2013

DIET COMPARISON AMONG NATIVE AND INTRODUCED SALMONIDS IN A TRIBUTARY TO LAKE SUPERIOR

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Recommended Citation
Howard, Julie L., "DIET COMPARISON AMONG NATIVE AND INTRODUCED SALMONIDS IN A TRIBUTARY TO LAKE SUPERIOR" (2013). *All NMU Master's Theses*. 412.
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DIET COMPARISON AMONG NATIVE AND INTRODUCED SALMONIDS IN A TRIBUTARY TO LAKE SUPERIOR

By

Julie L. Howard

THESIS

Submitted
To
Northern Michigan
University
In partial fulfillment of the
requirements
for the degree
of

MASTER OF BIOLOGY

Office of Graduate Education and Research

2013

SIGNATURE APPROVAL FORM

Title of Thesis: DIET COMPARISON AMONG NATIVE AND INTRODUCED SALMONIDS IN A TRIBUTARY TO LAKE SUPERIOR

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ABSTRACT

DIET COMPARISON AMONG NATIVE AND INTRODUCED SALMONIDS IN A TRIBUTARY OF LAKE SUPERIOR

By

Julie L. Howard

Nonnative salmonid introductions to Lake Superior and its tributaries have led to questions about potential competition with native brook trout (*Salvelinus fontinalis*). I examined invertebrate drift composition changes throughout one year in three habitat areas (beaver ponds, high and low gradient areas) and analyzed the diet composition, prey selectivity and diet overlap of three species of salmonids: brook trout, steelhead trout (*Oncorhynchus mykiss*), and coho salmon (*O. kisutch*). Invertebrate drift density and other drift metrics were 2-3 times higher in the summer than in the winter months; invertebrate drift metrics also varied with habitat and were 50-75% lower in the beaver ponds. Drift composition varied throughout the year and tended to reflect emerging invertebrates of both terrestrial and aquatic varieties. Prey selectivity was characterized more by avoidance of numerous, smaller prey items than by the positive selection of items from the drift. Diet overlap was 30% higher in the summer, reflecting the increase in available prey items in the drift and was highest among intracohort conspecifics. Young of year coho salmon are intermediate between age 1 and YOY fishes of other species with respect to prey consumed. Steelhead trout and brook trout, within a cohort, consumed very similar prey throughout the study. I found that there are

potential mechanisms for both introduced species to be negatively affecting the brook trout through prey and habitat resource overlap.

ACKNOWLEDGMENTS

This thesis follows the format prescribed by the *Canadian Journal of Fisheries and Aquatic Sciences* and the NMU Department of Biology as well as the Office of Graduate Studies.

The author wishes to thank the NMU Biology Department and the National Park Service as well as the Northern Michigan University Excellence in Education and Spooner grant programs and the Kalamazoo Valley Chapter of Trout Unlimited for additional funding.

I thank the members of my committee: Dr. Alan Rebertus, Dr. Alec Lindsay and my thesis advisor Dr. Jill B.K. Leonard for supporting this project. I thank the large force of volunteer faculty, graduate and undergraduate students, many of which were associated with the NMU fish lab, that helped make this project possible with special thanks to Joseph Gerbyshek, Anna Varian, Chris Gagnon, Carla Vitale, Andy Jasonowicz, Kevin Duby and Alexis Raney.

Most of all, without the love, patience and support of my fella, Chris Butler, this project would never have been completed.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF ABBREVIATIONS

ANOVA: Analysis of Variance

CCA: Canonical Correspondence Analysis

K: Fulton's Condition Factor

K-W: Kruskal-Wallis

LSD: Least Significant Difference

M: Molarity

NEI: Net Energy Intake Rate

OFT: Optimal Foraging Theory

PIRO: Pictured Rocks National Lakeshore

SE: Standard Error

TL: Total Length

V: Volts

W_r: Relative Weight

W_s: Length-specific Standard Weight

YOY: Young-of-year

CHAPTER ONE: LITERATURE REVIEW

Historical Background

Lake Superior is the largest and northernmost of the Laurentian Great Lakes and is one of the largest freshwater lakes in the world. It is generally considered oligotrophic with low productivity resulting from low water temperatures, an abbreviated growing season and deep waters. There are over 80 species of fishes (Minnesota Sea Grant, 2011) that currently populate the lake including native species, such as brook trout (*Salvelinus fontinalis*), lake trout (*Salvelinus namaycush*) and lake whitefish (*Coreogonus clupeaformis*), as well as nonnative introduced species such as steelhead trout (*Oncorhynchus mykiss*), coho salmon (*Oncorhynchus kisutch*), sea lamprey (*Petromyzon marinus*), and round goby (*Neogobius melanostomus*).

Of the native salmonids inhabiting Lake Superior, only the brook trout is found in both the lake and its tributaries. There is considerable variation in the life history of brook trout within Lake Superior and its drainages (McLaughlin 2001). Variants include stream resident brook trout that spend their entire life cycle in their natal streams, adfluvial brook trout that migrate from lake habitat into tributaries for spawning (Northcote 1997), and lacustrine brook trout that complete their life cycle within the lake habitat. The adfluvial and lacustrine forms are referred to locally as coaster brook trout, or coasters (Becker 1983), because of their tendency to occupy near shore areas. The lake use of the coaster typically results in a larger body size compared to the average resident brook trout and they have, therefore, been considered a valued sport fishery. Although coaster brook trout were historically abundant in Lake Superior, and were an important fishery in the Great Lakes region in the mid 1800's (Roosevelt 1865), by the early 1900's the coaster populations in Lake Superior declined dramatically (Hansen 1994). The decline in the coaster population is thought to be due to overfishing as well as the loss of spawning habitat through logging and mining activities (Horns et al. 2003) and the introduction of nonnative organisms, particularly nonnative salmonids (Rose 1986).

Many nonnative salmonids were intentionally introduced into the Great Lakes to increase sport fishing opportunities and provide controls on introduced prey fish (Emery 1985). Some fishes such as steelhead (rainbow) trout and brown trout (*Salmo trutta*) were intentionally introduced as early as the 1890's while other species such as coho salmon were introduced as late as 1965 (Emery 1985). Some introductions were accidental, as was the case with pink salmon (*O. gorbuscha*) which escaped a fish hatchery into Lake Superior is 1956 (Mills et al. 1994). In Lake Superior and its drainages, *O. mykiss* show two life history patterns: resident stream fishes are referred to as rainbow trout and spend their entire life cycle in their natal streams, while adfluvial fishes, referred to as steelhead trout, migrate from natal streams to the lake and back again for spawning. All coho salmon are adfluvial within Lake Superior and its tributaries. Along with the native brook trout, these introduced species use stream habitat for spawning and rearing (Peck 1970; MacCrimmon and Gots 1972; Greeley 1932). Since the introductions of these fishes, brook trout have declined in distribution in the region (Hudy et al. 2008; Fausch 1988; Rose 1986); resident stream brook trout are still widespread in the drainages of Lake Superior, but coasters are less abundant (Hansen 1994). There are surviving populations of coaster brook trout around Lake Superior in the Salmon Trout River, Big Siskiwit River and Tobin Harbor (Isle Royale National Park), Thunder Bay tributaries, Nipigon River, Lake Nipigon and in Pictured Rocks National Lakeshore (Huckins et al. 2008). The area of focus for this study was Pictured Rocks National Lakeshore (PIRO) where adfluvial coasters have been documented within three tributaries: Sevenmile Creek, Mosquito Creek and Hurricane Creek (Leonard et al. 2013, Kusnierz et al. 2009). Sevenmile Creek was selected for this study.

Life Histories

Brook trout

Brook trout are iteroparous and spawn in the fall as photoperiod and water temperatures decline (Power 1980). The preferred habitat for redd construction consists of small gravel and sand substrate where upwelling of groundwater occurs. Mature females can deposit approximately 300 to 400 eggs per season (Becker 1983). The incubation period varies depending on water temperature, but can be up to 165 days at 2.8°C (Becker 1983). After hatching, larvae remain in the nest until the yolk is fully absorbed. Emergence may occur as early as January or as late as April depending on conditions. Young-of-year (YOY) and age one adfuvial coasters and resident brook trout have similar life histories and they coexist in tributaries (Becker 1983); adfluvial coasters mostly move into the lake in the fall of their second year (Huckins and Baker

2008, Kusnierz et al. 2009). Female brook trout reach sexual maturity at approximately four years of age while males mature at approximately three years of age (Power 1980). Brook trout are capable of surviving in water temperatures ranging from 0-24°C; however, they thrive at temperatures between 10-15°C (Power 1980).

Studies of adult and juvenile brook trout, both in the field and in a laboratory setting, indicate that they prefer slower velocity pool habitat (Becker 1983; Cunjak and Green 1983, 1984; Magoulich and Wilzbach 1998a, 1998b) with access to woody debris or other forms of in-stream cover (Power 1980; Becker 1983; Cunjak and Green 1983; Cunjak 1996). Larson and Moore (1985) and Rose (1986) found that YOY brook trout were generally found near the bottom in shallow low current areas.

Steelhead trout

Steelhead trout are generally considered semelparous; however, some populations show varying rates of iteroparity (Narum et al. 2008). The timing of spawning varies with location, but in Lake Superior steelhead trout typically spawn in the spring when water temperatures are rising (Becker 1983), although smaller fall runs have been documented (Dubois et al. 1989). The preferred habitat for redd construction consists of small gravel and sand substrate (Becker 1983). Mature females over 500 mm total length may deposit up to 3800 eggs (Niemuth 1970). The incubation period varies with water temperature, but incubation will last about 80 days at 4.4°C (Becker 1983). After hatching larvae emerge from the gravel within two to three weeks (Becker 1983) and emergence has been documented to occur from May to July (Rose 1986). Some fish become resident stream fishes, not migrating out of the stream (rainbow trout), while those termed ‘steelhead’ migrate into the lake sometime before their second winter (Becker 1983). Steelhead trout (and rainbows) may reach sexual maturity at three years of age depending on the available resources and growth rate (Becker 1983). Steelhead trout are capable of surviving in water temperatures ranging from 0-28.3°C; however, they thrive at temperatures between 15-21°C (Becker 1983).

Juvenile steelhead trout are found in shallow low velocity areas with a substrate of gravel covered by cobble, woody debris or leaves (Larson and Moore 1985; Rose 1986). Everest and Chapman (1972) observed that young-of-year steelhead trout dispersed into faster moving water when they grew large enough. Larger steelhead trout, both residents and migrants, typically show a preference for faster, shallower waters in stream systems (Bisson et al. 1988).

Coho salmon

Coho salmon are semelparous and perish after spawning (Becker 1983). They spawn in the fall at approximately the same time as brook trout. Preferred habitat for redd construction is typically near the start of a riffle with small and medium gravel for substrate (Becker 1983). Mature females have an average of 3800 eggs depending on size (Avery 1974). The incubation period varies with water temperature, but may be up to 150 days at 0-2°C (Avery 1974). After hatching larvae emerge from the gravel two to three weeks after the yolksac has been absorbed and typically emerge two months prior to brook trout (Young 2004) from November to March. Sometime after a year in the stream, coho salmon smolts migrate downstream and out to Lake Superior where they remain before returning to a stream to spawn (Becker 1983).

Laboratory and field studies have shown that while in streams, coho salmon tend towards pool habitat with deep, slow-moving waters (Becker, 1983; Cunjak and Green, 1983, 1984; Bisson et al. 1988).

Invertebrate drift

Salmonids will feed on many prey items including aquatic insects, terrestrial insects, crustaceans, fish and annelids (Becker 1983), but as visually orientated predators they seem to prefer drifting invertebrates to other prey (Nilsson 1957; Larson et al. 1995). Any organism that is transported downstream by the current is considered part of the drift (Needham 1930). Drifting invertebrates may include dead or dying terrestrial invertebrates as well as adults and larvae or nymphs of the following aquatic orders depending on the season, habitat and time of day: Ephemeroptera (mayflies), Trichoptera (caddisflies), Plecoptera (stoneflies), Diptera (flies), Coleoptera (beetles), and Hemiptera (true bugs) (Needham 1930; Becker 1983; Bechara et al. 1993; LaVoie IV and Hubert 1994; Hilderbrand and Kershner 2004). Invertebrate drift can be categorized, according to Waters (1965), into three groups: catastrophic drift resulting from disturbance of the benthos (floods, water temperature surges, etc), constant drift which is the continual drift of low numbers of most species of stream invertebrates, and behavioral drift demonstrated by characteristic patterns of behavior resulting in a predictable diel periodicity.

Drift density and composition varies with the time of day and is mostly dependent on behavioral drift (McLay 1968; Clifford 1972; Huryn et al. 2008). Diel patterns in the drift can be attributed to two different types of behavior. The first is true behavioral drift where individuals launch themselves into the current at a specific time of day or night as a means of relocation to areas with more favorable conditions and resource availability. The second type of behavior reflects the increase in activity of invertebrates, for example during active foraging, at certain times of the day or night which inevitably leads to a higher likelihood of accidental drift due to risky behavior (Huryn et al. 2008). LaVoie and Hubert (1994) were able to show that some aquatic invertebrates are selective about when, during the day or night, they drift. They showed an increase in drift density beginning at sunset through the night and just before morning with lower densities throughout the daylight hours. Many studies point to aquatic invertebrates preferring to enter the drift when the risk of being eaten by drift-feeding fishes is low; drift increases at night when visibility is low (Flecker 1992; McIntosh et al. 2002; McIntosh and Peckarsky 1996).

Not only does drift composition and density vary with time of day, but drift shows variation with the seasons as well. Seasonal variation in drift density and composition is common in temperate zones and drift abundance is typically higher in the summer and lowest in the winter (McLay 1968; Clifford 1972; Brittain and Eikeland 1988). Part of the reason for the increase in drift in the summer is the increase of terrestrial invertebrate input into the stream which has been shown to be a substantial contributor to the drift during the summer, spring, and fall (Nakano et al. 1999a; Kawaguchi and Nakano 2001, Allan et al. 2003; Romaniszyn et al. 2007). Terrestrial invertebrate input is seasonally variable, but also varies depending on the composition of overhanging vegetation. Allan et al. (2003) showed that there were differences in terrestrial invertebrate composition and density between deciduous overhanging vegetation and coniferous overhanging vegetation. Similarly, Kawaguchi and Nakano (2001) and Edwards and Huryn (1996) showed that stream sections with trees had more terrestrial input than stream sections with mostly grasses as overhanging vegetation.

A similar pattern is seen within the aquatic invertebrate component of the drift which shows variation in composition and density according to streambed substrate and water velocity. Aquatic invertebrates flourish in cool water streams (Resh et al. 2008) with intermingling swift and slow velocity areas (Minshall and Minshall 1977). The variation in flow results in the deposition of an assortment of different size substrata (e.g. sand, gravel, cobble, boulders); areas with heterogeneous substrata have more available invertebrate microhabitats than areas with more homogenous substrata (Pennak and Van Gerpen 1947; Ward 1975; Flecker and Allan 1984; Jowett et al. 1991). Sections of a stream with low velocity and a small array of available substrata have lower drift densities than areas with high substrata diversity and high velocity (Flecker and Allan 1984; Jowett et al. 1991).

Salmonidae foraging

Salmonids are visually oriented predators which, in streams, primarily feed from the invertebrate drift. When drifting invertebrate densities are high salmonids will forage from the drift, however, during periods of low drift density as occurs in the winter, foraging may focus on benthic, or bottom-dwelling, invertebrates (Nakano et al. 1999b). Salmonid foraging often follows the diel pattern of invertebrate drift and foraging occurs during early morning and evening periods of low light (Becker 1983);

salmonids feed when both visibility and drift density are fairly high. Successful capture of prey items from the drift is influenced by many factors including water velocity, temperature, depth, turbidity, and interspecific/intraspecific competition (Cunjak et al. 1987; Hughes and Dill 1990; Sweka and Hartman 2001).

Fishes are more successful at capturing prey from the drift when invertebrate density is high; however, an increase in either turbidity or water velocity influences prey capture success by decreasing the fish's ability to successfully locate and capture prey from the drift. Sweka and Hartman (2001) showed that the ability of fish to detect prey declined as turbidity increased, reflecting a decline in the prey detection distance of brook trout to drifting invertebrates. Piccolo et al. (2008) also showed a decline in prey detection distance followed by a decline in prey capture probability with increasing water velocity; as water velocity increases prey capture success also declines. Hill and Grossman (1993) delved into the effects of net energy intake rate (NEI) on the selection of foraging locations and showed that rainbow trout chose locations with intermediate velocities for foraging, but maintained foraging positions within lower velocity areas, possibly to limit energy expenditure. Water depth has also been implicated as affecting prey capture success; however, as Piccolo et al. (2007) surmised, the increase in prey captured with increasing depth was due to the increase in prey encounter rate. As depth increases velocity tends to decrease which directly affects the size, or volume, of the foraging area where a fish may encounter prey. An increase in foraging area size potentially results in an increase in prey encounter rate and therefore an increase in capture success (Piccolo et al. 2007).

Water temperature influences foraging strategy for fishes; although capture success has not been directly related to water temperature, most fish are ectotherms whose body temperature fluctuates with the ambient temperature. Changes in body temperature heavily influence biological processes and both gastric evacuation rate and metabolic rate are affected which may, in turn, change the amount and frequency of prey consumption necessary to maintain condition and growth. Gastric evacuation rates, or how rapidly prey items are digested, have been shown to increase along with water temperature in many species; however, the relationship between water temperature and gastric evacuation rate varies depending on fish size, species, and prey (Elliot 1972; Ruggerone 1989; Benkwitt et al. 2009; Principe et al. 2007). Metabolic rates have been shown to increase with increasing ambient temperature for many organisms (Krogh 1916), and Smith et al. (1978) illustrated this pattern well for fishes, including salmonids. As temperature increases, energy intake must increase, but once temperatures reach the upper optimal threshold for fishes, the energy intake increases at a slower rate than maintenance requirements and the fish is at a disadvantage. Many abiotic factors affect the successful foraging of fishes in natural systems, yet they are able to survive and, in many situations, thrive.

Organisms must expend less energy than they consume in order to grow and reproduce. In aquatic systems, fishes select for microhabitat sites that provide access to prey while minimizing the energy needed to maintain their foraging position in the water column (Guensch et al. 2001). The Optimal Foraging Theory (OFT) assumes that organisms will forage by selecting for prey items that will maximize the rate of energy intake while minimizing costs associated with searching and capturing prey (Beauchamp et al. 2007) and that an organism will consume the most prey possible in any given unit of time (MacArthur and Pianka 1966). Salmonid prime foraging locations within stream systems are sites where prey encounter rates are high and where fish can maintain position within the water column with minimal energy expenditure, or areas with a low velocity microhabitat bordered by areas of medium to high water velocity. Fausch (1984) showed that fishes selected foraging locations that maximized the net energy intake rate (NEI) by providing adequate access to prey while requiring minimal energy expenditure. Typically these sites are in and among large woody debris and other substrates or along the shoreline where low velocity habitat is available due to the obstruction of flow (Inoue and Nakano 2002; Nislow et al. 1999; Cunjak and Green 1984; Hill and Grossman 1993; Baker and Coon 1997). Riley and Fausch (1995) showed that the addition of large woody debris to a system led to an increase in low velocity pool habitat resulting in a higher density of trout or higher usage. Identification of these preferred foraging locations is an important tool in determining potential foraging strategy.

When salmonids select foraging locations in streams there may be agonistic interactions among individuals seeking to occupy the same location. These interactions lead to a size-mediated dominance hierarchy where the larger fishes (either by total length or mass) select prime foraging locations while the positions taken up by subordinate, smaller fishes are determined by the net energy intake rate (NEI) available at each position (Hughes 1992; Nakano 1994; Fausch 1984). Prey availability is directly related to foraging location in that preferred sites may offer access to larger or more frequent invertebrates in the drift (Fausch 1984). As the dominance hierarchy is determined by aggressive interactions among individuals, typically the dominant individual is the largest and selects the foraging location with the highest potential NEI (Faush 1984; Nakano 1995). Although adult or subadult fishes within a pool or reach compete for positions within the hierarchy and tend to prefer deeper or faster flowing water (Bisson et al. 1988; Everest and Chapman 1972), some fishes, particularly YOY fishes, show preferences for foraging locations with different habitat characteristics. Preferred YOY foraging locations are characterized by slower moving waters along the edges of streams (Hartman 1965; Cunjak and Green 1984; Fausch and White 1986; Rose 1986). As these individuals grow in size they will join the struggle for a foraging site and establish a place in the existing hierarchy.

Shoreline, low velocity areas provide good foraging locations for young fishes and may offer slight protection from predation as the fishes begin to forage from the drift. As individuals age and grow, the fish gain experience in foraging and become more successful at capturing prey as well as determining which prey is suitable (Godin 1978; McLaughlin et al. 2000; Blaxter 1986). McLaughlin et al. (2000) showed that as fish age and gain foraging experience foraging success and efficiency increase. This effect could be, in part, influenced by an increase in gape size (Wankowski 1979) which leads to a larger range of prey available for consumption.

Interspecific interactions

The tributaries of Lake Superior may provide adequate rearing habitat for adfluvial fishes and resident fishes alike; however, in seasons and years when resources are limiting the potential for competitive interactions exists. Rose (1986) illustrated a decline in the growth of brook trout which coincided with the emergence of steelhead trout in the spring and pointed out that those fishes shared both habitat and prey resources. Rose (1986) also found that the taxonomic composition of the diets of young-of-year steelhead trout and brook trout were very similar and that those fishes occupied the same shallow areas along the banks of streams until growing large enough to disperse. The sympatric salmonids focused on during this study forage from the drift if invertebrate drift density is adequate; however, when resource availability declines, as was investigated by Fausch et al. (1997), the subordinate species may shift to a secondary foraging strategy such as benthic feeding. Shifts in foraging strategy may be recognizable in diet comparison studies as a shift in prey items within stomach samples in combination with declines in invertebrate drift density.

Studies of sympatric populations of introduced rainbow trout (steelhead) and native brook trout in the Great Smoky Mountains National Park illustrated a pattern in which the areas in the stream that the brook trout occupy declined and were limited to upstream sections while rainbow trout occupied the downstream areas (Larson and Moore 1985). Prior to the introduction of rainbow trout, the brook trout utilized the entire stream. A similar pattern of brook trout distribution has been documented in Sevenmile Creek in PIRO, but the mechanisms explaining the assumed shift in distribution are still unknown (J. Leonard, Northern Michigan University, pers. comm.). Illustrating the extent of diet overlap and similarities in prey selectivity may help determine if an overlap in preferred prey resources could be a contributing factor to spatial segregation and may shed some light on the potential for competition between species.

The potential for competition between brook trout and coho salmon also exists as both species share an affinity for deep pool type habitat (Becker 1983; Cunjak and Green 1983, 1984; Bisson et al. 1988). Since coho salmon only reside in Sevenmile Creek for a little over one year (J. Leonard, Northern Michigan University, pers. comm.), negative effects on the brook trout may be more limited temporally when compared to the effects of steelhead trout on brook trout. Since both brook trout and coho salmon prefer similar habitat, there is potential for competitive exclusion for the subordinate species or individuals in the selection of both prey items from the drift and foraging locations within pool habitat (Fausch and White 1986). Coho salmon may also negatively affect brook trout during spawning season as both species spawn in the fall and prefer gravel areas for redd construction (Becker 1983). Salmonids that spawn simultaneously have been shown to disturb previously constructed redds and to superimpose new redds on top of old ones (Essington et al. 1998). Coho salmon invasions of tributaries for spawning have also been shown to disrupt normal brook trout movement within streams resulting in the temporary upstream migration of brook trout (Janetski et al. 2011)

Diet comparison metrics

Diet studies commonly examine metrics based on count or abundance of prey items within samples as well as the biomass of prey items within samples. Abundance estimates allow direct comparison of what type of prey are consumed while biomass estimates allow similar comparison, but take into account the size of each prey item. Neither abundance nor biomass provide insight into nutritional value of prey items in the diet of the fishes. Many studies will convert abundance and biomass into proportional values in order to eliminate biases due to differences in the quantities of items consumed among individuals.

Common comparisons made in diet studies include diet overlap indices as well as prey selectivity indices. The diet overlap index that Schoener (1970, 1971) developed requires very few assumptions and is commonly used (Crowder 1990). The index compares the proportion of each prey item consumed by species *A* versus what was consumed by species B. This index reflects a symmetrical overlap where the overlap of diet items of species *A* with species *B* is the same as the overlap of diet items of species *B* with species *A.* Asymmetrical indices are available, but are much more complicated and are accompanied by more assumptions (Crowder 1990). If overlap is very high then the species being compared may be selecting for and potentially competing for specific prey items, if they are in limited supply. If overlap is low then those species being compared could be consuming different prey and are not occupying overlapping niches, or it could also be reflecting a pattern where one species, the subordinate species, has shifted its diet in response to direct competition with the dominant species (Fausch et al. 1997). A diet overlap index alone is not sufficient in determining niche overlap among species as there can be some doubt as to the cause of high or low overlap indices.

Another analysis that can be used, in combination with diet overlap indices, to elucidate patterns in the diet with the potential to further explain the extent of niche overlap is prey selectivity. Prey selectivity indices are a comparison of the relative abundance of a prey item in the diet to the relative abundance of the same prey item in the environment (Bowen 1996). These indices are useful in determining if certain prey items were selected for, selected against (avoided), or consumed at the same frequency that they occurred in the environment. In combination with the diet overlap index, the prey selectivity index can shed some light on what prey items each species were interested in consuming or avoiding at times when diet overlap was high or low. For example, if diet overlap is high between species *A* and species *B* in the month of June, but not in August, the selectivity index may help identify a potential pattern in resource use. Perhaps an invertebrate was emerging as an adult in June and was vulnerable to predation with both species *A* and *B* focused on consuming while during August those same invertebrates were rare leading to a more varied diet for both species *A* and *B*. The selection of the emerging adult in June corroborates the high diet overlap value for that month while the lower selection values for August does the same for the low diet overlap values. Prey selectivity indices can be useful in determining patterns in diet, and they can be useful in determining the specifics of resource use in regards to niche overlap.

Summary

The purpose of this study was to determine whether native and introduced salmonids experience niche overlap through prey preference and diet composition. I examined which prey items each salmonid species consumed, how it was affected by habitat and how changes in drift availability through the year affected diet composition. This study focused on diet composition of sympatric steelhead trout and brook trout of two age classes as well as sympatric coho salmon young-of-year. The goal of the study was to determine whether there was potential for competition among the three salmonids and how each group of introduced fishes (age class and/or species) may have affected native brook trout of both age classes.

CHAPTER TWO: DIET COMPARISON AMONG NATIVE AND INTRODUCED SALMONIDS IN A TRIBUTARY TO LAKE SUPERIOR

Chapter Overview (Abstract)

Nonnative salmonid introductions to Lake Superior and its tributaries have led to questions about potential competition with native brook trout (*Salvelinus fontinalis*). I examined stream drift composition changes throughout one year within three habitat areas (beaver ponds, high and low gradient areas) and analyzed the diet composition, prey selectivity and diet overlap of three species of salmonids: brook trout, steelhead trout (*Oncorhynchus mykiss*), and coho salmon (*O. kisutch*). Invertebrate drift density and other drift metrics were 2-3 times higher in the summer than in the winter months; the invertebrate drift metrics also varied with habitat and were 50-75% lower in the beaver ponds. Drift composition varied throughout the year and was related to emerging invertebrates of both terrestrial and aquatic varieties. Prey selectivity was characterized by avoidance of more numerous, smaller prey items rather than by the positive selection of items from the drift. Diet overlap was 30% higher in the summer, coinciding with an increase in prey items in the drift and was highest among intracohort conspecifics. Coho salmon diets were intermediate between other age 1 and YOY fishes. Steelhead trout and brook trout within the same size class consumed very

similar prey throughout the study. I identified mechanisms that may allow both introduced species to negatively affect brook trout through prey and habitat resource overlap.

Introduction

In aquatic systems, the introduction of nonnative species, planned and unintentional, has had serious negative impacts on native communities affecting many organisms including microbes, plants, invertebrates and fishes (Colautti et al. 2006; Krueger and May 1991; Litchman 2010; Mills et al. 1994). The introduction of nonnative fish species has been shown to negatively impact native fish communities by a variety of mechanisms including interspecific competition, predation, and disturbance (Krueger and May 1991; Moyle and Light 1996). With the introduction of salmonids to streams and lakes of the eastern United States, declines in native brook trout (*Salvelinus fontinalis*) populations have been widespread from the Appalachians to the Great Lakes region (Fausch and White 1981, 1986; Fausch 1988; Larson and Moore 1985).

In Lake Superior and its tributaries, steelhead trout (*Oncorhynchus mykiss*) and coho salmon (*O. kisutch*) were intentionally introduced in 1895 and 1965, respectively, to increase sport fishing opportunities in the region (Emery 1985). The introduced fishes and brook trout utilize stream habitats for spawning and rearing (Peck 1970; MacCrimmon and Gots 1972; Greeley 1932). Declining brook trout distribution and density throughout their historical range may be related to anthropogenic influences such as habitat destruction due to water diversion, mining, logging, and overharvesting (Hudy et al. 2008; Larson and Moore 1985, Becker 1983) as well as negative interactions with introduced species resulting from competition for spawning, rearing and foraging habitat (Fausch 1988; Rose 1986).

Salmonids are visually oriented predators that, in streams, primarily feed from the invertebrate drift. The drift is composed of aquatic and terrestrial invertebrates floating downstream in the current (Nilsson 1957; Larson et al. 1995). Successful capture of prey items from the drift is influenced by many environmental factors including water velocity, temperature, depth, turbidity, successful foraging locations, and interspecific and intraspecific competition (Cunjak et al. 1987; Hughes and Dill 1990; Sweka and Hartman 2001). Fishes may increase their foraging efficiency by selecting a foraging location that provides the optimum combination of environmental factors resulting in increased access to prey and minimizing energy expenditure. Fish size is commonly an important factor when fishes vie for a prime foraging location; larger individuals typically dominate smaller fishes (Nakano 1994). Coho salmon fry emerge approximately two months earlier than brook trout in the spring resulting in a larger average body size (Young 2004). Laboratory and field studies have shown that coho salmon and brook trout have similar tendencies for occupation of pool habitat with deep, slow-moving waters (Becker 1983; Cunjak and Green 1983, 1984; Bisson et al. 1988). Coho salmon in these systems could be displacing brook trout from prime foraging locations, and diet analysis may help illustrate potentially negative interactions. Steelhead trout and brook trout fry emerge about the same time in the spring and are therefore very close in size when they begin to feed on drift (Rose 1986). Steelhead trout presence in streams may be depressing brook trout growth for the first few months until steelhead trout disperse into faster moving water when they grow large enough (Everest and Chapman 1972; Rose 1986). Again, describing diet composition of YOY and age 1 steelhead trout, brook trout and coho salmon could help illustrate any negative interactions resulting from shared spatial and prey resources.

As brook trout in the northern Great Lakes and in Lake Superior have dwindled, many of the introduced salmonids have flourished (Minnesota Sea Grant, 2011). Naturally reproducing salmonids now occupying Lake Superior share important spawning and rearing habitat in the lake's tributaries. The increase in habitat use in tributaries via spawning and rearing activities of introduced salmonids could be an important example of how introductions are negatively influencing the native resident and adfluvial brook trout. Information such as prey availability and fish distribution that is gathered in stream habitats which are shared by native and introduced salmonids can improve our understanding of why and how native fish populations are being affected by the introduction of non-native species.

In this paper I present information on prey availability, consumption, and selectivity of prey by native brook trout, and introduced coho salmon and steelhead trout within a Lake Superior tributary of Pictured Rocks National Lakeshore and assess overlap in resource use to characterize mechanisms for potential interspecific competition. This project examines the composition of available year-round invertebrate drift and the effects of seasonality and fish macrohabitat type on prey availability, diet composition, selectivity for prey items, and diet overlap between these salmonids.

Methods

Study Area

This study was conducted on Sevenmile Creek, a second order tributary of Lake Superior, located about 29 km west of Grand Marais, Michigan in Pictured Rocks National Lakeshore (PIRO; Figure 1). There was an exotic salmonid removal project ongoing in Sevenmile Creek that began in May of 2008 and ended in November of 2010 which coincided with this study.

PIRO's climate is characterized by mean summer temperatures of 21.7±5.9°C, mean spring/fall temperatures of 5.5±6.4°C, and mean winter temperatures of -5.6±4.9°C (National Park Service Website-PIRO). Annual precipitation averages about 88 cm of rain and about 357 cm of snowfall. The study area encompassed approximately 2.4 km of the creek from the mouth (46° 37'N, 86° 15'W) to the beaver pond areas upstream; the drainage basin lies at an altitude of approximately 210 m above sea level. The stream flows through hardwood-conifer boreal forest composed of eastern hemlock (*Tsuga canadensis*), northern white cedar (*Thuja occidentalis*), balsam fir (*Abies balsamea*), yellow birch (*Betula alleghaniensis*), red maple (*Acer rubrum*), American beech (*Fagus grandifolia*), and eastern white pine (*Pinus strobus*). The shoreline habitat in the beaver ponds is primarily northern white cedar and tag alder (*Alnus rugosa).*

Experimental Design

Habitat metrics were used to define the borders of three habitat areas within Sevenmile Creek: high gradient (closest to the mouth), low gradient, and beaver pond areas (farthest from the mouth). Both the high gradient and beaver pond areas were approximately 750 m of stream, while the low gradient area comprised approximately 600 m of stream. Beginning in May 2009, invertebrate drift sampling occurred within each habitat area for two consecutive evenings, once a month for twelve months. During each sampling event, two drift nets were set up within each habitat area (twelve samples per month). Drift net locations were randomly selected within a 150 m representative section of each habitat; net locations were different for each two-day sampling event.

Stomach content samples were collected on the first or second day of drift sampling once a month from May through November 2009. During each sampling event, within each habitat area, up to ten stomach samples were collected for each of the five fish categories included in this study: young-of-year (YOY) brook trout (age 0), age 1 brook trout, YOY steelhead trout, age 1 steelhead trout, and YOY coho salmon; no age 1 coho salmon were included because they leave the stream after approximately one year.

Habitat Sampling

Mean stream slope (gradient) was calculated for each habitat area using a laser level. Substrate sizes and proportions were determined for each habitat area using Wolman pebble counts collected over the study period throughout each habitat area (Kondolf and Li 1992). Mean slope (*ln* transformed), mean velocity (Marsh-McBirney Flo-Mate, Loveland, CO; May-November 2008-2009), substrate size and salmonid density (total, non-native and brook trout) were determined by month in each habitat area and compared using either Analysis of Variance (ANOVA) with a Least Significant Difference (LSD) for pre-planned comparisons of means or nonparametric Kruskal-Wallis test with Bonferroni-corrected Mann-Whitney U or Dunn's post-hoc tests to determine if there were differences among the three habitat areas. Mean water temperature for each habitat area was calculated by month using data collected over the study period (May-November 2009).

Invertebrate Drift Samples

Invertebrate drift samples were collected with aquatic drift nets (363 µm mesh; mouth opening 30 cm x 46 cm) set within a 150 m representative reach in each of the three habitat areas as previously described. The nets were placed 30 min before sunset and removed 30 min after sunset to encompass the time when invertebrate drift is high and fishes are feeding (Bechara et al. 1993; Hilderbrand and Kershner 2004). Water velocity was measured at the mouth of each drift net during each net set by recording the time it took for a cork to travel one meter (McMahon et al. 1996). The velocity measurement was used to calculate total water volume sampled and drift density (Hilderbrand and Kershnew 2004). Drift samples were collected, immersed in 95% alcohol and stored. Each sample was later inundated with a sucrose solution with a specific gravity of 1.12 (0.87 M), causing the invertebrates to float while the inorganic matter and organic matter settled to the bottom of the container (Anderson 1959). Invertebrates and other items such as larval fish and fish eggs were collected from the sucrose solution and the invertebrates were identified by life stage (larvae, pupae or adult), to order or family (when possible), enumerated, and head capsule width and length measured. Larval fish and fish eggs were identified to species. The origin (terrestrial versus aquatic) of the insects was also determined when possible. Terrestrial invertebrates were defined as any organism entering the water from the surface (winged adult insects or known terrestrial invertebrates). Aquatic invertebrates included all aquatic larvae and any adult aquatic invertebrates whose primary habitat is water (Hilderbrand and Kershner 2004). These definitions reflect the purpose of the study, the feeding strategies of fishes, and not necessarily the carbon source of the potential prey items.

Mean invertebrate abundance, density, richness, biomass, Simpson's diversity index, and proportion of terrestrial invertebrates (by biomass and abundance) were calculated for the drift within each habitat area for each month. Data were transformed using a fourth root transformation when necessary in order to satisfy normality requirements. These data were compared using either ANOVA with a LSD post-hoc test or nonparametric Kruskal-Wallis test with Dunn's post-hoc test to determine if there were differences among the drift in the three habitat areas.

Invertebrate length to biomass regression lines specific to life stage and family, previously published in the literature, were used to estimate biomass of drift samples (Baumgartner and Rothhaupt 2003; Benke et al. 1999; Burgherr and Meyer 1997; Gruner 2003; Hodar 1996; Johnson and Strong 2002; Meyer 1989; Miyasaka et al. 2008; Rogers et al. 1977; Sabo et al. 2002; Sample et al. 1993; Smock 1980; Appendix A). Order-specific length-biomass regressions were used when family level information was unavailable (Benke et al. 1999). Prey items were categorized, using biomass, into prey size categories (Table 1). The proportions of each prey size category within drift samples were calculated and used to determine fluctuations in availability. These data were compared using either ANOVA with a LSD post-hoc test or nonparametric Kruskal-Wallis test with Dunn's post-hoc test to determine if there were differences among the drift in the three habitat areas and within different months.

Fish Collection/Stomach Sampling

Within each habitat, up to ten fish from each fish category were collected by single pass backpack electrofishing (Badger model, University of Wisconsin, Madison, WI, USA; voltage range 225-350V) during each sampling event. Young-of-year fish (all species) were *a priori* defined as having a total length below 100 mm while age one fish were defined by a total length above 100 mm and below 180 mm (Kusnierz et al. 2009, Leonard unpublished data); time of year was also taken into account when determining fish age. Stomach content samples were collected using gastric lavage, a non-lethal and effective method for removal of stomach contents (Light et al. 1983; Strange and Kennedy 1981). Samples were taken from all fish fitting the age criteria, excluding fishes under 50 mm where the gastric lavage apparatus was too large to be used without mortalities (Hakala and Johnson 2004; Hodgson et al. 1989; Meehan and Miller 1978, Strange and Kennedy 1981). Regurgitation was induced by forcing up to 100 ml of water into the stomach of the fish using a syringe with a modified Pasteur pipette tip and the stomach flushing was continued until the regurgitated fluid was visually particle free. The stomach contents were collected in a plastic dish modified with a removable sieve sleeve (363 µm mesh) in one corner (Figure 2) which allowed for transfer of the sample from the dish into a sample jar via ethanol wash. The proportion of stomach contents removed using this technique on small salmonids has been reported in the literature as ranging from 93% (Meehan and Miller 1978) to 98.9% (Strange and Kennedy 1981). Each stomach content sample was placed in ethanol and fish category, location, total length, and weight were recorded. Stomach content samples were identified by life stage, to order and family (when possible), and enumerated. Other measurements included head capsule width and body length, when available, of all ingested invertebrates as well as the terrestrial or aquatic origin.

Invertebrates from stomach content samples were commonly identified by head capsule only. Using head capsule size from invertebrates collected in the drift, regression relationships predicting prey length were created; outliers were removed when they were more than 2.5 standard deviations from the regression line. Linear regressions were used unless the scatter plot had an obvious curve in which case polynomial regression was utilized to better fit the data. If the relationships were not statistically significant at the family level, a regression was created at the order level. Regressions including both larvae and pupae, due to higher R^2 values resulting from higher sample size, were utilized to calculate pupal lengths (Appendix B). Length, when missing, was then calculated for the invertebrates in the stomach content samples using the length-head capsule size regressions developed from drift samples. Biomass was calculated using the same length-biomass regressions used for the drift samples (Appendix A). Larval fish found in the stomach content samples were measured directly for biomass and mean biomass was calculated for these items. It should be noted that the larval longnose sucker (*Catostomus catostomus*) biomass utilized in this study was taken from individuals preserved in 95% ethanol; therefore, the biomass of these animals was most likely underestimated due to shrinkage from preservation (Fowler and Smith 1983). The mean mass of coho salmon and steelhead trout eggs was calculated using samples collected from Sevenmile Creek (K. Duby, NMU, unpublished data). Using total length and species, genus or family of ingested fish, biomass was estimated by calculating the mean mass of all fish of the same length and taxonomic group using data collected on Sevenmile Creek (2003-2010; Table 2).

The total number of individuals from each fish category was tallied, and mean total length and weight were calculated for each fish category. Fish condition for each was determined by calculating the mean Fulton's condition factor (K; Anderson and Neumann 1996) using the following equation:

$$K = (W/L^3)*100{,}000$$

where W is the weight (g) and L is the length (mm). Relative weight (W_r; Wege and Anderson 1978) was also calculated for age 1 fishes using the following equation:

$$W_r = (W/W_s)*100$$

where W is individual fish weight and W_s is a length-specific standard weight gathered from the literature. Young-of-year fishes were too small to be included in relative weight calculations as published W_s values for steelhead trout and brook trout are only valid for individuals over 120 mm (Hyatt and Hubert 2001; Pope and Kruse 2007; Blackwell et al. 2000). Fulton's condition factor and relative weight were compared among habitat areas for all appropriate fish categories using nonparametric Kruskal-Wallis tests and a Dunn's post-hoc test.

Common prey items in the stomach content samples were determined by calculating the proportion of each prey item category within stomach content samples separately for abundance data and biomass data. The total biomass in each stomach content sample was calculated and Pearson correlations were used to determine if relationships existed between total stomach biomass and habitat type, salmonid density, nonnative salmonid density, or brook trout density.

The abundance of individuals within each stomach, the richness present per stomach, terrestrial invertebrate proportion (by biomass and abundance), and biomass per stomach were compared by fish category and habitat area using ANOVA and LSD post-hoc tests where total length was used as a blocked covariate to correct for fish size. In cases when data were nonparametric, a Kruskal-Wallis test with Dunn's post-hoc test was used and no fish size correction was applied.

Stomach content proportions (abundance and biomass) were analyzed in Canoco 4.56 using Canonical Correspondence Analysis (CCA) with fish category, habitat area and month as environmental factors (Fairchild et al. 1998, Jackson 1997). The effects any differences in the number of prey items in stomach content samples may have had were negated by using proportion in these analyses. Each CCA was run with biplot scaling and interspecies distances. Rare prey items were down-weighted by the program and suppressed in the final representation; rare species were defined as prey items which occurred in less than 1% of the samples. Forward automatic selection was used to determine the order of importance of the environmental variables, and a Monte Carlo test was also performed with restricted temporal permutations. In Canodraw, all environmental variables were nominal and each environmental variable was classified into the appropriate category: month, habitat area or fish category.

In order to determine whether the fishes, by habitat or month, reflected a prey size preference, prey items in stomach content samples were re-categorized using the same technique described for the invertebrate drift (Table 1). Kruskal-Wallis tests with Dunn's post-hoc tests, one for each prey category, were run using fish category and habitat type or month as independent variables.

Diet overlap was calculated for each individual fish for each fish category combination (Table 3), such as coho salmon age 1 compared with young-of-year steelhead trout, per month, for each habitat type using the following equation:

$$C_{xy} = 1 - 0.5\left(\sum |p_{xi} - p_{yi}|\right)$$

where C_{xy} is the diet overlap index value, p_{xi} is the proportion of food type *i* used by species *x*, p_{yi} is the proportion of food type *i* used by species *y*, and the vertical bars result in absolute values of the difference. Values range between 0 and 1, with 0 indicating no overlap and 1 indicating complete overlap (Bowen 1996, Bozek et al. 1994, Schoener 1970, 1971). Kruskal-Wallis with Dunn's post-hoc tests were run to compare diet overlap by habitat area, month and FCC. Pearson's correlation was used to determine if there was a relationship between diet overlap and salmonid density, nonnative salmonid density, or brook trout density.

Prey selectivity for individual fish was calculated for both biomass and abundance data according to the linear food selection index (L) of Strauss (1979):

$L = r_i - p_i$

where r_i represents the relative proportion of a prey item *i* in the diet and p_i is the relative proportion of a prey item *i* in the stream based on drift sampling. This selectivity index ranges between -1 (complete avoidance) and +1 (strongly selected for). Kruskal-Wallis tests with a Dunn's post-hoc test were used to determine whether the highest maximum selection (highest value) and the highest avoidance (lowest value) were different among fish categories, month and habitat. Mann-Whitney U tests were used to compare the number of prey items selected for versus the number avoided for both count and biomass selectivity. A Kruskal-Wallis test with a Dunn's post-hoc test were used to determine if there were differences among the fish categories, month and habitat in the number of prey items selected for and avoided for both biomass and abundance selectivity.

Data Analysis

All analyses were performed using SPSS 17.0 (SPSS Inc., Chicago, Illinois USA), Sigmaplot 11.0 (Systat Software, Inc., San Jose, California USA, www.sigmaplot.com), Microsoft Excel (2010), and Canoco 4.56 (Microcomputer Power, Ithaca, New York USA). Alpha was set at 0.05 to determine significance in all statistical analyses.

Results

Habitat Sampling

The environmental metrics supported the establishment of the three different habitat types within the study stream: the high gradient areas were closest to the mouth of the stream, the beaver pond areas were furthest upstream and the middle reaches were intermediate, low gradient areas. The gradient was approximately three times higher (2.16±0.42%) in the high gradient areas than the low gradient areas (0.65±0.19%) and approximately four times higher than the beaver ponds (0.48±0.19%; Table 4). Velocity was approximately two times higher in the high gradient areas (0.73±0.05 m/s) than the low gradient areas (0.39±0.03 m/s) and approximately three times higher than the beaver ponds (0.24±0.02 m/s; Table 4). Water temperature appeared to increase downstream, but no significant differences were found among habitats (12.34-15.21°C; Table 4). Water temperatures measured within habitat areas fluctuated throughout the study ranging from 4°C in November to 19.9°C in the summer months. In the high gradient areas, larger substrate dominated the stream bed while low gradient areas showed a more variable substrate and beaver ponds were dominated by sand and silt (Figure 3). Mean salmonid density ranged from 0.00-0.17 fish/m^2 and did not differ among habitat areas (Table 5). Nonnative salmonid density ranged from 0.00-0.16 fish/m^2 and was lowest in the beaver ponds ($p=0.001$) while brook trout density ranged from 0.00-0.06 fish/m^2 and was highest in the beaver ponds ($p<0.001$; Table 5). As expected, brook trout density was slightly negatively correlated with nonnative salmonid density ($r=-0.199$, $p<0.001$).

Invertebrate Drift samples

Drift samples were composed of invertebrates from three different phyla and six classes. Within those six classes, there were approximately 18 orders collected with more than 79 families of invertebrates ranging in life stage from larval to adult. Over 31,000 invertebrates were collected from drift samples during the duration of the study (Appendices C, D).

Invertebrate drift samples taken throughout the study indicated that fewer prey items were available in beaver ponds. Invertebrate drift abundance was lowest in the beaver ponds (F=12.519, df=2, p<0.001), where invertebrate drift samples contained a median of 28.5 invertebrates/sample (range = 5-314), while high gradient area samples contained a median of 110 invertebrates/sample (18-12666) and low gradient area samples contained a median of 96 invertebrates/sample (12-305). Invertebrate density is the most reliable measurement when comparing habitats with varying water velocity because density takes into account the volume of water sampled. Invertebrate drift density was lowest in the beaver ponds (F=5.273, df=2, p=0.006) where samples contained a median density of 0.26 invertebrates/m^3 (0.04-2.52) while high gradient area samples contained a median density of 0.54 invertebrates/m^3 (0.07-58.79) and low gradient area samples contained a median density of 0.76 invertebrates/m^3 (0.04-5.33). Invertebrate richness in drift samples was lowest in beaver ponds (F=19.111, df=2, p<0.001) where samples contained a median richness of 10 invertebrate families/sample (4-24) while high gradient area samples contained a median richness of 21 families/sample (6-47) and low gradient area sampled contained a median richness of 20 families/sample (7-35). The Simpson's diversity index was lowest in the beaver ponds (H=33.193, df=2, p<0.001) where samples contained a median index value of 4.8 (1.5-10.1) while high gradient area samples contained a median index value of 8.9 (1.0-18.4) and low gradient area samples contained a median index value of 7.7 (1.4-15.6). Invertebrate drift biomass was lowest in the beaver ponds (H=28.778, df=2, p<0.001) where samples contained a median of 16.7 mg/sample (1.4-153.4) while high gradient area samples contained a median of 61.9 mg/sample (3.2-280.3) and low gradient area samples contained a median of 37.3 mg/sample (7.5-373.9). Beaver ponds had a lower proportion of terrestrial invertebrate abundance (H=9.121, df=2, p=0.01) with a median of 10% terrestrial invertebrates (0-57%), than high gradient area samples that contained a median of 21% terrestrial invertebrates (0-99%). The proportion of terrestrial invertebrate biomass in drift samples was lowest in beaver ponds (H=6.887, df=2, p=0.032) where samples contained a median of 5% terrestrial invertebrates (0-93%), while high gradient area samples contained a median of 18% terrestrial invertebrates (0-75%) and low gradient area samples contained a median of 16% terrestrial invertebrates (0-69%).

Invertebrate drift was highest during the summer months and lowest during the winter. The composition of the drift varied less by habitat than by month. Invertebrate drift abundance increased from spring to summer when it reached its peak (August) and decreased in the fall to winter when it was the lowest (January) (H=57.008, df=11, p<0.001). There was a detectible increase in drift in February when ice break up occurred (Figure 4). Invertebrate drift density showed a similar pattern with an increasing trend through the spring and summer reaching a peak in August and declining again through fall into winter (H=59.776, df=11, p<0.001) mimicking abundance with a slight increase in February (Figure 4). Invertebrate drift richness showed a similar pattern (H=48.978, df=11, p<0.001) where August had the greatest richness and January the lowest within the study (Figure 4). There were differences in Simpson's diversity among the twelve months of the study (H=27.943, df=11, p=0.003); however, post hoc tests were unable to further identify pairwise differences. August samples had the highest invertebrate biomass in the drift while January samples had the lowest (H=31.008, df=11, p=0.001); low biomass and drift abundance values for September could be attributed to a high water event just prior to and during sampling (Figure 4).

Terrestrial invertebrates contributed to the drift during months when the stream was open to input from overhanging vegetation; ice covering the stream in winter months may have prevented the input of terrestrial invertebrates into the drift. The summer months showed up to 40 times higher proportions of terrestrial invertebrates biomass and abundance than winter months (H=69.819, df=11, p<0.001, H=89.649, df=11, p<0.001, respectively; Figure 5). Invertebrate drift abundance was dominated by aquatic invertebrates with the exception of August when approximately half of the drift was terrestrial (Figure 6). Invertebrate drift biomass was dominated by aquatic invertebrates, with the exception of the summer months of July through September when terrestrial invertebrates composed approximately 50% of the drift (Figure 6).

The size of prey available within the drift did not differ among habitats (Table 6); however, variation in size by sampling month was evident. Larger invertebrate instars became available in the drift as the growing season progressed from spring to fall, resulting in shifting quantities of the prey size categories. The summer months of July, August and September had, on average, 41% more prey items in size category 2 (0.01-0.1 mg) than spring or fall months (F=6.827, df=6, p<0.001). The fall months of October and November had, on average, 40% more prey items in size category 3 (0.1-1 mg) than summer months (F=5.333, df=6, p<0.001) and November had, on average, 32% more prey items in size category 4 (1-10 mg) than all other months (H=23.363, df=, p<0.001).

Fish Collection/Stomach Sampling

Efforts were made to sample each fish category in equal proportion for the duration of the study. Each fish category composed approximately 20% (17-22%) of the total number of stomach content samples collected (Table 7). Empty stomach content samples accounted for 11.7% of all fish sampled. Age 1 brook trout (22.7%) and steelhead trout (18.3%) showed the highest occurrence of empty stomach samples. However, 30% of age 1 steelhead trout and 24% of age 1 brook trout samples were collected in May, the month having the highest occurrence of empty samples (37.5%) in the study (Table 8). As May was the first month that samples were collected, the results may reflect potential sampling error due to inexperience with the gastric lavage technique and equipment.

Sample collection was equally distributed among the three habitats; however, within each habitat the five fish category samples were not equally collected due to the lack of availability. Based on samples taken during this study, brook trout of both age classes were found more frequently in low gradient and beaver pond areas while steelhead trout of both age classes were found more frequently in high gradient areas. Coho salmon were nearly equally distributed among the three habitats (Table 9).

Total length and weight for all fishes varied greatly throughout the study; however, the mean total length and weight for all fish categories increased from May to November (Figure 7). The mean total length and weight for age 1 brook trout were approximately 2.5 % larger, on average, than those of age 1 steelhead trout. The total length and weight of young-of-year brook trout were approximately 10% larger, on average, than those of YOY steelhead trout. The mean weight of the YOY coho salmon, having emerged earlier, was approximately 30% higher than the other YOY fishes (Table 10).

Beaver ponds, where brook trout occurred most frequently, were also where age 1 brook trout condition was highest for both Fulton's condition factor (K) and relative weight (W_r). Direct comparisons of K among fish species is not common practice because each species exhibits unique growth rates and body shape. The K for YOY brook trout ranged between 0.42-1.18 and although there were differences found among mean K for the three habitat areas (H=6.329, df=2, p=0.042), the nonparametric post-hoc test was not significant (Table 11). The K for age 1 brook trout ranged between 0.76-1.39 and was higher in the beaver pond areas than in low gradient areas (H=12.858, df=2, p=0.002; Table 11). Fishes with W_r values between 95 and 105 are considered to be in good condition with an optimum value of 100 (Pope and Kruse 2007). The W_r for age 1 brook trout ranged between 73.93-137.31 and was also higher in the beaver pond areas than the low gradient areas (H=7.001, df=2, p=0.03; Table 12).

The K for YOY steelhead trout ranged between 0.59-1.33 and there were no differences among the habitats (H=2.144, df=2, p=0.342; Table 11). The K for age 1 steelhead trout ranged from 0.71-1.34 and there were no differences among the habitats (H=1.006, df=2, p=0.605; Table 11). The W_r for age 1 steelhead trout ranged between 15.794-117.802 and no differences were found among habitats (H=2.521, df=2, p=0.284; Table 12). The K for YOY coho salmon ranged between 0.34-1.53 and there were no differences found among the habitats (H=1.771, df=2, p=0.413; Table 11).

Stomach content samples were composed of invertebrates from three different phyla and seven classes. Within the seven classes there were approximately 18 orders represented with more than 65 families of invertebrates ranging in life stage from larval to adult. Longnose sucker eggs and larvae, coho salmon eggs and a few other fishes were found in stomach samples as well as invertebrates. Over 10,000 prey items were collected from stomach content samples throughout the study.

The most common prey items based on abundance in the stomach content samples were larval Chironomidae, larval Baetidae, larval Lepidostomatidae, and larval Philopotamidae. Some items were found to reflect seasonal availability due to either hatching or spawning events such as coho salmon and longnose sucker eggs, adult Philopotamidae, adult Curculionidae, and many adult flies including Empididae, Sciaridae, Phoridae, Chironomidae, and Simuliidae (Tables 13, 14). The most common prey items in the stomach content samples based on biomass were more variable; most items were found to reflect seasonal availability due to hatching or spawning events such as coho salmon and longnose sucker eggs, adult Philopotamidae, Curculionidae, Corixidae and many adult flies including Empididae and Sciaridae (Tables 13, 15). Total stomach content biomass for all fish categories was not related to habitat (p=0.089), nor was it related to salmonid density (p=0.082), nonnative salmonid density (p=0.243), or brook trout density (p=0.150).

Although available invertebrate drift (abundance, richness, biomass, terrestrial proportion) was lowest in the beaver ponds, stomach content analyses indicated fishes in the beaver ponds consumed more prey items than in other areas. Stomach content samples in the beaver ponds had higher abundance than those in either the low or high gradient areas (H=14.942, df=2, p<0.001). Stomach content prey item richness was higher in the beaver ponds than in the low and high gradient areas (H=10.924, df=2, p=0.004). Fish in the beaver ponds had higher stomach content biomass than in the low gradient areas (H=10.545, df=2, p=0.005). The proportion of terrestrial invertebrate biomass in stomach content samples was not different among the three habitat areas (H=2.166, df=2, p=0.339); however, the proportion of terrestrial invertebrates by abundance in stomach content samples was higher in the low and high gradient areas than in the beaver ponds (H=17.099, df=2, p<0.001).

Stomach content prey abundance for most fish categories and biomass for age 1 brook trout were affected by habitat. In beaver ponds, stomach content samples of age 1 (p=0.007) and YOY (p=0.026) brook trout as well as YOY coho salmon (p=0.016) contained a greater abundance of prey items (H=25.486, df=4, p<0.001) than the other habitat types; YOY coho salmon samples contained the highest number of prey items. Age 1 brook trout had higher stomach content biomass in the beaver ponds than the other habitat areas (H=5.695, df=2, p=0.039). Young-of-year brook trout (p=0.058), steelhead trout (p=0.299) and coho salmon (p=0.237) as well as the age 1 steelhead trout (p=0.102) showed no differences in stomach content biomass among sites.

Young-of-year coho salmon were highest in stomach content metrics throughout the stream. Young-of-year steelhead trout and coho salmon stomach content samples contained higher numbers of prey items than the other fish categories in the study (H=106.029, df=4, p<0.001) as well as higher stomach content richness (H=96.997, df=4, p<0.001). Young-of-year coho salmon had higher stomach content biomass than YOY and age 1 brook trout. Young-of-year coho salmon had a higher proportion of terrestrial invertebrate biomass in their stomachs than any of the other fish categories (H=51.656, df=4, p<0.001). Young-of-year coho salmon and age 1 brook trout had a higher proportion of terrestrial invertebrates by abundance than YOY and age 1 steelhead trout (H=54.947, df=4, p<0.001).

Stomach content metrics varied throughout the months of the study and were typically lower in the spring, increasing through the summer and into fall. Fish sampled in May had fewer prey items in stomach content samples (H=89.248, df=6, p<0.001), biomass (H=68.144, df=6,p<0.001), richness (H=73.916, df=6, p<0.001) and terrestrial invertebrate proportion (H=23.398, df=6, p<0.001) than all other months in the study which may be due to sampling error or the lack of experience with the gastric lavage technique. Fishes sampled in June had higher stomach content biomass than every month except November (H=68.144, df=6, p<0.001). Many fishes sampled in June had the opportunity to consume longnose sucker eggs, a large contributor to biomass in stomach content samples, while fishes sampled in November had the opportunity to consume another high biomass item, coho salmon eggs (Table 13). The number of prey items in stomach content samples from July and August was higher than October and November ($H=89.248$, $df=6$, $p<0.001$), showing an increase during the summer and a decline into fall. Fishes collected during July showed a higher proportion of terrestrial invertebrate biomass in the stomach content samples than September through November ($H=63.795$, $df=6$, $p<0.001$); differences were also found using proportion based on abundance, but the post-hoc test was inconclusive ($H=23.398$, $df=6$, $p<0.001$). There was a slight positive correlation between the proportion of terrestrial invertebrates in the drift and what was consumed for both biomass and abundance metrics ($\rho=0.175$, $p<0.001$; $\rho=0.139$, $p<0.001$, respectively).

The CCA utilized in this study was helpful in illustrating similarities in diet by composition which may, depending on resource availability, lead to potential for competition among fish categories who are closely grouped and may demonstrate relationships between habitats and months of the study. Both the CCA's showed that month, specifically June and November, strongly influenced stomach content composition (Tables 16, 17). The strong effect on stomach content composition of the month of June is most likely due to particular invertebrates (adult Leptophlebiidae) and prey items (longnose sucker eggs) being consumed only within that month. November also showed a strong effect on stomach content composition most likely due to the seasonal addition of coho salmon eggs into the system as well as a few other invertebrates (Figures 8, 9, Table 13).

The CCA using proportion of prey item abundance (Figure 8) showed that habitat areas were much less influential than month which is illustrated by the tight grouping at the center of Figure 8. The CCA using proportion of biomass (Figure 9) also showed that habitat was less influential than month; however, high gradient areas were slightly separated from the other habitats aligning more with YOY coho salmon and age 1 steelhead trout; 36% of YOY coho salmon in this study were sampled from high gradient areas while 46% of age 1 steelhead trout in this study were sampled in high gradient areas. In both analyses, YOY brook trout and YOY steelhead trout were grouped together illustrating some similarity in stomach content composition by both abundance and biomass. In the CCA based on abundance, age 1 brook trout and age 1 steelhead trout were grouped together; however, in the CCA based on biomass, these fishes did not group together indicating that the numbers of each prey item consumed may have been similar, but the size of prey items consumed were different between the two fishes. This difference may reflect the habitats in which each fish category is most commonly found; brook trout were common in beaver ponds and steelhead trout were common in the high gradient areas. Interestingly, YOY coho salmon did not group with any fish category, but were consistently intermediate between the other YOY fishes and the age 1 fishes. Other CCA's with different environmental variable configurations were performed, however the CCA's that included all environmental variables provided the most comprehensive analyses.

Prey item preference by size was reflected in habitat, month and fish category. Age 1 fishes consumed less small prey than YOY fishes. Young-of-year coho salmon, as well as the age 1 fishes, consumed more large prey items than the other YOY fishes (Table 18). There were differences among habitat areas for the smallest prey category consumed (category 1) (H=6.181, df=2, p=0.045) and the largest prey (category 5) (H=14.565, df=2, p<0.001); however, post-hoc tests were unable to characterize differences among the habitats. In June more prey items in categories 4 (H=38.072, df=6, p<0.001) and 5 (H=33.62, df=6, p<0.001) were consumed than all months reflecting the timing of longnose sucker egg deposition within the stream.

The highest diet overlap values for the study occurred when YOY steelhead trout were involved in the comparison and comparisons involving YOY coho salmon resulted in the next highest diet overlap values. Young-of-year steelhead trout mean diet overlap was 0.217±0.002 and was the highest among all fish categories (H=586.164, df=4, p<0.001) and was highest in the high gradient areas (H=11.373, df=2, p=0.003). Diet overlap between YOY steelhead trout intracohort conspecifics was higher than all other fish category comparisons (FCC's) in the study (H=1186.828, df=14, p<0.001) and was the highest among YOY steelhead trout comparisons (H=1003.450, df=4, p<0.001). The lowest diet overlap calculated for YOY steelhead trout occurred with age 1 brook trout (Figure 10). Young-of-year coho salmon mean diet overlap was 0.174±0.003. Once again, intracohort conspecific diet overlap was highest (Figure 10); however diet overlap was lowest for YOY coho salmon in the high gradient areas. Again, the lowest diet overlap calculated for YOY coho salmon occurred with age 1 brook trout. Diet overlap of YOY coho salmon was highest with fishes of the same cohort; however, CCA analyses of stomach content samples showed that YOY coho salmon consumed prey items preferred by both age 1 fishes and the other YOY fishes, earning the YOY coho salmon an intermediate position between YOY fishes and age 1 fishes. Mean diet overlap for young-of-year brook trout was 0.179±0.003. The highest diet overlap occurred among fishes of the same cohort where it was highest in the beaver ponds (H=32.701, df=2, p<0.001). Diet overlap with age 1 fishes was lower than diet overlap with YOY fishes (H =109.499, df=4, p<0.001) (Figure 10). Age 1 brook trout mean diet overlap was 0.182±0.003 and they exhibited the lowest diet overlap among fish categories in the study (H=586.164, df=4, p<0.001). Differences were found among age 1 brook trout diet overlap comparisons (15.205, df=4, p=0.004); however, post-hoc tests were unsuccessful (Figure 10). Diet overlap with age 1 steelhead trout was highest in the low gradient areas (H=8.801,df=2,p=0.0012) and with YOY steelhead trout was highest in the beaver ponds (H=16.357,df=2,p<0.001). Age 1 steelhead trout mean diet overlap was 0.167±0.003, and diet overlap was high between both steelhead trout age classes (Figure 10) illustrating higher intraspecific diet overlap regardless of size class. Diet overlap between age 1 steelhead trout and YOY steelhead trout was lowest in the low gradient areas and high in the high gradient and beaver pond areas. Overlap between intracohort conspecifics did not differ among habitats.

Diet overlap was affected by sampling habitat, month and the density of salmonids. Mean diet overlap was 0.188±0.003 in high gradient areas and 0.183±0.002 in beaver ponds; both the high gradient and beaver pond areas had higher diet overlap than the low gradient areas with a mean diet overlap of 0.175±0.003 (H=30.255, df=2, p<0.001). Diet overlap was slightly positively correlated with total salmonid density (r=0.049, p<0.001), non-native salmonid density (r=0.030, p=0.001), and brook trout density (r=0.022, p=0.016) showing that as salmonid density increases diet overlap increases. Diet overlap for all FCC's in May, which was limited to age 1 steelhead trout and brook trout, was lower than all other months of the study (H=409.988, df=6, p<0.001). The summer months (June through September) showed higher diet overlap values than the fall months of October and November (Figure 11). Diet overlap increased as drift density, abundance (Figure 12), and richness increased and was slightly positively correlated with invertebrate drift abundance (r=0.0846, p<0.001), invertebrate drift density (r=0.0816, p<0.001), and richness (r=0.0608, p<0.001).

Both positive selection and avoidance of prey items relative to what was available in the drift occurred and were related to fish species and sampling habitat. Using the biomass data set, maximum positive selection in high gradient areas was greater than that of beaver ponds (H=8.874, df=2, p=0.012), suggesting that fishes were potentially more selective of prey items in high gradient areas where the richness and abundance of invertebrates in the drift was highest. There were no differences among the habitat areas in maximum positive selection for the abundance data set (H=1.579, df=2, p=0.454). Maximum avoidance was highest in the beaver pond areas for both biomass and abundance (H=16.117, df=2, p<0.001, H=323.789, df=2, p<0.001, respectively), showing that fishes in beaver ponds more strongly avoided prey items such as adult Chironomidae, Corixidae, Curculionidae and adult Empidae than fishes in the other habitat areas. Fishes avoided more items than they selected for both by abundance and biomass (U=2607.5, p<0.001 and U=1.5, p<0.001, respectively);

selection in this system, therefore, seems to represent an avoidance of available items in the drift more than a positive selection of items from the drift.

Selection, both the maximum value and the number of items selected for, varied among fish categories. Using the biomass data set, age 1 brook trout and steelhead trout had larger maximum positive selection than YOY steelhead trout and coho salmon (H=36.531, df-4, p<0.001); however, YOY coho salmon and steelhead trout positively selected more prey items (abundance and biomass) than YOY brook trout and age 1 steelhead trout and brook trout (H=92.061, df=4, p<0.001; H=74.451, df=4, p<0.001). Age 1 fishes selected for fewer prey more strongly, such as longnose sucker eggs, coho salmon eggs, adult Empididae and Curculionidae (Tables 15-17), than YOY steelhead trout and coho salmon which selected for a larger variety of prey items. There were no differences in maximum positive selection among the fish categories using abundance (H=1.579, df=2, p=0.454).

Avoidance, both the maximum value and the number of items avoided, varied among fish categories. Using the biomass data set, the maximum avoidance of prey items by YOY brook trout was greater than age 1 fishes (H=22.491, df=4, p<0.001); however, age 1 steelhead trout and brook trout avoided more items than YOY brook trout and coho salmon (H=26.924, df=4, p<0.001). Young-of-year brook trout more strongly avoided a few larger prey items such as adult Chironomidae, Curculionidae, adult Empididae and larval Limnephilidae while age 1 fishes avoided more prey items. Using the abundance data set, YOY steelhead trout and coho salmon had higher maximum avoidance than all other fish categories (H=45.551, df=4, p<0.001); however, both age 1 steelhead trout and brook trout avoided more items than all YOY fishes (H=32.239, df=4, p<0.001). Similar to the biomass data, age 1 fishes avoided more prey items than YOY fishes; however, YOY steelhead trout and coho salmon more strongly avoided a few prey items such as Corixidae, adult Sciaridae, adult Chironomidae, larval Leptophlebiidae and larval Simuliidae.

Selection and avoidance varied throughout the months of the study. Maximum positive selection was highest in June for both abundance and biomass (152.263, df=6, p<0.001, H=23.897, df=6, p<0.001) coinciding with higher diet overlap values. Some prey items that were positively selected in June were longnose sucker eggs and adult Empididae. Fewer items were selected for in May for both abundance and biomass (H=62.836, df=6, p<0.001, H=36.587, df=6, p<0.001) which reflects low diet overlap values in May. Using the biomass data set, maximum avoidance was highest in August (H=126.225, df=6, p<0.001) and in August fishes avoided more prey items than all months except June (H-=219.081, df=6, p<0.001). Prey items avoided in August included adult Sciaridae, adult Chironomidae and larval Baetidae. Using the abundance data set, maximum avoidance was highest in May, August and October (H=152.263, df=6, p<0.001) and more items were avoided by fishes in August than all other months (H=245.308, df=6, p<0.001).

Discussion:

Invertebrate drift:

Patterns in invertebrate drift have been studied extensively and have documented drift increasing from spring to mid-summer followed by a decline in density and abundance into winter (McLay 1968; Clifford 1972; Kawaguchi and Nakano 2001). The drift collected for the duration of this study illustrated a similar pattern with a peak in abundance in August followed by a decline into fall. One factor influencing the seasonal increase in drift may be the contribution of terrestrial invertebrates which can account for over 50% of available drift in streams (Cloe and Garman 1996; Kawaguchi and Nakano 2001; Mason and McDonald 1982; Nakano et al. 1999a; Romaniszyn et al. 2007; Wipfli 1997). In our system, the contribution of terrestrial invertebrates accounted for an average of 21% of the drift during the ice free season and between 31-51% during the peak in August.

Variation in the invertebrate drift was documented among the habitat areas, which presented different substrate and flow regimes (Flecker and Allan 1984; Jowett et al. 1991). Drift was less abundant, had lower density, and lower richness in the beaver pond areas where water velocity was low and the substrate was less complex. Further, as habitat areas were arranged linearly along the study reach (upstream to downstream: beaver ponds, low gradient, high gradient) the upstream beaver pond sites showed lower drift abundance, density, and richness than those further downstream which corresponds to studies showing higher invertebrate drift further downstream (Allan 1981; Williams and Hynes 1976; Bird and Hynes 1981; Waters 1972). One or both of these explanations may have contributed to the invertebrate drift patterns documented during this study.

Stomach samples:

Several studies have shown salmonids to be opportunistic foragers, with diets closely reflecting the composition of drift (Allan 1981; Bres 1986; Esteban and Marchetti 2004; Fausch and White 1986; Hilderbrand and Kershner 2004; Irvine and Northcote 1982). In this study invertebrate drift, and therefore diet composition, was strongly influenced by time of year or month. An increase in prey consumption (abundance and biomass) occurred from spring to midsummer as invertebrate drift increased, and as drift declined into fall fishes consumed less (Cada et al. 1987; Elliot 1970; Kawaguchi and Nakano 2001). The increase in prey consumption during the summer was most likely related to increasing metabolic rates due to increased water temperatures (Brett and Groves 1979), although another factor affecting prey consumption could be the increase in foraging success that may occur as a result of higher drift density (Galarowicz and Wahl 2005; Mathias and Li 1982; Ware 1972).

Changes in the foraging success of fishes are not solely mediated by changes in drift density, but rather are affected by many environmental factors such as water velocity and depth as well as fish density, since high fish densities can lead to interference or exploitative competition. Piccolo et al. (2007, 2008) showed that coho salmon and steelhead trout prey detection and foraging area were inversely related to water velocity and increased with water depth. Hughes and Dill (1990) as well as Grant and Noakes (1987) were able to show an increase in capture efficiency rates as water velocity declined. Areas with deep pools and low velocity would be beneficial to prey detection and capture rates as long as competitor density was low, negating interference competition for foraging locations. As long as drift density was at sufficient levels, exploitative competition would also be negated. The beaver ponds were characterized by deep, lower temperature pools with low water velocity, low drift, and low fish densities when compared with the other areas. Interestingly, stomach samples taken from the beaver ponds consistently contained higher biomass and abundance of invertebrates. Individuals within beaver ponds seem to have had higher foraging success; however, the amount consumed and collected in stomach samples could also be a function of lower metabolic rates in areas where temperatures were an average of 3°C lower (Brett and Glass, 1973; Brett and Groves 1979) or lower energy expended in maintaining foraging position due to lower water velocity (Piccolo et al. 2008; Rosenfeld and Boss 2001).

Many studies have shown that brook trout tend to have fewer items in their stomachs than other sympatric species (Hilderbrand and Kershner 2004, Dunham et al. 2000), but few studies examine condition as well as stomach content. In this study, brook trout consumed fewer items and less biomass than other fishes in the beaver ponds; however, age 1 brook trout had higher stomach content biomass and prey item abundance in the beaver ponds than in other habitats. If age 1 brook trout were better foragers in areas with habitat characteristics similar to beaver ponds one would expect to see higher condition as compared to other habitats. I calculated Fulton’s condition factor and relative weight for age 1 brook trout and these metrics were highest in the beaver ponds. Brook trout preference for pool habitat is well documented (Becker, 1983; Cunjak and Green, 1983, 1984) and, in our study, it would seem that preference is based, partially, in energetics. Despite a lower drift density in the beaver ponds, age 1 brook trout condition was higher which points to either high foraging success or low energy expenditure or a combination of the two. A study examining brook trout condition and stomach contents within similar habitat without a nonnative presence, when compared to this study, may determine if and to what extent interference competition is affecting brook trout condition and habitat selection.

When salmonids are selecting foraging locations in streams, there are typically interactions among individuals selecting the same location. These interactions tend to lead to a size-mediated dominance hierarchy where access to prime foraging locations is dominated by larger fish. These prime foraging locations are selected because they provide maximum access to prey while minimizing energy expenditure (Fausch 1984; Kristiansen 1999; Nakano 1994). Not all salmonids vie for the same foraging sites, as YOY fishes tend to prefer slower moving waters along the edges of streams (Hartman 1965; Cunjak and Green 1984; Fausch and White 1986; Rose 1986) while larger fishes tend to prefer deeper or faster flowing water (Bisson et al. 1988; Everest and Chapman 1972). Prey availability is directly related to foraging location in that preferred sites may offer access to larger prey items or a higher density of invertebrates in the drift (Fausch 1984). Age 1 fishes in our study consumed more large prey items than YOY fishes, a pattern seen throughout the literature (Allan 1981; Nakano 1995; Syrjanen et al. 2011; Werner and Hall 1974). Of the YOY fishes, coho salmon consumed more large items from the drift. Coho salmon emerge approximately two months earlier than brook trout or steelhead trout in the spring resulting in not only a larger body size (30% larger weight) earlier in the summer, but most likely a larger gape. Not only do larger fishes have a better chance at maintaining profitable foraging positions, but many studies have shown an improvement in foraging efficiency over time, allowing older fishes the advantage of experience in capturing and selecting appropriate prey items (Godin 1978, Blaxter 1986, McLaughlin et al. 2000). Both the larger size and the foraging experience of coho salmon would give them a great advantage in the struggle with other small fishes for foraging locations and may explain the difference in prey selection and usage seen among YOY fishes.

In general, fishes tend towards habitats that fulfill certain habitat requirements and preferences. In a system without density driven space limitations the selection of foraging locations would be limited to preferred habitats. For example, YOY coho salmon are known to prefer deeper pool habitat over riffles (Becker 1983; Bisson et al. 1988) as do brook trout (Cunjak and Green 1983, 1984). Those preferences would, in theory, limit the selection of foraging locations to the preferred pool areas, leaving potential foraging sites in riffles available for steelhead trout that show a preference for faster, shallower waters (Bisson et al. 1988; Rose 1986). In this study, coho salmon were found equally throughout all habitat areas, while steelhead trout occupied the areas with lower depth and higher water velocity in the lower reaches of the stream. Although brook trout were found throughout the study stream, they showed a biased occupation toward the beaver ponds and the deeper pool habitats. In theory, interference competition for foraging locations between brook trout and steelhead trout would be at a minimum because they prefer different habitat areas; however, density driven space limitations complicate the matter. If brook trout density were to reach high levels in the preferred pool habitat, subordinate fishes would be forced into less ideal habitat (Bult et al. 1999; Rosenfeld et al. 2005) and into steelhead trout areas where interference competition would occur for foraging locations. Competitive pressure, between rainbow trout (steelhead) and brook trout, which alters stream occupation locations, has been documented in the Great Smoky Mountains National Park, where brook trout ranges have shifted and were limited to upstream reaches (Larson and Moore 1985). The relationship between brook trout and coho salmon seems more complicated as YOY coho salmon are much larger than YOY brook trout, but are smaller than age 1 brook trout. Young-of-year coho salmon have been shown to occupy deep pools and to forage at the surface frequently (Piccolo et al. 2007) while YOY brook trout spend time in shallower pools (McLaughlin et al. 1994; Rose 1986). Age 1 brook trout tend to occupy deeper pools and forage throughout the water column (Fausch and White 1981). The YOY coho salmon then seem to hold an intermediate position between the two brook trout cohorts, most likely affecting both, but perhaps with moderate intensity. Habitat preferences in both allopatric and sympatric populations should also be examined to determine if the presence of other fishes influences preferred habitat selection.

Habitat preference and foraging location selection can influence prey availability and consumption thereby influencing patterns in diet overlap among fishes.

Unfortunately, due to normality and variance problems, only analyses with one independent variable were valid; there are most likely other patterns involving habitat and possibly month that could not be identified. Repeatedly the highest diet overlap values occurred first between conspecifics of the same cohort and then with other fishes in the same cohort. It is not surprising to find that fishes of the same size and species consume very similar items as they most likely occupy very similar habitat and foraging locations.

Differences in prey selection can be related to the optimal foraging theory which states that individuals maximize consumption, perhaps consuming more items or selecting for large, energy-rich prey items, while minimizing energy expenditure during foraging (Stephens and Krebs 1987). As invertebrate drift density changes, shifts in foraging strategies or in preferred prey may occur as predicted. Fausch et al. (1997) found that when invertebrate drift density was low, salmonids shifted to benthic feeding to supplement available prey from the drift. Newman (1987) showed that when drift density was low, benthic foraging supplemented or even supplanted drift foraging which was prominent in summer when drift density was high. Foraging shifts are not limited to seasonality, but also may shift within a 24-hour period. Kreivi et al. (1999) and Nakagawa et al. (2012) documented diel shifts in salmonid foraging further demonstrating the plasticity in salmonid foraging strategies. During this study, I saw variable diet composition throughout the year as well as variable diet overlap index values. Our mean diet overlap values ranged between 0.1 and 0.4 with some of the highest values occurring in August when invertebrate drift density was at its peak. A study by Deus and Petrere-Junior (2003) documented a similar increase in diet overlap when prey increased and explained the pattern by documenting seasonal shifts in prey utilization and foraging strategy of fishes which was dependent upon prey availability patterns as well as inter- and intraspecific competitive pressure. In a study from 2003, Miyasaka and coworkers documented low diet overlap values and hypothesized that pattern was due to a shift in foraging strategy following seasonal resource limitations. It is possible that the low diet overlap values in this study are a result of changing foraging strategies for these species depending on resource availability which is influenced by season and time of day. Nilsson and Northcote (1981) were able to determine that resource and foraging strategy shifts were occurring in sympatric populations of rainbow trout and cutthroat trout (*Salmo clarki*) by comparing sympatric populations to allopatric populations of each species. A similar comparison of resource use and foraging strategies between allopatric and sympatric populations of brook trout, coho salmon and steelhead trout would be useful in attempting to identify any potential for competition that may exist.

Diet overlap increased when invertebrate drift increased indicating that fishes were more selective, or choosier, of prey during times when prey density was high. Both selectivity and avoidance were strongest in summer when drift density was high suggesting that fishes did indeed show prey preference. One pattern that became apparent was that more prey items were avoided than preferentially selected from the drift and selection values were lower than avoidance values overall. Selectivity is not necessarily about positively selecting for items or avoiding them, but it is about choosiness. The choosiness of fishes increased as drift density increased, increasing diet overlap. As the optimal foraging theory states, fishes will choose the highest quality prey items available, and when drift density is high the opportunity to be more selective also increases.

The effects that the introduced species are having on the brook trout vary by age class as well as species. Coho salmon, perhaps because of their earlier emergence and larger size, are intermediate between the age 1 and YOY fishes wih respect to prey use and habitat-prey use interactions. The coho salmon are utilizing similar habitat as brook trout and could therefore be forcing smaller, subdominant YOY brook trout out of preferred habitat and into the faster and shallower foraging areas. It would be difficult to document a habitat shift such as this in the field unless direct observation via snorkeling combined with the manipulation of the presence or absence of each species were possible (see Nakano 1995). Not only are coho salmon potentially having a negative effect on YOY brook trout via habitat interactions, but as coho salmon grow larger through the summer and begin to select for larger prey items there may be increasing negative interactions with age 1 brook trout that also prefer larger prey. Prey consumed by YOY brook trout were very similar to prey consumed by YOY steelhead trout, but unless resources are limiting there may be little in the way of negative interactions between fishes of this size.

When both brook trout and steelhead trout are newly emerged, they occupy similar habitat in slower water near shore and are therefore occupying similar niches (Rose 1986). As they increase in size, steelhead trout move into faster shallow water and brook trout move into deeper water thereby decreasing negative interactions between species. The addition of YOY coho salmon, however, that prefer similar foraging locations to those preferred by YOY brook trout has the potential to increase the duration and frequency of negative interactions between the YOY steelhead trout and brook trout by limiting available pool habitat into which brook trout would normally move. The negative effects of steelhead trout on brook trout range illustrated by other studies (see Larson and Moore 1985) suggest that some type of competitive pressure occurs between species resulting in a brook trout range reduction and concentration in upstream reaches of the system. Age 1 steelhead trout in this study consumed similar sizes and quantities of prey items to that of the age 1 brook trout and although the literature points out that these two species prefer different habitats (Cunjak and Green 1983; Bisson et al. 1988; Rose 1986) perhaps access to preferred prey, when foraging locations are limited, is the driving force behind negative interaction between species for preferred foraging locations.

Diet comparisons in an uncontrolled environment, where competitive pressure may influence both access to prey and prey selection, serves as a preliminary view of the potential for competitive interactions in a natural system. The salmonids in the study, overall, consumed similar prey items and although diet overlap was below Schoener's suggested value, during periods of low invertebrate drift density when resources are limited, competition for foraging locations and prey could occur. Overall, this study has shown that introduced salmonids in a tributary of Lake Superior may be negatively affecting survival and growth of the native brook trout. An investigation into habitat preference and the selection of foraging locations via direct observation in streams would be a desirable next step in determining the likelihood and frequency of competition among these salmonids.

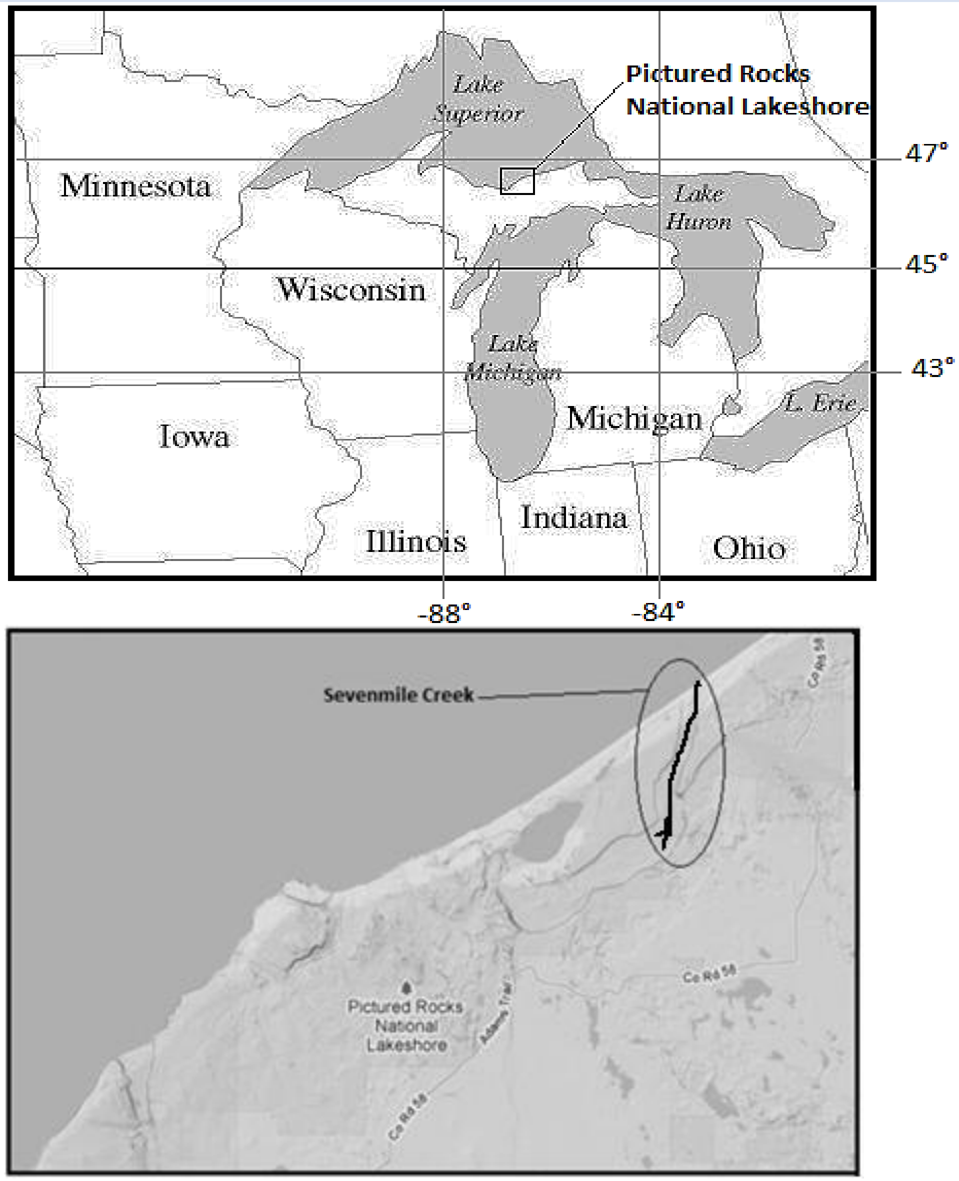

Figure 1: Location of Sevenmile Creek study site within Pictured Rocks National Lakeshore in the Upper Peninsula of Michigan on Lake Superior’s southern shore.

Figure 2: Photo of device used to collect stomach samples showing syringe and capture pan with sieve.

Table 1: Prey size categories used for both drift and stomach content samples.

Group	Biomass (mg)
5	x>10
4	10>x>1
3	1>x>0.1
2	0.1>x>0.01
1	x<0.01

Table 2: Biomass values used for non-invertebrate items in stomach content and drift samples.

Item	Biomass	Source
sucker egg	72.92 mg	mean from PIRO samples (n=10) in alcohol
coho egg	126 mg	mean from PIRO samples (n=110)
steelhead egg	82 mg	unpublished data; Duby and Leonard
larval fish	4 mg	mean from PIRO samples (n=10) in alcohol
Burbot (tl=60mm)	1300 mg	based on PIRO samples of equal length (n=10)
brook trout (tl=60mm)	1850 mg	based on PIRO samples of equal length (n=65)
red belly dace (tl=12mm)	100 mg	based on PIRO samples of equal length (n=45)
unknown salmonid (tl=30mm)	178 mg	based on PIRO samples of equal length (n=50)

Table 3: Fish category comparisons used during diet overlap calculations (15 total combinations).

	YOY Brook trout	**Age 1 Brook trout**	**Age 1 Steelhead**	**YOY Steelhead**	**YOY Coho**
YOY brook trout	**x**				
Age 1 brook trout	**x**	**x**			
Age 1 Steelhead	**x**	**x**	**x**		
YOY Steelhead	**x**	**x**	**x**	**x**	
YOY Coho	**x**	**x**	**x**	**x**	**x**

Table 4: Mean and standard error (SE) for gradient, velocity and water temperature in habitat areas. Includes results of statistical analyses and significantly highest values for each category are marked by an asterisk.

	Slope (%)	SE	Velocity (m/s)	SE	Water Temp (°C)	SE
High Gradient	2.16*	0.42	0.73*	0.05	15.21	6.30
Low Gradient	0.65	0.19	0.39	0.03	14.73	6.00
Beaver Ponds	0.48	0.19	0.24	0.02	12.34	7.30
Test Results	F=10.384, df=2, p=0.003		H=133.52, df=2, p<0.001		H=0.178, df=2, p=0.915	

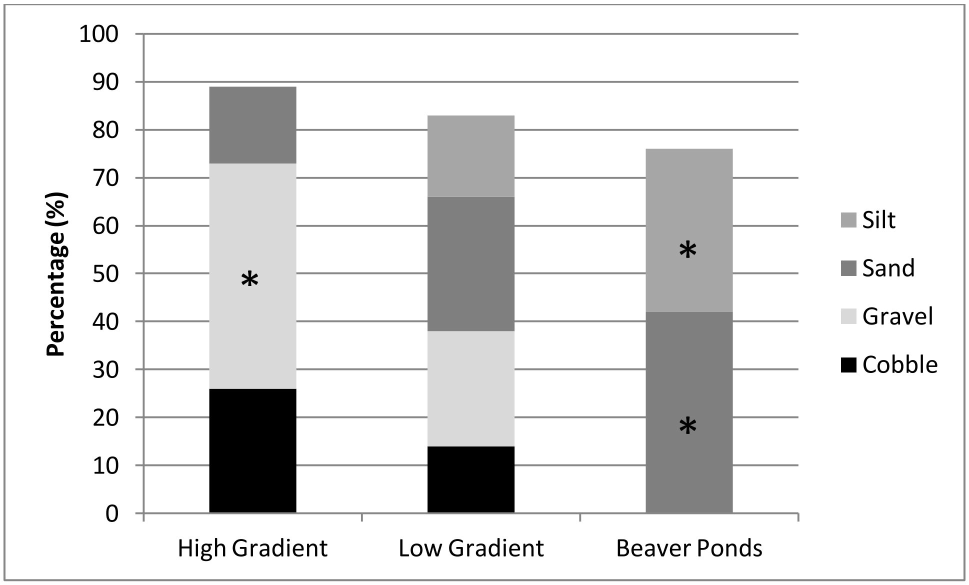

Figure 3: Composition of substrate for habitat areas. Asterisks show most common substrate type (H=47.693, df=2, p<0.001).

Table 5: Mean and standard error of fish densities by habitat. Including asterisks showing significantly higher values and ^ marking significantly lower values.

	Salmonid density (Fish/m²)	**SE**	**Nonnative salmonid density (Fish/m²)**	**SE**	**Brook trout density (Fish/m²)**	**SE**
High Gradient	0.023	0.003	0.021	0.003	0.002	0.000
Low Gradient	0.020	0.007	0.017	0.003	0.003	0.000
Beaver Ponds	0.015	0.005	0.007^	0.002	0.008*	0.002
Test Results	H=2.111, df=2, p=0.348		H=13.556, df=2, p=0.001		H=17.651, df=2, p<0.001	

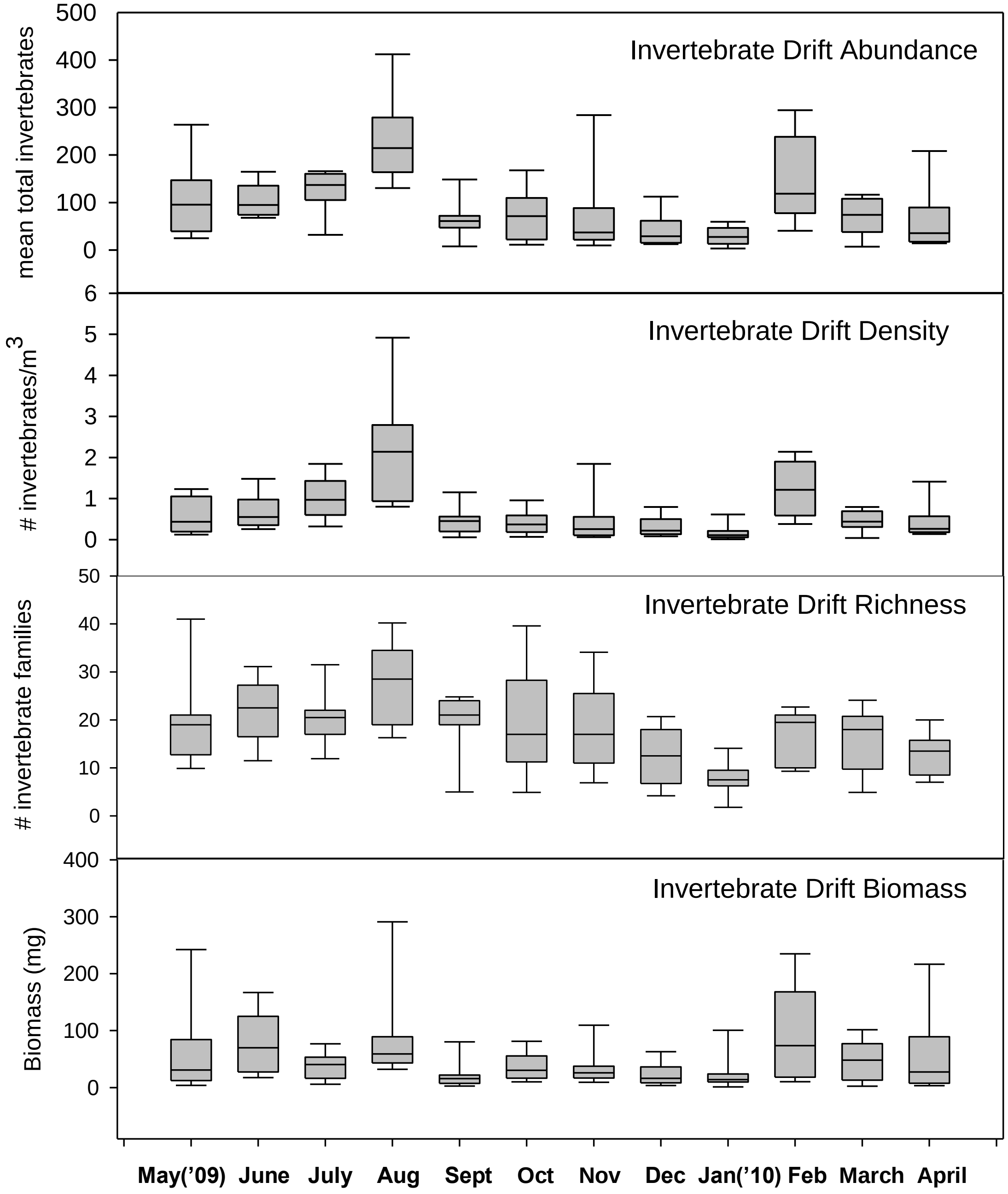

Figure 4: Invertebrate drift metrics showing drift abundance, density, richness and biomass from top to bottom, shown as medians (line), first and third quartiles (box) and 5th/95th percentile (whiskers) by month.

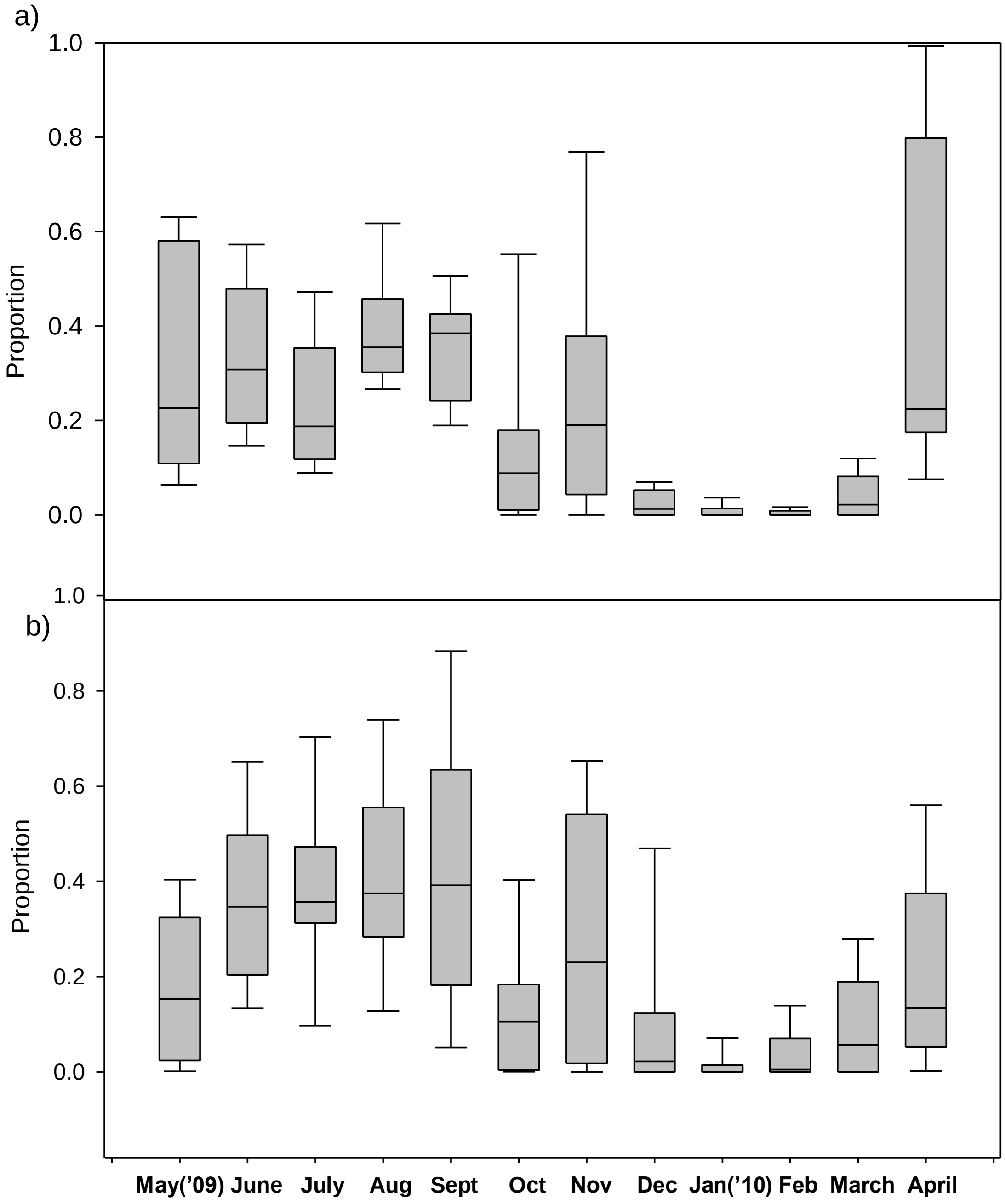

Figure 5: Terrestrial invertebrate proportion of the drift for both a) abundance and b) biomass, shown as medians (line), first and third quartiles (box) and 5th/95th percentile (whiskers) by month.

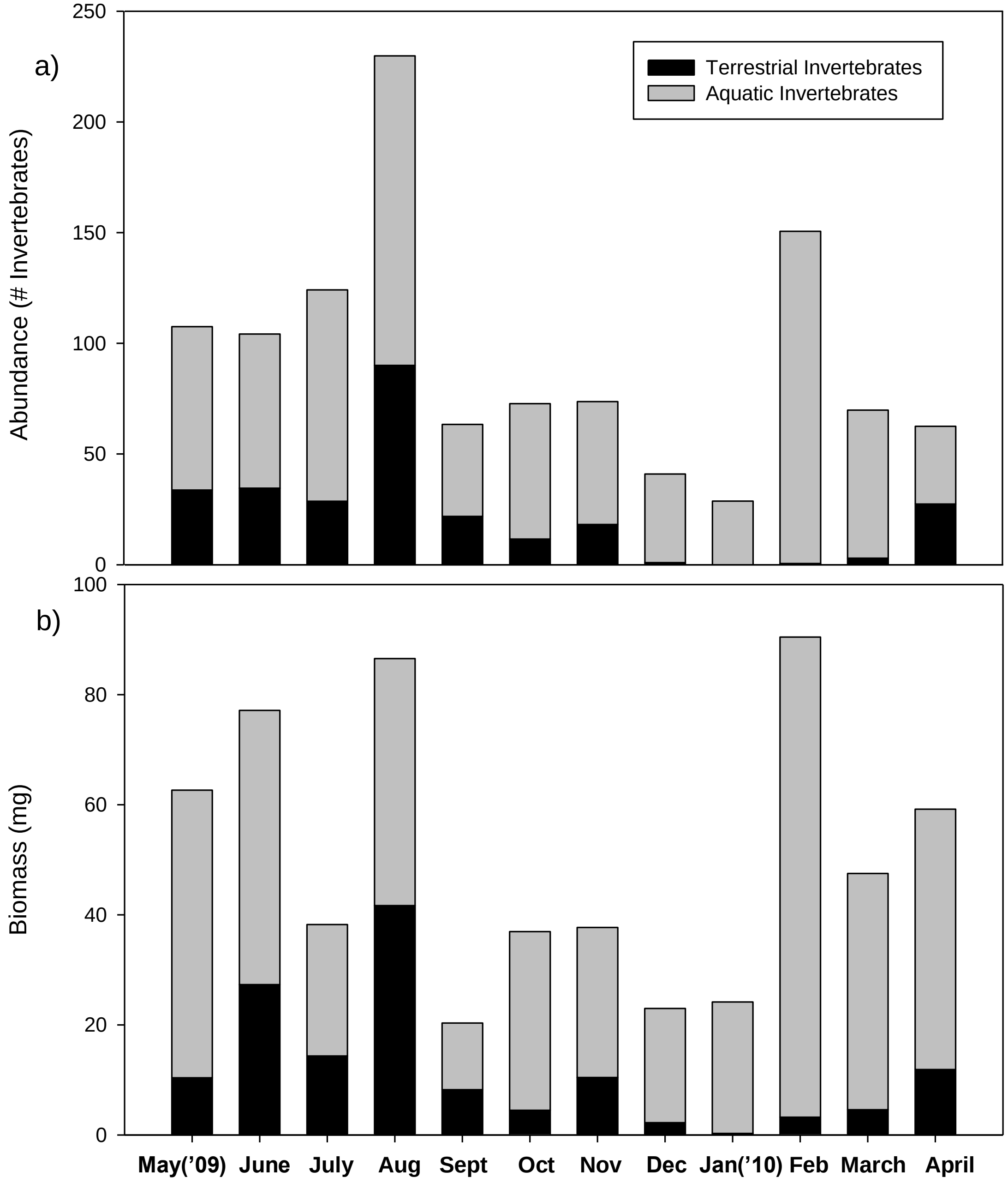

Figure 6: Invertebrate drift divided into terrestrial (dark portion of bar) and aquatic components (light portion of bar) for a) abundance and b) biomass.

Table 6: Results for comparison of available drift prey size categories among the three habitat areas (K-W =Kruskal-Wallace).

	test	**H/F**	**df**	**p**
Prey Category 1	K-W	0.0277	2	0.986
Prey Category 2	ANOVA	0.122	2	0.886
Prey Category 3	ANOVA	0.785	2	0.46
Prey Category 4	K-W	0.284	2	0.867
Prey Category 5	K-W	3.736	2	0.154

Table 7: Summary of species collected by month and habitat area. Values indicate number of evaluated individuals for each combination of habitat area, species and month.

		May	**June**	**July**	**August**	**September**	**October**	**November**	***Total***
Brook Trout YOY	**High Gradient**				6	9	7	7	*29*
n=121	**Low Gradient**				7	9	10	7	*33*
	Beaver Ponds			10	10	11	10	18	*59*
Brook Trout Age 1	**High Gradient**	14	4	4	5	3	3	1	*34*
n=141	**Low Gradient**	9	10	4	10	8	9	6	*56*
	Beaver Ponds	11	10	9	11	4	1	5	*51*
Steelhead YOY	**High Gradient**			8	9	12	10	10	*49*
n=122	**Low Gradient**				10	12	9	12	*43*
	Beaver Ponds				6	10	2	12	*30*
Steelhead Age 1	**High Gradient**	20	10	10	9	8	6	3	*66*
n=142	**Low Gradient**	14	10	6	10	2	7	8	*57*
	Beaver Ponds	8	1	1	3	2		4	*19*
Coho YOY	**High Gradient**		7	10	10	10	10	10	*57*
n=158	**Low Gradient**			10	10	10	10	9	*49*
	Beaver Ponds			10	9	10	3	20	*52*
Total		*76*	*52*	*82*	*125*	*120*	*97*	*132*	*684*

Table 8: Empty stomach samples by fish category and month. The total number (italics) of empty stomach samples and percentage of empty stomach samples by month and fish category. Large percentages are emboldened.

	Brook trout YOY	**Brook trout age 1**	**Steelhead YOY**	**Steelhead age 1**	**Coho YOY**	**# of empty stomachs**
May	0%	**44%**	0%	**62%**	0%	*30*
June	0%	0%	0%	8%	0%	*2*
July	0%	13%	0%	0%	0%	*4*
August	7%	9%	0%	23%	50%	*13*
September	33%	19%	0%	4%	0%	*12*
October	27%	13%	0%	0%	17%	*9*
November	33%	3%	100%	4%	33%	*10*
# of empty stomachs	*15*	*32*	*1*	*26*	*6*	*80*

Table 9: Fish category sampling distribution representing the proportion of each species sampled within each habitat. Total number of fish collected per fish category represented by (*n*).

	High gradient	**Low gradient**	**Beaver ponds**
Brook trout YOY (*121*)	24%	27%	49%
Brook trout Age 1 (*141*)	24%	40%	36%
Steelhead YOY (*122*)	40%	35%	25%
Steelhead Age 1 (*142*)	46%	40%	14%
Coho YOY (*158*)	36%	31%	33%
All Fishes	34%	35%	31%

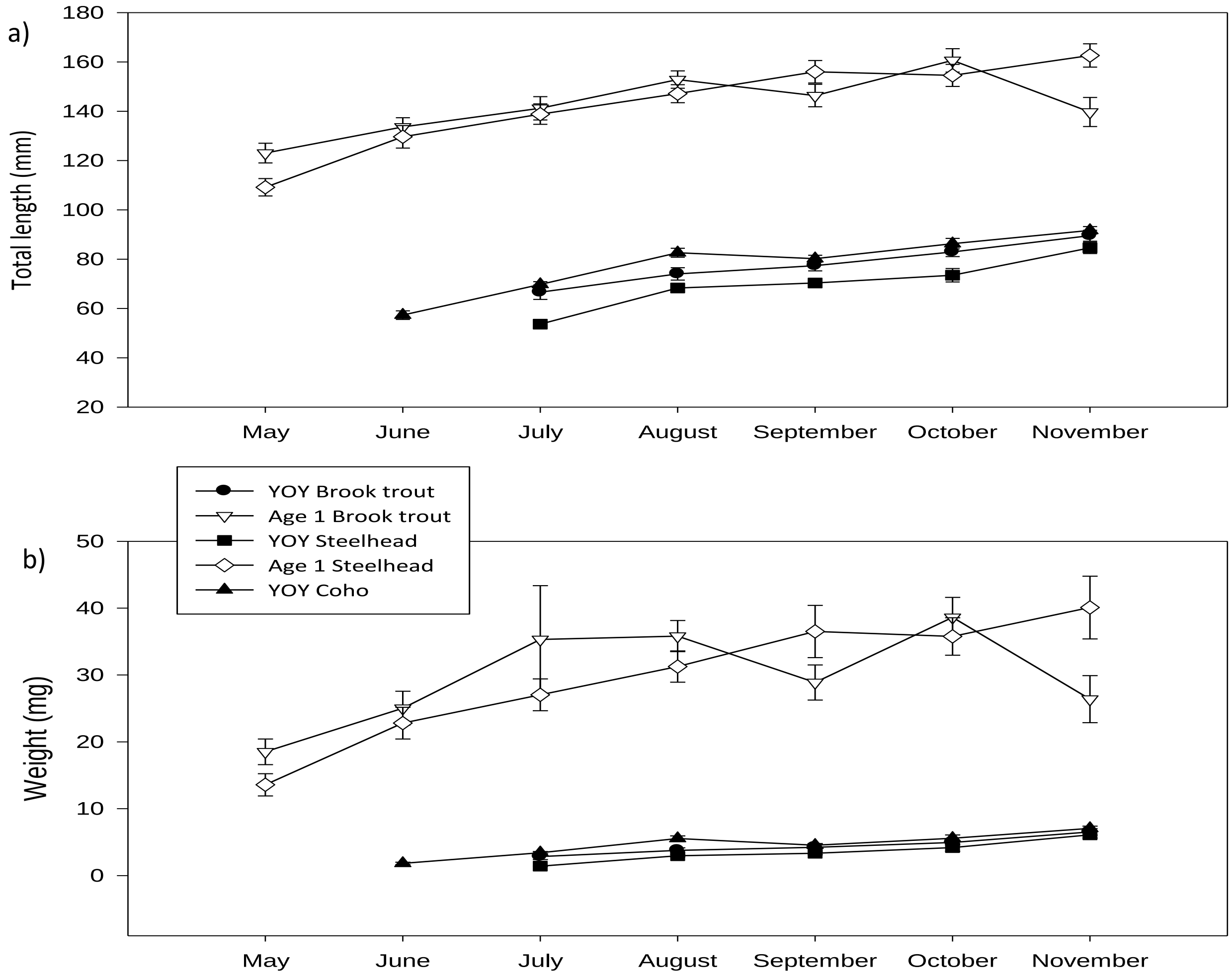

Figure 7: Mean (SE) total length (a) and weight (b) of individuals in each fish category.

Table 10: Mean total length and weight of all fishes sampled. Bolded values highlight mean weight among YOY fishes where significant differences were found.

	Mean Total Length	Std. Error	Mean Weight	Std. Error
Brook Trout YOY	80.21	1.20	**4.78**	0.22
Brook Trout Age 1	139.87	1.93	27.64	1.12
Steelhead YOY	73.29	1.22	**4.05**	0.22
Steelhead Age 1	136.26	2.26	26.53	1.28
Coho YOY	81.41	0.99	**6.19**	0.77

Table 11: Mean Fulton's condition factor (standard error) for all fish sampled within each habitat. The asterix shows a significantly higher condition factor in the beaver ponds for age 1 brook trout.

	Brook trout YOY	Brook trout age 1	Steelhead YOY	Steelhead age 1	Coho YOY
High Gradient	0.84 (0.01)	0.93 (0.02)	0.93 (0.01)	0.94 (0.01)	0.89 (0.01)
Low Gradient	0.83 (0.02)	0.91 (0.01)	0.94 (0.02)	0.96 (0.01)	0.92 (0.01)
Beaver ponds	0.88 (0.01)	0.98 (0.02)*	0.91 (0.02)	0.93 (0.02)	0.92 (0.02)

Table 12: Mean relative weight (standard error) for age 1 fish sampled within each habitat. The asterix shows a significantly higher relative weight in the beaver ponds for age 1 brook trout.

	Brook trout age 1	Steelhead age 1
High Gradient	89.03 (0.99)	87.50 (0.96)
Low Gradient	88.42 (1.30)	87.87 (2.15)
Beaver Ponds	92.77 (1.68)*	84.91 (2.06)

Table 13: Invertebrate abbreviations used in common prey item tables (Tables 14, 15) as well as CCA analyses (Figures 7, 8)

Code	Organism	Code	Organism	Code	Organism
Abaeti	Adult Baetidae	**Astaph**	Adult Staphylinidae	**Lgloss**	Larval Glossosomatidae
Abibio	Adult Bibionidae	**Atipul**	Adult Tipulidae	**Lgomph**	Larval Gomphidae
Acarab	Adult Carabidae	**Atrico**	Adult Trichoptera	**Lhepta**	Larval Heptageniidae
Achiro	Adult Chironomidae	**amphip**	Amphipoda	**Lhydro**	Larval Hydropsychidae
Acoleo	Adult Coleoptera	**aphid**	Aphididae	**Lhydo**	Larval Hydrophilidae
Acorix	Adult Corixidae	**aracmi**	Acari	**Lhymen**	Larval Hymenoptera
Aculic	Adult Culicidae	**aracsp**	Araneae	**Lhypti**	Larval Hydroptilidae
Acurcu	Adult Curculionidae	**cohegg**	Coho Egg	**Llepdo**	Larval Lepidoptera
Adipte	Adult Diptera	**collum**	*Collembola*	**Llephl**	Larval Leptophlebiidae
Adytis	Adult Dytiscidae	**Pchiro**	Pupal Chironimidae	**Llimne**	Larval Limnephilidae
Aelmid	Adult Elmidae	**Pdipte**	Pupal Diptera	**Lodona**	Larval Odonata
Aempid	Adult Empididae	**Pphilo**	Pupal Philopotamidae	**Lperli**	Larval Perlidae
Aephem	Adult Ephemeroptera	**Lather**	Larval Athericidae	**Lpleco**	Larval Plecoptera
Aformi	Adult Formicidae	**Lbaeti**	Larval Baetidae	**Lptero**	Larval Pteronarcyidae
Ahemip	Adult Hemiptera	**Lbrach**	Larval Brachycentridae	**Lrhyac**	Larval Rhyacophilidae
Ahymen	Adult Hymenoptera	**Lcalop**	Larval Calopterygidae	**Lsimul**	Larval Simuliidae
Ahypti	Adult Hydroptilidae	**Lcerat**	Larval Ceratopogonidae	**Ltaeni**	Larval Taeniopterygidae
Alephl	Adult Leptophlebiidae	**Lchiro**	Larval Chironomidae	**Ltipul**	Larval Tipulidae
Amecop	Adult Mecoptera	**Lcoleo**	Larval Coleoptera	**fish**	Fish
Amyceto	Adult Mycetophilidae	**Lcordu**	Larval Corduliidae	**gastro**	Gastropoda
Aortho	Adult Orthoptera	**Ldipte**	Larval Diptera	**larfish**	Larval longnose sucker
Aphilo	Adult Philopotamidae	**Lelmid**	Larval Elmidae	**sucegg**	Longnose sucker egg
Aphori	Adult Phoridae	**Lempid**	Larval Empididae	**Ltrico**	Larval Trichoptera
Asciar	Adult Sciaridae	**Lephem**	Larval Ephemeroptera		
Asimul	Adult Simuliidae	**Lephll**	Larval Ephemerellidae		

Table 14: Top four items by proportion (abundance) found in stomach content samples of each fish category by month and habitat area. Prey items are listed 1-4 from the left to right starting on the first line. See Table 13 for explanations of invertebrate abbreviations. Blank spaces occur when no fish were sampled for the month, species and habitat.

May	**Brook trout age 1**		**Steelhead age 1**	
High Gradient	Lsimul	Pphilo	Lhepta	Lsimul
	collum	oligoc	Lbaeti	Pphilo
Low Gradient	Llephl	Pchiro	Adipte	Ahymen
	Lchiro	Achiro	Llephl	collum
Beaver Ponds	Llepid	Lbrach	Llephl	Lhepta
	collum	Pphilo	Lbrach	Lephll

June	**Brook trout age 1**		**Steelhead age 1**		**Coho YOY**	
High Gradient	Aempid	collum	sucegg	Ldipte	Aempid	Lcerat
	sucegg	Llepid	collum	Lbaeti	sucegg	Lphilo
Low Gradient	Aempid	Llephl	Aempid	Alephl		
	Alephl	collum	Llephl	Lchiro		
Beaver Ponds	Aempid	Acoleo	Llephl	Aelmid		
	Lbaeti	Lchiro	Ltrico	aracsp		

July	**Brook trout age 1**		**Steelhead age 1**		**Brook trout YOY**		**Steelhead YOY**		**Coho YOY**	
High Gradient	Lbaeti		Lbaeti	Lhepta			Lbaeti	Lsimul	Lphilo	Adipte
			gastro	Lsimul			Lchiro	aphid	Lchiro	Llepid
Low Gradient	Acurcu	Achiro	Acurcu	Lbaeti					Lchiro	Adipte
	Lbrach	Aculic	Lchiro	Llepid					Achiro	Lbaeti
Beaver Ponds	Acurcu	Aempid	Lphilo	Pphilo	Lchiro	Lbaeti			Lchiro	Pdipte
	Llepid	Achiro	Acurcu	Lchiro	Lsimul	Achiro			Achiro	Pchiro

August	**Brook trout age 1**		**Steelhead age 1**		**Brook trout YOY**		**Steelhead YOY**		**Coho YOY**	
High Gradient	gastro	Acarab	Lbaeti	Lphilo	Lbaeti	gastro	Lbaeti	Abaeti	Asciar	Lbaeti
	Asciar	Ltrico	Lsimul	Asciar	Asciar	aracmi	Lchiro	Asciar	Lchiro	Achiro
Low Gradient	aracsp	Lcerat	Asciar	Ahypti	Asciar	aphid	Ltipul	Lbaeti	Asciar	Achiro
	Ahemip	Pchiro	Achiro	Lpleco	Achiro	Lchiro	Lchiro	Pchiro	Pchiro	Lchiro
Beaver Ponds	Acurcu	psocop	Lbaeti	Lbrach	Lbaeti	Lchiro	Lbaeti	Asciar	Lchiro	Pchiro
	Lephll	Lbaeti	aracsp	aphid	gastro	Asciar	Lchiro	gastro	Aempid	Asciar
September	**Brook trout age 1**		**Steelhead age 1**		**Brook trout YOY**		**Steelhead YOY**		**Coho YOY**	
High Gradient	fish	Lbaeti	Llepid	Lperli	psocop	aracsp	Lchiro	Lrhyac	Lchiro	Pchiro
	Lperli	Lphilo	Lbaeti	Lrhyac	Llepid	Lather	Llepid	Lbaeti	psocop	Ltipul
Low Gradient	Lgloss	Abaeti	Lcerat	Lchiro	gastro	Lchiro	Lchiro	Lephll	Lchiro	Adipte
	Lbrach	gastro	Lphilo	Ltipul	Ltrico	Llepid	Lhydro	Llepid	Achiro	Aempid
Beaver Ponds	Lphilo	gastro	gastro	Lphilo	gastro	Lhydro	Lbaeti	Ltipul	Lchiro	Aempid
	psocop	Llepdo	Lbrach	Lbaeti	Lpleco	Lchiro	Lchiro	Lphilo	Pchiro	Aphori
October	**Brook trout age 1**		**Steelhead age 1**		**Brook trout YOY**		**Steelhead YOY**		**Coho YOY**	
High Gradient	Llimne	Llepid	Lhydro	gastro	Lhydro	Llepid	Lphilo	Lhydro	Lphilo	Lchiro
	Adipte	oligoc	Lphilo	Lbrach	Lphilo	gastro	Llepid	Ltaeni	Lhydro	oligoc
Low Gradient	Llimne	Lphilo	Lhydro	Llepid	Llepid	Ltrico	Llepid	Lphilo	Lpleco	aphid
	Lhydro	oligoc	Lphilo	Lbrach	oligoc	Llimne	Lhydro	Ltaeni	Lcerat	Ahymen
Beaver Ponds					aphid	Lcerat	Lbaeti	Lephll	oligoc	Adipte
					Lhypti	Llepdo	Lpleco	Lhypti	Lphilo	psocop
November	**Brook trout age 1**		**Steelhead age 1**		**Brook trout YOY**		**Steelhead YOY**		**Coho YOY**	
High Gradient	cohegg	Lphilo	Lpleco	Lperli	Aphilo	Llepid	Aphilo	Lbaeti	Aphilo	Lcoleo
	Aphilo	Lrhyac	Lhydro	oligoc	Atrico	Ahemip	cohegg	Ltaeni	Lchiro	Pphilo
Low Gradient	collum	Lchiro	cohegg	Lphilo	Aphilo	Llepid	collum	Ltaeni	collum	Aphilo
	cohegg	Aphilo	collum	gastro	Lchiro	collum	Llepid	Lhydro	Lhydro	Lpleco
Beaver Ponds	Pphilo	Llepid	Lbrach	Lphilo	Lhypti	Aphilo	Llepid	Lhypti	Lhypti	Acorix
	Lphilo	Lbrach	Lcalop	gastro	Lphilo	Lchiro	Lphilo	Ltaeni	Lhydro	Llepid

Table 15: Top four items by proportion (biomass) found in stomach samples of each fish category by month and habitat area. Prey items are listed 1-4 from the left to right starting on the first line. See Table 13 for explanations of invertebrate abbreviations. Blank spaces occur when no fish were sampled for the month, species and habitat.

May	**Brook trout age 1**	**Steelhead age 1**
High Gradient	oligoc Lpleco Lsimul Pphilo	Lhepta Lephem Lbaeti Lchiro
Low Gradient	Fish aracmi Llephl Achiro	Llephl Ahymen Adipte Asimul
Beaver Ponds	Llepid Lbrach collem Lbaeti	Llephl Lbrach Lhepta Lephll

June	**Brook trout age 1**	**Steelhead age 1**	**Coho YOY**
High Gradient	Aempid Acoleo sucegg Abibio	sucegg larfish collem Fish	sucegg Lhepta Aempid Lphilo
Low Gradient	Aempid Alephl gastro Llephl	Aempid Lhepta Llephl Alephl	
Beaver Ponds	Aempid Lbaeti Acoleo Lchiro	Llephl Aelmid Ltrico aracsp	

July	**Brook trout age 1**	**Steelhead age 1**	**Brook trout YOY**	**Steelhead YOY**	**Coho YOY**
High Gradient	Lbaeti	Lbaeti Acurcu Lhepta gastro		Lbaeti Acurcu Lhepta Aracsp	Lphilo Lcoleo psocop Aphilo
Low Gradient	Acurcu Achiro Adytis Lbrach	Acurcu Lodona Llepid Lbrach			Lchiro Adipte Achiro Lbaeti
Beaver Ponds	Acurcu gastro fish aracsp	Acurcu Pphilo Lphilo Aphilo	Lbaeti Lchiro Lphilo Aphilo		Aphilo Achiro Aempid Lphilo

August	**Brook trout age 1**		**Steelhead age 1**		**Brook trout YOY**		**Steelhead YOY**		**Coho YOY**	
High Gradient	gastro	Ltrico	Lbaeti	Lcoleo	Lbaeti	Asciar	Lbaeti	Abaeti	Asciar	Aempid
	Acarab	Asciar	gastro	Lphilo	gastro	Adipte	Aempid	Lchiro	Abaeti	Lbaeti
Low Gradient	Acurcu	Aracsp	Asciar	Aformi	Asciar	Aphilo	Lbaeti	Adipt	Asciar	Aempid
	Asciar	Ahemip	Ahypti	Adipte	Lrhyac	gastro	Lhydo	Asciar	Achiro	Lhydro
Beaver Ponds	Acurcu	psocop	gastro	Acurcu	Lbaeti	Aempid	Lbaeti	Pphilo	Aempid	Lchiro
	Lephll	Ptrico	Lperli	Ahemip	gastro	Asciar	Lchiro	Asciar	Acurcu	Amecop
September	**Brook trout age 1**		**Steelhead age 1**		**Brook trout YOY**		**Steelhead YOY**		**Coho YOY**	
High Gradient	fish	gastro	Lperli	Lbaeti	psocop	Lhymen	Lrhyac	Lbaeti	aracsp	Psocop
	Llepid	Lperli	Lperlo	Llepid	aracsp	Lsimul	Llepid	Lhymen	Aempid	Gastro
Low Gradient	Lgloss	gastro	Lcerat	Lchiro	gastro	Lbaeti	Lephll	Lbaeti	Lpleco	Aempid
	Lbrach	Abaeti	Lphilo	Ltipul	Lcoleo	aracsp	Lphilo	aracsp	Achiro	oligoc
Beaver Ponds	Lphilo	gastro	gastro	Lpleco	Lpleco	gastro	Lbaeti	Ltipul	aracsp	Aempid
	Lpleco	Lbaeti	Lbrach	oligoc	oligoc	Lodona	Lpleco	Lphilo	oligoc	Lpleco
October	**Brook trout age 1**		**Steelhead age 1**		**Brook trout YOY**		**Steelhead YOY**		**Coho YOY**	
High Gradient	Llimne	Adipte	oligoc	gastro	Lhydro	gastro	Lphilo	Lhydro	oligoc	Lptero
	fish	Llepid	Llepid	Lpleco	Lphilo	aracsp	aracsp	Lrhyac	Ahemip	Lhydro
Low Gradient	Llimne	Lphilo	Lhydro	Lbrach	oligoc	Ltrico	Lpleco	Lphilo	Lpleco	Lhydo
	Lhydro	oligoc	Aortho	Lgomph	Llepid	Lrhyac	Lhydro	gastro	Lcerat	aracsp
Beaver Ponds					aphid	Ltipul	Lbaeti	Lephll	oligoc	psocop
					gastro	Lcerat	Lpleco	Ldipte	Aformi	Ahymen
November	**Brook trout age 1**		**Steelhead age 1**		**Brook trout YOY**		**Steelhead YOY**		**Coho YOY**	
High Gradient	cohegg	Lrhyac	Lpleco	Lperli	Aphilo	oligoc	Aphilo	Lhydro	Aphilo	Lcoleo
	Aphilo	Lphilo	Lhydro	gastro	Atrico	Pphilo	cohegg	Lbaeti	aracsp	cohegg
Low Gradient	cohegg	Aphilo	cohegg	gastro	Aphilo	cohegg	Llepid	Ltaeni	aracsp	Atrico
	Lcordu	Lhydro	fish	oligoc	Atrico	Lhydro	collem	Lhydro	Aphilo	collem
Beaver Ponds	Llimne	fish	Lbrach	gastro	Lhypti	Lphilo	Lphilo	Aphilo	Acorix	Lhydro
	Lphilo	Pphilo	Lcalop	Lphilo	Aphilo	Lhepta	Ltaeni	Lhydro	Llimne	Lpleco

Table 16: Summary of forward selection Monte Carlo test for count proportion in stomach samples CCA (number of permutations=499).

Environmental Variable	P-value	F-value
June	0.0120	9.91
November	0.0100	8.93
August	0.0060	5.33
May	0.0020	4.71
July	0.0120	4.90
Steelhead YOY	0.0040	3.76
Brook trout age 1	0.0040	3.20
Low gradient	0.0020	2.97
Steelhead age 1	0.0020	2.75
September	0.0700	2.55
High Gradient	0.0100	2.57
Brook trout YOY	0.0240	1.86

Table 17: Summary of forward selection Monte Carlo test for biomass proportion in stomach samples CCA (number of permutations=499).

Environmental Variable	P-value	F-value
June	0.0040	8.14
November	0.0040	6.02
August	0.0040	3.39
July	0.0020	3.46
May	0.0060	3.22
Brook trout age 1	0.0180	2.94
Steelhead YOY	0.0360	2.78
Steelhead age 1	0.0200	2.80
High gradient	0.0340	2.56
Low gradient	0.1140	1.91
September	0.0560	1.52
Brook trout YOY	0.0820	1.41

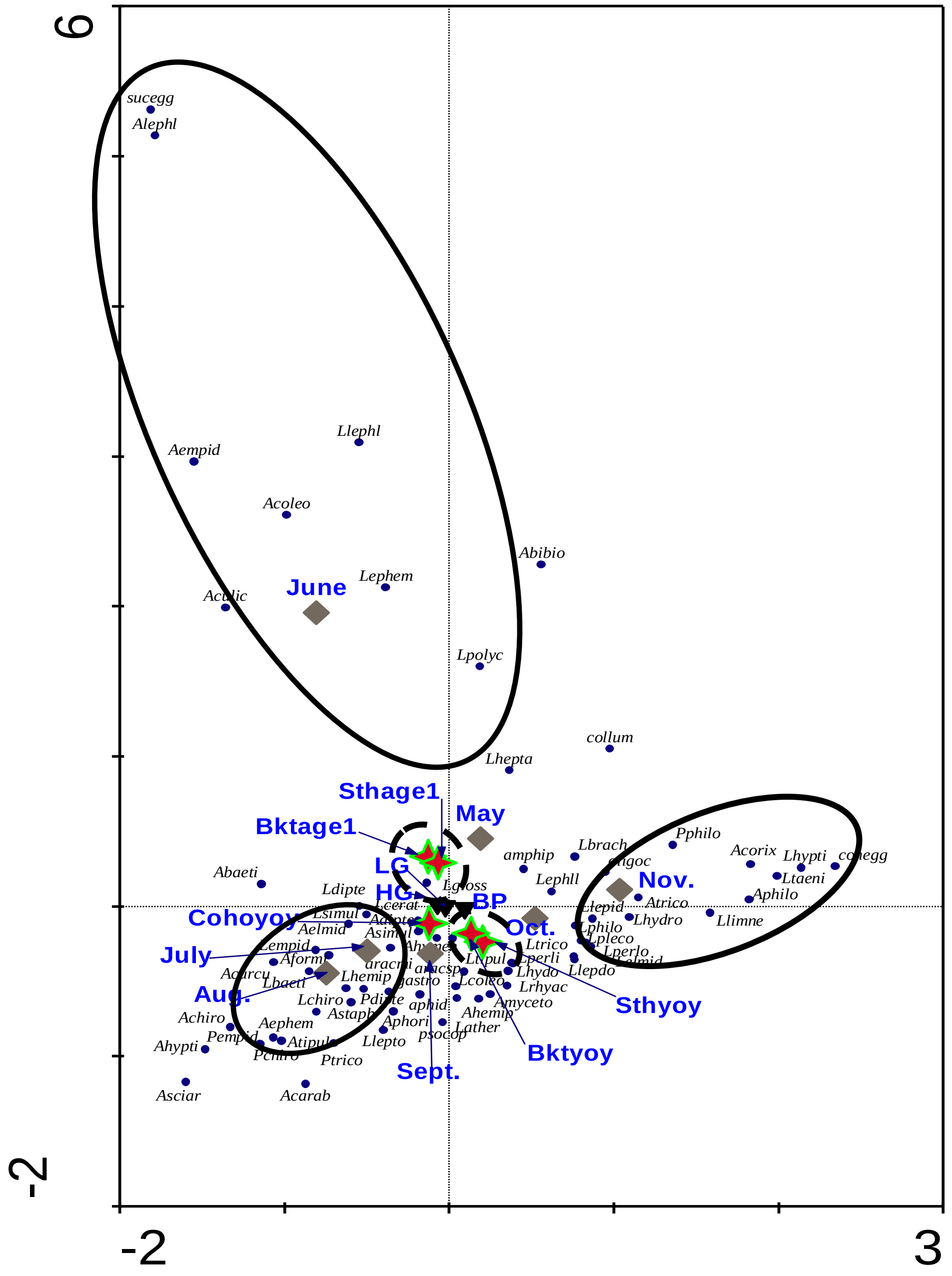

Figure 8: CCA using the proportion of prey items by abundance. Centroids for month are shown as diamonds, for habitat are shown as black triangles and for fish category are shown as stars. Axes 1 and 2 represented 45.2% and 36.9% of the species-environment relationship, respectively. The ovals emphasize the effect of month on the prey items within stomach contents while the dashed-line ovals emphasize the relationship among fish categories. Invertebrates are labeled with life stage (first letter) and family name (next five letters). Habitat area categories are shown as HG=high gradient, LG=low gradient, BP=beaver pond.

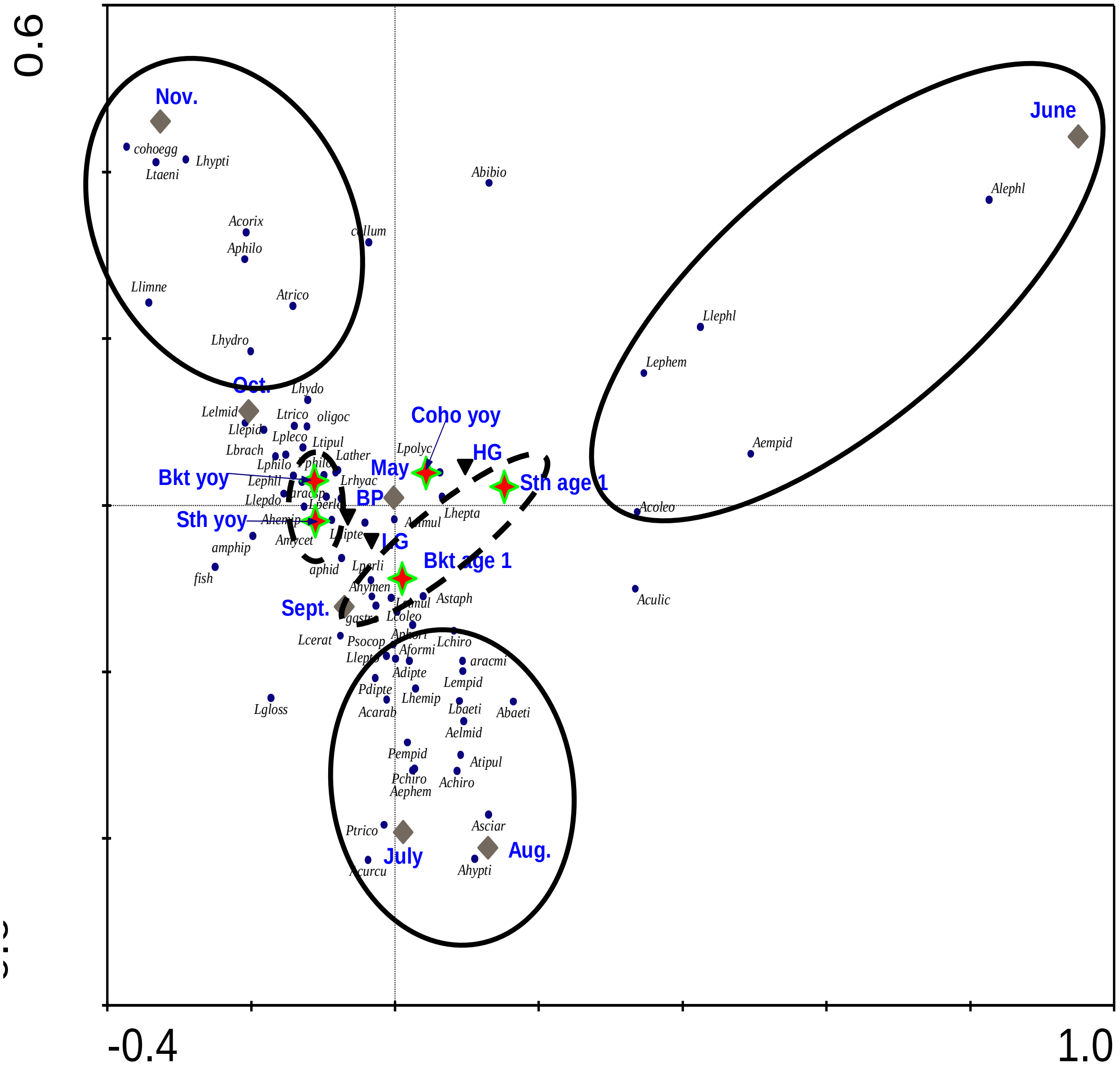

Figure 9: CCA using the proportion of prey items in diet by biomass. Centroids for month are shown as diamonds, for habitat are shown as black triangles and for fish category are shown as stars. Axes 1 and 2 represented 56.9% and 40.0% of the species-environment relationship, respectively. The ovals emphasize the effect of month on the prey items within stomach contents while the dashed-line oval emphasizes the relationship among fish categories. Invertebrates are labeled with life stage (first letter) and family name (next five letters). Habitat area categories are shown as HG=high gradient, LG=low gradient, BP=beaver pond.

Table 18: Prey size category preference. Symbols '↑' represent a higher preference (white), '↓' represent a lower preference (dark grey) and '=' was used when no preference was determined (light grey).

	Prey Size Category				
	1	2	3	4	5
Age 1 brook trout	↓	↓	=	↑	=
YOY brook trout	↑	↑	=	↓	↓
Age 1 steelhead	↓	↓	=	↑	↑
YOY steelhead	↑	↑	=	↓	=
YOY coho	↑	↑	=	↑	=
Test Results: Kruskal-Wallis	H=60.631, df=4, p<0.001	H=81.314, df=4, p<0.001	H=3.287, df=4, p=0.511	H=64.666, df=4, p<0.001	H=32.761, df=4, p<0.001

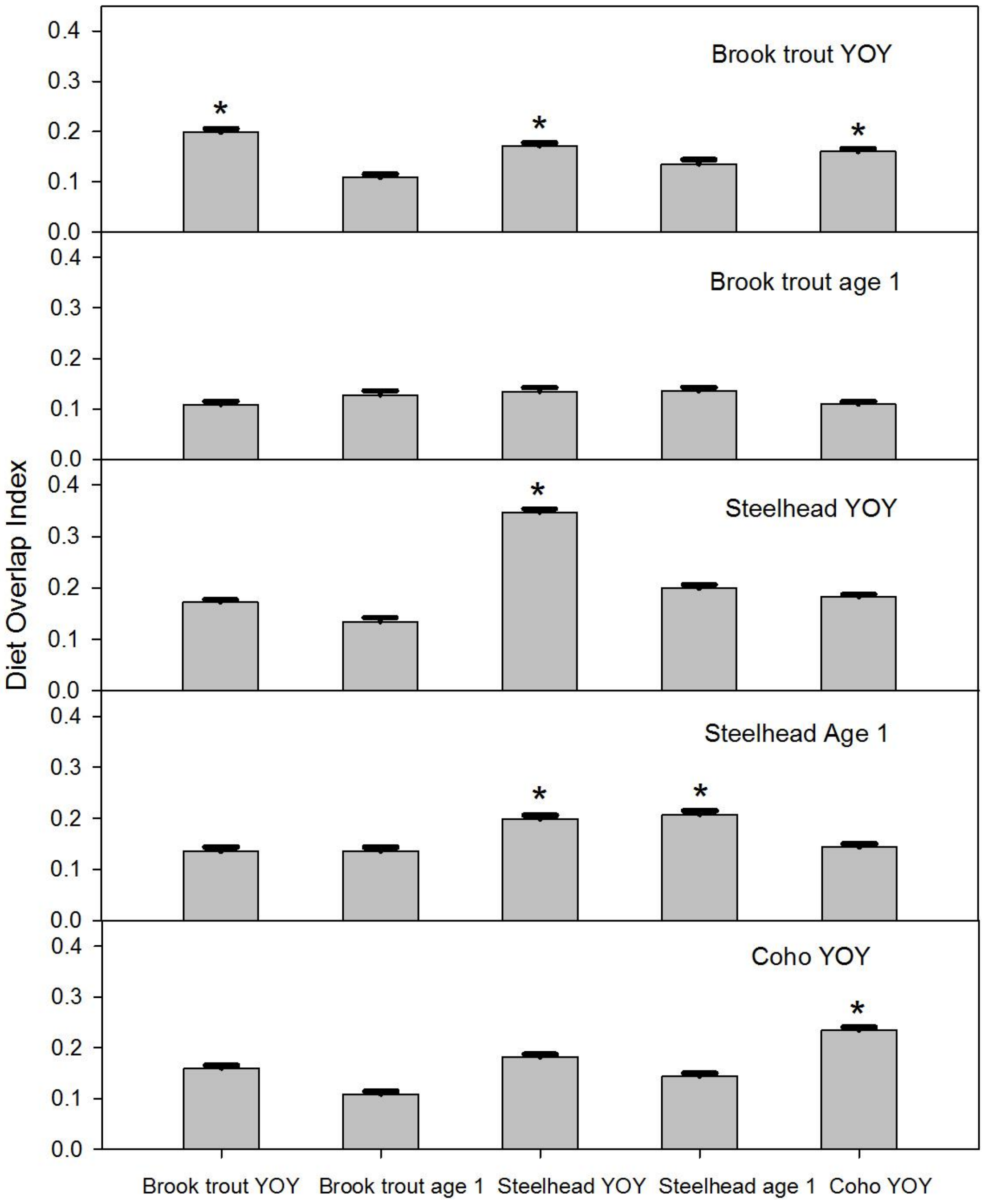

Figure 10: Mean diet overlap among fish categories. The asterisks mark significantly higher diet overlap values within each fish category and standard error bars are included.

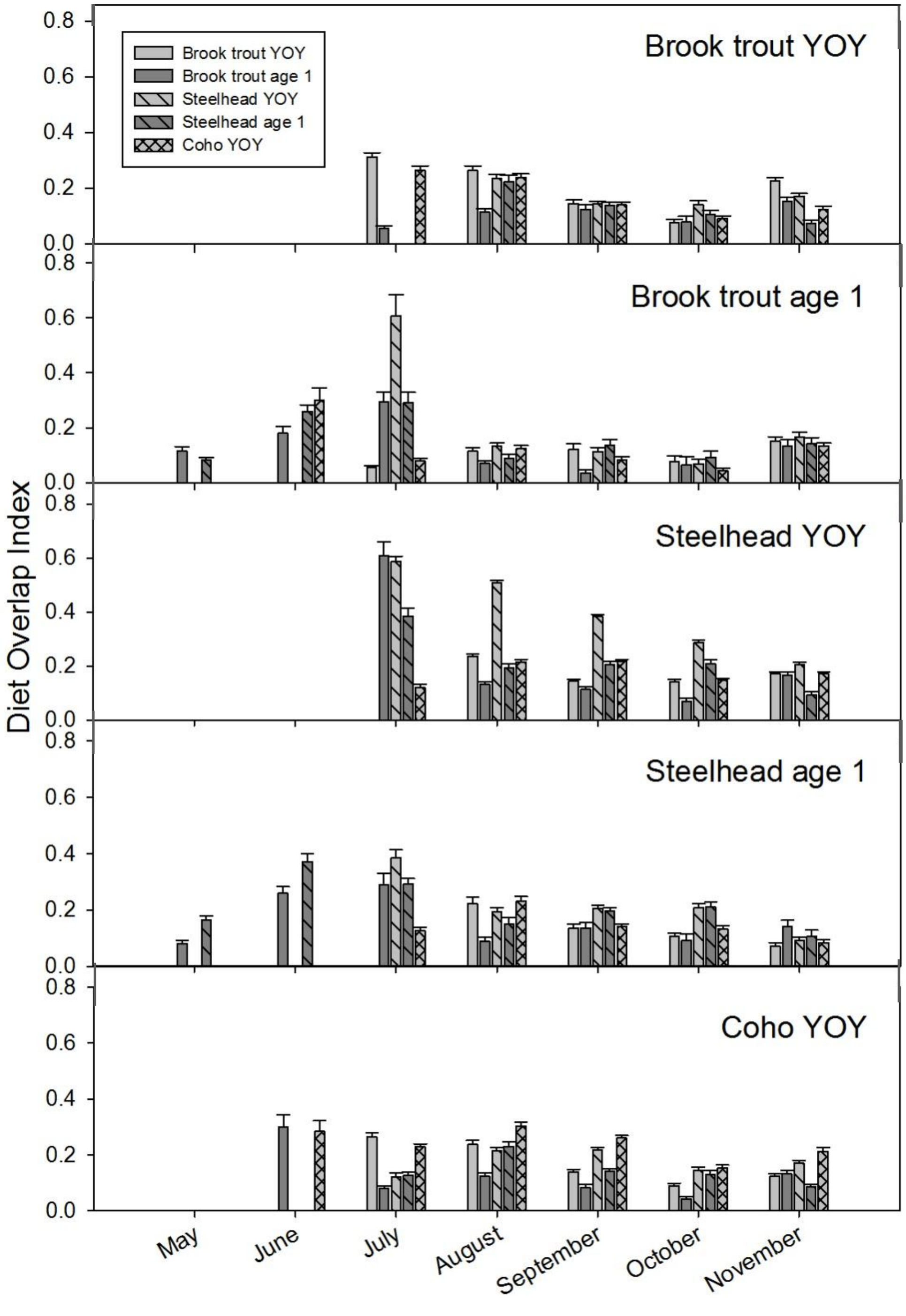

Figure 11: Mean diet overlap among fish categories by month.

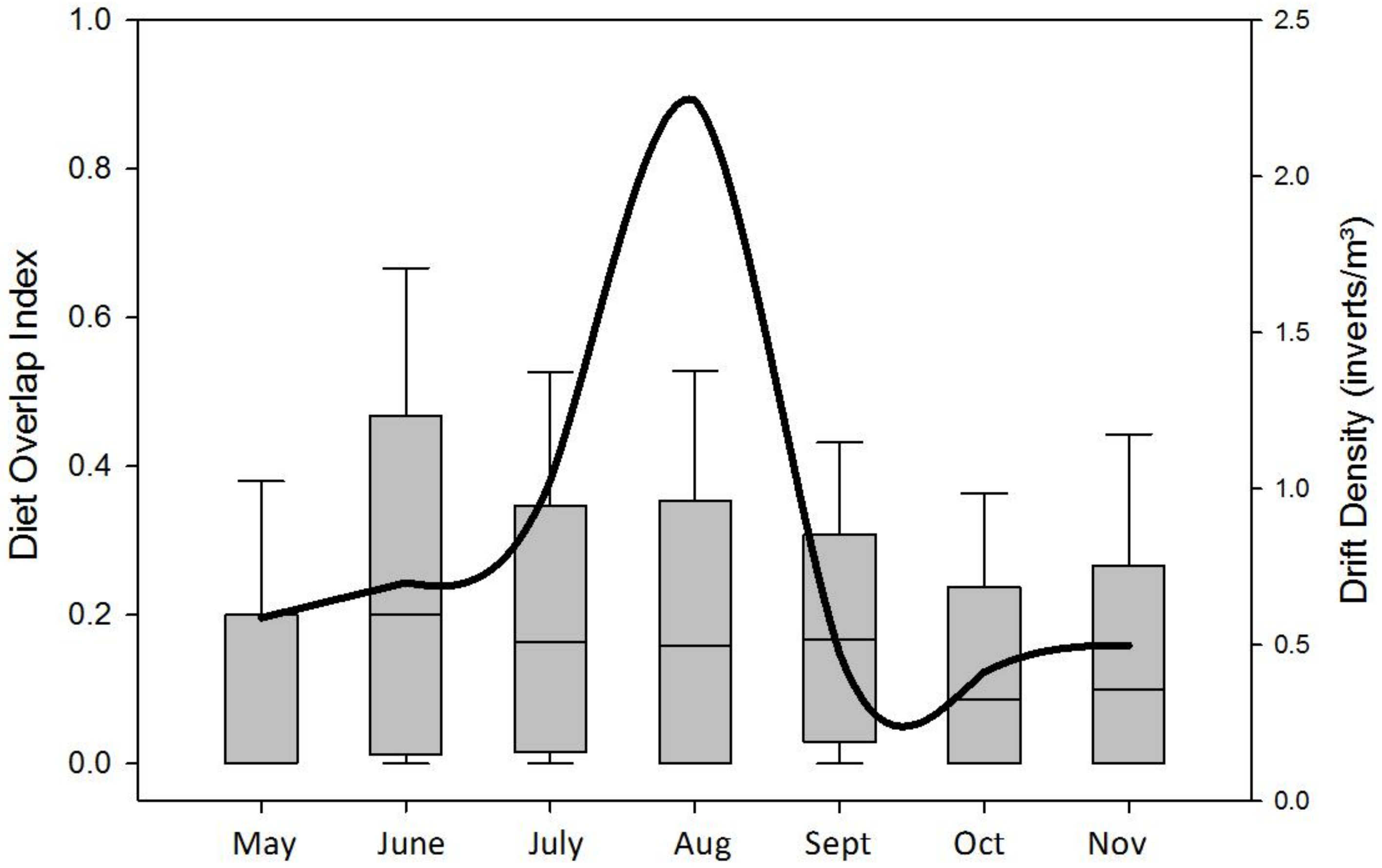

Figure 12: Diet overlap shown as medians (line within box), first and third quartiles (box) and 5th/95th percentile (whiskers) and drift density (line) by month.

CHAPTER THREE: SUMMARY AND CONCLUSIONS

Introductions of nonnative species, both planned and unintentional, into aquatic systems such as streams, rivers, and lakes have had serious negative impacts on native communities and have affected many organisms including plants, invertebrates and fishes (Colautti et al. 2006; Krueger and May 1991; Litchman 2010; Mills et al. 1994). In particular, the introduction of nonnative fish species has been shown to negatively impact native fish communities by a variety of mechanisms including competition for resources, predation, and disturbance (Krueger and May 1991; Moyle and Light 1996). With the introduction of salmon and trout to streams and lakes of the eastern United States, declines in native brook trout (*Salvelinus fontinalis*) populations have been widespread from the Appalachians to the Great Lakes region (Fausch and White 1981, 1986; Fausch 1988; Larson and Moore 1985).

In Lake Superior and its tributaries, steelhead trout (*Oncorhynchus mykiss*) and coho salmon (*O. kisutch*) were intentionally introduced, in 1895 and 1965 respectively, to increase sport fishing opportunities in the region (Emery 1985). The introduced fishes and brook trout utilize stream habitats for spawning and rearing (Peck 1970; MacCrimmon and Gots 1972; Greeley 1932). Declining brook trout distribution and density throughout their historical range may be related to human activities such as water diversion, mining, logging, and overfishing (Hudy et al. 2008; Larson and Moore 1985, Becker 1983) as well as negative interactions with introduced species resulting from competition for spawning, rearing and foraging habitat (Fausch 1988; Rose 1986).

Salmon and trout in streams feed mainly from the invertebrates drifting in the current which is referred to as the ‘drift’. The drift is composed of aquatic and terrestrial bugs (Nilsson 1957; Larson et al. 1995). Successful capture of food items from the drift is affected by many environmental factors including water speed, temperature, depth, clarity, where the fish are feeding, and competition with other fish (Cunjak et al. 1987; Hughes and Dill 1990; Sweka and Hartman 2001). Typically the larger a fish the better the opportunity it has to find a good place to feed (Nakano 1994). The best feeding locations are those spots where the fish doesn’t have to expend a lot of energy capturing food and where access to drifting invertebrates is high.

One of the introduced species, coho salmon, hatches earlier and is typically larger than the newly hatched brook trout (Young 2004). Both the coho salmon and brook trout prefer pool habitat with deep, slow-moving waters (Becker 1983; Cunjak and Green 1983, 1984; Bisson et al. 1988). As the young-of-year coho salmon in these systems tend to be larger than the young-of-year brook trout, the coho salmon may be taking the good feeding spots in pools from the brook trout. Steelhead trout, on the other hand, hatch around the same time as the brook trout and are similar in size when they begin to feed on the drift (Rose 1986). The steelhead trout presence may be slowing down the rate of growth in the brook trout until the steelhead trout move out into faster water as they grow larger (Everest and Chapman 1972; Rose 1986). By examining and comparing what these fishes were eating, I was able to determine if the introduced salmon and trout could be putting competitive pressure on the native brook trout via competition for prey resources.

In this paper I presented information on food availability in the drift and what was eaten by native brook trout, coho salmon and steelhead trout within a Lake Superior tributary of Pictured Rocks National Lakeshore. I examined how much the diets of the different fishes overlaped in order to determine how similar or dissimilar were their feeding habits. This project examined which invertebrates made up the drift and how it changed depending on time of year and habitat, what the fish were eating and what they prefered to eat as well as how similar were the diets of the different species.

The seasonal pattern seen in the drift throughout the study was similar to patterns seen in other studies where the number of invertebrates in the drift increased from spring to mid-summer declining into fall and winter (McLay 1968; Clifford 1972; Kawaguchi and Nakano 2001). The amount of invertebrates in the drift also varied with habitat which differed in water velocity as well as the size of rocks and the amount of sand or silt on the bottom of the stream (Flecker and Allan 1984; Jowett et al. 1991). In the areas where water velocity was low and where the bottom of the stream was mostly sand and silt, such as the beaver ponds, there were fewer invertebrates in the drift.

Many studies, including this one, have shown that salmon and trout diets closely reflect the type of invertebrates available in the drift (Allan 1981; Bres 1986; Esteban and Marchetti 2004; Fausch and White 1986; Hilderbrand and Kershner 2004; Irvine and Northcote 1982). In this study, drift and what the fish consumed were strongly influenced by time of year. From spring to midsummer as the invertebrates in the drift increased so also did the number of invertebrates and the weight of the invertebrates that were eaten by the salmon and trout in the study; as the invertebrates in the drift declined so did the number and weight of invertebrates eaten by salmon and trout (Cada et al. 1987; Elliot 1970; Kawaguchi and Nakano 2001). The reason for the higher number of invertebrates consumed in the summer may be higher summer water temperatures which increase the metabolism of the fishes and therefore require more food to be consumed (Brett and Groves 1979). Another potential explanation for the increase in the number and weight of invertebrates eaten by the fishes is that fish may have been more successful capturing invertebrates when there were more invertebrates available (Galarowicz and Wahl 2005; Mathias and Li 1982; Ware 1972).

The success of fishes in capturing invertebrates is not only related to how many prey are available in the drift, but also to water velocity and depth. Piccolo et al. (2007, 2008) showed that coho salmon and steelhead trout could detect invertebrates within a larger area in the stream in slower moving, deep water. Hughes and Dill (1990) as well as Grant and Noakes (1987) also showed that fish were able to capture invertebrates more efficiently in slower moving water. The beaver ponds were characterized by deep, lower temperature pools with slow moving water and low numbers of invertebrates in the drift. Interestingly, fishes in the beaver ponds consistently ate more invertebrates; individuals within beaver ponds seem to have been more efficient at capturing invertebrates.

The fishes found in beaver ponds ate more invertebrates than those fishes in the other habitat areas and within the beaver ponds the brook trout ate fewer items than the other fishes. Many studies have shown that brook trout tend to have fewer items in their stomachs compared to other fish (Hilderbrand and Kershner 2004, Dunham et al. 2000), but few studies examine how healthy the fish are as well as how much they are eating. If the larger brook trout were better foragers in areas with slow moving water and deep pools like the beaver ponds, one would expect to see brook trout in better condition as compared to other habitats. I examined two metrics that measure fish status and both the Fulton's condition factor and relative weight for larger brook trout were highest in the beaver ponds. Brook trout preference for pool habitat is well documented (Becker, 1983; Cunjak and Green, 1983, 1984) and, in my study, it would seem that preference is based on expending less energy than fish are able to eat. Although the number of invertebrates drifting in the beaver ponds was lower, the condition of the larger brook trout was better which means that the brook trout were better at catching food or that they were expending less energy to do it, or a combination of both.

When salmon and trout select a location from which to catch invertebrates in streams, there are typically interactions among individuals which would prefer the same location. These interactions tend to lead to a pattern where the best locations for catching invertebrates are dominated by larger fish. The best locations are selected because they provide maximum access to invertebrates while minimizing the amount of energy it takes to catch invertebrates and stay in position within the stream (Fausch 1984; Kristiansen 1999; Nakano 1994). Not all salmon and trout vie for the same sites, as YOY fishes tend to prefer slower moving waters along the edges of streams (Hartman 1965; Cunjak and Green 1984; Fausch and White 1986; Rose 1986) while larger fishes tend to prefer deeper or faster flowing water (Bisson et al. 1988; Everest and Chapman 1972). The larger fishes, both steelhead trout and brook trout, in my study consumed more large prey items than YOY fishes, a pattern seen in many other studies (Allan 1981; Nakano 1995; Syrjanen et al. 2011; Werner and Hall 1974). Of the YOY fishes, coho salmon ate more large items from the drift. Coho salmon hatch approximately two months earlier than brook trout or steelhead trout in the spring resulting in not only a larger body size (30% larger weight) earlier in the summer, but most likely a larger gape. Not only do larger fishes have a better chance at getting the best sites to catch invertebrates from, but many studies have shown that as fish age they get better at catching invertebrates, allowing older fishes the advantage of experience in catching invertebrates (Godin 1978, Blaxter 1986, McLaughlin et al. 2000). Both the larger size and the experience of coho salmon would give them a great advantage in the struggle with other small fishes for prey capture sites and may explain the difference in what invertebrates were eaten among YOY fishes.

Habitat preference and sites for catching invertebrates can influence how many and what invertebrates are eaten, which in turn influences how similar the diets are among fishes or how much the diets overlap. Repeatedly the highest diet overlap values occurred first between fishes of the same species that hatched at the same time. It is not surprising to find that fishes of the same size and species eat very similar items as they are most likely found in very similar habitat and in similar sites for catching invertebrates. During this study, the invertebrates that were eaten varied throughout the year and diet overlap also varied. Our mean diet overlap values ranged between 0.1

and 0.4 with the highest values occurring in August when the number of invertebrates in the drift was at its peak. A study by Deus and Petrere-Junior (2003) documented a similar increase in diet overlap when prey increased and explained the pattern by showing that fish shifted what they ate and where and how they caught invertebrates dependent upon what invertebrates were available and on whether other fishes of the same or different species were eating the same things. In a study from 2003, Miyasaka and coworkers showed low diet overlap values and suggested that it was because individuals of the nondominant species shifted to a different strategy for catching and eating invertebrates as the number of invertebrates available declined. It is possible that the low diet overlap values in this study are a result of changing foraging strategies for these species depending on resource availability which is influenced by season and time of day. Nilsson and Northcote (1981) were able to determine that resource and foraging strategy shifts were occurring in sympatric populations of rainbow trout and cutthroat trout (*Salmo clarki*) by comparing sympatric populations to allopatric populations of each species. A similar comparison of resource use and foraging strategies between allopatric and sympatric populations of brook trout, coho salmon and steelhead trout would be useful in attempting to identify any potential for competition that may exist.

Diet overlap increased when invertebrate drift increased lending credence to the idea that fishes were more selective, or choosier, of invertebrates during times when lots of invertebrates were available in the drift. In the summer when the number of drifting invertebrates was high, fishes more strongly avoided or selected for certain invertebrates showing that the fishes did actually have preference for certain prey. One pattern that became apparent was that more prey items were avoided than preferentially selected from the drift and selection values were lower than avoidance values overall. Selectivity isn't necessarily about positively selecting for items or avoiding them, but it is about choosiness. The choosiness of fishes increased as the number of invertebrates in the drift increased which led to an increase in diet overlap.

The effects that introduced fishes had on the brook trout varied by age class as well as species. Coho salmon, perhaps because of earlier hatching and larger size, were intermediate between the larger fish and YOY fishes in habitat use and prey use. The coho salmon are using similar habitat as brook trout and could therefore be forcing those smaller YOY brook trout out of preferred habitat and into the faster and shallower foraging areas. It would be difficult to document a habitat usage shift such as this in the field, but direct observation via snorkeling may be a useful tool to observe these types of patterns (see Nakano 1995). Not only are coho salmon having a negative effect on brook trout by attempting to occupy the same type of habitat, but as coho salmon grow larger through the summer they eat large prey items which increases the potential for negative effects on larger brook trout that also prefer to eat large invertebrates. Prey eaten by YOY brook trout was very similar to prey eaten by YOY steelhead trout, but unless the number of invertebrates in the drift is limited, the negative effects between these fishes may be small; however, when both brook trout and steelhead trout are newly emerged they prefer similar habitat in slower water near shore (Rose 1986). As steelhead trout increase in size they move into faster shallow water, and as brook trout increase in size they move into deeper water. Many studies have examined the potential negative effects of steelhead trout on brook trout distribution throughout the stream (see Larson and Moore 1985), and those studies suggest that some type of pressure occurs between species resulting in a brook trout distribution reduction, concentrating them in the upstream reaches of the system. Larger steelhead trout and brook trout in this study consumed similar numbers and sizes of prey items and although the literature points out that these two species prefer different habitats (Cunjak and Green 1983; Bisson et al. 1988; Rose 1986) perhaps access to preferred prey, when good sites for catching invertebrates are limited, is the driving force that results in negative interaction between species for preferred sites for catching prey.

Diet comparisons in the field where many variables are uncontrolled may be subject to undocumented competitive pressure among species that may influence both access to prey and which invertebrates are eaten as prey, and such comparisons serve as a preliminary view of whether the potential for competitive interactions among species exists in the natural system. The salmon and trout in the study, overall, ate similar invertebrates and although diet overlap was below Schoener's suggested value, during periods when the number of invertebrates in the drift is low, when resources are limited, competition for sites for catching invertebrates and which invertebrates are eaten could occur. Overall, this study has shown that introduced salmon and trout in a tributary of Lake Superior could be negatively affecting survival and growth of the native brook trout.

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APPENDIX A

LENGTH-BIOMASS REGRESSIONS FROM THE LITERATURE AND USED TO CALCULATE DRIFT AND STOMACH SAMPLE BIOMASS

Phylum	Class	Order	Family	Source	LifeStage	a	b	Taxon	SourceForLWRegression
Annelida	Oligochaeta	Oligochaeta	Oligochaeta	aquatic	any	0.008	1.888	class	Miyasak et al. 2008
Arthropoda	Arachnida	Acari	Hydrachnidia	aquatic	any	0.133	1.66	order	Hodar 1996
Arthropoda	Arachnida	Arachnida	Arachnida	terrestrial	any	0.0562	2.332	class	Gruner 2003
Arthropoda	Arachnida	Araneae	Araneae	terrestrial	any	0.05	2.74	order	Sabo et al. 2002
Arthropoda	Arachnida	Pseudoscorpiones	Pseudoscorpiones	terrestrial	any	0.04088	2.218	order	Johnson and Strong 2000
Arthropoda	Diplopoda	Diplopoda	Diplopoda	terrestrial	any	0.00012	3.909	class	Hodar 1996
Arthropoda	Insecta	Coleoptera	Cantharidae	terrestrial	adult	0.04	2.64	order	Sabo et al. 2002
Arthropoda	Insecta	Coleoptera	Carabidae	terrestrial	adult	0.072	2.401	family	Sabo et al. 2002
Arthropoda	Insecta	Coleoptera	Coleoptera	both	adult	0.0339	2.384	order	Gruner 2003
Arthropoda	Insecta	Coleoptera	Coleoptera	both	larva	0.011657	2.472	order	Meyer 1989
Arthropoda	Insecta	Coleoptera	Curculionidae	terrestrial	adult	0.04	2.64	order	Sabo et al. 2002
Arthropoda	Insecta	Coleoptera	Dryopidae	aquatic	adult	0.0339	2.384	order	Gruner 2003
Arthropoda	Insecta	Coleoptera	Dryopidae	aquatic	larva	0.011657	2.472	order	Gruner 2003
Arthropoda	Insecta	Coleoptera	Dytiscidae	aquatic	adult	0.0618	2.502	family	Benke et al. 1999
Arthropoda	Insecta	Coleoptera	Dytiscidae	aquatic	larva	0.011657	2.472	order	Gruner 2003
Arthropoda	Insecta	Coleoptera	Elmidae	aquatic	adult	0.0339	2.384	order	Gruner 2003
Arthropoda	Insecta	Coleoptera	Elmidae	aquatic	larva	0.0074	2.879	family	Benke et al. 1999

Arthropoda	Insecta	Coleoptera	Gyrinidae	aquatic	adult	0.04	2.64	order	Sabo et al. 2002
Arthropoda	Insecta	Coleoptera	Haliplidae	aquatic	adult	0.0271	2.744	family	Benke et al. 1999
Arthropoda	Insecta	Coleoptera	Haliplidae	aquatic	larva	0.011657	2.472	order	Gruner 2003
Arthropoda	Insecta	Coleoptera	Hydrophilidae	aquatic	adult	0.0339	2.384	order	Gruner 2003
Arthropoda	Insecta	Coleoptera	Hydrophilidae	aquatic	larva	0.011657	2.472	order	Gruner 2003
Arthropoda	Insecta	Coleoptera	Psephenidae	aquatic	adult	0.0123	2.906	family	Benke et al. 1999
Arthropoda	Insecta	Coleoptera	Scarabaeidae	terrestrial	adult	0.0746	2.582	family	Hodar 1996
Arthropoda	Insecta	Coleoptera	Staphylinidae	terrestrial	adult	0.001	4.026	family	Sabo et al. 2002
Arthropoda	Insecta	Coleoptera	Staphylinidae	terrestrial	larva	0.011657	2.472	order	Meyer 1989
Arthropoda	Insecta	Collembola	Collembola	terrestrial	any	0.0056	2.809	order	Gruner 2003
Arthropoda	Insecta	Collembola	Collembola	terrestrial	any	0.0056	2.809	order	Gruner 2003
Arthropoda	Insecta	Diptera	Athericidae	aquatic	adult	0.164	1.558	family	Sabo et al. 2002
Arthropoda	Insecta	Diptera	Athericidae	aquatic	larva	0.004	2.586	family	Benke et al. 1999
Arthropoda	Insecta	Diptera	Bibionidae	terrestrial	adult	0.021	2.081	suborder	Hodar 1996
Arthropoda	Insecta	Diptera	Camillidae	terrestrial	adult	0.0304	2.081	suborder	Hodar 1996
Arthropoda	Insecta	Diptera	Ceratopogonidae	both	adult	0.021	2.081	suborder	Hodar 1996
Arthropoda	Insecta	Diptera	Ceratopogonidae	both	larva	0.0025	2.469	family	Benke et al. 1999
Arthropoda	Insecta	Diptera	Ceratopogonidae	aquatic	pupa	0.0025	2.469	family	Benke et al 1999
Arthropoda	Insecta	Diptera	Chironomidae	aquatic	larva	0.0018	2.617	family	Benke et al. 1999
Arthropoda	Insecta	Diptera	Chironomidae	aquatic	pupa	0.0052	2.24	family	Burgherr and Meyer 1997
Arthropoda	Insecta	Diptera	Chironomidae	aquatic	adult	0.021	2.081	suborder	Hodar 1996
Arthropoda	Insecta	Diptera	Culicidae	aquatic	adult	0.021	2.081	suborder	Hodar 1996
Arthropoda	Insecta	Diptera	Diptera	both	adult	0.006	3.05	order	Sabo et al. 2002
Arthropoda	Insecta	Diptera	Diptera	both	larva	0.0025	2.692	order	Benke et al. 1999
Arthropoda	Insecta	Diptera	Diptera	both	pupa	0.009817	2.27	order	FSL
Arthropoda	Insecta	Diptera	Dixidae	aquatic	larva	0.0025	2.692	family	Hodar 1996
Arthropoda	Insecta	Diptera	Dolichopodidae	both	adult	0.0304	2.63	suborder	Hodar 1996

Arthropoda	Insecta	Diptera	Drosophilidae	terrestrial	adult	0.0304	2.63	suborder	Hodar 1996
Arthropoda	Insecta	Diptera	Empididae	both	adult	0.0304	2.63	suborder	Hodar 1996
Arthropoda	Insecta	Diptera	Empididae	both	larva	0.0054	2.546	family	Benke et al. 1999
Arthropoda	Insecta	Diptera	Empididae	both	pupa	0.03714	2.366	family	FSL
Arthropoda	Insecta	Diptera	Ephydridae	aquatic	adult	0.0304	2.081	suborder	Hodar 1996
Arthropoda	Insecta	Diptera	Mycetophilidae	terrestrial	adult	0.021	2.081	suborder	Hodar 1996
Arthropoda	Insecta	Diptera	Phoridae	terrestrial	adult	0.0304	2.63	suborder	Hodar 1996
Arthropoda	Insecta	Diptera	Sciaridae	terrestrial	adult	0.021	2.081	suborder	Hodar 1996
Arthropoda	Insecta	Diptera	Simuliidae	aquatic	larva	0.002	3.011	family	Benke et al. 1999
Arthropoda	Insecta	Diptera	Simuliidae	aquatic	pupa	0.006	3.05	family	FSL
Arthropoda	Insecta	Diptera	Simuliidae	aquatic	adult	0.021	2.081	suborder	Hodar 1996
Arthropoda	Insecta	Diptera	Sphaeroceridae	terrestrial	adult	0.0304	2.63	suborder	Hodar 1996
Arthropoda	Insecta	Diptera	Tipulidae	both	larva	0.0029	2.681	family	Benke et al. 1999
Arthropoda	Insecta	Diptera	Tipulidae	both	adult	0.021	2.081	suborder	Hodar 1996
Arthropoda	Insecta	Diptera	Tipulidae	aquatic	pupa	0.0029	2.681	family	Benke et al. 1999
Arthropoda	Insecta	Ephemeroptera	Baetidae	aquatic	adult	0.014	2.49	order	Benke et al. 1999
Arthropoda	Insecta	Ephemeroptera	Baetidae	aquatic	larva	0.0053	2.875	family	Benke et al. 1999
Arthropoda	Insecta	Ephemeroptera	Baetiscidae	aquatic	larval	0.0116	2.905	family	Benke et al. 1999
Arthropoda	Insecta	Ephemeroptera	Ephemerellidae	aquatic	larva	0.0103	2.676	family	Benke et al. 1999
Arthropoda	Insecta	Ephemeroptera	Ephemerellidae	aquatic	adult	0.014	2.49	order	Sabo et al. 2002
Arthropoda	Insecta	Ephemeroptera	Ephemeridae	aquatic	larval	0.0034	2.764	family	Benke et al. 1999
Arthropoda	Insecta	Ephemeroptera	Ephemeroptera	aquatic	adult	0.014	2.49	order	Sabo et al. 2002
Arthropoda	Insecta	Ephemeroptera	Ephemeroptera	aquatic	larva	0.0071	2.832	order	Benke et al. 1999
Arthropoda	Insecta	Ephemeroptera	Heptageniidae	aquatic	larva	0.0108	2.754	family	Benke et al. 1999
Arthropoda	Insecta	Ephemeroptera	Heptageniidae	aquatic	adult	0.014	2.49	order	Sabo et al. 2002
Arthropoda	Insecta	Ephemeroptera	Leptohyphidae	aquatic	larval	0.0071	2.832	order	Benke et al. 1999
Arthropoda	Insecta	Ephemeroptera	Leptophlebiidae	aquatic	adult	0.014	2.49	order	Benke et al. 1999

Arthropoda	Insecta	Ephemeroptera	Leptophlebiidae	aquatic	larva	0.0047	2.686	family	Benke et al. 1999
Arthropoda	Insecta	Ephemeroptera	Siphlonuridae	aquatic	larva	0.0027	3.446	family	Benke et al. 1999
Arthropoda	Insecta	Ephemeroptera	Siphlonuridae	aquatic	adult	0.014	2.49	order	Benke et al. 1999
Arthropoda	Insecta	Hemiptera	Aphididae	terrestrial	any	0.005	3.33	order	Sabo et al. 2002
Arthropoda	Insecta	Hemiptera	Belostomatidae	aquatic	adult	0.005	3.33	order	Sabo et al. 2002
Arthropoda	Insecta	Hemiptera	Corixidae	aquatic	adult	0.005	3.33	order	Sabo et al. 2002
Arthropoda	Insecta	Hemiptera	Corixidae	aquatic	larval	0.0031	2.904	family	Smock 1980
Arthropoda	Insecta	Hemiptera	Gerridae	aquatic	larval	0.015	2.596	family	Smock 1980
Arthropoda	Insecta	Hemiptera	Gerridae	aquatic	adult	0.005	3.33	order	Sabo et al. 2002
Arthropoda	Insecta	Hemiptera	Hemiptera	aquatic	larval	0.0108	2.734	order	Benke et al. 1999
Arthropoda	Insecta	Hemiptera	Hemiptera	both	adult	0.005	3.33	order	Sabo et al. 2002
Arthropoda	Insecta	Hemiptera	Hydrometridae	aquatic	adult	0.005	3.33	order	Sabo et al. 2002
Arthropoda	Insecta	Hemiptera	Mesoveliidae	aquatic	adult	0.02147	2.794	order	Johnson and Strong 2000
Arthropoda	Insecta	Hemiptera	Mesoveliidae	aquatic	larval	0.0108	2.734	order	Benke et al. 1999
Arthropoda	Insecta	Hemiptera	Nepidae	aquatic	adult	0.005	3.33	order	Sabo et al. 2002
Arthropoda	Insecta	Hemiptera	Notonectidae	aquatic	any	0.02147	2.794	order	Johnson and Strong 2000
Arthropoda	Insecta	Hemiptera	Pleidae	aquatic	adult	0.005	3.33	order	Sabo et al. 2002
Arthropoda	Insecta	Hemiptera	Triozidae	terrestrial	adult	0.005	3.33	order	Sabo et al. 2002
Arthropoda	Insecta	Hemiptera	Veliidae	aquatic	adult	0.02147	2.794	order	Johnson and Strong 2000
Arthropoda	Insecta	Hemiptera	Veliidae	aquatic	larval	0.0108	2.734	order	Benke et al. 1999
Arthropoda	Insecta	Hymenoptera	Formicidae	terrestrial	adult	0.027	2.666	family	Sabo et al. 2002
Arthropoda	Insecta	Hymenoptera	Hymenoptera	terrestrial	both	0.56	1.56	order	Sabo et al. 2002
Arthropoda	Insecta	Insecta	Insecta	both	larva	0.003231	2.258	class	Johnson and Strong 2000
Arthropoda	Insecta	Insecta	Insecta	terrestrial	adult	0.0305	3.628	class	Rogers et al. 1976
Arthropoda	Insecta	Lepidoptera	Lepidoptera	both	larva	0.002715	2.959	order	Sample et al. 1993
Arthropoda	Insecta	Lepidoptera	Lepidoptera	terrestrial	adult	0.012	2.69	order	Sabo et al. 2002
Arthropoda	Insecta	Mecoptera	Mecoptera	terrestrial	adult	0.09	2.41	class	Sabo et al. 2002

Arthropoda	Insecta	Megaloptera	Megaloptera	aquatic	larva	0.0037	2.838	order	Benke et al. 1999
Arthropoda	Insecta	Megaloptera	Sialidae	aquatic	adult	0.0037	2.753	family	Benke et al. 1999
Arthropoda	Insecta	Megaloptera	Sialidae	aquatic	larval	0.0037	2.753	family	Benke et al. 1999
Arthropoda	Insecta	Odonata	Aeshnidae	aquatic	larval	0.0082	2.813	family	Smock 1980
Arthropoda	Insecta	Odonata	Calopterygidae	aquatic	larval	0.005	2.742	family	Smock 1980
Arthropoda	Insecta	Odonata	Coenagrionidae	aquatic	larval	0.0051	2.785	family	Benke et al. 1999
Arthropoda	Insecta	Odonata	Coenagrionidae	aquatic	adult	0.001	2.672	family	Sabo et al. 2002
Arthropoda	Insecta	Odonata	Cordulegastridae	aquatic	larval	0.0067	2.782	family	Smock 1980
Arthropoda	Insecta	Odonata	Gomphidae	aquatic	larval	0.0088	2.787	family	Benke et al. 1999
Arthropoda	Insecta	Odonata	Odonata	aquatic	larval	0.0078	2.792	order	Benke et al. 1999
Arthropoda	Insecta	Orthoptera	Orthoptera	terrestrial	adult	0.0255	2.637	order	Hodar 1996
Arthropoda	Insecta	Plecoptera	Capniidae	aquatic	adult	0.26	1.69	order	Sabo et al. 2002
Arthropoda	Insecta	Plecoptera	Capniidae	aquatic	larva	0.0049	2.562	family	Benke et al. 1999
Arthropoda	Insecta	Plecoptera	Chloroperlidae	aquatic	larva	0.0065	2.724	family	Benke et al. 1999
Arthropoda	Insecta	Plecoptera	Chloroperlidae	aquatic	adult	0.005	2.732	family	Sabo et al. 2002
Arthropoda	Insecta	Plecoptera	Nemouridae	aquatic	larva	0.0056	2.762	family	Benke et al. 1999
Arthropoda	Insecta	Plecoptera	Perlidae	aquatic	larva	0.0099	2.879	family	Benke et al. 1999
Arthropoda	Insecta	Plecoptera	Perlodidae	aquatic	adult	0.26	1.69	order	Sabo et al. 2002
Arthropoda	Insecta	Plecoptera	Perlodidae	aquatic	larva	0.0196	2.742	family	Benke et al. 1999
Arthropoda	Insecta	Plecoptera	Plecoptera	aquatic	larva	0.0094	2.754	order	Benke et al. 1999
Arthropoda	Insecta	Plecoptera	Plecoptera	aquatic	adult	0.26	1.69	order	Sabo et al. 2002
Arthropoda	Insecta	Pscoptera	Psocoptera	terrestrial	any	0.0425	1.637	order	Hodar 1996
Arthropoda	Insecta	Plecoptera	Pteronarcyidae	aquatic	larva	0.0324	2.573	family	Benke et al. 1999
Arthropoda	Insecta	Plecoptera	Taeniopterygidae	aquatic	larval	0.0071	2.655	family	Benke et al. 1999
Arthropoda	Insecta	Trichoptera	Brachycentridae	aquatic	larva	0.0083	2.818	family	Benke et al. 1999
Arthropoda	Insecta	Trichoptera	Brachycentridae	aquatic	pupa	0.0083	2.818	family	Benke et al. 1999
Arthropoda	Insecta	Trichoptera	Glossosomatidae	aquatic	larva	0.0082	2.958	family	Benke et al. 1999

Arthropoda	Insecta	Trichoptera	Glossossomatidae	aquatic	pupa	0.082	2.958	family	Benke et al. 1999
Arthropoda	Insecta	Tricoptera	Glossossomatidae	aquatic	adult	0.01	2.9	order	Sabo et al. 2002
Arthropoda	Insecta	Trichoptera	Hydropsychidae	aquatic	adult	0.049	2.295	family	Sabo et al. 2002
Arthropoda	Insecta	Trichoptera	Hydropsychidae	aquatic	larva	0.0046	2.926	family	Benke et al. 1999
Arthropoda	Insecta	Trichoptera	Hydroptilidae	aquatic	larva	0.0122	2.57	family	Baumgartner and Rothhaupt 2003
Arthropoda	Insecta	Trichoptera	Hydroptilidae	aquatic	pupa	0.0122	2.57	family	Baumgartner and Rothhaupt 2003
Arthropoda	Insecta	Tricoptera	Hydroptilidae	aquatic	adult	0.01	2.9	order	Sabo et al. 2002
Arthropoda	Insecta	Trichoptera	Lepidostomatidae	aquatic	larva	0.0079	2.649	family	Benke et al. 1999
Arthropoda	Insecta	Trichoptera	Lepidostomatidae	aquatic	adult	0.01	2.9	order	Sabo et al. 2002
Arthropoda	Insecta	Trichoptera	Leptoceridae	aquatic	larva	0.0034	3.212	family	Benke et al. 1999
Arthropoda	Insecta	Trichoptera	Leptoceridae	aquatic	adult	0.01	2.9	order	Sabo et al. 2002
Arthropoda	Insecta	Trichoptera	Limnephilidae	aquatic	adult	0.004	2.933	family	Benke et al. 1999
Arthropoda	Insecta	Trichoptera	Limnephilidae	aquatic	larva	0.004	2.933	family	Benke et al. 1999
Arthropoda	Insecta	Trichoptera	Philopotamidae	aquatic	adult	0.01	2.9	order	Sabo et al. 2002
Arthropoda	Insecta	Trichoptera	Philopotamidae	aquatic	larva	0.005	2.511	family	Benke et al. 1999
Arthropoda	Insecta	Trichoptera	philopotamidae	aquatic	pupa	0.005	2.511	family	Benke et al. 1999
Arthropoda	Insecta	Trichoptera	Phryganeidae	aquatic	larva	0.0054	2.811	family	Benke et al. 1999
Arthropoda	Insecta	Trichoptera	Polycentropodidae	aquatic	larva	0.0047	2.705	family	Benke et al. 1999
Arthropoda	Insecta	Trichoptera	Psychomyiidae	aquatic	adult	0.01	2.9	order	Sabo et al. 2002
Arthropoda	Insecta	Trichoptera	Psychomyiidae	aquatic	larva	0.0056	2.839	order	Benke et al. 1999
Arthropoda	Insecta	Trichoptera	Psychomyiidae	aquatic	pupa	0.0039	2.873	family	Smock 1980
Arthropoda	Insecta	Trichoptera	Rhyacophilidae	aquatic	adult	0.01	2.9	order	Sabo et al. 2002
Arthropoda	Insecta	Trichoptera	Rhyacophilidae	aquatic	larva	0.0099	2.48	family	Benke et al. 1999
Arthropoda	Insecta	Trichoptera	Rhyacophilidae	aquatic	pupa	0.0099	2.48	family	Smock 1980
Arthropoda	Insecta	Trichoptera	Trichoptera	aquatic	adult	0.01	2.9	order	Sabo et al. 2002
Arthropoda	Insecta	Trichoptera	Trichoptera	aquatic	larva	0.0056	2.839	order	Benke et al. 1999

Arthropoda	Insecta	Trichoptera	Trichoptera	aquatic	Pupa	0.0056	2.839	order	Benke et al. 1999
Arthropoda	Malacostroca	Amphipoda	Amphipoda	aquatic	any	0.007828	2.56	order	Baumgartner and Rothhaupt 2003
Arthropoda	Malacostroca	Isopoda	Isopoda	aquatic	any	0.0054	2.948	order	Benke et al. 1999
Mollusca	Gastropoda	Gastropoda	Gastropoda	aquatic	any	0.03572	3.14	class	Meyer 1989
Mollusca	Mollusca	Mollusca	Mollusca	aquatic	any	0.0321	2.3	phylum	Baumgartner and Rothhaupt 2003

APPENDIX B

HEAD WIDTH-LENGTH REGRESSION LINES BUILT USING INVERTEBRATES COLLECTED VIA DRIFT SHOWING PERCENTAGE OF LENGTHS CALUCLATED IN STOMACH SAMPLES (*POLYNOMIAL REGRESSION MORE APPROPRIATE)

% calc.	Phylum	Class	Order	Family	Life stage	Taxon	a(SE)	b(SE)	r^2	Head Width	n	p
9%	Arthropoda	Arachnida	Araneae	Araneae	adult	class *	1.666+3.275(HW)-0.867(HW^2)		0.215	0.1-4.0	57	<0.001
17%	Arthropoda	Diplopoda	Diplopoda	Diplopoda	both	class	1.969(0.0274)	3.412(0.068)	0.482	0.05-2.0	2704	<0.001
34%	Arthropoda	Insecta	Coleoptera	Coleoptera	larva	order	4.186(0.295)	2.582(0.831)	0.11	0.1-1.0	80	0.003
33%	Arthropoda	Insecta	Coleoptera	Coleoptera	adult	order	2.910(0.181)	1.641(0.317)	0.135	0.1-1.5	173	<0.001
38%	Arthropoda	Insecta	Coleoptera	Curculionidae	adult	order	2.910(0.181)	1.641(0.317)	0.135	0.1-1.5	173	<0.001
40%	Arthropoda	Insecta	Coleoptera	Hydrophilidae	larva	family	1.177(1.158)	8.548(1.675)	0.839	0.1-1.0	7	0.004
10%	Arthropoda	Insecta	Coleoptera	Staphylinidae	adult	family	1.649(0.234)	7.433(0.838)	0.626	0.1-0.8	49	<0.001
20%	Arthropoda	Insecta	Diptera	Bibionidae	adult	order	1.879(0.0269)	3.603(0.0903)	0.423	0.05-2.0	2172	<0.001
7%	Arthropoda	Insecta	Diptera	Ceratopogonidae	larva	order	2.695(0.0415)	3.733(0.185)	0.132	0.02-2.0	2679	<0.001
20%	Arthropoda	Insecta	Diptera	Ceratopogonidae	adult	order	1.879(0.0269)	3.603(0.0903)	0.423	0.05-2.0	2172	<0.001
21%	Arthropoda	Insecta	Diptera	Chironimidae	larva	family	2.474(0.063)	7.020(0.431)	0.138	0.02-0.8	1661	<0.001
57%	Arthropoda	Insecta	Diptera	Chironimidae	pupa	family	2.096(0.055)	3.398(0.264)	0.16	0.1-0.8	871	<0.001
80%	Arthropoda	Insecta	Diptera	Chironimidae	adult	family	1.651(0.0519)	4.177(0.27)	0.168	0.05-	1187	<0.001

										0.7		
15%	Arthropoda	Insecta	Diptera	Culicidae	adult	family	2.969(0.501)	4.802(1.237)	0.537	0.1-0.8	15	0.002
5%	Arthropoda	Insecta	Diptera	Diptera	larva	order	2.695(0.0415)	3.733(0.185)	0.132	0.02-2.0	2679	<0.001
19%	Arthropoda	Insecta	Diptera	Diptera	larva/ pupa	order	2.535(0.0387)	4.076(0.164)	0.141	0.02-2.0	3648	<0.001
82%	Arthropoda	Insecta	Diptera	Diptera	adult	order	1.879(0.0269)	3.603(0.0903)	0.423	0.05-2.0	2172	<0.001
13%	Arthropoda	Insecta	Diptera	Empididae	larva/ pupa	order	2.535(0.0387)	4.076(0.164)	0.141	0.02-2.0	3648	<0.001
27%	Arthropoda	Insecta	Diptera	Empididae	adult	family	2.127(0.208)	3.686(0.293)	0.627	0.1-1.0	96	<0.001
17%	Arthropoda	Insecta	Diptera	Mycetophilidae	adult	family	1.732(0.383)	5.083(0.795)	0.759	0.1-0.8	15	<0.001
32%	Arthropoda	Insecta	Diptera	Phoridae	adult	family	1.701(0.234)	2.635(0.823)	0.243	0.1-0.5	34	0.003
60%	Arthropoda	Insecta	Diptera	Sciaridae	adult	family	1.631(0.0517)	5.743(0.27)	0.415	0.1-0.4	639	<0.001
26%	Arthropoda	Insecta	Diptera	Simuliidae	larva	family	1.426(0.0597)	6.338(0.186)	0.563	0.1-0.8	906	<0.001
16%	Arthropoda	Insecta	Diptera	Simuliidae	adult	family	2.608(0.258)	1.569(0.504)	0.152	0.2-1.0	56	0.003
10%	Arthropoda	Insecta	Diptera	Tipulidae	larva	family	1.537(0.599)	14.559(1.596)	0.569	0.1-1.25	65	<0.001
23%	Arthropoda	Insecta	Diptera	Tipulidae	adult	family	2.667(1.351)	8.218(2.314)	0.492	0.1-1.5	15	0.004
50%	Arthropoda	Insecta	Ephemeroptera	Baetidae	larva	family	1.652(0.0473)	4.852(0.13)	0.545	0.1-1.0	1158	<0.001
27%	Arthropoda	Insecta	Ephemeroptera	Baetidae	adult	family	3.141(0.246)	1.993(0.502)	0.33	0.02-1.0	34	<0.001
39%	Arthropoda	Insecta	Ephemeroptera	Ephemerellidae	larva	family	2.471(0.309)	4.005(0.302)	0.576	0.1-2.0	132	<0.001
100%	Arthropoda	Insecta	Ephemeroptera	Ephemeridae	larva	order	2.067(0.0359)	3.131(0.0634)	0.466	0.1-3.0	2795	<0.001
61%	Arthropoda	Insecta	Ephemeroptera	Ephemeroptera	larva	order	2.067(0.0359)	3.131(0.0634)	0.466	0.1-3.0	2795	<0.001
20%	Arthropoda	Insecta	Ephemeroptera	Ephemeroptera	adult	order	3.858(0.183)	1.962(0.189)	0.445	0.2-2.0	136	<0.001
30%	Arthropoda	Insecta	Ephemeroptera	Heptageniidae	larva	family	1.574(0.121)	1.999(0.134)	0.43	0.2-3.0	297	<0.001
40%	Arthropoda	Insecta	Ephemeroptera	Leptophlebiidae	larva	family	1.823(0.0491)	3.779(0.0898)	0.595	0.1-1.5	1209	<0.001
13%	Arthropoda	Insecta	Ephemeroptera	Leptophlebiidae	adult	order	3.858(0.183)	1.962(0.189)	0.445	0.2-2.0	136	<0.001
3%	Arthropoda	Insecta	Hemiptera	Aphididae	adult	family	1.316(0.143)	1.837(0.405)	0.255	0.1-0.8	62	<0.001
71%	Arthropoda	Insecta	Hemiptera	Corixidae	adult	family	2.667(0.72)	2.333(0.43)	0.907	1.0-2.0	5	0.012

47%	Arthropoda	Insecta	Hemiptera	Hemiptera	larva	order	1.568(0.292)	2.644(0.160)	0.841	0.1-3.0	54	<0.001
19%	Arthropoda	Insecta	Hemiptera	Hemiptera	adult	order	0.852(0.15)	3.812(0.249)	0.755	0.1-2.0	78	<0.001
67%	Arthropoda	Insecta	Hemiptera	Triozidae	adult	order	0.852(0.15)	3.812(0.249)	0.755	0.1-2.0	78	<0.001
19%	Arthropoda	Insecta	Hymenoptera	Hymenoptera	adult	order	1.808(0.19)	2.852(0.296)	0.715	0.1-2.0	39	<0.001
40%	Arthropoda	Insecta	Hymenoptera	Formicidae	adult	family	2.024(0.316)	2.651(0.384)	0.737	0.2-2.0	19	<0.001
29%	Arthropoda	Insecta	Insecta	Insecta	adult	class	1.969(0.0274)	3.412(0.068)	0.482	0.05-2.0	2704	<0.001
34%	Arthropoda	Insecta	Lepidoptera	Lepidoptera	larva	order	3.525(0.609)	3.741(1.497)	0.294	0.1-0.8	17	0.025
100%	Arthropoda	Insecta	Megaloptera	Corydalidae	larva	class	2.446(0.0216)	3.27(0.0418)	0.429	0.1-8.0	8151	<0.001
60%	Arthropoda	Insecta	Megaloptera	Sialidae	larva	class	2.446(0.0216)	3.27(0.0418)	0.429	0.1-8.0	8151	<0.001
80%	Arthropoda	Insecta	Odonota	Aeshnidae	larva	family	2.325(0.868)	1.759(0.273)	0.892	0.2-2.0	7	<0.001
29%	Arthropoda	Insecta	Odonota	Gomphidae	larva	family	0.847(0.546)	4.39(0.283)	0.964	0.2-5.0	11	<0.001
50%	Arthropoda	Insecta	Odonota	Odonata	larva	order	2.327(0.473)	2.064(0.243)	0.775	0.1-8.0	23	<0.001
100%	Arthropoda	Insecta	Orthoptera	Orthoptera	adult	class	1.969(0.0274)	3.412(0.068)	0.482	0.05-2.0	2704	<0.001
100%	Arthropoda	Insecta	Plecoptera	Chloroperlidae	adult	order	0.913(0.472)	6.522(0.813)	0.889	0.4-1.0	10	<0.001
88%	Arthropoda	Insecta	Plecoptera	Perlidae	larva	family	1.127(0.67)	3.694(0.349)	0.8	0.3-5.0	30	<0.001
25%	Arthropoda	Insecta	Plecoptera	Perlodidae	larva	family	1.844(0.221)	3.271(0.233)	0.57	0.1-2.0	151	<0.001
64%	Arthropoda	Insecta	Plecoptera	Plecoptera	larva	order	2.640(0.0772)	3.244(0.106)	0.536	0.1-5.0	808	<0.001
67%	Arthropoda	Insecta	Plecoptera	Plecoptera	adult	order	0.913(0.472)	6.522(0.813)	0.889	0.4-1.0	10	<0.001
13%	Arthropoda	Insecta	Plecoptera	Taeniopterygidae	larva	family	0.828(0.776)	6.544(0.835)	0.417	0.3-1.5	88	<0.001
60%	Arthropoda	Insecta	Psocoptera	Psocoptera	adult	order	1.316(0.11)	2.372(0.359)	0.509	0.1-1.0	44	<0.001
15%	Arthropoda	Insecta	Trichoptera	Brachycentridae	larva	family	1.357(0.117)	5.160(0.278)	0.647	0.1-1.5	189	<0.001
32%	Arthropoda	Insecta	Trichoptera	Hydropsychidae	larva	family	1.142(0.184)	5.917(0.282)	0.635	0.1-1.5	256	<0.001
12%	Arthropoda	Insecta	Trichoptera	Hydroptilidae	larva	order	1.386(0.0487)	6.071(0.0915)	0.719	0.1-2.5	1724	<0.001
16%	Arthropoda	Insecta	Trichoptera	Lepidostomatidae	larvae	family	1.951(0.0958)	5.473(0.204)	0.574	0.1-1.5	537	<0.001
18%	Arthropoda	Insecta	Trichoptera	Leptoceridae	larvae	family	2.128(0.439)	2.027(0.889)	0.336	0.1-1.5	11	0.048
62%	Arthropoda	Insecta	Trichoptera	Limnephilidae	larvae	family	0.560(0.191)	8.687(0.247)	0.858	0.1-2.5	207	<0.001

67%	Arthropoda	Insecta	Trichoptera	Philopotamidae	larvae	family	1.162(0.19)	5.784(0.282)	0.666	0.1-1.5	213	<0.001
54%	Arthropoda	Insecta	Trichoptera	Philopotamidae	pupa	order	3.678(0.588)	3.157(0.601)	0.427	0.1-2.0	39	<0.001
68%	Arthropoda	Insecta	Trichoptera	Philopotamidae	adult	family	3.878(0.452)	2.160(0.565)	0.268	0.4-1.25	42	<0.001
50%	Arthropoda	Insecta	Trichoptera	Phryganeidae	larvae	order	1.386(0.0487)	6.071(0.0915)	0.719	0.1-2.5	1724	<0.001
21%	Arthropoda	Insecta	Trichoptera	Psychomyiidae	larvae	order	1.386(0.0487)	6.071(0.0915)	0.719	0.1-2.5	1724	<0.001
15%	Arthropoda	Insecta	Trichoptera	Rhyacophilidae	larvae	family	1.723(0.55)	6.933(0.788)	0.665	0.1-2.0	41	<0.001
60%	Arthropoda	Insecta	Trichoptera	Trichoptera	larvae	order	1.386(0.0487)	6.071(0.0915)	0.719	0.1-2.5	1724	<0.001
60%	Arthropoda	Insecta	Trichoptera	Trichoptera	pupa	order	3.678(0.588)	3.157(0.601)	0.427	0.1-2.0	39	<0.001
87%	Arthropoda	Insecta	Trichoptera	Trichoptera	adult	order	2.116(0.255)	4.191(0.381)	0.654	0.1-1.25	66	<0.001

APPENDIX C

COMPOSITION OF DRIFT BY HABITAT AREA (L=LARVAE, P=PUPA, A=ADULT, X=UNKNOWN LIFESTAGE PRESENT) WITH SOURCE, TERRESTRIAL OR AQUATIC, DESIGNATION

Phylum	Class	Order	Family	Source	High Gradient	Low Gradient	Beaver Ponds
Arthropoda	Insecta	Plecoptera	Plecoptera	aquatic	L	L	L
Arthropoda	Insecta	Plecoptera	Pteronarcyidae	aquatic	L	L	
Arthropoda	Insecta	Plecoptera	Perlidae	aquatic	L	L	
Arthropoda	Insecta	Plecoptera	Perlodidae	aquatic	L	L	L
Arthropoda	Insecta	Plecoptera	Chloroperlidae	L=aquatic, A=terrestrial	LA	LA	L
Arthropoda	Insecta	Plecoptera	Taeniopterygidae	aquatic	L	LA	L
Arthropoda	Insecta	Plecoptera	Capniidae	L=aquatic, A=terrestrial	LA	LA	LA
Arthropoda	Insecta	Plecoptera	Nemouridae	aquatic	L	L	
Arthropoda	Insecta	Ephemeroptera	Ephemeroptera	L=aquatic, A=terrestrial	LA	A	LA
Arthropoda	Insecta	Ephemeroptera	Siphlonuridae	aquatic	L		L
Arthropoda	Insecta	Ephemeroptera	Baetidae	L=aquatic, A=terrestrial	LA	LA	LA
Arthropoda	Insecta	Ephemeroptera	Leptophlebiidae	L=aquatic, A=terrestrial	LA	LA	LA
Arthropoda	Insecta	Ephemeroptera	Leptohyphidae	aquatic	L		
Arthropoda	Insecta	Ephemeroptera	Ephemeridae	aquatic	L		

Arthropoda	Insecta	Ephemeroptera	Baetiscidae	aquatic		L	
Arthropoda	Insecta	Ephemeroptera	Ephemerellidae	L=aquatic, A=terrestrial	LA	L	L
Arthropoda	Insecta	Ephemeroptera	Potomanthidae	aquatic	L		
Arthropoda	Insecta	Ephemeroptera	Heptageniidae	L=aquatic, A=terrestrial	LA	LA	L
Arthropoda	Insecta	Trichoptera	Trichoptera	LP=aquatic, A=terrestrial	LPA	LPA	LPA
Arthropoda	Insecta	Trichoptera	Hydropsychidae	aquatic	L	L	L
Arthropoda	Insecta	Trichoptera	Philopotamidae	LP=aquatic, A=terrestrial	LA	LPA	LP
Arthropoda	Insecta	Trichoptera	Polycentropodidae	aquatic	L		
Arthropoda	Insecta	Trichoptera	Psychomyiidae	aquatic	L	L	L
Arthropoda	Insecta	Trichoptera	Rhyacophilidae	aquatic	L	LP	L
Arthropoda	Insecta	Trichoptera	Glossossomatidae	LP=aquatic, A=terrestrial	LPA	LA	L
Arthropoda	Insecta	Trichoptera	Hydroptilidae	L=aquatic, A=terrestrial	LA	LA	LPA
Arthropoda	Insecta	Trichoptera	Brachycentridae	aquatic	L	LP	L
Arthropoda	Insecta	Trichoptera	Lepidostomatidae	aquatic	L	L	L
Arthropoda	Insecta	Trichoptera	Limnephilidae	L=aquatic, A=terrestrial	LA	L	L
Arthropoda	Insecta	Trichoptera	Phryganeidae	aquatic	L		
Arthropoda	Insecta	Trichoptera	Leptoceridae	aquatic	L	L	L
Arthropoda	Insecta	Diptera	Diptera	LP=aquatic, A=terrestrial	LPA	PA	LPA
Arthropoda	Insecta	Diptera	Chironomidae	LP=aquatic, A=terrestrial	LPA	LPA	LPA
Arthropoda	Insecta	Diptera	Simuliidae	LP=aquatic, A=terrestrial	LPA	LPA	LA
Arthropoda	Insecta	Diptera	Tipulidae	LP=aquatic, A=terrestrial	LPA	LPA	L
Arthropoda	Insecta	Diptera	Athericidae	aquatic	L	L	L
Arthropoda	Insecta	Diptera	Ceratopogonidae	LP=aquatic, A=terrestrial	LA	LP	LP
Arthropoda	Insecta	Diptera	Empididae	LP=aquatic, A=terrestrial	LPA	LA	LPA

Arthropoda	Insecta	Diptera	Dixidae	aquatic			L
Arthropoda	Insecta	Diptera	Phoridae	terrestrial	A	A	A
Arthropoda	Insecta	Diptera	Drosophilidae	terrestrial	A	A	A
Arthropoda	Insecta	Diptera	Bibionidae	terrestrial	A	A	A
Arthropoda	Insecta	Diptera	Sciaridae	terrestrial	A	A	A
Arthropoda	Insecta	Diptera	Dolichopodidae	terrestrial	A	A	
Arthropoda	Insecta	Diptera	Sphaeroceridae	terrestrial	A		A
Arthropoda	Insecta	Diptera	Culicidae	terrestrial	A	A	A
Arthropoda	Insecta	Diptera	Camillidae	terrestrial			A
Arthropoda	Insecta	Diptera	Cecidomyiidae	terrestrial	A		
Arthropoda	Insecta	Diptera	Ephydridae	terrestrial	A	A	
Arthropoda	Insecta	Diptera	Mycetophilidae	terrestrial	A	A	
Arthropoda	Insecta	Odonota	Odonata	aquatic	L	L	L
Arthropoda	Insecta	Odonota	Aeshnidae	aquatic	L	L	L
Arthropoda	Insecta	Odonota	Cordulagastridae	aquatic		L	
Arthropoda	Insecta	Odonota	Corduliidae	aquatic		L	
Arthropoda	Insecta	Odonota	Gomphidae	L=aquatic, A=terrestrial	L	A	
Arthropoda	Insecta	Odonota	Coenagrionidae	aquatic		L	
Arthropoda	Insecta	Odonota	Calopterygidae	aquatic		L	
Arthropoda	Insecta	Coleoptera	Coleoptera	aquatic	LA	LA	LA
Arthropoda	Insecta	Coleoptera	Dryopidae	aquatic			
Arthropoda	Insecta	Coleoptera	Elmidae	aquatic	LA	LA	LA
Arthropoda	Insecta	Coleoptera	Haliplidae	aquatic	A	A	
Arthropoda	Insecta	Coleoptera	Dytiscidae	aquatic	A	L	A

Arthropoda	Insecta	Coleoptera	Gyrinidae	aquatic	A	A	
Arthropoda	Insecta	Coleoptera	Hydrophilidae	aquatic	LA	LA	L
Arthropoda	Insecta	Coleoptera	Curculionidae	terrestrial	A	A	A
Arthropoda	Insecta	Coleoptera	Staphylinidae	terrestrial	A	A	A
Arthropoda	Insecta	Coleoptera	Scarabaeidae	terrestrial	A		
Arthropoda	Insecta	Coleoptera	Cantharidae	terrestrial			A
Arthropoda	Insecta	Coleoptera	Carabidae	terrestrial	A		
Arthropoda	Insecta	Megaloptera	Sialidae	aquatic		L	
Arthropoda	Insecta	Hemiptera	Hemiptera	aquatic	LA	LA	LA
Arthropoda	Insecta	Hemiptera	Gerridae	aquatic	A	L	
Arthropoda	Insecta	Hemiptera	Mesoveliidae	aquatic	A		
Arthropoda	Insecta	Hemiptera	Corixidae	aquatic	A	A	A
Arthropoda	Insecta	Hemiptera	Triozidae	terrestrial			A
Arthropoda	Insecta	Hemiptera	Aphididae	terrestrial		A	A
Arthropoda	Insecta	Lepidoptera	Lepidoptera	terrestrial	L	LA	L
Arthropoda	Insecta	Hymenoptera	Hymenoptera	terrestrial	A	A	A
Arthropoda	Insecta	Hymenoptera	Formicidae	terrestrial	A	A	A
Arthropoda	Insecta	Orthoptera	Orthoptera	terrestrial			A
Annelida	Oligochaeta	Oligochaeta	Oligochaeta	terrestrial	X	X	
Arthropoda	Malacostroca	Amphipoda	Amphipoda	aquatic		X	X
Arthropoda	Malacostroca	Isopoda	Isopoda	aquatic		X	
Mollusca	Mollusca	Mollusca	Mollusca	aquatic	X	X	X
Mollusca	Gastropoda	Gastopoda	Gastropoda	aquatic	X	X	X
Arthropoda	Arachnida	Araneae	Araneae	terrestrial	X	X	X

Arthropoda	Arachnida	Acari	Acari	aquatic	X	X	X
Arthropoda	Arachnida	Pseudoscorpiones	Pseudoscorpiones	terrestrial	X	X	X
Arthropoda	Insecta	Collembola	Colluembola	terrestrial	X	X	X
Arthropoda	Insecta	Psocoptera	Psocoptera	terrestrial	X	X	

APPENDIX D

COMPOSITION OF THE DRIFT BY MONTH (L=LARVAE, P=PUPA, A=ADULT, X=UNKNOWN LIFESTAGE PRESENT) WITH SOURCE, TERRESTRIAL OR AQUATIC, DESIGNATION

Phylum	Class	Order	Family	Source	May	Jun	Jul	Aug	Sept	Oct	Nov	Dec	Jan	Feb	Mar	Apr
Arthropoda	Insecta	Plecoptera	Plecoptera	aquatic		L	L	L	L	L	L	L	L	L	LA	L
Arthropoda	Insecta	Plecoptera	Pteronarcyidae	aquatic	L	L				L				L		
Arthropoda	Insecta	Plecoptera	Perlidae	aquatic	L			L		L	L	L	L	L	L	
Arthropoda	Insecta	Plecoptera	Perlodidae	aquatic	L	L		L	L	L	L	L	L	L	L	L
Arthropoda	Insecta	Plecoptera	Chloroperlidae	L=aquatic, A=terrestrial	L	LA		L		L	L	L	L	L	L	L
Arthropoda	Insecta	Plecoptera	Taeniopterygidae	aquatic						L	L	L	L	L	LA	
Arthropoda	Insecta	Plecoptera	Capniidae	L=aquatic, A=terrestrial								L	L	L	LA	A
Arthropoda	Insecta	Plecoptera	Nemouridae	aquatic											L	L
Arthropoda	Insecta	Plecoptera	Leuctridae	L=aquatic, A=terrestrial											A	
Arthropoda	Insecta	Ephemeroptera	Ephemeroptera	L=aquatic, A=terrestrial	LA	LA	A	LA	LA	L					A	
Arthropoda	Insecta	Ephemeroptera	Siphlonuridae	aquatic		L	L									
Arthropoda	Insecta	Ephemeroptera	Baetidae	L=aquatic, A=terrestrial	L	LA	LA	LA	LA	L	LA	L	L	L	L	L

Arthropoda	Insecta	Ephemeroptera	Leptophlebiidae	L=aquatic, A=terrestrial	LA	LA	LA	L	L	L	L	L	L	L		L
Arthropoda	Insecta	Ephemeroptera	Leptohyphidae	aquatic				L								
Arthropoda	Insecta	Ephemeroptera	Ephemeridae	aquatic											A	L
Arthropoda	Insecta	Ephemeroptera	Baetiscidae	aquatic										L		
Arthropoda	Insecta	Ephemeroptera	Ephemerellidae	L=aquatic, A=terrestrial	L	LA		L	L	L	L	L	L	L	LA	L
Arthropoda	Insecta	Ephemeroptera	Potomanthidae	aquatic												
Arthropoda	Insecta	Ephemeroptera	Heptageniidae	L=aquatic, A=terrestrial	L	LA	LA	L	L	L	L	L	L	L	L	L
Arthropoda	Insecta	Trichoptera	Trichoptera	LP=aquatic, A=terrestrial	LA	LA	LPA	LP	LP	LP	L	LA			L	L
Arthropoda	Insecta	Trichoptera	Hydropsychidae	aquatic	L	LA	L	L	L	L	L	L	L	L	L	L
Arthropoda	Insecta	Trichoptera	Philopotamidae	LP=aquatic, A=terrestrial	LPA	L	LPA	LPA	L	L	LPA	LA	A	LPA	LA	LPA
Arthropoda	Insecta	Trichoptera	Polycentropodidae	aquatic											L	
Arthropoda	Insecta	Trichoptera	Psychomyiidae	aquatic						L					L	L
Arthropoda	Insecta	Trichoptera	Rhyacophilidae	aquatic	L	P		L	L	L	L	L			LA	L
Arthropoda	Insecta	Trichoptera	Glossossomatidae	LP=aquatic, A=terrestrial	LP	LPA	L	LP	LP	L	L	L		L		
Arthropoda	Insecta	Trichoptera	Hydroptilidae	L=aquatic, A=terrestrial	A		LPA	P		L	L	LA	L	L	L	L
Arthropoda	Insecta	Trichoptera	Brachycentridae	aquatic	L	L	L	LP	L	L	L	L	L	L	L	L
Arthropoda	Insecta	Trichoptera	Lepidostomatidae	aquatic	L	L	L	L	L	L	L	L	L	L	L	L
Arthropoda	Insecta	Trichoptera	Limnephilidae	L=aquatic, A=terrestrial	LA	L		L	L	L	L	L	L	L	L	L
Arthropoda	Insecta	Trichoptera	Phryganeidae	aquatic											A	
Arthropoda	Insecta	Trichoptera	Leptoceridae	aquatic	L	L	L			L	L				L	
Arthropoda	Insecta	Diptera	Diptera	LP=aquatic, A=terrestrial	LA	LPA	LPA	LPA	PA	A	A		L	L	A	P

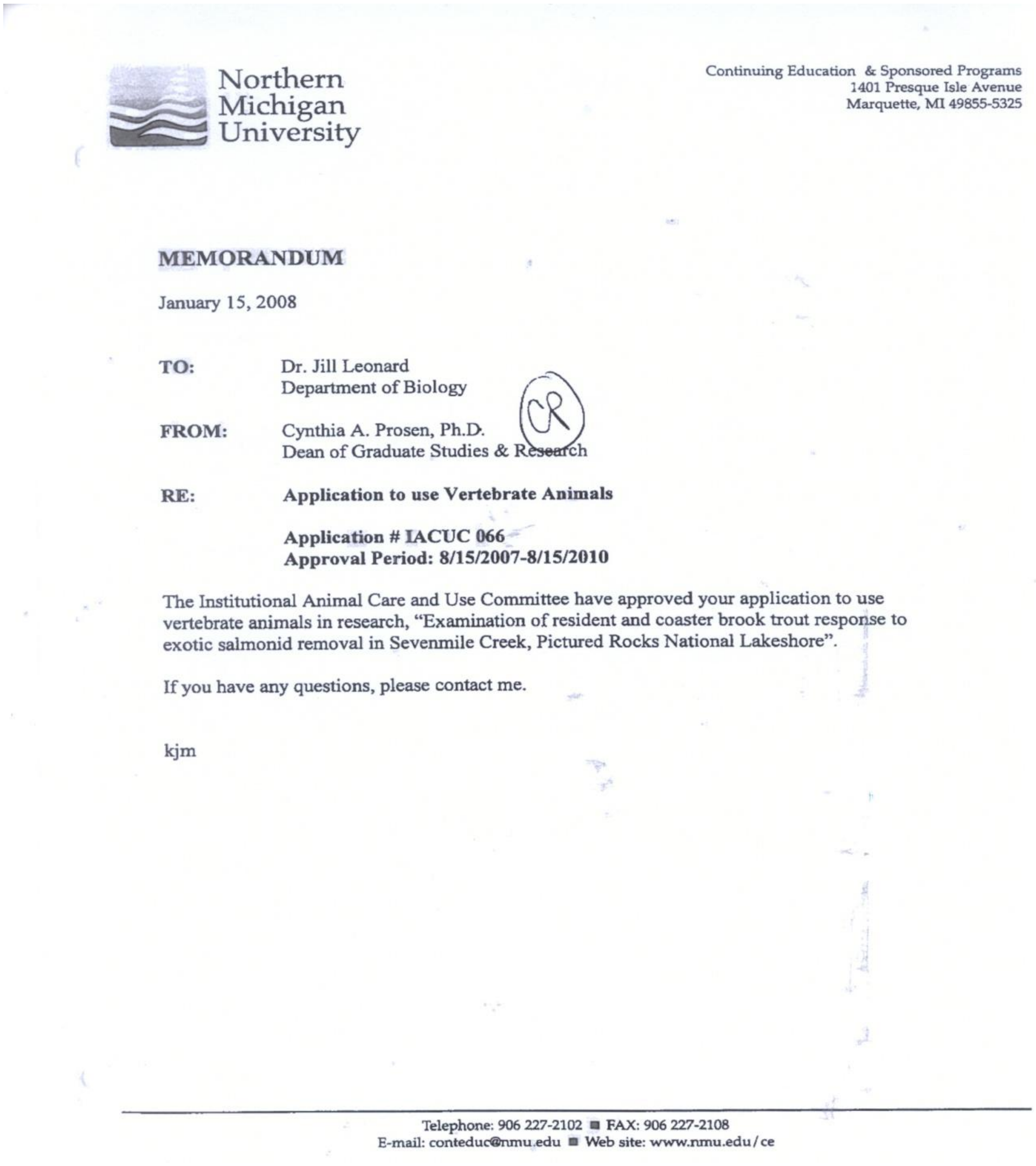
Arthropoda	Insecta	Diptera	Chironomidae	LP=aquatic, A=terrestrial	LPA	LPA	LPA	LPA	LPA	LPA	LPA	L		L	L	LPA
Arthropoda	Insecta	Diptera	Simuliidae	LP=aquatic, A=terrestrial	LPA	LPA	LPA	LPA	LPA	L	LA	L	L	L	LA	LP
Arthropoda	Insecta	Diptera	Tipulidae	LP=aquatic, A=terrestrial	LA	LA	LA	LA	LP	LP	LA	L	LA	L	L	L
Arthropoda	Insecta	Diptera	Athericidae	aquatic	L		L	L	L	L	L	L	L	L	LA	
Arthropoda	Insecta	Diptera	Ceratopogonidae	LP=aquatic, A=terrestrial	L	LP	LPA					L			L	L
Arthropoda	Insecta	Diptera	Empididae	LP=aquatic, A=terrestrial	A	LPA	LPA	LPA	LA	LA	A	L			A	
Arthropoda	Insecta	Diptera	Dixidae	aquatic					L							
Arthropoda	Insecta	Diptera	Phoridae	terrestrial	A	A	A	A	A	A	A				A	
Arthropoda	Insecta	Diptera	Drosophilidae	terrestrial	A	A		A	A		A					
Arthropoda	Insecta	Diptera	Bibionidae	terrestrial	A	A					A					
Arthropoda	Insecta	Diptera	Sciaridae	terrestrial	A	A	A	A	A	A	A	A			A	
Arthropoda	Insecta	Diptera	Dolichopodidae	terrestrial				A								
Arthropoda	Insecta	Diptera	Sphaeroceridae	terrestrial		A										
Arthropoda	Insecta	Diptera	Culicidae	terrestrial		A	A		A							
Arthropoda	Insecta	Diptera	Camillidae	terrestrial			A									
Arthropoda	Insecta	Diptera	Cecidomyiidae	terrestrial						A						
Arthropoda	Insecta	Diptera	Ephydridae	terrestrial	A											
Arthropoda	Insecta	Diptera	Mycetophilidae	terrestrial	A	A		A	A	A	A				A	A
Arthropoda	Insecta	Odonota	Odonata	aquatic				L						L		
Arthropoda	Insecta	Odonota	Aeshnidae	aquatic					L		L			L	L	
Arthropoda	Insecta	Odonota	Cordulagastridae	aquatic					L			L				
Arthropoda	Insecta	Odonota	Corduliidae	aquatic		L										
Arthropoda	Insecta	Odonota	Gomphidae	L=aquatic, A=terrestrial	A	L	L			L		L			L	

Arthropoda	Insecta	Odonota	Coenagrionidae	aquatic						L						
Arthropoda	Insecta	Odonota	Calopterygidae	aquatic			L	L								
Arthropoda	Insecta	Coleoptera	Coleoptera	aquatic	A		LA	LA	L		A	L				
Arthropoda	Insecta	Coleoptera	Dryopidae	aquatic												
Arthropoda	Insecta	Coleoptera	Elmidae	aquatic	A	A	LA	LA	LA	LA	LA	L	L	L	LA	L
Arthropoda	Insecta	Coleoptera	Haliplidae	aquatic		A			A							A
Arthropoda	Insecta	Coleoptera	Dytiscidae	aquatic		A	A	L								A
Arthropoda	Insecta	Coleoptera	Gyrinidae	aquatic		A								A	A	
Arthropoda	Insecta	Coleoptera	Hydrophilidae	aquatic	A	L	L	L	LA	L						A
Arthropoda	Insecta	Coleoptera	Curculionidae	terrestrial	A	A	A	A	A	A						A
Arthropoda	Insecta	Coleoptera	Staphylinidae	terrestrial	A	A	A	A	A	A	A					
Arthropoda	Insecta	Coleoptera	Scarabaeidae	terrestrial			A	A								
Arthropoda	Insecta	Coleoptera	Cantharidae	terrestrial				A								
Arthropoda	Insecta	Coleoptera	Carabidae	terrestrial				A								
Arthropoda	Insecta	Megaloptera	Sialidae	aquatic							L					
Arthropoda	Insecta	Hemiptera	Hemiptera	aquatic		LA	L	LA	A	A						
Arthropoda	Insecta	Hemiptera	Gerridae	aquatic	A		L									
Arthropoda	Insecta	Hemiptera	Mesoveliidae	aquatic												A
Arthropoda	Insecta	Hemiptera	Corixidae	aquatic							A	A		A	A	A
Arthropoda	Insecta	Hemiptera	Triozidae	terrestrial							A					
Arthropoda	Insecta	Hemiptera	Aphididae	terrestrial	A			A	A	A	A					
Arthropoda	Insecta	Lepidoptera	Lepidoptera	terrestrial	L	L	L	LA	L	L	L					
Arthropoda	Insecta	Hymenoptera	Hymenoptera	terrestrial	A	A		A	A	A	A	A				
Arthropoda	Insecta	Hymenoptera	Formicidae	terrestrial	A	A		A	A	A	A					
Arthropoda	Insecta	Orthoptera	Orthoptera	terrestrial	A										A	
Annelida	Oligochaeta	Oligochaeta	Oligochaeta	terrestrial	X	X		X	X	X	X			X	X	X
Arthropoda	Malacostroca	Amphipoda	Amphipoda	aquatic	X			X	X	X	X		X	X	X	X

Arthropoda	Malacostroca	Isopoda	Isopoda	aquatic				X			X	X				
Mollusca	Mollusca	Mollusca	Mollusca	aquatic	X			X		X	X			X		
Mollusca	Gastropoda	Gastopoda	Gastropoda	aquatic	X	X	X	X	X	X	X	X		X		X
Arthropoda	Arachnida	Araneae	Araneae	terrestrial	X	X	X	X	X	X	X	X			X	X
Arthropoda	Arachnida	Acari	Acari	aquatic	X	X	X	X	X	X	X			X		X
Arthropoda	Arachnida	Pseudoscorpiones	Pseudoscorpiones	terrestrial		X	X	X	X	X						
Arthropoda	Insecta	Collembola	Colluembola	terrestrial	X		X	X		X	X	X			X	X
Arthropoda	Insecta	Psocoptera	Psocoptera	terrestrial		X	X	X	X	X	X					
			Steelhead egg	aquatic												X
			Longnose Sucker egg	aquatic		X										
			Larval fish	aquatic		X	X									

APPENDIX E

IACUC 066



Northern
Michigan
University

Continuing Education & Sponsored Programs
1401 Presque Isle Avenue
Marquette, MI 49855-5325

MEMORANDUM

January 15, 2008

TO: Dr. Jill Leonard
Department of Biology

FROM: Cynthia A. Prosen, Ph.D. CR
Dean of Graduate Studies & Research

RE: **Application to use Vertebrate Animals**

Application # IACUC 066
Approval Period: 8/15/2007-8/15/2010

The Institutional Animal Care and Use Committee have approved your application to use vertebrate animals in research, "Examination of resident and coaster brook trout response to exotic salmonid removal in Sevenmile Creek, Pictured Rocks National Lakeshore".

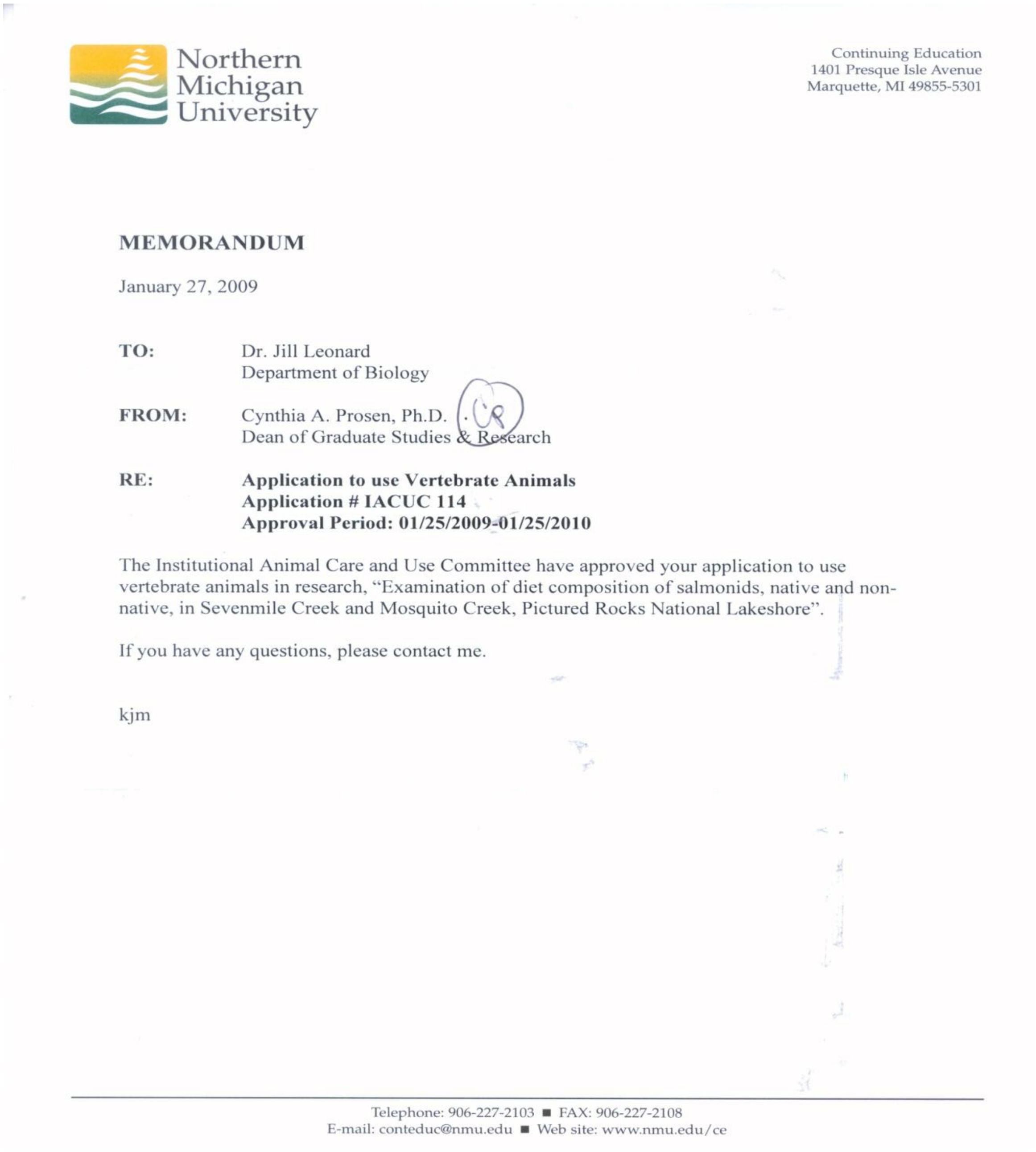
If you have any questions, please contact me.

kjm

Telephone: 906 227-2102 ■ FAX: 906 227-2108
E-mail: conteduc@nmu.edu ■ Web site: www.nmu.edu/ce

APPENDIX F

IACUC 114



Northern
Michigan
University

Continuing Education
1401 Presque Isle Avenue
Marquette, MI 49855-5301

MEMORANDUM

January 27, 2009

TO: Dr. Jill Leonard
Department of Biology

FROM: Cynthia A. Prosen, Ph.D.
Dean of Graduate Studies & Research

RE: **Application to use Vertebrate Animals**
Application # IACUC 114
Approval Period: 01/25/2009-01/25/2010

The Institutional Animal Care and Use Committee have approved your application to use vertebrate animals in research, "Examination of diet composition of salmonids, native and non-native, in Sevenmile Creek and Mosquito Creek, Pictured Rocks National Lakeshore".

If you have any questions, please contact me.

kjm

Telephone: 906-227-2103 ■ FAX: 906-227-2108
E-mail: conteduc@nmu.edu ■ Web site: www.nmu.edu/ce