A STUDY OF THE ROLE OF INTRAGUILD PREDATION IN THE POPULATION

DYNAMICS OF THREE SPECIES OF *RHYACOPHILA*

by

Charles Stewart Wright IV

Submitted in partial fulfilment of the requirements
for the degree of Master of Science

at

Dalhousie University
Halifax, Nova Scotia
July 2011

DALHOUSIE UNIVERSITY

DEPARTMENT OF BIOLOGY

The undersigned hereby certify that they have read and recommend to the Faculty of

Graduate Studies for acceptance a thesis entitled "A STUDY OF THE ROLE OF

INTRAGUILD PREDATION IN THE POPULATION DYNAMICS OF THREE SPECIES

OF *RHYACOPHILA*" by Charles Stewart Wright IV in partial fulfillment of the requirements

for the degree of Master of Science.

Dated: July 5, 2011

Supervisor: _____

Readers: _____

                     _____

DALHOUSIE UNIVERSITY

DATE: July 5, 2011

AUTHOR: Charles Stewart Wright IV

TITLE: A STUDY OF THE ROLE OF INTRAGUILD PREDATION IN THE
POPULATION DYNAMICS OF THREE SPECIES OF *RHYACOPHILA*

DEPARTMENT OR SCHOOL: Department of Biology

DEGREE: MSc   CONVOCATION: October   YEAR: 2011

_____
Signature of Author

Table Of Contents

List Of Tables

List Of Figures

Abstract

Intraguild (IG) predation, where species within the same guild prey on each other, is common in aquatic communities. I used the abundance and distributional patterns of three species of *Rhyacophila* (Trichoptera), derived from a survey of 25 streams in Nova Scotia, Canada, to test several predictions of IG theory. I first sampled microhabitats and conducted behavioural observations to establish that the species do co-occur and prey on each other. Abundance patterns did not conform to two key model predictions: (1) Neither of the IG prey (*R. minor, R. vibox*) was excluded from the most productive streams, and (2) IG prey densities were not inversely related to productivity in streams with the IG predator (R. fuscula). It remains possible that intraguild predation occurs between these species of *Rhyacophilia*, the measured abundances do not indicate any measurable effects from IGP, the abundance being determined instead by the availability of prey.

List Of Abbreviations Used

BH   Black Hole

BM   Bedrock with Moss

BN   Brown

BP   Bedrock without Moss

CH   Chipman

CI   Cobby Irving

CIup   Cobby Irving upstream

CPOM   Coarse Particulate Organic Matter

CV   Church Vault

FR   Fraser

FPOM   Fine Particulate Organic Matter

FT   Foote

GL   Granville Line

GK   Gaskill

HE   Healy

HEup   Healy upstream

IG   Intraguild

IGP   Intraguild Predation

LB   Long Beach

LP   Leaf Pack

NF   Number Five

PL   Poole

PV	Pineo Vault
RB	Robinson
RC	Ross Creek
SB	Saunder's
SC	Schoolhouse
SE	Cobble from edge of stream
SS	Sheapshearer
SM	Cobble from middle of stream
ST	Starrat
SV	Sullivan's Vault
TB	Turner Brook
WH	Wheaton
WW	Woodworth

Acknowledgements

It is my great honour to thank all the people who made this thesis possible: my supervisor Sandra Walde and the other students in the Walde lab for their camaraderie and help, including Julie Sircom, Anna Calvert and Kincaid Chan. I appreciate the assistance of Rod Stewart in biology stores and Steve Fry for help with equipment.

I would like to thank my parents for all their support over the years and my brother for all of the good natured encouragement.

Lastly, I'd like to thank my car for only breaking down once in all the thousands of kilometers I put on it for my many trips into the field.

Chapter 1 Introduction

The traditional approach to food web ecology has involved the study of interactions among species and populations separated by discrete trophic levels (Daugherty et al. 2007). More recently approaches have changed in recognition of the important role played by omnivory in many food webs (HilleRisLambers et al. 2006). Theoretical work and observational studies have shown that omnivory can have stabilizing effects on food webs whether the food webs are based on competition, predatory interactions or polyphagy (HilleRisLambers et al. 2006, Vandermeer 2006). The potential importance of one type of omnivory is explored in the 1989 paper by Polis, Myers and Holt which laid out the basis for the dynamics of intraguild predation (IGP). Intraguild predation is predation that occurs between two species that occupy the same guild. More specifically IGP is the consumption of prey species by a predator that can consume the resources of that prey (Holt and Polis 1997). For the purposes of this study, a guild will be defined as a set of species that consume the same type of resources in the same way (Polis et al. 1989).

Intraguild predation is found in terrestrial, marine and freshwater food webs, and across taxonomic groups, ranging from microorganisms (Morin 1999) to fish, amphibians and mammals (Polis et al. 1989). Intraguild predation has been estimated to occur in 58% to 78% of the species that are capable of participating in IGP (top carnivores and omnivores as well as intermediate omnivores, herbivores and detritivores) (Arim and Marquet 2004). Trophic position affects the likelihood of participating in intraguild interactions. Herbivore-detritivore species are more likely to be IG prey than predicted by null models, and intermediate trophic level species more likely to be IG predators than predicted by null models. (Arim and Marquet 2004).

1.1 Holt And Polis (1997) Model

Intraguild predation is a predatory interaction that can allow for the coexistence of two competitors on a single resource (Holt and Polis 1997). The Holt and Polis (1997) intraguild model consists of three elements, two predators which feed on a shared resource, and the resource which they share. The dominant predator (called the intraguild predator (IG predator)) also feeds on the other predator (called the intraguild prey (IG prey)). Coexistence between the IG predator and the IG prey occurs when the IG prey is a superior (more efficient) competitor for the shared resource compared with the IG predator (Daugherty et al. 2007) so that negative predation effects are moderated by greater success in feeding on the shared prey. In this case, coexistence would be expected at intermediate levels of the shared resource. At low levels of shared resource productivity the IG prey is able to competitively exclude the IG predator due to its superior competitive. At intermediate productivity levels the IG predator and the IG prey coexist because the IG prey's superior competitive ability is balanced by the fitness gain of the IG predator from consumption of the IG prey. In contrast, the IG predator should eliminate the IG prey at high levels of resource productivity because high population numbers of the IG predator increase predation pressure on the IG prey. This relationship between productivity and coexistence leads to the following expected abundance relationships: (1) A negative relationship between the IG prey and productivity in the presence of the IG predator, (2) A positive relationship between the IG prey and productivity in the absence of the IG predator, (3) A positive relationship between the IG predator and productivity.

The expected changes in the relative abundances of IG prey and IG predators along a productivity gradient predicted by the Holt & Polis (1997) model have been documented in a

number of different systems, primarily those related to biological control of agricultural pests. One of the best examples comes from parasitoids introduced to control California red scale, a pest of citrus crops. Borer et al. (2007) manipulated resource abundance, and found an inverse relationship between the abundances of the two parasitoids, the IG predator, *Aphytis melinus,* and the IG prey, *Encarisa perniciosi,* along with a positive relationship between the shared resource (California red scale) and the IG predator. The same patterns of abundance were observed in a laboratory study using two ciliates, where one, *Blepharisma* (IG predator) preyed on the other, *Tetrahymena* (IG prey) in addition to their common resource (bacteria) (Diehl and Feissel 2001). There is also evidence that IGP may influence natural abundances. An inverse relationship was found for two species that feed on aphids, a parasitoid and a coccinellid predator that also consumes the parasitoid (Raymond et al. 2000).

A number of studies have found empirical patterns inconsistent with predictions of the Holt and Polis (1997) theory; in particular, patterns where the IG predator and IG prey continue to coexist, even into high levels of the shared resource. Most studies showing these patterns point to physical or biological complexities not accounted for in the original formulation of the model as probable explanations. For example, Finke and Denno (2002, 2003) found that habitat complexity affected the intensity of intraguild predation by the wolf spider (*Paradosa littoralis)* on the mirid bug (*Thytthus vagus)* both of whom feed upon Pronkelisia planthoppers, and this change in complexity affected planthopper densities. A meta-analysis of published studies confirmed that the presence of more complex or more highly structured environments usually reduces the rate of intraguild predation, by providing a physical refuge for the IG prey (Janssesn et al. 2007). Reduced rates of intraguild predation limit exclusion by the IG predator, even at high levels of shared resource productivity

(Janssen et al. 2007). Amarasekare (2007) found that temporal refuges played a similar role, promoting coexistence of two parasitoids at high resource levels.

Real world experimentation is not as straightforward as deterministic (as opposed to stochastic) models of IGP which generate consistent results. In a laboratory experiment by Montserrat et al. (2008) involving a pair of predatory mite species (IG predator: *Iphiseius degenerans,* IG prey: *Neoseiulus cucumeris*) the outcome showed that even when the model conditions regarding resource utilization efficiency were satisfied, the predictions regarding coexistence were not always met. In some cases, the IG predator was eliminated at high productivity and in some cases the IG prey was eliminated at low productivity. In most but not all cases IGP was able to predict the outcome of the system but it was not possible in all cases to predict what mix of species would persist in the system. It was thought that this was due to chaotic effects generated by small differences in the initial conditions of the experiments (Monserrat et al. 2008).

1.2 More Complex Models Of Intraguild Predation

Most natural systems consist of more than three simple elements and may include alternative food sources for either the IG predator or IG prey, or predator-plant feeding (Daugherty et al. 2007, Holt and Huxel 2007). These complex food webs have also been shown to influence the range of productivities over which coexistence can be expected. When the IG predator has access to an additional resource not exploitable by the IG prey, then the predicted range of coexistence is greatly truncated because the IG predator can persist, and exclude the IG prey at much lower shared resource productivities. However, providing the IG prey with additional resources greatly expands the range of productivities

over which the IG predator and IG prey can coexist because the additional resource allows the IG prey to sustain its numbers into higher predatory pressure from the IG predator. Additional exclusive resources for the IG prey can also allow for coexistence through IGP without the need for the IG prey to be a more efficient competitor (Holt and Huxel 2007).

Dispersal strategies also affect the interaction between the IG predator and IG prey. In a theoretical study by Amaresekare (2007) it was assumed that both the IG predator and the IG prey would exhibit the same dispersal patterns since they were from the same guild. If the IG prey and the IG predator exhibit density-dependent dispersal, the asymmetry between the IG predator and the IG prey leads to a large fitness decrease for the IG prey as well as the IG predator and can lead to interspecific aggregations. In the case where the IG predator and the IG prey disperse in response to resource productivity a more optimal outcome is achieved for both species. This is because there is no fitness decrease for the IG predator while greater movement to resources will only result in greater mortality for the IG prey. The dispersal strategy of the IG prey leaves the Holt and Polis productivity-abundance relationship for the IG predator unaffected whereas the relationship for the IG prey is dependent on dispersal strategy and dispersal behavior.

Another factor that can affect the outcome of IGP interactions is species behaviour, for example whether IG prey are "vigilant", and can avoid predation by the IG predator. A study of theoretical models which included vigilance showed that when the IG prey was vigilant and the consumption rate of the IG prey by the IG predator was low, the system could stay stable as long as the attack rate of the IG predator on the IG prey was sustained at high levels (Kimbrell et al. 2007).

Finally, some studies may obtain results that are not consistent with the models due to their experimental design. A study by Briggs and Borer (2005) has shown that short term lab experiments testing IGP may not reach the same conclusions when compared with long-term or field observations due to a number of factors that are difficult to measure over the short term. Since the basis of the theory underlying IGP is based on equilibrium models, short term experiments that are not allowed to reach equilibrium may create results not reflecting the realities of a system.

1.3 Intraguild Predation In Stream Communities

The potential for intraguild predation to occur in stream communities appears to be large, as most predators (both invertebrate and vertebrate) are generalist, size-dependent predators that go through major shifts in size and diet during ontogeny. IGP in stream systems has been linked to asymmetries in body size between the IG predator and the IG prey (Woodward and Hildrew 2002), where predators feed on taxa or life stages sufficiently small to be exploited. Size dependent IGP adds complexity to intraguild interactions, as earlier but not later stages of some taxa may act as IG prey, and the later but not earlier stages of some taxa may act as IG predators. A single species can potentially act as an IG prey while young and an IG predator when older. Including size-dependence in IGP models has been found to decrease the likelihood of coexistence between the IG predator and IG prey when compared to unstructured models (Wolfshaar et al. 2006).

There is empirical evidence that intraguild predation influences species composition and abundances in aquatic communities, though there have been few attempts to explicitly test for effects of productivity on the outcomes of intraguild interactions. Size dependent IGP was found to influence the ability of an introduced trout species to invade a river system

(Taniguchi et al. 2002). In this system, although Age-0 introduced rainbow trout (*Oncorhynchus mykiss*) were dominated by Age-0 salmon (*O. Masou*), the larger Age-1 rainbow trout where able to dominate Age-0 salmon through both competition and predation allowing rainbow trout to invade this stream (Taniguchi et al. 2002). Intraguild predation can facilitate a species invasion. In an example including two species of family Crustacea (order Amphipoda), a muscle wasting parasite makes the native species (*Gammarus duebeni*) (acting as IG prey) more susceptible to predation from a non-native invading species that acts as the IG predator (*Gammarus pulex*) which is immune to the effect of the parasite (MacNeil et al. 2004).

Physical and biological factors can influence the intensity of intraguild predation in streams. For example, IGP has been reported within a guild of caddisflies in temporary or ephemeral Colorado wetlands, where there is a significant size difference between species, but not in permanent wetlands where the size difference is not present (Wissinger et al. 1996). Resource availability appears to influence the likelihood of significant intraguild predation. In a study of the predators of mosquito larvae it was found that IGP did not occur until populations of alternative prey numbers were reduced (Griswold and Lounibos 2006). The exclusion of leaf litter from a stream was found to enhance the amount of IGP occurring in stream communities, increasing the contribution of IGP to total predator consumption from 16 – 21% with natural levels of leaf input, to 16 – 27% where leaf litter was excluded (Hall et al. 2000).

A mesocosm experiment by Gustafson (1993) studied IGP in a system of salamanders inhabiting stream pools. This showed that in a system of salamander species which exploited stream invertebrates and microinvertebrates, the IG predator species decreased both the

survival and growth rate of a species that acted as a size dependent IG prey or IG predator (*Pseudotriton rubber*). The decrease of survival due to predation in the IG prey phase and the decrease in growth rate were due to asymmetric competition in the IG predator phase. Additionally, the presence of IG prey did not increase the growth rate of the IG predators. This is thought to be due to a balancing act between the negative effects of competition with the IG prey and the benefits of the additional energy source provided by the IG prey. IGP can be a highly important factor in structuring stream communities with just as many factors affecting it as the IGP found in terrestrial systems.

There are two major sources of energy supporting food webs in a stream (Giller and Malmqvist 1999). These include autochthonous input and allochthonous input. Autochthonous input is derived from within stream primary productivity (algae and other plants inhabiting the stream). Allochthonous inputs are primarily derived from primary productivity occurring adjacent to the stream (trees and other plants in the catchment area), this allochthonous input is washed and/or blown into the stream where it is consumed by detritivores, shredders and processed by various microorganisms (Giller and Malmqvist 1999). There are numerous studies which examine the importance of these inputs in nutrient supplies for stream communities. The river continuum concept states that as streams move from low order to high order they become wider. As streams become wider the main input shifts from allochthonous input where streams are narrow and shaded to autochthonous input as they widen and are no longer light limited. (Rosi-Marshall and Wallace 2002). A study from the Coweeta Hydrologic Laboratory showed that when leaf litter was excluded from a stream that there are other sources of energy in a stream, including the processing of wood detritus and showed the importance of autochthonous input even in low order streams

(Webster et al. 1999). It was determined in this study that autochthonous primary productivity would be used rather then a combination of autochthonous and allochthonous measurements primarily due to logistical concerns. Allochthonous input to the community in any area of the stream is highly dependent on upstream effects as this input is more likely to be transported downstream then be broken down and utilized where it is introduced into the stream (Webster et al. 1999). Thus it was felt that primary productivity would provide a better indication of the productivity of the stream at the sites where sampling was taking place. This may provides an incomplete picture of the nutrient flow into the stream and may cause a mischaracterization of the production of some guilds.

1.4 Biology Of Rhyacophila

Rhyacophila are a diverse and widespread group of free-living (caseless) caddisflies. The genus contains over 100 species, distributed widely through the northern hemisphere (Wiggins 2004). Life cycles of *Rhyacophila* species are usually univoltine (e.g. *R. minor* (Singh et al. 1984a)) or semivoltine (e.g. *R. vao*, (Dixon and Wrona 1992)), but voltinism can be flexible, responding to differences in water temperature (Lavandier and Cereghino 1995). *Rhyacophila* are commonly located in the rapids of cool running waters. They are often found associated with large cobble (Malmqvist and Sjostrom 1984, Martin 1985, Muotka 1993, Singh et al. 1984a). *Rhyacophila* may aggregate in response to their prey, which include Chironomidae and Simuliidae (Muotka 1993, Tokeshi and Pinder 1985, Malmqvist and Sjostrom 1984). *Rhyacophila* are found in streams of circumneutral (Muotka, 1993) or acidic pH (Kobuszewski & Perry, 1994). *Rhyacophila* are located in streams with temperatures ranging from near freezing up to 20°C (Fjellheim 1980, Singh et al. 1984a, Cereghino 2002).

Most *Rhyacophila spp.* are predaceous, at least in later instars (Singh et al. 1984a, Cereghino 2002, Lavandier and Cereghino 1995, Elliott 2005). Like most aquatic invertebrate predators they tend to have generalist food habits, consuming prey that can be caught and subdued, including early instars and smaller predatory species, as well as detritivorous and herbivorous invertebrates. Species of *Rhyacophila* consume only portions of their prey, usually discarding the "hard" sclerotized portions of the prey (Martin and Mackay 1982). As the sclerotized fragments are key to identifying prey in gut content analysis, the use of gut contents to determine prey consumption is likely to miss important components of the predator diet (Martin and Mackay 1982). Some *Rhyacophila* show shifts in resource use as they progress from smaller to larger size instars. Many species begin primarily as herbivorous in early instars and become carnivorous in later instars (*R. minor* Singh et al. 1984a), *R. intermedia* (Lavandier and Cereghino 1995), *R. occidentalis R. meridionalis*, *R. mocsaryl* and *R. tristis* (Cereghino 2002) and *R. dorsalis* (Elliott 2005). Some species appear to be mostly carnivorous throughout their life cycles (e.g. *R. vofixa*: Irons 1988, *R. intermedia* and *R. evoluta*: Lavandier and Cereghino 1995). A number of studies have found that blackflies (Simuliidae) are a principal component of the diet of several *Rhyacophila*, including *R. dorsalis* (Wotton et al. 1993, Elliott 2005), *R. nubila* (Otto 1993, Muotka 1993), *R. inculta* (Dudgeon and Richardson 1988) and *R. obliterata* (Muotka 1993, Muotka et al. 2006). Chironomids have been found to make up a large portion of the diet of *R. intermedia* (Lavandier and Cereghino 1995), *R. evoluta (*Lavandier and Cereghino 1995), *R. occidentalis*, *R. meridionalis*, R. *mocsaryl*, and *R. tristis* (Cereghino 2002), *R. nubila* and *R. obliterata* (Muotka 1993), *R. arnaudi* (Thut 1969)*, R. vagrita, R. vepulsa, R. vaccua,* and *R. vaefes* (Thut 1969) and *R. dorsalis* (Elliott 2005). Baetids (Ephemeroptera)

have also been found to make up a smaller portion of a number of species including *R. intermedia* and *R. evoluta* (Lavandier and Cereghino 1995), *R. nubila* (Otto 1993), *R. occidentalis*, *R. meridionalis, R. mocsaryl* and *R. tristis* (Cereghino 2002), *R. nubila* and *R. obliterata* (Muotka 1993). At least one study has found that Trichoptera (caddisflies) and Plecoptera (stoneflies) made up a large portion of the diet of *R. acutiloba, R. fuscula, R minor* and *R. nigrita* (Manuel and Folsom 1982).

Diel activity patterns of *Rhyacophila* also vary with instar which could also influence whether IGP occurs. A common pattern is for larvae to switch from aperiodic activity patterns in early instars (larval activity is unrelated to time of day) to a periodic activity pattern in late instar larvae where activity decreases during the day and peaks at night (*R. dorsalis* (Elliott 2005), *R. nubila* (Fjellheim 1980)). *R. nubila* was found to change its day/night activity pattern dependent on the presence or absence of fish. In the absence of fish, activity of *R. nubila* was aperiodic, but individuals became nocturnal in the presence of fish or fish chemicals (Huhta et al. 1999).

There is evidence of intraguild predation among sympatric species of *Rhyacophila*. Remains of *Rhyacophila sp*. have been found in *Rhyacophila obliterata* (Muotka 1993) and *Rhyacophila evoluta* (Lavandier and Cereghino 1995). In addition, there is evidence of habitat shifts by smaller species in the presence of larger *Rhyacophila* species (Martin 1985), therefore *Rhyacophila* should prove to be a useful group in which to study IGP.

Three species of *Rhyacophila* are common in the study streams, *R. fuscula, R. minor* and *R. vibox* (Sircom and Walde 2009). *R. fuscula* is the most widespread species of *Rhyacophila* in eastern North America. It is found from Newfoundland south to Georgia (Flint 1962) and is the largest of the three species in the study streams at maturity. It has a

univoltine life cycle with an extended flight period (four months) and thus a range of instars is present for most of the year. *R. fuscula* larvae are carnivorous, feeding on a range of prey (Martin and Mackay 1983) and tend to partially consume their prey (Manuel and Folsom 1982, Martin and Mackay 1982, Martin 1985).

R. vibox has been reported from central Canada/north-central USA to eastern Canada/north-eastern USA (Flint 1962). It also has a predominantly univoltine life cycle, but a more restricted flight period of approximately one month, beginning in May or June (Karl and Hilsenhoff 1979, Singh et al. 1984b, Sircom and Walde 2009). *R. vibox* tends to be found in small cold streams (Flint 1962, Karl and Hilsenhoff 1979) and in the study area reaches its highest densities in streams without fish (Sircom and Walde 2009). Early instars prefer slightly slower currents (< 45 cm/s) but later instars can be found in the full range of current velocities (Karl and Hilsenhoff 1979). Later instars of *R. vibox* are carnivorous (Shapas and Hilsenhoff 1976).

R. minor is found from Newfoundland south to the Appalachian Mountains (Flint 1962). It is the smallest of the three species at maturity, and is reported to have a univoltine life cycle in Ontario and the Appalachians, with spring emergence (Manuel and Folsom 1982, Singh et al. 1984b, Kobuszewski and Perry 1994). Early instars are herbivorous and found mostly on gravel substrate while later instars are predominantly carnivorous and prefer larger substrate (Singh et al. 1984a).

An important aspect in studying the role of an IGP model in structuring a population in a stream is establishing the secondary productivity reflected in the shared resource of the IG predator and the IG prey. Measuring abundances of prey is one route for this to be established, however it is difficult to directly determine the shared prey of these species of

Rhyacophila. Gut content analysis is difficult in these species is difficult and subject to uncertainty (see Martin and Mackay 1982 for study of gut content analysis in *Rhyacophila*) and the opportunistic nature of their predation leads to the assumption there diet may be highly variable through the year (with ontology and changes in prey composition). It was thus decided that a measure of primary productivity would be a better choice as a surrogate for the shared resource rather then attempting to measure the abundance of their prey.

1.5 Study Area

The study streams were located on the North Mountain of Nova Scotia's Annapolis Valley. The North Mountain is a ridge of basalt that stretches for ~200 km and is 220-260 m high. There are roughly 100 independent streams that drain the North Mountain and flow into the Bay of Fundy. Stream pH was near-neutral in stream measures to date (6.8 to 7.4). High flows come in the spring from the melting of snow, and heavy rainfall can produce intermittent spates in the early summer and autumn. Periods of low flow can occur in August and September during which some streams are reduced to pools of standing water. The forests surrounding the streams are dominated by red spruce, yellow birch and white birch as well as maples (Sircom and Walde 2011). Anthropogenic influences include farming (mostly hayfields and pastures), small-scale woodcutting and a few larger areas with clear-cutting (personal observation). Many of the streams were characterized by coarse substrate and this precluded the wide use of area based sampling devices (e.g. Surber or Hess sampler) (Sircom and Walde 2011). Streams were found in one of three different glacial till types; scour, stony and silty. The scour till type had a relatively thin till layer in which large amounts of material had been scoured. The stony type included streams with till that originated from the south

and included relatively coarse grains. The silty type included streams which had a finer grain that originated from the north and east (known as Lawrencetown till). Of the 25 study streams, 9 were located in scour zones (GK, LB, FR, CIUP, CI, BH, PV, WW and RC), 7 in silty (PL, GL, SC, ST, NF, HE and SS and 9 in stony till(RB, BN, TB, SB, CV, FT, CH, SV and WH). (Stea et al. 1992)

1.6 Objectives

Rhyacophila minor, *R. fuscula* and *R. vibox* co-exist in some of the study streams (Sircom and Walde 2009), but it is not known if individuals co-occur at spatial scales that would allow for behavioural interactions in the field. It is also not known if any of the study species will attack/consume conspecifics or individuals belonging to another species. Lastly, it is not known if the *Rhyacophila* found in these streams conform to the productivity – abundance relationship that would be expected under intraguild predation.

The main objective of this study was to determine whether or not the abundance patterns of the species of *Rhyacophila* being studied are consistent with the Holt and Polis (1997) model of intraguild predation:

This was accomplished by:

(a) Conducting a survey of microhabitats at a small spatial scale within two of the study streams to determine if individuals belonging to different species of *Rhyacophila* occur in close proximity.

(b) Conducting experiments with live *Rhyacophila* to determine if cannibalism or intraguild

predation occurs in a laboratory setting and if so, which species will act as IG predators and

which will act as IG prey

(c) Using a survey of 25 streams to determine whether the abundance patterns found over the

range of streams sampled are consistent with the predictions of a particular model of

intraguild predation (Holt and Polis 1997).

Chapter 2 Methods

This study is made up of three sections to test whether intraguild predation is structuring the population abundances of the three species of *Rhyacophila* (*R. minor*, *R. vibox* and *R. fuscula*) are structured by some form of intraguild predation. Section one consists of microhabitat sampling to confirm that it is likely and/or plausible that these species are interacting in their natural environment. Section two consists of feeding experiments to determine the roles within the Holt and Polis (1997) model of IGP that these species will take (IG predator or IG prey) in their interactions with each other. Section three consists of the benthic samples through the full set of 25 streams and was used to test the predicted relationships between the elements of an IGP model and productivity.

Before establishing whether or not the interactions between two species meet the predictions of an intraguild predation model, it was first necessary to establish that predation occurs and that there is a dominance hierarchy. Short of observing the species in their natural habitat, a common method of establishing this is to examine the digestive tract contents of individuals from the species. Gut content analysis, a method used to determine diet in most studies of predation, would not provide a good measure of the diets of species of *Rhyacophila*. They feed on the soft, high energy portions of the body of their prey, often opening and excavating the soft contents of the abdomen (Martin and Mackay 1982, personal observation). They discard or ignore the hard sclerotized portions of their prey which are normally used for species or genus identification (e.g. head capsule, legs or anal hooks). It was necessary instead to use a combination of two indirect methods consisting of microhabitat surveys (which provides indications of co-occurrence at small spatial scales) and observed interactions between the species in artificial streams (which provides an

indication as to whether predation between these species occurs or is at all possible). These indirect methods provide only evidence of the possibility that IGP is occurring and do not provide a measure of the extent to which it actually occurs in the field.

2.1 Microhabitat Sampling

Over two days (November 2nd and 3rd 2008) microhabitat samples were taken from two streams that were selected to represent streams that have different abundances of *R. minor*, *R. vibox* and *R. fuscula*. The streams selected were Ross Creek (RC) and Sullivans Vault (SV) (See Figure 2.1). Ross Creek was selected because it is a stream dominated by *R. minor* whereas Sullivans Vault has more equal abundance of the three species. It was hoped that with these two different abundance patterns any microhabitat shifting by the species of *Rhyacophila* would be evident. Five different microhabitat types were sampled in each stream: bedrock with moss (BM), bedrock without moss (BP), cobble in the middle of the stream (SM), cobble at the edge of the stream (SE) and leaf packs (LP). Each sample was taken using a Surber sampler (30 cm X 30 cm). Six replicates of each microhabitat type were collected at Sullivans Vault and seven replicates were collected at Ross Creek using a stratified sampling design, where each microhabitat type was sampled in the vicinity of the five predetermined benthic sampling site (Section 2.3). Additional replicates were obtained from upstream or downstream of the sampling section. For each sample, local current velocity and water depth were measured at the time of the sampling. Depths were measured so as to reflect the deepest portion of the Surber sample area, current velocity was measured within, or as close as possible to the middle of the Surber sample site either before or after the Surber sampler was deployed (some sample sites were too shallow to allow measuring of

current velocity from within Surber sample area and so current was measured either slightly upstream or downstream as appropriate) For the cobble samples the size of the cobble was estimated by recording the numbers of stones between 5 cm and 10 cm in diameter and the number of stones larger than 10 cm in diameter in each of the cobble sample quadrats.

The inherent difference between microhabitat types required different methodology in sampling within the stream. Bedrocks samples were taken from either bare bedrock or from large rocks with surface areas that exceeded that of the Surber sampler. Organisms were removed from the bedrock samples using a scrub brush. Cobble sites were selected so as to be removed from other stream features such as waterfalls or fallen logs so as to provide as close as possible to a "classic" riffle. The cobble locations were disturbed with a trowel. The methodology in sampling leaf packs was different then the other samples. Leaf packs were sampled by placing the sampler over a dense area of leaf pack and the area of leaf pack within the sample quadrat was manually directed into the net. Samples were preserved in 70% ethanol in the field, and organisms removed at 6.4X power in the lab. Head widths of all *Rhyacophila* larvae were determined at 40X power. The collected detritus was sieved into 3 size fractions (2mm+ (Detritus), 1mm-2mm (coarse particulate organic matter (CPOM)) and 1mm-500μm (fine particulate organic matter (FPOM)), dried at room temperature and then at 50°C (48 h) in a drying oven and weighed.

Analysis

To determine if the different species of *Rhyacophila* co-occurred more or less frequently than expected by chance, a chi squared test was applied to their co-occurrence in different microhabitat samples. The chi squared test used a null model where species were randomly distributed, expected numbers of co-occurrences were calculated from the product of

18

observed frequencies of presence/absence for each species. Lastly general linear modelling was used to relate the abundances of the species to measured stream characteristics and the abundances of various prey types.

2.2 Feeding / Behaviour Trials

Behavioural trials were conducted three times over the course of the study, early April, late November and early December of 2008. All trials were conducted in artificial stream tanks located in a refrigerated room (~ 5°C). Artificial streams were 19 cm in diameter with an internal hub 7.5 cm in diameter. They were filled with dechlorinated tap water and had an approximate flow rate of 10 cm/s. Aquarium gravel was added as a substrate. The artificial streams were placed on a day-night cycle corresponding to natural conditions at the time. Daytime light exposure was approximately 200 lux.

Prior to each trial, *Rhyacophila* larvae were collected from streams (Ross Creek (RC), Cobby Irving (CI), Cobby Irving upstream (CIup), Number Five (NF) and/or Healy upstream (HEup)), transported back to the laboratory on ice, and used within 24 hours. Desired larvae were identified with the use of a dissecting microscope. Experimental larvae were wet-weighed prior to the beginning of each run and two larvae were placed in each tank and held there up to seven days. Except for the December run, all experiments were conducted in the absence of shared prey. Individuals were observed at intervals over the course of the trials (detailed later). Specific observation times varied with time of year, but observations were carried out pre-dawn and post-dawn, pre-dusk and post-dusk as well as mid-day and during the night. For the pre-dawn, post-dusk and during the night periods, observations were carried out with the aid of a red light. An effort was made to standardize observation effort,

19

but generally observation continued until both larvae were located. At each observation, the individual was classified as:

Hiding: on the side of or under a rock, relatively still (most often characterized by clinging to or curling around a rock)

Passive: On the top or side of a rock or in the open, not moving but "looking" from side to side

Active: Moving, either under a rock, on top of a rock or in the open or actively drifting

Eating: Actively attacking or consuming

At each observation time evidence of predation was checked for by looking for dead or missing individuals. In the April trial if one of the individuals had disappeared or if predation had been witnessed, the remaining individual was removed and preserved in 95% alcohol to allow for later analysis. In the fall trials (November and December), the surviving larvae were left until the end of the experiment. The tank was also scrutinized for any remaining part or parts of the presumed deceased individual.

The differences between experimental conditions and those found in the natural habitat were likely to result in an overestimation rather than underestimation of natural rates of IGP. The most significant of these differences were the lack of prey in the first two sets of behavioural experiments, and less complex substrate in all trials that probably increased encounter rates. Stream flow velocity in the experimental aquariums (~ 10 cm/s) corresponded to the lower end of the range of velocities measured in July and October (maximum at over 100 cm/s, minimum at 6 cm/s and mean at 34 cm/s) and the light intensity in the lab was ~ 200 lux which was within the range of natural light levels under deciduous

canopy (minimum 2 lux, mean 4000 lux, mode 2000 lux)) but much lower than direct

sunlight (over 98000 lux maximum).

Feeding Trial 1:

Experimental animals were collected from Ross Creek and 2 sections of Cobby Irving

Brook, and were placed in the laboratory streams on April 8 on a 13 hour light and 11 hour

dark cycle with sunup at 0700 and sundown at 2000 hours. Tanks were observed at 0600,

0800, 1200, 1900, 2100 and 2400 h for a period of up to seven days, with an additional

observation at 0300 on the second and third day. Experimental treatments all consisted of 2

larvae per stream tank: *R. fuscula-R. minor* (4 replicates), *R. fuscula- R. vibox* (4 replicates),

R. vibox- R. minor (12 replicates), *R. minor-R. minor* (2 replicates) and *R. vibox-R. vibox* (2

replicates). The largest *R. vibox* were paired with the smallest *R. minor* and vice versa.

Number of replicates was determined by number of available larvae of each species.

Behavioral data were collected for this run, however it was not differentiated by species in

collection.

Feeding Trial 2:

Larvae collected from Ross Creek and Cobby Irving were placed in the laboratory

streams on November 18 and 19 under a 9 h / 15 h light / dark cycle (0800 sunup and 1700

sundown). Observations were conducted at 0700, 0900, 1200, 1600, 1800 and 1900 h for a

period of up to five days. Experimental treatments were *R.minor-R.vibox* (6 replicates),

R.minor-R.fuscula (3 replicates), *R.minor-R.minor* (4 replicates), *R. vibox-R. fuscula* (1

replicate), *R. vibox-R. vibox* (2 replicates). Observations of the remaining tanks were stopped

when it was noticed that errors had been made in identification of some of the larvae

(*Polycentropus* was mistaken for *R. minor* in several replicates).

Feeding Trial 3:

Larvae were collected from Number Five, Ross Creek, Cobby Irving, and Healy Brooks and the experiments begun on November 29. Experimental treatments were *R.minor-R.vibox* without prey (5 replicates) and *R.minor-R.vibox* with prey (4 replicates). Prey were ten small stonefly larvae (Nemouridae). Light regime and observation times were as for the November 2008 trial however the experiment length was up to 7 days.

Analysis

The primary goal of the feeding/behaviour trials were to establish the pattern of IGP that might be expected from these species of *Rhyacophila*. Mortality rates were determined in each of the three possible pairings of *Rhyacophila* and the species in the pairing which inflicted the higher mortality was then expected to act as an IG predator and the species in the pairing which suffered the higher mortality was expected to act as IG prey. Chi squared analysis was used to determine whether the mortality rates differed among species or runs.

to measure any behavioural response to the presence of other species (especially predatory and/or anti-predator responses) an activity index was calculated for each individual *Rhyacophila* for each of 6 time periods: pre-dawn (within 2 h before lights on), post-dawn (within 2 hours after lights on), midday (between 1200 and 0200), pre-dusk (within 2 h before lights-off), post-dusk (within 2 hours after lights off) and night (between post-dusk or pre-dawn). Individuals were considered active if they were moving, or if they were stationary and moving their heads. The activity of an individual for a given time period was the number of active observations divided by the total number of observations during that time period. All proportions were transformed using an arcsine square root transformed prior to analysis. The effect of other species, presence of prey and time of day on activity index was then

analyzed with Generalized Linear Modeling using repeated measures (ANOVA) analysis. The repeated measure was the time of day the observation was taken.

2.3 Benthic Samples

Abundances of three species of *Rhyacophila* (*R. minor, R. vibox and R. fuscula*) were determined from benthic samples (5 sample sites per stream, numbered 1 to 5 and marked with stakes) taken in April of 2008. Each sample consisted of a kick sample across the width of the stream and back, using a D-net (mesh size 250 µm). These samples produced a semi-quantitative estimate of abundances, based on the area of stream bottom disturbed (using width measurements and an approximate kick disturbance length of 60cm). This was the most practical sampling method for streams of this type because of the large size of the substrate. More quantitative samplers such as the Hess or Surber would have restricted sampling to only a few microhabitat types. All sampling locations were from riffles within a 300m section of the stream (figure 2.1) (appendix 1).

All invertebrates retained on a 500 micron mesh sieve were removed from the debris using a dissecting microscope. The *Rhyacophila* were sorted to species using a dissecting microscope with the help of Merritt et al. (2008) and the head widths were measured at their widest point at 40X power.

Along with the benthic samples stream width and depth were measured. Additional measures such as the presence or absence of fish came from previous studies (Sircom and Walde 2011).

Analysis

      The abundances collected from the benthic sampling were tested to determine whether or not they met the outcomes predicted from a model of IGP structuring the population patterns found in the 25 streams. The measure of primary productivity (see section 2.4 for measurement of primary productivity) which best correlated with the measured abundances of the three species of *Rhyacophila* was used to test for these predictions.

      For each of the IGP pairings determined from the feeding experiment, three tests were done, derived from three predictions based on the expected relationship between species abundances and resource productivity from the model of IGP. Each prediction required a different test.

      For the first prediction, "Is coexistence less likely at high and at low productivity levels?" the average productivity was calculated for where the IG prey was found without the IG predator, where the IG prey and IG predator were found together (coexisting) and where the IG predator was found without the IG prey (although many of the pairings lacked data for at least one of these circumstances). A one-sided t-test was then applied on these sets of streams to determine if the difference in the productivity between these sets of streams was significant.

      For the second prediction, "Do densities of the IG predator increase with productivity? ", regression analysis was used to determine whether the relationship between the abundance of the species of *Rhyacophila* expected to act solely as an IG predator and the productivity of the streams they are found in are both significant and positive.

      For the third prediction, "do densities of the IG prey decline with productivity or IG predator density if the IG predator is present?", was also tested with regression analysis to

determine whether the densities of the IG prey showed a negative relationship with either the measured productivity or the density of its IG predator.

Size patterns may have an effect on patterns of predation by these species of *Rhyacophila* because of the opportunistic feeding displayed by species of *Rhyacophila* (Martin and Mackay 1982). Head widths measured from both the benthic sampling and microhabitat sampling were rendered into a histogram.

Looking for explanations other then IGP, general linear modeling was used to determine the factors statistically related to the observed abundances of the three species of *Rhyacophila*.

2.4 Measurement Of Primary Productivity

Primary productivity (algal growth) was measured at two points in time, June/July 2008 (June 23 – July 14) and September/October 2008 (September 19 - October 8). Unglazed ceramic tiles (4.6 cm by 4.6 cm) were placed in the streams as a substrate and algae was allowed to colonize for 2 weeks (Cattaneo and Amireault 1992). To reduce grazing, each tile was secured with the use of wire in the bottom of a 10 cm by 10 cm by 9 cm plastic container with 1.5 mm mesh glued over openings on the upstream and downstream sides to allow for the circulation of water. These containers were designed to limit grazers from gaining access to the growing periphyton on the artificial substrate tiles. However, water levels were sometimes above the level of the plastic containers and this may have allowed access by some grazers.

Five sets of 3 tiles were placed in each stream (at locations corresponding to the benthic samples). Measurements of light, depth and temperature were taken at each site. At

the time of tile removal, water samples were taken at each site for measurement of pH and

conductivity.

Tiles were immediately placed in Ziploc bags containing 50 ml of 90% acetone.

Chlorophyll samples were extracted in a refrigerator in darkness for a period of at least 3

days (Wasmund et al. 2006). The concentration of chlorophyll in the acetone was then

measured with a spectrophotometer using the trichromatic method (Palumbo et al. 1987,

Strickland and Parsons 1972). Chlorophyll concentrations were calculated using the

Strickland and Parsons trichromatic formula (Chlorophyll a =(11.6*(abs665)-1.31*(abs645)-

0.14(abs630))*50) and values rendered as milligrams (mg.) of chlorophyll per centimeter

squared of tile.

During the September/October 2008 sampling (October 3 - October 8, samples of

algae covered rocks were taken in addition to substrate tile samples. Two sets of three or four

rocks were removed from each stream. Each set came from an arbitrary location by the bank

edge of a riffle from two points between the uppermost and lowermost benthic sample

locations usually between site 1 and 2 and then usually between sites 4 and 5. Sites were

chosen to be under an area which minimized the amount of shading on the rocks. Rock

samples were processed in the same manner as tile samples. Surface area of rocks was

measured by wrapping rocks with tin foil and using the mass of tin foil to determine surface

area. The surface area of rocks was divided in half since only the top half of the rock would

be exposed to light.

Analysis

A correlation analysis between the three measures of productivity and various

physical and biological factors was conducted to determine the factors which were most

closely linked to differences in productivity. Then general linear modeling was used to create

a model of the most correlated factors in order to determine the most important factors that

relate to the measured productivity.
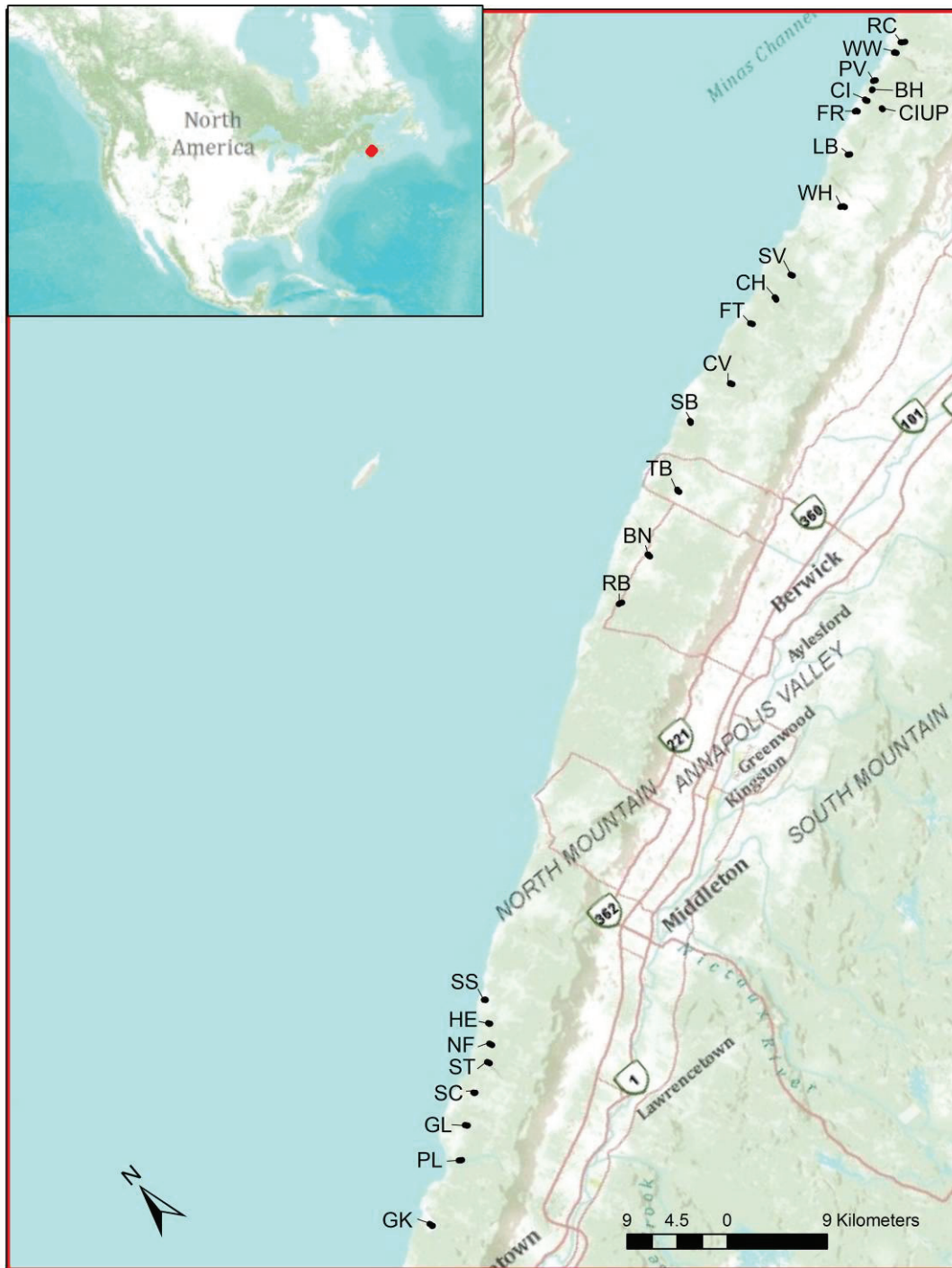
Figure 2.1: Map of the Stream sampling sites on the North Mountain of the Annapolis Valley in Nova Scotia, Canada.

Chapter 3 Results

3.1 Microhabitat

The two streams selected for microhabitat sampling, Ross Creek (RC) and Sullivan`s Vault Brook (SV) are approximately 16 km apart. The streams were similar in width at the point of sampling, and had similar water chemistry (pH and conductivity) and substrate (Table 3.1). Average current velocity in the locations sampled was slightly lower in Sullivan's Vault but more variable in Ross Creek.

The three species of *Rhyacophila* co-occurred in both streams at the spatial scale of 30 X 30 cm quadrats. Species tended to occur together about as often as expected if individuals of each species were randomly allocated to sample locations (RC chi squared = 1.52 p= 0.678 , SV chi squared = 4.583 p= 0.205) (Expected numbers of co-occurrences were calculated from the product of observed frequencies of presence/absence for each species)(Table 3.2). *R. fuscula* co-occurred with at least one other *Rhyacophila* species in 37% (RC) and 80% (SV) of the samples it was present. Co-occurrence for *R. vibox* was 67% (RC) and 80% (SV) of the samples it was present. For *R. minor* co-occurrence with at least one other species was 36% (RC) and 60% (SV) of the samples it was present.

Densities of the three species were not significantly correlated with each other in Ross Creek, but in Sullivan's Vault there were significant positive correlations between *R. vibox* and *R. fuscula* (P = 0.009) and between *R. vibox* and *R. minor* (P = 0.025).

The relative abundances of the three species differed between streams (P < 0.001); *R. minor* were much more abundant than either *R. vibox* or *R. fuscula* in Ross Creek, but differences were smaller in Sullivan's Vault (Table 3.1). Differences in microhabitat use by the species did not vary significantly between the streams (P = 0.157) (Table 3.3). However,

the species did differ in microhabitat use (P < 0.001) (Table 3.3). In the measured microhabitats; densities of *R. minor* were highest in cobble substrate found mid-stream, *R. fuscula* were most abundant in leaf packs and on moss-covered bedrock, while *R. vibox* were more evenly distributed among the microhabitat types, and most were collected from moss, leaf packs and cobble substrate mid-stream (Fig. 3.1).

All species tended to be more abundant in locations that were deeper and had more macrodetritus (particles > 2mm) (see Table 3.3, depth parameter). Species varied in their relationship with CPOM (1 – 2 mm) (interaction term, P < 0.001, Table 3.3). *R. minor* abundances increased positively with CPOM, while there was no relationship between CPOM and *R. vibox* or *R. fuscula*. There were no significant interactions between species and velocity, depth or large detritus.

Most *Rhyacophila* species showed a significant relationship with at least one prey type. *R. minor* was significantly related to Ephemeroptera (p <0.001) (Table 3.4). *R. vibox* was not significantly related to Simuliidae (p = 0.058) (Table 3.4). Lastly *R. fuscula* was significantly related with both stoneflies (p >0.001) and Simuliidae (p>0.001) (Table 3.4).

3.2 Feeding And Behaviour Experiments

Mortality Rates

Over all runs, mortality rates were higher for *R. minor* (30%, 13/44) than for *R. vibox* (6%, 2/36) or *R. fuscula* (0%, 0/12) (p =0.055 (chi squared)). Mortality rates over all species tended to be higher in the spring (Run 1) (25%, 11/44) than in fall experiments (Runs 2 and 3) (9%, 4/47) (p=0.079 (chi squared)).

In the April experiment, all *R. minor* held alone or with another *R. minor* survived, but half or more died when held with *R. fuscula* or *R. vibox* (Table 3.5). *R. vibox* died in 25% (1 of 4) of its interactions with *R. fuscula,* and only 7% of its interactions with *R. minor* (2 of 36) and never when with an *R. vibox* conspecific. *R. fuscula* survived in all stream tanks (Table 3.5).

In the fall studies, *R. minor* died in 17% (1 of 6) (November) and 45% (4 of 9) (December) interactions with *R. vibox* (Table 3.5). The presence of prey did not significantly affect survival of *R. minor* in the presence of *R. vibox* (60% vs. 0%) (p = 0.26). One *R. vibox* died in the presence of *R. minor* in the November trial.

Activity

R. minor tended to be less active than *R. vibox* (April and November runs: P = 0.029, December Run: P = 0.067) (table 3.6). Overall activity of *Rhyacophila* did not change in response to the presence of another species (Table 3.6, Figure 3.2). Diel pattern of activity did change, but in different ways for *R. vibox* vs. *R. minor* (Fig. 3.2). *R. vibox* was less active during daylight observations (post-dawn, mid-day, pre-dusk) in the presence of *R. minor* than when with other *R. vibox*. *R. minor* reduced activity in response to other *Rhyacophila*, but mostly during the dark period (post-dusk, night, pre-dawn) (Fig. 3.2).

In the third trial, *R. minor* and *R. vibox* showed significantly different diel patterns of activity (P = 0.001) and different responses to the presence of prey (P = 0.040) (Table 3.6). *R. vibox* was much less active during the pre and post dawn periods in the presence of prey (Fig. 3.3).

Behavioral data were only obtained for *R. fuscula* for the November run (Run 2), and low replication precluded testing for interaction terms. Activity levels of *R. fuscula* tended to

be high, and did not seem to vary significantly with time of day or the other species present except for a notable peak in *R. fuscula* activity in the post-dusk hours (Fig 3.2).

3.3. Tests Of Predictions Of Holt & Polis (1997) Model

3.3.1 Is Coexistence Less Likely At High And At Low Productivity Levels?

R. minor - R. fuscula: Streams with both *R. minor* and *R. fuscula* have higher primary productivity than streams without *R. fuscula*, as expected from the feeding experiments (Fig. 3.4b). However, streams with only *R. fuscula* or only *R. minor* also have lower productivity than streams with both species (Fig. 3.4b). *R. fuscula* was not found in three of the streams containing *R. minor*, and the two species coexisted in 18 streams. The average chlorophyll a level (on rocks, in October) was significantly lower in the streams without *R. fuscula* (0.176 mg/cm2 $\pm$ 0.118) (mean $\pm$ SD) than in streams where *R. fuscula* was also present (0.512 + 0.453) (P = 0.009, one-sided t-test). (*R. vibox* was present in both sets of streams.).

R. minor - R. vibox: Streams containing *R. vibox* but not *R. minor* have a lower productivity than those with *R. vibox* and *R. minor* together. *R. minor* was not found in three of the streams containing *R. vibox*, and the two species coexisted in 21 streams. The average chlorophyll a level (on rocks, in October) was significantly lower in the streams without *R. minor* (0.128 mg/cm2 $\pm$ 0.048) (mean $\pm$ SD) than in streams where *R. minor* was also present (0.464 + 0.435) (P = 0.0012, one-sided t-test). (*R. fuscula* was present in one stream where *R. minor* was absent). The streams containing *R. vibox* in the absence of *R. minor* were lower in periphyton level than streams that contained *R. minor* and *R. vibox* together. This is the opposite of what is predicted by the Holt and Polis (1997) model (Figure 3.4a)

R. vibox - R. fuscula: Streams containing *R. vibox* but not *R. fuscula* have lower productivity than those with *R. vibox* and *R. fuscula* together (Fig. 3.4a). Six streams contained *R. vibox* but not *R. fuscula,* and the two species coexisted in 19 streams. The average chlorophyll a level (on rocks, in October) was significantly lower in the streams without *R. fuscula* (0.162 mg/cm2 $\pm$ 0.078) (mean $\pm$ 1 SD) than in streams where *R. fuscula* was also present (0.489 + 0.451) (P = 0.0014, one-sided t-test). There were no streams without *R. vibox*.

3.3.2 Do Densities Of The IG Predator Increase With Productivity?

Significant and positive relationships existed between productivity (measured as chlorophyll a levels on the rock samples from October) and total density of *R. fuscula* (table 3.7) (p = 0.005) the only species as *Rhyacophila* expected to act solely as an IG predator. Positive relationships were also present if smaller (1st and 2nd) instars (p = 0.023) and larger (3rd through 5th) instars (p = 0.033) were considered separately (table 3.8).

3.3.3 Do Densities Of The IG Prey Decline With Productivity Or Predator Density If The IG Predator Is Present?

In the streams where *R. fuscula* was present, the density of *R. minor* increased with primary productivity as measured on rock samples from October (p=0.018) (table 3.8), and increased with the density of *R. fuscula* (p = 0.0014). In the same streams, the density *of R. vibox* showed no relationship with productivity, and a weak tendency to increase with the abundance of *R. fuscula* (P = 0.091).

Over the range of streams where *R. fuscula* was absent, the relationship between *R. vibox* density and productivity was non-significant (p=0.117) (Figure 3.5). Over this same

range of streams the relationship between productivity and *R. minor* density was also non-significant (p=0.253) (Figure 3.6).

3.4 Observed Rhyacophila Size Patterns

The distribution of head widths from the Rhyacophila collected in the spring benthic sampling (Figure 3.7a and Figure 3.7b) and the fall microhabitat sampling (Figure 3.8a and Figure 3.8b) reveals that species are divided into multiple size classes. *R. minor* sampled in the spring displays a distinct bi-modal distribution which peaks at 0.48 mm (3rd instar) and 0.96 mm (5th instar). This pattern changes into a possible trimodal pattern in the fall sample with maxima at 0.384 mm (3rd instar), 0.72 mm (5th instar) and 0.96 mm (5th instar). *R. vibox* shows a similar bimodal pattern in the spring with peaks at 0.432 mm (3rd instar) and 0.864 mm (5th instar). *R. vibox* also shows this bimodal pattern in the fall with peaks at 0.48 mm (3rd instar) and 0.96 mm (5th instar). The distribution of *R. fuscula* in the spring seems to follow a unimodal distribution with a peak at 0.672 mm (3rd instar) and a distribution in the fall which is potentially made up of four different size groups (Figure 3.8b). Given that these maxima represent markedly different instars it is probable they are different size classes.

3.5 Factors Affecting Productivity

None of the measured variables were correlated with the among stream variation in algal growth on tiles in June (growth measured as concentration of chlorophyll a) (Table 3.8). Average light ratio (p=0.045) (Table 3.8) (measured as the light intensity at the sample site divided by the maximum light intensity) was positively correlated with the among stream variation in algal growth in October. Among stream variation in algal growth on rocks collected in October depended significantly on glacial till type (p= 0.026) and on pH

(p=0.044) (Table 3.8). The scour till had the highest levels of chlorophyll a (0.751 mg/cm^2), followed by the stony till (0.295 mg/cm^2), and silty till the lowest (0.119 mg/cm^2).

3.6 Alternative Explanations For Observed Abundance Patterns

I used general linear modelling to test if the variation among streams in density of the three predators could be explained by differences in prey abundance, water temperature or presence/absence of fish (brook trout). Abundance of *R. minor* was positively correlated with densities of Chironomidae, the abundance of *R. vibox* was also positively related to Chironomidae numbers and negatively related to the presence of fish, and *R. fuscula* densities were positively associated with the number of Ephemeroptera (Table 3.9).

Table 3.1: Average characteristics of the two streams used for microhabitat sampling, Ross Creek and Sullivan's Vault. Values for density, current velocity, water depth, substrate and detritus are means of the 30 (SV) or 35 (RC) samples along with their standard error taken in November 2008. The pH values and conductivity were measured in October 2008, and bank-full width is the mean of 5 measurements taken during benthic sampling, standard error is also given.

	Sullivan's Vault N=30	Ross Creek N=35
Location (UTM coordinates)	20 T 371483 5004454	20 T 386454 5010952
Species densities (#/m^2)		
R. minor	10.4 ± 3.7	52.4 ± 12.4
R. vibox	2.2 ± 1.0	3.5 ± 1.1
R. fuscula	6.7 ± 2.0	4.8 ± 1.7
Current velocity (cm/s)	29 ± 1.63	37 ± 3.9
# cobbles per quadrat		
5 – 10 cm	3.3 ± 0.45	3.4 ± 0.6
> 10 cm	1.8 ± 0.32	2.7 ± 0.4
Bank-full width (m)	4.7 ± 0.32	4.4 ± 0.14
Depth (cm)	12.7 ± 0.66	9.2 ± 0.5
Fine Particulate Organic Matter (FPOM) (g) (500 μm - 1 mm)	0.25 ± 0.030	0.45 ± 0.14
Coarse Particulate Organic Matter (CPOM) (g) (Particles 1mm – 2mm diameter)	0.16 ± 0.02	0.40 ± 0.10
Large Detritus (Detpack) (g) (Matter greater then 2mm)	5.21 ± 1.09	3.95 ± 0.71
Conductivity (μS/cm)	93.4 ± 0.52	73.3 ± 0.58
pH	6.8 ± 0.049	6.8 ± 0.10

Table 3.2: Presence and co-occurrence (observed and expected) over all microhabitat samples of the species of Rhyacophila in microhabitat samples (30 X 30 cm) taken from Ross Creek and Sullivan's Vault Brook in November 2008.

	Ross Creek (35 Total)	Sullivan's Vault (30 Total)
Species	**Presence (% locations)**	
R. fuscula	23	37
R. vibox	26	17
R. minor	80	33
Species	**Co-Occurrence** **% Co-occurrence (% Expected)**	
R. fuscula – R. vibox	9 (5)	7 (6)
R. fuscula – R. minor	20 (18)	13 (12)
R. vibox - R. minor	17 (21)	17 (6)
R. vibox - R. minor - R. fuscula	9 (5)	7 (2)

Table 3.3: Results of general linear models used to analyze (1) effects of microhabitat on the distribution of *R. minor*, *R. vibox* and *R. fuscula* within streams and (2) relationships between environmental factors and species abundances. Species abundances were square-root transformed for analysis.

Model Parameters	Type III SS	df	Mean Square	F-ratio	p-value
Stream	7.215	1	7.215	15.013	**<0.001**
Species	29.657	2	14.828	30.855	**<0.001**
Habitat	8.178	4	2.045	4.254	**0.003**
Species*Habitat	16.478	8	2.060	4.286	**<0.001**
Stream*Species	16.823	2	8.411	17.503	**<0.001**
Stream*Habitat	5.646	4	1.412	2.937	**0.022**
Species*Habitat*Stream	5.809	8	0.726	1.511	0.157
Error	79.296	165	0.481		

Model Parameters	Type III SS	df	Mean Square	F-ratio	p-value
Stream	6.612	1	6.612	11.431	**0.001**
Species	1.185	2	0.592	1.024	0.361
Velocity	0.540	1	0.540	0.933	0.335
Depth	2.782	1	2.782	4.809	**0.030**
CPOM	3.630	1	3.630	6.276	**0.013**
Macrodetritus	2.290	1	2.290	3.959	**0.048**
Species*Velocity	0.090	2	0.045	0.078	0.925
Species*Depth	0.070	2	0.035	0.060	0.942
Species*CPOM	17.246	2	8.623	14.908	**<0.001**
Species*Macrodetritus	0.324	2	0.162	0.280	0.756
Error	101.799	176	0.578		

Table 3.4: Results of general linear models testing for relationships between the abundance (square root transformed) of the three species of *Rhyacophila* collected in the microhabitat survey and the velocity, depth and abundance of three prey species (Plecoptera, Simuliidae and Ephemeroptera)

R. minor abundance: All relationships positive.

Independent Variables	Type III SS	df	Mean Squares	F-ratio	p-value
Stream	**7.838**	**1**	**7.838**	**10.406**	**0.002**
Velocity	2.846	1	2.846	3.778	0.057
Depth	0.347	1	0.347	0.460	0.500
Plecoptera abundance	0.010	1	0.010	0.014	0.907
Simuliidae abundance	0.200	1	0.200	0.266	0.608
Ephemeroptera abundance	**24.258**	**1**	**24.258**	**32.206**	**0.000**
Error	41.427	55	0.753		

R. vibox abundance: All relationships positive.

Independent Variables	Type III SS	df	Mean Squares	F-ratio	p-value
Stream	0.014	1	0.014	0.070	0.793
Velocity	0.318	1	0.318	1.563	0.216
Depth	0.051	1	0.051	0.249	0.620
Plecoptera abundance	0.524	1	0.524	2.575	0.114
Simuliidae abundance	0.761	1	0.761	3.740	0.058
Ephemeroptera abundance	0.018	1	0.018	0.087	0.769
Error	11.191	55	0.203		

R. fuscula abundance: All relationships positive.

Independent Variables	Type III SS	df	Mean Squares	F-ratio	p-value
Stream	0.812	1	0.812	3.344	0.073
Velocity	0.148	1	0.148	0.607	0.439
Depth	0.459	1	0.459	1.888	0.175
Plecoptera abundance	**4.337**	**1**	**4.337**	**17.853**	**0.000**
Simuliidae abundance	**7.467**	**1**	**7.467**	**30.740**	**0.000**
Ephemeroptera abundance	0.479	1	0.479	1.974	0.166
Error	13.360	55	0.243		

Table 3.5: Mortality of *R. minor*, *R. vibox* and *R. fuscula* in experiments conducted in laboratory streams in April, November and December 2008. Average mass (wet weight in mg) of the larvae is in brackets. Low mortalities in Run 2 are most likely due to the truncated experiment time.

Species Combination	% Mortality [average mass (mg)]		
Run1 (April)	*R. minor*	*R. vibox*	*R. fuscula*
R. minor – R. minor (N=2)	0% [5.3]	-	-
R. minor – R. vibox (N=12)	67% [6.0]	0% [13]	-
R. minor – R. fuscula (N=4)	50% [20]	-	0% [11]
R. vibox – R. fuscula (N=4)	-	25% [13]	0% [30]
R. vibox – R. vibox (N=2)	-	0% [9]	-
Run 2 (November)			
R. minor – R. minor (N=4)	0% [3]	-	-
R. vibox – R. vibox (N=2)		0% [5]	
R. minor – R. vibox (N=6)	0% [3]	17% [4]	-
R. minor- R. fuscula (N=3)	0% [4]	-	0% [5]
R. vibox – R. fuscula (N=1)	-	0% [1]	0% [2]
Run 3 (December)			
R. minor – R. vibox (N=5)	60% [4]	0% [7]	-
R. minor – R. vibox with prey (N=4)	0% [4]	25% [3]	-

Table 3.6: Results of repeated measures analysis to test for effects of species combinations and time of day on the activity of *R. minor* and *R. vibox*. The dependent variable in each case was the activity index (arcsine square root transformed)) and the repeated measure was time of day the observation was taken. (A) Differences in activity level among species (*R. vibox, R. minor, R. fuscula*), type of co-occupant (conspecific vs. other species) and runs (April vs. November). (B) Difference in activity level in December among species (*R. vibox, R. minor*) and in the presence/absence of prey.

A)

Between Subjects					
Source	SS	df	Mean Squares	F-ratio	p-value
Species	**1.242**	**1**	**1.242**	**5.362**	**0.029**
Co-occupant	0.867	2	0.433	1.871	0.174
Run	0.214	1	0.214	0.924	0.345
Co-occupant*Species	0.228	2	0.114	0.493	0.616
Error	6.023	26	0.232		

Within Subjects					
Source	SS	df	Mean Squares	F-ratio	p-value
Time	0.392	5	0.078	1.215	0.306
Time*Species	0.552	5	0.110	1.713	0.136
Time*Co-occupant	0.675	10	0.067	1.046	0.409
Time*Run	0.382	5	0.076	1.184	0.321
Time*Co-occupant*Species	**2.338**	**10**	**0.234**	**3.624**	**<0.001**
Error	8.386	130	0.065		

B)

Between Subjects					
Source	SS	df	Mean Squares	F-ratio	p-value
Species	0.927	1	0.927	3.939	0.067
Prey	0.359	1	0.359	1.524	0.237
Prey*Species	0.385	1	0.385	1.635	0.222
Error	3.294	14	0.235		

Within Subjects							
Source	SS	df	Mean Squares	F-ratio	p-value	G-G	H-F
Time	**1.232**	**5**	**0.246**	**4.825**	**0.001**	**0.004**	**0.001**
Time*Species	**1.190**	**5**	**0.238**	**4.658**	**0.001**	**0.005**	**0.001**
Time*Prey	**0.623**	**5**	**0.125**	**2.438**	**0.043**	**0.069**	**0.043**
Time*Prey*Species	**0.632**	**5**	**0.126**	**2.474**	**0.040**	**0.066**	**0.040**
Error	3.575	70	0.051				

Table 3.7: Results of regression of predator density on productivity level. The dependent variables are the average densities of individuals. Total denotes all individuals collected while small denotes 1st and 2nd instar only while large denotes 3rd, 4th and 5th instar.

A) All streams included

Dependent Variables		R. fuscula			R. minor	R. vibox
		total	1st and 2nd instars	3rd, 4th and 5th instars	Total	Total
June chl a (tiles)	P-value	0.778	0.737	0.819	0.499	0.657
	R^2	0.0039	0.0055	0.0026	0.022	0.0096
	slope	0.047	0.077	0.051	0.038	0.036
Oct chl a (rocks)	P-value	**0.005**	0.023	**0.0033**	**0.002**	0.636
	R^2	0.29	0.21	0.32	0.36	0.0099
	Slope	0.21	0.75	0.91	0.067	0.06
Oct chl a (tiles)	P-value	**0.021**	**0.017**	**0.028**	**0.004**	0.164
	R^2	0.21	0.22	0.19	0.3	0.083
	slope	0.36	0.5	0.46	0.14	0.11

B) Streams with *R. fuscula* present

Dependent Variables		R. fuscula			R. minor	R. vibox
		total	1st and 2nd instars	3rd, 4th and 5th instars	total	total
June chl a (tiles)	P-value	0.737	0.708	0.791	0.431	0.989
	R^2	0.0073	0.009	0.0045	0.039	1.2E-05
	slope	0.07	0.093	0.075	0.045	0.0012
Oct chl a (rocks)	P-value	0.053	0.145	**0.034**	**0.018**	0.368
	R^2	0.2	0.12	0.24	0.29	0.048
	Slope	0.69	0.62	1.03	0.22	0.15
Oct chl a (tiles)	P-value	**0.033**	**0.042**	**0.042**	**0.017**	0.135
	R^2	0.24	0.22	0.22	0.29	0.13
	slope	0.49	0.55	0.65	0.15	0.16

Table 3.8: Results of general linear models constructed to determine if glacial till type, actual (not bankfull) stream width, or measured abiotic factors were related to the measured chlorophyll a levels. Analyses were conducted separately for chl a on tiles placed in the streams in (A) June and (B) October, and (C) on rocks collected from the streambed in October. Abiotic measures were taken at the time of sampling (June or October).

(A) June Chlorophyll a on tiles N=23 r^2=0.386

Dependent variables	Type III SS	df	Mean Squares	F-ratio	p-value
Soil Till	0.036	2	0.018	0.268	0.768
pH	0.062	1	0.062	0.921	0.353
Conductivity	0.000	1	0.000	0.000	0.993
Light Ratio	0.004	1	0.004	0.062	0.807
Depth	0.077	1	0.077	1.143	0.303
Water Temperature	0.068	1	0.068	1.014	0.331
Stream Width	0.148	1	0.148	2.194	0.161
Error	0.942	14	0.067		

(B) October Chlorophyll a on tiles N=23 r^2=0.489

Dependent variables	Type III SS	df	Mean Squares	F-ratio	p-value
Soil Till	0.037	2	0.018	0.296	0.748
Stream Width	0.182	1	0.182	2.942	0.108
October pH	0.061	1	0.061	0.989	0.337
October Conductivity	0.001	1	0.001	0.018	0.894
October Light Ratio	0.299	1	0.299	4.836	**0.045**
October Depth	0.001	1	0.001	0.015	0.903
October Water Temperature	0.004	1	0.004	0.060	0.810
Error	0.865	14	0.062		

(C) October Chlorophyll a on rocks N=23 r^2=0.585

Dependent variables	Type III SS	df	Mean Squares	F-ratio	p-value
Soil Till	1.079	2	0.539	4.789	**0.026**
Stream Width	0.051	1	0.051	0.450	0.513
October pH	0.555	1	0.555	4.922	**0.044**
October Conductivity	0.043	1	0.043	0.381	0.547
October Light Ratio	0.256	1	0.256	2.272	0.154
October Depth	0.057	1	0.057	0.503	0.490
October Water Temperature	0.051	1	0.051	0.450	0.513
Error	1.577	14	0.113		

Table 3.9: Results of General Linear models constructed to determine if the measured stream variables which are statistically related to the population density of *R. minor, R. vibox* and *R. fuscula*.

N = 25 r^2 = 0.686

Squareroot *R. Minor* density	Type III SS	df	Mean Squares	F-ratio	p-value
Simulid density	0.772	1	0.772	1.826	0.193
Chironomid Density	3.365	1	3.365	7.962	**0.011**
Ephemeroptera Density	0.734	1	0.734	1.736	0.203
Fish presence	0.370	1	0.370	0.875	0.361
October water temperature	0.078	1	0.078	0.184	0.672
Error	8.031	19	0.423		

N=25 r^2 = 0.781

Squareroot *R. vibox* density	Type III SS	df	Mean Squares	F-ratio	p-value
Simulid density	0.000	1	0.000	0.000	0.985
Chironomid density	1.183	1	8.831	8.831	**0.008**
Ephemeroptera density	0.027	1	0.027	0.198	0.661
Fish Presence	3.014	1	3.014	22.502	**0.000**
October water temperature	0.012	1	0.012	0.091	0.766
Error	2.545	19	0.134		

N=25 r^2=0.712

Squareroot *R. fuscula* density	Type III SS	df	Mean Squares	F-ratio	p-value
Simulid density	0.000	1	0.000	0.004	0.948
Chironomid density	0.001	1	0.001	0.022	0.883
Ephemeroptera density	0.444	1	0.444	10.166	**0.005**
Fish presence	0.038	1	0.038	0.864	0.364
October water temperature	0.032	1	0.032	0.733	0.403
Error	0.830	19	0.044		
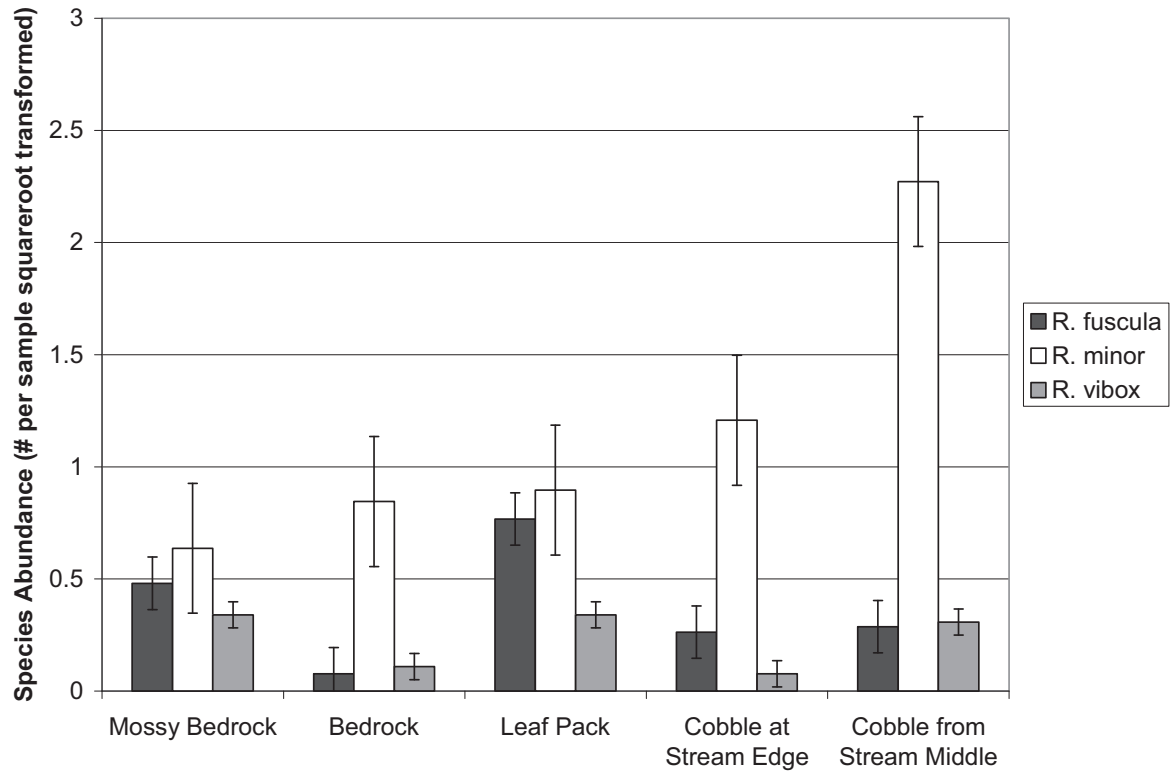
Figure 3.1: Variation among microhabitat types in average abundance (# per sample, square root transformed) of *R. fuscula*, *R. minor* and *R. vibox*. Values are averages across samples from both streams, and error bars are standard errors.
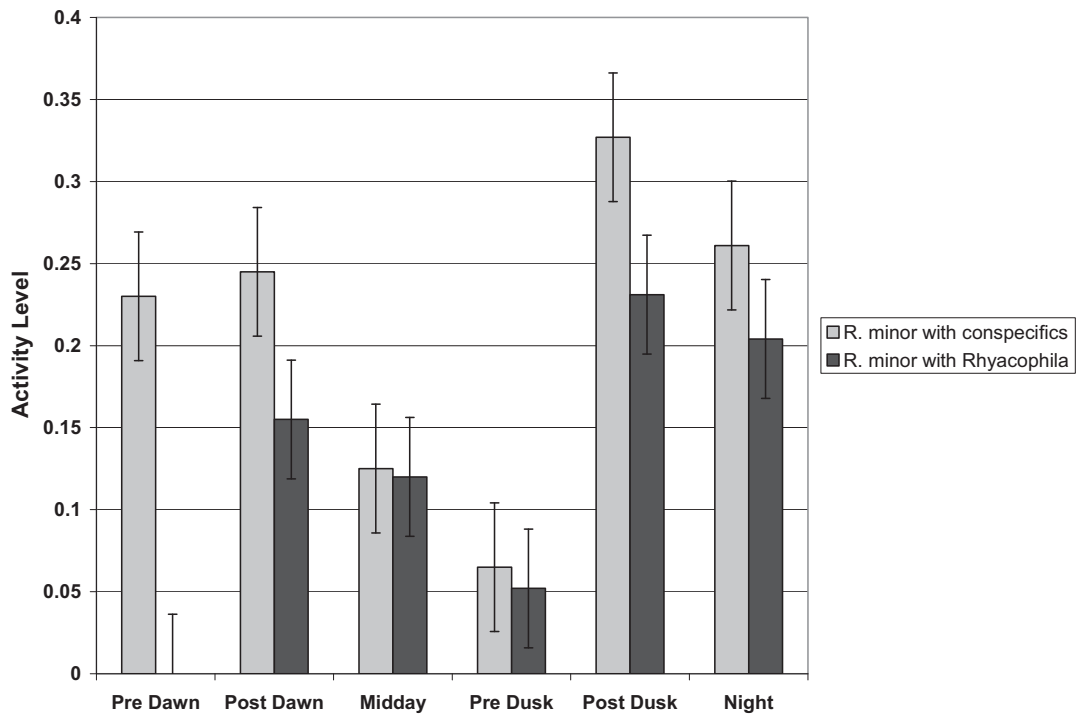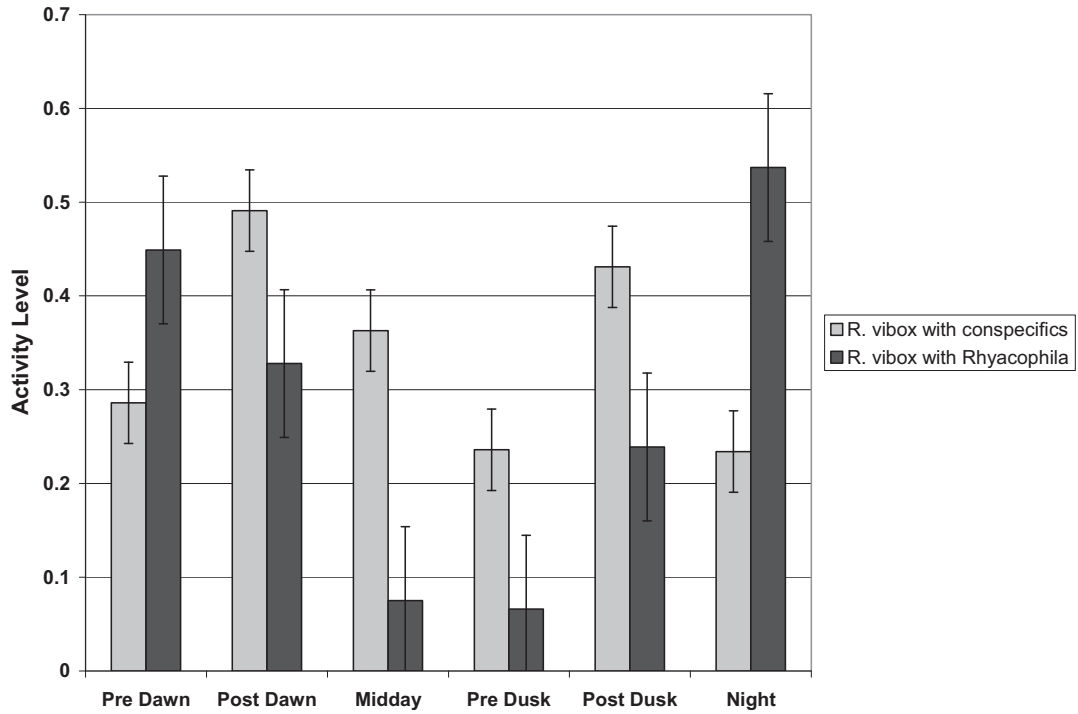
Figure 3.2: Mean activity level for *R. minor* and *R. vibox* in the presence of a conspecific or other species of *Rhyacophila*. Data are from the first and second run of the behavioural feeding experiments. Error bars show standard error.
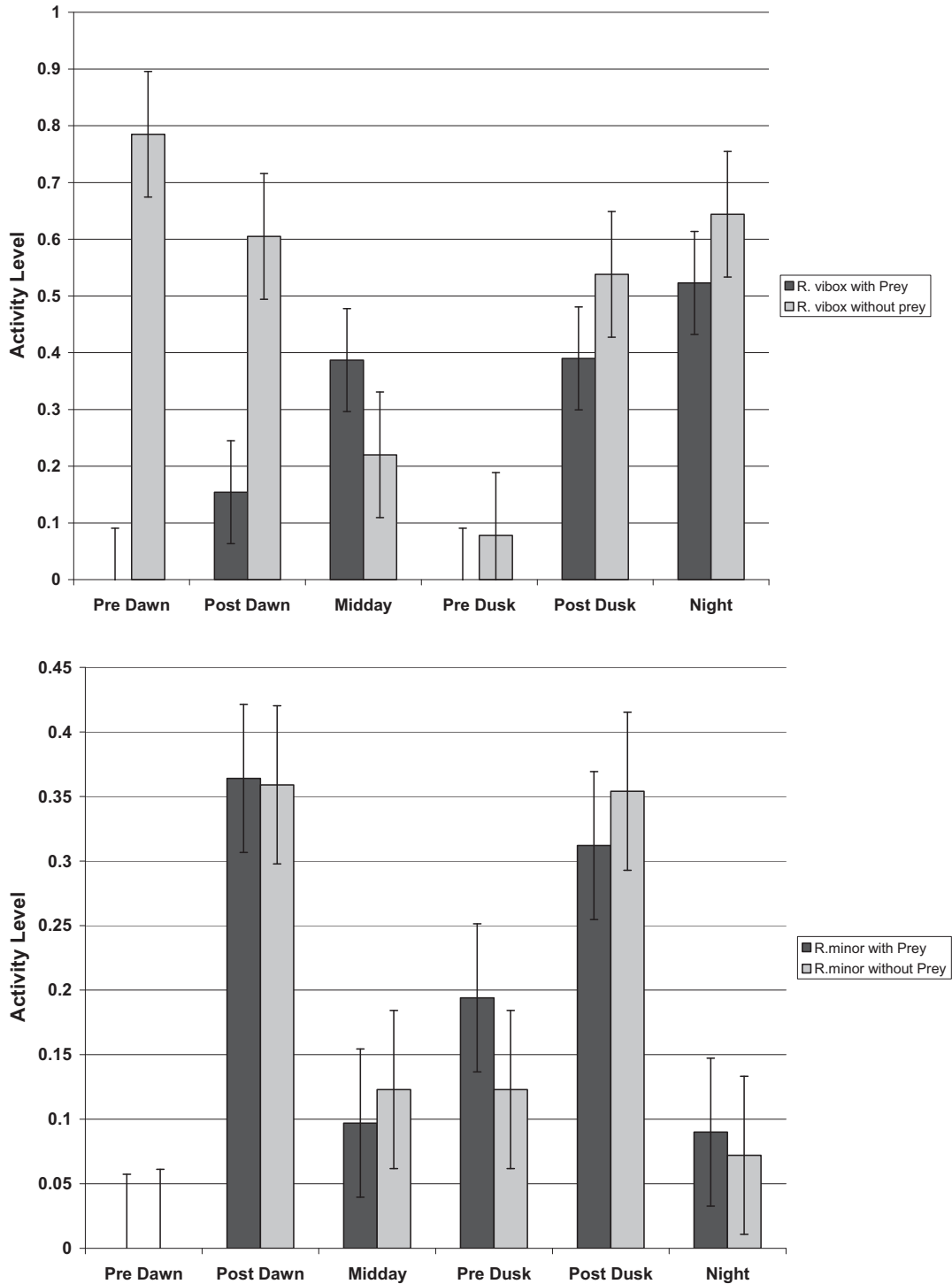
Figure 3.3: Effect of the presence/absence of prey on the mean activity levels of (a) R. vibox in the presence of R. minor and (b) R. minor in the presence of R. vibox. Mean Activity level for *R. minor* and *R. vibox* in the absence and presence of prey. Data comes from the outcomes of the third run of the behavioural feeding experiments. Error bars show standard error
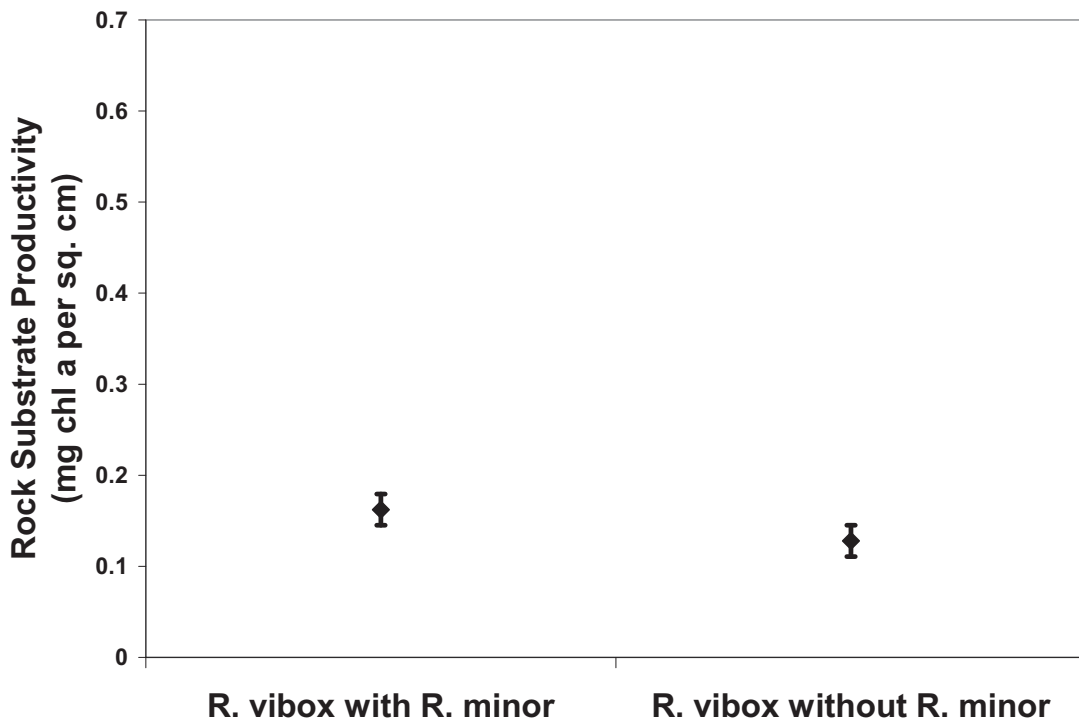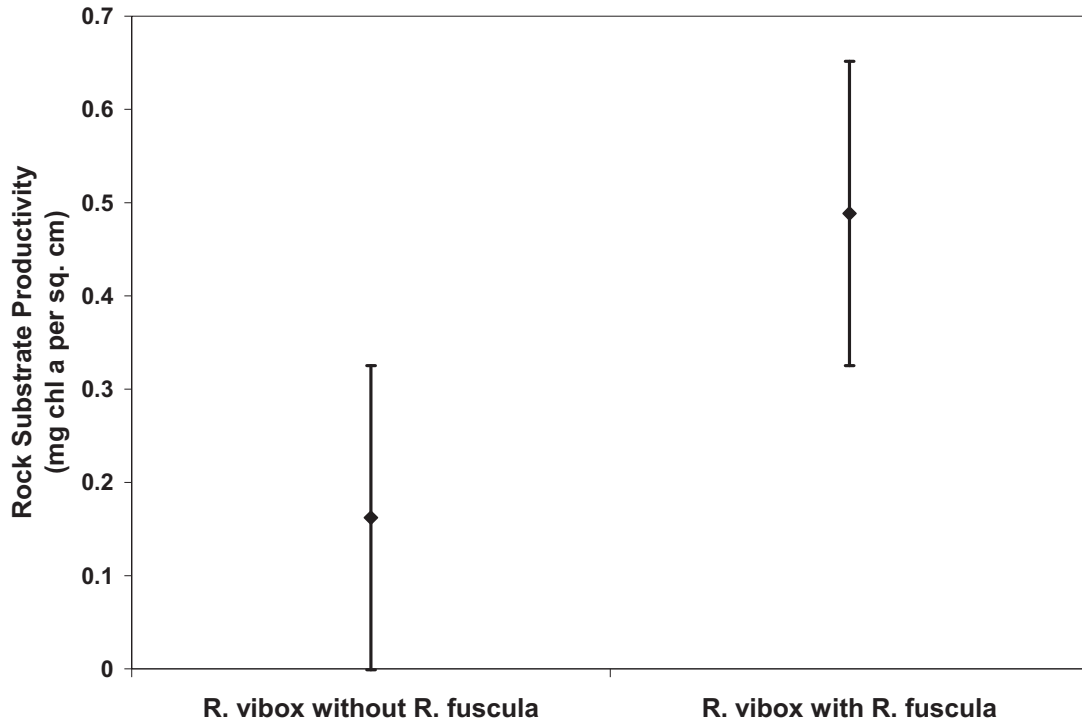
Figure 3.4a: Average productivity (chlorophyll a on rocks in October) between subsets of streams containing different combinations of predators.
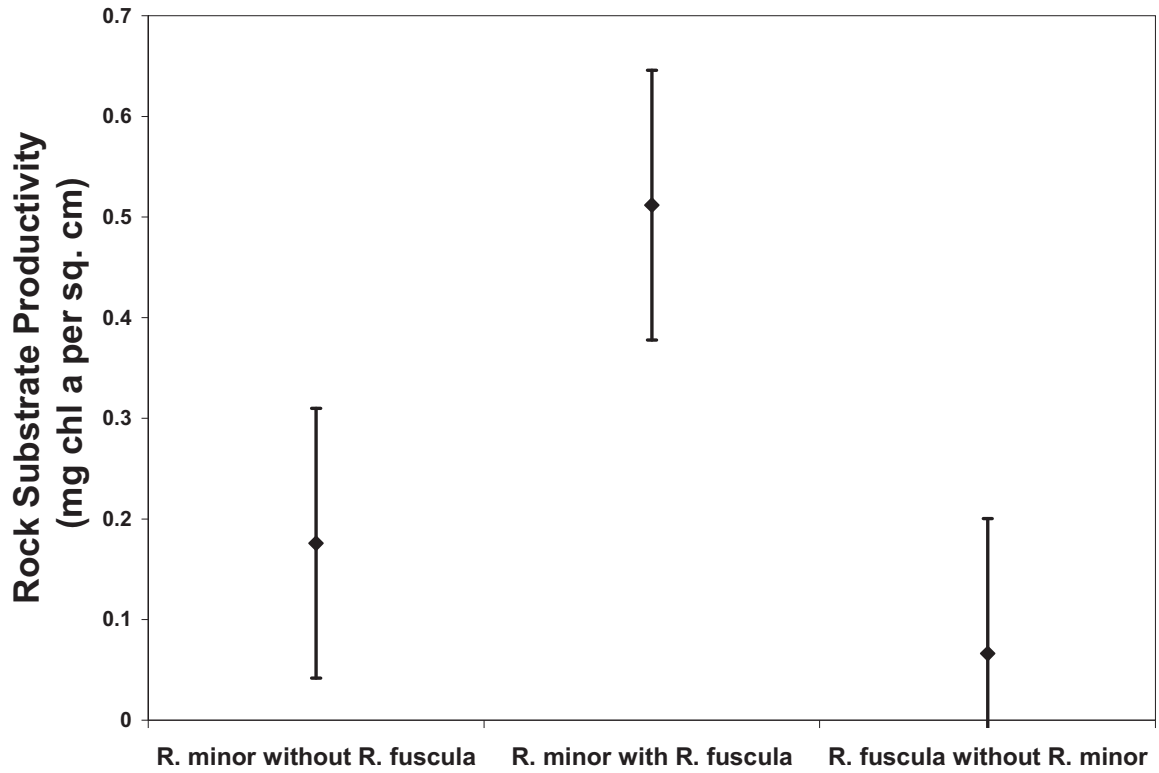
Figure 3.4b: Average productivity (chlorophyll a on rocks in October) between subsets of streams containing different combinations of predators.

R. vibox with R. fuscula not present

$$y = 3.9967x + 0.3864$$
$$R^2 = 0.1737$$

R. vibox density (# per sample) (y-axis)

Rock Productivity (mg chl a per sq. cm) (x-axis)

R. vibox with R. fuscula present

$$y = 0.3234x + 0.4629$$
$$R^2 = 0.0478$$

R. vibox density (# per sample) (y-axis)

Rock Productivity (mg chl a per sq. cm) (x-axis)
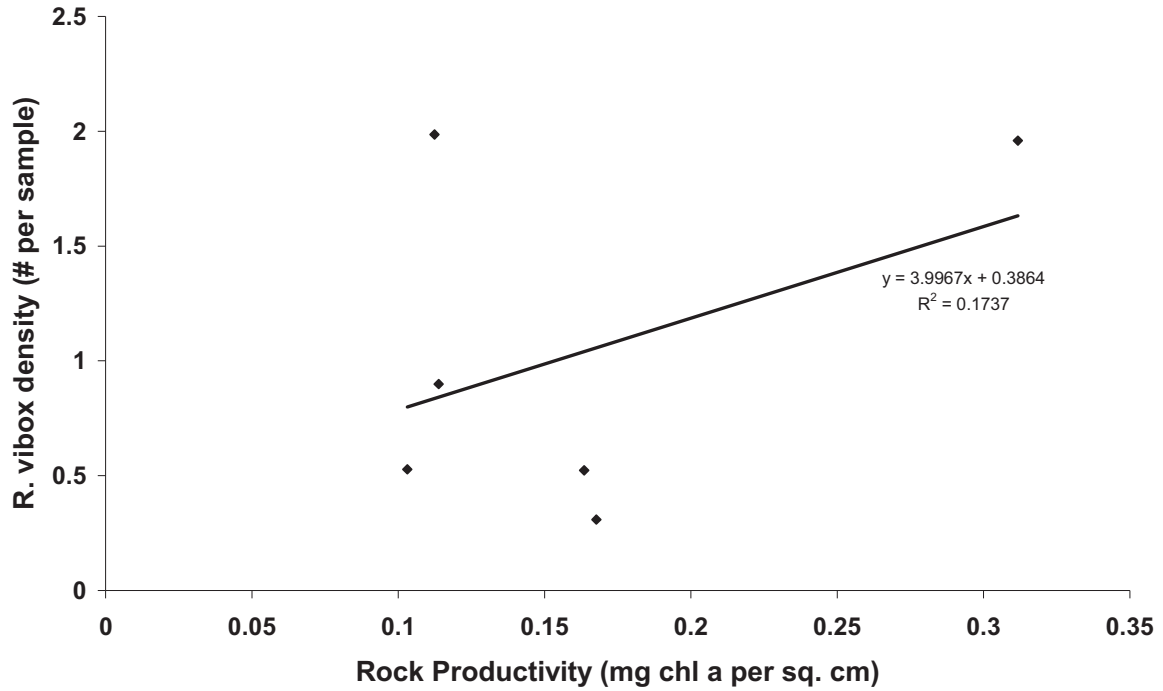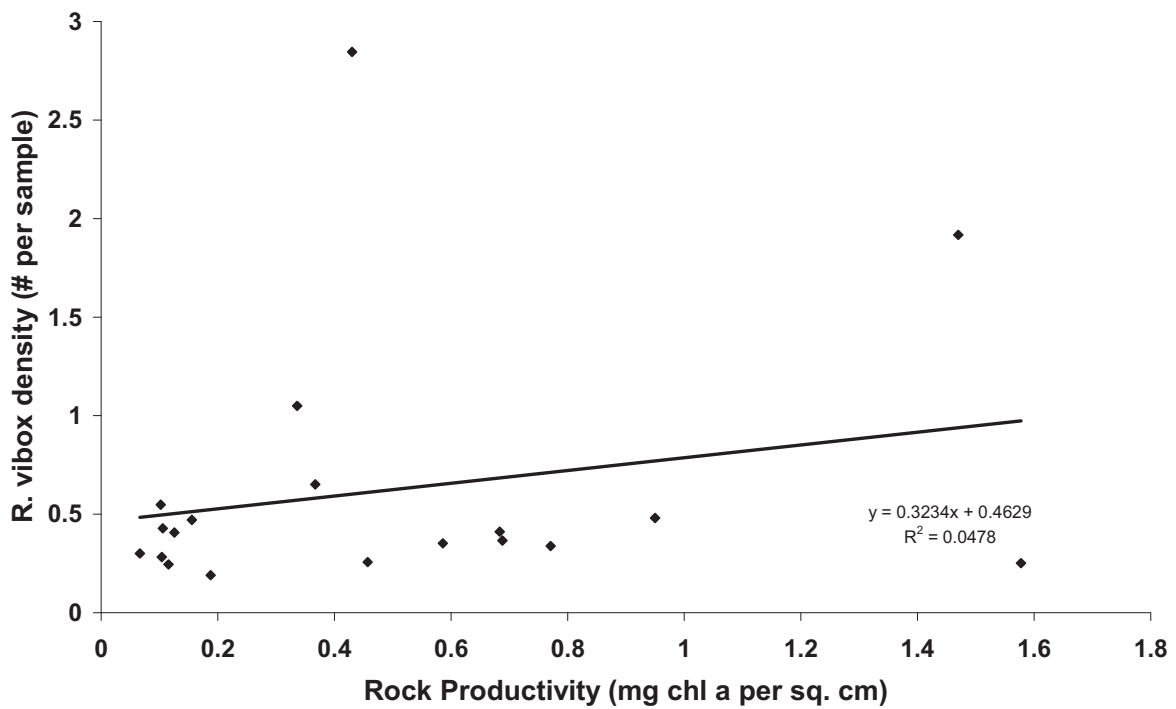
Figure 3.5: The relationship of R. vibox and productivity over different ranges of streams, used to test for the existence of IGP.

R. Minor with R. Fuscula not present

$$y = 1.2041x - 0.0532$$
$$R^2 = 0.308$$

R. minor with R. fuscula present

$$y = 1.2834x + 0.5006$$
$$R^2 = 0.2872$$
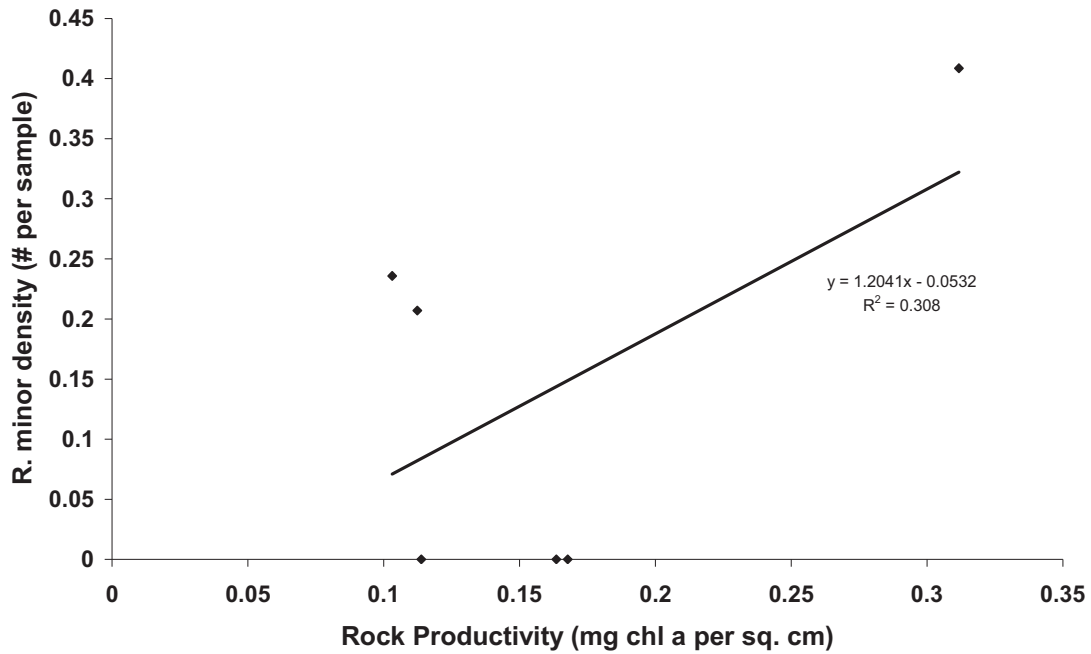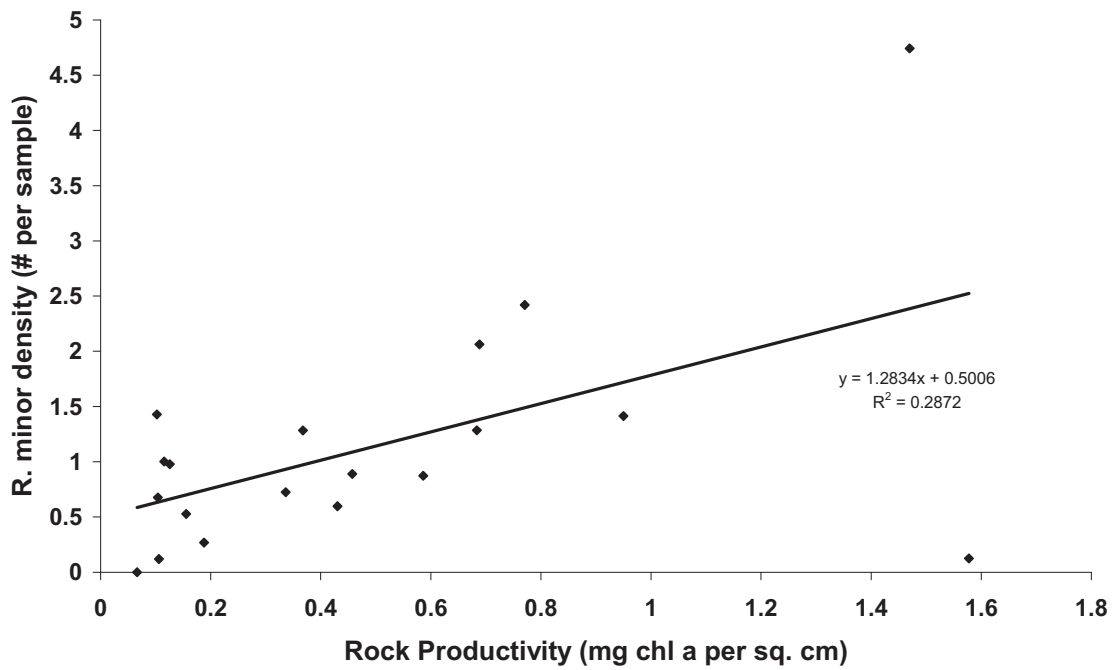
Figure 3.6: The relationship of *R. minor* and productivity over different ranges of streams, used to test for the existence of IGP.

R. minor

R. vibox
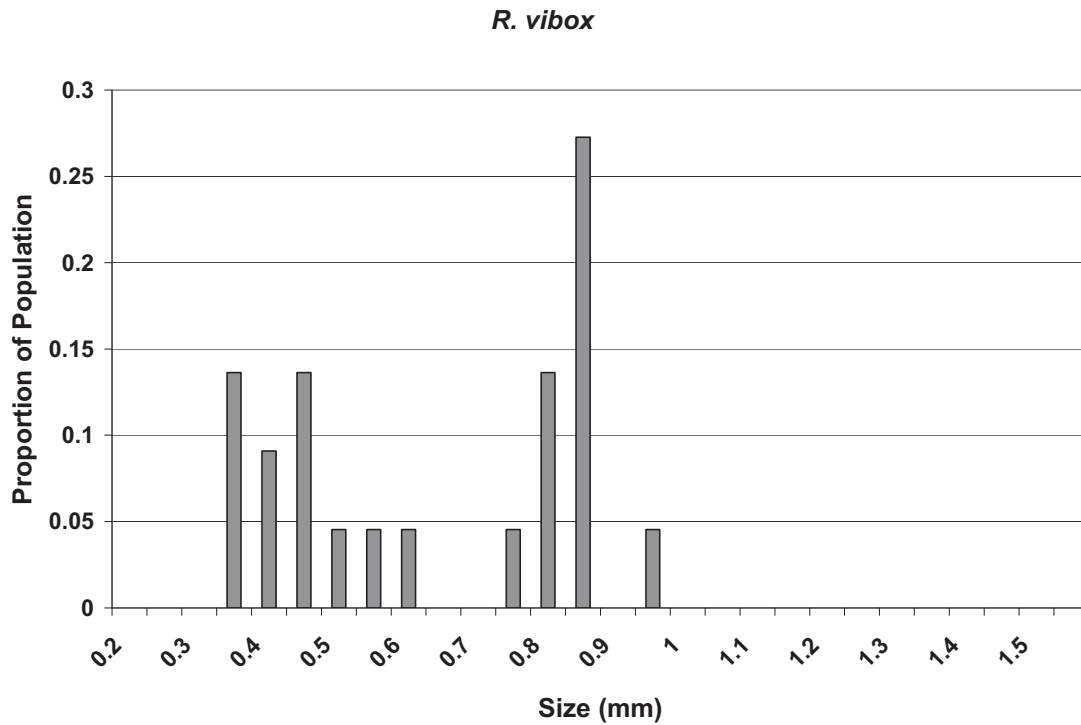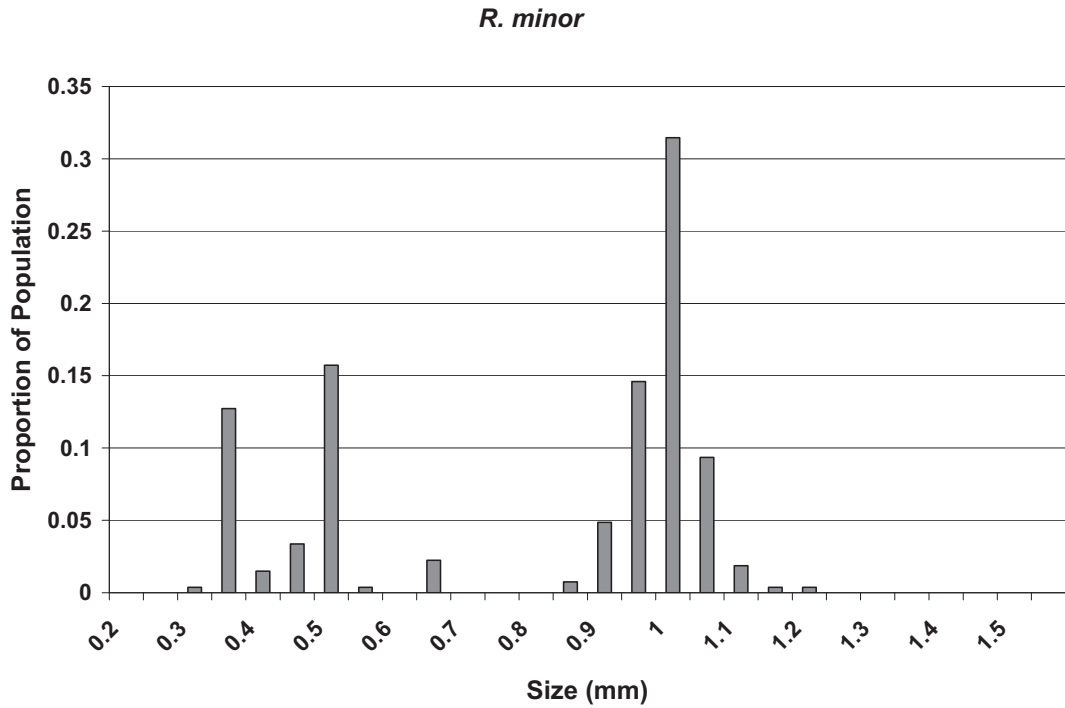
Figure 3.7a: Distribution of the Head Width of the three species of *Rhyacophila* collected during benthic sampling (April) from Ross Creek and Sullivan's Vault

R. fuscula
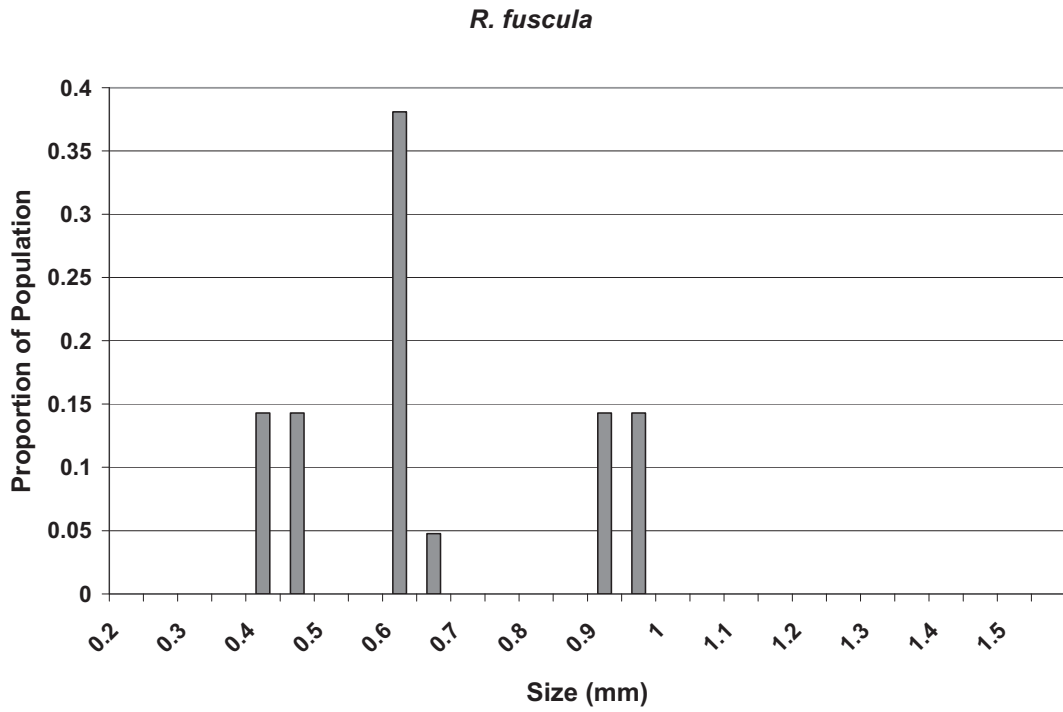
Figure 3.7b: Distribution of the Head Width of the three species of *Rhyacophila* collected during benthic sampling (April) from Ross Creek and Sullivan's Vault

R. minor

R. vibox
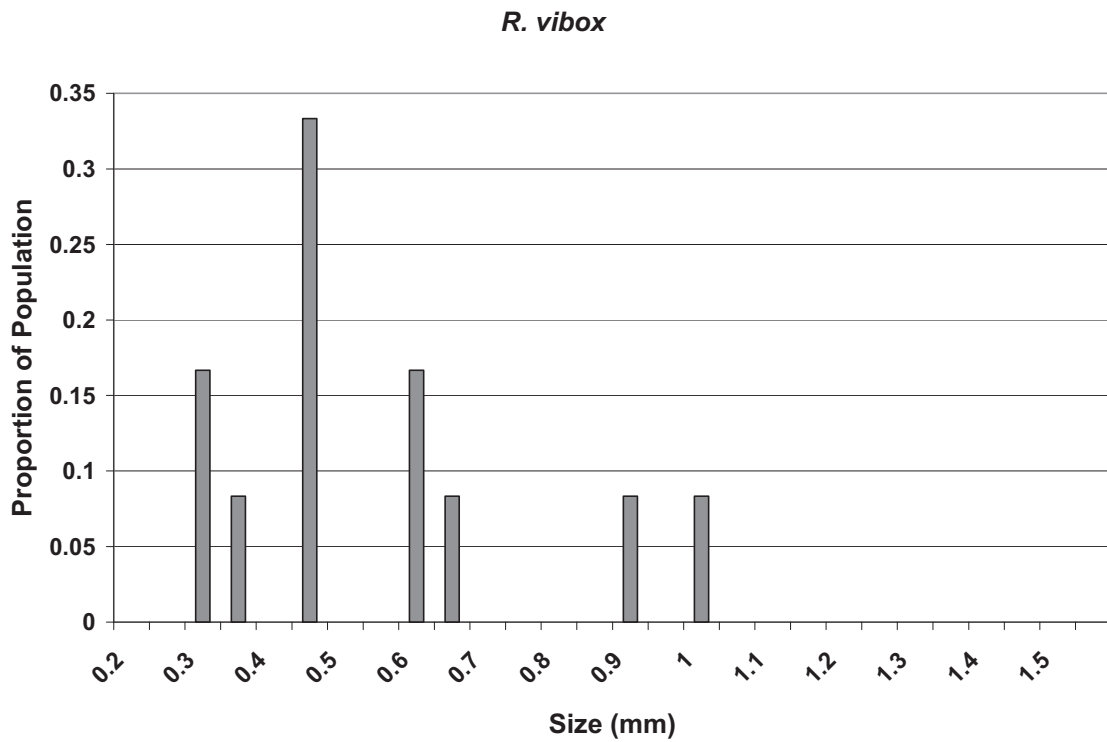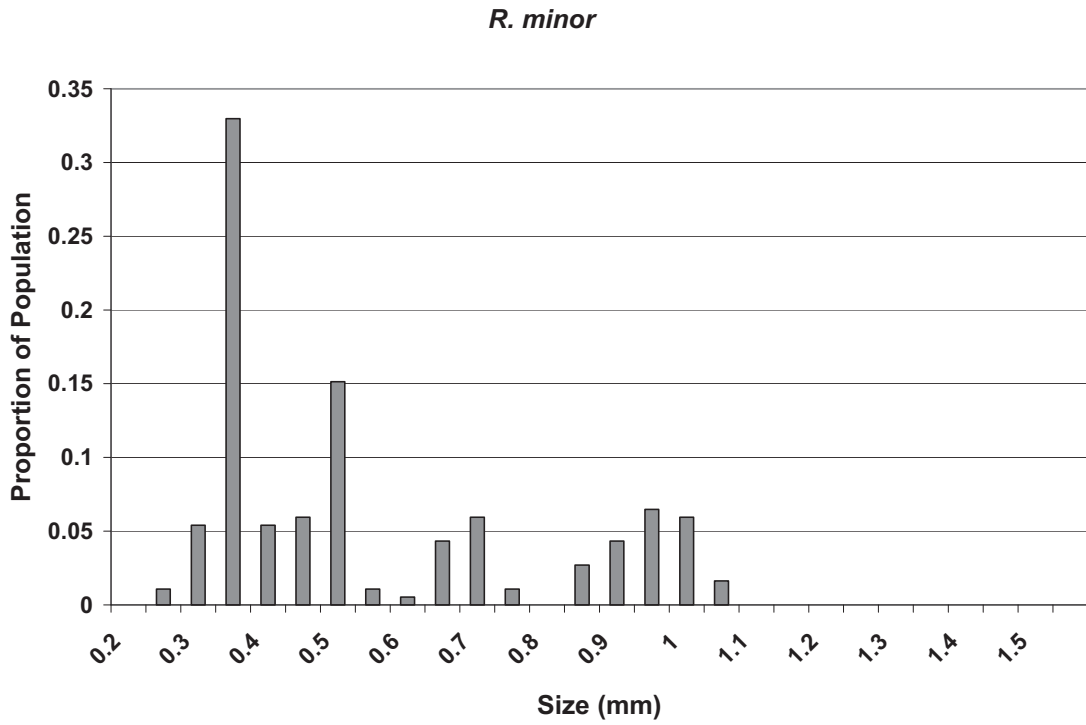
Figure 3.8a: Distribution of the head width of the three species of *Rhyacophila* collected during microhabitat sampling (Fall)

R. fuscula
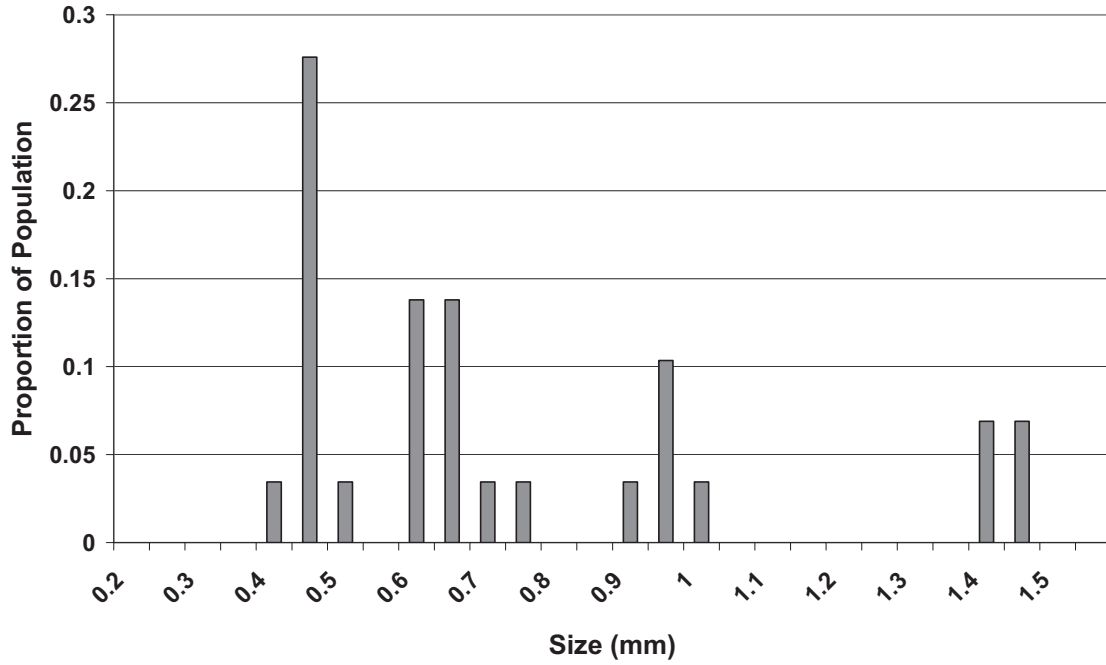
Figure 3.8b: Distribution of the head width of the three species of *Rhyacophila* collected during microhabitat sampling (Fall)

Chapter 4 Discussion

Intraguild predation has the potential to significantly alter relative abundances within a guild and to influence patterns of species coexistence (Polis et al. 1989). The Holt and Polis (1997) model predicts that an IG predator should show increased abundance as productivity increases, but that an IG prey should be negatively related to productivity if the IG predator is present. None of three species of *Rhyacophila* studied showed any indication of a negative relationship between species abundance and productivity; *R. minor* and *R. fuscula* had positive relationships and *R. vibox* numbers were unrelated to primary productivity. While it is still possible that intraguild predation occurs in these streams, it does not appear to drive these species abundance patterns.

4.1: Microhabitat – Do The Species Have The Potential To Interact?

Three lines of evidence suggest that there is the potential for behavioural interaction between these three species of *Rhyacophila*. More than one species was collected in 36% (Ross Creek) and 88% (Sullivan's Vault) of the sampling quadrats (30 by 30 cm), and all species were found in all the microhabitat types sampled. In addition, the distribution of *R. vibox* was positively correlated with the distributions of the other two species in Sullivan's vault. The fact that substantial overlap was found in both sampled streams, despite having very different densities of *Rhyacophila minor*, and coming from different soil till types, suggests that overlap in distribution is likely to occur in other streams, provided densities are at least moderately high.

The 30 cm by 30 cm spatial scale used in the microhabitat survey covered a large enough area to collect a sufficient number of individuals for statistical purposes while still being small enough to allow for the specific sampling of specific microhabitat types.

Rhyacophila initiates attacks on prey over distances of only millimetres (Otto 1993, personal observation), but 30 cm is well within the range of movement of *Rhyacophila*, which have been shown to disperse 10 to 13 m over the course of a single day (Elliott 2003).

Despite the considerable overlap in distributions, the three species of *Rhyacophila* clearly showed differences in their microhabitat use. *R. minor* was more abundant in cobble habitats than on bedrock or in leaf pack habitats. Their abundances were highest in the cobble in the middle of the stream, consistent with observations from an Ontario stream where *R. minor* was found to prefer stones (cobble) over either gravel or bedrock (Singh et al. 1984). The highest numbers of *R. fuscula* were found in leaf packs and on mossy bedrock. Leaf packs and moss are physically complex habitats which tend to support high numbers of prey (e.g. Meissner et al. 2009). Abundance of *R. vibox* did not differ among microhabitats, indicating the absence of strong microhabitat preferences. However the numbers of *R. vibox* were relatively low in the sampled streams, and it is possible that larger differences would be seen in streams where it is very abundant. The lack of a strong habitat preference among *R. vibox* may to some extent explain its ubiquity among the 25 streams in the benthic samples. *R. vibox* may be more adaptable to the various microhabitats, though further testing would be required to confirm this.

At the scale of 30 x 30 cm quadrats, relationships between *Rhyacophila* and prey abundances were usually stronger than between *Rhyacophila* and physical factors. The significant relationships between *R. fuscula* and the abundances of Simuliidae and stoneflies and the significant relationship between *R. minor* and mayflies suggests that these species of *Rhyacophila* may aggregate in response to their prey. This is also consistent with the prey species for *Rhyacophila* as found in studies on *Rhyacophila* diet which determined that not

57

only are Simuliidae and stoneflies prey species of *Rhyacophila* but that *Rhyacophila* were also found to associate with them (Malmqvist and Sjostrom 1984, Muotka 1993, Tokeshi and Pinder 1985).

While the species exhibited different patterns of apparent microhabitat preference, there was considerable overlap in the spatial distributions of all three species in both streams. The frequency of co-occurrence and the lack of negative correlations suggest that at this spatial scale, none of the species shifts its distribution in response to another, in contrast to what has been observed for other sympatric pairs of *Rhyacophila* species (Martin 1985, Lavandier and Cereghino 1995). *R. minor* and *R. fuscula* seem to differ most in microhabitat use, and their abundances were not correlated in either stream. However, due to high densities of *R. minor* (especially in Ross Creek), the potential for encounter (as measured by presence in the same quadrat) was still quite high. *R. vibox* seemed to show strong overlap with the microhabitat use of *R. fuscula* and *R. minor* with significant correlations with both species present in data collected from Sullivan's Vault Brook. The greatest overlap, and thus most likely the highest encounter rates, occurred in leaf packs and on mossy bedrock for *R. vibox* and *R. fuscula*, and in cobble substrate in the middle of the stream for *R. minor* with the other two species.

4.2: Behaviour Study – Which Species Dominate Behaviourally?

The predator-prey interactions between these three species are important in understanding any IGP which may be occurring. *R. minor* experienced a high level of mortality when with *R. fuscula* or *R. vibox*. This suggests that *R. minor* could act as IG prey and conversely that *R. vibox* and *R. fuscula* would act as IG predators. This concurs with a study in which *R. vibox* was found to act as an IG predator in interactions with *Sweltsa onkos*

(Plecoptera: Chloroperlidae) a species which is comparable in size to early instar

Rhyacophila (Sircom and Walde 2009). Two examples of an *R. vibox* perishing in the

presence of *R. minor* shows that when *R. minor* is significantly larger than *R. vibox* , *R. minor*

could have the potential to act as an IG predator. *R. vibox* mortality in the presence of *R.*

fuscula also indicates that *R. vibox* will switch between a role as an IG predator (with *R.*

minor) and an IG prey (with the larger *R. fuscula*). *R. fuscula* was found to act as an IG

predator in all of its interactions with the other species (based on the lack of any mortality in

interactions with other species of *Rhyacophila*).

Predation among these species of *Rhyacophila* may be size-dependent rather than

species-based. Through most of the year *R. fuscula* are the largest of the three species of

Rhyacophila and is a likely predator for both *R. minor* and *R. vibox*. *R. vibox* for the most

part are larger then *R. minor* in the spring. In the fall, however, there were a large number of

R. vibox which are smaller than some of the *R. minor*. The small *R. vibox* could be preyed

upon by these second year *R. minor* which would be a reverse of the expected interaction.

Size-dependent symmetric IGP has also been found in other aquatic IGP systems. Von May

et al. (2009) found in mosquito larvae and tadpoles who were engaged in IGP there was a

critical size threshold which determined which species acted as IG predator and IG prey.

Size-dependent predation has been observed for other benthic invertebrate intraguild

interactions (Elliott 2005, Taniguchi et al. 2002, Wissinger et al. 1996). Woodward and

Hildrew (2002) found body size was the overriding factor in determining trophic position and

predator diet in a stream food web. The single interaction of a large *R. minor* and small *R.*

vibox in which the *R. minor* was able to successfully kill *R. vibox* supports the hypothesis of

size-dependent predator-prey relationships, but more tests would be required to confirm this.

Thus, *R. fuscula* appears to be the least vulnerable of the species in its interactions, while the vulnerabilities of *R. vibox* and *R. minor* may have the potential to shift depending on the season and the demographic makeup of their populations.

Non-lethal interactions (i.e. injury or interference) between species can create an effect between species that mirrors the fitness consequences of classic predation. Non-lethal interactions have been found in experiments in which chloroperlids lost appendages in the presence of *R. vibox*, presumably as the results of failed attacks (Sircom and Walde 2009). Non-consumptive attacks on prey by *R. dorsalis* have also been reported (Wotton et al. 1993). Non-lethal interactions can also include changes in activity induced by the presence of another species. Examples of non-lethal interactions from other species of caddisflies include an interaction with a cased caddisfly in which prey retreat into their case in response to an attack (Wissinger et al. 1996). The retreat interrupts the feeding of the prey and thus has a non-lethal effect on the fitness of the individual. The mere presence of a predator can alter the behavior of prey. McIntosh and Peckarsky (1996) found that the simple "odour" of trout would decrease mayfly activity levels (decreased drift, less exposure) and that the presence of multiple predator species could create a conflict in predator avoidance behaviors (avoidance of stoneflies by mayflies entails entering drift, a conflict with trout avoidance behavior). It is likely that species which exhibit non-lethal attacks in conventional predator-prey interactions will also exhibit these in interactions with intraguild prey. If non-lethal effects are present they would be expected to augment the expected results from an IGP model since they would decrease the survival of the target prey. *R. minor* and *R. vibox* differed in their responses to con-generic predators. *R. vibox* had lower activity in daylight periods as compared with night in the presence of other species (as was found with *R. nubila*

in the presence of fish (Huhta et al. 1999)). This is a possible generic response to the presence of other species that would lower the risk of predation, though at the cost of decreased foraging. Both *R. minor* and *R. vibox* seemed to show response in their diel activity patterns in response to the presence of either predators or prey. The presence of IG predators causing the use of predator avoidance behaviors by prey could induce non-lethal effects like those found in Wissinger et al. (1996) since predator avoidance behavior would entail additional expenditure of energy.

The mortality rates derived from these experiments likely reflect the maximum possible rates which can occur since the majority of these interactions took place in the absence of prey. Absence of prey could also lead to an increased activity level (Otto 1993). The lack of any lethal predation upon *R. minor* in the presence of prey indicates that IGP may be rarer than would be expected based on mortality in these experiments, though it is also possible that the large *R. vibox* present in April are more aggressive. Significantly different rates of mortality between the different experimental runs may have been partly due to the differences in the experimental length. The high mortality that occurred in run 1 may also be due to the larger sizes of *Rhyacophila* in the spring. Individuals of *R. fuscula* are generally larger than either *R. vibox* or *R. minor* which may be why there was no recorded *R. fuscula* mortality. Stream flow velocity in the experimental aquariums (~ 10 cm/s) corresponded to the lower end of the range of velocities measured in July and October and the light intensity corresponded to natural light levels under deciduous canopy (~ 200 lux).

4.3: Stream Survey – Do The Streams Reflect The Predictions Of Holt And Polis (1997) IGP model?

The pattern of coexistence for *R. minor* and *R. fuscula* was partly consistent with the predictions of the Holt & Polis (1997) model. As predicted, streams with both *R. minor* and *R. fuscula* present had higher primary productivity than streams with *R. minor* (IG prey) but no *R. fuscula* (IG predator). However, streams with *R. fuscula* but no *R. minor* were not the most productive, but rather, much less productive. What seems to be driving the pattern is that R. minor is absent from the least productive streams within the study area. *R. fuscula* was expected to be acting in the IG predator role in interactions with *R. minor* and so this finding runs contrary to the expectations under the Holt and Polis (1997) model of IGP. The fact that *R. fuscula* was found without *R. minor* in the lowest productivity streams seems to definitely indicate that IGP, as modelled by Holt and Polis (1997) does not structure these population abundances.

The patterns of coexistence for *R. vibox* with *R. minor* and *R. fuscula* are consistent, in part, with the predictions of Holt & Polis (1997), if *R. vibox* is considered the IG prey in the interactions with *R. fuscula* and IG predation in the interactions with *R. minor*. Primary productivity was, on average, higher for streams with both *R. vibox* and *R. minor* and in those with both *R. vibox* and R. *fuscula* than in those without *R. minor* or *R. fuscula.* However, *R. vibox* was not excluded from the most productive streams. As in the patterns in the earlier paragraph, since *R. vibox* is expected to be acting as IG prey in its interactions with *R. fuscula* it would not be expected to be found in the streams with the highest productivities (this is assuming these streams are sufficiently productive to allow for the exclusion of *R. vibox*). The failure to exclude *R. vibox* even at high productivities could potentially the

indicate it is following the predictions of a Holt and Polis (1997) model that includes alternate prey, or some other source of alternative resource however, even in that case it would be expected to see a negative relationship with productivity when the IG predator (*R. fuscula*) is present. It is possible and quite likely that these streams do not reflect the full range of productivities to allow the exclusion of the IG predator at low productivities and the IG prey at high productivities. This is most evident in the case of *R. vibox* a species which may be able to switch between IG prey and IG predator and was not excluded in any of the streams.

Streams have two sources of energy the first is energy made within the stream by autotrophs (algae and other plants) the second is from external inputs (leaf litter and detritus). The measures of chlorophyll a from the substrate samples are important in establishing the density-productivity relationship that is crucial to the identification and examination of the existence of IGP. Primary productivity was used because it supports a wider spectrum of the stream community then external inputs. Analysis showed there were no stream variables that had a significant relationship with the chlorophyll a measures on tiles from the June substrate samples. The measures for the October tile substrate samples were found to be significantly correlated with the light ratio This is consistent with the results of previous studies that have found a relationship between the available light and the growth of periphyton (Kiffney 2008, Kiffney et al. 2003). Lastly, the measures of chlorophyll taken from the October rock samples were found to be correlated with both the stream soil till and the water pH. A likely explanation for the lower levels of periphyton in the silty soil tills is decreased levels of light reaching the periphyton due to an increased light absorption created by silt suspended in the stream water column the deposition of silt may also interfere with the growth of periphyton.

The water pH was also significantly correlated with the chlorophyll measures from the rock samples taken in October. pH can have a large effect on stream periphyton. Artificial acidification of streams was found to cause increases in a stream's periphyton biomass (Hall et al. 1980).

Beyond the patterns of coexistence, the density patterns of the species are also important part of testing for intraguild predation within a predator-prey relationship. Firstly, it is expected that the density of an IG predator will increase positively along with the stream productivity. While *R. fuscula* does display a positive relationship with productivity (rock chlorophyll a) (this relationship is also shown to be significant over the full range of productivities). However, the elimination of streams where *R. fuscula* was not present renders this relationship non-significant. Analysis of the density patterns over which *R. minor* is present along with *R. fuscula* reveals *R. minor* has a positive and significant relationship with productivity over this range of streams as well as significant relationship with *R. fuscula* density. This result is contrary to expectations under a scenario where IGP is occurring since *R. minor* would be expected to have a negative relationship with productivity in a situation where it is found along with its IG predator. This finding would seem to rule out an IGP relationship between *R. fuscula* and *R. minor* structuring their population abundances.

R. vibox in its potential role as an IG predator under the Holt and Polis (1997) model of IGP is expected to have a positive relationship with productivity over the range of productivities where *R. fuscula* is not present. The relationship between *R. vibox* and productivity over this range of productivities is shown to be non-significant but positive. This is based on a sample of only six streams and there is one stream (NF) that has large leverage and another (WH) on which this positive relationship is largely based. Similar issues with

64

statistics are encountered with analysis of *R. minor* over this range of productivities. One

stream (WH) is largely responsible for a non-significant but positive relationship between *R.*

minor density and the productivity of the stream. *R. minor* is expected to have a negative

relationship with productivity when it coexists with either *R. vibox* or *R. fuscula*. *R. minor*

displays positive relationships with productivity in both these cases, which seems to rule out

an IG prey / IG predator relationship between *R. minor* and either *R. fuscula* or *R. vibox*

Studies of *Rhyacophila* diet have found that species of *Rhyacophila* display herbivory

in the early instar stages (Stages 1 -3) or a change in the size of consumed prey as species

progress through instar 1-5 (Lavandier and Cereghino 1995, Cereghino 2002, Elliott 2005).

Of the *Rhyacophila* found in these streams, data on diet only exists for *R. minor*. *R. minor*

was found to shift from a mostly herbivorous diet, to a carnivorous diet as they transitioned

from instar 1 to 3 with the majority of its diet deriving from carnivory in instars 3-5

(Lavandier and Cereghino 1995, Cereghino 2002, Elliott 2005). It is therefore possible that if

instars of the three species of *Rhyacophila* are not maturing at the same rates then a temporal

refuge is being created. In the spring the majority of *R. fuscula* larvae are in the instar 3

stage, while the majority of *R. minor* and *R. vibox* have already entered the instar 5 stage. In

the fall the three species reach an even distribution of instars where all three species of

Rhyacophila show a similar mix of instars ranging from 2nd stage instars to 5th stage instars.

It is possible therefore that in the spring both *R. minor* and *R. vibox* are free from predation

pressure from *R. fuscula* since the largest *R. fuscula* are only 3rd instar and *R. minor* and *R.*

vibox are then vulnerable to predation in the fall. Looking past instar and looking instead at

head widths reveals an important part of this picture. In the spring the head widths of the

three species are within the same range and *R. fuscula* has smaller head widths than the older

R. minor (likely due to the 2 year life cycle of *R. minor* compared to the 1 year life cycle of *R. fuscula* and *R. vibox*). In the fall there are a large portion of *R. fuscula* with a head width much larger than *R. minor* and there is a definite opportunity in the fall for *R. minor* or *R. vibox* to be small enough to be prey for *R. fuscula*. While there are *R. minor* or *R. vibox* likely too large to be preyed upon in the fall by *R. fuscula*, smaller individuals would be present upon which *R. fuscula* can prey (shown by the ability of *R. fuscula* to prey upon both *R. vibox* and *R. minor* in behavior experiments). If a temporal refuge does exist it may not be eliminating IGP but it may be diminishing its effect allowing other factors to become more important in determining population distribution patterns. This is demonstrated in studies where refuges where found to lower the intensity of IGP (Finke and Denno 2002, Janssen et al. 2007).

There are alternative formulations of Holt & Polis' IGP model that can alter the relationships between the species densities and productivity. However, modifications only change the range of productivities over which coexistence is expected to occur (Daugherty et al. 2007, Holt and Huxel 2007). These modifications can include an additional resource exclusive to the IG predator or an additional resource which is exclusive to the IG prey. In such a situation only the range of productivities where coexistence is expected will shift. When there is a supplement to the IG predator, the range of coexistence is greatly narrowed and is much lower in the range of productivities. This occurs as the IG predator is able to persist at much lower productivities since it has access to a resource that the IG prey does not. Alternatively when the IG prey is given an exclusive additional resource, the range of coexistence between the IG prey and IG predator is greatly expanded. The IG prey is able to coexist with the IG predator at much higher levels of productivity because the IG prey is not

competing with the IG predator for its use. Predation pressure from the IG predator is still expected to eliminate the IG prey population, it simply occurs at a higher productivity. Neither of these two additions to the IGP model is expected to change the relationship between the IG prey or IG predator and productivity and thus it is likely that neither of these two situations are occurring in this case. Other alternate formulations of the IGP model have also been created. These generally change the model outcome to very closely reflect the outcomes outlined above. A study by Amarasekare (2007) examined IGP in a parasitoid system. This long term study (12 years) found that when the IG prey was able to utilize a refuge, it could coexist with the IG predator to a very high productivity and had in fact never been excluded during the experiment. However, while coexistence did still occur up to high productivities the IG prey still displayed a negative relationship with productivity and the IG predator displayed a positive relationship with productivity. Even when complicating factors are present which are distorting and altering the outcomes of the standard Holt and Polis (1997) model of IGP the three conditions being tested for still hold. Coexistence between the IG predator and IG prey is expected over a range of intermediate productivities. While the IG predator is expected to display a positive relationship with productivity, the IG prey is expected to display a negative relationship with productivity when in the presence of the IG predator. Even with major reformulations to the Holt and Polis (1997) model the fundamental predictions of the model remain intact. Given that all these of these species of *Rhyacophila* coexist in the same streams it is possible that a form of complex IGP is occurring with more then one IG predator and IG prey. A model in this system could potentially be similar to figure 4.1. However, further theoretical study would be required to gauge the ramifications of such an addition to an IGP model.

The microhabitat usage patterns provide at least one clue as to why IGP is not structuring the overall population distribution of these three species of *Rhyacophila*. *R. vibox* was found through all of the streams sampled and had a non-significant relationship with the productivity of the stream as opposed to either *R. fuscula* or *R. minor*. It is most likely that the population distribution of *R. vibox* was influenced by fish presence since it was the only *Rhyacophila* to show a significant relationship with fish (p=<0.001). Eliminating *R. vibox,* it is still possible that *R. minor* and *R. fuscula* may be engaging in IGP. However, the results from the microhabitat survey show that *R. fuscula* and *R. minor* tend to occupy differing microhabitats. *R. minor* was found in the highest densities in cobble mid-stream while *R. fuscula* was found most abundant in leaf packs and on moss-covered bedrock. While *R. fuscula* and *R. minor* did overlap in their habitat usage, the level of overlap may not have been sufficient for the expectations of IGP to be reflected in their population distribution patterns even if IGP was occurring between the species. This is similar to microhabitat shifting found in other species of *Rhyacophila* and interactions between *R. fuscula* and other species of *Rhyacophila* (Lavandier and Cereghino 1995) (Martin 1985). This could reflect a change created by intraguild predation pressure, but more work would be required to confirm this possibility.

4.4: Alternate Explanations To Patterns Of Species Distribution?

Analysis of *R. minor* abundance patterns shows a significant relationship with the in stream population abundances of both Ephemeroptera and Chironomidae over the full range of streams. Both of these genera consist largely of species that are prey to *R. minor* (Lavandier and Cereghino 1995, Cereghino 2002, Muotka 1993, Elliott 2005). It is consistent with the microhabitat results where *R. minor* was found to aggregate with Ephemeroptera and

with past studies that *R. minor* density would be found to have a positive and significant relationship with the density of their prey. A greater density of prey species would be expected to support a larger density of predator species. A number of studies have found that species of *Rhyacophila* have been associated with prey species in studies of microdistributions within streams (Malmqvist and Sjostrom 1984, Muotka 1993, Tokeshi and Pinder 1985). Association with prey species on the microhabitat scale found in the microhabitat portion of this study could be used to explain the correlation with prey density across a whole stream. A small scale interaction such as this which finds predators associating with prey could easily be amplified and used as a mechanism to explain why you might expect greater levels of predator abundance in concert with greater prey abundance over a larger system,

A similar analysis of *R. vibox* density patterns revealed that its population density is significantly and positively correlated with chironomiidae density which, as with *R. minor*, is consistent with past studies of *Rhyacophila* prey associations (Lavandier and Cereghino 1995, Cereghino 2002, Muotka 1993, Elliott 2005). Secondly, *R. vibox* was also significantly correlated with the presence or absence of fish. *R. vibox* had a higher density in streams without fish. This is also consistent with previous studies, since fish are predators of *Rhyacophila*. However, there is no evidence to suggest why *R. vibox* and not *R. minor* or *R. fuscula* are not also correlated with fish presence.

R. fuscula was also positively and significantly correlated with Ephemeroptera density. This is consistent with the results from both *R. minor* density and *R. vibox* density patterns as *Rhyacophila* have been found to associate with prey species in the microhabitat portion of this study and in other studies. (Lavandier and Cereghino 1995, Cereghino 2002,

69

Muotka 1993, Elliott 2005). This finding contrasts with the results of the microhabitat survey in which *R. fuscula* was found to aggregate with Simulids and stoneflies. However, these are still known prey species and this discrepancy could be due to the limited number of streams sampled.

There are additional possible factors which could additionally be the overriding factor which is determining *Rhyacophila* abundance however the above mentioned relationships with prey abundances exhibited the strongest relationship with *Rhyacophila* density of the factors measured in this study. However, there are a number of other possible factors that could be useful to examine in future work on these species. The availability of the species preferred habitat in each individual stream could be a very important factor and one which was not measured here. Additionally, greater examination of stream velocity and other abiotic factors could reveal differences between streams which might affect the species' abundance patterns.

Conclusion:

This study has looked at a number of the factors that would indicate whether or not abundance patterns of *R. minor*, *R. vibox* and *R. fuscula* are consistent with that predicted by intraguild predation models. A number of steps were required to establish whether or not these species were interacting with each other at all and whether or not they could be involved in intraguild predation.

The microhabitat survey and behaviour study established that these three species do interact lethally with each other, at least in the lab, and that all three species exhibited significant spatial overlap within streams. Despite potential issues with the behaviour study because species were kept in artificial tanks the evidence did confirm that it is likely these

species would interact in a natural setting, particularly if they were hungry. This was confirmed with firsthand sightings of active predation between the species.

The behaviour and feeding experiments allowed for the creation of an intraguild hierarchy which could act as a framework of expected roles and interactions. *R. fuscula* was found to be dominant over both *R. vibox* and *R, minor* largely because *R. fuscula* is significantly larger. The interaction between *R. vibox* and *R. minor* was more complex due to their being closer in size. It was concluded that interactions were likely to be size dependent with *R. vibox* tending to dominate *R. minor* unless *R. minor* is sufficiently large and *R. vibox* sufficiently small. This established a generalized food web in which *R. fuscula* would always act as IG predator, *R. vibox* would act as IG prey with *R. fuscula* and an IG predator with *R, minor* and *R, minor* usually acting as IG prey.

The abundance patterns of the three species were then analyzed in the context of the model of intraguild predation as formulated in Holt and Polis (1997). Comparing average productivities over select ranges of streams showed that they did not adhere to what was expected if intraguild predation was structuring population abundances. Most crucially neither *R. minor* nor *R. vibox* showed a negative relationship with productivity when it was thought to be acting as an IG prey.

It was concluded therefore that it was most likely that intraguild predation was not structuring the population abundances observed in the benthic samples. While it does seem likely that intraguild predation occurs between these species of *Rhyacophila*, there is little evidence to conclude that the population abundance patterns at the scale of streams conform to the predictions of the Holt and Polis (1997) model of intraguild predation nor any variant of such.

Since it was likely that intraguild predation was not responsible for structuring these species populations abundances, measured variables were analyzed to determine what factor or factors seemed to determine or affect the population abundances of these species of *Rhyacophila.* Of the variables measured in this study it was the abundance of prey which was most closely associated with the *Rhyacophila* abundance the prey species included Simuliidae, Ephemeroptera and Plecoptera.

While it remains possible that intraguild predation occurs between the three species of *Rhyacophilia* being studied since laboratory studies indicate that they can and do engage in IGP, the measured population abundances do not indicate any measurable effects on these species population abundances. There are two lines of inquiry that extends from this point: First, An examination of a wider range of stream characteristics to identify the underlying characteristics that ultimately influence population abundance, focusing especially on the composition and availability of preferred habitat. Secondly, longer duration lab experiments which quantify the rate at which IGP is occurring between these species to directly determine the role IGP plays in this system. It would be necessary in these experiments to better replicate the natural habitat and to alter conditions to better reflect natural prey abundances.
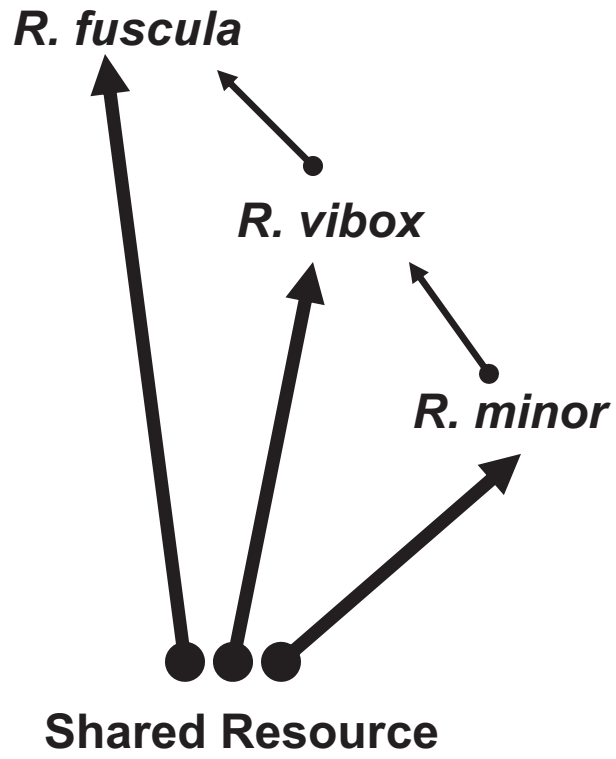
Figure 4.1: Alternate food web of species interaction

Appendix 1

Benthic Sample Collection Sites:

      Streams (25) were selected based on (1) prior knowledge of predator distributions (approx. 10 streams), and (2) hypothesized productivity based on land use. Selected streams were (from east to west): RC (Ross Creek), WW (Woodworth), PV (Pineo Vault), BH (Black Hole), CI (Cobby Irving), CI up (Cobby Irving Upstream), FR (Fraser), LB (Long Beach), WH (Wheaton), SV (Sullivan Vault), CH (Chipman), FT (Foote), CV (Church Vault), SB (Saunder's), TB (Turner), BN (Brown), RB (Robinson), SS (Sheapshearer), HE (Healy), NF (Number Five), ST (Starratt), SC (Schoolhouse), GL (Granville Line), PL (Poole), GK (Gaskill)

Stream	Location (UTM NAD83)	CV	20 T 364054 5001788
GK	20 T 314238 4974386	FT	20 T 367515 5003807
PL	20 T 318325 4976166	CH	20 T 369766 5004016
GL	20 T 320110 4977593	SV	20 T 371483 5004454
SC	20 T 321900 4978790	WH	20 T 376699 5005601
ST	20 T 323847 4979657	LB	20 T 379237 5007791
NF	20 T 324730 4980447	FR	20 T 381377 5009577
HE	20 T 325544 4981466	CI up	20 T 382797 5008576
SS	20 T 326333 4982755	CI	20 T 382357 5009690
RB	20 T 349465 4995928	BH	20 T 383075 5009845
BN	20 T 352924 4997081	PV	20 T 383518 5010243
TB	20 T 357062 4998932	WW	20 T 385703 5010735
SB	20 T 360553 5001680	RC	20 T 386454 5010952

Appendix 2

Feeding/Behavior experiment: pairings and outcomes

MF – *R. minor* and *R. fuscula*
MV – *R. minor* and *R. vibox*
MVP – *R. minor* and *R. vibox* with prey
VF – *R. vibox* and *R. fuscula*
V – *R. vibox* alone
M – *R. minor* alone
MM – *R. minor* and *R. minor*
VV – *R. vibox* and *R. vibox*

Run	Treat	Rack	Tank	Mass(g)	Mass(g)	Who Died?	Day of Death
1	MF	1	1	M=0.059	F=0.0287	M	6
1	MV	1	2	V=0.0142	M=0.0083	M	4
1	MV	1	3	V=0.012	M=0.0061	M	7
1	VF	1	4	V=0.0107	F=0.0207	V	7
1	MF	1	5	M=0.0084	F=0.0071	N	0
1	VF	1	6	F=0.0442	V=0.0048	N	0
1	MV	2	1	V=0.0184	M=0.008	M	6
1	MV	2	2	M=0.0051	V=0.0247	N	0
1	MV	2	3	M=0.0087	V=0.0092	N	0
1	MF	2	4	F=0.004	M=0.01	N	0
1	MV	2	5	V=0.012	M=0.007	M	6
1	V	2	6	V=0.0117		N	0
1	MV	3	1	M=0.0055	V=0.0127	M	3
1	MV	3	2	V=0.0201	M=0.0036	M	6
1	M	3	3	M=0.0055		N	0
1	MV	3	4	M=0.0051	V=0.0117	N	0
1	VF	3	5	V=0.0171	F=0.0024	N	0
1	MV	3	6	M=0.0056	V=0.0134	M	4
1	VF	4	1	V=0.0174	F=0.0521	N	0
1	M	4	2	M=0.0053		N	0
1	V	4	3	V=0.0096		N	0
1	MF	4	4	F=0.003	M=0.002	M	6
1	MV	4	5	M=0.0065	V=0.0132	M	4
1	MV	4	6	M=0.0083	V=0.0034	N	0
2	VF	1	4	V=0.0007	F=0.0017	N	0
2	MM	1	6	M=0.0046	M=0.0042	N	0
2	MV	2	1	M=0.0030	V=0.0017	N	0
2	MV	2	2	V=0.0033	M=0.0026	N	0
2	MM	2	3	M=0.0015	M=0.0030	N	0
2	MV	2	4	V=0.0088	M=0.0062	N	0
2	MV	2	5	M=0.0010	V=0.0018	V	5
2	MF	2	6	F=0.0049	M=0.0028	N	0
2	VV	3	1	V=0.0033	V=0.0062	N	0

Run	Treat	Rack	Tank	Mass(g)	Mass(g)	Who Died?	Day of Death
2	MF	3	3	F=0.0034	M=0.0022	N	0
2	MM	3	4	M=0.0027	M=0.0020	N	0
2	MV	3	5	M=0.0029	V=0.0038	N	0
2	MM	4	1	M=0.0034	M=0.0025	N	0
2	MV	4	3	V=0.0088	M=0.0024	N	0
2	MF	4	5	M=0.0040	F=0.0071	N	0
3	MV	1	2	V=0.0099	M=0.0036	M	8
3	MV	1	4	M=0.0049	V=0.0080	N	0
3	MVP	1	6	M=0.0027	V=0.0030	M	5
3	MVP	2	4	V=0.0018	M=0.0043	N	0
3	MV	2	6	V=0.0050	M=0.0030	N	0
3	MVP	3	5	M=0.0038	V=0.0031	V	8
3	MV	3	6	V=0.0070	M=0.0035	M	8
3	MV	4	5	V=0.0029	M=0.0036	M	8
3	MVP	4	6	M=0.0055	V=0.0047	N	0

Reference List

Amarasekare, P. 2007. Trade-offs, temporal variation, and species coexistence in communities with intraguild predation. Ecology 88: 2720-2728

Arim, M. and Marquet, P. A. 2004: Intraguild predation: a widespread interaction related to species biology. Ecology Letters 7:557-564

Borer, E., C. Briggs and Holt, R, 2007. Predators, Parasitoids, and Pathogens: A cross-cutting examination of intraguild predation theory. Ecology 88: 2681-2688

Briggs, C.J. and Borer, E.T. 2005. Why short-term experiments may not allow long-term predictions about intraguild predation. Ecological Applications 15: 1111-1117

Cattaneo, A. and Amireault, M.C. 1992. How artificial are artificial substrata for periphyton? Journal of the North American Benthological Society 11(2): 244-256

Cereghino, C. 2002. Shift from a herbivorous to a carnivorous diet during the larval development of some *Rhyacophila* species (Trichoptera). Aquatic Insects 24: 129-135

Daugherty, M.P., Harmon, J.P. and Briggs, C.J. 2007. Trophic supplements to intraguild predation. Oikos. 116: 662-677

Diehl, S. and M. Feissel. 2001. Intraguild prey suffer from enrichment of their resources: a microscosm experiment with ciliates. Ecology 82: 2977-2983

Dixon, R.W.J. and Wrona, F.J. 1992. Life history and production of the predatory caddisfly *Rhyacophila vao* Milne in a spring-fed stream. Freshwater Biology 27: 1-11

Dudgeon, D. and Richardson, J. 1988: Dietary variations of a predaceous caddisfly larvae (Trichoptera: Rhyacophiladae, Polycentropidae and Artopsychidae) from British Columbian streams. Hydrobiologia 160: 33-43

Elliott, J.M. 2003. A comparative study of the dispersal of 10 species of stream invertebrates. Freshwater Biology. 48: 1652-1668

Elliott, J. 2005. Contrasting diel activity and feeding patterns of four instars of *Rhyacophila dorsalis* (Trichoptera). Freshwater Biology 50: 1022-1033

Finke, D. and Denno, R. 2002. Intraguild predation diminished in complex-structured vegetation: implications for prey suppression. Ecology 83:643-652

Finke, D. and Denno, R. F. 2003. Intra-guild predation relaxes natural enemy impacts on herbivore populations. Ecological Entomology 28: 67-73

Fjellheim, A. 1980. Differences in drifting of larval stages of *Rhyacophila nubila* (Trichoptera). Holarctic Ecology 3: 99-103

Flint, O.S., 1962. Larvae of the caddis fly genus *Rhyacophila* in eastern North America (Trichoptera: rhyacophilidae) Proceedings of the United States National Museum 113: 465-493

Giller, P.S. and Malmqvist,B. 1999. The Biology of Streams and Rivers. Oxford University Press 304pp

Griswold, M.W. and Lounibos, L.P. 2006. Predator identity and additive effects in a treehole community. Ecology 87: 987-995

Gustafson, M. P. 1993. Intraguild predation among larval plethodontid salamanders: a field experiment in artificial stream pools. Oecologia 96: 271-275

Hall, R.O., Wallace, J.B. and Eggert, S.L. 2000. Organic matter flow in stream food webs with reduced detrital resource base. Ecology 81: 3445-3463

Hall, R.J., Likens, G.E., Fiance, S.B. and Hendrey, G.R. 1980. Experimental Acidification of a stream in the Hubbard Brook experimental forest, New Hampshire. Ecology. 61: 976-989

HilleRisLambers. R., van de Koppel, J. and Herman P.M.J. 2006. Persistence despite omnivory: benthic communities and the discrepancy between theory and observation. Oikos 113: 23-32

Holt, R. and Polis, G. 1997. A theoretical framework for intraguild predation. The American Naturalist 149: 745-764

Holt, R. and Huxel, G. 2007. Alternative prey and the dynamics of intraguild predation: theoretical perspectives. Ecology 88: 2706-2712

Huhta, A, T. Muotka, A. Juntunen and Yrjonen, M. 1999. Behavioural interactions in stream food webs: the case of drift-feeding fish, predatory invertebrates and grazing mayflies. The Journal of Animal Ecology 68: 917-927

Irons, J. 1988. Life history patterns and trophic ecology of trichoptera in two Alaska (U.S.A.) subarctic stream. Canadian Journal of Zoology 66: 1258-1265

Janssen, A., Sabelis, M.W., Magalhaes, S., Montserrat, M. and van der Hammen, T. 2007. Habitat Structure Affects Intraguild Predation. Ecology 88: 2713-2719

Karl, T., and Hilsenhoff, W. 1979. The caddisflies (Trichoptera) of Parfrey`s glen creek, Wisconsin. Transactions of the Wisconsin Academy of Sciences, Arts and Letters 67: 31-42

Kiffney, P.M. 2008. Response of lotic producer and consumer trophic levels to gradients of resource supply and predation pressure. Oikos 117: 1428-1440

Kiffney, P.M., Richardson, J.S. and Bull, J.P. 2003. Responses of periphyton and insects to experimental manipulation of riparian buffer width along forest streams. Journal of Applied Ecology. 40: 1060-1076

Kimbrell, T., Holt, R.D. and Lundberg, P. 2007. The influence of vigilance on intraguild predation. Journal of Theoretical Biology 249: 218-234

Kobuszewski, D., and Perry, S. 1994. Secondary production of *Rhyacophila minora, Ameletus sp.,* and *Isonychia bicolour* from streams of low and circumneutral pH in the Appalachian Mountains of West Virginia. Hydrobiologia. 273: 163-169

Lavandier, P. and Cereghino, R. 1995. Use and partition of space and resources by two coexisting *Rhyacophila* species (Trichoptera) in a high mountain stream. Hydrobiologia 300: 157-162

MacNeil, C., Dick, J.T.A. and Johnson, M.P. 2004. A species invasion mediated through habitat structure, intraguild predation, and parasitism. Limnology and Oceanography 49: 1848-1856

Malmqvist, B. and Sjostrom, P. 1984. The microdistribution of some lotic insect predators in relation to their prey and to abiotic factors. Freshwater Biology 14: 649-656

Manuel, K. and Folsom, T. 1982. Instar sizes, life cycles, and food habits of five *Rhyacophila* (Trichoptera: Rhyacophilidae) species from the Appalachian Mountains of South Carolina, U.S.A. Hydrobiologia 97: 281-285

Martin, I. 1985. Microhabitat selection and life cycle patterns of two *Rhyacophila* species (Trichoptera: Rhyacophilidae) in southern Ontario streams. Freshwater Biology 15:1-14

Martin, I. and Mackay, R.. 1982. Interpreting the diet of *Rhyacophila* larvae (Trichoptera) from gut analyses: an evaluation of techniques. Canadian Journal of Zoology 60:783-789

Martin, I. and Mackay, R. 1983. Growth rates and prey selection of two congeneric predatory caddisflies (Trichoptera: Rhyacophilidae) Canadian Journal of Zoology 61: 895-900

McIntosh, A.R. and Peckarsky, B.L. 1999. Criteria determining behavioural responses to multiple predators by a stream mayfly. Oikos 85: 554-564

Meissner, K., Juntunen, A., Malmqvist, B. and Muotka, T. 2009. Predator-prey interactions in a variable environment: responses of a caddis larva and its blackfly prey to variations in stream flow. Annales Zoologici Fennici 46: 193-204

Merritt, R.W., Cummins, K.W., and Berg, M.B. (Eds) 2008. An introduction to the Aquatic Insects of North America, 4th edn. Kendall/Hunt, Dubuque.

Montserrat, M., Magalhaes, S., Sabelis, M.W., de Roos, A.M. and Janssen, A. 2008. Patterns of Exclusion in an intraguild predator-prey system depend on initial conditions. Journal of Animal Ecology 77: 624-630

Morin, P. 1999. Productivity, Intraguild Predation, and Population Dynamics in Experimental Food Webs. Ecology 80: 752-760

Muotka, T. 1993. Microhabitat use by predaceous stream insects in relation to seasonal changes in prey availability. Ann. Zool. Fennici 30:287-297

Muotka, T., Juntunen, A. and Meissner, K. 2006. Differential vulnerability determines the diet of a slow-moving predatory stream insect. Freshwater Biology 51: 1486-1495

Otto, C. 1993. Long-term risk sensitive foraging in *Rhyacophila nubila (*Trichoptera) larvae from two streams. Oikos 68: 67-74

Palumbo, A.V., Mulholland, P.J. and Elwood, J.W. 1987. Extraction with DMSO to Simultaneously Measure Periphyton Photosynthesis, Chlorophyll, and ATP. Limnology and Oceanography 2(32) 464-471

Polis, G., Myers, C. and Holt, R. 1989. The ecology and evolution of intraguild predation: potential competitors that eat each other. Annual Review of Ecology and Systematics 20: 297-330

Raymond, B. Darby, A.C. and Douglas, A.E. 2000, Intraguild Predators and the Spatial Distribution of a Parasitoid. Oecologia 124: 367-372

Rosi-Marshall, E.J. and Wallace, J.B. 2002. Invertebrate food webs along a stream resource gradient. Freshwater Biology 47: 129-141

Shapas, T.J. and Hilsenhoff, W.L. 1976. Feeding habits of Wisconsin's predominant lotic Plecoptera, Ephemeroptera and Trichoptera. The Great Lakes entomologist 9: 175-188

Singh, M., Smith, S. and Harrison, A. 1984a. Life cycles, microdistribution, and food of two species of caddisflies (Trichoptera) in a wooded stream in southern Ontario. Canadian Journal of Zoology 62(12): 2582-2588.

Singh, M., Smith, S. M. and Harrison, A.D. 1984b. Emergence of some caddisflies (Trichoptera) from a wooded stream in southern Ontario. Hydrobiologia 112: 223-232

Sircom, J. and Walde, S.J. 2009. Intraguild interactions and large-scale population patterns. Journal of the North American Benthological Society 28: 649-658

Sircom, J. and Walde, S.J. 2011. Niches and neutral processes contribute to the resource-diversity relationships of stream detritivores. Freshwater Biology 56: 877-888

Strickland, J.D., and Parsons T.R. 1972. A practical handbook of seawater analysis, 2nd ed. Bull. Fish. Res. Bd. Can. 167pp

Taniguchi, Y., Dausch, K. and Nakano, S.. 2002. Size-structured interactions between native and introduced species: Can intraguild predation facilitate invasion by stream salmonids?. Biological Invasions 4: 223-233

Tokeshi, M. and Pinder, L. 1985. Microhabitats of stream invertebrates on two submersed macrophytes with contrasting leaf morphology. Holarctic Ecology 8: 313-319

Thut, R. 1969. Feeding habits of larvae of seven *Rhyacophila* (Trichoptera: Rhyacophilidae*)* species with notes on other life-history features. Annals of the Entomological. Society of America 62: 894-898

Vandermeer, J. 2006. Omnivory and the stability of food webs. Journal of Theoretical Biology 238: 497-504

von May, R., Reider, K.E. and Summers, K. 2009. Effect of body size on intraguild predation between tadpoles of bamboo-breeding poison frogs and predaceous mosquito larvae. Journal of Freshwater Ecology 24: 431-435

Wasmund, N., Topp, I. and Schories, D. 2006. Optimising the storage and extraction of chlorophyll samples. Oceanologia. 48 (1): 125-144

Webster, J.R., Benfield, E.F., Ehrman, T.P., Schaeffer, M.A., Tank, J.L., Hutchens, J.J. and D'Angelo, D.J. 1999. What happens to allochthonous material that falls into streams? A synthesis of new and published information from Coweeta. Freshwater Biology 41: 687-705

Wissinger, S.A., Sparks, G.B., Rouse, G.L., Brown, W.S. and Steltzer, H. 1996. Intraguild predation and cannibalism among larvae of detritivorous caddisflies in subalpine wetlands. Ecology 77: 2421-2430

Wiggins, G.B. 2004. Caddisflies: the Underwater Architects. University of Toronto Press. Toronto. 292pp.

Wolfshaar, van de K.E., Roos, A.M. and Persson, L. 2006. Size-dependent interactions inhibit coexistence in intraguild predation systems with life-history omnivory. The American Naturalist 168: 62-75

Woodward, G. and Hildrew, A.G.. 2002. Body-size determinants of niche overlap and intraguild predation with a complex food web. Journal of Animal Ecology 71: 1063-1074

Wotton, R, M. Wipfli, L. Watson, and Merritt, R. 1993. Feeding variability among individual aquatic predators in experimental channels. Canadian Journal of Zoology 71: 2033-2037