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# It's Complicated: Does Food Web Structure Affect Detrital Processing in Streams?

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## It's complicated: Does food web structure affect detrital processing in streams? Stephen Tentinger

An Abstract of a Thesis In Biology

Submitted in Partial Fulfillment Of the Requirements For the Degree of Master of Arts December 2016

Buffalo State State University of New York Department of Biology

#### ABSTRACT OF THESIS

It's complicated: Does food web structure affect detrital processing in streams?

Trophic cascades involve powerful feeding interactions that can alter the flow of energy and the abundance of species in an ecosystem. In western NY streams, the negative impacts of a new benthic invertivore, the round goby (*Neogobius melanostomus*) is altering benthic community structure and leaf litter decomposition. Streams with round gobies have a reduced abundance of shredders and slower leaf decay than streams without gobies. However, crayfish, as shredders of leaf litter, may be large or aggressive enough to avoid predation by round gobies. I used a 30-day full factorial field experiment with blocks to determine if round gobies affected the role of the crayfish (Orconectes propinguus) in the breakdown of detritus. I found no significant difference (P > 0.05) in the decay rates of red maple leaves (*Acer rubrum*) among treatments. However, I observed a difference in the number of prey consumed by predators among treatments (P<0.001). Round gobies ate significantly more prey when crayfish were present than with other round gobies. Though direct effects on prey abundance were strong when round gobies were with crayfish, they weren't strong enough to indirectly affect leaf litter decomposition rates. This suggest that a trophic cascade was not evident. Knowledge of these community shifts can better help us understand how invasive species can affect the biotic integrity of heterotrophic streams.

Buffalo State State University of New York Department of Biology

It's complicated: Does food web structure affect detrital processing in streams?

A Thesis in Biology

by

Stephen Tentinger

Submitted in Partial Fulfillment of the Requirements for the Degree of Master of Arts

December 2016

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#### Introduction:

#### Trophic Cascades:

Trophic cascades involve powerful feeding interactions that can alter the flow of energy and the abundance of species in ecosystems. They occur when predators reduce the impact their prey have on the next trophic level to the point of affecting primary producers (Hairston et al. 1960). For example, a typical trophic cascade occurs in lakes when piscivorous fish reduce the biomass of planktivores via predation. The result indirectly increases the biomass of zooplankton which leads to a decrease in the biomass of algae (Carpenter et al. 1985).

A wide variety of vertebrate and invertebrate predators are responsible for initiating cascade effects in both aquatic and terrestrial food webs (Pace et al. 1999). These predators can initiate trophic cascades by consuming their prey directly (density-mediated) or by altering the behavior or life history of their prey (trait-mediated) (Kerfoot & Sih 1987; Abrams 1995; Werner & Pecor 2003). For example, Schmitz (1994) observed an increase in the biomass of perennial dicots and grasses when dominant grasshopper species were introduced to predatory spiders. The spiders' predation on grasshoppers greatly reduced the population of grasshoppers causing the rate of herbivory by grasshoppers on perennial dicots and grasses to decrease as well. Similarly, Tronstad et al. (2010) documented that the introduction of lake trout (*Salvelinus namaycush*) in Yellowstone Lake, Wyoming in 1985 caused a decrease in the number Yellowstone cutthroat trout led to an increase in the biomass of large zooplankton which then led to a decrease in the biomass of phytoplankton. Tronstad et al. (2010) also documented Yellowstone cutthroat trout hiding to avoid being preyed upon by lake trout. This trait-mediated behavior reduced their time preying upon large zooplankton.

Predators might initiate trophic cascades by altering the behavior or life history of their prey so that the prey avoids being eaten (trait-mediated) (Kerfoot & Sih 1987; Abrams 1995; Werner & Pecor 2003). When the intermediate predator spends more time avoiding its own predator, the prey's biomass increases. For example, in a marine ecosystem off the coast of Western Australia, tiger sharks (*Galeocerdo cuvier*) play an important role in regulating herbivore consumption of seagrass beds (Burkholder et al. 2013). Burkholder et al. (2013) suggested that sea cows (*Dugong dugon*), a marine herbivore, alter their behavior to avoid predation when tiger sharks are present. Using caged sea cows in areas where tiger sharks were present or absent, Burkholder et al. (2013) observed a doubling of seagrass consumption in areas where tiger sharks were absent compared to cages with sea cows in locations with tiger sharks were present.

Trait-mediated trophic cascades also have been observed in river or lotic ecosystems. In alpine streams of the western Rocky Mountains, McIntosh et al. (2004) observed that streams with brook trout (*Salvelinus fontinalis*) had higher densities of periphyton growing on substrate than in streams where brook trout were absent. The study suggested that brook trout alter the behavior of mayfly larvae (*Baetis bicaudatus*) reducing their grazing on periphyton when they avoid predation (McIntosh et al. 2004). By experimentally exposing mayfly larvae to brook trout odor in laboratory settings, McIntosh et al. (2004) observed a behavioral increase in mayfly larvae hiding behavior, leading to a reduction in periphyton consumption. All these examples indirectly effects the biomass of living autotrophs such as plants and periphyton. These examples can also indirectly affect the biomass of dead plant material such as detritus.

#### **Detrital Based Food Webs:**

Traditionally, trophic cascade studies (both density-mediated and trait-mediated) have looked for top predator effects on herbivores grazing on living plant material in the green world (Ruetz et al. 2002; Schmitz 2010). However, most plant material produced by primary production is not consumed by herbivores and ends up being decomposed and becoming part of the "brown world" in the form of detritus (Polis & Strong 1996; Schmitz 2010). This material is important for nutrient recycling as microbes and detritivores break down the decomposed plant material releasing nutrients that are then taken up by primary producers. However, detrital-based food webs also have examples of trophic cascades where top predators can slow the breakdown of detrital resources by altering the behavior or reducing the biomass of detritivores (Wallace et al. 1982; Benfield & Webster 1985; Mulholland et al. 1985; Hall et al. 2001; Schmitz 2010). Several studies have observed detritus-based trophic cascades in laboratory settings (Short & Holomuzki 1992; Malmqvist 1993) Konishi et al. (2001) observed the same results in a field enclosure experiment by manipulating the presence or absence of rainbow trout (*Onchorhynchus mykiss*) and fresh water sculpin (*Cottus nozawae*) in streams of northern Japan. Streams with these invertivorous fish present had a significant reduction in the breakdown rate of oak leaves (*Quercus crispla*) compared to streams that were fishless (Konishi et al. 2001). The reduction in leaf breakdown was the result of fish predation on the amphipod shredder (*Jesogammarus jezoensis*). A similar study from streams in Virginia showed no fish-induced cascade to leaf litter decomposition (Wach & Chambers 2007). Wach and Chambers (2007) compared mosquitofish (*Gambusia holbrooki*) and Rosyside dace (*Clinostomus funduloides*) effects on leaf litter decomposition and observed a significant decrease in the number of amphipods present (*Gammarus pseudolimnaeus*) when either invertivorous fish was present. However, there was no significant reduction in the rate of leaf litter breakdown have been mixed.

Detritus plays an important role as an allochthonous carbon energy input into streams. In river systems, the first, second and third-order streams comprise about 85% of the total length of the running water (Leopold et al. 1964; Anderson & Sedell 1979). Headwater streams are maximally influenced by riparian vegetation through shading and as the source of organic matter inputs (Anderson & Sedell 1979). As the order of the stream increases, the role of allochthonous energy input decreases as there is a shift from heterotrophy to autotrophy (Meehan & Lindroth 2007).

When leaves fall into a stream during the autumn season, they lose soluble organic and inorganic materials rapidly (Webster and Benfield 1986). After the first few days, the leaves are then colonized by aquatic microbes and fungi producing polysaccharide hydrolyzing exoenzymes that soften the leaf material (Webster and Benfield 1986). The percent lignin and complex nitrogen content in the detritus determines how long it takes for bacteria and fungi to colonize the leaf litter (Cummins & Klug 1979). Multiple studies have shown different plants have leaves with varying decay rates (Figure 1), with submerged herbaceous plants generally decaying more quickly than emergent herbaceous plants or leaves from woody species. As the leaves become colonized by fungi and bacteria, they become more palatable to shredders, a feeding guild of macroinvertebrates consuming leaf litter (Cummins and Klug 1979).

Many aquatic insects and crustaceans belong to the shredder functional feeding group and play an important role in streams for the breakdown of leaf litter (Cummins & Klug 1979). Shredders prefer detritus in the form of coarse particulate organic matter (CPOM) that has been conditioned and colonized by bacteria and fungi (more than 50% of the biomass) (Bärlocher & Kendrick 1974; Suberkopp & Klug 1974; Suberkopp & Klug 1976; Cummins & Klug 1979). The consumption of bacteria and fungi as well as the consumption of CPOM, supports shredder growth and secondary production and the production of fine particulate organic matter (FPOM) and dissolved organic matter (DOM) (Bärlocher & Kendrick 1974; Cummins & Klug 1979) (Figure 2). Wallace et al. (1982) showed that the breakdown of leaf litter was significantly reduced when shredder density was experimentally reduced. This reduction was more noticeable in leaf species that had more lignin. In Ellicott Creek, leaf litter breakdown occurs more rapidly in upstream sections of the system where no round gobies occur (Cudney and Pennuto, unpublished data) compared to downstream sections where round gobies are present. Additionally, the density of shredding amphipods is significantly lower at sites with round gobies compared to sites without them (Fischer 2014).

#### Crayfish:

In addition to insect taxa, crayfish also play a role in breaking down detritus (Cummins & Klug 1979; Creed 1994). Crayfish are distributed throughout the world and are generally considered omnivores (Holdich & Lowery, 1988). Omnivores in general are opportunistic feeders and are able to consume both plant and animal material (Olsson et al. 2008; Stenroth et al. 2008). Crayfish can consume both leaf litter and the macroinvertebrates that break down the leaf litter and are able to shift their trophic position either seasonally, ontogenetically, or when there are anthropogenic changes in the local environment (Weins & Wolf 1993; Usio 2000; Anderson & Cabana; 2007; Stenroth et al. 2008). Despoite being omnivorous, crayfish could initiate trophic cascades. For example, Lodge et al. (1994) conducted an experiment in a series of lakes in Wisconsin using enclosures and exclosures containing crayfish (*Orconectes*)

*rusticus*) to determine if grazing pressures caused crayfish to change their diets. The diets of crayfish in enclosures shifted from consuming algae to consuming algivorous snails whereas the diets of excluded crayfish stayed the same (Lodge et al. 1994). The reduction in algal consumption indirectly caused an increase in primary production inside enclosures compared to lakes with exclosures (Lodge et al. 1994). However, these trophic cascades were not permanent since crayfish could switch back to consuming algae depending on which food item was available (Lodge et al. 1994).

In streams of western New York, the northern clearwater crayfish, (*Orconectes propinquus*) is a common crayfish which is a generalist omnivore consuming detritus, periphyton, algae, macrophytes, and benthic invertebrates such as mayfly nymphs and chironomids (Stein et. al 1977). Several behavioral studies have shown *O. propinquus* avoids being eaten by sensing specific kairomones released by its predator and avoiding danger (Stein & Magnuson 1976; Hazzlet 1994; Bouwma & Hazlett 2001). However, the role of *O. propinquus* on the breakdown on leaf litter in northern temperate streams remains unstudied.

#### Invasive Species:

Throughout history, many species of flora and fauna have been introduced into habitats where they are considered non-native or exotic. In some cases, these species can become invasive when they become fully established in their new habitat and are able to expand and colonize new areas (Elton 1958). Some invasive species alter ecosystem functions where they become established (Simberloff & Von Holle 1999). For example, dreissenid mussels (*Dreissena polymorpha & Dreissena rostriformis bugensis*) are notorious for being an invasive species in the Great Lakes. They have been known to decrease the biomass of both zooplankton and phytoplankton and increase the biomass of benthic algae, macrophytes, and benthic macroinvertebrates (Stewart and Haynes 1994, Bridgeman et al. 1995, Fahnenstiel et al. 1995, Lowe and Pillsbury 1995, Skubinna et al. 1995). In a study by Stewart et al. (1998), macroinvertebrate community composition was measured in Fishery Bay off the coast of Lake Erie in Put-In-Bay, Ohio. Using sites with both high and low densities of dreissenid mussels present, macroinvertebrate density and richness were higher in samples from sites with high

dreissenid densities than in sites with low dreissenid densities (Stewart et al. 1998). However, many of the macroinvertebrate taxa found in samples from high dreissenid density only fed on pseudo-feces produced by dreissenid mussels such as oligochaetes, leeches, limpets and snails (Stewart et al. 1998). These taxa do not provide the same nutritional value to fishes as some other important taxa such as *Diporeia hoyi*. The density of *Diporeia hoyi* was significantly lower in samples from sites with high densities of dreissenid mussels than in samples from sites with low dreissenid mussel densities (Stewart et al. 1998). This can cause planktivorous fish species to expend more effort in foraging so that they can obtain the optimal nutritional requirements they need for optimal growth (Stewart et al. 1998).

In an old field ecosystem, Lopezaraiza-Mikel et al. (2007) examined how an invasive plant, the Himalayan Balsam (*Impatiens glandulifera*), interacted with insect pollinators among native plants using a plant-pollinator interaction matrix model. The model gives several scenarios on how invasive plants can interact with pollinators: they can add new interactions with existing pollinators, they can compete with other native plants for existing pollinators, or they can introduce new pollinators to the community (Lopezaraiza-Mikel 2007). By manipulating sites with or without Himalayan Balsam in an experimental field outside Bristol, United Kingdom, they showed sites that had Himalayan Balsam had high numbers of pollinating-generalist such as *Hymenoptera spp*. and *Hemiptera spp*. (Lopezaraiza-Mikel 2007). These insects carried out most of the pollination with Himalayan Balsam, as well as pollinating native plants creating more links than previously predicted in the plant-pollinator interaction matrix model. (Lopezaraiza-Mikel 2007). Thus, invasive species can be capable of changing the distribution and functional role of species within an ecosystem.

#### Round Goby:

Within the last 10 years, invasion by a generalist benthic invertivorous fish, the round goby (*Neogobius melanostomus*) has altered much of the eosystems's structure and function of the Laurentian Great lakes and their tributaries. Round gobies were first introduced into the Great Lakes in the mid 1990's and were first discovered in the St. Claire River (Jude et al. 1992). According to Hayden & Miner (2009), they found their way to the Great Lakes as pelagic larvae

transported in ballast water from ships originating from the Caspian Sea. They are aggressive and compete for space and food with native fishes of the Great Lakes. In particular, they have negatively affected other species with similar habits and habitat preferences like the mottled sculpin (*Cottus bairdi*) and logperch (*Percina caprodes*) (Jude et. al 1995). Jansen & Jude (2001) showed that round gobies competed for food resources with mottled sculpin when <60 mm, competed for space when 60 to 100 mm and competed for spawning grounds when >100 mm. Rounds gobies also prey upon eggs and larva of predatory fish such as lake trout (*Salvelinus namaycush*) smallmouth bass (*Micropterus dolomieu*) and lake sturgeon (*Acipenser fulvescens*) (Chotkowski &Marsden 1999; Corkum et al. 2004)

Round gobies are considered habitat generalists, tolerating a large range of salinity (up to 37‰) and have a broad diet (Smirnov 1986; Charlebois et. al 1997). Round gobies were introduced to the Aral Sea in the 1950's and survived until the late 1980's when increasing salinity levels restricted their distribution (Moskalkova 1996). In 1968, round gobies were observed in the Kuybyshev Reservoir, which flows in to the Volga River, and allowed them to spread throughout much of Europe (Tsyplakov 1974).

Round gobies have invaded many tributary streams and rivers entering the Great Lakes (Krakowiak & Pennuto 2008; Kornis et al. 2012). They consume much of the macroinvertebrate community that are important to the breakdown of detritus from CPOM to FPOM. (Carman et al. 2006; Krakowiak & Pennuto 2008; Pennuto et al. 2010). Our lab is working with this invasive predator, and investigating its potential to initiate trophic cascade effects in the small, detritusbased tributary streams that flow into Lake Erie.

#### Purpose of Experiment:

Prior experiments have shown that round gobies consume important invertebrate shredders (invertebrates that break down leaf material in streams), thereby increasing the time needed for leaves to decompose (Fischer 2014). However, no experiment has examined how round gobies, a generalist invertivore, might alter the role of crayfish, a generalist omnivore in the breakdown of leaf litter. In this experiment, I conducted a full factorial field enclosure experiment to determine if round gobies affect leaf litter decay by altering the role of the crayfish in a stream community. By observing changes in the rates of decay in leaf litter and changes in the abundance of benthic invertebrates, I tried to determine if a trophic cascade was occurring in either the presence of round gobies or crayfish alone or when round gobies and crayfish were present together.

I expected the abundance of shredders to be reduced in treatments where round gobies were present compared to treatments where no predators were present (Figure 3a). This would indicate that round gobies were either preying upon shredders or eliciting a predator avoidance behavior by shredders. In either case, I expected to see an increase the time needed for leaves to break down indicating a trophic cascade. In treatments where crayfish are present (Figure 3b), I also expected to see a reduction in the number of shredders present by elicitation of a predator avoidance behavior by shredders relative to treatments where there were no predators present. However, it is also possible that crayfish competed with shredders for detrital resources. Thus, it was possible to expect an increase in leaf litter decay rates in treatments where only crayfish were present compared to treatments where both predators were absent or when just round gobies were absent (Figure 3b). In treatments where both round gobies and crayfish were present, I expected to see either leaf litter decay rates that were slower, faster or about the same as in treatments where round gobies and crayfish were absent (Figure 3c). If leaf decay rates were slower, this would indicate that either round gobies outcompeted crayfish for food and space or that both crayfish and round gobies consumed shredders and/or induced a predator avoidance behavior by shredders, resulting in a trophic cascade. If leaf decay rates are faster or remain the same, this would indicate that either crayfish outcompeted round gobies and that both crayfish and shredders were consuming leaf litter or that crayfish and round gobies competed with each other equally resulting in a decrease in consumption of shredders.

#### Methods:

#### Field Site Description:

Predation intensity and predator identity effects on leaf litter breakdown were assessed with a full factorial, cage enclosure experiment in Ellicott Creek. Ellicott Creek is a fourth-order

stream located in Erie County in Western New York. It originates near Darien Lake State Park east of Alden, New York and ends by joining Tonawanda Creek before flowing into the Niagara River. Ellicott Creek runs through a variety of rural, suburban and urban landscapes. According to a 2001 study by the New York Department of Environmental Conservation, the upper portion of Ellicott Creek is characterized by slow-moving water to near standing water while the middle and lower portions of the streams are characterized by more constant-moving water (Bode et. al 2002). The field site for the enclosure experiment took place within portion of the creek near the University at Buffalo North Campus near St. Rita's Lane in Williamsville, New York (43.006501°N,78.775492°W) (Figure 4). In 2010, the site had an average dissolved oxygen content of 11.51 mg/ml and an average annual water temperature of 12.01 °C and an average temp of 20.50 °C during the summer months (June, July, August) (Pennuto unpub. data).

Round gobies were first observed in Ellicott Creek in 2004 (Pennuto, unpublished data). Their diets at this site are dominated by chironomids and net-spinning caddisflies (Pennuto et al. 2010). The pre-goby (2001) macroinvertebrate community has been altered significantly by round gobies; amphipods and caddisflies have decreased in relative abundance whereas chironomids and riffle beetles have increased in relative abundance post-goby arrival (Pennuto unpublished data).

#### Experimental Setup:

The field experiment took place from 23 June 2014 to 2 August 2014. There were four treatments: gobies only (GG), crayfish only (CC) (*Orconectes propinquus*), gobies and crayfish (GC), and control (N). Each treatment was replicated 12 times, arranged as a randomized block design among four riffles that were 20 m from each other (Figure 5a, 5b). Each riffle had three strings of four cages, one cage with each treatment. Each string was attach to a length of rebar driven into the stream bed (Figure 5b). Cage strings were spaced 1 m from each other to avoid trap interaction effects.

Cage enclosures consisted of standard Gee<sup>®</sup> minnow traps (41.9-cm long by 22.9-cm wide) that were modified by placing wire mesh across the entry holes on the cage (Figure 6). Each cage had a leaf pack of red maple (*Acer rubrum*) leaves (5±0.1g) that were collected during autumn abscission in 2013. Leaves were stored at 0°C until time of experiment and were dried to a constant weight in a drying oven (VWR XZ97, 60°C). Each leaf pack was created with 5.0 g of dried leaf material (Ohaus Adventurer electric scale) carefully placed in nylon mesh bags (2cm mesh size) and zip-tied to the inside of a cage. Forty-eight experimental cages were created (4 treatments x 4 riffles (blocks) x 3 replicate strings per riffle). An additional four cages with leaf packs were created to determine handling loss (Benfield 2006). All cages were deployed on 23 June, 2014. The four handling loss cages were also deployed and retrieved immediately after submersion. These cages were then treated as the experiment cages were (see below).

Round gobies and crayfish were collected from Ellicott Creek between June 23, 2014 to July 2, 2014 using kick nets and seines. Gobies and crayfish were placed in separate aerated aquarium tanks (~38 L). On July 3, 2014, round goby total length (mm) and mass (g) were measured. Crayfish carapace length and width (mm) and mass (g) also were measured. Round gobies and crayfish were paired by similar mass ( $\pm$  0.1 g) and added to the following treatments: CC = two crayfish, GG = two gobies, GC = one goby and one crayfish and N = neither. Goby and crayfish pairings were placed in labeled zip lock bags and transported to the field site where they were placed in their respective cages as depicted in Figure 4. Thus, leaf packs had conditioned and been colonized by macroinvertebrates for 11 days prior to adding fish or crayfish.

On each of the three collection dates, one string of cages was randomly selected from each riffle for determining leaf litter loss and macroinvertebrate community structure. Removal dates were July 10 (Week 1) July 17 (Week 2), and August 2 (Week 4). Thus a total of 16 cages were retrieved on each sampling date. However, over one third of all the cages used became vandalized or destroyed during a flooding event that occurred between July 17, 20145 and August 2, 2014. Therefore, treatments for Week 4 are not included in the results and only treatments from Week 1 and Week 2 were analyzed.

The velocity of each cage was determined prior to cage removal (Swoffer 2100 flow meter). Each cage was removed by placing a kick net downstream from each cage and using the net the lift the cage out of the water. Cages were carefully placed into sampling trays and

opened. Gobies and crayfish were removed from cages and placed into labeled zip-locked bags. Leaf pack bags also were taken out of cages and placed in zip-lock bags. All zip-lock bags were placed in a cooler and were immediately transported to SUNY Buffalo State College where they were processed.

#### Processing Samples:

Gobies were measured by total length (mm) and weighed (g). Crayfish were measured by carapace length and width (mm) and weighed (g). Both gobies and crayfish were then stored at 0°C. Leaf litter bags were placed in a large sorting tray and carefully opened. Each piece of leaf material was carefully washed using distilled water to collect and remove any debris and invertebrates. Once leaves were clean, they were placed into 50-mm aluminum weigh boats and dried to a constant weight using a drying oven (VWR XZ97, 60°C) for > 24 hours.

The contents in the sorting tray were washed through a mesh strainer (0.9 mm), and elutriated in a 10% sodium chloride solution to separate invertebrates from debris. Invertebrates were preserved in 70-% ETOH in labeled 20-ml glass scintillation vials. Preserved invertebrates were then sorted to genus (Peckarsky et al. 1990) and assigned to functional feeding groups (Bode et al. 1990). All of the Chironomidae were counted, then Tanypodinae were removed and counted and assigned to a predator functional feeding group (Bode 1990). Next, a random subsample of 10 chironomids was mounted on microscope slides and identified to Genus using keys from Bode et al. (1990) and assigned to functional feeding groups. Since the genera richness within the Chironomidae was low, I assigned identity and functional feeding group to the remaining midges in proportion to the count from the 10-midge subsample.

Once leaves were dried to a constant weight, they were weighed (g) using an analytical balance (O'Haus Adventurer) to determine dry mass remaining. Leaves were ground to a fine powder in a mini-Wiley mill (Thomas Scientific). Three two-to-four mg subsamples of ground tissue were made from each leaf pack using a microbalance (Mettler Toledo XP6). Subsamples were placed in tin capsules (5x9 mm) and were analyzed for carbon and nitrogen content using a CE Elantech elemental analyzer. B-BOT (72.53% C, 6.51% N) (Thermo Scientific) was used as a standard to calibrate the instrument. The remaining leaf material was weighed (g) and placed in

a muffle furnace (Lindberg/Blue) and burned for 20 minutes at 500° C. Ash was then weighed (g) and the ash-free dry mass (AFDM) was determined using methods from Benfield (2006). Gobies and crayfish that were stored at 0°C were thawed and stomachs were removed. Stomachs were dissected and analyzed for number of prey consumed by identifying head capsules as either chironomid, hydropscychid, or other.

#### Statistical Analysis.

All data analyses were done using the R-statistical package version 3.2.3 for Microsoft Windows. All significant results are represented with an alpha of 0.05 and all marginally significant results are represented with an alpha of 0.1. Treatment effects on leaf decays rates were analyzed by a two-way ANCOVA. Decay rates were determined by taking the slope of the natural log of the mean percent AFDM remaining for each of the treatments through time. The velocity which was measured in front of each cage was used as the covariate for the two-way ANCOVA. Treatment effects on the number of invertebrates present in leaf packs between weeks were compared using a two-way ANOVA block design. The number of invertebrates present in each leaf pack were scaled to the amount of AFDM remaining. Treatment effects on the number of invertebrates within each functional feeding groups between weeks were compared using a two-way ANOVA block design. Invertebrate numbers were scaled to the amount of ash free dry mass remaining. Treatment effects on the number of chironomids were compared using a two-way ANOVA block design. Number of chironomids were scaled to AFDM remaining. Treatment effects on carbon: nitrogen ratios between weeks were analyzed by a two-way ANOVA block design. Goby and crayfish measurements after experiment completion were averaged and compared across treatments using a one-way ANOVA. The number of prey found in the guts of gobies and crayfish from each treatment were compared between weeks using a two-way analysis of deviance. I used this method since the number of prey were discrete number counts that did not follow a normal distribution. I assumed that the distributions were quasipoisson to take into account non-normality and over-dispersion.

I compared the relative strengths of direct and indirect effects of predator treatment by plotting the mean change in shredder abundance (x-axis) against the mean change in leaf decay

rate (y-axis) (Schmitz 2010) from the July 12 (week 2) treatments (see figure 8). The Y axis represents the strength of directs effects on prey while the X axis represents the strength of indirect effects on prey. The 45 degree line represents the equivalence of both the direct and indirect effects. The change in shredder abundance was calculated as: LN (D<sub>C+</sub>/D<sub>C</sub>) and the change in leaf decay rate was calculated as LN ( $K_{C+}/K_{C-}$ ) (Schmitz 2010).  $D_{C+}$  represent the number of shredder in leaf packs of a specific predator treatments whereas D<sub>C</sub>-represents the number of shredder in leaf packs of the control treatments. K<sub>C+</sub> represents the leaf decay rate of leaf packs with a specific predator treatments whereas K<sub>C</sub>-represents the leaf decay rate of leaf packs of the control treatments. Using these equations to plot the strengths of both the direct and indirect effects of a study, a point in the lower left quadrant of the graph indicates that predators have negative indirect effects (i.e. slower detrital breakdown rates) on prey that are stronger than their direct effect (i.e. consumption) on prey (Schmitz 2010). This indicates that a trophic cascade is occurring. I derived 95% confidence intervals around the mean for direct effects to assess predation strength. If the 95% CI bars overlapped, the direct predation effects were considered similar. If the 95% CI bars did not overlap, the direct predation effects were considered different.

#### **Results:**

#### Leaf Breakdown:

Leaf packs decayed at the same rate across treatments. The natural log of the percent AFDM (Figure 8) did not differ across any of the treatments (Table 1). The mean breakdown rates for leaf packs collected from cages from July 10, 2014 (Week1) through July 17, 2014 (Week 2) differ slightly (Table 2). C:N ratios were similar across treatments for both Week 1 and Week 2 (Figure 9). However, C:N ratios did differ between Week 1 and Week 2 as a whole (Table 3) having a fewer moles of carbon per mole of nitrogen in Week 2 than in Week 1.

#### Invertebrate counts:

All invertebrate identities and counts from Week 1 and Week 2 are summarized in Appendix A and B, respectively. There were 24 different genera of invertebrates collected coming from 17 different families (Appendix A and B). The mean number of invertebrates per gram of ash free dry mass did not differ across treatments nor did it differ between Week 1 and Week 2 (Figure 10 and Table 4). All five functional feeding groups were observed in Week 1 and in Week 2 (Figures 11-15). Each functional feeding group did not differ between treatments but predators and shredders did differ between weeks (Predators p = 0.035, Shredders p = 0.034) while grazers differed marginally between weeks (p = 0.083) (Table 5).

#### Gobies and Crayfish:

Growth rates of gobies and crayfish collected on Week 2 (Figure 16) did not differ among treatments (p = 0.194) (Table 6). However, the consumption of prey did differ between gobies and crayfish collected from treatments from both Week 1 and Week 2 (p = <0.001) (Table 7). When gobies were placed in treatments with crayfish, they consumed significantly more prey than gobies placed in treatments with other gobies (Figure 17).

According to the results on the direct (detritivore consumption) and indirect (leaf breakdown rates) effects by round gobies and crayfish (Figure 18), only treatments that had both round gobies and crayfish present (GC) showed direct effects outweighing indirect effects. The mixed taxa predator treatment (GC) had fewer detritivores present in the leaf packs compared to the other treatments. Single predator taxa treatments (GG and CC) had direct effects that were weaker than the indirect effects and had an increase in the number of detritivores present. However, none of these treatment outcomes were strong enough to cause decreases in the break down rates of leaf litter.

#### Discussion:

Trophic cascades are important to maintain ecosystem function. Predators can initiate trophic cascades by direct consumption on prey (density-mediated) or by altering the prey's behavior (trait-mediated). When trophic cascades occur, the preys' response to predators indirectly impacts the biomass of the next trophic level (Harriston et al. 1960). Trophic cascades can be initiated in food webs supported by primary production (Hunter & Price 1992; Strong 1992; Carpenter & Kitchell 1993; Polis & Strong 1996) or by detritus (Moore et al. 2004; Schmitz 2010). Invasive species have initiated trophic cascades after outcompeting native predators for the same ecological niche (Pimm 1989; Pagnucco et al. 2016). I Investigated whether the invasive invertivorous round goby initiated a trophic cascade by altering shredder dynamics and leading to a reduction in the breakdown of detritus. I also investigated whether leaf decomposition by a native crayfish differed in the presence of round gobies. To answer these questions, I conducted a field enclosure experiment in Ellicott Creek in Western New York during the summer of 2014.

Leaf pack ash-free dry mass remaining did not differ between treatments (Figure 8), suggesting that cages with round gobies and/or crayfish present did not alter leaf decomposition rates relative to the control (Table 1). Fischer (2014) observed leaf breakdown rate in Ellicott Creek as high as 0.058 day<sup>-1</sup> where round gobies were absent and as low as 0.028 day<sup>-1</sup> where round gobies were present. My leaf packs had breakdowns rate which were faster than those reported by Fischer (2014), and were about 0.060 day<sup>-1</sup> regardless of whether round gobies were present or not. There are possible reasons for why my leaf packs did not differ in decay rates across treatments.

First, since microbial communities are important for leaf decomposition (Benfield 2007), it is possible that during the time frame of my experiment they dominated leaf decay dynamics more than macroinvertebrates. Fischer (2014) investigated whether microbial assemblages on red maple leaves differed in the presence or absence of round gobies in Ellicott Creek. She placed leaf litter bags where round gobies were present and where they are not during the spring and fall of 2012 (Fischer 2014). There were no differences in microbial communities between sites (Fischer 2014). Fischer (2014) suggested the lack of differences in microbial communities could be due to factors such as water chemistry, nutrient input, and fungi and bacterial growth. Most of these factors are dependent on one another and are very difficult to separate out. Unfortunately, none of these factors were recorded during my experiment.

Another potential reason why I did not see any differences in leaf decay rates across treatments could be due to the low taxa richness and diversity of invertebrates found in the stream that colonized the leaf packs. Studies by Jonsson & Malmqvist (2000) and Jonsson et al. (2001) showed that increasing taxa richness of macroinvertebrates decreased the time needed for leaves to be broken down. The number of taxa found in my study was 24 and the average Shannon Diversity index across treatments for both Week 1 and Week 2 was 1.383. Many studies have correlated low taxa richness and diversity of colonizing macroinvertebrates to anthropogenic perturbations such as low amounts of dissolved oxygen (Huryn et al. 2002; Mckie et al. 2009) and low pH (Dangles et al. 2004; Mckie et al. 2009). These are common in streams that run through urbanized areas. The stretch of Ellicott Creek where the field experiment took placed is heavily impacted by urban perturbations such as surface runoff from paved roads, parking lots, and highways. Runoff from these sites can sometimes have low amounts of dissolved oxygen and low pH. This can possibly cause poor water quality which only a few genera of macroinvertebrates can tolerate. The most abundant macroinvertebrates that colonized my leaf packs were net spinning caddisflies (Hydropsychidae) and the non-biting midge, *Polypedilum sp.* (Chironomidae) (Appendix A & B). Both of these taxa are moderately to very tolerant of poor water quality, having Hilsenhoff Biotic Indexes between five and seven (Bode et al. 1990).

Other studies have correlated low taxa richness and diversity of macroinvertebrates to low species richness of leaf litter that make up a leaf pack (McArthur et al. 1994; Swan & Palmer 2004; Kominoski et al. 2007). Kominoski et al. (2007) observed an increase in the diversity of detritivores when using leaf packs made up of mixed leaf species compared to using leaves from just one species. My leaf packs were only made up of red maple leaves. Using leaves from one species could have resulted in only a few taxa of macroinvertebrates being able to colonize my leaf packs regardless of treatment. Although C:N ratios of the red maple leaves did decrease between Week 1 and Week 2 (Figure 9), making the leaves more nutritious, there was no difference in taxa richness nor diversity of macroinvertebrates between Week 1 and Week 2 leaf packs regardless of treatment causing no difference in leaf breakdown rates.

Macroinvertebrates in the functional feeding group "Shredder" are important for breaking down CPOM to FPOM (Cummins & Klug 1976). The abundance of shredders did differ between Week 1 and Week 2 (Figure 15) but did not differ between treatments (Table 5). It is important to understand that not all shredders break down CPOM to FPOM equally. Amphipod shredders such as species from the genus *Gammarus* are able to break down CPOM more efficiently than shredders from the midge family Chironomidae (Graca et al. 2001). In Fischer (2014), Gammarus was the most abundant shredder out of all of her leaf packs. Fischer (2014) observed an average of 142 *Gammarus* amphipod shredders in leaf packs where round gobies were absent regardless of when leaf packs were collected. She also observed an average of only three *Gammarus* in leaf packs were round gobies were present regardless of when leaf packs were collected (Fischer 2014). Leaf packs with a high abundance of *Gammarus* broke down significantly faster than leaf packs with a low abundance of *Gammarus*. My experiments all took place were round gobies were present and observed on average eight *Gammarus* in leaf packs regardless of week or treatment (Appendix A & B). Having a low abundance of efficient shredders regardless of treatments could have resulted in no difference in leaf breakdown rates. However, I also observed over 100 *Polypedilum* g<sup>-1</sup> AFDM, a chironomid shredder, in all treatments regardless of week.

Polypedilum is the most diverse genera of shredders in the Family Chironomidae and is found in almost all rivers and streams throughout the world (Benke 1998). Benke (1998) observed the annual productivity rate for *Polypedilum* was extremely high during the summer when temperatures were around 24°C to 30°C. This resulted in a turnover rate for *Polypedilum* almost once every day which is far faster than other macroinvertebrate species (Benke 1998). Water temperature for Ellicott Creek was very warm during the summer of 2014. This could have caused a high abundance of *Polypedilum* during my field experiment trial. The abundance of *Polypedilum* could have been so numerous that neither round gobies nor crayfish were able to control their density. This would have resulted in there being no difference in the breakdown of leaf material across treatments. This phenomenon is known as prey-swamping.

Prey-swamping occurs when prey are in high numbers and have high mobility rates. Unlike predator-swamping where the emergence of prey are too numerous for predators to regulate by direct consumption (Holling 1973), prey-swamping creates difficulty for predators to regulate because prey move between and recolonize habitats at very fast rates (Cooper et al. 1990; Lancaster et al. 1991; Malmqvist 1993). For example, Malmqvist (1993) observed a reduction in the decomposition rate of alder leaves when two shredder species, *Protonmemura meyeri* and *Nemoura avicularis*, were in the presence of a predatory stonefly larvae, *Diura*  *nanseni*. However, a third shredder, *Taeniopteryx nebulosi*, occurred in very high numbers in streams in northern Sweden. When in the same stream as the other shredders, *P. meyeri* and *N. avicularis*, the fast mobility rate by the abundant *T. nebulosi* shredder shadowed the reduction in the decomposition rate of alder leaves when *D. nanseni* is present (Malmqvist 1993). The abundance of *Polypedilum* could have swamped both predator's ability to regulate them causing no differences in leaf breakdown rates across treatments.

The numerical dominance of *Polypedilum* in leaf packs may have increased intraspecific competition between other *Polypedilum*. I suspected this because trends in the abundance of *Polypedilum* in both Week 1 and Week 2 looked like there were fewer in the control cages than goby cages (GG) and crayfish cages (CC). Round gobies are generalist invertivores and have been known to consume much of the macroinvertebrate community (Krakowiak & Pennuto 2008; Pennuto et al. 2010). In treatments where round gobies are present, *Polypedilum* could have increased predator-avoidance behavior leading to greater refuge use within leaf litter. If round gobies increased refuge seeking behavior in *Polypedilum*, there would be no apparent reduction in *Polypedilum* abundance. However, in the absence of round gobies and under heightened intraspecific interactions, *Polypedilum* abundance in control cages would appear to decline, leading to what appears to be an increase in the abundance of *Polypedilum* in cages with gobies (GG) over control cages.

Crayfish are opportunistic predators. They can decrease macroinvertebrate abundances in streams (Crowl & Covich 1990, Weber and Lodge 1990, Lodge et al. 1994, Usio & Townsend 2002). They can also facilitate macroinvertebrate abundances. Crayfish shred leaf material, producing smaller organic particulates that are favorable to *Polypedilum* and other smaller macroinvertebrates (Heard & Richardson 1995). I suspect crayfish treatments (CC) were facilitating macroinvertebrate abundances. These treatments had the highest abundance of *Polypedilum* and other smaller macroinvertebrates. When round gobies were in cages with crayfish (GC), the gut contents suggest that crayfish didn't change their feeding behavior (Figure 17). However, the gut contents of round gobies showed that they ate significantly more invertebrates, including *Polypedilum*, when with crayfish (GC) than by themselves (GG) (Table 7). I suspected round gobies could have benefited from the shredding of leaf litter by crayfish as a way to expose smaller macroinvertebrates for round gobies to prey upon. It is also possible that round gobies expressed intraspecific competition when placed with other round gobies (GG) causing then to consume fewer prey (Kornis et al. 2014). However, there was no differences in leaf litter breakdown rates suggesting the changes in the abundance of *Polypedilum* across treatments did not indirectly affect leaf litter decomposition.

Trophic cascades have been shown to occur repeatedly in many primary production base resource ecosystems (Kerfoot & Sih 1987; Abrams 1995; Werner & Pecor 2003; McIntosh et al. 2004; Tronstead et al. 2011; Burkholder et al. 2013). Trophic cascades can also occur in detrital base resource ecosystems (Wallace et al. 1982; Benfield & Webster 1985; Mulholland et al. 1985; Short & Holomuzki 1992; Malmqvist 1993; Polis & Strong 1996; Hall et al. 2001; Konishi et al. 2001; Wach & Chambers 2007; Schmitz 2010). In order for a trophic cascade to occur in a detrital food web depends on the magnitudes of both the direct and indirect effects that occurs between a predator and its prey (Schmitz 2010). Direct effects are the result of prey being predated by predators (i.e. being consumed or changing behavior or life history). Indirect effects are the consequence caused by the results of prey being predated by predators (i.e. changes in the breakdown rate of detritus).

I conducted the same procedure and used the same equation (Schmitz 2010) to determine the strengths of the direct effects (i.e. number of prey consumed) and indirect effects (i.e. breakdown rates of red maple leaves) that round gobies and crayfish had on detritivores (Figure 18). Treatments with either gobies only (GG) or crayfish only (CC) had slightly positive direct effects on detritivores that were slightly stronger than the indirect effects. Treatments with both gobies and crayfish (GC) had slightly negative direct effects on detritivores that were slightly weaker than the indirect effects. Since all of my treatments fell along the zero X axis in my study (Figure 18), there were no treatments that had a strong negative indirect effect that would initiate a trophic cascade. Several trophic cascade studies performed in streams (Rosemond et al. 2001, Ruetz et al. 2002, Miyashita & Niwa 2006) have shown top predators can successfully reduce the number of detritivores in a heterotrophic stream. However, reductions in the shredder abundance were not strong enough the significantly reduce the decomposition rate of detritus. My results follow this same pattern (Figure 18). Treatments with round gobies and crayfish together (GC) had strong direct effects in reducing the abundance of shredders. However, the direct effects were not strong enough to cause strong indirect effects in reducing the decomposition rate of red maple leaves. Because lotic system can be quite variable in physical and chemical conditions through time, it can be quite difficult to see any pattern of changes in food web structure (Benfield 2006). With high variability in the abundance of invertebrate taxa and the possibility of prey-swamping occurring for the dominant shredder, *Polypedilum*, it makes it difficult to observe how round gobies alter the role of crayfish in the decomposition of leaf litter. If I could take prey-swamping into account, I would have expected to see round gobies, when placed with crayfish (GC), negatively impacting shredder abundance (Figure 3c). The impact would have been strong enough that it could have resulted in slower breakdown rates of red maple leaves. However, my results did not show evidence that round gobies alter crayfish behavior, and that this alteration lead to a reduction in leaf litter decomposition. Therefore, I did not observe a trophic cascade when the invasive round goby was in the presence of a native crayfish.

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Figure 1: The breakdown rates for various woody and non woody plants, based on 596 estimates compiled from field studies in all types of freshwater ecosystems (Webster and Benfield 1986.)

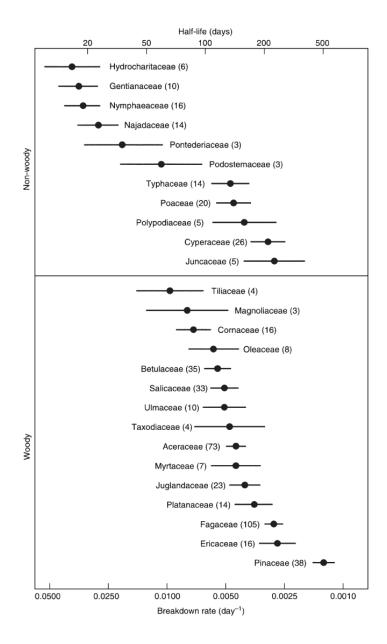


Figure 2: The shredder: CPOM: fungal-bacterial system (Cummins & Klug 1979).

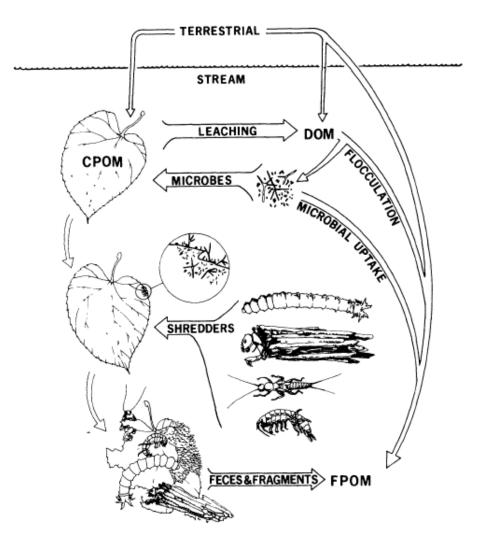
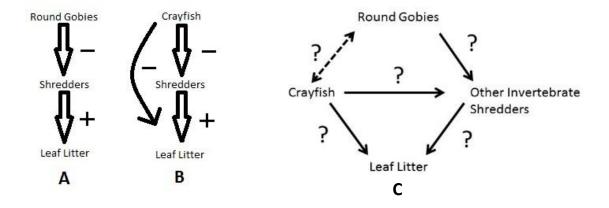


Figure 3: Predicted shifts between trophic levels in enclosure experiment performed in Ellicott Creek in summer 2014. A = treatments with gobies only, B = treatments with crayfish only, C = treatments with gobies and crayfish



## Figure 4: Map of Ellicott Creek Field Site. Yellow marks on map represent boundary lines of field site



Figure 5a: Layout of Treatments within cages during field experiment Figure 5b: Example of how cages were set up in each riffle.

## RIFFLE 4

 $\langle \rangle$ 

GC	СС	CC
GG	GC	GG
N	N	GC
CC	GG	N
	RIFFLE 3	
GG	GC	CC
Ν	GG	GC
GC	CC	N
CC	Ν	GG
	RIFFLE 2	
GG	GG	GC
N	CC	GG
GC	N	CC
CC	GC	N
	RIFFLE 1	
GG	GC	GC
GC	CC	Ν
Ν	Ν	CC
CC	GG	GG



Figure 6: Example of cage used in field experiment

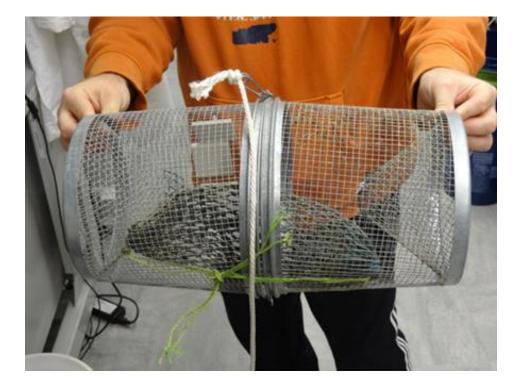


Figure 7: Model used to determine relative strengths of direct and indirect effects on predator treatments derived from Schmitz (2010a).

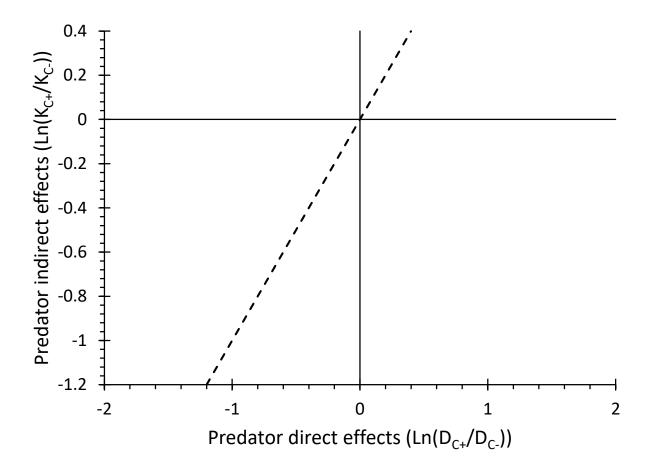


Figure 8. Mean percent ash free dry mass remaining among treatments assessing round goby and crayfish effects on leaf decompositin in Ellicott Creek, summer 2014. Error bars = 1 s.e.

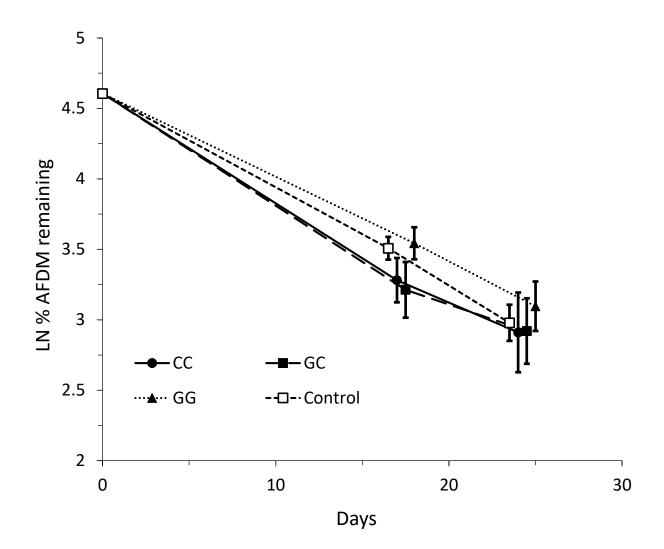
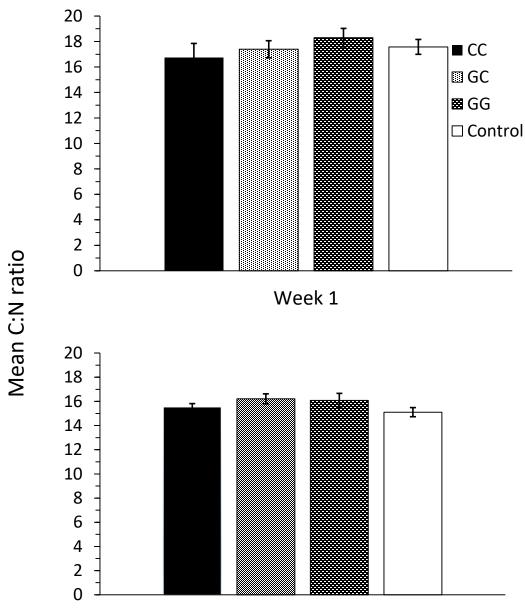


Figure 9. C:N ratio of leaf litter collected from Ellicott Creek on July 10, 2014 (Week 1) and July 17, 2014 (Week2) between treatments. Error bars = 1 s.e.



Week 2

Figure 10. Mean number of invertebrates per gram of ash free dry mass between treatments collected from Ellicott Creek from July 10, 2014 (week 1) and July 17, 2014 (week 2). Error bars= 1 s.e.

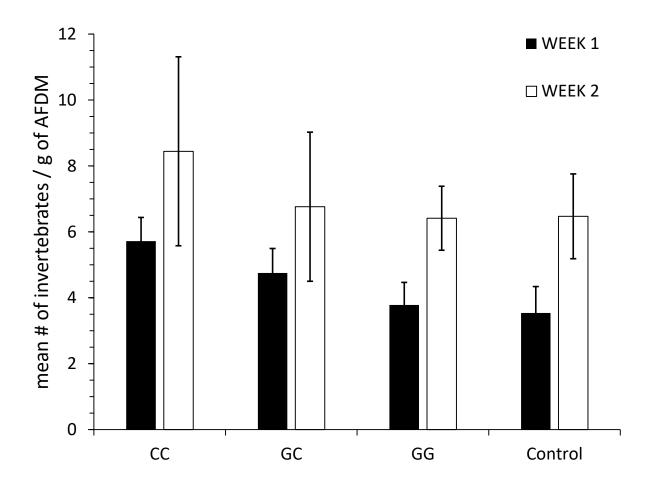


Figure 11. Mean number of collector-filters across treatments collected on July 10, 2014 (Week 1) and July 17, 2014 (Week 2) from Ellicott Creek. Error bars = 1 s.e.

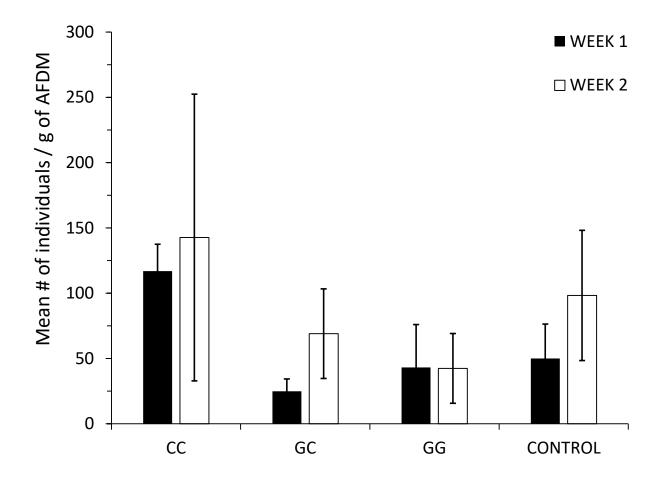


Figure 12. Mean number of collector-gatherers across treatments collected on July 10, 2014 (Week 1) and July 17, 2014 (Week 2) from Ellicott Creek. Error bars = 1 s.e.

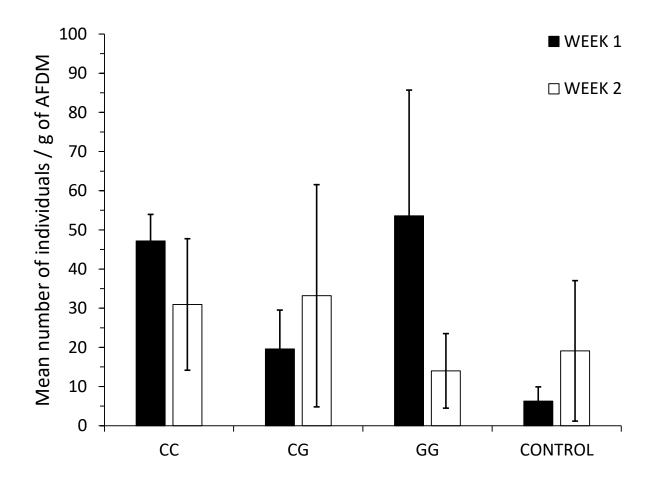


Figure 13. Mean number of predators across treatments collected on July 10, 2014 (Week 1) and July 17, 2014 (Week 2) from Ellicott Creek. Error bars = 1 s.e.

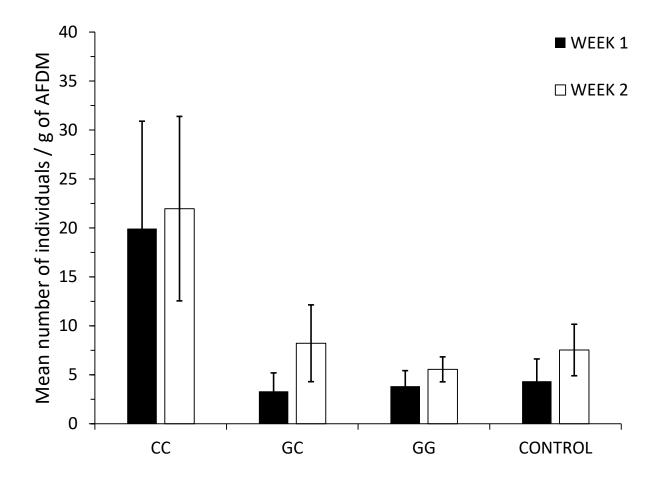


Figure 14. Mean number of grazers across treatments collected on July 10, 2014 (Week 1) and July 17, 2014 (Week 2) from Ellicott Creek. Error bars = 1 s.e.

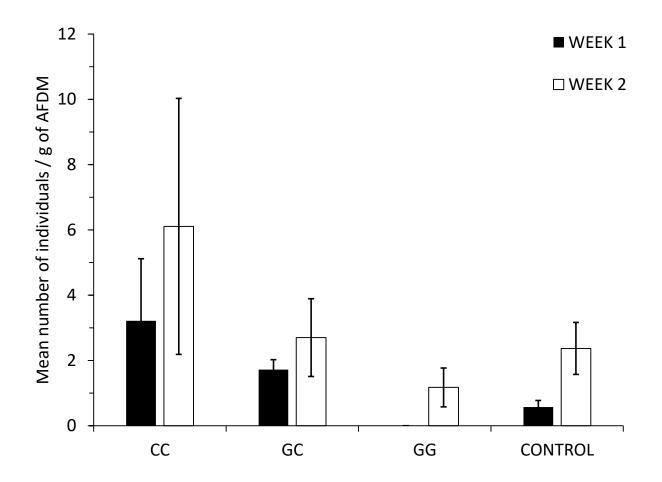


Figure 15. Mean number of shredders across treatments collected on July 10, 2014 (Week 1) and July 17, 2014 (Week 2) from Ellicott Creek. Error bars = 1 s.e.

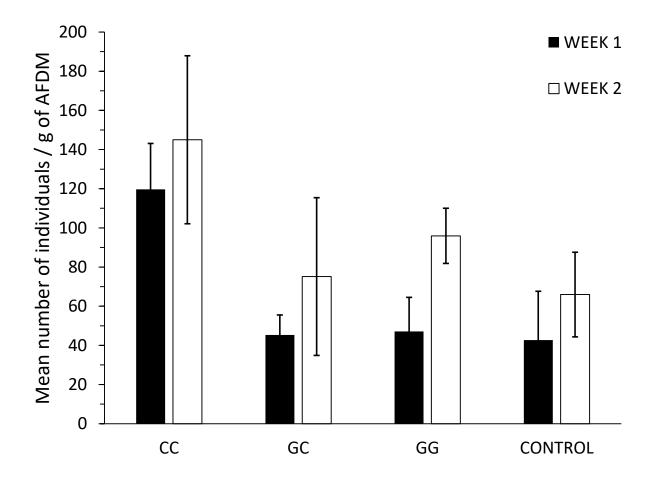


Figure 16. Growth rates of gobies and crayfish when placed in their respective treatments. Results were compared from July 3, 2014 (Week 0) to July 17, 2014 (Week 2). Error bars = 1 s.e.

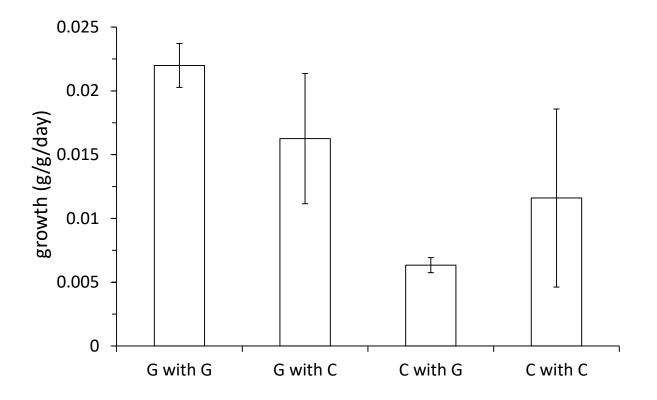


Figure 17 Mean number of invertebrate prey consumed by gobies (G) and crayfish (C) from treatments collected on July 10, 2014 (week 1) and July 17, 2014 (week 2) from Ellicott Creek. Error bars = 1 s.e.

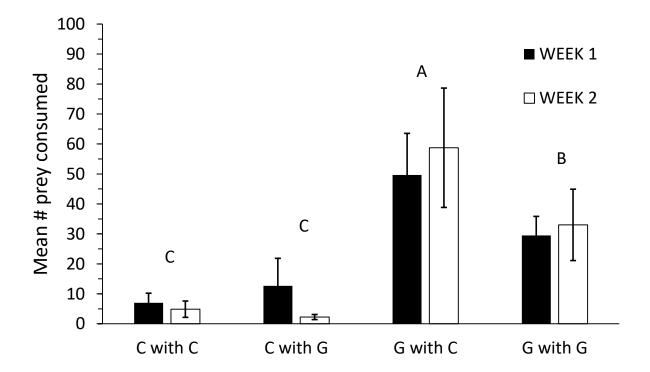
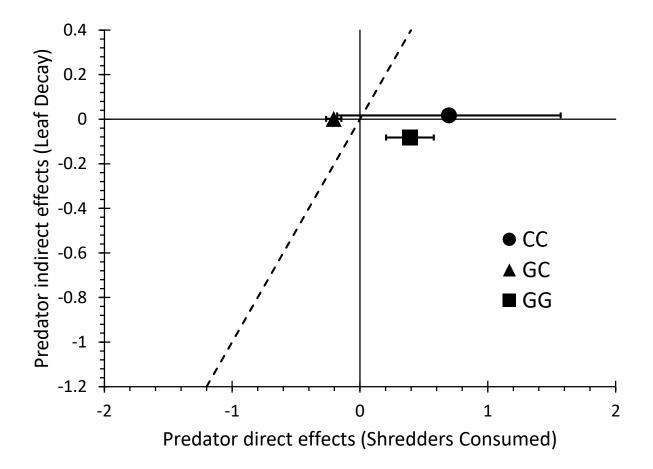


Figure 18. Interactions between the strengths of direct effects (Number of Shredders being consumed) and indirect effects (The rate of leaf litter being broken down by shredders) across treatments compared to the control collected on July 17, 2014 (Week 2). Error bars = 95 % confidence intervals.



Factor	df	MS	F	Р
Week	1	1.3785	13.363	0.00148
Treatments	3	0.0108	0.987	0.41808
Interaction	3	0.0203	0.197	0.89278
Velocity (Covariate)	1	0.6127	5.940	0.02379
Error	21	0.1032		

Table 1. Results of ANCOVA on leaf decay rates of red maple (Acer rubrum) among treatments during June 23, 2014 through July 17, 2014.

Treatment	Number of cages retrieved	Breakdown rate <u>+</u> 1 SE (day <sup>-1</sup> )
Crayfish Only	7	0.0695 <u>+</u> 0.0201
Gobies Only	8	0.0627 <u>+</u> 0.0126
Gobies and Crayfish	7	0.0685 <u>+</u> 0.0184
Control	8	0.0684 <u>+</u> 0.0092

Table 2. Mean breakdown rates of red maple (*Acer rubrum*) leaves among treatments collected from July 10, 2014 (Week 1) to July 17, 2014 (Week 2), from Ellicott Creek.

Factor	df	MS	F	Р
Riffle (block)	3	3.16	•	
Treatment	3	1.39	1.44	0.263
Week	1	22.23	22.88	<0.001
Interaction	3	0.99	1.02	0.406
Error	19	0.97		

Table 3. Results of two-way, randomized complete block ANOVA testing Treatment and Week effects on the C:N ratios in leaf litter collected from Ellicott Creek.

Table 4. Results of a two-way, randomized complete block ANOVA testing Treatment and Week effects on total abundance of invertebrates per gram of leaf ash-free dry mass remaining.

Factor	df	MS	F	Р
Riffle (block)	3	35097.5		
Treatment	3	52439.1	1.93	0.161
Week	1	19255.3	0.71	0.411
Interaction	3	2150.0	0.08	0.970
Error	18	27144.3		

Table 5. Results of two-way, randomized complete block ANOVA testing Treatment and Week	
effects on abundance of invertebrates per gram of leaf ash-free dry mass remaining per	
functional feeding group on July 10, 2014 (Week 1) and July 17, 2014 (Week 2). All data were	
(In+1)-transformed to meet variance assumptions.	

Functional feeding					
group	Factor	df	MS	F	Р
	Riffle (block)	3	17.95		
	Treatment	3	7.67	0.78	0.522
Collector/filterer	Week	1	15.99	1.62	0.219
	Interaction	3	0.53	0.05	0.983
	Error	18	9.87		
	Riffle (block)	3	13.05		
	Treatment	3	8.86	1.74	0.194
Collector/gatherer	Week	1	2.54	0.50	0.489
	Interaction	3	0.83	0.16	0.923
	Error	18	5.09		
	Riffle (block)	3	5.34		
	Treatment	3	4.36	2.26	0.117
Predator	Week	1	10.09	5.22	0.035
	Interaction	3	0.29	0.15	0.925
	Error	18	1.93		
	Riffle (block)	3	1.64		
	Treatment	3	2.36	1.98	0.153
Grazer	Week	1	4.02	3.37	0.083
	Interaction	3	0.32	0.27	0.845
	Error	18	1.19		
	Riffle (block)	3	8.56		
	Treatment	3	5.13	0.90	0.461
Shredder	Week	1	29.74	5.20	0.034
	Interaction	3	0.98	0.17	0.914
	Error	18	5.72		

Factor	df	MS	F	Р
Treatment	3	0.000156	1.862	0.194
Error	11	8.35*10 <sup>-5</sup>		

Table 6. Results of one way ANOVA on growth rates (g/g/day) of gobies and crayfish between treatments collected on July 17, 2014 (Week 2).

Factor	df	Deviance	Residual df	Residual Deviance	Р
Null			27	719.24	
Week	1	0.19	26	719.05	0.8956
Treatment	3	476.43	23	242.62	1.362*10 <sup>-9</sup>
Interaction	3	33.12	20	209.5	0.3805

Table 7. Results of two-way analysis of deviance testing number of invertebrate prey found in guts of crayfish and gobies between treatments and weeks. Post-hoc results shown in figure 11.

	Functional Feeding					
	Group	C-C	G-G	G-C	Contro	
MOLLUSCA						
GASTRAPODA						
BASOMMATOPHORA						
Lymmaeidae						
Fossaria sp.	Collector-Gatherer	0	2	0	0	
PELECYPODA	Collector-Gatheren	0	2	0	0	
VENEROIDEA						
Sphaeriidae						
Sphaerium sp.	Collector-Filterer	0	0	0	0	
ARTHROPODA						
CRUSTACEA						
AMPHIPODA						
Gammeridae						
Gammarus sp.	Shredder	4	4	1	5	
INSECTA						
EPHEMEROPETERA						
Heptageniidae						
Heptagenia sp.	Scraper	0	0	1	2	
Caenidae						
Caenis sp.	Collector-Gatherer	0	0	0	0	
ODONATA						
Calopterygidae						
Calopteryx sp.	Predator	1	0	0	0	
COLEOPTERA						
Elmidae						
Macronychus sp.	Predator	0	0	0	0	
Stenelmis sp.	Scraper	9	0	3	1	
TRICHOPTERA						
Hydropshychidae		102	00		124	
Cheumatopsyche sp.	Collector-Filterer	192	96	41	121	
Hysropsyche sp.	Collector-Filterer	179	105	32		
Hydoptilidae	Foronor	2	0	1	0	
Hydroptila sp.	Scraper	2	0	I	0	
Leptoceridae Unknown Leptoceridae sp.	Collector-Gatherer	0	0	0	0	
DIPTERA	conector-Gatheren	0	0	0	0	
Tipulidae						
Tipula sp.	Shredder	0	6	0	1	
Simuliidae	Sinedder	0	Ū	Ū	-	
Simulium sp.	Collector-Filterer	_		_	_	
	Collector-Filterer	0	1	0	0	
Empididae		10	10	_	4.6	
Hemerodromia sp.	Predator	12	13	7	16	
Chironomidae Tanypodinae						
Thienemannimyia sp.	Predator	11	1	2	4	
Orthocladiiinae	Fredator	11	T	2	4	
Cricotopus sp.	Shredder	0	0	0	0	
Eukiefferiella sp.	Collector-Gatherer	144	244	64	33	
Orthocladius sp.	Collector-Gatherer	0	0	0	0	
Trissocladius sp.	Collector-Gatherer	0	0	0	0	
Chironominae		5	Ũ	č	č	
Endochironomus sp.	Shredder	0	0	0	0	
Paratanytarsus sp.	Collector-Filterer	0	0	10	13	
Polypedilum sp.	Shredder	469	230	144	194	
UNKNOWN GENERA						
Water mite sp.	Predator	9	5	3	3	

## Appendix A. List of taxa collected from July 10, 2014 (Week1).

Functional Feeding						
	Group	C-C	G-G	G-C	Control	
MOLLUSCA						
GASTRAPODA						
BASOMMATOPHORA						
Lymmaeidae						
Fossaria sp.	Collector-Gatherer	0	0	1	0	
PELECYPODA						
VENEROIDEA						
Sphaeriidae						
, Sphaerium sp.	Collector-Filterer	0	3	1	0	
ARTHROPODA						
CRUSTACEA						
AMPHIPODA						
Gammeridae						
Gammarus sp.	Shredder	32	1	0	14	
INSECTA	Sinedder	52	I	0	14	
EPHEMEROPETERA						
Heptageniidae	<u> </u>	0		0	2	
Heptagenia sp.	Scraper	0	1	0	3	
Caenidae			-			
Caenis sp.	Collector-Gatherer	1	0	1	0	
ODONATA						
Calopterygidae						
Calopteryx sp.	Predator	1	0	0	0	
COLEOPTERA						
Elmidae						
Macronychus sp.	Predator	1	0	0	0	
Stenelmis sp.	Scraper	11	2	6	3	
TRICHOPTERA						
Hydropshychidae						
Cheumatopsyche sp.	Collector-Filterer	122	34	81	107	
Hysropsyche sp.	Collector-Filterer	104	56	54	140	
Hydoptilidae						
Hydroptila sp.	Scraper	0	0	0	1	
Leptoceridae		-	-	-	_	
Unknown						
Leptoceridae sp.	Collector-Gatherer	0	0	0	0	
DIPTERA						
Tipulidae						
Tipula sp.	Shredder	4	2	1	0	
Simuliidae			_	_	-	
Simulium sp.	Collector-Filterer	1	0	10	0	
Empididae		-	Ŭ	10	Ŭ	
Hemerodromia sp.	Predator	15	4	12	9	
Chironomidae	redator	15	4	12	5	
Tanypodinae <i>Thienemannimyia sp.</i>	Predator	20	5	0	7	
	Predator	20	5	0	/	
Orthocladiiinae	Character 1	0	0	0		
Cricotopus sp.	Shredder	0	0	0	11	
Eukiefferiella sp.	Collector-Gatherer	78	20	58	45	
Orthocladius sp.	Collector-Gatherer	0	10	0	0	
Trissocladius sp.	Collector-Gatherer	0	0	1	0	
Chironominae						
Endochironomus sp.	Shredder	0	0	1	25	
Paratanytarsus sp.	Collector-Filterer	0	0	0	0	
Polypedilum sp.	Shredder	352	211	156	144	
UNKNOWN GENERA						
Water mite sp.	Predator	14	3	8	5	

## Appendix B. List of Taxa collected from July 17, 2014 (Week 2).