

EFFECTS OF A LOW HEAD DAM ON A DOMINANT DETRITIVORE AND
DETRITAL PROCESSING IN A HEADWATER STREAM.

A Thesis
by
BRETT MATTHEW TORNWALL

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APPROVED BY:

Robert Creed
Chairperson, Thesis Committee

Michael Gangloff
Member, Thesis Committee

Michael Madritch
Member, Thesis Committee

Steven Seagle
Chairperson, Department of Biology

Edelma D. Huntley
Dean, Research and Graduate Studies

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FOREWARD

The research detailed in this thesis will be submitted to *Oikos*, an international peer-reviewed journal owned by John Wiley and Sons Inc. and published by the John Wiley and Sons Inc. Press.

The thesis has been prepared according to the guidelines of this journal.

ABSTRACT

EFFECTS OF A LOW HEAD DAM ON A DOMINANT DETRITIVORE AND DETRITAL PROCESSING IN A HEADWATER STREAM. (May 2011)

Brett Matthew Tornwall, B.S., University of Florida

M.S., Appalachian State University

Chairperson: Robert Creed

The caddisfly *Pycnopsyche gentilis* is a dominant detritivore in southern Appalachian streams. A dam on Sims Creek selectively removes *P. gentilis* from downstream reaches. I evaluated the breakdown of yellow birch leaves in the presence and absence of *P. gentilis* using a leaf pack breakdown experiment. Leaf packs were placed in reaches above the dam where *P. gentilis* is present and below the dam where it is essentially absent. I also conducted experiments to determine why *P. gentilis* was uncommon below the dam. Using enclosures, I evaluated whether there were differences in the survival and growth of *P. gentilis* in the two stream sections. I also evaluated the potential for intraguild predation by a larger caddisfly, *Pycnopsyche luculenta*, which is more abundant below the dam. *Pycnopsyche gentilis* larvae were placed in enclosures with or without *P. luculenta* above and below the dam; all enclosures included leaf packs. Leaf breakdown was significantly slower in the downstream section. *Pycnopsyche gentilis* was absent from downstream leaf packs. The stonefly *Tallaperla* was also less abundant below the dam. Detritivore diversity indices were similar for both stream sections. Calculations of *P. gentilis* per capita leaf ingestion in enclosures

suggest that *P. gentilis* was primarily responsible for the higher breakdown rates in the upstream reach. Survival and growth of *P. gentilis* were similar in up and downstream sections and *P. luculenta* had no effect on *P. gentilis* growth or survival. My results are consistent with those of other studies that suggest that it is the presence of *P. gentilis* and not detritivore diversity that drives detrital breakdown in southern Appalachian streams. The absence of *P. gentilis* below the dam may be due to the dam and reservoir preventing downstream dispersal of larvae.

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INTRODUCTION

Dams and impoundments can have major effects on stream ecosystems (Ward and Stanford 1983, Williams and Wolman 1985, Ligon et al. 1995). Dams are capable of altering chemical, physical, and biological aspects of lotic ecosystems, although the specific effects are dependent on characteristics of both the dam and the stream or river on which the dam is built (Ward and Stanford 1983, Poff and Hart 2002, Hart et al. 2002). For example, tall dams with large reservoirs on large rivers with hypolimnetic releases are likely to capture large amounts of sediment and release water of lower than normal temperatures into downstream reaches from spring to fall (Ward and Stanford 1983, Poff and Hart 2002). In contrast, small dams with surface release into headwater streams are likely to elevate downstream summer water temperatures and may have less of an effect on sediment transport because resident times are shorter in small reservoirs (Poff and Hart 2002). Surprisingly, much more is known about the effects of large hydroelectric dams on rivers than is known about small, surface release dams despite the fact that small dams are much more common in North America (Poff and Hart 2002).

The effects of dams and their impoundments on lotic communities have been examined in many different studies (Ward 1976a, 1976b, Cortes et al. 1998, Bunn and Arthington 2002, Lessard and Hayes 2003, Mantel et al. 2010a, 2010b). Dams alter species richness, diversity, and/or composition of downstream communities (Ward 1976a, 1976b,

Mantel et al. 2010a, 2010b). For example, filter-feeding hydropsychid caddisflies and black fly larvae (Simuliidae) increase in abundance downstream of dams (Spence and Hynes 1971, MacKay and Waters 1986). Some species exhibit reductions in numbers below dams, particularly detritivorous taxa (i.e., shredders) (Short and Ward 1980, Freeman et al. 2003, Mendoza-Lera et al. 2010). Changes in filter feeder and detritivore abundance could affect ecosystem functions including nutrient cycling and detrital processing. However, few studies have examined the effects of impoundments on stream ecosystem functions, particularly detrital processing (Short and Ward 1980, Mendoza-Lera et al. 2010).

Understanding effects of dams on detrital processing in headwater streams is important because temperate woodland headwater streams receive virtually all of their energy in the form of allochthonous detritus, primarily leaves (Cummins 1974, Cummins et al. 1989). Leaf decomposition consists of an initial leaching stage during which soluble organic and inorganic materials are lost, followed by microbial colonization (Webster and Benfield 1986). Invertebrate shredding and mechanical breakdown combine to further fragment the leaves into fine particulate organic matter (FPOM) (Webster and Benfield 1986). FPOM is believed to be an important source of energy and nutrients for downstream communities (Vannote et al. 1980), although there is little evidence to support this hypothesis (Heard and Richardson 1995). Few studies have explicitly evaluated the relationship between FPOM production and secondary production and the results are mixed (Usio et al. 2001, Jonsson and Malmqvist 2005).

As mentioned above, dams are capable of altering stream biodiversity. The relationship between biodiversity and ecosystem function has been the subject of considerable research (Naeem et al. 1994, Tilman and Downing 1994, McGrady-Steed et al.

1997, Naeem 1998, Loreau et al. 2001, Mittelbach et al. 2001, Hooper et al. 2005, Cardinale et al. 2006, Creed et al. 2009). Many researchers have reported a positive relationship between diversity and ecosystem function (e.g., Naeem et al. 1994, Tilman and Downing 1994, McGrady-Steed et al. 1997, Naeem 1998, Jonsson and Malmqvist 2000, 2003, Crutsinger et al. 2006). More recently, researchers have reported negative relationships between diversity and function (e.g., Cardinale and Palmer 2002, Boyero et al. 2007, Creed et al. 2009). One mechanism that could potentially explain a negative relationship between biodiversity and ecosystem function is the effect of species that are both functional and competitive dominants (Creed et al. 2009). Functional and competitive dominants can lower diversity by excluding other organisms from habitats while simultaneously increasing function if the competitively subordinate taxa were functionally inferior. Competitively dominant taxa that are not functionally dominant can also create a negative relationship between biodiversity and function by lowering the performance of more diverse assemblages (Cardinale and Palmer 2002).

Experiments exploring the relationship between biodiversity and ecosystem function are often highly artificial (Bracken et al. 2008, Srivastava et al. 2009) or suffer from experimental artifacts (Huston 1997). Synthetic-assemblage experiments (SAE), in which species are artificially assembled into communities can differ in their responses to changes in diversity compared to natural systems (Díaz et al. 2003). Additionally, SAE may produce a statistical effect where larger assemblages are more likely to contain functionally dominant species i.e., the sampling effect (Huston 1997). In many cases, the positive association between biodiversity and ecosystem function can be attributed to poorly performing monocultures in experiments where different levels of biodiversity were experimentally

manipulated (see Bracken et al. 2008, Rollins 2010). However, if the best performing monoculture performs at least as well as the multi-species treatments then that is strong evidence for a dominant species effect (Rollins 2010). However, if only the mean monoculture performance is reported this increases the likelihood of reporting a positive but spurious relationship between function and diversity when a dominant species is really the driving force behind the relationship, not increasing diversity.

An alternative to SAE is the selective removal of species from the community (Díaz et al. 2003). Some experiments altered species compositions through random removals or additions and found that the more species in an assemblage, the higher the ecosystem function of that assemblage (see Bracken et al. 2008). Bracken et al. (2008) point out that experiments randomly adding or removing species to an assemblage are not realistic because species are not lost or removed randomly from ecosystems. Díaz et al. (2003) and Bracken et al. (2008) argue that non-random removals, in which species are removed from communities in a way that mimics the effect of natural or anthropogenic effects, is potentially a more realistic approach to examining the effects of species deletions on ecosystem function. For example, some land use practices may result in the selective removal or reduced abundance of a specific taxon (e.g., Creed et al. 2009). In headwater streams, dams appear to selectively affect particular detritivore taxa (Short and Ward 1980, Cherry 2000, Mendoza-Lera et al. 2010). Thus, streams with dams on them provide an opportunity to explore the effects of selective reduction or deletion of particular detritivore taxa on ecosystem function.

This study examines the effects of a small surface release dam on detrital processing in a headwater stream. A previous leaf pack breakdown experiment found that a dominant detritivorous taxon, the limnephilid caddisfly *Pycnopsyche gentilis* (Creed et al. 2009), was

rare downstream of the dam on Sims Creek (Cherry 2000). Cherry (2000) also found that leaf breakdown rates were low below the dam despite the presence of other detritivore taxa. I hypothesized that the presence of the dam and reservoir was the cause of the reduced densities of *P. gentilis* below the dam, which would result in a decrease in leaf breakdown rates in the downstream section. I also evaluated whether or not there was a significant effect of detritivore richness or diversity on leaf breakdown. Finally, I evaluated whether *P. gentilis* was able to survive and grow below the dam and whether it might be excluded from the downstream habitat by intraguild predation by a larger species of *Pycnopsyche*.

METHODS

Study site

Sims Creek is a second order stream located on the Blue Ridge Parkway in the Southern Appalachian Mountains. A dam on the creek creates a small reservoir approximately 1 hectare in size. The dam has a spillway that releases surface water to the downstream section of stream. The riparian zones along the stream above and below the reservoir are similarly vegetated with *Rhododendron maximum*, *Betula alleghaniensis*, *Tsuga caroliniana*, *Tsuga canadensis*, *Acer saccharum*, *Quercus alba*, and *Quercus rubra* comprising the majority of the vegetation. Yellow birch (*B. alleghaniensis*) leaves were chosen for my experiments because it is the most abundant leaf in the stream (see leaf survey results). Sites were chosen in the up and downstream sections with similar substrate, depth, and flow conditions. Depth and stream flow were measured at each site on the first day of the leaf pack breakdown experiment. Depths for the upstream site ranged from 13 - 37 cm with a mean depth of 21.9 cm and at the downstream site ranged from 12 - 21 cm with a mean of 16.2 cm. Stream width for both sites ranged from 1.5 m-3 m. Current velocity was 18 cm/s for the upstream site and 15 cm/s for the downstream site.

Water temperatures were monitored at both sites with temperature loggers (HOBO U22 Water Temp Pro v2) during the winters of 2008/2009 and 2009/2010 (Figures 1A and 1B). Mean temperature differences for late winter/early spring of 2008/2009 (not the year of the experiments) were greater with a mean temperature of 5.81 (\pm 2.28) °C upstream and 7.00

(± 2.28) °C downstream. Mean temperature differences between the upstream and downstream stream sections for the winter of 2009/2010 were negligible, with a mean of 3.46 (± 2.31) °C upstream and a mean of 3.54 (± 2.23) °C downstream. The reservoir was frozen over for the most of the 2009/2010 winter and for the entire duration of the leaf pack breakdown experiment.

Leaf surveys

Leaf surveys were primarily designed to give an indication of the relative availability of different leaf species in the stream, not to estimate leaf mass on a per area basis. Leaves were surveyed in the stream on 15 Nov 2010 and 11 Dec 2010. On 1 Dec 2010 a rain storm caused Sims Creek to flood which washed out many of the debris dams containing leaves. A 26 cm X 26 cm quadrat was haphazardly placed on an aggregation of leaves and all leaves within the quadrat were placed in a plastic bag and later identified in the lab to species. Leaves of both sugar (*Acer saccharum*) and red maple (*A. rubrum*) were grouped together as maple due to difficulty identifying partially decomposed leaves. Leaves were then oven dried at 60 °C for 5 d and dry mass was determined.

Caddisfly surveys

Detritivorous caddisfly surveys were conducted from 0-80 m upstream from the reservoir and from 20-100 m below the reservoir on 1 Apr 2009. Surveys were standardized on a per unit effort basis with ten 8 minute sampling periods per section. Debris dams and leaf accumulations were searched for 8 minutes and all caddisflies were collected and later identified. One-way analysis of variance (ANOVA) was used to determine if significant differences in caddisfly abundance occurred with respect to location.

Leaf pack breakdown experiment

Leaf packs were composed of 5 g of air dried yellow birch leaves collected just prior to abscission in mid-October 2009. Leaves were soaked overnight in reverse osmosis water in order to soften them for leaf pack construction. Leaf packs were held together using binder clips and attached to the upstream side of bricks using cable ties (Creed et al. 2009). Forty-two leaf packs were placed upstream and downstream of the pond on 4 Dec 2009 to determine mass loss over time. Downstream leaf packs were between 60 and 120 m downstream of the dam spillway and upstream leaf packs were 25-50 meters upstream from the reservoir. An additional 6 leaf packs were placed in the stream but were removed after 1 minute to serve as handling controls (day 0 sample). On days 1, 7, 14, 28, 42, 51, and 91, 12 leaf packs (6 upstream and 6 downstream) were randomly sampled. Leaf packs were removed from the stream and placed into sealable plastic bags. In the lab, leaves were gently cleaned to remove debris and macroinvertebrates. Leaves were dried for 4 days at 60 °C and weighed to the nearest 0.01 g to determine dry mass. Next, leaves were ashed at 550 °C for 3 hours to determine ash free dry mass (AFDM).

AFDM values were compared by date and location using a general linear model ANOVA. Levene's test was used to check for equal variances and log transformations were performed if needed. Leaf breakdown rates were calculated by taking the natural log of the mean percent of leaf AFDM remaining on a particular date and then performing regression analysis to determine k , the slope of the regression line (Benfield 1996).

Macroinvertebrates were removed from leaf packs and preserved in 70% ethanol and later identified to the lowest taxonomic level possible, usually genus or species. Two-way ANOVAs were used to test for location and date effects on the abundance of major

detritivore taxa (e.g. *P. gentilis*, *Tallaperla maria*, or *Tipula abdominalis*), two diversity indices (Shannon-Weiner and Simpson's Index), and detritivore richness. ANOVAs were also performed to determine if detritivore richness was significantly different between the two stream sections on a particular sampling date. Correlation analyses were performed to determine if the presence of any major detritivore affected the abundance of any other major detritivore.

***P. gentilis* survival and growth experiment.**

Previous field surveys and an experiment (Cherry 2000) determined that *P. gentilis* was essentially absent downstream of the dam. In order to determine if survival and growth of *P. gentilis* larvae differed above and below the dam I conducted an enclosure experiment. Sixteen plastic enclosures (35 cm X 20 cm X 20 cm) with 243 μ m mesh on the upstream and downstream ends were placed in Sims Creek up and downstream of the pond on 18 Feb 2010. Each enclosure contained 5 g of air-dried yellow birch leaves. Leaves were allowed to condition (i.e., microbial colonization) in the stream for 14 days. One pre-weighed (blotted wet mass, to the nearest 0.0001 g) *P. gentilis* larva was placed into each cage on 5 Mar 2010. All larvae were judged to be in the 3rd instar based on case size and body mass. Cages were randomly assigned positions at each site.

After the larvae had been in the cages for 28 d all larvae and leaf packs were collected. The final blotted wet mass of the larvae and AFDM of the remaining leaf material were determined. The procedures for determining AFDM were the same as in the leaf pack experiment. Changes in mass of *P. gentilis* in the two stream sections were compared using a one-way ANOVA. Differences in mortality were compared using Fisher's exact test.

Intraguild predation experiment

Large detritivorous caddisflies may occasionally feed on conspecifics and other small caddisflies (Wissinger et al. 1996). Two other large caddisflies (*P. luculenta* and *Hydatophylax argus*) are present in Sims Creek and both are more abundant below the dam (see results of caddisfly surveys). I examined the potential for intraguild predation by the more common species (*P. luculenta*) on *P. gentilis*. The effect of *P. luculenta* on *P. gentilis* was evaluated using a similar procedure to the *P. gentilis* survival and growth experiment. Enclosure setup and leaf conditioning were the same. Eight of the enclosures contained one larva of each species and 8 of the enclosures contained a single *P. gentilis* larva. Each stream section received 8 enclosures (4 with both species and 4 with only *P. gentilis*). Containers were placed approximately 60 m up and downstream of the reservoir on 18, Feb 2010. Two cages were lost due to increased flow during rain events (1 downstream *P. gentilis*/*P. luculenta* enclosure and 1 upstream *P. gentilis* enclosure). Final sample sizes were 4 upstream enclosures with both species, 3 upstream enclosures with only *P. gentilis*, 3 downstream enclosures with both species, and 4 downstream enclosures with only *P. gentilis*. After 28 d all larvae and leaf packs were collected. Mortality of the caddisflies and AFDM of the remaining leaf material were determined. AFDM was determined using the methods previously described. Differences in mortality were compared using Fisher's exact test.

RESULTS

Leaf Surveys

Yellow birch leaves were the dominant leaf by biomass in debris dams after the autumn leaf drop in both stream sections. Yellow birch accounted for 60% of leaf mass at the upstream site and 84% at the downstream site on 15 Nov 2010 (Figures 2A and 2B). After the flood on 1 Dec 2010, overall leaf mass in the debris dams declined dramatically (Figures 3A and 3B). Yellow birch and rhododendron were co-dominant species in the post-flood disturbed habitat.

Caddisfly Surveys

A significant difference was detected in *P. gentilis* abundances ($F_{1,14}=31.84$, $p<0.001$) between the two locations. Sixty-four *P. gentilis* were found upstream and 3 were found downstream. Thirty *P. luculenta* were found upstream and 83 were found downstream but the difference was not significant ($F_{1,14}=3.56$, $p=0.08$). One *H. argus* was found upstream and 9 were found downstream and the difference was significant ($F_{1,14}=7.23$, $p=0.018$). .

Leaf pack breakdown experiment

There was a significant effect of both date ($F_{7,73}= 65.66$, $p<0.001$) and location ($F_{1,73}=18.79$, $p<0.001$) as well as a significant date*location interaction ($F_{7,73}=3.26$, $p=0.005$) on leaf breakdown (Figure 4). Leaf pack AFDM remaining was significantly lower for upstream leaf packs on days 1 ($F_{1,10}=5.43$, $p=0.042$), 42 ($F_{1,10}=8.5$, $p=0.015$), and 51 ($F_{1,10}=9.2$, $p=0.013$) compared to downstream leaf packs. The difference in AFDM

remaining on day 91 was marginally significant ($F_{1,9}=4.74$, $p=0.058$). The k value for leaves at the upstream site for the entire period (0.0138) was approximately twice that for leaves at the downstream site (0.007).

No *P. gentilis* were found on downstream leaf packs. This species was present on upstream leaf packs and was most abundant on day 42 (Figure 5A). *Tallaperla maria* was most abundant on day 51 and was significantly more abundant at the upstream site on days 28 ($F_{1,10}=23.75$, $p<0.001$) and 51 ($F_{1,10}=9.16$, $p=0.013$) (Figure 5B). *Tipula abdominalis* exhibited patchy distribution and was not significantly more abundant on any date for either location ($F_{1,10}=0.1658$, $p=0.69$) (Figure 5C). No significant correlations were detected between *P. gentilis*, *T. maria*, and *T. abdominalis* densities on leaf packs. There were no significant differences in the Shannon-Weiner indices for upstream and downstream sites on any date ($F_{1,59}=1.748$, $p=0.191$) (Figure 8). There was a significant overall effect of location on Simpson's index ($F_{1,59}=4.991$, $p=0.021$). Further analysis indicated that on day 7 ($F_{1,10}=5.454$, $p=0.042$) and 28 ($F_{1,10}=6.008$, $p=0.034$) Simpson's index was significantly higher in the upstream section (Figure 7). Differences were not significant on any other date. Detritivore richness was not significantly different between stream sections on any day (day 7 $F_{1,10}=1$, $p=0.34$; day 14 $F_{1,10}=0.47$, $p=0.51$; day 28 $F_{1,10}=2.24$, $p=0.17$; day 42 $F_{1,10}=3.79$, $p=0.08$; day 51 $F_{1,10}=2.17$, $p=0.17$). *P. luculenta* and *H. argus* were present in both stream sections, although densities were patchy. Most leaf packs (85%) had none of either species although on day 42 one upstream leaf pack had 10 *H. argus*, 8 *P. luculenta*, and 4 *P. gentilis*.

Correlations of leaf pack AFDM remaining on day 42 and densities of major invertebrate detritivores (*P. gentilis*, *T. maria*, and *T. abdominalis*) on upstream leaf packs indicated that almost 92% of the variation in leaf pack AFDM remaining was explained by

the densities of *P. gentilis* on the leaf packs. ($r^2 = 0.9187$, $p = 0.003$) (Figure 6). The densities of *T. maria* and *T. abdominalis* did not have a significant correlation with leaf pack AFDM remaining on day 42 for the upstream site.

***P. gentilis* survival and growth experiment**

There were no significant differences in caddisfly survival (Fishers exact test $p = 1.0$), initial mass ($F_{1, 14} = 0.0104$, $p = 0.92$) or growth ($F_{1, 14} = 0.471$, $p = 0.504$) between upstream and downstream sections. *P. gentilis* at both sites exhibited similar mean mass losses of approximately 50 mg (upstream site $61 \text{ mg} \pm 16$; downstream site $54 \text{ mg} \pm 13$). No differences in feeding rates as measured by leaf pack AFDM remaining were detected between the two sites ($F_{1, 14} = 0.746$, $p = 0.402$).

Intraguild predation experiment

Pycnopsyche luculenta had no significant effect on the survival of *P. gentilis* (Fishers exact test $p = 1.0$). Additionally, no significant difference in survival was detected for solitary *P. gentilis* in either stream section (Fishers exact test $p = 1.0$).

Leaf mass loss in enclosures did not differ significantly among location ($F_{1, 12} = 0.964$, $p = 0.345$) but did differ significantly in response to caddisfly treatments ($F_{1, 12} = 13.49$, $p = 0.0032$). Specifically, cages with both *P. gentilis* and *P. luculenta* lost significantly more leaf mass than cages that contained a single *P. gentilis* (Figure 9).

DISCUSSION

Selective deletion of a dominant species

Reduced leaf breakdown rates downstream of dams have been observed in previous studies (Cummins 1979, Mendoza-Lera et al. 2010), although the mechanism(s) responsible for this phenomenon remain unclear. The mechanism in my study appears to be the selective removal of a dominant detritivore (*P. gentilis*) from the stream below the dam. The removal of a functionally dominant species such as *P. gentilis* from a stream could have large impacts on ecosystem function (Creed et al. 2009). The virtual absence of *P. gentilis* below the dam is the most likely explanation for decreased leaf pack breakdown rates downstream of the dam. Similar results were reported by Cherry (2000).

Pycnopsyche gentilis, *T. maria*, and *T. abdominalis* have been reported to be important leaf shredders in Southern Appalachian streams (Stout et al. 1993). *Tipula abdominalis* densities on leaf packs did not significantly differ between the up and downstream section which suggests that it had little impact on leaf breakdown. Both *P. gentilis* and *T. maria* were significantly more abundant in the upstream section suggesting that both taxa may contribute significantly to leaf breakdown. Several lines of evidence suggest that *T. maria* is not an important shredder in Sims Creek. Cherry (2000) conducted a leaf breakdown experiment in Sims Creek in the late 1990's approximately 1km downstream of the dam. *Tallaperla maria* was abundant in this section but *P. gentilis* was not (Cherry 2000). Leaf breakdown appeared to be mostly microbial driven in this section of stream

below the dam despite the presence of *T. maria* (Cherry 2000). This further supports the idea that reduced densities of *P. gentilis* are the primary reason for slower leaf breakdown rates I observed in the stream downstream of the dam.

Furthermore, feeding rates of *P. gentilis* are high compared to other taxa (Eggert and Wallace 2007, Rollins 2010). Data from the enclosure experiment suggests that a single *P. gentilis* is capable of consuming 0.010 g leaf/day for 42 d. Leaf packs in the enclosure experiment had a 14 d microbial colonization period and were then consumed by *P. gentilis* for 28 d, analogous to natural conditions. In contrast, the entire detritivore community in the downstream section consumed 0.014 g leaf/d whereas the upstream detritivore community, which included an average of 2.67 *P. gentilis*/leaf pack on day 42, consumed an average of 0.024 g leaf/d. These data indicate that a single *P. gentilis* can have nearly the same effect on leaf breakdown as an entire guild of detritivores devoid of *P. gentilis*. When the upstream densities of *P. gentilis* are considered in conjunction with the potential feeding rates, *P. gentilis* feeding could account for all leaf mass loss upstream. This is supported by the significant relationship between *P. gentilis* density and leaf mass AFDM remaining on day 42. On day 42 of the experiment, no relationship was detected between *T. maria* density and leaf pack AFDM remaining. Additionally, leaves displayed evidence of heavy *P. gentilis* feeding activity (e.g., entire portions of the leaf missing, including veins) but little evidence of *T. maria* feeding (e.g., leaf material removed between small veins resulting in a net-like pattern).

These results are correlational and not experimental. However, results from other experiments have demonstrated that *P. gentilis* has a higher feeding rate than other detritivores, including potentially dominant species like *T. maria* and *T. abdominalis* (Eggert

and Wallace 2007, Rollins 2010). Eggert and Wallace (2007) found that *P. gentilis* had a feeding rate 5X higher on leaves than that of *T. maria* and 3-4X higher than that of *T. abdominalis*. Additionally, Rollins (2010) reported that experimental per capita consumption of yellow birch leaves by *P. gentilis* was significantly higher than either *T. maria* or *T. abdominalis*. Leaf mass loss in treatments with *T. maria* was not different from microbial controls in a field enclosure experiment (Rollins 2010).

Detritivore richness was not significantly different between the two stream sections on any sampling date. Additionally, both Simpson's Index and the Shannon-Weiner Index were not significantly different between the two stream sections (except on day 7 and 28 for Simpson's Index). This indicates that detritivore diversity may not be the primary driver of leaf breakdown in Sims Creek. Previous studies report a positive relationship between shredder species richness and detrital processing in streams (Jonsson and Malmqvist 2000, Ruesink and Srivastava 2001, Jonsson and Malmqvist 2003, Dangles and Malmqvist 2004). In contrast, other recent studies report either no effect of species richness on detrital processing or a negative relationship (Boyero et al. 2007, Creed et al. 2009, McKie et al. 2009, Rollins 2010).

Other possible explanations for the reduced breakdown rate of leaves downstream of the dam on Sims Creek are differences in leaching rates, differences in physical processes (i.e., fragmentation due to high current, impacts from particles suspended in the water column etc.) (Gessner et al. 1999), or differences in microbial breakdown rates. However, I found little support for these potential mechanisms.

On day 1, upstream leaf packs had lost significantly more mass due to leaching than leaf packs at the downstream site. The reason for this difference is unknown although other

studies have reported similar results (Gelroth and Marzolf 1978, Short and Ward 1980). According to Petersen and Cummins (1974) leaching is a physical process and should not differ between stream sections. By day 7 there were no significant differences in leaf pack AFDM remaining. Therefore it is unlikely that differences in leaching rates contributed much to overall breakdown rates.

Physical processes are another potential driver of leaf breakdown (Gessner et al. 1999). However, in Sims Creek the upstream and downstream sections showed little differences in stream width, stream depth or current velocity and therefore should not differ greatly in physical effects on the leaf packs. It is possible that during high flow events less suspended sediment could be present in the downstream section because much of the sediment has been removed from the water column by the reservoir (Poff and Hart 2002). Reduced sediment could lessen leaf abrasion downstream of the reservoir during high flow events. However, this is an unlikely cause of the differences in leaf breakdown rates seen in my study because the only significant rain event occurred on day 52 of the study and there were significant differences in remaining leaf pack AFDM on days 42 and 51.

Differences in microbial breakdown rates are another possible contributor to the differences in leaf pack breakdown rates seen in the two different stream sections. However, I found no evidence that microbial breakdown rates differed between the two sections. First, on days 7 and 14 no significant differences in leaf pack breakdown rates were present. This time period is commonly thought of as the period where microbial breakdown is most important (Webster and Benfield 1986, Allan 1995). It was only after this time period when macroinvertebrate shredder (e.g., *P. gentilis*) densities began to increase that a significant difference in leaf pack breakdown rates was observed. Second, no differences in remaining

leaf pack AFDM were present in the *P. gentilis* survival and growth experiment between the two stream sections. If microbial decomposition was faster in the upstream section then there should have been less AFDM remaining in the upstream enclosures. This was not observed.

Why is *P. gentilis* rare downstream of the reservoir?

The reason for *P. gentilis*'s relative absence below the reservoir has not yet been determined. However, some causes can be ruled out. Since *P. gentilis* could survive in cages when transplanted downstream, winter water chemistry or temperature differences are not likely to be the mechanism that excludes *P. gentilis* from the downstream section. Also, *P. gentilis* growth did not differ between the two sections. If growth and survival of *P. gentilis* does not differ between the two stream sections in the winter, some other factor must be responsible for excluding *P. gentilis* from the downstream habitat.

Differences in predation pressure on *P. gentilis* could explain the virtual absence of *P. gentilis* downstream of the dam. Caddisflies are known to engage in intraguild predation (Wissinger et al. 1996) and two larger caddisflies (*H. argus* and *P. luculenta*) were present at higher densities below the dam. Intraguild predation by the larger and more common *P. luculenta* does not appear to explain the absence of *P. gentilis* since there was no significant difference in mortality between enclosures that contained *P. luculenta* and those that did not. I did not evaluate effects of *H. argus* on *P. gentilis*. It is also a potential intraguild predator that is more abundant below the dam. Other predators such as crayfish or trout could be more abundant below the dam and hence contribute to low *P. gentilis* densities but their effects were not investigated as part of this study.

Elevated summer water temperatures downstream from the reservoir may affect the distribution of *P. gentilis*. Warmer water temperatures have been shown to alter stream macroinvertebrate communities in a variety of ways. For example, elevated water temperatures were found to cause earlier adult emergence in aquatic insects and altered sex ratios (Hogg and Williams 1996). It is possible that increased temperatures in the downstream section during the summer affect *P. gentilis* densities throughout the rest of the year. Temperature differences have been shown to have an effect on the metabolic rates of other Trichopteran species (Howell and Voshell Jr. 1982). Many univoltine caddisfly species undergo a period of diapause in the last larval instar before pupation (Novak 1960). This period of diapause occurs during the summer. Elevated summer water temperatures in the downstream section could affect *P. gentilis* during diapause resulting in reduced pupation rates. If *P. gentilis* has high site fidelity recolonization rates of the downstream section could be slow. Winter water temperatures in both 2008/2009 and 2009/2010 did not exhibit the large differences between the two stream sections as was seen in summer temperatures in 2004. Therefore slightly warmer water temperatures in the downstream section during the winter are unlikely to be responsible for the differences in *P. gentilis* densities.

A more likely scenario for the absence of *P. gentilis* at the downstream site is that the reservoir acts as a barrier to downstream larval dispersal via drift. Many insects with aquatic larvae and terrestrial adults (e.g. Ephemeroptera, Trichoptera, and Plecoptera) have directed upstream flight (Müller 1954). Adults fly upstream to oviposit presumably to counter downstream drift of larvae (e.g., the colonization cycle) (Müller 1954, 1982, Madsen 1977). Neves (1979) found that *Pycnopsyche guttifer* adults, a closely related species to *P. gentilis*, displayed directed upstream flight and that *P. guttifer* larvae drifted 400-700 m downstream

prior to pupation. If *P. gentilis* behaves in a similar manner, the larvae may not be capable of drifting through the reservoir and as a result do not reach the section of stream downstream of the dam. *Pycnopsyche gentilis* larvae may either suffer high mortality in attempts to drift through the reservoir or may crawl back upstream to avoid the lentic habitat of the reservoir. Current velocities in the pond are probably low which could result in *P. gentilis* not being able to drift at all when in the pond. Additionally, the pond has introduced brown trout (*Salmo trutta*) (RP Creed, personal observation) that could prey upon large caddisfly larvae. As a result, adult *P. gentilis* will only emerge from stream sections above the pond. If they exhibit directed flight up the stream valley no eggs will be laid in the stream section below the dam. Under this scenario, *P. gentilis* would be lost quickly from downstream habitats once a dam is built.

In conclusion, this study demonstrates the usefulness of evaluating changes in an ecosystem function as a result of the selective removal of a dominant species. Dams have been shown to decrease detritivore densities which allow for the evaluation of the effects of this decrease on detrital processing. In cases where a deleted species is a functional dominant, large changes in function may be seen with relatively little change in detritivore diversity.

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FIGURE LEGENDS

Figure 1A. Water temperatures for the upstream and downstream locations on Sims Creek from 23 February 2009 – 18 April 2009.

Figure 1B. Water temperatures for the upstream and downstream locations on Sims Creek from 4 Dec 2009 until 4 April 2010.

Figure 2A. Mean (\pm 1SE) leaf species abundances in leaf accumulations before a flood on December 1, 2010. (Birch= *B. allegheniensis*, Maple= *A. rubrum*, *A. saccharum*, Rhodo= *R. maximum*, Red Oak=*Q. rubra*, Magnolia= *Magnolia acuminata*, T. Poplar= *Tulipifera liriodendron*, Beech= *Fagus grandifolia*, Witchazel= *Hamamelis virginiana*)

Figure 2B. Mean (\pm 1SE) leaf species percent abundance in leaf accumulations before a flood on December 1, 2010.

Figure 3A. Mean (\pm 1SE) leaf species abundances in leaf accumulations after a flood on December 1, 2010.

Figure 3B. Mean (\pm 1SE) leaf species percent abundance in leaf accumulations after a flood on December 1, 2010.

Figure 4. Mean (\pm 1SE) leaf pack AFDM remaining plotted by day and location. Dates with significantly different ($p < 0.05$) mean leaf pack AFDM remaining between the two sections are denoted with an *. Dates marginally significant ($p < 0.07$) are denoted with a +.

Figure 5A. Mean (\pm 1SE) number of *P. gentilis*/g of leaf pack AFDM remaining in a location as a function of date. No *P. gentilis* were found downstream of the reservoir on a leaf pack.

Figure 5B. Mean (\pm 1SE) number of *T. maria*/g of leaf pack AFDM remaining in a location as a function of date. Dates that are significantly different ($p < 0.05$) are denoted with an *.

Figure 5C. Mean (\pm 1SE) number of *T. abdominalis*/g of leaf pack AFDM remaining in a location as a function of date.

Figure 6. Linear regression of leaf pack AFDM remaining (g) as a function of *P. gentilis* density (*P. gentilis*/g) at the upstream site for day 42.

Figure 7. Simpson's Diversity Index (1-D) for detritivores on each sample date for both upstream and downstream sections. Data are means (\pm 1SE) for all leaf packs collected at a particular site on a particular date.

Figure 8. Shannon-Weiner Index for detritivores on each sample date for both upstream and downstream sections. Data are means (\pm 1SE) for all leaf packs collected at a particular site on a particular date.

Figure 9. Mean (\pm 1SE) leaf pack AFDM remaining after 28 days for enclosures with a single *P. gentilis* (P.g) and enclosures with a one *P. gentilis* and one *P. luculenta* (P.L).

Figure 1A.

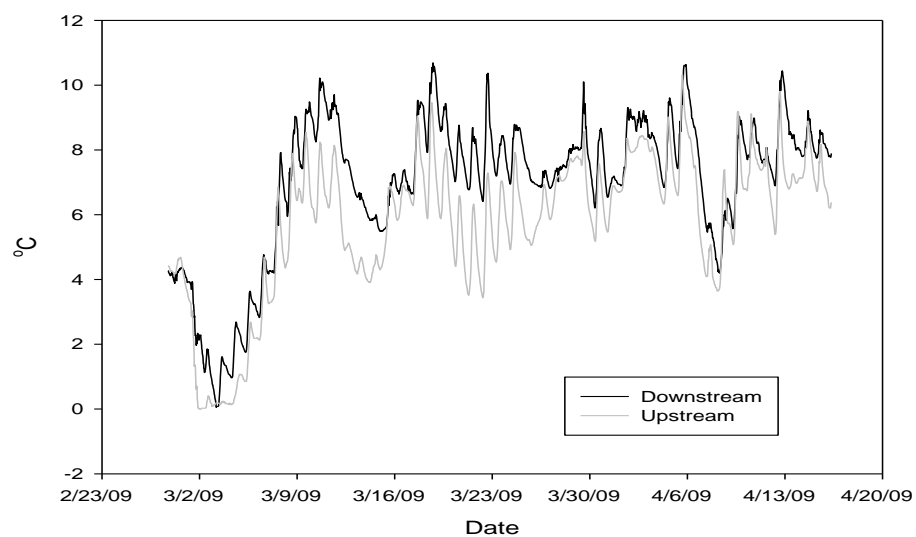


Figure 1B.

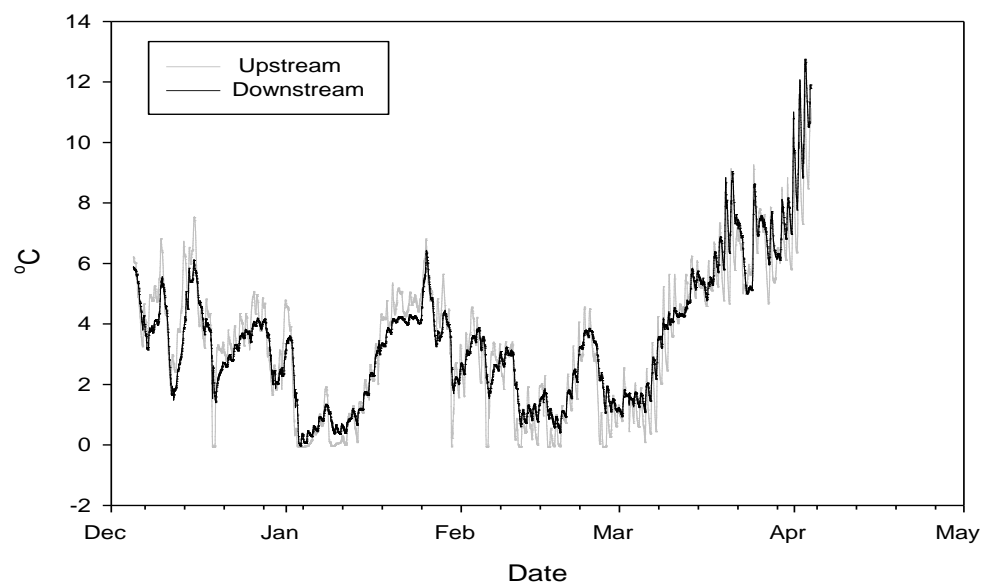


Figure 2A.

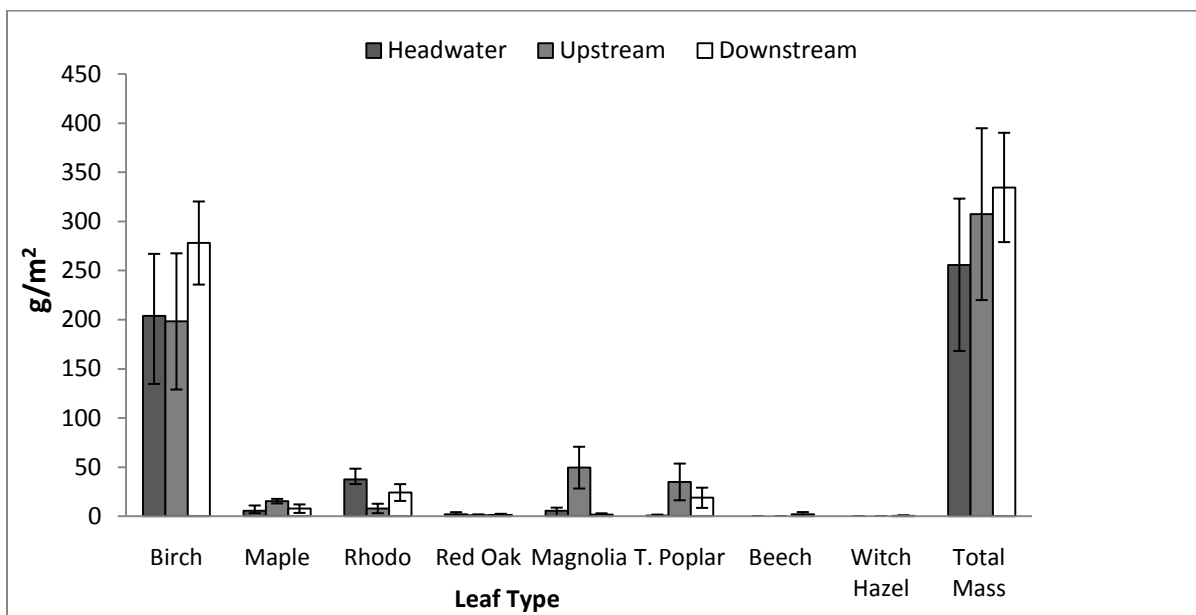


Figure 2B.

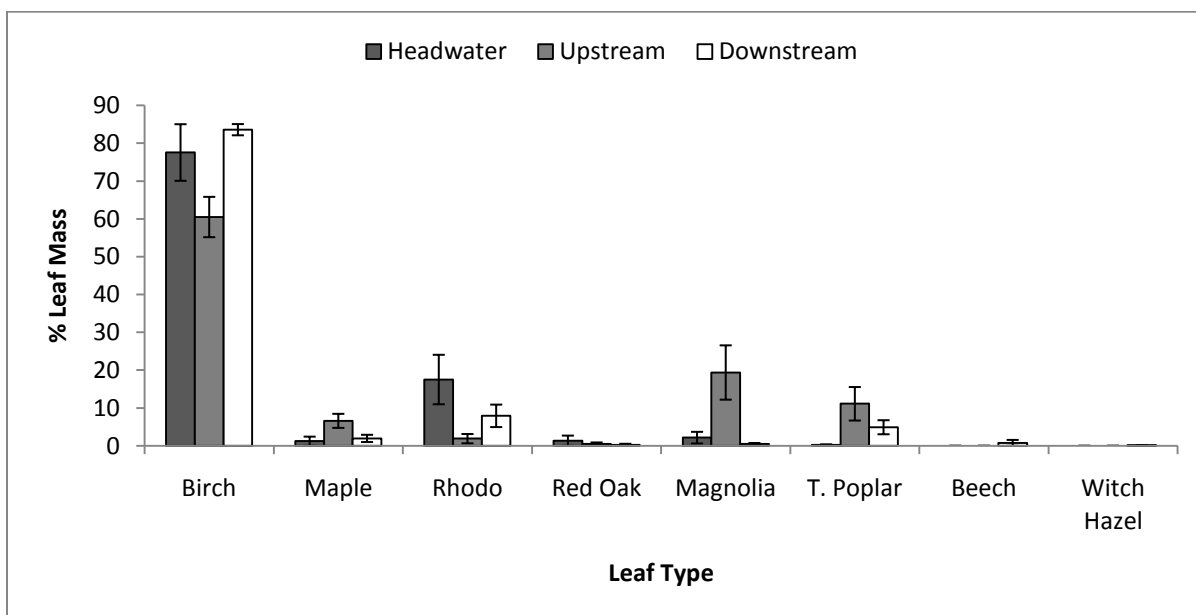


Figure 3A.

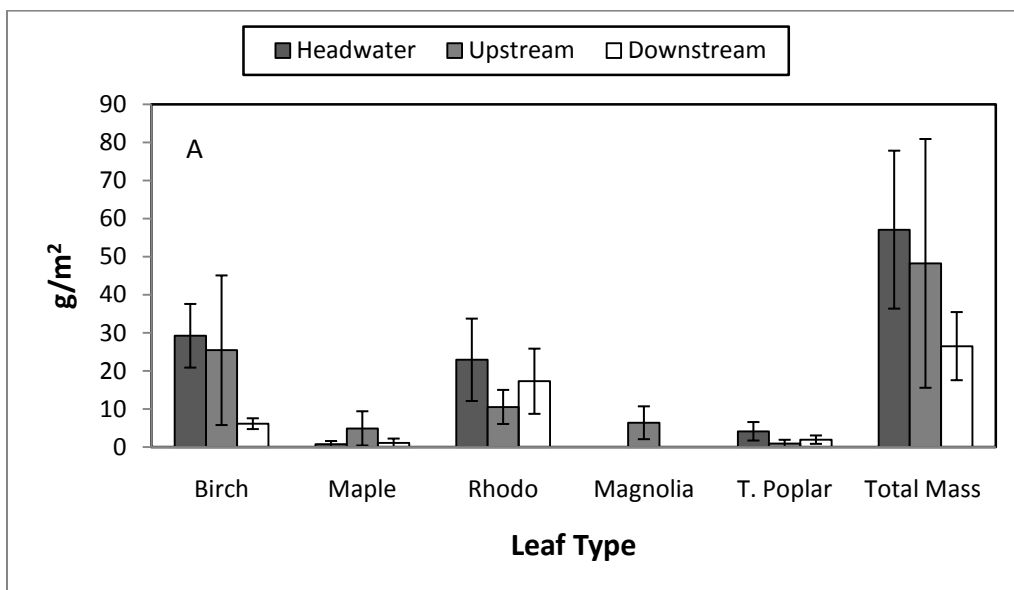


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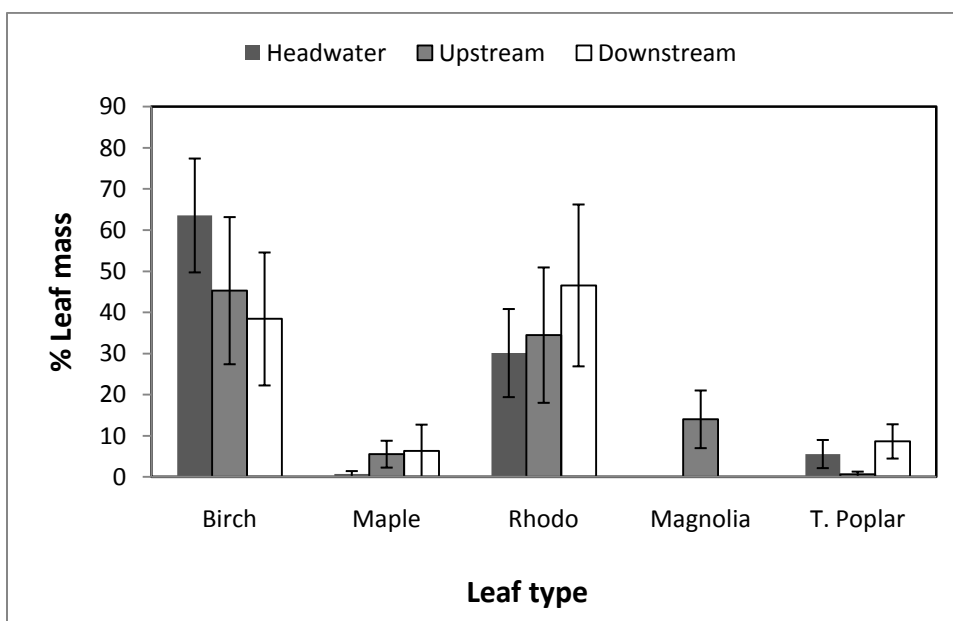


Figure 4.

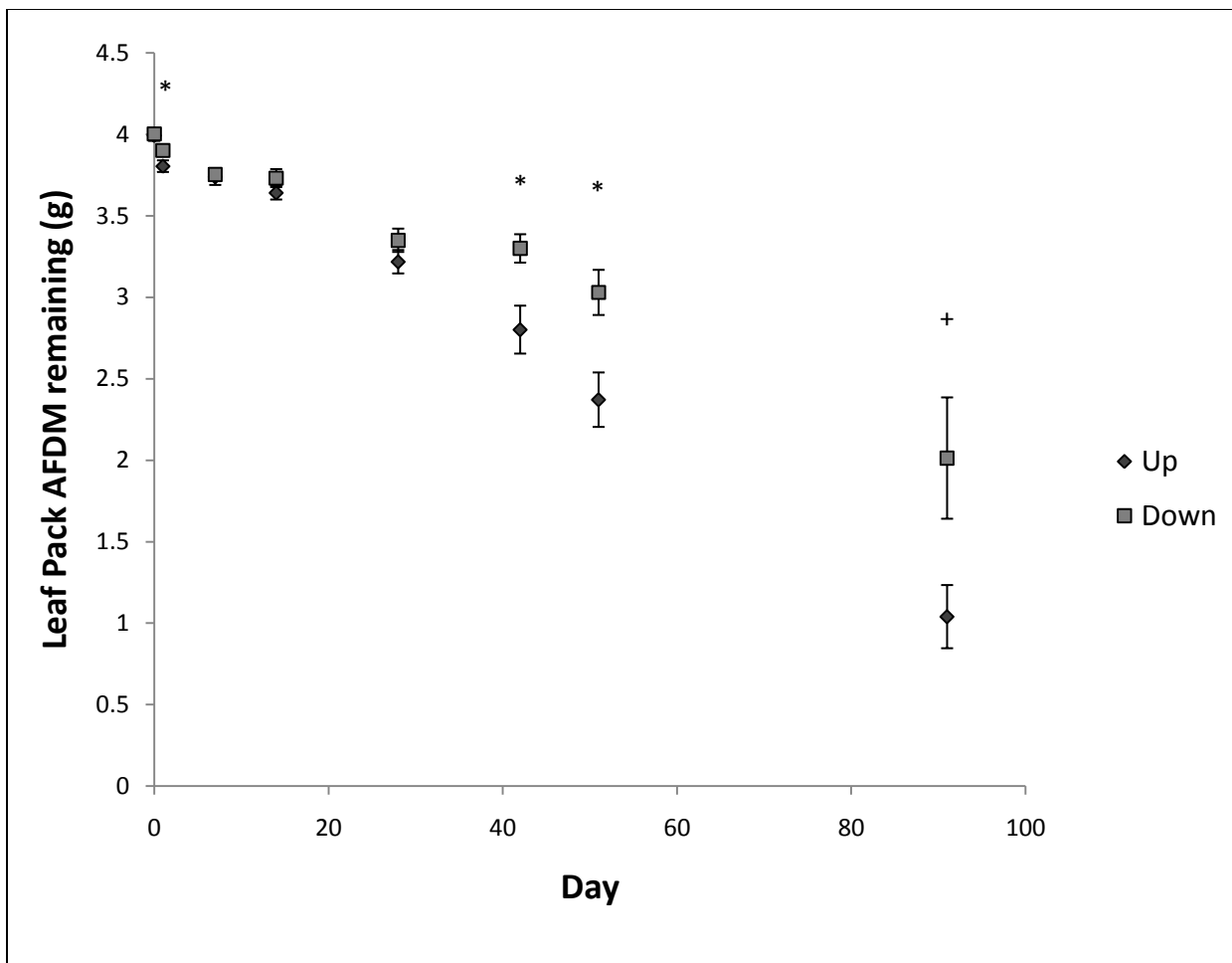


Figure 5A.

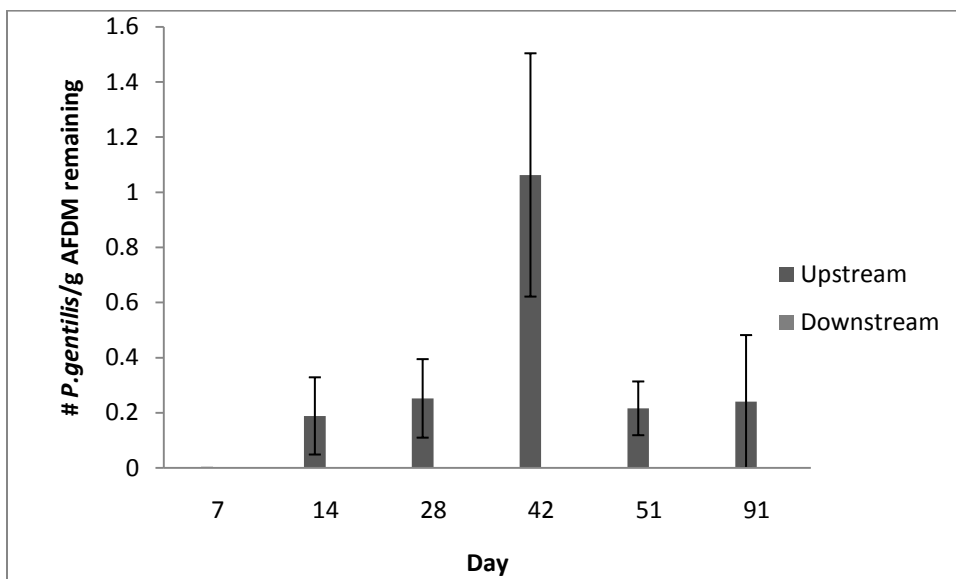


Figure 5B.

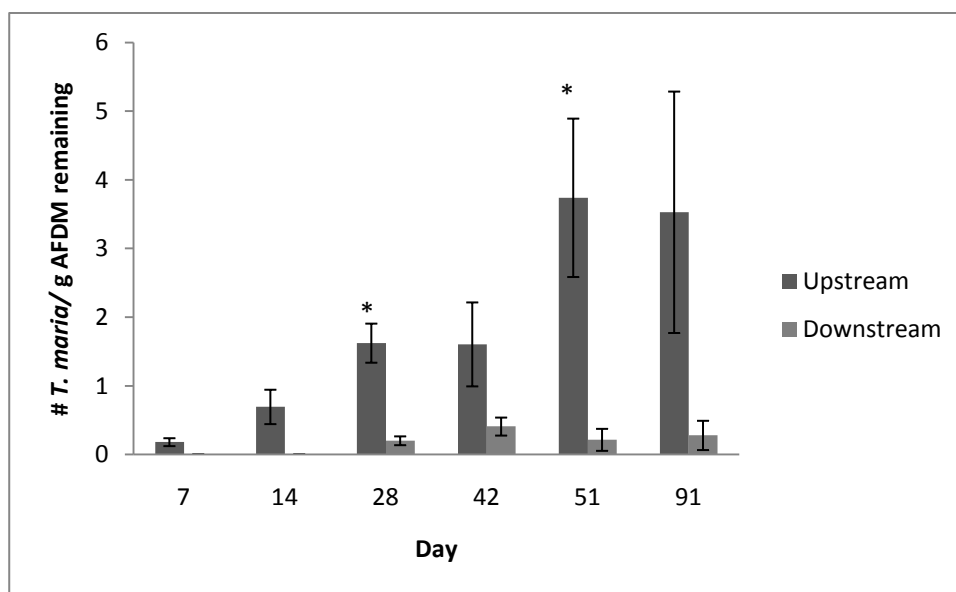


Figure 5C.

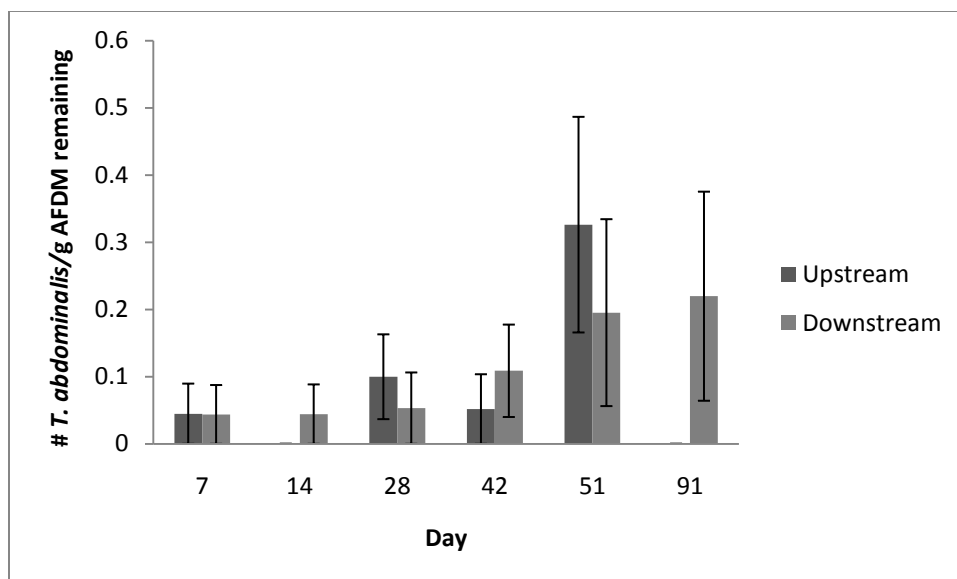


Figure 6.

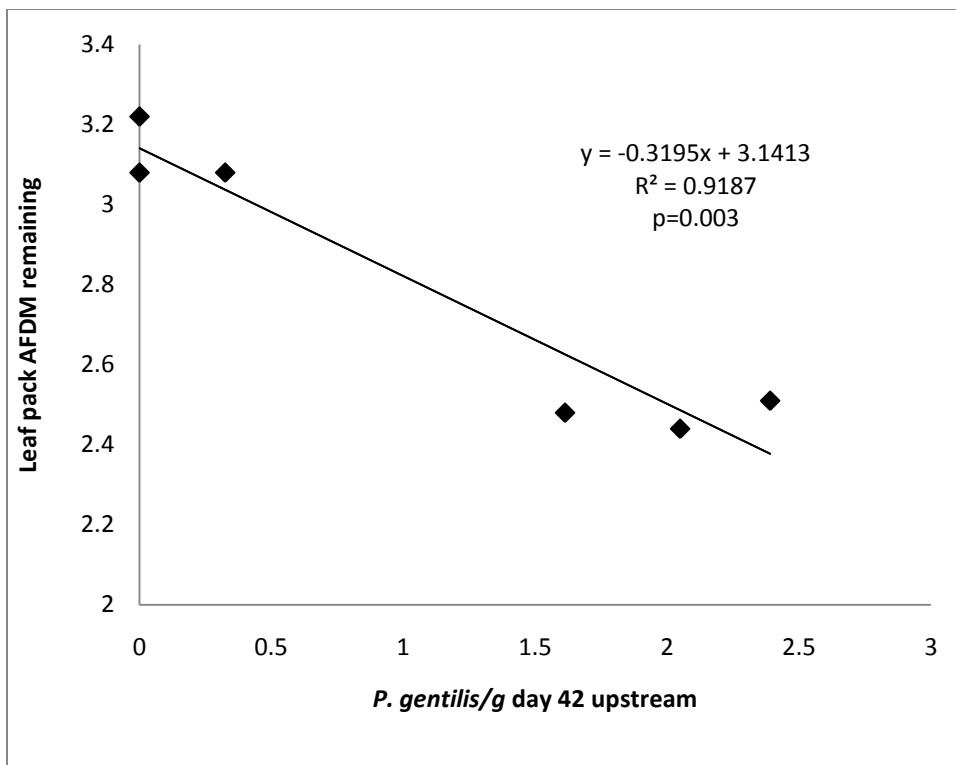


Figure 7.

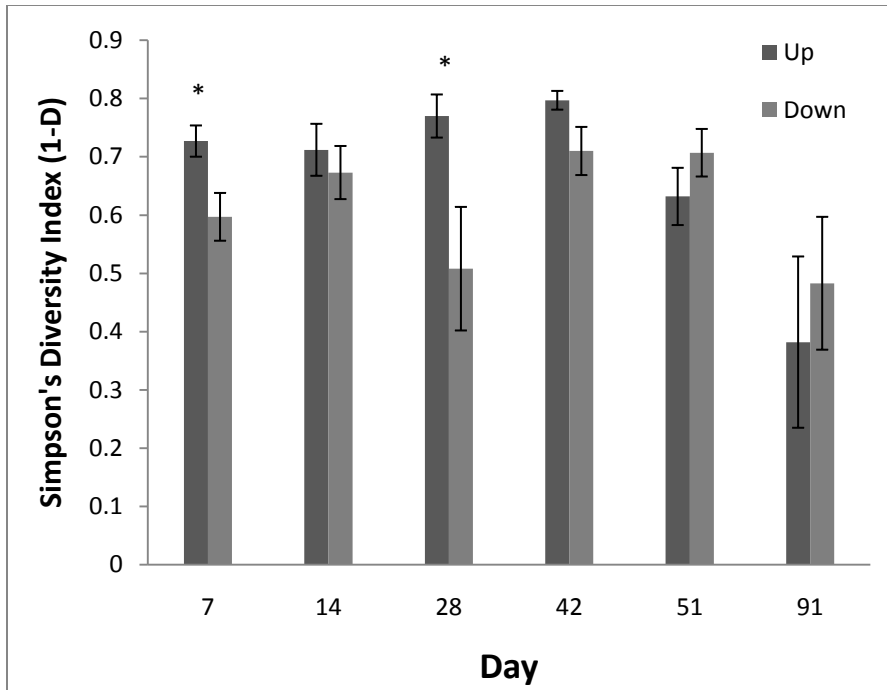


Figure 8.

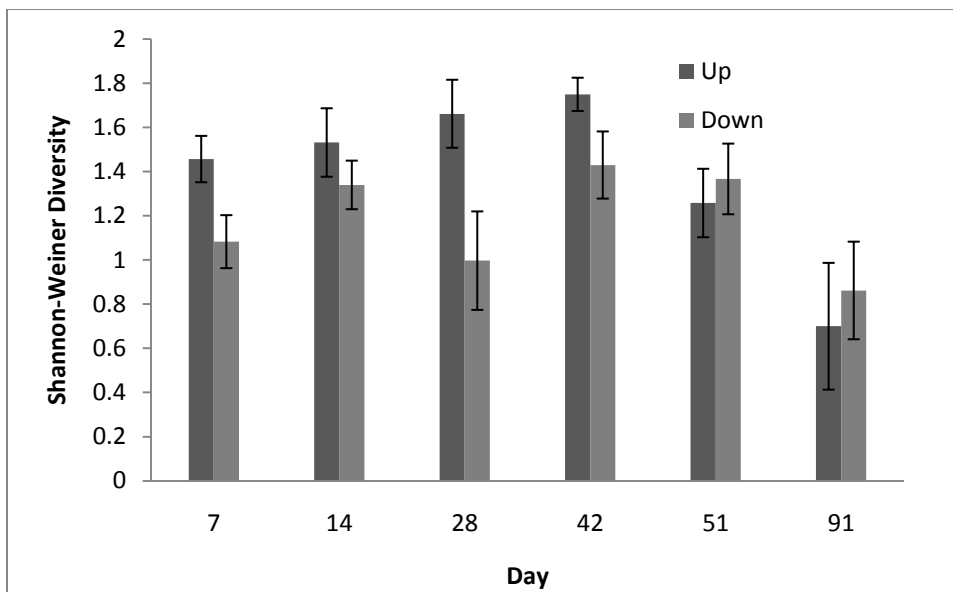
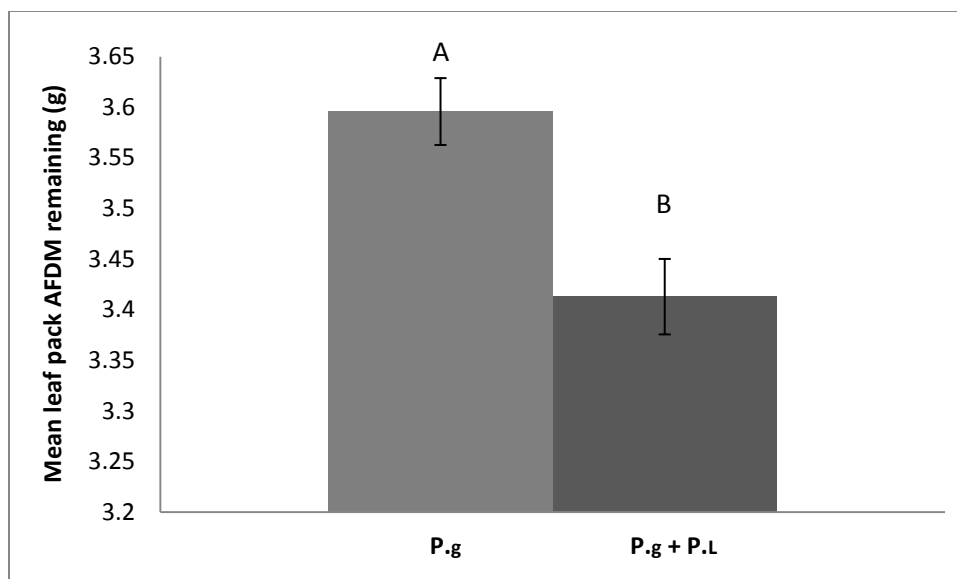


Figure 9.



VITA

Brett Matthew Tornwall was born in Gainesville, FL in March of 1985. He attended elementary and high school in Keystone Heights, FL and graduated from high school in May of 2003. The following autumn he entered the University of Florida to study Wildlife Ecology and was awarded a Bachelor of Science degree in December of 2007. In the fall of 2008 he accepted a teaching assistantship in the Biology Department of Appalachian State University and began study towards a Master of Science degree. The M.S. was awarded in May 2011. In August of 2011 Mr. Tornwall will commence work toward his Ph.D in biological sciences at the Virginia Polytechnical Institute and State University.