

The Pennsylvania State University

The Graduate School

College of Agricultural Sciences

**DAMS, DREDGING, AND DARTERS:
EFFECTS OF ANTHROPOGENIC DISTURBANCES
ON BENTHIC FISH ECOLOGY**

A Dissertation in

Wildlife and Fisheries Science

by

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Submitted in Partial Fulfillment
of the Requirements
for the Degree of

Doctor of Philosophy

August 2010

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ABSTRACT

Human activities can shape fish ecology in a variety of ways. Large-scale and long-term disturbances such as the construction of dams and commercial dredging operations can affect the hydrodynamics and nutrient flow within rivers. Habitat heterogeneity is decreased as the natural riffle-pool-run sequences are lost to continuous pools and, as a consequence, lotic species are displaced by lentic species, while generalist and invasive species displace native riverine habitat-specialists. Sediment and organic detritus accumulate in deep, dredged reaches and behind dams, disrupting nutrient flow and destroying habitat for lithophilic (“rock-loving”) species. I used standard ecological metrics such as species richness and diversity, as well as stable isotope analysis of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, to quantify differences in fish assemblages among dredged and non-dredged sites, and dam-influenced and free-flowing sites, in the Allegheny River, Pennsylvania. I also examined logperch darters (*Percina caprodes*) to see whether the reduction of water velocity due to navigation and flood-control dams is correlated with morphological changes in this species.

For benthic trawl samples, dredged sites had the lowest species diversity, while undredged sites had the highest diversity. Species diversity and abundance were relatively consistent across bank, near-channel, and mid-channel sampling locations at undredged sites, but appeared show a negative trend at dredged sites. Species abundance and diversity were negatively correlated with depth of individual benthic trawl samples, although near-shore shallow water trawls at dredged sites had lower diversity than those similar depths at undredged sites. These differences were largely driven by the virtual absence of species in lithophilic reproductive guilds at dredged sites, as revealed by

principal components analysis. Data from boat electrofishing did not reveal any apparent differences among dredged and undredged sites, possibly due to sampling locations being located in shallow water along banks, rather than in the channel.

Stable isotope analysis revealed shifts from benthic-derived nutrients at free-flowing sites to increased reliance on pelagic nutrients and terrestrial detritus as water depth increased at dam-influenced sites. There was a similar trend in small benthic fishes from undredged to dredged sites suggesting a loss of benthic nutrient pathways in deeper water. This is consistent with my observations while SCUBA diving that there was effectively no light penetration deeper than 8 to 10 m, while dredged areas could be more than 20 m deep. Larger fishes appeared to show more reliance on benthic nutrients at dredged sites, which could indicate increased foraging in shallow water near the banks, which was also the source of most sampling pressure.

Logperch darters had more interspecific morphological variation than intraspecific variation, particularly among outgroups to *Percina caprodes* (*P. kathae* and *P. bimaculata*), but also between the Ohio (*P. c. caprodes*) and Northern (*P. c. semifasciata*) logperch subgenera. There was some evidence for ecomorphological adaptation as *P. c. caprodes* from sites in streams and free-flowing rivers with faster water velocities had deeper and thicker caudal peduncles and bodies than those from dam-influenced sites where water velocities are slower. This trend was not apparent in *P. c. semifasciata* from Lake Erie and its tributary streams.

The primary objectives of my dissertation were to investigate fish assemblages in large-river habitats of the Ohio River Drainage of Pennsylvania. In particular, I evaluated the putative impacts of anthropogenic disturbances (large-scale commercial

gravel dredging, and navigation and flood-control dams) on fishes at several ecological scales, while focusing on benthic and lithophilic species. I accomplished this by examining the effects of these ecological perturbations on fish morphology, populations, and assemblages. I also fulfilled my secondary objectives by using the knowledge and understanding gained about these large-river fish communities to inform management strategies and provide suggestions for mitigation and minimization of the ecological effects from dams and dredging.

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ACKNOWLEDGEMENTS

I would like to thank my parents, Janet and David, for all of their support throughout my life. They've always been there for me and I quite literally owe them my life. My sister, Rachel, despite our not-infrequent disagreements, has always had my back (only occasionally with a knife in-hand) and I'd like to thank her for proofreading drafts of this dissertation. Who ever said that an English degree was useless?

Terrie Vasilopoulos has been my rock for almost the entire time that I've been at Penn State: maintaining my sanity and always providing a shoulder to vent on, and I look forward to our future collaborations.

My research could not have been conducted without the field and laboratory assistance of a number of people. In no particular order: Tim Stecko, Ben Lorson, Rich Taylor, Jeremy Harper, Howie Goldstein, Rachel Cleaver Yoder, Amanda Horning, Dan Gray, Evan Goldstrohm, Ashley Anderson, Drake Cooper, Aaron Henning, Mary Lundeba, Terrie Vasilopoulos, Vicky Cavener, Bonnie Lu, & Rob Criswell.

My office mates over the years: Dave Lieb, Jeremy Harper, Andy Filipczak, Aubrey Lashaway, Melissa May, and Laura Madden who somehow managed to put up with me without killing me. I know that I benefitted greatly from bouncing ideas off them, and I can only hope that they feel the same.

The Pennsylvania Cooperative Fish and Wildlife Research Unit: Duane Diefenbach, Ty Wagner, and all of the graduate students provided logistic, in-kind, and moral support. And what can I say about Kay Christine? While Jay and Bob may have been my advisors, I was always Kay's student. The meatball subs helped too.

Tim White, Rob Crane, and the Penn State Science Diving Program greatly improved my SCUBA ability and gave me many opportunities for diving, for which I am very grateful.

My committee members: Paola Ferreri and Chuck Fisher, were always ready with excellent suggestions and feedback, and greatly improved the quality of my research and my dissertation.

John Arway at the Pennsylvania Fish and Boat Commission, for bringing his years of knowledge of Pennsylvania's fisheries and dredging issues. I can't think of a better person to be the Director of the Fish and Boat Commission. The State Wildlife Grant Program (administered by the PA Fish and Boat Commission) and Wild Resource Conservation Program (administered by the PA Department of Conservation and Natural Resources) funded my research.

My academic advisors: Bob Carline who brought me here, and Jay Stauffer who adopted me when Bob retired. I couldn't have done it without them, and I've really benefited from their decades of accrued knowledge.

Chapter 1

General Introduction

Study Area – Upper Ohio River Drainage

The Three Rivers of western Pennsylvania are the Allegheny, Monongahela, and Ohio (Figure 1.1). With a total length of 523 km and with a watershed of about 30,000 km², the Allegheny River has historically received the least anthropogenic stressors of the three drainages. From its headwaters in Pennsylvania near Coudersport, the Allegheny River flows north into New York before re-entering Pennsylvania where a dam forms the Kinzua reservoir. Below the Kinzua Dam, the river is free-flowing for 211 km until East Brady, PA, upon which it is regulated by eight locks-and-dams for the final 116 km to the Ohio River. Glacial alluvial gravel and rocks comprise the dominant substrate in the Allegheny River.

The Monongahela River originates at the confluence of the West Fork and Tygart rivers near Fairmont, West Virginia from whence it flows 206 km (146 km in Pennsylvania) to the confluence with the Allegheny River. With an overall watershed draining 19,011 km², and regulated by nine locks-and-dams (six in Pennsylvania), the substrate of the Monongahela River primarily consists of mud and sand. In the 19th century, anthropogenic stresses increased as mining (and the subsequent downstream shipping of coal) and steel plants became the dominant industries in the watershed (Pearson and Krumholz 1984).

The Ohio River forms at the confluence of the Allegheny and Monongahela rivers in Pittsburgh; it drains an area of 490,601 km² and flows 1,579 km to its mouth on the Mississippi River at Cairo, IL. Sixty-four km of the Ohio River, and three locks-and-dams, are located within Pennsylvania. The substrate of the Ohio River is a combination of the glacial alluvial deposits of

the Allegheny River and the sand and silt of the Monongahela River. Being downstream from Pittsburgh during the steel-boom meant that the Ohio River was historically subjected to many anthropogenic stressors. While water quality has improved in recent decades as the steel industry has declined and environmental practices have become more standard, the Ohio River is downstream from the approximately 2.5 million residents of metropolitan Pittsburgh, and the associated commercial, industrial, and residential stressors.

Biogeography and Fish Distribution

At various times in its history, parts of what is now the Ohio River basin have been part of, or connected to, a number of different drainages, including the Great Lakes and Atlantic Ocean (Robison 1986). For instance, prior to the last glacial maximum in the Wisconsin, the Monongahela River fed the Allegheny River which flowed north into the Laurentian system, while much of what is now the Ohio River flowed west into the ancient Teays River system and the rest flowed north into the Laurentian system. Direct glacial action, the blocking of northern outflows by glaciers, and glacial melting largely prevented the northerly flow of water, and caused new connections among basins. As the Allegheny River reversed flow, it forced a route west with the Monongahela and connected with what became the Ohio River. As the bulk of the upper Ohio River basin was covered with glaciers during the glacial maxima, fishes were forced into refugia from which they later recolonized glaciated areas. The majority of Ohio River species recolonized from the Mississippian glacial refugium (southern Mississippi River basin), but some may also have colonized from the Atlantic (Chesapeake basin and south) and Missourian (western Missouri River basin) refugia (Crossman and McAllister 1986, Hocutt et al. 1986). As a result of these recolonizations from a variety of glacial refugia, the upper Ohio River (River kilometre 0-526) ichthyofauna comprises 128 fish species, of which 117 are native to the

drainage (Table 1.1). The Allegheny River also contains a rich ichthyofauna, with 110 species (102 native) having been reported from this drainage (Table 1.1).

The first scientific accounts of the fishes of the Ohio River drainage come from Samuel Rafinesque who, from 1818-1819 undertook the first systematic study of the fishes of the Ohio River (Rafinesque 1820). Rafinesque (1820) described approximately 90 new species, and correctly noted their biogeographic distinction from those of the Atlantic drainage. Rafinesque (1820) also noted the presence of anadromous fish species such as herrings, sturgeon, and eels as far upstream as Pittsburgh, located about 3,190 km from the Mississippi River's mouth in the Gulf of Mexico, although he suggests that these are resident populations rather than anadromous. American eel, *Anguilla rostrata*, of which Rafinesque describes four species (Rafinesque 1820), are now known to breed only in the Sargasso Sea region of the Atlantic Ocean (Comparini and Rodino 1980), and would therefore have been catadromous.

While anthropogenic activities have had adverse effects on many fish species, others have thrived and conditions have been improving (Pearson and Krumholz 1984, Pearson and Pearson 1989, Argent and Kimmel 2003, Thomas et al. 2005, Argent et al. 2007). Development of cumulative effects-driven fisheries assessments have indicated that small benthic fishes are most susceptible to anthropogenic effects due to limited home-range size and reliance on local, aquatic-derived nutrients (Munkittrick et al. 2000). Sampling small, benthic species from large-rivers presents challenges that are not adequately addressed by most sampling gears (e.g., electrofishing and gill-nets), in part because fisheries assessments are commonly focused on large and economically important species. More recently, sampling methods to assess small, benthic species in large river habitats have been developed (Herzog et al. 2005, Argent et al. 2007, Koryak et al. 2008). While these methods provide a great deal of information about small benthic fish distribution, historical comparisons are confounded by the use of a novel gear. That is to say,

it raises the question of whether the absence of a species from prior studies is due to its actual absence, or to its habitat not being sampled efficiently.

History of Anthropogenic Activities

Rafinesque (1820) described the Ohio River as being between 1m at low water and 10 m deep at high water, with an average depth of approximately 5 m. Navigation dams and channel dredging now maintain a minimum depth of approximately 3 m (Figure 1.2). He also described the Allegheny River as being “almost perfectly clear” while the Monongahela and Ohio rivers as being slightly turbid, but almost clear at low stage “and at all times very salubrious” (Rafinesque 1820:50). He mentions that the turbidity is caused by very fine particles which have low rates of deposition. At the time, the rivers were relative pristine, not yet having been subjected to large-scale industrial or municipal waste. By the mid 1800s, however, it was noted that the rivers were very turbid, in the words of Walt Whitman, quoted in (Pearson and Krumholz 1984) “...they are always and excessively muddy...” (p. 39). (Trautman 1957) noted the negative effects that siltation has on many species, including logperch *Percina caprodes*, which is generally more tolerant of siltation than many other darter species.

The Falls of the Ohio near Louisville, KY presented a major obstacle to early navigation, and were circumvented by the Louisville and Portland Canal, which included the first locks on the river, and was completed in 1830. Although the canal had not yet been completed by the time of Rafinesque’s survey, shipping was increasing in importance and the first steam ships were plying their trade on the river. At the time, Pittsburgh had a population of about 15,000, compared to over 300,000 in the city and almost 2.5 million in the metropolitan area today (Bureau 2010). Though renowned for its steel industry, this growth in human population density has also had a profound effect on water quality. Pearson and Krumholz (1984) reported that

while there were between 7 and 14 municipal sewage discharges per 160 km in the lower and middle Ohio River, there were more than 40 in the first 138 km from Pittsburgh, PA to Wheeling, WV.

Humans have relied on fishes and mussels for sustenance since their earliest habitations in the Ohio River basin. Mussel shells, fishing artifacts, and fish bones have been found in Paleoindian middens, including the Meadowcroft Rockshelter near Pittsburgh, which has been occupied by humans since at least 14 thousand years ago (Adovasio et al. 1978, Adovasio et al. 1990), indicating their importance as food sources. Rafinesque (1820: 47) also made reference to the importance of commercial fisheries in the Ohio River, stating that Ohio River fish “afford excellent food...equal to the best sea fish”. In 1950, “Downstream from factory outlets, I’ve seen crawfish crawling out of the water to escape the acid; and I’ve seen fish ‘piping’ with their snouts half out the water, trying to get a fresh breath” (Simpich 1950). By 1962, it was reported that commercial fishing was impossible as “fishes from the upper third of the Ohio River have long possessed objectionable taste (usually reported as oily, muddy, or gasoline flavors)” (Pearson and Krumholz 1984). While there have been continuing concerns about the levels of contaminants in Ohio River fishes, the general tissue concentrations seem to have been declining since these earlier reports, and most species are safe for at least limited consumption (Pearson and Krumholz 1984, Protection 2009).

Dredging

Dredging for resource removal and navigation purposes are common in many river systems, and can have profound effects on the physical and biological characteristics of the river (Rivier and Seguiet 1985, Kanehl and Lyons 1992, Meador and Layher 1998, Roell 1999, Kondolf et al. 2001). Dredging causes structural changes to the river (Figure 1.2), such as head-

cutting (erosion from the upstream extent of a dredged hole) and bank erosion (Rivier and Segquier 1985, Kanehl and Lyons 1992, Kondolf 1997, Gob et al. 2005). Fine sediment loads increase, while overall sediment dynamics are altered as larger gravel and rocks are removed and replaced by fine organic and inorganic silts (Veshchev 1982, Petit et al. 1996, Wilcock et al. 1996a, Wilcock et al. 1996b, Kondolf 1997, Gaillardet and Piegay 1999, Kondolf et al. 2001, Wyzga 2001, Gob et al. 2005, Rinaldi et al. 2005, Rovira et al. 2005). Natural replenishment of the substrate post-dredging can take hundreds of years, and may best be measured on geological time scales (Kanehl and Lyons 1992, Kondolf 1997, Meador and Layher 1998, Kondolf et al. 2001, Rovira et al. 2005). Habitat restoration, such as the reestablishment of gravel bars in streams, can help restore invertebrate and fish community populations (Merz and Ochikubo Chan 2005).

Dredging has detrimental effects on macrophyte and algal plant diversity and biomass, by a combination of altered substrates, increased turbidity and sedimentation, and reduced light penetration and photosynthesis (Rivier and Segquier 1985, Kanehl and Lyons 1992, Brown et al. 1998, Ameziame et al. 2002). Invertebrate populations are also affected by dredging as sedimentation reduces reproduction and fitness and substrate removal eliminates habitat (Rivier and Segquier 1985, Kanehl and Lyons 1992, Aldridge 2000, Greenwood et al. 2002, Merz and Ochikubo Chan 2005). Fishes can be adversely affected indirectly because of changes in the plant and macroinvertebrate communities. Additionally fishes can be stressed directly, as species with specific habitat requirements (e.g. riffles and gravel habitat) are affected first, followed by those intolerant of sedimentation (Rivier and Segquier 1985). Due to their specific habitat requirements and their sensitivity to sedimentation, particularly for spawning, fish species that spawn in gravel and rocky substrates (lithophilic species) are most likely to be affected by riverine dredging (Rivier and Segquier 1985, Berkman and Rabeni 1987, Kanehl and Lyons 1992, Kondolf et al. 1993, Kondolf 2000, Kondolf et al. 2001).

Stable Isotope Analysis

Stable isotope analysis relies on the principle that “you are what you eat.” In other words, consumers incorporate the chemical composition of their prey, and we can use this to trace nutrients through food-webs. The most common stable isotopes used in food web studies are carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$). The ratio of ^{13}C to ^{12}C in a sample, compared to the same ratio in a known standard, is known as $\delta^{13}\text{C}$ and varies with different primary producers, while $\delta^{15}\text{N}$ is the ratio of ^{15}N to ^{14}N and is enriched with increasing trophic levels (Peterson and Fry 1987).

In aquatic systems, primary producers from deep water habitats are depleted in ^{13}C relative to those from shallow habitats due to their reliance on respired CO_2 as a source of inorganic carbon (Vander Zanden and Rasmussen 1999, Post 2002b). Similarly, producers in slower moving water are depleted relative to those in faster water due to the boundary layer effect and decreased CO_2 availability (Finlay et al. 1999, Trudeau and Rasmussen 2003). Terrestrial (allochthonous) derived carbon differs from aquatic (autochthonous) $\delta^{13}\text{C}$ as aquatic sources are generally relatively depleted in lower order streams but enriched in higher order rivers (Jones et al. 1998, Finlay 2001, Grey and Harper 2002, Flotemersch and Jackson 2003, Pace et al. 2004, Carpenter et al. 2005). Certain compounds, such as methane (CH_4) have extremely depleted $\delta^{13}\text{C}$ signatures, and can be used to trace such inputs into higher consumers via microbial food webs (Jones and Grey 2004, Grey and Deines 2005). $\delta^{15}\text{N}$ accumulates in step-wise fashion at each trophic level within food webs, at an average increment of approximately 3.4‰ per trophic level, and can be used as an indicator of relative trophic position within a food-web (Vander Zanden and Rasmussen 1999, 2001, Post 2002b, Post 2002a, Vanderklift and Ponsard 2003). Because baseline $\delta^{15}\text{N}$ varies across systems and habitats, it is important to apply baseline-correction using either primary producers or known primary consumers (Vander Zanden and Rasmussen 1999, Post 2002b).

Because of their ability to delineate nutrient flow through food-webs, stable isotopes are frequently used to investigate the sources of anthropogenic inputs to aquatic systems, and to determine the effects of anthropogenic activities, including species introductions or invasions (Vander Zanden et al. 1999, Curry et al. 2007), cultural eutrophication (Vadeboncoeur et al. 2002, Vadeboncoeur et al. 2003, Vander Zanden et al. 2003, Chandra et al. 2005), agriculture (Harrington et al. 1998, Anderson and Cabana 2005, Gray et al. 2005), point-source pollutants such as sewage (Hobbie et al. 1990, Costanzo et al. 2001, Wayland and Hobson 2001, Savage and Elmgren 2004, Aguilar et al. 2008) and pulp-mill effluent (Wassenaar and Culp 1996, Wayland and Hobson 2001, Dube et al. 2006, Skinner et al. in press), and tracing contaminants (Cabana et al. 1994, Campbell et al. 2003, Jardine et al. 2005, Jardine et al. 2006).

Objectives of Dissertation

The objectives of this dissertation are to investigate fish assemblages in large-river habitats of the Ohio River Drainage of Pennsylvania. In particular, I evaluate the putative impacts of anthropogenic disturbances (large-scale commercial gravel dredging, and navigation and flood-control dams) on fishes, especially on benthic and lithophilic species. I accomplish this by examining the effects of these ecological perturbations on fish morphology, populations, and assemblages. Secondary objectives are to use this knowledge and understanding about these large-river fish communities to inform management strategies and provide suggestions for mitigation and minimization of the ecological effects from dams and dredging.

My research is organized into seven chapters. In this first chapter, “General Introduction,” I have given an overview of the history of the Ohio River Basin, including its tributaries the Allegheny and Monongahela rivers. I have discussed the geology, biogeography, and changes in water quality and fish distribution over time. In the second chapter, “Extensions

of the Known Ranges of *Percina shumardi* Girard and Three Species of *Etheostoma* (subgenus *Nothonotus*) in Pennsylvania” (Freedman et al. 2009a), I discuss range expansions of four darter species in the Ohio River, including documenting River Darter, *Percina shumardi*, for the first time in Pennsylvania. My third chapter, “Development and Efficacy of an Electrified Benthic Trawl for Sampling Riverine Fishes,” introduces the PSU trawl, which greatly increased the sampling efficiency for small benthic fishes and was used to sample fishes in my other chapters (Freedman et al. 2009b). In my fourth chapter, “Effects of Gravel Dredging on Fish Populations and Assemblages,” I have examined relationships between fish populations and assemblages with dredging history and sampling depth. My fifth chapter, “Effects of Anthropogenic Activities on Fish Assemblages: Food-web and Trophic Consequences” uses stable isotope analysis of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ to examine differences in fish food-web structure and nutrient dynamics due to navigation dams and commercial gravel dredging. For my sixth chapter, “Ecomorphology and Intergrression Confound Biogeography in Logperch Darters,” I investigate the role of water velocity and dams in defining the morphology of logperch, and investigate the biogeography of logperch in Pennsylvania. My seventh and final chapter is a General Discussion, in which I synthesize and suggest management implications of my research.

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Table 1.1. List of native (N) and introduced (I) fish species documented from the Upper Ohio River (0-526 km) and the Allegheny River. PA Status denotes conservation status in Pennsylvania: Ex – Extirpated, E – Endangered, T – Threatened, C – Candidate. Sources: Freedman et al. (2009a), Lorson (2010), Pearson & Krumholz (1984), Pearson & Pearson (1989).

Scientific Name	Common Name	Upper Ohio	Allegheny	PA Status
Petromyzontidae				
<i>Ichthyomyzon bdellium</i>	Ohio Lamprey	N	N	C
<i>Ichthyomyzon castaneus</i>	Chestnut Lamprey	N		
<i>Ichthyomyzon fossor</i>	Northern Brook Lamprey		N	E
<i>Ichthyomyzon greeleyi</i>	Mountain Brook Lamprey		N	T
<i>Ichthyomyzon unicuspis</i>	Silver Lamprey	N		
<i>Lampetra aepyptera</i>	Least Brook Lamprey	N	N	C
<i>Lampetra appendix</i>	American Brook Lamprey	N	N	C
Acipenseridae				
<i>Acipenser fulvescens</i>	Lake Sturgeon	N		E
<i>Scaphirynchus platyrhynchus</i>	Shovelnose Sturgeon	N		
Polyodontidae				
<i>Polyodon spathula</i>	Paddlefish	N	N	
Lepisosteidae				
<i>Lepisosteus osseus</i>	Longnose Gar	N	N	
<i>Lepisosteus platostomus</i>	Shortnose Gar	N		
Amiidae				
<i>Amia calva</i>	Bowfin	N	N	C
Anguillidae				
<i>Anguilla rostrata</i>	American Eel	N		
Clupeidae				
<i>Alosa chrysochloris</i>	Skipjack Herring	N		T
<i>Alosa pseudoharengus</i>	Alewife	I		
<i>Dorosoma cepedianum</i>	Gizzard Shad	N	N	
Hiodontidae				
<i>Hiodon alosoides</i>	Goldeye	N		T
<i>Hiodon tergisus</i>	Mooneye	N	N	T
Salmonidae				
<i>Oncorhynchus mykiss</i>	Rainbow Trout	I	I	
<i>Salmo trutta</i>	Brown Trout	I	I	
<i>Salvelinus fontinalis</i>	Brook Charr		N	
Gadidae				
<i>Lota lota</i>	Burbot		N	E
Esocidae				
<i>Esox americanus vermiculatus</i>	Grass Pickerel	N	N	
<i>Esox lucius</i>	Northern Pike	I	I	
<i>Esox masquinongy</i>	Muskellunge	N	N	
Cyprinidae				

<i>Campostoma anomalum</i>	Central Stoneroller	N	N	
<i>Carassius auratus</i>	Goldfish	I	I	
<i>Chrosomus erythrogaster</i>	Southern Redbelly Dace	N		T
<i>Clinostomus elongatus</i>	Redside Dace		N	
<i>Cyprinella spiloptera</i>	Spotfin Shiner	N	N	
<i>Cyprinus carpio</i>	Eurasian Carp	I	I	
<i>Notropis buccatus</i>	Silverjaw Minnow	N	N	
<i>Erimystax dissimilis</i>	Streamline Chub	N	N	
<i>Erimystax x-punctatus</i>	Gravel Chub	N	N	E
<i>Exoglossum laurae</i>	Tongetied Minnow		N	
<i>Hybognathus nuchalis</i>	Mississippi Silvery Minnow	N		
<i>Hybopsis amblops</i>	Bigeye Chub	N	N	
<i>Luxilus chrysocephalus</i>	Striped Shiner	N	N	
<i>Luxilus cornutus</i>	Common Shiner	N	N	
<i>Lythrurus umbratilis</i>	Redfin Shiner		N	E
<i>Macrhybopsis aestivalis</i>	Speckled Chub	N		
<i>Macrhybopsis storeriana</i>	Silver Chub	N	N	E
<i>Margariscus margarita</i>	Pearl Dace		N	
<i>Nocomis biguttatus</i>	Hornyhead Chub		N	C
<i>Nocomis micropogon</i>	River Chub	N	N	
<i>Notemigonus crysoleucas</i>	Golden Shiner	N	N	
<i>Notropis ariomnus</i>	Popeye Shiner		N	Ex
<i>Notropis atherinoides</i>	Emerald Shiner	N	N	
<i>Notropis blennioides</i>	River Shiner	N		E
<i>Notropis boops</i>	Bigeye Shiner	N		
<i>Notropis buccatus</i>	Silverjaw Minnow	N	N	
<i>Notropis burchanani</i>	Ghost Shiner	N	N	E
<i>Notropis dorsalis</i>	Bigmouth Shiner		N	T
<i>Notropis heterolepis</i>	Blacknose Shiner	N	N	
<i>Notropis hudsonius</i>	Spottail Shiner	N	I	
<i>Notropis photogenis</i>	Silver Shiner	N	N	
<i>Notropis rubellus</i>	Rosyface Shiner	N	N	
<i>Notropis stramineus</i>	Sand Shiner	N	N	
<i>Notropis volucellus</i>	Mimic Shiner	N	N	
<i>Notropis whipplei</i>	Steelcolor Shiner	N		
<i>Notropis wickliffi</i>	Channel Shiner	N	N	
<i>Notropis heterodon</i>	Blackchin Shiner		N	E
<i>Phenacobius mirabilis</i>	Suckermouth Minnow	N		
<i>Pimephales notatus</i>	Bluntnose Minnow	N	N	
<i>Pimephales promelas</i>	Fathead Minnow	N	I	
<i>Pimephales vigilax</i>	Bullhead Minnow	N		
<i>Rhinichthys cataractae</i>	Longnose Dace		N	
<i>Rhinichthys obtusus</i>	Western Blacknose Dace	N	N	
<i>Semotilus atromaculatus</i>	Creek Chub	N		
Catostomidae				
<i>Carpiodes carpio</i>	River Carpsucker	N	N	
<i>Carpiodes cyprinus</i>	Quillback	N	N	
<i>Carpiodes velifer</i>	Highfin Carpsucker	N	N	
<i>Catostomus commersoni</i>	White Sucker	N	N	

<i>Cycleptus elongatus</i>	Blue Sucker	N		
<i>Erimyzon sucetta</i>	Lake Chubsucker	N		
<i>Hypentelium nigricans</i>	Northern Hogsucker	N	N	
<i>Ictiobus bubalus</i>	Smallmouth Buffalo	N	N	
<i>Ictiobus cyprinellus</i>	Bigmouth Buffalo	N		E
<i>Ictiobus niger</i>	Black Buffalo	N	N	
<i>Minytrema melanops</i>	Spotted Sucker	N		T
<i>Moxostoma anisurum</i>	Silver Redhorse	N	N	
<i>Moxostoma breviceps</i>	Shorthead Redhorse	N	N	
<i>Moxostoma carinatum</i>	River Redhorse	N	N	
<i>Moxostoma duquesnei</i>	Black Redhorse	N	N	
<i>Moxostoma erythrurum</i>	Golden Redhorse	N	N	
Ictaluridae				
<i>Ameiurus catus</i>	White Catfish	I		
<i>Ameiurus melas</i>	Black Bullhead	N		E
<i>Ameiurus natalis</i>	Yellow Bullhead	N	N	
<i>Ameiurus nebulosus</i>	Brown Bullhead	N	N	
<i>Ictalurus furcatus</i>	Blue Catfish	N		
<i>Ictalurus punctatus</i>	Channel Catfish	N	N	
<i>Noturus eleutherus</i>	Mountain Madtom	N	N	E
<i>Noturus flavus</i>	Stonecat	N	N	
<i>Noturus gyrinus</i>	Tadpole Madtom	N	N	E
<i>Noturus miurus</i>	Brindled Madtom	N	N	T
<i>Noturus stigmosus</i>	Northern Madtom		N	E
<i>Pylodictus olivaris</i>	Flathead Catfish	N	N	
Percopsidae				
<i>Percopsis omyscomaycus</i>	Troutperch	N	N	
Fundulidae				
<i>Fundulus diaphanus</i>	Banded Killifish	N	N	
<i>Fundulus heteroclitus</i>	Mummichog	I		
<i>Fundulus notatus</i>	Blackstripe Topminnow	I		
Gasterosteidae				
<i>Culaea inconstans</i>	Brook Stickleback		N	C
Atherinopsidae				
<i>Labidesthes sicculus</i>	Brook Silverside	N	N	C
Moronidae				
<i>Morone americana</i>	White Perch		I	
<i>Morone chrysops</i>	White Bass	N	N	
<i>Morone chrysops x saxatilis</i>	Hybrid Striped Bass	I		
<i>Morone saxatilis</i>	Striped Bass	I		
Centrarchidae				
<i>Ambloplites rupestris</i>	Rockbass	N	N	
<i>Lepomis cyanellus</i>	Green Sunfish	N	N	
<i>Lepomis gibbosus</i>	Pumpkinseed	N	N	
<i>Lepomis gulosus</i>	Warmouth	N	N	E
<i>Lepomis humilis</i>	Orangespotted Sunfish	N		
<i>Lepomis macrochirus</i>	Bluegill	N	N	
<i>Lepomis megalotis</i>	Longear Sunfish	N	N	E
<i>Lepomis microlophus</i>	Redear Sunfish	N		

<i>Micropterus dolomieu</i>	Smallmouth Bass	N	N	
<i>Micropterus punctulatus</i>	Spotted Bass	N	N	
<i>Micropterus salmoides</i>	Largemouth Bass	N	N	
<i>Pomoxis annularis</i>	White Crappie	N	N	
<i>Pomoxis nigromaculatus</i>	Black Crappie	N	N	
Percidae				
<i>Ammocrypta pellucida</i>	Eastern Sand Darter	N	N	E
<i>Crystallaria asprella</i>	Crystal Darter	N		
<i>Etheostoma blennioides</i>	Greenside Darter	N	N	
<i>Etheostoma caeruleum</i>	Rainbow Darter	N	N	
<i>Etheostoma camurum</i>	Bluebreast Darter	N	N	T
<i>Etheostoma exile</i>	Iowa Darter		N	E
<i>Etheostoma flabellare</i>	Fantail Darter	N	N	
<i>Etheostoma maculatum</i>	Spotted Darter	N	N	T
<i>Etheostoma nigrum</i>	Johnny Darter	N	N	
<i>Etheostoma spectabile</i>	Orangethroat Darter	N		
<i>Etheostoma tippecanoe</i>	Tippecanoe Darter	N	N	T
<i>Etheostoma variatum</i>	Variegated Darter	N	N	
<i>Etheostoma zonale</i>	Banded Darter	N	N	
<i>Perca flavescens</i>	Yellow Perch	N	N	
<i>Percina caprodes</i>	Logperch	N	N	
<i>Percina copelandi</i>	Channel Darter	N	N	
<i>Percina evides</i>	Gilt Darter	N	N	T
<i>Percina macrocephala</i>	Longhead Darter	N	N	
<i>Percina maculata</i>	Blackside Darter	N	N	
<i>Percina sciera</i>	Dusky Darter	N		
<i>Percina shumardi</i>	River Darter	N		
<i>Sander canadense</i>	Sauger	N	N	
<i>Sander vitreus</i>	Walleye	N	N	
Scianidae				
<i>Aplodinotus grunniens</i>	Freshwater Drum	N	N	
Cottidae				
<i>Cottus bairdi</i>	Mottled Sculpin	N	N	

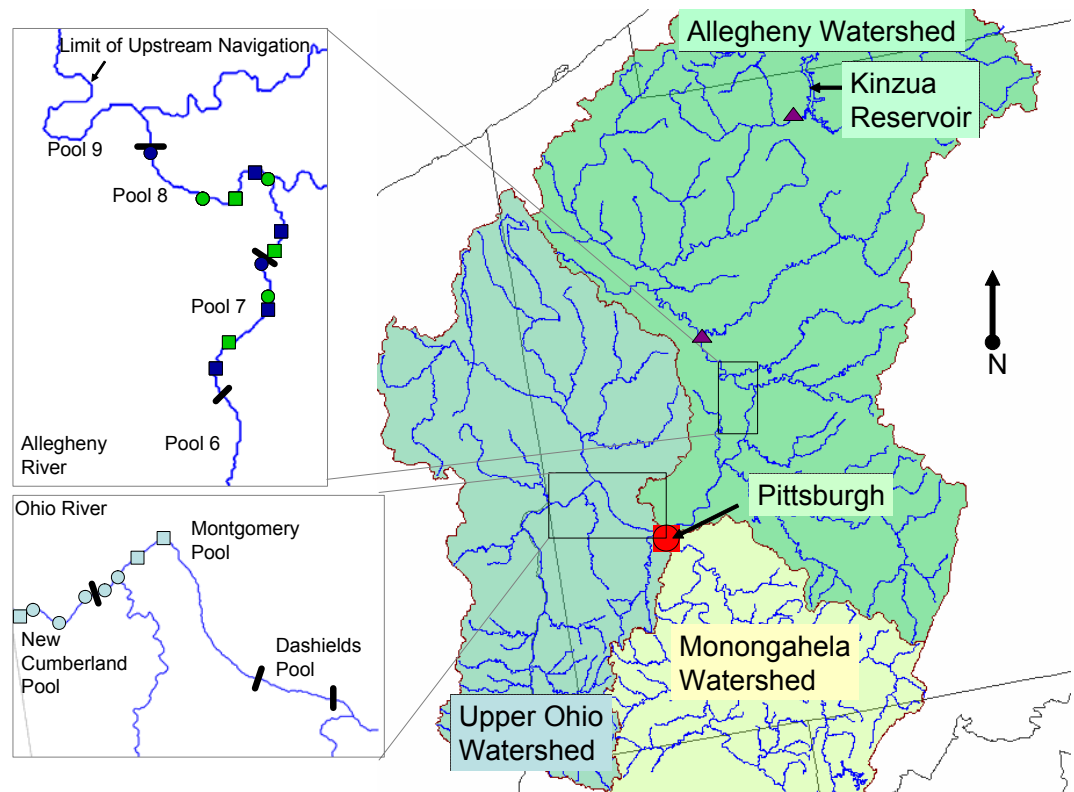


Figure 1.1: Map of Upper Ohio River, Allegheny River, and Monongahela River drainages in western Pennsylvania. Solid black bars indicate dams. Triangles (free-flowing), circles (undredged), and squares (dredged) represent sampling site locations while colours indicate sampling type as follows: light blue (electrofishing only), dark blue (trawling & electrofishing), green (stable isotope, electrofishing, & trawling), and purple (stable isotope only).

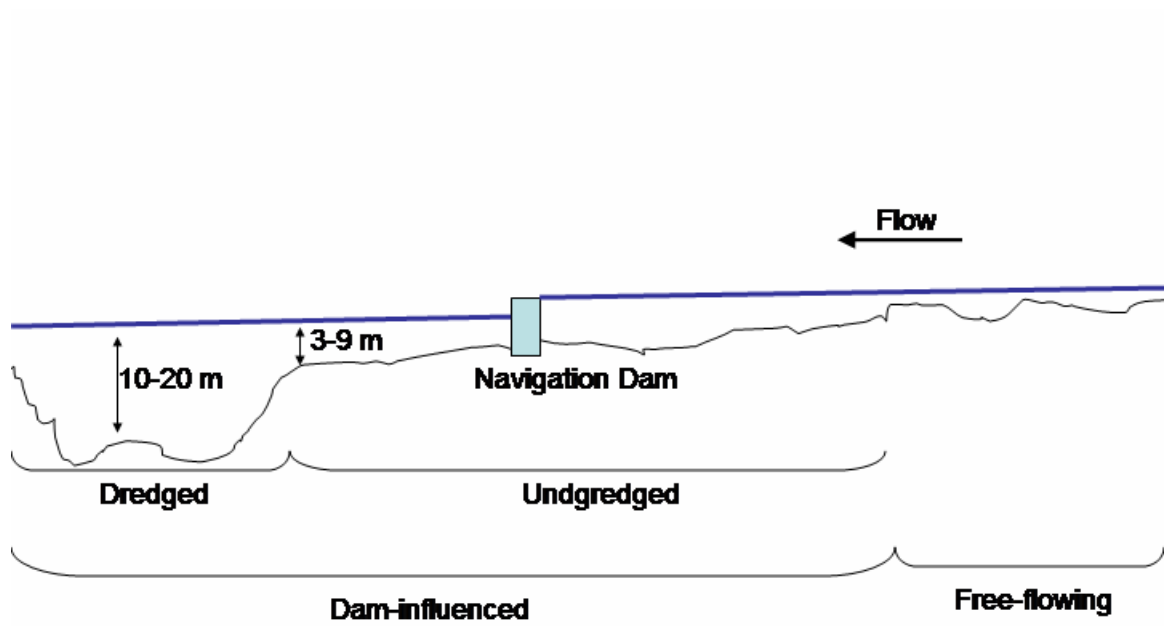


Figure 1.2. Diagrammatic representation of the impact of dams and dredging on river reaches.

Chapter 2

Extensions of the Known Ranges of *Percina shumardi* Girard and Three Species of *Etheostoma* (subgenus *Nothonotus*) in Pennsylvania

Freedman, J.A., T.D. Stecko, R.W. Criswell & J.R. Stauffer Jr. 2009. Extensions of the Known Ranges of *Percina shumardi* Girard and Three Species of *Etheostoma* (subgenus *Nothonotus*) in Pennsylvania. *Journal of the Pennsylvania Academy of Science*. 83: 42-44.

Introduction

Over the past several years while conducting mussel surveys, we have noted the abundance of many species of darters (Percidae: Etheostomatini) in the deep pools and runs of large rivers. These habitats are difficult to sample for small fishes; thus they have been underrepresented in ichthyological surveys. The development of the Missouri benthic trawl (Herzog et al. 2005) for sampling small benthic fishes has greatly improved the effectiveness of our sampling large riverine habitats; hence, our knowledge of the distribution and abundance of these species has increased. As a result of utilizing these sampling techniques, we extended the known ranges of the River Darter, *Percina shumardi* Girard, and three species of *Etheostoma* (subgenus *Nothonotus*) in Pennsylvania.

Methods and Materials

We sampled the Ohio River in Pennsylvania at regular 1.0 km intervals from its formation at the confluence of the Allegheny and Monongahela rivers in Pittsburgh to the Ohio and West Virginia border (Fig. 1) in August 2007. We sampled the tailwaters of the Montgomery

Dam (New Cumberland Pool) and the Dashields Dam (Montgomery Pool) in October 2007. Sampling was conducted using a Missouri benthic trawl according to the sampling protocols established by Herzog et al. (2005). Trawls were conducted in the central channel as well as near-shore, at depths ranging between 1.5 - 6.7 m. All fishes were identified in the field, with voucher specimens retained for laboratory verification.

Results and Discussion

We captured a total of 35 River Darters, *Percina shumardi*, (Fig. 2) from the Ohio River. We collected four individuals in the New Cumberland Pool of the Ohio River; two individuals each at two sites located approximately 7 km and 11 km upstream from the Ohio/West Virginia border respectively (PSU 4477, Fig. 1). Further targeted sampling revealed that their range within Pennsylvania extends at least 34 km upstream on the Ohio River to the Dashields Dam (PSU 4459, 4460, 4476).

The River Darter is distributed throughout the Mississippi River drainage, and is locally abundant in the Ohio River into West Virginia and Ohio, as well as being the most common darter collected from the Mississippi River (Kuehne and Barbour 1983, Page 1983). While River Darters have never been collected from Pennsylvania prior to this study, Cooper (1983) suggested that they may be a future migrant into Pennsylvania as water quality improved. Although River Darters have been thought to be invertebrate-generalist feeders (Trautman 1957, 1981, Page 1983), it has been determined that they may also specialize in feeding on snails, similar to other species of *Percina*, subgenus *Imostoma* (Haag and Warren Jr. 2006).

River Darter habitat consists primarily of large rivers with gravel/cobble/boulder substrates and with moderate to fast currents (Trautman 1957, Scott and Crossman 1973, Trautman 1981, Cooper 1983, Page 1983), with younger individuals inhabiting shallower water. Specimens have been collected, however, from areas which are too turbid for many other darter

species (Trautman 1957, Scott and Crossman 1973, Trautman 1981, Kuehne and Barbour 1983), and also from streams (Haag and Warren Jr. 2006); thus, these range extensions for *P. shumardi* within Pennsylvania may underestimate their true distribution within the state.

We collected three Bluebreast Darters, *Etheostoma caeruleum* (Cope), from Montgomery Dam tailwaters (New Cumberland Pool, PSU 4459). Seven Bluebreast Darters, five Spotted Darters, *Etheostoma maculatum* Kirtland, and one Tippecanoe Darter, *Etheostoma tippecanoe* Jordan and Evermann, were collected from the Dashields Dam tailwaters (Montgomery Pool, PSU 4476). These dams are located approximately 13 km and 34 km from the Ohio/West Virginia border, respectively (Figure 1).

These three species are presently classified as threatened within Pennsylvania by the (Commission 2007). The Tippecanoe Darter has heretofore been reported only from the Allegheny River system. The Bluebreast Darter and Spotted Darter were collected from the Allegheny and Mahoning rivers, but have been extirpated from the latter (Bean 1892, Cooper 1983). The closest records downstream of the state line for the Bluebreast Darter and Tippecanoe Darter are from the lower Muskingum River, but they probably occurred in the unimpounded Ohio River as well (Trautman 1981). The nearest downstream records of the Spotted Darter include the middle sections of the Elk River in West Virginia (Stauffer Jr. et al. 1995) and Muskingum and Scioto rivers in Ohio (Trautman 1981), but there are none from the mainstem Ohio River. Water quality in the Ohio River has been improving over the last 50 years, with marked improvement since the Clean Water Act was implemented in 1972, and is closely correlated with marked improvements in fish diversity and assemblages from 1957-2001 (Thomas et al., 2005). Our recent records, facilitated by the use of benthic trawls as a novel sampling gear, therefore most likely represent an expansion of the Allegheny River populations of all three species as a result of improved water quality.

Additional sampling is warranted to elucidate the full range of these species throughout the Ohio River drainage in Pennsylvania, including both the Allegheny and Monongahela rivers.

It is likely that further sampling using benthic trawls will yield more new species records for Pennsylvania and document additional range extensions.

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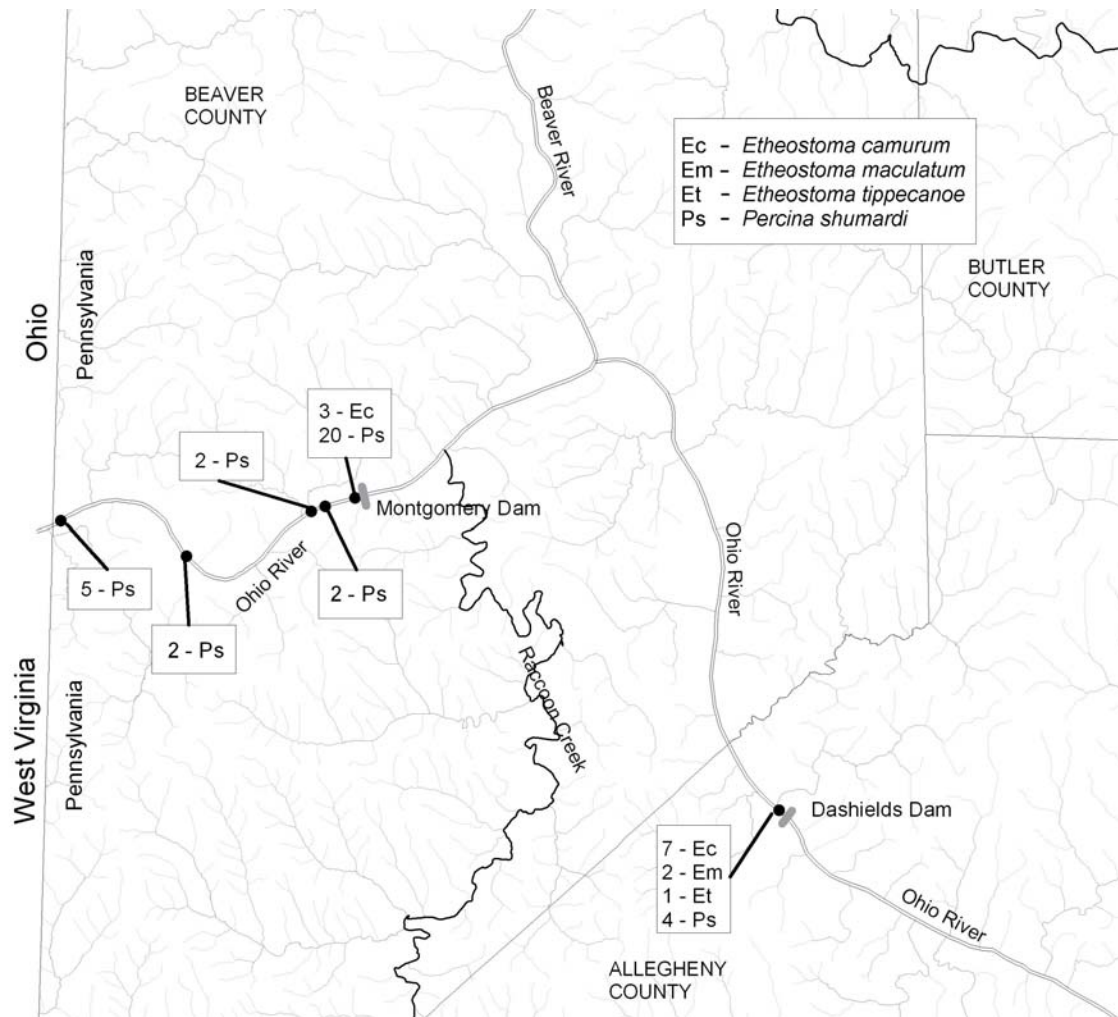


Figure 2.1: Map showing capture data for rare darter species caught during benthic trawl sampling of the Ohio River.



Figure 2.2: River Darter (*Percina shumardi*), New Cumberland Pool, Ohio River, Beaver County, PA . 7 October 2007 . Photo: R.W. Criswell.

Chapter 3

Development and efficacy of an electrified benthic trawl for sampling large-river fish assemblages

Freedman, J.A., T.D. Stecko, B.D. Lorson, & J.R. Stauffer Jr. 2009. Development and efficacy of an electrified benthic trawl for sampling riverine fishes. *North American Journal of Fisheries Management*. 29: 1001-1005.

Introduction

Sampling small benthic, lithophilic fishes in large rivers is challenging, because they are not vulnerable to nets (e.g., trap nets, gill nets) nor electrofishing gear when they inhabit deep water. Small fishes may be captured using beach seines, minnow or Windermere traps, or electrofishing, but these methods are most effective close to shore (Murphy and Willis 1996). Together, these methods result in samples biased against small-bodied benthic and deeper-water fish species. Since presence/absence and abundance data are often used to make inferences about species-specific habitat use, incorrect conclusions could be made when using data from survey methods that have intrinsic size or species biases.

The Missouri-trawl (Herzog et al. 2005) was designed to remedy this situation by securing a fine-mesh net to the exterior of a benthic trawl. The Missouri-trawl has proven effective in sampling these small benthic fishes in rivers throughout North America, thereby extending known distribution and abundance estimates for many species (Stewart et al. 2005, Argent et al. 2007, Koryak et al. 2008, Freedman et al. *in press*) and supplementing other gear types (Argent et al. 2007, Koryak et al. 2008). Our observations by SCUBA of the Missouri-trawl in action, however, has revealed avoidance of the trawls by some species, especially in gravel-cobble substrates where fish could easily avoid the trawl

by seeking refuge in the interstitial spaces. During our trawling of the Allegheny and Ohio rivers of Pennsylvania, we have observed that there seems to be a bias towards juveniles of many darter and minnow species, with larger individuals and adults seldom being captured. Some species also seem to be abundant during SCUBA surveys, but may be rare or absent in the trawls. In short, it seemed that while the Missouri-trawl is relatively effective in capturing these small-bodied fishes, improvements are possible.

Electrical currents have been used successfully to capture fishes for several decades (Reynolds 1996). While electrofishing gear, including electrified seines, has been successfully used to capture fishes in wadeable streams (Bayley et al. 1989, Peterson and Rabeni 2001), its utility has been limited due to its inability to sample fishes from deeper water (depth greater than 1.2 m). Exceptions include the capture of sea lamprey, *Petromyzon marinus*, ammocoetes by deep-water electrofishing (McLain and Dahl 1968, Bergstedt and Genovese 1994, Moser et al. 2007). While most of these deep-water methods have used a combination of electrical currents and suction to capture ammocoetes, McLain and Dahl (1968) modified a sled-mounted benthic trawl by electrifying it and pulling it along the lake bottom. While it was considered to be effective in capturing ammocoetes, it also had a high by-catch rate 23 species, representing 19 genera. This technology was seldom used through the intervening years; however, Peterson (1996) used an electrified benthic trawl for sampling fishes in non-wadeable reaches of Ozark streams, where it proved effective.

Since electrical currents have the dual abilities to attract and incapacitate fishes, we electrified a Missouri-trawl. We hypothesized that an electrified trawl would be more efficient than the non-electrified trawl, capturing both greater numbers of species and higher numbers of fishes, as well as larger individuals. We tested the trawls in the Ohio, Allegheny, and Monongahela rivers in Pennsylvania. The substrate of the Allegheny River is primarily composed of glacial alluvial gravel and rocks while Monongahela River substrate is primarily sand and mud. The Ohio River forms at the confluence of the Allegheny and Monongahela rivers in Pittsburgh, and has a substrate intermediate between these tributaries. This allowed us to test the trawls in a variety of riverine habitats.

Methods

We modified a Missouri-trawl consisting of a 19.05 mm stretch inner mesh bag and a 4.76 mm stretch outer mesh bag, with a 2.44 m headrope (Herzog et al. 2005) from Innovative Net Systems, Louisiana. The trawl was modified with 15 cm stretch mesh across the opening of the net functioning as a rock-exclusion device or rock-skirt. To electrify the trawl, we added five, 30 cm-long wire “ticklers” (called cathodes in DC mode and electrodes in AC mode) to each of the tow ropes above the otter boards, and a wire running along the headrope (anode in DC mode and electrode in AC mode). Electrodes were connected to a Smith-Root VI-A electrofishing controller unit connected to a Honda 3500 W generator. Trawls were conducted using a 5.3 m jonboat powered by a 25-HP outboard motor (Figure 1).

We sampled a total of 40 sites in the Allegheny (28 sites), Ohio (4), and Monongahela (8) rivers in Pennsylvania, using paired trials to compare the trawls. Sampling sites for these comparisons were selected randomly from sites which we were sampling as part of a larger study. At each site, we randomly selected either the PSU- or the Missouri-trawl to be tested first, and randomly selected the location within the river – either bank or mid-channel. We then conducted a two minute trawl with each method at the same speed in close parallel transects.

We used the same trawl for all comparisons to eliminate potential bias due to trawl differences - it was electrified for the PSU-trawl replicates, and used without electricity for the Missouri-trawls. These trawls were conducted 3 to 8 m apart so as to sample the same or similar habitats while minimizing any effects that the previous trawl may have had in attracting or repelling fishes along its transect. In addition, trawls were conducted 30 to 60 minutes apart to minimize the potential effects of disturbance on the fishes. Trawls were conducted with, and slightly faster than, the current. Depths ranged from 2 to 10 m, with mean depths of 4.37 m for PSU-trawls and 4.53 m for Missouri-trawls. Secchi depths ranged from 60 to 160 cm. Fishes were identified to species in the field, photo vouchers were recorded, and

representative fishes were placed in permanent storage in the Pennsylvania State University Fish Museum. Most shiners (*Notropis* spp.) were too small to identify reliably; hence, all were conservatively grouped together as “Shiner species.”

We used a paired-sample Wilcoxon signed rank test with continuity correction to test whether the PSU-trawl captured more fishes and more species than the Missouri-trawl. Statistical analyses were performed using R 2.5.1 (R Development Core Team 2008).

Results and Discussion

In 40 paired trials, we caught significantly more fishes using the PSU-trawl than the Missouri-trawl (Wilcoxon, $p = 0.0001628$; Table 1; Figure 2). The PSU-trawl caught more fishes in 80% of trials, compared to 12.5% for the Missouri-trawl. We caught significantly more species with the PSU-trawl than with the Missouri-trawl (Wilcoxon, $p = 0.0002281$; Table 1; Figure 2). With the PSU-trawl, we caught more species in 62.5% of trials and also caught eight species not sampled with the Missouri-trawl, while the Missouri-trawl was more successful in 12.5% of trials and only captured one species not collected with the electrified trawl (Table 1). While the Missouri-trawl failed to catch any fishes in 30% of trials, the PSU-trawl captured no fish in only 2.5% of trawls. These trends held across all three rivers, as we caught more individuals and species with the PSU-trawl in each river as well as cumulatively. The PSU trawl was tested first in 53% of trials, while on average the first trawl to be tested in each trial caught more fishes 46% of the time, suggesting no influence of trawl order on catch rate.

While we did not measure every fish that we caught, we did classify all fishes measuring >20 cm TL as “large”. Despite the rock-skirt acting as a potential and indeed probable barrier to these large fishes entering the trawl, we caught a total of seven such “large” fishes in all trawls: six in the PSU-trawl and only one in the Missouri-trawl. We have observed that the rock-skirt is very effective in reducing snags and wear-and-tear induced by dragging rocks in the trawl and is therefore recommended

for trawling rocky substrates. Herzog et al. (2005) regularly captured larger-bodied fishes in the Mississippi River using the Missouri-trawl. Their relative success in capturing larger species was likely due, in addition to the absence of a rock-skirt, to a combination of higher turbidity and softer substrate in the Mississippi River than at our study sites. Secchi depths in the Mississippi ranged from 2 - 61 cm and averaged 28 cm, while in our study Secchi depths ranged from 60 to 160 cm, and averaged approximately 100 cm. Higher turbidity may make trawls less noticeable to fishes either by vision or sound. A softer substrate than the rock comprising the majority of the substrate in the Allegheny and Ohio rivers may reduce avoidance by hiding in interstitial spaces between rocks. In the Monongahela River, however, which features a softer substrate than the Allegheny or Ohio rivers, we caught more individuals in six of the eight comparisons performed, and only caught more species with the Missouri-trawl in one comparison. However, since the sampling-area footprint of the PSU-trawl is intrinsically limited by the width of the trawl, this is likely the limiting factor in capturing larger fishes, rather than habitat-specific differences or the rock-skirt.

Benthic trawls have been modified with anode-cathode electrical arrays for sampling deep lakes (McLain and Dahl 1968) and non-wadeable stream reaches (Peterson 1996). McLain and Dahl's (1968) sled-based trawl was effective at capturing a variety of benthic fishes as well as the targeted sea lamprey ammocoetes. Such a sled, however, may prove unwieldy and difficult to bring into the boat on repeated trawls. Peterson's (1996) electrified trawl was smaller than the Missouri-trawls used in our study (1 m across compared to 2.44 m) and therefore may have been less efficient in sampling large rivers. Herzog et al. (2005) used Missouri-trawls with headropes of 4.87 m which have proven very successful in sampling the Mississippi River. While we used the smaller trawl in large part to minimize snags in the rocky substrates of the Allegheny and Ohio rivers, we expect it is possible to electrify the larger trawl and gain similar results. The electricity did not appear to affect mortality of fishes or bycatch (e.g., turtles, amphibians, crayfishes).

In conclusion, we caught more than twice as many fishes and eight more species using the PSU-trawl than with the Missouri-trawl, as well as more large individuals. Further testing in different

watersheds and water conditions (e.g., depth, turbidity, conductivity, temperature, and substrate) will likely support our results. Further research will determine the effectiveness of the PSU-trawl in capturing specific species, sizes, and life-history stages of fishes in comparison with other sampling methods, and attempt to determine relative susceptibility between otherwise similar species. The rock-skirt is effective in preventing snags and excluding rocks from the trawl, but it is important to examine to what degree it may be excluding larger fishes. Further testing should also compare AC and DC currents, and seek to determine ideal electrical settings for these trawls. There are inherent risks associated with any sampling conducted using electricity, and to minimize potential hazards we therefore recommend observing the safety guidelines in Reynolds (1996).

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Table 3.1: Total abundance of fishes caught in 40 paired comparisons of the PSU-trawl and the Missouri-trawl, and the mean and median catch per trawl, in the Ohio, Allegheny, and Monongahela rivers, Pennsylvania

Family and Common		Trawl Type	
Name	Species	Missouri	PSU
Catostomidae			
Northern hog sucker	<i>Hypentelium nigricans</i>	1	0
Smallmouth buffalo	<i>Ictiobus bubalus</i>	0	1
Golden redhorse	<i>Moxostoma erythrurum</i>	1	1
Smallmouth redhorse	<i>Moxostoma breviceps</i>	0	2
Cyprinidae			
Streamline chub	<i>Erimystax dissimilis</i>	44	11
Shiner species	<i>Notropis spp.</i>	20	32
Bluntnose minnow	<i>Pimephales notatus</i>	4	2
Ictaluridae			
Channel catfish	<i>Ictalurus punctatus</i>	3	27
Centrarchidae			
Rock bass	<i>Ambloplites rupestris</i>	0	1
Smallmouth bass	<i>Micropterus dolomieu</i>	1	3
Percidae			
Greenside darter	<i>Etheostoma blennioides</i>	9	33
Rainbow darter	<i>Etheostoma caeruleum</i>	1	17
Bluebreast darter	<i>Etheostoma camurum</i>	11	81
Fantail darter	<i>Etheostoma flabellare</i>	0	6

Spotted darter	<i>Etheostoma maculatum</i>	0	6
Johnny darter	<i>Etheostoma nigrum</i>	1	5
Tippecanoe darter	<i>Etheostoma tippecanoe</i>	6	31
Banded darter	<i>Etheostoma zonale</i>	1	1
Logperch	<i>Percina caprodes</i>	21	57
Channel darter	<i>Percina copelandi</i>	283	601
Gilt darter	<i>Percina evides</i>	17	17
Longhead darter	<i>Percina macrocephala</i>	11	11
River darter	<i>Percina shumardi</i>	10	16
Sauger	<i>Sander canadense</i>	0	2
Walleye	<i>Sander vitreus</i>	1	1
Sciaenidae			
Freshwater drum	<i>Aplodinotus grunniens</i>	0	4
Cottidae			
Mottled sculpin	<i>Cottus bairdi</i>	0	9
Number of Individuals		448	988
Mean (\pm Standard deviation)		11.2 (23.0)	24.7 (35.4)
Median (\pm Standard deviation)		2.5 (23.0)	7.5 (35.4)
Number of Species		19	26
Mean (\pm Standard deviation)		1.9 (1.9)	3.2 (2.4)
Median (\pm Standard deviation)		1.0 (1.9)	2.0 (2.4)

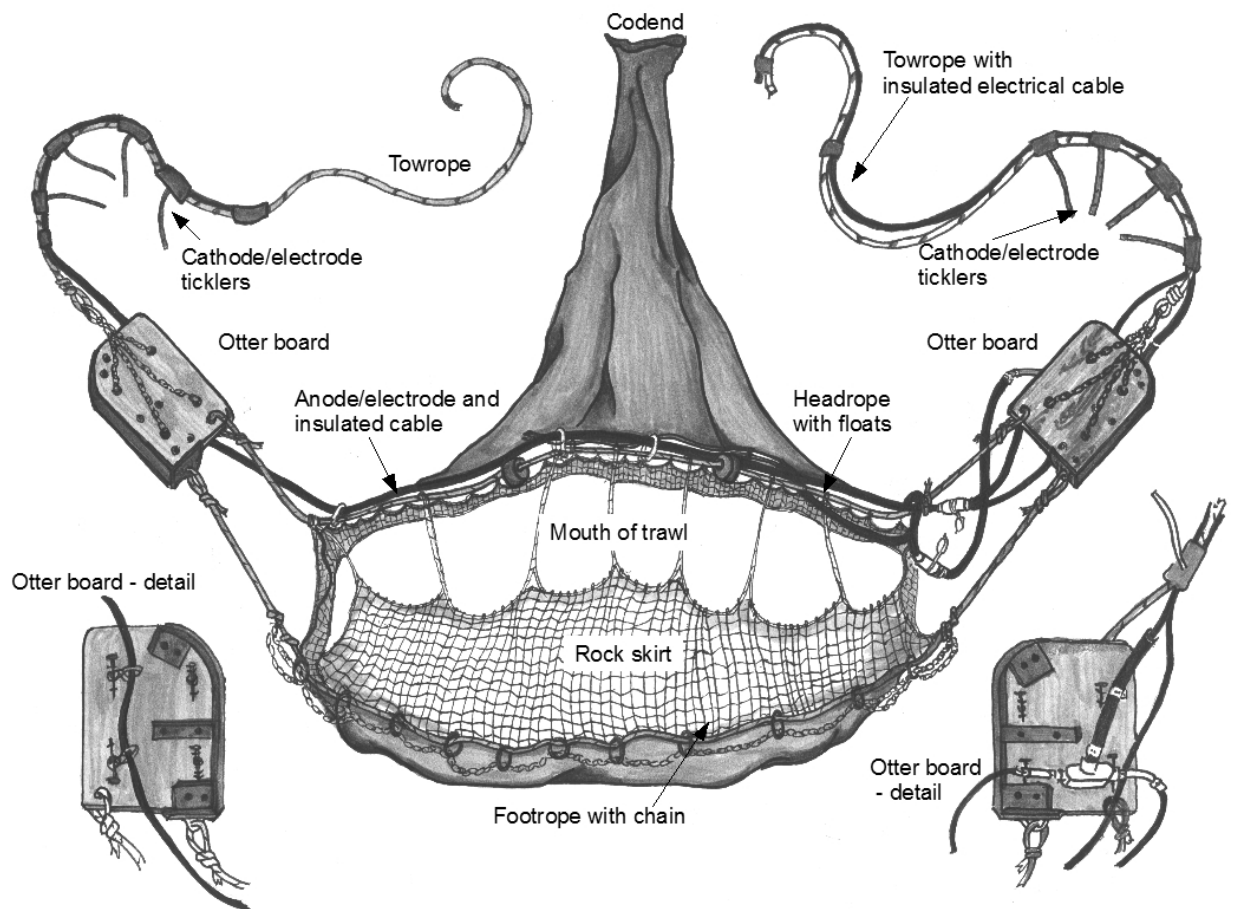


Figure 3.1: Diagram of a PSU-trawl, illustrating the modifications for electrifying the trawl. The insulated electrical cable attached to the towrope contains separate leads for both the cathodes and the anode, which in turn are attached to an electrofishing controller unit using standard amphenol connectors (illustration is not to scale).

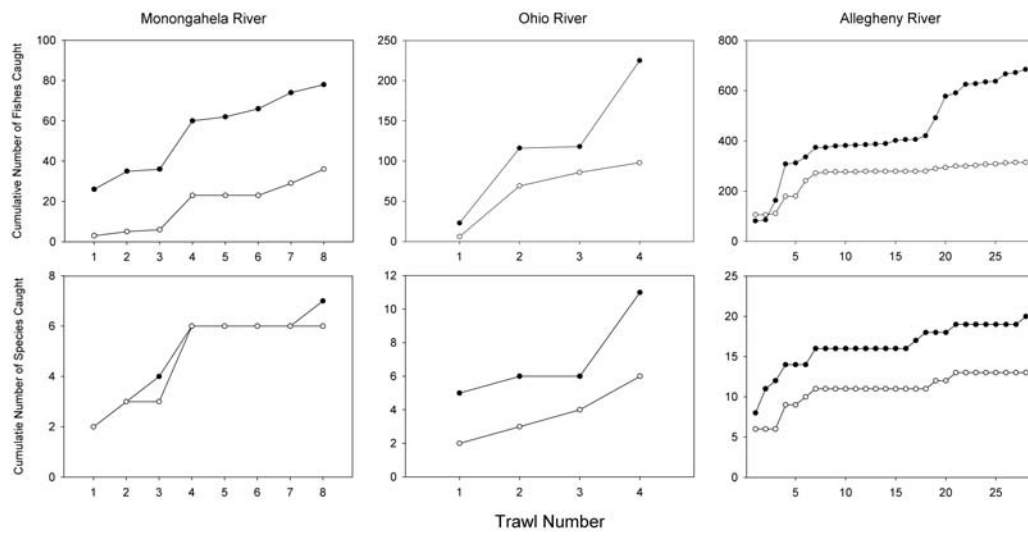


Figure 3.2: Cumulative number of fishes (upper row) and number of species (lower row) caught using the PSU-trawl (solid) and Missouri-trawl (open) in paired comparisons in each of the Monongahela, Ohio, and Allegheny rivers, Pennsylvania.

Chapter 4

Effects of Gravel Dredging on Fish Populations and Assemblages

Introduction

Understanding the effects of human activities on aquatic systems can be challenging (Munkittrick et al. 2000). Dredging or substrate removal is a relatively common anthropogenic disturbance in freshwater systems (Kanehl and Lyons 1992, Meador and Layher 1998), and is often used to provide a minimum depth for commercial shipping or recreational boating. In heavily polluted systems, dredging may be used to remove contaminated substrate (Reimold and Durant 1974, Rice and White 1987). Commercial dredging to either access material in the substrate (e.g., gold) or for the substrate itself (sand, gravel) is also common in many rivers and streams (Harvey 1986, Berkman and Rabeni 1987, Hall 1988, Kanehl and Lyons 1992, Meador and Layher 1998, Davis et al. 2000, Milner and Piorkowski 2004). In-stream removal of substrate can affect the physical characteristics of the river as the channel is frequently modified, creating relatively homogenous, deep reaches (Berkman and Rabeni 1987, Kanehl and Lyons 1992, Petit et al. 1996, Kondolf 1997, Wyzga 2001, Gob et al. 2005). These deep reaches then alter water flow and velocity, and can accumulate sediment and organic detritus, thus disrupting nutrient dynamics in the system (Brown et al. 1998, Rinaldi et al. 2005). Headcutting (the erosion of the upstream end of the dredged area) and subsequent bank erosion can also result, further homogenizing the aquatic habitat with a further loss of littoral and shallow habitats (Kanehl and Lyons 1992, Rinaldi et al. 2005). Combined, the removal of coarse gravel and cobble and the accumulation of fine sediment and detritus can greatly alter habitat characteristics

required by aquatic species (Berkman and Rabeni 1987, Kanehl and Lyons 1992, Kondolf and Wolman 1993, Kondolf 1997, 2000, Milner and Piorkowski 2004, Rinaldi et al. 2005).

As a result, riverine gravel dredging can have lethal, sublethal, or behavioural effects on fishes that inhabit dredged sites (Rees 1959, Veshchev 1982, Harvey 1986, Newcombe and MacDonald 1991, Larimore and Bayley 1996, Wilcock et al. 1996b, Kondolf 1997, Harvey and Lisle 1998, Harvey and Lisle 1999). In addition to direct effects on fishes resulting from the dredging, substrate habitat may be altered as gravel is dredged, coarse woody debris and other structure may be removed, and macrophyte beds may be destroyed. Suspended sediments may affect fishes downstream by increasing turbidity and reducing visibility; fine sediments may settle into the substrate and smother sensitive fish, fish eggs, and benthic invertebrates downstream from the dredging site. A review of the literature showed that salmonid reactions to suspended sediments ranged from simple avoidance and other behavioural responses at lower suspended sediment concentrations and episode durations to sublethal and lethal (up to 100% mortality in eggs and juveniles) effects at higher concentrations and durations (Newcombe and MacDonald 1991). Changes in turbidity thus alter species composition, as species requiring high visibility will suffer while tolerant species will become dominant in the community, and may cause behavioural changes in species that remain.

Once dredged, it is highly unlikely that a site will return to its previous state for decades (Irizarry 1969). Macroinvertebrate assemblages in dredged streams were significantly different from reference streams (lower abundance, biomass, and community evenness), even >50 years later (Milner and Piorkowski 2004). Restoration of gravel bars used by salmonids as spawning substrate has benefits to macroinvertebrate communities, with restored sites equalling and even surpassing unenhanced sites within weeks (Merz and Ochikubo Chan 2005), although it should be noted that this study dealt with habitat augmentation rather than removal. Fish community response to sand dredging in the Kansas River showed higher fish diversity at sites that had been dredged 26 years earlier than at undredged sites, although most of this diversity was due to an

increased prevalence of non-native and lentic species at the disturbed sites, while native lotic species declined (Paukert et al. 2008). Fish community compositions in the undredged (control) sites were thus more similar over time than were the dredged sites.

To assess the effects of gravel dredging on fish assemblages, I used electrofishing to sample large-bodied fishes and electrified benthic trawling to sample small benthic fishes. I predicted that dredging would have an adverse effect on fish populations and diversity, with fewer fishes living in deep areas. Furthermore, due to an overall loss of suitable habitat, I predicted that diversity would also be lower in shallower areas at dredged sites than at similar depths in undredged sites. Because larger fishes may be better able to avoid dredging activities and to thrive in more variable habitats, I hypothesized that small benthic fishes would be more negatively impacted by past dredging operations than would larger fishes. Specifically, small species in lithophilic or “rock-loving” reproductive guilds should experience the strongest declines at dredged sites relative to undredged sites. Lithophilic species include brood hiders, which are defined as those species that deposit eggs in gravel depressions or the interstitial spaces among rocks, and substrate choosers that guard eggs that are buried in the gravel (Simon 1998).

Methods

Study Area

The Allegheny River flows 523 km from its headwaters in Pennsylvania, into New York State, before flowing in a generally southerly direction to Pittsburgh where it forms the Ohio River at the confluence with the Monongahela River. Glacial alluvial gravel and rocks comprise the dominant substrate in the Allegheny River, and commercial gravel dredging operations operate in seven of the nine navigation pools that comprise the lower 113 km of the river. The

Ohio River flows 1,579 km from Pittsburgh until it joins the Mississippi River at Cairo, IL. Like the Allegheny River, the Ohio River's substrate is largely comprised of glacial alluvial gravel and rocks, although with a greater proportion of fine sediments from the Monongahela River. The 64 km of the Ohio River in Pennsylvania is comprised of four navigation pools and has historically been subjected to far more anthropogenic stressors than has the Allegheny River (Pearson and Krumholz 1984).

Sampling

I sampled 19 sites using boat electrofishing gear during the nights of June 7-11, 2009, on the Allegheny and Ohio rivers (Figure 1.1). Eleven sites were located in Pools 7 and 8 of the Allegheny River, while 8 were located in the New Cumberland and Montgomery Pools of the Ohio River. Crews consisted of 3-4 persons, and electrofishing time ranged from 14 to 40 minutes. Data were converted to catch-per-unit-effort (CPUE), with a unit of effort defined as one hour of sampling time.

I conducted ten, two-minute electrified benthic trawls (Freedman et al. 2009b) at each of nine sites in Pools 7 and 8 of the Allegheny River from July 13 to 15, 2009 (Figure 1.1). Two trawls were pulled along each bank, two in the center channel, and two each to the right and left of the mid-channel. Two sites were located immediately below dams and had no history of gravel dredging; three sites were located away from dams and had not been dredged; and four sites were both away from dams and had been dredged. Where possible, all fishes were identified to species in the field; representative samples were retained as voucher specimens, and photo vouchers were taken. Smaller species and juveniles were retained for laboratory examination and verification.

Data Analysis

Study sites were compared with non-metric multidimensional scaling (nMDS), using Bray-Curtis dissimilarity to assess site relationships, with dredging history and presence of dams as factors. In nMDS ordination, samples that are more dissimilar to one another are further apart, while those with similar communities are placed closely together (Legendre and Legendre 1998). Individual trawl samples were also analyzed using nMDS with depth, dredging history, and location within the river (bank, near channel, and mid channel) as factors using Primer 5 software. Species richness, total catch, and Brillouin's Diversity Index were compared among trawl samples, with maximum depth as a factor. To assess whether the reproductive guild is a factor in determining which fish are more susceptible to dredging, I used the reproductive guilds established in (Balon 1975, 1978, 1981, Simon 1998) Table 4.1). Because I hypothesized that small fishes that breed in and around gravel and rocks are most susceptible to gravel dredging, I calculated the percent of the catch in each trawl that was composed of lithophilic brood hiders and substrate choosers. I used regression analysis to analyze differences in species richness, total catch, Brillouin Index, and percent lithophilic substrate choosers and brood hiders between dredged and undredged sites at a significance level of $p < 0.05$ using the MASS package for R.

2.8.1. The relative proportion of fishes using different reproductive guilds at different depths and between dredged and undredged sites was analyzed using principal components analysis (PCA) using Primer 5. Graphs were made in Primer 5 or SigmaPlot 8.0.

Results

Electrofishing

I caught 779 fishes, of which 322 (41.3%) were small minnows (Cyprinidae); 174 (22.3%) were sunfishes or bass (Centrarchidae); 147 (18.9%) were suckers (Catostomidae); 50 (6.4%) were darters, walleye, and sauger (Percidae); and 21 (2.7%) were catfishes (Ictaluridae). *Notropis atherinoides* (Emerald Shiners) were the most abundant species in our sampling, with 261 individuals (33.5% of the total catch). The following Pennsylvania-listed Endangered (E), Threatened (T), and Candidate (C) species were caught during our electrofishing sampling: *Macrhybopsis storeriana* (E), *Hiodon tergisus* (T), *Ictiobus bubalus* (T), *Ichthyomyzon bdellium* (C), *Lepisosteus osseus* (C), and *Moxostoma carinatum* (C). There was clear differentiation in fish assemblages between the Allegheny and Ohio rivers, but not between navigation pools within rivers (Figure 4.1A). There were no detectable differences in large-fish assemblages correlated with dredging history (Figure 4.1B).

Comprehensive Trawling

In 90 trawls I captured 5942 fishes comprising at least 32 species. In all three comparisons, dredged sites had the lowest catch and number of species per site, and the lowest catch per trawl, while below-dam sites had the highest number of species and undredged sites have the most species per trawl and the highest overall catches (Figure 4.2). Fish assemblages caught using benthic trawls grouped together according to dredging history when analyzed using MDS. There was no such apparent relationship when these data were examined using depth as a factor rather than dredging history (Figure 4.3).

I caught the most fishes at undredged sites while dam sites generally had the most species; the lowest catches and number of species were at dredged sites (Figure 4.2). Non-metric multidimensional scaling revealed clustering of fish assemblages by dredging history (Figure 4.3). Comparing species and total catch by the trawl location revealed differences among locations. Dredged sites had fewer species at each location than undredged and near-dam sites, with a trend of declining species richness from bank (6.44) to near channel (3.31) to mid channel (2.88) locations. Undredged and near-dam sites had similar trends, with species richness declining from 9.25 to 8.38 to 7.00 at near-dam sites and from 9.42 to 9.75 to 8.17 at undredged sites (Figure 4.4). Mean catch-per-trawl declined from bank to near channel to mid channel locations at both near-dam (66.13 to 55.13 to 44.50 fishes) and dredged (87.06 to 24.81 to 11.63 fishes) sites. At undredged sites the highest mean catches were at near channel locations (107.67) while bank and mid channel catches were similar at 90.25 and 89.33, respectively (Figure 4.4). Dredged sites thus had the fewest species-per-trawl at all locations, and the lowest mean catches at both near channel and mid channel sites. Undredged and near-dam sites did not have strong trends across locations, while dredged sites trended towards fewer species and lower catches in channel locations relative to the bank locations.

Comparison of benthic trawl data by depth revealed negative relationships among total catch (total $R^2 = 0.22$; undredged $R^2 = 0.059$, dredged, $R^2 = 0.25$), number of species (total $R^2 = 0.40$, undredged: $R^2 = 0.15$; dredged $R^2 = 0.32$), and Brillouin Index (total $R^2 = 0.4047$; undredged $R^2 = 0.16$; dredged $R^2 = 0.27$) with depth (Figure 4.5). Lithophilic brood hidiers and substrate choosers also had a negative correlation with depth (total $R^2 = 0.15$; undredged $R^2 = 0.12$; dredged $R^2 = 0.07$) (Figure 4.6). Regression analysis showed significant main effects for depth and dredged status in number of species, Brillouin Index, and percent lithophils, but not for total catch (Table 4.3). There was a significant interaction between depth and dredged status for percent lithophilic species, but not for the other variables (Table 4.3). PCA showed a bimodal distribution for undredged trawls along PC1, correlated with brood-hiding lithophils and

substrate-choosing phytophils, or with most dredged trawls and open-substrate lithopelagophils and phytolithophils. Trawl catches at dredged sites were generally more correlated with open-substrate lithophils, and trawls at undredged sites with substrate-choosing lithophils and open-substrate phytolithophils (Table 4.2, Figure 4.7).

Discussion

There was an overall decline in fish abundance, species richness, and diversity among smaller fishes at dredged sites. There are several potential reasons for this, including direct effects from gravel dredging, decreased food availability or foraging efficiency, lack of suitable spawning habitat, and direct effects of sedimentation on fishes. Depth in the Allegheny River is maintained at a minimum of 3 to 4 m in the navigation channels, and in undredged sites seldom exceeds 6 m (pers. obs.). Dredged sites, however, may approach 20 m, and frequently exceed 10 m in depth. These dredged “holes” accumulate sediment and detritus (Pers. Obs.), rendering them inhospitable to lithophilic species. While these rivers are often turbid (secchi depth up to 167 cm in the Allegheny River), light penetration is reduced to almost zero by 10 m, so that primary productivity is limited and turbidity is such that visual predators are unable to forage effectively.

Shallower trawls at dredged sites (<8 m) had lower abundance, species richness, and diversity than equivalent depths at undredged sites. This difference cannot be assigned to increased sedimentation, because most of these trawls were conducted along the banks and should not be any different from bank sites at undredged sites. This suggests instead that there must be some other ecological process affecting this system. Assuming that the bank sites at dredged and undredged sites contain similar habitats, lower diversity may best be explained by changes in water flow and subsequent effects on nutrient dynamics and sediment flow as it is channelled into

the center of the river away from the banks. The overall loss of shallow benthic habitat may reduce populations to unsustainable numbers and result in a sink-environment for the overall metapopulation of the species. Piscivorous fishes may also exert some top-down control on smaller fishes whose population is also limited by a reduction in prey.

There was a sharp decline in the proportion of lithophilic species in both deeper water dredged sites (Figures 4.6 and 4.7). Sedimentation can have a range of effects on fishes. Sedimentation has detrimental effects on the survival of fish eggs and larvae in coarse gravel (Cordone and Kelly 1961, Newcombe and MacDonald 1991, Kondolf 2000). While such studies have traditionally focused on economically important game fishes such as salmonids, other species with similar reproductive habits would be expected to have similar responses. Along with salmonids, several darter species are classified as lithophilic brood-hiders (Simon 1998), and lithophilic substrate choosers would be expected to have similar negative responses to sedimentation. Decreases in lithophilic breeders was also found in a study of the effects of siltation on stream fishes in Missouri, which also noted an increase in fish assemblage homogeneity among riffle, run, and pool habitats (Berkman and Rabeni 1987). This was due primarily to a loss in riffle-dwelling species, which would be expected to be most susceptible to sedimentation due to their preference for clean, flowing water. Rivier and Segulier (1985) showed that there were three stages of changes in fish assemblages due to stream dredging: 1) reduction in lotic species, and an increase in lentic species; 2) reduction in lithophilic lentic species; 3) decline in overall diversity, with a fish assemblage dominated by eurytopic generalist, silt-tolerant, and deeper-water species.

There was no detectable difference in large-fish assemblages between dredged and undredged sites based on electrofishing data. Large benthivores that can filter invertebrates out of detritus, or consume the detritus itself (such as suckers and carp), may be less affected by turbidity than invertivores such as darters that rely on ambush or active hunting to acquire prey – strategies that would be detrimentally affected by high turbidity (Rivier and Segulier 1985).

(Forshage and Carter 1973, Kanehl and Lyons 1992) found that gravel dredging was associated with the reduction or elimination of minnow and darter species, and an increase in some sucker species. Many sucker (Catostomidae) species exhibit a preference for spawning in gravel, but are known for sometimes long-migrations to natal streams (Doherty 2004), and in the Ohio and Allegheny rivers they may be spawning below dams. Smaller species such as darters are unlikely to make such migrations and, as such, would be more susceptible to the effects of sedimentation in a localized environment.

Gravel dredging and mining can have long-term consequences on fish habitat. In a study of gravel mining in Spain, (Rovira et al. 2005) found that between 1956 and 1987 gravel was mined at 14 times the rate of replenishment. This affected not only the river dynamics, but also the groundwater system, and by the later 1990s the sedimentation rate was still higher than before and erosion of the riverbed continued. They calculated that, at the current rate of deposition, it would take up to 420 years for the river to recover to the pre-extraction bed-level. Since riverbed incision was only on the order of 2 m, compared to the 10+ m in the Allegheny and Ohio rivers, it would likely take much longer for these rivers to recover, particularly with the presence of dams interfering with deposition (Kondolf 1997). This is consistent with the findings of (Rinaldi et al. 2005) who found that the effects of gravel mining are especially difficult to reverse when the rate of gravel extraction greatly exceeds the rate of replenishment, and is compounded by other human activities reducing sediment delivery. Rinaldi et al. (2005) concluded by recommending that instream mining should be prohibited except in rivers with exceptionally high rates of replenishment.

Conclusions and Suggestions for Future Research

While in the short term, active gravel dredging can cause sedimentation rates to increase, the longer term consequences can be significant. By increasing the depth of the channel by two to four times its original depth, fine sedimentation rates will increase in these dredged holes, thus diminishing habitat quality for lithophilic species. Even as dredged areas are replenished, due to the dams this new substrate will be dominated by fine sediments which will smother any gravel. It seems unlikely that these dredged areas will naturally replenish to create suitable habitat for lithophilic species in anything short of a geological time-scale. Head-cutting and erosion of the sides of dredged holes and the bank may help to replenish the holes (Davis et al. 2000), but only at the cost of shallow benthic habitat in the surrounding areas, and to no tangible benefit as the gravel will be buried under fine sediments. Most damage to fish populations likely occurs as a result of indirect effects such as the loss of suitable spawning habitat, rather than to direct effects on adult fishes (Kanehl and Lyons 1992). Fish will either avoid these areas or, if they do spawn, their eggs and larvae will have low survivorship due to sedimentation. (Irizarry 1969) found that areas on the Salmon River in Idaho, dredged 30 years earlier, produced 97% less biomass of trout and whitefish than undredged areas.

Future studies could incorporate a before-after-control-impact study design to track changes in fish populations through time. Detailed recording of water quality parameters and sedimentation rates could allow causation to be assigned for any changes observed in fish populations. Long-term, periodic sampling to observe restoration and resettlement would also be beneficial. Such studies would allow changes in fish assemblages to be causally assigned to dredging practices, although long-term monitoring would be required to assess recolonization and long-term consequences from dredging.

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Table 4.1: Fish species captured during benthic trawling, including reproductive guild (adapted from Simon, 1998).

Family	Common Name	Scientific Name	Reproductive Guild
Petromyzontidae	Lamprey Species	<i>Petromyzon</i> or <i>Ichthyomyzon</i> <i>spp.</i>	Brood Hider - Lithophil
Cyprinidae	bluntnose minnow	<i>Pimephales notatus</i>	Nest Spawner - Speleophil
Cyprinidae	streamline chub	<i>Erimystax dissimilis</i>	Open Substrate - Lithophil
Cyprinidae	mimic shiner	<i>Notropis volucellus</i>	Open Substrate - Phytophil
Catostomidae	smallmouth buffalo	<i>Ictiobus bubalus</i>	Open Substrate - Lithopelagophil
Catostomidae	Sucker Species	<i>Catostomus spp.</i>	Open Substrate - Lithophil
Catostomidae	river redhorse	<i>Moxostoma carinatum</i>	Open Substrate - Lithophil
Catostomidae	golden redhorse	<i>Moxostoma erythrurum</i>	Open Substrate - Lithophil
Catostomidae	shorthead redhorse	<i>Moxostoma macrolepidotum</i>	Open Substrate - Lithophil
Ictaluridae	channel catfish	<i>Ictalurus punctatus</i>	Nest Spawner - Speleophil
Ictaluridae	stonecat	<i>Noturus flavus</i>	Nest Spawner - Speleophil
Ictaluridae	flathead catfish	<i>Pylodictus olivaris</i>	Nest Spawner - Speleophil
Percopsidae	trout-perch	<i>Percopsis omiscomaycus</i>	Open Substrate - Lithophil
Moronidae	white bass	<i>Morone chrysops</i>	Open Substrate - Phytolithophil
Centrarchidae	rockbass	<i>Ambloplites rupestris</i>	Nest Spawner - Polyphil
Centrarchidae	bluegill	<i>Lepomis macrochirus</i>	Nest Spawner - Polyphil
Centrarchidae	smallmouth bass	<i>Micropterus dolomieu</i>	Nest Spawner - Polyphil
Percidae	rainbow darter	<i>Etheostoma caeruleum</i>	Brood Hider - Lithophil
Percidae	logperch	<i>Percina caprodes</i>	Brood Hider - Lithophil
Percidae	channel darter	<i>Percina copelandi</i>	Brood Hider - Lithophil
Percidae	gilt darter	<i>Percina evides</i>	Brood Hider - Lithophil
Percidae	longhead darter	<i>Percina macrocephala</i>	Brood Hider - Lithophil
Percidae	fantail darter	<i>Etheostoma flabellare</i>	Nest Spawner - Speleophil
Percidae	Johnny darter	<i>Etheostoma nigrum</i>	Nest Spawner - Speleophil
Percidae	walleye	<i>Sander vitreus</i>	Open Substrate - Lithopelagophil
Percidae	yellow perch	<i>Perca flavescens</i>	Open Substrate - Phytolithophil
Percidae	bluebreast darter	<i>Etheostoma camurum</i>	Substrate Chooser - Lithophil
Percidae	Tippecanoe darter	<i>Etheostoma tippecanoe</i>	Substrate Chooser - Lithophil
Percidae	variegated darter	<i>Etheostoma variatum</i>	Substrate Chooser - Lithophil

Percidae	greenside darter	<i>Etheostoma blennioides</i>	Substrate Chooser - Phytophil
Percidae	banded darter	<i>Etheostoma zonale</i>	Substrate Chooser - Phytophil
Scianidae	freshwater drum	<i>Aplodinotus grunniens</i>	Open Substrate - Pelagophil

Table 4.2: Table of Principal Components of reproductive guilds analysis at dredged and undredged sites.

Variable		PC1	PC2	PC3	PC4	PC5
Brood-Hider	Lithophil	0.477	-0.26	0.012	0.262	0.07
Nest-Spawner	Polyphil	0.134	-0.16	0.335	-0.365	0.246
Nest-Spawner	Speleophil	0.201	0.249	-0.545	-0.451	-0.219
Open-Substrate	Lithopelagophil	-0.351	-0.201	-0.174	-0.204	-0.059
Open-Substrate	Lithophil	-0.216	0.468	0.525	0.18	-0.08
Open-Substrate	Pelagophil	-0.058	0.218	-0.23	-0.132	0.856
Open-Substrate	Phytolithophil	-0.404	-0.395	-0.077	-0.119	-0.053
Open-Substrate	Phytophil	-0.39	-0.094	-0.037	0.263	0.32
Substrate-Chooser	Lithophil	-0.125	-0.543	0.027	0.019	-0.028
Substrate-Chooser	Phytophil	0.448	-0.279	0.213	-0.065	0.196
Unknown/Other		0.094	-0.007	-0.423	0.645	0.016
% Variation		24.2	16.2	11	9.8	8.9
Cumulative Variation		24.2	40.5	51.4	61.3	70.2

Table 4.3: Estimates and results of significance test ($p < 0.05$) for undredged ($n=50$) and dredged ($n=40$) sites in navigations pools 7 and 8 in the Allegheny River.

		Estimate	Standard Error	t-value	p
Total Catch	Depth	-2.9074	1.7424	-1.669	0.0988
	Dredged	-10.5810	27.1443	-0.390	0.6976
	Depth x Dredged	0.2442	1.8796	0.130	0.8969
# Species	Depth	-0.19784	0.07409	-2.670	0.00909
	Dredged	-3.83067	1.15428	-3.319	0.00133
	Depth x Dredged	0.06167	0.07993	0.772	0.443251
Brillouin	Depth	-0.02489	0.010491	-2.372	0.019901
	Dredged	-0.62675	0.163444	-3.835	0.000239
	Depth x Dredged	0.005697	0.011317	0.503	0.615994
% Lithophils	Depth	-0.029141	0.008876	-3.283	0.00149
	Dredged	-0.618718	0.138281	-4.474	0.000023
	Depth x Dredged	0.026584	0.009575	2.776	0.00675

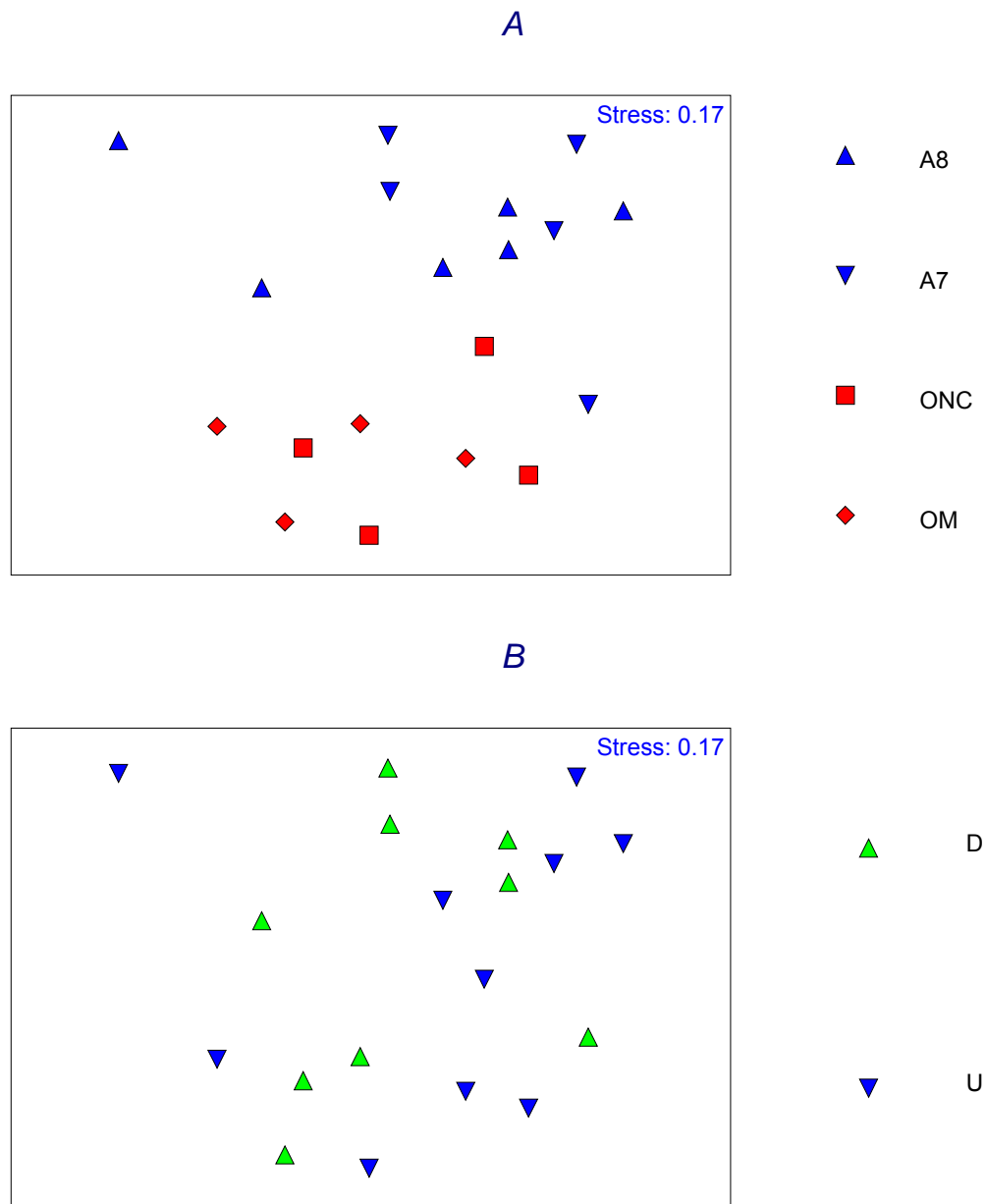


Figure 4.1: A) nMDS plot of boat electrofishing data for Allegheny River Navigation Pool 7 (A7) and Pool 8 (A8), and Ohio River Montgomery Pool (OM) and New Cumberland Pool (ONC); B) nMDS plot of boat electrofishing data for undredged (U) and dredged (D) sites in the Allegheny and Ohio rivers.

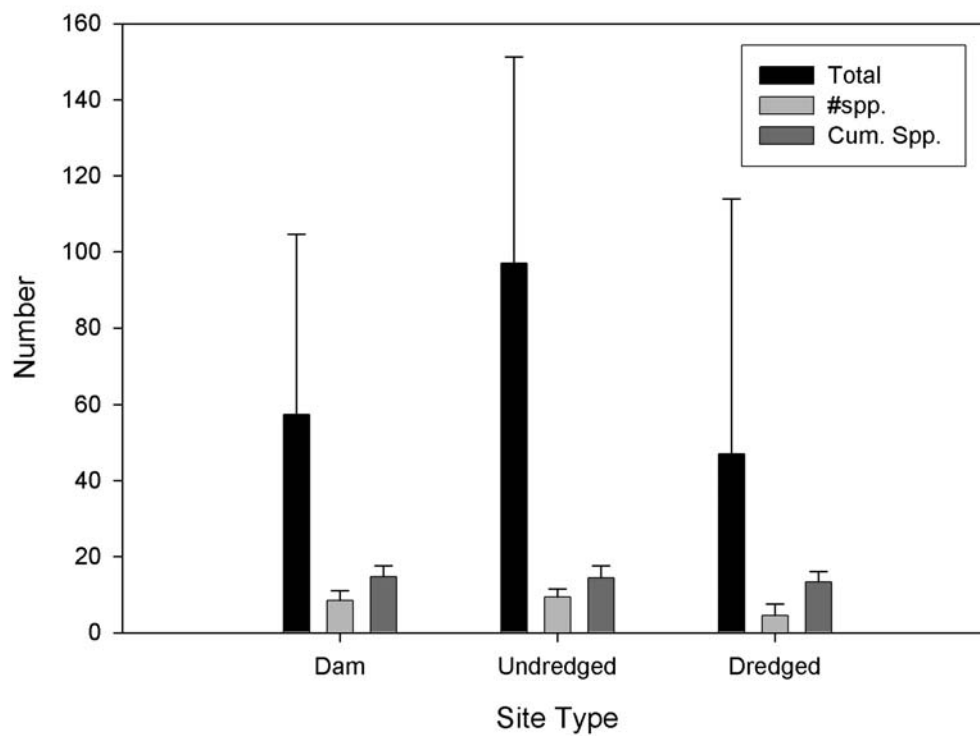


Figure 4.2: Mean total catch (number of fishes) and number of species per trawl, and cumulative catch per site, using electrified benthic trawl in navigation pools 7 & 8 in the Allegheny River. Error bars represent standard deviation.

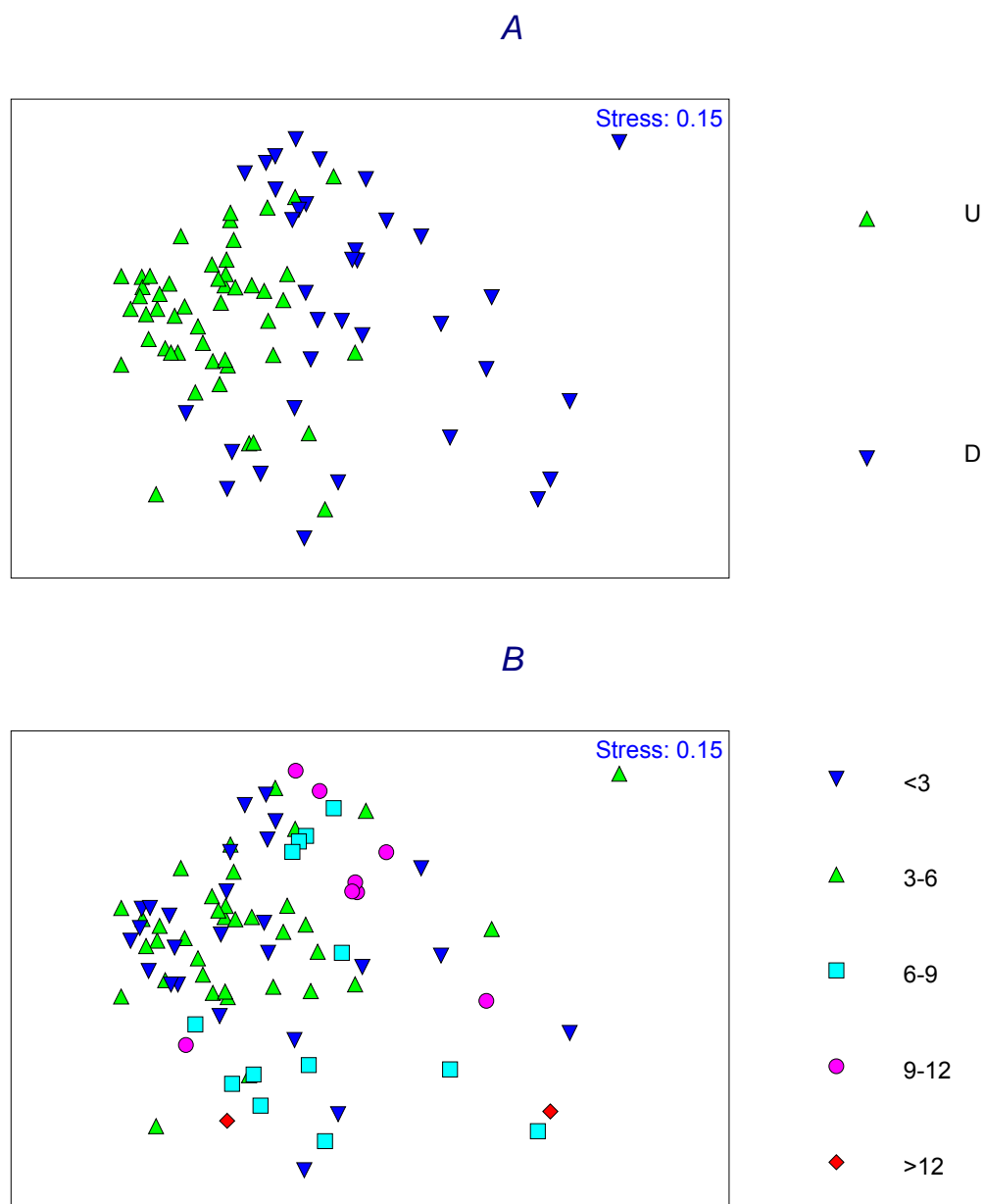


Figure 4.3: nMDS plots of electrified benthic trawl data in Allegheny River Navigation Pools 7 & 8 for trawls by A) undredged (U) and dredged (D) sites and B) depth class (in metres).

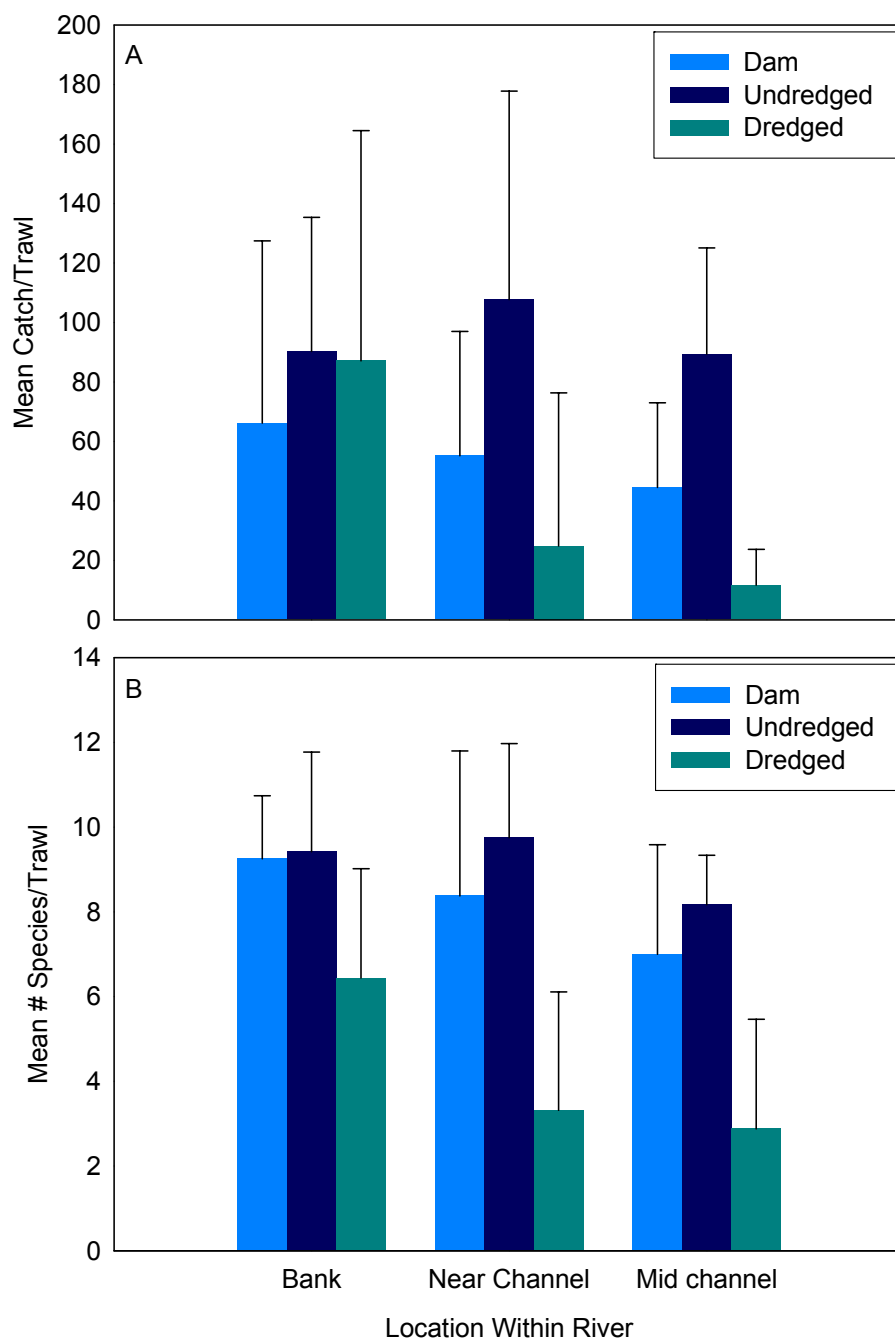


Figure 4.4: A) Mean (\pm SD) total catch per trawl, B) Mean (\pm SD) number of species per trawl for Bank, Near Channel, and Mid Channel locations at Near Dam, Undredged, and Dredged sites in navigation pools 7 & 8 of the Allegheny River, Pennsylvania.

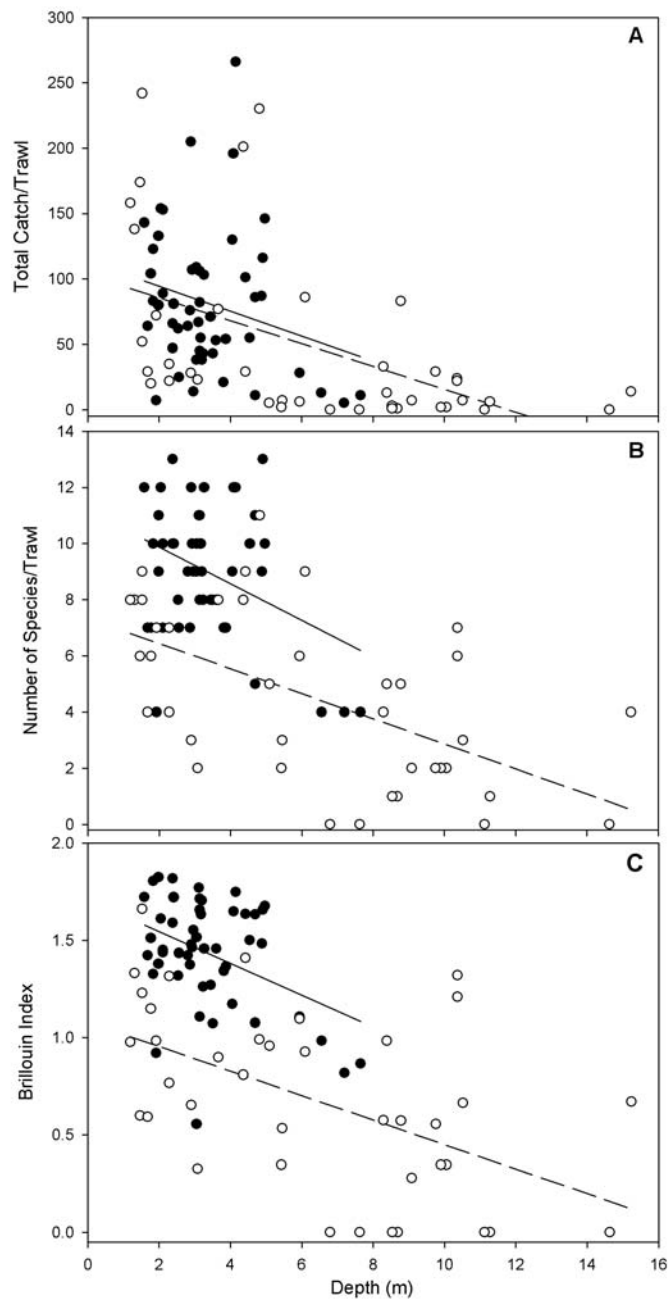


Figure 4.5: A) total catch per trawl, B) number of species per trawl, C) Brillouin Index per trawl, with regression lines for undredged (solid symbols, solid lines) and dredged sites (open symbols, dotted lines) in navigation pools 7 & 8 in the Allegheny River using an electrified benthic trawl.

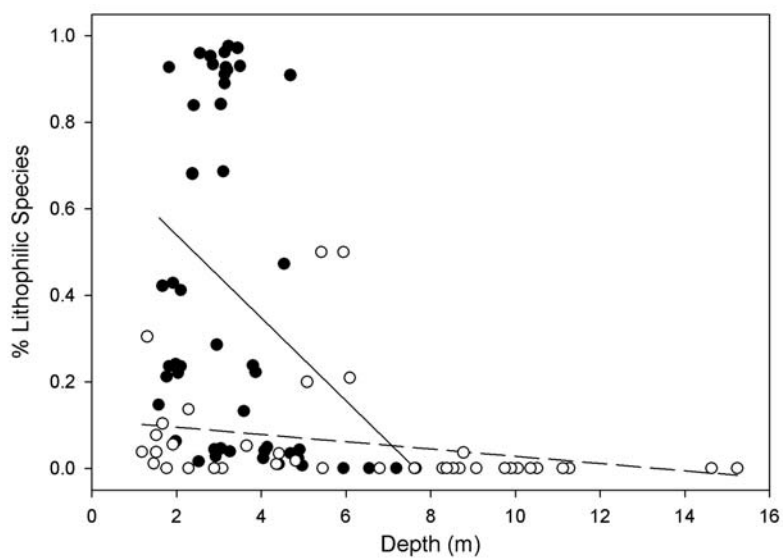


Figure 4.6: Proportion of total catch per trawl consisting of lithophilic substrate choosers and brood hiders, in Allegheny River navigation pools 7 & 8 using an electrified benthic trawl, at undredged (closed symbols, solid line) and dredged (open symbols, dotted line) sites.

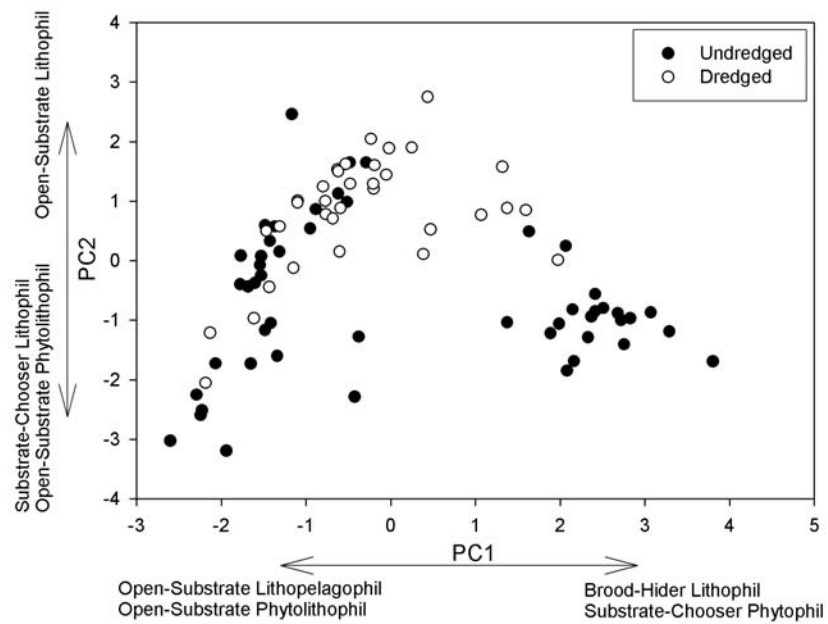


Figure 4.7: PCA plot of proportionate reproductive guilds at undredged (closed symbols) and dredged sites (open symbols).

Chapter 5

Effects of anthropogenic activities on fish assemblages: Food-web and trophic consequences

Introduction

Dams and gravel dredging are common anthropogenic features of many rivers. Constructed for flood-control, hydroelectric power generation, and to facilitate navigation or recreation, the presence of dams affects not only the natural flow of rivers but also nutrient and sediment dynamics, as nutrients and sediments can accumulate behind dams, thus becoming unavailable downstream (Kondolf 1997). Whether to facilitate navigation by maintaining a constant depth or for commercial removal, gravel dredging consists of the removal of substrate and habitat structure; the subsequent increase in depth can have profound effects on aquatic food webs (Berkman and Rabeni 1987, Kanehl and Lyons 1992, Brown et al. 1998, Ameziane et al. 2002, Milner and Piorkowski 2004). Dams and dredging can each decrease the natural heterogeneity of rivers, as pool and lentic habitats come to dominate, and the only proxy for riffle habitats may be immediately downstream of dams where turbulence and oxygen content of the water are highest (Kondolf 1997).

The resource base of any food web is driven by autochthonous primary producers, or by allochthonous inputs which derive primarily from terrestrial sources (Vanotte et al. 1980). Periphyton, macrophytes, epiphytes, and diatoms can be negatively affected by higher turbidity and sedimentation rates, and the subsequent reductions in light penetration and changes in substrate composition, associated with dredging (Rivier and Seguiet 1985). Moreover, many

fishes themselves depend on these structured habitats for protection from predators and as refugia from the current (Kanehl and Lyons 1992). Lithophilic (“rock-loving”) species, such as many darters (Percidae: Etheostomatini) require rocky and gravel habitats in which to spawn and care for their eggs (Page 1983, Simon 1998). The loss of this habitat, as well as increased turbidity and sedimentation due to dredging, can render habitats unsuitable for reproduction even if adults are able to survive (Berkman and Rabeni 1987). Given that many small fishes have short life-spans and generation times (Page 1983, Berkman and Rabeni 1987), such disruptions to reproduction, even if temporary, can be devastating to a population (Berkman and Rabeni 1987). Changes in aquatic invertebrate assemblages, from collector-gatherers and grazers living and feeding on and under rocks to shredders and decomposers feeding on terrestrial detritus, can affect fish foraging behaviour and efficiency (Harvey 1986, Berkman and Rabeni 1987, Greenwood et al. 2002, Milner and Piorkowski 2004). While it can be relatively easy to assess direct effects of these types of disturbance on fish assemblages (i.e., presence/absence and relative abundance), determining behavioural changes and ecological shifts mediated by dams and dredging present a greater challenge.

Stable isotopes can be used to provide information about both realized trophic scenopoetic (environmental conditions) and bionomic (interactions with other organisms) niche dimensions (Newsome et al. 2007). In other words, they can inform us not only *what* an organism was eating, but also *where* it was feeding (Post 2002b, Vander Zanden and Vadeboncoeur 2002, Vander Zanden et al. 2005, Newsome et al. 2007). Stable carbon isotope signatures ($\delta^{13}\text{C}$) vary across different taxa of primary producers, as well as in response to differences in environmental variables. For instance, in freshwater aquatic systems, epiphytes, periphyton, and phytoplankton differ in $\delta^{13}\text{C}$ signatures, as do periphyton from lentic and lotic environments, or from deep or shallow water (Vander Zanden and Rasmussen 1999, Post 2002b). Variation in primary producer $\delta^{13}\text{C}$ in streams and rivers is largely driven by CO_2 availability: in shallow or turbulent water the boundary layer effect increases the availability of “fresh” CO_2 ,

while in slow or deep water CO₂ is less available and is therefore “recycled” by primary producers (Peterson and Fry 1987, Finlay et al. 1999, Trudeau and Rasmussen 2003). The heavier stable isotope of nitrogen (¹⁵N) is conserved in organic tissues, and passes to higher consumers in a form of bioaccumulation. $\delta^{15}\text{N}$ is thus enriched at a relatively constant rate (2-5‰) across trophic levels, and therefore serves to estimate trophic position within a food-web (Vander Zanden and Rasmussen 1999, 2001, Post 2002a, Post 2002b). $\delta^{15}\text{N}$ varies across habitats (e.g., freshwater vs. marine), and is also enriched in ¹⁵N at greater water depth, thus providing further information about the scenopoetic niche dimensions of the organism (Newsome et al. 2007). While stable isotope analysis has been used to gain insights into biotic changes that occur as a response to anthropomorphic stress, such research has tended to focus on point- and non-point-source additions to aquatic environments (Costanzo et al. 2001, Vadeboncoeur et al. 2003, Gray et al. 2004, Grey et al. 2004, Anderson and Cabana 2005, Vander Zanden et al. 2005); however, other physical alterations to the environment can also have profound effects on nutrient flow and resource availability. While stable isotope analysis has not, to date, been used to examine the effects of dams or dredging on large-river fish assemblages, its ability to differentiate food sources and detect trophic positions makes it a powerful tool for examining the effects of dams and dredging on riverine fish assemblages.

The Allegheny River originates in Pennsylvania, flowing north into New York before proceeding in a generally southerly direction to converge with the Monongahela River in Pittsburgh, where they form the Ohio River. The lower 113 km are regulated by a series of eight navigation lock-and-dam systems, while the middle section, regulated by the Kinzua Dam located 317 km upstream from the confluence flows relatively unimpeded. Commercial gravel dredging has occurred throughout most of the nine navigation pools on the Allegheny River, but only at one site above the navigation pool influence. While subject to some point- and non-point source stressors such as sewage discharges and agriculture, 139 km of the middle section of the

Allegheny River have been designated as a National Wild and Scenic River, and remain relatively pristine.

By comparing patterns in stable isotope distribution at both dredged and undredged sites, I will be able to examine both direct and indirect effects of gravel dredging on fish communities. While standard census techniques can reveal species presence or absence and relative abundance, they do not reveal other changes in fish behaviour or ecology. Stable isotope analysis can reveal dietary shifts, as well as changes in habitat and food-resource use between dredged and undredged sites. I expect that the food-webs at dredged sites will be simpler, with relatively species depauperate fish assemblages, and shifts in resource use as littoral and shallow benthic production are diminished while terrestrial detritus accumulates at dredged sites. Consumers will thus likely show a decreased reliance on littoral (inshore) resources as the availability decreases due to reduced habitat, and a subsequent increase in reliance on terrestrial and pelagic-derived nutrients. Similarly, by comparing stable isotopes from fishes at free-flowing sites not impacted by dams with those from dam-influenced sites, I will be able to determine whether dams affect fish assemblages in a similar way. As mean depth is increased, and habitat is homogenized into pools due to dams, I expect that fishes will rely more on pelagic-derived nutrients relative to free-flowing sites. Stable isotope and species abundance data are complementary, so integration of both sets of data into one analysis using canonical correspondence analysis will provide results that are more informative and revealing than either would be alone.

Methods

Study Site and Sample Collection

Two sites were sampled above the influence of navigation dams (Free-flowing Sites), and six sites were sampled in the upper navigation pools of the Allegheny River (Pools 7-8) during late summer, 2007: three sites which had never been dredged (Undredged Sites) and three which had been dredged (Dredged Sites) at some point (Figure 1.1). Since definitive dredging history was unavailable, dredged sites were defined as those with maximum depths of at least 10 m. For undredged “control” sites, I used areas at which dredging was not permitted (two sites at the bases of bridges) and a section in Pool 8 that had not been dredged; maximum depths averaged 3-6 m at these undredged sites. Invertebrates and fishes from each site were sampled at three habitats, defined as (1) near-shore, (2) near-channel, and (3) mid-channel. All fishes were identified to species, while invertebrates were identified to Family, and were assigned to trophic guilds. Benthic invertebrates (mussels, snails, crayfishes, and insects) were collected by SCUBA divers, trawls, and ponar samplers. Adult fishes were collected using a combination of Missouri- and PSU-benthic trawls (Herzog et al. 2005, Freedman et al. 2009b), multiple-mesh experimental gill-nets, beach-seines, and electrofishing. This use of multiple sampling methods provided a comprehensive and representative sample of the fish assemblage at each site. Fish samples were immediately frozen until processing in the laboratory. Due to their small size, invertebrates were analyzed whole, and were preserved in 70% ethanol until preparation to allow for laboratory identification. Correction of invertebrate samples for preservation in ethanol was applied prior to statistical analysis and interpretation (Sarakinos et al. 2002).

Several individuals of each fish and invertebrate taxon (to compensate for inherent inter-individual variability), and of different size-classes where relevant (e.g., species in which juveniles and adults may undergo trophic ontogeny), were sampled for stable isotope analysis.

White muscle tissues was used where possible for fish samples, as previous studies have shown it to be less variable than other tissues, with a moderate stable isotope turnover rate on the order of weeks to months (Hobson 1999). For smaller species and juveniles, samples consisted of whole fillets, or whole fishes. Excised muscle samples were taken from live larger species and individuals using a biopsy punch and the fishes were released. Deceased specimens were sampled by removing a fillet of white muscle tissue. Gut contents were taken by dissecting the guts from sampled fishes in the field or in the lab, and were preserved in 70% ethanol for laboratory identification prior to preparation. Gut contents were identified to the lowest taxonomic level possible, and were then used for stable isotope analysis.

All samples were prepared as follows: each sample was placed into a clean glass vial and dried in a drying oven at 60°C for 24-48 hours, and then homogenized to a fine powder using mortar-and-pestle, or within the vial using a glass stirring rod. Samples were weighed into 0.2 mg ($\pm 10\%$) aliquots, placed into 5 mm x 3.5 mm tin capsules, and analyzed for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ using either a Thermo-Finnigan Delta Plus or Delta XP isotope-ratio mass spectrometer interfaced with a Carlo Erba NC2500 Elemental Analyzer via the Conflo II or Conflo III at the Stable Isotopes in Nature Laboratory at the University of New Brunswick, Canada.

From each sample, the ratios of ^{14}N to ^{15}N and of ^{12}C to ^{13}C were determined, and $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ were calculated using the formula:

$$\delta X = [(R_{\text{sample}}/R_{\text{standard}})-1] \times 1000$$

where X refers to the rare, heavy isotope, and R is the ratio of the heavy isotope (^{15}N , ^{13}C) to the light isotope (^{14}N , ^{12}C) in the sample and in a standard. The standard for nitrogen is atmospheric nitrogen (AIR), and for carbon is carbon dioxide derived from calcium carbonate in the Pee Dee

Bee formation of South Carolina (PDB). As lipids are rich in carbon relative to tissues, variable tissue-lipid contents among samples can increase overall variability of samples. To account for this, I used a lipid correction that uses C:N to standardize lipid content across samples (Post et al. 2007).

Statistical Analysis

I used circular statistics (Schmidt et al. 2007) to assess differences between fish stable isotope signatures by assessing directional changes from sites above the navigation dam influence (free-flowing) to both undredged and dredged sites in the navigation pools, and from undredged to dredged sites, using the software package Oriana 3.0 (Kovach Computing Services 2009). In circular statistics, the stable isotope data are transformed into linear vectors for each fish species, with an origin that is standardized as 0,0. $\delta^{13}\text{C}$ is plotted on the X-axis, with ^{13}C -depletion (indicative of pelagic and terrestrial carbon sources) to the left (270°), and ^{13}C -enrichment (littoral and shallow benthic carbon sources) to the right (90°). $\delta^{15}\text{N}$ is plotted on the Y-axis, with ^{15}N -enrichment (higher trophic level) at 0° and ^{15}N -depletion (lower trophic level) at 180° . I defined the origin as being the site with the least anthropogenic disturbances (free-flowing or undredged) while the other end of the vector represents the impacted site (undredged or dredged). The length of each vector represents the magnitude of change of stable isotopic signatures for that species, while the angle of the vector represents the directionality of that change. Free-flowing sites were only sampled using PSU trawls; hence analyses including these sites include only the trawl data and not the gill-net data, so large ($> 15\text{cm}$ fork length) and small fishes ($< 15\text{cm}$ fork length) were analyzed separately. I used Rayleigh's Test for Circular Uniformity to test whether the distribution of vectors was random or uniform.

To incorporate stable isotope analysis with species abundance data, I used canonical correspondence analysis (CCA) using the statistical package *vegan* for R 2.5.1 (R Development

Core Team 2008). Canonical correspondence analysis allowed me to combine a site-by-species matrix and a site-by-environmental variable matrix. I used fish abundance data for the site-by-species matrix, and maximum depth and mean stable isotope signatures ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) of invertebrate consumers as indicators of environmental gradients at each site. Because CCA does not recognize negative integers, the $\delta^{13}\text{C}$ data (given as negative values since most organisms are depleted in ^{13}C relative to the IAEA standard) were transformed by taking the absolute values. The sign is not important to the analysis as the relevant information is the absolute value, but it is imperative to recognize that the $\delta^{13}\text{C}$ vectors are therefore the opposite of the usual interpretation, and thus that the direction of the vector suggests greater absolute values of $\delta^{13}\text{C}$ (i.e. more depleted in $\delta^{13}\text{C}$, or towards pelagic or deeper-water nutrients). Species abbreviations are given in Table 5.1. Complete stable isotope values for fishes and invertebrates are provided in the Appendix.

Results

Trends in Stable Isotope Signatures

Small fishes from free-flowing sites had the least ^{13}C depleted $\delta^{13}\text{C}$ signatures, consistent with a reliance on shallow and benthic-derived nutrients (Figure 5.1A). Small fishes from dredged sites (Figure 5.1C) had ^{13}C depleted $\delta^{13}\text{C}$ signatures, which are consistent with a reliance on pelagic and deep-derived nutrients rather than shallow or benthic-derived nutrients. No small fishes from free-flowing sites had $\delta^{13}\text{C}$ signatures more negative than -24.00 ‰, while only two fishes from dredged sites had $\delta^{13}\text{C}$ signatures that were less negative than -24.00 ‰. Small fishes from undredged sites incorporated a range of $\delta^{13}\text{C}$ signatures, consistent with being supported by a range of nutrient sources (Figure 5.1C). There was a negative trend in small fish $\delta^{15}\text{N}$ from

free-flowing to undredged to dredged sites (Figure 5.1A,B,C), consistent with increasing reliance on pelagic or terrestrial nutrients, and decreased reliance on shallow benthic derived nutrients. There were no apparent trends as large fishes from dredged and undredged had similar $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ranges (Figure 5.1D,E). Invertebrate assemblages had similar trends in $\delta^{13}\text{C}$ to small fishes, as invertebrate $\delta^{13}\text{C}$ was more depleted, on average, at dredged sites than undredged or free-flowing sites for common trophic guilds (Figure 5.2).

Circular Statistics

There was a directional shift in $\delta^{13}\text{C}$ from free-flowing to dam-influenced sites. Circular statistics revealed that fishes from both undredged (Rayleigh's Test, $p < 0.01$; Figure 5.3) and dredged (Rayleigh's Test, $p < 0.01$; Figure 5.3) sites were shifted from reliance on benthic production at free-flowing sites to increased reliance on pelagic-derived nutrients at dam-influenced sites. There was no significant effect of dam influence on the trophic position of fishes. Fantail darter, *Etheostoma flabellare*, (from $\delta^{15}\text{N}$ 13.30 ± 0.38 at free-flowing sites to 14.61 ± 1.41 at undredged sites) and Johnny darter, *Etheostoma nigrum*, (from $\delta^{15}\text{N}$ 10.99 ± 0.25 to 12.93 ± 1.00) were exceptions as they both increased mean trophic position from free-flowing to undredged sites. From free-flowing to dredged sites, Rainbow darter, *Etheostoma caeruleum*, (from $\delta^{15}\text{N}$ 14.68 ± 0.39 to 11.96 ± 0.21) and Banded darter, *Etheostoma zonale*, (from $\delta^{15}\text{N}$ 12.97 ± 0.50 to 11.88 [$n=1$ so no SD]) both decreased in trophic position.

Both small (Rayleigh's Test, $p=0.012$) and large fishes (Rayleigh's Test, $p=0.035$) had significantly lower mean $\delta^{15}\text{N}$ values at dredged relative to undredged sites (Figure 5.3). Shifts in $\delta^{13}\text{C}$ were not consistent, as large fishes tended towards an increased use of benthic nutrients, while small fishes trended towards increased reliance on pelagic nutrients. At dredged sites, Gizzard shad, *Dorosoma cepedianum*, ($\delta^{13}\text{C}$ -29.32 [no SD, $n=1$] to -25.19 ± 1.28) and Golden redhorse, *Moxostoma erythrurum*, ($\delta^{13}\text{C}$ -26.18 [no SD, $n=1$] to -23.79 [no SD, $n=1$]) both had

clear shifts towards an increased reliance on benthic nutrients, while Streamline chub, *Erimystax dissimilis*, (-24.22 ± 1.25 to -28.05 ± 0.43) and *Notropis* minnow species (-25.79 ± 1.55 to -27.48 ± 2.02) had an increased reliance on pelagic nutrients.

Nutrient Dynamics and Food-webs

Canonical correspondence analysis revealed that dredged sites were associated not only with increased depth, but also with enriched $\delta^{15}\text{N}$ of filter-feeder and scraper-grazer invertebrates, and with depleted $\delta^{13}\text{C}$ of filter-feeder and collector-gatherer invertebrates. Undredged sites were generally correlated with depleted filter-feeder and scraper-grazer $\delta^{15}\text{N}$, and with enriched $\delta^{13}\text{C}$ of collector-gatherers but depleted $\delta^{13}\text{C}$ of scraper-grazers. Free-flowing sites were correlated with enriched collector-gatherer $\delta^{15}\text{N}$ and enriched scraper-grazer $\delta^{13}\text{C}$ (Figure 5.4).

Darter species (*Etheostoma* and *Percina* genera) were likewise associated with undredged and free-flowing sites. This included species classified as Threatened by the State of Pennsylvania (*E. tippecanoe*, *P. maculata*, and *P. evides*). Considered relative habitat generalists, *P. caprodes* and *P. copelandi* did not appear to be correlated with any sites, while another habitat generalist, *E. nigrum* was correlated with dredged sites. Large benthic generalists such as catfishes (*Ictalurus punctatus* and *Pylodictus olivaris*), suckers (Genera *Ictiobus*, *Carpionodes*, and *Moxostoma*), carp (*Cyprinus carpio*) and drum (*Aplodinotus grunniens*) were associated with dredged sites, although their stable isotope signatures were generally consistent with shallower benthic areas (Figure 5.4).

Discussion

Effects of dams on nutrient dynamics

Because only benthic trawling was used to sample fishes at free-flowing sites, with its inherent capture bias towards smaller fish species (Herzog et al. 2005, Argent et al. 2007, Koryak et al. 2008, Freedman et al. 2009b), it was not possible to compare stable isotope signatures of large fishes between the free-flowing and dam-influenced sites. Small fish species, however, shifted from reliance on benthic-derived nutrients (relatively enriched ^{13}C) at free-flowing sites to terrestrial and pelagic-derived (depleted ^{13}C) nutrients at both dredged and undredged sites. This trend is consistent with patterns of increased depth caused by the downstream presence of dams at these sites.

These results are also consistent with shifts from benthic-driven primary production (e.g., periphyton) to pelagic-production (e.g., phytoplankton) as a result of cultural eutrophication (Vadeboncoeur et al. 2003, Chandra et al. 2005, Vander Zanden et al. 2005). Such shifts are generally considered to be the result of eutrophication increasing concentration and productivity of pelagic primary producers, thus starving benthic producers of both nutrients for growth and sunlight for photosynthesis (Vadeboncoeur et al. 2003, Chandra et al. 2005). Anthropogenically increased depth may have similar effects. As average depth increases, from mere centimetres in headwater streams to many metres in high-order rivers, relatively less light reaches the river floor, from near 100% of non-refracted light in small clear streams to zero in turbid and deep water, thus decreasing benthic production. Building dams and thus increasing the mean depth from ~2-3 m in pools in the free-flowing Allegheny River to a constant minimum of 4-5 m (or more) in dam-influenced reaches can therefore decrease benthic production without any influences from eutrophication or other increases in relative turbidity. Since the free-flowing reach of the river includes runs and riffles as well as pools, while the homogenous dam-influenced reaches

effectively consist only of long pools possibly with minimal riffle- or run-type habitat immediately downstream of dams, a loss of benthic nutrient pathways becomes even more likely.

Reliance on shallow and benthic-derived nutrients at free-flowing sites appears to be high while at undredged sites $\delta^{13}\text{C}$ signatures suggest a trend towards increasing reliance on pelagic-derived nutrients. While a full range of benthic and pelagic nutrients seem to be available, fishes are relying more on pelagic nutrients; this is consistent with the theory that reliance on pelagic nutrients (and decreased reliance on benthic nutrients) would increase with the increased depth due to the navigation dams. While most small fishes at free-flowing sites relied on shallow and benthic nutrients while a few relied on pelagic nutrients, this trend was not apparent at undredged sites.

Rafinesque (1820) referred to the Allegheny River as being “almost perfectly clear” while our Secchi depths ranged from 142-145cm downstream of an active dredging operation and 157-198cm in other dam-influenced areas of the river (Pers. Obs.), thus offering supporting evidence that this is no longer the case. However, we found Secchi depths in the range of 330cm above the dam influence, so there does appear to be a negative effect of dams on water clarity. The approximately 214 km of the Allegheny River between the Kinzua Dam and the end of the navigation dam influence near East Brady PA, likely experience full light penetration except during times of high discharge. Free-flowing sites, therefore, likely represent similar reference states to the historical condition, and with similar fish assemblages and food-web structure.

Effects of dredging on nutrients

Examination of stable isotope data suggest that small fishes at dredged sites generally consumed more pelagic-derived nutrients, while their conspecifics at undredged sites relied more on benthic-derived nutrients. This is consistent with my hypothesis that dredging reduces benthic productivity, mediated by increased depth, increased turbidity, and a decrease in suitable habitat

for periphyton to colonize. Large fishes, however, confounded this hypothesis by relying more on benthic nutrients at dredged sites relative to undredged sites. Gizzard shad had a strong influence on this trend, which may be indicative of increased motility in large fishes relative to small fishes. Small fishes, being less motile, may shift diets towards phytoplankton- and terrestrial-based nutrients, since these are readily available in their home-ranges. Larger fishes, however, which in this study mostly include generalist benthivores such as suckers and carp, move into shallower water to feed and hence are able to take advantage of benthic productivity in these areas.

In deep dredged areas, there is zero light penetration beyond about 10m depth (Pers. Obs.) and so there is likely no photosynthesis or benthic primary production at these depths, with the exception of the microbial and detritus-based food webs. (Rivier and Segurier 1985) found 54-94% declines in diatom populations and reduced densities of algae and plants as a result of dredging in the Doubs River in France, and attributed these changes to increased turbidity and sedimentation, decreased light penetration, and changes to the substrate. In the Allegheny River, bubbles of gas were seen to be rising from depth and breaking the surface at dredged sites (JAF Pers. Obs.). As methane has $\delta^{13}\text{C}$ of approximately -70‰, and has been traced into biological food webs (Jones and Grey 2004, Grey and Deines 2005), I therefore expected to see some extremely negative $\delta^{13}\text{C}$ signatures in some fishes. In a study in Mactaquac Lake, New Brunswick, 6.2% of yellow perch, and 2.6% of white sucker had stable isotope signatures consistent with a dietary contribution from methane (Freedman and Curry in prep.). As I did not find any such signatures in the Allegheny River, it appears that methane is not an important nutrient source; it is not being assimilated into the food-web, or was not detected due to limited sample size of fishes at these sites.

As the availability of CO_2 decreases, for instance at deeper depths and in slow-flowing water, $\delta^{13}\text{C}$ becomes more negative due to the recycling of CO_2 and subsequent depletion of ^{13}C during primary producer respiration (Peterson and Fry 1987, Finlay et al. 1999, Trudeau and

Rasmussen 2003). This is consistent with the correlation of depleted $\delta^{13}\text{C}$ at deep dredged sites. Undredged sites are correlated with depleted scraper-grazer $\delta^{13}\text{C}$ relative to free-flowing sites, which suggests that the deeper average depths associated with the navigation dams have a similar effect. Dredged sites were not strongly correlated with scraper-grazer $\delta^{13}\text{C}$, which may result from diminished (benthic) algal resources available to these primary consumers at dredged sites.

It is difficult to assign correlations of species abundance and stable isotope signatures to specific causes. The positive correlations of lithophilic species such as most darters with undredged and free-flowing sites support my hypothesis that dredged sites do not contain the habitat required to support such species. Large benthic generalists may utilize deeper areas as thermal refugia, moving into shallow water at night to feed. As generalists, they may also be consuming invertebrates in the terrestrial detritus which accumulates in dredged holes.

The positive correlation between enriched primary consumer invertebrate $\delta^{15}\text{N}$ and dredged sites is the opposite of the negative correlation between fish $\delta^{15}\text{N}$ with dredged sites. Enriched $\delta^{15}\text{N}$ is correlated with depth in lakes (Vander Zanden and Rasmussen 1999), which is consistent with invertebrate data from this study. If fishes were feeding at a consistent trophic level (e.g. secondary consumers) they would therefore be expected to show a similar trend. Since fishes at dredged sites have lower $\delta^{15}\text{N}$, both overall and in relation to primary consumer “baselines,” it is safe to extrapolate that they are feeding at lower trophic levels at these sites and is further support of my hypothesis that food-chain length would be diminished due to dredging. In effect, there is a simpler food-web present within the dredged sites than the undredged and free-flowing sites. Lower $\delta^{15}\text{N}$ at dredged sites is correlated with a decrease in species diversity and overall fish abundance, and may be indicative of simpler food-web structure and reduced food-chain length. (Post et al. 2000) found that food-chain length is negatively correlated with ecosystem size, which is consistent with the findings of the present study.

Conclusions

Stable isotope analysis of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ is an appropriate tool for assessing differences in fish assemblages at dredged and undredged sites, and comparing these to sites which have no influence from dams. There is a clear shift towards increased reliance on pelagic nutrients at dam-influenced and particularly at dredged sites among smaller fishes. Larger fishes appear to be less affected by dredging, but are correlated with benthic nutrients and dredged sites. The overall food web at dredged sites appears to be compressed as fishes at dredged sites also occupy lower relative trophic positions and lower $\delta^{15}\text{N}$ relative to undredged sites. Lithophilic species are particularly affected by dredging and are correlated with undredged and free-flowing sites, while eurytopic generalist species are relatively abundant at dredged sites. Future studies could examine differences in food webs and nutrient dynamics before, and at various intervals after, dredging in order to directly determine both long- and short-term food-web consequences to dredging.

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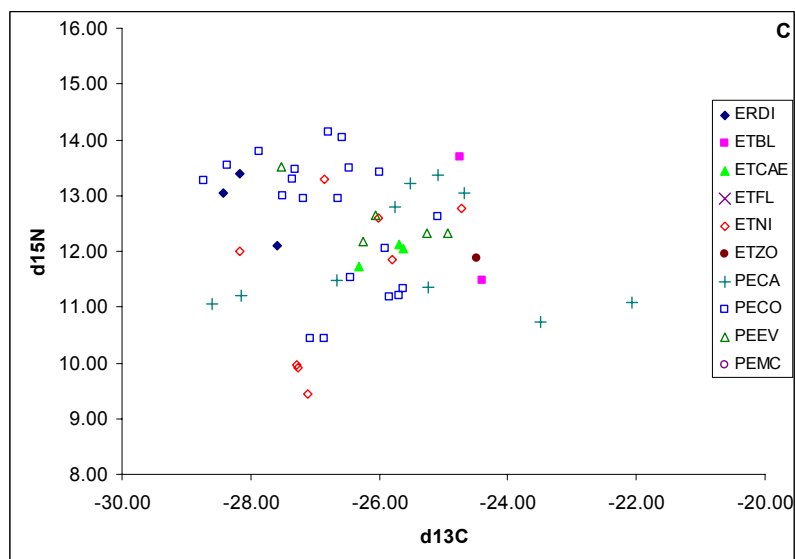
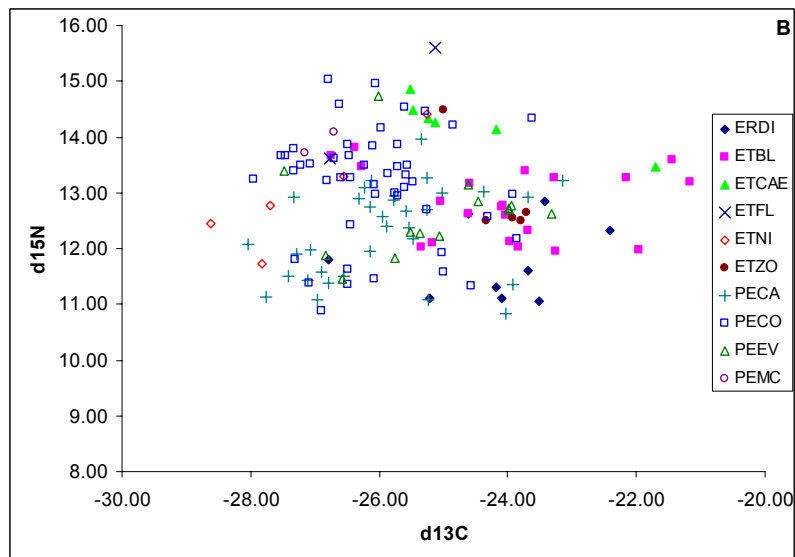
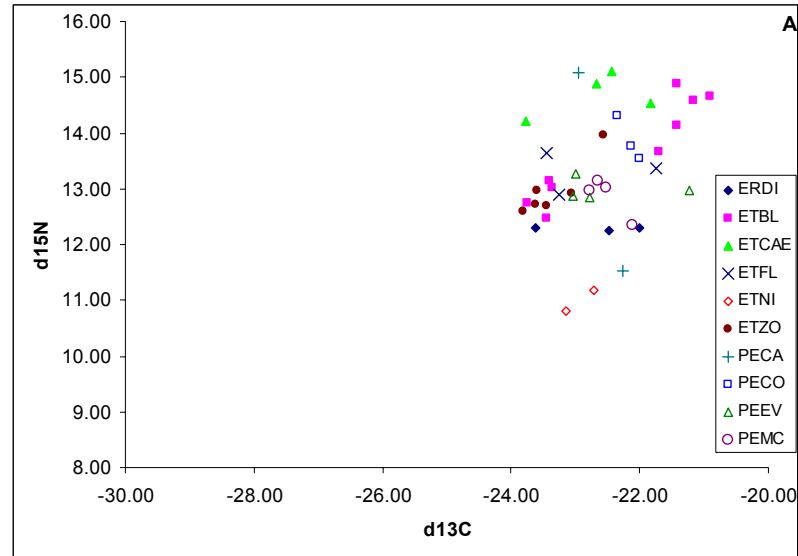
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Table 5.1. List of fish species caught during stable isotope analysis sampling, with abbreviation code used in analyses.

Family	Common Name	Scientific Name	Code
Clupeidae	gizzard shad	<i>Dorosoma cepedianum</i>	DOCE
Catostomidae	river carpsucker	<i>Carpionodes spp.</i>	CASP
Catostomidae	smallmouth buffalo	<i>Ictiobus bubalus</i>	IBBU
Catostomidae	redhorse spp.	<i>Moxostoma spp.</i>	MXSP
Cyprinidae	common carp	<i>Cyprinus carpio</i>	CYCA
Cyprinidae	streamline chub	<i>Erimystax dissimilis</i>	ERDI
Cyprinidae	minnow species	<i>Notropis spp.</i>	NOSP
Ictaluridae	channel catfish	<i>Ictalurus punctatus</i>	ICPU
Ictaluridae	flathead catfish	<i>Pylodictus olivaris</i>	PYOL
Centrarchidae	rockbass	<i>Ambloplites rupestris</i>	AMRU
Centrarchidae	smallmouth bass	<i>Micropterus dolomieu</i>	MIDO
Percidae	greenside darter	<i>Etheostoma blennioides</i>	ETBL
Percidae	rainbow darter	<i>Etheostoma caeruleum</i>	ETCA
Percidae	bluebreast darter	<i>Etheostoma camurum</i>	ETCM
Percidae	fantail darter	<i>Etheostoma flabellare</i>	ETFL
Percidae	Johnny darter	<i>Etheostoma nigrum</i>	ETNI
Percidae	Tippecanoe darter	<i>Etheostoma tippecanoe</i>	ETTI
Percidae	banded darter	<i>Etheostoma zonale</i>	ETZO
Percidae	logperch	<i>Percina caprodes</i>	PECA
Percidae	channel darter	<i>Percina copelandi</i>	PECO
Percidae	gilt darter	<i>Percina evides</i>	PEEV
Percidae	longhead darter	<i>Percina macrocephala</i>	PEMC
Percidae	walleye	<i>Sander vitreus</i>	SAVI
Scianidae	freshwater drum	<i>Aplodinotus grunniens</i>	APGR

Table 5.2. Vector angles and lengths for fish species used in circular statistics analysis. Species abbreviations are provided in Table 5.1.

Species	Free-flowing to Undredged		Free-flowing to Dredged		Undredged to Dredged	
	Angle	Length	Angle	Length	Angle	Length
APGR					179.32	0.84
CASP					281.50	0.60
CYCA					123.69	0.47
DOCE					78.50	4.22
ERDI	250.78	1.61	276.08	5.38	286.02	3.99
ETBL <40 mm					196.93	0.96
ETBL >40 mm	261.52	1.63	269.77	2.46	285.14	0.88
ETCA	257.28	1.91	229.64	4.20	210.23	2.66
ETCM	272.43	2.12				
ETFL	292.65	3.40				
ETNI	294.48	4.68	277.50	3.75	159.57	1.55
ETTI						
ETZO	267.85	0.80	226.28	1.58	197.78	1.11
IBBU					154.26	0.62
ICPU					188.43	0.55
LASI					119.31	1.96
LEMA					205.38	0.86
MIDO yoy					193.95	1.58
MXAN					178.36	0.70
MXER					82.37	2.41
NOSP	264.21	3.67	273.22	5.35	291.63	1.82
PECA <50 mm					118.81	0.23
PECA >50 mm	259.99	3.28	253.76	2.40	96.14	0.94
PECO <30 mm					225.47	0.86
PECO >30 mm	266.45	4.04	264.28	4.91	254.41	0.89
PEEV	262.61	2.72	263.64	3.52	267.14	0.80
PEMR	270.17	3.41				
PYOL					175.52	0.51



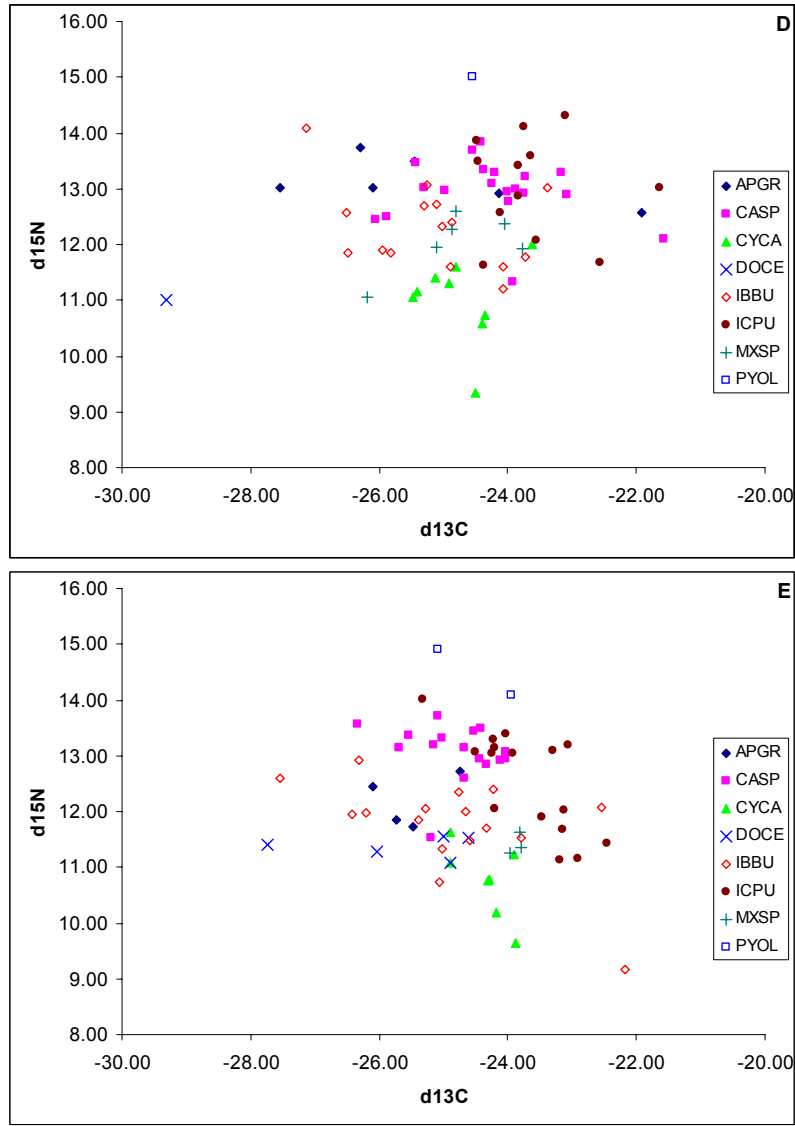


Figure 5.1: Stable isotope biplots of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for small fishes at (A) free-flowing, (B) undredged, and (C) dredged sites; and for large fishes at (D) undredged and (E) dredged sites in the Allegheny River, Pennsylvania. Species abbreviations are provided in Table 5.1.

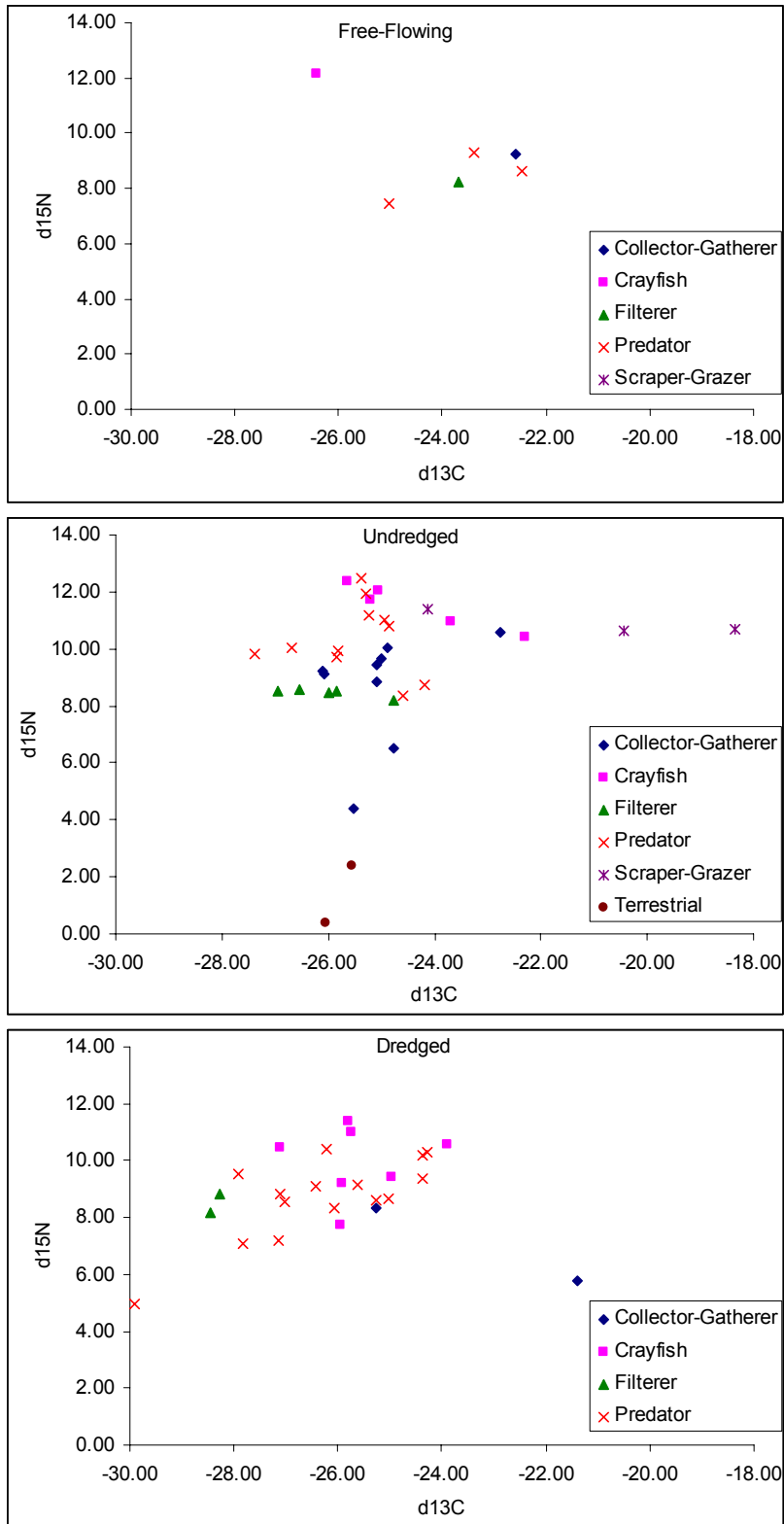


Figure 5.2: Stable isotope biplots of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for invertebrate guilds at free-flowing, undredged, and dredged sites in the Allegheny River, Pennsylvania.

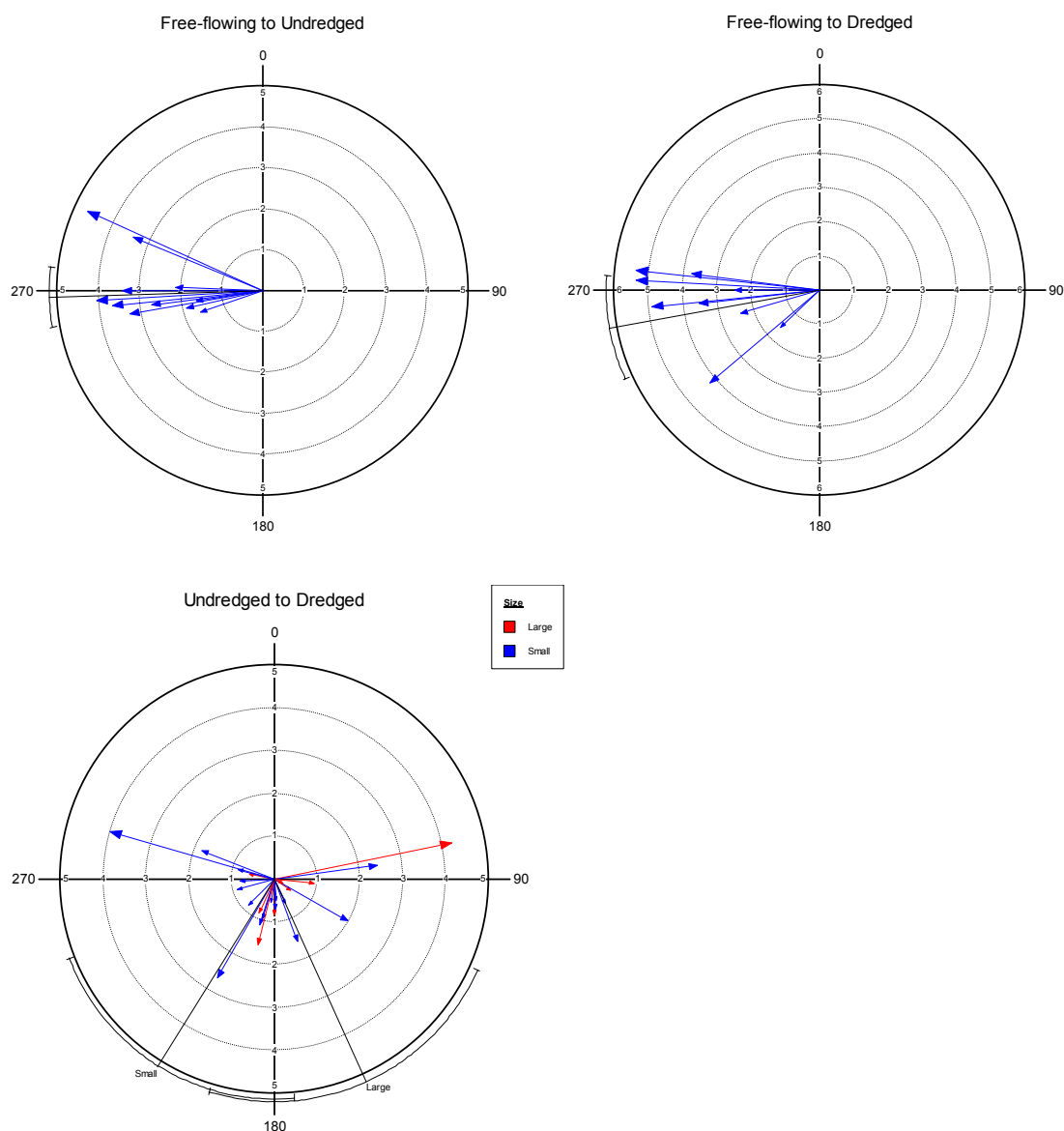


Figure 5.3: Circular distribution plots of: free-flowing to undredged sites, free-flowing to dredged sites, and undredged to dredged sites in the Allegheny River, Pennsylvania. Each vector represents a fish species or size-class, with angle representing change in the appropriate direction and length indicating relative strength of directionality. Vector directionality towards 0° indicates higher $\delta^{15}\text{N}$ while 180° is lower $\delta^{15}\text{N}$, and 90° and 270° respectively are enriched and depleted ^{13}C . Blue vectors are small species while red vectors are large species. Lines at the circumference of the plot represent the 95% confidence interval around the mean.

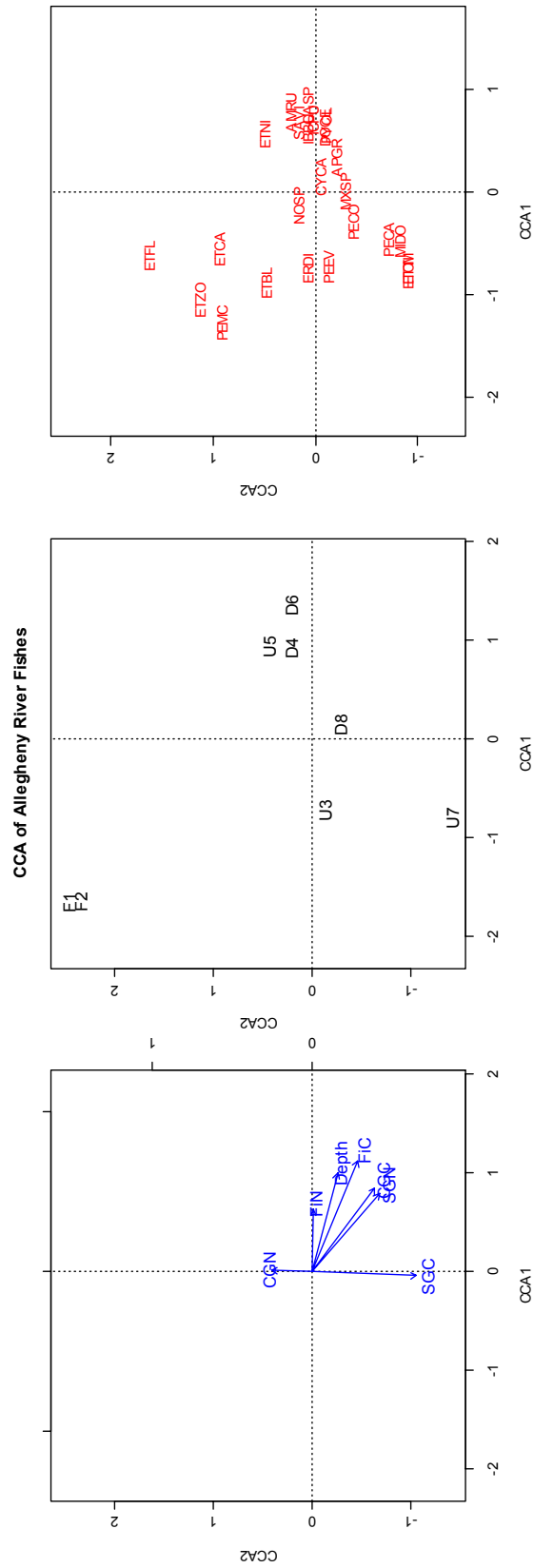


Figure 5.4: Canonical correspondence analysis plots of environmental variables, sites, and fish species abundance in the Allegheny River. Environmental variables are depth and $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of invertebrate baseline fauna (SG: scraper-grazer; Fi: Filterer, CG: Collector-Gatherer), while the suffixes C and N refer to $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively. Sites are free-flowing (F), undredged (U), and dredged (D), while fish species abbreviations are given in Table 5.1.

Chapter 6

Ecomorphology and Introgression Confound Phylogeography in Logperch Darters

Introduction

Environmental conditions are well known to drive morphological divergence and adaptation. Icelandic charr, for instance, occur in four morphotypes: piscivore, planktivore, and small and large benthivores (Robinson and Wilson 1994, Guiguer et al. 2002). While clearly distinguishable morphologically, these morphotypes are not recognized as being taxonomically distinct. Benthic and pelagic morphs of three-spined sticklebacks have been extensively studied in western North America (Schluter and McPhail 1992, Schluter 1993, 1996), while land-locked populations of rainbow smelt, *Osmersus mordax*, ((Curry et al. 2004, Jardine and Curry 2006) and alewife, *Alosa pseudoharangus* ((Palkovacs et al. 2008, Post and Palkovacs 2009) in eastern North America are morphologically and behaviourally distinct from their anadromous cousins.

Selection of riverine and lacustrine morphs in some taxa (Robinson and Wilson 1994) may be driven by differential water velocity. Brook trout, *Salvelinus fontinalis*, exhibit phenotypic plasticity in response to varying water velocities, having more slender bodies, deeper caudal peduncles, and larger caudal fins when raised in faster-flowing water (Imre et al. 2001, 2002). Sculpin, *Cottus* spp., have likewise been shown to be adapted to varying water velocities, with different morphs at different currents (Kerfoot and Schaefer 2006). The cyprinid *Notropis wickliffi* was, until recently, considered to be a large-river variety or subspecies of the stream dwelling *N. volucellus* (Hrabik 1996), and it is not unreasonable to speculate that the speciation event resulted from parapatric separation due to habitat preference.

It is well established that darter morphology is related to habitat and environmental conditions. Analysis of several relative body proportions, such as relative pectoral fin size and body shape, reveals more similarity between species inhabiting similar habitats across subgenera than within subgenera (Page 1983, Page and Swofford 1984). Despite this, character displacement within species has only been documented in Johnny Darter (*Etheostoma nigrum*) (Robinson and Wilson 1994) in which riverine and lacustrine forms are considered separate morphs, and for which a genetic mechanism has been thought to be at least partially responsible (Lagler and Bailey 1947).

Logperch, *Percina caprodes* Rafinesque, are relatively large-bodied (up to 18 cm) darters which are ubiquitous across many habitats in the upper Ohio River and upper Saint Lawrence drainages, ranging from streams to lakes. (Rafinesque 1820) described the logperch as being the most common species of darters or “hogfishes” found in the Ohio River and surrounding drainages. Two subspecies of *Percina caprodes* are recognized: Ohio Logperch *P. c. caprodes* are primarily found in the Ohio River drainage, while Northern logperch *P. c. semifasciata*, are found in the Great Lakes drainage and throughout most of its Canadian range (Page 1983). Both forms are also found in other drainages, probably due to a combination of natural (stream-capture events) and anthropogenic (transplants, bait-bucket introductions, and connectivity among drainages as a result of shipping canals) factors. Intergrades are common where their ranges overlap, for instance in Lake Erie (Trautman 1981), and there is not a consistent pattern of occurrence in New York where both subspecies occur (Smith 1985).

If logperch from different habitats (stream, river, and lake) are morphologically distinct from one another, this is evidence of adaptive character displacement and may be indicative of phenotypic plasticity or selective pressures. Specifically, I expect logperch from slower moving water, such as the Lower Allegheny, which is regulated by navigation dams, and from the Allegheny or Kinzua Reservoir, which is an impoundment created by a flood-control dam, to be relatively stout and to have relatively large caudal peduncles compared to fishes from faster

flowing water. The relative influences of phylogeny and ecomorphological adaptation will be examined by comparing morphology both within and among *P. c. caprodes* and *P. c. semifasciata* in the Ohio and Great Lakes drainages, respectively. These will be compared to Chesapeake logperch, *Percina bimaculata* Haldeman 1844, a closely related species found in the Potomac and Susquehanna drainages (Near 2008) and Mobile Logperch, *Percina kathae* Thompson 1997, from Georgia (Thompson 1997). To further parse the effects of phylogeography, I will also examine *P. c. caprodes* from West Virginia, where no intergradation should occur with other logperch taxa, and *P. c. caprodes* from the Genesee River in New York State, which drains to Lake Ontario, and hence may be more closely related to, or may represent intergrades with *P. bimaculata*. Proper taxonomy and species identifications are vital for understanding fish ecology and management (Stauffer and Kocovsky 2007), and so it is important to understand the relative importance of environmental conditions in influencing the morphology of fishes.

Methods

Logperch were sampled from three habitats in the Allegheny River drainage (stream, river, and lake) and two habitats in the Lake Erie drainage (stream and lake). To test whether introgression was occurring, logperch were also sampled from known *P. c. caprodes* populations in the Monogahela River drainage of West Virginia, while *P. bimaculata* and *P. kathae* from the Susquehanna and Mobile river drainages respectively, were also compared to examine whether differences between *P. c. caprodes* and *P. c. semifasciata* appear to be specific. Only logperch >70mm total length were measured in this study in order to ensure that all fishes were mature (Scott & Crossman 1973). Collection data for all specimens measured in this study are given in Table 6.1. Fishes were either collected by backpack electrofishing in streams, or by using a Missouri or PSU electrified trawl (Herzog et al. 2005, Freedman et al. 2009b) in the main stem of

the Allegheny River. All fishes are either catalogued in the Pennsylvania State University Fish Museum, or will be catalogued there shortly.

The 30 morphometric and 11 meristic measurements used in this analysis are summarized in Table 6.2. All morphometric measurements were to the nearest 0.01 mm using Fowler Sylvac digital calipers, while meristic counts were exact counts of the number of fin spines, fin rays, and scales. Morphometric data were analyzed using sheared principal components analysis (SPCA) in which size is regressed against the covariance matrix, thus providing information about the shape of the organism independent of size (Humphries et al. 1981). Meristic counts were analyzed using principal component analysis (PCA) from a correlation matrix. Comparisons among drainages and habitats were illustrated by plotting the second sheared principal component of morphometric data (SPC2) against the first principal component of meristic data (PC1). Multivariate analysis of variance (MANOVA) with Duncan's multiple range test was used to test for significant ($p < 0.05$) differences both among populations and species, and for differences among habitats within populations. All statistical analyses were performed using SAS, and graphs were made using SigmaPlot 8.0.

Results

Differences in Logperch Among Drainages

Percina kathae were significantly different from all other logperch in meristic data, but were not significantly different from Allegheny and Monongahela *P. c. caprodes* and *P. c. semifasciata* in morphometric data. Figure 6.1 shows that, when all data is considered, *P. kathae* is distinct from other logperch taxa (Tables 6.3, 6.4, and 6.5). *Percina bimaculata* and *P. c. semifasciata* were not significantly different morphometrically but did differ meristically, and *P.*

bimaculata appeared to be distinct from other logperch in Figure 6.1, albeit with only two individuals of *P. bimaculata* in the analyses (Tables 6.3, 6.4, and 6.5). Despite *P. c. caprodes* from the upper Genesee River drainage appearing darker in colouration from those from other drainages, *Percina c. caprodes* populations were not significantly different from one another in either analysis, but were significantly different from *P. c. semifasciata* in both analyses (Tables 6.3, 6.4, and 6.5; Figure 6.1).

Percina kathae had higher fin ray and scale counts, while *P. c. semifasciata* and *P. bimaculata* were lowest in these counts and *P. c. caprodes* were intermediate (Table 6.3 and Figure 6.1). *Percina bimaculata* were stouter in morphometric measurements than other the logperches. *Percina c. semifasciata* had a relatively long head and short dorsal and anal fins, consistent with the lower fin spine and ray counts.

Differences in Logperch Among Habitats

Analysis of the SPCA and PCA and Duncan's multiple range test revealed no differences between *P. c. semifasciata* from Lake Erie and its tributary streams (Figure 6.2). There were, however, differences among *P. c. caprodes* among habitats. *Percina c. caprodes* from lake habitat were significantly different from *P. c. caprodes* from the Middle and Lower Allegheny River in both meristics and morphometrics, but were not different from Lower Allegheny River populations in meristics, or from stream habitat fish in either factor (Tables 6.6, 6.7, and 6.8; Figure 6.3).

Lake habitat logperch had generally lower scale counts than did those from other habitats (Table 6.6). While logperch from the Lower Allegheny River and Allegheny Lake habitats were not similar in overall morphometric analysis, they did differ from other habitats in some key measurements relating to ecomorphology. Lake and Lower Allegheny River logperch had

relatively slender heads and bodies (HD, HW, BD, AD2AA) compared to those from other habitats. Relative caudal peduncle size (LCPD and CPW), however, was lower than those from other habitats (Table 6.6). Analysis of all *P. c. caprodes* (those from different habitats in the Allegheny drainage, from the Genesee River, and the Monongahela River drainage) revealed that Allegheny Lake fish were morphometrically distinct from all other *P. c. caprodes*, while Middle River and Stream fish were also distinct from one another. There were no differences in meristic counts among populations (Table 6.6; Figure 6.3).

Discussion

Logperch Speciation and Distribution

Percina c. caprodes and *P. c. semifasciata* are as dissimilar to one another as either is from *P. kathae* or *P. bimaculata*, respectively (Figure 6.1). On the basis of meristic data alone it would be possible to argue that *P. bimaculata* and *P. c. semifasciata* are more similar to one another than either to *P. c. caprodes* (Table 6.3) and, in fact, they were considered synonymous until recently described as separate species (Near 2008). The lack of scales on the nape was considered to be a synapomorphic trait, suggestive of shared common ancestry for *P. bimaculata* and *P. c. semifasciata*. However, the phylogenetic evidence suggests that this is rather a homoplasy, while the presence of nape scales, present throughout the other logperch taxa and most other *Percina* species (Page 1983, Near 2008), is the plesiomorphic character state.

Percina c. caprodes and *P. c. semifasciata* occupy predominantly allopatric ranges, although their ranges overlap near the Great Lakes-Ohio River interface, where intergradation occurs (Trautman 1957, Smith 1985). Logperch in unglaciated regions of Ohio consist entirely of *P. c. caprodes* (Trautman 1981), while *P. c. semifasciata* are found throughout the northern range

of *P. caprodes*. Trautman (1981) noted that *P. c. semifasciata* were found near offshore islands in western Lake Erie, while along the shore and in tributary streams intergrades with *P. c. caprodes* were increasingly more common towards the eastern end of the lake, although pure *P. c. caprodes* were seldom encountered.

On the basis of intermittent nape scalation, it appears that logperch in the Allegheny Lake may be intergrades between *P. c. semifasciata* and *P. c. caprodes* which they otherwise resemble (Figures 6.1 and 6.3). In the Allegheny River basin of western Pennsylvania, evidence for intergrades was noted in the northern part of the basin (Raney 1939). (Moenkhaus 1894) noted a general decrease in the numbers of spines and anal rays with increasing latitude among logperches, as well as a broad overlap between *P. c. caprodes* and *P. c. semifasciata* colour patterns throughout the Great Lakes region.

In describing *P. bimaculata* as a distinct species “rescued from synonymy,” Near (2008) evaluated its phylogenetic relationships to other logperch species and populations. In his analysis, *P. caprodes* appears to be polyphyletic, with clear genetic distinctions between the eastern (*P. c. caprodes*) and western (*P. c. semifasciata*) drainages of the Mississippi River drainage. *Percina c. caprodes* is more closely related phylogenetically to other Mississippi and Atlantic drainage logperch species such as *P. bimaculata*, *P. kathae*, and *P. fulvitaenia* Morris and Page, than to *P. c. semifasciata*, which is genetically distinct from this clade. These phylogenies support the theory that *P. c. semifasciata* developed in allopatric isolation from the *P. c. caprodes* clade, and that the present sympatry of these taxa in parts of the Mississippi and Great Lakes drainage is a later development and likely occurred after the speciation events resulting in the other logperch species.

There are twelve recognized species of logperch. (Near and Benard 2004) documented speciation rates in logperch, and determined that rapid allopatric speciation occurs in this taxa. *Percina rex* diverged from other logperch taxa approximately 4.20 million years ago, while the clades containing *P. caprodes* and *P. kathae* diverged roughly 780 kya. *Percina bimaculata*,

described in (Near 2008), clusters with *P. kathae* rather than *P. caprodes* in this phylogenetic analysis. Biogeographically, *P. caprodes* and *P. bimaculata* would be expected to be closely associated as they are in adjacent drainages. Closely-related sister species pairs, *P. kathae* and *P. austroperca*, and *P. caprodes* and *P. suttkusi*, occur allopatrically, lending support to the theory that logperch speciation was allopatric rather than sympatric, and that co-occurrence of species is a more recent development (Near and Benard 2004). In fact, Near and Benard (2004) also showed that of the three instances of extensive sympatry in logperches, two consist of species which diverged over two million years ago.

Logperch from the Genesee River, a tributary of Lake Ontario within the Great Lakes drainage, are *P. c. caprodes* rather than *P. c. semifasciata* (Figure 6.1). While much darker in colouration (Pers. Obs.), they are no different from Allegheny or Monogahela drainage *P. c. caprodes* in meristic or morphometric analysis. Thus, while *P. c. semifasciata* colonized the Great Lakes drainage above Niagara Falls, this is evidence that Lake Ontario, and perhaps the rest of the eastern Saint Lawrence Drainage, were colonized by *P. c. caprodes* from the Ohio River drainage. The Genesee River was connected with both the Susquehanna and Allegheny Rivers at various times during the Pleistocene, with stream capture events acting as a likely route for fish species dispersal between these basins (Hocutt et al. 1986). It is not unreasonable to suppose that *P. c. caprodes* colonized the Susquehanna and Potomac river basins through this route and, upon glacial retreat and loss of connectivity with the Genesee and Allegheny drainages, evolved into *P. bimaculata* in allopatric isolation. Genesee River *P. c. caprodes*, meanwhile, remained connected to the Allegheny River for a longer period of time and have not been isolated for a sufficient time to form a new species. The relatively recent speciation events of logperches (Near and Benard 2004) suggest that this is a more likely route than direct connectivity during the Pliocene, although later stream-capture events between the Allegheny and Suquehanna or the Potomac and Youghiogheny are also a possibility (Hocutt et al. 1986).

Alternatively, since *P. bimaculata*, *P. kathae*, and *P. austroperca* are phylogenetically related, diverging approximately 0.50 to 0.42 mya (Near and Benard 2004, Near 2008) and inhabit Atlantic (*P. bimaculata*) and Gulf (*P. kathae* and *P. austroperca*) drainages, we can posit dispersal along the Atlantic coast. *Percina bimaculata* would then have survived in the Atlantic glacial refugium during the Wisconsin glacial maximum. *Percina c. caprodes* is most closely related to *P. fulvitaenia*, found in the Ozarks, and its range includes much of the eastern Mississippi drainage (Near and Benard 2004, Near 2008). This supports survival in the Mississippian glacial refugium and subsequent invasion into the Ohio River system. *Percina c. semifasciata* are genetically distinct from other logperches (Near and Benard 2004, Near 2008) and may have survived glaciation in the Missourian glacial refugium. They could have subsequently invaded the western Mississippi Valley in the Pleistocene from preglacial Hudson Bay or Laurentian stream systems (Pflieger 1970, Robison 1986), or dispersed throughout their range via the ancient Lake Agassiz, which would help to explain their range up to the Hudson Bay drainage.

Ecomorphology

Many fish species can inhabit different habitats, and may have different ecological, life-history, and morphological traits depending on where they reside. Phenotypic plasticity and character displacement are well-documented in fishes (Robinson and Wilson 1994, Stauffer and Gray 2004). Behavioural and life-history traits may also vary among different habitats, which can have evolutionary consequences (Schluter and McPhail 1992, Freedman and Noakes 2002, McKinnon et al. 2004), but may be difficult to detect in morphology or meristic counts.

While there were no differences between *P. c. semifasciata* from streams and lake habitats, there were differences among habitats for *P. c. caprodes* from the Allegheny River

drainage. *P. c. caprodes* from lake and dam-influenced sites had caudal peduncles that were less deep and less wide than *P. c. caprodes* from more lotic environments. Imre et al. (2002) showed that brook charr raised in higher velocities had deeper and wider caudal peduncles than those from slower flowing water. They also found, however, that brook charr from lower velocities had deeper bodies, which is the opposite of my findings with logperch which had larger heads and bodies in higher velocities. Kerfoot and Schaefer (2006) found that *Cottus* from deeper and slower streams had larger heads and bodies, but also narrower caudal peduncles, while those from faster velocity streams had deeper caudal peduncles. Larger caudal peduncles are clearly associated with adaptation to higher velocities, as are relatively larger heads and bodies.

Relative to most other darters, logperch are habitat generalists. In a study of darter habitat partitioning in West Virginia streams, logperch were associated with riffle-pool transition areas, and were typically found hovering above the substrate (Welsh and Perry 1998). This behaviour is consistent with logperch having relatively large swim bladders (23.9-26.5% standard length) compared to other darters, a trait which is also associated with slower-flowing pool habitats (Evans and Page 2003). (Stauffer et al. 1996) found that logperch were associated with deeper habitats than most other darter species in French Creek, Pennsylvania, resulting in strong microhabitat segregation with other darters. Logperch were also associated with deeper, slower water in the Little River of Tennessee, than were most other, smaller darter species (Greenberg 1991). Greenberg (1991) hypothesized that this segregation by body size resulted from size-selective predation on smaller fishes by predators in the deeper areas rather than habitat preference of the darters themselves, although it seems likely that other variables are also a factor.

Percina caprodes acquired the specific name, *caprodes*, meaning “pig-like” in reference to the shape of their snout that is shared with other members of the group (Rafinesque 1820, Scott and Crossman 1973). While young logperch feed predominantly on zooplankton such as cladocerans and copepods, they switch to a diet of chironomid larvae, amphipods, isopods, dragonfly nymphs, and mayfly nymphs as they grow (Scott and Crossman 1973). Indeed, the

shape of their snout appears to be an adaptation for rolling or flipping small stones in their search for food. This suggests alternate foraging behaviours – either flipping rocks during active foraging, or hovering in the water column and waiting for benthic prey to emerge. Particularly during hover foraging, the ability to maintain position in the water column would be vital to efficient foraging.

There is an apparent lack of ecomorphological adaptations in Lake Erie drainage *P. c. semifasciata*, as there are no differences either in the MANOVA or direct comparisons of morphological data (Figure 6.2). *Percina c. semifasciata* from Lake Erie have LCPD similar to stream-dwelling Allegheny drainage *P. c. caprodes*, but CPW consistent with lentic *P. c. caprodes* (Tables 6.4 and 6.7). I assumed that logperch captured in the mouths of streams in Lake Erie were lake-resident forms that had moved in to the streams to spawn. Likewise, I assumed that logperch that were captured well above the mouths in streams were resident forms, particularly if they were above falls or other potential barriers to upstream movements. The lack of morphological and meristic differentiation between the purported lake and stream forms likely indicates that there is no ecomorphological differentiation in this population. Possible reasons include the spawning migration of lake forms, which may select for increased swimming ability both in reaching and swimming within natal streams, relative to non-migratory lake forms. It is also possible that the reason for a lack of differentiation results from their actually being part of a contiguous population, or that intergradation in this population may be resulting in evolution towards generalized morphology rather than ecological specialization.

The Allegheny Reservoir, also known as Kinzua Lake, was formed in 1965 by the construction of the Kinzua Dam. Lock-and-dams have influenced the Allegheny River for up to 100 years. At generation times of 1-2 years, this would suggest either rapid adaptive evolution or phenotypic plasticity in the logperch to provide differences in body depth and caudal peduncle morphology. Such character displacement, including phenotypic plasticity, in fishes is well documented, especially among Cichlidae, Centrarchidae, and Salmonidae, but among many other

taxa as well (Robinson and Wilson 1994). Character displacement due to habitat preference, leading to divergence by benthic and limnetic forms and littoral and pelagic forms, is especially well documented, as are trophic polymorphisms due to feeding preference. Many salmonids have morphological responses to differing environmental conditions (Bourke et al. 1997, Imre et al. 2002, Peres-Neto and Magnan 2004, Grunbaum et al. 2007). Sticklebacks may exhibit character release in the absence of competitors and rapidly evolve different forms or morphs to effectively exploit all available niches (Schluter and McPhail 1992). European perch (*Perca fluviatilis*) exhibit morphological differences depending on diet (Svanback and Eklov 2002, 2006). (Palkovacs et al. 2008, Palkovacs and Post 2008, Post and Palkovacs 2009) showed that alewife have rapid evolution in gill-raker morphology when subjected to land-locked conditions as a result of the rapidly changing prey base community. To the best of my knowledge, however, there are no published studies specifically showing changes in velocity-adapted ecomorphology as a result of dam construction, although many of the studies on charr could certainly be extrapolated to expect similar results (Imre et al. 2001, 2002, Grunbaum et al. 2007).

Conclusions and Future Research

While phylogeny plays a major role in determining morphology, the roles that phylogeography and ecomorphology play in differentiating such species should not be underestimated. As Moenkhaus (1894) noted, there is a trend towards higher dorsal and anal fin rays counts with increasing latitude, while I have observed that Genesee River *P. c. caprodes* had different pigmentation than Ohio River drainage *P. c. caprodes*. Superficial similarities in morphology, such as the lack of nape scales in *P. c. semifasciata* and *P. bimaculata* can be misleading, as it was in this case where the two taxa were synonymized for decades.

Morphological adaptation to different current velocities was apparent in the Allegheny drainage

logperch. Analysis of morphometric data could lead a researcher to falsely conclude that Genesee and Allegheny drainage logperch are separate species if only the lake habitat in the Allegheny was sampled. Understanding the role of environment and habitat in structuring fish morphology is therefore important in understanding taxonomy, particularly in a species which is able to adapt to various habitat types.

While *P. c. caprodes* from lake habitats are morphometrically distinct from other populations, and those from the Lower Allegheny River also show morphological adaptations to slower moving water, the mechanism behind these adaptations is not clear. There may be energetic savings in having these ecological adaptations, thus improving fitness. Alternatively, phenotypic plasticity may be playing a role, as larval or juvenile logperch may have phenotypic responses to their habitat and form their bodies accordingly. If these *P. c. caprodes* are breeding in these lentic habitats rather than migrating to faster flowing waters, this could be support for phenotypic plasticity. Such adaptations could also help explain why there are no ecomorphological differences in *P. c. semifasciata*: if they are spawning in streams, larval fish may be subject to higher velocities during a critical imprinting period. The only way to truly test the mechanism would be to conduct a common-garden experiment in which logperch larvae and juveniles of different lineages are raised and subjected to differing water velocities. If differences are due to phenotypic plasticity, then morphology should be primarily affected by water velocity; while if there is genetic structuring then parental origin should be reflected in juvenile morphology.

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Table 6.1: Collection Information for logperch examined in this study with species, number (number of individuals), collection locality, and PSU Fish Museum Catalogue Number (PSU-xx) or sampling collection number if not yet catalogued into PSU Fish Museum.

Species	Number	Collection Locality	Museum Collection Number
<i>Percina c. caprodes</i>	1	Allegheny River, Pool 8, Templeton, PA	JAF-06-14
<i>Percina c. caprodes</i>	1	Allegheny River, Pool 8, Templeton, PA	JAF-06-15
<i>Percina c. caprodes</i>	1	Allegheny River, Pool 7, Kittanning, PA	JAF-06-29
<i>Percina c. caprodes</i>	1	Allegheny River, Pool 7, Kittanning, PA	JAF-06-32
<i>Percina c. caprodes</i>	1	Allegheny River, Pool 8, Templeton, PA	JAF-06-35
<i>Percina c. caprodes</i>	1	Allegheny River, Pool 8, Templeton, PA	JAF-06-36
<i>Percina c. caprodes</i>	3	Allegheny River, near Salamanca NY	PSU-4799
<i>Percina c. caprodes</i>	1	Allegheny River at Parker City, PA	BDL-08-215
<i>Percina c. caprodes</i>	4	Allegheny River, Warren Co., PA	BDL-09-16
<i>Percina c. caprodes</i>	1	Allegheny River, Pool 7 – below dam, PA	JAF-08-06
<i>Percina c. caprodes</i>	1	Allegheny River at Oil Creek, PA	BDL-08-213
<i>Percina c. caprodes</i>	1	Allegheny River, Hunter PA	BDL-08-203
<i>Percina c. caprodes</i>	1	Allegheny River, Hickory Bridge PA	BDL-08-199
<i>Percina c. caprodes</i>	1	Allegheny River, Trunkville PA	BDL-08-198
<i>Percina c. caprodes</i>	5	French Creek, Cochran PA	PSU-1832
<i>Percina c. caprodes</i>	5	French Creek, Venango PA	PSU-2240
<i>Percina c. caprodes</i>	6	Kinzua Lake at mouth of Kinzua Creek, Warren Co. PA	JAF-09-07
<i>Percina c. caprodes</i>	7	Genesee River, Wellsville NY	PSU-4938
<i>Percina c. caprodes</i>	8	West Fork River, Weston WV	PSU-1817
<i>Percina c. semifasciata</i>	3	Presque Isle Bay, Erie Co. PA	PSU-2348
<i>Percina c. semifasciata</i>	4	Walnut Creek mouth, Erie Co. PA	PSU-1628
<i>Percina c. semifasciata</i>	5	16-Mile Creek mouth, Erie Co. PA	JAF-09-02
<i>Percina c. semifasciata</i>	3	16-Mile Creek above falls, Erie Co. PA	JAF-09-03
<i>Percina c. semifasciata</i>	6	Crooked Creek upstream, Erie Co. PA	JAF-09-06
<i>Percina c. semifasciata</i>	1	Raccoon Creek upstream, Erie Co. PA	PSU-1618
<i>Percina c. semifasciata</i>	3	West Branch Conneaut Creek upstream, Erie Co. PA	PSU-1514

<i>Percina bimaculata</i>	1	West Branch Octoraro Creek, Lancaster Co. PA	PSU-10062
<i>Percina bimaculata</i>	1	Octoraro Creek, Chester-Lancaster Co. PA	PSU-10063
<i>Percina kathae</i>	6	West Armuchee Creek, Chattooga Co. GA	PSU-2082

Table 6.2: Morphometric measurements and meristic counts for assessing logperch morphology, adapted from (Hubbs and Lagler 1958, Page 1983).

Morphometric		Meristic	
SL	Standard length	DSPINES	Dorsal fin spines
HL	Head length	DRAYS	Dorsal fin rays
HW	Head width	P1RAYS	Pectoral fin rays
SNL	Snout length	P2RAYS	Pelvic fin rays
POHL	Post-orbital head length	ARAYS	Anal fin spines + rays
HED	Horizontal eye diameter	LLS	Lateral line scales
VED	Vertical eye diameter	PLS	Post-lateral line scales
HD	Head depth	LCPS	Least caudal peduncle scales
UJL	Upper jaw length	SALL	Scales above lateral line
LJL	Lower jaw length	SBLL	Scales below lateral line
SNDOR	Snout to dorsal fin length	STLL	Scales transverse lateral line
SNP2	Snout to pelvic fin length		
BD	Body depth		
DFBL1	First dorsal fin base length		
DFBL2	Second dorsal fin base length		
AD1AA	Anterior 1 st dorsal fin to anterior anal fin		
AD1PA	Anterior 1 st dorsal fin to posterior anal fin		
AD2PA	Anterior 2 nd dorsal fin to posterior anal fin		
AD2AA	Anterior 2 nd dorsal fin to anterior anal fin		
PD2AA	Posterior 2 nd dorsal fin to anterior anal fin		

PD2VC	Posterior 2 nd dorsal fin to ventral caudal fin base
PADC	Posterior anal fin to dorsal caudal fin base
P2PA	Pelvic fin to posterior anal fin
P2AA	Pelvic fin to anterior anal fin
ABL	Anal fin base length
PD2P2	Posterior 2 nd dorsal fin to pelvic fin
CPL	Caudal peduncle fin length
LCPD	Least caudal peduncle depth
CPW	Caudal peduncle width
P1L	Pectoral fin length

Table 6.3: Meristic count distribution for *Percina c. caprodes* from the Allegheny, Monongahela, and Genesee river drainages, *P. c. semifasciata* from the Lake Erie drainage, *P. bimaculata* from the Susquehanna River drainage, and *P. kathae* from the Mobile River drainage.

Dorsal Spines				
	13	14	15	16
<i>P. c. caprodes</i> - Allegheny	2	3	27	3
<i>P. c. caprodes</i> - WV		1	6	1
<i>P. c. caprodes</i> - Genesee	1	3	2	1
<i>P. c. semifasciata</i> - Erie	1	13	11	
<i>P. bimaculata</i>	2			
<i>P. kathae</i>			1	5
Dorsal Rays				
	14	15	16	17
<i>P. c. caprodes</i> - Allegheny	4	16	13	2
<i>P. c. caprodes</i> - WV		2	6	
<i>P. c. caprodes</i> - Genesee	1	3	2	1
<i>P. c. semifasciata</i> - Erie	7	7	8	3
<i>P. bimaculata</i>		1	1	
<i>P. kathae</i>		2	4	
Pectoral Rays				
	12	13	14	15 16
<i>P. c. caprodes</i> - Allegheny			4	23 8
<i>P. c. caprodes</i> - WV			2	5 1
<i>P. c. caprodes</i> - Genesee			3	4
<i>P. c. semifasciata</i> - Erie	1		7	12 5
<i>P. bimaculata</i>			2	

P. kathae 3 2 1

Pelvic Rays			
	5	6	7
<i>P. c. caprodes</i> - Allegheny	8	27	
<i>P. c. caprodes</i> - WV	8		
<i>P. c. caprodes</i> - Genesee	7		
<i>P. c. semifasciata</i> - Erie	1	10	14
<i>P. bimaculata</i>	2		
<i>P. kathae</i>	5	1	

Anal Spines + Rays				
	10	11	12	13 14
<i>P. c. caprodes</i> - Allegheny	12	23		
<i>P. c. caprodes</i> - WV	8			
<i>P. c. caprodes</i> - Genesee	2	3	2	
<i>P. c. semifasciata</i> - Erie	2	7	11	5
<i>P. bimaculata</i>	1	1		
<i>P. kathae</i>	2	3	1	

Lateral Line Scales																	
	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91 92 93
<i>P. c. caprodes</i> - Allegheny								1	1	4	5	6	7	6	1		
<i>P. c. caprodes</i> - WV									1		1	1	1	3	1		
<i>P. c. caprodes</i> - Genesee											2	3	1		1		
<i>P. c. semifasciata</i> - Erie	1		2	2	1	6	6	2	3		2						
<i>P. bimaculata</i>		1	1														
<i>P. kathae</i>													1		2		1 1 1

Post-lateral line scales												
	0	1	2	3								
<i>P. c. caprodes</i> - Allegheny	2	3	18	12								
<i>P. c. caprodes</i> - WV	1	3	2	2								
<i>P. c. caprodes</i> - Genesee		1	6									
<i>P. c. semifasciata</i> - Erie		5	14	6								
<i>P. bimaculata</i>		2										
<i>P. kathae</i>	1		3	2								

Least Caudal Peduncle Scales												
	25	26	27	28	29	30	31	32	33	34	35	36 37
<i>P. c. caprodes</i> - Allegheny					1	7	6	8	9	4		
<i>P. c. caprodes</i> - WV						3	2		2		1	
<i>P. c. caprodes</i> - Genesee						1	5				1	
<i>P. c. semifasciata</i> - Erie	3	2	4	3	10	1	2					
<i>P. bimaculata</i>			2									
<i>P. kathae</i>								2		2	1	1

Scales Above Lateral Line												
	5	6	7	8	9	10	11	12	13	14		
<i>P. c. caprodes</i> - Allegheny		2	2	11	16	3			1			
<i>P. c. caprodes</i> - WV			1		1	4	1	1				
<i>P. c. caprodes</i> - Genesee				2	2	3						
<i>P. c. semifasciata</i> - Erie	3	3	12	3	3	1						
<i>P. bimaculata</i>			2									
<i>P. kathae</i>							4	1		1		

Scales Below Lateral Line																	
	11	12	13	14	15	16	17	18	19	20	21						
<i>P. c. caprodes</i> - Allegheny		1	3	4	16	8	3										
<i>P. c. caprodes</i> - WV				1	3	2		1	1								
<i>P. c. caprodes</i> - Genesee			3	1	1	1	1										
<i>P. c. semifasciata</i> - Erie	3	6	10	3	2	1											
<i>P. bimaculata</i>				2													
<i>P. kathae</i>							1	2	1		2						
Scales Transverse Lateral Line																	
	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35
<i>P. c. caprodes</i> - Allegheny					1	4	5	10	9	4	2						
<i>P. c. caprodes</i> - WV						1	2	2		1		1	1				
<i>P. c. caprodes</i> - Genesee					2	1		1	1	1	1						
<i>P. c. semifasciata</i> - Erie	1	2	6	4	3	4	4		1								
<i>P. bimaculata</i>					2												
<i>P. kathae</i>													1	1	2	1	1

Table 6.4: Morphometric measurements for *Percina c. caprodes* from the Allegheny, Monongahela, and Genesee river drainages, *P. c. semifasciata* from Lake Erie drainage, *P. bimaculata* from the Susquehanna River drainage, and *P. kathae* from the Mobile River drainage.

	<i>Percina c. caprodes</i>				<i>Percina c. caprodes</i>				<i>Percina c. caprodes</i>			
	(Allegheny), n=35				(Monongahela), n=8				(Genesee), n=7			
Variable	Mean	SD	Min	Max	Mean	SD	Min	Max	Mean	SD	Min	Max
SL (mm)	89.0	11.7	72.0	126.3	91.8	10.8	72.5	103.8	93.7	1.6	91.6	96.0
HL(mm)	22.9	3.0	18.5	32.0	23.2	2.6	18.4	26.3	23.8	0.8	22.8	24.9
Percent of Head Length												
HW	46.6	3.3	40.0	53.0	49.1	2.2	46.0	52.0	47.0	2.8	42.0	50.0
SNL	33.1	2.2	28.0	37.0	34.5	2.0	31.0	38.0	35.0	1.4	33.0	37.0
POHL	47.1	1.8	41.0	51.0	48.9	1.6	46.0	51.0	47.0	1.2	45.0	48.0
HED	22.5	1.8	19.0	27.0	22.4	1.7	19.0	24.0	20.1	0.7	19.0	21.0
VED	20.9	1.4	19.0	25.0	21.8	1.3	20.0	24.0	21.1	1.9	19.0	25.0
HD	48.6	4.5	39.0	56.0	53.9	4.3	46.0	61.0	49.0	2.9	44.0	52.0
UJL	21.1	2.9	16.0	29.0	19.8	1.7	17.0	22.0	20.0	2.1	17.0	23.0
LJL	15.1	2.6	11.0	23.0	15.4	1.5	13.0	17.0	14.7	1.3	13.0	16.0
Percent of Standard Length												
SNDOR	31.1	1.2	27.0	33.0	31.9	1.4	30.0	34.0	31.7	0.5	31.0	32.0
SNP2	29.5	1.1	27.0	31.0	29.0	1.1	27.0	30.0	28.0	0.6	27.0	29.0
BD	14.1	2.4	9.4	21.6	14.5	1.9	10.8	16.7	15.1	0.7	14.5	16.5
DFBL1	31.5	1.5	29.0	35.0	31.4	1.1	30.0	33.0	31.9	0.9	31.0	33.0
DFBL2	22.5	1.4	19.0	25.0	23.1	1.2	21.0	25.0	23.9	0.9	23.0	25.0
AD1AA	35.9	1.3	32.0	39.0	36.0	1.2	35.0	38.0	35.6	1.5	34.0	38.0
AD1PA	50.9	1.8	47.0	53.0	50.8	0.9	50.0	52.0	51.6	1.4	49.0	53.0
AD2PA	18.1	3.0	13.9	26.3	19.6	2.9	14.1	22.9	19.7	1.1	18.2	21.6
AD2AA	12.6	2.1	9.4	19.0	13.8	1.7	10.4	15.8	13.4	0.4	13.1	14.0
PD2AA	21.5	4.0	15.8	34.1	22.6	3.3	16.2	26.6	23.8	1.0	22.7	25.1

PD2VC	18.3	1.1	16.0	20.0	18.4	1.1	17.0	20.0	17.9	0.7	17.0	19.0
PADC	23.6	1.6	20.0	26.0	23.3	1.3	22.0	25.0	24.3	0.8	23.0	25.0
P2PA	50.2	1.5	45.0	53.0	50.4	1.2	49.0	52.0	50.1	0.4	50.0	51.0
P2AA	34.5	1.3	32.0	37.0	34.1	0.6	33.0	35.0	33.6	1.0	32.0	35.0
ABL	15.8	1.2	14.0	20.0	16.9	0.8	16.0	18.0	16.6	1.0	15.0	18.0
PD2P2	55.8	2.1	50.0	59.0	52.3	11.1	25.0	58.0	57.4	0.8	56.0	58.0
CPL	22.3	1.4	18.0	25.0	22.0	1.1	21.0	24.0	23.3	1.3	21.0	25.0
LCPD	7.6	0.5	7.0	8.0	7.9	0.4	7.0	8.0	7.3	0.5	7.0	8.0
CPW	4.8	0.6	4.0	6.0	5.5	0.8	5.0	7.0	5.0	0.0	5.0	5.0
PL1	18.6	1.2	17.0	21.0	18.8	1.0	17.0	20.0	19.4	0.5	19.0	20.0
HL	25.7	1.0	24.0	28.0	25.1	0.6	24.0	26.0	25.3	1.0	24.0	27.0

	<i>Percina c. semifasciata</i>				<i>Percina kathae</i>				<i>Percina bimaculata</i>			
	(Erie), n=25				(Mobile), n=6				(Susquehanna), n=2			
Variable	Mean	SD	Min	Max	Mean	SD	Min	Max	Mean	SD	Min	Max
SL (mm)	95.0	11.4	72.2	120.6	110.7	4.9	104.1	115.2	93.3	10.5	85.9	100.7
HL(mm)	25.1	3.2	19.0	32.1	28.8	1.4	26.9	30.2	22.8	1.0	22.1	23.5
Percent of Head Length												
HW	48.9	3.0	44.0	55.0	49.5	1.6	48.0	52.0	54.0	1.4	53.0	55.0
SNL	33.1	1.7	29.0	36.0	34.8	0.8	34.0	36.0	33.5	0.7	33.0	34.0
POHL	46.6	1.3	44.0	49.0	49.7	1.0	48.0	51.0	51.0	2.8	49.0	53.0
HED	22.2	1.6	20.0	25.0	20.0	0.6	19.0	21.0	22.5	0.7	22.0	23.0
VED	21.1	1.5	19.0	24.0	18.8	1.0	18.0	20.0	21.0	1.4	20.0	22.0
HD	51.5	3.0	45.0	57.0	52.3	1.9	50.0	54.0	55.0	2.8	53.0	57.0
UJL	23.4	2.8	20.0	32.0	23.0	1.8	20.0	25.0	19.5	0.7	19.0	20.0
LJL	15.6	1.3	13.0	18.0	16.2	1.2	14.0	17.0	15.5	0.7	15.0	16.0
Percent of Standard Length												

SNDOR	32.1	1.1	30.0	34.0	31.2	0.4	31.0	32.0	31.0	0.0	31.0	31.0
SNP2	31.0	1.7	27.0	34.0	30.7	1.5	29.0	33.0	29.5	2.1	28.0	31.0
BD	15.9	2.2	12.1	19.7	19.1	0.9	17.5	19.8	15.5	1.4	14.5	16.5
DFBL1	29.7	1.9	26.0	32.0	33.5	2.0	32.0	36.0	32.0	0.0	32.0	32.0
DFBL2	20.6	1.6	18.0	23.0	22.3	0.5	22.0	23.0	22.0	0.0	22.0	22.0
AD1AA	36.5	1.3	34.0	39.0	36.8	1.3	36.0	39.0	36.5	0.7	36.0	37.0
AD1PA	49.0	2.9	36.0	51.0	52.2	1.2	51.0	54.0	51.5	0.7	51.0	52.0
AD2PA	19.1	3.0	14.8	25.4	23.1	1.1	21.5	24.2	20.2	2.2	18.6	21.7
AD2AA	14.4	3.6	8.6	25.6	17.0	0.8	16.0	17.8	14.5	1.4	13.5	15.5
PD2AA	21.6	3.0	16.0	27.9	28.0	1.7	24.9	29.5	22.6	3.0	20.5	24.7
PD2VC	18.4	1.0	16.0	20.0	18.7	2.2	17.0	23.0	19.0	0.0	19.0	19.0
PADC	24.0	1.0	22.0	26.0	22.3	0.8	21.0	23.0	24.5	0.7	24.0	25.0
P2PA	49.3	1.3	47.0	52.0	49.3	1.2	48.0	51.0	49.5	2.1	48.0	51.0
P2AA	35.4	1.3	33.0	37.0	33.2	1.0	32.0	34.0	34.5	2.1	33.0	36.0
ABL	14.3	1.2	12.0	17.0	17.2	1.0	16.0	18.0	17.0	0.0	17.0	17.0
PD2P2	55.6	1.5	53.0	60.0	56.2	0.8	55.0	57.0	55.0	2.8	53.0	57.0
CPL	22.8	1.6	18.0	25.0	21.5	0.8	20.0	22.0	21.5	0.7	21.0	22.0
LCPD	7.8	0.5	7.0	9.0	8.0	0.0	8.0	8.0	8.0	0.0	8.0	8.0
CPW	4.4	0.6	4.0	6.0	4.3	0.5	4.0	5.0	5.0	0.0	5.0	5.0
PL1	20.0	1.3	17.0	22.0	19.3	0.8	18.0	20.0	20.0	2.8	18.0	22.0
HL	26.4	0.8	25.0	28.0	26.0	0.0	26.0	26.0	24.5	2.1	23	26

Table 6.5: Differences in morphometric measurements (SPC2, upper diagonal) and meristic counts (PC1, lower diagonal) for logperches from the Allegheny River (*Percina c. caprodes*), Lake Erie (*P. c. semifasciata*), Genesee River (*P. c. caprodes*), Monongahela River (*P. c. caprodes*), Mobile River (*P. kathae*), and Susquehanna River (*P. bimaculata*) drainages. “X” denotes statistically significant (Duncan’s Multiple Range Test; $p < 0.05$) differences in that variable between drainages.

Meristic Data – PC1	Morphometric Data – SPC2						
		Allegheny	Erie	Genesee	Mon.	Mobile	Susq.
	Allegheny		X				
	Erie	X		X	X		X
	Genesee		X			X	
	Mon.		X	X			
	Mobile	X	X	X	X		X
	Susq.	X		X	X	X	

Table 6.6: Meristic Counts for Allegheny River drainage *Percina c. caprodes* in lake and stream habitats, and in the lower (dam influenced), middle, and upper Allegheny River.

Dorsal Spines				
	13	14	15	16
Allegheny Lake (Kinzua)	1		5	
Lower Allegheny River		1	6	
Middle Allegheny River		1	6	2
Upper Allegheny River			3	
Allegheny Stream (French Ck.)	1	1	7	1
Dorsal Rays				
	14	15	16	17
Allegheny Lake (Kinzua)		4	2	
Lower Allegheny River	3	1	2	1
Middle Allegheny River		5	3	1
Upper Allegheny River	1	2		
Allegheny Stream (French Ck.)		4	6	
Pectoral Rays				
	14	15	16	
Allegheny Lake (Kinzua)		6		
Lower Allegheny River		3	4	
Middle Allegheny River	2	5	2	
Upper Allegheny River		2	1	
Allegheny Stream (French Ck.)	2	7	1	
Pelvic Rays				
	6	7		

Allegheny Lake (Kinzua)	6
Lower Allegheny River	1 6
Middle Allegheny River	5 4
Upper Allegheny River	1 2
Allegheny Stream (French Ck.)	1 9

Anal Spines + Rays

12 13 14

Allegheny Lake (Kinzua)	4 2
Lower Allegheny River	1 6
Middle Allegheny River	3 6
Upper Allegheny River	1 2
Allegheny Stream (French Ck.)	3 7

Lateral Line Scales

82 83 84 85 86 87 88 89 90

Allegheny Lake (Kinzua)	1	1	2	1		1			
Lower Allegheny River				1	1	2	1	1	1
Middle Allegheny River			1	1	1		4		2
Upper Allegheny River						2			1
Allegheny Stream (French Ck.)			1	2	4	2	1		

Post-lateral line scales

0 1 2 3

Allegheny Lake (Kinzua)			2	4
Lower Allegheny River			6	1
Middle Allegheny River	2	1	2	4

Upper Allegheny River	1	1	1
Allegheny Stream (French Ck.)	1	7	2

Least Caudal Peduncle Scales						
	29	30	31	32	33	34
Allegheny Lake (Kinzua)	1	1	1	2		1
Lower Allegheny River				2	3	2
Middle Allegheny River		2	4	1	2	
Upper Allegheny River				2	1	
Allegheny Stream (French Ck.)		4	1	1	3	1

Scales Above Lateral Line							
	7	8	9	10	11	12	13
Allegheny Lake (Kinzua)	2	2		2			
Lower Allegheny River			4	2	1		
Middle Allegheny River			1	6	2		
Upper Allegheny River			1	2			
Allegheny Stream (French Ck.)			5	4			1

Scales Below Lateral Line						
	12	13	14	15	16	17
Allegheny Lake (Kinzua)			2	3	1	
Lower Allegheny River	1	1		1	2	2
Middle Allegheny River			1	6	2	
Upper Allegheny River			1	1		1
Allegheny Stream (French Ck.)		2		5	3	

Scales Transverse Lateral Line						
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	23	24	25	26	27	28	29
Allegheny Lake (Kinzua)		2	1	1	1	1	
Lower Allegheny River	1	1		1	2	2	
Middle Allegheny River			1	4	2	1	1
Upper Allegheny River			1		1		1
Allegheny Stream (French Ck.)		1	2	4	3		

Table 6.7: Morphometric Measurements for Allegheny River drainage *Percina c. caprodes* in lake and stream habitats, and in the lower (dam influenced), middle, and upper Allegheny River.

Allegheny Lake (Kinzua),												
	n=6				Lower Allegheny River, n=7				Middle Allegheny River, n=9			
Variable	Mean	SD	Min	Max	Mean	SD	Min	Max	Mean	SD	Min	Max
SL (mm)	83.5	9.2	72.6	94.1	82.1	6.8	72.0	93.5	93.2	9.5	81.5	108.6
HL(mm)	21.7	1.9	19.9	24.6	20.7	1.6	18.5	23.0	24.1	2.1	21.0	27.2
Percent of Head Length												
HW	45.2	2.9	42.0	50.0	44.1	4.1	40.0	52.0	47.6	2.8	42.0	50.0
SNL	32.8	1.2	32.0	35.0	30.7	2.3	28.0	34.0	32.8	1.6	30.0	35.0
POHL	47.3	1.4	46.0	50.0	48.7	1.6	46.0	51.0	46.3	2.5	41.0	49.0
HED	21.8	1.5	20.0	24.0	23.7	2.0	22.0	27.0	21.9	1.3	20.0	24.0
VED	21.3	2.0	20.0	25.0	21.1	1.5	19.0	23.0	20.7	1.0	19.0	22.0
HD	45.3	2.2	42.0	48.0	48.7	4.1	43.0	54.0	49.8	4.1	43.0	54.0
UJL	23.5	1.0	22.0	25.0	18.9	1.5	16.0	20.0	20.0	2.0	16.0	23.0
LJL	17.3	3.9	12.0	23.0	14.6	1.6	12.0	16.0	13.8	2.6	11.0	18.0
Percent of Standard Length												
SNDOR	31.5	0.8	31.0	33.0	30.0	0.8	29.0	31.0	30.8	1.7	27.0	33.0
SNP2	29.5	1.0	28.0	31.0	29.3	1.4	27.0	31.0	29.6	0.9	29.0	31.0
BD	12.9	1.5	10.4	14.2	12.3	2.1	9.4	16.0	14.9	1.9	12.3	18.1
DFBL1	31.0	1.1	29.0	32.0	31.7	2.1	29.0	35.0	31.4	1.7	29.0	34.0
DFBL2	22.2	0.4	22.0	23.0	23.4	1.0	22.0	25.0	22.4	1.2	20.0	24.0
AD1AA	35.2	1.3	33.0	37.0	35.4	1.9	32.0	37.0	36.4	1.1	35.0	39.0
AD1PA	51.3	1.4	49.0	53.0	50.7	2.4	47.0	53.0	50.7	1.8	47.0	52.0
AD2PA	16.4	2.3	14.3	20.0	17.3	2.6	14.6	22.3	19.3	3.1	14.7	24.1
AD2AA	11.3	0.9	9.7	12.0	10.8	1.3	9.4	13.3	13.7	1.8	11.1	16.5
PD2AA	19.6	2.2	17.0	22.8	19.6	2.1	16.6	23.1	22.1	3.1	17.2	28.4
PD2VC	18.5	1.0	17.0	20.0	17.4	1.4	16.0	20.0	18.4	0.5	18.0	19.0

PADC	23.8	1.6	21.0	25.0	22.1	2.0	20.0	26.0	23.6	1.0	22.0	25.0
P2PA	49.8	1.2	49.0	52.0	49.6	2.1	45.0	51.0	50.9	1.1	50.0	53.0
P2AA	34.3	0.8	33.0	35.0	33.1	1.2	32.0	35.0	35.2	0.7	34.0	36.0
ABL	15.5	1.0	14.0	17.0	16.4	2.0	14.0	20.0	16.0	1.1	15.0	18.0
PD2P2	55.0	1.3	54.0	57.0	56.7	1.4	54.0	58.0	56.7	1.4	54.0	58.0
CPL	23.3	0.8	22.0	24.0	21.0	2.2	18.0	25.0	22.3	1.0	21.0	24.0
LCPD	7.2	0.4	7.0	8.0	7.4	0.5	7.0	8.0	7.8	0.4	7.0	8.0
CPW	4.5	0.5	4.0	5.0	4.4	0.5	4.0	5.0	4.9	0.6	4.0	6.0
PL1	20.0	1.1	18.0	21.0	18.0	1.0	17.0	19.0	18.4	1.2	17.0	21.0
HL	26.0	1.1	25.0	28.0	25.4	0.8	24.0	26.0	26.0	1.3	24.0	28.0

Upper Allegheny River,									
n=3					French Creek, n=10				
Variable	Mean	SD	Min	Max	Mean	SD	Min	Max	
SL (mm)	78.7	7.4	73.6	87.2	96.6	13.2	83.2	126.3	
HL(mm)	20.2	1.9	18.5	22.2	24.8	3.5	21.4	32.0	
Percent of Head Length									
HW	47.3	0.6	47.0	48.0	48.1	2.8	45.0	53.0	
SNL	34.0	1.0	33.0	35.0	34.8	1.8	32.0	37.0	
POHL	46.3	0.6	46.0	47.0	46.7	1.1	45.0	49.0	
HED	24.7	2.1	23.0	27.0	21.9	1.5	19.0	24.0	
VED	22.0	1.0	21.0	23.0	20.4	1.3	19.0	23.0	
HD	52.0	3.6	49.0	56.0	48.4	5.7	39.0	56.0	
UJL	19.3	2.5	17.0	22.0	22.7	3.3	19.0	29.0	
LJL	13.3	0.6	13.0	14.0	15.7	1.8	14.0	19.0	

Percent of Standard Length

SNDOR	32.0	0.0	32.0	32.0	31.5	0.8	30.0	33.0
SNP2	30.7	0.6	30.0	31.0	29.2	1.1	28.0	31.0
BD	13.1	1.6	12.0	14.9	15.8	2.7	12.8	21.6
DFBL1	32.3	1.2	31.0	33.0	31.4	1.1	30.0	34.0
DFBL2	20.3	1.5	19.0	22.0	22.8	1.5	20.0	25.0
AD1AA	36.3	1.2	35.0	37.0	36.0	1.1	34.0	37.0
AD1PA	49.3	2.1	47.0	51.0	51.4	1.4	49.0	53.0
AD2PA	15.0	1.8	13.9	17.0	19.8	2.8	17.5	26.3
AD2AA	11.5	1.4	10.5	13.1	14.0	2.2	12.5	19.0
PD2AA	18.1	3.2	15.8	21.7	24.5	4.8	19.8	34.1
PD2VC	19.7	0.6	19.0	20.0	18.1	1.1	17.0	20.0
PADC	24.3	0.6	24.0	25.0	24.3	1.3	22.0	26.0
P2PA	49.7	0.6	49.0	50.0	50.5	1.5	48.0	52.0
P2AA	34.0	0.0	34.0	34.0	35.1	1.4	32.0	37.0
ABL	15.3	0.6	15.0	16.0	15.6	0.8	14.0	17.0
PD2P2	51.7	2.1	50.0	54.0	56.2	1.8	53.0	59.0
CPL	23.0	1.0	22.0	24.0	22.4	0.8	21.0	24.0
LCPD	8.0	0.0	8.0	8.0	7.8	0.4	7.0	8.0
CPW	4.7	0.6	4.0	5.0	5.1	0.7	4.0	6.0
PL1	18.3	0.6	18.0	19.0	18.4	1.0	17.0	20.0
HL	25.3	0.6	25.0	26.0	25.6	0.8	25.0	27.0

Table 6.8: Differences in morphometric measurements (SPC2, upper diagonal) and meristic counts (PC1, lower diagonal) for *Percina c. caprodes* from Lake (Kinzua reservoir); Lower (impounded), Middle, and Upper Allegheny River; Monongahela River; and Genesee River. “X” denotes statistically significant (Duncan’s Multiple Range Test; $p < 0.05$) differences in that variable between habitats or drainages.

Morphometric Data – SPC2								
Meristic Data – PC1		Lake	Lower	Middle	Upper	Stream	Mon.	Genesee
	Lake		X	X	X	X	X	X
	Lower	X						
	Middle	X	X			X		
	Upper	X	X	X				
	Stream	X	X	X	X			
	Mon.	X	X	X	X	X		
	Genesee	X	X	X	X	X	X	

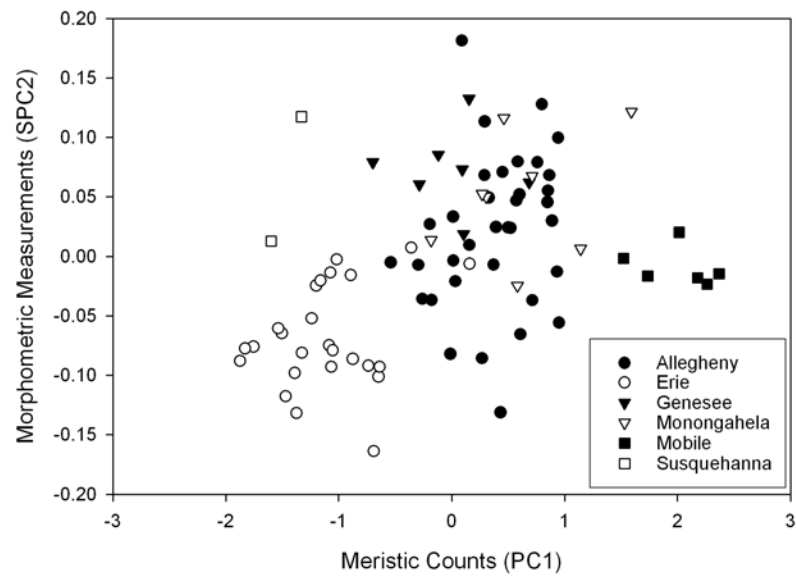
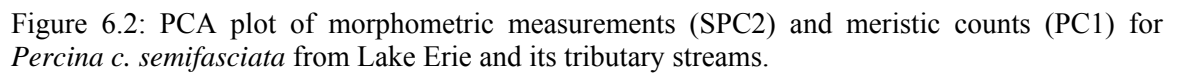


Figure 6.1: PCA plot of morphometric measurements (SPC2) and meristic counts (PC1) for logperches from the Allegheny River (*Percina c. caprodes*), Lake Erie (*P. c. semifasciata*), Genesee River (*P. c. caprodes*), Monongahela River (*P. c. caprodes*), Mobile River (*P. kathae*), and Susquehanna River (*P. bimaculata*) drainages.



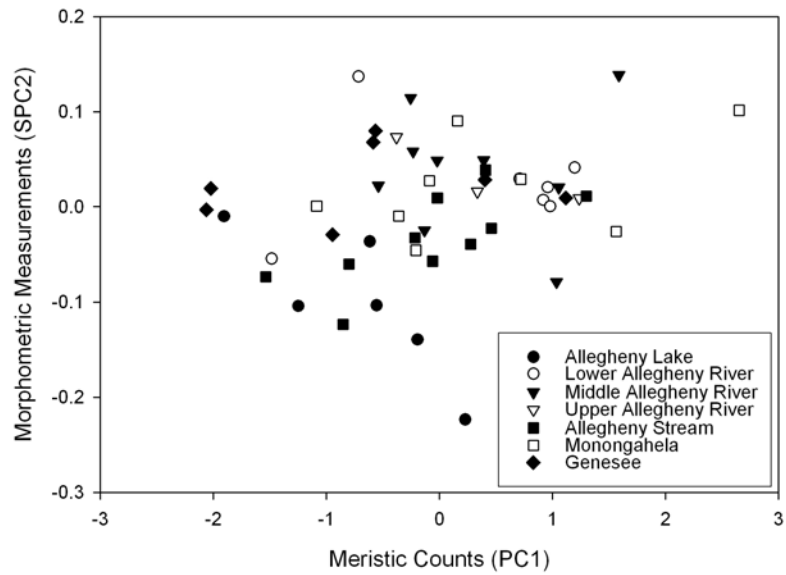


Figure 6.3: PCA plot of morphometric measurements (SPC2) and meristic counts (PC1) for *Percina c. caprodes* from Lake (Kinzua reservoir); Lower (impounded), Middle, and Upper Allegheny River; Monongahela River; and Genesee River.

Chapter 7

General Discussion

Review and Synthesis

I focused primarily on the ichthyofauna of the lock and dam portion of the Allegheny, Monongahela, and Ohio rivers in south-western Pennsylvania. In particular, I introduced and explained the concepts and rationale for evaluating the fish fauna in large rivers (Chapter 1). I followed these explanations with a discussion of the way in which range expansions of darters in the Ohio River could be attributed to a combination of improved sampling gear and improving water quality, but hypothesized that dispersal was limited by the presence of navigation dams (Chapter 2). The conservation status of River Darter, *Percina shumardi*, a new record for Pennsylvania, can now be determined. I specifically demonstrated that the PSU electrified benthic trawl is a more effective tool for sampling small benthic fish species in large rivers (Chapter 3). The PSU trawl was used extensively in my other research chapters, and its increased efficiency in sampling riverine fishes could have ramifications in studies of fish distribution and abundance, and in environmental assessment and monitoring programs.

I continued by examining the relationships among fish species to dredging history and water depth (Chapter 4). I found that while there were no mean differences in fish abundance at dredged and undredged sites, there were differences in species richness (number of species) and diversity (Brillouin Index). These differences were largely driven by a strong negative correlation of species in lithophilic reproductive guilds at dredged sites and in deeper areas. I used stable isotope analysis of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (Chapter 5) to examine differences in food webs among dredged and undredged sites within the influence of navigation dams, and sites upstream from the influence of navigation dams. Fishes from the dam-influenced sections were associated

with shifts from benthic to pelagic-derived nutrients. Food-webs from dredged sites included fewer trophic levels; larger fishes trended towards increased use of benthic or shallow-water nutrients, while smaller fishes showed a trend towards pelagic nutrients. I evaluated the biogeography logperch darters (Chapter 6), and how morphological adaptations to habitats can confound taxonomic studies. The three taxa of logperches found in Pennsylvania (*Percina caprodes caprodes*, *P. c. semifasciata*, and *P. bimaculata*) were morphologically distinct from one another, and there was evidence for ecomorphological adaptations among Logperches in response to dam-induced lacustrine environments. Finally, I synthesize the results of the research chapters and discuss management implications of this research in this Chapter (Chapter 7)

Understanding the Effects of Dams on Fish Ecology

While the locks in navigation lock-and-dam systems provide access between pools, the dams inhibit fish movement. As seen in Chapter 2, *Percina shumardi* was only captured to the base of the DaShields Dam in the Montgomery Pool of the Ohio River (Figure 1.1). Extensive sampling has not collected it in the DaShields or Emsworth pools of the Ohio River (Stauffer Jr. et al. 2010); this suggests that it is indeed recolonizing the Pennsylvania section of the Ohio River rather than simply having been missed in prior surveys. The range of this species will likely expand into the DaShields and Emsworth Pools, and into the Allegheny and Monongahela rivers, but upstream dispersal will likely be slowed by the presence of navigation dams. The extirpation from the Ohio River of anadromous species such as Lake Sturgeon, *Acipenser fulvescens*, can be at least partially explained by the presence of dams. The use of navigation lock chambers by fishes can be confirmed by lockchamber rotenone surveys performed by the Ohio River Sanitation Commission in which almost 3×10^6 fishes comprising 116 fish taxa were collected in 377 sampling events: an average of almost 8,000 fishes per collection (Thomas et al.

2005). Juvenile paddlefish, *Polyodon spathula*, stocked in the Ohio River were also confirmed to have passed through locks in both upstream and downstream directions (Barry et al. 2007).

Stable isotope analysis revealed a shift towards increased reliance on pelagic-derived nutrients by fishes at sites influenced by dams relative to the free-flowing sites above the navigation dam influence. This shift is consistent with shifts from allochthonous to autochthonous and benthic to pelagic nutrients from low-order streams to high-order rivers predicted and observed in other studies (Vannote et al. 1980, Finlay 2001). There were also changes in fish assemblages from free-flowing to dam-influenced sites, with relatively fewer species adapted to higher velocity streams and small rivers, and more large-river species.

Dams can also effect changes to fish morphology. In Chapter 6, I showed how Logperch from the Allegheny Reservoir (lake habitat) are morphologically distinct from Logperch from other habitats. Logperch from the lower Allegheny River, influenced by navigation dams, had similar morphological adaptations to those from a lentic environment, with more slender caudal peduncles but stockier bodies. These morphological changes are consistent with findings in sculpin (Kerfoot and Schaefer 2006), brook charr (Imre et al. 2001, 2002, Peres-Neto and Magnan 2004), and arctic charr (Peres-Neto and Magnan 2004, Grunbaum et al. 2007). Changes in morphology can also lead to trophic shifts and specialization and potentially even speciation events (Schluter and McPhail 1992, Schluter 1993, 2001, Guiguer et al. 2002). There is no evidence for sympatric speciation in logperches, as allopatric separation is the driving force in speciation for this group of fishes (Near and Benard 2004). In darters of the genus *Percina*, however, change in certain morphological characteristics is more rapid among co-occurring darter species enabling sympatry with minimized niche overlap (Carlson et al. 2009). Most of these characteristics were related to feeding adaptations, but there is evidence for morphological adaptations to different habitats within streams and rivers among darter species (Page 1983, Page and Swofford 1984). Whether such differential habitat use among darters could lead to allopatric

separation, particularly if a population were isolated in a lacustrine environment, remains an interesting question, albeit one unlikely to be answered.

Determining whether certain darter species have more phenotypic variation than others, and hence perhaps more phenotypic plasticity, is more likely to yield results. Most darter species are habitat specialists (Page 1983, Page and Swofford 1984). Logperches, however, are found in a variety of habitats – from streams to rivers to lakes (Trautman 1981, Kuehne and Barbour 1983, Page 1983). My findings that Logperch from the Allegheny Reservoir and Lower Allegheny River have caudal peduncle morphology consistent with adaptations to lentic environments are indicative of either rapid adaptive selection for this trait, or phenotypic plasticity with regards to water velocity. Since human-constructed dams are a relatively recent feature on the rivers (less than 200 years for navigations dams and about 40 years for the Kinzua Dam) (Pearson and Krumholz 1984), evolutionary selective pressures would have to be very strong for evolution to occur over such a time-frame. Darter speciation occurs over periods of thousands of years (Near et al. 2001, Near 2002, Near and Benard 2004) and thus, although rapid evolution is not out of the question, my findings may be more consistent with phenotypic plasticity. A common-garden rearing experiment, subjecting larval and juvenile Logperch and perhaps other darter species to differential water velocities could be used to test the underlying cause of these findings.

The ability to colonize different habitats also brings species into contact with different species communities. It would be interesting to test whether Logperch undergo trophic niche-shifts in response to such changing environmental conditions and in response to differential inter-specific competition, and whether any such changes differ across size classes in a form of trophic ontogeny. Indeed, my findings from Chapter 5 suggest that species do undergo trophic shifts in response to dam-mediated nutrient availability. Species that are adapted to faster-flowing water may find refugia below dams within rivers where turbulence is greatest, such as the *Etheostoma* darter species in Chapter 2. While dams provide several economic benefits, it is therefore

necessary to understand the effects that they can have on individual fish species, populations, and communities.

Applications to Environmental Assessments and Monitoring of Dredging

I have shown that there are differences in fish assemblages (Chapters 4 and 5) and food webs (Chapter 5) between dredged and undredged areas. Dredged sites have fewer small benthic species, particularly those in lithophilic reproductive guilds, and a higher proportion of eurytopic species. These trends also apply to shallow areas at dredged sites, which are relatively depauperate in these taxa than equivalent depths at undredged sites. Food webs at dredged sites have increased reliance on pelagic-derived nutrients than those at undredged sites, which is consistent with a loss of benthic nutrient pathways (Vander Zanden and Vadeboncoeur 2002, Vadeboncoeur et al. 2003, Chandra et al. 2005). Larger fish species do not follow the same trends, as they do not show population declines and they trend towards an increased reliance on benthic nutrients at dredged sites. This may be due to foraging forays into shallower water. Boat electrofishing is most efficient in shallow water and gill nets were set close to shore, so there may be a sampling bias towards shallow-water fishes. Unlike small benthic fishes, however, large fishes did not experience population differences in shallow areas of dredged sites but since the stable isotope data did show shifts in reliance on benthic nutrients there was an effect of dredging on their trophic dynamics.

Stable isotope analysis was used to reveal differences in nutrient dynamics and particularly the reliance on benthic nutrients within food webs. While stable isotopes have been used to trace the effects of a variety of point-source (Wassenaar and Culp 1996, Wayland and Hobson 2001, Dube et al. 2006) and non-point source (Harrington et al. 1998, Anderson and Cabana 2005, Gray et al. 2005) inputs to aquatic systems, this is the first time that they have been

used to determine the effects of commercial dredging on riverine food webs. Stable isotopes revealed differences in trophic structure between dredged and undredged sites, and are therefore a valuable tool for assessing the impacts of such large-scale and long-term disturbances on fish assemblages.

Lower populations of lithophilic species along banks at dredged sites may be a result of altered species interactions or nutrient dynamics. It may also result from the separation of viable populations by the breadth of the river. Benthic species are less likely to disperse across deep, silty, turbid environments (Freedman 2005), and so environmental perturbations resulting in diminished populations can have profound effects. While recolonization would be facilitated in a contiguous, undredged habitat, shallow banks at dredged sites and undredged areas near dams and bridges might function as isolated population source patches or habitat corridors for small benthic fish species, thus having profound effects on metapopulation dynamics within the river.

Management Implications and Conclusions

Dams create lentic habitats that, in turn, can affect fish morphology while dams and dredging both have profound effects on fish populations, assemblages, and food webs. Dams increase river depth and can act as barriers to fish migrations and dispersal. As fishes adapt to slower water velocity resulting from dams, there are also shifts in nutrient availability and utilizations. Deeper water is correlated with shifts from benthic to pelagic nutrients due to increased turbidity and sedimentation, which also in turn are negatively correlated with abundance of lithophilic species. Understanding the interactions between dams and dredging on the ecology of riverine fishes is imperative in formulating sound management policy. Stable isotope analysis revealed many of these interactions.

Dams alter sediment and nutrient dynamics in rivers. Sediment accumulates behind the dams, reducing natural replenishment of the substrate (Kondolf 1997). This is a particular issue

in dredged areas, where natural replenishment and restoration to pre-dredged conditions may take at least hundreds of years (Kondolf 1997, Rinaldi et al. 2005, Rovira et al. 2005). The retention of sediments (particularly coarse sediments such as gravel and cobble) behind dams may diminish natural replenishment by orders of magnitude. While gravel restoration can lead to rapid recolonization by benthic macroinvertebrates in smaller rivers and streams (Merz and Ochikubo Chan 2005), gravel restoration in the Allegheny or Ohio rivers would be virtually impossible. It is therefore necessary for natural resources managers to weigh the relative benefits of commercial gravel extraction against those provided by ecosystem functionality. Several Pennsylvania-listed Threatened, Endangered, and Candidate fish species are found in the Allegheny and Ohio rivers, and these species tend to be associated with undredged sites (Chapters 4 and 5). Even shallow areas at dredged sites are species-depauperate, especially among lithophilic reproductive guilds. Since restoration of dredged areas to make them inhabitable by lithophilic species is likely impossible, it will be necessary to preserve undredged regions in these rivers in order to preserve these species. These rivers are no longer in pristine condition due to the presence of navigation dams and other anthropogenic influences, but dredging has the ability to diminish critical habitats.

The use of electrofishing, gill-nets, and other sampling gears which target large-bodied fishes in shallow water may lead to erroneous conclusions about the effects of dredging on fish assemblages. Many of these species, such as *Cyprinus carpio*, are eurytopic and can therefore tolerate a wide range of environmental conditions. Smaller fish species, furthermore, are less able to migrate to better conditions. Many of these smaller species, moreover, are in lithophilic reproductive guilds and are therefore highly sensitive to the high turbidity and sedimentation rates present at many dredged sites. In assessing whether dredging has a deleterious effect on fishes, using large-bodied species could cause a Type II error and the false conclusion that there is no effect of dredging on fish populations and assemblages. The use of benthic trawls, and particularly electrified benthic trawls, is therefore supported for targeted sampling of small

benthic fishes. Such assessment and monitoring studies should therefore focus on species that are *a priori* hypothesized to be sensitive to habitat disruption associated with dredging and dredged sites.

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Appendix A

List of Fish and Invertebrate Stable Isotope Samples, with Fish Abbreviations.

Family	Common Name	Scientific Name	Abbreviation
Amiidae	bowfin	<i>Amia calva</i>	AACA
Lepisosteidae	longnose gar	<i>Lepisosteus osseus</i>	LSOS
Clupeidae	skipjack herring	<i>Alosa chrysochloris</i>	ALCH
Clupeidae	gizzard shad	<i>Dorosoma cepedianum</i>	DOCE
Catostomidae	river carpsucker	<i>Carpionodes spp.</i>	CASP
	northern		
Catostomidae	hogsucker	<i>Hypentelium nigricans</i>	HYNH
	smallmouth		
Catostomidae	buffalo	<i>Ictiobus bubalus</i>	IBBU
Catostomidae	black buffalo	<i>Ictiobus niger</i>	IBNI
Catostomidae	silver redhorse	<i>Moxostoma anisurum</i>	MXAN
Catostomidae	river redhorse	<i>Moxostoma carinatum</i>	MXCA
Catostomidae	black redhorse	<i>Moxostoma duquesnei</i>	MXDU
Catostomidae	golden redhorse	<i>Moxostoma erythrurum</i>	MXER
	shorthead	<i>Moxostoma</i>	
Catostomidae	redhorse	<i>macrolepidotum</i>	MXMA
Cyprinidae	common carp	<i>Cyprinus carpio</i>	CYCA
Cyprinidae	streamline chub	<i>Erimystax dissimilis</i>	ERDI
	tonguetied		
Cyprinidae	minnow	<i>Exoglossum laurae</i>	EXGL
Cyprinidae	river chub	<i>Nocomis micropogon</i>	NCMI
Cyprinidae	emerald shiner	<i>Notropis atherinoides</i>	NOAT
Cyprinidae	minnow species	<i>Notropis spp.</i>	NOSP
Cyprinidae	mimic shiner	<i>Notropis volucellus</i>	NOVO
Cyprinidae	channel shiner	<i>Notropis wickliffi</i>	NOWI
	bluntnose		
Cyprinidae	minnow	<i>Pimephales notatus</i>	PINO
Esocidae	northern pike	<i>Esox lucius</i>	ESLU
Hiodontidae	goldeneye	<i>Hiodon alosoides</i>	HIAL
Hiodontidae	mooneye	<i>Hiodon tergisus</i>	HITE
Ictaluridae	channel catfish	<i>Ictalurus punctatus</i>	ICPU
	mountain		
Ictaluridae	madtom	<i>Noturus eleutherus</i>	NTEL
Ictaluridae	northern madtom	<i>Noturus stigmosus</i>	NTST
Ictaluridae	flathead catfish	<i>Pylodictus olivaris</i>	PYOL
Atherinopsidae	brook silverside	<i>Labidesthes sicculus</i>	LASI
Moronidae	white bass	<i>Morone chrysops</i>	MOCH
Moronidae	striped bass	<i>Morone saxatilis</i>	MOSA
Moronidae	hybrid striper	<i>Morone chrysops x saxatilis</i>	MOXX
Centrarchidae	rockbass	<i>Ambloplites rupestris</i>	AMRU

Centrarchidae	green sunfish	<i>Lepomis cyanellus</i>	LECY
Centrarchidae	bluegill	<i>Lepomis macrochirus</i>	LEMA
Centrarchidae	sunfish species	<i>Lepomis spp.</i>	LESP
Centrarchidae	smallmouth bass	<i>Micropterus dolomieu</i>	MIDO
Centrarchidae	spotted bass	<i>Micropterus punctulatus</i>	MIPU
Centrarchidae	largemouth bass	<i>Micropterus salmoides</i>	MISA
Centrarchidae	white crappie	<i>Pomoxis annularis</i>	POAN
Centrarchidae	black crappie	<i>Pomoxis nigromaculatus</i>	PONI
Percidae	greenside darter	<i>Etheostoma blennioides</i>	ETBL
Percidae	rainbow darter	<i>Etheostoma caeruleum</i>	ETCA
Percidae	bluebreast darter	<i>Etheostoma camurum</i>	ETCM
Percidae	fantail darter	<i>Etheostoma flabellare</i>	ETFL
Percidae	spotted darter	<i>Etheostoma maculatum</i>	ETMA
Percidae	Johnny darter	<i>Etheostoma nigrum</i>	ETNI
Percidae	darter species	<i>Etheostoma spp</i>	ETSP
Percidae	Tippecanoe darter	<i>Etheostoma tippecanoe</i>	ETTI
Percidae	banded darter	<i>Etheostoma zonale</i>	ETZO
Percidae	logperch	<i>Percina caprodes</i>	PECA
Percidae	channel darter	<i>Percina copelandi</i>	PECO
Percidae	gilt darter	<i>Percina evides</i>	PEEV
Percidae	blackside darter	<i>Percina maculata</i>	PEMA
Percidae	longhead darter	<i>Percina macrocephala</i>	PEMC
Percidae	river darter	<i>Percina shumardi</i>	PESH
Percidae	yellow perch	<i>Perca flavescens</i>	PRFL
Percidae	sauger	<i>Sander canadense</i>	SACA
Percidae	walleye	<i>Sander vitreus</i>	SAVI
Scianidae	freshwater drum	<i>Aplodinotus grunniens</i>	APGR
Cottidae	mottled sculpin	<i>Cottus bairdi</i>	COBA

Site	Family	Species	Length	δ13Ccorr	δ15N
D	Centrarchidae	AMRU	143	-24.66	12.94
D	Centrarchidae	AMRU	144	-24.16	13.07
D	Scianidae	APGR	22	-26.36	11.09
D	Scianidae	APGR	25	-26.88	10.39
D	Scianidae	APGR	28	-26.31	11.06
D	Scianidae	APGR	30	-27.01	11.28
D	Cyprinidae	ERDI	37	-28.16	13.39
D	Cyprinidae	ERDI	39	-28.42	13.04
D	Cyprinidae	ERDI	40	-27.58	12.11
D	Percidae	ETBL	27	-24.41	11.49
D	Percidae	ETBL	42	-24.75	13.69
D	Percidae	ETCAE	22	-25.63	12.04
D	Percidae	ETCAE	23	-26.31	11.73
D	Percidae	ETCAE	24	-25.69	12.12
D	Percidae	ETNI	26	-26.01	12.59
D	Percidae	ETNI	27	-27.11	9.44
D	Percidae	ETNI	29	-24.72	12.78

D	Percidae	ETNI	29	-27.27	9.92
D	Percidae	ETNI	29	-27.28	9.96
D	Percidae	ETNI	30	-25.79	11.85
D	Percidae	ETNI	35	-26.85	13.29
D	Percidae	ETNI	42	-28.17	12.00
D	Percidae	ETZO	27	-24.49	11.88
D	Ictaluridae	ICPU	15	-23.75	14.34
D	Ictaluridae	ICPU	17	-24.70	12.71
D	Ictaluridae	ICPU	18	-24.80	13.44
D	Ictaluridae	ICPU	22	-25.53	14.35
D	Ictaluridae	ICPU	23	-24.84	11.93
D	Ictaluridae	ICPU	25	-25.89	13.49
D	Ictaluridae	ICPU	25	-25.22	14.62
D	Ictaluridae	ICPU	25	-25.36	13.96
D	Ictaluridae	ICPU	27	-25.30	11.63
D	Ictaluridae	ICPU	31	-25.86	13.04
D	Atherinidae	LASI	67	-24.96	11.74
D	Atherinidae	LASI	69	-25.00	11.20
D	Atherinidae	LASI	70	-26.11	12.66
D	Atherinidae	LASI	73	-24.48	11.15
D	Atherinidae	LASI	76	-27.63	13.21
D	Centrarchidae	LEMA	44	-26.98	12.76
D	Centrarchidae	MIDO	26	-25.20	11.48
D	Cyprinidae	NOSP	25	-25.51	9.58
D	Cyprinidae	NOSP	31	-28.12	11.21
D	Cyprinidae	NOSP	33	-28.70	11.47
D	Cyprinidae	NOSP	35	-24.30	10.91
D	Cyprinidae	NOSP	35	-25.38	10.91
D	Cyprinidae	NOSP	38	-26.77	12.83
D	Cyprinidae	NOSP	38	-28.24	11.47
D	Cyprinidae	NOSP	39	-26.22	12.64
D	Cyprinidae	NOSP	39	-28.96	11.93
D	Cyprinidae	NOSP	42	-28.87	11.45
D	Cyprinidae	NOSP	43	-28.78	13.21
D	Cyprinidae	NOSP	45	-29.80	12.06
D	Cyprinidae	NOSP	50	-28.07	12.15
D	Cyprinidae	NOSP	51	-29.07	12.39
D	Cyprinidae	NOSP	52	-29.24	11.97
D	Cyprinidae	NOSP	54	-29.65	12.14
D	Cyprinidae	NOSP	55	-22.76	11.14
D	Cyprinidae	NOSP	56	-29.72	11.24
D	Cyprinidae	NOSP	56	-27.94	12.93
D	Cyprinidae	NOSP	56	-28.77	12.53
D	Cyprinidae	NOSP	57	-23.19	11.44
D	Cyprinidae	NOSP	58	-29.43	10.98
D	Cyprinidae	NOSP	58	-28.27	12.48
D	Cyprinidae	NOSP	62	-25.87	9.26
D	Cyprinidae	NOSP	65	-26.10	9.76
D	Cyprinidae	NOSP	67	-26.69	11.75

D	Percidae	PECA	38	-28.15	11.21
D	Percidae	PECA	38	-22.07	11.09
D	Percidae	PECA	41	-25.23	11.36
D	Percidae	PECA	43	-26.65	11.48
D	Percidae	PECA	43	-28.60	11.04
D	Percidae	PECA	73	-25.51	13.22
D	Percidae	PECA	74	-23.49	10.74
D	Percidae	PECA	78	-25.76	12.79
D	Percidae	PECA	80	-25.09	13.36
D	Percidae	PECA	80	-24.68	13.05
D	Percidae	PECO	24	-25.62	11.33
D	Percidae	PECO	25	-25.83	11.17
D	Percidae	PECO	25	-25.69	11.20
D	Percidae	PECO	27	-25.91	12.06
D	Percidae	PECO	27	-27.06	10.43
D	Percidae	PECO	27	-26.85	10.43
D	Percidae	PECO	27	-26.45	11.53
D	Percidae	PECO	35	-27.35	13.28
D	Percidae	PECO	35	-26.63	12.95
D	Percidae	PECO	35	-28.36	13.54
D	Percidae	PECO	36	-27.30	13.47
D	Percidae	PECO	36	-28.73	13.27
D	Percidae	PECO	36	-26.46	13.50
D	Percidae	PECO	37	-25.08	12.63
D	Percidae	PECO	38	-27.18	12.94
D	Percidae	PECO	38	-26.58	14.03
D	Percidae	PECO	39	-26.80	14.14
D	Percidae	PECO	40	-27.86	13.78
D	Percidae	PECO	42	-27.50	12.99
D	Percidae	PECO	45	-25.99	13.43
D	Percidae	PEEV	25	-24.94	12.33
D	Percidae	PEEV	27	-26.26	12.16
D	Percidae	PEEV	27	-26.05	12.64
D	Percidae	PEEV	27	-25.26	12.32
D	Percidae	PEEV	41	-27.53	13.52
D	Cyprinidae	PINO	38	-23.42	10.46
D	Cyprinidae	PINO	42	-25.15	9.92
D	Cyprinidae	PINO	43	-23.96	10.33
D	Cyprinidae	PINO	58	-29.00	11.47
D	Ictaluridae	PYOL	14	-24.76	11.70
D	Percidae	SAVI	69	-22.91	13.74
D	Amiidae	AACA	560	-22.35	14.01
D	Amiidae	AACA	560	-24.11	14.28
D	Clupeidae	ALCH	241	-28.05	15.66
D	Scianidae	APGR	332	-25.73	11.85
D	Scianidae	APGR	336	-25.47	11.73
D	Scianidae	APGR	340	-24.75	12.71
D	Scianidae	APGR	348	-26.10	12.45
D	Catostomidae	CASP	270	-24.13	12.92

D	Catostomidae	CASP	282	-25.20	11.53
D	Catostomidae	CASP	339	-24.02	13.06
D	Catostomidae	CASP	351	-25.69	13.13
D	Catostomidae	CASP	359	-25.16	13.19
D	Catostomidae	CASP	363	-24.41	13.50
D	Catostomidae	CASP	365	-24.67	12.61
D	Catostomidae	CASP	381	-25.01	13.32
D	Catostomidae	CASP	382	-24.45	12.95
D	Catostomidae	CASP	385	-25.55	13.37
D	Catostomidae	CASP	385	-24.67	13.14
D	Catostomidae	CASP	392	-24.52	13.44
D	Catostomidae	CASP	398	-24.04	12.93
D	Catostomidae	CASP	405	-25.09	13.72
D	Catostomidae	CASP	434	-26.35	13.56
D	Catostomidae	CASP	440	-24.34	12.86
D	Cyprinidae	CYCA	572	-23.88	9.64
D	Cyprinidae	CYCA	587	-23.89	11.22
D	Cyprinidae	CYCA	614	-24.19	10.19
D	Cyprinidae	CYCA	630	-24.90	11.63
D	Cyprinidae	CYCA	655	-24.29	10.77
D	Cyprinidae	CYCA	690	-24.31	10.75
D	Cyprinidae	CYCA	746	-24.89	11.09
D	Clupeidae	DOCE	300	-24.88	11.09
D	Clupeidae	DOCE	327	-25.01	11.56
D	Clupeidae	DOCE	333	-24.60	11.53
D	Clupeidae	DOCE	335	-26.03	11.27
D	Clupeidae	DOCE	360	-27.73	11.40
D	Esocidae	ESLU	370	-22.86	14.69
D	Catostomidae	IBBU	451	-24.22	12.41
D	Catostomidae	IBBU	465	-27.54	12.59
D	Catostomidae	IBBU	474	-26.32	12.92
D	Catostomidae	IBBU	484	-26.43	11.96
D	Catostomidae	IBBU	487	-24.59	11.48
D	Catostomidae	IBBU	491	-26.21	11.97
D	Catostomidae	IBBU	500	-24.66	11.99
D	Catostomidae	IBBU	511	-22.55	12.07
D	Catostomidae	IBBU	515	-22.17	9.17
D	Catostomidae	IBBU	515	-25.27	12.05
D	Catostomidae	IBBU	517	-25.40	11.85
D	Catostomidae	IBBU	548	-25.03	11.32
D	Catostomidae	IBBU	550	-25.06	10.72
D	Catostomidae	IBBU	559	-24.32	11.71
D	Catostomidae	IBBU	562	-23.80	11.52
D	Catostomidae	IBBU	574	-24.77	12.35
D	Ictaluridae	ICPU	418	-24.20	12.05
D	Ictaluridae	ICPU	440	-22.46	11.43
D	Ictaluridae	ICPU	442	-23.46	11.91
D	Ictaluridae	ICPU	451	-23.06	13.19
D	Ictaluridae	ICPU	459	-23.19	11.14

D	Ictaluridae	ICPU	461	-23.29	13.10
D	Ictaluridae	ICPU	463	-23.13	12.04
D	Ictaluridae	ICPU	469	-24.26	13.05
D	Ictaluridae	ICPU	471	-24.19	13.15
D	Ictaluridae	ICPU	473	-24.50	13.07
D	Ictaluridae	ICPU	473	-23.14	11.67
D	Ictaluridae	ICPU	482	-22.92	11.16
D	Ictaluridae	ICPU	497	-24.02	13.40
D	Ictaluridae	ICPU	500	-25.32	14.00
D	Ictaluridae	ICPU	545	-24.22	13.30
D	Ictaluridae	ICPU	663	-23.93	13.05
D	Lepistosteidae	LSOS	650	-24.61	14.55
D	Centrarchidae	MISA	372	-19.63	13.75
D	Catostomidae	MXAN	388	-23.97	11.25
D	Catostomidae	MXAN	397	-23.81	11.62
D	Catostomidae	MXER	393	-23.79	11.36
D	Ictaluridae	PYOL	487	-23.93	14.08
D	Ictaluridae	PYOL	603	-25.09	14.92
D	Percidae	SAVI	265	-28.64	14.40
D	Percidae	SAVI	269	-27.40	13.96
D	Percidae	SAVI	473	-23.37	15.05
F	Cottidae	COBA	19	-24.10	13.64
F	Cottidae	COBA	19	-24.64	13.89
F	Cottidae	COBA	21	-23.36	13.39
F	Cottidae	COBA	21	-26.39	14.09
F	Cottidae	COBA	24	-25.72	13.95
F	Cottidae	COBA	25	-24.76	13.61
F	Cottidae	COBA	58	-23.11	12.94
F	Cottidae	COBA	64	-26.05	13.54
F	Cottidae	COBA	67	-26.28	14.24
F	Cottidae	COBA	68	-25.90	14.24
F	Cyprinidae	ERDI	60	-22.01	12.29
F	Cyprinidae	ERDI	62	-22.49	12.24
F	Cyprinidae	ERDI	65	-23.61	12.31
F	Percidae	ETBL	46	-23.36	13.01
F	Percidae	ETBL	47	-23.44	12.47
F	Percidae	ETBL	47	-23.76	12.73
F	Percidae	ETBL	50	-23.41	13.14
F	Percidae	ETBL	58	-21.42	14.87
F	Percidae	ETBL	62	-20.91	14.65
F	Percidae	ETBL	64	-21.16	14.58
F	Percidae	ETBL	65	-21.43	14.14
F	Percidae	ETBL	69	-21.71	13.67
F	Percidae	ETCA	43	-22.45	12.86
F	Percidae	ETCA	44	-22.41	13.31
F	Percidae	ETCA	45	-22.88	13.36
F	Percidae	ETCA	47	-22.34	13.15
F	Percidae	ETCAE	38	-23.77	14.22
F	Percidae	ETCAE	38	-22.66	14.87

F	Percidae	ETCAE	39	-21.84	14.53
F	Percidae	ETCAE	40	-22.44	15.11
F	Percidae	ETFL	40	-23.44	13.65
F	Percidae	ETFL	44	-23.26	12.89
F	Percidae	ETFL	48	-21.75	13.37
F	Percidae	ETNI	42	-23.14	10.81
F	Percidae	ETNI	43	-22.72	11.17
F	Percidae	ETZO	30	-23.81	12.59
F	Percidae	ETZO	35	-23.44	12.69
F	Percidae	ETZO	35	-23.61	12.71
F	Percidae	ETZO	35	-23.07	12.92
F	Percidae	ETZO	37	-23.59	12.96
F	Percidae	ETZO	49	-22.57	13.96
F	Cyprinidae	EXGL	77	-23.98	14.85
F	Cyprinidae	EXGL	77	-24.06	15.29
F	Cyprinidae	EXGL	77	-24.11	15.37
F	Cyprinidae	NCMI	71	-26.00	14.09
F	Cyprinidae	NCMI	71	-25.78	14.83
F	Cyprinidae	NCMI	92	-25.32	13.77
F	Cyprinidae	NCMI	100	-26.41	14.29
F	Cyprinidae	NCMI	120	-25.87	15.85
F	Cyprinidae	NOSP	32	-21.91	12.00
F	Cyprinidae	NOSP	32	-22.49	11.23
F	Cyprinidae	NOSP	33	-21.82	10.50
F	Cyprinidae	NOSP	34	-22.07	11.63
F	Cyprinidae	NOSP	35	-21.43	12.06
F	Cyprinidae	NOSP	35	-23.36	11.64
F	Cyprinidae	NOSP	36	-23.15	10.59
F	Cyprinidae	NOSP	36	-21.32	11.42
F	Cyprinidae	NOSP	37	-21.16	12.05
F	Cyprinidae	NOSP	43	-22.10	10.52
F	Cyprinidae	NOSP	50	-22.66	10.82
F	Cyprinidae	NOSP	50	-22.26	11.26
F	Ictaluridae	NTEL	32	-21.82	12.53
F	Percidae	PECA	70	-22.27	11.53
F	Percidae	PECA	86	-22.94	15.08
F	Percidae	PECO	42	-22.01	13.54
F	Percidae	PECO	43	-22.36	14.31
F	Percidae	PECO	43	-22.14	13.76
F	Percidae	PEEV	30	-21.23	12.97
F	Percidae	PEEV	43	-23.03	12.87
F	Percidae	PEEV	45	-22.78	12.85
F	Percidae	PEEV	45	-23.00	13.28
F	Percidae	PEMAC	61	-24.08	14.21
F	Percidae	PEMAC	65	-22.71	13.86
F	Percidae	PEMAC	66	-23.84	13.68
F	Percidae	PEMAC	69	-23.45	13.83
F	Percidae	PEMC	52	-22.10	12.35
F	Percidae	PEMC	53	-22.78	12.96

F	Percidae	PEMC	54	-22.65	13.14
F	Percidae	PEMC	55	-22.51	13.01
U	Cyprinidae	ERDI	41	-24.10	11.11
U	Cyprinidae	ERDI	41	-24.18	11.31
U	Cyprinidae	ERDI	58	-26.80	11.81
U	Cyprinidae	ERDI	60	-24.61	12.62
U	Cyprinidae	ERDI	66	-23.51	11.05
U	Cyprinidae	ERDI	66	-23.69	11.60
U	Cyprinidae	ERDI	67	-23.44	12.84
U	Cyprinidae	ERDI	67	-25.21	11.12
U	Cyprinidae	ERDI	100	-22.41	12.33
U	Percidae	ETBL	25	-21.96	11.97
U	Percidae	ETBL	26	-23.84	12.04
U	Percidae	ETBL	27	-24.10	12.75
U	Percidae	ETBL	27	-23.97	12.13
U	Percidae	ETBL	28	-24.60	13.17
U	Percidae	ETBL	28	-25.35	12.03
U	Percidae	ETBL	29	-24.61	12.61
U	Percidae	ETBL	29	-23.68	12.33
U	Percidae	ETBL	29	-24.08	12.77
U	Percidae	ETBL	29	-25.17	12.10
U	Percidae	ETBL	30	-23.26	11.94
U	Percidae	ETBL	31	-24.03	12.60
U	Percidae	ETBL	32	-25.04	12.85
U	Percidae	ETBL	41	-23.28	13.27
U	Percidae	ETBL	42	-26.75	13.66
U	Percidae	ETBL	43	-26.38	13.80
U	Percidae	ETBL	44	-26.28	13.47
U	Percidae	ETBL	50	-22.15	13.27
U	Percidae	ETBL	51	-23.73	13.40
U	Percidae	ETBL	60	-21.16	13.19
U	Percidae	ETBL	64	-21.45	13.60
U	Percidae	ETCAE	25	-25.23	14.33
U	Percidae	ETCAE	30	-25.47	14.50
U	Percidae	ETCAE	31	-25.13	14.26
U	Percidae	ETCAE	32	-25.52	14.86
U	Percidae	ETCAE	33	-24.17	14.13
U	Percidae	ETCAE	40	-21.71	13.47
U	Percidae	ETCM	20	-24.60	12.15
U	Percidae	ETCM	32	-24.07	13.41
U	Percidae	ETCM	33	-22.62	13.86
U	Percidae	ETCM	33	-25.90	13.39
U	Percidae	ETCM	35	-25.99	13.51
U	Percidae	ETFL	35	-25.13	15.61
U	Percidae	ETFL	39	-26.77	13.62
U	Percidae	ETNI	39	-28.61	12.46
U	Percidae	ETNI	42	-26.55	13.28
U	Percidae	ETNI	42	-27.69	12.77
U	Percidae	ETNI	43	-27.83	11.73

U	Percidae	ETNI	45	-25.27	14.41
U	Percidae	ETTI	22	-23.32	14.31
U	Percidae	ETTI	26	-25.67	13.05
U	Percidae	ETTI	28	-24.00	13.00
U	Percidae	ETTI	29	-23.77	13.13
U	Percidae	ETTI	30	-25.96	12.94
U	Percidae	ETZO	23	-23.78	12.50
U	Percidae	ETZO	24	-24.34	12.51
U	Percidae	ETZO	25	-23.93	12.56
U	Percidae	ETZO	25	-23.71	12.65
U	Percidae	ETZO	32	-24.99	14.49
U	Catostomidae	HYNI	78	-21.65	12.78
U	Atherinidae	LASI	58	-26.12	12.84
U	Atherinidae	LASI	61	-26.40	12.86
U	Atherinidae	LASI	66	-28.29	13.47
U	Atherinidae	LASI	66	-26.68	13.01
U	Atherinidae	LASI	70	-27.33	12.90
U	Atherinidae	LASI	73	-27.75	12.83
U	Atherinidae	LASI	75	-27.42	12.84
U	Atherinidae	LASI	77	-28.84	12.88
U	Centrarchidae	LEMA	48	-26.61	13.54
U	Centrarchidae	MIDO	26	-24.07	11.12
U	Centrarchidae	MIDO	26	-25.85	11.72
U	Centrarchidae	MIDO	28	-23.75	13.20
U	Centrarchidae	MIDO	29	-24.13	13.00
U	Centrarchidae	MIDO	35	-23.97	13.25
U	Centrarchidae	MIDO	36	-24.19	12.57
U	Centrarchidae	MIDO	37	-21.03	12.51
U	Centrarchidae	MIDO	45	-23.54	13.49
U	Centrarchidae	MIDO	50	-25.80	13.45
U	Centrarchidae	MIDO	72	-25.60	12.48
U	Centrarchidae	MIDO	74	-25.02	13.16
U	Centrarchidae	MIDO	81	-24.52	13.74
U	Centrarchidae	MIDO	83	-27.39	13.76
U	Centrarchidae	MIDO	93	-28.10	13.90
U	Centrarchidae	MIDO	94	-25.39	13.82
U	Cyprinidae	NOSP	42	-26.39	11.38
U	Cyprinidae	NOSP	44	-24.14	10.88
U	Cyprinidae	NOSP	44	-24.68	10.85
U	Cyprinidae	NOSP	45	-23.80	10.73
U	Cyprinidae	NOSP	46	-26.86	10.17
U	Cyprinidae	NOSP	56	-28.27	11.77
U	Cyprinidae	NOSP	57	-27.66	11.27
U	Cyprinidae	NOSP	58	-28.55	11.82
U	Cyprinidae	NOSP	59	-27.58	12.55
U	Cyprinidae	NOSP	62	-27.45	11.75
U	Cyprinidae	NOSP	67	-27.17	11.32
U	Cyprinidae	NOSP	69	-23.47	10.62
U	Cyprinidae	NOSP	69	-25.18	10.78

U	Cyprinidae	NOSP	69	-24.36	11.24
U	Cyprinidae	NOSP	69	-24.90	9.50
U	Cyprinidae	NOSP	70	-25.59	10.55
U	Cyprinidae	NOSP	70	-25.29	10.44
U	Cyprinidae	NOSP	70	-25.27	9.61
U	Cyprinidae	NOSP	72	-24.42	11.31
U	Cyprinidae	NOSP	74	-24.32	9.91
U	Cyprinidae	NOSP	86	-26.28	11.36
U	Percidae	PECA	34	-23.92	11.35
U	Percidae	PECA	35	-26.55	11.50
U	Percidae	PECA	36	-25.24	11.09
U	Percidae	PECA	36	-26.79	11.38
U	Percidae	PECA	39	-24.02	10.84
U	Percidae	PECA	39	-27.07	11.96
U	Percidae	PECA	41	-27.42	11.51
U	Percidae	PECA	43	-26.95	11.09
U	Percidae	PECA	44	-27.12	11.42
U	Percidae	PECA	45	-27.75	11.12
U	Percidae	PECA	47	-26.89	11.57
U	Percidae	PECA	59	-25.34	13.96
U	Percidae	PECA	62	-26.14	12.76
U	Percidae	PECA	63	-23.16	13.23
U	Percidae	PECA	63	-27.32	12.93
U	Percidae	PECA	63	-27.29	11.89
U	Percidae	PECA	67	-28.04	12.08
U	Percidae	PECA	72	-26.12	13.21
U	Percidae	PECA	73	-26.22	13.08
U	Percidae	PECA	74	-25.77	12.86
U	Percidae	PECA	74	-25.94	12.56
U	Percidae	PECA	75	-25.76	12.94
U	Percidae	PECA	76	-25.59	12.66
U	Percidae	PECA	77	-26.32	12.90
U	Percidae	PECA	77	-25.48	12.17
U	Percidae	PECA	78	-25.88	12.39
U	Percidae	PECA	79	-25.54	12.38
U	Percidae	PECA	80	-24.37	13.01
U	Percidae	PECA	82	-25.25	12.69
U	Percidae	PECA	82	-26.13	11.96
U	Percidae	PECA	83	-25.02	12.99
U	Percidae	PECA	100	-25.25	13.27
U	Percidae	PECA	112	-23.68	12.92
U	Percidae	PECO	22	-23.92	12.96
U	Percidae	PECO	24	-26.09	11.46
U	Percidae	PECO	25	-25.02	11.92
U	Percidae	PECO	25	-24.32	12.58
U	Percidae	PECO	25	-25.00	11.57
U	Percidae	PECO	25	-26.48	11.34
U	Percidae	PECO	25	-26.49	11.64
U	Percidae	PECO	26	-26.90	10.88

U	Percidae	PECO	27	-23.86	12.18
U	Percidae	PECO	27	-27.09	11.39
U	Percidae	PECO	27	-27.31	11.81
U	Percidae	PECO	28	-24.57	11.32
U	Percidae	PECO	32	-26.46	13.65
U	Percidae	PECO	33	-23.62	14.34
U	Percidae	PECO	33	-26.45	12.42
U	Percidae	PECO	34	-26.49	13.86
U	Percidae	PECO	34	-26.81	13.22
U	Percidae	PECO	34	-25.57	13.32
U	Percidae	PECO	34	-26.07	14.95
U	Percidae	PECO	34	-26.60	13.27
U	Percidae	PECO	35	-25.96	14.17
U	Percidae	PECO	35	-24.86	14.21
U	Percidae	PECO	35	-25.29	14.46
U	Percidae	PECO	35	-25.70	13.87
U	Percidae	PECO	35	-26.78	15.02
U	Percidae	PECO	35	-27.47	13.66
U	Percidae	PECO	36	-26.62	14.59
U	Percidae	PECO	36	-27.07	13.53
U	Percidae	PECO	36	-26.24	13.49
U	Percidae	PECO	36	-26.06	12.96
U	Percidae	PECO	37	-25.72	13.47
U	Percidae	PECO	37	-25.60	14.53
U	Percidae	PECO	37	-27.22	13.49
U	Percidae	PECO	37	-27.95	13.24
U	Percidae	PECO	37	-27.33	13.39
U	Percidae	PECO	37	-26.45	13.26
U	Percidae	PECO	37	-25.87	13.34
U	Percidae	PECO	37	-26.70	13.61
U	Percidae	PECO	37	-25.60	13.11
U	Percidae	PECO	37	-25.71	12.93
U	Percidae	PECO	38	-25.57	13.50
U	Percidae	PECO	38	-25.25	12.69
U	Percidae	PECO	39	-27.52	13.66
U	Percidae	PECO	40	-27.32	13.78
U	Percidae	PECO	41	-25.48	13.20
U	Percidae	PECO	44	-26.08	13.15
U	Percidae	PECO	45	-25.75	12.98
U	Percidae	PECO	46	-26.09	13.85
U	Percidae	PEEV	24	-25.07	12.23
U	Percidae	PEEV	26	-25.36	12.27
U	Percidae	PEEV	26	-26.58	11.45
U	Percidae	PEEV	27	-23.32	12.63
U	Percidae	PEEV	27	-24.46	12.84
U	Percidae	PEEV	27	-25.75	11.83
U	Percidae	PEEV	27	-25.51	12.30
U	Percidae	PEEV	31	-26.83	11.89
U	Percidae	PEEV	32	-23.99	12.72

U	Percidae	PEEV	32	-23.94	12.78
U	Percidae	PEEV	32	-23.99	12.70
U	Percidae	PEEV	32	-24.61	13.15
U	Percidae	PEEV	37	-27.47	13.40
U	Percidae	PEEV	38	-26.01	14.73
U	Percidae	PEMC	52	-27.15	13.71
U	Percidae	PEMC	60	-26.71	14.08
U	Scianidae	APGR	361	-24.14	12.92
U	Scianidae	APGR	371	-21.92	12.56
U	Scianidae	APGR	551	-27.54	13.01
U	Scianidae	APGR	627	-26.09	13.02
U	Scianidae	APGR	647	-26.30	13.75
U	Scianidae	APGR	738	-25.44	13.49
U	Catostomidae	CASP	344	-24.41	13.83
U	Catostomidae	CASP	349	-23.88	13.00
U	Catostomidae	CASP	350	-25.44	13.47
U	Catostomidae	CASP	351	-23.07	12.89
U	Catostomidae	CASP	351	-24.24	13.09
U	Catostomidae	CASP	357	-24.01	12.96
U	Catostomidae	CASP	358	-23.17	13.28
U	Catostomidae	CASP	361	-24.37	13.35
U	Catostomidae	CASP	372	-24.98	12.98
U	Catostomidae	CASP	384	-23.74	12.92
U	Catostomidae	CASP	389	-25.89	12.50
U	Catostomidae	CASP	392	-24.20	13.28
U	Catostomidae	CASP	394	-21.57	12.11
U	Catostomidae	CASP	394	-23.72	13.21
U	Catostomidae	CASP	395	-25.31	13.02
U	Catostomidae	CASP	399	-24.55	13.70
U	Catostomidae	CASP	400	-26.06	12.44
U	Catostomidae	CASP	404	-23.99	12.77
U	Catostomidae	CASP	412	-23.93	11.34
U	Cyprinidae	CYCA	466	-24.39	10.58
U	Cyprinidae	CYCA	570	-24.35	10.73
U	Cyprinidae	CYCA	570	-25.47	11.06
U	Cyprinidae	CYCA	580	-24.92	11.30
U	Cyprinidae	CYCA	586	-24.80	11.61
U	Cyprinidae	CYCA	614	-24.50	9.35
U	Cyprinidae	CYCA	634	-25.12	11.40
U	Cyprinidae	CYCA	659	-23.61	12.00
U	Cyprinidae	CYCA	699	-25.41	11.15
U	Clupeidae	DOCE	341	-29.32	11.00
U	Catostomidae	IBBU	406	-25.01	12.32
U	Catostomidae	IBBU	413	-25.29	12.70
U	Catostomidae	IBBU	438	-24.88	12.39
U	Catostomidae	IBBU	471	-25.11	12.72
U	Catostomidae	IBBU	474	-25.27	13.06
U	Catostomidae	IBBU	475	-26.52	12.56
U	Catostomidae	IBBU	476	-24.90	11.60

U	Catostomidae	IBBU	481	-24.08	11.61
U	Catostomidae	IBBU	481	-25.95	11.90
U	Catostomidae	IBBU	485	-23.38	13.01
U	Catostomidae	IBBU	520	-26.48	11.84
U	Catostomidae	IBBU	546	-24.07	11.19
U	Catostomidae	IBBU	613	-25.81	11.85
U	Catostomidae	IBBU	634	-23.72	11.77
U	Catostomidae	IBBU	N/A	-27.14	14.10
U	Ictaluridae	ICPU	424	-23.11	14.31
U	Ictaluridae	ICPU	465	-24.11	12.58
U	Ictaluridae	ICPU	471	-23.56	12.08
U	Ictaluridae	ICPU	472	-24.48	13.85
U	Ictaluridae	ICPU	472	-22.55	11.68
U	Ictaluridae	ICPU	474	-23.64	13.59
U	Ictaluridae	ICPU	475	-24.36	11.64
U	Ictaluridae	ICPU	532	-23.83	12.88
U	Ictaluridae	ICPU	543	-24.46	13.50
U	Ictaluridae	ICPU	620	-21.63	13.01
U	Ictaluridae	ICPU	631	-23.84	13.43
U	Ictaluridae	ICPU	634	-23.75	14.12
U	Centrarchidae	MIDO	190	-25.20	12.62
U	Catostomidae	MXAN	381	-24.05	12.37
U	Catostomidae	MXAN	408	-23.76	11.92
U	Catostomidae	MXCA	421	-25.11	11.94
U	Catostomidae	MXCA	492	-24.81	12.60
U	Catostomidae	MXCA	574	-24.88	12.26
U	Catostomidae	MXER	196	-26.18	11.04
U	Centrarchidae	PONI	282	-26.17	13.76
U	Ictaluridae	PYOL	760	-24.55	15.01

Site	Guild	Species	%C	%N	C/N	lipid corrected $\delta^{13}C$	$\delta^{15}N$
D	C-G	Ephemeroptera - Ephemeridae	11.90	3.10	3.84	-25.27	8.31
D	C-G	Orconectes obscurus	40.73	11.25	3.62	-24.97	9.41
D	C-G	Orconectes obscurus	41.17	11.17	3.69	-25.96	7.75
D	C-G	Orconectes obscurus	41.81	11.86	3.52	-25.92	9.18
D	C-G	Orconectes obscurus	43.37	12.82	3.38	-27.10	10.47
D	C-G	Orconectes obscurus	41.36	13.12	3.15	-23.91	10.55
D	C-G	Orconectes obscurus	44.26	13.23	3.35	-25.73	10.99
D	C-G	Orconectes obscurus	37.15	9.74	3.82	-25.79	11.38
D	C-G	Gammarus	25.38	4.61	5.50	-21.40	5.79
F	C-G	Hemiptera - Corixidae	48.70	12.36	3.94	-22.58	9.23
F	C-G	crayfish remains	44.26	12.39	3.57	-26.43	12.16
U	C-G	Ephemeroptera - Ephemeridae	42.33	11.49	3.68	-25.08	8.86
U	C-G	Hemiptera - Corixidae	46.98	12.10	3.88	-25.00	9.65
U	C-G	Orconectes obscurus	40.61	11.56	3.51	-22.30	10.42
U	C-G	Ephemeroptera - Oligoneuriidae	40.41	11.31	3.57	-22.75	10.56
U	C-G	Orconectes obscurus	43.12	12.06	3.57	-25.07	12.04
U	C-G	Hemiptera - Corixidae	50.77	10.18	4.99	-26.11	9.22
U	C-G	Orconectes obscurus	43.96	12.47	3.53	-23.69	10.95

U	C-G	Orconectes obscurus	41.94	12.29	3.41	-25.65	12.37
U	C-G	Orconectes obscurus	41.53	11.84	3.51	-25.21	11.73
U	C-G	Ephemeroptera - Oligoneuriidae	16.24	3.15	5.16	-24.77	6.50
U	C-G	Ephemeroptera - Ephemeridae	44.40	7.98	5.56	-25.52	4.40
U	C-G	invert remains - Ephemeridae	9.09	1.90	4.79	-25.08	9.47
U	C-G	Hemiptera - Corixidae	48.00	12.91	3.72	-26.08	9.11
U	C-G	Plecoptera - Pteronarcyidae	44.14	11.59	3.81	-24.88	10.06
D	Fi	Corbicula	47.08	14.06	3.35	-28.26	8.82
D	Fi	Dreissena polymorpha	40.48	12.83	3.16	-28.45	8.17
F	Fi	Corbicula	44.33	13.94	3.18	-23.70	8.22
U	Fi	Dreissena polymorpha	44.69	12.51	3.57	-24.77	8.17
U	Fi	Corbicula	43.07	8.16	5.28	-26.94	8.51
U	Fi	Corbicula	39.96	7.53	5.30	-26.53	8.55
U	Fi	Corbicula & Unionid	38.14	6.07	6.28	-25.85	8.50
U	Fi	Corbicula	43.62	6.40	6.81	-26.00	8.46
U	Fi	Corbicula	34.60	9.16	3.77	-26.13	9.52
D	Pr	Odonata - Macromiidae	47.58	13.09	3.63	-26.21	10.39
D	Pr	Odonata - Gomphidae	43.31	11.49	3.77	-27.92	9.52
D	Pr	Odonata - Gomphidae	43.47	10.55	4.12	-27.83	7.10
D	Pr	Odonata - Macromiidae	42.09	11.15	3.77	-24.38	9.39
D	Pr	Odonata - Macromiidae	44.16	11.75	3.76	-26.06	8.32
D	Pr	Odonata - Macromiidae	44.14	11.68	3.78	-25.02	8.68
D	Pr	Odonata - Gomphidae	45.54	11.76	3.87	-29.91	4.96
D	Pr	Odonata - Macromiidae	44.46	12.43	3.58	-24.38	10.19
D	Pr	Odonata - Macromiidae	45.55	11.09	4.11	-24.28	10.32
D	Pr	Odonata - Macromiidae	45.96	12.02	3.82	-25.61	9.17
D	Pr	Odonata - Macromiidae	45.01	11.83	3.80	-26.42	9.08
D	Pr	Odonata - Macromiidae	42.39	11.53	3.68	-27.11	8.80
D	Pr	Odonata - Macromiidae	42.99	11.41	3.77	-27.01	8.54
D	Pr	Odonata - Macromiidae	44.52	11.79	3.78	-25.26	8.62
D	Pr	Odonata - Macromiidae	43.09	10.35	4.16	-27.13	7.21
F	Pr	Odonata - Gomphidae	45.61	11.68	3.90	-25.03	7.47
F	Pr	Odonata - Corduliidae	48.36	9.39	5.15	-23.38	9.30
F	Pr	Odonata - Corduliidae	44.90	12.08	3.72	-22.47	8.61
U	Pr	Odonata - Macromiidae	42.78	11.64	3.67	-25.23	11.17
U	Pr	Odonata - Corduliidae	43.07	11.45	3.76	-24.85	10.77
U	Pr	Odonata - Gomphidae	45.27	11.90	3.81	-24.95	11.00
U	Pr	Odonata - Macromiidae	46.63	11.25	4.14	-25.29	11.92
U	Pr	Odonata - Macromiidae	45.87	11.07	4.14	-25.39	12.46
U	Pr	Odonata - Anisoptera	43.77	10.55	4.15	-26.68	10.04
U	Pr	Odonata - Gomphidae	43.51	11.14	3.91	-24.60	8.35
U	Pr	Coleoptera - Gyrinidae	54.83	8.39	6.54	-24.18	8.75
U	Pr	Odonata - Macromiidae	44.23	12.82	3.45	-25.81	9.91
U	Pr	Odonata - Macromiidae	38.66	10.56	3.66	-25.83	9.72
U	Pr	Odonata - Corduliidae	46.83	11.55	4.05	-27.39	9.82
F	S-G	snail - Bithyniidae	46.52	9.39	4.96	-20.39	5.01
U	S-G	small snail	18.43	3.28	5.62	-18.34	10.69
U	S-G	snail - Bithyniidae	28.21	5.89	4.79	-20.44	10.62
U	S-G	snail - Bithyniidae	41.86	10.20	4.11	-24.13	11.39
U	TERR	caterpillar	58.78	7.61	7.72	-26.06	0.37
U	TERR	earwig parts	48.12	10.39	4.63	-25.55	2.38

VITA

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Education

- 2010 Ph.D. Wildlife and Fisheries Science, Pennsylvania State University, PA
2005 M.Sc. Biology, University of New Brunswick, Fredericton NB
2001 B.Sc. Zoology (Honours), University of Guelph, Guelph ON

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