Abstract

BREWSTER, JESSICA R. Trophic Relations of Introduced Flathead Catfish in a North Carolina Piedmont River. (Under the direction of Dr. Thomas J. Kwak.)

The flathead catfish *Pylodictis olivaris* is a large piscivorous ictalurid that is native to the Mississippi and Rio Grande river drainages, but has been widely introduced across the United States. I studied the trophic relations of introduced flathead catfish in the upper Cape Fear River basin, located in the piedmont region of North Carolina. My specific objectives for this study were to (1) quantify the diet of the flathead catfish and determine an ontogentic shift in diet; (2) determine selectivity for different prey fishes based on their occurrence in the flathead catfish diet and abundance in the river system; (3) determine diel chronology in feeding; (4) calculate daily ration and gastric evacuation rate to quantify the rate of food consumption; and (5) conduct field experiments to elucidate the mechanisms of the predator-prey relationship by determining preferences in introduced flathead catfish and channel catfish feeding between prey species, prey location in the water column, and accessibility to cover.

River ecologists and fisheries managers are concerned with introductions of flathead catfish because of negative impacts to native fish communities associated with direct predation and indirect competition from these apex predators. There are also concerns with introductions that result in co-occurrence with imperiled species, and within my study site, introduced flathead catfish occur with the federally endangered Cape Fear shiner *Notropis mekistocholas* and the Carolina redhorse *Moxostoma* sp., a federal species of concern.

I sampled a section of the Deep River in North Carolina that was hydrologically divided into unimpounded and impounded reaches, to quantify diet and determine diet selectivity. A second study site, located at the confluence of the Deep and Haw rivers where

the Cape Fear River is formed, was sampled in conjunction with the first field site to determine diel feeding chronology, daily ration, and gastric evacuation rate. Flathead catfish were collected using non-lethal, low-frequency, pulsed-DC electrofishing, and diets were sampled using non-lethal, pulsed gastric lavage. A randomized prey curve determined that the number of stomachs sampled was sufficient to accurately describe flathead catfish diet.

The prey taxon with the greatest occurrence in the diet was crayfish, while sunfish *Lepomis* spp. composed the greatest percent of the diet by weight; neither imperiled fish species was found in any stomach sampled. An ontogenetic shift in diet was evident when flathead catfish reached about 300 mm in total length, and flathead catfish length significantly explained variation in percent-composition-by-weight of crayfish, sunfish, and darters *Etheostoma* and *Percina*. Flathead catfish showed positive prey selectivity for taxa that occupied similar benthic microhabitat as this predator, highlighting the importance of prey encounter rates to the predatory behavior of flathead catfish. Flathead catfish ranged in size from 91 mm to 1,127 mm in total length and fed throughout the 24-h period. Flathead catfish displayed a highly variable diel feeding chronology for July with a mean stomach fullness of 0.32%, but showed a single mid-day peak in feeding during August (mean fullness = 0.52%). The gastric evacuation rate for flathead catfish increased between July (0.40/h) and August (0.59/h), as did daily ration, which more than doubled between the two months (3.06% in July, 7.37% in August).

A tethering experimental approach proved effective in determining prey selection dynamics for two contrasting large catfish species in the field, when they were presented choices among prey differing in species, location in the water column, and access to shelter from the predator. The flathead catfish, an obligate carnivore, showed no preference among all three treatment effects, whereas channel catfish, a feeding generalist, showed strong specificity for redbreast sunfish that were located higher in the water column. These research findings under controlled conditions in a field setting offer additional insight into prey selection dynamics of these introduced catfish predators as it occurs in a natural setting that could not be gained by traditional sampling and observational approaches. Understanding the trophic relations of introduced flathead catfish and the degree of vulnerability among prey taxa will allow resource managers to make science-based decisions that may decrease the impacts of introduced flathead catfish on native fish populations and allow enhanced protection for imperiled species.

Trophic Relations of Introduced

Flathead Catfish in a North Carolina Piedmont River

by

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A thesis submitted to the Graduate Faculty of
North Carolina State University
in partial fulfillment of the requirements for the
Degree of Master of Science

FISHERIES AND WILDLIFE SCIENCES

Raleigh, North Carolina
2007

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Biography

Jessica Robin Brewster was born in Atlanta, Georgia, on July 1, 1979, and was the only child of Frank and Jane Brewster. Her father was in the military, so she spent part of her childhood in Atlanta and Augusta, Georgia, as well as in Fort Leonard Wood, Missouri. She spent her youth racing sail boats and showing horses. She really enjoyed the competition that both offered, but it was being outside and active that really caused Jessica to love these sports. When Jessica was in eighth grade, her family moved back to Augusta for the last time, and she graduated from Lakeside High School in 1997.

Jessica was hoping to move off to college and attend University of Georgia (Go Dawgs!!), but her parents convinced her to stay in town and attend Augusta State University until she completed her non-major courses. This was a decision that Jessica was not thrilled about at the time, but in the end, she would thank her parents, because while at ASU, she met the professor that ended up shaping her professional career. Dr. Bruce Saul was the fisheries professor at ASU, and at a time when Jessica was unsure of what she wanted to do with her life, friends convinced her to take his aquatic biology course. The first field trip was to the mountains, and as soon as Jessica put on the backpack electrofishing equipment and started chasing down fish she was “hooked” . She knew that she wanted a job that involved fisheries, and with Dr. Saul’s support and guidance, she was provided with all the opportunities to allow her to accomplish her goals.

In the winter of 2002, Jessica graduated from Augusta State University with a Bachelor of Science in Biology, and the following summer, took her first fisheries job with the Georgia Department of Natural Resources “Stream Team” . She spent that summer sampling the streams of Georgia in the piedmont region and enjoyed it so much that she came back the next year to help sample streams in the mountain region. During that second summer, she began to realize that although she enjoyed collecting data, she also wanted to be able to create something meaningful from it. She knew then that she wanted to become a fisheries biologist, so Jessica decided to go back to school and get a Master's degree.

During 2004, Jessica met Dr. Tom Kwak and accepted a position as a Master's student studying the trophic relations of introduced flathead catfish. In December of that year, Jessica and her fiancé, JJ, packed up their stuff, loaded up their beautiful black lab, Onyx, and headed up to Raleigh, North Carolina. The following pages describe the activities that took place for Jessica to accomplish her goal of receiving her Master's degree.

Acknowledgments

I would first like to thank Dr. Tom Kwak for his support and guidance during the past two and a half years. Working with him has allowed me to gain a great deal of knowledge and confidence in the fisheries field. I would also like to thank my committee members, Dr. Jim Rice and Dr. Cavell Brownie, for their suggestions and logistic help during this research. This project was funded by the North Carolina Wildlife Resources Commission through Federal Aid in Sport Fish Restoration funds (Project F-68).

I want to thank Dr. Bruce Saul for first showing me how awesome it was to do fisheries work. His enthusiasm and mentorship allowed me to get excited about pursuing a career as a "fish head" and gave me the opportunities to make my goal of becoming a fisheries biologist possible. The base of my fisheries knowledge was expanded by Jeff Jones, who allowed me to help every time he went sampling and who was brave enough to teach me to drive a shock boat.

Along with my committee members, there is a plethora of people at North Carolina State University who I would like to thank for helping me along the way. Edward Malindzak gave me invaluable insight into the world of graduate school and flathead catfish. Wendy Moore was there to help with all logistic issues, including paperwork that kept me in school and paid. My field technician, Michael Fisk, helped make field work enjoyable and kept me calm when things weren't going exactly the way I planned. Patrick Cooney, who assisted with all nighttime sampling and helped proof read my thesis. I thank everyone that assisted me in the field: Micheal Fisk, Patrick Cooney, Edward Malindzak, Rupert Medford, Ryan Spidel, Jenny Winters, Aya Tajiri, Julie Harris, Christin Brown, Scott Favrot, Frank

Brewster, and JJ Baumann. Wayne Starnes helped identify shiners and suckers that were collected in diets. Ryan Heise and Wayne Starnes helped in the sampling design for estimating prey fish populations, and a large crew assisted in collecting data for those estimates. Keith Ashley, Christian Waters, Tom Rachels, Kent Nelson, Scott Van Horn, and Bob Curry who assisted with designing field methods and grant administration. Bill Pine refined some of the techniques used in my study and provided early ideas on tethering. Chris Butler assisted in understanding cumulative prey curves. Along with their help in the field, I would like to thank Christin Brown, Julie Harris, Michael Fisk, Patrick Cooney, Scott Favrot, and Warren Mitchell for their emotional support and camaraderie.

A special thanks goes to my family and friends. My wonderful parents, Frank and Jane Brewster, for supporting and encouraging me no matter what I was trying to accomplish. I'm very lucky to have such loving parents, and I truly would not be the person I am today without them. My grandparents, Jim and Wilma Brewer, provide constant support and are always there to cheer me along. I thank Sally Crunkleberry, Keith Gibbs, Onyx, and the gang for always being able to provide laughter and a smile. Last, but definitely not least, I would like to thank my loving and amazing fiancé, JJ Baumann, who has provided patience and understanding and has been my emotional rock throughout graduate school and life. Thank you!!!!!

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Introduction

The flathead catfish *Pylodictis olivaris* is a large piscivorous ictalurid that was first described from the Ohio River in 1818 (Jackson 1999) and can be found across the United States. The flathead catfish is native to the southern Great Lakes, as well as the Mississippi, Mobile, and Rio Grande river drainages and has been widely introduced, both legally and illegally, across the United States (Jenkins and Burkhead 1994; Jackson 1999). Flathead catfish were first introduced in the Atlantic Slope region of the United States in the Flint River of southern Georgia around 1950, and these introductions have continued as far north as the Delaware and Susquehanna rivers in eastern Pennsylvania (Quinn 1987; Fuller et al. 1999; Jackson 1999; Brown et al. 2005).

The biology of this fish has been extensively studied both in it's native and introduced ranges. The maximum age reported for an introduced flathead catfish in a riverine system is 17 years (Kwak et al. 2006), but estimates for flathead catfish in their native range exceed 25 years (Nash and Irwin 1999). Sexual maturity is reached between 3 and 5 years for males and 4 and 7 years for females (Minckley and Deacon 1960; Turner and Summerfelt 1970; Munger et al. 1994). Flathead catfish are the second largest ictalurid, with total lengths ranging up to 900 mm and record weights of over 45 kg (Jenkins and Burkhead 1994; Jackson 1999). Juveniles occupy swift, rubble-bottomed riffles until they reach 5 to 10 cm, when they distribute into surrounding habitats that include pools and deeper riffles (Minckley and Deacon 1960; Jenkins and Burkhead 1994). Adults favor moderate to deep pools in large streams, rivers, lakes, and reservoirs that contain large woody debris, deep holes, or any physical objects that can be used for cover (Minckley and Deacon 1960; Jenkins and Burkhead 1994).

Flathead catfish are considered highly mobile in their introduced and native ranges (Kwak et al. 2004; Vokoun and Rabeni 2005; Malindzak 2006). In a study conducted in the coastal region of North Carolina, flathead catfish were reported to occupy linear home ranges from 13 km to 25 km (Kwak et al. 2004). Malindzak (2006) found that flathead catfish constrained to a closed section of river, between two dams, on the upper Cape Fear River drainage occupied an annual linear range of 16.2 km, but that these fish could have a linear range greater than 28 km during the spawning season. Flathead catfish in their native range show mean annual movements greater than 60 km (Vokoun and Rabeni 2005).

Ontogenetic shifts in diet occur in most fishes (Gerking 1994), and biotic and environmental factors can influence these shifts in feeding. During early life stages, flathead catfish are invertivores, relying on aquatic insects and crayfish for food, but as they mature and grow they become obligate carnivores, feeding mainly on live fish (Layher and Boles 1980; Jackson 1999; Pine 2003). This ontogenetic shift in diet from invertebrates to fish usually occurs when flathead catfish exceed 300 mm in length (Quinn 1987; Jackson 1999; Weller and Robbins 1999; Herndon and Waters 2000), but may occur earlier in reservoir flathead catfish populations than those in a riverine environment (Layher and Boles 1980). Along with fish length and environment, the ontogenetic shift in diet is affected by the abundance of available prey items (Minckley and Deacon 1960). Invertebrates remain a substantial component of the diet as the fish matures as long as invertebrate prey remain abundant, but flathead catfish begin to feed on fish at a smaller size when aquatic invertebrates are scarce (Minckley and Deacon 1960). Adult flathead catfish may also completely shift their diet if abundance in prey availability changes (Haas et al. 2001).

Seasonal variation in feeding is influenced by changing water temperatures, spawning events, and other environmental factors. Seasonal migration, feeding patterns, and digestion rates of the flathead catfish are associated with changes in water temperature. Rising water temperature may play a role in the movement of flathead catfish upstream to spawning grounds and then back into deepwater wintering sites when water temperatures begin cooling (Kwak et al. 2004). Increasing water temperatures also trigger increased feeding activity and rates of digestion (Minckley and Deacon 1960; Haas et al. 2001). Feeding starts to increase at the beginning of spring and peaks before spawning in April and May, decreases between May and August concurrent with spawning, and then peaks again in August after spawning is completed, with the greatest diet diversity occurring in spring and summer (Turner and Summerfelt 1970; Layher and Boles 1980). An increase in feeding post-spawning was shown in pond experiments where fathead minnows *Pimephales promelas* increased in number while co-occurring with only flathead catfish until June, when their abundance began to decline, and by August they had almost been eliminated (Swingle 1967). However, not all trophic studies detected seasonal trends in feeding. Quinn (1987) detected no seasonal trend in the diets of flathead catfish in the Flint River of Georgia.

Flathead catfish are primarily nocturnal fish, increasing both their movements and feeding activity at night (Minckley and Deacon 1960; Quinn 1987; Malindzak 2006). During the day flathead catfish show little to no movement, but at night, they become more active and move toward deeper waters (Malindzak 2006). Quinn (1987) suggested that introduced flathead catfish in Georgia feed in the early morning hours, and Minckley and Deacon (1960) reported that native flathead catfish in Kansas collected from dawn to mid-day and dusk to midnight had the highest average number of organisms in the stomach, suggesting a crepuscular feeding pattern for flathead catfish.

Flathead catfish interact intensively with native fish by direct predation and indirect competition for food sources. Descriptions of flathead catfish feeding behavior indicate that they remain motionless and either leave their mouths wide open until prey swim in seeking cover (Trautman 1957) or actively lunge at prey that swim close enough to seize (Minckley and Deacon 1960). Flathead catfish are opportunistic feeders, consuming the largest and most abundant prey item at the time of feeding (Minckley and Deacon 1960; Swingle 1967; Turner and Summerfelt 1970). They consume large amounts of prey, and the large gape-width of their mouths allows them to consume prey items that are large relative to their size (Turner and Summerfelt 1970; Herndon and Waters 2000). The dominant prey items in the diet of flathead catfish are members of the Centrarchidae, Clupeidae, and Ictaluridae fish families, as well as crayfish and aquatic insects (Guier et al. 1981; Ashley and Buff 1987; Quinn 1987; Weller and Robbins 1999). Ecosystem simulation modeling demonstrated both direct effects of predation and indirect competition by flathead catfish on native fishes and projected that native apex predators experience the greatest response to introduced flathead catfish due to increased interspecific competition for food resources (Pine et al. 2007).

The desire of anglers to pursue a big-game catfish in their local system that is aggressive, with the ability to reach large sizes and a good flavor to its flesh, has resulted in introductions of the flathead catfish outside of its native range (Jenkins and Burkhead 1994; Jackson 1999). Attitudes among biologists, resource managers, and anglers about this introduced species vary because of the flathead catfish's value as a sport fish and its ability to alter fish communities and traditional fisheries (Jackson 1999). Invasive flathead catfish have been considered among the most ecologically harmful introductions in the United States (Fuller et al. 1999; USFWS Memorandum dated 3 November 1999). Anglers are divided between those that prize catching flathead catfish and those that are concerned with the impact they have on native sport fish populations, but both groups agree that sport fishing should be the only means of reducing flathead catfish abundance (Weller and Geihsler 1999).

Introduced flathead catfish populations establish themselves and expand rapidly within a system (Guier et al. 1981; Ashley and Buff 1987; Thomas 1993). The first known introduction of the flathead catfish in North Carolina was into the Cape Fear River in 1966, when 11 adults with a combined weight of 107 kg were released near Fayetteville, North Carolina (Ashley and Buff 1987). It took only 10 years for the flathead catfish to establish itself, expand its range to inhabit 200 km of the mainstem Cape Fear River, and become the predominant apex predator in the system (Guier et al. 1981; Ashley and Buff 1987). Guier et al. (1981) believed that the flathead catfish would have expanded its range in the Cape Fear River even further if not hampered by physical obstructions, such as dams, and the presence of saline water.

Introduced flathead catfish have raised concern among river ecologists and fisheries managers because of the possible negative affects on native fish communities (Guier et al. 1981; Thomas 1993; Bart et al. 1994; Ashley and Rachels 1998; Weller and Robbins 1999). The greatest impact on native fish populations is reported to occur shortly after flathead catfish have been introduced into a system (Ashley and Buff 1987; Thomas 1993; Jackson 1999; Kwak et al. 2004). Thomas (1993) reported that the introduction of this species resulted in the near eradication of bullhead *Ameiurus* spp. populations in the Altamaha River system of Georgia, and that this severe decline in bullhead populations could have caused a shift in the flathead catfish diet to the redbreast sunfish *Lepomis auritus,* that had subsequently experienced a population decline. Species that have become targets of direct predation by introduced flathead catfish include the silver redhorse *Moxostoma anisurum,* robust redhorse *Moxostoma robustum,* and most ictalurids and *Lepomis* spp. (Guier et al. 1981; Thomas 1993; Bart et al. 1994; Ashley and Rachels 1998; Weller and Robbins 1999; Pine et al. 2005). Guier et al. (1981) concluded that there was strong evidence that the decline in bullhead and channel catfish *Ictalurus punctatus* populations in the Cape Fear River of North Carolina was a result of predation by flathead catfish. Food-web simulation modeling by Pine et al. (2007) projected declines of up to 50% in the biomass of native fish groups after the establishment of introduced flathead catfish. In contrast, several investigators could not detect an adverse impact on native fish populations despite an increase in flathead catfish predation (Ashley and Buff 1987; Quinn 1987). Ashley and Buff (1987) concluded that centrarchids made up only a small proportion of the flathead catfish stomach contents they collected, suggesting that the increased concerns among local anglers over the decrease in sunfish populations could not be attributed to flathead catfish predation.

Flathead catfish have been introduced into waters that are inhabited by rare and endangered fishes, and the impact of co-occurrence with these species is unknown. The Deep River, a major tributary of the Cape Fear River, is inhabited by the federally endangered Cape Fear shiner *Notropis mekistocholas,* and there are only five known metapopulations of Cape Fear shiners remaining (Howard 2003; Hewitt et al. 2006). The co-occurrence of flathead catfish creates the potential for negative effects on these species, as flathead catfish have been reported to feed on other members of the Cyprinidae family (Gueir et al. 1981; Pine et al. 2005). Howard (2003) found that Cape Fear shiners inhabit riffles most of the year and move into deeper water to spawn. These same macrohabitats are used by both juvenile and adult flathead catfish (Minckley and Deacon 1960; Jenkins and Burkhead 1994; Irwin et al. 1999; Malindzak 2006). The rare and undescribed Carolina redhorse (*Moxostoma* sp.) is a federal species of concern that also inhabits the same sections of the Cape Fear River as the flathead catfish (Starnes et al. 2005). Little is known about the biology of this species, but other members of the Catostomidae family have been found in the stomach contents of flathead catfish (Guier et. al 1981; Pine et al. 2005), and there has been a negative correlation between the introduction of flathead catfish and the abundance of other redhorse species (Bart et al. 1994). It has also been suggested that introduced flathead catfish feed upon juvenile Gulf sturgeon *Acipenser oxyrinchus desotoi*, resulting in declines of this federally threatened benthic fish (Fuller et al. 1999). Understanding the relationships between flathead catfish and these rare and endangered species is a fundamental step toward protecting imperiled fish populations and ensuring that precautions are taken to maintain or increase their survival rates.

Determining feeding behaviors and how a fish's diet affects the nutrition and growth of the fish is essential to understanding the ecological role of the population in a system (Bowen 1996). Thus, I initiated research on the trophic relations of introduced flathead catfish to better understand the ecological impacts of this invasive species. My research approach included a quantitative description of the diet using the frequency of occurrence for a prey item, which suggests the consistency of prey selection over the entire group of a studied predator, while the importance level of prey items to the nutritional needs of a fish was determined using percent-composition-by-weight for prey items in the diet (Bowen 1996). I then quantified feeding selectivity using the frequency of prey items found in stomach contents relative to the availability in the system, an important analysis when determining the potential impact this introduced species has on native fish communities (Chesson 1978; Pine et al. 2005). And finally, I estimated daily ration and gastric evacuation rate to quantify predation as a dynamic function (Bromley 1994) and further explain the interactions and effects of predation and competition between introduced flathead catfish and native fish communities.

Objectives

The goal of my research is to determine the dietary requirements of introduced flathead catfish and potential ecological effects on native species. My research is one component of a larger study that also includes estimating population size, seasonal and diel movements, and habitat use of the flathead catfish in its introduced range. Understanding how the flathead catfish fulfills its nutritional needs will assist in understanding its impacts on native species in the piedmont rivers of North Carolina, including the endangered Cape Fear shiner and the imperiled Carolina redhorse.

My specific objectives are to (1) quantify the diet of the flathead catfish and determine ontogenetic shift in diet for different prey items; (2) determine selectivity for different prey items based on occurrence in the flathead catfish diet and the abundance of those prey in the river system; (3) determine diel periodicity in feeding; and (4) calculate daily ration and gastric evacuation rate to quantify the rate of food consumption.

Methods

Site Description

I conducted field sampling in two river reaches within the upper Cape Fear River drainage basin. The first site was used to quantify the flathead catfish diet and determine diet selectivity. It was also used in conjunction with a second field site to determine diel periodicity in feeding, daily ration, and gastric evacuation rate. This site was located on a section of the Deep River, a medium-sized piedmont river in the upper Cape Fear drainage in Moore and Lee counties of North Carolina (Figure 1). I sampled the section of river between Highfalls Dam and Carbonton Dam, which was about 35 river km in length. The site is about 25 km west of Sanford, North Carolina, and 220 km from where the Cape Fear River discharges into the Atlantic Ocean. This section of river is hydrologically divided into two distinct reaches (Figure 1). The upper reach is composed of fast-flowing, shallow water that contains a series of pools and riffles and is located between Highfalls Dam and the Glendon-Carthage Road Bridge. The lower reach is composed of impounded water that is deep and slow moving and is located between the Glendon-Carthage Road Bridge and Carbonton Dam.

The second field site was sampled in conjunction with the first field site to determine diel periodicity in feeding, daily ration and evacuation rate. It was located at the confluence of the Deep and Haw rivers where the Cape Fear River is formed, in Chatham and Lee counties of North Carolina (Figure 2), downstream of Moncure Dam on the Deep River and Jordan Dam on the Haw River and upstream of Buckhorn Dam on the Cape Fear River. The site is about 16 km east of Sanford, North Carolina and 165 km from the mouth of the Cape Fear River.

Diet Sampling Procedures

Flathead catfish were collected and diets sampled using techniques proven effective in previous research conducted for the larger project (Kwak et al. 2004). Fish were collected using non-lethal, low-frequency, pulsed-DC electrofishing (Smith-Root Inc., Mark VI electrofisher) and then temporarily placed in a holding tank. Flathead catfish diets were sampled by removal of stomach contents within an hour of capture to minimize digestion and chances of regurgitation in the holding tank.

Sampling was conducted at the first field site and began on May 12, 2005, when water temperatures exceeded the 18ºC minimum threshold for effective flathead catfish capture by electrofishing (Kwak et al. 2004). The 35-km section of the Deep River was stratified into two sampling reaches, an upper unimpounded reach and a lower impounded reach as described above. Daily sampling began at sunrise, between 06:30 and 07:00 hours, and continued until sampling of the reach was complete. Sampling occurred within each reach at least once per week during three successive weeks in a month, and sampling ceased one week to allow the flathead catfish to recover from electrofishing. Flathead catfish exhibit reduced vulnerability to successive electrofishing during a 24-48 h recovery period after initially being collected (Kwak et al. 2004), consequently sampling sites were not electrofished more than once in a 48-h period.

In related research within this same river section, Malindzak (2006) was conducting a radio-telemetry study on 19 flathead catfish. Information from these tagged fish was used to determine when sampling in the upper reach, an area utilized only during the spawning season, would begin and end. The upper reach was sampled until the tagged flathead catfish began moving back downstream to deeper waters, whereas the lower reach was sampled during the entire sampling season. Sampling ended on September 28, 2005, when the water temperature dropped below 18ºC.

Once flathead catfish were collected, the total length (± 1 mm) and weight (± 1 g) of each fish was measured and recorded. Then their stomach contents were collected using pulsed gastric lavage (PGL), a technique shown to quickly, efficiently, and non-lethally remove all food types and sizes (Foster 1977; Waters et al. 2004). After removal, stomach contents were placed in a resealable plastic bag and labeled with an identification number and the date, then placed on ice for transfer back to the lab. The diet samples were transported to the North Carolina Cooperative Fish and Wildlife Research Unit laboratory and frozen for further analysis. In the laboratory, the items from each stomach were sorted to the lowest taxon possible, and the total number and wet weight (± 0.01 g) were recorded for each taxon.

Diet Composition

A cumulative prey curve was developed to determine if the number of flathead catfish stomachs sampled was adequate to describe their diet (Ferry and Cailliet 1996; Bizzarro et al. In press). Prey items were grouped by family, and means and standard deviations of the cumulative number of unique prey taxa were calculated (Adams 2004). The mean cumulative number of unique prey taxa in each sample was randomized 500 times and then plotted against the number of stomachs (Bizzarro et al. In press). The sample size is considered adequate if the curve reaches an asymptote (Ferry and Cailliet 1996); to quantitatively determine if an asymptote was reached, a linear regression was performed on the last four endpoints (Bizzarro et al. In press). If the slope of the last four endpoints was not significantly different from zero (Zar 1996), an asymptote was reached, and the sample was considered adequate.

A quantitative description of the flathead catfish diets sampled was developed using two methods. I used frequency of occurrence to suggest the consistency of prey selection over all flathead catfish sampled, while the importance level of the prey taxa to the nutritional needs of the flathead catfish was determined using percent-composition-by-weight (Bowen 1996). Prey items were grouped by family and graphed to qualitatively determine which families were more prevalent and which were more nutritionally valuable.

Ontogenetic shifts in diet occur in most fish (Gerking 1994), and in flathead catfish this shift is reported to occur around 300 mm (Jackson 1999). The data used to quantify the overall diet of flathead catfish were used to determine if this ontogentic shift was detectable within my study. I used logistic regression to examine if month sampled, flathead catfish length, and the interaction between month and flathead catfish length could be used to predict occurrence of certain prey taxa in the diet. I used a two-factor ANOVA to examine the effects of flathead catfish length and month on the percent-composition-by-weight of specific prey taxa in the diet. The proportion-by-weight of prey taxa for each stomach sample was arcsine transformed to stabilize error variance (Zar 1999). If the ANOVA resulted in a significant treatment effect, I stratified the flathead catfish into five length classes, < 250 mm, 250 - 299 mm, 300 - 349 mm, 350 - 449 mm, and > 450 mm, and performed a Tukey's multiple contrast test to identify differences among treatment categories.

Diet Selectivity

Chesson's (1978) selectivity index was used to measure the flathead catfish's selective predation of different prey items. A Chesson's (1978) alpha (α) is calculated for individual prey items and is defined as

$$\alpha_i = \frac{r_i / p_i}{\sum_{j=1}^{m} (r_j / p_j)},$$

where r_i is the percent of a prey taxon in the diet, p_i is the percent of that prey taxon available in the system, and r_j and p_j are those values for all prey taxa. The index ranges between 0 and 1, with random feeding occurring at $1/m$, where m is the number of prey taxa available in the system. Prey items with a Chesson's alpha value greater than the random feeding value are positively selected and considered preferred. Prey items with an alpha less than the random feeding value are negatively selected and considered avoided. I assigned an alpha of 1.0 for prey items occurring in the diet but not found in availability sampling.

The availability of prey items in the Deep River study site (Table 1) was determined using electrofishing gears and a three-pass removal method. I estimated prey availability separately within the two sampling reaches of this site (Table 2) (see site description section above); one was located in the upper unimpounded reach where Buffalo Creek drains into the Deep River, and the other was in the lower impounded reach at the Carbonton boat ramp, approximately 34 river km upstream of Carbonton Dam. The Buffalo Creek site was located in an area consisting of pools and riffles, necessitating use of both backback and boat electrofishing units. Each unit was used to complete three sampling passes of suitable habitat for that gear, with equal effort among passes. The boat unit was used to sample the pool area, and the backpack unit to sample the riffle area. The Carbonton boat ramp site was located in an impounded area of the Deep River and was sampled using two boat electrofishing units following the same three-pass protocol. Each site was sampled in October of 2004 and May of 2005. I employed a maximum-likelihood method to estimate the population sizes of fish prey items available in the system based on the electrofishing catches among passes (Seber 1982; Bohlin et al. 1989; Kwak 1992). When a population was not sufficiently reduced among successive passes, the overall number of individuals sampled was used as a minimum estimate of the total population.

The 35-km section of Deep River was divided into 3 reaches based on habitat, and a Chesson's (1978) alpha was calculated for individual prey families within each of the reaches over the two seasons that prey availability was sampled. Alpha values for diet samples collected before June 21 were calculated using the fish population estimates estimated from the prey availability sampling in May, and alphas for diet samples collected after June 21 incorporated fish population estimates from the October prey availability sampling. The site location of prey availability data used for each reach was based on habitat similarity; therefore, prey availability data from the Buffalo Creek upstream estimates were applied to the diet samples of fish from the two upstream reaches and prey availability for the downstream Carbonton boat ramp estimates were applied to the downstream reach diet samples. I calculated two series of Chesson's alpha values each for the middle and downstream reaches, representing stomach content and prey availability sampled before and after June 21. The upper reach was only utilized by flathead catfish during spawning, so I calculated only one Chesson's alpha for diet and prey availability sampled before June 21 in that reach. Based on habitat similarity and proximity to the prey availability sampling sites, the results for the two upstream reaches were averaged to obtain a mean Chesson's alpha for each prey taxa representing diet selectivity of flathead catfish in shallow, fast moving water. A mean Chesson's alpha was also calculated, averaging values of alpha for the two seasons from the lower reach, to represent diet selectivity in deep, slow moving water.

Diel Chronology

Field sampling to determine the diel feeding chronology of flathead catfish was conducted during July and August of 2005 and 2006. The 2005 samples were collected at the first field site located on the Deep River of North Carolina (Figure 1), and the 2006 samples were collected at the second field site located at the confluence of the Haw and Deep Rivers (Figure 2). Flathead catfish diet samples were collected over two 6-h periods and one 12-h period in 2005, over a single 24-h period in July of 2006, and during one 21-h period and one 3-h period in August of 2006 (due to equipment failure). The results for July 2005 and 2006 and for August 2005 and 2006 were each combined based on similar environmental factors and to increase sample size. Mean temperatures were 26ºC in July and 27ºC in August. Flathead catfish and diet samples were collected and processed following the methods described above (Diet Sampling Procedures). The stomach fullness (F_t), an index of fish feeding intensity (Hyslop 1980), of fish sampled at time t was calculated using the equation

$$F_t = \frac{W_t}{W_f} \times 100,$$

where W_t is the wet weight of stomach contents, and W_f is the live, wet weight of the flathead catfish. I stratified the 24-h period into 2-h time intervals, and the mean fullness for fish collected in each interval, including empty stomachs and those with contents, was calculated and graphed over the 24-h period.

Daily Ration and Evacuation Rate

The field data collected to determine diel feeding chronology were also used to estimate a daily ration and a gastric evacuation rate for flathead catfish. Daily ration calculated from the field is an ideal approach, because the fish are subjected to natural conditions rendering more realistic results (Jarre et al. 1991; Bromley 1994; Grant and Kott 1999). Daily ration (C_{24}) was calculated using the method of Elliot and Persson (1978)

$$C_{24} = \sum_{t=1}^{p} \frac{(F_{t+1} - F_t e^{-Rt})RT}{(1 - e^{-RT})},$$

where F_t and F_{t+1} are the mean stomach fullness of fish at two successive time (t) periods, R is the gastric evacuation rate, T is the time interval between successive samples, and p is the number of sampling intervals in the 24-h period. The reliability of this method to estimate daily ration from field sampling was verified by Cochran and Adelman (1982), Kwak et al. (1992), and Héroux and Magnan (1996). The Elliot and Persson (1978) model estimates the amount of food consumed over a 24-h period and is most suitable when each sample period is 3-h or less; therefore, the sampling period, T, used in my study was 2 h.

A gastric evacuation rate (R) was calculated for each 2-h time interval (T) using the slope of the relationship between stomach fullness (F_i) and time

$$R = \frac{\log_e F_{(t+1)} - \log_e F_{(t)}}{T},$$

where $F_{(t)}$ and $F_{(t+1)}$ are the mean stomach fullness at the beginning and end of the time interval (Boisclair and Leggett 1988; Boisclair and Marchand 1993; Héroux and Magnan 1996). The evacuation rate used when calculating daily ration with the Elliot and Persson (1978) model was derived from the time interval with the steepest slope (Boisclair and Legget 1988). In July of 2005 and 2006, peak feeding occurred between 16:00 and 18:00 hours, therefore, the evacuation rate I used was the slope calculated from this peak to the next successive time interval (18:00 – 20:00 hours) to determine a daily ration for the combined July data. Peaks in feeding occurred between 10:00 and 12:00 hours during August of 2005 and 2006; therefore, the evacuation rate I used was the slope calculated from this peak to the next successive time interval (12:00 – 14:00 hours) to determine a daily ration for the combined August data.

Results

A total of 608 flathead catfish were collected, excluding those from diel sampling, between May 12, 2005, and September 28, 2005, and of these, the stomachs of 338 (45%) contained food items. Stomach contents were identified to phylum for clams and snails, infraorder for freshwater shrimp and crayfish, order for aquatic insects, and family for fish. Unidentifiable material included pieces of flesh, scales, and bone fragments and were included in analysis as unidentified fish.

Diet Composition

The randomized cumulative prey curve reached an asymptote (*P* = 0.3258; Figure 3) indicating that a sample size of 338 was adequate for analysis of flathead catfish diet. I identified 95% of prey consumed by flathead catfish, while the remaining stomach contents were in advanced stages of digestion and could not be identified beyond being fish material. Stomach contents included prey items from seven fish families, two orders of aquatic insects, two infraorders of aquatic invertebrates, as well as snails and clams representing the phylum Mollusca (Figure 4). Crayfish (Astacidae) were the most common prey item by occurrence (25%), but members of the fish family Centrarchidae made up the greatest percent of the diet by weight (44%). Centrarchidae was mainly represented by *Lepomis* species (89%), but also included six largemouth bass *Micropterus salmoides* ranging from 0.14g to 301g. Clupeidae were the second greatest proportion of the diet weight (26%), although this family was only represented by four large gizzard shad *Dorosoma cepedianum*. Flathead catfish consumed members of both the Catostomidae and Cyprinidae fish families that included satinfin shiner *Cyprinella analostana,* sandbar shiner *Notropis scepticus*, and brassy jumprock *Moxostoma* sp., but neither the Cape Fear shiner nor Carolina redhorse were present in any of the diets examined. The family Percidae was represented by two genera of darters, *Etheostoma* and *Percina*, and cannibalism was evident by the occurence of juvenile flathead catfish in the diet, but the ictalurid component also included madtoms *Noturus* spp. and channel catfish *Ictalurus punctatus*.

An ontogentic shift in diet was apparent between flathead catfish less than 300 mm and those greater or equal to 300 mm (Figure 5). Of the 12 identified prey taxa groups, five had sufficient data for statistical comparison. I found that as flathead catfish increase in size the consumption of both Odonata and Percidae decreased; however, the occurrence of Centrarchidae increased with flathead catfish size (Figure 6). Logistic regression models for flathead catfish length significantly explained occurrence in the diet for these three prey taxa, Odonata (χ^2 = 20.89; P <0.0001), Centrarchidae (χ^2 = 32.55; P <0.0001), and Percidae (χ^2 = 11.12; P = 0.0009). Odonata was the only prey taxon that showed a significant effect of month (χ^2 = 11.35; P = 0.0229) or the interaction (χ^2 = 11.56; P = 0.0209), but when the model was reduced to main effects of month and fish length, the month treatment was no longer significant (χ^2 = 1.27; P =0.8658), but fish length remained so (χ^2 = 12.91; P = 0.0003). Neither factor examined (fish length or month) showed a significant effect for predicting occurrence in the diet for Astacidae or Ictaluridae.

Similar results were found when examining the percent-composition-by-weight of the five statistically significant size groups within the flathead catfish diet using two-factor ANOVA. Odonata (P = 0.0001), Centrarchidae (P = 0.0025), and Percidae (P = 0.0174) all showed a significant main effect of flathead catfish length on the percent-composition-by-weight of the diet, and these results were further examined by the Tukey multiple contrast test among flathead catfish length groups (Figure 6). For these three taxa, the primary ontogentic shift occurred around 300 mm. The greatest differences in diet for Odonata and Centrarchidae occurred between the smallest and largest flathead catfish. The results for Percidae revealed greatest differences in diet between flathead catfish

that were 300-349 mm in length and greater than 450 mm in length. Neither treatment showed a significant effect for weight of the prey groups Astacide and Ictaluridae.

Anguillidae, Catostomidae and Clupeidae were found exclusively in the diet of flathead catfish that were greater than 300 mm (Figure 5).

Diet Selectivity

Relative rankings of fish prey in the diet differed from the prey's availability in the system for both the impounded and unimpounded study reaches. Diet and prey available in the impounded reach showed similar rankings during the fall and spring seasons (Table 1). Rankings for prey availability were determined from population estimates calculated for both the unimpounded and impounded reaches during the fall of 2004 and spring of 2005 (Table 2). *Lepomis* spp. were consistently most prevalent in the diet and available during both seasons. Other intensively consumed prey taxa were members of Ictaluridae and Percidae. Ranks of prey taxa consumed and available in the unimpounded reach varied between seasons (Table 1), but members of the Percidae and Centrarchidae families were the most consumed prey items of flathead catfish during both seasons. Predation pressure on specific prey items did not correspond to their availability in the unimpounded portion of the system, except for the most prevalent prey items, including *Lepomis* spp. in the spring and Percidae in the fall. Flathead catfish diet selectivity was generally similar between the unimpounded and impounded reaches (Figure 7). Mean selectivity (Chesson's alpha) values for each reach showed positive selectivity for members of the Ictaluridae and Percidae families and negative selectivity for members of the Catostomidae, Cyprinidae, and Lepisosteidae families. Mean selectivity values showed positive selectivity for Clupeidae and Anguillidae in the unimpounded reach, but this is due to prey taxa rarely being consumed and not found in availability sampling. *Lepomis* spp. and *Micropterus* spp. showed neutral to positive selectivity in the unimpounded reach, but negative selectivity in the impounded reach.

Diel Chronology and Daily Ration

Diel feeding chronology patterns for flathead catfish varied between the months of July and August (Figure 8). Feeding peaked during several hours during July, whereas, only one large peak in feeding occurred during the afternoon in August. A total of 199 flathead catfish were collected during July, and of these, 115 (58%) had empty stomachs (Table 3). Mean stomach fullness among 2-h intervals ranged between 0.05% and 0.67% during July (Figure 8), and the daily ration for that month was 3.06% of flathead catfish body weight (Table 3). A total of 235 flathead catfish stomach were sampled in August, and of these, 138 (59%) were empty (Table 3). The mean fullness among intervals ranged between 0% and 1.96% during August (Figure 8), and the daily ration was 7.37% of flathead catfish weight (Table 3). Mean stomach fullness, gastric evacuation rate, and daily ration all increased from July to August (Table 3), and flathead catfish doubled their daily nutritional requirement between the two months, according to daily ration estimates.

Flathead catfish consumed a variety of prey items throughout the 24-h period, but there was no distinct pattern to the prey taxa consumed over this period (Figure 9). Centrarchidae were consumed throughout daylight hours and intermittently during dark hours during July and August. Percidae were fed upon throughout the 24-h period during July, but were only consumed in daylight hours during August. Crayfish (Astacidae) were mostly consumed during daylight hours, except for the post-dusk period in July and the pre-dawn period in August. Ictalurids were also consumed during daylight hours, except for July when they were fed upon between 22:00 and 24:00 hours. Ephemeroptera was absent from the flathead catfish diet during August, but present in July in the hours preceding dusk. This is likely due to an observed hatching event that occurred during the July diel sampling but not during August sampling.

Discussion

Previous investigators have described the flathead catfish diet in a quantitative manner to assess how introduced flathead catfish impact native fish populations (Guier et al. 1981; Ashley and Buff 1987; Quinn 1987; Weller and Robbins 1999; Herndon and Waters 2000), but I was able to more specifically identify mechanisms that affect the predator-prey relationship. To better understand how these introduced predators affect native fish communities through direct predation and competition for food resources, I quantified the diet of introduced flathead catfish, and then further explored ontogenetic variation and diet patterns, and estimated gastric evacuation rates and daily ration.

Sunfish are important to recreational fishing and to the river food web and are strongly affected by the occurrence of introduced flathead catfish. I was unable to address the direct predation of specific sunfish species, but the large amount of centrarchid biomass that flathead catfish consumed in my research supports the hypothesis that introduced flathead catfish negatively impact native redbreast sunfish populations due to direct predation (Bart et al. 1994; Ashley and Rachels 1998; Herndon and Waters 2000). Based on ecosystem simulation modeling, Pine et al. (2007) projected that once flathead catfish were introduced into a system, the native apex predators showed the greatest response due to increased competition for food. In the section of Deep River where my research was conducted, largemouth bass are the native apex predator, and even though they were not consumed in large quantities, they indirectly compete for food resources with flathead catfish. Bluegills are a dominant prey item for largemouth bass (Cochran and Adelman 1982; Olson and Young 2003), and my findings along with other reports (Weller and Robbins 1999; Herndon and Waters 2000; Pine et al. 2005) demonstrate that sunfish are also dominant prey for introduced flathead catfish. Further, my results according to fish size (Figure 5) suggest that as flathead catfish increase in size, so does the competition for these sunfish. This large consumption of an important forage fish indirectly affects other native predators by reducing the amount of food available in the system, further exemplifying the negative impacts of introduced flathead catfish. Crayfish are also a shared resource between native largemouth bass and introduced flathead catfish, with similar indirect competitive pressure (Lewis et al. 1974; Olson and Young 2003). Increased competition for food sources could result in the decreased health and status of native predator populations.

In addition to important sport fishes, rare and imperiled native fish species may be impacted by introduced flathead catfish. These introduced apex predators inhabit the same waters as a number of threatened and endangered fish species. In my research, flathead catfish selected against Cyprinidae or Catostomidae even though they were abundant in the system, decreasing concerns of direct predation on the Cape Fear shiner and Carolina redhorse. However, previous studies demonstrated that flathead catfish feed on members of both these families with varying intensity (Guier et al. 1981; Ashley and Buff 1987; Quinn 1987; Pine et al. 2005). Cyprinid fishes were generally abundant in the Deep River system (Table 1), but the low representation in flathead catfish diets could be related to use of different microhabitats. These species overlaped habitat in the unimpounded reach during the flathead catfish spawning season when feeding was decreased. For deeper waters, Cyprinidae generally inhabit shallow habitat, whereas flathead catfish occupy deep benthic microhabitat. Catostomidae ranked among the most abundant among available fishes for all sites and seasons (Table 1), but were also negatively selected by flathead catfish. Both of these species share benthic microhabitats, and thus, it is unclear why flathead catfish did not consume this family more as a food source.

My findings support those of Quinn (1987) that identified darters as one of the first fish species that flathead catfish feed upon as juveniles. As flathead catfish increase in size, the use of darters as food decreases, but biologists monitoring imperiled darters that co-exist with flathead catfish should be concerned about predation effects. Juvenile flathead catfish are found in microhabitats similar to those of darter species and are not excluded from habitat that darters usually use as protection, such as shelter under large rocks (Schlosser 1987; Chipps et al. 1994; Irwin et al. 1999). Snails and the Asian clam *Corbicula* were most likely incidental prey items that were consumed when feeding on other benthic prey, as all snails and Asian clams were found in stomachs that also contained crayfish and darters.

Quantifying a predator's selection of prey relative to its abundance in the environment is essential information when studying predator-prey interactions (Lechowicz 1982). I used a selectivity index to quantitatively describe the relative vulnerability among prey fish families to flathead catfish predation. Quantifying the diet alone elucidates sources of prey and population effects on native species, but does not convey information on feeding preferences or relative vulnerability of prey. Of the previous investigators that analyzed the diet of introduced flathead catfish (Guier et al. 1981; Ashley and Buff 1987; Quinn 1987; Weller and Robbins 1999; Herndon and Waters 2000; Pine et al. 2005), only one quantified selectivity of specific prey taxa by flathead catfish in their introduced ranges (Pine et al. 2005). The results of my study and those reported by Pine et al. (2005) both showed that flathead catfish, in both the piedmont and coastal regions, only displayed a positive selectivity for benthic fish species. When I analyzed the overall diet, the impact to Centrarchidae is evident by the large amount of biomass consumed by flathead catfish, but the mechanisms for this intensive predation are not clear. My selectivity analysis of flathead catfish feeding shows the high availability of this family in the Deep River and a corresponding high abundance in the flathead catfish diet (Table1) but not a strong or consistent selection (Figure 7), suggesting that flathead catfish opportunistically feed on prevalent prey items, but this trend in feeding is not consistent among less prevalent prey taxa. For example, in the impounded reach the second most abundant prey family was Cyprinidae, which did not occur in the flathead catfish diet, and the second most prevalent item in the flathead catfish diet was Percidae, a relatively rare taxon in availability. One hypothesis that could explain this finding is that flathead catfish may exploit the most abundant prey taxa in any microhabitat, but pursue less abundant prey only in the benthic microhabitats that they occupy.

I found that flathead catfish positively selected other prey species that shared their benthic microhabitat. Positive selectivity for benthic fishes was also documented by Pine et al. (2005), who found positive selectivity by flathead catfish in coastal rivers only for Ictaluridae and Soleidae, both benthic species. This positive selectivity for benthic species may partially explain observed decreases in native catfish populations following introduction of flathead catfish (Guier et al. 1981; Thomas 1993; Bart et al. 1994; Weller and Robbins 1999). Thomas (1993) found that bullhead populations were nearly extirpated after the introduction of flathead catfish, but these conclusions were based on correlative evidence, and no diets were examined. The positive selection of ictalurids in both my study and Pine et al. (2005) suggests that bullhead species are more vulnerable to predation by flathead catfish, and this vulnerability could lead to the observed negative impacts at the population level.

Flathead catfish are reported to display both crepuscular and nocturnal patterns in feeding (Minckley and Deacon 1960; Quinn 1987). However, my results did not show a distinct crepuscular or nocturnal pattern in feeding during July or August (Figure 8). During July, flathead catfish fed continuously throughout the day, but none of the peaks occurred during time intervals immediately preceding or following dusk and dawn, but a single, prolonged peak in feeding occurred during the night between 0:00 and 4:00 hours. Flathead catfish also fed throughout the 24-h period in August, with only one peak in feeding, and it occurred mid-day. Radio telemetry studies that have examined the diel movement of flathead catfish report increased activity during dusk, night, and dawn (Daugherty and Sutton 2005; Malindzak 2006). I found slight peaks in feeding during both months between 0:00 and 4:00 hours that could be associated with increased nocturnal movement, but most peaks in feeding found during my study occurred during daylight hours, a time of little to no movement in radio telemetry studies. Flathead catfish are opportunistic feeders, and feeding could be affected by diel habitat use and activity patterns of prey items, but I detected no obvious pattern in prey taxa that were consumed during peaks in feeding for July or August that would attribute these peaks to prey behavior (Figure 9). One contributing factor to the varying patterns in feeding between July and August may be reproductive seasonality. Malindzak (2006) found that flathead catfish spawning in the Deep River concluded in June. Thus, post-spawning condition of individuals and related behaviors associated with activity and feeding may affect the July diel feeding pattern and intensity, relative to that in August. The increase in mean stomach fullness and daily ration from July to August is in accord with reports of increased feeding after the spawning period for this species (Turner and Summerfelt 1970; Layher and Boles 1980).

I calculated daily ration for introduced flathead catfish to determine nutritional requirements of this apex predator and to compare them to those of other fish species. The daily ration estimates that I calculated for flathead catfish were similar to those estimated for largemouth bass (Cochran and Adelman 1982), the native apex predator of my study site. Cochran and Adelman (1982) estimated largemouth bass daily ration with a mean range of 1.67 and 4.52 % in the month of July, and this range encompasses the daily ration that I calculated for flathead catfish in July of 3.06 % (Table 3). During August, their mean range for daily ration estimates of largemouth bass did not vary much from July (1.13-5.58 %), whereas daily ration for flathead catfish greatly increased to 7.37 %. However, the daily ration that I calculated for flathead catfish during August was less than the greatest daily ration of 9.48% calculated for largemouth bass. Temperatures during Cochran and Adelman's (1982) August sampling (25ºC) were similar to those during my August sampling (27ºC).

Another introduced catfish to the piedmont rivers of North Carolina is the channel catfish. Channel catfish in a riverine environment were reported to have a daily ration of 5-10 % (Kwak et al. 1992), while Vigg et al. (1991) estimated channel catfish daily ration in lentic environments as 10-16 %. These daily ration estimates for channel catfish were calculated during the same months as those of my study under generally similar temperature regimes (26ºC , Kwak et al. 1992; 22-26ºC, Vigg et al. 1991), and in both environments the omnivorous channel catfish required a greater daily ration than the carnivorous flathead catfish. The daily rations that I estimated for introduced flathead catfish will serve to better understand the impacts that this fish has on the available prey biomass and are important when analyzing food-web dynamics. My estimates may also be used to incorporate into bioenergetics models and to better inform aquaculturists of the amount of food needed to sustain this fish.

Summary and Management Implications

The ecological impacts of introduced flathead catfish are a valid and serious resource management concern. Flathead catfish in the upper Cape Fear River drainage consume large amounts of sunfish biomass, a family that supports a popular, local sport fishery and serves as important forage for native predators. The co-existence of flathead catfish and imperiled species is also an important management issue. My results support and strengthen the assertion of Malindzak (2006) that due to minimal overlap in microhabitat use between the flathead catfish and Cape Fear shiner, there is reduced risk of direct predation by flathead catfish. Due to the increased vulnerability to flathead catfish, managers should be concerned with species that inhabit similar benthic microhabitats as the flathead catfish, such as native darters and catfish species that exhibit a positive selectivity in flathead catfish feeding. The diel pattern varied between months, and impacts to prey communities will be greater in August when the daily nutritional requirement of the flathead catfish exceed 7% of its body weight.

Related research by Pine et al. (2005) and my study are the only research efforts that analyzed the diet selectivity of introduced flathead catfish, but my research expanded upon and differed from that of Pine et al. (2005) in a number of ways. The two studies were conducted in different physiographic regions of North Carolina, in which the flathead catfish sampled had access to different prey bases. There were marine influences in the coastal rivers sampled by Pine et al. (2005) that flathead catfish in my study did not encounter upstream of a series of dams, including a marine prey base and varying salinity. Unlike the coastal river sites, my study was conducted on a river system that was closed on both ends by dams; therefore, I was able to better estimate prey availability, because neither flathead catfish nor their prey were able to migrate into or from the study site. I was able to expand upon the selectivity of introduced flathead catfish by more than doubling the sampling sizes used to analyze coastal rivers, increasing the accuracy and resolution when examining selectivity of flathead catfish in the piedmont rivers of North Carolina. I also determined patterns in diel feeding chronology, and estimated evacuation rate and daily ration, that improved our understanding of the trophic relations of introduced flathead catfish.

My research findings build on previous investigations of negative impacts of introduced flathead catfish on native fish communities by further elucidating some of the mechanisms of the predator-prey relationships associated with these impacts. Natural resource managers can use this information to better understand how introduced flathead catfish are affecting fish assemblages in their region and plan management steps that may be implemented. The trophic impacts of the flathead catfish are relevant to dam removal or construction projects, because removal of a dam could facilitate dispersal of flathead catfish to areas supporting imperiled species and native sport fish populations; but removal would also decrease the amount of impounded habitat that is the most suitable for flathead catfish (Malindzak 2006). Understanding the trophic relations of introduced flathead catfish and the degree of vulnerability among prey taxa will allow resource managers to make science-based decisions that may decrease the impacts of introduced flathead catfish on native fish populations and allow enhanced protection for those imperiled species.

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Table 1.—Rank by number of fish taxa identified in the flathead catfish diet and population estimates of fish prey available in the unimpounded and impounded reaches of the Deep River, North Carolina, during spring and fall. Blanks represent prey taxa that were not detected in the diet or availability sampling.

	Unimpounded reach				Impounded reach			
	Spring		Fall		Spring		Fall	
Family or genus	Prey rank	Availability rank	Prey rank	Availability rank	Prey rank	Availability rank	Prey rank	Availability rank
Anguillidae	4							
Catostomidae		3	3	2		4	4	4
Clupeidae	4			7	4	5	4	5
Cyprinidae		6		1	4	2		2
Gadidae		8		9				
Ictaluridae	3	4		4	3	6	3	
Lepisosteidae		2		6		6		
Lepomis sp.	2	1	2	5	1	1	1	1
Micropterus sp.		7	2	8	4	3	3	3
Moronidae				9				
Percidae	1	5	1	3	2		2	6

Table 2.—Population estimates (± SE) calculated for prey fish availability in the unimpounded and impounded reaches of the Deep River, North Carolina, during the fall of 2004 and spring of 2005.

	Fall 2004		Spring 2005	
Family and species	Unimpounded	Impounded	Unimpounded	Impounded
Catostomidae				
Brassy jumprock	298.0 (± 417.3)		81.9 (± 25.4)	
Carolina redhorse		1.0	2.0	
Notchlip redhorse	77.2 (± 55.4)		39.6 (± 16.8)	2.0
Shorthead redhorse	51.0		42.4 (± 0.3)	1.0
Spotted sucker	6.9 (± 1.5)	3.0 (± 2.8)	5.6	2.0 (± 1.7)
V-lip redhorse	27.6 (± 16.8)		17.1 (± 24.4)	0.5 (± 0.0)
Centrarchidae				
Black Crappie	1.0			
Bluegill	6.0	185.2 (± 45.8)	3.3	423.5 (± 409.6)
Green sunfish		1.0		1.0
Largemouth bass	8.3 (± 3.0)	8.3 (± 5.3)	5.9	15.4 (± 8.5)
Redbreast sunfish	60.9 (± 113.0)		466.6 (± 2,487.6)	
Redear sunfish		2.0	0.6	0.5 (± 0.0)
Warmouth		1.0		
White crappie				1.0
Clupeidae				
Gizzard Shad	13.3 (± 16.8)	4.0		4.0
Threadfin shad		2.0		
Cyprinidae				
Bluehead chub	539.9 (± 3,341.4)		20.1 (± 3.0)	
Cape Fear shiner	2.2 (± 0.4)			
Comely shiner	3.0	10.5 (± 4.0)	1.7	12.4 (± 4.6)
Common carp		2.0		3.0
Coastal shiner		9.0 (± 1.2)		9.0
Golden shiner		0.5		1.0
Grass carp		1.0		
Highfin shiner	3.0		0.6 (± 0.0)	
Sandbar shiner	1,258.7 (± 1,063.1)	6.5 (± 1.6)	58.9 (± 5.0)	
Satinfin shiner	1.0			
Spotfin shiner			1.1 (± 0.0)	

Table 2.—Extended.

	Fall 2004		Spring 2005	
Family and species	Unimpounded	Impounded	Unimpounded	Impounded
Spottail shiner	301.1 (± 335.2)	5.0	30.1 (± 3.6)	
Swallowtail shiner	5.4 (± 0.5)		16.1 (± 11.1)	
White shiner	3.0		11.3 (± 0.3)	
Whitefin shiner	2.1		2.22 (± 0.4)	
Cyprinodontidae				
Speckled killifish	1.0		1.22 (± 0.4)	
Ictaluridae				
Channel catfish	2.0		7.0	1.0
Flat bullhead	1.13 (± 0.4)		1.0	
Flathead catfish				0.5 (± 0.0)
Margined madtom	97.8 (± 32.2)		147.1 (± 171.7)	
Snail bullhead	21.0		22.3 (± 2.2)	
Piedmont darter	177.6 (± 74.0)	0.5	58.7 (± 20.1)	
Lepisosteidae				
Longnose gar	54.0		242.8 (± 1,231.7)	2.0
Moronidae				
White perch	1.0			
Percidae				
Fantail darter	23.1 (± 2.1)		13.3 (± 2.0)	
Tessellated darter	57.4 (± 23.1)		74.3 (± 22.5)	

Table 3.─ Summary statistics from four diel feeding samples for flathead catfish during July and August 2005, and July and August 2006, from the upper Cape Fear River drainage in North Carolina. Results for July 2005 and 2006 were combined, as were those results for August 2005 and 2006, based on similar environmental conditions.

Statistic	July	August
Total number of fish sampled	199	235
Mean TL (mm) (± SE)	321.8 (± 14.0)	340.7 (± 13.9)
Mean weight (g) (± SE)	933.2 (± 139.0)	1,165.1 (± 173.4)
Empty stomachs (%)	58.4	59.3
Mean fullness (g/100g) (± SE)	0.32 (± 0.06)	0.52 (± 0.14)
Gastric evacuation rate (/h)	0.40	0.59
Daily ration (%)	3.06	7.37

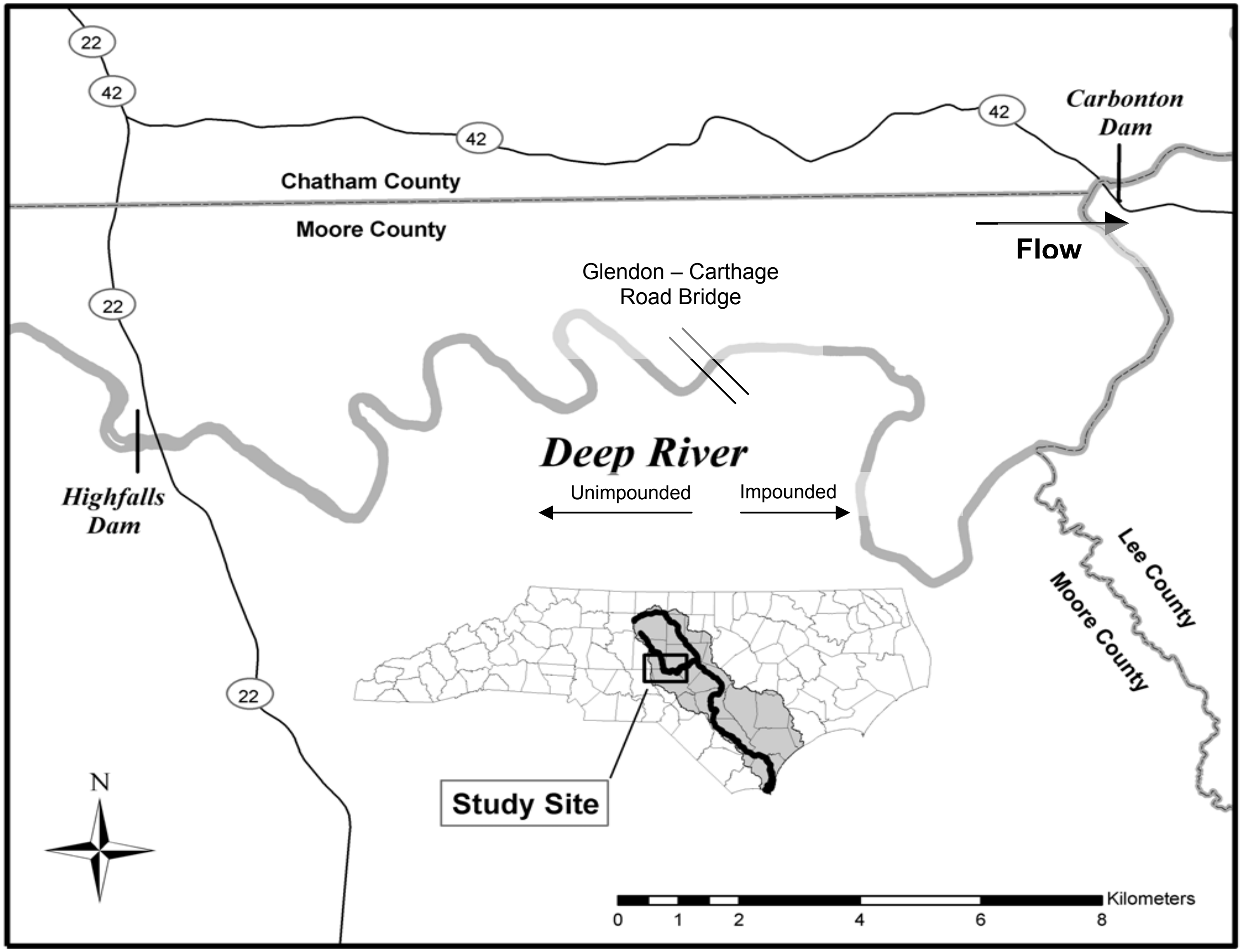


Figure 1.— Map of study site for sampling trophic relations of introduced flathead catfish on the Deep River, North Carolina.

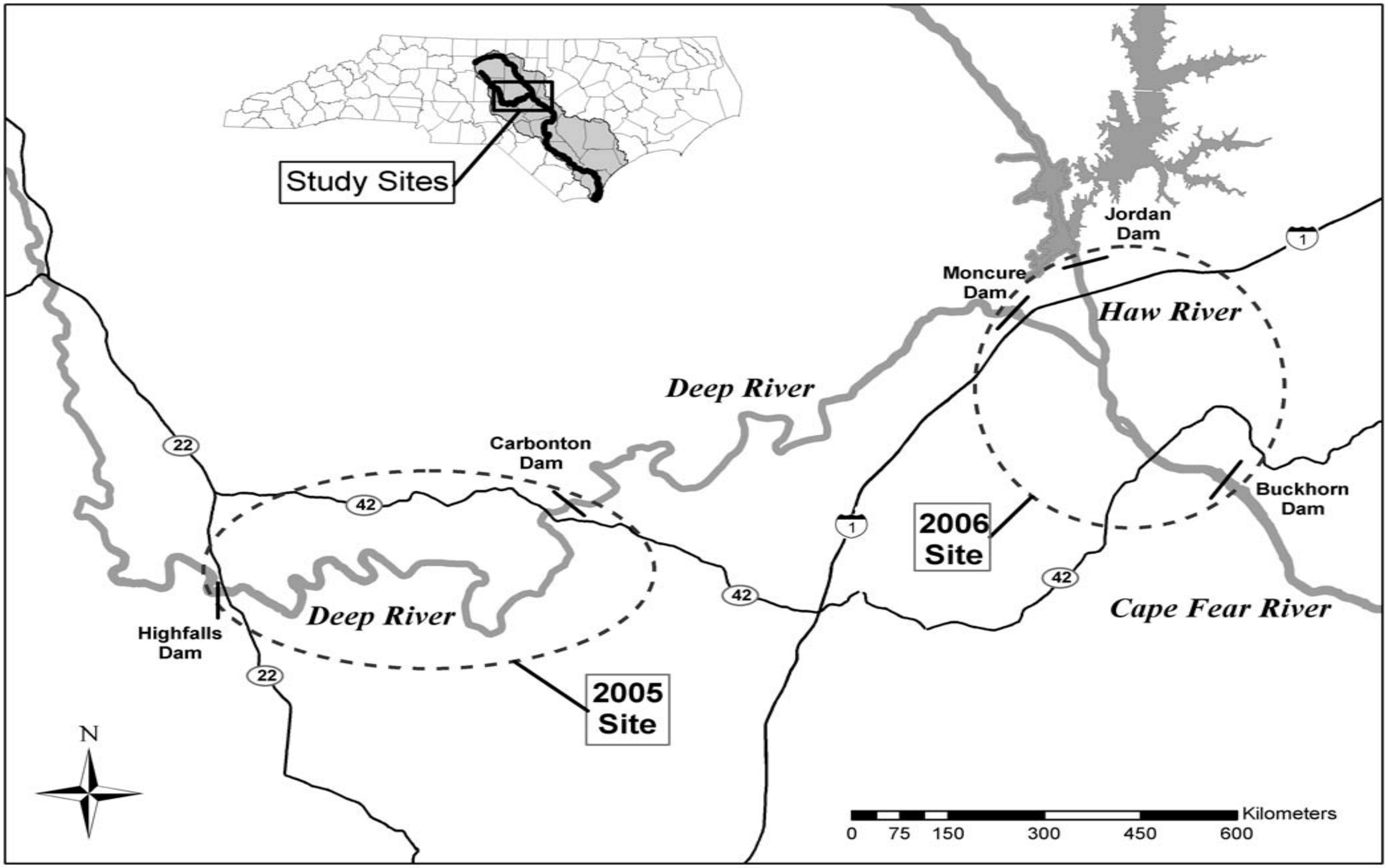


Figure 2.— Study site for analysis of diel chronology and daily ration of flathead catfish in the upper Cape Fear River drainage, North Carolina.

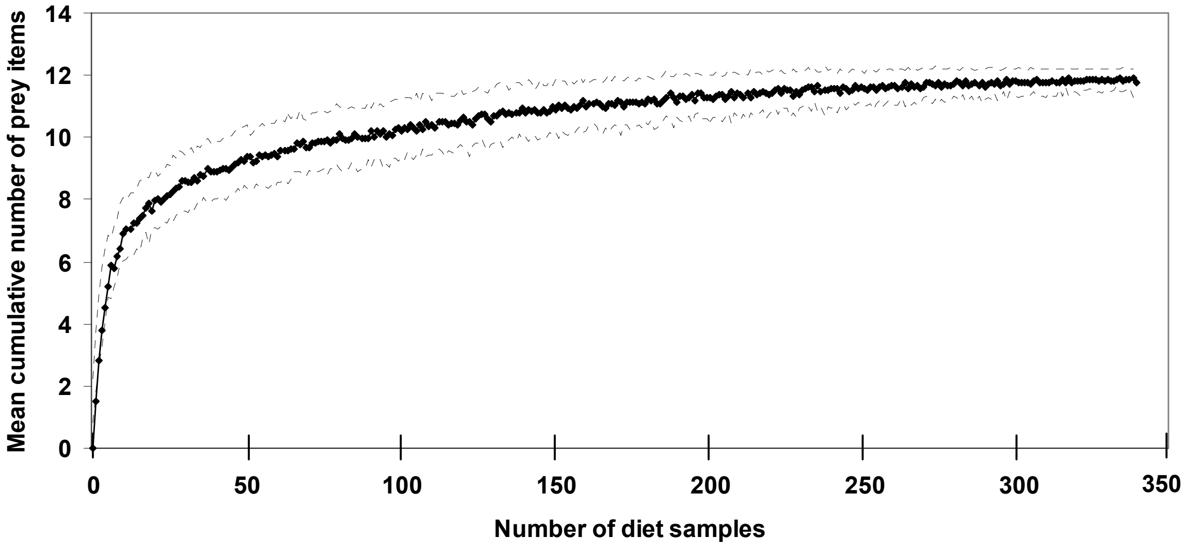


Figure 3.—Randomized cumulative prey curves for flathead catfish (N = 338 diet samples) collected from the Deep River, North Carolina, May to September 2005. Broken lines represent standard deviation values about the mean.

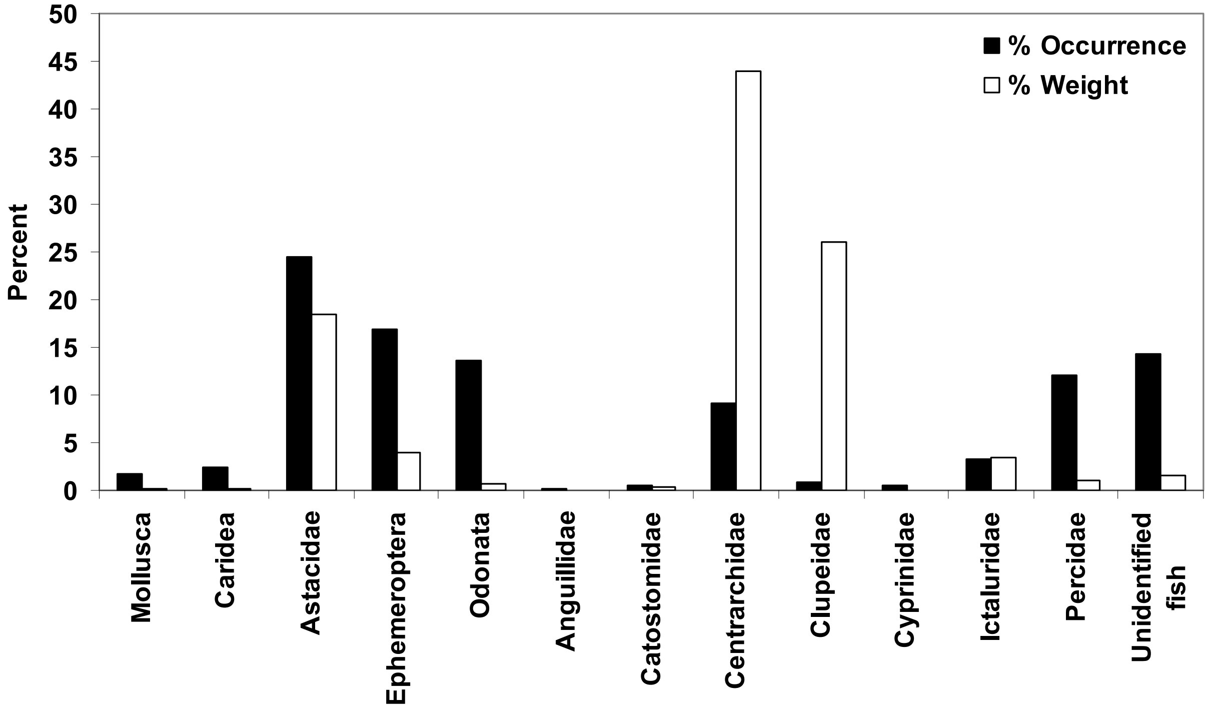


Figure 4.—The percent frequency of occurrence and percent composition by weight of prey taxa in flathead catfish diet (*N* = 338) collected May to September 2005, from the Deep River, North Carolina.

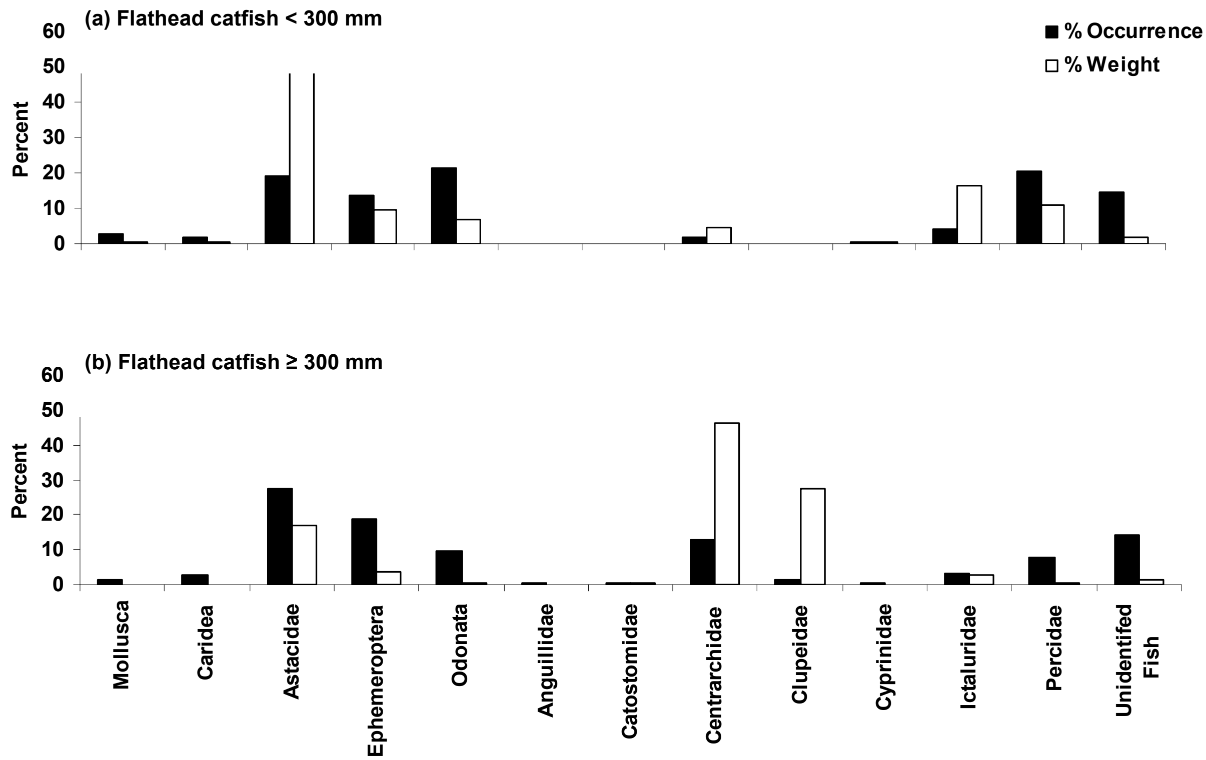
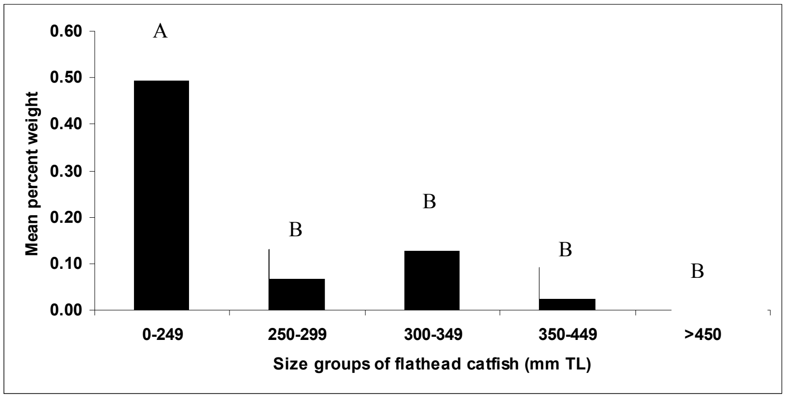
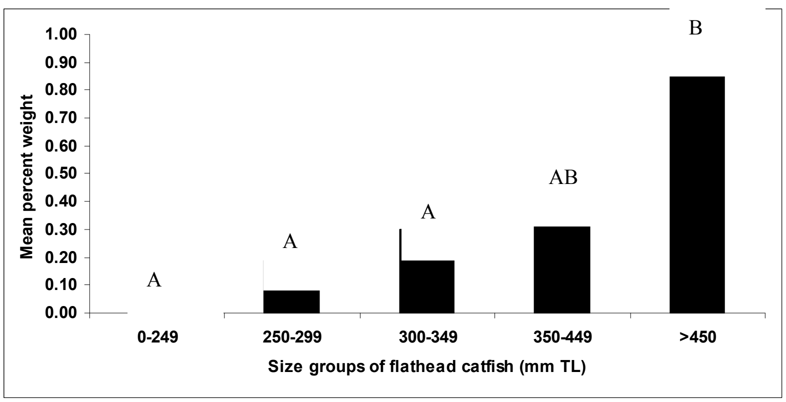


Figure 5.—Percent frequency of occurrence and percent composition by weight of prey taxa in the diet of flathead catfish (a) less than 300 mm in total length (*N* =125) and (b) greater than or equal to 300 mm in total length (*N* = 213) collected May to September 2005, from the Deep River, North Carolina. Astacide, Odonata, Centrarchidae, Ictaluridae, and Percidae all had sufficient data for comparison, but only Odonata, Centrarchidae and Percidae showed a significant treatment effect of flathead catfish length on occurrence in the diet.

(a) Odonata, ANOVA *F* = 12.01, *P* = 0.0001



(b) Centrarchidae, ANOVA *F* = 6.57, *P* = 0.0025



(c) Percidae, ANOVA *F* = 4.13, *P* = 0.0174

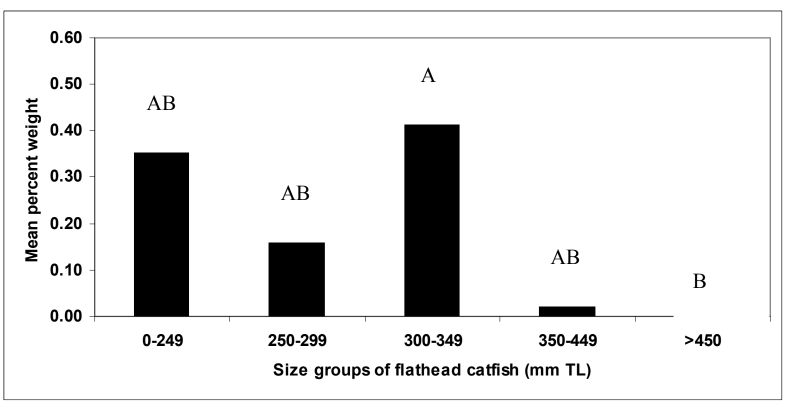


Figure 6.— Results of the two-factor ANOVA and Tukey's multiple contrast test performed on prey taxa with a significant treatment effect of flathead catfish length on percent-composition-by-weight of the diet. Size groups with common letters are not significantly different.

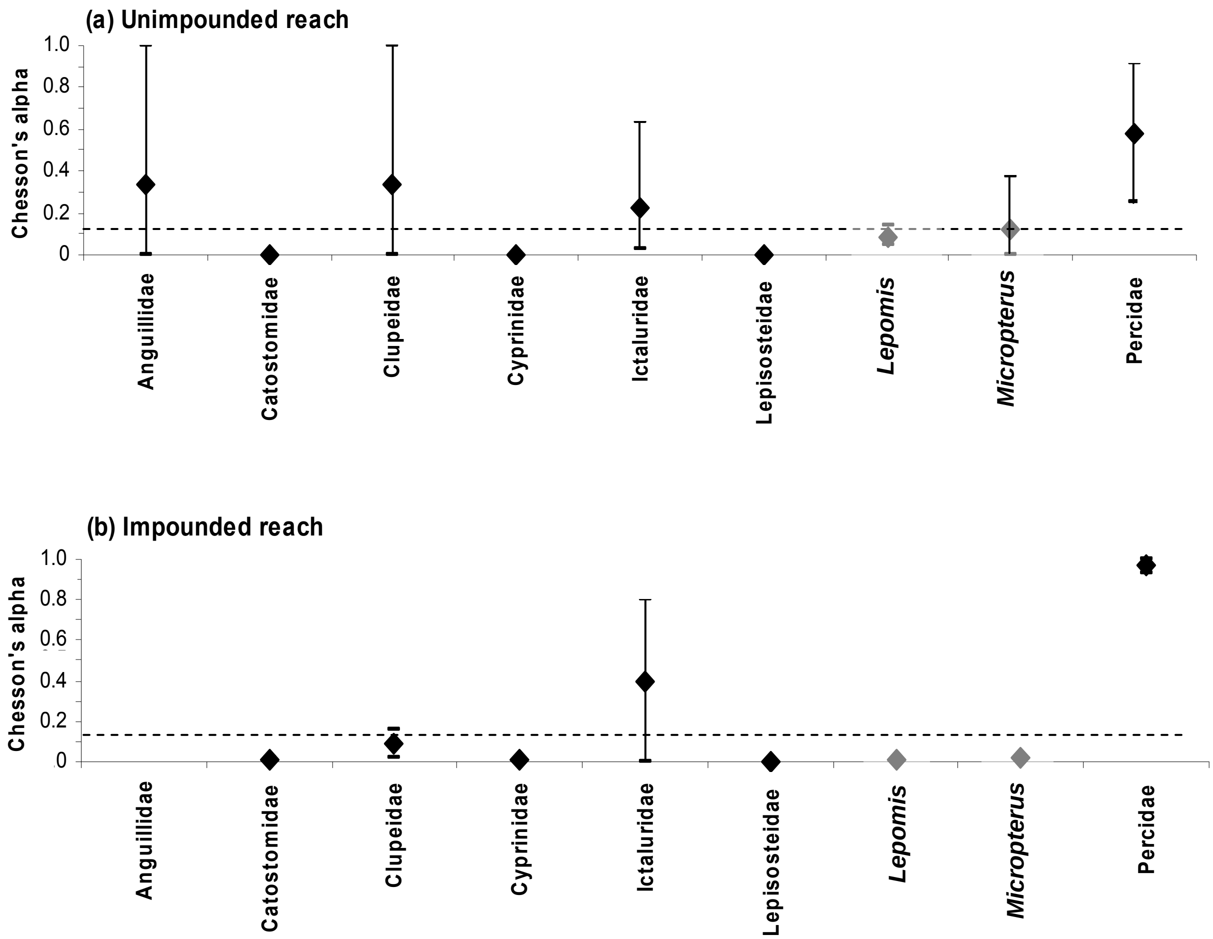


Figure 7.— Mean Chesson's alpha index of selectivity for prey taxa found in the diet of flathead catfish (N = 338) collected May to September 2005, from the (a) unimpounded and (b) impounded study reaches of the Deep River, North Carolina. Error bars represent the range of values among three population-level estimates during fall 2004 and spring 2005 in the unimpounded reach and two population-level estimates during fall 2004 and spring 2005 in the impounded reach. The horizontal dashed lines represent neutral selectivity ($1/m$, where m is the total number of prey categories). A value above this line indicates positive selectivity for a particular prey taxon, a value below this line indicates negative selectivity. Taxa without values were not available as prey during the respective season within the reach.

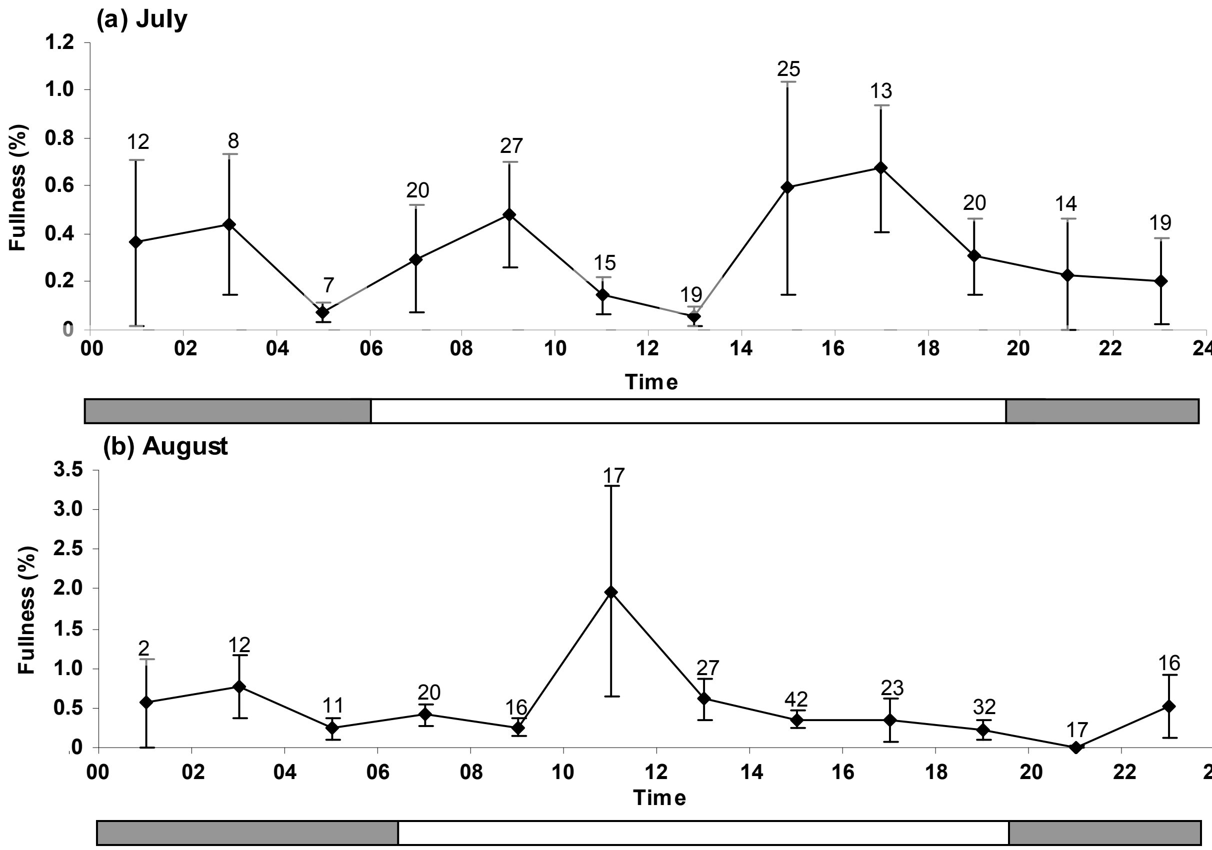


Figure 8.─Diel feeding chronology of flathead catfish from the upper Cape Fear River drainage, North Carolina, as determined from changes of stomach fullness (mean fullness ± SE) over a 24-h period during (a) July (N = 199) and (b) August (N = 235) of 2005 and 2006. Number of observations is indicated above the error bars. Open and solid portions of horizontal bars represent daylight and night hours, respectively.

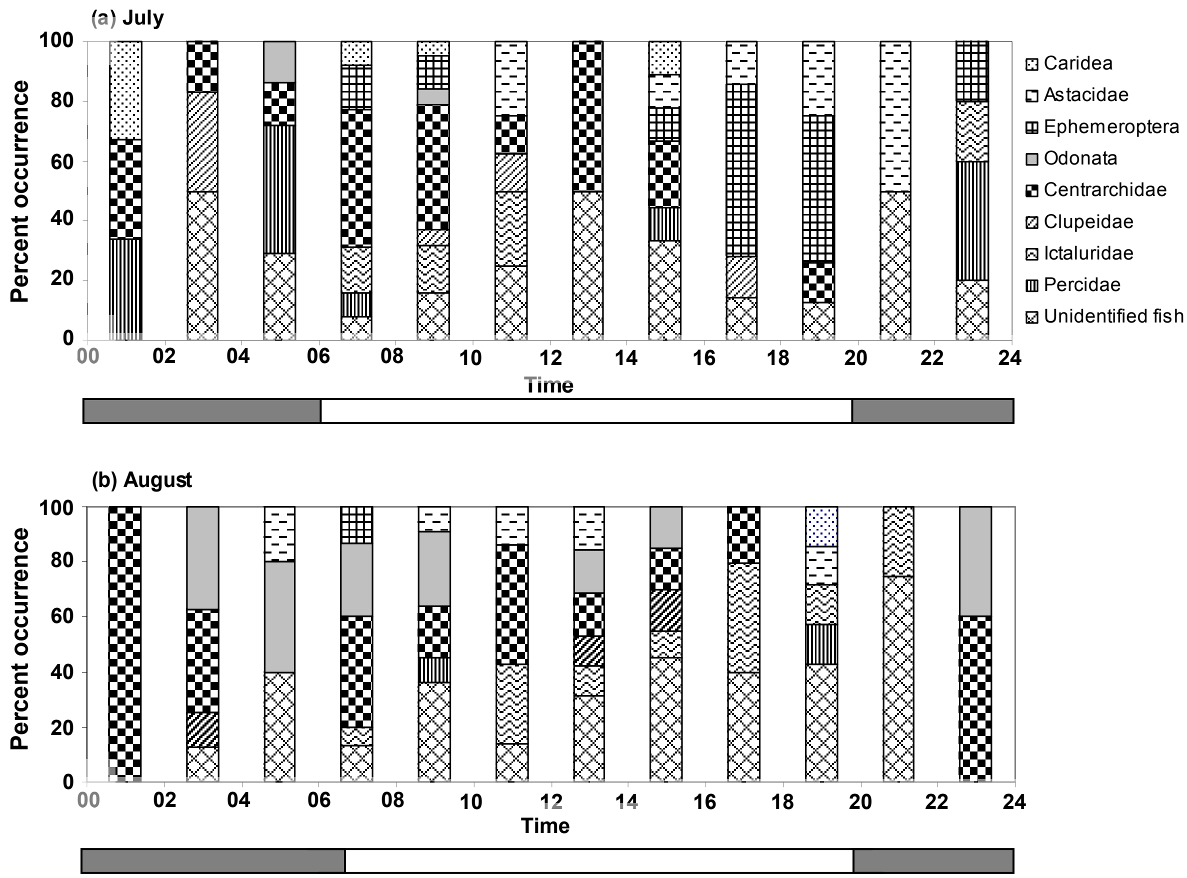


Figure 9.— Percent occurrence of prey taxa in the flathead catfish diet for each 2-h time interval during diel sampling in (a) July and (b) August of 2005 and 2006 on the upper Cape Fear River drainage of North Carolina. Open and solid portions of horizontal bars represent daylight and night hours, respectively.

Chapter II – Prey selection dynamics of two introduced catfish species: a tethering experiment.

Introduction

Flathead catfish *Pylodictis olivaris* and channel catfish *Ictalurus punctatus* are two large ictalurids that have been widely introduced across the United States (Etnier and Starnes 1993; Jenkins and Burkhead 1994). Introductions are the result of anglers' desire to create new fisheries in their local systems or by agency stockings; such introductions have raised ecological issues that require the attention of resource managers (Hubert 1999; Jackson 1999). A primary concern of these introductions is the impact that predation by flathead catfish, an obligate carnivore, and channel catfish, a generalist omnivore, could have on native fish communities (Hubert 1999; Jackson 1999).

The flathead catfish is a large and long-lived obligate carnivore that has been widely introduced beyond its native range (Jackson 1999). It is the second largest ictalurid, with total lengths ranging up to 900 mm and weights exceeding 45 kg (Jenkins and Burkhead 1994; Jackson 1999). The maximum age reported for an introduced flathead catfish in a riverine system is 17 years (Kwak et al. 2006), but estimates in their native range exceed 25 years (Nash and Irwin 1999). During early stages of life flathead catfish are invertivores, relying on aquatic insects and crayfish for food, but as they mature and grow they become primarily piscivorous (Layher and Boles 1980; Jackson 1999; Pine 2003).

The flathead catfish is native to the southern Great Lakes region, as well as the Mississippi, Mobile, and Rio Grande river drainages, but the desire of anglers to pursue a big-game catfish in their local system that is aggressive, can to reach large sizes, and has a good flavor to its flesh, has resulted in both legal and illegal introductions of this fish outside of its native range (Jenkins and Burkhead 1994; Jackson 1999). Flathead catfish were first introduced to the Atlantic Slope region of the United States in the Flint River of southern Georgia about 1950, and introductions range as far north as the Deleware and Susquehanna rivers in eastern Pennsylvania (Quinn 1987; Fuller et al. 1999; Jackson 1999; Brown et al. 2005). Attitudes among biologists, resource managers, and anglers about this introduced species vary because of the flathead catfish's value as a sport fish and its ability to alter native fish communities and traditional fisheries (Jackson 1999). Invasive flathead catfish have been considered one of the most ecologically harmful introductions in the United States (Fuller et al. 1999; USFWS Memorandum dated 3 November 1999).

Once introduced into a system, flathead catfish rapidly establish populations and expand throughout the system (Guier et al. 1981; Ashley and Buff 1987; Thomas 1993). The first known introduction of the flathead catfish in North Carolina was into the Cape Fear River in 1966, when 11 adults with a combined weight of 107 kg were released near Fayetteville, North Carolina (Ashley and Buff 1987). Within 10 years flathead catfish became established, expanded its range to inhabit 200 km of the mainstem Cape Fear River, and dominateed the food web as an apex predator within the system (Guier et al. 1981; Ashley and Buff 1987). Guier et al. (1981) believed that the flathead catfish would have expanded its range in the Cape Fear River even further if not hampered by physical obstructions, such as dams, and the presence of saline water.

Introductions of flathead catfish have raised concern among river ecologists and fisheries managers because of the possible negative effects to native fish communities (Guier et al. 1981; Thomas 1993; Bart et al. 1994; Ashley and Rachels 1998; Weller and Robbins 1999). The greatest impact to native fish populations is reported to occur shortly after flathead catfish have been introduced into a system (Ashley and Buff 1987; Thomas 1993; Jackson 1999; Kwak et al. 2004). Thomas (1993) reported that the introduction of this species resulted in the near eradication of bullhead *Ameiurus* spp. populations in the Altamaha River system of Georgia, and that this severe decline in bullhead populations may have shifted the flathead catfish diet to the redbreast sunfish *Lepomis auritus,* which also subsequently experienced a population decline. Species that have become targets of direct predation by introduced flathead catfish include the silver redhorse *Moxostoma anisurum,* robust redhorse *Moxostoma robustum* and most ictalurids and sunfish species *Lepomis* (Guier et al. 1981; Thomas 1993; Bart et al. 1994; Ashley and Rachels 1998; Weller and Robbins 1999; Pine et al. 2005). Guier et al. (1981) concluded the decline in bullhead and channel catfish populations in the Cape Fear River of North Carolina was likely a result of predation by the flathead catfish. Food-web simulation modeling by Pine et al. (2007) projected declines of up to 50% in the biomass of native fish groups after the establishment of introduced flathead catfish. In contrast, several investigators could detect no adverse impact on native fish populations despite an increase in flathead catfish predation (Ashley and Buff 1987; Quinn 1987). Ashley and Buff (1987) found that centrarchids made up only a small proportion of the flathead catfish diet, suggesting that the increased concerns among local anglers over the decrease in sunfish populations could not be attributed to flathead catfish predation. However, the abundance and availability of centrarchids were not reported in their assessment.

These reports of negative impacts to native fish communities due to flathead catfish introductions have been based entirely on correlative evidence. The linear decline of ictalurid and centrarchid populations in river systems has been attributed to expanding populations of introduced flathead catfish (Guier et al. 1981; Thomas 1993; Ashley and Rachels 1998) when a suite of concomitant biotic and abiotic factors could also be contributing to decline of native fish communities (Pine et al. 2005). Thomas (1993) surmised that the eradication of native bullhead populations caused a shift in the diet of introduced flathead catfish to native redbreast sunfish. However, whether this direct shift was a result of flathead catfish altering their feeding microhabitat selection or a switch in specific prey species is not known.

The channel catfish is another large catfish that has been introduced widely beyond its native range. Channel catfish also attain large sizes, exceeding 530 mm in length and 23 kg (Etnier and Starnes 1993). However, the introduction of this species is of less concern to ecologists and managers, relative to that of the flathead catfish, because the channel catfish is an omnivore. This is evident by widespread supplemental stocking of channel catfish for fishery enhancement when recruitment is low in lentic environments (Hubert 1999). The channel catfish typically inhabits warmwater rivers and reservoirs and is associated with a variety of substrates, but generally found in pools that provide some sort of cover (Etnier and Starnes 1993; Jenkins and Burkhead 1994). Channel catfish are generalist feeders, consuming prey items in proportion to their availability, and they concentrate in areas where food is abundant (Hubert 1999). The exact natural range of this catfish is unclear, but it is known to include all central drainages of the United States from the Great Lakes and Mississippi basins to the Gulf slope (Etnier and Starnes 1993; Jenkins and Burkhead 1994). The native range of channel catfish is believed to encompass some of the eastern Atlantic slope drainages, but this does not include the piedmont region and coastal regions of North Carolina, South Carolina, or Virginia (Etnier and Starnes 1993).

There is a need for, but lack of, experimental evidence to determine what mechanisms of the predator-prey relationship control predation events of large introduced catfishes. Tethering experiments have been conducted with other species in both freshwater and marine environments to elucidate mechanisms associated with feeding and to estimate predation risk in a natural environment, while retaining control of some factors associated with predation. The change in predation risk associated with varying degrees of depth, cover, habitat, and water quality have all been estimated in tethering experiments (Gregory and Levings 1998; Post et al. 1998; Linehan et al. 2001; White and Harvey 2001; Laurel et al. 2003).

In this study, I conducted tethering experiments to estimate how environmental and biotic factors affect the predation risk of prey fishes by introduced flathead catfish and channel catfish in a piedmont river system in North Carolina. With most previous tethering experiments, the overall predation risk was measured by presence or absence of tethered prey items with little emphasis or data on the predator, but in this study, I estimated predation risk associated with two specific predators. My objective was to conduct field experiments to elucidate the mechanisms of the predator-prey relationship by determining preferences of introduced flathead catfish and channel catfish feeding as a function of prey species, the prey's location in the water column, and accessibility to cover.

Methods

Site Description

This research was conducted on an impounded section of a river system in the piedmont region of North Carolina (Figure 1). The study site was located at the confluence of the Deep and Haw rivers, where the Cape Fear River is formed in Chatham and Lee counties. Experiments were conducted in the section of the Deep River downstream of Moncure Dam, the section of the Haw River downstream of Jordan Dam, and on the Cape Fear River upstream Buckhorn Dam, during the summer of 2006. The study site is approximately 16 km east of Sanford, North Carolina, and 275 km from the mouth of the Cape Fear River.

Estimates of Predation Risk

Tethers were constructed and deployed to determine prey selection and associated factors of introduced catfishes in the upper Cape Fear drainage from 16 May to 11 October 2006. Each tether line was constructed using 6.4-mm rope that was weighed down at eight points by bricks that were placed 3.0 m apart from each other. At each brick, an experimental unit with a treatment corresponding to the combination of three factor settings was attached. Each treatment combination was randomly assigned where it would be placed along the tether, but each treatment was equally represented within a tether line. Units were made from braided nylon rope and suspended upward into the water column with floats. A 0.5-m length of the 3-mm rope was attached on one side to three-way swivels located on each unit, and circle hooks (size 6/0) were attached on the terminal end to tether prey fish.

Tethers and prey were deployed and allowed to soak overnight, and a series of three factors, corresponding to eight treatment combinations, were tested to quantify large catfish predators' feeding preferences. The first factor was a choice of two live prey fishes, redbreast sunfish or snail bullhead *Ameiurus brunneus*, two native fishes reported to be negatively affected by the introduction of flathead catfish (Guier et al. 1981; Thomas 1993; Bart et al. 1994; Ashley and Rachels 1998; Weller and Robbins 1999). These prey items were collected using a boat-mounted electrofisher in the upper Cape Fear River drainage where the Haw River flows into Jordan Lake and were then transported the same day to the study site farther downstream on the Cape Fear River. We selected size 6/0 modified circle hooks to tether prey items, as they were among the most effective hooks for sampling flathead catfish (Arterburn and Berry 2002). Prey items were tethered through the muscle tissue at a location slightly behind the dorsal fin (Gregory and Levings 1998; Linehan et al. 2001; Laurel et al. 2003). The other two test factors were included to determine habitat-specific predation risks by (a) placing the prey items at two distances from the river bottom, either 0.6 m or 1.8 m, and (b) allowing for presence or absence of artificial cover. Cover was located above the prey item at a location where it could be easily accessed and was provided by attaching a flexible, corrugated pipe that was large enough for the tethered prey fish to comfortably swim into and was sealed on one end to avoid tangling.

Data on placement of treatment combinations, prey size, and predators sampled were collected for all tethers. When tethers were deployed, the order of treatments along the line was recorded, as well as the total length (± 1 mm) of each prey item. Location in the river, time, and date were noted when the tethers were deployed and collected. As the tethers were collected, presence or absence of flathead catfish or channel catfish was recorded for each unit along with total length (± 1 mm) and weight (± 1 g) for flathead catfish and channel catfish sampled. The presence or absence of prey items was recorded for each unit, as well as if the prey item was dead or alive. The presence of any other predators was also noted.

Redbreast sunfish and snail bullheads were collected in the field and brought back to the laboratory to assess the use of artificial cover by tethered prey and any behavioral effects the tethering method had on the prey item. Prey items were placed in a tank that was 1.83 m in diameter and 1.22 m deep for at least 24 h to allow them to acclimate, but in three attempts, no snail bullheads survived this acclimation period. However, redbreast sunfish survived the acclimation period, and one of the tethering units that provided cover was placed into the tank. A redbreast sunfish was tethered and then video-taped for 6 h to observe any attempt to use the artificial cover that was provided and if its movement was hampered by the weight or placement of the hook.

Statistical Analysis

I performed logistic regression separately for flathead catfish and channel catfish predation to determine if any factor (prey species, distance from the bottom, or cover availability) could significantly predict predation events by either of these predators. Logistic regression was performed using a generalized estimation equations analysis, and each whole tether experiment was considered a block. I initially performed this analysis assuming that all tether units were available at the time of flathead catfish or channel catfish predation. I then repeated it assuming that predation by another species occurred first, rendering the tethering unit unavailable to the specific study predator, and I thus excluded those units from the analysis for the respective predator. This analysis was initially performed with the full model and then reduced models were fitted by sequentially eliminating interactions that were not significant. No factor (prey, position, or cover) significantly affected flathead catfish predation; therefore, I used a chi-square of equality to determine if there was a combination of treatments that increased the chances of a predation event occurring based only on treatments where flathead catfish predation occurred. For both flathead catfish and channel catfish, I also performed logistic regression to determine if prey size affected the chance of a predation event, as well as an ANOVA to examine the effect of prey length on the size of the predator. All statistical analyses were performed using SAS 9.1 software (SAS Institute Inc., Cary, North Carolina).

Results

A total of 65 tether lines were deployed, each with eight units of different treatment combinations, between 16 May 2006 and 11 October 2006. Twenty-seven units (of 520 total) were omitted from the analysis due to entanglement, either by the prey fish or a captured predator entangling several units. Except for one blue catfish *Ictalurus furcatus*, flathead catfish ($N = 61$) and channel catfish ($N = 27$) were the only predators that were captured. Of the remaining units that did not experience a predation event or entanglement, 50% of the prey items remained attached to the tether unit and only 11% of those were dead at termination of each experiment. The video recording of redbreast sunfish in the laboratory showed that the tethered prey item had full mobility and the weight or placement of the hook did not hamper the fish's ability to swim up and down through the water column or to circle the tether. The tethered sunfish did not use the cover provided, but I observed other untethered free-swimming sunfish in the tank occupying the cover.

Flathead catfish preyed randomly on all treatment combinations (Table 1). Chi-square results from combinations that resulted in a flathead catfish predation event revealed no equality attributed to any individual factor (χ^2 = 0.5333; P = 0.9993; df = 7). Examination of predation events blocking on the whole tether, including all units, those that experienced predation events and those where a predation event did not occur, detected no factor that was significant in predicting a predation event, even within the most reduced model and including or excluding units preyed upon by other species (Table 2). I detected no relationship between the size of prey items and predation by flathead catfish (χ^2 = 1.27; P = 0.2595) or the size of the prey item and size of the flathead catfish (F = 2.94, P = 0.0926).

Channel catfish feeding was more specific than that of flathead catfish, with a high percentage (93 % of total predation events) of redbreast sunfish predation occurring by channel catfish (Table 1). The combination that resulted in the greatest number of predation events was redbreast sunfish as prey, located 1.8 m from the river bottom, with no cover available (Figure 2). Channel catfish appeared to avoid bullheads as prey when positioned higher (1.8 m) in the water column (i.e. no predation events with this combination). Tethers analyzed by blocking on the whole tether revealed a significant relationship between channel catfish predation and the type of prey species (χ^2 = 6.31; P = 0.0120) when calculating the full logistical regression model (Table 2). After eliminating unimportant interactions, the model showed that prey species (χ^2 = 20.72; P <0.0001), as well as cover (χ^2 = 8.79; P = 0.0030), were highly significant predictors of predation by channel catfish (Table 2). Logistic regression results yielded identical conclusions when performed including or excluding units preyed upon by other species (Table 2). I detected a highly significant relationship between the size of prey items and predation by channel catfish (χ^2 = 24.80; *P* <0.0001), but there was no relationship detected between the size of the prey item and the size of the channel catfish (*F* = 0.65, *P* = 0.4269).

Discussion

I experimentally determined prey selectivity for two contrasting large catfish species in-situ, presented with choices of prey, prey location in the water column, and prey accessibility of shelter from the predator. Other tethering experiments have examined predation risk associated with specific prey items (Gregory and Levings 1998; Post et al. 1998; Linehan et al. 2001; White and Harvey 2001; Laurel et al. 2003), but I found no other published research that applied tethering experiments to examine feeding dynamics of specific predators toward different prey items. In associated research in this thesis (Chapter 1), I examined the selectivity and overall quantity of prey consumed by flathead catfish, but these parameter estimates were based on encounter rates in the environment, rather than onwhat the flathead catfish would prefer to feed upon given a choice of prey, location, and habitat complexity.

I designed the tethering treatments based on insight from published literature and personal field observations of flathead catfish diets. The choice of prey species reflected observations of decreases in redbeast sunfish and snail bullhead populations as a result of flathead catfish introductions (Guier et al. 1981; Thomas 1993; Bart et al. 1994; Ashley and Rachels 1998), as well as my own findings on flathead catfish trophic dynamics (Chapter 1).

When I quantified the flathead catfish diet in the Deep River of North Carolina (Chapter 1), sunfish were consumed in proportion to the high abundance in the system, and bullheads were highly selected prey items based on similar microhabitat use as flathead catfish. The tethering experimental approach allowed the removal of these environmental factors, and thus clearly described the feeding mechanisms behind the increased consumption of both these prey items, by making them equally available for flathead catfish or channel catfish predation. The increased selectivity for prey items within similar benthic microhabitats (Chapter 1) was also eliminated by placing the same number of tethered prey items within a benthic microhabitat as were located higher in the water column. The ability of prey to display an escape response was addressed by providing cover to allow shelter-seeking behaviors, providing insight on the effects of prey behavior and habitat complexity.

Tethering experiments have been applied rather widely in aquatic and marine environments to study fish and invertebrate predation risk and associated trophic dynamics, but the approach has been closely scrutinized for ecological realism. The tethering approach is particularly useful to study predation dynamics in habitats where direct observation is not possible (e.g., marine benthic environments, turbid or deep freshwater systems). However, marine benthic ecologists have questioned the interpretation of tethering data, based on experimental artifacts and bias (Aronson and Heck 1995; Curran and Able 1998; Kneib and Scheele 2000). Other investigators have addressed concerns such as a predator’s response to a tethered versus free-swimming prey item, release of predator-attracting body fluids by tethered prey, and a prey organism’s inability to use their natural escape behavior to avoid predators. The assumption that an absent prey item represents a predation event raises another argument of exactly what parameters the tethering experiment is estimating (Kneib and Scheele 2000). The difference between previous tethering studies and the design that I developed is the focus of the study. I was interested in the behavior of specific predators relative to three applied treatments, rather than the predation rates of specific prey items. Therefore, the concern of increased feeding on tethered prey doesn't apply to my design, as well as the debate of what parameters I estimated with these tethering units. I determined how these predators feed when given a choice of prey items under varying environmental conditions, and I was not interested in applying my results to estimate the probability of these prey species being consumed under natural conditions. The artifact of fluids that could be released from tethered prey items pertains to studies that use tethers to estimate predation risks in a natural environment, where bodily fluids could possibly increase the potential of being consumed, but since I was interested in the decision of predators to feed upon prey that were all tethered using the same method, this artifact does not apply differentially between the prey species. One concern of tethering that is applicable to my study is the inability of prey items to use their natural predator avoidance behaviors. The use of constraints does not allow prey items to respond to the threat of a predator with certain behaviors, such as finding complex structures as refuge or high-speed swimming, to avoid the risk of predation (Eklöv and Persson 1996). However, incorporating artificial structure as a treatment likely mitigates that bias and may offer associated insight.

I hypothesized that flathead catfish, an obligate carnivore, would demonstrate a preference of prey items among the test treatments, either based on the prey item's body morphology or behavior, similar microhabitats, or habitat complexity, and that trophic generalist channel catfish would not show specificity for any treatment; however results for these predator species were markedly different. The selectivity results (Chapter 1) suggested a preference toward prey items that occupied the same benthic microhabitat as flathead catfish, but flathead catfish fed equally on prey items with no regard to location in the water column. The availability of cover should have allowed prey items to seek shelter, thus decreasing the probability of predation, but the inability to confirm that prey items were actively using these shelters in the field limits my ability to draw conclusions on the effect of this treatment based solely on flathead catfish predation (Curran and Able 2000). The similarity in predation risks among treatments supports the broad conclusion that flathead catfish feed opportunistically.

Flathead catfish selected prey randomly among all treatment effects, whereas channel catfish showed strong specificity for certain test treatments. Channel catfish, a feeding generalist, would not be expected to show a preference for any of the test treatments, but channel catfish chose to consume redbreast sunfish 93% of the time, showing a clear preference for this prey type. I detected a positive relationship between the size of the prey item and the predation by a channel catfish, but this was due to the preference for redbreast sunfish, a smaller prey item when compared to snail bullheads. The preference of redbreast sunfish did not appear to be purely size-selective because there was an overlap in the size of the smallest snail bullheads and the larger redbreast sunfish that were consumed. However, body morphology (e.g. shape or presence of spines) may play a role in the observed selection pattern. Depth was not a statistically significant treatment effect, but channel catfish consumed prey that were located higher in the water column 59% of the time. The accessibility to shelter also had an effect on the risk of predation by channel catfish, and the strong preference for prey without access to cover suggests the experimental design for this treatment was effective and results are valid for both channel and flathead catfish. These findings demonstrate that channel catfish, a generalist feeder, is very specific when selecting fish prey, and that flathead catfish, an obligate carnivore, is very general in prey fish selection. These unexpected, contrasting results between two introduced catfish predators confirm the validity of tethers as a valid experimental approach for my objectives.

My results suggest that flathead catfish are not specifically choosing prey items and consumption depends on encounter rates of these predators with certain prey items. Previous studies showing declines in specific prey (Guier et al. 1981; Thomas 1993; Bart et al. 1994; Ashley and Rachels 1998) correlate these declines with the introduction of flathead catfish when there is a suite of biotic and abiotic factors that could be affecting these populations. Thomas (1993) observed that after introduced flathead catfish eradicated a native bullhead population, they began systematically consuming redbreast sunfish, and while my research revealed no evidence to support a preference for snail bullheads over redbreast sunfish, variable encounter rates in a natural riverine setting could explain the pattern. The conclusive findings of my research under controlled conditions in a field setting offer additional insight into prey selection dynamics of these introduced catfish predators as it occurs in a natural setting that could not be gained by traditional sampling and observational approaches.

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Table 1.—Number of predation events by flathead catfish and channel catfish according to experimental treatment combinations (prey species, distance from river bottom, and cover availability) for 65 tether lines and 493 predation opportunities (tether units).

			Number (percent) of predation events		
Distance from river bottom (m)	Cover availability		Redbreast sunfish	Snail bullhead	Total
Flathead catfish					
0.6	Present		6 (10.0)	8 (13.1)	14 (23.1)
0.6	Absent		8 (13.1)	7 (11.4)	15 (24.5)
1.8	Present		7 (11.4)	8 (13.1)	16 (24.5)
1.8	Absent		8 (13.1)	9 (14.8)	17 (27.9)
		Total	29 (47.6)	32 (52.4)	61 (100.0)
Channel catfish					
0.6	Present		3 (11.1)	0 (0)	3 (11.1)
0.6	Absent		6 (22.2)	2 (7.5)	8 (29.7)
1.8	Present		2 (7.4)	0 (0)	2 (7.4)
1.8	Absent		14 (51.8)	0 (0)	14 (51.8)
		Total	25 (92.5)	2 (7.5)	27 (100.0)

Table 2.—Logistic regression results of flathead catfish ($N = 61$) and channel catfish ($N = 27$) predation events according to treatment effects (prey species, depth in the water column, and cover availability) and their interactions for full and reduced models. Logistic regression was performed assuming all units were available at time of flathead catfish or channel catfish predation. It was also performed assuming predation by other predators occurred first, therefore excluding those units from predation by flathead catfish or channel catfish. Degree of freedom is one for all main and interaction treatment effects.

	Equal availability		Excluding predation by other species	
Source of variation	X^2	P	X^2	P
Flathead catfish full model				
Prey Species	0.25	0.6171	0.00	0.9935
Depth	0.08	0.7803	0.31	0.5769
Cover	0.05	0.8157	0.36	0.5482
Prey Species * Depth	<0.01	0.9960	<0.01	0.9935
Prey Species * Cover	0.28	0.5948	0.62	0.4316
Depth * Cover	<0.01	0.9728	0.10	0.7488
Flathead catfish reduced main-effects model				
Prey Species	0.23	0.6325	<0.01	0.9909
Depth	0.07	0.7874	0.31	0.5789
Cover	0.05	0.8314	0.42	0.5155
Channel catfish full model				
Prey Species	6.31	0.0120	15.65	<0.0001
Depth	0.04	0.8361	0.10	0.7475
Cover	0.36	0.5499	0.84	0.3589
Prey Species * Depth	0.08	0.7841	0.08	0.7732
Prey Species * Cover	0.42	0.5182	0.94	0.3318
Depth * Cover	0.51	0.4744	0.73	0.3941
Channel catfish reduced main-effects model				
Prey Species	20.72	<0.0001	21.11	<0.0001
Depth	1.85	0.1740	1.85	0.1734
Cover	8.79	0.0030	9.36	0.0022

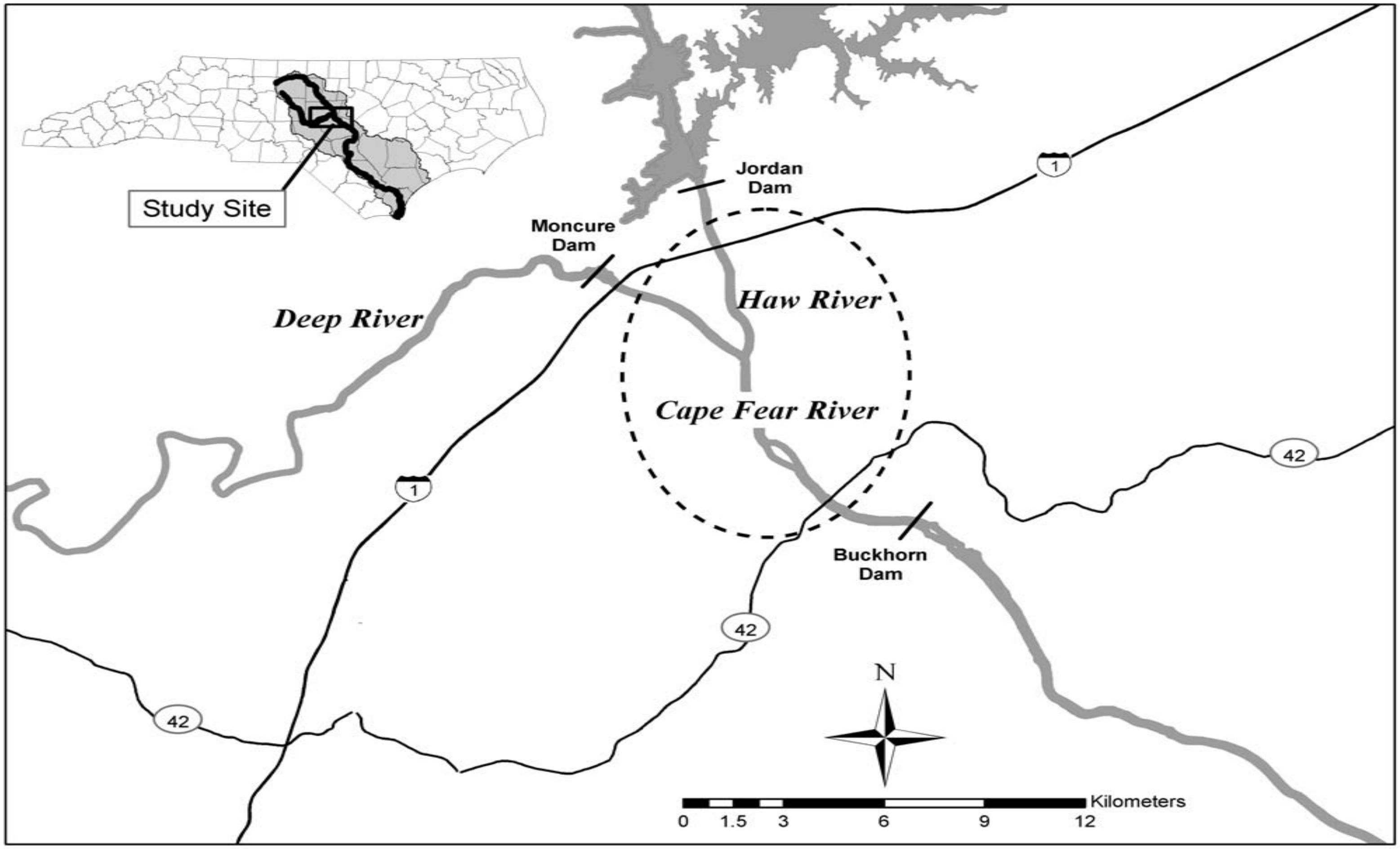

Figure 1.— Study site for conducting prey selection tethering experiments for flathead catfish and channel catfish in the upper Cape Fear River drainage, North Carolina.

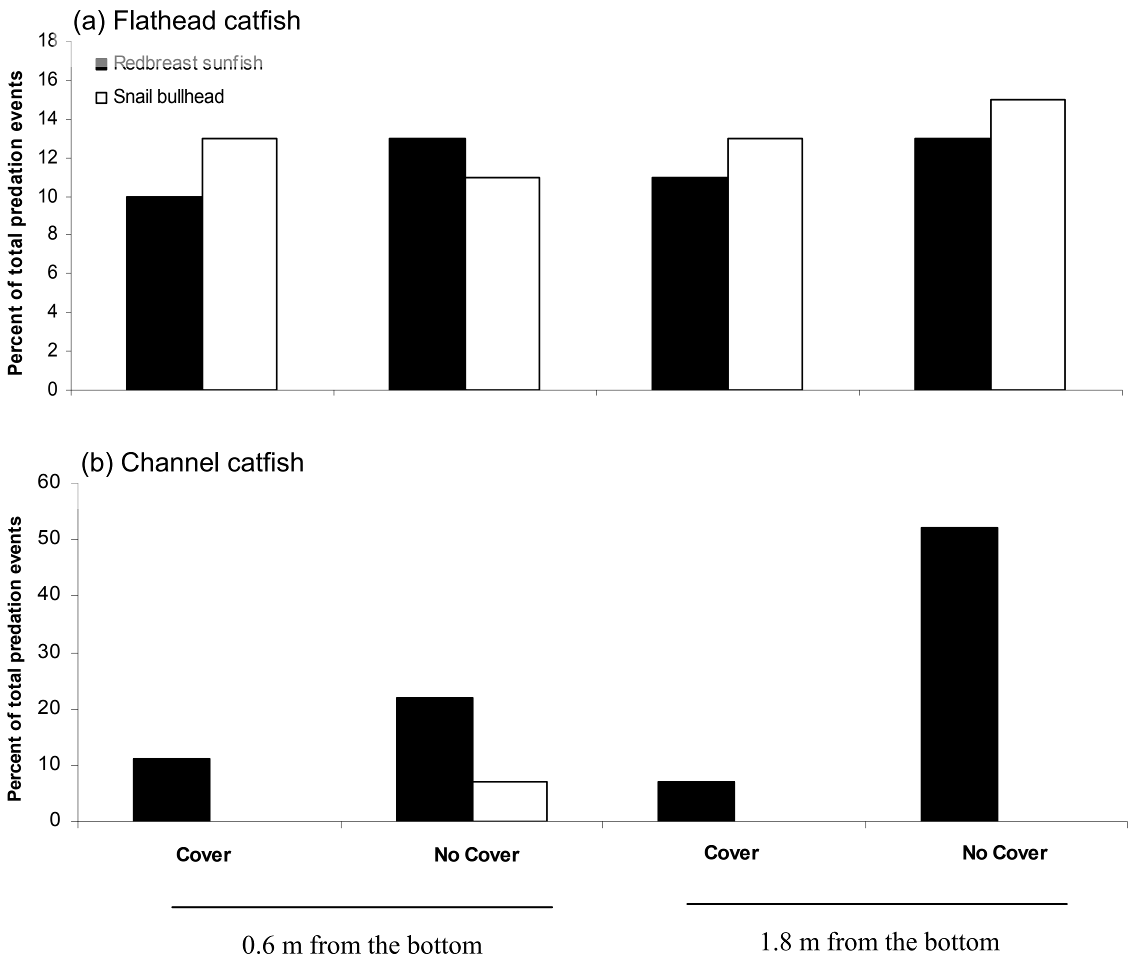

Figure 2.—Percentages of total predation events by (a) flathead catfish ($N = 61$) and (b) channel catfish ($N = 27$) according to treatment combinations (prey species, distance from the river bottom, and cover availability) for 65 tether lines and 493 predation opportunities (tether units).