Can replacement of native by non-native trout alter stream-riparian food webs?

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SUMMARY

1. Non-native species can affect food web and community structure, including the flow of resources from one habitat to another. In many streams of western North America, non-native brook trout (*Salvelinus fontinalis*) have replaced native cutthroat trout (*Oncorhynchus clarkii*). Because brook trout naturally occur at higher densities and exhibit different feeding habits, this replacement may have consequences for a range of organisms in stream-riparian food webs.

2. We conducted a large-scale, 2-month field experiment to test whether, compared with cutthroat trout, brook trout reduce benthic insects, cause an increase in stream algae, and reduce emerging adult aquatic insects as well as riparian spiders that rely on emergence as prey. Twenty enclosed reaches from which trout were removed were treated by adding age-1 and older: (i) cutthroat trout at natural density (0.15 fish m^{-2}); (ii) brook trout at a natural density (0.40 fish m^{-2}); (iii) brook trout at a low density equal to the cutthroat trout treatment (0.15 fish m^{-2}) or (iv) no trout added.

3. Brook trout reduced the flux of emerging insects by 55% compared with cutthroat trout, but, surprisingly, only at the lower density. This reduction in emergent insects was predicted to reduce spider abundance by 20%, provided that sufficient branches were available to support riparian spider webs. We also detected an effect of trout on large-bodied benthic and emerging insects, but not on the entire assemblage of benthic insects, or periphyton.

4. We hypothesise that our results were influenced by trout foraging behaviour mediated by their density and size structure. Regardless of the mechanisms responsible, our results indicate that non-native brook trout can reduce the flux of emerging insects, and further analysis showed that this could reduce riparian spiders and birds that prey on them. Similar effects of non-native fish are likely to occur in lotic and lentic waters beyond the western United States.

Keywords: food webs, non-native invasions, *Oncorhynchus clarkii*, *Salvelinus fontinalis*, species replacement

Introduction

Replacement of native species by non-native species is a common outcome of invasions in freshwater ecosystems. The strongest impacts of such replacement are generally thought to be associated with invasive species that have functional characteristics not already present in the invaded habitat. For example, drastic changes in community structure and ecosystem function have accompanied invasions by molluscs, crayfish and fish that have

traits unique to the invaded communities (Strayer *et al.*, 1999; Simon & Townsend, 2003; Olden *et al.*, 2006). However, it is frequently the case that species invade habitats occupied by what is perceived as a functionally similar native counterpart, and our understanding of impacts in such circumstances is incomplete. The focus of investigation has typically been on the negative consequences for populations of the native species being replaced, whereas the direct and indirect effects on the food web and community structure have been less

studied. At present, in such cases, it is often assumed that non-native species are essentially 'analogues' to the closely related native species they replace, and will affect communities similarly (e.g. Quist & Hubert, 2004). Although this assumption has been evaluated in a few instances (e.g. replacement of native by invasive ants, Holway *et al.*, 2002), it remains largely untested in freshwater ecosystems.

When wholesale replacement occurs, broader effects on communities may depend on the traits of the invader in comparison with the native species and whether replacement occurs at higher, equal or lower density. For example, even if replacement occurs at a similar abundance, the non-native species could have stronger effects on the food web if species-specific traits differ (Parker *et al.*, 1999). Therefore, it is important to understand whether effects on food webs are caused by greater density and/or different traits (Benjamin, Fausch & Baxter, 2011). However, few experimental manipulations have measured the differences between the effects of native and non-native species on food webs. Knowledge of these causal relationships, measured via experiments, may be critical for those who manage non-native species. If there is no difference in effects and only the species identity has been changed, then the public may ask whether resources would be better used elsewhere.

In many streams worldwide, non-native salmonid fishes have been introduced where native salmonids already occur (Rahel, 2002), often resulting in species replacement. In the western U.S.A., brook trout (*Salvelinus fontinalis*) have invaded most streams to which they have access and are now the most widespread and abundant non-native fish (Schade & Bonar, 2005). The outcome is often that brook trout replace native cutthroat trout (*Oncorhynchus clarkii*; Dunham *et al.*, 2002; Fausch, 2008), and afterwards exhibit greater density and production (Benjamin & Baxter, 2010, 2012). In addition, brook trout have a greater propensity for picking invertebrate prey directly from the substrate, whereas cutthroat trout predominantly capture drifting prey, including terrestrial invertebrates from the stream surface (Griffith, 1974; Nakano *et al.*, 1998; Lepori *et al.*, 2012). Thus, brook trout could reduce benthic invertebrates more than the cutthroat they replace, owing to differences in abundance and/or foraging behaviour. Although this invasion has been widely studied, most research has focused on mechanisms of replacement or the consequences for cutthroat trout (Peterson, Fausch & White, 2004), whereas impacts on stream-riparian food webs remain largely uninvestigated.

Recent research has shown that non-native salmonid fishes can reduce insects emerging from aquatic ecosystems to riparian zones, which is an important resource flow that supports riparian predators such as spiders, lizards, birds and bats (Baxter, Fausch & Saunders, 2005). For example, in a large-scale field experiment, adding non-native rainbow trout (*O. mykiss*) to a Japanese stream not only had negative effects on benthic insects that led to increased streambed algae, but also reduced aquatic insect emergence, which, in turn, reduced riparian spiders that depend on these prey (Baxter *et al.*, 2004). Similarly, trout introduced to historically fishless lakes apparently reduced emerging insects and their amphibian and avian predators (Finlay & Vredenburg, 2007; Epanchin, Knapp & Lawler, 2010). However, neither of these studies investigated, the effects of replacement of one salmonid by another, which is an increasingly common outcome. In an earlier study, we found that emergence was 36% lower from streams in two Rocky Mountain regions where brook trout had replaced cutthroat trout, and projected that the loss in total emergence flux would reduce spiders by 6–20% (Benjamin *et al.*, 2011). However, experimental evidence is lacking, and the relative effects of differences in foraging traits versus the differences in trout density are uncertain.

Here, we compared direct and indirect effects on stream-riparian food webs of native cutthroat trout and the brook trout that replace them, via a large-scale field experiment. We manipulated the abundance of age-1 and older brook trout or cutthroat trout to test three main hypotheses. First, we hypothesised that compared with cutthroat trout, brook trout reduce benthic insects, owing to their greater natural density and benthic foraging. This would cause a trophic cascade that increases periphyton, as well as reducing emerging insects and the riparian spiders that feed on them. Second, we hypothesised that the two species have different effects, such that even when they are at equal density, the greater consumption of benthic insects by brook trout causes stronger cascading effects than cutthroat trout. Third, we hypothesised that trout of either species cause effects to these trophic levels, compared with no trout.

Methods

The experiment was conducted in Mahogany Creek, a small mountain stream in the Teton River basin, Idaho from 5 July to 3 September 2007. We chose this stream because brook trout (87% relative abundance) and cutthroat trout (13%) were sympatric (Colyer, 2006) and

because there was no road along the stream and little recreational activity. No other fish species were present. Average water temperature during the experiment was 9.7 °C ($\pm$0.11 SE) and discharge was 0.11 m^3 s^{-1} ($\pm$0.004). The stream was relatively small (mean width: 2.5–4.3 m), of moderate gradient (2–5% measured from a topographical map), the substratum was mainly cobble and gravel, and the riparian vegetation was primarily willow (*Salix* sp.).

Study design

To test our hypotheses, we manipulated fish presence and density in enclosed stream reaches, each 100 m^2 in surface area ($\pm$3.1 m^2). Enclosures were separated by at least 30 m of unmanipulated stream (henceforth referred to as buffers), which were effective in removing potential bias from upstream reaches in a previous experiment (Forrester, 1994; see Lepori *et al.*, 2012 for details). To increase realism, we included at least one of each mesohabitat type (i.e. pools, riffles and runs), because habitat complexity can influence predator–prey interactions (Crowder & Cooper, 1982; Bechara, Moreau & Hare, 1993). Movement of fish $\geq$ 45 mm (but not drifting benthic invertebrates) in and out of each enclosure was prevented by plastic mesh fences (6.4-mm mesh), which were buried in the stream bed, supported by metal posts, and sealed with sand bags. Set-up of the experiment took approximately 3 weeks and began immediately after spring run-off. The experiment ended just as leaf fall began, which would have compromised our enclosures by obstructing the mesh. Thus, owing to logistic constraints, we chose to run the experiment for approximately 60 days, which was sufficient time to detect food-web effects in similar experiments (Forrester, Chace & McCarthy, 1994; Baxter *et al.*, 2004).

The four treatments included cutthroat trout at natural density (0.15 fish m^{-2}; CT), brook trout at the higher natural density measured in this and other streams in the region (0.40 fish m^{-2}; BK-high), brook trout at the same density as the cutthroat trout (BK-low) and a very low trout density that remained after removing all fish possible (hereafter, No Fish; NF). We mimicked the natural size and age structure of age-1 and older trout in the first three treatments. Cutthroat trout were 60% age-1 [<100 mm fork length (FL)], 23% age-2 (100–170 mm FL) and 17% age-3 and older (>170 mm FL). Brook trout were 36% age-1 (<125 mm FL), 29% age-2 (125–160 mm FL) and 35% age-3 and older (>160 mm FL). The densities and size structures were based on surveys by Colyer (2006) and Benjamin & Baxter (2010) during the previous 2 years in this stream and others in the Teton River basin where each species was allopatric, as well as across the historical range of cutthroat trout (Benjamin & Baxter, 2012). We acknowledge that the NF treatment may have been affected by chemical cues from either trout species, which can affect drift behaviour and life histories of invertebrates (Peckarsky *et al.*, 2002; McIntosh & Peckarsky, 2004). However, we assumed that in our large-scale experimental reaches (length: 32.2 m $\pm$ 0.93 SE), the effects of trout on prey biomass would be predominately caused by consumptive, rather than non-consumptive effects (Englund, Cooper & Sarnelle, 2001).

We used a randomised incomplete block design with 20 enclosed reaches along 1.4 km of stream, divided into six blocks. Blocking was applied because we anticipated upstream reaches might differ from downstream reaches in habitat or biotic variables. The four treatments were randomly assigned within four complete blocks. The two incomplete blocks were assigned only the CT and BK-high treatments, to increase statistical power for comparing these two treatments, which were judged most relevant to managing brook trout invasions. Although the incomplete blocks had only two treatments, the total length of each block was similar. Before the experiment, we removed trout from the enclosed reaches with four-pass electrofishing (12B electrofisher; Smith-Root, Vancouver, WA, U.S.A.). These same trout were then stocked in enclosures to create the treatments, based on the densities and size structures described above.

Benthic insects and periphyton

Benthic insects were collected at the end of the experiment using two complementary methods, electrobugging (Taylor, McIntosh & Peckarsky, 2001) and stone picking (for details see Lepori *et al.*, 2012). Six electrobugging samples were collected at evenly spaced locations 3 m apart along the length of each enclosure, and randomly placed left, right or in the centre of the channel. Because electrobugging requires flow to carry invertebrates into the net, locations with no current were relocated laterally to the nearest microhabitat with flow. The upstream sample in each enclosure was collected approximately 6 m downstream of the upper fence to minimise the chance that insects from the upstream buffer would enter the sample. Each electrobugging sample was collected by passing the electrofisher anode (diameter = 0.15 m; 400 V DC at 20 Hz) six times (7 s per pass) in a downstream direction for 1 m to the centre of a 70-cm-wide kick net. The area sampled (0.40 m^2) was calculated by multiplying the electrical field diameter (estimated to be

0.35 m diameter) by the distance sampled upstream of the net, and included the additional semi-circular field upstream of the 1-m mark. Because electrobugging may underestimate non-drifting taxa (i.e. cased caddisflies and Diptera; Taylor *et al.*, 2001), we also picked insects directly from stones collected from the streambed. The stone-picking samples involved removing insects from the surface of 10 cobbles, collected at 3-m intervals along each reach. The cobbles were traced onto plastic sheets, and weights of the tracings were converted to area following methods in Bergey & Getty (2006).

Samples were stored in 95% ethanol and identified to species (Ephemeroptera, Coleoptera, Plecoptera, Trichoptera) or family (Diptera). Large (>1 mm) individuals from the electrobugging samples were separated from small (250 μm–1 mm) ones using sieves. All small taxa in electrobugging samples and chironomids in stone-picking samples were subsampled if their abundance exceeded 200 individuals, and these values were used to calculate total abundance for the whole sample. Head capsule widths or total lengths were measured to estimate biomass of individuals based on equations from Benke *et al.* (1999). Because fish often target large-bodied, predatory benthic insects, and these can cause indirect effects in stream food webs (Meissner & Muotka, 2006), we calculated biomass of predatory benthic insects separately. In addition, because we wanted to identify potential mechanisms behind any treatment effects on periphyton, we also calculated biomass separately for benthic taxa in the grazer–scraper functional feeding group. Predator and grazer–scraper designations were based on Merritt, Cummins & Berg (2008).

To sample periphyton, 10 cobbles were collected from the wetted channel, spaced at 2–3 m intervals along each enclosure, at the mid-point (30 July–3 August 2007) and end (31 August–3 September 2007) of the experiment. Their surfaces were scrubbed, and the periphyton collected was pooled into one container, and the cobbles were traced to estimate surface area. Samples were placed on ice and later frozen for laboratory analysis. Pooled samples were filtered (Whatman GF/F; pore size = 0.7 μm), filters were placed in 10 mL of methanol overnight to extract chlorophyll-*a* and biomass was estimated, after correcting for pheophytin, using a spectrophotometer (APHA, 1995).

Emerging insects and riparian spiders

Adult insects emerging from each enclosure were sampled using four emergence traps (0.33 m^2, mesh size = 0.2 mm; Malison, Benjamin & Baxter, 2010), two

in pools, one in a run and one along the bank of a run. These sampling strata encompassed different habitats and accounted for different modes of emergence among taxa (i.e. some crawl up the bank versus emerging from the water surface; Malison *et al.*, 2010). Emerging insects were collected during five 4-day periods (divided into two 2-day intervals) separated by 6–10 days. Insects were removed from traps using an aspirator and stored in 95% ethanol. Adult insects were identified to genus, except Diptera which were identified to family. All insects were counted, dried (60 °C at least 24 h) and weighed to the nearest 0.001 mg. In addition, because the presence of trout may reduce the size of insects, including size of emerging adults (Peckarsky *et al.*, 2002), we estimated the average biomass of emerging adults for the dominant taxa (Table S1) by dividing the total biomass of these taxa by their counts.

We surveyed adult and juvenile riparian spiders that rely on emerging insects as prey. Because spiders are relatively mobile, they can track variation in aquatic insect emergence at the stream-reach scale (Power *et al.*, 2004). Spiders were identified to family based on web and body morphology (Ubick *et al.*, 2005). Within each reach, spiders found overhanging the stream and riparian zone, up to a maximum height of 2.5 m and within 1 m from the active channel, were counted at night when they are most visible (Kato *et al.*, 2003). Counts were made twice during the experiment, midway and at the end. Reaches within blocks were surveyed on the same night, and all were surveyed within the 5-day periods that periphyton was sampled. Double-observer sampling (Nichols *et al.*, 2000) in a randomly located 5-m reach in most enclosures yielded a median detection probability of 0.93, indicating that most spiders were detected by our sampling method.

Fish diets and abundance

We sampled diets of trout in the CT and BK-high treatments using gastric lavage twice during the experiment, midway and at the end (see Lepori *et al.*, 2012 for details). Comparison between these two treatments was judged the most important to inform management of brook trout invasions. Logistical constraints prevented sampling other treatments. We collected stomach contents from 6 to 19 (median = 12) trout of each species and age class (age-1, -2 and -3 and older) during each sampling occasion. Samples were stored in 95% ethanol and identified to the lowest taxonomic level recognisable. To measure the biomass contribution of each taxon to trout diets, we measured the head capsule width of each

individual invertebrate and reconstructed their mass using equations from the literature (Collins, 1992; Sample et al., 1993; Rogers, Buschbom & Watson, 1997; Benke et al., 1999; Sabo, Bastow & Power, 2002; Gruner, 2003). When diet samples included more than 15 individuals of a given taxon, we used the average head capsule width from 15 individuals chosen at random to represent the rest. We classified individual taxa as either aquatic or terrestrial and report the biomass for each category. For more detail on presence and abundance of taxa in the diets of fish, benthos and drift, see Lepori et al. (2012).

Final trout densities were measured by three-pass depletion electrofishing at the end of the experiment. Capture probabilities and densities were estimated with Program MARK (White & Burnham, 1999), using a Huggins estimator with fish length as an individual covariate. Separate estimates were calculated for each species, and for age-0 versus age-1 and older trout, which were separated by length (see Table 1 in Lepori et al., 2012). Eleven *a priori* models were compared that included combinations of trout species, block, stream position (blocks 1–3 versus 4–6) and habitat complexity (defined as high or low). Estimates were model-averaged to calculate the final density (Burnham & Anderson, 2002).

Terrestrial invertebrate input and habitat measurements

We measured terrestrial invertebrate input, and biotic and abiotic habitat variables that might influence the distribution and abundance of fish, benthic and emerging insects, periphyton and spiders. Because terrestrial invertebrates falling in the stream may reduce predation pressure on benthic invertebrates (Nakano, Miyasaka & Kuhara, 1999a), we sampled this input twice during the experiment, once just after the mid-point (in the 5th week) and once at the end. We collected falling invertebrates at two random locations along each reach using pan traps (0.41 m²) filled with 5 cm of water and 2–3 drops of odourless surfactant. Contents were collected after 4 days. Invertebrates were separated into terrestrial or aquatic taxa (only adults whose larvae reside in the stream), dried and weighed to the nearest 0.1 mg.

Habitat variables were measured to assess the similarity among enclosures, and for use as covariates in models that predict benthic insects and spiders. To measure aquatic habitat, width (m) was measured on channel cross-sections spaced at 2-m intervals along the active channel, and depth (m) was measured at three

Table 1 Mean values (±1 SE) for ecosystem response variables in each treatment during each sampling period. Adult aquatic insects are those whose larvae reside in water

Sample period	Treatment	Periphyton chlorophyll-a (mg m^{-2})	Riparian spider counts	Fish diet			Terrestrial invertebrate input (mg m^{-2})
				Benthic insects (mg)	Terrestrial insects (mg)	Adult aquatic insects (mg)	
Mid	Cutthroat	3.7 (0.2)	61 (10)	15.6 (5.3)	2.3 (0.9)	0.7 (0.4)	225 (76)
	Brook low	4.8 (1.3)	63 (8)				296 (69)
	Brook high	4.2 (0.7)	112 (19)	14.5 (3.0)	5.1 (1.7)	0.3 (0.2)	410 (51)
	No fish	4.1 (1.2)	61 (5)				359 (41)
End	Cutthroat	5.8 (1.5)	79 (14)	24.0 (3.9)	3.0 (1.4)	0.9 (0.6)	39 (10)
	Brook low	5.8 (0.9)	73 (11)				39 (16)
	Brook high	4.8 (0.5)	90 (7)	22.7 (3.8)	0.8 (0.3)	0.4 (0.2)	43 (14)
	No fish	5.7 (1.3)	92 (14)				71 (19)

equally spaced locations along each cross-section (¼, ½, ¾ the width). At the midpoint of each cross-section, we visually classified the dominant and subdominant sub-strata (i.e. cobble, pebble, fine). Because spiders need structures, such as branches, to support webs (Power *et al.*, 2004), we visually estimated branch density in categories for each 2-m interval (no branches, 1–5, 6–25, 26–50 and >50 branches, defined as <5 cm diameter at the base and >50 cm long). Branch density was esti-mated to a height of 2.5 m above the water surface, and the mid-point for each category was used in analyses (75 was used for the >50 category).

Data analysis

To evaluate trout treatment effects on periphyton, ben-thic and emerging insects, riparian spiders and fish diet biomass, we used ANOVA, with repeated measures when appropriate (Littell *et al.*, 2006; SAS Version 9.1; SAS Institute 2003, Cary, NC, U.S.A.). We refer to these as treatment-effects models. To test our main hypothesis, we conducted two planned comparisons. First, we tested whether brook trout at their natural density had stronger effects on stream-riparian food webs than the cutthroat trout they replaced (BK-high versus CT). Second, we tested whether the effects of brook trout were stronger when the two species were at equal density (BK-low versus CT). This pair of contrasts allowed us to infer whether any effect of brook trout compared with cutthroat trout was simply because of their greater density, or to an inherent difference between the species. Third, we also tested whether the trout treatments, on average, had a stronger effect than when most trout were removed (CT, BK-high and BK-low versus NF). This was a relevant hypothesis because trout have been introduced worldwide, often into fishless bodies of water (Rahel, 2002; Fausch, 2008), studies of the effects of fish on aquatic-riparian commu-nities are limited (Baxter *et al.*, 2005), and the generality of the top-down effects of fish has been questioned (Meissner & Muotka, 2006).

Before analysis, benthic insect biomass data (including those used in separate analyses of grazers and predators), were log-transformed, and emergence density and fish diet biomass were square-root-transformed, to meet the assumption of homogeneous variance. The six blocks were located in the only segment of the study stream that met all our criteria for low gradient and similar habitat conditions. Hence, block and treatment were considered fixed effects. Because benthic invertebrates were sampled using two methods, a categorical variable for sampling

technique was included. Emergence density was analysed similarly, with a variable for mid-channel versus bank traps. Additional covariates in the analysis included the biomass of terrestrial invertebrate input, substrate, width and depth for benthos models; and mean branch density for spider models. We adjusted the denominator degrees of freedom using the Kenward–Rogers method, which accounts for estimation of any additional variance and covariance parameters, and makes these tests conserva-tive (Littell *et al.*, 2006). Covariates and blocking were removed from models when not significant ($P > 0.05$).

Detecting and quantifying complex indirect effects such as those hypothesised in this study can require a combination of analytical approaches (Polis *et al.*, 1998; Wootton, 2002). One problem is that when there are many mechanistic steps between treatment (e.g. brook trout) and response (spiders), more replication is needed to provide statistical power to account for other covariates that may affect the outcome of treatments. For example, to detect the effects of trout treatments on spiders, other covariates may need to be included such as substrate (which affects benthic invertebrates), depth (affects trout foraging), reach area (affects the emer-gence of adult aquatic insects; see below) and branch density (affects the response of spiders to this emer-gence). A second problem is that some covariates can-not be used because they are confounded with the treatments. For example, emergence could not be included in the treatment-effects model predicting spi-ders because we assumed it was controlled by the trout treatments themselves. Unfortunately, methods such as structural equation modelling (SEM) and path analysis (Wootton, 1994; Grace *et al.*, 2010), developed to identify important indirect effects caused by multiple factors, require a higher level of replication than our large-scale study allowed.

Therefore, as an alternative that is similar to SEM (Wootton, 2002), we developed complementary mecha-nistic ANOVA models based on *a priori* causal hypotheses to evaluate direct relationships underlying hypothes-ised indirect effects. For example, we fit models of periphyton and emergence as a function of benthic insect biomass, rather than trout treatments. Likewise, we fit a model of spider counts as a function of total emergence flux and branch density. Total emergence flux was estimated as emergence density (calculated from emergence traps) times surface area of the reach (estimated as length times mean width). This covariate was used because spiders respond to the total flux of emerging prey that crosses the stream-riparian boundary where they place their webs, not the mean flux per unit

area across the stream surface (Gratton & Vander Zanden, 2009; Benjamin *et al.*, 2011). Lastly, we linked the treatment effect model with the mechanistic model to estimate the potential change in spiders that could occur if cutthroat trout were replaced by brook trout.

We expected some differences among treatments might occur because of differences in insect composition, life history or traits (e.g. vulnerability to predation) and because such differences might mediate multitrophic-level effects. Therefore, we also used non-metric multidimensional scaling (NMDS) ordination with a Sørensen distance matrix to evaluate patterns of insect assemblage structure among treatments, followed by a multiresponse permutation procedure (MRPP) to test for differences in insect assemblage among treatments (McCune & Grace, 2002; PC-ORD Version 6, MJM Software Designs, Gleneden Beach, OR, U.S.A.). Based on these results, we conducted ANOVA similar to those described above for treatment effects on individual taxa (i.e. the caddisfly *Apatania* and chironomids) or groups of taxa (i.e. large-bodied taxa, which tend to be predators) that may have decoupled the linkages we predicted.

Results

Habitat and fish density

Overall, experimental enclosures were similar in aquatic and riparian habitat throughout. There were no significant differences in branch density, width, depth, width/depth ratio, substrate, pool volume, pool/riffle surface area, discharge or water chemistry among treatments ($P > 0.18$) or blocks ($P > 0.10$). Terrestrial invertebrate input did not differ among treatments ($P = 0.09$), but varied among blocks and through time. The three upstream blocks had 29% more input than those downstream ($P = 0.02$), and input was almost seven times greater at the mid-point (321 ± 34 mg m^{-2}) than at the end of the experiment (47 ± 7 mg m^{-2}; $P < 0.001$; Table 1).

Densities of age-1 and older trout at the end of the experiment were similar to those planned for all treatments (Table 2). Small numbers of the other species were present in each treatment (and both species in NF), but most were small age-1 trout that probably evaded capture when treatments were set up. On average, these fish consisted of two to four trout of the other species and made up only 6–12% of the total trout biomass in the trout treatments. In NF, two brook trout and five cutthroat trout were found, on average, but most were also small age-1 trout.

Table 2 Mean density (± 1 SE) of age-1 and older trout in each treatment at the end of the experiment (after Lepori *et al.*, 2012)

| Treatment | Trout density (fish m^{-2}) | |
	Cutthroat	Brook
Cutthroat	0.156 (0.019)	0.016 (0.007)
Brook low	0.041 (0.019)	0.152 (0.012)
Brook high	0.040 (0.017)	0.321 (0.015)
No fish	0.048 (0.002)	0.022 (0.019)

Benthic insects and periphyton

At the end of the experiment, the biomass of benthic insects differed among treatments ($P = 0.05$ by ANOVA on log-transformed data; Fig. 1a). Brook trout did not reduce the biomass of benthic insects more than cutthroat trout, at either high ($P = 0.10$ for BK-high versus CT contrast) or equal densities ($P = 0.15$ for BK-low versus CT contrast). However, the biomass of benthic insects in BK-low was nearly double that in BK-high ($P = 0.03$ by Tukey's HSD). Removing most trout produced no detectable increase in benthic biomass ($P = 0.89$ for fish versus no fish contrast). The model accounted for differences in biomass of benthic insects among blocks ($P = 0.04$) and sampling method ($P < 0.001$). The biomass of benthic grazers (not shown) was also significantly different among treatments ($P = 0.03$), which, like total benthic biomass, was owing to greater grazer biomass in BK-low than BK-high ($P = 0.02$ by Tukey's HSD). In contrast, the biomass of predatory invertebrates in the benthos did not differ among treatments ($P = 0.65$).

Ordination of the relative biomass of benthic insects revealed no significant difference among fish treatments ($P = 0.64$), but the two axes (67% variation explained) were strongly influenced by the biomass of three taxonomic groups, *Apatania* (Pearson's $r = 0.55$), chironomids ($r = 0.88$) and large-bodied benthic taxa, which consisted solely of large stoneflies during the experiment (i.e. *Hesperoperla*, *Kogotus*, and *Megarcys*; $r = -0.90$). The BK-low treatment had the greatest biomass of *Apatania* (379 ± 186 mg m^{-2}) and chironomids (1088 ± 608 mg m^{-2}), whereas BK-high had the lowest (*Apatania* $= 157 \pm 64$ mg m^{-2}, chironomids $= 183 \pm 57$ mg m^{-2}; Table S1). The combined biomass of these two taxa was different between these two treatments ($P = 0.05$ by ANOVA; $P = 0.04$ between the treatments by Tukey's HSD). Finally, biomass of the large-bodied benthic taxa did not differ among treatments ($P = 0.15$). However, in NF, their biomass was five times the average of the three trout treatments (Fig. 2a), although there was modest evidence for this
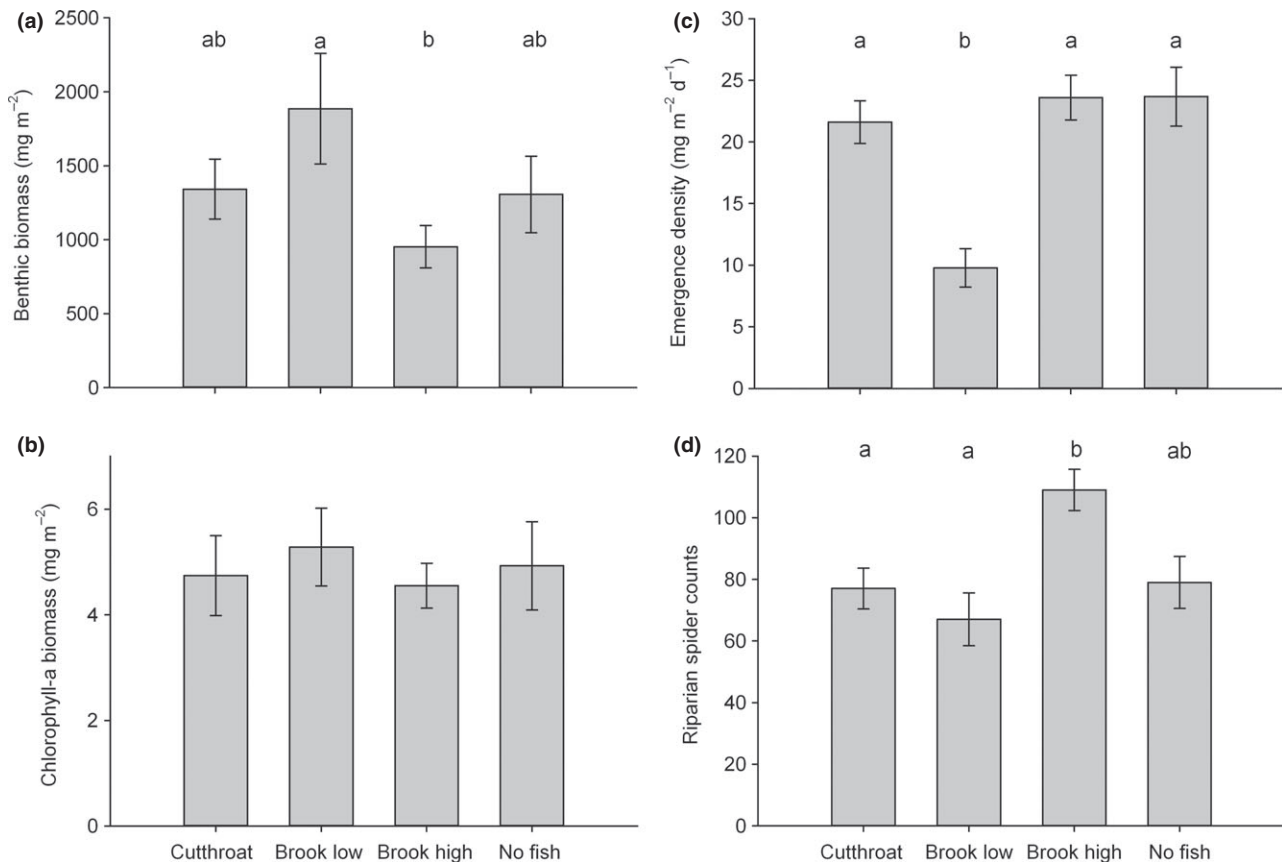
Fig. 1 Effects of treatments on the biomass of (a) benthic insects, (b) chlorophyll-*a* in periphyton, (c) flux of emerging insects and (d) the number of riparian spiders. Least-square means (±1 SE) shown are adjusted for covariates. The biomass of benthic insect was log-transformed, and the flux of emerging insects was square-root-transformed for analysis, so means and SE in the figure are back-transformed. Benthic insect biomass is from the end of the experiment, spider and periphyton data were averaged over the two sample periods, and emergence flux was averaged over five sampling periods (see Table 1 and Fig. 3). Treatments with different lower-case letters are significantly different ($P < 0.05$) based on Tukey's HSD.

difference owing to high variation ($P = 0.06$ for fish versus no fish contrast).

We found no difference in periphyton biomass, measured as chlorophyll-*a*, across treatments ($P = 0.87$; Fig. 1b). There was 32% greater biomass of periphyton chlorophyll-*a* during the final sampling period than at the mid-point, but this difference was not significant ($P = 0.14$; Table 1). In a separate model fit without treatments to test mechanisms, we did not detect an effect of benthic invertebrate grazer biomass on periphyton biomass ($P = 0.40$).

Emerging insects and riparian spiders

The flux of emerging insects differed among treatments (Fig. 1c; $P < 0.0001$). There was no detectable difference between brook trout at high density and cutthroat trout ($P = 0.41$ for BK-high versus CT contrast), but when the species were at equal density brook trout reduced

emergence by more than half (55%) compared with cutthroat trout ($P < 0.0001$ for BK-low versus CT contrast). Trout, in general, reduced the flux of emerging insects ($P = 0.01$ for fish versus no fish contrast), primarily because the emergence from BK-low was 41% of that from NF. The model accounted for significant effects of sampling method, block and time ($P \leq 0.04$). Emergence density from BK-low reaches was consistently lower than from any other treatment throughout the experiment (Fig. 3). There were no significant differences among treatments with respect to the size of adult insects within taxa ($P \geq 0.15$). In the mechanistic model where treatment was excluded, the biomass of benthic insects had no detectable effect on the flux of emerging insects ($P = 0.24$).

Ordination of the relative biomass of emerging insects revealed no significant differences among treatments ($P = 0.47$), but some large-bodied taxa influenced variation along the two axes (76%), including large
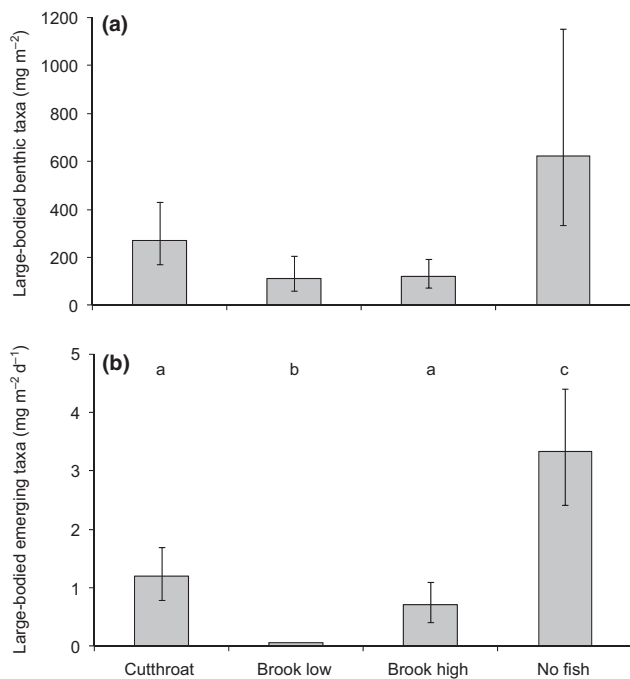
Fig. 2 Effects of fish treatments on (a) the biomass of large-bodied benthic insects (the stoneflies *Hesperoperla*, *Kogotus* and *Megarcys*) and (b) the flux of large-bodied emerging insects (the caddisflies *Chyranda*, *Dicosmoecus*, *Hesperophylax* and *Onocosmoecus*, and the stoneflies *Isoperla*, *Kogotus* and *Pictetiella*). The biomass of large-bodied benthic insect was log-transformed, and the flux of large-bodied emerging insects was square-root-transformed for analysis, so least-squares means and SE in the figure are back-transformed. Treatments with different lower-case letters are significantly different ($P < 0.05$) based on Tukey's HSD.

limnephilid caddisflies (i.e. *Chyranda*, *Dicosmoecus*, *Hesperophylax* and *Onocosmoecus*; Pearson's $r = 0.80$) and large stoneflies (*Isoperla*, *Kogotus* and *Pictetiella*; $r = 0.50$; see Table S1). We detected an effect of fish treatment on these large taxa ($P < 0.01$; Fig. 2b). Planned contrasts detected no difference in emergence of large-bodied taxa between CT and BK-high ($P = 0.39$ for BK-high versus CT contrast), but emergence from CT treatments was 20 times that from BK-low ($P = 0.02$ for BK-low versus CT contrast). Moreover, there was an overall effect of trout on these large taxa ($P < 0.01$ by fish versus no fish contrast).

Riparian spiders were dominated by the families Tetragnathidae (60% on average), Araneidae (37%) and Linyphiidae (1%). Counts of riparian spiders differed among treatments ($P = 0.01$; Fig. 1d), but contrary to our hypothesis, 42% more spiders were found along reaches with brook trout at high density (BK-high) than those with cutthroat trout (CT; $P = 0.008$ for planned contrast). As predicted, fewer spiders were counted along reaches with
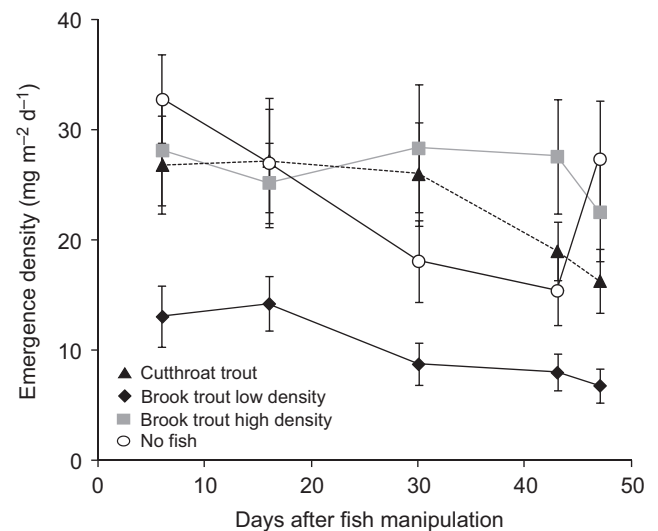

Fig. 3 Density of emergence flux (means ± SE) from the four treatments during the experiment. Day 0 is the beginning of the experiment.
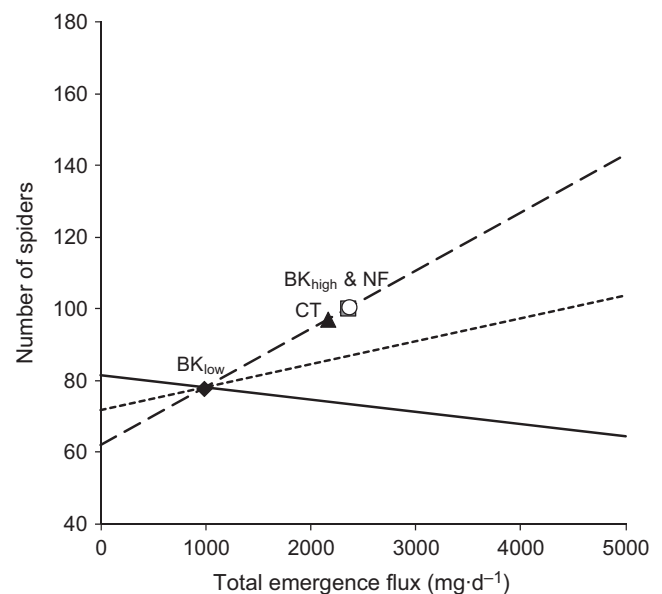

Fig. 4 Predicted increase in number of spiders of three families with total emergence flux at three different mean branch densities: 80 (solid line), 240 (short dashed) and 400 (long dashed) branches per treatment reach. Points show number of spiders projected for reaches with each treatment, based on their estimated mean total emergence fluxes. The three branch densities are at approximately the 10th, 50th and 85th percentiles in the data (range = 30–413 branches per reach).

brook trout (BK-low) than cutthroat trout (CT) when the two species were at equal density, but this difference was not significant ($P = 0.36$). No difference was detected between the NF treatment and those with fish ($P = 0.57$

for planned contrast). In this analysis of treatment effects, branch density also had a positive effect on spiders ($P = 0.01$), but this was independent of treatment (treatment x branch density interaction; $P = 0.73$). In the mechanistic model without treatments, branch density and insect emergence were both important. In that model, the number of spiders increased with total emergence flux from experimental reaches, but only at higher branch densities ($P = 0.04$ for interaction; Fig. 4; Figure S1).

Predicted effects of trout on spiders

By combining the model for emergence based on treatment effects with the mechanistic model for spiders, we infer that brook trout could reduce riparian spiders compared with cutthroat trout when the two trout species are at equal density (BK-low versus CT), and web-building habitat is available. Based on the treatment effects for emergence, we calculated that brook trout reduced total emergence flux by 55% from our 100 m^2 treatments compared with cutthroat trout at equal density. In turn, using the mechanistic model for spiders, we estimated that this reduced emergence flux caused by brook trout would result in 20% fewer spiders, when calculated at the high branch density needed to provide web support (Fig. 4). In contrast, treatments with brook trout at high density (BK-high) or no added trout (NF) are predicted to have slightly more spiders than the treatment with cutthroat trout, given high branch density.

Trout diets

Diets of brook trout at high density and cutthroat trout were similar in the proportions of terrestrial and aquatic (adult and benthic) invertebrates consumed during both periods. At the mid-point sample, the ratio in biomass of terrestrial to benthic aquatic invertebrates for brook trout diets was 25 : 73%, and for cutthroat trout was 12 : 84% (in all cases, the remainder was adult aquatic insects; Table 1). At the end, the ratio for brook trout was 3 : 95% and for cutthroat trout was 11 : 86%. We found no significant difference between trout species in the total biomass of benthic aquatic invertebrates in their diets ($P = 0.94$). Trout consumed more benthic aquatic invertebrates at the end of the experiment compared with the middle ($P = 0.02$).

Discussion

In this large-scale field experiment, we found that non-native brook trout can have stronger effects on stream-riparian food webs than the native cutthroat trout they replace, particularly on insect emergence and riparian spiders. However, the effects were complex and depended on brook trout density. When brook trout were at the higher density, we detected no difference in emergence compared with cutthroat trout. However, when at the same density, brook trout reduced emerging insects by 55% compared with cutthroat trout, which was consistent with our hypothesis. Our mechanistic model from this same experiment predicted that if the natural density of cutthroat trout was replaced with an equal density of brook trout, spiders would be reduced by 20%, provided that sufficient riparian branches were available as web support. Compared to the treatment with no added trout, the overall top-down effect of trout was strong on emerging insects of large-bodied taxa, and there was some evidence of an effect on large benthic taxa, but no effect could be detected on total benthic insect biomass, periphyton or riparian spiders. Below, we offer hypotheses that may explain these complex results.

Non-native versus native trout

We expected brook trout at high density to cause the greatest reduction in biomass of benthic insects and thus emerging insects, but instead found that brook trout at low density reduced emergence most. In a comparative study of 10 pairs of mountain streams (similar to Mahogany Creek) where brook trout had replaced cutthroat trout, versus those where cutthroat trout remained, we found that emergence was 36% less from the brook trout streams, and 24% less even after adjusting for the greater biomass of brook trout (Benjamin *et al.*, 2011). That comparative study measured the long-term effects of invasion and replacement by brook trout, compared with the short-term effects of removal and manipulation of trout species and density in this experiment. Overall, the combined results support the hypothesis that non-native brook trout can reduce emerging insects to a greater degree than the cutthroat trout they replace.

An important question is why low brook trout density caused higher benthic biomass but lower emergence than high brook trout density. Along with other mechanisms identified below, one explanation is that density alters both territorial and foraging behaviour of trout, as for other organisms (e.g. Fretwell & Lucas, 1970). For example, larger trout dominate optimal foraging positions and attack smaller fish that make forays for drifting invertebrates, restricting them to marginal locations

(e.g. Fausch & White, 1986) and to picking benthic invertebrates directly from the streambed (Nakano, Fausch & Kitano, 1999b). More large brook trout were present in the high-density treatment, and they could have relegated smaller fish to benthic foraging (cf. Grant & Noakes, 1987). If so, benthic foraging by the smaller brook trout may explain the low biomass of benthic insects in this treatment. In contrast, in the low-density treatment, there were fewer large fish, which may have allowed more of the smaller brook trout to forage on insects as they were emerging rather than picking immature benthic insects from the stream bed. This shift in foraging modes by brook trout with density is a hypothesis worth investigating.

The low emergence caused by brook trout at low density was consistent throughout the experiment and across blocks, and apparently occurred quickly, because it was evident by the sixth day of the experiment. Others have found similar rapid effects of trout in field experiments (Forrester *et al.*, 1994; Baxter *et al.*, 2004). Enclosures with low-density brook trout also had very low emergence of large-bodied taxa compared with others, and some of these larger taxa may be important for supporting spiders.

In contrast, the high benthic biomass caused by the low-density brook trout treatment by the end of the experiment was explained mainly by dominance of *Apatania* and chironomids. Nevertheless, these taxa did not affect emergence biomass because *Apatania* emergence peaked just before the experiment began, and the chironomids were small bodied. In the high-density treatment, we speculate that smaller brook trout were more likely to pick *Apatania* and chironomids directly from the stream bed (see above), thus reducing the benthic biomass. Taken together, these results suggest that at low-density more brook trout captured insects as they emerged towards the stream surface, whereas at high density, they more often picked insects from the stream bed.

If brook trout reduce emergence more than cutthroat trout when they are at equal density, then we expected indirect consequences for riparian consumers like spiders. At first, we found no significant difference in spider counts between these two treatments, but this analysis does not account for differences in wetted area among reaches that affects total emergence flux and is calculated at the mean branch density. In contrast, our mechanistic model that accounts for these factors showed that spider counts increased at higher total emergence flux that supplies food, and when more branches were available to support webs. As a result, when sufficient branches are available for web support,

we predict that the 55% reduction in emergence caused by the low-density brook trout treatment would reduce spiders by 20% compared with cutthroat trout at equal density. This result is similar to our comparative study, where we used a similar mechanistic model to project 6–20% lower spider numbers along streams where brook trout had replaced cutthroat trout, based on 36% lower total emergence flux (Benjamin *et al.*, 2011). When branch habitat is limiting, spiders are unable to track increases in food (Power *et al.*, 2004), adding variation that can prevent detecting this food-web linkage.

The loss of emergence owing to the replacement of cutthroat trout by brook trout at equal density could have consequences for other riparian predators like birds that rely on this subsidy. For instance, we estimated that the reduction of total prey energy exported to the riparian zone of Mahogany Creek would be 81 601 kJ km^{-1} during the 100-day summer season, which is when migrant birds like flycatchers and warblers are breeding (Appendix S1). Migrant birds of this weight require 64.0 kJ day^{-1} to support active foraging (Walsberg, 1983), and depend on emerging insects for 29% of their diet over summer (Nakano & Murakami, 2001; Uesugi & Murakami, 2007). Therefore, loss of emerging insects caused by replacement of cutthroat trout by brook trout at equal density is predicted to result in the loss of prey for 44 birds per km from the riparian zone for the summer, which was two-thirds the bird density reported from the riparian zone of a coldwater stream in northern Japan (Nakano & Murakami, 2001).

Top-down effects of trout

Reports regarding top-down influences of trout on benthic macroinvertebrates have ranged from no effect (Allan, 1982; Nakano *et al.*, 1999a; Zimmerman & Vondracek, 2007) to strong reductions (Dahl & Greenberg, 1999). Here, we detected modest effects of trout on large-bodied taxa of benthic insects, and strong effects on large-bodied emerging insects. This result is not surprising given that trout are visual predators and select larger prey (Meissner & Muotka, 2006), and because insects are especially vulnerable when they are emerging (Rader, 1997). However, we did not detect an effect of trout on the total benthic insect biomass, which included most of the principal grazer taxa, and this helps explain why we did not detect cascading effects on periphyton. Here, we consider six possible reasons to explain these results, including the effects of study design, timing, non-consumptive effects and intermediate predators.

The first reason that may explain why we did not detect strong trout effects on all benthic taxa is that we used large enclosures to incorporate realistic habitat complexity. Ecologists have long recognised that this complexity can lessen the impacts of predators on prey (e.g. Huffaker, 1958). Second, our 2-month experiment may not have been long enough to detect the effects of fish we hypothesised, although others (e.g. Forrester *et al.*, 1994) measured effects sooner in large enclosures. Third, seasonal timing can also influence the top-down effects of fish (Flecker & Townsend, 1994). For instance, peak emergence apparently occurred just before the experiment (JRB and FL, personal observation), so a stronger effect on emergence (and perhaps benthic insects and periphyton) may have been detected if our experiment could have been started earlier or been extended to encompass more of the invertebrate prey life cycles.

A fourth possible reason is that we were unable to control the presence of small trout fry in the treatments because of the mesh size of enclosures. Age-0 fry (19–45 mm) could move through the mesh fences and were emerging from the gravel throughout the stream during the first half of the study. Nevertheless, although trout fry were present in all our treatments, there were no differences in their density ($P = 0.32$ by ANOVA), so we considered it an ambient condition for the experiment. In a companion study, we found that consumption of benthic macroinvertebrates by these fry made up only about one-fifth of the total (Lepori *et al.*, 2012), and this small effect of age-0 salmonids on benthic macroinvertebrates is consistent with previous tests (Culp, 1986; Zimmerman & Vondracek, 2007). If a smaller mesh had been used to exclude fry, the fences would have quickly clogged with organic matter and failed, compromising our treatments.

Fifth, it is possible that non-consumptive effects influenced invertebrate prey movement, growth, or foraging behaviour in our experiment. For instance, chemical cues from brook trout and cutthroat trout in other Rocky Mountain streams and mesocosms have altered the drift behaviour of mayfly species (McIntosh, Peckarsky & Taylor, 1999, 2002; McIntosh & Peckarsky, 2004) and reduced their size and fecundity at emergence (Peckarsky *et al.*, 2002). However, in a concurrent study (Lepori *et al.*, 2012), an analysis of population fluxes suggested that the abundance of only a minority of taxa could have been influenced by induced changes in migration rates. Nor did we detect any differences in the size of individual emerging taxa among treatments, suggesting that growth was mostly unaffected.

Because brook trout and cutthroat trout were originally present in our study stream, and their chemical cues may travel up to 30 m (Peckarsky *et al.*, 2002), it is likely trout essence was present as a background condition throughout our stream (McIntosh *et al.*, 2002). Consequently, the results of our experiment, and in particular the No Fish treatment, should be interpreted as tests of only consumptive effects of fish on invertebrate prey.

Lastly, it is possible that the effects of predatory insects occupying an intermediate trophic level or the presence of invertebrates relatively invulnerable to fish predation may have influenced our results. Other studies have shown that invertebrate predators and invulnerable herbivores can play a role in the trophic control of stream communities (e.g. Peckarsky *et al.*, 2008; Power, Parker & Dietrich, 2008). We found that fish consumed all of the dominant invertebrate taxa in our study stream, including larvae of small, cased caddisflies (Lepori *et al.*, 2012), which suggests prey vulnerability was unlikely to explain differences we observed. Although predatory benthic insects did occur in our study stream, as a group, their biomass did not vary among treatments, so this also seems unlikely to explain our findings. Nevertheless, there was weak evidence that compared with No Fish treatments, fish reduced large-bodied predatory stoneflies in the benthos. If this was the case, then we might have expected some grazing invertebrates to show evidence of a release from stonefly predation. This could be part of the reason we observed greater biomass of grazing taxa in the BK-low treatment (largely owing to *Apatania* and chironomids), but if so it is not clear why such an effect did not manifest itself in other fish treatments. To address such uncertainties, studies are needed that explicitly investigate the potential for invertebrate traits, including feeding and behaviour of predatory insects, to mediate effects of fish on food webs.

Future directions

Through a large-scale field experiment, we show that non-native brook trout can alter ecosystem functions like insect emergence compared with the native cutthroat trout they replace. These findings confirm similar results of our broad comparative study in 20 other streams in two Rocky Mountain regions (Benjamin *et al.*, 2011). Together, these studies help refute an earlier report that predicted that brook trout have ecosystem consequences similar to cutthroat trout (Quist & Hubert, 2004), which led those authors to conclude that this species

replacement is relatively benign. In contrast to that view, brook trout invasion could have important consequences not only by replacing native cutthroat trout, but also by reducing important food resources for riparian predators like spiders and birds, which rely on insect emergence for 25–100% of their diet (Nakano & Murakami, 2001; Baxter *et al.*, 2005). Likewise, loss of emergence will likely reduce nutrient fluxes from streams to their riparian zones, as has been demonstrated for lakes (Gratton & Vander Zanden, 2009).

Detecting and accurately quantifying these complex indirect effects require careful analysis and a thorough understanding of individual species ecology and behaviour. Here, we found that simply testing treatment effects is inadequate, because confounding variables can enter at each link in the food web. Only by linking direct treatment effects with mechanistic models of indirect effects were we able to estimate the effects of non-native trout on spiders. Likewise, we suspect that changes in trout foraging behaviour with trout density mediated effects on the food web, a hypothesis that will require more research to test. Moreover, a more comprehensive approach to these effects is needed, which explores not only the effects of direct consumption by trout on invertebrate prey, but also considers non-consumptive effects on invertebrate drift behaviour, growth and life history traits (Peckarsky *et al.*, 2008).

Overall, these results should be useful to ecologists testing indirect effects in field experiments, as well as to managers who increasingly must think beyond the direct effects of non-native species on a single native species. Our results add to the growing body of evidence that the indirect effects of non-native species can cascade to affect diverse taxa in distant habitats by altering food-web subsidies (Baxter *et al.*, 2004; Benjamin *et al.*, 2011), even when they simply replace native species that are apparently similar.

Acknowledgments

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Percent composition of benthic and emergence biomass.

Figure S1. Spider counts as a function of total emergence flux and total branch density for the 4 treatments in 20 study reaches, each sampled at the midpoint and end of the experiment.

Appendix S1. Riparian summer migrant birds lost owing to replacement of cutthroat trout by brook trout at equal density.

[Correction added on February 5 2016, after first online publication on 6 May 2013: The supporting information has been amended]

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