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Early Round Goby (Neogobius melanostomus) Invasion Into Lake Michigan Tributaries and Competitive Interactions with Two Native Benthic Fishes.

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EARLY ROUND GOBY (*NEOGOBIUS MELANOSTOMUS*) INVASION INTO LAKE

MICHIGAN TRIBUTARIES AND COMPETITIVE INTERACTIONS WITH

TWO NATIVE BENTHIC FISHES.

A THESIS SUBMITTED TO

THE FACULTY OF THE GRADUATE SCHOOL

IN CANDIDACY FOR THE DEGREE OF

MASTER OF SCIENCE

PROGRAM IN BIOLOGY

BY

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CHICAGO, ILLINOIS

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ACKNOWLEDGEMENTS

Where there is water, there are fish. And where there are fish, they can be collected.
- Carl L. Hubbs

Yet the most skillful naturalist from an examination of the species… could not have foreseen this result.
- Charles Darwin

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ABSTRACT

The round goby (*Neogobius melanostomus*) is a prolific invasive species and is currently spreading into tributary streams of Laurentian Great Lakes. There is a high potential for negative impacts on native benthic fishes in these stream habitats and the aim of this study is to assess the impacts of the round goby on two native darter species, johnny darter (*Etheostoma nigrum*) and blackside darter (*Percina maculata*). I review the history of round goby invasion in the Great Lakes and summarize hypotheses of the invasive characters of the round goby. Using game theory, I provide a G-function approach to understanding the outcomes of the round goby invasion in tributary streams. I conducted a field based laboratory study compare the fish communities in invaded and non-invaded reaches of two streams and found differences attributed to the catch per unit effort (CPUE) of round gobies. CPUE of the johnny darter was different in invaded and non-invaded reaches, while it was not different for blackside darter. Stomach contents of the round goby and darter were analyzed and overlap was found between the invasive and native species. Finally, a laboratory experiment assessed the competitive behaviors of the round goby and the johnny darter and found that there were behavioral differences. The results for this study provide a baseline during the early invasion of two Lake Michigan tributaries and provide evidence of both exploitative and interference competition between the round goby and johnny darter. It is likely that these competitive interactions resulted in a realized niche shift of the johnny darter and there is a high likelihood that

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continued competition between the johnny darter and round goby will possibly result in

population decline of the johnny darter or even local extirpation.

CHAPTER 1

INTRODUCTION

Ecology and Evolution of the Round Goby: A Pervasive Invader

Neogobius melanostomus (Actinopterygii, Perciformes, Gobiidae) (Pallas 1811),

the round goby, is one of the most wide ranging-invasive species worldwide (reviews:

Corkum et al. 2004, Kornis et al. 2012). In their native range, the round goby was

confined to shallow brackish waters of the Ponto-Caspian region (Azov, Black, and

Caspian Seas), including the surrounding estuaries and tributaries (Miller 1986). Over

the last two decades, the round goby has considerably expanded its range into further

reaches of Ponto-Caspian tributaries. This is especially true in the Danube River, where

the round goby has doubled their habitat range (Pinchuck et al. 2003). They have also

successfully invaded major European and American waterways, presumably via ballast

water transport (Charlebois et al. 1997). In Eurasia, the round goby is commonly found

in the following regions in order by date of invasion: Kuybyshev, Tsimlyansk, and

Volgorgrad reservoirs (since the 1960s-1970s), Moscow river (1980s), Danube river

(1990s) Baltic sea (1990), North Sea basin (2004), Lek River (2004) and Albert Canal in

Belgium (reviewed in Kornis et al. 2012). Their current distribution in North America

includes all five Laurentian Great Lakes and their tributaries, stretching down the Illinois

River towards the Mississippi River (USGS.gov). Kornis and VanderZanden (2010)

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predicted that with increasing global temperatures the round goby will continue to expand its range in the Great Lakes, with mainly physical barriers preventing spread into streams and rivers. With such a broad habitat range and projected expansion it is important to understand potential impacts on native fish communities.

As the round goby invades new habitats it becomes integrated into local fish communities and interacts with fish species that have not evolved with the round goby as a predator or competitor. These interactions are of interest to many ecologists studying invasion biology. The round goby has already been attributed to the extirpation of mottled sculpin (*Cottus bairdii*) and johnny darter (*Etheostoma nigrum*) from regions of the Great Lakes (Janssen and Jude 2001) and researchers predict negative impacts on other native benthic fishes through predation, as well as both direct and indirect competition (Poos et al. 2010).

In order to better understand the potential impacts the round goby may have on native fishes, many researchers have investigated biological characteristics that contribute to their widespread invasion success. Some of these characteristics are found in both native and invasive populations of round gobies, while others are unique to invasive or founder populations of the round goby (Brandner et al. 2013, Hôrková & Kováč 2013).

Like many invasive species, the round goby can thrive in a wide range of habitats. They are capable of eating a breadth of prey items, and reproduce multiple times in a reproductive season (Kornis et al. 2012). Behavioral attributes such as boldness, dispersal tendency, exploratory behavior, intraspecific aggression, and interspecific aggression are

common traits of invasive species (Hudina et al. 2014), and the round goby exhibits these behaviors. Researchers have described both intra and interspecific aggressive behaviors of round gobies (Dubs and Corkum 1996, Balshine et al. 2005), with high site fidelity and territoriality. While most round gobies exhibit site fidelity and territoriality, some exhibit dispersal behavior and move long distances. Dispersing individuals may account for range expansion (Bronnenhuber et al. 2011).

Balázová & Kováč (2007) hypothesize that phenotypic plasticity in developmental phenology is a unique attribute in invasive populations and leads to goby success. They found precocial and altricial developmental patterns in invasive and native round goby populations, respectively. The round goby develops earlier in invaded habitats and attains reproductive maturity at a smaller size than those found in the Ponto-Caspian region (Hôrková & Kováč 2013).

Finally, founder populations of the round goby at an invasion front were larger and heavier than those in established invasive populations (Brandner et al. 2013). This difference in size may contribute to their increase competitive ability at the invasion front. In addition, round gobies in founder populations fed at higher trophic levels (Keane & Crawley 2002), even though founder populations did exhibit higher parasitic load (Brandner et al. 2013). This higher parasitic load may contribute to invasiveness if these individuals have less to lose and therefore will be more likely to disperse.

Although these physiological, biological, and ecological attributes contribute to the invasiveness of round gobies, a major morphological attribute is often ignored. The

round goby has a rare morphology of fused pharyngeal jaws that enable it to crush

molluscs. Fused lower pharyngeal jaws are a morphological trait found only in

durophageous species. Pharyngognapthy is the presence of three characters used for

feeding: 1) fused lower pharyngeal jaw, 2) presence of a muscular sling uniting the

neurocranium with the lower pharyngeal jaw and 3) diarthrosis of the upper pharyngeal

jaws along the neurocranium at the synovial joint (Figure 1) a9Wainwright et al. 2012).

These traits are described as a "key innovation" in other fishes including labrids, cichlids,

and embiotocids (Liem 1973, Hulsey 2006) and have only evolved 6-10 times in all

percomorphs (comprising of over 14,000 species (TOL.org)).

The evolutionary history of gobies, including the Ponto Capsian gobies, have

been studied extensively (Thacker 2009, Neilson and Stepien 2009a, Neilson and Stepien

2009b, Neilson and Stepien 2011, Stepien and Neilson 2013). The family Gobiidae

consists of over 2,000 marine and freshwater species. Within the Gobiidae clade, the

Ponto-Caspian gobies originated during the Messinian salinity crisis 5.3-6 mya when sea

level dropped due to climatic and tectonic changes in the region. This left the region

isolated until 5.33 mya when the region was flooded and reconnected with the

surrounding water bodies. During this time period the genus *Neogobius* evolved. The

phylogeny and taxonomy of *Neogobius* and close relatives have often been contested

(Neilson and Stepien 2009a, Stepien and Neilson 2013). The genus (as currently

described) consists of 24 species, 11 of which are considered invasive: including the

round goby (*N. melanostomus),* monkey goby (*N. fluviatillis*), bighead goby (*N. kessleri*),

racer goby (*N. gymnotrachelus*), and tubenose goby (*Proterorhinus semilunaris*) (Stepien and Neilson 2013).

Understanding the evolutionary origins of the round goby and the phenotypic characters that contribute to its widespread success are important to the study of invasion biology and assessing the potential impacts within invaded ecosystems.

Invasion Biology and Evolutionary Game Theory

Invasive species have been well studied to understand the process and sequence of invasion, and thereby predict future patterns of species invasion. The invasion process starts when organisms are introduced to a new habitat through transportation (often anthropogenic). Once in a new habitat the organisms may become established and maintain a breeding population. The population may then grow and spread to new regions. If the species maintains a population within a non-native habitat it is considered naturalized. A species is determined "invasive" if it has negative impacts within its new habitat. Not all introduced species become naturalized, and not all naturalized species are considered invasive (Kolar and Lodge 2001).

Kolar and Lodge (2001) discuss the technique of quantifying invasion potential through the presence of "invasive" characters. They looked at a suite of biological characters for plants and animals and assessed whether there was a relationship between the character and the establishment or spread of a species. This approach has many benefits. However, it may be limited based on how a researcher defines an invasive character. With this in mind, Pintor et al. (2011) developed a set of *a priori* hypotheses

grounded in evolutionary game theory that can used to test for potential invasion success. Their approach utilizes the G-function (fitness generating function) to model the relationship between strategies (traits) of the invader, strategies present in the native population or community, and the population sizes within the community. The G-function can be interpreted within an ecological context as the change in population size of the invader over time. Evolutionarily, the G-function represents changes in strategies (or traits) of the invasive species. I will apply the theory developed by Pintor et al. (2011) to the invasion biology of the round goby in Lake Michigan tributaries to develop hypotheses on the impact of round goby in these fluvial systems.

Using the pathways presented in Pintor et al. (2011) it must first be determined if the round goby is a novel G-function or the same G-function as native fishes in tributary streams. Based on the novel trait of fused pharyngeal jaws, the round goby has the ability to crush hard prey (such as pea clams, Sphaeriidae), and therefore I suggest has a novel G-function. An invader with a novel G-function must next be hypothesized to have a superior or non-superior G-function. Invasive dreissenid mussels are not yet prolific in tributaries of Lake Michigan; therefore the round goby does not have access to this as a food source over native fishes. However, there are freshwater clams that may be available to stream round gobies as a food source. Depending on the abundance of hard prey I hypothesize that round gobies have a superior G-function in tributaries with a high abundance of hard prey, and a non-superior G-function in tributaries without abundant bivalve prey.

If the round goby has a superior G-function, the only outcome is species replacement. An example of this is southern Lake Michigan, where superior round gobies replaced johnny darters and mottled sculpin. If the round goby does not have a superior G-function in tributary streams, I expect species coexistence if there is an empty niche available, or species replacement if the community is a non-evolutionary stable strategy. Field and laboratory studies are necessary to verify if the strategy of the round goby (the trait of fused pharyngeal jaws) give the round goby a superior G-function. This study will provide information on round goby habitat and prey use in recently invaded streams.
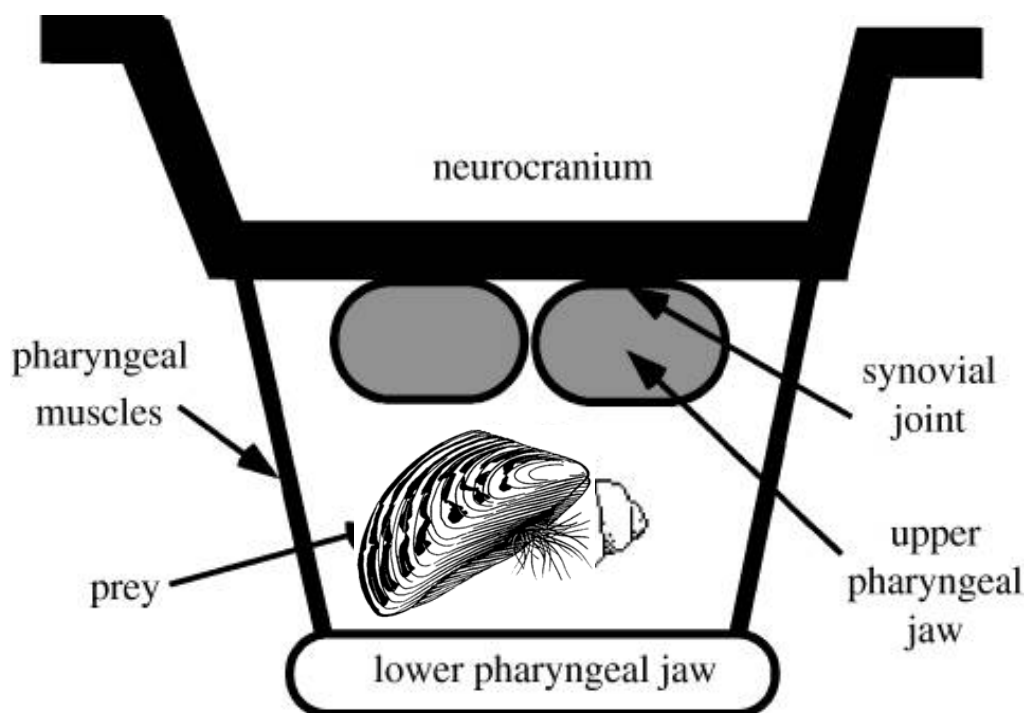
Figure 1. Diagram of the round goby pharyngeal jaw apparatus modified from Hulsey (2006), zebra mussel from seagrant.umn.edu.

Goals and Objectives

The objective of this research is to assess the competitive interactions between the invasive round goby and two native darter species in recently invaded Wisconsin tributary streams of Lake Michigan. This project will address the following research questions: (1) How do invasive round gobies utilize habitat in two Lake Michigan tributaries? (2) How do two native darter species and gobies utilize habitat in invaded and non-invaded reaches? (3) Is there a difference in prey of round gobies and darters in invaded reaches? (4) Is there a difference in prey of native darters in invaded and non-invaded reaches? Finally, (5) how do round gobies and native darters utilize depletable food patches in a laboratory setting? I hypothesize that the round goby will have similar diet and habitat preferences as native benthic darters and that the goby is a better competitor. Findings from this study with contribute to the growing literature addressing effects of round goby invasion into tributary streams and foraging theory techniques in aquatic systems.

CHAPTER 2

COMPETITIVE INTERACTIONS IN NEWLY INVADED STREAMS

Introduction

Invasion biology studies the ecological processes of exotic species colonizing new

habitats (Lodge 1993). The process of biological invasion can be viewed in

chronological steps: first with transport, then introduction, subsequent establishment, and

spread (Kolar & Lodge 2001). Throughout the invasion process, several factors may

influence the success of a species as an invader, including competition with indigenous

species for resources such as food and/or space. Competitive interactions with

indigenous species may explain many failed establishments of introduced species (Sakai

et al. 2001). However, once a non-native species becomes established in a community, it

may have negative impacts on indigenous species. Non-native species that are successful

in establishing populations and cause environmental impacts are often referred to as

"invasive" species (Lodge 1993). Invasive species tend to have adverse impacts on

native communities through predation, direct competition (via aggressive behaviors) or

indirect competition (through exploitative or apparent competition).

The invasive round goby, *Neogobius melanostomus* (Pallas 1814), was first

reported in the Great Lakes in 1991 in the St. Clair River, Michigan (Jude et al. 1992).

Within the next five years, the round goby spread throughout all five of the Laurentian

Great Lakes through both human mediated and natural dispersal methods (Charlebois

al. 2001). The round goby achieved population densities as high as 100 /m^2 in preferred habitats, such as the rocky coast of Lake Michigan (Chotkowski & Marsden 1999). Its impacts on native lentic benthic species have been significant. The decline and subsequent extirpation of *Cottus bairdii* (mottled sculpin) and *Etheostoma nigrum* (johnny darter) from Lake Michigan has been attributed to the round goby due to competition for space (Janssen & Jude 2001, Lauer et al. 2004). In the laboratory, round goby displaced *C. bairdii* from spawning nests (Dubs & Corkum 1996) and outcompeted *Percina caprodes* (logperch) from preferred habitats (Balshine et al. 2005). The success of the round goby in the Great Lakes is attributed, in part, to its aggressive behavior (Balshine et al. 2005), use of invasive dreissenid mussels as a primary food source (Charlebois et al. 1997), opportunistic foraging (French and Jude 2001, Carman et al. 2006), plastic environmental tolerances (Ray and Corkum 2001), and high fecundity (Corkum et al. 1998).

Recently, the round goby has expanded its range from shallow, rocky habitats into deeper waters, and tributary streams of Lake Michigan (reviewed in Kornis et al. 2012). The range expansion into lotic systems has been deemed the "secondary invasion" of the round goby (Poos et al. 2010, Kornis et al. 2013) and is likely to pose new threats to native benthic species (Poos et al 2010). In particular, native darters (*Etheostoma* spp. and *Percina* spp.) are likely to be impacted due to similar habitat and dietary preferences (French and Jude 2001). The round goby has high site fidelity on rocky substrates (Ray and Corkum 2001), the preferred habitat of many darter species, and both are diurnal,

visual foragers. While round gobies are primarily durophageous in the Great Lakes and in native habitats, they have a wide breadth in prey items and are opportunistic foragers. The potential for interference and exploitative competition between the round goby and native darters in tributaries is high. However, the full extent of competitive interactions in tributaries is unknown.

Research Objective

The objective of this research is to assess the possible competitive interactions between the invasive round goby and native percid species in recently invaded Wisconsin tributary streams. This project will address the following research questions: (1) How do invasive round gobies utilize habitat in two Lake Michigan tributaries? (2) How do two native darter species utilize habitat in round goby-invaded and non-invaded reaches? (3) Is there a difference in prey selection of round gobies and darters in invaded reaches? And finally, (4) is there a difference in prey selection of native darters in invaded and non-invaded reaches? I hypothesize that the round goby will have similar diet and habitat preferences as native benthic darters in streams lacking dreissenid mussels. Findings from this study with contribute to the growing literature addressing effects of round goby invasion into tributaries.

<center>**Materials and Methods**</center>

Site Selection

Two wadeable Lake Michigan tributaries were surveyed for this study. Silver Creek is a second- order stream that originates in Manitowoc, Wisconsin. Pigeon River

is a third- order tributary originating in Sheboygan Co., Wisconsin (Figure 1). These streams were selected for known co-habitation of round goby and darters (personal communication, Matt Kornis). Four invaded sample sites (Figure 2, Sites 1 & 2; Figure 3, Site 1 & 2) were selected along an invasion gradient away from the source (Lake Michigan), two non-invaded sites (Figure 2, Site 3; Figure 3, Site 3) were selected further upstream for comparison. On August 16, 2011 a round goby was collected from non-invaded site in Pigeon River (Figure 3, Site 3). Therefore, a third non-invaded site (Figure 3, Site 4) was added to the study and sampled for the remaining trips. Distance from Lake Michigan was calculated for each sampling site using GIS (Geographic Information Systems) (ArcGis v.10.1). No downstream barriers were present within sampling streams to prevent round goby invasion. Sites were sampled once monthly in May, July, August, and September 2011, except for site PR4, which was sampled only in August and September 2011.

Sample Site Characteristics

Habitat data were collected using techniques from US EPA Field Operations for Wadeable Streams (Peck et al. 1997) and WI DNR fish habitat assessment (Simonson et al. 1994). I located measured stream wetted width, bank-full height, stream depth profile, riparian land use, bank erosion, substrate size, percentage habitat coverage (riffle and non-riffle, large woody debris, macroalgae cover), current velocity, water temperature, salinity, specific conductance, and dissolved oxygen concentration (YSI PRO2030)

Fish Community

Sampling area for fish collections was standardized by using a sample reach of five times the wetted width. Fishes were collected within each reach using a bank-full single pass approach with a Smith-Root LR-20B backpack electrofisher set at 200 volts, duty cycle 30%, and 40 hertz. Fishes were collected and separated into habitat type, "riffle" or "non-riffle," based on microhabitat types of Grossman and Freeman (1987). Fishes were identified, counted, measured for total length, and released except for those included in the dietary analysis. Sampling time was recorded for each habitat type within the sampling area. Voucher specimens for fish that could not be identified in the field were euthanized using an overdose of MS-222, preserved in 10% formalin solution, and returned to the laboratory for identification. All round gobies collected were euthanized, and preserved for laboratory diet analysis. A subset of johnny and blackside darters were euthanized and preserved for dietary analysis.

Dietary Analysis

All round gobies, johnny darters, and blackside darters collected were measured for total length and sexed via genital papillae in the laboratory. The complete digestive tract was dissected from esophagus to vent, removed, and measured for wet weight (0.01 g). The digestive tract was opened and relative fullness estimated. All prey items were counted and identified to lowest possible taxonomic level. Content volume was estimated and weight measured (0.01g).

Habitat and Dietary Statistical Analyses

Fish catch per unit effort (CPUE) was transformed via the Hellinger transformation (Bocard et al. 2011). This transformation is common in fish community analyses and reduces the importance of rare species. CPUE data was averaged across all invaded and non-invaded sites,

Principal components analysis (PCA) was used to analyze fish communities in invaded and non-invaded reaches of Silver Creek and Pigeon River. ANOVA and t-tests were used to compare CPUE data between invaded and non-invaded reaches of study streams, and to test for difference between microhabitats (riffle and non-riffle). Percent abundance and mean percent abundance were calculated as an unbiased method to analyze dietary contents (Hulbert 1984).

Table 1. Stream, site ID, location and invasion status of study reaches in Pigeon River and Silver Creek, Wisconsin. *Site PR3 was initially indicated as goby absent, however this site became invaded during this study.

Stream	Site ID	Latitude	Longitude	Distance from Lake Michigan (km)	Invasion Status
Silver Creek	SC1	44°03.680	87°39.253	.09	Goby Present
Silver Creek	SC2	44°03.696	87°39.348	.26	Goby Present
Silver Creek	SC3	44°03.795	87°39.586	.78	Goby Absent
Pigeon River	PR1	43°47.139	87°43.818	1.65	Goby Present
Pigeon River	PR2	42°46.951	87°44.792	2.91	Goby Present
Pigeon River	PR3	43°45.945	87°46.826	8.00	Goby Absent*
Pigeon River	PR4	43°47.272	87°47.206	11.09	Goby Absent

Figure 2. Map of study areas in western Lake Michigan (Google Maps) with reference polygons indicating study location of Silver Creek, (Manitowoc, WI) and Pigeon River, (Sheboygan, WI).
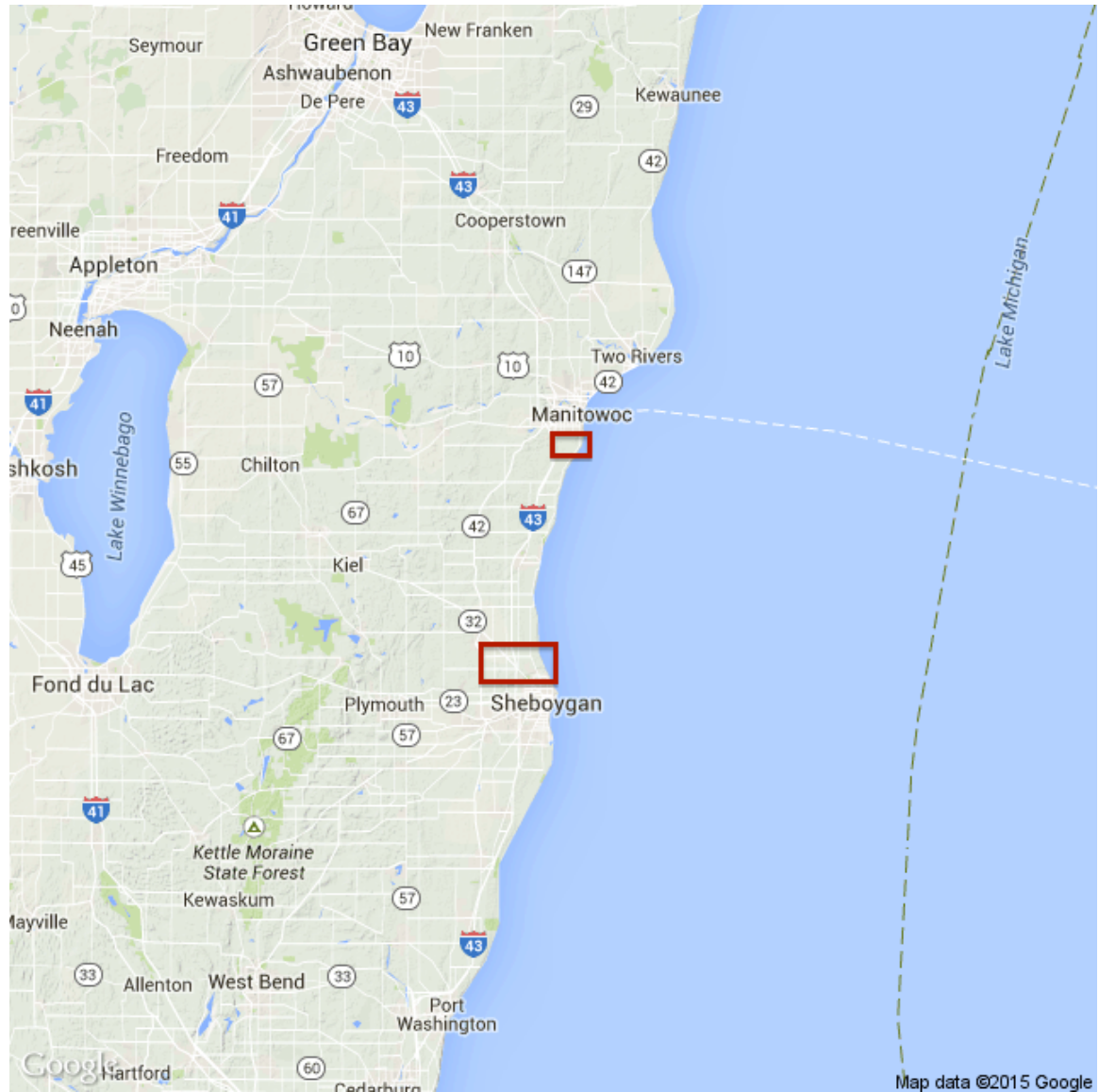
Figure 3.   Map of Silver Creek, Manitowoc, WI indicating three sample site locations (round goby presence indicated in red, round goby absence indicated in blue).
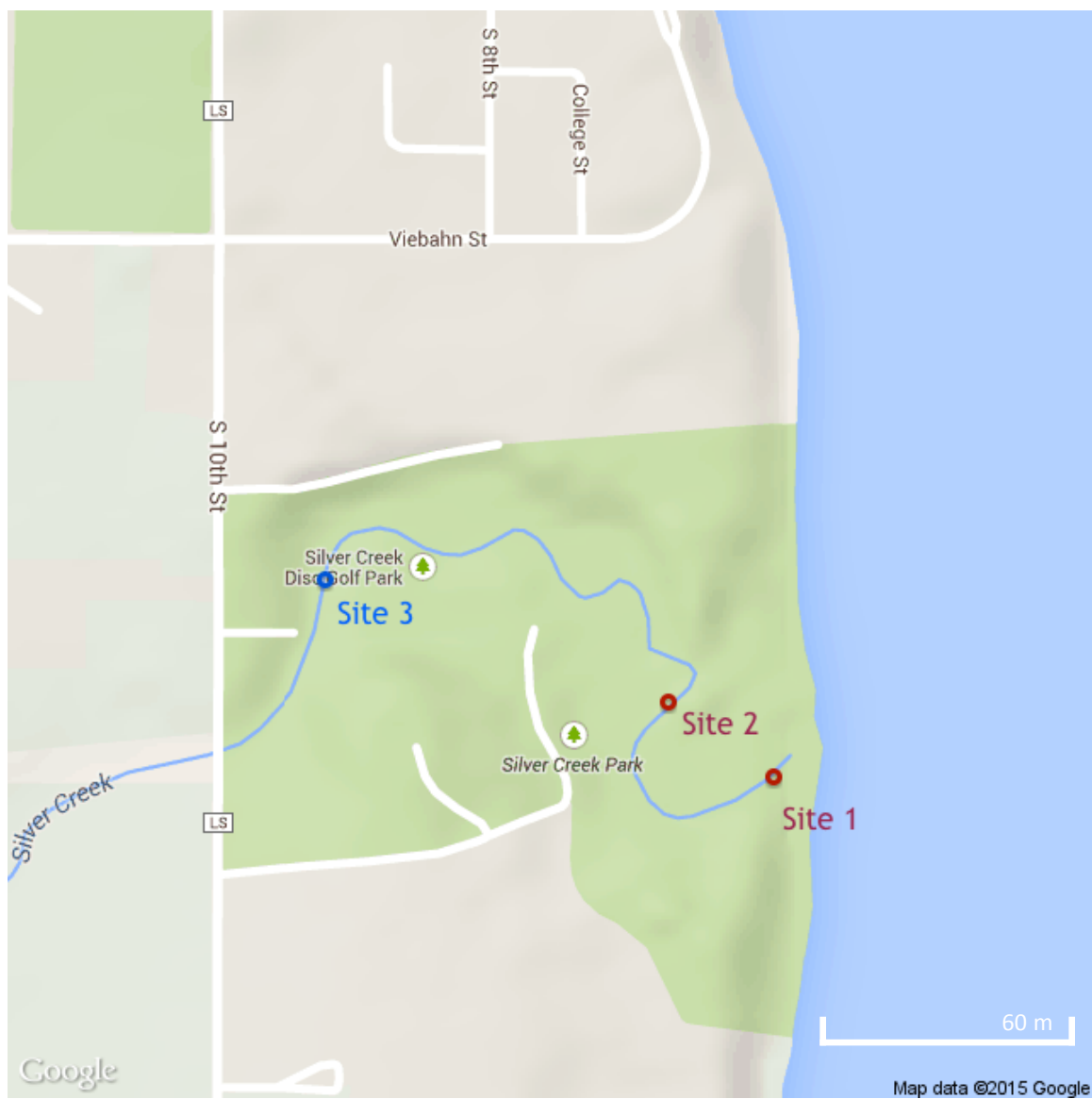
Figure 4. Map of Pigeon River, Sheboygan, WI indicating sample sites (round goby presence indicated in red, round goby absence indicated in blue).
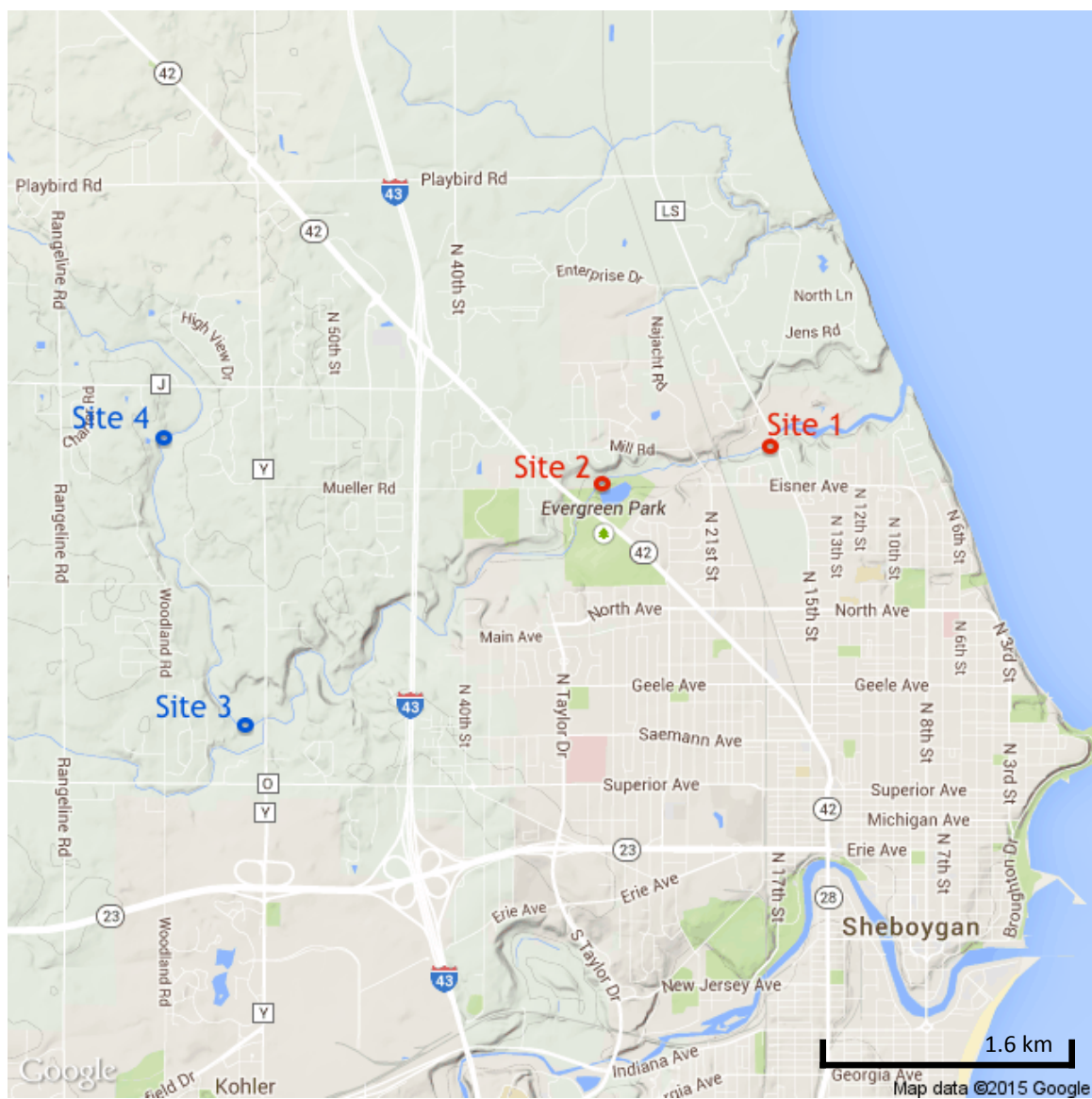
Results

Sample Site Characteristics

The two tributary streams were similar in water chemistry and hydraulic conditions (Table 2), and varied in physical characteristics (Table 3). Pigeon River is larger than Silver Creek, but both steams exhibited higher velocity at downstream sites than upstream. Riffle habitats had a higher percentage of cobble substrate or larger, while substrate type varied at non-riffle sites. Both streams flowed through agricultural, suburban, and recreational land use areas.

Fish Community

A total of 1504 fishes comprising 9 families and 27 species were collected from the Pigeon River and Silver Creek, Wisconsin during summer of 2011 (Table 4). The most abundant species collected in both rivers was the longnose dace (*Rhinichthys cataractae*) (relative abundance = 26.5%). Round gobies (n = 156) were collected from 4 invaded sites on the Pigeon River and Silver Creek (relative abundance = 10.3%). Male and female round gobies were collected in similar numbers (79 males and 77 females) with an average total length of 48.1mm (s.d. = ±19.3mm). A total of 128 johnny darters (relative abundance = 8.5%) and 113 (relative abundance = 7.5%) blackside darters were also collected from both rivers. An endangered species, the striped shiner (*Luxilus chrysocephalus*), was collected from Pigeon River (relative abundance = .001). The specimen was returned to the stream and no voucher was maintained to verify the field identification.

Fish diversity was not significantly different in invaded and non-invaded reaches for any of the indices examined (t-test, p>0.05) (Table 4). Because invasive species can often add to diversity index values, analyses were re-run excluding round gobies from diversity calculations. This also resulted in no significant differences between invaded and non-invaded reaches of streams (t-test, p>0.05).

Stream Site	Goby Present	Wetted Width (m)	Sample Reach (m)	Temperature (°C)	Specific Conductivity (µS)	D.O. (mg/L)	Salinity (ppt)	Velocity (ft/sec)	Max Depth (cm)	% Riffle	% Non-Riffle
PR1	Y	12.05	52.00	17.65	661	9.90	0.30	1.86	34.75	50	50
PR2	Y	10.35	44.88	18.98	632	10.46	0.30	1.69	26.75	40	60
PR3	N*	11.55	56.75	20.35	635	9.99	0.35	0.24	66.50	30	70
PR4	N	11.32	51.21	18.99	643	10.11	0.32	1.26	42.67	40	60
SC1	Y	7.33	32.88	15.83	595	9.42	0.37	0.27	66.00	50	50
SC2	Y	5.83	24.63	17.38	593	10.21	0.30	0.46	26.50	50	50
SC3	N	4.23	18.00	17.25	630	10.13	0.33	0.89	29.00	60	40

Table 2. Mean environmental and hydraulic parameters of stream sites in Silver Creek and Pigeon River.

Table 3. Substrate percentages in riffle and non-riffle microhabitats in Pigeon River and Silver Creek.

Site	Microhabitat	Boulder	Cobble	Gravel	Sand	Silt	Slate Rock
PR1	Riffle	5	95	0	0	0	0
PR1	Non-Riffle	0	10	50	40	0	0
PR2	Riffle	15	70	0	15	0	0
PR2	Non-Riffle	5	40	0	5	0	50
PR3	Riffle	5	95	0	0	0	0
PR3	Non-Riffle	10	80	0	0	10	0
PR4	Riffle	0	50	30	0	20	0
PR4	Non-Riffle	10	10	5	0	75	0
SC1	Riffle	10	40	0	50	0	0
SC1	Non-Riffle	20	80	0	0	0	0
SC2	Riffle	75	25	0	0	0	0
SC2	Non-Riffle	50	0	0	0	50	0
SC3	Riffle	0	80	20	0	0	0
SC3	Non-Riffle	0	10	0	40	40	0

Table 4. Fishes collected from Silver Creek and Pigeon River, Wisconsin

Family	Genus species	Common Name (Abbreviation)
Gobiidae	*Neogobius melanostomus*	Round goby (NM)
Cyprinidae	*Campostoma anomalum*	Central stoneroller (CA)
	Campostoma oligolepis	Largescale stoneroller (CO)
	Luxilus chrysocephalus	Striped Shiner (LC)
	Luxilus cornutus	Common Shiner (LC.x)
	Lythrurus umbratilis	Redfin Shiner (LU)
	Nocomis biguttatus	Hornyhead chub (NB)
	Rhinichthys atratulus	Blacknose dace (RA)
	Rhinichthys cataractae	Longnose dace (RC)
	Semotilus atromaculatus	Creek chub (SA)
Catastomidae	*Catostomus commersoni*	White sucker (CC)
Ictaluridae	*Ameiurus melas*	Black bullhead (AM)
	Noturus flavus	Stonecat madtom (NF)
Esocidae	*Esox lucius*	Northern pike (EL)
Umbridae	*Umbra limi*	Central mudminnow (UL)
Salmonidae	*Oncorhynchus mykiss*	Rainbow trout (OM)
	Salmo trutta	Brown trout (ST)
Centrarchidae	*Ambloplites rupestris*	Rock bass (AR)
	Lepomis cyanellus	Green sunfish (LCN)
	Lepomis gibbosus	Pumpkinseed (LG)
	Lepomis macrochirus	Bluegill (LM)
	Micropterus dolomieu	Smallmouth bass (MD)
	Micropterus salmoides	Largemouth bass (MS)
Percidae	*Perca flavescens*	Yellow perch (PF)
	Percina maculata	Blackside darter (PM)
	Etheostoma nigrum	Johnny darter (EN)
	Etheostoma exile	Iowa darter (EE)

Table 5. Means, standard error, and paired t-test results of diversity indices invaded and non-invaded stream sites. Index values were calculated by including and excluding round gobies.

	Index	Mean ± S.E. (Non-Invaded)	Mean ± S.E. (Invaded)	p-value
	Shannon Diversity	1.46 ± 0.34	1.44 ± 0.40	0.894
	Simpson Diversity	0.69 ± 0.13	0.69 ± 0.13	0.973
Goby Included	Inverse Simpson	3.67 ± 1.39	3.82 ± 1.66	0.762
	Shannon Diversity	1.30 ± 0.36	1.43 ± 0.41	0.317
	Simpson Diversity	0.63 ± 0.14	0.69 ± 0.13	0.248
Goby Excluded	Inverse Simpson	3.12 ± 1.21	3.80 ± 1.68	0.145

Figure 5. Percentage variation as explained through % eigenvalue and the Broken stick model from a principal components analysis of fish communities in invaded and non-invaded reaches of Pigeon River and Silver Creek, WI. PC1 and PC2 explain account for over 75% of the variation within the fish community dataset. The Broken Stick model is less than % eigenvalue for both PC1 and PC2. Therefore both % variation and broken stick model support interpretation of PC1 and PC2.
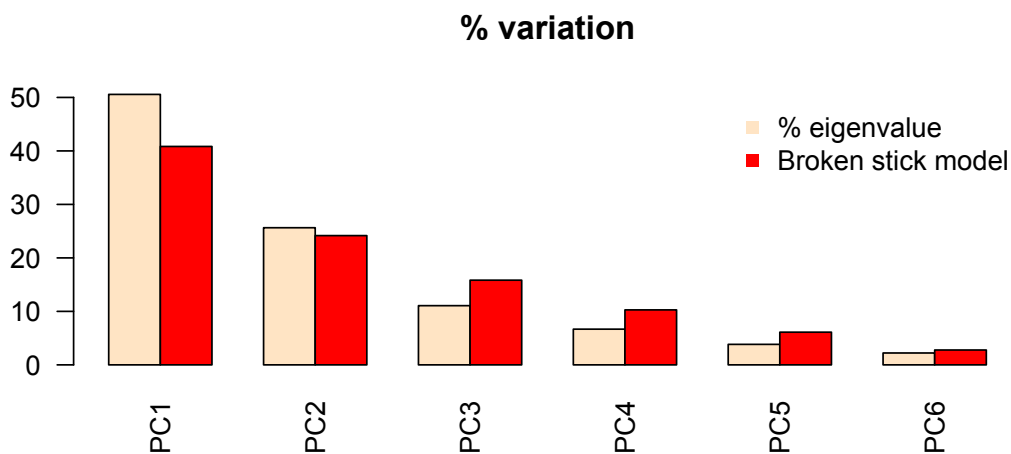
Figure 6. Principal components analysis of Hellinger transformed average fish CPUE for each site at Silver Creek (SC) and Pigeon River (PR), WI. PC1 and PC2 account for over 75% of variation in fish community data. Fish species abbreviations as in Table 3.
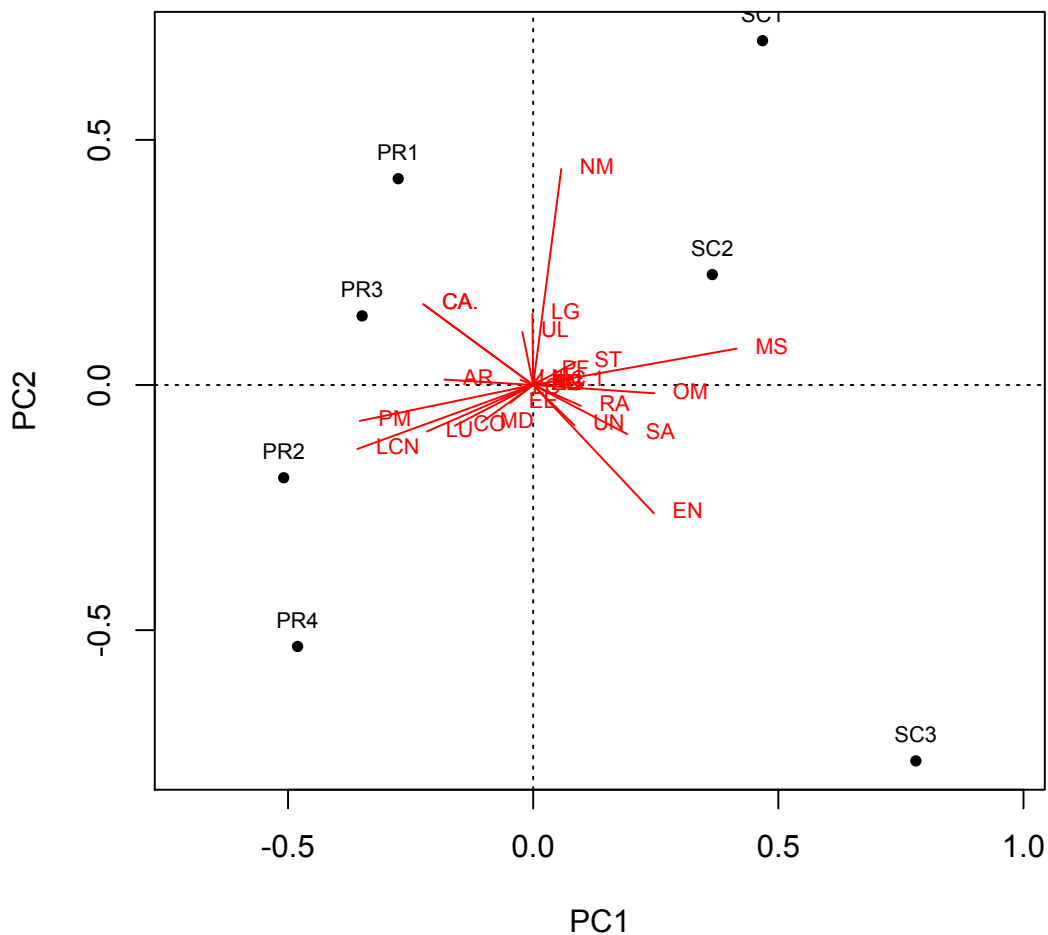
The principal component analysis of average fish CPUE resulted in two significant axes that represent over 75% of variation in the fish community data collected from Pigeon River and Silver Creek. The percent eigenvalues are further supported by the broken stick model, which represents less than the percentage eigenvalues in PC1 and PC2 (Figure 4). Therefore, both PC1 and PC2 were interpreted.

Principal component 1 represented 50.6 % of the variation in fish CPUE and distinguishes between the two stream systems. PC2 represents 25.6 % of the variation in average CPUE and distinguishes along the distance from Lake Michigan (Figure 5). Fish taxa closer together on the PCA are more likely to co-occur with one another. *Etheostoma nigrum* (johnny darter), *Micropterus salmoides* (largemouth bass) and *Oncorhynchus mykiss* (rainbow trout) are positively associated with Silver Creek sites: with (*E.nigrum*) positively associated with upstream (non-invaded) sites at Silver Creek, whereas *N. melanostomus* is positivity associated with downstream sites. *Percina maculata* (blackside darter) and *Lepomis cyanellus* (green sunfish) are positively associated with Pigeon River sites: with *P. maculata* positively associated upstream, and *N. melanostomus* and *Luxilus cornutus* (common shiner) associated downstream.

Differences in microhabitat use were analyzed for the invasive goby and the two target darter species in Silver Creek and Pigeon River. On average, the round goby had three times higher CPUE in riffle habitats ($\bar{x}$ = 1.432 individuals/minute, s.e. = ± 0.604) than in non-riffle ($\bar{x}$ = 0.466 individuals/minute, s.e. = ± 0.174) (Figure 6). However, there was no statistically significant difference in round goby CPUE in riffle and non-riffle areas (t-test t = -1.57, df = 20, p = 0.066).

There was a significant difference between johnny darter CPUE in invaded and non-invaded sites (Two-way ANOVA df = 1, F = 9.3, p = 0.004) (Figure 7) with average johnny darter CPUE in invaded sites four times higher than non-invaded sites (invaded $\bar{x}$ = 1.211 individuals/minute, s.e. = ± 0.325; non-invaded $\bar{x}$ = 0.307 individuals/minute, s.e.

= ± 0.106). There was no difference in johnny darter CPUE in different microhabitats

(ANOVA df = 1, F = 0.24, p = 0.627), or the interaction of microhabitat type and

invasion status (ANOVA df = 1, F = 1.14, p = 0.293).

Finally, there were no significant differences between blackside darter CPUE in

invaded and non-invaded sites (ANOVA df = 1, F = 1.09, p = 0.303) (Figure 8),

microhabitat type (ANOVA df = 1, F = 0.55, p = 0.463), or the interaction of

microhabitat type and invasion status (ANOVA df = 1, F = 1.27, p = 0.267).

Figure 7. Average round goby catch per unit effort (CPUE; number of
individuals/minute), in riffle and non-riffle areas of invaded and sites (error bars
represent standard error).
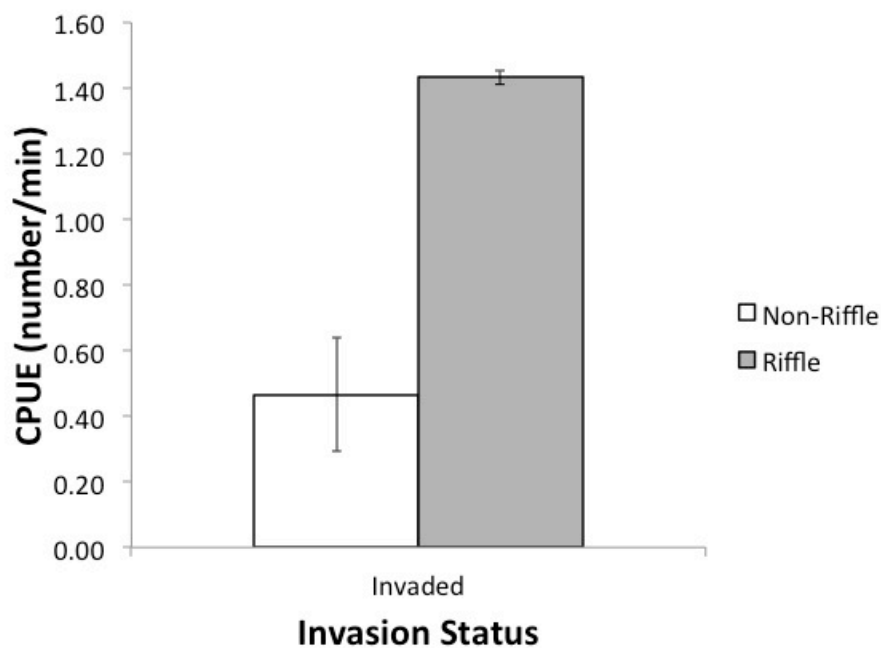
Figure 8. Average johnny darter catch per unit effort (CPUE; number of individuals/minute), in riffle and non-riffle areas of invaded and non-invaded sites (error bars represent standard error).
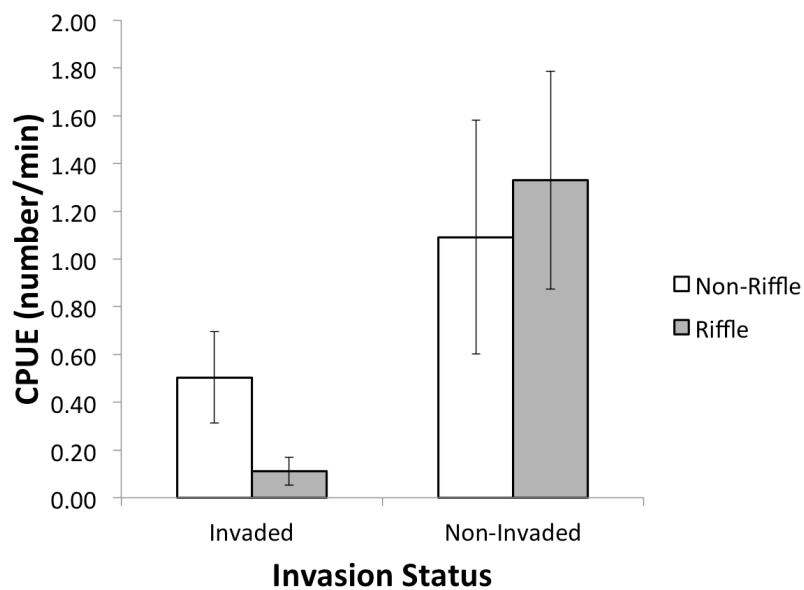
Figure 9. Average blackside darter catch per unit effort (CPUE; number of individuals/minute), in riffle and non-riffle areas of invaded and non-invaded sites (error bars represent standard error).
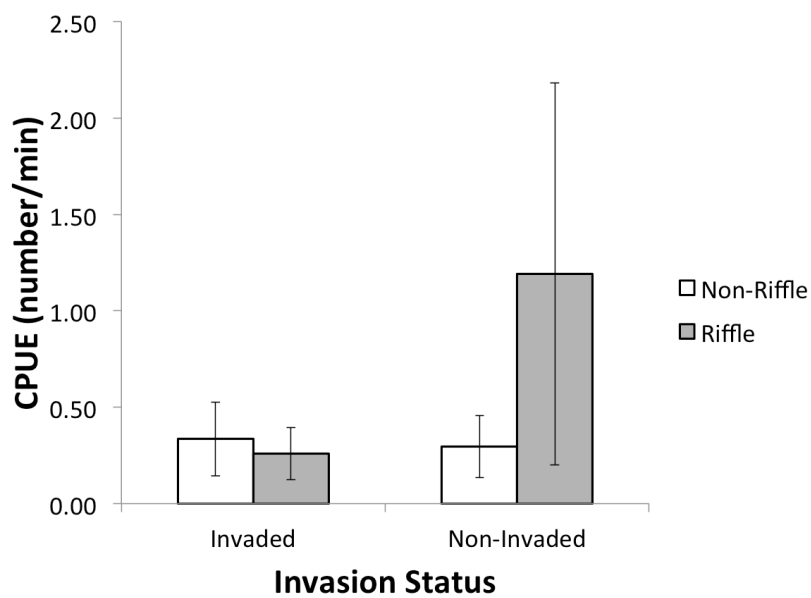
Dietary Analysis

I analyzed the contents of 156 round gobies, 128 johnny darters, and 113 blackside darters collected from Silver Creek and Pigeon River. Darters were categorized as non-invaded (n = 71 johnny darters, 81 blackside darters) and invaded (n = 57 johnny darters, 32 blackside darters). Of all stomachs analyzed, 5.0% were empty (n=21), while the average fullness of all stomachs was 84%. I identified a total of 7,499 prey items in the contents of all fish species stomachs from over 30 aquatic invertebrate families (Bouchard 2004). A very small proportion (1.5%) of prey items were categorized as unidentified due to the advanced state of digestion.

Diets of gobies and darters in both invaded and non-invaded reaches of both streams (Figure 9) were dominated by chronomids and ranged from 35% for johnny darter to 67 % for round gobies. Johnny darter diet in non-invaded reaches shifted to include a higher percentage of crustaceans (30.8%), while blackside darters in non-invaded reaches almost entirely consisted of small minnow and flat head mayflies (93%).

I saw clear differences in goby stomach content data when analyzed by stream. The round goby diets from Silver Creek had a higher percent abundance of crustaceans (Amphipoda, Isopoda, and Cladocera), which could be due to the close proximity of Silver Creek sites to Lake Michigan (Figure 10). Round gobies collected from Pigeon River also had a higher relative abundance of trichoptera (Hydropsychidae and Hydroptilidae), Johnny and blackside darter diets were not separated by stream since

johnny darters were most associated with Silver Creek, and blackside darters entirely

represented in Pigeon River (Figure 5).

Figure 10. Percent abundance of prey from stomach contents for *N. melanostomus* (n=156), *E. nigrum* from invaded stream sites (n=71), *E. nigrum* from goby absent sites (n=57), *P. maculata* from invaded stream sites (n = 81), and *P. maculata* from goby absent sites (n=32).
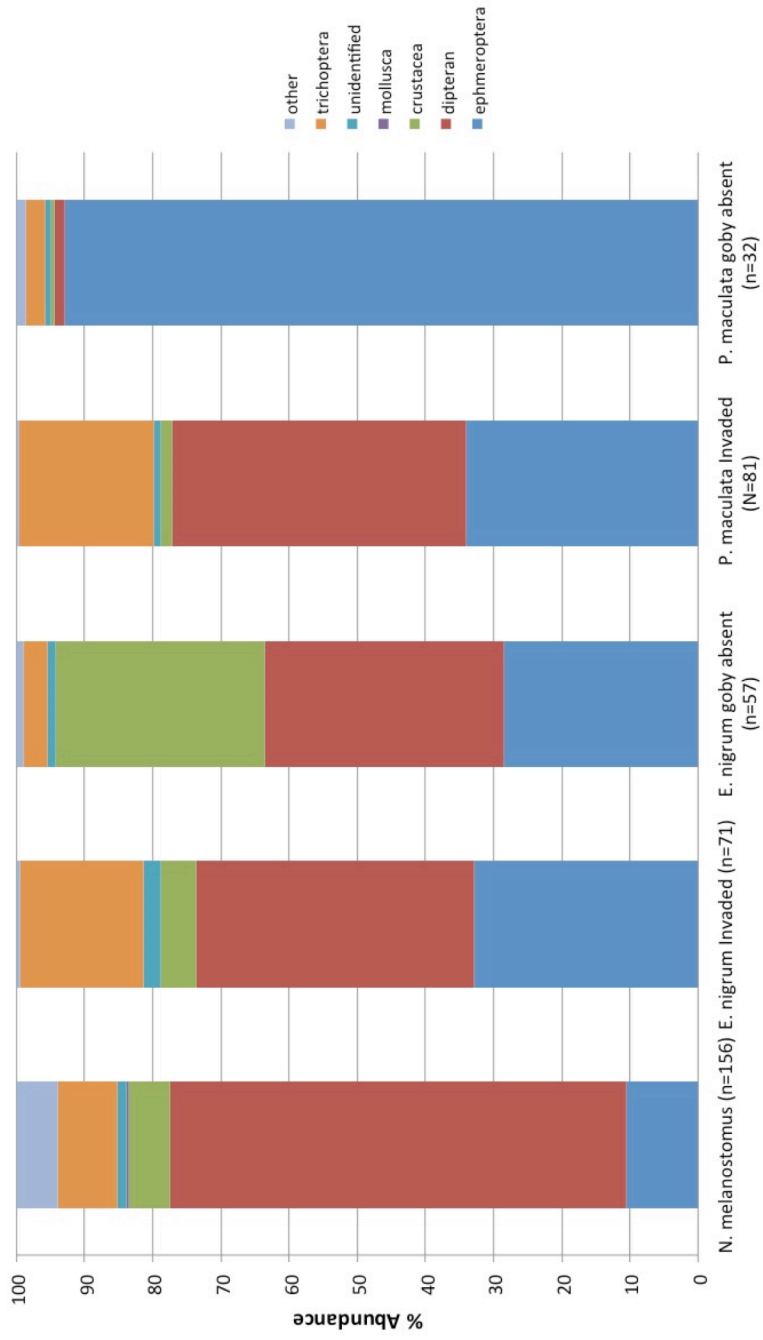
Figure 11. Round goby diet data separated by study site Pigeon River (n= 99) and Silver Creek (n = 57).
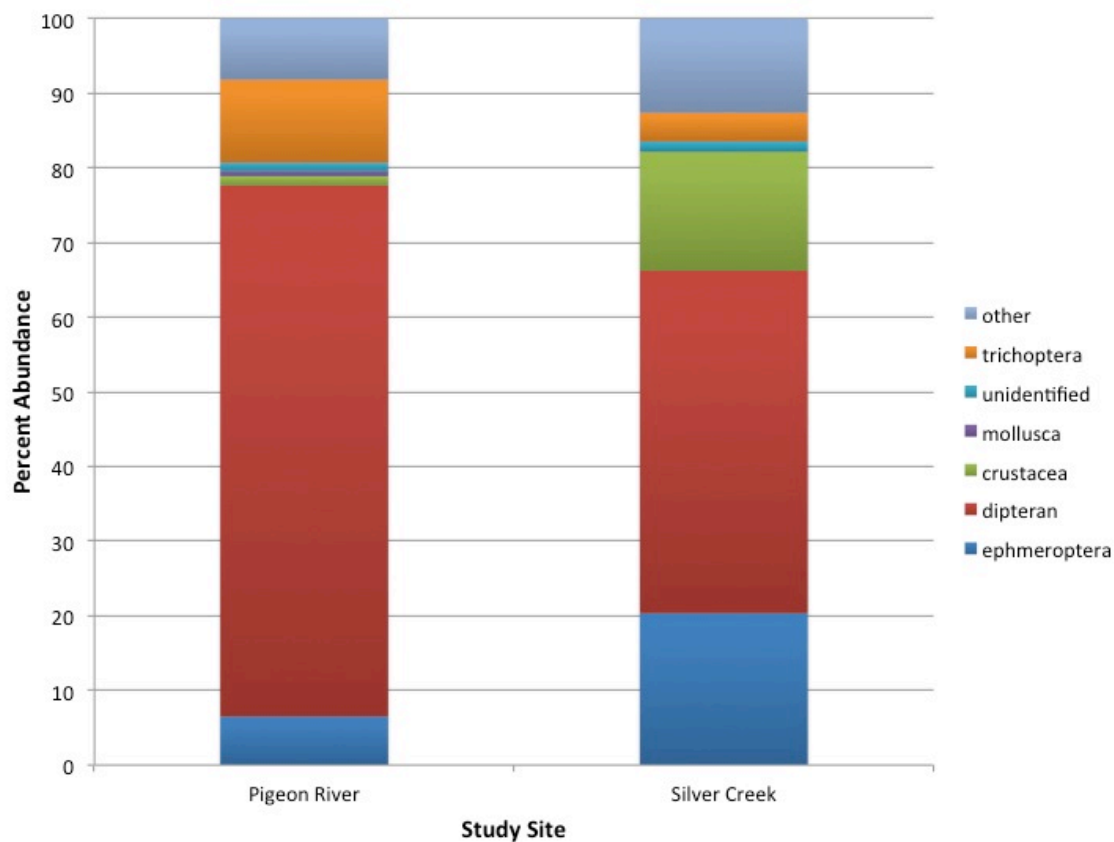
Discussion

Fish Community

Unexpectedly, I found no difference in fish diversity in round goby-invaded stream reaches compared to non-invaded reaches in both results excluding the goby from analyses and those including goby in analyses. Round gobies have been reported to cause declines in both the abundance and diversity of fishes (i.e. *Etheostoma nigrum*, johnny darter; *Cottus bairdii*, mottled sculpin) in the Great Lakes (Balshine et al. 2005,

Dubs and Corkum 1996, Janssen and Jude 2001, Lauer et al 2004). A likely explanation

for these contrasting results could be due to the early invasion status of streams in this

study.

Although fish species diversity in invaded and non-invaded reaches were not

different, johnny darter CPUE was lower in invaded stream reaches. Johnny darters have

been extirpated from Lake Michigan habitats by round gobies (Lauer et al. 2004) and

have been indicated as threatened in lotic habitats due to round goby range expansion

(Poos et al. 2010). Declines in CPUE may be initial signs of extirpation in tributary

habitats.

Round gobies collected from Silver Creek and Pigeon River were relatively small

in size (x = 48.1 mm TL). Maximum length of adult males is reported as 246 mm TL

(fishbase.org). The presence of mostly small individuals in our samples could be an effect

of sampling technique (i.e. the backpack electroshocker voltage and frequency target

smaller species). However, larger round gobies were collected (maximum TL = 125 mm)

in this study, and larger individuals of other species (ex. *Onchorynchus mykiss*) were also

collected. Backpack electroshocker might also affect sampling of round goby populations

due to the lack a swim bladder (which prevents the fish from floating to the surface after

the application of electrical shock) or due to the presence of rocky substrates, however

Brander et al. (2013a) tested goby and benthic fish population sampling techniques and

found the electroshocker was the least selective and most effective technique. The gobies

collected, therefore, most likely reflect the populations in Silver Creek and Pigeon River.

The small size round gobies could indicate new invaders from Lake Michigan. Territorial adult round gobies in Lake Michigan may outcompete for habitat and therefore, smaller individuals are invading into tributary streams. Some studies looking at invasion fronts have indicated that larger gobies tend to be expanding habitat ranges (Brander et al. 2013b., Gutowsky & Fox 2011), while others have found that gobies in newly invaded habitats were smaller and reproduced earlier than in established populations (Corkum et al. 2004, Hôrková & Kováč 2013). Bradner et al. (2013b) also found more males in newly invaded populations, which I collected equal proportions of males (51%) and females (49%).

It is important to note that sampling of the fish community in Pigeon River resulted in collection of a currently endangered species, the striped shiner (dnr.wi.gov 2014). This species was not verified with a voucher specimen, however it is important to consider the indirect impacts the round goby invasion may have on rare, non-benthic fish species. Prior work (and the work of this study) focuses on the impacts of round gobies on native benthic species due to habitat and dietary overlap (Poos et al. 2010). The round goby may still compete for food with non-benthic species. They may also prey upon the eggs and fry of non-benthic species (Chotkowski & Marsden 1999).

Multivariate analyses revealed that fish communities in invaded reaches of two Lake Michigan tributary streams are different than fish communities in non-invaded reaches. This may be due to the differences between upstream and downstream locations of our study sites (Lyons 1996), however this is unlikely as both Silver Creek and Pigeon

River did not change stream order from the furthest upstream site to the furthest downstream sites sampled. Differences in stream fish communities can be attributed to the presence of the invasive round goby at downstream locations. Downstream sites are likely to be invaded first to due movements of round goby from the source (Lake Michigan), rather than from transport upstream as fishing bait (Carmen et al. 2006). Fish taxa in upstream sites were different than those found in downstream sites, with the upstream sites communities comprised of benthic fishes johnny darter, blackside darter, and longnose dace, while downstream sites comprised of round gobies, central stonerollers, and largemouth bass (Figure 6).

Round gobies can alter the fish and macroinvertibrate communities of invaded habitats (Kuhns & Berg 1999, Krakowiak & Pennuto 2008, Kornis et al. 2013). One hypothesis in invasion biology is that communities with high diversity are less vulnerable to invasion (Lodge 1993). However, round gobies have invaded into high diversity tributaries (Kornis & VanderZanden 2010, Poos 2010, Phillips et al. 2003, Bronnenhuber et al. 2011, and this study), and while it has taken a long time for round gobies to invade Great Lake tributaries (approximately 20 years from introduction into the Great Lakes), this range expansion or secondary invasion into lotic habitats is unlikely to be prevented due to high diversity fish diversity in streams. In fact, with the only physical barriers preventing invasion to upstream habitats, the round goby is predicted to invade throughout the Lake Michigan, Wisconsin watershed (Kornis & VanderZanden 2010) and may change the fish and macroinvertebrate communities of these habitats.

Dietary Analysis

Diets of the round goby, blackside darter, and johnny darter overlap as all three species fed primarily on chironomids. This may suggest is the potential for competition for prey between invasive and native species. Not only do I see an overlap in diet between the goby and darters, but also there is a shift in both the blackside darter and the johnny darter stomach contents in non-invaded sites. Johnny darters shifted to a diet more abundant in trichopterans in invaded reaches of the streams. Further investigation is needed to determine if trichopterans are considered a suboptimal prey item, which would indicate shift in realized niche of the johnny darter due to competition. The blackside darter on the other hand had a higher richness in prey species when found with gobies, than in non-invaded sites. The high abundance of ephemeroptera in blackside darter diets from non-invaded reaches of the streams may be due to a localized abundance in upstream sites.

Many studies have looked at the diet of round gobies in native and invaded habitats (reviewed in Kornis et al. 2012). My findings are consistent with those previously published on goby diets in tributary streams, where dipterans made up 64% - 53% dietary mass and 32% - 8% ephemeroptera. Round gobies have a wide dietary breadth, and are known to do well in invaded habitats that do not have the presence of dreissenid mussels (a main prey item in native habitats and in the Great Lakes) (Carmen et al. 2006). Round gobies do exhibit ontogenetic shifts in diet (Kornis et al 2012), however the gobies analyzed in this represented adults and juveniles and there were no

differences in diet due to age.

High diet overlap suggests competition between goby and native darters is possible via both exploitation and interference competition. If prey or primary habitats are a limiting resource in tributary streams, the round goby may outcompete benthic fishes for these resources. Interference competition is likely as the goby and both the johnny and blackside darters were collected at the same sites in Silver Creek and Pigeon River and are diurnal species. The round goby is notoriously aggressive for rocky habitat (Balshine et al. 2005) and has displaced native benthic species from primary habitat in the Great Lakes. The diet shift of johnny darters in this study does suggest character displacement. With historic extirpation of benthic fishes in mind, displacement of darter species in Silver Creek and Pigeon River is a likely outcome.

Finally, there was no evidence round goby predation on native fish eggs or fry in this dietary analysis. These soft-bodied prey types may pass through the dietary track of the goby quickly and potentially be overlooked in this study. Predation on sculpin and johnny darter eggs may be a major cause for the extirpation of these two species from Lake Michigan (Janssen and Jude 2001, Lauer et al. 2004) and further research should assess if predation is occurring on native fish species.

Conclusions

This study documented the fish community and dietary contents of fishes in two Lake Michigan tributary streams during early stages of round goby invasion. The fish communities in invaded reaches of the streams and goby-absent reaches were different,

and the variation in communities is attributed to goby presence. Abundant benthic fishes were analyzed in depth and I found that the CPUE of johnny darters was different in invaded and non-invaded reaches of the streams. This, in combination with dietary overlap of the round goby and native darter species suggests that there may be competition between the species. Finally, a dietary shift was observed in the johnny darter that may indicate displacement into a new realized niche.

While the relative abundance of round gobies in tributary streams at the time of this study was low compared to abundance in Lake Michigan, it is possible that exploitation or interference competition may impact benthic fish communities in streams. This analysis of the early invasion of round gobies into tributaries of Lake Michigan provides a baseline of comparison for future studies on the impact of round gobies on native fish communities and subsequent changes in diets as the invasion of round gobies into streams proceeds.

CHAPTER 3

ROUND GOBY AND JOHNNY DARTER PATCH USE

Introduction

According to optimal foraging theory, organisms use heterogeneous (i.e. patchy)

resources in an efficient and predictable way (MacArthur & Pianka, 1966). Organisms

should forage from a patch until they reach a point where the value of foraging is no

longer greater than the costs. The amount of food left in a patch when the forager quits is

known as a giving up density (GUD) (Brown 1988).   Patch use experiments have been

used to measure GUDs as an indicator of harvest rate (H). The harvest rate takes into

account the energetic cost of predation (P), foraging costs (C), and missed opportunity

costs (MOC) and can be expressed in the formula: $H = P + C + MOC$. Through

manipulating or holding constant variables such as predation risk and missed opportunity

cost, one can measure the harvest rate. This has been used to approximate the cost of

interspecific competitive interactions in terms of energetic value (Brown 1988, Brown et

al. 1997, Abrahamsky et al. 2001, Ovadia & Zu 2003).   A superior competitor may

exclude an inferior competitor from utilizing resources within a patch. Coexistence may

occur in a heterogeneous environment if species partition resources (MacArthur and

Pianka 1966). On evolutionary time scales coexistence may occur via absolute

partitioning of resources and environmental differences (Tokeshi 2009). In an ecological

time scale, overlap of resource utilization is often observed (Tokeshi 2009). The

resulting effects may impact resource utilization of competing species.

Streams and rivers are heterogeneous environments exposed to frequent perturbation (Grossman and Freeman 1987). Coexistence of lotic fishes may occur via temporal, spatial and food resource partitioning (Ross, 1986, Grossman and Freeman 1987, Greenburg 1991). Studies have shown that undisturbed lotic systems are resistant to invasion by non-native fishes (Baltz and Moyle 1993) because of predation, in addition to lack of morphological specialization, and competitive interactions.

Tributaries of the Laurentian Great Lakes are subjected to a round goby secondary invasion (Kornis & Vander Zanden 2010, Poos et al. 2010, Carman et al. 2006). This is surprising as the round goby is a lentic species in its native habitat, the Black and Caspian Seas (Charlebois et al. 1997). The success of the round goby in tributary streams has been attributed to environmental factors such as watershed area and stream gradient (Kornis & Vander Zanden 2010), stream size (Krakowiak & Pennuto 2008) and low concentrations of dissolved ions (Baldwin et al. 2012). Round goby tributary invasion has occurred in both low diversity streams (Carmen et al. 2006, Krokowiak & Pennuto 2008), as well as biodiversity hotspots (Poos et al. 2010).

Although environmental and biological factors contributing to the round goby's success in streams is poorly understood, there is no question that it is spreading into new habitats and thereby interacting with new species. Much of the concern about round goby range expansion is the effect on native fish populations. The round goby can cause a decline in both the abundance and diversity of fishes (i.e. *Etheostoma nigrum*, johnny

darter; *Cottus bairdii*, mottled sculpin) in the Great Lakes (Balshine et al. 2005, Dubs and Corkum 1996, Janssen and Jude 2001, Lauer et al. 2004), and may potentially extirpate native fishes (Poos et al. 2010).

Research Objective

In this study I will investigate the short-term competitive behaviors of the invasive round goby, *Neogobius melanostomus*, and native johnny darter, *Etheostoma nigrum*, through the application of foraging theory and patch use experiments. The round goby was initially reported in southern Lake Michigan in 1998 and by 2002 johnny darters were considered extirpated from the region (Lauer et al. 2004). Both species feed diurnally on benthic macroinvertebrates (Kornis et al. 2012, Kuehne & Barbour 1983) and therefore have the potential for direct competitive interactions. Poos et al. (2010) hypothesized that the round goby competes with the johnny darter based on overlap in habitat and declining populations of johnny darter in invaded habitats. I hypothesize that the round goby will negatively impact johnny darter harvest rates from benthic food patches in a laboratory setting through competitive exclusion.

Materials and Methods

Patch Use Experimental Fishes

Twenty (20) *Neogobius melanostomus* were collected via hook and line and minnow traps from Lake Michigan at Calumet Harbor, Chicago, Illinois. Gobies were adults of total length (TL) ranging from 86 mm - 112 mm and both males and females were collected. Twenty *Etheostoma nigrum* were collected from Lawrence Creek,

Chemung, Illinois via backpack electroshocker. Johnny darter total length ranged from 66 mm – 89 mm and both sexes were represented. Johnny darters and round gobies feed on benthic prey.

Patch Use Experiments

Patch use experiments were conducted in January and March 2013 to test the effects of competition on foraging behavior. Experiments were performed in the Artificial Stream Laboratory of Quinlan Life Sciences Building, Loyola University Chicago, Illinois. All trials took place in one circular pond (1.5m radius, h=1.0 m) during daylight hours. Drop- in dividers (Rubbermaid Sterilite 30 gallon storage box) were used to keep the two species separated within the pond for long- term housing. A third experimental divider (Rubbermaid Sterilite 18 gallon storage box) was used for all foraging trials. Water quality was maintained via an EHEIM water filter, and an Aqua Logic Cyclone brand drop in chiller that maintained water temperature between 14 and 18°C. Depleteble food patches were made from 10 cm diameter (470 mL) petri dishes filled with a pea gravel substrate. Thirty live black worms of 20 mm length were mixed into the substrate. except for two initial trials that had an initial food density of twenty blackworms/patch. Black worms were selected as the food type for these foraging trials because they mimic the movement of common prey of *N. melanostomus* and *E. nigrum,* larval chironomids, and are readily eaten by both species.

Three trial types were performed for this experiment: (1) one round goby foraging, (2) one johnny darter foraging, and (3) one round goby/ one johnny darter

foraging together, each replicated 9, 9, and 5 times, respectively. Fishes were fasted 24-36 hours prior to foraging trials and were not used more than once per experiment to avoid habituation. Fish(es) were placed into an experimental tank for 1h prior to the trial. A prepared food patch was then placed into the center of the experimental tank. Fish(es) foraging behavior was filmed via overhead Logitech webcam and/or underwater GoPro Camera with a MacroLens Underwater Case. Video was transferred to a computer for laboratory analysis. All trials lasted for 60 minutes. After each trial, the food patch was removed and remaining prey items were counted.

Foraging Behavior Analysis

Laboratory video analysis allowed us to quantify foraging behaviors. Response variables of total gain, GUD, and Patch Residence Time (PRT) (the amount of time spent in the food patch) (Stenberg and Persson, 2005) were quantified along with any displays of aggressive behavior. Latency to foraging was measured as the amount of time from the start of experiment to foraging from food patch first occurred. Total gain is the number of food items consumed by the fish(es) during the trial, while GUD is reported as the proportion of the number of food items remaining in the food patch. Both were obtained from the food patch and are indirect measurements of quitting harvest rate (Brown 1988). Patch residence time, first feeding time, and aggressive behaviors (approaches, chases, bites) were obtained from video analysis. A One-way analysis of variance (ANOVA) was used to examine total gain, GUD, and PRT when species foraged alone or with a potential competitor

Results

Nearly all round gobies (n=9), except for 1, foraged from artificial food patches. The average proportion GUD was 0.47 (s.e. = 0.135) (Figure 1). Round goby latency to foraging, (first foraging time) was 8 minutes 47 seconds (Figure 2). The amount of time spent in a patch either foraging or resting was determined through patch residence time and averaged at 10 minutes and 12 seconds (Figure 3).

Of the 17 trials with individual johnny darters foraging, only 9 trials were completed with active foraging. Johnny darters ate less food (x = 6.44 worms, s.e. = 5.24) and their average proportion GUD was 0.79 (s.e. = .06) (Figure 1). Mean latency to foraging 11 minutes 5 seconds (Figure 2). The average johnny darter patch residence time was 18.43 minutes (Figure 3).

I obtained 5 competition trials where foraging took place when fish were competing. I only observed foraging of round gobies under competition trials, and no foraging of johnny darters took place. Average round goby total gain was 10.6 worms (proportion GUD = 0.64), whereas johnny darter total gain was zero.

The patch residence time of round goby under competition was 45.55 minutes, while the patch residence time of the johnny darter under competition was 6.13 minutes. While johnny darters approached the food patch, they did not foraging from it.

Of the 5 successful competition trials, only 3 videos were clear enough to obtain data on aggressive displays of behavior. Of these three trials, the average number of displayed aggressive behaviors was 5.33 displays/hour (s.e. = 1.67) and involved

defending the food patch via chasing and approaches. These displays almost entirely

prevented the johnny darter from approaching the food patch and did result in total

exclusion of johnny darter from foraging at the patch.

Round gobies had a significantly greater gain than johnny darters when each

foraged alone (1-way ANOVA, $F_{3,24} = 4.05$, $p = 0.018$), however round goby gain when

in the presence of johnny darters could not be analyzed because johnny darters had 0 gain

in all trials. There was no difference between round goby giving up densities as an

individual or under competition with the johnny darter, nor was there a difference

between round goby and johnny darter giving up densities.

Figure 12. Average proportion GUD of round gobies and johnny darters foraging
individually (n=9) and the round goby when johnny darter was present (Round Goby*,
n=5) (error bars represent standard error).
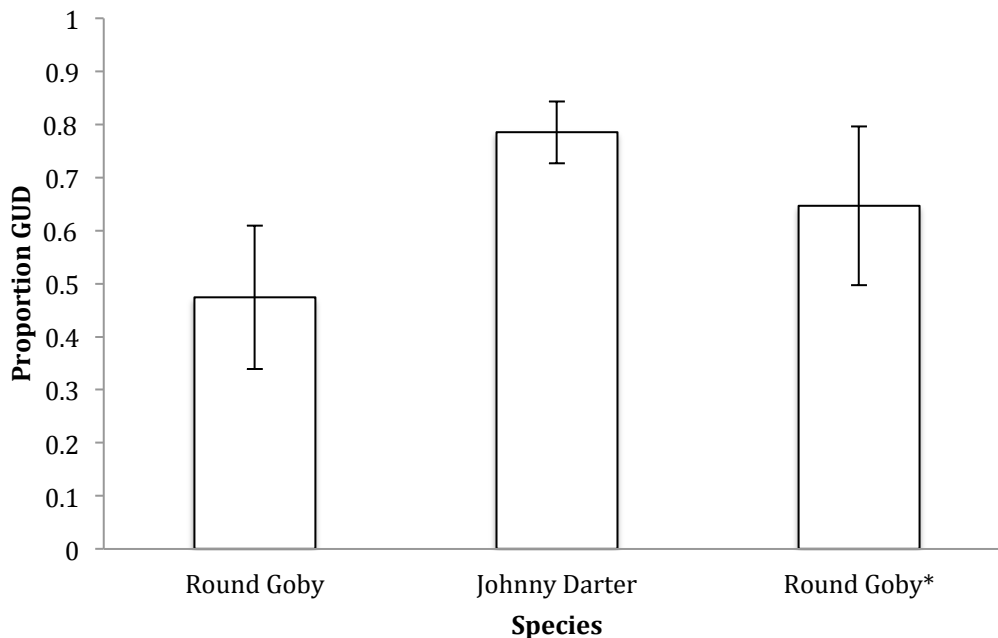
Figure 13. Average latency to foraging time for round gobies and johnny darters foraging individually (n=9) and under competition treatment (n=5). Error bars represent standard error.
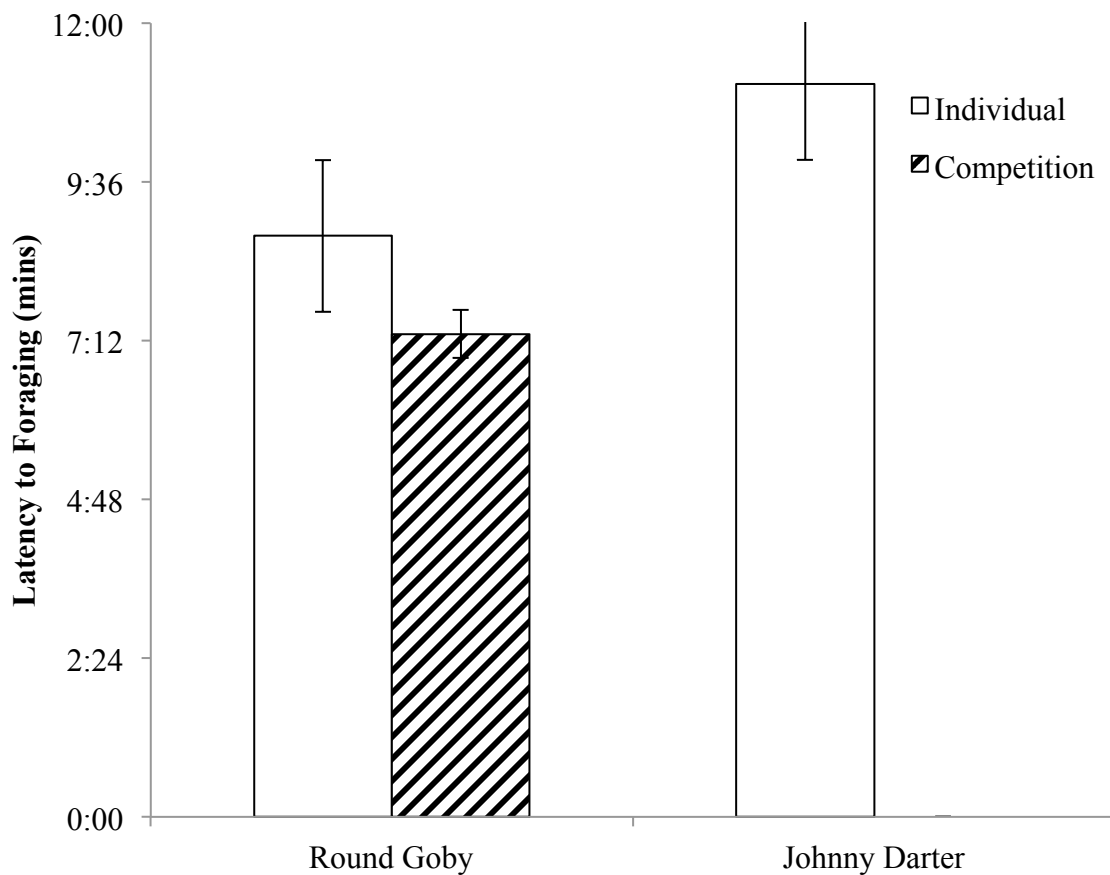
Figure 14. Average patch residence time (PRT) of round gobies and johnny darters foraging individually (n=9) and under the competition treatment (n=5) (error bars represent standard error).
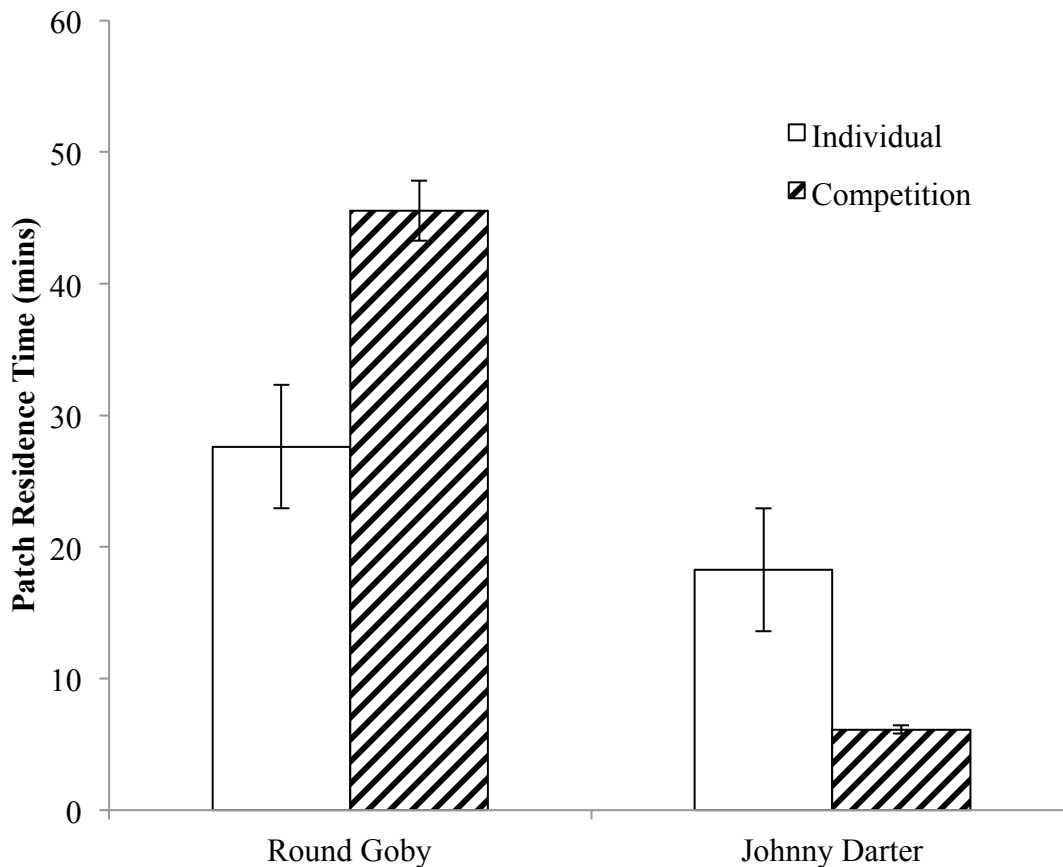
Discussion

Round gobies in this experiment foraged more effectively than johnny darters in artificial food patches and exhibited aggressive behaviors that prevented johnny darters from foraging during competition trials. Round gobies were also more effective in patch residence time and time of first feeding in individual foraging trials, as well as competitive trials. Round gobies have negative impacts on johnny darter populations in southern Lake Michigan (Lauer et al 2004) and were hypothesized to impact tributary

populations as well (Poos et al. 2010). Jude (1995) hypothesized that round gobies outcompete native benthic fishes for food, shelter, and spawning habitats. Round goby aggressive behavior has been observed toward native species for habitat. Laboratory experiments provided evidence for round goby competitive interactions with the mottled sculpin (*Cottus bairdii*) (Dubs and Corkum 1996) and logperch (*Percina caprodes*) (Balshine et al. 2005). In this study, aggressive behaviors of round gobies toward johnny darters for a common food resource were also observed.

Dubs and Corkum (1996) concluded that aggressive behaviors of round gobies toward benthic fishes would ultimately result in the demise of native species. Direct observations of competition for food in the laboratory showed that there is a negative impact of the gobies on the johnny darter. This competition may explain the declines in johnny darter population abundance observed in streams during early round goby stream invasion (Kornis et al. 2013, and this study: Chapter Two).

Patch use experiments have been used as a common experimental technique for assessing the foraging behavior of mammals and have extensive applications. Giving up densities have provided estimates of target species abundance, activity, behavioral responses, forager identities, growth estimates, habitat usage, food handling time, harvesting speed, morphological adaptations, age structure, searching pattern, and stress levels (Bedoya-Perez et al. 2013). Patch use experiments have also been used to assess the effects of intraspecific and interspecific competition between small mammals such as gerbils (Abramsky et al. 2001, Ovadia & Zu 2003) and between birds and gerbils (Brown

et al. 1997).   These studies found that the GUD of foragers increased with increased competition. This could be due to increasing the cost (C) of foraging in that particular patch. Aggressive behaviors can outweigh the benefits from foraging and also lead to increased GUDs. The round goby exhibited aggressive behavior toward the johnny darter resulting in an increase in the foraging cost of the johnny darter and a decrease in foraging behavior of the round goby. Ultimately, the round goby completely prevented the johnny darter from utilizing the food patch.

This experiment is one of the first uses of artificial food patches and giving up densities shown in fishes. Stenberg and Persson (2005, 2006) demonstrated that the technique could be successfully used to analyze effects of group foraging and growth prospects for benthic foraging fishes. Fishes patch use behavior has also been used in lakes and pond habitats as an approximation of productivity (Persson & Neilson 2007). Finally, field enclosure experiments have shown competitive effects of foraging on euryhaline cottids (Polivka 2007, Polivka 2011). Patch use experiments can be a powerful tool to answer questions pertaining to foraging and predation ecology.   While the technique is widely practiced in terrestrial systems, its use in aquatic biology is still in its early application. I propose more patch use experiments will help answer fundamental questions in invasion biology and quantify the impacts of round goby on native benthic fishes.

CHAPTER 4

CONCLUSIONS

My goal for this thesis was to assess the potential impacts of the round goby tributary stream invasion on native benthic fishes. I first reviewed the history of round goby invasion and the characteristics of the round goby that may be attributed to its widespread invasion success. The round goby possesses many characters of invasive species such as high fecundity, territoriality, wide dietary breadth, and ability to thrive in a wide range of environmental parameters. However, one character potentially overlooked is the round goby's ability to eat hard prey items due to the fusion of their lower pharyngeal jaw. Phayngognathy is a trait that many ichthyologists attribute to the widespread success of other fish families (Cichlids and Labrids) and this is certainly a trait that has helped the round goby co-invade the Great Lakes with zebra and quagga mussels. With this novel character in mind, I assessed the possible outcomes of the round goby invasion in tributary streams through a game theory perspective using the G-Function. The G-Function approach allows for *a priori* hypotheses on the outcome of an invasion. If the round goby has a superior G-Function, the only outcome of an invasion is species replacement.

In Chapter 2, I conducted a field-based study using the invasion front as a natural experiment to assess the differences in fish communities in newly invaded reaches and non-invaded reaches. I found that these communities did differ, and that the variation in

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invaded and non-invaded reaches was attributed to round goby CPUE. I next assessed the microhabitat usage of the round goby, and while I did not find a significant difference in riffle and non-riffle habitat use, there was a trend towards higher CPUE in riffle habitats. The blackside darter did not show any differences in CPUE in invaded and non-invaded, nor riffle, non-riffle habitats. The johnny darter on the other hand did show differences in CPUE from invaded and non-invaded sites. Finally, I assessed the stomach contents of the round goby, johnny darter, and blackside darter from invaded and non-invaded reaches of streams. The diets of all species did overlap in invaded reaches and primarily consisted of chironomids. The johnny darter's diet shifted in non-invaded reaches to comprise of a higher abundance of crustaceans, while the blackside darter was almost entirely ephemeroptera. These findings suggest that competitive interactions with johnny darter may result in changes in their habitat use and diet, suggesting a displacement into a new realized niche.

In Chapter 3, I conducted a laboratory behavioral experiment where I used depletable food patches to assess competitive interactions of the round goby and johnny darter. I found differences in patch use in the proportion of food left at an experimental patch, the time spent at a food patch, and the first foraging time. These findings were expected as the round goby is known to be a territorial and aggressive species and suggests that when competing for foraging habitat, the round goby will outcompete via both exploitative and interference competition.

With the findings of my field and laboratory experiments in mind, I return to

assessing the potential outcome of the round goby through the G-Function approach. There is no doubt that the round goby possessed a novel, superior G-Function in the Great Lakes due to their pharygognathy feeding strategy. However, the tributary streams in my study lacked invasive dressinid mussels and I did not find a significant proportion of their diet to consist of hard-bodied prey. If the ability to feed on hard-bodied prey does not give the round goby a superior G-function in tributary streams, species replacement is still likely, as the recipient community is unlikely to have an empty niche available. Therefore, based on my findings there may be reductions in population size, and potentially local extirpation of johnny darters in invaded tributary streams. Further research is needed to assess impacts on blackside darters.

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VITA

Margaret Ann (Meg) Malone graduated from the College of Charleston, South Carolina in May 2007 with a B.S. in Marine Biology. As an undergraduate she studied pelagic fish feeding and aggregating behavior in the Fish Behavioral Ecology lab of Dr. Gorka Sancho. Malone also obtained a National Science Foundation (NSF) Research Experience for Undergraduate (REU) at Rutgers University Marine Field Station, where she studied estuarine fish distributions through acoustic telemetry. Malone's undergraduate research resulted in two peer-reviewed articles, an oral presentation at American Fisheries Society Student Colloquium, and multiple poster presentations.

Upon graduating from the College of Charleston, Malone moved back to the Midwest. She worked as a laboratory manager at on optometry office, and as a research assistant at the Great Lakes WATER Institute in the Aguilar-Cuhel biogeochemistry Lab. At the WATER Institute she participated in off-shore research cruises, collecting benthos and zooplankton samples. She also worked on digitizing historical zooplankton records from Lake Michigan prior to the dreissenid and round goby invasion.

Malone began her master of science in Biology at Loyola University Chicago in 2010, focusing on aquatic ecology and invasive fish species. This thesis was presented in part at two Joint Meetings of Ichthyologists and Herpetologists (JMIH 2011 and 2013). During her time at Loyola, Malone enjoyed teaching Ecology Laboratory (BIO 266) at Lake Shore campus and LUREC. She also oversaw the independent research of Loyola

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