Fausch 1995). Care was taken to secure the bottom of the seines with rocks to prevent fish from escaping. Fish captured in each pass were anesthetized, measured (FL, nearest 1 mm), and retained in live baskets until the electrofishing was completed. For abundance estimation, fish of each species were divided into two age classes (age 0 vs. age 1 and older) identified from length-frequency histograms. Maximum likelihood population estimates and profile likelihood 95% confidence intervals (Otis et al. 1978) were calculated for each age class of each species using the program CAPTURE (White et al. 1982). The biomass of each species and age class in each site was estimated by multiplying the population estimate by the mean mass of individual fish. The latter was estimated using length-weight regressions developed for Dolly Varden from another stream in the basin and for rainbow trout from Horonai Stream (C.V. Baxter and K.D. Fausch, unpublished data).

Characteristics of the stream habitat and riparian vegetation were also measured at each site. Channel units were classified as pools, runs, or riffles, and the length of each was measured. Depth was measured at three equidistant points on a transect perpendicular to the flow at the midpoint of each channel unit, along with wetted width. In the pools, depths and width were measured the same way on three transects at the midpoints of the lower, middle and upper thirds of the unit, respectively. Measurements were then used to estimate habitat volume for each site. The number of pieces of large wood (≥ 30 cm diameter, ≥ 1 m length) in each reach and the dominant substrate type [modified Wentworth scale (Orth 1983), estimated visually at each depth measurement] were also recorded. Water temperature was monitored at 24-min intervals near the mid-point of each site from mid-June to mid-July using a data logger (Onset Corp., Pocasset, Mass.). At each site, the dominant species of understory and overstory riparian vegetation were visually assessed and leaf area index (LAI, leaf area per unit ground area) was measured at 10-m intervals along the reach (LAI-2000 Plant Canopy Analyzer; Li-COR Biosciences, Lincoln, Neb.). Data from the comparative study were analyzed using one-way ANOVA in which sites were nested within treatment. Planned comparisons among sites of the three types, as well as between the two fish species, were conducted by the LSD method (SAS 1999).

Results

Field experiment

During the experiment, the falling input of terrestrial invertebrates into Horonai Stream was reduced nearly 70% by

the greenhouse cover [12.9 ± 2.5 vs. 41.7 ± 6.0 mg $m^{-2} day^{-1}$ (mean ± 1 SE) in the eight reaches with greenhouses vs. eight without; $P < 0.001$ by *t*-test], whereas the drifting input of terrestrial invertebrates was similar between these treatments (0.04 ± 0.01 vs. 0.04 ± 0.007 mg m^{-3}). However, falling input to control reaches during the first 3 weeks [hereafter period 1; 59.0 ± 7.7 mg $m^{-2} day^{-1}$ (mean ± 1 SE)] was more than twice that during the last 3 weeks (period 2; 24.4 ± 3.3 mg $m^{-2} day^{-1}$; $P = 0.01$ by ANOVA for time effect). There were no differences in terrestrial invertebrate inputs among blocks during the experiment ($P = 0.85$), nor were there significant block or block \times treatment effects for any of the response variables measured ($P > 0.10$).

Dolly Varden in control reaches tracked the changes in terrestrial invertebrate input through time, because their diets contained twice as much terrestrial prey biomass during period 1 as in period 2 (Fig. 1; $P = 0.01$ by LSD after ANOVA). Likewise, the growth in mass of charr captured at the end of period 2 was, on average, less than double that of those captured at the end of period 1 in control reaches (Fig. 2), indicating that they grew more during period 1 when the prey subsidy was higher. For each period, growth was measured from the start of the experiment to enable all of the data to be used because a different subset of fish was recaptured in each sample. Fish in all treatments grew during the experiment, indicating that the size of enclosures and the densities of fish were appropriate.

Experimentally reducing terrestrial invertebrate input to the stream using mesh greenhouses resulted in a lower biomass of terrestrial prey in the diets of Dolly Varden charr (Fig. 1) and more biomass of benthic stream insects. The main effect of the greenhouse cover on terrestrial prey biomass was not significant ($P = 0.46$), but there was a significant two-way interaction (rainbow trout \times greenhouse; $P = 0.009$), and a greenhouse \times time interaction was detected though not significant ($P = 0.08$). When data from each sampling period were examined separately, two-way interactions between the main effects were significant for both time periods (period 1: $P = 0.0001$; period 2: $P = 0.03$). Therefore, LSD comparisons were made, which showed that Dolly Varden diets consisted of 46–70% less terrestrial prey in greenhouse versus the control reaches during periods 1 and 2 (period 1: $P = 0.004$, period 2: $P = 0.04$ by LSD after ANOVA). Due to the loss of terrestrial prey, the diets of Dolly Varden in reaches with greenhouses consisted of a 3.1- to 7.5-fold higher biomass of benthic stream insects than those in control reaches [period 1: 1.90 ± 0.80 vs. 0.62 ± 0.13 mg (mean ± 1 SE), period 2: 1.20 ± 0.38 vs. 0.16 ± 0.06 mg]. The main effect of the greenhouse cover on the biomass of benthic prey in Dolly Varden diets was significant ($P = 0.04$), as was the effect of time ($P = 0.005$). For period 2, the two-way interaction was

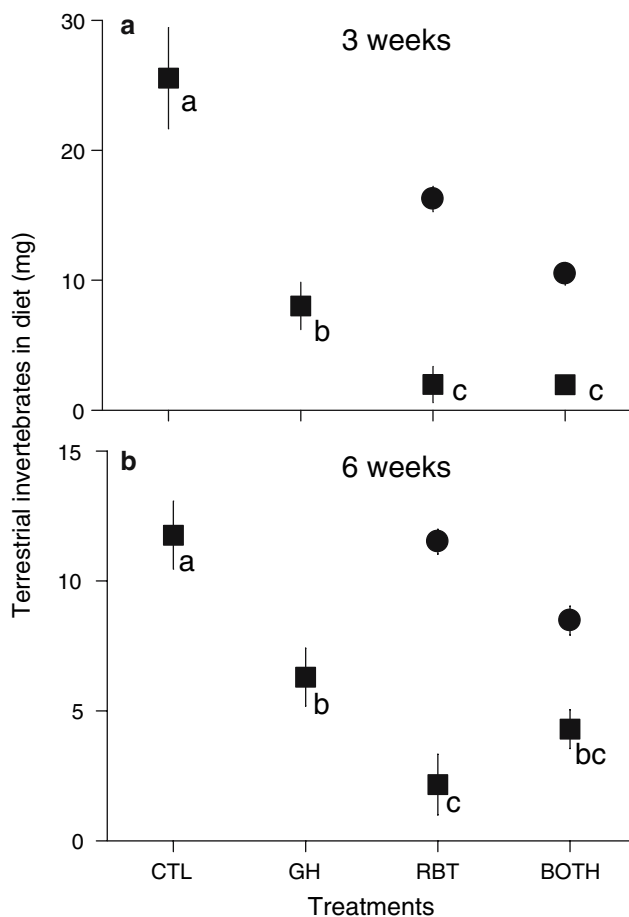


Fig. 1 Mean biomass of terrestrial invertebrates in diets of individual Dolly Varden (*Salvelinus malma*, filled square) and rainbow trout (*Oncorhynchus mykiss*, filled circle) after 3 (a) and 6 weeks (b) in four treatments – control (native Dolly Varden only, CTL), greenhouse cover (reduced subsidy of terrestrial invertebrates to stream, GH), rainbow trout (non-native rainbow trout added, RBT), and both greenhouse and trout added (BOTH) – in reaches of Horonai Stream during the summer of 2002. Values are means \pm 1 SE ($n = 4$ except $n = 3$ for RBT treatment; see text). Different lowercase letters indicate significant differences ($P < 0.05$) among treatments within periods based on LSD comparisons after ANOVA of log-transformed data. Data for panel b are from Baxter et al. (2004)

also significant (rainbow trout \times greenhouse; $P = 0.04$), and the subsequent LSD comparison showed that the diets of Dolly Varden in the greenhouse reaches had significantly more biomass of benthic insects than those in the control reaches during this period ($P = 0.002$).

When terrestrial prey inputs were reduced with the greenhouse cover, the growth of Dolly Varden charr also decreased, but this effect was not manifested until the end of the experiment. The main effect of the greenhouse cover on growth was not significant ($P = 0.28$), but the effect of time was ($P = 0.001$), and a three-way interaction (rainbow trout \times greenhouse \times time) was detected, although it was not significant ($P = 0.09$). When data from each time period were examined separately, two-way interactions between the

main effects were not significant after 3 weeks ($P = 0.84$), but they were nearly significant after 6 weeks ($P = 0.06$). The greenhouse had no detectable effect on charr growth after the first 3 weeks (Fig. 2; $P = 0.70$ for greenhouse main effect), but charr growth was 25% lower in the greenhouse versus the control reaches by the end of the experiment, which was a significant difference ($P = 0.03$, by LSD).

In the treatment where rainbow trout were added, they consumed most of the terrestrial invertebrates, apparently forcing Dolly Varden to shift to foraging on benthic insects from the streambed. Rainbow trout caused an 82–93% reduction in the biomass of terrestrial prey in Dolly Varden diets during the two sample periods compared to control reaches (Fig. 1; period 1: $P < 0.0001$, period 2: $P = 0.0004$, by LSD; see above for interaction effects). In turn, this resulted in a 1.6- to 4.5-fold increase in the biomass of benthic insects in Dolly Varden diets compared to controls [period 1: 0.97 ± 0.34 vs. 0.62 ± 0.13 mg (mean \pm 1 SE), $P = 0.49$ for rainbow trout main effect; period 2: 0.72 ± 0.12 vs. 0.16 ± 0.06 mg, $P = 0.008$, by LSD; see above for interaction. However, the switch to benthic foraging did not occur as soon or as strongly as that induced by the greenhouse treatment.

The addition of rainbow trout also caused a 38 and 31% reduction in the growth of Dolly Varden by the end of periods 1 and 2, respectively (Fig. 2), with the decreased growth appearing sooner than in the greenhouse cover treatment in which prey inputs were directly reduced. Charr growth was lower in reaches with rainbow trout than in control reaches during period 1 ($P = 0.009$ for rainbow trout main effect; see above for non-significant rainbow trout \times greenhouse interaction) and was also significantly lower by the end of the experiment ($P = 0.02$ by LSD; see above for interaction). Furthermore, rainbow trout gained significantly more weight than sympatric Dolly Varden when averaged over the entire experiment (Fig. 2; $P = 0.02$ by LSD; the effect of time was not significant, $P = 0.13$) but grew a similar amount as Dolly Varden in control reaches. Taken together, the results from the two single treatments showed that the effect of adding rainbow trout on diet and growth of native Dolly Varden was as strong, or stronger, in every case than experimentally excluding terrestrial prey input using a mesh greenhouse.

Adding both the greenhouse and rainbow trout treatments together produced similar results to adding either alone (Figs. 1, 2). In these reaches, there was a similar reduction of terrestrial prey in charr diets compared to controls (period 1: $P < 0.0001$, period 2: $P = 0.02$, by LSD), and a corresponding increase in benthic insects consumed [period 1: 1.04 ± 0.24 vs. 0.62 ± 0.13 mg (mean \pm 1 SE), see significant greenhouse main effect above; period 2: 0.95 ± 0.22 vs. 0.16 ± 0.06 mg, $P = 0.002$, by LSD]. Charr growth was reduced relative to control reaches by 41% during the first 3 weeks and 24% over 6 weeks (period 1:

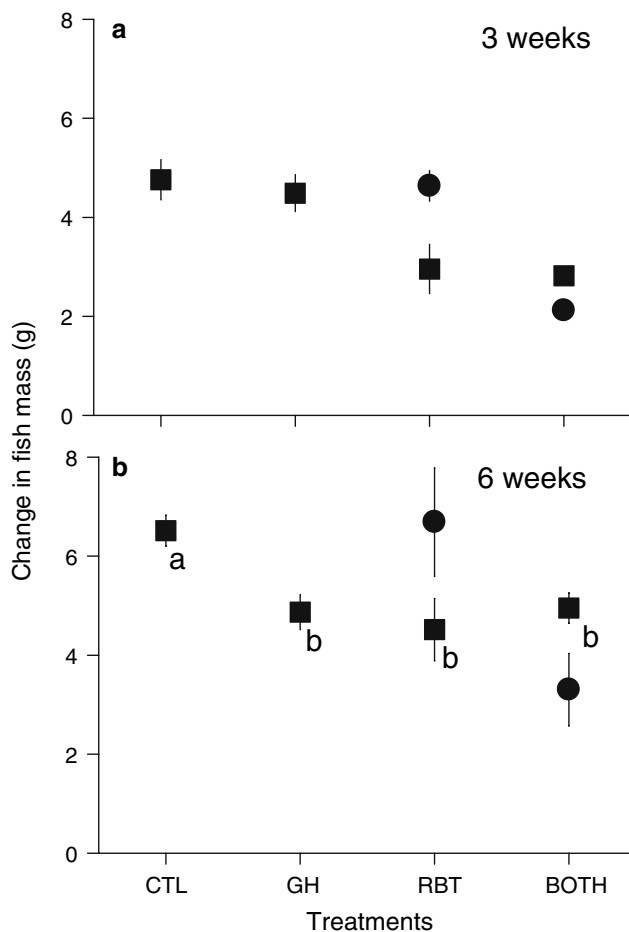


Fig. 2 Growth of Dolly Varden (filled square) and rainbow trout (filled circle) after 3 (a) and 6 weeks (b) in four treatments – control (CTL), greenhouse cover (GH), rainbow trout (RBT), and both greenhouse cover and trout (BOTH) – in reaches of Horonai Stream during the summer of 2002. Values are means \pm 1 SE ($n = 4$ replicates except $n = 3$ for RBT treatment, see text). See text for significance of treatment effects for the 3-week period. Different lowercase letters indicate significant differences ($P < 0.05$) among treatments for the 6-week-period based on LSD comparisons after ANOVA of log-transformed data

$P = 0.015$; period 2: $P = 0.04$, by LSD). We had expected that the effects of rainbow trout on charr might be exacerbated by excluding terrestrial prey, but instead we observed that either treatment alone reduced charr growth to a threshold beyond which the added treatment elicited no further response. Rainbow trout growth was diminished even more than charr growth when terrestrial prey inputs were reduced, but the greenhouse effect for rainbow trout was marginally significant due to the high variation relative to sample size ($P = 0.06$; neither the effect of time or the time \times greenhouse interaction were significant, $P > 0.10$).

Comparative study

The six sites selected for the comparative study had a similar stream habitat and riparian vegetation (S2), and stream

width, depth, habitat volume, large wood, and leaf area index did not differ between sites with and without rainbow trout ($P \geq 0.25$ by one-way ANOVA). However, sites without rainbow trout had lower (though not significantly different) mean temperatures in June–July 2003 than those with rainbow trout [S2; 7.0 ± 0.1 vs. $10.5 \pm 0.6^\circ\text{C}$ (mean \pm 1 SE); $P = 0.09$ by ANOVA]. We saw no evidence of angling at any site.

In accordance with our experimental results, Dolly Varden at sites with rainbow trout had a 78% lower biomass of terrestrial invertebrate prey in their diets, on average, than charr at sites without the invading species (Fig. 3a; $P = 0.05$ by one-way ANOVA). This was true whether rainbow trout were present at low or approximately equal relative abundance ($P = 0.04$ and 0.03 , respectively, by LSD after ANOVA) and could not be explained by differences in the sizes of charr sampled for diets, which were similar among the three groups of sites [FL = 126 ± 2.8 mm (mean \pm 1 SE); $P = 0.50$ by ANOVA]. With respect to proportions, terrestrial prey constituted 78% of the biomass of diets of Dolly Varden in allopatry but made up a significantly lower proportion (48%, on average, with a corresponding increase in the proportion of benthic stream insects) when rainbow trout were present ($P = 0.04$ by ANOVA after arcsine square root transformation). This reduction was greater when the relative abundance of rainbow trout was equal to that of Dolly Varden than when it was lower [35 ± 6 vs. $60 \pm 6\%$ terrestrial prey (mean \pm 1 SE); $P = 0.02$ by LSD]. At invaded sites, rainbow trout consumed a similar biomass and proportion of terrestrial invertebrates as Dolly Varden did at allopatric sites (Fig. 3a; $P = 0.80$ and 0.30 , respectively, by ANOVA), suggesting that differences in Dolly Varden diets were driven by the presence of rainbow trout rather than by differences in terrestrial prey availability among sites.

The abundance (Table 1) and biomass (Fig. 3b) of Dolly Varden was lower at sites where rainbow trout were present than at sites where they were absent. The biomass of all age classes of Dolly Varden combined was 77% lower, on average, at sites with rainbow trout than at those where Dolly Varden were allopatric ($P = 0.008$ by ANOVA). Moreover, the biomass of Dolly Varden was similarly reduced whether rainbow trout were present at low or about equal relative abundance ($P = 0.004$ and 0.006 , respectively, by LSD). Age-0 Dolly Varden were also least abundant at sites with rainbow trout and most abundant at one of the sites without rainbow trout (Table 1). Likewise, a high abundance of juvenile (age-1) Dolly Varden at sites without rainbow trout was associated with lower mean lengths of age-1+ charr than at sites with rainbow trout (Table 1; $P < 0.003$ by LSD after ANOVA). In contrast, age-0 rainbow trout were captured at sites with higher abundance of rainbow trout but not at those with low abundance of

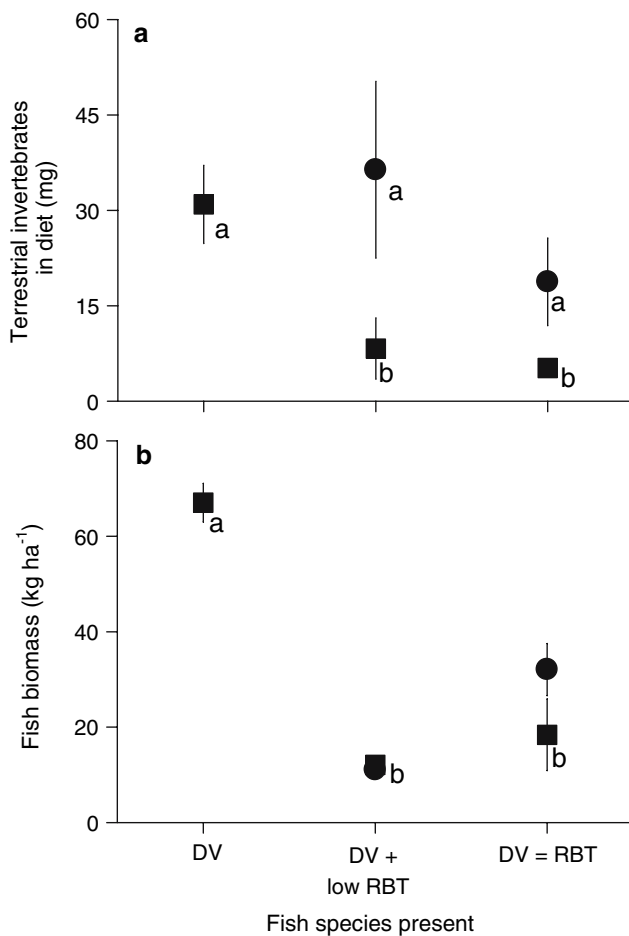


Fig. 3 Biomass of terrestrial invertebrates in fish diets (**a**) and of two salmonids (all age classes) (**b**) in stream reaches in southwestern Hokkaido with native Dolly Varden alone (DV), Dolly Varden and low densities of non-native rainbow trout (DV + low RBT), or Dolly Varden and rainbow trout in about equal relative abundance (DV = RBT) during the summer of 2003. Diets and biomass of Dolly Varden (filled square) and rainbow trout (filled circle) are shown. Values are means \pm 1 SE ($n = 2$). Different lowercase letters indicate significant differences ($P < 0.05$) among treatments based on LSD comparisons after one-way ANOVA

rainbow trout (Table 1), suggesting that little recruitment was occurring for either species at the latter sites. When estimates for Dolly Varden and rainbow trout were combined, we found that total salmonid biomass was similar at sites with a higher relative abundance of rainbow trout compared to those with only Dolly Varden ($P = 0.23$ by LSD), but that it was nearly 70% lower at sites where rainbow trout were present at low densities ($P = 0.03$ by LSD).

Discussion

The combined results of our experimental and comparative studies, coupled with our previous work (Baxter et al. 2004), indicate that invading rainbow trout disrupt the

subsidy of terrestrial prey to small spring streams in Hokkaido, with strong consequences for the behavior, growth, and abundance of native charr that depend on this resource. Our experiment showed that terrestrial invertebrates were not only an important component of the diets of native Dolly Varden charr (see also Nakano et al. 1999c; Kawaguchi and Nakano 2001; Nakano and Murakami 2001) but that they also strongly affected their growth. Dolly Varden in control reaches grew the most during the first half of the experiment, when ambient terrestrial prey flux to the stream was the highest. Experimentally reducing this subsidy to Dolly Varden using a mesh greenhouse caused the fish to shift to foraging on benthic stream insects (Nakano et al. 1999a, c) and reduced their growth by 25% over 6 weeks. Moreover, this effect was likely conservative because terrestrial invertebrate input into Horonai Stream in the summer of 2002 was 34–63% lower than that measured during the summer in two earlier studies (Nakano et al. 1999c; Nakano and Murakami 2001). Kawaguchi et al. (2003) conducted a similar short-term experiment in the same stream and showed that when terrestrial invertebrate input was reduced using greenhouse covers, fish biomass in unfenced 50-m reaches (those in our study were fenced) quickly decreased by nearly 50% because fish emigrated, apparently redistributing themselves in proportion to prey availability. Together, these findings indicate that any factor that alters the characteristics or fate of this prey subsidy is likely to reduce the growth or the abundance of native charr populations.

Our combined studies also demonstrated that invading rainbow trout directly usurped the subsidy of terrestrial invertebrate prey from Dolly Varden. Fish diet data from our experiment showed that rainbow trout were effective at monopolizing the prey subsidy, and forced the native charr to shift their foraging to picking benthic insects from the streambed (see Fausch et al. 1997; Nakano et al. 1999a). The comparative study showed that the biomass of terrestrial prey in Dolly Varden diets in other small spring streams in Hokkaido was reduced by more than 75% when rainbow trout were present at either lesser or equal densities, indicating that this shift in foraging behavior is a general phenomenon. Moreover, in the experiment, rainbow trout reduced the biomass of terrestrial prey in diets of Dolly Varden during both periods by 82–93%, which was more reduction than was caused by the direct exclusion of terrestrial prey using the greenhouse. Likewise, the 31% reduction in charr growth caused by rainbow trout during the experiment was greater than that caused by excluding terrestrial prey inputs altogether. Underwater observations suggested that the main mechanism for these effects was that rainbow trout not only usurped the prey subsidy, but also dominated the charr behaviorally, forcing them to leave locations profitable for drift foraging (Baxter et al. 2004) and reducing their total daytime foraging rate (drift

Table 1 Estimates of fish abundance for age-0 and age-1 and older (age-1+) fish from the six sites surveyed in the comparative study of streams in southwestern Hokkaido during the summer of 2003. Data are based on maximum likelihood population estimates from removal electrofishing. Numbers in parentheses show the profile likelihood

95% confidence intervals. The total number of fish captured is shown for three cases where either a small sample size or the lack of depletion precluded calculating abundance estimates. Also shown are fork lengths (mm, mean \pm 1 SE) for age-1+ fish

Salmonid composition ^a	Site ^b	Dolly Varden			Rainbow trout		
		Abundance		Age-1 + mean length	Abundance		Age-1 + mean length
		Age-0	Age-1+		Age-0	Age-1+	
DV	NN	345 (287–475)	364 (349–386)	92.5 (1.0)	0	0	–
DV	SN	27 ^c	199 (179–240)	88.5 (1.6)	0	0	–
DV + low RBT	UM	24 (22–35)	10 (10–13)	126.2 (7.5)	0	9 (9–9)	133.3 (14.5)
DV + low RBT	UK	4 (4–5)	22 (22–24)	123.8 (4.9)	0	7 (7–7)	176.3 (16.0)
DV = RBT	LM	51 (45–74)	11 (11–13)	142 (6.8)	15 (15–21)	19 (19–19)	144.7 (8.2)
DV = RBT	LK	2	11 (11–13)	134.2 (8.7)	6	27 (27–42)	132.1 (9.0)

^a Sites had either native Dolly Varden charr in allopatry (DV), Dolly Varden and low relative abundance of non-native rainbow trout (DV + low RBT), or Dolly Varden and rainbow trout in approximately equal relative abundance (DV = RBT)

^b NN, North Fork Nanbetsu Stream; SN, South Fork Nanbetsu Stream; UM, Upper Mohanrin Stream; UK, Upper Kashunbetsu Stream; LM, Lower Mohanrin Stream; LK, Lower Kashunbetsu Stream

^c Shallow, complex, side-channel habitat prevented adequate depletion of age-0 Dolly Varden at this site

and benthic combined) by 66% (D.J. Jordan and C.V. Baxter, unpublished data). Thus, despite being similar in size, the invader was apparently superior due to a combination of both exploitative and interference competition.

An alternative hypothesis to explain the reduced charr growth caused by rainbow trout in the field experiment is that the increased total fish density specified by the additive design simply reduced average prey availability to all fish. However, in addition to the behavioral observations reported just above, the observational study showed that the biomass of terrestrial invertebrates in Dolly Varden diets was greatly reduced in the presence of either a low or high abundance of rainbow trout, even when total fish biomass was lower than when charr were alone. Taken together, this evidence indicates that the foraging shift by Dolly Varden and the resulting effects on charr growth were due primarily to the presence of rainbow trout, and not solely to differences in fish density. We suspect that native salmonids in other regions might be similarly affected because many of these consume terrestrial prey (Baxter et al. 2005), and rainbow trout are the most widely introduced fish species in the world (Fausch et al. 2001).

Our experimental and comparative study results indicate that domination of the terrestrial invertebrate subsidy by rainbow trout, coupled with interference competition, may be the primary reason that native Dolly Varden populations were lower when rainbow trout were present. Rainbow trout invasion apparently resulted in a 77% decrease in Dolly Varden biomass, on average, at the invaded sites in the comparative study, even though the habitat was similar. To our knowledge, there are no reasons other than the presence of rainbow trout that can explain this low Dolly

Varden abundance. Dolly Varden were historically common in small streams of this region (Ishigaki 1984; Fausch et al. 1994), the habitat was suitable at all sites and throughout the length of invaded streams to sustain abundant Dolly Varden, and there was no evidence of angling. Likewise, the temperature was within the optimum range for charr at all sites sampled (Kitano et al. 1995; Nakano et al. 1996; Takami et al. 1997). Although the mechanisms responsible for native charr declines are uncertain, loss of the terrestrial subsidy diminishes Dolly Varden growth, which probably reduces fecundity and recruitment. Indeed, at most of the sites where rainbow trout were present, we found few age-0 or juvenile Dolly Varden. Rainbow trout might also reduce Dolly Varden by predation on age-0 charr (see Taniguchi et al. 2002) and by disturbing charr redds (nests) by building their own in the same streambed locations and displacing charr eggs or newly hatched fry (Taniguchi et al. 2000). In addition, Kawaguchi et al. (2003) showed that excluding terrestrial prey, as rainbow trout do, caused Dolly Varden to emigrate. Regardless of the combination of mechanisms, the problem is likely to be widespread because rainbow trout are rapidly invading other Hokkaido streams (Takami and Aoyama 1999) and have been reported to displace Dolly Varden as well as other native salmonids such as white-spotted charr (*Salvelinus leucomaenis*), Sakhalin taimen (*Hucho perryi*), and masu salmon (*O. masou*; Hasegawa et al. 2004; Kitano 2004; Morita et al. 2004).

Our use of complementary experimental and comparative studies provided us with a more thorough perspective on the importance of the prey subsidy and the effects of the non-native fish invasion than either approach alone could have. The controlled experiment allowed us to measure the

effects on behavior, diet, and short-term growth responses of the consumer, but not on movement (but see Kawaguchi et al. 2003) or long-term demographic responses. In contrast, the comparative study did not allow for the control of other external factors (e.g., fish density, differences in stream and riparian forest productivity, time since invasion) but did increase confidence in the realism of the experiment and the generality of our findings and enabled an investigation of population responses over a longer term and at larger spatial scales. Other investigators reported that ecological processes measured in small-scale laboratory and field experiments often could not be successfully extrapolated to larger scales (e.g., Peckarsky et al. 1997; Cooper et al. 1998). In contrast, the processes we discovered using relatively large-scale field manipulations in approximately 30-m reaches arrayed over a 1.7-km stream segment matched those measured in a set of similar small streams elsewhere in Hokkaido. This gave us confidence that the field experiment encompassed critical ecological processes and spatial heterogeneity, and that it was conducted over sufficient time to detect important ecological effects (Englund and Cooper 2003), such as those on fish diet and fish growth. Such integrated, multi-scale approaches have been proposed as the way forward in ecology (Polis et al. 1998; Power et al. 1998), and are needed to gain a fuller understanding of the role of prey subsidies in food webs as well as the possible consequences should they be disrupted or lost (Baxter et al. 2005).

In the literature on invasion biology, most direct effects reported for invading species are overt, such as driving native species extinct by predation, monopolizing space, or transmitting diseases (Simberloff 1997; Parker et al. 1999). However, our studies have demonstrated that invading species can also disrupt the flow of allochthonous resources across habitat boundaries by directly usurping prey organisms that would otherwise subsidize native consumers. Recent investigations have shown that other similar effects are also possible, such as invaders that monopolize resources which are important to consumers in other habitats. For example, non-native trout introduced to high-elevation lakes in California reduce amphibian larvae through predation, which may decrease garter snakes (*Thamnophis elegans*) that also prey on these amphibians in both aquatic and adjacent terrestrial habitats (Matthews et al. 2002). In addition, invaders may compete directly with the species that provides the cross-habitat subsidy, as occurred when introduced opossum shrimp (*Mysis relicta*) exploited prey of kokanee salmon (*O. nerka*) in Flathead Lake, Montana, which reduced the subsidy of migrating adult salmon to eagles and bears (Spencer et al. 1991). Similarly, the invasion of riparian areas by non-native bamboo (*Bambusa* spp.) or saltcedar (*Tamarix remosissima*) altered the flux of plant detritus to streams (O'Connor et al. 2000; Kennedy

and Hobbie 2004), a subsidy that fuels many aquatic organisms. By any of these means, disruption of resource fluxes that connect habitats may be an unforeseen impact of invasions and an additional mechanism contributing to the loss of native species.

Acknowledgments This research could not have been completed without the help of J. Jordan, K. Tatara, Y. Miyake, A. Uesugi, S. Laeser, H. Asano, K. Ono, S. Bailey, K. Ross, J. Monroe, Y. Inagaki, T. Ishii, Y. Taniguchi, M. Inoue, and L. Weaver-Baxter. We also received assistance from D. Fukui, K. Hasegawa, T. Iwata, K. Kasugai, N. Kazahari, D. Kishi, B. Kondratieff, M. Matsuda, M. Miura, H. Miyata, K. Motomori, E. Nabeshima, T. Nakahara, F. Okabe, K. Onishi, T. Sugata, K. Takahashi, G. Takimoto, T. Tosuji, H. Urabe, H. Yorozuya, and the staff at the Tomakomai Research Station. We thank J. Dunham, J. Olden, J. Monroe, and four anonymous reviewers for comments that improved the manuscript. Protocols for fish sampling were approved by the Animal Care and Use Committee of Colorado State University (Protocol 01-164A). This study was supported by a National Science Foundation grant (DEB 0108222) to K.D. Fausch, fellowships from the Japan Society for the Promotion of Science to C.V. Baxter and K.D. Fausch, and Japanese Ministry of Education, Science, Sport, and Culture grants to M. Murakami.

References

- Baxter CV, Fausch KD, Murakami M, Chapman PL (2004) Non-native stream fish invasion restructures stream and forest food webs by interrupting reciprocal prey subsidies. *Ecology* 85:2656–2663
- Baxter CV, Fausch KD, Saunders WC (2005) Tangled webs: reciprocal flows of invertebrate prey link streams and riparian zones. *Freshw Biol* 50:201–220
- Cooper SD, Diehl S, Kratz K, Sarnelle O (1998) Implications of scale for patterns and processes in stream ecology. *Aust J Ecol* 23:27–40
- Diamond J (1986) Overview: laboratory experiments, field experiments, and natural experiments. In: Diamond J, Case T (eds) *Community ecology*. Harper & Row, New York, pp 3–22
- Duggins DO, Simenstad CA, Estes JA (1989) Magnification of secondary production by kelp detritus in coastal marine ecosystems. *Science* 24:170–173
- Englund G, Cooper SD (2003) Scale effects and extrapolation in ecological experiments. *Adv Ecol Res* 33:161–213
- Fausch KD (1998) Interspecific competition and juvenile Atlantic salmon (*Salmo salar*): on testing effects and evaluating the evidence across scales. *Can J Fish Aquat Sci* 55:218–231
- Fausch KD, Nakano S, Ishigaki K (1994) Distribution of two congeneric charrs in streams of Hokkaido Island, Japan: considering multiple factors across scales. *Oecologia* 100:1–12
- Fausch KD, Nakano S, Kitano S (1997) Experimentally induced foraging mode shift by sympatric charrs in a Japanese mountain stream. *Behav Ecol* 8:414–420
- Fausch KD, Taniguchi Y, Nakano S, Grossman GD, Townsend CR (2001) Flood disturbance regimes influence rainbow trout invasion success among five holarctic regions. *Ecol Appl* 11:1438–1455
- Giles N (1980) A stomach sampler for use on live fish. *J Fish Biol* 16:139–153
- Hasegawa K, Yamamoto T, Murakami M, Maekawa K (2004) Comparison of competitive ability between native and introduced salmonids: evidence from pairwise contests. *Ichthyol Res* 51:191–194
- Ishigaki K (1984) Exploring the mystery of charrs. Iwanamishoten, Tokyo

- Kawaguchi Y, Nakano S (2001) Contribution of terrestrial invertebrates to the annual resource budget for salmonids in forest and grassland reaches of a headwater stream. *Freshw Biol* 46:303–316
- Kawaguchi Y, Nakano S, Taniguchi Y (2003) Terrestrial invertebrate inputs determine the local abundance of stream fishes in a forested stream. *Ecology* 84:701–708
- Kennedy TA, Hobbie SA (2004) Saltcedar (*Tamarix remosissima*) invasion alters organic matter dynamics in a desert stream. *Freshw Biol* 49:65–76
- Kitano S (2004) Ecological impacts of rainbow, brown and brook trout in Japanese inland waters. *Glob Environ Res* 8:41–50
- Kitano F, Nakano S, Maekawa K, Ono Y (1995) Effect of stream temperatures on longitudinal distribution of fluvial Dolly Varden and potential loss due to global warming. *Wildl Conserv* 1:1–11
- Matthews KR, Knapp RA, Pope KL (2002) Garter snake distributions in high-elevation aquatic ecosystems: is there a link with declining amphibian populations and non-native trout introductions? *J Herpetol* 36:16–22
- Morita K, Tsuboi J, Matsuda H (2004) The impact of exotic trout on native charr in a Japanese stream. *J Appl Ecol* 41:962–972
- Murakami M, Nakano S (2002) Indirect effect of aquatic insect emergence on a terrestrial insect population through bird predation. *Ecol Lett* 5:333–337
- Nakano S, Murakami M (2001) Reciprocal subsidies: dynamic interdependence between terrestrial and aquatic food webs. *Proc Natl Acad Sci USA* 98:166–170
- Nakano S, Kitano F, Maekawa K (1996) Potential fragmentation and loss of thermal habitats for charrs in the Japanese archipelago due to climatic warming. *Freshw Biol* 36:711–722
- Nakano S, Fausch KD, Kitano S (1999) Flexible niche partitioning via a foraging mode shift: a proposed mechanism for coexistence in stream-dwelling charrs. *J Anim Ecol* 68:1079–1092
- Nakano S, Kawaguchi Y, Taniguchi Y, Miyasaka H, Shibata Y, Urabe H, Kuhara N (1999) Selective foraging on terrestrial invertebrates by rainbow trout in a forested headwater stream in northern Japan. *Ecol Res* 14:351–360
- Nakano S, Miyasaka H, Kuhara N (1999) Terrestrial-aquatic linkages: riparian arthropod inputs alter trophic cascades in a stream food web. *Ecology* 80:2435–2441
- O'Connor PJ, Covich AP, Scatena FN, Loope LL (2000) Non-indigenous bamboo along headwater streams of the Loquillo Mountains, Puerto Rico: leaf fall, aquatic leaf decay and patterns of invasion. *J Trop Ecol* 16:499–516
- Orth DJ (1983) Aquatic habitat measurements. In: Nielson LA, Johnson DL (eds) *Fisheries techniques*. American Fisheries Society, Bethesda, pp 61–84
- Otis D, Burnham KP, White GC, Anderson DR (1978) Statistical inference from capture data on closed animal populations. *Wildl Monogr* 62:1–135
- Parker IM, Simberloff D, Lonsdale WM, Goodell K, Wonham M, Kareiva PM, Williamson MH, Von Holle B, Moyle PB, Byers JE, Goldwasser L (1999) Impact: toward a framework for understanding the ecological effects of invaders. *Biol Invasions* 1:3–19
- Peacor SD, Werner EE (1997) Trait-mediated indirect interactions in a simple aquatic food web. *Ecology* 78:1146–1156
- Peckarsky BL, Cooper SD, McIntosh AR (1997) Extrapolating from individual behavior to populations and communities in streams. *J North Am Benthol Soc* 16:375–390
- Peterson DP, Fausch KD (2003) Testing population-level mechanisms of invasion by a mobile invertebrate: a simple conceptual framework for salmonids in streams. *Biol Invasions* 5:239–259
- Polis GA, Anderson WB, Holt RD (1997) Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. *Annu Rev Ecol Syst* 28:289–316
- Polis GA, Power ME, Huxel GR (2004) Food webs at the landscape level. University of Chicago Press, Chicago
- Polis GA, Wise DH, Hurd SD, Sanchez-Pinero F, Wagner JD, Jackson CT, Barnes JD (1998) The interplay between natural history and field experimentation. In: Resetarits WJ Jr, Bernardo J (eds) *Experimental ecology*. Oxford University Press, New York, pp 254–280
- Power ME, Deitrich WE, Sullivan KO (1998) Experimentation, observation, and inference in river and watershed investigations. In: Resetarits WJ Jr, Bernardo J (eds) *Experimental ecology*. Oxford University Press, New York, pp 113–132
- Power ME, Rainey WE (2000) Food webs and resource sheds: towards spatially delimiting trophic interactions. In: Hutchings MJ, John EA, Stewart AJA (eds) *Ecological consequences of habitat heterogeneity*. Blackwell, Oxford, pp 291–314
- Resetarits WJ Jr, Bernardo J (eds) (1998) *Experimental ecology: issues and perspectives*. Oxford University Press, New York
- Riley SC, Fausch KD (1995) Trout population response to habitat enhancement in six northern Colorado streams. *Can J Fish Aquat Sci* 52:34–53
- Sabo JL, Power ME (2002) Numerical response of lizards to aquatic insects and short-term consequences for terrestrial prey. *Ecology* 83:3023–3036
- Sabo JL, Power ME (2002) River-watershed exchange: effects of riverine subsidies on riparian lizards and their terrestrial prey. *Ecology* 83:1860–1869
- SAS Institute (1999) SAS version 8 e. SAS Institute, Cary, N.C.
- Simberloff D (1997) The biology of invasions. In: Simberloff D, Schmitz DC, Brown TC (eds) *Strangers in paradise: impact and management of nonindigenous species in Florida*. Island Press, Covelo, pp 3–20
- Spencer CN, McClelland BR, Stanford JA (1991) Shrimp stocking, salmon collapse, and eagle displacement: cascading interactions in the food web of a large aquatic ecosystem. *BioScience* 41:14–21
- Takami T, Aoyama T (1999) Distributions of rainbow trout and brown trout in Hokkaido, northern Japan. *Wildl Conserv* 4:41–48
- Takami T, Kitano F, Nakano S (1997) High water temperature influences on foraging responses and thermal deaths of Dolly Varden *Salvelinus malma* and white-spotted charr *S. leucomaenis* in a laboratory. *Fish Sci* 63:6–8
- Taniguchi Y, Fausch KD, Nakano S (2002) Size-structured interactions between native and introduced species: can intraguild predation facilitate invasion by stream salmonids? *Biol Invasions* 4:223–233
- Taniguchi Y, Miyake Y, Saito T, Urabe H, Nakano S (2000) Redd superimposition by introduced rainbow trout, *Oncorhynchus mykiss*, on native charrs in a Japanese stream. *Ichthyol Res* 47:149–156
- Trussell GC, Ewanchuk PJ, Bertness MD (2003) Trait-mediated effects in rocky intertidal food chains: predator risk cues alter prey feeding rates. *Ecology* 84:629–640
- Werner EE (1992) Individual behavior and higher-order species interactions. *Am Nat* 140[Supplement]:S5–S32
- White GC, Anderson DR, Burnham KP, Otis D (1982) Capture-recapture and removal methods for sampling closed populations. Los Alamos National Laboratory LA-8787-NERP, Los Alamos