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Piscivore addition causes a trophic cascade within and across ecosystem boundaries

Seth M. Rudman, Julian Heavyside, Diana J. Rennison and Dolph Schluter

S. M. Rudman (rudman@zoology.ubc.ca), J. Heavyside, D. J. Rennison and D. Schluter, Dept of Zoology, Univ. of British Columbia 4200-6270 University Blvd. Vancouver, BC, V6T1Z4, Canada.

The addition of predators can play a key role in structuring ecological communities through both consumptive and non-consumptive effects. Stocking of piscivorous fish in lakes and similar experimental introductions have provided fundamental evidence in support of trophic cascade theory. Yet, the impact of piscivore addition on cross ecosystem subsidies and meso-predator resource use has not been well studied. Here, we use a replicated pond experiment to document the trophic impacts of a piscivore, cutthroat trout *Onchorhynchus clarkii*, on aquatic communities already containing a meso-predatory fish (threespine stickleback *Gasterosteus aculeatus*) and neighbouring terrestrial ecosystems. We find that piscivore addition led to a trophic cascade that extended across an ecosystem boundary: trout addition increased the biomass and average size of insects emerging into the terrestrial system. Piscivores caused a diet shift in stickleback, a non-consumptive effect that was likely mainly responsible for the increase in emerging insect biomass. We additionally show that heterogeneity in the strength of the pelagic trophic cascade was more closely correlated with the magnitude of diet shift (reflecting a non-consumptive effect) than decreases in stickleback abundance (a consumptive effect). Taken together, our experiment demonstrates that the addition of a piscivore causes a trophic cascade that can extend beyond the aquatic system and suggests that non-consumptive effects may more strongly influence the strength of a trophic cascade than has been previously recognized.

Trophic cascades, in which top–down control of community structure leads to indirect effects two or more trophic levels below, form the backbone of a predictive framework for the extended outcomes of trophic interactions (Paine 1980, Carpenter et al. 1985). Manipulations of the species present in aquatic communities, often through fish stocking, have provided many of the strongest empirical examples of trophic cascades (Henrikson et al. 1980, Benndorf 1987, Carpenter et al. 1987, Elser and Carpenter 1988, Mittlebach et al. 1995). However important gaps remain. For example, the extent to which a trophic cascade crosses the ecosystem boundary between aquatic habitats and neighbouring terrestrial ecosystems is largely unknown. Also, little is known about the relative contribution of consumptive and non-consumptive effects as mechanisms driving trophic responses (Peckarsky et al. 2008).

One way in which top–down control in aquatic systems might have effects that cross an ecosystem boundary is via the production of aquatic insects. Many insects spend the larval portion of their life cycle in the littoral and benthic zone of aquatic environments and emerge as adults to feed and reproduce in the terrestrial landscape, where they are an important subsidy for birds, frogs, bats, and even fish in other watersheds (McCarty 1997, Finlay and Vredenburg 2007, Epanchin et al. 2010, Fukui et al. 2006, Uno and Power 2015). Fish can have profound consumptive effects on the benthic aquatic larval stages of these insects, which can alter insect emergence (McCarty 1997, Pope et al. 2009) and ultimately influence important ecosystem functions of terrestrial environments, such as pollination (Knight et al. 2005).

To date studies examining the link between predatory fish addition and insect emergence have focused on aquatic systems that previously didn't contain fish, with the result that the added fish species largely consumed benthic invertebrates (Baxter et al. 2005, Knight et al. 2005, Pope et al. 2009, Epanchin et al. 2010). These studies have found that the addition of one trophic level of fish depletes predatory emerging insects (Knight et al. 2005, Pope et al. 2009) but may facilitate the emergence of small herbivorous larvae such as chironomids (Pope et al. 2009). Yet, many lakes that are stocked with predatory fish already contain smaller benthivorous or planktivorous fish (meso-predators), as in classic whole-lake piscivore addition experiments that have documented trophic cascades (Henrikson et al. 1980, Benndorf 1987, Carpenter et al. 1987, Elser and Carpenter 1988, Mittlebach et al. 1995). The presence of these meso-predatory fish reverses the expected impacts of top predator addition on emerging insects. Trophic cascade theory would lead us to predict that the addition of a piscivore would reduce the numbers of meso-predatory fish, facilitate emergence of large predatory insects, and decrease emergence of chironomids. The trophic level of the stocked species, influenced both by the biology of the species and the pre-stocking species composition, thus determines the predicted effects of fish stocking. Understanding how predator addition impacts the emergence of adult aquatic insects in longer food chains is key to understanding both the scope of the trophic cascade and the wider impacts of fish stocking on ecosystem dynamics.

Predictions about the impacts of predator addition into areas already containing meso-predators hold if we assume that the effects of adding a piscivore are mainly consumptive. Whole lake experiments have documented decreases in meso-predatory fish biomass as a result of piscivore introduction (i.e. a consumptive effect) and these consumptive effects could be a key component of the trophic cascade (Mittlebach et al. 1995, Carpenter and Kitchell 1996). However, predator presence can also lead to changes in phenotypes such as foraging efficiency or habitat use, which are often termed non-consumptive effects. These non-consumptive effects can strongly impact other species and can be sufficiently strong to cause shifts in community composition in some experimental systems (Nyström et al. 2001, Peacor and Werner 2001, Schmitz et al. 2004, Peckarsky et al. 2008). The role of non-consumptive effects of piscivores in driving changes in habitat use and diet of meso-predatory fish is not well known. This is because the outcomes of consumptive and non-consumptive effects on the pelagic food web are expected to be similar. Addition of a piscivore might cause a habitat shift in meso-predatory fish that reduces predation on zooplankton, leading to an increase in zooplankton biomass and a decrease in phytoplankton biomass. A consumptive effect, namely reducing the number of meso-predatory fish, would be expected to produce a similar pelagic food web cascade. Yet, in the community of emerging insects, predictions from consumptive and non-consumptive effects differ in this system because trout forage mainly in the open water (Nowak et al. 2004) and the trophic interactions among benthic invertebrates are complex (Diehl 1992, Majdi et al. 2015). A consumptive effect that reduces meso-predatory fish would lead to a reduction in benthic foraging, an increase in large benthic invertebrates, and a decrease in emerging chironomids. In contrast, a habitat shift (a non-consumptive effect) by meso-predatory fish would increase foraging effort in the more spatially complex benthic environment leading to a decrease in large benthic invertebrates and a subsequent increase in emerging chironomids. Determining the role of the consumptive and non-consumptive effects is a critical part of understanding trophic cascades and is also important for making predictions about the timing of compositional shifts associated with predator addition.

We utilized a system of experimental ponds to test the predictions of trophic cascade theory on the trophic response following the introduction of top predator. We added a piscivore, cutthroat trout, into ponds containing threespine stickleback and measured both the open water (phytoplankton and zooplankton) and cross ecosystem (emerging insect) trophic cascade. Trophic cascade theory for consumptive effects led us to the prediction that the introduction of trout would cause a decrease in stickleback abundance, an increase in zooplankton biomass, and a decrease in phytoplankton biomass. In the benthic habitat we predicted that trout addition would lead to greater emerging insect biomass, stemming largely from a non-consumptive effect of increased stickleback foraging in the benthic environment, which has been shown to lead to increases in chironomid abundance (Harmon et al. 2009, Rudman et al. 2015) and emergence (Rudman and Schluter 2016). We additionally include a preliminary comparison of insectivorous bat activity over experimental ponds, with the expectation that bat foraging would be greater over aquatic environments where the biomass of emerging insects is greatest. Based on the above logic we expected this to be the ponds that contain cutthroat trout.

Methods

Experimental setup

We conducted the experiment in a system of 10 experimental ponds (25 × 15 m, max depth of 6 m) (see Arnegard et al. 2014 for more details). We stocked stickleback into the ponds from two sources: 1) four F_1 crosses between benthic and limnetic ecotypes of threespine stickleback taken from Paxton Lake (Texada Island, British Columbia) made in 2011 and 2) fish collected from First lake (Texada Island, British Columbia), which was seeded with F_1 crosses between benthic and limnetic ecotypes from Paxton Lake in 1980. Paxton Lake houses a pair of stickleback species that differ in their morphology and diet preferences (Schluter and McPhail 1992, Schluter 1993). Benthic ecotypes primarily consume aquatic insect larvae and limnetic ecotypes mainly consume zooplankton (Schluter and McPhail 1992). We used hybrid stickleback to maximize the amount of intraspecific phenotypic and genetic diversity in experimental populations. In the spring of 2012, each of the four F_1 families was split in half and 21–31 individuals were introduced into each of two ponds. Thirty one fish from First Lake were added to each of the remaining two ponds. Each pair of ponds was matched based on a variety of biotic criteria (i.e. macrophyte coverage, phytoplankton and zooplankton abundance) before stickleback introduction. Stickleback in all 10 ponds reproduced in the summer of 2012, producing advanced generation hybrid fish with a range of phenotypes that encompassed most of the variation between benthic and limnetic ecotypes (Arnegard et al. 2014). We introduced two (> 285 mm) cutthroat trout to a randomly chosen pond within each matched pair as a predator addition treatment in September 2012 (total of five trout addition and five control ponds).

We estimated the number of stickleback using mark–recapture methods in November 2012 and January, March and November 2013. We used six-week intervals between marking and recapturing fish to reduce any tendency for marked fish to avoid traps. We employed a Bayesian framework to generate population estimates, which took into account measured population sizes from similar experiments to set bounds on the maximum number of fish (Gazey and Staley 1986). Estimates with standard errors are listed in Table 1.

Table 1. Estimates of mean stickleback abundance from each experimental treatment. The final sample period is from the subsequent generation.

	11/1/12		1/22/13		3/7/13		11/10/13	
Treatment	Mean	SE	Mean	SE	Mean	SE	Mean	SE
No trout	1691	887	1047	252	1262	246	693	153
Trout	1977	689	1108	305	710	131	1173	703

Table 2. Standard effect sizes for the addition of piscivorous trout to ecological response variables.

Response	Cohen's D	Hedges G
Phytoplankton biomass	1.35	1.22
Zooplankton biomass	1.63	1.47
Zooplankton average mass	0.71	0.65
Emerged insect biomass	0.74	0.67
Emerged insect average mass	1.03	0.93
Bat activity	1.14	0.91

Phytoplankton, zooplankton and emerging insect measurements

Phytoplankton abundance was measured in the epilimnion (~10 cm below the surface) using spectroflourometry (fluorometer with an in-vivo module). This flourometric data was converted to ug l^{-1} of phytoplankton using a calibration curve created from lab standards (CHLa = (0.0137 × Reflectance) –0.434). Spectrofluorometry has been shown to be effective at estimating densities of natural phytoplankton, but can become inaccurate when particular species are present, particularly cyanobacteria (Gregor and Maršálek 2004). Zooplankton were sampled by taking 4.5 m vertical tows with a 30 cm diameter cod end net made from 80 µm mesh from the deepest area of each pond. Zooplankton samples were preserved in 70% ethanol, stained with rose bengal's solution, and sub-sampled to 1/20 before being classified to the lowest feasible taxonomic unit. Both phytoplankton and zooplankton were collected four times between September 2012 and February 2014. The total length of each zooplankton individual in each sample was also recorded. Published length–weight regressions were used to convert these measurements to biomass (Watkins et al. 2011).

To collect insects as they emerged from the experimental ponds, we constructed cone-shaped floating traps (33 cm in diameter) using wire and 400 µm mesh. We placed one trap in the shallows (~1.5 m depth) and one in the deep (~6 m depth) of each pond anchored with rope in the late afternoon on 11, 12, 13 and 25 June 2013. Traps were emptied the following morning using a modified hand vacuum and insects were deposited directly into vials containing 95% ethanol. Each insect was measured and identified to the lowest readily identifiable taxonomic unit. Published length–weight regressions were used to estimate the dry mass of each individual insect (Sabo et al. 2002).

To assess the impact of trout addition on phytoplankton and zooplankton biomass we took the difference between paired ponds (control – trout addition) at each sample point after trout introduction. We then used a repeated measures ANOVA to determine whether the difference between paired ponds differed significantly from 0 over time (i.e. testing for a treatment by time interaction). As insect data were collected over a two week time period we combined the emergence from each night for each pond and used a paired t-test to determine the effects of trout addition on mean emerging insect biomass and average size. We also calculated the standard effect size (Cohen's D and Hedges G) of response variables to allow comparison of effects within and across the boundary of aquatic ecosystem (Table 2). All statistical analyses were performed in R ver. 3.1.3 (<www.r-project.org>).

Consumptive versus non-consumptive effects

We used diet as a metric of non-consumptive effects of trout on stickleback habitat. Fish were collected using a combination of dip netting and open water seining (beach seine with 2 m net depth) and were immediately euthanized and preserved in 95% ethanol to maximize our ability to identify prey items. The stickleback were collected in December 2012, which was three months after trout addition but before we detected any consumptive effects (decrease in stickleback numbers in ponds with trout compared to control ponds) (Table 1). We identified and counted stomach contents of 10 fish from each of the four predator addition ponds and four control ponds that were stocked with Paxton lake F_1 crosses. We chose not to euthanize any fish from ponds stocked with fish from First Lake due to concerns about low population size. Diet items were identified to the lowest feasible taxonomic unit (often genus or family). Small zooplankton (e.g. *Bosmina*, *Alonella*, etc.) were grouped together.

To visualize differences in diet associated with predator addition, we created a two-dimensional NMDS from diet data using Bray–Curtis dissimilarities (*vegan* package in R). We then tested for differences in the diet community structure between predator addition and control ponds by creating a dissimilarity matrix between all fish and using a permutational MANOVA (Anderson 2001) to test effect of predator addition on species composition of stomach contents.

We also sought to investigate whether the strength of any trophic cascade we observed was more strongly correlated with the consumptive effects of predators on stickleback abundance or the non-consumptive effects of predators, measured by a shift in stickleback diet. The strength of the pelagic trophic cascade was calculated as the difference between the biomass of phytoplankton in matched control and piscivore addition ponds (in µg l^{-1} in the spring (April) sample. The consumptive effect of predator addition was calculated by taking the difference in stickleback abundance between matched control and predator addition ponds in the spring (March) mark–recapture study. There was a ~five-week lag between the estimation of stickleback numbers and the measurement of phytoplankton and zooplankton over which the abundance of stickleback may have changed somewhat. The non-consumptive effect was estimated using the Bray–Curtis dissimilarity matrix between stomach contents for each of the matched control and predator addition pond replicates. Diet shift was calculated as the mean dissimilarity between fish from different ponds minus the average of the dissimilarity between fish from the same pond. The correlations between the strength of the trophic cascade and the consumptive and non-consumptive effects were calculated using pearson correlation coefficients.

Bat activity

We used passive echolocation recording equipment to estimate the amount of bat activity above the experimental ponds on 26, 29 and 30 June. Each night, we placed recording equipment at the edge of two neighbouring control and at two neighbouring predator addition ponds that were ~120 m away from each other. Recording equipment can detect echolocation calls from a distance of 30 m (Adams et al. 2012), so each recorder was deployed adjacent to two ponds of the same treatment within the array. The recording equipment was oriented so that data were recorded only from ponds within 40 m of the sensor, enabling us to record over ponds of the desired treatment. Recordings began at 10 p.m. each night and were stopped at 6 a.m. We used callViewer software to manually count and identify the genus of bat emitting each of a subset of echolocation calls. The only genera present were *Myotis* and *Eptesicus*. Using the manually counted files as a guide, we used frequency and amplitude information for each recorded call to count the total number of calls from both *Myotis* (80–40 kHz) and *Eptesicus* (34–25 kHz). We used the 'seewave' package in R to transform wave files and perform a fast fourier transformation before automated counting was done in R. We refrained from significance testing on bat data as our experimental recording setup was not replicated (i.e. only one recording location for each treatment).

Data deposition

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.6gj64> (Rudman et al. 2016).

Results

Phytoplankton, zooplankton, insect emergence

We found evidence of a pelagic trophic cascade driven by trout presence: trout addition led to 34% greater zooplankton biomass on average (Fig. 1, DF = 3, F = 11.91, p = 0.0007). The average body size of zooplankton was 51% greater with trout present than without trout (Fig. 1 DF = 3, F = 3.94, p = 0.036). We observed a corresponding 174% decrease in the total biomass of phytoplankton (Fig. 1, DF = 3, F = 7.84, p = 0.004) with trout present, which demonstrates the indirect effect of trout on the pelagic environment.

We also found effects on benthic insect emergence. Over four nights of insect emergence trapping we collected 318 insects comprising a total biomass of 17 275.39 mg. We found a significant effect of trout addition on the total biomass of emerging insects (Fig. 2, DF = 4, t = 3.21, p = 0.033), with a 93% increase in log-biomass relative to ponds without trout. Trout addition ponds also showed an increased mean body mass (i.e. log-biomass) of insects (Fig. 2, DF = 4, t = 4.07, p = 0.015), with insects emerging from trout-addition ponds having 125% greater body mass on average. Chironomids, which made up 93% of the total number of insects sampled and showed a trend towards a larger average size in ponds with trout (DF = 4, t = 2.03, p = 0.11). Although four out of five pond pairs showed a greater biomass of chironomids emerging when trout were present, there was no treatment effect (DF = 4, t = 0.76, p = 0.49).

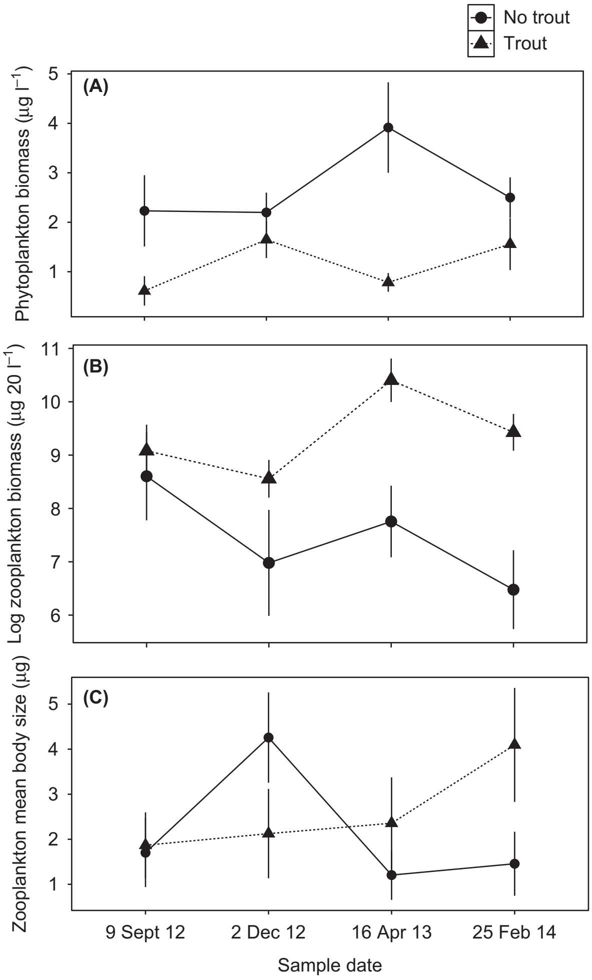

Figure 1. The trophic cascade within the open water of the aquatic ecosystem. (A) the biomass of phytoplankton (B) the log-transformed biomass of zooplankton (C) average zooplankton body size (mass). Data for all panels show data just before trout introduction (25 September 2012); analysis for the impacts of trout addition were conducted only on data from later dates. Points represent means for individual ponds with standard errors around each mean, with lines connecting means of each treatment.

Bat activity

We recorded a total of 74 240 bat echolocation calls over three nights of monitoring. The number of bat calls, and hence activity, was greater over the experimental area that contained trout in each of the 3 nights of recording by an average of 34% (Fig. 2C). Bat activity data are bulked rather than replicate measurements due to limitations of the experimental array, so uncertainty of the treatment effect is not measured. As such, these data only give a preliminary indication of the effect of piscivore addition on bat foraging.

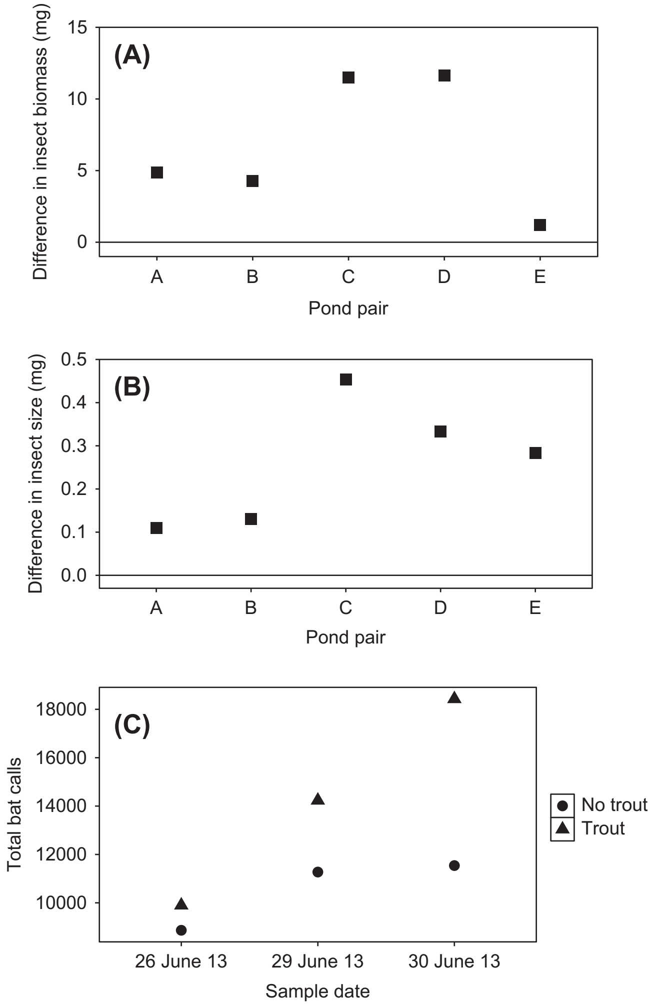

Figure 2. The effects of trout addition on: (A) the biomass of insects emerging from experimental ponds; (B) the average body mass of insects emerging from experimental ponds; and (C) bat activity as measured by passive echolocation. (A) and (B) show the differences between paired ponds with each point representing the difference between one pair of ponds. Values greater than zero indicate an increase in ponds with trout addition.

Habitat shifts, non-consumptive effects, and the trophic cascade

To assess treatment effects on habitat use, we identified 6297 prey items from the stomachs of 80 stickleback. A permutational MANOVA illustrated a significant difference in diet composition between stickleback from predation and control ponds (DF = 1, F = 12.72, p = 0.002). This corresponded with a shift away from zooplankton and towards increased consumption of benthic invertebrates in predator addition ponds (Fig. 3). Fish stomachs from control ponds had ~9-fold more small zooplankton than those from ponds with piscivores. The second most numerous taxon in the stickleback diet was chironomid larvae, which were ~4-fold more abundant in fish taken from predator addition ponds than those without predators.

We measured diet only three months after trout addition, which was before we had observed any significant declines in stickleback abundance (Table 1, Fig. 4). This suggests that predator addition influenced stickleback habitat use, reducing their consumption of open water zooplankton and increasing their consumption of benthic insect larvae. To test whether this might influence the strength of the pelagic trophic cascade, we plotted measures of both the consumptive and non-consumptive effects of trout against

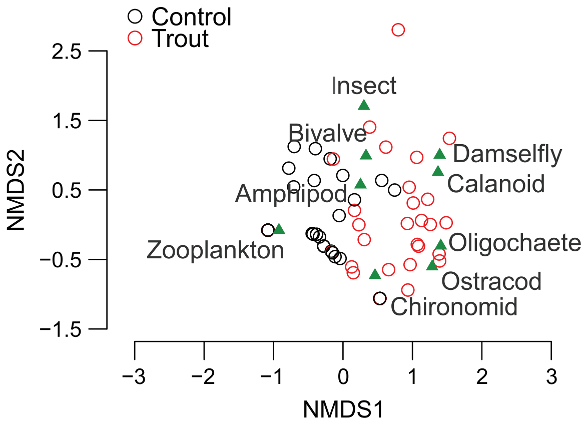

Figure 3. A NMDS plot of stomach contents of threespine stickleback collected ten weeks after piscivore addition. Taxa names are included only for taxa that were represented by > 3 individuals in stomach contents (taxa positions shown as green triangles).

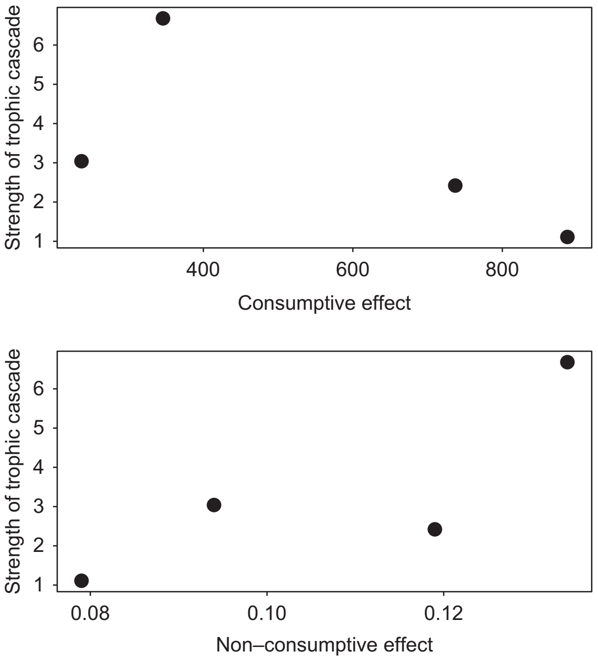

Figure 4. The relationship between the strength of the pelagic trophic cascade and measures of (A) consumptive effects; and (B) non-consumptive effects. Consumptive effects were measured as the reduction in number of stickleback in predator addition ponds relative to control ponds. Non-consumptive effects were measured as the shift in diet composition (e.g. the reduction in zooplankton consumption) between predator addition and control ponds. The strength of the trophic cascade was measured as the phytoplankton biomass in control pond – phytoplankton biomass in the matched predator addition pond.

the strength of the pelagic trophic cascade at peak summer conditions and tested for a correlation with a Pearson's product moment correlation coefficient (Fig. 4). The consumptive effect of predator addition showed a weak negative relationship to the strength of the trophic cascade ($r = -0.68$ $SE = 0.37$). In contrast, the non-consumptive effect had a positive relationship with the strength of the pelagic trophic cascade ($r = 0.82$, $SE = 0.28$).

Discussion

Aquatic trophic cascades following piscivore addition to lake ecosystems are a classic example of the indirect effects of predators on lower trophic levels (Carpenter et al. 1985, Carpenter and Kitchell 1996). Our study demonstrates that the addition of a piscivore initiates a trophic cascade that can impact a cross-ecosystem subsidy (Fig. 1, 2). Trout addition led to an increase in the biomass and average body size of emerging insects, which can be explained by at least two mechanisms. First, it could be due to decreased predation pressure by stickleback on benthic invertebrates stemming from the consumptive effects of trout on stickleback density (Table 1). With decreased predation pressure from stickleback, a greater proportion of aquatic insect larvae could have survived to pupate. Second, this change in insect emergence could also have come from an induced habitat shift and increased stickleback foraging in benthic environments (i.e. a non-consumptive effect), leading to a reduction in the number of predatory benthic invertebrates, and a release of benthic grazers and filter feeders (i.e. chironomids). Greater foraging activity by stickleback in benthic environments could also have lead to changes in benthic invertebrate foraging behaviour and growth rates, which could further release benthic invertebrate grazers (Diehl 1992, Ball and Baker 1996, Weber and Traunspurger 2015). Previous experiments have suggested that increased foraging on benthic invertebrates by stickleback increases the abundance of chironomids (Harmon et al. 2009, Rudman et al. 2015). In the current experiment, increased insect emergence observed in piscivore addition replicates is more consistent with a non-consumptive effect, as increases in chironomid abundance, which made up the vast majority of emerging insects, are associated with increased benthic foraging of stickleback. However, the increase in chironomid emergence cannot explain the entirety of the differences in emerging insect biomass between predator addition and control treatments. The introduction of fish can have a large effect on insect emergence (Pope et al. 2009) and on terrestrial species that rely on them as a subsidy (McCarty 1997, Finlay and Vredenburg 2007, Epanchin et al. 2010). Our study demonstrates that the effects of trout introductions on emerging insects, and hence the cross-ecosystem component of the trophic cascade, depends strongly on the fish community present before introduction.

The relative roles of consumptive and non-consumptive effects in driving trophic cascades are not well understood. There is evidence that piscivores consume prey fish species in trophic cascade studies (Carpenter et al. 1987, Elser and Carpenter 1988, Mittlebach et al. 1995), but there is also evidence for non-consumptive effects of predators on prey fish (Werner et al. 1983, Carpenter et al. 1987, He and Kitchell 1990). Although our study was not designed to disentangle consumptive and non-consumptive effects and had limited power to explore this relationship, we did find some evidence that the diet shift following predator addition may play a role in determining the strength of the pelagic trophic cascade (Fig. 4). Surprisingly, we observed a negative relationship between the consumptive effects of predators and the strength of the observed pelagic trophic cascade (Fig. 4). This result, combined with a positive correlation between the diet shift in stickleback and the strength of the trophic cascade suggest that diet shifts associated with predator introduction may be an important part of trophic cascades in freshwater systems. Non-consumptive effects have been shown to be a component of trophic cascades in other systems (Schmitz et al. 2004, but see Bestion et al. 2015), suggesting that they may be play a role in the outcome of many trophic cascades. Future work aimed at disentangling the consumptive and non-consumptive effects would be informative both from an ecological and management standpoint.

Chironomids, which made up the vast majority of insects we captured, are an important prey item for *Myotis* bats (Clare et al. 2014), which feed preferentially over water (LaVal et al. 1977). We found some evidence that trout addition led to a shift in insectivorous bat foraging within our experimental array that corresponded with increased foraging over ponds with greater emerging insect biomass (Fig. 2). The experimental ponds are all located within a single clearing and the two recording units were set up adjacent to ponds that were ~120 m apart, well within the foraging range of both *Myotis* and *Eptesicus* bats. This suggests any difference in bat foraging can be ascribed to choice, as opposed to distance from roosting habitat or migratory routes. Previous studies have documented that bats alter foraging patterns based on insect availability (Fukui et al. 2006). Many species rely on the cross-ecosystem subsidy of emerging insects from aquatic environments, and given that the timing of insect emergence coincides with the reproductive season for both *Myotis* and *Eptesicus* bats (Crichton and Krutzsch 2000) emerging insects could be an important subsidy for some of these populations. However, our bat monitoring data was bulked and we consider these findings preliminary. Further work to understand the interplay between aquatic community structure, insect emergence, and bat foraging could help determine the strength of these relationships and if there are management actions that could promote foraging by insectivorous bats, many populations of which are currently threatened in North American (Blehert et al. 2009).

Our study demonstrates that the trophic cascade from piscivore addition extends beyond the aquatic system. The average effect size for the aquatic response variables was larger (1.11) than those from the cross-ecosystem insect and bat responses (0.84), but the effects across the ecosystem boundary were still appreciably strong (Table 2). Trophic cascades can result from both prey reduction due to predator consumption or non-consumptive effects of predation, namely a shift in prey species behaviour (Peckarsky et al. 2008). We observed a decline in stickleback abundance in piscivore addition ponds in the spring of the first year. Surprisingly this pattern was reversed in following generation, perhaps due to strong competition (and hence small size and reproductive output) in ponds without predators. We also observed a non-consumptive effect, the shift of stickleback diet (Fig. 3), which seemed to correlate more strongly to the strength of the trophic cascade. In addition, we found that species compositional changes in the herbivore community and non-consumptive effects were better predictors of the strength of the trophic cascade than anticipated. As a whole, our results demonstrate some of the important mechanisms of a trophic cascade and that the effects of a trophic cascade can extend across ecosystem boundaries.

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