

**The influence of stream-derived detritus subsidies on lake benthic
community composition and trophic interactions**

by

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Abstract

Cross-ecosystem subsidies are important for the structure and functioning of communities within many ecosystems. Increases in subsidies have been modeled to increase trophic cascade strength within recipient systems, because of the donor-controlled addition of a resource. Streams receive high inputs of detrital subsidies and what is not processed within the system is transported downstream. Therefore, streams that flow into lakes have the potential to provide large amounts of detritus to lakes compared to the transfer of detritus from forested lake edges.

I hypothesized that streams would increase detritus standing stocks around stream mouths in lakes, that streams would affect the benthic invertebrate community composition, and that those effects would change with distance from the lake shore. To test this I conducted a survey of detritus standing stocks and benthic invertebrate communities at six stream/lake interface and six forest/lake interface sites within two lakes. I found that streams and distance into lakes affected detritus standing stocks, but the effect was only seen when individual pairings of stream and forest sites were examined. I also found that headwater streams significantly altered invertebrate community composition in the lake littoral zone, even up to a distance of 27 meters into the lakes, with some taxa only found at stream/lake interfaces. These results suggest that streams alter the amount of basal resources through subsidies and contribute to whole lake biodiversity.

My second hypothesis was that increased detritus in lakes would increase trophic cascade strength. To test this hypothesis, I conducted an in-lake cage experiment in which I manipulated detritus standing stocks (5 densities) and presence of a top-predator

(trout). I found that increasing subsidies altered strength of trophic cascades. But unexpectedly, low detritus treatments experienced the strongest positive effect on algal biomass. At intermediate detritus levels there was a switch in the indirect effects of predators, and at the highest detritus densities predators had a negative indirect effect on algal biomass. These results provide evidence that along a gradient of detritus subsidies, trophic cascade strength experiences threshold responses in where predators may have strong, but opposite indirect effects on primary production.

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Dedication

To Hamish Greig

- my personal at-home ecologist, best friend, and husband

Foreword

“Take chances, make mistakes, get messy!”

-Miss Frizzle, ‘The Magic School Bus’

“It is the systems so formed which, from the point of view of the ecologist, are the basic units of nature on the face of the earth. Our natural human prejudices force us to consider the organisms (in the sense of the biologist) as the most important parts of these systems, but certainly the inorganic " factors" are also parts there could be no systems without them, and there is constant interchange of the most various kinds within each system, not only between the organisms but between the organic and the inorganic. These ecosystems, as we may call them, are of the most various kinds and sizes. They form one category of the multitudinous physical systems of the universe, which range from the universe as a whole down to the atom. The whole method of science, as H. Levy ('32) has most convincingly pointed out, is to isolate systems mentally for the purposes of study, so that the series of isolates we make become the actual objects of our study, whether the isolate be a solar system, a planet, a climatic region, a plant or animal community, an individual organism, an organic molecule or an atom. Actually the systems we isolate mentally are not only included as parts of larger ones, but they also overlap, interlock and interact with one another. The isolation is partly artificial, but is the only possible way in which we can proceed.”

-A. G. Tansley. 1935. The use and abuse of vegetational concepts and terms.
Ecology 16:284-307.

Chapter 1: Introduction

An ecological community is composed of organisms that live and interact together within a habitat (Leibold et al. 2004). Within a community, there are often multiple trophic levels, which are groupings of organisms that feed on common resources (primary producers, primary consumers, secondary consumers or predators) (Lindeman 1942). Different mechanisms can determine how a community is assembled. Characteristics of species can make them suitable to live in particular patches in the landscape, called niches (MacArthur and Levins 1967, Tokeshi 1993), that are defined by a combination of biotic and abiotic factors. Communities can also form because of more stochastic processes such as ecological drift or dispersal limitations (Hubbell 2001). And last, there may be a combination of both where communities form via stochastic processes and then deterministic factors cause them to organize in different niches (Chase 2003).

Top-down and bottom-up community regulation

Bottom-up limitation on a community occurs when consumers are limited by their food resources (White 1978). The amount of primary production limits primary consumers which then limits predators. A top-down approach was proposed by Hairston, Smith, and Slobodkin (1960) called “the world is green” hypothesis, and occurs in a three-tiered food web where predators regulate primary consumers, releasing primary production from consumption. An organism’s position in the food chain then determines whether they are top-down or bottom-up regulated (Hairston et al. 1960). These models assume that primary production and other resources are regulated from within the system, but what if there are external processes contributing to resources within the community?

Cross-ecosystem subsidies

Ecosystems are open entities that receive energy and nutrients from adjacent systems, have mobile predators that feed across boundaries, and include organisms that have complex life stages that are larvae in one system and emerge to be adults in another (Polis et al. 1997, Richardson et al. 2010). A cross-ecosystem subsidy (also known as resource subsidies or allochthonous resources) is energy or material that crosses from one system to another and is donor controlled, meaning interactions within the recipient system will not regulate the amount of subsidy that is received (Richardson et al. 2010). Subsidies can be received at different trophic levels, such as terrestrial leaves entering a stream as food for primary consumers (Richardson 1992a) or adult freshwater insects entering the terrestrial environment as food for predators (Sabo and Power 2002b, Marczak and Richardson 2007).

The exchange of subsidies is an ubiquitous process that occurs between a multitude of systems (Polis et al. 1997). There are freshwater subsidies such as invertebrates emerging to terrestrial systems (Sabo and Power 2002b, Marczak et al. 2007a), fine organic matter moving from lakes to streams (Richardson and Mackay 1991), or streams transporting resources to estuaries (Sakamaki et al. 2010). Oceans can supply such materials as seaweed resources to beach communities (Polis and Hurd 1996b) or salmon that spawn and die in stream systems (Bilby et al. 1996, Wipfli et al. 1998). And last, terrestrial systems can provide insects to feed stream fish (Nakano et al. 1999) and leaves that support freshwater invertebrate populations (Richardson 1991).

Terrestrial leaves that fall into freshwater systems, also known as leaf detritus, are important to the functioning of freshwater communities because they provide resources to nutrient poor systems and can support populations of primary consumers (detritivores) that feed

mainly on detritus (Richardson 1991, Dobson and Hildrew 1992, Wallace et al. 1999). Additions or depletions in detritus resources can cause quick responses in freshwater invertebrate communities (Wallace et al. 1999, Rowe and Richardson 2001) and can drastically alter ecosystem productivity (Wallace et al. 1999). Because detritus causes an increase in productivity that is donor controlled, it has the potential to affect trophic dynamics in the recipient community other than those posed by top-down and bottom-up regulation in food chains with only primary production.

Trophic cascades

Trophic cascades occur when predators, through regulation of primary consumers, have indirect effects on non-adjacent trophic levels (Carpenter et al. 1985). This indirect predator regulation was first observed in aquatic systems (Carpenter et al. 1985, Power 1990) and has now been observed in a multitude of habitats (McLaren and Peterson 1994, Estes et al. 1998, Micheli 1999, Pace et al. 1999, Schmitz et al. 2000, Halaj and Wise 2001). For example, wolves have been linked to annual increases in primary productivity mediated by reduction in herbivores by predation (McLaren and Peterson 1994) and sea otters reduce urchin populations indirectly enabling an increase in kelp abundance (Estes et al. 1998). Although there are examples from different systems, trophic cascades remain strongest in aquatic systems (Shurin et al. 2002). There are many theories as to what affects trophic cascade strength (Borer et al. 2005, Shurin and Seabloom 2005, Shurin et al. 2006, Hall et al. 2007), but not until recently has trophic cascade strength been linked to the amount of subsidies a system receives (Leroux and Loreau 2008).

Outline of thesis

Chapter 2

Streams receive high amounts of terrestrial leaf detritus each year (Richardson et al. 2005) and what is not processed by the stream is transported down the catchment (Webster et al. 1999, Wipfli et al. 2007). Up to 286 g of detritus / stream / day can be exported out of streams (Wipfli and Gregovich 2002), which may come to be deposited in lakes. I investigated stream effects on detritus standing stocks and associated benthic invertebrate communities in lakes. I hypothesized that streams would increase benthic detritus around stream/lake interfaces compared to forest/lake interfaces, but this difference would decrease with distance into the lake. I also hypothesized that streams would alter benthic invertebrate community composition, and those effects would change with distance into the lake. Last, I predicted that stream-altered detritus patches (stream derived subsidies) would be a significant predictor of invertebrate composition in lakes. To test these hypotheses I conducted an in-lake survey around stream/lake boundaries and forest/lake boundaries in two lakes in British Columbia, Canada.

Chapter 3

The functioning of many ecosystems relies on subsidies, especially freshwater environments. Recently it has been proposed that the amount of subsidies a system receives can impact the strength of trophic cascades in that system. I wanted to investigate the effect of a range of subsidy quantities on trophic cascade strength in lakes, which would allow me to explore cause-effect relationships that are predicted from the results in Chapter 2. I hypothesized that as alder leaf detritus subsidies increased in a lake ecosystem, the trophic cascade strength would increase. I ran an in-lake cage experiment in which I manipulated alder leaf detritus (5

input rates) along with the presence/absence of trout, and measured algal biomass and invertebrate community responses.

Summary

The following two chapters investigate the role of stream detritus subsidies on lake benthic invertebrate communities and how those subsidies affect trophic cascade strength within different areas of the lake ecosystem. These chapters outline the role of subsidies in recipient communities and how subsidies alter the interactions within those communities. The thesis concludes with a discussion on the general implications of these results, limitations to my studies, and the future direction of research on subsidies and trophic cascade strength.

Chapter 2: The influence of streams on inputs of detrital standing stocks and benthic invertebrate community structure in lakes

Introduction

For years ecosystems were studied as discrete units, even though when the term ‘ecosystem’ was created they were thought to “overlap, interlock and interact with one another” (Tansley 1935). We now know that ecosystems are connected through the exchange of nutrients and energy, known as subsidies (Polis et al. 1997, Baxter et al. 2005, Richardson et al. 2010). In addition, ecosystems are also connected through organisms with complex life cycles (Knight et al. 2005) and by organisms that feed across boundaries. We also know that at the boundary of ecosystems, or ecotones, there are unique habitats formed by the interconnecting systems, such as waves creating sandy beaches at the marine-terrestrial ecotone or braided rivers forming gravel bars that are utilised by specialist terrestrial spiders (Greenwood and McIntosh 2008). These processes are formalised in the field of landscape ecology, where adjacent ecosystems are studied together as interactive units across landscape scales (Polis et al. 1997, Polis et al. 2004).

A landscape is formed by patches of ecosystems that can be heterogeneous (non-similar systems; e.g. forest and stream ecosystems) or homogeneous (similar systems; e.g. stream and lake ecosystems) (Addicott et al. 1987). It is heterogeneous habitats that are involved in most classic studies of subsidies (Richardson 1991, Polis and Hurd 1996b, Webster et al. 1999, Sabo and Power 2002b). For example algal wrack and carrion from the ocean supports specialist terrestrial consumers on beach shores and can also change trophic dynamics (Polis and Hurd 1996b, Piovia-Scott et al. 2011). Similarly, emerging aquatic invertebrates can subsidize terrestrial spiders and lizards (Sabo and Power 2002b, Marczak and Richardson 2007) and can have complex, unexpected indirect effects such as altering pollen limitation in terrestrial plants

(Knight et al. 2005). Many of these subsidy exchanges are reciprocal. For example, freshwater insects emerge in spring and supplement terrestrial spider populations, but then in summer terrestrial insect numbers are high and fall into streams to subsidize fish (Nakano and Murakami 2001).

Resource subsidies also move between homogeneous systems with less distinct boundaries, for example between headwater streams and larger rivers or between streams and lakes (Richardson et al. 2010). Aquatic invertebrates drift down-stream providing food to fish in larger rivers (Wipfli and Gregovich 2002). Similarly, terrestrial detritus subsidies that are not processed in headwater streams can provide basal resources for communities further down in a river (Malmqvist et al. 1978, Webster et al. 1999, Malmqvist et al. 2001). Spawning fish such as salmon can also transport energy up a stream network connecting oceans to small streams (Bilby et al. 1996, Wipfli et al. 1998). Finally, lakes outflow into streams and can provide high quality food for stream filter feeders (Richardson 1984, Richardson and Mackay 1991). However, the flow of energy and nutrients from streams to lakes is relatively unstudied (but see: Balogh et al. 2003, Donohue and Irvine 2004, Arp et al. 2007).

In addition to the heterogeneity of adjacent ecosystems, the edge-to-area ratio of a system can also affect input rates of subsidies (Polis and Hurd 1996b, Polis et al. 1997). The boundary between the land-water interface can be the most productive part of the ecosystem (Wetzel 1990), and the percent contribution of terrestrial leaf detritus to production in lakes depends on the perimeter and size of the lakes (Gasith and Hasler 1976). In river networks, headwater streams with large edge-to-area ratios receive high inputs of terrestrial subsidies. This changes down the catchment where larger rivers with lower edge-to-area ratios receive fewer subsidies

from the terrestrial environment and depend more on autochthonous resources as a consequence (Minshall et al. 1985, Finlay 2001).

In comparison to headwater streams, lakes have a small edge-to-area ratio with a smaller percentage of production coming from terrestrial leaf subsidies (Gasith and Hasler 1976, Wetzel 1990). Nevertheless, lake benthic invertebrate production is still highly dependant on allochthonous resources relative to autochthonous production (Solomon et al. 2008, Northington et al. 2010) and this dependence is highest in the shallow littoral regions of lakes (Babler et al. 2008). While little is known on how stream inlets influence benthic invertebrates in lakes (Donohue and Irvine 2004, Takamura et al. 2009), some observational studies suggest that streams affect the distribution of taxa in lakes (Winterbourn 1971).

In this study I investigated the interface between stream inlets and lakes. Headwater streams receive high inputs of terrestrial leaf litter with amounts up to 400-700 g of ash-free dry mass / m² / year (Richardson et al. 2005). Detritus that is not processed by the stream will be transported to downstream ecosystems (Webster et al. 1999). The purpose of this study was to determine how standing stocks of coarse leaf detritus and benthic invertebrate community composition in lakes are influenced by inflowing streams. I investigated this question by conducting a survey of lake benthic invertebrates and littoral standing stock of detritus around lake/stream interfaces and lake/forest interfaces. I hypothesized that streams that flow into lakes have the potential to transport large quantities of unprocessed coarse leaf litter into lakes, and deposit this subsidy farther into the lake than at the lake/forest interface. Detritus transported downstream accumulates in plumes near river mouths in estuaries (Sakamaki and Richardson 2008) and I predicted the same patterns will occur in lakes. I also predicted that benthic invertebrate communities around the homogeneous lake/stream ecotone will differ from

communities around the heterogeneous lake/forest ecotone, which will correlate with the increase in leaf detritus around stream inlets. Lastly, I predicted that there would be an interface by distance interaction, where there would be significant differences between detritus and invertebrate communities at near shore sites (0 – 3m) but these differences would converge at large distances into the lake (27 m).

Methods

Study site

My study took place at the Malcolm Knapp Research Forest (MKRF) located 40 km east of Vancouver, British Columbia in the Coast Mountain Range. MKRF is a temperate rainforest with the main canopy consisting of western hemlock (*Tsuga heterophylla*), western red cedar (*Thuja plicata*) and Douglas-fir (*Pseudotsuga menziesii*) with deciduous trees such as red alder (*Alnus rubra*) and vine maple (*Acer circinatum*) around riparian zones (Kominoski et al. 2011). Loon Lake and Marion Lake were chosen for this study because of their multiple inflowing streams, accessibility, and representation of a range of lake characteristics at Malcolm Knapp. Loon Lake is a deep lake (maximum depth 62 m) (S. Hinch, UBC, pers. comm.), while Marion Lake is a shallow lake (maximum depth 7 m) (Winterbourn 1971).

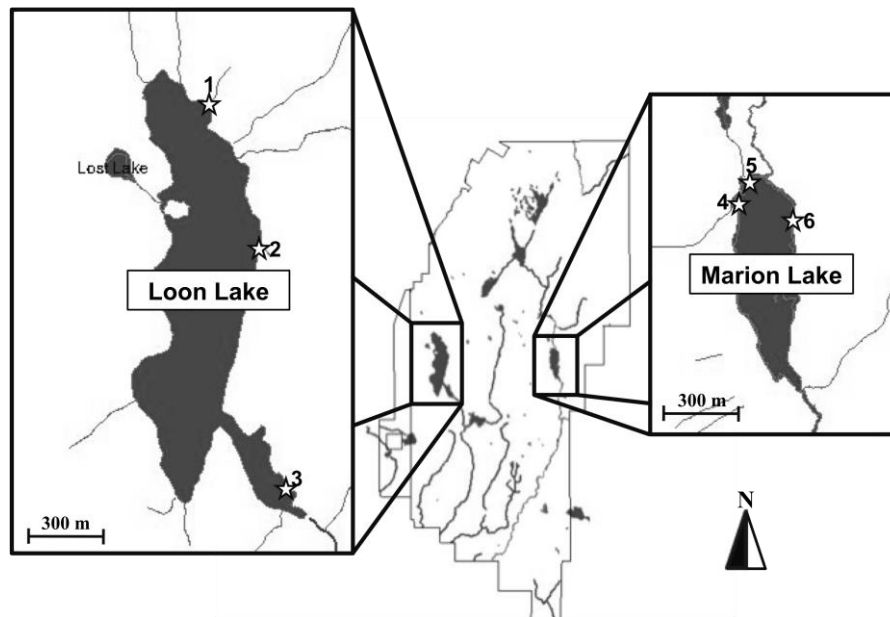


Figure 2.1: Map of Loon Lake and Marion Lake at the University of British Columbia's Malcolm Knapp Research Forest. The stars represent study sites: 1) Faraway Stream, 2) Cobble Creek, 3) Lilypad Stream, 4) Piddiley Stream, 5) Marion Creek, 6) Paper Stream.

Survey design

Survey data collection took place between October 15 and October 20, 2010 in two lakes at the Malcolm Knapp Research Forest with three sites in each lake (Figure 2.1). Each site consisted of an area that had a stream inlet (stream interface) and an adjacent area that was >20 m from the stream inlet (forest interface). Samples were taken at each stream and forest interface site along a transect extending into the lake, perpendicular to shore. I sampled five distances along the transect (0, 1, 3, 9, 27 m) and three samples were taken at each distance, for a total of 15 samples at each lake/stream and lake/forest site (Figure 2.2). The 0 m sample for forest interface was taken at the lake edge (wetted region) and for stream interface was taken at the transect with the lake edge. Habitat variables (depth (m), dissolved oxygen (D.O. mg/L), and temperature (°C)) were measured at each distance along each transect (Appendix 1).

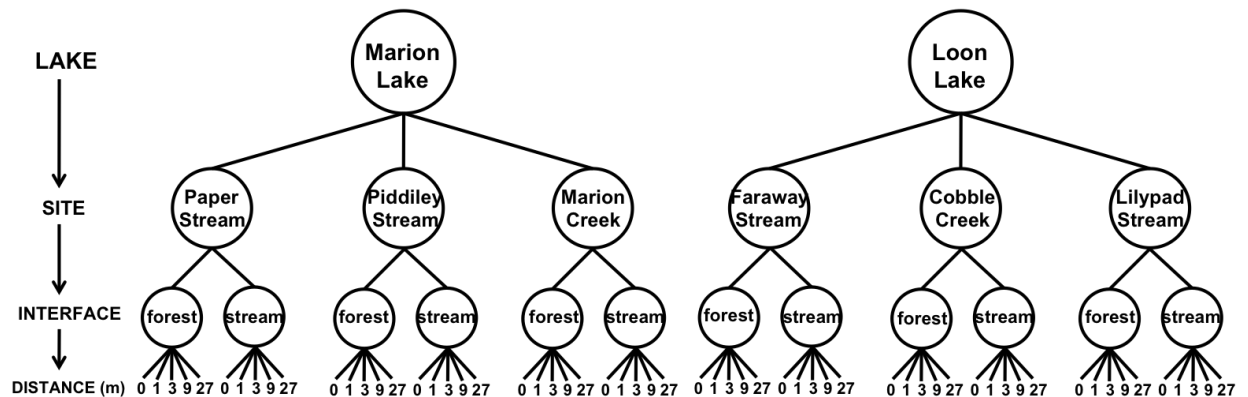


Figure 2.2: Hierarchical design of lake surveys with 6 sites nested in 2 lakes, 2 interfaces at each site and 5 distances sampled for coarse detritus and benthic invertebrates along each transect.

Benthic invertebrate community

Benthic invertebrates were sampled using a 0.023 m² Eckman dredge sampler, the contents of which was then washed over a 1 mm mesh sieve. The samples retained in the sieve

were placed in plastic bags with water from the lake and invertebrates were kept alive (< 48 hours) until they could be separated from substrate. The invertebrates were then preserved in 70% ethanol and measured (length of body or width of shell) using an ocular micrometer and identified to genus where possible or the lowest practical taxonomic level using standard keys (Cannings and Stuart 1977, Thorp and Covich 1991, Wiggins 1996, Merritt et al. 2008). Taxa were assigned to functional groups (collector/filterer, collector/gatherer, scraper, shredder, herbivore/piercer, predator) using published classifications (Merritt et al. 2008). The dry mass of each individual was estimated using published and unpublished length-mass regressions (Appendix 2). Total biomass, total abundance, and taxa richness were used as response variables in analyses. To avoid pseudo-replication, the average of each of the response variables were taken for the three samples at each distance for each interface. Mussels (*Anodonata* sp.), which were rarely encountered, were removed from total biomass analysis because my sampling was not designed to accurately estimate their abundances and their disproportionately high individual body mass would skew the results.

Detritus standing stock

Detritus standing stock was sampled along with the invertebrate samples using the Eckman dredge sampler. Following the removal of the invertebrates, samples were separated through a 1 mm mesh sieve so all the remaining detritus was coarse particulate organic matter (CPOM; > 1 mm) (Cummins 1974). The samples were frozen until processing, then dried at 55°C, weighed, ashed at 500°C, and then weighed again. These data were used to calculate ash-free dry mass (AFDM) using the formula:

$$\text{AFDM} = \text{dry mass (g)} - \text{ash mass (g)}.$$

Three samples were taken at each distance for each transect, so the average of those three samples was used in analyses to avoid pseudo-replication.

Statistical analyses

The effect of interface (stream or forest), distance into the lake, and detritus biomass on univariate response variables (total invertebrate biomass, total invertebrate abundance, and taxa richness) was analysed with linear mixed-effects models that accounted for the spatially hierarchical nature of my design (Figure 2.2). Distance, interface, and detritus were set as fixed factors while lake and site nested within lake were included as random factors. I nested site inside lake because variation between sites may be accounted for by variation between lakes. Distance, interface, and detritus were fixed factors as they were the main predictors of my hypotheses. All response variables and detritus were ln-transformed to meet the assumptions of statistical tests. Analyses were conducted using the nlme package (Pinheiro et al. 2011) in R (R-Development-Core-Team 2011).

To test the effect of stream and distance on detritus biomass, I ran a linear mixed-effects model with detritus as the response variable, distance and interface as fixed-effect predictors, and lake and stream nested within lake as random factors. Detritus was ln-transformed to meet assumptions of normality and the analysis was conducted using the nlme package (Pinheiro et al. 2011) in R (R-Development-Core-Team 2011).

I used a direct gradient ordination analysis to test for associations between benthic invertebrate community composition and abiotic habitat variables (lake, site, interface, distance, detritus, temperature, D.O., depth). A detrended correspondence analysis (DCA) was performed on community composition to determine the appropriate ordination method (linear or unimodal). Gradient length terms (a measure of difference in community composition between sites) under

3.0 indicates a linear method is appropriate, between 3.0 and 4.0 is either linear or unimodal, and over 4.0 a unimodal method is appropriate (Lepš and Šmilauer 2003). My largest gradient length of the first four DCA axes was >4 , therefore I used the unimodal ordination method, canonical correspondence analysis (CCA), for my analyses. CCA is a direct gradient analysis technique where species composition is directly related to measured environmental variables and takes advantage of the additional environmental data. This differs from indirect gradient analysis where environmental variables are inferred from patterns seen in community composition (Palmer 1993). Samples and habitat variables were visually expressed using a biplot. Habitat variables are represented as arrows on the biplot and the length of the arrow indicates its relative importance in the ordination. The direction of the arrow indicates the correlation of variables with species composition axes (Palmer 1993).

I first ran a CCA ordination on species composition and all habitat variables. Based on the results, I ran another CCA ordination with the variance explained by lake partitioned out by treating lake as a block in the design. Lastly, I ran a CCA with variance explained by all habitat variables, except interface and distance, partitioned out to look at the independent effects of interface (stream or forest) and distance into the lake on species composition. All ordinations were conducted using the vegan package (Oksanen et al. 2011) in R (R-Development-Core-Team 2011).

Results

Detritus subsidy

The standing stock of coarse detritus was not significantly affected by either interface or distance when analysed across all streams (Table 2.1a). However, patterns emerged when individual sites with forest and stream interface pairs were considered (Figure 2.3). Cobble and Marion streams both had higher amounts of detritus at near-shore, forest-interface sites. Lilypad, Paper, Faraway, and Piddiley had higher detritus amounts at 0 m and 1 m distances at stream interfaces compared to forest interfaces. Detritus at 27 m distances was similar for stream and forest interfaces at all sites (Figure 2.3)

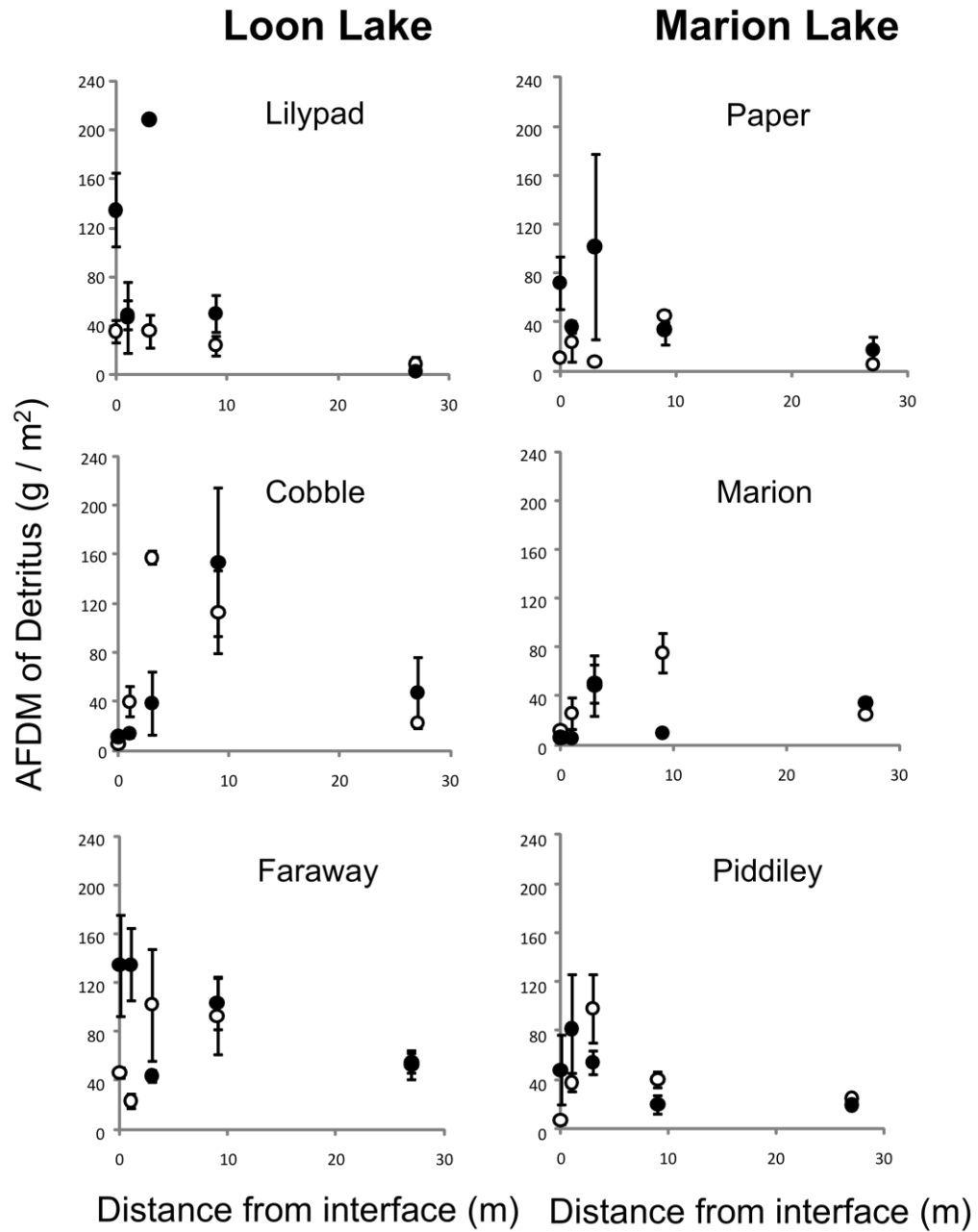


Figure 2.3: Plots of ash-free dry mass (AFDM) of coarse detritus (g / m^2) against distance into the lake (m) for each site. Open circles are forest/lake interface and black circles are stream/lake interface. Bars indicate standard error ($n=3$, not included as replicates in the analysis).

Table 2.1: Mixed-effects model results with response variables a) ash-free dry mass of detritus, b) total invertebrate biomass, c) total invertebrate abundance, and d) taxa richness. Fixed predictors were interface, distance, and detritus while random predictors were lake and site nested in lake. Bold P values are significant ($P < 0.05$) and F values are presented as $F_{\text{degrees of freedom, error}}$.

Response variable	Predictors	Variance	F	P
(a) Ash-free dry mass of detritus*				
	Lake	0.34		
	Site(Lake)	0.11		
	Interface		0.99 _{1,51}	0.33
	Distance		2.54 _{1,51}	0.12
	Interface x Distance		0.39 _{1,51}	0.53
(b) Total Biomass*				
	Lake	0.31		
	Site(Lake)	0.03		
	Interface		0.01 _{1,50}	0.91
	Distance		16.09 _{1,50}	0.0002
	Detritus*		3.86 _{1,50}	0.05
	Interface x Distance		1.32 _{1,50}	0.26
(c) Total Abundance*				
	Lake	0.17		
	Site(Lake)	0.14		
	Interface		5.21 _{1,50}	0.03
	Distance		34.15 _{1,50}	< 0.0001
	Detritus*		8.32 _{1,50}	0.006
	Interface x Distance		2.78 _{1,50}	0.10
(d) Taxa Richness*				
	Lake	0.13		
	Site(Lake)	0.18		
	Interface		1.09 _{1,50}	0.29
	Distance		26.63 _{1,50}	< 0.0001
	Detritus*		5.89 _{1,50}	0.02
	Interface x Distance		0.06 _{1,50}	0.80

* ln-transformed data

Invertebrate community composition

There was a total of 53 taxa found in Loon and Marion Lake. Fifteen taxa occurred only in Marion Lake and 11 taxa were only observed in Loon Lake (Appendix 3). Of the 42 taxa in Marion Lake and 38 taxa in Loon Lake, 28.8 % and 23.7 %, respectively, were found only at

stream interface sites. For Marion Lake, some of the taxa at stream interface sites were *Aeshna* dragonfly larvae, *Gammotaulius* and *Oxyethira* caddisfly larvae, and morpho-taxon mite 2 and mite 3. At Loon Lake, the taxa at stream interface sites included *Cordulia* dragonfly larvae, *Cryptochia* and *Lepidostoma* caddisfly larvae, and Tipulidae. Stream interface sites had more taxa than forest sites in both lakes, but stream sites in both lakes shared only 3 taxa: morpho-taxon, mite 3; *Psychoglypha* caddisflies; and *Lenarchus* caddisflies (Appendix 3).

Total benthic invertebrate biomass, total abundance, and taxa richness all significantly decreased with distance into the lake (Table 2.1b, c, d). Detritus standing stock had a significant positive effect on taxa richness and total abundance (Table 2.1c, d), while it had a marginally non-significant effect on total biomass (Table 2.1b). Only total abundance was significantly increased by stream interface (Table 2.1c).

Community composition was significantly influenced by lake (Table 2.2a), which is evident in the separation of sites within the different lakes along CCA axis 1 (Figure 2.4a). Distance, depth, interface, and detritus also significantly affected community composition, with the combined effect of all variables accounting for 23% of variation in the invertebrate community composition (Table 2.2a). After the variance explained by lake (7%) was partitioned out, depth had a strong effect on community composition, which was negatively correlated with both axes (Figure 2.4b, Table 2.2b). Morpho-taxon, mite 3, Chironomini, and *Polycentropus* caddisflies were all associated with depth on the ordination (Appendix 4). Distance, interface, and detritus also had significant effects on community composition, and together these variables explained 16% of the variation in the model (Table 2.2b). Interface and distance were associated with CCA axis 1, but in opposite directions, and there was overlap on the biplot between forest and stream interface points (Figure 2.4b). After the variance (17%) of all habitat variables was

partitioned out of the model leaving interface and distance (5% of explained variation), there was clear grouping of the stream interface and forest interface sites along CCA axis 2 (Figure 2.4c).

Distance had an effect on composition along CCA axis 1, with samples at 27 m from the shoreline clustering in the bottom left corner of the ordination (Figure 2.4c, Table 2.2c).

Table 2.2: Permutation significance tests of environmental variables from the canonical correspondence analysis (CCA) ordination of invertebrate community composition. a) Whole model with all habitat variables constrained. b) Model controlling for the effect of lake by partitioning it out as a constrained variable. c) Model controlling for the effect of all habitat variables, except for interface and distance, by partitioning them out as a constrained variable. Bold P values are significant ($P < 0.05$) and F values are presented as $F_{\text{degrees of freedom, error}}$.

Variable	Term	Variation	$F_{1,52}$	P
a) All habitat variables		0.23		
	Lake		4.75	0.001
	Interface		1.82	0.03
	Distance		2.37	0.001
	Depth		2.61	0.001
	DO		1.06	0.44
	Temp		1.47	0.11
	Detritus		1.71	0.04
b) Partitioned (Lake)		0.07		
Remaining habitat variables		0.16		
	Interface		1.82	0.02
	Distance		2.37	0.006
	Depth		2.61	0.001
	DO		1.06	0.41
	Temp		1.47	0.14
	Detritus		1.71	0.04
c) Partitioned (habitat variables)		0.17		
Interface and distance		0.05		
	Interface		1.71	0.04
	Distance		1.99	0.01

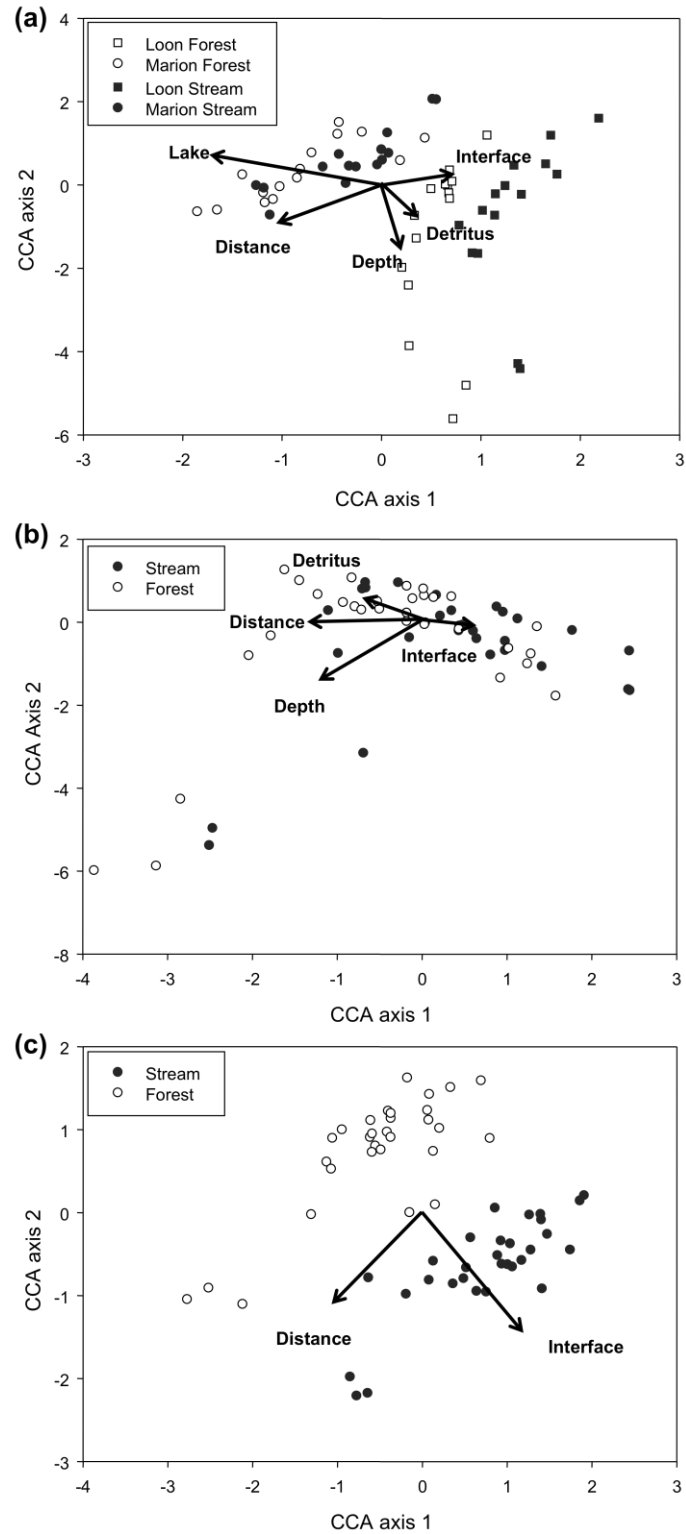


Figure 2.4: Canonical correspondence analyses (CCA) of benthic invertebrate community composition with a) all habitat variables in model, b) all habitat variables in model except for the variance of lake partitioned out, and c) interface and distance in model with all other habitat variables partitioned out. Arrows indicate significant constrained habitat variables and length of arrow is representative of its effect on the community. Points on plots are site scores.

Discussion

I predicted that benthic detritus standing stocks in lakes would be influenced by the type of interface (stream/lake and stream/forest) and by distance into the lake. Habitats closer to lake edges were more likely to receive inputs from the surrounding forest than those further into the lake. As streams transport high amounts of coarse particulate organic matter to downstream systems (Cuffney and Wallace 1988, Wipfli and Gregovich 2002, Wipfli et al. 2007), one of which is lakes, streams could generate detritus plumes where they enter the lakes, creating subsidy hotspots. Alternatively, streams may push detritus further into the lake, creating patches low in subsidy abundance. Surprisingly, my results supported both of these predictions. Smaller streams had higher amounts of detritus standing stock near shore, but larger streams had less detritus near shore compared to forest interface sites.

I further predicted that streams would influence benthic invertebrate community composition and these effects would change with distance into the lake. I also predicted that these effects would be associated with detritus standing stocks. While streams did not affect total invertebrate biomass or taxa richness, they did have a significant positive effect on total abundance of invertebrates and overall community composition, as ~25% of taxa in both lakes were restricted to stream-influenced sites (Marion Lake had 8% of taxa and Loon Lake 21% of taxa only found in forest interface sites). Unexpectedly, the effect of streams on invertebrate communities continued up to 27 m into the lake, evident by the separation of stream and forest sites at all distances in the ordinations and the non-significant interface by distance interaction in the mixed-effects models. Despite the fact that detritus was not consistently affected by stream and distance, detritus itself was a significant predictor of total abundance, taxa richness, and

overall community composition. Thus, detritus itself was important in shaping the benthic invertebrate communities in lakes.

Detritus subsidies and their effect on benthic invertebrates

The type of ecotone and the proximity to the lake edge did not have overall significant effects on lake benthic detritus standing stocks in my study. This was an unexpected result as streams receive high inputs of detritus subsidies each year (Richardson et al. 2005) and detritus that is not processed by streams is transported to ecosystems lower in the catchment (Webster et al. 1999, Wipfli et al. 2007). Visual plumes of leaf detritus were apparent around some of my stream interface sites (e.g., Lilypad and Piddely) but this varied from stream to stream. There were two obvious exceptions where I did not see a plume of detritus: Cobble Creek and Marion Creek. The substrate at the inlet (0, 1, and 3 m distances) of these two streams was dominated by inorganic cobble and was devoid of detritus. These were also the largest of the six streams, with Marion being about 8 m wide. The absence of detritus in these streams was likely a result of scouring around the stream inlets during high flow events that transported the detritus further into the lake (Racine et al. 1995). For example at Cobble Creek (0.7 m wide), plumes of detritus were not observed until 9 m into the lake when stream interface detritus had larger biomass than forest interface detritus. This effect was not seen in Marion Creek (8 m wide), and it is possible that any detritus was transported further into the lake than my sampling could detect (> 27 m) or between measurements (>9 m but <27 m).

Although Cobble Creek and Marion Creek did not increase detritus at the lake edge, I did observe this effect at the other four stream interface sites. Piddely, Paper, Faraway, and Lilypad stream sites each increased biomass of detritus at the 0, 1, and sometimes 3 m sites compared to the forest interface. These streams were all smaller in width (Lilypad was only 0.3 m wide) and

may subsequently have had less scouring force at the inlets (Ractliffe et al. 1995) during the low flow season when I sampled. Because of the size of the streams, it may be that peak flows were not large enough to flush leaves from the inlets and they were able to accumulate detritus plumes (Ractliffe et al. 1995). These results indicate that streams do affect benthic detritus in lakes, but the nature of the effect is dependant on other characteristics of streams, such as size and discharge. Scour from flow disturbance from larger streams may actually remove detritus deposited around stream inlets in lakes, while small streams enhance the deposition of detritus creating plumes of resources adjacent to stream inlets.

Streams and distance into the lake did not significantly affect lake benthic detritus, but detritus was a significant predictor of benthic invertebrate community responses. Detritus had significant positive effects on total abundance of invertebrates and taxa richness. It was also a significant predictor of invertebrate community composition with and without lake incorporated into the model. This is not surprising given that detritus can be a limiting resource for invertebrate communities in streams (Richardson 1991, Wallace et al. 1999) and ponds/lakes (Klemmer et al. In Review). In conclusion, stream and distance effects on detritus standing stocks varied between sites and detritus was an important predictor of invertebrate communities.

Environmental correlates of invertebrate community composition

There were many environmental variables that affected community composition, including lake, depth, detritus standing stocks, interface, and distance into the lake. It is not surprising that lakes had the greatest effect on composition as Marion Lake and Loon Lake only shared 27 out of 53 taxa. The most notable difference between the lakes is depth and area. Loon Lake is over 60 m deep whereas Marion is a relatively shallow lake (< 7 m deep). The depth of a lake can significantly affect the benthic invertebrate communities, with shallow lakes shown to

have higher benthic invertebrate biomass (Jeppesen et al. 1997). Depth was the largest driving force in community composition after lake variance was removed. Babler et al. (2008) found that the total number of taxa peaked at 1.5 m depth in lakes and composition of secondary production shifted to being dominated by Chironomidae. This supports my results of depth being an important driver in composition and there were similar patterns of Chironomidae dominate deep sites.

Stream interface and distance into the lake had a significant effect on invertebrate composition in my study. After removing variance due to all other habitat variables, stream and distance still explained 5% of total variation in invertebrate community composition. Streams as small as 0.3 m wide still affected composition 27 m into the lake as seen by complete separation of stream and forest sites along the distance gradient. Although detritus biomass was not consistently related to stream interface and distance, there may be other aspects that are related. An explanation for why I did not see an overall effect of streams on detritus could be that the quality of detritus differs among streams, rather than just the quantity. Leaf detritus being transported to lakes by streams may be preconditioned with microbes and fungi, and therefore more readily accessible to invertebrates (Cummins 1974, Gessner et al. 1999). Another explanation is that streams influenced detritus flux across the lake boundary, but overall standing stock did not change because it was already processed by benthic invertebrates (Cuffney et al. 1990, Wallace et al. 1995). This would contribute to detecting an invertebrate community response without seeing a difference in detritus standing stock around streams. My methods of detritus collection did not account for the flux across the forest/lake and stream/lake boundaries. This may have greatly improved my understanding by allowing me to capture total detritus that

was transported across boundaries, not the net detritus left over after processing of lake invertebrates.

There are likely to be several physical characteristics of streams that influence invertebrate composition that were not described by my sampling regime. As mentioned previously, there was a visually obvious deposition of inorganic sediment near some of the stream/lake interfaces. Donohue and Irvine (2004) found that inorganic sediment load from streams significantly decreased benthic invertebrate biomass in lakes. Streams have been shown to also increase dissolved organic carbon (DOC) and humic substances in lakes (Balogh et al. 2003), but I did not observe a stream effect on invertebrate biomass which suggests that streams do not alter basal resources. Temperature is another stream characteristic that could affect benthic composition (Vannote and Sweeney 1980), but did not significantly affect composition in my study. This may be due to measurement limitations rather than actual trends at the stream sites. I took temperature readings during invertebrate sampling which occurred at different times during the day. Therefore, time of day could have affected considerably the temperature of the inflowing stream water (Crisp 1990, Webb et al. 2008) and the temperature of the lake (Bussieres and Granger 2007). Stream temperature affects the presence and abundance of stream invertebrates (Vannote and Sweeney 1980) and may have affected distribution of taxa within the lakes.

Stream interface and distance were important drivers in stream communities (composition, biomass, abundance, and taxa richness). This may be because streams created novel ecotonal habitat that supports a different community of invertebrates. Greenwood and McIntosh (2008) found that streams affected the ability of consumers to respond to resources across the terrestrial/stream boundary by creating novel habitat along braided river cobble beds. I

found that a quarter of taxa in both lakes were found only near stream/lake interface sites, so streams could potentially be adding novel habitat that increases the biodiversity of lake ecosystems.

Conclusions

Stream interfaces significantly influenced invertebrate community composition, adding species to the lake ecosystem that are only found near stream sites. These effects on composition were observed up to 27 m into the lake, even though some of the streams were only 0.3 m wide. While detritus subsidies deposited by streams seems like an obvious driver of composition, physical habitat changes may be equally important. Streams may create novel ecotone habitats within lakes, creating higher diversity of invertebrate taxa within lakes. This has whole system consequences for a drainage network. Upstream modifications of landscapes (dams, foresting, etc.) may not only directly affect headwater streams and their transport of materials (Wipfli et al. 2007), but may also affect downstream lake invertebrate composition and detritus resources.

Chapter 3: Increase of detritus subsidy along a gradient of input rates causes switch in trophic cascade strength

Introduction

Donor-controlled materials and organisms that move across ecosystem boundaries (allochthonous subsidies) are accepted as an integral part of the composition and function of recipient ecosystems (Polis et al. 1997, Richardson et al. 2010). The classic examples of subsidies, such as kelp detritus on beaches or spawning salmon transferring marine-derived nutrients up-stream (Naiman et al. 2002, Spiller et al. 2010), are now understood to have important interactions with the recipient community (Sabo and Power 2002b, Marczak et al. 2007b, Yang et al. 2010). Subsidies have bottom-up effects on consumers at multiple levels that influence communities beyond the controls of *in situ* production (Polis and Strong 1996). Subsidies, besides directly affecting consumers, may also influence indirect effects of predators in food webs such as trophic cascades (indirect effects of predators on *in-situ* producers) (Nakano et al. 1999, Knight et al. 2005, Piovia-Scott et al. 2011).

Consumer-resource models predict stronger trophic cascades with an increase in the supply of allochthonous resources. For example, Leroux and Loreau's (2008) model predicts that trophic cascades are stronger with higher input rates of subsidies. The magnitude of the increase in trophic cascade strength is predicted to vary depending on the trophic level receiving the subsidy and will be most prominent when subsidies enter at the primary producer level (subsidizing primary consumers, e.g. leaf detritus) (Leroux and Loreau 2008). For example, an increase in detritus resources at the primary producer level will cause an increase in detritivores, potentially supporting a higher abundance of predators. The high abundance of predators will

then suppress higher levels of herbivores releasing primary production from feeding pressure (Polis and Hurd 1995).

While theoretical evidence points to stronger trophic cascades with increasing subsidy inputs (Huxel and McCann 1998, Huxel et al. 2002, Leroux and Loreau 2008), empirical studies show varied responses of trophic cascade strength to increased allochthonous inputs. Inputs of subsidies to terrestrial/riparian zones and terrestrial/marine zones, for example, induced stronger trophic cascades than sites without subsidies (Polis and Hurd 1995, Henschel et al. 2001, Knight et al. 2005). Subsidies increased primary consumer numbers, which supported higher numbers of predators than could have been supported by *in-situ* production, allowing predators to have stronger top-down effects (Polis and Hurd 1995). In other instances, the removal of a subsidy created stronger trophic cascades as predators that were supported by primary consumer subsidies switched to feeding on species that consumed *in situ* production, thereby having an indirect positive effect on primary production (Nakano et al. 1999, Piovia-Scott et al. 2011). Lastly, subsidy inputs may have no effect on trophic cascade strength (Halaj and Wise 2002). The differences in empirical results could be due to the binary manipulation of subsidies (reduced or added by a singular amount), when naturally there are thresholds that might not be captured with presence/absence studies (Schmitz et al. 2008).

Both theoretical and empirical studies contain simplifications that do not reflect the range of processes, nor the complex relations (non-additivities, non-linearities, etc.) by which consumer-resource dynamics may operate in communities. For example, experimental manipulations of subsidies have mainly investigated changes in trophic interactions with the presence or absence of an allochthonous resource. In nature, subsidy input rates often differ along a continuous gradient (Vannote et al. 1980) and can be patchy in abundance in both space

and time (Polis and Hurd 1996a, Callaway and Hastings 2002, Hoover et al. 2006, Holt 2008, Wesner 2010). Therefore manipulating subsidies on a discrete scale (presence/absence) is unlikely to reflect the true dynamics of the effects of subsidies on complex species interactions. Although theoretical models have addressed the effects of gradients of subsidies on food webs (Huxel and McCann 1998, Leroux and Loreau 2008), they lack other complexities such as the physical structure often provided by subsidies in recipient habitats (Richardson 1992b). Subsidies, such as accumulations of detritus, can provide refugia for prey and predators (Reice 1991, Richardson 1992b, Lewis and Denno 2009) which could alter species interactions that affect trophic cascade strength by mechanisms other than providing a nutritional or energetic resource. Incorporating these complexities into theoretical and empirical studies is the next step in revealing how subsidies affect trophic cascade strength.

The purpose of this study was to investigate whether trophic cascade strength changes along a gradient of allochthonous resource supply. I conducted an in-lake cage experiment in which I manipulated the biomass of alder detritus and the presence/absence of a top predator (trout). I hypothesized that, in the absence of trout, an increase in detritus resources would increase primary consumer biomass (Polis and Hurd 1995) and therefore decrease algal biomass (Figure 3.1a,b). But, in the presence of trout, increasing detritus would not affect primary consumer biomass and therefore algal biomass, because of suppression of primary consumers by trout (Figure 3.1a,b). This would lead to strong trophic cascades at high detritus densities (Figure 3.1b). Because leaf detritus can add structure to a recipient system in addition to nutrients and energy (Richardson 1992b), I also conducted an in-lake artificial leaf addition experiment. I hypothesized that the structure provided by artificial leaves would increase the biomass of

invertebrates compared to the absence of leaves, but this increase would be less than observed with equivalent quantities of real leaf detritus.

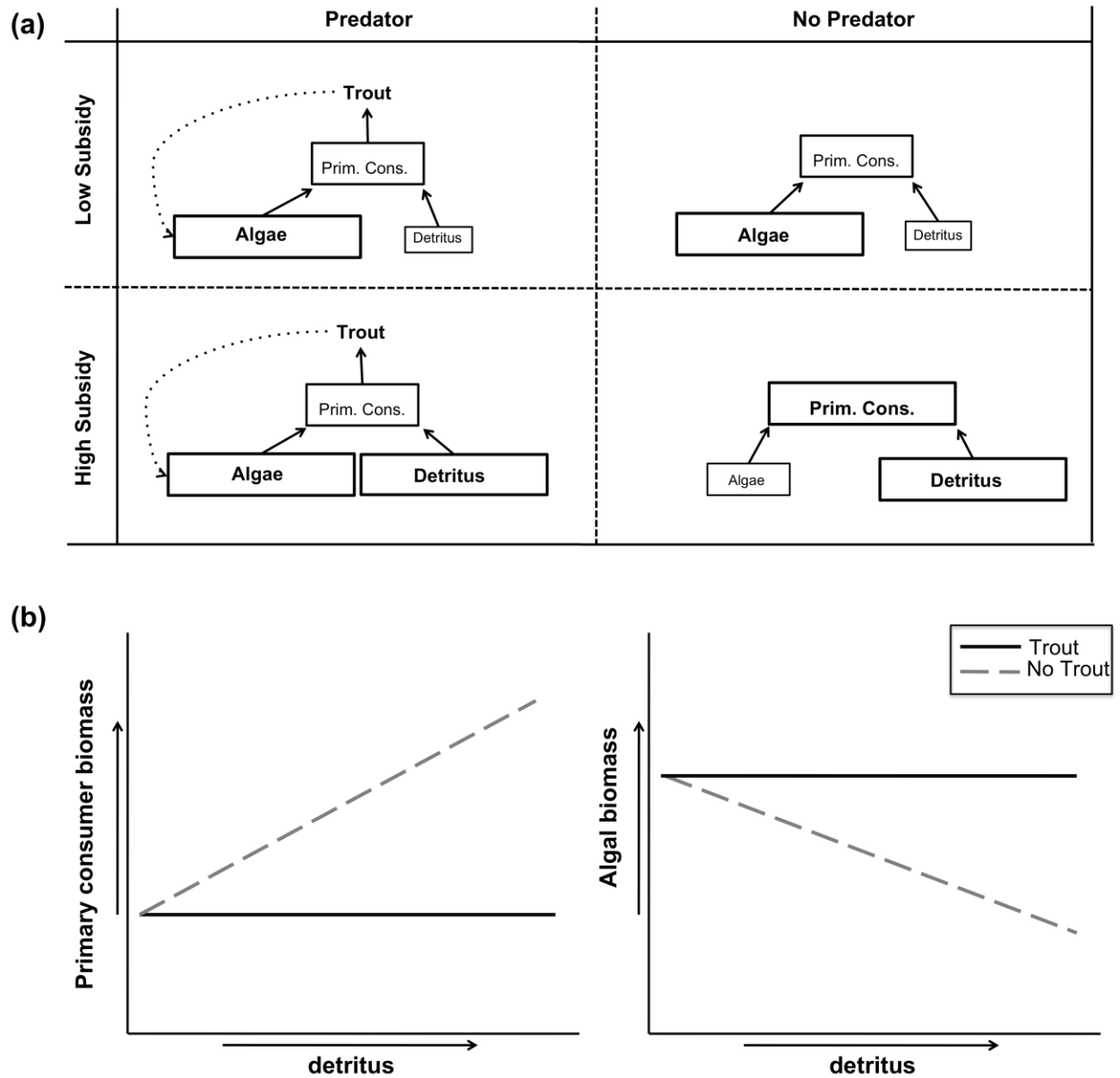


Figure 3.1: (a) Mechanistic predictions of the effects of increasing detritus with and without predators present. “Prim. Cons.” stands for primary consumers. Solid arrows indicate the movement of energy up the food web. Dashed arrows indicate indirect effects of predators on primary production. The size of boxes and text indicates the amount of biomass in that trophic position. (b) Predictions of increasing detritus on response variables: primary consumer biomass and algal biomass.

Methods

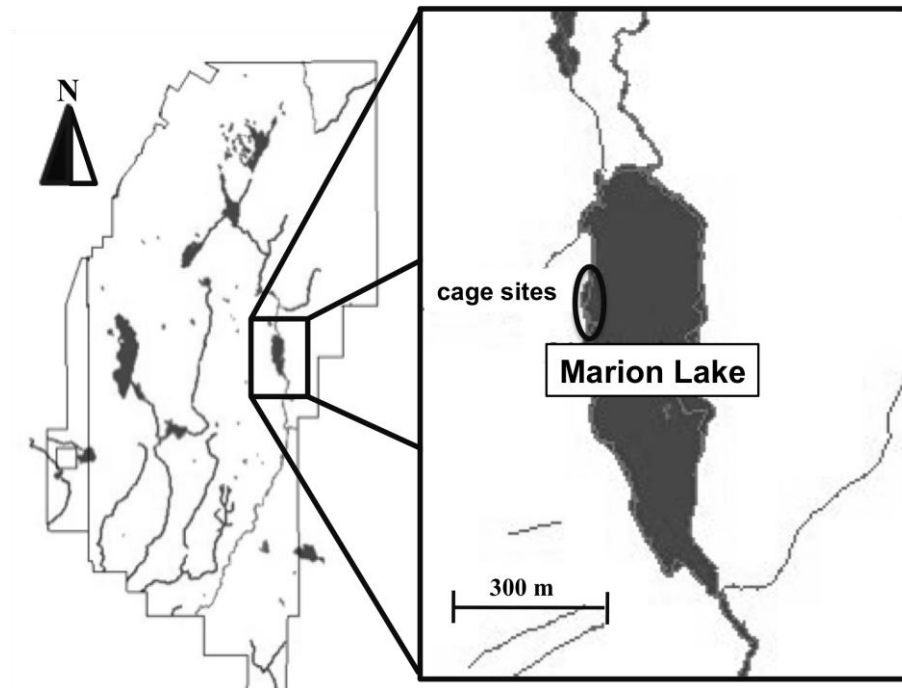


Figure 3.2: Map of Marion Lake at the Malcolm Knapp Research Forest located in the Coast Range Mountains of British Columbia, Canada. The location of cages for the *in situ* cage experiment is marked by an oval.

Study site

My study took place at the Malcolm Knapp Research Forest (MKRF) located 40 km east of Vancouver, British Columbia in the Coast Mountain Range. MKRF is a temperate rainforest with the main canopy consisting of western hemlock (*Tsuga heterophylla*), western red cedar (*Thuja plicata*) and Douglas-fir (*Pseudotsuga menziesii*) with deciduous trees such as red alder (*Alnus rubra*) and vine maple (*Acer circinatum*) around riparian zones (Kominoski et al. 2011). Marion Lake is a shallow lake (maximum depth 7 m) at an altitude of 300 m (Winterbourn 1971). Marion Lake has multiple inflowing streams and is surrounded by boggy zones prone to fluctuations in water inundation due to rainfall events (Winterbourn 1971).

Experimental design

In October 2010, I placed 30 experimental cages (0.81 m² surface area, 0.50 m height) along the western shore of Marion Lake (Figure 3.2) ~ 1 to 2 m from shore and in ~ 0.25 m water depth. The bottom and sides of the cages were covered with 1 cm mesh screening to allow for open colonization and movement of lake benthic communities yet contain added leaf detritus. The tops of the cages were covered with 0.3 cm mesh screening to contain the cutthroat trout in case there was a rise in lake water level. The experiment was designed as a replicated regression (Cottingham et al. 2005) with three replicates of each of five densities of detritus (0, 5, 10, 20, 40 g air dried mass) crossed by the presence or absence of cutthroat trout. Treatments were randomly assigned to the cages using stratified randomization to account for variation along the lake shoreline. Cages were pushed into lake sediment with 3 large rocks inside to provide substrate. Cages were situated at least 0.25 m apart, but distances varied due to large wood on the lake bottom.

Red alder leaves (*Alnus rubra*) were gathered in October 2009 from alder trees around the University of British Columbia's campus and air dried for 11 months. On September 24, 2010, the appropriate detritus density (0, 5, 10, 20, or 40 g / 0.81 m²) was added to each of the cages and allowed to inoculate for 7 days to encourage microbial colonization of the detritus and benthic invertebrate colonization of the cages. One cutthroat trout (*Oncorhynchus clarkii*) (~ 10 cm fork length) was added to half of the cages on October 1, 2010, day 1 of the experiment.

After 25 days, on October 26 the cages were removed from the lake by sliding a 0.1 cm mesh net around the cages to capture the benthic invertebrate community. All coarse detritus (>1 mm) and invertebrates were frozen until processing. Any three-spined stickleback (*Gasterosteus*

aculeatus) that were found in the cages were counted and released back into the lake and the cutthroat trout were returned to their original habitat.

Benthic invertebrate composition

Invertebrate samples were thawed and preserved in 70% ethanol. Invertebrates were measured (length of body mm or width of shell mm) using an optical micrometer and identified to genus, or lowest taxonomic level (Cannings and Stuart 1977, Thorp and Covich 1991, Wiggins 1996, Merritt et al. 2008). Taxa were assigned to functional feeding groups (collector/filterer, collector/gatherer, scraper, shredder, herbivore/piercer, predator) (Merritt et al. 2008). Collector/gatherer, scraper, and shredder groupings were combined to form the grouping “primary consumers”. Herbivore/piercers and collector/filterers were excluded from this grouping because they do not feed on algae or detritus, my two primary production response variables. The predator functional group is referred to henceforth as “predatory invertebrates” to distinguish between trout, stickleback, and invertebrate secondary consumers. The dry mass of each individual was estimated using length-mass regressions (Appendix 2).

Detritus decomposition

All coarse detritus (> 1 mm) from each cage was collected and frozen at the end of the experiment. The detritus samples were then thawed and alder leaf detritus was separated from all other coarse detritus (ambient) which did not significantly differ between treatments (2-way ANOVA, coarse detritus ln-transformed, treatments and interaction $P > 0.12$) (Figure 3.3). Alder detritus and other coarse detritus were dried separately at 55°C, weighed, ashed at 500°C, and then weighed again. Ash free dry mass (AFDM) was calculated using the formula:

$$\text{AFDM} = \text{dry mass (g)} - \text{ash mass (g)}.$$

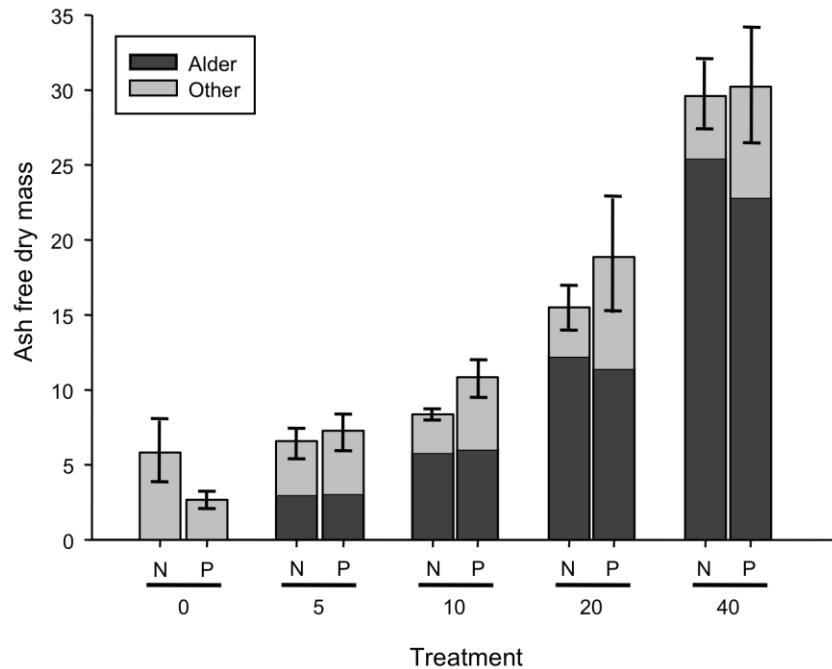


Figure 3.3: Bar graph of total coarse particulate organic matter (>1 mm) in g of ash free dry mass (AFDM) at the end of the experiment. Dark grey portion of bars is experimentally added alder detritus; light grey portion of bars is ambient detritus that entered cages. On the x-axis: N= no trout cages; P= trout cages; 0, 5, 10, 20, and 40 is alder detritus mass treatment in g per cage. Bars indicate standard error of combined coarse particulate organic matter and alder detritus.

Benthic algal biomass

Three 25 cm², non-glazed, ceramic tiles were placed in the south-west corner of each cage to measure final net benthic algae biomass. Tiles were removed and placed on ice for transport then frozen at -18°C until analysis. Tiles were placed in 30 mL of 90% acetone to lyse the cells and release photosynthetic pigments. After approximately 21 hours, 8 mL of the acetone extract were then analysed for chlorophyll *a* (chl *a*) with a Turner Designs Fluorometer (model: TD-700, Sunnyvale, CA 94085), treated with 0.24 mL of 0.1 N HCL, then re-analysed to account for pheophytin *a* (using USEPA method 445.0). Resulting values were converted to chl *a* (mg / m²). There were three tiles in each cage, and the average of the three tiles was used for cage chl *a*.

Trophic cascade strength

Relative predator (trout) impact on the non-adjacent trophic level (benthic algae biomass) was calculated using primary producer trophic index (PTI) (Shurin et al. 2002, Leroux and Loreau 2008):

$$PTI = \ln (P_I / P_0)$$

where P_I is chl a (mg / m^2) in cages with trout and P_0 is chl a (mg / m^2) in cages without trout. All possible PTI combinations were calculated for each detritus density (three trout cages and three non-trout cages per detritus density for a total of nine PTI combinations) and then the mean PTI value was calculated for each detritus density with standard error. Positive PTI values indicate a positive indirect effect on algal biomass and negative PTI values indicate a negative indirect effect on algal biomass. Larger values indicate strong predator regulation (stronger trophic cascades).

Artificial leaf addition experiment

To investigate how the physical structure of the alder leaves influenced benthic invertebrate colonization, I conducted an artificial leaf addition experiment. Designed to mimic the $10 \text{ g} / 0.81 \text{ m}^2$ density of alder leaves, six cages with 25 fabric, alder-shaped leaves were randomly distributed among the 30 experimental cages. The cages were set up exactly as described for the trophic cascade experiment, with three cages receiving one cutthroat trout each and three cages without cutthroat trout.

Statistical analyses

The effect of increasing allochthonous inputs on response variables (total abundance, total dry-mass, algal biomass (chl a), primary consumer dry-mass, snail abundance, predatory invertebrate abundance, and stickleback abundance) for trout and non-trout treatments were

analysed using a linear model that included trout presence/absence (trout), increasing detritus density (mass) as a continuous variable, and trout by detritus-mass interaction. Response variables with a significant trout by mass interaction were subsequently analysed with separate linear regressions for trout and non-trout treatments. Response variables without a significant trout by mass interaction, but with a significant mass effect, were analysed using linear regression for the effect of mass on the response variable (trout presence or absence removed from analysis). When assumptions of normality and equal variance were not met, variables were \ln or $\ln(x + 1)$ transformed to meet assumptions. All statistical analyses were analysed using R (R-Development-Core-Team 2011).

The effect of alder leaf structure on response variables (algal biomass (chl *a*) and primary consumer dry-mass, and total invertebrate biomass) was analysed using a two-way analysis of variance (ANOVA) with presence/absence of trout (trout) and leaf type (no leaves, fabric leaves, 10 g alder leaves) as fixed factors.

Results

Trophic cascade experiment

Total abundance of invertebrates inside the cages increased with increasing allochthonous subsidy inputs, but only in the presence of trout (Table 3.1a, Table 3.2a, Figure 3.4a). There were three main taxa that had observed differences between trout and no trout treatments, *Sphaeriidae* fingernail clams, *Hirudinea* leeches, and *Gyraulus* snails (Appendix 5). The average density of invertebrates per cage was $109 / \text{m}^2$. Interestingly, the same trend was observed with total invertebrate biomass (Table 3.1b, Table 3.2b, Figure 3.4b), where there was a significant increase in biomass in the trout cages, but no significant change in the no-trout cages. At the highest detritus density, there was a 3- to 4-fold increase in invertebrate biomass when trout were present (Figure 3.4b).

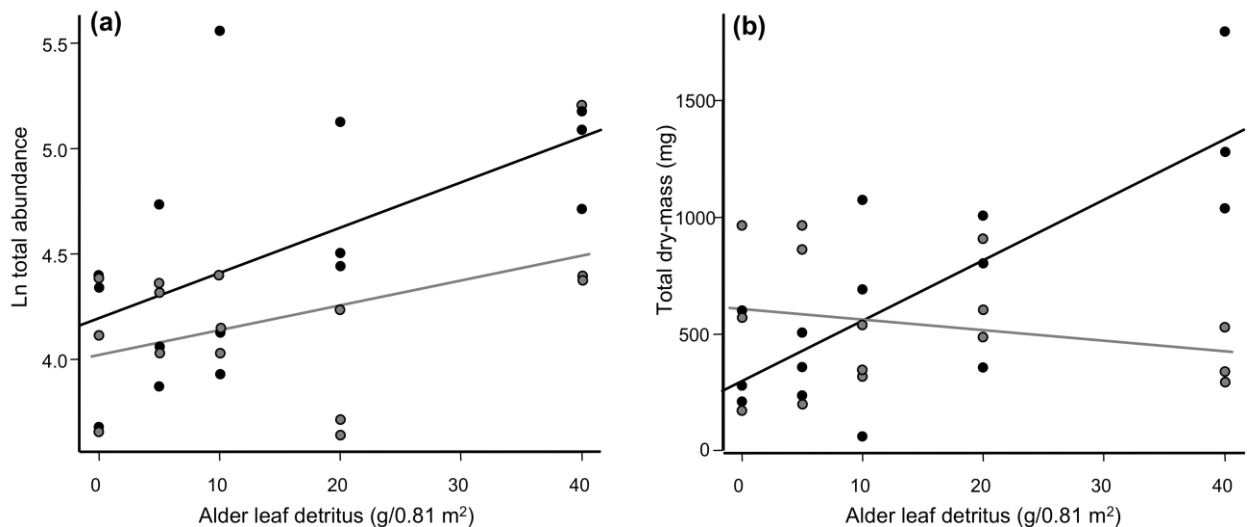


Figure 3.4: (a) Effect of alder leaf detritus mass on total invertebrate abundance (ln transformed) for the cage experiment. Grey circles and line are for the no-trout treatment; black circles and line are for the trout cages treatment. (b) Effect of alder leaf detritus mass on total invertebrate dry mass (mg) for the cage experiment. Grey circles and line are for the no-trout treatment; black circles and line are for the trout cages treatment.

Table 3.1: Linear model results for total abundance, total dry-mass, chl *a*, primary consumer dry-mass, snail abundance, predatory invertebrate abundance, and stickleback abundance in cage experiment. P values that are bold are significant ($P < 0.05$) and F values are presented as $F_{\text{degrees of freedom, error}}$.

Variable	$F_{1,26}$	P
a) Total abundance*		
Trout presence	4.32	0.04
Mass of Alder	9.30	0.005
Trout x Mass	0.86	0.36
b) Total dry-mass (mg)		
Trout presence	1.89	0.18
Mass of Alder	8.13	0.008
Trout x Mass	16.11	0.0005
c) Chl <i>a</i> (mg/m ²)		
Trout presence	1.41	0.25
Mass of Alder	2.59	0.12
Trout x Mass	5.35	0.03
d) Primary consumer dry-mass (mg)		
Trout presence	3.36	0.08
Mass of Alder	7.08	0.01
Trout x Mass	17.61	0.0003
e) Snail abundance*		
Trout presence	1.35	0.26
Mass of Alder	8.51	0.007
Trout x Mass	2.07	0.16
f) Predatory Invertebrate abundance*		
Trout presence	2.99	0.10
Mass of Alder	9.99	0.004
Trout x Mass	0.08	0.78
g) Stickleback abundance**		
Trout presence	2.17	0.15
Mass of Alder	4.32	0.04
Trout x Mass	0.67	0.42

* ln-transformed data

** ln (x+1)-transformed data

At 0 g of alder allochthonous additions, PTI was the highest, indicating a strong positive trophic cascade. The trophic cascade strength decreased, until 10 g of alder detritus, when there was a switch to trout having a negative indirect impact on algal biomass. The strongest negative trophic cascades occurred at the high levels of allochthonous inputs (Figure 3.5).

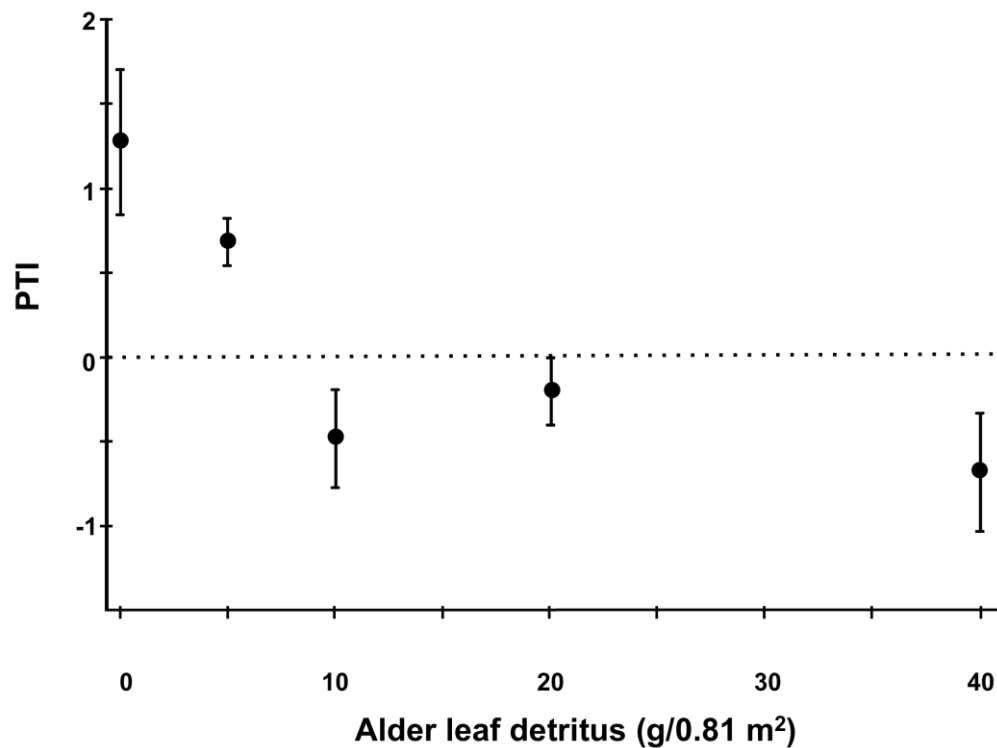


Figure 3.5: Effect of alder leaf detritus mass on average PTI values (algal biomass) for the cage experiment. Dotted line indicates 0 PTI which indicates no effect of trout on algal biomass. Bars indicate standard error ($n = 9$). Positive values indicate trout having a positive indirect effect on algal biomass, negative values indicate trout having a negative indirect effect on algal biomass. Larger values indicate stronger trophic cascade.

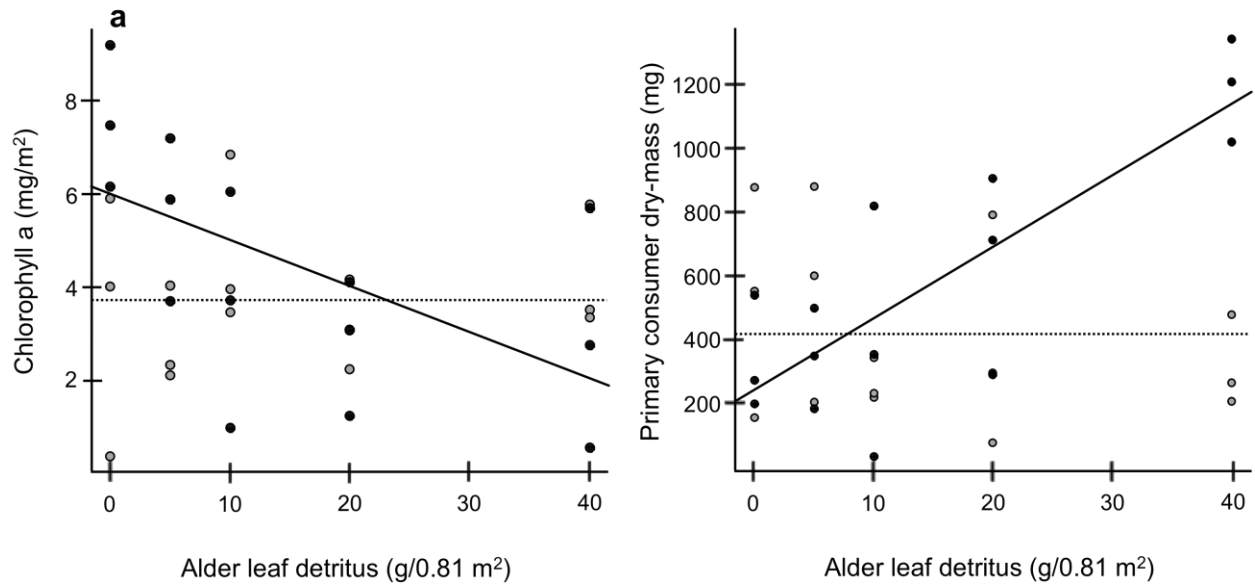


Figure 3.6: (a) Effect of alder leaf detritus mass on chlorophyll *a* for the cage experiment. Black circles and solid line are trout treatment; grey circles are no-trout treatment and dotted line is mean of no-trout chl *a* (3.8 mg/m²) as linear model was non-significant. (b) Effect of alder leaf detritus mass on primary invertebrate consumer dry mass for the cage experiment. Black circles and solid line are trout treatment; grey circles are no-trout treatment and dotted line is mean of no-trout chl *a* (410 mg) as linear model was non-significant.

The switch of positive to negative indirect effects of trout on algal biomass was also observed in the linear model of chl *a*. At the lowest allochthonous inputs, algal biomass doubled in cages with trout compared to cages with no trout. But above 10 g of alder leaf detritus inputs, trout had a negative impact on algal biomass, peaking at a 33% decrease of algal biomass at 40 g of alder leaves. In the absence of trout, there was no effect of detritus on algal biomass (Figure 3.6a, Table 3.1c, Table 3.2c). Trout had the opposite effect on primary consumer biomass (Table 3.1d, Table 3.2d). When trout were present, primary consumer biomass increased until it was 4 times greater than the no trout treatment at the highest alder detritus density. But, in the absence of trout, there was no significant change in primary consumer biomass with the increase of detritus (Figure 3.6b). Increasing alder detritus had an overall positive effect on snail abundance (Table 3.1e, Table 3.2e, Figure 3.7a) and predatory invertebrate abundance (Table

3.1f, Table 3.2f, Figure 3.7b), but a negative effect on stickleback fish abundance (Table 3.1g, Table 3.2g, Figure 3.7c) while trout had no effect on any of the three variables (Table 3.1e, f, g; Table 3.2e, f, g).

Table 3.2: Regression equations for total abundance, total dry-mass, chl *a*, primary consumer dry-mass, snail abundance, predatory invertebrate abundance, and stickleback abundance in cage experiment. Bold P values are significant ($P < 0.05$) and F values are presented as $F_{\text{degrees of freedom, error}}$.

Variable	intercept	slope	F	P	r^2
a) Total abundance*					
No Trout	4.02	0.01	3.04 _{1,13}	0.11	0.19
Trout	4.19	0.02	6.28 _{1,13}	0.03	0.33
b) Total dry-mass (mg)					
No Trout	604.94	-4.38	0.77 _{1,13}	0.34	0.05
Trout	297.65	25.89	21.02 _{1,13}	0.0005	0.62
c) Chl <i>a</i> (mg/m ²)					
No Trout	3.41	0.02	0.33 _{1,13}	0.57	0.03
Trout	6.00	-0.09	6.11 _{1,13}	0.03	0.32
d) Primary consumer dry-mass (mg)					
No Trout	485.60	-5.03	1.05 _{1,13}	0.32	0.07
Trout	242.98	22.48	26.8 _{1,13}	0.0001	0.67
e) Snail abundance*	1.88	0.03	8.10 _{1,28}	0.008	0.22
f) Predatory Invertebrate abundance*	2.49	0.02	9.63 _{1,28}	0.004	0.26
g) Stickleback abundance**	1.57	-0.01	4.20 _{1,28}	0.04	0.13

* ln-transformed data

** ln (x +1)-transformed data

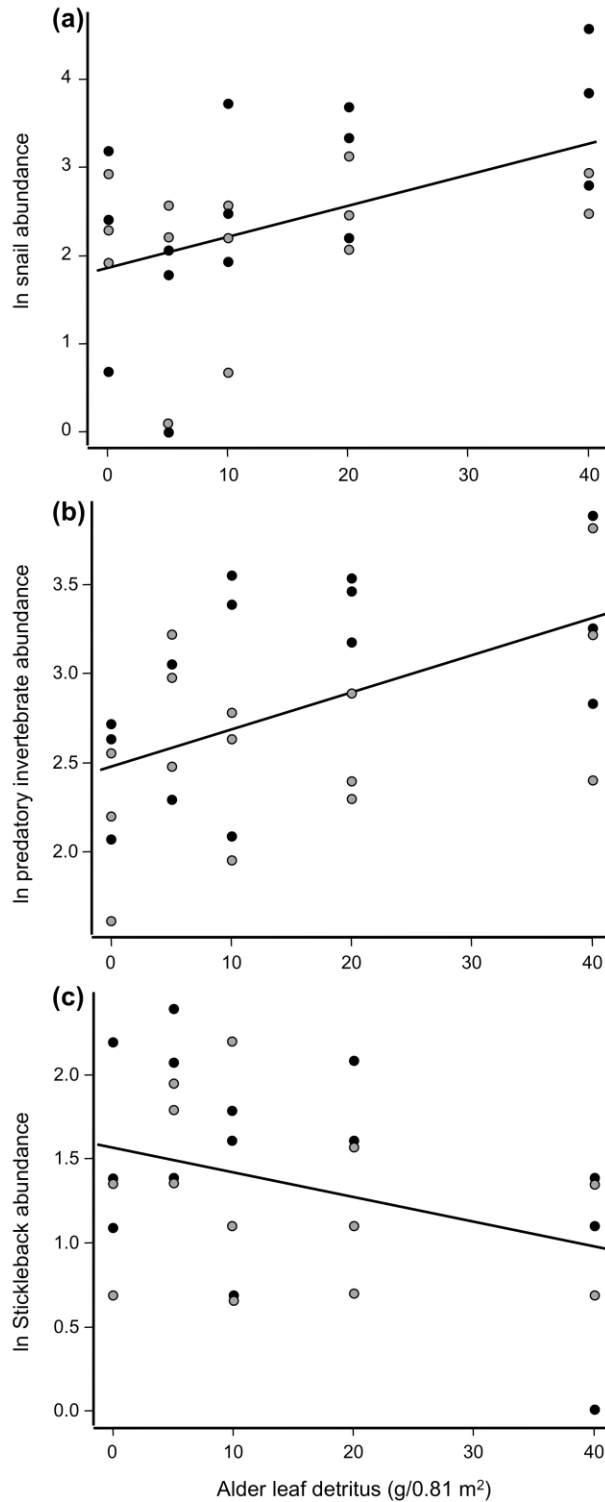


Figure 3.7: Effect of alder leaf mass on (a) snail abundance (ln-transformed), (b) predatory invertebrate abundance (ln-transformed), and (c) stickleback abundance (ln-transformed) per 0.81 m² for the cage experiment. Grey circles are no trout treatments and black circles are trout treatments.

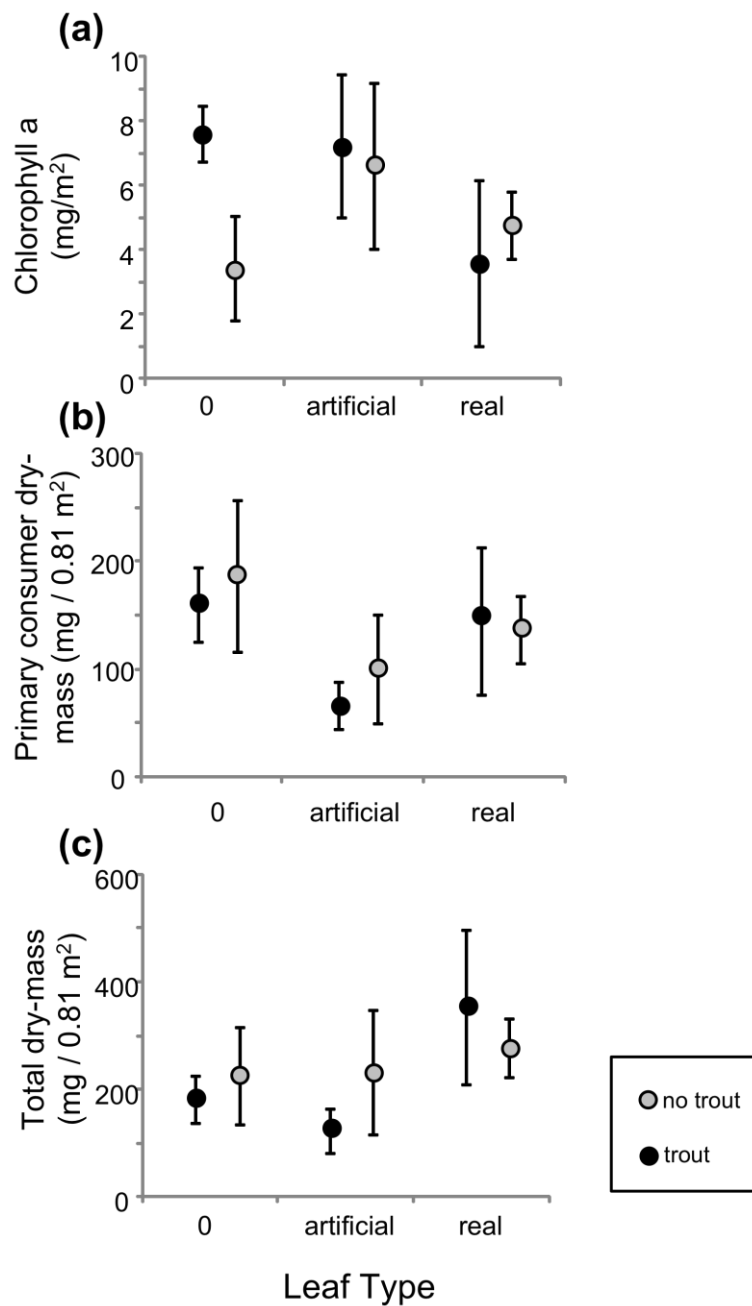


Figure 3.8: (a) Effect of leaf type (no leaves, 25 artificial, fabric leaves, 10 g alder leaf detritus) on (a) algal biomass (chl *a*), (b) invertebrate primary consumer dry-mass (mg), and (c) total invertebrate dry mass (mg). Bars indicate standard error (n=3).

Artificial leaf addition experiment

The physical presence of leaves did not have an effect on algal biomass (Figure 3.8a), primary consumer biomass (Figure 3.8b), or total invertebrate biomass (Figure 3.8c) when compared to equivalent amounts of real leaves and the absence of leaves (Table 3.3).

Table 3.3: Linear model statistical results for algal biomass, primary consumer dry-mass, and total invertebrate dry-mass in artificial leaf experiment. F values are presented as $F_{\text{degrees of freedom, error}}$.

Variable	F	P
a) Algal biomass (chl <i>a</i>)		
Trout presence	0.72 _{1,12}	0.41
Leaf type	1.25 _{2,12}	0.32
Trout x Leaf	1.22 _{2,12}	0.33
b) Primary consumer dry-mass		
Trout presence	0.19 _{1,12}	0.66
Leaf type	1.69 _{2,12}	0.22
Trout x Leaf	0.10 _{2,12}	0.90
c) Total invertebrate dry-mass		
Trout presence	0.12 _{1,12}	0.74
Leaf type	1.32 _{2,12}	0.30
Trout x Leaf	0.54 _{2,12}	0.60

Discussion

I predicted that trophic cascade strength would increase with an increased supply of detritus inside my experimental cages. This was because detritus would provide an alternative food resource for primary consumers that would otherwise feed on benthic algae. I hypothesized that in the absence of trout, primary consumer numbers would increase which would decrease algal biomass, but when trout were present, primary consumer numbers would be suppressed, therefore releasing algal biomass from grazing. In high detritus treatments, this would mean that cages without trout would have low algal biomass and cages with trout would have higher algal biomass, creating high PTI values.

My results did not support these predictions. The lowest detritus treatments (0, 5 g alder leaves) showed strong positive trophic cascades, where trout had a positive indirect effect on algal biomass. Conversely, the highest detritus treatment (40 g alder leaves) exhibited strong negative trophic cascades, where trout had a negative indirect effect on algal biomass. This switch of the direction of indirect effects was unexpected, and challenges our understanding of the effects of subsidies on species interactions (Polis and Hurd 1995, Nakano et al. 1999, Leroux and Loreau 2008).

Trophic cascade strength

Theoretical and empirical studies have provided mixed results on how allochthonous resources affect trophic cascade strength; some provide evidence for increasing in trophic cascade strength with increasing detrital inputs, while others provide evidence for decreasing trophic cascade strength with increasing detrital inputs (Polis and Hurd 1995, Nakano et al. 1999, Halaj and Wise 2002, Leroux and Loreau 2008). I found that as subsidies increased along a gradient of inputs, trophic cascade strength decreased from strong positive effect on algae, and

passed a threshold at intermediate detritus levels, beyond which predators induced a strong negative effect on algae. Piovia-Scott et al. (2011) showed that in the absence of an experimentally added seaweed subsidy, predators had a strong impact on herbivores, reducing herbivory, and creating a strong positive trophic cascade. When seaweed was added to the beaches, detritivore numbers increased, and predators switched to feeding on detritivores which reduced the positive indirect effect of predators on plants (Piovia-Scott et al. 2011). Their study only included the presence or absence of the seaweed on beaches. Similarly, my results show that in the absence of alder detritus, cutthroat trout have a positive indirect effect on algal biomass which decreased with the addition of alder leaf detritus. However midway along the gradient of detritus density, I observed a switch from a positive indirect effect of trout on algae to a negative indirect effect where algal biomass was lower in the presence of trout. Evidence for thresholds of allochthonous resource supply where indirect predator effects change from positive to negative have not been observed before in empirical studies of subsidy effects on trophic cascades. However, models by Huxel et al. (1998) revealed a threshold in food web stability with subsidy abundance, where food web stability peaked at intermediate subsidy levels. Huxel et al. (1998) did not directly measure trophic cascade strength, but suggested that changes in the strength of species interactions were responsible for this threshold.

The threshold responses I observed in trophic cascade strength and algal biomass could be explained by trout having a positive effect on primary consumer biomass with increasing detritus density. In contrast to my predictions, increasing alder detritus had no effect on primary consumer biomass in the absence of trout, but when trout were present, primary consumer biomass increased to four times that of biomass in cages without trout.

Community responses

The abundance of primary consumers increased with detritus density, but only in the presence of trout. While this potentially explains the switch in trophic cascade strength, it is still unclear what the mechanism is behind the increase in primary consumers with a top predator present. Several hypotheses may explain this unexpected result.

The first explanation for the increase in primary consumers with detritus density in the presence of trout is that the detritus acts as a refuge for the primary consumers (Holomuzki and Hoyle 1990, Richardson 1992b). Trout are visual predators (McIntosh 2000), so low detritus densities likely provide less structural refuge from predation than in higher detritus densities. Although I observed this in the trout cages, this trend did not occur in cages without trout. If detritus was acting as a refuge, I would expect that there would be similar patterns of primary consumers in cages with and without trout (Reice 1991), yet trout cages had higher abundance of primary consumers. Therefore this explanation, on its own, does not account for the increase in primary consumers in the presence of trout.

A second explanation is that there were less intermediate predators (stickleback fish and predatory invertebrates) in cages with trout, which released primary consumers from predation (Meissner and Muotka 2006). While I observed a decrease in stickleback with increasing detritus density, there was an increase in predatory invertebrates with detritus density and both of these effects were not significantly affected by the presence of trout (Diehl 1992). Low experimental power arising from the variability of stickleback and predatory invertebrate abundance within treatments likely obscured the detection of weak effects of trout. Therefore I cannot rule out that

trout negatively affected intermediate predator abundance indirectly increasing primary consumers.

A final explanation could be that trout preferentially consumed vulnerable soft bodied primary consumers (such as mayfly larvae), which has been observed in other systems (Rosenfeld 2000, McIntosh 2002, Nystrom et al. 2003, Herbst et al. 2009). This may have released armoured primary consumers (such as snails) from competition, increasing their numbers. McNeely et al. (2007) found that armoured grazers can alter community composition and the transfer of carbon up the food web. I observed an increase in snail abundance with increasing detritus and there was a trend towards higher snail abundance with trout at high detritus densities. However, much like the intermediate predator abundances, the variability of the snail abundance within treatments lead to low power to detect trout effect. This data would benefit from additional observational and quantitative experiments to see if trout prefer soft bodied primary consumers, and whether this enables snails to increase in abundance. Because of my low predictive power due to high variability, I also cannot rule out that an increase in snail abundance in the presence of trout created higher primary consumer biomass with high detritus densities.

My data provide inconclusive support for multiple hypotheses as to why primary consumer biomass increases with detritus density in the presence of trout. Trout-induced increase in primary consumer biomass with increasing detritus may have been from detritus acting as a refuge from predation for the consumer, a decrease in secondary consumers in the presence of trout, or an increase in armoured primary consumers (snails) in the presence of trout. Increasing the number of replicates within a treatment may increase the ability to detect these trends. The collection of the community data from the open mesh cages at the end of the experiment may

have contributed to unexplained variation within treatments. Invertebrates and fish that were present throughout the experiment may have been disturbed during sample collection or actively emigrated from the cages as resources diminished during the final few days. Due to these reasons, the mechanisms behind the unexpected, trout-induced increase in primary consumers with detritus increase remain unclear.

Subsidies as a structural habitat

Resource subsidies, besides providing energy and nutrition to a system, may also provide increased complexity of habitat structure (Holomuzki and Hoyle 1990, Richardson 1992b, Rosenfeld 2000). Leroux and Loreau (2008) predicted that as allochthonous resources increase, especially at the primary consumer level (detritus), trophic cascade strength should increase. These predictions were not supported by my findings. Although their model included some natural characteristics of subsidies, such as recycling of subsidy nutrients, it did not include the physical effect that subsidies could have on interactions within the recipient community (Leroux and Loreau 2008). Even at low density, subsidies can impact foraging rates of predators and can provide physical refuge from predation (Richardson 1992b) and from weather extremes (Lewis and Denno 2009). The results from my artificial leaf addition experiment did not show a difference in total biomass, primary consumer biomass, and algal biomass between the fabric and natural leaf treatments, which suggests that invertebrates utilise detrital subsidies for resources other than nutrient and energetic requirements. However, because the artificial leaves did not significantly differ from no leaf-addition treatments I cannot conclude that leaves physically change interactions within the community. I chose to mimic the 10 g detritus treatment with artificial leaves because it was an intermediate manipulation of subsidy input, but I found that the 10 g treatment did not differ in total invertebrate biomass, primary consumer biomass, or algal

biomass from the 0 g treatment, so a higher level of subsidy (20 g or 40 g) might have been more appropriate to mimic with the artificial leaves.

Conclusions

My results provide evidence that different levels of allochthonous resources will affect trophic cascade strength in a non-linear way. Along a continuous gradient of subsidies, trophic cascade strength experienced a threshold response, where there was a complete switch in cascade influence at mid subsidy densities. This threshold response of cascade strength due to subsidies is a novel empirical result. But a limitation to this study, as with most empirical research, is that the time-scale of the observed effects were limited to a short period within the generation time of interacting species. Theoretical predictions of trophic cascade strength and food web stability with increasing allochthonous resources come from models spanning thousands of time steps and measure multi-generational responses of food webs (Huxel and McCann 1998, Leroux and Loreau 2008). However, this study and numerous other experiments (Nakano et al. 1999, Sabo and Power 2002a, Piovia-Scott et al. 2011) have measured community response within one generation or season, and therefore can only comment on the short-term effects of predators on trophic dynamics. At these time scales, changes in species interactions reflect shifts in diet of consumers or short-term aggregation of predators or prey, rather than changes in predator, prey, or producer population dynamics. Future experiments need to incorporate long-term, multi-generational responses into the effects of subsidy inputs on trophic cascades in order to bridge the gap between theory and empirical evidence. Nevertheless, my findings reveal that complex species interactions such as trophic cascades can exhibit non-linear threshold responses to gradients of allochthonous inputs. Thus, even moderate changes in the magnitude of subsidies could have profound effects on food web dynamics.

Chapter 4: Concluding remarks

Synthesis

The results from Chapter 2 provided evidence that streams affect leaf detritus standing stocks in lakes and benthic invertebrate community composition. My results supported my hypothesis that in lakes, detritus would increase around stream mouths compared to forest boundaries and that increase would diminish with distance into the lake. However these results were not expressed as an overall trend across all streams, as patterns of detritus accumulation differed between stream sites. I also found that streams, distance into the lake, and detritus affected benthic invertebrate communities. Thus streams contribute to the patchiness of both resource subsidies and benthic invertebrates in lakes, potentially enhancing whole-lake biodiversity. The influence of inflowing streams on lakes is therefore important to incorporate into catchment-scale models of subsidy transport in streams (Wipfli et al. 2007).

Chapter 3 provided evidence that resource subsidies alter the strength of trophic cascades (Leroux and Loreau 2008), although my results did not support my original hypothesis. I predicted that trophic cascade strength would increase as subsidy inputs were experimentally increased to lake benthic communities. However, I found that predators exhibited strong, positive, top-down control on non-adjacent trophic levels (algae) at the lowest detritus densities. At intermediate detritus levels there was a switch of indirect predator effects such that at high levels of detritus predators exerted strong negative top-down effects on algae. Although my results suggest several possible mechanisms (detritus acts as refuge for primary consumers from predators, intermediate predator abundance decreases with trout, or armoured primary consumers increase in abundance with trout), further experiments are required tease apart these hypotheses.

I found that streams alter detritus standing stocks in lakes, potentially creating patches of subsidies within the lake ecosystem (Hoover et al. 2006) having bottom-up effects on community composition. My results also showed that the quantity of detritus subsidies influence the indirect, top-down effects of predators. Therefore it is likely that within a lake ecosystem, benthic food webs associated with different quantities of detrital inputs experience different levels of top-down control that is mediated by a mobile predator (trout) yet are still affected by bottom-up forces. Regulation of top-down and bottom-up forces in detritus-based systems has been observed (McIntosh et al. 2005). Patch dynamics are consistent with the hypothesis of spatial food web compartments in habitats that are connected by mobile predators (McCann et al. 2005). However as this patchiness appears associated with detritus and other subsidies from streams, my work indicates incorporating cross-ecosystem resource transfers into theory on spatial food web compartments will be advantageous.

Limitations

There are several limitations to my study and scale of inference that limit my conclusions. For example, in my survey I used detritus standing stocks as a proxy for the quantity of detritus that was being transported across the stream/lake and forest/lake boundaries. In order to gain a better understanding of exactly how streams impact lake communities and their interactions, it would be informative to monitor the actual flux of subsidies (i.e., biomass per unit time) across the two boundaries. It would also be useful to quantify other sources of subsidies, such as fine organic matter, nutrients, and inorganic sediment, rather than focusing on the standing stock of coarse organic matter alone. These additional data would provide a better understanding of exactly how streams affect this unique ecotone within lakes.

My survey took place during autumnal leaf drop, when leaf input was high but surface water discharge was low. It would be interesting to compare the streams' influence on lake detritus and invertebrates throughout the different seasons where leaf input and stream discharge differ. Streams effects on detritus dynamics in lakes may be seasonal and different invertebrate taxa occur in the lakes during different parts of the year (Winterbourn 1971). Sakamaki and Richardson (2008) found that standing stocks of detritus around river inlets to estuaries was highest in autumn and decreased to its lowest abundance in spring. This same trend in lakes is likely to produce different stream-induced effects throughout the year.

My experimental results provided evidence for a switch in trophic cascades from positive indirect effects on algae to negative effects along a gradient of increasing detritus biomass. A limitation of many empirical studies, as well as mine, is the time frame of observed results (Nakano et al. 1999, Sabo and Power 2002a, Piovita-Scott et al. 2011). My results differed from those predicted by theoretical models, which may be due to the short time frame of my

experiment (Huxel and McCann 1998, Huxel et al. 2002, Leroux and Loreau 2008). Multiple generation time scales enable feedbacks in the population dynamics of consumers (e.g., grazers) and resources (such as algae) to be incorporated into species interactions. Therefore long-term experimental manipulation of a gradient of detritus subsidies that spans multiple generations is needed to fully understand how systems and interactions within those systems are formed around subsidies.

My results from freshwater communities suggest that increases in subsidies along a gradient of input rates causes a switch in the indirect effects of predators on primary production. There are differences between freshwater, terrestrial, and marine ecosystems that would need to be considered to draw more general conclusion on the top-down influence of predators under different subsidy regimes. Particular aspects include: 1) the difference in size between primary consumers and primary producers, e.g. zooplankton (consumer) size to phytoplankton size (producer) in lakes compared to caterpillar (consumer) size to tree (producer) size in forests; 2) prevalence of ectotherms or endotherms; 3) turnover time of species; and 4) how productive the system is (Shurin and Seabloom 2005). Because of the differences between these four characteristics between freshwater, marine, and terrestrial ecosystems it is important to conduct similar experiments across systems to enhance our general understanding of subsidies effect on trophic cascades.

Prospects

Spatial subsidies are a crucial resource input that influence the structure and function of many ecosystems (Polis et al. 1997, Richardson et al. 2010). Therefore understanding the impacts of altering subsidy quantity and quality to recipient ecosystems is an important consideration for upland systems and how they are managed (Wipfli et al. 2007). This is especially true in stream networks where there is a natural down-catchment flow of subsidies from headwater streams to downstream ecosystems (lakes, rivers, estuaries) (Wipfli et al. 2007). My study provides evidence that streams affect a) leaf detritus subsidies to lakes, b) the benthic invertebrate community associated with that subsidy, and c) that detritus subsidies can affect trophic cascade strength and these effects are dependant on the amount of subsidy. Each of these conclusions suggests that the alteration of upstream ecosystems will have consequences for the invertebrate community composition and top-down regulation of food webs in lakes downstream. For example, forest harvesting is known to affect the quality and quantity of leaf litter that falls into streams and the processing rates and storage once in the streams (Benfield et al. 2001, Lecerf and Richardson 2010). These impacts may flow downstream and affect lake ecosystems by altering the amount and quality of detritus received from streams. Future studies need to focus on how impacting subsidy flows and water hydrology from headwater streams will affect the overall functioning of downstream systems, such as lakes (Wipfli et al. 2007, Richardson et al. 2010). Incorporation of lakes into policy and management of headwater streams may provide incentives for conservation that are more relevant to society, as lakes are recreationally and aesthetically valued ecosystems (Siderelis and Perrygo 1996).

While my study provides evidence that streams affect detritus subsidies and benthic invertebrate communities, there are many unanswered questions that, if addressed, will enhance

our understanding of these complex systems (Jones 2010). Also, understanding the range of amounts of subsidy exchanges and where they are entering the recipient community will help to better predict the extent of top-down predator control. Future studies need to expand their focus from how a unidirectional subsidy affects one system, to incorporating the bidirectional exchange of subsidies between ecosystems, and how altering the amount of subsidies entering a system may also affect subsidies leaving the system.

The study of cross-ecosystem subsidies will benefit from understanding interactions between anthropogenic changes in fluxes of cross-ecosystem subsidies, e.g. how changing nutrient load and detritus inputs interact to affect lake communities. Human activities are altering the flows of subsidies between ecosystems all over the world (Benfield et al. 2001, Hebblewhite et al. 2005, Burcher et al. 2007, Lecerf and Richardson 2010). Subsidies are critical to community composition and the structure and function of food webs (Polis et al. 1997, Richardson et al. 2010). Therefore understanding the change in rates of subsidy transfer, the effects on recipient communities and their interactions, and bidirectional exchanges between systems will be crucial to predicting and managing future human impacts on ecosystems (Polis et al. 1997, Leroux and Loreau 2008, Richardson et al. 2010).

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Appendix 1: Stream habitat variables

Appendix 1: Habitat variables for each stream interface and forest interface sites in the Loon Lake and Marion Lake survey. “Lk.” stands for lake, “St.” stands for stream interfaces, and “Ft.” stands for forest interfaces.

	Stream Width (m)	Stream Depth (m)	0 m			1 m			3 m			9 m			27 m		
			depth (m)	DO (mg/L)	temp (C)	depth (m)	DO (mg/L)	temp (C)	depth (m)	DO (mg/L)	temp (C)	depth (m)	DO (mg/L)	temp (C)	depth (m)	DO (mg/L)	temp (C)
Loon Lk.																	
Faraway St.	0.6	0.06	0.67	9.74	13.5	0.93	9.89	11.0	1.75	9.55	13.7	5.00	9.50	13.7	14.50	9.49	6.7
Faraway Ft.	-	-	0.25	9.32	13.6	0.35	9.53	13.8	1.00	9.61	13.8	5.00	9.64	13.7	18.00	9.91	6.6
Cobble St.	0.7	0.09	0.03	10.31	8.3	0.19	9.65	12.0	0.42	9.83	12.7	1.75	9.61	13.4	15.50	10.08	6.5
Cobble Ft.	-	-	0.37	9.42	13.3	0.57	9.39	13.3	2.10	9.41	13.4	6.00	9.17	13.4	17.00	10.15	6.5
Lilypad St.	0.3	0.04	0.10	10.76	7.7	0.19	9.45	10.7	0.52	9.16	13.2	3.00	8.96	12.9	10.00	10.05	12.8
Lilypad Ft.	-	-	0.40	9.00	13.7	0.71	8.93	13.3	1.50	8.94	13.1	3.5	8.89	12.9	-	8.79	12.8
Marion Lk.																	
Paper St.	0.53	0.1	0.15	9.52	9.5	0.18	9.05	9.6	0.34	9.25	10.7	0.46	10.00	11.6	0.83	10.24	11.6
Paper Ft.	-	-	0.14	7.82	3.9	0.15	7.63	4.5	0.28	9.70	7.2	0.53	10.32	8.7	0.89	10.02	8.8
Marion St.	8.4	0.8	0.76	11.52	7.2	0.79	11.55	7.3	1.30	11.75	7.3	1.30	11.52	7.4	2.50	10.70	9.5
Marion Ft.	-	-	0.32	10.84	8.8	0.44	11.54	8.9	0.61	10.62	9.1	0.79	10.29	9.2	1.10	10.38	8.4
Piddiley St.	0.5	0.13	0.16	10.52	9.1	0.24	10.41	10.1	0.61	10.33	10.7	0.71	10.35	10.9	1.00	10.34	10.8
Piddiley Ft.	-	-	0.33	10.75	9.6	0.45	10.35	10.1	0.63	10.03	10.4	0.95	10.02	10.5	-	10.25	10.1

Appendix 2: Length-mass regression equations

Appendix 2: Length –mass regression equations based on total body length. Where DM = dry mass (mg), BL = body length (mm), and SL = shell length (longest or widest part) (mm). Shell weight was not included in any of the Mollusca regressions. A.J. Klemmer unpublished data are regressions by Amanda J. Klemmer. H.S. Greig unpublished data are regressions by Hamish S. Greig.

Taxa	Taxonomic resolution of regression	Regression	Reference
<i>Aeshna</i> sp.	Aeshnidae	$DM = 0.0082 * BL^{2.813}$	Benke et al. 1999
<i>Agabus</i> sp. larvae	Colembetinae	$DM = 0.0016 * BL^{3.0302}$	H.S. Greig unpublished data
<i>Agrypnia</i> sp.	Phryganeidae	$DM = 0.0054 * BL^{2.811}$	Benke et al. 1999
<i>Ampumixis</i> sp. larvae	Coleoptera (larvae)	$DM = e^{-5.97} + 2.76 * \ln(BL)$	Burgherr & Meyer 1997
<i>Bezzia</i> spp.	Ceratopogonidae	$DM = 0.0025 * BL^{2.469}$	Benke et al. 1999
Hydracarina 1	Hydracarina	$DM = e^{-2.02} + 1.66 * \ln(BL)$	Baumgartner & Rothhaupt 2003
<i>Caenis</i> sp.	Caenidae	$DM = 0.0054 * BL^{2.772}$	Benke et al. 1999
<i>Callibaetis</i> sp.	Callibaetis sp.	$DM = 0.00081 * BL^{3.547}$	Benke et al. 1999
<i>Cernotina</i> sp.	Polycentropodidae	$DM = 0.0047 * BL^{2.705}$	Benke et al. 1999
Chironomini <i>Chrysomelidae</i> sp. larvae	Chironomini Coleoptera (larvae)	$DM = 0.0007 * BL^{2.952}$ $DM = e^{-5.97} + 2.76 * \ln(BL)$	Benke et al. 1999 Burgherr & Meyer 1997
<i>Cordulia</i> sp.	Corduliidae	$DM = 0.0096 * BL^{2.787}$	Benke et al. 1999
<i>Cryptochia</i> sp.	Limnephilidae	$DM = 0.004 * BL^{2.933}$	Benke et al. 1999
<i>Culicoides</i> sp.	Ceratopogonidae	$DM = 0.0025 * BL^{2.469}$	Benke et al. 1999
<i>Curculionidae</i> sp. larvae	Coleoptera (larvae)	$DM = e^{-5.97} + 2.76 * \ln(BL)$	Burgherr & Meyer 1997
<i>Dixella</i> sp.	Diptera	$DM = 0.0025 * BL^{2.692}$	Benke et al. 1999
<i>Enallagma</i> sp.	Coenagrionidae	$DM = 0.0051 * BL^{2.785}$	Benke et al. 1999
Sphaeriidae	Sphaeriidae	$DM = 0.0163 * BL^{2.477}$	Benke et al. 1999
Turbellaria	Turbellaria	$DM = 0.0082 * BL^{2.168}$	Benke et al. 1999
Gammarus	Amphipoda	$DM = 0.0058 * BL^{3.015}$	Benke et al. 1999
<i>Grammotaulis</i> sp.	Limnephilidae	$DM = 0.004 * BL^{2.933}$	Benke et al. 1999
<i>Gyraulis</i> sp.	<i>Gyraulis</i> sp.	$DM = (0.0219 * BL^{2.423}) * 0.334$	H.S. Greig unpublished data
<i>Gyrinus</i> sp. adult	Coleoptera (adults)	$DM = e^{-5.46} + 4.33 * \ln(BL)$	Burgherr & Meyer 1997
<i>Haliphus</i> sp. adult	Coleoptera (adults)	$DM = e^{-5.46} + 4.33 * \ln(BL)$	Burgherr & Meyer 1997
<i>Hybomitra</i> sp.	Tabanidae	$DM = 0.005 * BL^{2.591}$	Benke et al. 1999
leech (experiment)*	leech	$DM = 0.0083 * BL^{1.9196}$	A.J. Klemmer unpublished data
leech (survey)**	leech	$DM = 0.0266 * BL^{2.0555}$	A.J. Klemmer unpublished data

* Experiment leeches were frozen and then preserved in 70% ethanol. Regression was made from preserved length and mass.

** Survey leeches were preserved in 70% ethanol. Regression was made from preserved length and mass.

Appendix 2 continued.

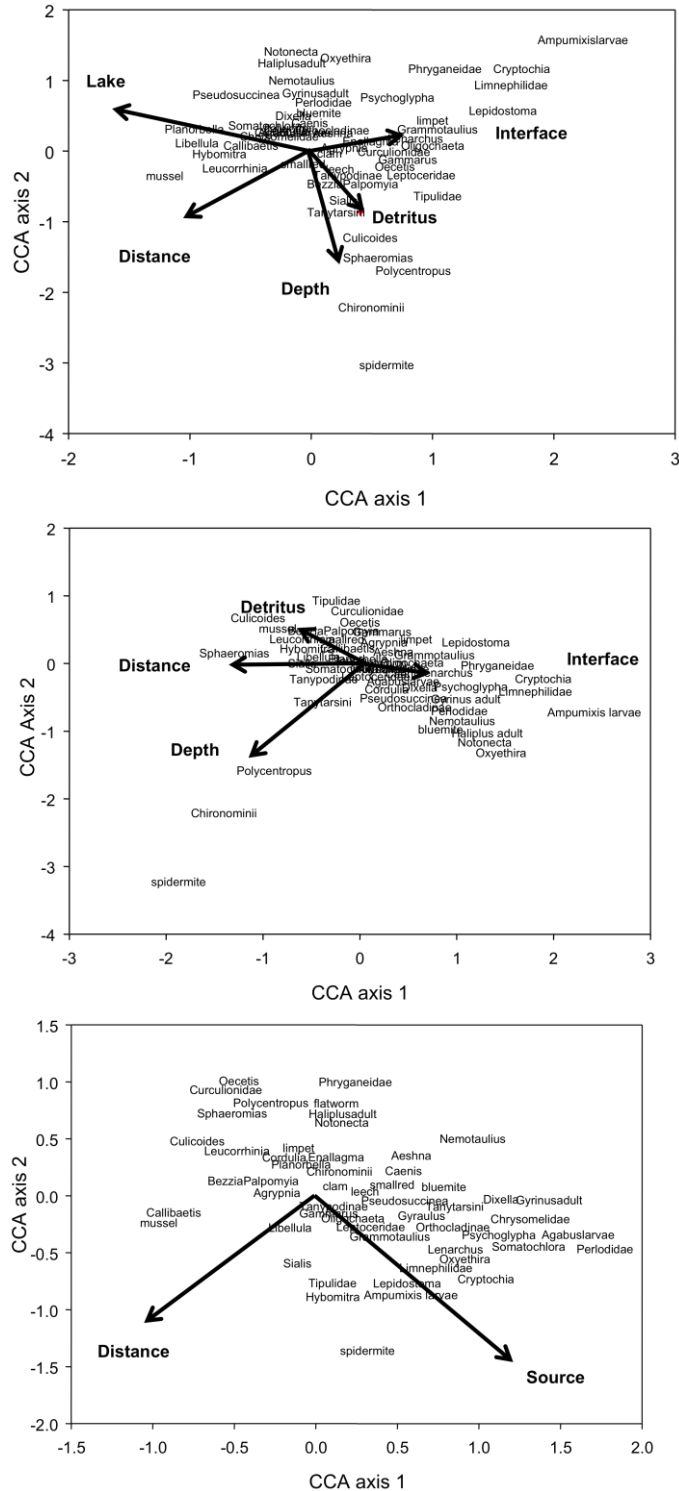
Taxa	Taxonomic resolution of regression	Regression	Reference
<i>Lenarchus</i> sp.	Limnephilidae	$DM = 0.004 * BL^{2.933}$	Benke et al. 1999
<i>Lepidostoma</i> sp.	<i>Lepidostoma</i> sp.	$DM = 0.0079 * BL^{2.649}$	Benke et al. 1999
<i>Leucorrhinia</i> sp.	Libellulidae	$DM = 0.0076 * BL^{2.809}$	Benke et al. 1999
<i>Libellula</i> sp.	Libellulidae	$DM = 0.0076 * BL^{2.809}$	Benke et al. 1999
limpet	Sphaeriidae	$DM = 0.0163 * BL^{2.477}$	Benke et al. 1999
mussel	Unionidae	$DM = 0.0023 * BL^{3.156}$	Benke et al. 1999
<i>Mystacides</i> sp.	<i>Oecetis</i> sp.	$DM = 0.0034 * BL^{3.212}$	Benke et al. 1999
Nectopsyche	<i>Oecetis</i> sp.	$DM = 0.0034 * BL^{3.212}$	Benke et al. 1999
Nemotaulis	Limnephilidae	$DM = 0.004 * BL^{2.933}$	Benke et al. 1999
<i>Notonecta</i> sp.	<i>Notonecta</i> sp.	$DM = 0.844 * e^{(BL/10) * 3.065}$	H.S. Greig unpublished data
<i>Oecetis</i> sp.	<i>Oecetis</i> sp.	$DM = 0.0034 * BL^{3.212}$	Benke et al. 1999
Oligochaeta	Oligochaeta	$DM = 10^{-2.618} * BL^{1.875}$	Stoffels et al. 2003
Orthoclaadiinae	Orthoclaadiinae	$DM = 0.002 * BL^{2.254}$	Benke et al. 1999
<i>Oxyethira</i> sp.	Hydroptilidae	$DM = 10^{-1.897} * BL^{2.901}$	Stoffels et al. 2003
Perlodidae	Perlodidae	$DM = 0.0196 * BL^{2.742}$	Benke et al. 1999
<i>Planorbella</i> sp.	Planorbidae	$DM = (10^{2.885} * \log_{10}(SL) + -1.1) * 0.334$	Madsen & Frandsen 1979
<i>Polycentropus</i> sp.	<i>Polycentropus</i> sp.	$DM = 0.0071 * BL^{2.531}$	Benke et al. 1999
<i>Pseudosuccinea</i> sp.	Gastropoda	$DM = (0.046 * SL^{3.2341}) * 0.85$	H.S. Greig unpublished data
<i>Psychoglypha</i> sp.	Limnephilidae	$DM = 0.004 * BL^{2.933}$	Benke et al. 1999
Hydracarina 2	Hydracarina	$DM = e^{-2.02} + 1.66 * \ln(BL)$	Baumgartner & Rothhaupt 2003
<i>Sialis</i> sp.	<i>Sialis</i> sp.	$DM = 0.0031 * BL^{2.801}$	Benke et al. 1999
Hydracarina 3	Hydracarina	$DM = e^{-2.02} + 1.66 * \ln(BL)$	Baumgartner & Rothhaupt 2003
<i>Somatochlora</i> sp.	Corduliidae	$DM = 0.0096 * BL^{2.787}$	Benke et al. 1999
<i>Sphaeromias</i> sp.	Ceratopogonidae	$DM = 0.0025 * BL^{2.469}$	Benke et al. 1999
Hydracarina 4	Hydracarina	$DM = e^{-2.02} + 1.66 * \ln(BL)$	Baumgartner & Rothhaupt 2003
Tanypodinae	Tanypodinae	$DM = 0.0038 * BL^{2.411}$	Benke et al. 1999
Tanytarsini	Tanytarsini	$DM = 0.0008 * BL^{2.728}$	Benke et al. 1999
tiny Leptoceridae	<i>Oecetis</i> sp.	$DM = 0.0034 * BL^{3.212}$	Benke et al. 1999
tiny Limnephilidae	Limnephilidae	$DM = 0.004 * BL^{2.933}$	Benke et al. 1999
tiny Phryganeidae	Phryganeidae	$DM = 0.0054 * BL^{2.811}$	Benke et al. 1999
Tipulidae	Tipulidae	$DM = 0.0029 * BL^{2.681}$	Benke et al. 1999

Appendix 3: Taxon present in survey

Appendix 3: Taxa present in samples from survey separated by lake and then interface within lake. “X” indicates taxon being present.

Class/Order	Taxon	Loon	Forest	Stream	Marion	Forest	Stream
Acari	mite 1				X	X	X
Acari	mite 2	X	X		X		X
Acari	mite 3	X		X	X		X
Amphipoda	<i>Gammarus</i>	X	X	X	X	X	X
Annelida	Oligochaeta	X	X	X	X	X	X
Bivalvia	<i>Anodonata</i> sp.				X	X	X
Bivalvia	Sphaeriidae	X	X	X	X	X	X
Clitellata	Hirudinea	X	X	X	X	X	X
Coleoptera	<i>Agabus</i> larvae				X		X
Coleoptera	<i>Ampumixis</i> larvae	X		X			
Coleoptera	<i>Chrysomelidae</i> larvae				X		X
Coleoptera	<i>Curculionidae</i> larvae	X	X				
Coleoptera	<i>Gyrinus</i> adult				X		X
Coleoptera	<i>Halipus</i> adult				X	X	
Diptera	<i>Bezzia/Palpomyia</i>	X	X	X	X	X	X
Diptera	Chironomini	X	X	X	X	X	X
Diptera	<i>Culicoides</i>	X	X	X			
Diptera	<i>Dixella</i>				X	X	X
Diptera	<i>Hybomitra</i>				X	X	X
Diptera	Orthocladinae	X		X	X	X	X
Diptera	<i>Sphaeromias</i>	X	X	X			
Diptera	Tanypodinae	X	X	X	X	X	X
Diptera	Tanytarsini	X	X	X	X	X	X
Diptera	Tipulidae	X		X			
Ephemeroptera	<i>Caenis</i>	X	X	X	X	X	X
Ephemeroptera	<i>Callibaetis</i>	X	X		X	X	X
Gastropoda	<i>Gyraulus</i>	X	X	X	X	X	X
Gastropoda	limpet	X	X	X			
Gastropoda	<i>Planorbella</i>				X	X	X
Gastropoda	<i>Pseudosuccinea</i>				X	X	X
Hemiptera	<i>Notonecta</i>				X	X	
Megaloptera	<i>Sialis</i>	X	X	X	X	X	X
Odonata	<i>Aeshna</i>	X	X		X		X
Odonata	<i>Cordulia</i>	X		X	X	X	
Odonata	<i>Enallagma</i>	X	X	X	X	X	X
Odonata	<i>Leucorrhinia</i>	X	X		X	X	X
Odonata	<i>Libellula</i>				X	X	X
Odonata	<i>Somatochlora</i>				X		X
Plecoptera	Perlodidae				X		X
Trichoptera	<i>Agrypnia</i>	X	X	X	X	X	X
Trichoptera	<i>Cryptochia</i>	X		X			
Trichoptera	<i>Grammotaulius</i>	X	X	X	X		X
Trichoptera	<i>Lenarchus</i>	X		X	X		X
Trichoptera	<i>Lepidostoma</i>	X		X			
Trichoptera	<i>Nemotaulius</i>	X	X	X	X	X	X
Trichoptera	<i>Oecetis</i>	X	X				
Trichoptera	<i>Oxyethira</i>				X		X
Trichoptera	<i>Polycentropus</i>	X	X	X			
Trichoptera	<i>Psychoglypha</i>	X		X	X		X
Trichoptera	tiny Leptoceridae	X	X	X	X	X	X
Trichoptera	tiny Limnephilidae	X	X	X	X	X	X
Trichoptera	tiny Phryganeidae	X	X				
Turbellaria	Turbellaria	X	X		X	X	X
Total Taxa		38	29	30	42	30	39

Appendix 4: Survey ordination with taxa



Appendix 4: Canonical correspondence analyses (CCA) of benthic invertebrate community composition with a) all habitat variables in model, b) all habitat variables in model except for the variance of lake partitioned out, and c) interface and distance in model with all other habitat variables partitioned out. Arrows indicate significant constrained habitat variables and length of arrow is representative of its effect on the community.

Appendix 5: Taxon abundance per cage for experiment

Appendix 5: Average abundance of taxa per cage (0.81 m²) for trout cages and no trout cages per detritus density. Detritus density is expressed as 0, 5, 10, 20, and 40 g / 0.81 m². “<1” indicates any abundance average that was less than 1 / 0.81 m², “lv” stands for larvae, and “ad” stands for adult. Blank spaces indicate absence of taxa from treatment.

Class/Order	Taxon	No Trout	Trout	No Trout					Trout				
		total	total	0	5	10	20	40	0	5	10	20	40
Acari	mite 1		<1										<1
Acari	mite 2	1	<1	1	<1	<1		2	<1	<1		1	
Acari	mite 3	<1	<1	<1	<1	<1		<1			1	<1	<1
Amphipoda	<i>Gammarus</i>	3	5	4	3	3	1	5	7	7	2	6	4
Bivalvia	<i>Sphaeriidae</i>	15	28	18	15	8	14	18	12	10	61	29	26
Clitellata	Hirudinea	6	11	4	8	2	8	7	6	6	13	14	15
Coleoptera	<i>Agabus</i> lv	<1	<1			1							<1
Coleoptera	<i>Chrysomelidae</i> lv	<1	<1	<1								<1	
Coleoptera	<i>Haliphus</i> ad	<1	<1					<1					<1
Diptera	<i>Bezzia/Palpomysia</i>	<1	<1	<1		<1				<1			1
Diptera	Chironomini	4	6	5	2	5	1	7	2	5	4	5	12
Diptera	<i>Hybomitra</i>		<1							<1	1		1
Diptera	Orthocladinae	1	2	1	1	1			1	<1	4	2	2
Diptera	<i>Sphaeromias</i>	<1	<1		<1					<1	<1	<1	1
Diptera	Tanypodinae	3	4	1	4	2	2	9	3	1	6	6	5
Diptera	Tanytarsini	<1	1	<1		2		<1		1	1	1	2
Ephemeroptera	<i>Caenis</i>	10	9	5	7	14	1	23	8	13	5	9	10
Ephemeroptera	<i>Callibaetis</i>	<1	1		<1		1	<1	<1	1	1	2	1
Gastropoda	<i>Gyraulus</i>	5	16	6	2	4	9	6	9	2	15	14	40
Gastropoda	<i>Planorbella</i>	5	6	6	5	3	5	5	3	3	5	8	11
Gastropoda	<i>Pseudosuccinea</i>	1	2	<1	1	2	<1	2	1		<1	4	3
Hemiptera	<i>Notonecta</i>	<1				<1	<1						
Odonata	<i>Aeshna</i>	1	<1	<1	<1	1	1				1	1	1
Odonata	<i>Cordulia</i>	1	1	<1	<1	1	<1	1	<1	<1	2	1	1
Odonata	<i>Enallagma</i>	3	3	2	4	4	1	5	2	4		6	4
Odonata	<i>Leucorrhinia</i>		<1								<1		
Trichoptera	<i>Agrypnia</i>	4	3	2	4	6	2	7	4	5	<1	2	3
Trichoptera	<i>Cernotina</i>	1	1		2	1	<1	2	<1		1	1	1
Trichoptera	<i>Mystacides</i>		<1							<1			
Trichoptera	<i>Nectopsyche</i>		<1										<1
Trichoptera	<i>Nemotaulius</i>	2	1	1	2	2	1	1	1	<1	1	1	1
Trichoptera	<i>Oecetis</i>	<1	<1	<1							<1		
Trichoptera	<i>Oxyethira</i>	5	5	2	8	4	1	8	6	10	1	2	5
Trichoptera	<i>Polycentropus</i>	<1						<1					
Trichoptera	tiny Leptoceridae	1	<1	<1	1	1		1		<1			<1
Trichoptera	tiny Libellulidae		<1							<1			
Turbellaria	Turbellaria		<1							<1			