Trophic interactions across lake–stream boundaries in mountain lakes

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ABSTRACT

Fish can affect the mass flux of invertebrates across aquatic ecosystem boundaries, as shown by the effects of fish on export of zooplankton from lakes to outlet streams in 12 oligotrophic lakes in Rocky Mountain National Park (RMNP), Colorado (6 lakes and streams with fish; 6 without fish). Lakes without fish exported to streams 5 times as much zooplankton biomass as lakes with fish because of strong suppression of large zooplankton in lakes with fish. Of the zooplankton biomass exported to streams from both types of lakes, 95% was lost within 500 m of the lakes; the greatest rate of loss occurred within 10 m. Higher rates of loss for large zooplankton in streams below lakes without fish suggest that fish predation is not the primary cause for loss of zooplankton below lakes. In streams with and without fish, small zooplankton were lost at much lower rates downstream than large zooplankton. Daylight and nocturnal sampling showed much higher exports of zooplankton and, especially for large taxa, from lakes to streams at night, presumably because of diel vertical migration. Stream locations near a lake outlet had high total macroinvertebrate biomass, especially for filtering and gathering collectors as well as detritivores, indicating that macroinvertebrate predation is likely related to zooplankton mass flux. Large zooplankton also could have high vulnerability to interception by the channel substrate, which could stimulate detritivory. Biomass of all macroinvertebrates, and specifically of the filtering and gathering collectors, was lower in streams with fish because fish suppressed the export of zooplankton food for macroinvertebrates from the lakes and directly consumed macroinvertebrates. Therefore, the RMNP lakes and their outlet streams demonstrate trophic compression of stream macroinvertebrates by fish, during which macroinvertebrates are simultaneously pressured by increasing top-down forces from direct predation and reduced bottom-up forces because zooplankton are suppressed by fish in lakes.

Introduction

Lakes export biomass and energy to streams through the entrainment of zooplankton in outlet water (e.g., Chandler 1937, Walks and Cyr 2004, Chang et al. 2008). By reinforcing food supply that could be used by consumers in stream reaches below lakes, lacustrine zooplankton influence the abundance and species composition of invertivorous communities (Robinson and Minshall 1990, Richardson and Mackay 1991, Eriksson 2001).

Because fish suppress the biomass of zooplankton in lakes (Carlisle and Hawkins 1998, Parker et al. 2001, Schabetsberger et al. 2009), subsidies of zooplankton to food webs downstream of lakes are likely reduced by the presence of fish. Several aspects of fish-driven changes in export of zooplankton to streams below lakes are poorly understood, including the distance over which zooplankton are removed in streams below lakes with and without fish, the degree to which zooplankton exported to streams are consumed (macroinvertebrates, fish), and the effect of zooplankton vertical migration in lakes on invertebrate export to streams.

Quantification of trophic interactions across lake to stream boundaries is best achieved by comparison of multiple lake and stream pairs that are physically similar but in some cases have fish and in other cases do not. Such studies are possible, as reported here, for lakes of Rocky Mountain National Park (RMNP), which contains numerous small, oligotrophic lake and stream pairs with and without fish. Comparisons were used here to test 3 hypotheses: (1) export and the mass flux of lacustrine zooplankton is greater in streams below lakes without fish than below lakes with fish; (2) the mass flux of zooplankton and distance below lakes influences the community composition and biomass of stream benthic macroinvertebrates; and (3) for lakes with and without fish, nocturnal
vertical migration accentuates export of zooplankton from lakes to streams.

**Methods and study site**

Study sites included 6 lakes with fish and 6 without fish in the headwaters of the North Fork of St. Vrain Creek, RMNP, Colorado (Table 1). Sampling alternated between lake and stream pairs with fish and without fish between 29 July and 22 August 2013, when zooplankton biomass in these lakes is near its annual peak (Detmer et al. 2017) and production in nearby streams is nearing its peak (McCutchan and Lewis 2002). Peak discharge in the basin typically occurs in June (McCutchan and Lewis 2002) when all surface waters are nutrient poor (McCutchan and Lewis 2002, Detmer et al. 2017). August discharge in 2013 was slightly lower than average.

Records provided by the US Fish and Wildlife Service show that, of the 6 fishless lakes, 2 were never stocked and the remaining 4 were stocked but became fishless because of inadequate spawning habitat. The 4 lakes that were stocked but became fishless have been fishless for more than 30 years and therefore have likely reverted to their historical faunal conditions (Knapp et al. 2001). These records also show that lakes with fish contain naturally reproducing populations of cutthroat trout (*Oncorhyncus clarkii*), brook trout (*Salvelinus fontinalis*), or both (Table 1), both of which have demonstrated strong negative effects on zooplankton biomass and body size in lakes at high elevation (Carlisle and Hawkins 1998). Fish were present in all streams below lakes containing fish, but not in streams below lakes without fish because waterfalls downstream of the study reaches act as a barrier to entry from lower elevation streams containing fish.

Bathymetric maps were created for each lake with a global positioning system (GPS) unit and a portable sonar device at 45–200 points, depending on the lake size. Geographic information models and calculations for mean and maximum depth were conducted with a triangulated irregular network in ArcGIS 10.2.2.

All lakes had an area ≥1 m deep within 50 m of the outlet and had no macrophytes within 20 m of the outlet. Lake temperature was measured near noon at the lake outlet. Stream discharge was calculated at the same time from the sum of 10 velocity–depth profiles obtained with a current meter (Gordon et al. 2004). Physical characteristics of lakes and streams did not differ significantly between lakes with and without fish (Table 1).

Lacustrine zooplankton were sampled with vertical tows of a conical zooplankton net from near the bottom to the surface (20 cm diameter, 53 μm mesh) at the deepest location and at 3–8 additional arbitrary locations of ≥1 m depth; the mean densities of zooplankton for these sites were used in analyses. These samples were taken within 90 min of noon. Efficiency of the net was assumed to be 50% (Walters and Vincent 1973, Lewis 1979).

Based on the rapid reduction of zooplankton abundance with increasing distance from lakes as shown by previous studies (Chandler 1937, Chang et al. 2008, Doi et al. 2008), zooplankton samples in streams below lakes were collected at 1, 10, 50, 100, 200, and 500 m below the first riffle at approximately the same time as lacustrine samples. Zooplankton in streams were collected from near the thalweg of the stream 30 times with a 1 L bottle at each sampling site; the water was poured through a conical zooplankton net.

Diel variation in zooplankton export from lakes to streams was evaluated for Thunder Lake, with fish, and Bluebird Lake, with no fish. Zooplankton were collected 1 m downstream of the lake over 24 h at intervals of 2 to 4 h. Longitudinal sampling of the downstream waters was conducted at all distances mentioned earlier at midday.

**Table 1.** Characteristics of RMNP lakes with and without fish on the day of sampling. BT = brook trout; CT = cutthroat trout.

| Lake            | Fish | Elevation (m) | Lake area (ha) | Maximum lake depth (m) | Mean lake depth (m) | Temperature (°C) | Discharge (m³ s⁻¹) |
|-----------------|------|---------------|----------------|------------------------|---------------------|------------------|-------------------|
| **Lakes without fish**                      |      |               |                |                        |                     |                  |                   |
| Bluebird        |      | 3371          | 5.0            | 9.3                    | 3.4                 | 12.7             | 0.29              |
| Eagle           |      | 3296          | 5.2            | 16.2                   | 4.7                 | 10.4             | 0.19              |
| Falcon          |      | 3371          | 1.1            | 7.7                    | 2.5                 | 10.1             | 0.22              |
| Finch           |      | 3021          | 2.6            | 2.6                    | 1.3                 | 16.2             | 0.01              |
| Lion Lake 1     |      | 3373          | 1.8            | 12.8                   | 4.3                 | 11.0             | 0.17              |
| Lion Lake 2     |      | 3460          | 1.5            | 8.5 (2.2)              | 2.8 (0.6)           | 12.0 (0.9)       | 0.18 (0.03)       |
| Mean (SE)       |      | 3316 (63)     | 2.8 (0.7)      | 8.5 (2.2)              | 2.8 (0.6)           | 12.0 (0.9)       | 0.18 (0.03)       |
| **Lakes with fish**                             |      |               |                |                        |                     |                  |                   |
| Box             | BT   | 3266          | 1.6            | 9.3                    | 3.9                 | 11.7             | 0.23              |
| Lower Hutcheson | CT   | 3304          | 1.7            | 7.6                    | 2.9                 | 13.4             | 0.19              |
| Ouzel           | BT & CT | 3052 | 2.0            | 2.7                    | 0.7                 | 9.3              | 0.39              |
| Pear            | CT   | 3225          | 6.0            | 16.8                   | 6.2                 | 12.9             | 0.08              |
| Sandbeach       | CT   | 3135          | 4.8            | 7.9                    | 2.4                 | 15.5             | 0.05              |
| Thunder         | CT   | 3225          | 5.9            | 12.9                   | 4.3                 | 10.7             | 0.42              |
| Mean (SE)       |      | 3201 (37)     | 3.7 (0.8)      | 9.5 (2.0)              | 3.4 (0.8)           | 12.2 (0.8)       | 0.22 (0.06)       |
and midnight. Vertical zooplankton tows in the lake were collected only at midday because, although the vertical distribution of zooplankton differs between day and night, their biomass per unit area does not (e.g., Pennak 1944, Masson et al. 2001, Brosseau et al. 2012).

For both lakes and streams, all samples were fixed in 95% ethanol and then washed and preserved in 70% ethanol (Black and Dodson 2003). For counting, zooplankton were concentrated to 100 mL, and at least 4 subsamples ranging in size from 1 to 20 mL were analyzed in a modified Bogorov sampler for identification, measurement, and counting, except when the density was low, when the entire sample was processed. Zooplankton were identified to the lowest practicable taxonomic level (typically genus or species: Stemberger 1979, Pennak 1989, Thorp and Covich 1991). For abundant taxa, body lengths of at least 100 organisms were measured with an optical micrometer; for taxa with fewer than 100 organisms per subsample, all organisms were measured. Allometric equations were used to calculate dry mass of individual zooplankton (Dumont and Balvay 1979, USEPA 2003).

For streams, 2–4 macroinvertebrate samples were collected at each zooplankton sampling site with a Surber sampler (0.09 m², 243 μm mesh), pooled, and preserved in 70% ethanol. All macroinvertebrates were identified (Thorp and Covich 1991, Ward et al., 1992, Merritt and Cummins 2008) and counted. With the exception of Oligochaeta, Ostracoda, Hirudinea, Acarina, Coleoptera, and Diptera, all taxa were identified to genus or species. Coleoptera were identified to family or genus. Diptera were categorized as nontanypodinate chironomids, tanypodinate Chironomidae, Simuliidae, Empididae, Psychodidae, Tipulidae, and other. All taxa were assigned to functional feeding groups per Merritt and Cummins (2008). When at least 100 organisms were found in a sample of a particular taxon, at least 100 organisms were measured. For less abundant taxa, all organisms were measured. Individual dry mass was calculated based on allometric equations from Baumgartner and Rothaupt (2003), Benke et al. (1999), Johnston and Cunjak (1999), and Misenerendino (2001).

**Statistical methods**

Regressions were used to relate zooplankton within lakes to zooplankton entering streams below lakes. Contrasts in means between lake and stream pair categories (fish, no fish) were conducted with an independent samples Student’s t test. Zooplankton were sorted into small (<0.1 μg), medium (0.1–1.0 μg), and large (>1 μg) size categories for contrast between lakes with plankton in lakes (Brooks and Dodson 1965, Carlisle and Hawkins 1998, Knapp et al. 2001, Detmer et al. 2017).

Progressive downstream loss of zooplankton in streams below lakes (mass flux, g dry mass m⁻² d⁻¹) was calculated as the difference in zooplankton dry biomass per unit volume (μg m⁻³) between the upstream and downstream points of the reach multiplied by the flow (m³ s⁻¹) and divided by the area of the stream reach between the 2 points (m²), and converted to appropriate units (g m⁻² d⁻¹). An ANCOVA was used to test the relationship between the mass flux of zooplankton and fish with each reaches' upstream distance below lake outlet as a covariate for all zooplankton and for zooplankton of the 3 size categories. For this analysis 100 μg m⁻² d⁻¹ was added to normalize the data. The same technique, except with no addition, was applied to noon and midnight comparisons of total zooplankton mass flux below a single lake with fish (Thunder Lake) and a single lake without fish (Bluebird Lake).

Densities of macroinvertebrates were used to calculate a similarity matrix for nonmetric multidimensional scaling (NMDS; Minchin 1987) with the Bray-Curtis distance matrix (Bray and Curtis 1957) to create an image of changes in community structure with increasing distance from lakes with and without fish. A permutational analysis of variance (PERMANOVA) was used via the adonis function within the vegan package to test for differences in macroinvertebrate community structure with increasing distance streams below lakes with and without fish (Oksanen et al. 2016).

For comparisons with zooplankton mass flux based on midday synoptic sampling, macroinvertebrate biomass was estimated for each taxon in each stream reach (interval between sampling points) as the mean for the upstream and downstream sampling site for each study reach. An ANCOVA followed by model simplification (Crawley 2007) was used with these values to evaluate the interaction and independent effects of fish and zooplankton mass flux on total macroinvertebrate biomass and biomass of functional feeding groups of macroinvertebrates.

In all analyses, data were log₁₀ transformed as necessary to normalize data, except for distances below lakes, which were normalized with a square root transformation. For all statistical tests, alpha was 0.05 except where multiple tests were applied to a single response variable (size categories of zooplankton and functional feeding groups), which were corrected by the Bonferroni method (Zar 1984).

**Results**

Mean body size of zooplankton, measured as micrograms dry mass per individual, was smaller at the deepest location in lakes containing fish (0.40 ± 0.04 μg) than in lakes without fish (2.33 ± 1.24 μg; t₁₀ = 5.41, P = 0.0008). Likewise, biomass of zooplankton was greater within
lakes without fish (58024 ± 18589 μg m⁻³) than with fish (14377 ± 5405, μg m⁻³; t₁₀ = 2.25, P < 0.05; see also Detmer et al. 2017).

In streams 1 m below lakes, body size of zooplankton was closely related to the body size of zooplankton within lakes (R² = 0.68, P < 0.001):

\[
\log_{10}[\text{stream body size}] = -0.12 + 1.08 \\
\times \log_{10}[\text{lake body size}].
\]

Zooplankton body size 1 m below lakes without fish (2.26 ± 0.07 μg) was almost 10 times greater (P < 0.01) than 1 m below lakes with fish (0.26 ± 0.07 μg). Biomass of zooplankton (μg m⁻³) 1 m below lakes also was closely related to zooplankton biomass in lakes (R² = 0.58, P < 0.01):

\[
\log_{10}[\text{stream biomass}] = 0.40 + 0.60 \\
\times \log_{10}[\text{lake biomass}].
\]

Mean body size in streams below lakes without fish decreased with increasing distance (R² = 0.29, P < 0.001):

\[
\log_{10}[\text{zooplankton body size}] = 1.3917 + -0.8963 \\
\times \text{distance}^{0.5}.
\]

In streams below lakes with fish, where zooplankton body size entering streams is smaller than for streams below lakes without fish, no significant reduction in mean body size was observed with increasing distance from the lake (P > 0.05).

Zooplankton biomass per unit volume 1 m downstream of lakes without fish (3456 ± 1571 μg m⁻³) was greater (t₁₀ = 2.37, P = 0.04) than zooplankton biomass entering streams below lakes with fish (658 ± 291 μg m⁻³). As could be expected because of the reduced body size of zooplankton entering streams below lakes with fish, pairwise comparisons of zooplankton biomass 1 m below the lake outlet differed among size categories of zooplankton (Fig. 1). Differences between streams with and without fish were greatest for large zooplankton because biomass of large zooplankton was lower below lakes with fish (>1 μg; ANOVA F₁,₁₀ = 10.83, P = 0.01; Fig. 1). Export of small- and intermediate-sized zooplankton to streams below lakes did not differ in relation to presence or absence of fish (P > 0.05).

The mass flux of all zooplankton to streams per unit area of stream surface (g dry mass m⁻² d⁻¹) was greatest upstream and decreased downstream more rapidly in streams below lakes without fish than below lakes with fish (ANCOVA distance⁰.⁵ × fish, F₁,₅₆ = 5.71, P = 0.02). This pattern is explained primarily by large zooplankton, which initially had a greater maximum flux but were lost more rapidly in streams below lakes without fish than below lakes with fish (Fig. 2; ANCOVA distance⁰.⁵ × fish, F₁,₅₆ = 3.90, P = 0.05). The mass flux of medium zooplankton was not influenced by fish independently or in combination with distance but was influenced directly by distance (ANCOVA distance⁰.⁵ F₁,₅₆ = 62.27, P < 0.001).

**Diel variation in zooplankton export**

Zooplankton biomass per unit volume entering the stream below Bluebird Lake (without fish) and the stream below Thunder Lake (with fish) varied greatly over the 24 h sampling periods (Fig. 3). Export for both lakes was greater at night than during the day. Zooplankton biomass entering the stream below Bluebird Lake was dominated by *Daphnia middendorffiana*, a large zooplankter. Export of *D. middendorffiana* from Bluebird Lake was highest at night and lowest near sunrise and sunset. *Diaptomus* sp., another large zooplankter, showed consistent, moderate export during the day and night but low export around sunrise and sunset. Zooplankton export from Thunder Lake was dominated by *Diacyclops* sp., a zooplankter of medium size, which peaked around midnight.

Mass flux of zooplankton was greater at night than during the day for both Bluebird Lake and Thunder Lake (Fig. 4; F₁,₁₂ = 22.12, P < 0.001). Mass flux of zooplankton also was greatest closest to the lake and showed a more rapid reduction with increasing distance below Bluebird Lake than Thunder Lake (F₁,₁₂ = 5.56, P = 0.04). The change in mass flux over time did not differ, however, relative to distance and lake type (ANCOVA time × distance⁰.⁵ × lake F₁,₁₂ = 0.41, P = 0.53), suggesting that patterns in mass flux at noon are consistent with those observed at midnight, except that noon estimates of export are underestimates of diel mass flux.

**Stream macroinvertebrates**

Across all streams, 52 macroinvertebrate taxa were encountered. Species richness in streams below lakes with...
from the lake. The shift in community structure moving away from the lake was greater in streams below lakes with fish than below lakes without fish (Fig. 5). Results of the PERMANOVA supported the NMDS, indicating that macroinvertebrate communities were significantly related to both the presence of fish ($F_{1,68} = 2.62, R^2 = 0.04, P = 0.02$) and increasing distance from lake ($F_{1,68} = 3.38, R^2 = 0.05, P = 0.01$), but that presence of fish and distance did not interact ($P > 0.05$).

Total macroinvertebrate biomass in the stream channel was significantly related to both the presence of fish (ANCOVA fish $F_{1,56} = 19.67, P < 0.001$) and the mass flux of zooplankton (ANCOVA log$_{10}$ zooplankton $F_{1,56} = 39.56, P < 0.001$) and did not show interaction between the two ($P > 0.05$; Fig. 6). Filter feeding and gathering collecting macroinvertebrates, as expected, showed a strong relationship to both fish (ANCOVA fish $F_{1,56} = 11.79, P < 0.001$) and the mass flux of zooplankton ($F_{1,56} = 12.22, P < 0.001$), but no interaction was observed between the two ($P > 0.05$). Additionally, detritivorous macroinvertebrates showed a relationship to zooplankton mass flux ($F_{1,56} = 11.73, P < 0.001$) but not to the presence of fish ($P > 0.05$) or to the interaction between zooplankton mass flux and presence of fish ($P > 0.05$). None of the other functional feeding groups showed a relationship to zooplankton mass flux, presence of fish, or interaction between the two ($P > 0.05$).

**Discussion**

The present study shows that trophic cascades induced by fish in lakes cross the lake and stream boundary; they influence streams below lakes by reducing the mass flux of zooplankton to streams below lakes. The reduction in zooplankton mass flux decreases the bottom-up influence of zooplankton in streams, which corresponds with lower macroinvertebrate biomass, especially for filtering and gathering collectors and detritivores. Macroinvertebrate biomass also was lower in streams with fish than would be predicted based only on zooplankton mass flux, indicating that fish likely suppress macroinvertebrates in streams below lakes. Macroinvertebrates of streams below lakes therefore experience a trophic compression from the presence of fish because they are reduced directly by fish predation and indirectly by suppression of nutrition provided by zooplankton export from lakes.

Demi et al. (2012) showed in a comparison of 3 lakes with a dominant planktivore and 3 lakes without a dominant planktivore, consistent with the literature and the present study, that planktivorous fish (alewife [*Alosa pseudoharengus*]) reduced body size of zooplankton and biomass of large zooplankton within lakes. Contrary to the present study, however, Demi et al. (2012) showed that alewife in lakes did not reduce zooplankton in

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**Figure 2.** Relationship between zooplankton mass flux per unit area for reaches below lakes (designated by top of each reach, m) with and without fish with increasing distance (D) from the lake for 3 size classes of zooplankton: large >1 μg, medium 0.1–1 μg, and small <0.1 μg. To adjust for sites below the minimum detection limit, 100 μg m$^{-2}$ d$^{-1}$ was added to all sites. The mass fluxes of large zooplankton was influenced by distance and fish ($P = 0.05$); medium zooplankton were influenced only by increasing distance from the lake; and small zooplankton were not influenced by fish, distance, or a combination of the two ($P > 0.05$). Note y-axis intervals are log$_{10}$ and x-axis intervals are square roots.
substantial even over the first 10 m (~50%), so the study by Demi et al. might have shown results similar to the present study if samples had been collected close to the lake outlets.

In reviewing the downstream persistence of zooplankton originating from lakes, Walks and Cyr (2004) concluded that the mass flux of zooplankton in streams below lakes is negatively related to stream depth. For the present study, streams were shallow (<0.5 m) and therefore had a high ratio of wetted channel surface area to volume, which could intensify losses of zooplankton to predation, physical interception by structural elements of the channel, or dilution from ungaged filtration. For RMNP, the persistence of small-bodied zooplankton in streams below lakes was greater than for larger-bodied zooplankton for streams with and without fish.

Because rate of decline in zooplankton biomass with distance downstream in RMNP was similar with and without fish for small- and medium-sized zooplankton and greater for large zooplankton in streams without fish, consumption of zooplankton by fish in streams below lakes is not likely the primary cause for reduction in biomass of zooplankton with increasing distance downstream; large zooplankton are likely selectively consumed by macroinvertebrates or intercepted by the channel substrate. Zooplankton of small to medium size may also be more likely to remain in suspension because they are more influenced by viscous forces than inertial forces than larger zooplankton and therefore are more likely to remain in suspension longer (i.e., smaller zooplankton have a lower Reynolds’s number). If small zooplankton are more likely to remain in suspension, they are also less likely to be intercepted by the channel surface or captured by macroinvertebrates and would travel farther downstream, as was observed.
In a study of 4 lakes, Walks and Cyr (2004) showed that shallow outlet streams varied greatly in relative abundance of *Daphnia* from <10% during the day to >90% at night. In the present study, the abundance of *Daphnia* entering the stream below Bluebird Lake (no fish) increased at night, as in the study by Walks and Cyr (2004). Because *Daphnia* was the dominant taxon, biomass exported at night was much greater than that observed during the day. Thunder Lake (fish), which was dominated by *Diacyclops* and had lower biomass of *Daphnia*, also showed an increase in zooplankton biomass leaving the outlet at night, but it was much smaller than that for Bluebird Lake. The study by Demi et al. (2012) showed no effect of fish on total zooplankton biomass exported to streams, whereas export was significantly affected by fish in the present study. The present study shows that zooplankton export to streams below lakes is closely related to lacustrine zooplankton biomass and community composition, both of which can be changed by fish, and that the difference between lake categories in zooplankton biomass entering streams below lakes changes with time of day. Therefore, differences in zooplankton mass flux are likely an enhancement of midday observations for many or most lakes. Although day and night differed, diel zooplankton export is likely related to midday export because of the relationships between macroinvertebrates and midday mass flux. Diel periodicity in export of zooplankton also could have ecological relevance for macroinvertebrates, some of which have been shown to have diel periodicity in behavior (Douglas et al. 1994, Huhta et al. 2000).

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The relationship between zooplankton mass flux to streams below lakes and macroinvertebrate biomass in streams is consistent with numerous studies suggesting that mass flux of zooplankton in streams provides a substantial resource for macroinvertebrates (Sheldon and Oswood 1977, Harding 1997, Edler and Georgian 2004, Walks and Cyr 2004, Doi et al. 2008). Macroinvertebrates in streams below lakes with fish are unusual in that they are negatively influenced both directly and indirectly by the presence of fish. Macroinvertebrates in streams with fish receive top-down suppression because fish reduce biomass and mean body size of macroinvertebrates in streams (Power 1990, Baxter et al. 2004), but macroinvertebrates in streams below lakes also experience negative bottom-up influence because fish reduce the export of zooplankton from lakes. Thus, fish cause trophic compression of macroinvertebrate communities in streams below lakes. Numerous studies have shown that fish alter the flow of energy from aquatic to terrestrial food webs through the suppression of emergent aquatic invertebrates (e.g., Knight et al. 2005, Finlay and Vredenburg 2007, Epanchin et al. 2010). The present study shows that effects of fish on macroinvertebrate communities in streams below lakes.
extend beyond predation of macroinvertebrates; fish in streams below lakes also reduce mass flux of zooplankton, a macroinvertebrate food source, to the stream.

Typically, introductions have a unique top-down or bottom-up effect on native communities, and trophic compression of stream macroinvertebrates is a byproduct of the interface between the lake and stream ecosystems. The top predator, fish, can occupy both sides of the ecosystem boundary, whereas macroinvertebrate prey, which are subordinate predators, can occupy only the stream side of the ecosystem boundary and therefore are subject to 2 qualitatively different types of suppression by the top predator: predation and removal of food. By this mechanism, the ecosystem boundary diversifies trophic interactions.

**Acknowledgements**

We thank the US National Park Service for logistical support, in particular C. Yost and P. McLaughlin. J. Roberson prepared figures and the manuscript. L. Chipman and several undergraduates at the University of Colorado at Boulder assisted in the collection of samples. We also thank the 2 anonymous reviewers and the associate editor, G. Boros, for insightful comments and suggestions that helped improve this manuscript.

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