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Diet Overlap and Competition Among Native and Non-Native Small-Bodied Fishes in the Colorado River, Grand Canyon, Arizona

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LOYOLA UNIVERSITY CHICAGO

DIET OVERLAP AND COMPETITION AMONG NATIVE AND NON-NATIVE SMALL-BODIED FISHES IN THE COLORADO RIVER, GRAND CANYON, ARIZONA

A THESIS SUBMITTED TO
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BY
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To my husband, Nathan, and my parents Rick and Rosan,
for all your love and support.

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ABSTRACT

Introductions of non-native fishes are threatening native fish communities in streams and rivers across the United States. The Colorado River especially has experienced numerous species invasions, and native fish populations throughout the basin are in decline. The native fish community in the Grand Canyon has been particularly affected, with half of the native fishes extirpated from the canyon. Many scientists blame interactions with non-native fishes for these declines. However, to date no one has conducted a thorough diet analysis of small-bodied fishes in the system to assess overlap between native and non-native fish diets. I analyzed the diets of native juvenile bluehead sucker, juvenile flannelmouth sucker, speckled dace, and non-native fathead minnow in multiple seasons and years. Small-bodied fishes in the Grand Canyon consumed a variety of resources, including diatoms, amorphous detritus, terrestrial vegetation, aquatic invertebrates, and terrestrial invertebrates. Diet composition depended on season, and was especially affected by turbidity during flood events. Generally, small-bodied fishes consumed more allochthonous carbon (e.g. amorphous detritus and terrestrial vegetation) during the monsoon season when tributaries were flooding and mainstem turbidity was high. Regardless of seasonal variability in diet, the juveniles of native suckers exhibited extensive diet overlap with non-native fathead minnows, but speckled dace diets did not overlap with fathead minnow diets. I therefore infer a potential for competition among fathead minnows and the juveniles of bluehead and flannelmouth suckers.

CHAPTER ONE

INTRODUCTION

Streams and rivers world-wide are experiencing unprecedented rates of invasion by non-native species. Globally, 1,354 international introductions of exotic fishes had occurred by 1990, and this number excludes the numerous translocations of species among river basins within a country's borders (Welcomme 1988). In the United States, over 530 fish species have been introduced (Tyus and Saunders 2000), and the majority of 125 important watersheds have experienced at least one fish invasion (Gido and Brown 1999). The mechanisms of fish introductions and invasions are varied, but include intentional introductions to establish sport fisheries, to support fish culture, and as biological control agents (Allan and Flecker 1993). Unintentional introductions also contribute to fish invasions via release or escape from aquariums or as "hitchhikers" in ballast water of ships, in shipments of other fish species, or in bait buckets (Allan and Flecker 1993).

Non-native species have been implicated in the wide-spread decline of native fishes in rivers and streams across the United States (Allan and Flecker 1993). Non-native fishes may interact with native fishes in many ways. Examples of non-native fishes reducing native fish populations via predation and competition are often cited. There is also evidence that hybridization with non-native fishes can degrade the genetic integrity of native fish populations (Allan and Flecker 1993, Tyus and Saunders 2000). Habitat degradation and the spread of diseases and parasites are additional mechanisms by which non-native fishes can damage native fish populations (Welcomme 1988, Allan and Flecker 1993).

Although most river basins are exposed to non-native fish introductions, the number of successful invasions varies greatly among rivers. In the United States, southwestern rivers are among the most heavily impacted by non-native fishes (Gido and Brown 1999). For example, over 100 fishes have been introduced to the Colorado River basin, at least half of which are now well established in the basin (Rinne and Janisch 1995, Tyus and Saunders 2000, Olden and Poff 2005). The dominance of non-native fishes in the Colorado River is especially striking in the Grand Canyon, where non-native species diversity is much larger than the diversity of remaining native species. Non-native trout were stocked in the Colorado River in Glen Canyon just above the Grand Canyon as game fish in the 1920s, and a successful trout fishery was established in the cold tailwaters of Glen Canyon Dam after its completion in 1963 (Minckley et al. 2003). Both rainbow (*Oncorhynchus mykiss*) and brown trout (*Salmo trutta*) contribute to this fishery. Common carp (*Cyprinus carpio*), channel catfish (*Ictalurus punctatus*), yellow bullhead (*Ictalurus melas*), fathead minnow (*Pimephales promelas*), plains killifish (*Fundulus zebrinus*), and red shiner (*Cyprinella lutrensis*) also occur commonly throughout the Grand Canyon (Tyus and Saunders 2000, Valdez et al. 2001, Minckley et al. 2003).

The extensive non-native fish assemblage in the Colorado River has been blamed for the dramatic declines of the native fish community (Minckley 1991, Tyus and

Saunders 2000). Historically, the native fish assemblage in the Grand Canyon was composed of eight species: Colorado squawfish (*Ptychocheilus lucius*), razorback sucker (*Xyrauchen texanus*), roundtail chub (*Gila robusta*), bonytail chub (*G. elegans*), humpback chub (*G. cypha*), flannelmouth sucker (*Catostomus latipinnis*), bluehead sucker (*C. discobolus*), and speckled dace (*Rhinichthys osculus*) (Minckley et al. 2003). Native species richness has declined by half, with only flannelmouth sucker, bluehead sucker, speckled dace, and the federally endangered humpback chub currently residing in the Grand Canyon.

Non-native fishes in the Grand Canyon may affect native fish populations through predation and competition for resources or spawning sites. The effects of large-bodied exotic species in the Grand Canyon (e.g. rainbow and brown trout, catfish) apparently include substantial effects of predation (Tyus and Saunders 2000). However, the small-bodied exotic fishes in this system (e.g., fathead minnows, red shiners, plains killifish) may compete with or prey upon both native small-bodied fishes (speckled dace) and the larvae or juveniles of large-bodied native fishes (humpback chub, flannelmouth sucker, and bluehead sucker). These small-bodied exotic fishes were unintentionally introduced via bait buckets, and may pose a serious threat to native species due to their aggressive behavior, such as chasing and physical threats, and via resource competition (Karp and Tyus 1990, Tyus and Saunders 2000). Fathead minnows, for example, are highly territorial and have been known to physically attack sucker larvae (Tyus and Saunders 2000). In addition, fathead minnows are the most abundant of the exotic small-bodied fishes in the system (Baxter et al. unpublished data, Gloss and Coggins 2005). Although alternatives could be imagined, it is most plausible that serious resource competition is most likely when native and non-native species inhabit the same locations. For example, backwater habitats and other potentially important nurseries for native fishes may create spaces for fierce resource competition with abundant fathead minnows and red shiners (Holden and Stalnaker 1975, Rees et al. 2005).

Although competition with non-native fishes has been widely implicated in the decline of native fishes in the Grand Canyon, competition has not been adequately studied in small-bodied fishes (Tyus and Saunders 2000). Trophic interactions of native and non-native fishes must be understood to assess the extent of resource competition between native and non-natives fishes. The niche concept is a useful construct in assessing these trophic interactions. The extent to which a species uses food resources and various habitats shapes its ecological niche. Grinnell (1917) first used the niche concept to describe the requirements of a species that limit its distribution. In 1927, Elton described a species' niche as its overall role in the ecological community, with special emphasis on trophic interactions. Hutchinson (1957) solidified the definition of a niche as an N-dimensional hypervolume, composed of both physical and biological factors. My discussion of ecological niches will reflect the Hutchinsonian niche concept.

The niche concept can be used to evaluate resource competition among species. For example, the complete range of biotic and abiotic environmental factors within which a species can survive in the absence of competition is its fundamental niche (Hutchinson 1957). Interspecific resource competition is only possible if three conditions are met: 1) two or more species share fundamental niches to some degree; 2) the shared resources are limited; and 3) all species involved are negatively affected by sharing the limited resource (Crombie 1947, Angermeier 1982). When faced with interspecific resource competition, species' niches are often constricted. These constricted niches are called realized niches (Hutchinson 1957). By partitioning shared resources into smaller realized niches that do not greatly overlap, competing species can coexist. The degree of niche restriction varies, and depends on the strength of competition. The degree of competition is affected by the amount of overlap among species' fundamental niches, the degree of resource limitation, and the competitive ability of each species involved. In extreme cases, a dominant competitor may drive the weaker competitor to local extinction, called "competitive exclusion" (Hutchinson 1957).

From these ideas of niche overlap and resource competition, I developed a diagram to illustrate the potential interactions of two species using habitat and diet as the dimensions of a two dimensional niche-space (Figure 1). In scenarios 1 and 2, resource competition is not possible because only one dimension of the species niches overlap. In scenario 1, the two species overlap in diet, but not habitat. Scenario 2 illustrates the reverse scenario, where two species' habitat overlaps, but their diets do not. Scenario 3 depicts two species experiencing resource competition; in this scenario the two species overlap in the two dimensions measured, diet and habitat.

Directly measuring the extent of competition involves a series of pair-wise exclusion or introduction experiments manipulating the abundances of the species of interest (Schoener 1983). Because these experiments can be logistically difficult in many systems, ecologists have sought metrics from which they can infer competition. In his review of early field experiments examining resource competition, Schoener (1983) concluded that resource competition could be inferred when two or more species overlap in microhabitat and diet. Field experiments in the mainstem Colorado River in the Grand Canyon would be extremely difficult and expensive; therefore, I used niche (i.e. habitat and diet) overlap to infer the potential for resource competition among native and non-native small-bodied fishes in the Grand Canyon (as in Greger and Deacon 1988, Quist et al. 2006).

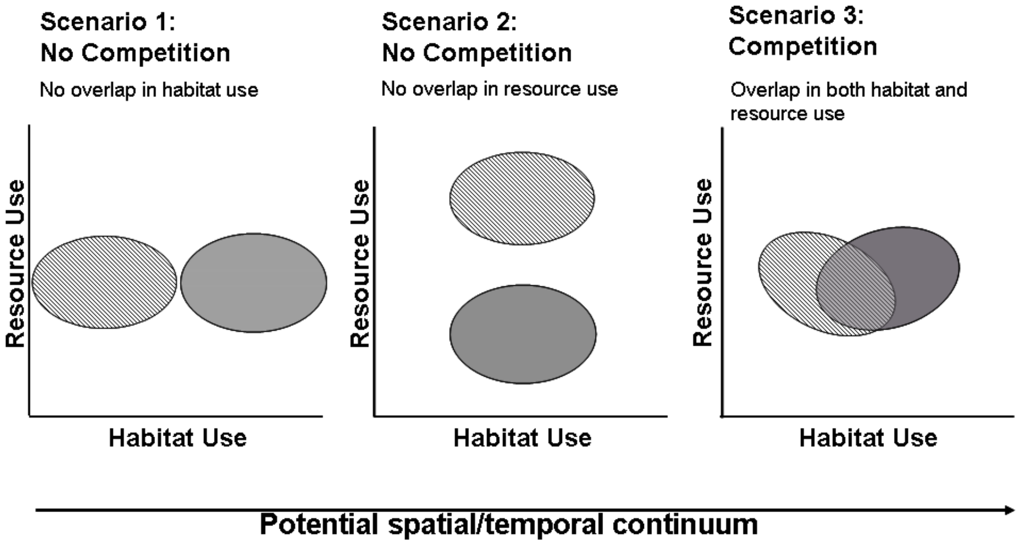

Figure 1. Three potential competition scenarios between two species. The ovals represent hypothetical 2-dimensional niches of two species with regards to diet and habitat. The arrow demonstrates that the nature of the interactions could change through time and/or space.

Diet and habitat use of the dominant small-bodied fishes (i.e., juvenile bluehead sucker, juvenile flannelmouth suckers, speckled dace, and fathead minnow) in the Colorado River in Grand Canyon have not been extensively studied. However, limited data from throughout the Colorado River basin suggest the occurrence of both diet and habitat overlap among the species commonly found in the lower Colorado River (Muth and Snyder 1995, Childs et al. 1998, Gido and Propst 1999, Bezzerides and Bestgen 2002, Rees et al. 2005, Ptacek et al. 2005, Gido et al. 2006). Habitat use among juvenile bluehead and flannelmouth suckers, speckled dace, and fathead minnow overlaps greatly; most of these small-bodied fishes prefer slow and shallow backwaters and mainstem near-shore habitats. However, speckled dace often occupied habitats with higher velocities (Childs et al. 1998, Gido and Propst 1999, Bezzerides and Bestgen 2002, Gido et al. 2006). Shallow backwaters provide protection from piscivorous fish and from fast moving water (Childs et al. 1998, Converse et al. 1998, Gido and Propst 1998, Valdez et al. 2001, Ward et al. 2002, Ralsten et al. 2007). Behavioral studies suggest that larvae of sucker species actively seek out backwater habitats (Bezzerides and Bestgen 2002, Rees et al. 2005, Ptacek et al. 2005). In addition, backwaters may provide warm water temperatures for improved larval and juvenile fish development (Clarkson and Childs 2000, Tyus and Saunders 2000). These studies and the co-occurrence of larval and juvenile flannelmouth and bluehead suckers, speckled dace and fathead minnows in the Grand Canyon (personal observation, Ralsten et al. 2007) indicate that these fishes overlap in habitat use.

These studies also provide some descriptions of the diet preferences of small-bodied fishes found in the lower Colorado River basin. Larval and juvenile native fishes (flannelmouth sucker, bluehead sucker, humpback chub, speckled dace) in the Little Colorado River consume larval chironomids. Sucker species consume large amounts of unidentifiable organic matter, and diatoms make up a small relative volume of sucker diets (<1%) (Childs et al. 1998). In the San Juan River, stable isotope analysis demonstrated that juvenile flannelmouth and bluehead sucker, speckled dace, and fathead minnow are at least partially invertivorous (Gido et al. 2006). Fathead minnows and bluehead suckers are considered herbivores/detritivores and speckled dace are considered invertivorous (Muth and Snyder 1995, Gido et al. 2006). Similarly, in backwater environments in the Green River, larval and juvenile flannelmouth and bluehead suckers consume diatoms, zooplankton, dipteran larvae and organic debris (Muth and Snyder 1995, Rees et al. 2005, Ptacek et al. 2005).

The habitat and food resources of fishes in the Grand Canyon are spatially variable (Minckley 1991, Blinn and Cole 1991, Ralsten et al. 2007). For example, temperature and water clarity are variable along the length of the river. The tailwaters of Glen Canyon Dam are relatively clear and cold but the Colorado River warms slightly and becomes progressively turbid downstream with inputs of more tributaries. This is especially prominent downstream of the two largest tributaries, the Little Colorado River and the Paria River (Figure 2). As a result, algal production is much lower downstream of these tributaries (Hall et al. unpublished data). Tributaries also deliver allochthonous carbon to the Colorado River and these resources are available to fishes for consumption (Kennedy et al. unpublished data). The invertebrate community in the Grand Canyon also changes longitudinally downstream of the dam. The tailwater invertebrate community is dominated by non-native gammarus, New Zealand mudsnail, and chironomid species, most of which are likely non-native (Kennedy and Gloss 2005). However, gammarus and New Zealand mudsnails become rarer downstream, and chironomids and simuliids dominate the downstream invertebrate community (Kennedy and Gloss 2005). In addition to changes in the invertebrate community, invertebrate abundance and biomass also decline with distance downstream from the dam (Kennedy and Gloss 2005).

The Colorado River is also laterally variable, with habitat patches created by differences in physical properties such as water depth and velocity, substrate type, and shoreline habitat. Historically, lateral heterogeneity was likely greater, because backwaters were more prevalent in the Grand Canyon prior to the construction of Glen Canyon Dam in 1963 (Converse et al. 1998). Backwaters are generally considered ideal habitat for small-bodied fishes. Small fish can take refuge from fast currents, cold temperatures, and large aquatic predators in backwater habitats (Goeking et al. 2003, Brouder et al. 1999). The operation of the dam has changed the stability of the backwaters currently present in the Grand Canyon (Brouder et al. 1999). The discharge from the dam fluctuates on a daily basis to meet daily changes in power demand, and these frequent changes in discharge result in short retention times of water in backwaters (Behn et al. 2010). The short retention time results in backwaters that do not resemble backwaters in less regulated systems (i.e. warmer, relatively stagnant water, higher phytoplankton and zooplankton densities, etc.) (Behn et al. 2010). Despite these changes to backwaters in the Grand Canyon, there is a perceived paradigm among researchers and managers that backwaters are critically important habitats for juvenile native fishes in the Grand Canyon (Brouder et al. 1999, Behn et al. 2010), but this paradigm has not been tested.

The longitudinal variation in turbidity is accentuated seasonally when flooding tributaries carry more sediment and organic matter into the mainstem Colorado River (Blinn and Cole, 1991). During the monsoon season (July 15 – September 30), tributaries deliver up to 500,000 metric tons of particulate organic matter to the mainstem (Kennedy et al. unpublished data), which may be an important food resource for fishes. This seasonal heterogeneity was likely greater prior to construction of Glen Canyon Dam (Andrews 1991, Lovich and Melis 2007). Before the dam was completed, the Colorado River in the Grand Canyon was punctuated by extreme variability in seasonal discharge, turbidity and temperature (Blinn and Cole 1991, Stevens et al. 1997). Now, Glen Canyon Dam retains the majority of suspended sediment and organic matter from upstream and releases uniformly clear and cold water from Lake Powell (Lovich and Melis 2007).

The Colorado River also exhibits less inter-annual heterogeneity than was likely historical and the sources of this heterogeneity have likely changed. Historically, the main sources of inter-annual heterogeneity were variation in spring snow-melt in the headwaters and the strength of monsoon season storms in late summer and early fall (White et al. 2005). However, the Glen Canyon Dam dampens the effects of spring snow-melt and to a lesser extent, monsoon flooding (Lovich and Melis 2007). Human activities now also contribute to inter-annual variability in habitat conditions in the river. The role of human activities is especially large in the Colorado River due to the predominance of dams in the riverscape (Minckley 1991, Graf 1999). The Glen Canyon Dam, just upstream of the Grand Canyon, is one of more than 117 major dams with impoundments greater than one million cubic meters on the Colorado River (Minckley 1991). These dams are operated to meet regional power demand and to maintain reservoirs that also meet regional demands for freshwater (Andrews 1991, Minckley 1991). Due to changes in power or water demand, average annual downstream discharge can change substantially. In addition, experimental flow treatments are used as an ecological management tool to improve downstream riverine habitat (Lovich and Melis 2007, Ralsten 2007, Coggins 2008). Examples of experimental flow treatments include the unrestricted release of water, simulating seasonal flooding, and periods of constant daily discharge, simulating normal river conditions in contrast to the daily fluctuations in discharge in normal dam operations (Lovich and Melis 2007, Ralsten 2007, Coggins 2008,). One such experimental "steady flow" regime was implemented September – October 2008 and this paper discusses the effect of this steady flow treatment on small-bodied fish diets.

Objectives and hypotheses

My goal was to describe the diets and niche overlap of the dominant small-bodied fishes: native juvenile flannelmouth and bluehead suckers (FMS and BHS, respectively), speckled dace (SPD), and non-native fathead minnows (FHM) and to infer potential resource competition among native and non-native fishes in the Grand Canyon. I defined "small-bodied" as smaller than 150 mm total length. This included all life stages of fathead minnow and speckled dace, and juveniles of flannelmouth and bluehead suckers. I examined the extent of diet overlap of these species via gut content analysis to evaluate the possibility that resource competition with non-natives is responsible, in part, for native species declines. I also assessed the importance of seasonal and spatial heterogeneity in river conditions to small-bodied fish diets by comparing fish diets from four seasons and from backwater and mainstem habitats. In September and October 2008, Glen Canyon Dam operators implemented an experimental flow regime in which daily discharge was held constant (i.e. there were no fluctuations in discharge). Thus, to address the consequences of this management action on small-bodied fish diets, I compared small-bodied fish diets from three monsoon seasons (2006, 2007, and 2008).

Study questions

In considering these objectives, I addressed the following research questions: 1) What are the diets of the dominant native and non-native small-bodied fishes in the Colorado River, Grand Canyon? 2) How does diet composition vary with habitat (backwater versus maistem) or season (spring, summer, autumn, winter)? 3) Do the diets of the dominant small-bodied fishes overlap? 4) Does the extent of diet overlap vary with habitat (backwater versus mainstem) or season? 5) Do dam operations (i.e. steady flow treatment) in the monsoon season affect diet composition and overlap among the dominant small-bodied fishes?

Based on these questions, I predicted that all small-bodied fishes would utilize most types of resources available to them in the system, e.g. aquatic invertebrates, especially *Simulium arcticum, Gammarus lacustris,* and chironomid spp., diatoms, plant debris, amorphous detritus, and terrestrial invertebrates, but that speckled dace would be the most invertivorous because of their feeding strategy and preferred habitat (Childs et al. 1998, Gido and Propst, 1999, Gido et al. 2006). I also predicted that organic debris, such as plant material and amorphous detritus, would be more available in backwater habitats than mainstem habitats due to lower water velocity and higher deposition rates, as described in Behn et al. (2010). Therefore, I predicted that the diets of small-bodied fishes caught in these habitats would reflect this difference in resource availability. Resource availability in the Colorado River changes seasonally, most notably in the monsoon season (July 15-September 30) when tributaries flood and deliver large amounts of allochthonous carbon to the mainstem. Therefore, I predicted that the diets of small-bodied fishes would reflect seasonal changes in resource availability. During turbid conditions, I predicted that juvenile suckers and fathead minnows would consume fewer diatoms and rely more heavily on allochthonous material, such as plant debris and potentially amorphous detritus. Conversely, I predicted that, because they are likely primarily invertivorous, speckled dace diets would not be affected by temporal variation in allochthonous resources.

I also predicted that the shift toward allochthonous material in juvenile sucker and fathead minnow diets would be exaggerated in strong monsoon years (i.e. higher tributary discharge and higher mainstem turbidity). Experimental low steady flows in the summer of 2000 reduced drift and resulted in higher chironomid densities in upstream reaches of the Grand Canyon (Rogers 2003). Based on this limited evidence, I predicted that the benthic-feeding juvenile suckers, fathead minnows, and to a lesser extent speckled dace, would consume more chironomids in periods of steady flows than in periods of fluctuating flow.

A conceptual diagram (Figure 1) outlines three potential scenarios for niche overlap between two species. Given the existing literature, I hypothesized that scenario 3 would best describe the interactions of fathead minnows with juvenile suckers. Because speckled dace are likely more invertivorous than juvenile suckers and fathead minnows (Childs et al. 1998, Gido et al. 2006), I hypothesized that scenario 2 (Figure 1) would best describe the interactions of speckled dace with fathead minnows and juvenile suckers. In addition, I hypothesized that the extent of interspecific competition would be more intense (greater diet overlap) in turbid conditions (i.e., during the monsoon season) due to low rates of primary production and limited resource availability. However, the reverse may also occur where allochthonous carbon from tributaries results in higher resource availability and diversity and decreases diet overlap among small-bodied fishes. I also predicted that all four taxa would utilize backwaters similarly based on studies in other parts of the Colorado River basin (Gido and Propst 1999), and thus the extent of overlap would not be affected by habitat.

CHAPTER TWO

METHODS

Study sites and sample collection

The Colorado River in the Grand Canyon is bounded upstream by Glen Canyon Dam and downstream by Lake Mead, the reservoir behind Hoover Dam. Six sites along this 225 mile reach were sampled (Figure 2). Sites were selected to encompass longitudinal gradients, to represent the dominant geomorphic reaches in the canyon (Stevens et al. 1997) and to bracket the major tributaries. Mean physical and chemical properties of each site were measured (Table 1).

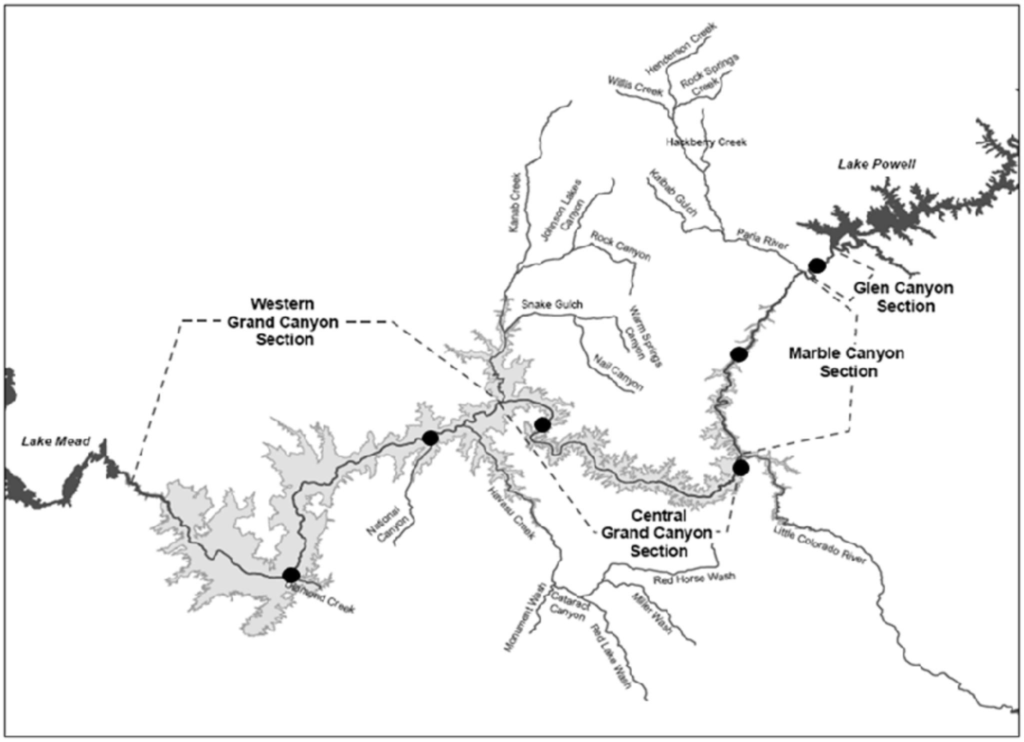

Figure 2. Map of collection sites on the Colorado River in the Grand Canyon.

Table 1. Approximate mean site characteristics.

Site	Annual Discharge m3/s (SD)	Catchment area (million ha)	Depth (m)	Width (m)
RM 0	329.89 (53.61)	28.96	6.3	131.4
RM 30	N/A	N/A	6.3	77.1
RM 62	> 346.68 (51.45)*	> 63.67*	7.8	110.3
RM 127	> 346.68 (51.45)*	> 63.67*	5.1	60.8
RM 167	N/A	38.31	6.2	74.4
RM 225	357.66 (48.90)	38.67	6.2	82.5

* site is located at RM 88. Annual discharge and catchment area were calculated using USGS Real-Time Water Data for Arizona. Annual discharge is calculated from the monthly mean discharges taken from July 2006 to May 2007. Catchment area is taken from the USGS station closest to the sites listed above.

Although six sites were sampled, the native small-bodied fishes (speckled dace and juvenile flannelmouth and bluehead suckers) were absent from the two upper-most sites (above RM 62). The same was true of fathead minnows, the dominant non-native small-bodied fish. These patterns are likely attributable to lack of suitable spawning habitat and to the high densities of piscivorous rainbow trout in the upper reaches of the Grand Canyon (Gloss and Coggins 2005). Because the majority of samples were captured downstream of the two major tributaries (Paria River and Little Colorado River), diet variability caused by longitudinal gradients was likely dampened. In addition, sample sizes from individual sites for each sample date were small (<10 individuals/species). Thus, there was low statistical power to assess the effect of longitudinal gradients on small-bodied fish diets. Therefore, I focused on seasonal and lateral (i.e. habitat) variability and pooled samples from the four sites to increase the statistical power of this analysis.

To evaluate seasonal variability in small-bodied fish diets, I collected samples in four seasons (April 2007, July 2007, September 2007, and January 2008). To examine inter-annual variability and the influence of a dam operational change, i.e., steady flows, I collected samples from September 2006 and 2007, during typical diel fluctuations in dam discharge and in September 2008 when dam operations were restricted to steady flows. The importance of habitat to small-bodied fish diets was examined by collecting samples from backwater and mainstem habitats at each site and for each sampling date.

Up to 10 individuals of each species were collected at each site through seining and electroshocking. Backwater habitats and sandy near-shore habitats in the mainstem were sampled during the day using seine nets. Other near-shore habitats in the mainstem were sampled via electrshocking shortly after dark. Fish were handled according to the USGS-Grand Canyon Monitoring and Research Center protocol. Fish were weighed and measured for fork length (FL) and total length (TL), and whole specimens were preserved in the field in 70% ethanol for later gut content analysis. I defined “small-bodied fish” as any specimen smaller than 150 mm total length, regardless of life stage. Sample collection was supervised by a collaborator (C.V. Baxter, Idaho State University IACUC protocol number 6261007).

Study species

Although many species of small-bodied fish were collected in small numbers, this analysis focuses on the species caught in consistently larger numbers. These include: juvenile bluehead sucker, juvenile flannelmouth sucker, speckled dace, and fathead minnow.

Bluehead sucker (BHS)

Bluehead sucker (*Catostomus discobolus*) is one of three endemic catostomids historically found in the Grand Canyon. Both males and females generally reach sexual maturity at lengths greater than 318 mm, but some reports indicate that sexual maturity can be reached at slightly smaller sizes (Ptacek et al. 2005). Bluehead sucker spawn in spring, but spawning activity may stretch into early summer. Spawning generally takes place over clean gravel. Once developed, larvae drift downstream to low velocity habitats such as backwaters. In the Upper Colorado River basin, young bluehead suckers grow to about 50 mm in their first year, and are approximately 90 mm after their second year (Ptacek et al. 2005).

Adult bluehead suckers are found in fast-flowing cobble areas and have a pronounced stiff scraping disc in their lower jaw. They are benthic feeders and scrape algae, associated invertebrates, and other organic matter off hard substrates (Ptacek et al. 2005). Larval and juvenile bluehead suckers generally inhabit areas of slower water velocity and consume more invertebrates than do adults (Ptacek et al. 2005).

Flannelmouth sucker (FMS)

Flannelmouth sucker (*Catostomus latipinnis*) is the second of three endemic catostomids historically found in the Grand Canyon. The third, razorback sucker (*Xyrauchen texanus*), has been reported occasionally in the Grand Canyon, but is generally considered extirpated from the canyon (Gloss and Coggins, 2005). On average, adult flannelmouth suckers reach lengths of about 500 mm, and most mature flannelmouth suckers caught in the Grand Canyon are between 400 and 650 mm (Rees et al. 2005). Flannelmouth suckers generally spawn in the spring and early summer, but there is some evidence of fall or even year round spawning in some tributaries in the Grand Canyon (Rees et al. 2005). Spawning is thought to occur over cobble substrate in tributaries near the confluence with the mainstem. Like larval bluehead suckers, larval flannelmouth suckers drift and can even actively seek out areas of low velocity, such as near-shore and backwater habitats.

Adult flannelmouth suckers inhabit areas of slower velocity than do adult bluehead suckers, such as pools, slow moving rivers, and backwaters (Rees et al. 2005). Flannelmouth suckers lack the cartilaginous ridges found in bluehead suckers, and adults are benthic omnivores, consuming invertebrates, algae and detritus (Rees et al. 2005). Larvae and juveniles are less benthic, but also consume mainly invertebrates and algae (Rees et al. 2005).

Speckled dace (SPD)

Speckled dace (*Rhinichthys osculus*) is a small-bodied fish, native to the Western United States (Moyle 1976, Lovich 2005). The species is highly adaptable and can inhabit a wide range of habitats from intermittent streams to lake environments (Moyle 1976). Speckled Dace maximum length is approximately 100 mm and they generally reach reproductive maturity at age 2 (Moyle 1976). Speckled dace spawn in spring and summer over gravel substrate. Larvae and fry seek out warm, shallow environments in the river’s margins (Moyle 1976).

Speckled dace are generally benthic foragers, consuming benthic invertebrates found among rocky substrate, but they are also known to consume zooplankton and terrestrial invertebrates on the surface. Their diets can change seasonally, and may include large amounts of algae in certain locations and seasons (Moyle 1976).

Fathead minnow (FHM)

Fathead minnow (*Pimephales promelas*) is non-native to the Colorado River basin and was likely introduced unintentionally via bait buckets (Tyus and Saunders 2000, Gloss and Coggins 2005). It is a small-bodied fish, with maximum lengths of around 100 mm TL (Moyle 1976). Fathead minnows can survive in a wide range of environments and are highly tolerant of poor water quality (Moyle 1976). Fathead minnows spawn in the summer, are highly fecund and may spawn multiple times in one summer. Males are territorial and establish nests under debris such as stones or branches (Moyle 1976).

Fathead minnows consume a wide range of food items, including diatoms, filamentous algae, benthic invertebrates, zooplankton, and other organic matter, often from the benthic environment (Moyle 1976). However, it is generally believed that they will consume the most available food items, in any part of the water column (Moyle 1976).

Gut content analysis

Gut contents were analyzed using a modification of the methods described in Rybczynski et al. (2008). I removed and examined the contents from the anterior portion of the gut to the first U-bend of cyprinids (fathead minnow and speckled dace) and juvenile catostomids (flannelmouth and bluehead suckers) because these families lack true stomachs (Greger and Deacon 1988, Childs et al. 1998, Gido et al. 2006, and Rybczynski et al. 2008). Gut contents were placed into a Petri dish and sorted into coarse and fine fractions and examined using microscopy. The coarse fraction was composed of macroscopic invertebrates and large pieces of plant material that were too large to place on a slide; the fine fraction consisted primarily of diatoms, amorphous detritus, plant material, and some invertebrate body parts. I spread the gut contents to an even depth and obtained relative proportions of each food item in the coarse fraction and of the whole fine fraction as percentages of the total area using a stereo microscope and image analysis software (ImagePro Plus ® Media Cybernetics, Bethesda, Maryland and Leica Application Suite © Leica Microsystems Ltd., Heerbrugg, Switzerland). The fine fraction was filtered onto 0.45 µm grided Metricel® membrane filters (Pall Corp., Ann Arbor, MI) and preserved on slides using immersion oil type B for further examination. Relative proportions of each food category in the fine fraction were calculated based on relative area measurements made using image analysis software (ImagePro Plus ® Media Cybernetics, Bethesda, Maryland and Leica Application Suite © Leica Microsystems Ltd., Heerbrugg, Switzerland) and a compound microscope at 100-400x magnification depending on particle density on the slide.

Because many standard gut content analytic methods are based on mass or volume rather than on area (Hellawell and Abel 1971, Hynes 1950) I also measured the relative proportions by mass of all food categories in both the coarse and the fine fraction, using ash-free dry mass (AFDM) in addition to using the area-based method described above.

Of the 569 small-bodied fish diets that I analyzed, 290 were analyzed using both area-based and mass-based methods to compare these methods and validate the area-based approach. Proportional contribution of each of the dominant food categories calculated by mass was highly correlated with the same measures calculated by area with correlation coefficients close to 1.0 for all seasons (Table 2). These data demonstrated that measures of relative area are representative of measures of relative mass. Therefore, I analyzed the remaining samples with the area-based method only and the data presented here are area-based measurements.

Digital imaging technology makes area-based measurement easier and less time consuming than volumetric or mass-based measurements. Area-based measurements may also provide more precise measurements than either volumetric or mass-based methods. For small volumes, visual estimates of relative volumes are often used (e.g., Muth and Snyder 1995, Childs et al. 1998) and these have large error associated with them if precise equipment is not available. In contrast, digital imaging allows for more precise and consistent measurements of relative diet composition. In addition, area-based measurements do not damage the sample as mass-based measurements do, and the samples can therefore be archived for future analysis.

Table 2. Correlation of percent diet resulting from mass and area measurements for each of the dominant food resources (>10% in diets) and each sampling date.

Season	Food Resource													
	Diatom		Am. Det.		Terr.Veg.		Chiro.		Sim.		Other Aq. Invert.		Terr. Invert.	
	R	p-value	R	p-value	R	p-value	R	p-value	R	p-value	R	p-value	R	p-value
Sep. 2006	0.975	<0.001	0.857	<0.001	0.834	<0.001	0.542	0.001	0.507	0.002	0.638	<0.001	0.821	<0.001
Apr. 2007	0.997	<0.001	0.987	<0.001	0.653	<0.001	0.868	<0.001	0.788	<0.001	0.845	<0.001	0.992	<0.001
Jul. 2007	0.880	<0.001	0.666	<0.001	0.848	<0.001	0.859	<0.001	0.880	<0.001	0.789	<0.001	0.939	<0.001
Sep. 2007	0.940	<0.001	0.892	<0.001	0.920	<0.001	0.874	<0.001	0.961	<0.001	0.811	<0.001	0.847	<0.001
Jan. 2008	0.974	<0.001	0.952	<0.001	0.818	<0.001	0.947	<0.001	0.953	<0.001	0.827	<0.001	N/A	N/A
Sep. 2008	0.883	<0.001	0.937	<0.001	0.832	<0.001	0.872	<0.001	0.874	<0.001	0.909	<0.001	0.849	<0.001

Of the 569 specimens analyzed, 194 were speckled dace; 40 were collected in backwater habitats, 141 were collected in mainstem habitats, and 13 lacked habitat data.

These samples were not included in the habitat analyses. The total lengths of speckled dace across all sampling dates ranged from 21 mm to 108 mm; length for 16 specimens was not recorded. The mean TL of speckled dace specimens was greatest in September 2007, but September 2006 and 2008 mean lengths were not different from other sampling dates. (1-way ANOVA; df = 5; F = 6.64; p-value < 0.001).

Sixty-two juvenile bluehead suckers were collected. Of these, 27 were from backwater habitats and 34 were from mainstem habitats (one fish did not have its habitat of origin recorded and was not included in the habitat analyses). For all sampling dates, bluehead sucker TL ranged from 31 mm to 135 mm. Mean TL was significantly greater in September 2007 than in January and September 2008 (1-way ANOVA; df = 4; F = 3.84; p-value = 0.008). Specimens collected in January had the smallest mean TL, but this pattern was not statistically significant.

Of the specimens analyzed, 129 were juvenile flannelmouth suckers; 46 of these were collected in backwater habitats, 71 were collected in mainstem habitats, and 12 lacked habitat data. These were not included in the habitat analyses. Total length of flannelmouth suckers ranged from 29 mm to 148 mm across all sampling dates, but 13 specimens were lacking length data. Mean TL was greatest in September 2006 and July 2007, but only TL in September 2006 was significantly different (1-way ANOVA; df = 5; F = 5.45; p-value <0.001).

I analyzed 184 were fathead minnows diets. Of these 127 were from mainstem habitats, 47 were from backwater habitats and 10 lacked habitat data and were not included in the habitat analyses. The range of TL for fathead minnows across all sampling dates was 27 mm to 104 mm, with only one specimen missing length data. Specimens collected in April and July 2007 had the longest mean TL, and these were significantly different from the mean TL of specimens collected in September 2007, which was the smallest mean TL (1-way ANOVA; df = 3; F = 3.70; p-value = 0.003). This was the only significant difference.

Data analysis

I compared the relative contribution of each food resource to the diet of each fish species among seasons (April 2007-January 2008) and among years (September 2006-2008) using 1-way Analysis of Variance (ANOVA). All proportional data were arcsine-square root transformed to meet the assumptions of ANOVA. I used a Tukey's post-hoc pairwise comparison test for all statistically significant ANOVAs (p-value < 0.05).

Turbidity

To examine the relationship between diet composition and turbidity, I used acoustic sediment data from the USGS Grand Canyon Monitoring and Research Center (http://www.gcmrc.gov/products/other_data/gcmrc.aspx). This data set was generated from the Laser Acoustic Monitoring System that records suspended sediment concentrations at 4 sites through the Grand Canyon every 15 minutes. My collection sites corresponded to the locations of the four acoustic monitoring stations. Primary production rates in the Colorado River in the Grand Canyon approach zero when sediment concentrations are above approximately 316 mg/l (Hall et al. unpublished data). The number of observations in the 30 days prior to sampling when silt concentrations were higher than 316 mg/l, and when gross primary production (GPP) = 0, provides a metric of biologically-relevant turbidity levels. I refer to this metric as MT (metric of turbidity). When MT is small, this corresponds to few observations of high turbidity and presumably high rates of GPP. The opposite is true when MT is large. I conducted a correlation analysis to test if there were associations between the percent of the diet of each dominant food resource and MT. All univariate statistical analyses were performed using the software package Systat® (v. 10.0) (SSI San Jose, California).

Diet overlap

The mean proportions of food categories in each species diet were calculated for all sampling dates. Mean proportions were used to compare the degree of diet overlap among species using Schoener's similarity index (Schoener 1970). The proportion of overlap is calculated with the following formula:

$$C=1-\tfrac{1}{2}(\Sigma|P_{x,i}-P_{y,i}|)$$

where $P_{x,i}$ and $P_{y,i}$ are the proportions of food category i in the diets of species x and species y, respectively. Index values range from 0 (no overlap) to 1 (complete overlap). Statistical analysis of Schoener's index is not possible, but index values of greater than 0.6 or less than 0.4 are generally accepted as ecologically important (Wallace 1981, Childs et al. 1998, Muth and Snyder 1995).

I also assessed patterns of diet overlap within and among species and season using Bray-Curtis resemblance matrices of square-root-transformed proportional data and non-metric multidimensional scaling (NMDS; PRIMER v6 © PRIMER-E Ltd., Plymouth, United Kingdom). The plot generated by NMDS reflects a "best-fit" illustration of the similarity matrix. The goodness of fit of the NMDS analysis to this similarity matrix is reflected in the stress value. Stress values range from 0 to 1 and any value less than 0.15 generally indicates a good fit to the data. Statistical differences among species groups (established a priori) in the NMDS analysis were identified using one-way analysis of similarity (ANOSIM; PRIMER v6 © PRIMER-E Ltd., Plymouth, United Kingdom). ANOSIM provides a test statistic R that ranges from -1 to 1 and is based on the rank similarities of samples within a priori groups versus among a priori groups. The R statistic is an indication of the similarity of samples within a group versus among groups. A value of R = 0 indicates that the rank similarities are the same within and among groups; that is, there is no difference in the degree of similarity of samples based on the groupings. A value of R = 1 indicates that samples within groups are more similar to each other than to samples in other groups. The significance of R is tested through a permutation test randomly assigning samples to groups. The significance level is the percentage (out of 1,000 permutations) of simulated values that are greater than the observed R value; if only 5% of simulated values are greater than the observed value, the significance level is 5% (Warwick et al. 1990). Both the value of R and the significance level must be considered when interpreting ANOSIM results. Proportional diet data were correlated with NMDS axes scores using Systat® (v. 10.0) (SSI San Jose, California).

CHAPTER THREE

RESULTS

Diet composition

The diets of juvenile bluehead and flannelmouth suckers, speckled dace, and fathead minnows consisted mainly of diatoms, terrestrial vegetation, amorphous detritus, aquatic insects (especially *S. arcticum* and chironomids, but including *G. lacustris*, Trichopterans, Hemipterans, Coleopterans, and other Dipteran species), and, to a lesser extent, various terrestrial invertebrates, including Hemipterans and Hymenopterans (Figure 3).

Seasonal variability

Bluehead sucker

The diets of juvenile bluehead suckers contained mostly fine organic material, including diatoms (3 – 71%), amorphous detritus (4 – 71%), and coarser material such as chironomids (0 – 50%), simuliids (0 – 21%) and terrestrial vegetation (0 – 26%) (Figure 3A; Table 3). The diets of juvenile bluehead suckers changed only slightly with season. The proportion of amorphous detritus in their diets was significantly larger in September (16%) than in April (4%) (1-way ANOVA; df = 3; F = 3.9; p-value = 0.020; Table 3). No other food resource in bluehead sucker diets exhibited significant differences among seasons (1-way ANOVA; Table 4).

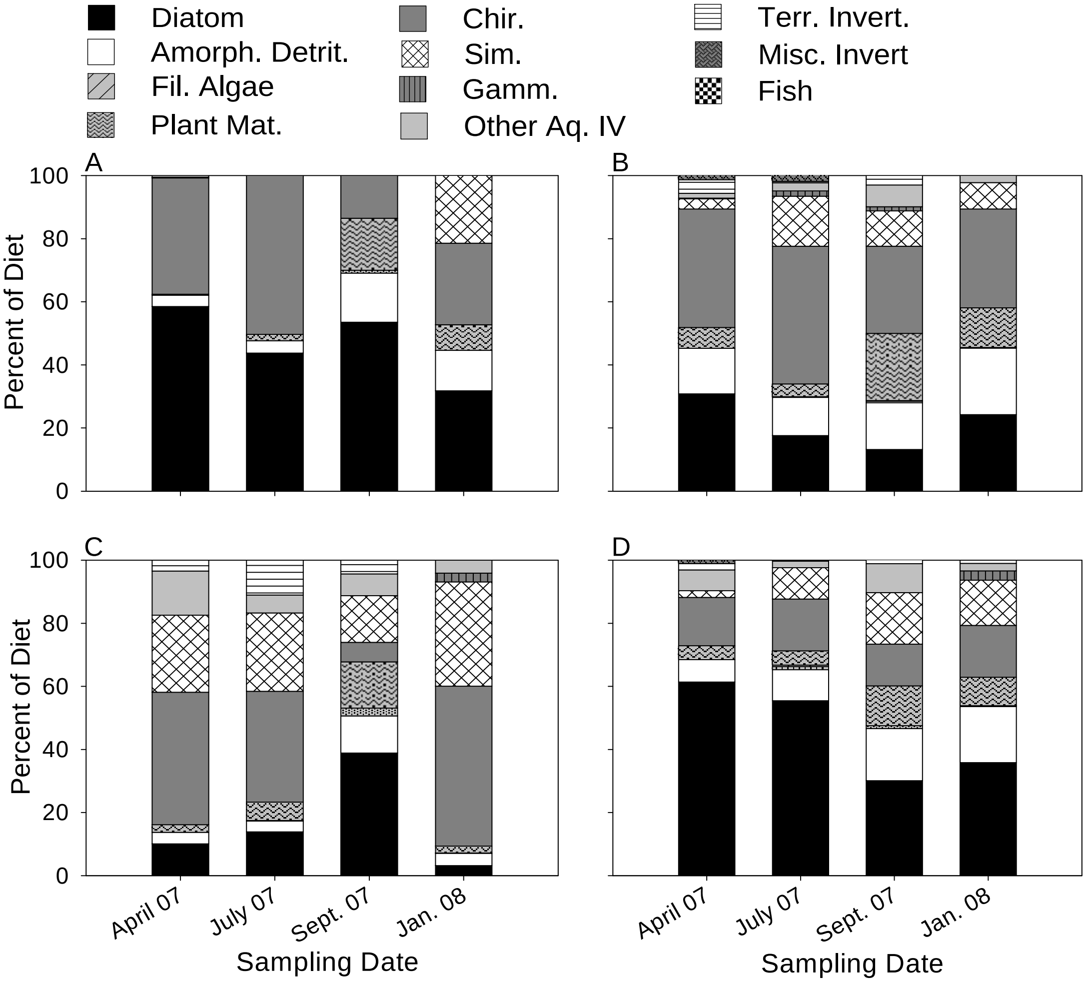

Figure 3. Seasonal variability in the diet composition of the four dominant small-bodied fish species: (A) juvenile bluehead sucker (n=29), (B) juvenile flannelmouth sucker (n=89), (C) speckled dace (n=134), and (D) fathead minnow (n=118). Values are averages across four sites for each sampling date.

Table 3: Mean diet composition by percent area with standard error for bluehead sucker (BHS), fathead minnow (FHM), flannelmouth sucker (FMS), and speckled dace (SPD).

Date	Diet Item	BHS		FHM		FMS		SPD	
Sep. 2006	Diatom	3.21	N/A	29.35	(3.9)	13.91	(7.8)	5.40	(3.2)
	Amorphous Detritus	71.14	N/A	33.32	(3.8)	34.20	(8.0)	18.76	(5.4)
	Macrophyte	0.00	N/A	4.31	(1.6)	0.00	(0.0)	2.09	(2.0)
	Filamentous Algae	0.00	N/A	0.00	(0.0)	0.00	(0.0)	0.00	(0.0)
	Terrestrial Vegetation	25.65	N/A	19.41	(2.2)	29.59	(5.9)	18.73	(4.1)
	Chironomid	0.00	N/A	4.55	(3.2)	15.36	(8.7)	15.61	(5.1)
	Simuliid	0.00	N/A	1.75	(1.0)	3.31	(2.6)	9.73	(4.3)
	Gammarus	0.00	N/A	0.00	(0.0)	0.00	(0.0)	0.29	(0.3)
	Other Aquatic Invertebrates	0.00	N/A	6.88	(3.3)	3.05	(1.6)	27.78	(5.9)
	Terrestrial Invertebrates	0.00	N/A	0.00	(0.0)	0.58	(0.3)	1.73	(1.6)
	Miscellaneous Invertebrates	0.00	N/A	0.57	(0.5)	0.00	(0.0)	0.00	(0.0)
Apr. 2007	Diatom	58.47	(23.4)	61.33	(6.4)	30.86	(6.4)	9.52	(4.0)
	Amorphous Detritus	3.63	(1.6)	7.12	(1.2)	14.40	(4.1)	3.46	(1.9)
	Macrophyte	0.00	(0.0)	0.00	(0.0)	0.00	(0.0)	0.00	(0.0)
	Filamentous Algae	0.00	(0.0)	0.00	(0.0)	0.00	(0.0)	0.00	(0.0)
	Terrestrial Vegetation	0.29	(0.1)	4.42	(1.7)	6.59	(2.1)	2.28	(0.7)
	Chironomid	36.85	(23.5)	15.26	(4.7)	37.53	(8.0)	42.67	(6.4)
	Simuliid	0.04	(0.0)	2.15	(1.8)	3.28	(2.1)	23.35	(5.4)
	Gammarus	0.22	(0.2)	0.00	(0.0)	0.21	(0.1)	0.00	(0.0)
	Other Aquatic Invertebrates	0.49	(0.5)	6.58	(2.8)	1.48	(0.7)	15.43	(4.5)
	Terrestrial Invertebrates	0.00	(0.0)	2.07	(1.5)	4.33	(3.0)	3.29	(2.1)
	Miscellaneous Invertebrates	0.00	(0.0)	1.06	(1.1)	1.32	(0.8)	0.00	(0.0)
Jul. 2007	Diatom	43.72	(43.7)	55.45	(7.4)	17.59	(7.4)	13.86	(4.7)
	Amorphous Detritus	3.92	(3.9)	9.84	(2.3)	12.11	(5.6)	3.49	(1.5)
	Macrophyte	0.00	(0.0)	1.00	(0.5)	0.22	(0.1)	0.15	(0.1)
	Filamentous Algae	0.00	(0.0)	0.45	(0.5)	0.00	(0.0)	0.00	(0.0)
	Terrestrial Vegetation	2.03	(2.0)	4.51	(1.0)	4.00	(0.9)	5.86	(2.4)
	Chironomid	50.33	(49.7)	16.43	(5.6)	43.67	(8.2)	35.06	(5.3)
	Simuliid	0.00	(0.0)	9.89	(4.4)	15.82	(4.8)	24.87	(4.3)
	Gammarus	0.00	(0.0)	0.00	(0.0)	1.70	(0.6)	0.00	(0.0)
	Other Aquatic Invertebrates	0.00	(0.0)	2.12	(1.0)	2.59	(1.3)	5.67	(2.6)
	Terrestrial Invertebrates	0.00	(0.0)	0.31	(0.3)	0.44	(0.3)	11.05	(4.2)
	Miscellaneous Invertebrates	0.00	(0.0)	0.00	(0.0)	1.84	(1.8)	0.00	(0.0)
Sep. 2007	Diatom	53.51	(8.7)	30.09	(6.6)	13.18	(4.0)	38.85	(5.6)
	Amorphous Detritus	15.57	(2.1)	16.49	(3.2)	14.80	(3.2)	11.77	(2.5)
	Macrophyte	0.92	(0.6)	0.91	(0.9)	0.50	(0.3)	2.47	(1.3)
	Filamentous Algae	0.00	(0.0)	0.00	(0.0)	0.23	(0.2)	0.00	(0.0)
	Terrestrial Vegetation	16.47	(6.3)	12.63	(2.2)	21.25	(3.9)	14.66	(3.1)
	Chironomid	7.06	(3.6)	13.24	(4.4)	27.64	(4.8)	6.17	(3.2)
	Simuliid	2.58	(1.2)	16.32	(6.8)	11.19	(4.8)	14.79	(4.8)
	Gammarus	0.42	(0.4)	0.00	(0.0)	1.32	(0.8)	0.00	(0.0)
	Other Aquatic Invertebrates	2.86	(1.5)	9.21	(3.4)	6.90	(1.9)	6.92	(2.8)
	Terrestrial Invertebrates	0.61	(0.5)	1.10	(1.1)	2.99	(1.0)	4.37	(2.3)
	Miscellaneous Invertebrates	0.00	(0.0)	0.00	(0.0)	0.00	(0.0)	0.00	(0.0)

Table 3. Continued.

Date	Diet Item	BHS		FHM		FMS		SPD	
Jan. 2008	Diatom	31.77	(11.0)	35.80	(5.2)	24.21	(6.4)	3.19	(2.5)
	Amorphous Detritus	12.83	(3.1)	17.84	(2.5)	21.10	(4.9)	3.88	(2.7)
	Macrophyte	0.00	(0.0)	0.21	(0.1)	0.19	(0.2)	0.09	(0.1)
	Filamentous Algae	0.00	(0.0)	0.00	(0.0)	0.00	(0.0)	0.00	(0.0)
	Terrestrial Vegetation	8.11	(4.6)	9.01	(1.6)	12.55	(3.7)	2.18	(1.0)
	Chironomid	25.84	(11.3)	16.41	(4.2)	31.31	(6.3)	50.69	(6.3)
	Simuliid	21.34	(12.5)	14.37	(4.0)	8.38	(2.7)	33.03	(5.8)
	Gammarus	0.00	(0.0)	2.92	(1.6)	0.00	(0.0)	2.82	(2.5)
	Other Aquatic Invertebrates	0.10	(0.1)	2.40	(1.0)	2.25	(1.0)	4.12	(1.8)
	Terrestrial Invertebrates	0.00	(0.0)	1.03	(1.0)	0.00	(0.0)	0.00	(0.0)
	Miscellaneous Invertebrates	0.00	(0.0)	0.00	(0.0)	0.00	(0.0)	0.00	(0.0)
Sep. 2008	Diatom	70.97	(3.8)	54.05	(4.6)	41.15	(5.3)	20.72	(4.7)
	Amorphous Detritus	16.37	(1.8)	26.45	(3.1)	19.82	(3.0)	8.48	(2.5)
	Macrophyte	0.00	(0.0)	0.00	(0.0)	0.09	(0.1)	0.10	(0.1)
	Filamentous Algae	0.00	(0.0)	0.00	(0.0)	0.00	(0.0)	0.00	(0.0)
	Terrestrial Vegetation	5.81	(1.3)	8.21	(1.6)	12.56	(3.4)	8.84	(2.1)
	Chironomid	5.13	(2.6)	3.32	(1.8)	15.57	(3.7)	21.91	(3.8)
	Simuliid	0.71	(0.5)	3.12	(1.9)	5.53	(2.2)	17.13	(3.4)
	Gammarus	0.02	(0.0)	0.01	(0.0)	0.20	(0.2)	1.49	(0.9)
	Other Aquatic Invertebrates	0.55	(0.4)	4.47	(2.6)	4.81	(1.4)	13.70	(3.1)
	Terrestrial Invertebrates	0.44	(0.3)	0.00	(0.0)	0.28	(0.1)	7.63	(2.9)
	Miscellaneous Invertebrates	0.00	(0.0)	0.00	(0.0)	0.00	(0.0)	0.00	(0.0)
	Fish	0.00	(0.0)	0.37	(0.4)	0.00	(0.0)	0.00	(0.0)

Table 4: Seasonal differences in each of the dominant food resources (>10% in diets) in the diets of bluehead sucker (BHS), flannelmouth sucker (FMS), speckled dace (SPD) and fathead minnow (FHM) (One-way ANOVAs with Tukey's pairwise comparisons). Significant values are bold (p-values <0.05). Non-significant (p-value > 0.05) ANOVA analyses are not shown.

Species	Food Resource	Date	Apr-07	Jul-07	Sep-07	Jan-08
BHS	Am. Detritus	df: 3; F: 3.9; p: 0.020				
		Apr-07	1.000			
		Jul-07	0.998	1.000		
		Sep-07	**0.040**	0.119	1.000	
		Jan-08	0.324	0.434	0.616	1.000
FMS	T. Veg.	df: 3; F: 8.0; p: <0.001				
		Apr-07	1.000			
		Jul-07	0.999	1.000		
		Sep-07	**<0.001**	**0.001**	1.000	
		Jan-08	0.355	0.388	0.059	1.000
FMS	Other Aq. Invert.	df: 3; F: 3.8; p: 0.012				
		Apr-07	1.000			
		Jul-07	0.847	1.000		
		Sep-07	**0.010**	0.195	1.000	
		Jan-08	0.925	0.994	0.065	1.000
SPD	Am. Detritus	df: 3; F: 8.4; p: <0.001				
		Apr-07	1.000			
		Jul-07	0.986	1.000		
		Sep-07	**<0.001**	**0.001**	1.000	
		Jan-08	0.999	0.970	**<0.001**	1.000
SPD	Diatom	df: 3; F: 13.6; p: <0.001				
		Apr-07	1.000			
		Jul-07	0.857	1.000		
		Sep-07	**<0.001**	**<0.001**	1.000	
		Jan-08	0.736	0.281	**<0.001**	1.000
SPD	T. Veg.	df: 3; F: 10.3; p: <0.001				
		Apr-07	1.000			
		Jul-07	0.549	1.000		
		Sep-07	**<0.001**	**0.003**	1.000	
		Jan-08	0.984	0.368	**<0.001**	1.000
SPD	Chironomid	df: 3; F: 14.0; p: <0.001				
		Apr-07	1.000			
		Jul-07	0.719	1.000		
		Sep-07	**<0.001**	**<0.001**	1.000	
		Jan-08	0.650	0.131	**<0.001**	1.000
SPD	Other Aq. Invert.	df: 3; F: 3.1; p: 0.030				
		Apr-07	1.000			
		Jul-07	0.071	1.000		
		Sep-07	0.204	0.975	1.000	
		Jan-08	**0.032**	0.972	0.841	1.000
FHM	Am. Detritus	df: 3; F: 3.0; p: 0.034				
		Apr-07	1.000			
		Jul-07	0.824	1.000		
		Sep-07	0.192	0.686	1.000	
		Jan-08	**0.031**	0.340	0.980	1.000
FHM	Diatom	df: 3; F: 5.1; p: 0.002				
		Apr-07	1.000			
		Jul-07	0.952	1.000		
		Sep-07	**0.013**	0.072	1.000	
		Jan-08	**0.017**	0.118	0.938	1.000
FHM	T. Veg.	df: 3; F: 4.9; p: 0.003				
		Apr-07	1.000			
		Jul-07	0.930	1.000		
		Sep-07	**0.004**	**0.032**	1.000	
		Jan-08	0.100	0.433	0.360	1.000

Flannelmouth sucker

The diets of juvenile flannelmouth suckers contained fine organic material, including diatoms (13 – 41%), amorphous detritus (12 – 34%), as well as substantial amounts of terrestrial vegetation (4 – 30%) and aquatic insects, especially chironomids (15 – 44%) (Figure 3B; Table 3). The diets of juvenile flannelmouth suckers varied significantly among seasons. The proportion of terrestrial vegetation increased significantly in September (21%) compared to April (7%) and July (18%) (1-way ANOVA; df = 3; F = 8.0; p-value <0.001; Table 3). Aquatic invertebrates other than chironomids and simuliids also made up a significantly larger portion of flannelmouth sucker diets in September (7%) than in April (1%) (1-way ANOVA; df = 3; F = 3.8; p-value = 0.012; Table 3).

Speckled dace

Speckled dace in this study were predominantly invertivorous (Figure 3C). Aquatic insects, especially chironomids (6 – 51%) and simuliids (10 – 33%), dominated their diets, but speckled dace also consumed smaller amounts of diatoms (3 – 39%), amorphous detritus (3 – 19%) and terrestrial vegetation (2 – 19%). The diets of speckled dace varied significantly among seasons, but did not follow the patterns observed in juvenile sucker diets. Speckled dace consumed fewer chironomids in September (6%) than in the April, July and January (43%, 35%, and 51%, respectively) (1-way ANOVA; df = 3; F = 14.0; p-value <0.001; Table 3). In contrast, the proportion of diatoms in speckled dace diets was significantly higher in September (39%) than in April, July, and January (10%, 14%, and 3%, respectively) (1-way ANOVA; df = 3; F = 13.6; p-value < 0.001; Table 3). Similarly, proportions of amorphous detritus were higher in September

(12%) than in April July and January (3%, 3%, and 4%, respectively) (1-way ANOVA; df = 3; F = 8.4; p-value <0.001; Table 3). The proportion of terrestrial vegetation in speckled dace diets was also higher in September (15%) than in April, July and January (2%, 6%, and 2%, respectively) (1-way ANOVA; df = 3; F = 10.3; p-value <0.001; Table 3).

<u>Fathead minnow</u>

Like juvenile bluehead suckers, fathead minnow diets were dominated by fine materials such as diatoms (29 – 61%), amorphous detritus (7 – 33%) and terrestrial vegetation (4 – 19%) (Figure 3D; Table 3). However, the proportion of fine materials in the diets of fathead minnows varied significantly among season. Diatoms were found in significantly higher proportions in April (61%) than in September (30%) and January (36%) (1-way ANOVA; df = 3; F = 5.1; p-value = 0.002; Table 3). The proportion of amorphous detritus in fathead minnow diets was significantly higher in January (18%) than in April (7%) (1-way ANOVA; df = 3; F = 3.0; p-value = 0.034; Table 3) and the proportion of terrestrial vegetation was significantly higher in September (13%) than in April (4%) and July (5%) (1-way ANOVA; df = 3; F = 4.9; p-value = 0.003; Table 3). The proportions of invertebrates in fathead minnow diets did not change significantly with season and was always less than 40% of their diets (1-way ANOVA; Table 4).

Diet overlap

I assessed diet overlap using Schoener's similarity index, and NMDS and ANOSIM and both methods revealed substantial overlap among juvenile bluehead sucker diets, flannelmouth sucker diets and fathead minnow diets. Speckled dace diets overlapped less consistently with flannelmouth sucker and fathead minnow diets (Figure

4; Tables 5 and 6). The Schoener's similarity index revealed that juvenile bluehead sucker diets overlapped substantially (index > 0.6) with fathead minnow diets, except in September 2006 (Table 5). Bluehead sucker diets overlapped with flannelmouth sucker diets on all sampling dates except September 2007. Speckled dace diets did not typically overlap with diets of bluehead sucker or fathead minnow, with the exception of overlap in September 2007. In contrast, speckled dace diets overlapped with flannelmouth sucker diets on all sampling dates except for January 2008. Flannelmouth sucker diets overlapped with fathead minnow diets on all sampling dates (Table 5).

Table 5: Schoener's similarity matrix for all species-species combinations for each sampling date. Scores are calculated from the mean proportion of each diet item. Scores above 0.600 (substantial overlap) are in bold.

Species	Season	BHS	FMS	FHM
FMS	Sep. 2006	**0.631**		
	Apr. 2007	**0.724**		
	Jul. 2007	**0.672**		
	Sep. 2007	0.585		
	Jan. 2008	**0.795**		
	Sep. 2008	**0.700**		
FHM	Sep. 2006	0.559	**0.759**	
	Apr. 2007	**0.782**	**0.644**	
	Jul. 2007	**0.661**	**0.604**	
	Sep. 2007	**0.723**	**0.735**	
	Jan. 2008	**0.836**	**0.783**	
	Sep. 2008	**0.808**	**0.801**	
SPD	Sep. 2006	0.406	**0.651**	0.580
	Apr. 2007	0.514	**0.619**	0.422
	Jul. 2007	0.544	**0.754**	0.508
	Sep. 2007	**0.784**	**0.673**	**0.844**
	Jan. 2008	0.565	0.513	0.453
	Sep. 2008	0.419	**0.645**	0.483

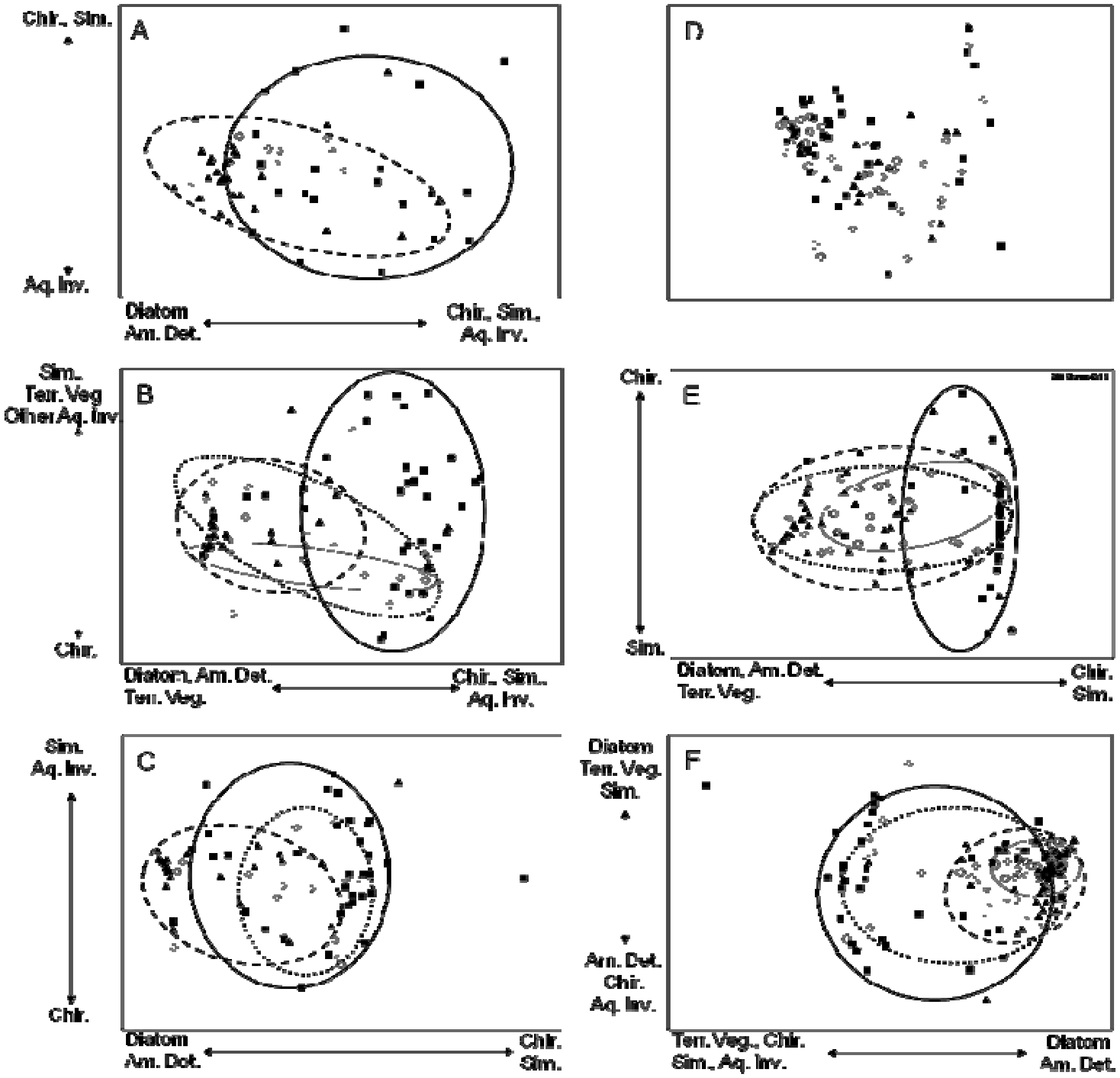

Figure 4. Seasonal changes in diet overlap among species. NMDS based on proportional diet composition of all species: juvenile bluehead suckers (BHS; circles), speckled dace (SPD; squares), juvenile flannelmouth suckers (FMS; diamonds), and fathead minnow (FHM; triangles) in all habitats for each sampling date (A) Sep. 2006 (stress = 0.14), (B) Apr. 2007 (stress = 0.12), (C) Jul. 2007 (stress = 0.10), (D) Sep. 2007 (stress = 0.14), (E) Jan. 2008 (stress = 0.11), and (F) Sep. 2008 (stress = 0.11). Ovals encompass >80% of specimens of species for which there were significant differences in diet (ANOSIM p-value < 0.05; ANOSIM results in Table 6).

Table 6: Results of one-way ANOSIM examining differences among species for each sampling date. Pairwise comparisons with significant (p-value < 0.05) differences in diet are bold. NS indicates that the global R statistic was not significant (p-value > 0.05).

Species	Season	BHS		FMS		FHM	
		R	P-value	R	P-value	R	P-value
FMS	Sep. 2006	-0.089	0.556				
	Apr. 2007	-0.08	0.722				
	Jul. 2007	0.133	0.212				
	Sep. 2007	NS	NS				
	Jan. 2008	-0.037	0.577				
	Sep. 2008	**0.198**	**0.002**				
FHM	Sep. 2006	0.025	0.367	0.21	0.061		
	Apr. 2007	-0.081	0.51	**0.158**	**0.008**		
	Jul. 2007	0.203	0.173	**0.185**	**0.024**		
	Sep. 2007	NS	NS	NS	NS		
	Jan. 2008	0.014	0.426	0.048	0.134		
	Sep. 2008	**0.07**	**0.02**	**0.121**	**0.001**		
SPD	Sep. 2006	0.042	0.5	-0.027	0.574	**0.386**	**0.001**
	Apr. 2007	**0.368**	**0.009**	**0.269**	**0.001**	**0.495**	**0.001**
	Jul. 2007	0.2	0.105	0.036	0.223	**0.236**	**0.001**
	Sep. 2007	NS	NS	NS	NS	NS	NS
	Jan. 2008	**0.461**	**0.009**	**0.383**	**0.001**	**0.362**	**0.001**
	Sep. 2008	**0.369**	**0.001**	**0.145**	**0.003**	**0.37**	**0.001**

There was a substantial amount of overlap in the NMDS plots among all species, especially fathead minnows, juvenile bluehead suckers, and juvenile flannelmouth suckers (Figure 4). However, diet overlap patterns were dependent on sampling date (Figure 4 and Table 6). For example, in September 2006, fathead minnow and speckled dace diets were moderately different (ANOSIM; R = 0.386, p-value = 0.001; Figure 4A; Table 6). This difference was associated with aquatic invertebrates in speckled dace diets and diatoms and amorphous detritus in fathead minnow diets (Figure 4A; Table 7).

Table 7: Axis correlation scores for each of the dominant food resources (>10% in diets) in the non-metric multi-dimensional scaling analysis illustrated in Figure 4. Axis 1 corresponds to the x-axis and Axis 2 corresponds to the y-axis in Figure 4.

Date	Food item	NMDS Axis			
		Axis 1 (x)		Axis 2 (y)	
		R	P-value	R	P-value
Sep. 2006					
	Diatom	**-0.673**	**<0.001**	-0.218	0.097
	Am. Det.	**-0.676**	**<0.001**	**0.302**	**0.020**
	Terr. Veg.	-0.168	0.203	0.037	0.783
	Chironomid	**0.616**	**<0.001**	**0.382**	**0.003**
	Simuliid	**0.352**	**0.006**	**0.418**	**0.001**
	Other Aq. Invert.	**0.682**	**<0.001**	**-0.569**	**<0.001**
Apr. 2007					
	Diatom	**-0.902**	**<0.001**	-0.139	0.180
	Am. Detritus	**-0.477**	**<0.001**	0.201	0.052
	Terr. Veg.	**-0.349**	**0.001**	**0.241**	**0.019**
	Chironomid	**0.723**	**<0.001**	**-0.530**	**<0.001**
	Simuliid	**0.289**	**0.005**	**0.685**	**<0.001**
	Other Aq. Invert.	**0.464**	**<0.001**	**0.317**	**0.002**
Jul. 2007					
	Diatom	**-0.836**	**<0.001**	0.154	0.178
	Am. Detritus	**-0.462**	**<0.001**	-0.221	0.052
	Terr. Veg.	-0.054	0.641	-0.166	0.147
	Chironomid	**0.451**	**<0.001**	**-0.622**	**<0.001**
	Simuliid	**0.506**	**<0.001**	**0.594**	**0.001**
	Other Aq. Invert.	0.028	0.806	**0.456**	**<0.001**
Sep. 2007					
	Diatom	**-0.823**	**<0.001**	**0.378**	**<0.001**
	Am. Detritus	**-0.472**	**<0.001**	-0.139	0.178
	Terr. Veg.	0.073	0.481	**-0.599**	**<0.001**
	Chironomid	**0.508**	**<0.001**	**-0.473**	**<0.001**
	Simuliid	**0.610**	**<0.001**	**0.665**	**<0.001**
	Other Aq. Invert.	**0.225**	**0.027**	**-0.395**	**<0.001**
Jan. 2008					
	Diatom	**-0.844**	**<0.001**	-0.154	0.121
	Am. Detritus	**-0.562**	**<0.001**	0.187	0.060
	Terr. Veg.	**-0.253**	**0.010**	0.068	0.500
	Chironomid	**0.705**	**<0.001**	**0.543**	**<0.001**
	Simuliid	**0.566**	**<0.001**	**-0.720**	**<0.001**
	Other Aq. Invert.	0.120	0.228	-0.110	0.273
Sep. 2008					
	Diatom	**0.849**	**<0.001**	**0.301**	**<0.001**
	Am. Detritus	**0.490**	**<0.001**	**-0.352**	**<0.001**
	Terr. Veg.	**-0.197**	**0.020**	**0.303**	**<0.001**
	Chironomid	**-0.717**	**<0.001**	**-0.222**	**0.009**
	Simuliid	**-0.645**	**<0.001**	**0.282**	**0.001**
	Other Aq. Invert.	**-0.258**	**0.002**	**-0.669**	**<0.001**

In April 2007, speckled dace diets exhibited some overlap with, but were significantly different than, diets of fathead minnows, bluehead suckers and flannelmouth suckers (ANOSIM; R = 0.495, 0.269, and 0.368, respectively; p-value = 0.001, 0.001, and 0.009, respectively; Figure 4B; Table 6). Speckled dace samples occupied the diet space most closely associated with aquatic invertebrates, especially chironomids and simuliids. The other species occupied space associated with high proportions of diatoms and amorphous detritus (Figure 4B; Table 7). In contrast, fathead minnows and flannelmouth suckers had very similar diets, with only minor differences (ANOSIM; R = 0.158; p-value = 0.008; Figure 4B; Table 6). The difference between flannelmouth sucker and fathead minnow diets was associated with chironomids and simuliids contributing to flannelmouth sucker diets, but not fathead minnow diets (Figure 4B; Table 7).

In July 2007, fathead minnow diets were again very similar to flannelmouth sucker diets with only minor differences (ANOSIM; R = 0.185; p-value = 0.024; Figure 4C; Table 6). However, fathead minnow diets were more substantially different than speckled dace diets in July 2007 (ANOSIM; R = 0.236; p-value = 0.001; Figure 4C; Table 6). These were the only significant differences in this sampling date (Figure 4C; Table 6). Speckled dace and flannelmouth sucker diets were associated with simuliids and aquatic invertebrates other than chironomids and fathead minnow diets were more associated with diatoms, amorphous detritus, and terrestrial vegetation (Figure 4C; Table 7).

There were no significant differences among diets in September 2007 (Figure 4D; Table 6), but speckled dace diets were moderately different from the diets of all other species in January 2008, mainly due to the predominance of simuliids and chironomids in speckled dace diets (ANOSIM; 0.2 < R < 0.5; p-value < 0.01; Figure 4E; Table 6; Table 7).

In September 2008, fathead minnow diets were very similar to diets of bluehead suckers and flannelmouth suckers with only minor differences (ANOSIM; R = 0.07 and 0.121, respectively; p-value = 0.02 and 0.001 respectively; Figure 4F; Table 6), but were different than speckled dace diets (ANOSIM; R = 0.370; p-value = 0.001; Figure 4F; Table 6). Bluehead sucker and flannelmouth sucker diets were very similar (ANOSIM; R = 0.198; p-value = 0.002; Figure 4F; Table 6). Flannelmouth sucker diets were also very similar to speckled dace diets (ANOSIM; R = 0.145; p-value = 0.003; Figure 4F; Table 6), but bluehead sucker diets were different than speckled dace diets (ANOSIM; R = 0.369; p-value = 0.001; Figure 4F; Table 6). These patterns were caused by the association of speckled dace and flannelmouth sucker diets with aquatic invertebrates, including simuliids and chironomids, and terrestrial vegetation. In contrast, bluehead sucker and fathead minnow diets were associated with diatoms and amorphous detritus (Figure 4F; Table 7).

Inter-annual patterns and dam operations

Diets of small-bodied fish caught during the monsoon season exhibited inter-annual variability (Figure 5). In general, allochthonous carbon sources, like amorphous detritus and terrestrial vegetation were more important in September 2006 than in other years, but this pattern was not always significant (Figure 5 and Table 8). Juvenile bluehead suckers consumed significantly more amorphous detritus in September 2006 (71%) than in September 2007 (16%) and 2008 (16%) (Table 3; 1-way ANOVA; df = 2; F = 9.6; p-value <0.001) and juvenile flannelmouth suckers and fathead minnows consumed significantly more amorphous detritus in fluctuating flows in September 2006 (34% and 33%, respectively) than in fluctuating flows in September 2007 (15% and 16%, respectively) (Table 3; 1-way ANOVA; df = 2; F = 4.4; p-value = 0.017 and F = 5.5; p-value = 0.006, respectively). In addition, speckled dace and fathead minnows consumed significantly more terrestrial vegetation in fluctuating flows in September 2006 (19%) than during steady flows in September 2008 (9% and 8%, respectively) (Table 3; 1-way ANOVA; df = 2; F = 3.4; p-value = 0.039 and F = 9.2; p-value <0.001, respectively).

Although there was clear inter-annual variability in small-bodied fish diets, I did not observe a consistent effect of steady flow dam operations in September 2008, when there were no daily fluctuations in discharge, except that diatoms were generally more important in September 2008 than in other years (Figure 5). For example, the proportion of diatoms in the diets of bluehead suckers was greater during steady flows in September 2008 (71%) than in fluctuating flows in 2007 (54%) and was significantly greater than in fluctuating flows in September 2006 (3%) (Table 3; 1-way ANOVA; df = 2; F = 5.0; p-value = 0.011). Fathead minnows also consumed significantly more diatoms in September 2008 (54%) than in September 2006 (29%) and September 2007 (30%) (Table 3; 1-way ANOVA; df = 2; F = 9.0; p-value < 0.001). Likewise, flannelmouth sucker diets had a significantly larger proportion of diatoms in steady flows in September 2008 (41%) than in fluctuating flows in September 2007 (13%) (Table 3; 1-way ANOVA; df = 2; F = 9; p-value < 0.001). The proportion of diatoms in flannelmouth sucker diets in September 2008 was also larger than in fluctuating flows in September 2006 (14%), but the difference was not significant (Table 3). The proportion of diatoms in speckled dace diets also varied among years, but the proportion was significantly higher in September 2007

(39%) than in September 2006 (5%) and in September 2008 (21%) (Table 3; 1-way ANOVA; df = 2; F = 9.5; p-value <0.001). The importance of invertebrates in small-bodied fish diets also varied among years, but there were no apparent patterns in their variability (Figure 5 and Table 8).

Table 8: Inter-annual differences in the proportion of each of the dominant food resources (>10% in diets) in the diets of bluehead sucker (BHS), flannelmouth sucker (FMS), speckled dace (SPD) and fathead minnow (FHM) during the monsoon season (July – September) (one-way ANOVAs). Bold values indicate significant p-values (<0.05). Non-significant ANOVAs (p-value > 0.05) are not shown.

Species	Food Resource	Date	Sep-06	Sep-07
BHS	Am. Detritus	df: 2; F: 9.6; p: <0.001		
		Sep-06	1.000	
		Sep-07	**<0.001**	1.000
		Sep-08	**<0.001**	1.000
BHS	Diatom	df: 2; F: 5.0; p: 0.011		
		Sep-06	1.000	
		Sep-07	0.158	1.000
		Sep-08	**0.036**	0.097
BHS	T. Veg.	df: 2; F: 3.3; p: 0.044		
		Sep-06	1.000	
		Sep-07	0.731	1.000
		Sep-08	0.316	0.072
FMS	Am. Detritus	df: 2; F: 4.4; p: 0.017		
		Sep-06	1.000	
		Sep-07	**0.013**	1.000
		Sep-08	0.128	0.300
FMS	Diatom	df: 2; F: 9.0; p: <0.001		
		Sep-06	1.000	
		Sep-07	0.896	1.000
		Sep-08	0.064	**<0.001**
FMS	T. Veg.	df: 2; F: 3.9; p: 0.026		
		Sep-06	1.000	
		Sep-07	0.745	1.000
		Sep-08	0.071	0.073
SPD	Diatom	df: 2; F: 9.5; p: <0.001		
		Sep-06	1.000	
		Sep-07	**<0.001**	1.000
		Sep-08	0.167	**0.012**
SPD	T. Veg.	df: 2; F: 3.4; p: 0.039		
		Sep-06	1.000	
		Sep-07	0.558	1.000
		Sep-08	**0.038**	0.236

Table 8. Continued.

Species	Food Resource	Date	Sep-06	Sep-07
SPD	Chironomid	df: 2; F: 6.0; p: 0.004		
		Sep-06	1.000	
		Sep-07	0.124	1.000
		Sep-08	0.616	**0.003**
SPD	Other Aq. Invert.	df: 2; F: 7.1; p: 0.001		
		Sep-06	1.000	
		Sep-07	**0.001**	1.000
		Sep-08	0.053	0.187
FHM	Am. Detritus	df: 2; F: 5.5; p: 0.006		
		Sep-06	1.000	
		Sep-07	**0.004**	1.000
		Sep-08	0.447	0.056
FHM	Diatom	df: 2; F: 9.0; p: <0.001		
		Sep-06	1.000	
		Sep-07	0.942	1.000
		Sep-08	**0.002**	**0.002**
FHM	T. Veg.	df: 2; F: 9.2; p: <0.001		
		Sep-06	1.000	
		Sep-07	0.063	1.000
		Sep-08	**<0.001**	0.270
FHM	Chironomid	df: 2; F: 4.3; p: 0.016		
		Sep-06	1.000	
		Sep-07	**0.039**	1.000
		Sep-08	0.989	**0.020**
FHM	Simuliid	df: 2; F: 5.0; p: 0.009		
		Sep-06	1.000	
		Sep-07	**0.016**	1.000
		Sep-08	0.980	**0.017**

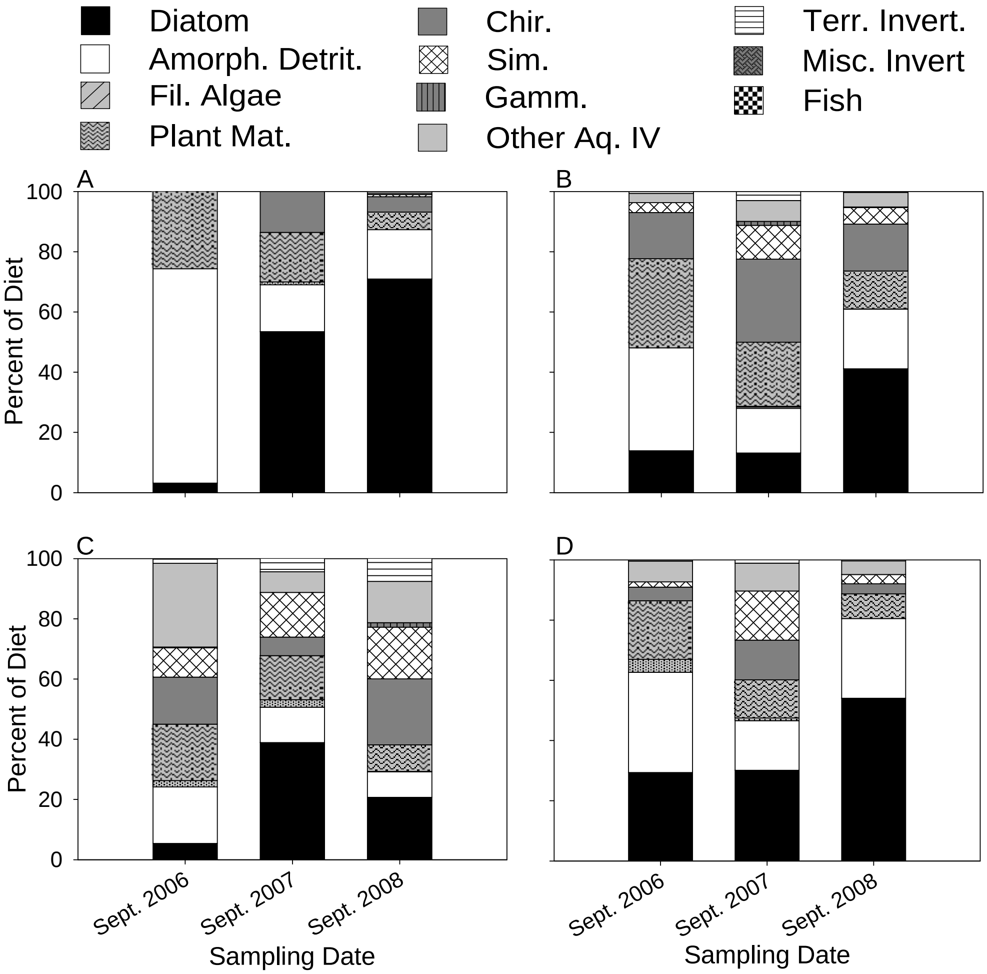

Figure 5. Inter-annual variability and effects of dam releases on fish diets during the monsoon season. Dam operations in September 2008 were constrained and there were no daily fluctuations in discharge. (A) juvenile bluehead sucker (n=48), (B) juvenile flannelmouth sucker (n=64), (C) speckled dace (n=94), and (D) fathead minnow (n=88). Values are averages across four sites for each sampling date.

Potential drivers of seasonal and inter-annual diet variability

Variation in small-bodied fish diets was associated with the amount of time prior to sampling that silt concentrations were above the threshold at which primary production shuts down, described by the metric of turbidity (MT) (Table 9). Silt concentrations varied significantly among sampling dates (Figure 6). Mean silt concentrations were lowest prior to sampling in April and July 2007 (Figure 6; 1-way ANOVA; df = 5; F = 2140.6; p-value < 0.001) and were highest prior to sampling in September 2006, followed by September 2007 and September 2008 (Figure 6; 1-way ANOVA; df = 5; F = 2140.6; p-value < 0.001). Therefore, MT was low in April and July 2007, and higher in September 2006, 2007, and 2008. When MT was high, amorphous detritus and terrestrial vegetation were important in flannelmouth sucker diets (Pearson's correlation coefficient = 0.234 and 0.357 respectively; p-value = 0.008 and <0.001 respectively) and the proportions of chironomids and simuliids in flannelmouth sucker diets were small (Pearson's correlation coefficient = 0.234 and 0.263 respectively; p-value = 0.003 and 0.008 respectively). Large proportions of amorphous detritus and terrestrial vegetation were observed in speckled dace diets when MT was high (Pearson's correlation coefficient = 0.233 and 0.395 respectively; p-value = 0.001 and <0.001 respectively). However, the proportions of chironomids, simuliids, and other invertebrates in speckled dace diets were small when MT was high (Pearson's correlation coefficient = 0.224, 0.210, and 0.184, respectively; p-value = 0.002, 0.003, and 0.010, respectively). Variation in fathead minnow diets was also related to MT. When MT was high, proportions of amorphous detritus and terrestrial vegetation in fathead minnow diets were large (Pearson's correlation coefficient = 0.425 and 0.390 respectively; p-value <0.001), but the proportion of diatoms was small (Pearson's correlation coefficient = 0.210; p-value = 0.004). Bluehead sucker diets were the exception; no food resources in bluehead sucker diets were correlated with MT (Table 9).

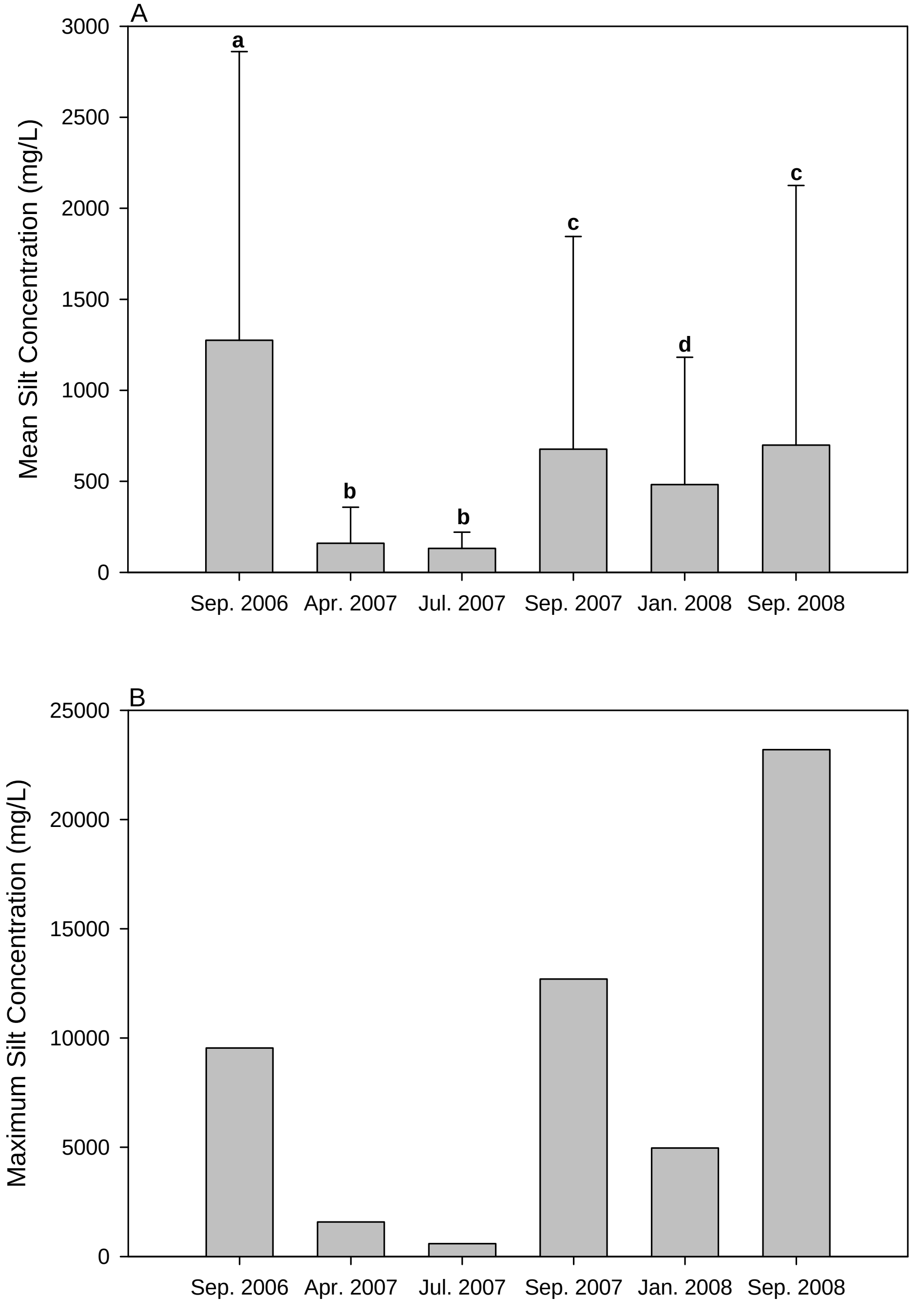

Figure 6. (A) Mean (+ 1 standard deviation) and (B) maximum silt concentrations in the 30 days prior to sampling for all sampling dates. Mean concentrations were compared using a one-way ANOVA with Tukey's post-hoc test (df = 5, F = 2140.6, $p < 0.001$).

Table 9: Correlations of the metric of turbidity (MT, the number of observations in the 30 days prior to sampling when silt concentrations were higher than 316 mg/l, and when GPP (gross primary production) = 0) with proportions of dominant items in bluehead sucker (BHS), flannelmouth sucker (FMS), speckled dace (SPD), and fathead minnow (FHM) diets. Bold values indicate significant relationships (p-value < 0.05). N/A indicates that data were not available for the analysis.

Food Resources	Species							
	BHS		FMS		SPD		FHM	
	R	p-value	R	p-value	R	p-value	R	p-value
Diatom	0.118	0.36	0.004	0.965	-0.01	0.888	**-0.21**	**0.004**
Am. Det.	0.006	0.964	**0.234**	**0.008**	**0.233**	**0.001**	**0.425**	**<0.001**
Terr. Veg.	-0.056	0.666	**0.357**	**<0.001**	**0.395**	**<0.001**	**0.39**	**<0.001**
Chiro.	-0.065	0.615	**-0.234**	**0.008**	**-0.224**	**0.002**	-0.142	0.055
Simuliid	-0.175	0.174	**-0.263**	**0.003**	**-0.21**	**0.003**	-0.098	0.186
Other Aq. Invert.	N/A	N/A	0.134	0.133	**-0.184**	**0.01**	N/A	N/A

Potential influences of habitat on diet composition

There were limited differences in what fish consumed in mainstem habitats compared to backwater habitats and there were no consistent patterns either within or among species (Figure 7). The diets of juvenile bluehead sucker, juvenile flannelmouth sucker, speckled dace, and fathead minnow were similar regardless of where they were caught (Figure 8A, B, C, and D, respectively) and ANOSIM supported no significant differences between habitats (Table 10).

Diet overlap patterns changed only slightly when habitat was considered and these changes depended on sampling date. In April 2007, patterns of diet overlap were similar in mainstem and backwater habitats, with few exceptions (Tables 11and 12). Bluehead sucker diets generally overlapped with flannelmouth sucker and fathead minnow diets in April 2007, but Schoener's index scores comparing bluehead and flannelmouth sucker diets did not indicate overlap in backwaters (Table 11). In addition, bluehead sucker diets overlapped with speckled dace diets in mainstem habitats, but not in backwater habitats (Tables 11 and 12). All other diet overlap patterns were the same in mainstem and backwater habitats in April 2007. Patterns of diet overlap in mainstem habitats compared to backwater habitats were also similar in January 2008, but there were some differences (Tables 11 and 12). For example, speckled dace diets were more similar to bluehead sucker and flannelmouth sucker diets in backwater habitats than in mainstem habitats (Tables 11 and 12). In contrast, fathead minnow diets overlapped with flannelmouth sucker diets in mainstem habitats, but were more distinct in backwater habitats (Tables 11 and 12). In addition, fathead minnow diets and speckled dace diets appear to be different in backwater habitats but not in mainstem habitats (ANOSIM; R = 0.240; p-value = 0.005; Tables 11 and 12).

Table 10: Differences between mainstem and backwater habitats in the diets of bluehead sucker (BHS), flannelmouth sucker (FMS), speckled dace (SPD), and fathead minnow (FHM) (One-way ANOSIMs for each species and for each sampling date). N/A indicates sampling dates and species for which samples from both habitats were not available. Bold values indicate significant results (p-value < 0.05).

Season	Species							
	BHS		FMS		SPD		FHM	
	R	P-value	R	P-value	R	P-value	R	P-value
Sep. 2006	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
Apr. 2007	-0.375	1.000	-0.017	0.518	**0.135**	**0.044**	N/A	N/A
Jul. 2007	N/A	N/A	N/A	N/A	-0.045	0.578	0.036	0.369
Sep. 2007	N/A	N/A	0.117	0.129	N/A	N/A	0.094	0.207
Jan. 2008	-0.103	0.625	-0.049	0.790	0.063	0.227	0.060	0.076
Sep. 2008	0.091	0.121	0.052	0.156	**0.148**	**0.009**	0.023	0.198

There were also some differences in patterns of diet overlap between mainstem and backwater habitats in September 2008 (Tables 11 and 12). There was less diet overlap in backwater habitats than in mainstem habitats. For example, bluehead sucker diets were different from the diets of speckled dace, and to a lesser extent flannelmouth suckers, in backwater habitats, but not in mainstem habitats (Tables 11 and 12).

Similarly, flannelmouth sucker diets overlapped more with fathead minnow and speckled dace diets in mainstem habitats than in backwaters (Tables 11 and 12).

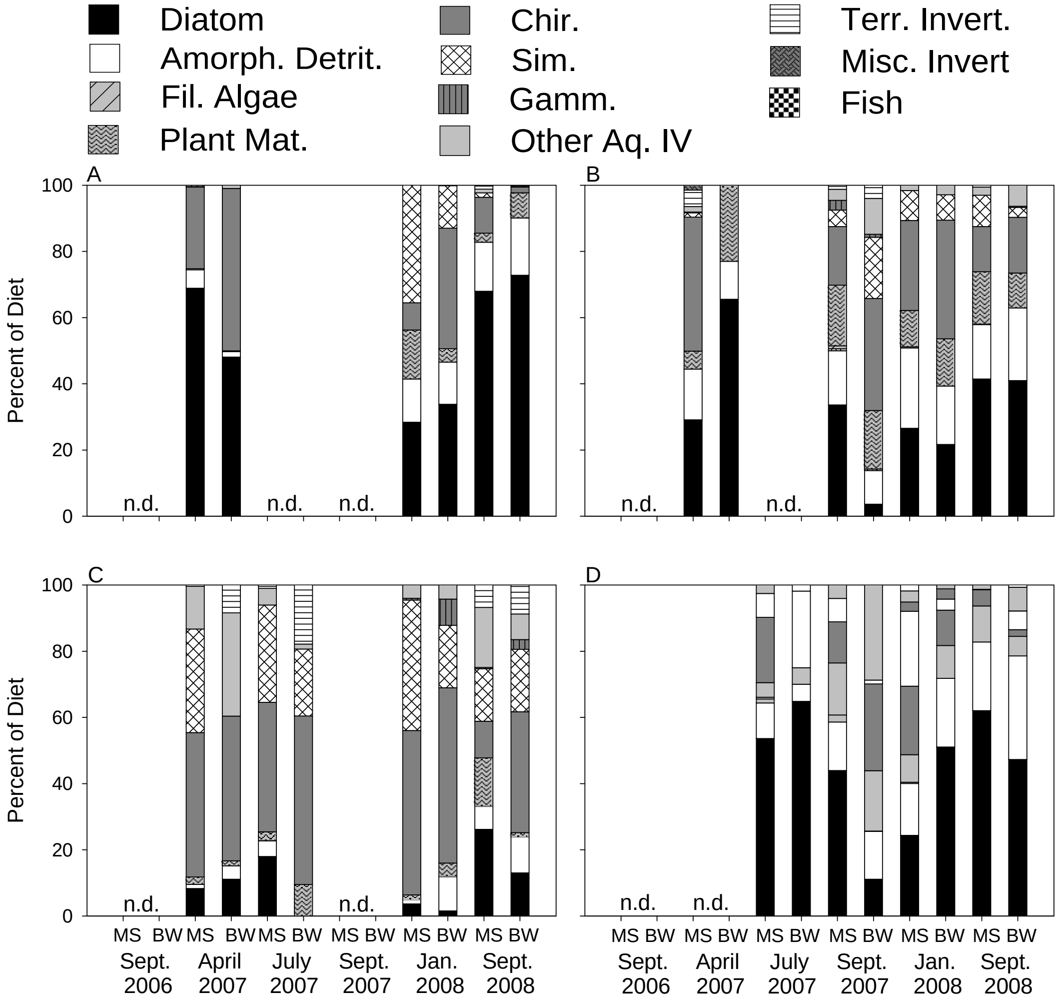

Figure 7. Variability of diets between backwater (BW) and mainstem (MS) habitats for (A) juvenile bluehead suckers, (B) juvenile flannelmouth suckers, (C) speckled dace, and (D) fathead minnows. No data (n.d.) represents sampling periods where data were not collected in mainstem and/or backwater habitats. Values are averaged across four sites for each sampling date.

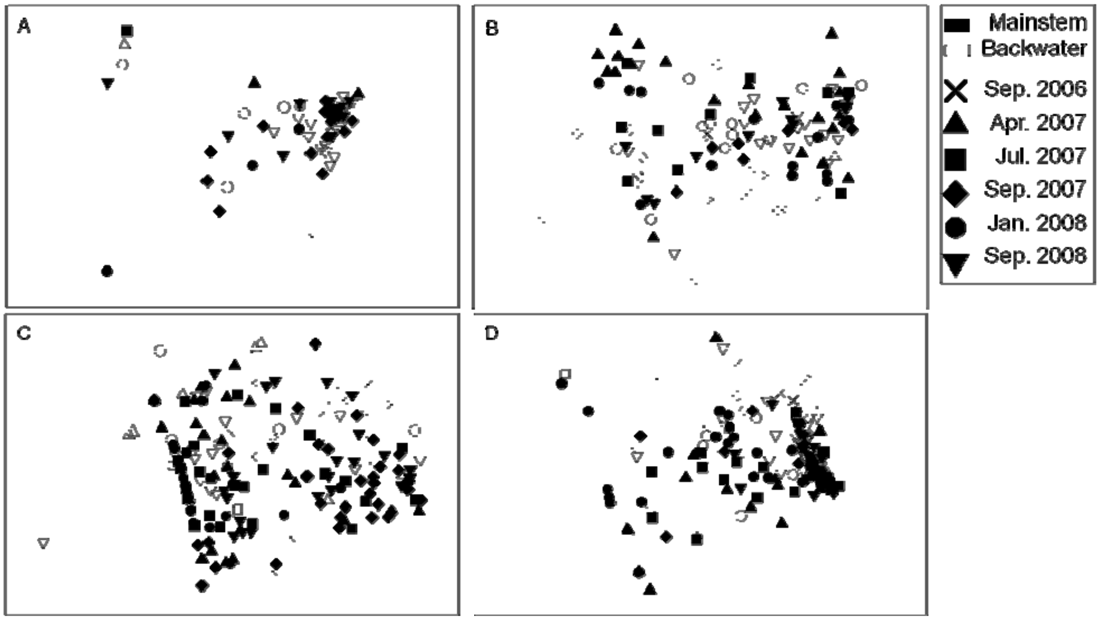

Figure 8. Non-metric multidimensional scaling (NMDS) illustrating variability between habitats (solid shapes are mainstem habitats; open shapes are backwater habitats) in (A) juvenile bluehead sucker diets (stress = 0.08), (B) juvenile flannelmouth sucker diets (stress = 0.13), (C) speckled dace diets (stress = 0.17), and (D) fathead minnow diets (stress = 0.12) in 6 sampling periods (NMDS).

Table 11: Schoener's similarity matrix for all species-species combinations for each sampling date and in mainstem (MS) and backwater (BW) habitats. Scores are calculated from the mean proportion of each diet item. Scores above 0.600 (substantial overlap) are in bold, and scores below 0.400 (substantial differences) are italicized.

Species	Season	BHS		FMS		FHM	
		MS	BW	MS	BW	MS	BW
FMS	Sep. 2006	N/A	N/A				
	Apr. 2007	**0.601**	0.500				
	Jul. 2007	**0.629**	N/A				
	Sep. 2007	**0.759**	N/A				
	Jan. 2008	**0.678**	**0.821**				
	Sep. 2008	**0.729**	**0.682**				
FHM	Sep. 2006	N/A	N/A	N/A	N/A		
	Apr. 2007	**0.826**	N/A	**0.620**	N/A		
	Jul. 2007	**0.694**	N/A	**0.690**	N/A		
	Sep. 2007	**0.837**	N/A	**0.853**	**0.697**		
	Jan. 2008	**0.766**	**0.648**	**0.801**	**0.645**		
	Sep. 2008	**0.857**	**0.731**	**0.751**	0.505		
SPD	Sep. 2006	N/A	N/A	N/A	N/A	N/A	N/A
	Apr. 2007	*0.346*	0.577	0.557	*0.167*	*0.362*	N/A
	Jul. 2007	**0.631**	N/A	**0.807**	N/A	0.549	*0.270*
	Sep. 2007	**0.751**	N/A	**0.764**	N/A	**0.848**	N/A
	Jan. 2008	0.501	**0.651**	0.442	**0.621**	0.535	*0.340*
	Sep. 2008	0.503	*0.274*	**0.714**	0.517	0.503	0.403

Table 12: Differences in diet overlap patterns in mainstem (MS) and backwater (BW) habitats for each sampling date (one-way ANOSIM). Species are bluehead sucker (BHS), flannelmouth sucker (FMS), fathead minnow (FHM), and speckled dace (SPD). Bold values indicate comparisons with significant R statistics (p-value < 0.05). N/A indicates an incomplete sample set.

Species	Season	Habitat	BHS		FMS		FHM	
			R	p-value	R	p-value	R	p-value
FMS	Apr-07	MS	-0.081	0.725				
		BW	<0.001	0.667				
	Jul-07	MS	0.133	0.212				
		BW	N/A	N/A				
	Sep-07	MS	0.175	0.059				
		BW	N/A	N/A				
	Jan-08	MS	-0.031	0.462				
		BW	-0.044	0.558				
	Sep-08	MS	0.045	0.144				
		BW	**0.248**	**0.001**				
FHM	Apr-07	MS	-0.081	0.51	**0.158**	**0.003**		
		BW	N/A	N/A	N/A	N/A		
	Jul-07	MS	0.203	0.173	**0.185**	**0.015**		
		BW	N/A	N/A	N/A	N/A		
	Sep-07	MS	0.046	0.203	-0.046	0.643		
		BW	N/A	N/A	-0.048	0.577		
	Jan-08	MS	-0.083	0.685	-0.063	0.883		
		BW	0.162	0.113	**0.24**	**0.005**		
	Sep-08	MS	0.004	0.401	**0.192**	**0.015**		
		BW	**0.104**	**0.006**	**0.081**	**0.007**		
SPD	Apr-07	MS	**0.444**	**0.012**	**0.251**	**0.001**	**0.495**	**0.001**
		BW	0.075	0.295	**0.443**	**0.013**	N/A	N/A
	Jul-07	MS	0.2	0.105	0.016	0.305	**0.232**	**0.003**
		BW	N/A	N/A	N/A	N/A	0.5	0.086
	Sep-07	MS	-0.1	0.951	-0.077	0.743	-0.053	0.679
		BW	N/A	N/A	N/A	N/A	N/A	N/A
	Jan-08	MS	**0.533**	**0.01**	**0.429**	**0.001**	**0.25**	**0.001**
		BW	0.132	0.134	**0.24**	**0.008**	**0.623**	**0.001**
	Sep-08	MS	**0.119**	**0.047**	-0.017	0.598	**0.248**	**0.002**
		BW	**0.628**	**0.001**	**0.328**	**0.001**	**0.517**	**0.001**

CHAPTER FOUR

DISCUSSION

This study represents one of the only comprehensive descriptions of the diets of small-bodied fishes in the Colorado River in the Grand Canyon. This is especially true for juveniles of the two native sucker species included in the analysis (*C. discobolus* and *C. latipinnis*). There is evidence that populations of these catostomids are declining throughout their range, though their populations in the Grand Canyon appear steady (Clarkson and Childs 2000, Ward et al. 2002, Paukert and Rogers 2004, Ptacek et al. 2005, Gloss and Coggins, 2005). Little is known about the diets of the vulnerable juvenile stages of these species. In this study, small-bodied fishes in the Grand Canyon consumed a variety of resources: diatoms, amorphous detritus, terrestrial vegetation, aquatic invertebrates (including chironomids and simuliids), and terrestrial invertebrates. These resources encompass most of the available resources in the system, which include filamentous algae, diatoms, aquatic invertebrates (dominated by chironomids, simuliids, *Gammarus lacustris*, and New Zealand mudsnail), and allochthonous carbon (including terrestrial vegetation and amorphous detritus) (Kennedy et al. unpublished data, Blinn and Cole 1991; Kennedy and Gloss 2005). I also found that small-bodied fish diets overlapped, indicating that competition may occur, both among native species and among native and non-native species. However, the diets and patterns of niche overlap depended on species and seasonal, inter-annual and habitat heterogeneity in the system.

Niche overlap

An important first step in understanding the ongoing declines of native fish populations in the Colorado River is to describe the ecology of the species, including the diets of juvenile life stages. A second important step is to understand how these species, especially the vulnerable early life stages, interact with other species. There are many types of inter-specific interactions, but I have focused on resource competition. As I predicted, bluehead sucker diets generally overlapped with flannelmouth sucker and fathead minnow diets. In contrast, fathead minnow diets were often significantly different than speckled dace diets. Flannelmouth sucker diets overlapped less consistently with fathead minnow and speckled dace diets. Significant differences in diet were typically associated with diatoms and amorphous detritus in bluehead sucker and fathead minnow diets, and with simuliids and chironomids in speckled dace diets.

Seasonal heterogeneity in diets and niche overlap

Diet overlap patterns changed with season. For instance, bluehead sucker diets were different than flannelmouth sucker and fathead minnow diets during the monsoon season and in steady flows in September 2008, when bluehead suckers ate diatoms, amorphous detritus and terrestrial vegetation more exclusively than did fathead minnows and flannelmouth suckers. In addition, fathead minnow diets were not significantly different than speckled dace diets during the monsoon season in fluctuating flows in September 2007, when there were no differences in diet among any fishes. Fathead minnow diets and flannelmouth sucker diets were different in April and July 2007, when turbidity was the lowest (Figure 9). However, fathead minnow and flannelmouth sucker diets were also different in September 2008, which had relatively high turbidity. This variation in diet overlap is likely attributable to underlying seasonal variability in the diets of individual species.

The diets of small-bodied fishes reflected the seasonal heterogeneity of resources in the Colorado River. Many seasonal patterns in resource availability are driven by a distinct monsoon season (July 15 – September 30). The carbon budget is dominated by allochthonous carbon during monsoon flooding (Kennedy et al. unpublished data) and as turbidity increases, primary production declines (Bob Hall, unpublished data). This temporal heterogeneity in resource availability was likely much greater historically, because Glen Canyon Dam now dampens the effects of spring snowmelt and monsoon flooding (Andrews 1991, Lovich and Melis 2007).

I found that small-bodied fish diets mirrored the seasonal heterogeneity of resources in the river. The extent of seasonal variability of diets, however, depended on species. For example, the diets of juvenile bluehead suckers changed only slightly with season, but the diets of flannelmouth suckers, speckled dace, and fathead minnows varied significantly among seasons. Flannelmouth sucker diets contained more terrestrial vegetation and aquatic invertebrates in turbid conditions in September. These invertebrates included highly degraded and unidentifiable specimens, as well as species that are rare or absent in invertebrate samples from the mainstem Colorado River. It is possible that the increase of these aquatic invertebrates in flannelmouth sucker diets in September reflects a scouring of tributary fauna during monsoon flooding. Speckled dace consumed more terrestrial vegetation, but fewer chironomids in September. The increased turbidity may have affected the ability of speckled dace to find their preferred food resource and forced them to rely on allochthonous carbon sources such as terrestrial vegetation.

Seasonal patterns in the diets of fish could also be attributable to ontogenetic shifts in diet associated with seasonal differences in the total length of fish samples. Such ontogenetic shifts have been documented in many fishes (Werner and Gilliam 1984). If there were consistent differences in the total lengths of samples from each sampling date in this study, some of the observed seasonal variation in diet might be due to variation in sample length. However, there were few differences in mean total length among sampling dates for all species. In particular, if total length of fish captured varied seasonally, I would expect fish caught in the same season of different years to vary predictably in length. This was not the case. Samples from September 2006, 2007, and 2008 were not consistently different from other sampling dates. Although there were some weak correlations between total length and diet composition (Table 13), I do not believe that sample length contributed greatly to the observed seasonal variation in the diets of small-bodied fishes. However, further research into ontogenetic shifts across a broader size range for these species, particularly the catostomids, could reveal additional important diet patterns.

Table 13: Correlations of total length and percent diet for each dominant food resource (> 10 % in diet) and each species: bluehead sucker (BHS), flannelmouth sucker (FMS), speckled dace (SPD), and fathead minnow (FHM). Bold values indicate significant relationships (p-value < 0.05).

Food Resource	Species							
	BHS		FMS		SPD		FHM	
	R	p-value	R	p-value	R	p-value	R	p-value
% Diatom	**0.411**	**<0.001**	-0.102	0.280	**0.320**	**<0.001**	**0.163**	**0.028**
% Amorphous Detritus	-0.040	0.076	**0.197**	**0.035**	0.002	0.983	-0.042	0.577
% Terrestrial Vegetation	-0.152	0.239	**0.188**	**0.045**	**0.253**	**<0.001**	0.128	0.085
% Chironomid	**-0.276**	**0.030**	-0.044	0.646	**-0.397**	**<0.001**	**-0.150**	**0.042**
% Simuliid	-0.187	0.145	-0.109	0.246	**0.167**	**0.026**	-0.036	0.630
% Other Aquatic Invertebrates	-0.150	0.243	**-0.193**	**0.040**	-0.115	0.125	-0.102	0.168
% Terrestrial Invertebrates	-0.206	0.109	0.041	0.667	-0.048	0.525	0.060	0.418

Inter-annual heterogeneity and dam operations

The diets of small-bodied fish caught during the steady flows in September 2008 were not consistently different than in other years for any species. However, bluehead suckers, flannelmouth suckers, and fathead minnows consumed more diatoms in the steady flows of 2008 than in other years. These results suggest that dam operations may affect small-bodied fish diets during the monsoon season, but could also reflect variability in the strength and timing of the monsoon seasons among years. Mean silt concentrations in August and September 2008 were similar to concentrations in August and September 2007, indicating that 2007 and 2008 experienced similar monsoon seasons. However, maximum silt concentrations during the same time period were approximately 4.5 times higher in 2008 than in 2007. The 2008 monsoon was likely much flashier, consisting of fewer, but stronger storms, resulting in shorter periods of high turbidity. These conditions may have allowed primary producers to recover more quickly than the conditions resulting from weaker, but more persistent storms during the

2007 monsoon. Inter-annual variability in small-bodied fish diets may be attributed to variations in the nature of monsoon storms rather than variations in dam operations.

Potential drivers of seasonal and inter-annual diet variability

I observed higher proportions of allochthonous carbon sources (amorphous detritus and terrestrial vegetation) in small-bodied fish diets during the monsoon season, and especially in strong monsoon seasons, and these patterns were associated with the MT (metric of turbidity). The MT describes the amount of time prior to sampling that silt concentrations were above the threshold at which the rate of primary production approaches zero. Turbidity could drive the observed diet patterns (decreased diatoms and increased allochthonous carbon in monsoon seasons) in two ways: 1. low light levels could limit photosynthesis, resulting in low availability of diatoms to consumers; and 2. tributary flooding could deliver large amounts of allochthonous carbon sources, such as terrestrial vegetation, to the mainstem channel.

Importance of backwaters

Backwater habitats may provide refuges from predators, swift currents, and colder water in mainstem habitats and thus can be important habitats for small-bodied fishes (Brouder et al. 1999, Bezzerides and Bestgen 2002, Goeking 2003). Because backwaters can, at times, have high densities of small-bodied fishes, they may be hotspots for diet overlap and competition (Muth and Snyder 1995). I compared diet and diet overlap patterns of small-bodied fishes between backwater and mainstem habitats. Despite the potential importance of backwater habitats, I did not find within-species differences in small-bodied fish diets between backwater and mainstem habitats. I also examined differences in the extent of diet overlap among species between backwater and mainstem habitats. During some seasons the extent of diet overlap among species was different in mainstem habitats than in backwater habitats. For example, in September 2008 species diet overlap was reduced in backwater habitats compared to mainstem habitats. In general, there were not consistent differences in the extent of diet overlap in backwaters versus mainstem habitats. Due to time constraints in the field and low densities of small-bodied fishes, not all sampling dates had sufficient samples from both mainstem and backwater habitats, which may have limited my ability to make robust comparisons (e.g. see Table 11 and Table 12). More sampling in these distinct habitats may elucidate if there are differences fish diet overlap in backwaters versus mainstem habitats.

Implications of niche overlap

Competition can be difficult and costly to assess directly, especially in remote field sites such as the Grand Canyon. Direct assessment of competition involves pair-wise enclosure experiments to measure the effect of controlled resource limitation on the fitness of each species in the presence and absence of other species. Because it is often difficult, or sometimes even impossible to conduct these experiments, competition is often inferred when certain dimensions of the species niches overlap, especially microhabitat and diet (Schoener 1983). Here, I infer the potential for competition by niche overlap in the form of diet overlap, and to some degree habitat overlap.

The four dominant small-bodied fishes in the Colorado River in the Grand Canyon commonly occur in the same habitats, as they are all commonly captured in the same sampling pass (personal observation and Ralsten et al. 2007). Hence, it is clear that they share similar habitats. For this reason, scenario 1 in Figure 1 is not an accurate depiction of small-bodied fish interactions in the Grand Canyon. I have also demonstrated, using two distinct analyses, that the diets of small-bodied fishes overlap, ruling out scenario 2 in Figure 1 as an accurate depiction of small-bodied fish interaction. The results presented here suggest that scenario 3 in Figure 1, i.e. niche overlap, accurately depicts many of the interactions among small-bodied fishes in the Grand Canyon and demonstrate that there is a large potential for resource competition among native and non-native fishes, and even among native species, especially among fathead minnows and juvenile bluehead and flannelmouth suckers.

The fathead minnow is an aggressive invasive species and is wide-spread in the Colorado River basin. Competition between fathead minnows and juvenile bluehead and flannelmouth suckers could be particularly harmful because these sucker populations are declining in much of their range and preservation of Grand Canyon populations may be important to species conservation. Negative effects of competition with non-natives at the juvenile stage could have a dramatic effect on bluehead and flannelmouth sucker recruitment and reproductive success. Although juvenile suckers may compete with fathead minnows, the diets of speckled dace do not overlap with the diets of fathead minnows and these species are not likely to compete for resources.

The diets of some native species also overlapped greatly, especially those of juvenile bluehead and flannelmouth suckers. This is counter-intuitive because these two closely related species evolved together and should not compete based on ecological theory. Ecological theory states that two closely related species that share a niche cannot coexist (competitive exclusion principle, Hutchinson 1957). However, these two species have similar early life histories, and may not diverge ecologically until later life stages. The juveniles of these two species occupy similar habitats, but the adults occupy different habitats (Ptacek et al. 2005 and Rees et al. 2005). These species may have evolved to have similar niches in early life stages, but avoid competition with distinct niches as adults.

I infer competition based on niche overlap, but cannot definitively conclude that small-bodied fishes in the Grand Canyon compete without assessing resource limitation in the system. Competition cannot occur if the shared resources are not limiting (Crombie 1947, Angermeier 1982). Resource limitation is often directly measured in the field via experimental food additions or exclusions (as in Weisberg and Lotrich 1986, Richardson 1991, and Wallace et al. 1999). If consumers respond positively to the addition of food (Weisberg and Lotrich 1986 and Richardson 1991), or negatively to food exclusion (as in Wallace et al. 1999), the consumers are food limited. However, such experiments are difficult in remote ecosystems, such as the Grand Canyon, and alternative methods of testing for resource limitation are necessary. An alternative approach to assess resource limitation is to let nature conduct the experiment. For example, Wellington and Victor (1985) used a sudden increase in resource availability on coral reefs in response to an El Niño event to assess resource limitation of damselfish. The damselfish population did not increase in response to increased resource availability and the authors concluded that the population was not resource limited (Wellington and Victor 1985). In addition, natural variation in resource availability is sometimes compared to fish growth. Food limitation can be inferred if resource availability and fish growth are correlated (Noble 1975). Other studies have relied on energetic calculations to assess resource limitation (e.g. Montgomerie and Gass 1981, Eadie and Keast 1982, Collie 1987, Rosi-Marshall and Wallace 2002). These studies use different methods and have focused on diverse taxa, but essentially all compare consumption rates to resource production rates or availability. If consumption rates approach or exceed resource production rates, resources are limited (e.g. Montgomerie and Gass 1981 and Eadie and Keast 1982). In contrast, if resource production is much greater than consumption rates, resources are not limited (e.g. Collie 1987, Rosi-Marshall and Wallace 2002). The energetic approach to assessing resource limitation does not require ecosystem manipulation and does not rely on natural experiments and therefore can be more feasible than other methods. Currently, a research team is applying the energetic approach to the Grand Canyon to assess resource limitation.

The specific resources in which diets overlap are also important because these resources can vary in quality and abundance. Diet overlap in an abundant resource may not be important for species interactions. Likewise, diet overlap in a poor-quality resource may not be important even if it is consumed in large quantities. For example, amorphous detritus is generally a low-quality food resource (i.e. low assimilation efficiency) and therefore may not be energetically important (Persson 1983). Persson (1983) found that roach diets overlapped greatly when all food items were considered, but did not overlap when low-quality amorphous detritus was excluded from the overlap analysis. Therefore, the quality of food resources should be considered in addition to resource availability when assessing the implications of overlap among fish diets.

Implications for management and recommendations for future research priorities

These results have potential implications for future management and research priorities. I inferred competition among native and non-native fishes from diet overlap, but experiments quantifying the extent of competition (i.e resource overlap plus resource limitation) would benefit managers as they try to understand the effects of non-native species on native fish populations. In addition, the potential for competition between juvenile suckers with non-native fathead minnow argues for management actions that could suppress fathead minnow populations. Although mechanical removal of other non-native fishes has been relatively successful (Coggins 2008), mechanical removal of fathead minnows would be difficult due to their small size. Another potential method for suppressing fathead minnow populations could be the implementation of periods of high flow releases from Glen Canyon Dam. Previous experimental high flows in the Grand Canyon have been shown to displace fathead minnows, but not native species (Valdez et al. 2001). Fathead minnow populations recovered within eight months of the high flow, but stronger or more frequent high flows may be effective tools to suppress populations (Valdez et al. 2001).

Dam managers have also implemented experimental periods of steady flows to improve fish habitat. Managers implemented steady flows during the 2008 monsoon season. I found that this management action had little effect on small-bodied fish diets. However, steady flows may benefit small-bodied fishes in other ways, perhaps by improving habitat quality. A low steady summer flow treatment in 2000 resulted in substantial warming of nearshore and backwater habitats, which would favor juvenile fish development (Trammell et al. 2002). More research should be conducted to fully understand the effects of steady flows on small-bodied fishes. This study demonstrates that inter-annual variability in the system, such as variation in monsoon strength, can alter fish feeding habits and this variability should be considered when evaluating effects of experimental dam operations or other management activities.

My results also suggest that more research investigating the importance of backwaters to small-bodied fish is needed. I did not find differences in small-bodied fish diets between fishes collected in backwater and mainstem habitats, but my study design did not allow me to fully address the question. For instance, I could not guarantee that fish were actively feeding in the habitat from which they were caught. Small-bodied fish may use backwaters as habitat refuges, but may rely on the mainstem for feeding habitats and this merits further research.

Conclusion

Competition with non-native fishes has been blamed for the declining populations of many native fishes in the southwestern United States (Tyus and Saunders 2000, Minckley et al. 2003). I observed significant diet overlap between native juvenile bluehead and flannelmouth sucker and non-native fathead minnows in the Grand Canyon and infer that competition among these species is possible. In contrast, speckled dace diets did not overlap with fathead minnow diets nor with juvenile flannelmouth sucker and bluehead sucker diets, and the potential for competition among these species is low.

These data provide a first look at the diets of these species in the Grand Canyon and at the effects of seasonal, inter-annual, and habitat heterogeneity on small-bodied fish diets. This study reveals the importance of riverine conditions for small-bodied fish diets. Different patterns emerge when spatial, seasonal, and inter-annual variability is considered. For example, turbidity can vary among years and is a particularly important factor for small-bodied fish diets. Future studies in the Colorado River and other systems should incorporate these sources of variability to develop a comprehensive understanding of small-bodied fish diets and diet overlap. Although more research in this area is warranted, managers should consider competition between fathead minnows and juvenile suckers in the development of management plans for the Colorado River in the Grand Canyon.

APPENDIX A

COMPLETE DIET COMPOSITION TABLE

Appendix 1. Mean (SD) percentage of food resources comprising juvenile bluehead sucker (BHS), juvenile flannelmouth sucker (FMS), speckled dace (SPD) and fathead minnow (FHM) diets on six sampling dates and at 4 sites in the Grand Canyon.

Season	Species	Food Resource	Site			
			62	127	167	225
Sep-06	BHS	Diatom	3.21 N/A	- -	- -	- -
		Amorphous Detritus	71.14 N/A	- -	- -	- -
		Aquatic Vegetation	- -	- -	- -	- -
		Filamentous Algae	- -	- -	- -	- -
		Terrestrial Vegetation	25.65 N/A	- -	- -	- -
		Aquatic Invertebrate				
		Diptera				
		Chironomid	- -	- -	- -	- -
		Simuliid	- -	- -	- -	- -
		Tipulid	- -	- -	- -	- -
		Ceratopogonid	- -	- -	- -	- -
		Unidentifiable	- -	- -	- -	- -
		Gammarus	- -	- -	- -	- -
		Aquatic Mite	- -	- -	- -	- -
		Planorbidae	- -	- -	- -	- -
		Trichoptera	- -	- -	- -	- -
		Coleoptera	- -	- -	- -	- -
		Ephemeroptera	- -	- -	- -	- -
		Odonata	- -	- -	- -	- -
		Megaloptera	- -	- -	- -	- -
		Hemiptera - Corixidae	- -	- -	- -	- -
		Copepod	- -	- -	- -	- -
		Cladacera	- -	- -	- -	- -
		Unidentifiable Aquatic Invertebrate	- -	- -	- -	- -
		Terrestrial Invertebrate				
		Hemiptera - Aphid	- -	- -	- -	- -
		Hemiptera - Unidentified	- -	- -	- -	- -
		Thysanoptera - Thrip	- -	- -	- -	- -
		Hymenoptera	- -	- -	- -	- -
		Coleoptera	- -	- -	- -	- -
		Diptera	- -	- -	- -	- -
		Orthoptera	- -	- -	- -	- -
		Terrestrial Mite	- -	- -	- -	- -
		Unidentifiable Terrestrial Invertebrate	- -	- -	- -	- -
		Miscellaneous Invertebrate	- -	- -	- -	- -
		Fungi	- -	- -	- -	- -
		Fish	- -	- -	- -	- -

Appendix 1. Continued.

Season	Species	Food Resource	Site 62		127		167		225
Sep-06	FMS	Diatom	3.22	N/A	20.32	(26.7)	14.45	(15.5)	- -
		Amorphous Detritus	10.58	N/A	46.66	(19.4)	29.65	(18.4)	- -
		Aquatic Vegetation	- -		- -		- -		- -
		Filamentous Algae	- -		- -		- -		- -
		Terrestrial Vegetation	43.38	N/A	29.16	(20.6)	22.83	(8.2)	- -
		Aquatic Invertebrate							
		Diptera							
		Chironomid	6.42	N/A	1.30	(1.6)	27.47	(31.7)	- -
		Simuliid	21.20	N/A	0.82	(1.8)	0.29	(0.6)	- -
		Tipulid	- -		- -		0.11	(0.2)	- -
		Ceratopogonid	- -		0.23	(0.5)	- -		- -
		Unidentifiable	2.49	N/A	- -		0.72	(1.4)	- -
		Gammarus	- -		- -		- -		- -
		Aquatic Mite	4.30	N/A	0.06	(0.1)	0.46	(0.9)	- -
		Planorbidae	- -		0.04	(0.1)	0.32	(0.4)	- -
		Trichoptera	- -		0.10	(0.2)	- -		- -
		Coleopteran	- -		- -		1.01	(2.0)	- -
		Ephemeropteran	- -		- -		- -		- -
		Odonata	- -		- -		- -		- -
		Megaloptera	- -		- -		- -		- -
		Hemiptera - Corixidae	- -		- -		- -		- -
		Copepod	- -		- -		- -		- -
		Cladacera	- -		- -		- -		- -
		Unidentifiable Aquatic Invertebrate	6.42	N/A	0.85	(1.9)	2.58	(4.9)	- -
		Terrestrial Invertebrate							
		Hemiptera - Aphid	1.59	N/A	- -		- -		- -
		Hemiptera - Unidentified	- -		- -		- -		- -
		Thysanoptera - Thrip	0.40	N/A	0.18	(0.2)	0.04	(0.1)	- -
		Hymenoptera	- -		- -		0.06	(0.1)	- -
		Coleoptera	- -		- -		- -		- -
		Diptera	- -		- -		- -		- -
		Orthoptera	- -		- -		- -		- -
		Terrestrial Mite	- -		- -		- -		- -
		Unidentifiable Terrestrial Invertebrate	- -		0.27	(0.6)	- -		- -
		Miscellaneous Invertebrate	- -		- -		- -		- -
		Fungi	- -		- -		- -		- -
		Fish	- -		- -		- -		- -

Appendix 1. Continued.

Season	Species	Food Resource	Site							
			62		127		167		225	
Sep-06	SPD	Diatom	4.06	N/A	5.92	(8.4)	7.48	(19.5)	1.27	(1.5)
		Amorphous Detritus	76.54	N/A	18.93	(26.8)	18.69	(24.0)	9.20	(16.4)
		Aquatic Vegetation	- -		- -		3.65	(11.8)	- -	
		Filamentous Algae	- -		- -		- -		- -	
		Terrestrial Vegetation	1.60	N/A	10.64	(15.0)	27.14	(19.8)	7.47	(8.6)
		Aquatic Invertebrate								
		Diptera								
		Chironomid	17.80	N/A	50.00	(70.7)	7.39	(11.4)	19.79	(15.3)
		Simuliid	- -		- -		13.50	(25.3)	7.06	(6.3)
		Tipulid	- -		- -		- -		- -	
		Ceratopogonid	- -		- -		- -		- -	
		Unidentifiable	- -		- -		- -		4.63	(6.5)
		Gammarus	- -		- -		0.50	(1.7)	- -	
		Aquatic Mite	- -		- -		4.71	(16.0)	0.96	(2.4)
		Planorbidae	- -		- -		0.30	(0.9)	- -	
		Trichoptera	- -		- -		- -		- -	
		Coleoptera	- -		- -		1.67	(5.3)	- -	
		Ephemeroptera	- -		- -		0.69	(2.1)	- -	
		Odonata	- -		- -		- -		1.10	(2.7)
		Megaloptera	- -		- -		- -		- -	
		Hemiptera - Corixidae	- -		- -		- -		- -	
		Copepod	- -		- -		- -		- -	
		Cladacera	- -		- -		- -		- -	
		Unidentifiable Aquatic Invertebrate	- -		14.51	(20.5)	14.77	(16.7)	42.44	(23.4)
		Terrestrial Invertebrate								
		Hemiptera - Aphid	- -		- -		- -		- -	
		Hemiptera - Unidentified	- -		- -		- -		- -	
		Thysanoptera - Thrip	- -		- -		- -		- -	
		Hymenoptera	- -		- -		- -		- -	
		Coleoptera	- -		- -		- -		- -	
		Diptera	- -		- -		- -		- -	
		Orthoptera	- -		- -		- -		- -	
		Terrestrial Mite	- -		- -		- -		- -	
		Unidentifiable Terrestrial Invertebrate	- -		- -		- -		6.07	(13.8)
		Miscellaneous Invertebrate	- -		- -		- -		- -	
		Fungi	- -		- -		- -		- -	
		Fish	- -		- -		- -		- -	

Appendix 1. Continued.

Season	Species	Food Resource	Site			
			62	127	167	225
Sep-06	FHM	Diatom	28.33 (26.0)	32.35 (15.1)	34.26 (23.3)	16.73 (15.6)
		Amorphous Detritus	22.70 (19.3)	47.97 (16.0)	32.00 (21.2)	30.34 (18.7)
		Aquatic Vegetation	2.58 (5.7)	2.76 (5.7)	5.10 (7.9)	7.30 (16.0)
		Filamentous Algae	- -	- -	- -	- -
		Terrestrial Vegetation	14.07 (7.8)	16.92 (10.6)	18.81 (13.9)	31.55 (3.3)
		Aquatic Invertebrate				
		Diptera				
		Chironomid	5.17 (8.1)	- -	9.18 (29.0)	- -
		Simuliid	7.21 (9.8)	- -	0.04 (0.1)	- -
		Tipulid	- -	- -	- -	- -
		Ceratopogonid	- -	- -	- -	- -
		Unidentifiable	- -	- -	- -	- -
		Gammarus	- -	- -	- -	- -
		Aquatic Mite	- -	- -	- -	- -
		Planorbidae	- -	- -	- -	- -
		Trichoptera	- -	- -	- -	- -
		Coleoptera	- -	- -	- -	- -
		Ephemeroptera	- -	- -	- -	- -
		Odonata	- -	- -	- -	- -
		Megaloptera	- -	- -	- -	- -
		Hemiptera - Corixidae	- -	- -	- -	- -
		Copepod	- -	- -	- -	- -
		Cladacera	- -	- -	- -	- -
		Unidentifiable Aquatic Invertebrate	17.76 (26.2)	- -	0.49 (1.6)	14.08 (27.0)
		Terrestrial Invertebrate		- -		
		Hemiptera - Aphid	- -	- -	- -	- -
		Hemiptera - Unidentified	- -	- -	- -	- -
		Thysanoptera - Thrip	- -	- -	- -	- -
		Hymenoptera	- -	- -	- -	- -
		Coleoptera	- -	- -	- -	- -
		Diptera	- -	- -	- -	- -
		Orthoptera	- -	- -	- -	- -
		Terrestrial Mite	- -	- -	- -	- -
		Unidentifiable Terrestrial Invertebrate	- -	- -	- -	- -
		Miscellaneous Invertebrate	2.18 (5.8)	- -	0.11 (0.4)	- -
		Fungi	- -	- -	- -	- -
		Fish	- -	- -	- -	- -

Appendix 1. Continued.

Season	Species	Food Resource	Site 62	127	167	225
Apr-07	BHS	Diatom	68.84 (39.0)	- -	48.10 (68.0)	- -
		Amorphous Detritus	5.62 (3.1)	- -	1.64 (2.3)	- -
		Aquatic Vegetation	- -	- -	- -	- -
		Filamentous Algae	- -	- -	- -	- -
		Terrestrial Vegetation	0.31 (0.2)	- -	0.26 (0.4)	- -
		Aquatic Invertebrate				
		Diptera				
		Chironomid	24.69 (34.9)	- -	49.01 (69.3)	- -
		Simuliid	0.09 (0.1)	- -	- -	- -
		Tipulid	- -	- -	- -	- -
		Ceratopogonid	- -	- -	- -	- -
		Unidentifiable	- -	- -	- -	- -
		Gammarus	0.45 (0.6)	- -	- -	- -
		Aquatic Mite	- -	- -	0.99 (1.4)	- -
		Planorbidae	- -	- -	- -	- -
		Trichoptera	- -	- -	- -	- -
		Coleoptera	- -	- -	- -	- -
		Ephemeroptera	- -	- -	- -	- -
		Odonata	- -	- -	- -	- -
		Megaloptera	- -	- -	- -	- -
		Hemiptera - Corixidae	- -	- -	- -	- -
		Copepod	- -	- -	- -	- -
		Cladacera	- -	- -	- -	- -
		Unidentifiable Aquatic Invertebrate	- -	- -	- -	- -
		Terrestrial Invertebrate				
		Hemiptera - Aphid	- -	- -	- -	- -
		Hemiptera - Unidentified	- -	- -	- -	- -
		Thysanoptera - Thrip	- -	- -	- -	- -
		Hymenoptera	- -	- -	- -	- -
		Coleoptera	- -	- -	- -	- -
		Diptera	- -	- -	- -	- -
		Orthoptera	- -	- -	- -	- -
		Terrestrial Mite	- -	- -	- -	- -
		Unidentifiable Terrestrial Invertebrate	- -	- -	- -	- -
		Miscellaneous Invertebrate	- -	- -	- -	- -
		Fungi	- -	- -	- -	- -
		Fish	- -	- -	- -	- -

Appendix 1. Continued.

Season	Species	Food Resource	Site			
			62	127	167	225
Apr-07	FMS	Diatom	44.07 (26.7)	57.06 (49.8)	34.44 (31.4)	13.04 (19.0)
		Amorphous Detritus	47.92 (33.5)	8.70 (9.8)	9.25 (10.5)	11.18 (18.6)
		Aquatic Vegetation	- -	- -	- -	- -
		Filamentous Algae	- -	- -	- -	- -
		Terrestrial Vegetation	6.60 (8.6)	9.50 (16.4)	3.18 (2.8)	5.12 (7.3)
		Aquatic Invertebrate				
		Diptera				
		Chironomid	1.42 (2.5)	5.08 (6.5)	35.33 (37.3)	60.30 (37.0)
		Simuliid	- -	2.38 (4.1)	1.56 (2.4)	6.61 (16.6)
		Tipulid	- -	- -	- -	0.75 (1.9)
		Ceratopogonid	- -	- -	- -	- -
		Unidentifiable	- -	- -	- -	0.94 (3.0)
		Gammarus	- -	- -	0.10 (0.3)	0.77 (2.0)
		Aquatic Mite	- -	- -	0.96 (2.3)	0.23 (0.7)
		Planorbidae	- -	- -	- -	- -
		Trichoptera	- -	- -	- -	- -
		Coleoptera	- -	- -	- -	- -
		Ephemeroptera	- -	- -	- -	- -
		Odonata	- -	- -	- -	- -
		Megaloptera	- -	- -	- -	- -
		Hemiptera - Corixidae	- -	- -	- -	- -
		Copepod	- -	- -	- -	- -
		Cladacera	- -	- -	- -	- -
		Unidentifiable Aquatic Invertebrate	- -	- -	2.40 (5.4)	0.01 (0.0)
		Terrestrial Invertebrate				
		Hemiptera - Aphid	- -	- -	- -	- -
		Hemiptera - Unidentified	- -	- -	- -	- -
		Thysanoptera - Thrip	- -	- -	- -	- -
		Hymenoptera	- -	- -	- -	- -
		Coleoptera	- -	- -	- -	- -
		Diptera	- -	- -	- -	- -
		Orthoptera	- -	- -	- -	- -
		Terrestrial Mite	- -	- -	- -	- -
		Unidentifiable Terrestrial Invertebrate	- -	17.28 (29.9)	9.40 (23.0)	- -
		Miscellaneous Invertebrate	- -	- -	3.76 (6.8)	1.06 (3.3)
		Fungi	- -	- -	- -	- -
		Fish	- -	- -	- -	- -

Appendix 1. Continued.

Season	Species	Food Resource	Site 62	127	167	225
Apr-07	SPD	Diatom	- -	- -	8.53 (20.6)	21.07 (34.8)
		Amorphous Detritus	- -	- -	3.77 (7.9)	6.85 (18.4)
		Aquatic Vegetation	- -	- -	- -	- -
		Filamentous Algae	- -	- -	- -	- -
		Terrestrial Vegetation	- -	2.61 (6.4)	3.05 (4.1)	2.45 (4.2)
		Aquatic Invertebrate				
		Diptera				
		Chironomid	41.77 (33.1)	33.54 (36.8)	51.43 (38.7)	32.48 (39.8)
		Simuliid	29.03 (43.3)	50.09 (37.8)	9.50 (15.4)	24.68 (33.5)
		Tipulid	- -	- -	- -	4.12 (12.3)
		Ceratopogonid	- -	- -	- -	- -
		Unidentifiable	- -	- -	- -	- -
		Gammarus	- -	- -	- -	- -
		Aquatic Mite	- -	- -	- -	- -
		Planorbidae	- -	- -	- -	- -
		Trichoptera	3.05 (6.8)	- -	- -	- -
		Coleoptera	- -	9.38 (23.0)	- -	- -
		Ephemeroptera	- -	- -	- -	- -
		Odonata	- -	- -	- -	- -
		Megaloptera	- -	- -	- -	- -
		Hemiptera - Corixidae	- -	- -	- -	- -
		Copepod	- -	- -	- -	- -
		Cladacera	- -	- -	- -	- -
		Unidentifiable Aquatic Invertebrate	16.04 (31.6)	4.38 (10.1)	22.96 (32.5)	3.08 (6.9)
		Terrestrial Invertebrate				
		Hemiptera - Aphid	- -	- -	- -	- -
		Hemiptera - Unidentified	- -	- -	- -	- -
		Thysanoptera - Thrip	- -	- -	- -	- -
		Hymenoptera	- -	- -	- -	- -
		Coleoptera	10.11 (22.6)	- -	0.68 (2.5)	5.27 (17.5)
		Diptera	- -	- -	- -	- -
		Orthoptera	- -	- -	- -	- -
		Terrestrial Mite	- -	- -	- -	- -
		Unidentifiable Terrestrial Invertebrate	- -	- -	0.08 (0.3)	- -
		Miscellaneous Invertebrate	- -	- -	- -	- -
		Fungi	- -	- -	- -	- -
		Fish	- -	- -	- -	- -

Appendix 1. Continued.

Season	Species	Food Resource	Site 62	127	167	225
Apr-07	FHM	Diatom	66.45 (39.0)	43.12 (35.9)	74.51 (34.1)	54.79 (31.3)
		Amorphous Detritus	6.35 (4.8)	8.45 (7.0)	7.42 (7.9)	6.98 (7.5)
		Aquatic Vegetation	- -	- -	- -	- -
		Filamentous Algae	- -	- -	- -	- -
		Terrestrial Vegetation	1.32 (1.3)	10.27 (21.6)	3.79 (5.6)	5.11 (5.3)
		Aquatic Invertebrate				
		Diptera				
		Chironomid	21.04 (36.0)	8.99 (12.3)	7.98 (21.1)	18.34 (22.7)
		Simuliid	- -	10.82 (24.2)	- -	1.30 (3.1)
		Tipulid	- -	- -	- -	- -
		Ceratopogonid	- -	- -	- -	- -
		Unidentifiable	4.77 (15.1)	- -	- -	0.34 (1.0)
		Gammarus	- -	- -	- -	- -
		Aquatic Mite	- -	- -	- -	- -
		Planorbidae	- -	- -	- -	- -
		Trichoptera	- -	- -	- -	- -
		Coleoptera	- -	- -	- -	- -
		Ephemeroptera	- -	- -	- -	- -
		Odonata	- -	- -	- -	- -
		Megaloptera	- -	- -	- -	- -
		Hemiptera - Corixidae	- -	- -	- -	- -
		Copepod	- -	- -	- -	- -
		Cladacera	- -	- -	- -	- -
		Unidentifiable Aquatic Invertebrate	- -	10.83 (24.2)	6.31 (16.7)	6.10 (9.7)
		Terrestrial Invertebrate				
		Hemiptera - Aphid	- -	- -	- -	- -
		Hemiptera - Unidentified	- -	- -	- -	- -
		Thysanoptera - Thrip	- -	- -	- -	- -
		Hymenoptera	- -	- -	- -	- -
		Coleoptera	- -	- -	- -	- -
		Diptera	- -	- -	- -	- -
		Orthoptera	- -	- -	- -	- -
		Terrestrial Mite	- -	- -	- -	- -
		Unidentifiable Terrestrial Invertebrate	- -	7.53 (16.8)	- -	3.05 (8.6)
		Miscellaneous Invertebrate	- -	- -	- -	3.99 (11.3)
		Fungi	0.07 (0.2)	- -	- -	- -
		Fish	- -	- -	- -	- -

Appendix 1. Continued.

Season	Species	Food Resource	Site			
			62	127	167	225
Jul-07	BHS	Diatom	43.72 (61.8)	- -	- -	- -
		Amorphous Detritus	3.92 (5.5)	- -	- -	- -
		Aquatic Vegetation	- -	- -	- -	- -
		Filamentous Algae	- -	- -	- -	- -
		Terrestrial Vegetation	2.03 (2.9)	- -	- -	- -
		Aquatic Invertebrate				
		Diptera				
		Chironomid	50.33 (70.2)	- -	- -	- -
		Simuliid	- -	- -	- -	- -
		Tipulid	- -	- -	- -	- -
		Ceratopogonid	- -	- -	- -	- -
		Unidentifiable	- -	- -	- -	- -
		Gammarus	- -	- -	- -	- -
		Aquatic Mite	- -	- -	- -	- -
		Planorbidae	- -	- -	- -	- -
		Trichoptera	- -	- -	- -	- -
		Coleoptera	- -	- -	- -	- -
		Ephemeroptera	- -	- -	- -	- -
		Odonata	- -	- -	- -	- -
		Megaloptera	- -	- -	- -	- -
		Hemiptera - Corixidae	- -	- -	- -	- -
		Copepod	- -	- -	- -	- -
		Cladacera	- -	- -	- -	- -
		Unidentifiable Aquatic Invertebrate	- -	- -	- -	- -
		Terrestrial Invertebrate				
		Hemiptera - Aphid	- -	- -	- -	- -
		Hemiptera - Unidentified	- -	- -	- -	- -
		Thysanoptera - Thrip	- -	- -	- -	- -
		Hymenoptera	- -	- -	- -	- -
		Coleoptera	- -	- -	- -	- -
		Diptera	- -	- -	- -	- -
		Orthoptera	- -	- -	- -	- -
		Terrestrial Mite	- -	- -	- -	- -
		Unidentifiable Terrestrial Invertebrate	- -	- -	- -	- -
		Miscellaneous Invertebrate	- -	- -	- -	- -
		Fungi	- -	- -	- -	- -
		Fish	- -	- -	- -	- -

Appendix 1. Continued.

Season	Species	Food Resource	Site 62	127	167	225
Jul-07	FMS	Diatom	3.97 (4.5)	1.36 (2.4)	- -	26.55 (34.8)
		Amorphous Detritus	29.48 (49.7)	1.46 (2.5)	- -	10.09 (11.4)
		Aquatic Vegetation	- -	- -	- -	0.35 (0.7)
		Filamentous Algae	- -	- -	- -	- -
		Terrestrial Vegetation	2.94 (1.5)	7.92 (4.9)	- -	3.15 (3.0)
		Aquatic Invertebrate				
		Diptera				
		Chironomid	44.65 (48.8)	31.31 (23.9)	- -	47.09 (33.0)
		Simuliid	16.59 (27.0)	44.11 (9.9)	- -	7.10 (9.6)
		Tipulid	- -	- -	- -	- -
		Ceratopogonid	- -	- -	- -	- -
		Unidentifiable	- -	- -	- -	0.52 (1.6)
		Gammarus	1.82 (3.2)	3.85 (4.2)	- -	1.02 (1.8)
		Aquatic Mite	0.22 (0.4)	0.39 (0.4)	- -	0.07 (0.2)
		Planorbidae	- -	0.10 (0.2)	- -	- -
		Trichoptera	0.11 (0.2)	1.95 (3.0)	- -	- -
		Coleoptera	- -	- -	- -	- -
		Ephemeroptera	- -	- -	- -	- -
		Odonata	- -	- -	- -	- -
		Megaloptera	- -	- -	- -	- -
		Hemiptera - Corixidae	- -	3.91 (3.5)	- -	- -
		Copepod	- -	- -	- -	0.13 (0.3)
		Cladacera	- -	- -	- -	- -
		Unidentifiable Aquatic Invertebrate	0.21 (0.4)	2.86 (4.9)	- -	0.50 (1.1)
		Terrestrial Invertebrate				
		Hemiptera - Aphid	- -	- -	- -	- -
		Hemiptera - Unidentified	- -	- -	- -	- -
		Thysanoptera - Thrip	- -	- -	- -	0.48 (1.2)
		Hymenoptera	- -	0.65 (1.1)	- -	- -
		Coleoptera	- -	- -	- -	- -
		Diptera	- -	- -	- -	- -
		Orthoptera	- -	- -	- -	- -
		Terrestrial Mite	- -	- -	- -	- -
		Unidentifiable Terrestrial Invertebrate	- -	0.13 (0.2)	- -	- -
		Miscellaneous Invertebrate	- -	- -	- -	2.95 (9.3)
		Fungi	- -	- -	- -	- -
		Fish	- -	- -	- -	- -

Appendix 1. Continued.

Season	Species	Food Resource	Site 62	127	167	225
Jul-07	SPD	Diatom	41.31 (35.7)	2.63 (7.9)	- -	10.34 (28.9)
		Amorphous Detritus	10.01 (15.9)	1.77 (5.3)	- -	1.96 (4.3)
		Aquatic Vegetation	0.09 (0.3)	- -	- -	0.46 (1.5)
		Filamentous Algae	- -	- -	- -	- -
		Terrestrial Vegetation	2.89 (6.1)	3.38 (4.0)	4.18 (9.9)	12.09 (24.7)
		Aquatic Invertebrate				
		Diptera				
		Chironomid	35.85 (41.6)	39.63 (30.3)	48.24 (29.7)	19.69 (22.6)
		Simuliid	7.66 (12.6)	43.37 (30.6)	35.29 (23.1)	15.37 (20.3)
		Tipulid	- -	- -	- -	- -
		Ceratopogonid	- -	- -	- -	- -
		Unidentifiable	- -	0.91 (2.7)	- -	0.91 (2.9)
		Gammarus	- -	- -	- -	- -
		Aquatic Mite	- -	- -	0.19 (0.5)	- -
		Planorbidae	- -	- -	- -	- -
		Trichoptera	2.09 (4.4)	4.93 (14.2)	- -	- -
		Coleoptera	- -	- -	- -	- -
		Ephemeroptera	- -	- -	- -	- -
		Odonata	- -	- -	- -	- -
		Megaloptera	- -	- -	1.02 (2.9)	- -
		Hemiptera - Corixidae	- -	2.30 (5.9)	- -	4.34 (13.7)
		Copepod	- -	- -	- -	- -
		Cladacera	- -	- -	- -	- -
		Unidentifiable Aquatic Invertebrate	0.12 (0.4)	0.36 (1.1)	2.33 (3.5)	2.70 (8.5)
		Terrestrial Invertebrate				
		Hemiptera - Aphid	- -	- -	- -	- -
		Hemiptera - Unidentified	- -	- -	- -	27.96 (35.1)
		Thysanoptera - Thrip	- -	- -	4.72 (9.4)	- -
		Hymenoptera	- -	- -	2.96 (4.3)	0.50 (1.6)
		Coleoptera	- -	0.57 (1.7)	1.08 (3.0)	- -
		Diptera	- -	- -	- -	- -
		Orthoptera	- -	- -	- -	- -
		Terrestrial Mite	- -	- -	- -	0.91 (2.7)
		Unidentifiable Terrestrial Invertebrate	- -	0.16 (0.5)	- -	2.77 (8.7)
		Miscellaneous Invertebrate	- -	- -	- -	- -
		Fungi	- -	- -	- -	- -
		Fish	- -	- -	- -	- -

Appendix 1. Continued.

Season	Species	Food Resource	Site			
			62	127	167	225
Jul-07	FHM	Diatom	43.01 (34.7)	29.62 (25.7)	79.46 (28.3)	68.12 N/A
		Amorphous Detritus	9.54 (5.9)	13.14 (19.9)	6.17 (2.7)	19.11 N/A
		Aquatic Vegetation	1.11 (1.9)	2.29 (3.2)	- -	8.35 N/A
		Filamentous Algae	1.20 (3.6)	- -	- -	- -
		Terrestrial Vegetation	3.81 (3.7)	6.99 (9.3)	4.37 (4.6)	4.42 N/A
		Aquatic Invertebrate				
		Diptera				
		Chironomid	33.19 (35.6)	20.44 (18.9)	- -	- -
		Simuliid	4.55 (8.4)	21.30 (15.7)	9.26 (29.3)	- -
		Tipulid	- -	- -	- -	- -
		Ceratopogonid	- -	- -	- -	- -
		Unidentifiable	1.18 (3.5)	1.65 (3.3)	- -	- -
		Gammarus	- -	- -	- -	- -
		Aquatic Mite	- -	- -	- -	- -
		Planorbidae	- -	- -	- -	- -
		Trichoptera	0.07 (0.2)	- -	- -	- -
		Coleoptera	- -	- -	- -	- -
		Ephemeroptera	- -	- -	- -	- -
		Odonata	- -	- -	- -	- -
		Megaloptera	- -	- -	- -	- -
		Hemiptera - Corixidae	- -	- -	- -	- -
		Copepod	- -	- -	- -	- -
		Cladacera	- -	- -	- -	- -
		Unidentifiable Aquatic Invertebrate	2.33 (5.3)	4.57 (6.0)	- -	- -
		Terrestrial Invertebrate				
		Hemiptera - Aphid	- -	- -	- -	- -
		Hemiptera - Unidentified	- -	- -	- -	- -
		Thysanoptera - Thrip	- -	- -	0.74 (2.3)	- -
		Hymenoptera	- -	- -	- -	- -
		Coleoptera	- -	- -	- -	- -
		Diptera	- -	- -	- -	- -
		Orthoptera	- -	- -	- -	- -
		Terrestrial Mite	- -	- -	- -	- -
		Unidentifiable Terrestrial Invertebrate	- -	- -	- -	- -
		Miscellaneous Invertebrate	- -	- -	- -	- -
		Fungi	- -	- -	- -	- -
		Fish	- -	- -	- -	- -

Appendix 1. Continued.

Season	Species	Food Resource	Site 62		127		167		225
Sep-07	BHS	Diatom	70.78	(15.8)	71.22	N/A	36.83	(37.4)	- -
		Amorphous Detritus	20.62	(13.0)	14.61	N/A	15.40	(4.4)	- -
		Aquatic Vegetation	0.50	(0.9)	- -		1.63	(3.6)	- -
		Filamentous Algae	- -		- -		- -		- -
		Terrestrial Vegetation	5.82	(7.5)	14.18	N/A	15.35	(14.4)	- -
		Aquatic Invertebrate							
		Diptera							
		Chironomid	0.05	(0.1)	- -		17.58	(17.8)	- -
		Simuliid	1.32	(2.5)	- -		4.70	(6.5)	- -
		Tipulid	- -		- -		- -		- -
		Ceratopogonid	- -		- -		- -		- -
		Unidentifiable	- -		- -		- -		- -
		Gammarus	- -		- -		1.06	(2.6)	- -
		Aquatic Mite	- -		- -		- -		- -
		Planorbidae	- -		- -		- -		- -
		Trichoptera	- -		- -		- -		- -
		Coleoptera	- -		- -		- -		- -
		Ephemeroptera	- -		- -		- -		- -
		Odonata	- -		- -		- -		- -
		Megaloptera	- -		- -		- -		- -
		Hemiptera - Corixidae	- -		- -		- -		- -
		Copepod	- -		- -		1.80	(3.9)	- -
		Cladacera	- -		- -		- -		- -
		Unidentifiable Aquatic Invertebrate	0.91	(2.6)	- -		4.14	(4.9)	- -
		Terrestrial Invertebrate							
		Hemiptera - Aphid	- -		- -		- -		- -
		Hemiptera - Unidentified	- -		- -		- -		- -
		Thysanoptera - Thrip	- -		- -		0.74	(1.3)	- -
		Hymenoptera	- -		- -		0.64	(1.6)	- -
		Coleoptera	- -		- -		0.14	(0.3)	- -
		Diptera	- -		- -		- -		- -
		Orthoptera	- -		- -		- -		- -
		Terrestrial Mite	- -		- -		- -		- -
		Unidentifiable Terrestrial Invertebrate	- -		- -		- -		- -
		Miscellaneous Invertebrate	- -		- -		- -		- -
		Fungi	- -		- -		- -		- -
		Fish	- -		- -		- -		- -

Appendix 1. Continued.

Season	Species	Food Resource	Site			
			62	127	167	225
Sep-07	FMS	Diatom	4.08 (6.7)	62.58 N/A	14.32 (21.4)	13.14 (17.9)
		Amorphous Detritus	4.82 (7.6)	8.58 N/A	15.53 (16.8)	24.76 (14.5)
		Aquatic Vegetation	0.97 (2.0)	- -	0.62 (2.0)	0.48 (0.7)
		Filamentous Algae	- -	- -	0.59 (1.9)	- -
		Terrestrial Vegetation	34.31 (39.1)	11.35 N/A	25.84 (12.3)	30.27 (26.4)
		Aquatic Invertebrate				
		Diptera				
		Chironomid	25.28 (29.4)	- -	23.42 (15.8)	23.37 (27.0)
		Simuliid	24.16 (32.6)	- -	2.91 (4.3)	1.56 (2.8)
		Tipulid	- -	- -	- -	- -
		Ceratopogonid	- -	- -	- -	- -
		Unidentifiable	0.15 (0.3)	- -	2.39 (5.1)	0.63 (1.2)
		Gammarus	0.71 (1.6)	17.48 N/A	0.77 (2.4)	0.21 (0.6)
		Aquatic Mite	0.07 (0.2)	- -	0.24 (0.8)	0.85 (0.9)
		Planorbidae	0.06 (0.2)	- -	0.04 (0.1)	0.05 (0.1)
		Trichoptera	0.20 (0.6)	- -	1.89 (4.1)	- -
		Coleoptera	0.06 (0.2)	- -	0.24 (0.6)	- -
		Ephemeroptera	- -	- -	- -	- -
		Odonata	- -	- -	- -	- -
		Megaloptera	- -	- -	- -	- -
		Hemiptera - Corixidae	- -	- -	0.26 (0.8)	- -
		Copepod	0.02 (0.1)	- -	0.65 (1.1)	- -
		Cladacera	0.10 (0.3)	- -	- -	- -
		Unidentifiable Aquatic Invertebrate	1.88 (3.4)	- -	7.60 (9.6)	2.41 (4.8)
		Terrestrial Invertebrate				
		Hemiptera - Aphid	- -	- -	- -	- -
		Hemiptera - Unidentified	- -	- -	0.31 (1.0)	0.29 (0.8)
		Thysanoptera - Thrip	0.79 (1.7)	- -	0.57 (1.0)	0.56 (1.4)
		Hymenoptera	1.24 (3.0)	- -	0.71 (1.9)	- -
		Coleoptera	0.61 (1.5)	- -	0.31 (0.5)	0.95 (2.0)
		Diptera	0.13 (0.4)	- -	- -	- -
		Orthoptera	- -	- -	- -	- -
		Terrestrial Mite	- -	- -	0.79 (1.5)	- -
		Unidentifiable Terrestrial Invertebrate	0.36 (1.2)	- -	- -	0.48 (1.4)
		Miscellaneous Invertebrate	- -	- -	- -	- -
		Fungi	- -	- -	- -	- -
		Fish	- -	- -	- -	- -

Appendix 1. Continued.

Season	Species	Food Resource	Site			
			62	127	167	225
Sep-07	SPD	Diatom	51.36 (36.9)	50.51 (31.1)	19.03 (24.0)	21.03 (19.7)
		Amorphous Detritus	8.13 (7.1)	9.85 (14.0)	13.89 (13.6)	17.39 (21.6)
		Aquatic Vegetation	2.57 (4.0)	1.03 (3.2)	0.54 (1.2)	5.36 (13.7)
		Filamentous Algae	- -	- -	- -	- -
		Terrestrial Vegetation	1.09 (1.7)	17.15 (24.0)	22.95 (16.0)	23.33 (12.7)
		Aquatic Invertebrate				
		Diptera				
		Chironomid	0.95 (2.2)	0.45 (1.2)	20.06 (44.7)	11.18 (10.8)
		Simuliid	35.29 (44.0)	10.47 (9.1)	0.25 (0.6)	3.65 (5.4)
		Tipulid	- -	- -	- -	- -
		Ceratopogonid	- -	- -	- -	- -
		Unidentifiable	0.11 (0.3)	- -	- -	1.61 (4.5)
		Gammarus	- -	- -	- -	- -
		Aquatic Mite	- -	- -	0.88 (2.0)	- -
		Planorbidae	- -	- -	- -	- -
		Trichoptera	0.16 (0.5)	- -	- -	- -
		Coleoptera	- -	- -	- -	- -
		Ephemeroptera	- -	- -	- -	- -
		Odonata	- -	- -	- -	- -
		Megaloptera	- -	- -	- -	- -
		Hemiptera - Corixidae	- -	- -	- -	- -
		Copepod	- -	- -	- -	- -
		Cladacera	- -	- -	- -	- -
		Unidentifiable Aquatic Invertebrate	0.35 (0.8)	2.63 (4.0)	22.39 (32.4)	8.33 (13.5)
		Terrestrial Invertebrate				
		Hemiptera - Aphid	- -	- -	- -	- -
		Hemiptera - Unidentified	- -	- -	- -	- -
		Thysanoptera - Thrip	- -	- -	- -	- -
		Hymenoptera	- -	1.07 (2.7)	- -	7.02 (14.9)
		Coleoptera	- -	- -	- -	- -
		Diptera	- -	- -	- -	- -
		Orthoptera	- -	2.78 (8.8)	- -	- -
		Terrestrial Mite	- -	- -	- -	- -
		Unidentifiable Terrestrial Invertebrate	- -	4.06 (10.5)	- -	1.11 (3.1)
		Miscellaneous Invertebrate	- -	- -	- -	- -
		Fungi	- -	- -	- -	- -
		Fish	- -	- -	- -	- -

Appendix 1. Continued.

Season	Species	Food Resource	Site 62		127		167		225
Sep-07	FHM	Diatom	31.86	(32.1)	35.30	(49.9)	27.28	(30.0)	- -
		Amorphous Detritus	18.83	(18.6)	4.01	(5.7)	16.66	(11.8)	- -
		Aquatic Vegetation	1.97	(6.2)	- -		0.04	(0.1)	- -
		Filamentous Algae	- -		- -		- -		- -
		Terrestrial Vegetation	7.75	(9.2)	19.53	(0.1)	16.12	(10.9)	- -
		Aquatic Invertebrate							
		Diptera							
		Chironomid	5.00	(12.3)	11.74	(16.6)	21.78	(25.3)	- -
		Simuliid	29.61	(41.2)	28.52	(40.3)	0.60	(1.7)	- -
		Tipulid	- -		- -		- -		- -
		Ceratopogonid	- -		- -		- -		- -
		Unidentifiable	- -		0.90	(1.3)	1.88	(4.2)	- -
		Gammarus	- -		- -		- -		- -
		Aquatic Mite	- -		- -		- -		- -
		Planorbidae	0.04	(0.1)	- -		- -		- -
		Trichoptera	- -		- -		1.22	(3.9)	- -
		Coleoptera	- -		- -		- -		- -
		Ephemeroptera	- -		- -		- -		- -
		Odonata	- -		- -		- -		- -
		Megaloptera	- -		- -		- -		- -
		Hemiptera - Corixidae	- -		- -		- -		- -
		Copepod	- -		- -		- -		- -
		Cladacera	- -		- -		- -		- -
		Unidentifiable Aquatic Invertebrate	2.52	(5.0)	- -		14.43	(19.0)	- -
		Terrestrial Invertebrate							
		Hemiptera - Aphid	- -		- -		- -		- -
		Hemiptera - Unidentified	- -		- -		- -		- -
		Thysanoptera - Thrip	0.33	(1.0)	- -		- -		- -
		Hymenoptera	- -		- -		- -		- -
		Coleoptera	- -		- -		- -		- -
		Diptera	1.38	(4.4)	- -		- -		- -
		Orthoptera	- -		- -		- -		- -
		Terrestrial Mite	- -		- -		- -		- -
		Unidentifiable Terrestrial Invertebrate	0.72	(2.3)	- -		- -		- -
		Miscellaneous Invertebrate	- -		- -		- -		- -
		Fungi	- -		- -		- -		- -
		Fish	- -		- -		- -		- -

Appendix 1. Continued.

Season	Species	Food Resource	Site 62	127	167	225
Jan-08	BHS	Diatom	11.77 (16.6)	50.47 (34.1)	- -	14.39 (12.6)
		Amorphous Detritus	8.15 (11.5)	12.15 (9.4)	- -	18.88 (4.8)
		Aquatic Vegetation	- -	- -	- -	- -
		Filamentous Algae	- -	- -	- -	- -
		Terrestrial Vegetation	19.02 (26.9)	1.95 (3.0)	- -	9.54 (4.6)
		Aquatic Invertebrate				
		Diptera				
		Chironomid	7.79 (11.0)	30.95 (42.0)	- -	33.67 (30.1)
		Simuliid	53.27 (66.1)	4.28 (5.2)	- -	23.53 (33.3)
		Tipulid	- -	- -	- -	- -
		Ceratopogonid	- -	- -	- -	- -
		Unidentifiable	- -	- -	- -	- -
		Gammarus	- -	- -	- -	- -
		Aquatic Mite	- -	- -	- -	- -
		Planorbidae	- -	- -	- -	- -
		Trichoptera	- -	- -	- -	- -
		Coleoptera	- -	- -	- -	- -
		Ephemeroptera	- -	- -	- -	- -
		Odonata	- -	- -	- -	- -
		Megaloptera	- -	- -	- -	- -
		Hemiptera - Corixidae	- -	- -	- -	- -
		Copepod	- -	0.20 (0.4)	- -	- -
		Cladacera	- -	- -	- -	- -
		Unidentifiable Aquatic Invertebrate	- -	- -	- -	- -
		Terrestrial Invertebrate				
		Hemiptera - Aphid	- -	- -	- -	- -
		Hemiptera - Unidentified	- -	- -	- -	- -
		Thysanoptera - Thrip	- -	- -	- -	- -
		Hymenoptera	- -	- -	- -	- -
		Coleoptera	- -	- -	- -	- -
		Diptera	- -	- -	- -	- -
		Orthoptera	- -	- -	- -	- -
		Terrestrial Mite	- -	- -	- -	- -
		Unidentifiable Terrestrial Invertebrate	- -	- -	- -	- -
		Miscellaneous Invertebrate	- -	- -	- -	- -
		Fungi	- -	- -	- -	- -
		Fish	- -	- -	- -	- -

Appendix 1. Continued.

Season	Species	Food Resource	Site			
			62	127	167	225
Jan-08	FMS	Diatom	63.59 (16.4)	58.46 (50.9)	9.22 (6.3)	13.48 (22.3)
		Amorphous Detritus	12.50 (5.4)	5.31 (4.9)	28.66 (22.7)	21.75 (30.0)
		Aquatic Vegetation	1.45 (2.5)	- -	- -	- -
		Filamentous Algae	- -	- -	- -	- -
		Terrestrial Vegetation	9.98 (10.0)	1.08 (1.0)	10.54 (7.9)	20.07 (27.3)
		Aquatic Invertebrate				
		Diptera				
		Chironomid	6.65 (11.2)	13.41 (19.3)	40.39 (24.5)	37.06 (38.5)
		Simuliid	5.07 (4.5)	14.32 (24.1)	9.14 (14.2)	6.53 (9.3)
		Tipulid	- -	- -	- -	- -
		Ceratopogonid	- -	- -	- -	- -
		Unidentifiable	- -	6.65 (11.5)	1.57 (4.7)	0.41 (1.2)
		Gammarus	- -	- -	- -	- -
		Aquatic Mite	- -	- -	- -	- -
		Planorbidae	- -	- -	0.08 (0.2)	- -
		Trichoptera	0.64 (1.1)	- -	0.15 (0.4)	- -
		Coleoptera	- -	- -	- -	- -
		Ephemeroptera	- -	- -	- -	- -
		Odonata	- -	- -	- -	- -
		Megaloptera	- -	- -	- -	- -
		Hemiptera - Corixidae	- -	- -	- -	- -
		Copepod	0.12 (0.2)	0.16 (0.1)	- -	- -
		Cladacera	- -	- -	- -	- -
		Unidentifiable Aquatic Invertebrate	- -	0.60 (1.0)	0.25 (0.5)	0.69 (2.0)
		Terrestrial Invertebrate				
		Hemiptera - Aphid	- -	- -	- -	- -
		Hemiptera - Unidentified	- -	- -	- -	- -
		Thysanoptera - Thrip	- -	- -	- -	- -
		Hymenoptera	- -	- -	- -	- -
		Coleoptera	- -	- -	- -	- -
		Diptera	- -	- -	- -	- -
		Orthoptera	- -	- -	- -	- -
		Terrestrial Mite	- -	- -	- -	- -
		Unidentifiable Terrestrial Invertebrate	- -	- -	- -	- -
		Miscellaneous Invertebrate	- -	- -	- -	- -
		Fungi	- -	- -	- -	- -
		Fish	- -	- -	- -	- -

Appendix 1. Continued.

Season	Species	Food Resource	Site 62	127	167	225
Jan-08	SPD	Diatom	8.99 (25.4)	- -	0.79 (1.8)	1.28 (4.1)
		Amorphous Detritus	0.78 (2.2)	- -	2.90 (6.1)	7.72 (24.4)
		Aquatic Vegetation	- -	- -	- -	0.26 (0.8)
		Filamentous Algae	- -	- -	- -	- -
		Terrestrial Vegetation	1.91 (3.8)	- -	0.56 (1.3)	4.24 (7.9)
		Aquatic Invertebrate				
		Diptera				
		Chironomid	47.85 (31.1)	26.00 N/A	45.23 (33.0)	60.90 (38.9)
		Simuliid	35.19 (30.1)	74.00 N/A	36.02 (31.6)	24.21 (32.2)
		Tipulid	- -	- -	- -	- -
		Ceratopogonid	- -	- -	- -	- -
		Unidentifiable	- -	- -	0.60 (1.9)	- -
		Gammarus	- -	- -	8.18 (22.5)	- -
		Aquatic Mite	- -	- -	- -	- -
		Planorbidae	- -	- -	- -	- -
		Trichoptera	0.34 (1.0)	- -	3.22 (10.2)	- -
		Coleoptera	- -	- -	- -	- -
		Ephemeroptera	- -	- -	- -	- -
		Odonata	- -	- -	- -	- -
		Megaloptera	- -	- -	- -	- -
		Hemiptera - Corixidae	- -	- -	- -	- -
		Copepod	- -	- -	- -	- -
		Cladacera	- -	- -	- -	- -
		Unidentifiable Aquatic Invertebrate	4.95 (10.2)	- -	2.50 (7.8)	1.39 (4.4)
		Terrestrial Invertebrate				
		Hemiptera - Aphid	- -	- -	- -	- -
		Hemiptera - Unidentified	- -	- -	- -	- -
		Thysanoptera - Thrip	- -	- -	- -	- -
		Hymenoptera	- -	- -	- -	- -
		Coleoptera	- -	- -	- -	- -
		Diptera	- -	- -	- -	- -
		Orthoptera	- -	- -	- -	- -
		Terrestrial Mite	- -	- -	- -	- -
		Unidentifiable Terrestrial Invertebrate	- -	- -	- -	- -
		Miscellaneous Invertebrate	- -	- -	- -	- -
		Fungi	- -	- -	- -	- -
		Fish	- -	- -	- -	- -

Appendix 1. Continued.

Season	Species	Food Resource	Site			
			62	127	167	225
Jan-08	FHM	Diatom	36.28 (24.4)	27.75 (38.6)	5.98 (5.8)	66.97 (25.3)
		Amorphous Detritus	19.15 (15.4)	9.87 (13.1)	29.04 (22.5)	14.07 (7.3)
		Aquatic Vegetation	- -	- -	0.52 (1.6)	0.31 (1.1)
		Filamentous Algae	- -	- -	- -	- -
		Terrestrial Vegetation	11.54 (12.2)	3.19 (5.6)	10.79 (9.3)	10.25 (11.9)
		Aquatic Invertebrate				
		Diptera				
		Chironomid	16.17 (31.0)	23.88 (34.4)	18.79 (11.1)	8.41 (28.8)
		Simuliid	4.60 (12.0)	33.25 (37.3)	22.51 (27.2)	- -
		Tipulid	- -	- -	- -	- -
		Ceratopogonid	- -	- -	- -	- -
		Unidentifiable	- -	- -	- -	- -
		Gammarus	9.51 (18.1)	- -	2.77 (8.8)	- -
		Aquatic Mite	- -	- -	- -	- -
		Planorbidae	- -	- -	- -	- -
		Trichoptera	- -	- -	- -	- -
		Coleoptera	- -	- -	- -	- -
		Ephemeroptera	- -	- -	- -	- -
		Odonata	- -	- -	- -	- -
		Megaloptera	- -	- -	- -	- -
		Hemiptera - Corixidae	- -	- -	- -	- -
		Copepod	- -	- -	0.03 (0.1)	- -
		Cladacera	- -	- -	- -	- -
		Unidentifiable Aquatic Invertebrate	2.76 (7.3)	2.06 (6.5)	5.24 (7.7)	- -
		Terrestrial Invertebrate				
		Hemiptera - Aphid	- -	- -	- -	- -
		Hemiptera - Unidentified	- -	- -	- -	- -
		Thysanoptera - Thrip	- -	- -	- -	- -
		Hymenoptera	- -	- -	- -	- -
		Coleoptera	- -	- -	4.33 (13.7)	- -
		Diptera	- -	- -	- -	- -
		Orthoptera	- -	- -	- -	- -
		Terrestrial Mite	- -	- -	- -	- -
		Unidentifiable Terrestrial Invertebrate	- -	- -	- -	- -
		Miscellaneous Invertebrate	- -	- -	- -	- -
		Fungi	- -	- -	- -	- -
		Fish	- -	- -	- -	- -

Appendix 1. Continued.

Season	Species	Food Resource	Site 62	127	167	225
Sep-08	BHS	Diatom	70.03 (17.1)	78.07 (15.2)	75.44 (13.1)	61.74 (30.8)
		Amorphous Detritus	20.91 (13.6)	14.55 (9.3)	15.88 (8.3)	15.76 (10.9)
		Aquatic Vegetation	- -	- -	- -	- -
		Filamentous Algae	- -	- -	- -	- -
		Terrestrial Vegetation	5.54 (3.8)	3.93 (4.5)	8.40 (6.4)	6.30 (11.0)
		Aquatic Invertebrate				
		Diptera				
		Chironomid	1.86 (4.6)	2.71 (3.3)	0.10 (0.2)	12.52 (25.6)
		Simuliid	1.09 (2.4)	0.10 (0.3)	- -	1.52 (4.8)
		Tipulid	- -	- -	- -	- -
		Ceratopogonid	- -	- -	- -	- -
		Unidentifiable	0.46 (1.1)	0.09 (0.3)	- -	- -
		Gammarus	0.09 (0.2)	- -	- -	- -
		Aquatic Mite	- -	- -	- -	0.27 (0.8)
		Planorbidae	- -	- -	- -	- -
		Trichoptera	- -	- -	- -	- -
		Coleoptera	- -	- -	- -	- -
		Ephemeroptera	- -	- -	- -	- -
		Odonata	- -	- -	- -	- -
		Megaloptera	- -	- -	- -	- -
		Hemiptera - Corixidae	- -	- -	- -	- -
		Copepod	0.01 (0.0)	0.03 (0.1)	0.16 (0.4)	0.39 (1.1)
		Cladacera	- -	- -	- -	- -
		Unidentifiable Aquatic Invertebrate	- -	- -	- -	0.62 (2.0)
		Terrestrial Invertebrate				
		Hemiptera - Aphid	- -	- -	- -	- -
		Hemiptera - Unidentified	- -	- -	- -	- -
		Thysanoptera - Thrip	- -	0.51 (1.6)	- -	0.89 (2.8)
		Hymenoptera	- -	- -	- -	- -
		Coleoptera	- -	- -	- -	- -
		Diptera	- -	- -	- -	- -
		Orthoptera	- -	- -	- -	- -
		Terrestrial Mite	- -	- -	- -	- -
		Unidentifiable Terrestrial Invertebrate	- -	- -	- -	- -
		Miscellaneous Invertebrate	- -	- -	- -	- -
		Fungi	- -	- -	- -	- -
		Fish	- -	- -	- -	- -

Appendix 1. Continued.

Season	Species	Food Resource	Site			
			62	127	167	225
Sep-08	FMS	Diatom	41.48 (29.0)	30.73 (29.0)	37.63 (33.6)	52.91 (26.7)
		Amorphous Detritus	24.07 (23.8)	24.84 (23.9)	16.74 (16.2)	17.62 (8.5)
		Aquatic Vegetation	- -	- -	0.28 (0.9)	- -
		Filamentous Algae	- -	- -	- -	- -
		Terrestrial Vegetation	2.66 (1.8)	7.92 (4.9)	17.04 (21.6)	14.76 (25.3)
		Aquatic Invertebrate				
		Diptera				
		Chironomid	25.46 (16.0)	25.10 (32.0)	13.79 (16.5)	6.74 (8.7)
		Simuliid	5.37 (4.7)	5.99 (16.9)	8.57 (15.4)	2.17 (5.4)
		Tipulid	- -	- -	- -	- -
		Ceratopogonid	- -	- -	- -	- -
		Unidentifiable	- -	3.33 (9.4)	- -	- -
		Gammarus	- -	- -	0.61 (1.9)	- -
		Aquatic Mite	- -	- -	0.23 (0.5)	- -
		Planorbidae	- -	- -	1.02 (3.1)	- -
		Trichoptera	- -	1.85 (3.5)	0.06 (0.2)	- -
		Coleoptera	- -	- -	- -	- -
		Ephemeroptera	- -	- -	- -	- -
		Odonata	- -	- -	- -	- -
		Megaloptera	- -	- -	- -	- -
		Hemiptera - Corixidae	- -	- -	- -	- -
		Copepod	0.49 (0.7)	0.09 (0.2)	3.17 (7.4)	3.94 (6.9)
		Cladacera	- -	- -	- -	- -
		Unidentifiable Aquatic Invertebrate	- -	- -	0.47 (0.9)	1.68 (3.1)
		Terrestrial Invertebrate				
		Hemiptera - Aphid	- -	- -	- -	- -
		Hemiptera - Unidentified	- -	- -	- -	- -
		Thysanoptera - Thrip	0.46 (0.8)	0.16 (0.4)	0.25 (0.6)	0.19 (0.6)
		Hymenoptera	- -	- -	0.16 (0.4)	- -
		Coleoptera	- -	- -	- -	- -
		Diptera	- -	- -	- -	- -
		Orthoptera	- -	- -	- -	- -
		Terrestrial Mite	- -	- -	- -	- -
		Unidentifiable Terrestrial Invertebrate	- -	- -	- -	- -
		Miscellaneous Invertebrate	- -	- -	- -	- -
		Fungi	- -	- -	- -	- -
		Fish	- -	- -	- -	- -

Appendix 1. Continued.

Season	Species	Food Resource	Site			
			62	127	167	225
Sep-08	SPD	Diatom	19.06 (29.2)	17.04 (31.7)	10.48 (22.9)	36.27 (32.4)
		Amorphous Detritus	7.39 (11.2)	5.78 (11.8)	11.71 (22.4)	9.04 (17.8)
		Aquatic Vegetation	- -	- -	0.06 (0.2)	0.36 (1.1)
		Filamentous Algae	- -	- -	- -	0.00 (0.0)
		Terrestrial Vegetation	1.22 (1.2)	11.53 (16.1)	13.55 (18.0)	9.06 (9.4)
		Aquatic Invertebrate				
		Diptera				
		Chironomid	26.85 (23.3)	15.38 (15.3)	22.14 (29.3)	23.28 (27.2)
		Simuliid	12.66 (19.5)	21.27 (27.3)	25.49 (21.8)	9.09 (14.3)
		Tipulid	- -	- -	- -	- -
		Ceratopogonid	- -	- -	- -	- -
		Unidentifiable	- -	4.74 (8.1)	- -	0.79 (2.5)
		Gammarus	2.06 (4.4)	3.49 (11.0)	0.41 (1.3)	- -
		Aquatic Mite	- -	- -	0.20 (0.6)	1.04 (2.5)
		Planorbidae	0.37 (1.2)	- -	- -	- -
		Trichoptera	26.12 (30.2)	- -	0.08 (0.2)	- -
		Coleoptera	- -	- -	- -	- -
		Ephemeroptera	- -	- -	- -	- -
		Odonata	- -	- -	- -	- -
		Megaloptera	- -	- -	- -	- -
		Hemiptera - Corixidae	- -	2.27 (7.2)	- -	- -
		Copepod	- -	- -	- -	- -
		Cladacera	- -	- -	- -	- -
		Unidentifiable Aquatic Invertebrate	4.18 (7.5)	7.81 (10.3)	0.93 (2.0)	6.27 (10.6)
		Terrestrial Invertebrate				
		Hemiptera - Aphid	- -	- -	- -	- -
		Hemiptera - Unidentified	- -	1.26 (2.4)	- -	- -
		Thysanoptera - Thrip	0.08 (0.2)	0.26 (0.8)	0.37 (1.2)	0.61 (1.5)
		Hymenoptera	- -	- -	14.58 (30.4)	2.21 (4.9)
		Coleoptera	- -	- -	- -	1.76 (5.6)
		Diptera	- -	1.92 (6.1)	- -	- -
		Orthoptera	- -	- -	- -	- -
		Terrestrial Mite	- -	- -	- -	- -
		Unidentifiable Terrestrial Invertebrate	- -	7.24 (16.8)	- -	0.23 (0.7)
		Miscellaneous Invertebrate	- -	- -	- -	- -
		Fungi	- -	- -	- -	- -
		Fish	- -	- -	- -	- -

Appendix 1. Continued.

Season	Species	Food Resource	Site 62	127	167	225
Sep-08	FHM	Diatom	63.91 (31.3)	56.30 (27.7)	58.30 (22.2)	39.90 (30.0)
		Amorphous Detritus	23.18 (21.7)	27.98 (19.5)	20.04 (9.6)	34.10 (23.0)
		Aquatic Vegetation	- -	- -	- -	- -
		Filamentous Algae	- -	- -	- -	- -
		Terrestrial Vegetation	10.35 (10.6)	2.97 (2.9)	13.18 (15.0)	6.23 (3.9)
		Aquatic Invertebrate				
		Diptera				
		Chironomid	1.02 (1.6)	- -	8.12 (18.8)	3.34 (9.8)
		Simuliid	1.53 (3.9)	- -	0.24 (0.8)	10.06 (21.2)
		Tipulid	- -	- -	- -	- -
		Ceratopogonid	- -	- -	- -	- -
		Unidentifiable	- -	- -	- -	- -
		Gammarus	- -	- -	- -	0.03 (0.1)
		Aquatic Mite	- -	- -	- -	- -
		Planorbidae	- -	- -	- -	- -
		Trichoptera	- -	- -	- -	- -
		Coleoptera	- -	- -	- -	- -
		Ephemeroptera	- -	- -	- -	- -
		Odonata	- -	- -	- -	- -
		Megaloptera	- -	- -	- -	- -
		Hemiptera - Corixidae	- -	- -	- -	- -
		Copepod	- -	- -	- -	2.64 (8.3)
		Cladacera	- -	- -	- -	- -
		Unidentifiable Aquatic Invertebrate	- -	11.22 (30.0)	0.12 (0.4)	3.70 (6.1)
		Terrestrial Invertebrate				
		Hemiptera - Aphid	- -	- -	- -	- -
		Hemiptera - Unidentified	- -	- -	- -	- -
		Thysanoptera - Thrip	- -	- -	- -	- -
		Hymenoptera	- -	- -	- -	- -
		Coleoptera	- -	- -	- -	- -
		Diptera	- -	- -	- -	- -
		Orthoptera	- -	- -	- -	- -
		Terrestrial Mite	- -	- -	- -	- -
		Unidentifiable Terrestrial Invertebrate	- -	- -	- -	- -
		Miscellaneous Invertebrate	- -	- -	- -	- -
		Fungi	- -	- -	- -	- -
		Fish	- -	1.53 (4.6)	- -	- -

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VITA

Sarah Seegert was born and raised in Stevens Point, Wisconsin. After graduating from the local high school in 2003, she enrolled at the University of Wisconsin–Madison. Sarah graduated in May 2007 with a Bachelor's of Science in Biology with honors and a certificate in Environmental Studies. While at UW–Madison , she conducted independent research for a senior honors thesis, which was titled "Submerged macrophytes in Big Spring Creek, WI: Distribution and influence on phosphorus dynamics." She was also involved in research investigating the influence of light on ecosystem structure and nutrient and carbon dynamics in the Wisconsin River and its floodplain.

In the summer of 2007, Sarah received a Research Assistantship at Loyola University Chicago, where she began her Master's thesis research with Dr. Emma Rosi-Marshall, investigating small-bodied fish diets in the Colorado River. While at Loyola, Sarah participated in five sample collection trips in the Grand Canyon, including sampling during an experimental high flow release from Glen Canyon Dam in 2008. She also served as teaching assistant for two courses at Loyola and participated in an intensive short-course in the Fundamentals of Ecosystem Ecology at the Cary Institute for Ecosystem Studies in January 2009. In August 2009, Sarah took a job with the Great Lakes Fishery Commission as a research program associate in Ann Arbor, MI, where she is currently living with her husband Nathan.