

PREDATION AS A MECHANISM FOR CONTROL OF WHITE PERCH: AN
INVESTIGATION OF FOOD HABITS IN TWO NEBRASKA RESERVOIRS

By

Nathan J.C. Gosch

A THESIS

Presented to the Faculty of

The Graduate College at the University of Nebraska

In Partial Fulfillment of Requirements

For the Degree of Master of Science

Major: Natural Resource Sciences

Under the Supervision of Professor Kevin L. Pope

Lincoln, Nebraska

August 2008

PREDATION AS A MECHANISM FOR CONTROL OF WHITE PERCH: AN
INVESTIGATION OF FOOD HABITS IN TWO NEBRASKA RESERVOIRS

Nathan J.C. Gosch, M.S.

University of Nebraska, 2008

Adviser: Kevin L. Pope

The white perch (*Morone americana*) is an invasive species that dominates the fish communities in Branched Oak and Pawnee reservoirs, Nebraska. The main objective of this study was to investigate predation as a potential mechanism for biological control of white perch. Predator size in relation to available prey sizes is an important factor affecting prey vulnerability; thus, I investigated prey length-predator length and prey body depth-predator gape width relations. Larger white perch were consumed in Branched Oak Lake than in Pawnee Lake; however, when accounting for predator size, few differences in the size of white perch consumed existed between reservoirs. White perch consumed in Branched Oak Lake were not only larger, but also older (age 0-6), whereas white perch consumed in Pawnee Lake were almost exclusively age 0. Stable isotopes analysis was used to complement the traditional food-habits techniques. Determining trophic position among fishes via $\delta^{15}\text{N}$ values was difficult in both reservoirs. Based on $\delta^{13}\text{C}$ values, white perch were assimilated into the muscle tissue of predators in both reservoirs. Largemouth bass, walleye and sauger were the most effective white perch predators on a per-kg basis. However, managing for these

predators is difficult in these two reservoirs because recruitment of these fishes is, at best, limited. Thus, predation is likely not a viable option for controlling white perch.

A secondary objective of this study was to document food habits of white perch from two population states (stunted [Branched Oak Lake] and non-stunted [Pawnee Lake]) to predict possible changes in food-web dynamics that might occur in situations where a stunted white perch population is altered to a non-stunted state. Cladocerans and dipterans dominated white perch diets in both reservoirs. Fish eggs and trichopterans were also important during spring and fish were important during autumn. The importance of invertebrates to the diet of white perch indicates that direct competition for limited food resources with young sportfishes is possible regardless of white perch population status.

Acknowledgements

First and foremost, I want to thank my family for their endless supply of support, understanding and encouragement and, most importantly, for leading me to faith in Jesus Christ. Thank you for always believing in me. I cannot express how important your influence has been in my life.

I must thank Dr. David Willis at South Dakota State University for giving me a jump-start in the fisheries world with the opportunity to conduct undergraduate research. I am certain that his influence greatly improved my performance in graduate school. Also, thank you for getting me in contact with my current adviser, Dr. Kevin Pope.

Dr. Kevin Pope, thank you for the guidance, an always open door and all the red ink you sacrificed for the betterment of my writing. From day one, I always felt like I could be myself around you. Thank you for always being a good sport and being able to dish it out as well as take it. I will forever be impressed by the number of pushups you can do in a suit. I must also thank you for demonstrating the uselessness of name tags because “those that know the Pope, know the Pope!”

The other members of my graduate committee were Dr. Mark Pegg, Dr. Richard Holland and Dr. Drew Tyre. Dr. Mark Pegg, thank you for all the guidance and suggestions and for your willingness to always join in when I was giving Dr. Pope a hard time. Dr. Richard Holland, thank you for always giving me new perspectives on research and management issues and for your terrific sense of humor. I must also thank you for providing me with additional motivation; I cannot think of a better motivational tool for a new graduate student than the “Terminator” poster on your file cabinet. Dr. Drew Tyre, thank for your advice and patience with statistical analyses, particularly in the program R.

I also must thank you for your willingness to put up with all my fish talk. I know that fishheads can be a handful at times.

Thank you to my technicians Jeff Stittle, Landon Pierce and John Walrath and my fellow graduate students Dustin Martin, Chris Lewis, Tony Barada, Mike Archer, Jen Hogue, Brenda Pracheil, Ben Neely, Aaron Lotz, Ryan Bjerke, Justin Williams and Kensey Riley for all of the field and laboratory assistance, and especially for your friendship. You guys really made it a blast going to work. All of your contributions will not be forgotten and I hope to return the favor someday.

Thank you to the Nebraska Game and Parks Commission employees, especially the District 5 fisheries office, for all of the help and support. You guys have no idea how much easier you made my life. Thank you for always trusting me with your shocking boat even though mine always seemed to be busted.

This work was jointly supported by funds from Federal Aid in Sport Fish Restoration, project F-172-R, administered by the Nebraska Game and Parks Commission, and by funds from U.S. Geological Survey, Research Work Order Number 03HQURU1586. The contents of this project are solely the responsibility of the author and do not necessarily represent official views of the Nebraska Game and Parks Commission or the U.S. Geological Survey. Reference to trade names does not imply endorsement by the author or any U.S. Government.

Table of Contents

Abstract	ii
Acknowledgements.....	iv
List of Tables	viii
List of Figures	x
List of Appendices	xv
Chapter 1. Introduction	1
Study Area	4
Branched Oak Lake.....	4
Pawnee Lake	5
Chapter 2. Predator-Prey Size Relations in a Fish Community with a Stunted White Perch Population and a Fish Community with a Non-stunted White Perch population	6
Methods.....	8
Results.....	10
Discussion.....	13
Chapter 3. Food Habits of Stunted and Non-stunted White Perch	19
Methods.....	20
Results.....	22
Discussion.....	24
Chapter 4. Predation as a Potential Mechanism for Biological Control	29
Methods.....	30
Results.....	35

Seasonal Quantitative Description of Diets	35	
Foraging Success on White Perch.....	37	
Foraging Success on White Perch and Gizzard Shad	38	
Predators Present in Both Reservoirs.....	39	
Estimates of Biomass and Consumption of White Perch	39	
Discussion	40	
Chapter 5. Using Stable Isotopes to Determine Trophic Position and Complement		
Traditional Food Habits Methods for Piscivores	49	
Methods.....	50	
Results.....	51	
Discussion	53	
Chapter 6. Future Management and Research		57
References.....	61	

List of Tables

Table 2-1. Upper and lower 95% confidence limits (CL) for quantile regression. Quantiles with confidence limits that include 0 have similar slopes between reservoirs.....	75
Table 4-1. Equations used to predict maximum stomach capacity (V; ml) of fish as a function of their total length (L, mm)	76
Table 4-2. Pairwise comparisons for foraging success on white perch between predators (LMB = largemouth bass, WHC = white crappie, BLC = black crappie, CHC = channel catfish, FHC = flathead catfish, HSB = hybrid striped bass, WAE = walleye) using Dunn’s multiple comparison procedure in Branched Oak Lake, Nebraska during 2006. An “*” indicates statistically significant comparisons ($\alpha = 0.05$) and “—“ indicates non-significant comparisons	77
Table 4-3. Pairwise comparisons for foraging success on white perch between predators (LMB = largemouth bass, CHC = channel catfish, FHC = flathead catfish, WHB = white bass, SAU = sauger, WAE = walleye) using Dunn’s multiple comparison procedure in Pawnee Lake, Nebraska during 2006. An “*” indicates statistically significant comparisons ($\alpha = 0.05$) and “—“ indicates non-significant comparisons	78
Table 4-4. Pairwise comparisons for foraging success on white perch between predators (WHC = white crappie, FHC = flathead catfish, HSB = hybrid striped bass, WAE = walleye) using Dunn’s multiple comparison procedure in Branched Oak Lake, Nebraska during 2007. An “*” indicates statistically significant comparisons ($\alpha = 0.05$) and “—“ indicates non-significant comparisons	79

Table 4-5. Pairwise comparisons for foraging success on white perch between predators (FHC = flathead catfish, WHB = white bass, SAU = sauger, WAE = walleye) using Dunn's multiple comparison procedure in Pawnee Lake, Nebraska during 2007. An "*" indicates statistically significant comparisons ($\alpha = 0.05$) and "--" indicates non-significant comparisons	80
Table 4-6. Estimated relative biomass of predators in Branched Oak (BO) and Pawnee (PA) reservoirs, Nebraska and their associated consumption of white perch based on calculated rates of foraging success	81

List of Figures

- Figure 2-1. Mean \pm SE predator size:prey size ratio in Branched Oak and Pawnee reservoirs, Nebraska during 2006 and 200782
- Figure 2-2. Length-frequency distributions of white perch consumed by predators in Branched Oak and Pawnee reservoirs, Nebraska. Ages were determined from Chizinski (2007).....83
- Figure 2-3. Length-frequency distributions of white perch consumed by predators (black fill) and white perch captured by the Nebraska Game and Park Commission (white fill) during annual autumn standardized sampling in Branched Oak (top 2 panels) and Pawnee reservoirs (bottom two panels), Nebraska.....84
- Figure 2-4. Relations between predator gape width and total length for fishes captured in Branched Oak and Pawnee reservoirs, Nebraska during 200785
- Figure 2-5. Relations between prey standard length (GZD = gizzard shad, WHP = white perch) and predator total length (left panels) and prey body depth and predator gape width (right panels) in Branched Oak (top and middle panels, respectively) and Pawnee (bottom panels) reservoirs, Nebraska during 2006 and 200786
- Figure 2-6. Quantile (0.1, 0.5 and 0.9) regressions between prey standard length (GZD = gizzard shad, WHP = white perch) and predator total length and between prey body depth and predator gape width in Branched Oak and Pawnee reservoirs, Nebraska during 2006 and 2007 (* indicates slope significantly different from zero)87
- Figure 2-7. Relation between white perch (prey) standard length and predator total length for species in which a minimum of 5 individuals were captured containing at least

one measurable white perch in their stomach contents in Branched and Pawnee reservoirs, Nebraska during 2006 and 200788

Figure 2-8. Relation between white perch (prey) body depth and predator gape width for species in which a minimum of 5 individuals were captured containing at least one measurable white perch in their stomach contents in Branched and Pawnee reservoirs, Nebraska during 2006 and 200789

Figure 3-1. Relation between maximum stomach capacity (V) and total length (L) of white perch. A point represents the maximum total volume of prey observed in an individual stomach plotted as the midpoint for each length group90

Figure 3-2. Frequency of occurrence \pm SE (left panels), percent composition of volume displaced (middle panels) and mean stomach fullness \pm SE (right panels) for prey consumed (CL = cladocera, CO = coleoptera, DI = diptera, HM = hemiptera, WP = white perch) by white perch during spring (top panels), summer (middle panels) and autumn (bottom panels) 2006 in Branched Oak Lake, Nebraska91

Figure 3-3. Frequency of occurrence \pm SE (left panels), percent composition of volume displaced (middle panels) and mean stomach fullness \pm SE (right panels) for prey consumed (CL = cladocera, CP = copepoda, DI = diptera, EG = fish eggs, UF = unidentifiable fish) by white perch during spring (top panels), summer (middle panels) and autumn (bottom panels) 2007 in Branched Oak Lake, Nebraska..92

Figure 3-4. Frequency of occurrence \pm SE (left panels), percent composition of volume displaced (middle panels) and mean stomach fullness \pm SE (right panels) for prey consumed (CL = cladocera, DI = diptera, WP = white perch) by white perch

during spring (top panels), summer (middle panels) and autumn (bottom panels)
 2006 in Pawnee Lake, Nebraska.....93

Figure 3-5. Frequency of occurrence \pm SE (left panels), percent composition of volume displaced (middle panels) and mean stomach fullness \pm SE (right panels) for prey consumed (CL = cladocera, CO = coleoptera, DI = diptera, TR = trichoptera, EG = fish eggs, UF = unidentifiable fish) by white perch during spring (top panels), summer (middle panels) and autumn (bottom panels) 2007 in Pawnee Lake, Nebraska94

Figure 3-6. Length-frequency distributions of white perch captured in Branched Oak and Pawnee reservoirs, Nebraska95

Figure 3-7. Scattergrams of the proportion (by volume) of fish prey in the stomachs of individual white perch plotted as a function of white perch total length for Branched Oak and Pawnee reservoirs, Nebraska96

Figure 4-1. Relation between maximum stomach capacity (V) and total length (L) of hybrid striped bass. A point represents the maximum total volume of prey observed in an individual stomach plotted as the midpoint for each length group.....97

Figure 4-2. Foraging success \pm SE on white perch for predators (LMB = largemouth bass, WHC = white crappie, BLC = black crappie, CHC = channel catfish, FHC = flathead catfish, WHB = white bass, HSB = hybrid striped bass, SAU = sauger, WAE = walleye) captured in Branched Oak and Pawnee reservoirs, Nebraska during 200698

- Figure 4-3. Foraging success \pm SE on white perch for predators (WHC = white crappie, FHC = flathead catfish, WHB = white bass, HSB = hybrid striped bass, SAU = sauger, WAE = walleye) captured in Branched Oak and Pawnee reservoirs, Nebraska during 200799
- Figure 4-4. Cumulative-frequency distributions of foraging success (ml/kg) on white perch (solid line) and gizzard shad (dotted line) for predators (LMB = largemouth bass, WHC = white crappie, BLC = black crappie, CHC = channel catfish, FHC = flathead catfish, HSB = hybrid striped bass, WAE = walleye) captured in Branched Oak Lake, Nebraska during 2006 and 2007100
- Figure 4-5. Cumulative-frequency distributions of foraging success (ml/kg) on white perch for largemouth bass (LMB), flathead catfish (FHC) and walleye (WAE) in Branched Oak Lake, Nebraska during 2006 and 2007101
- Figure 4-6. Cumulative-frequency distributions of foraging success (ml/kg) on white perch for predators (LMB = largemouth bass, CHC = channel catfish, FHC = flathead catfish, WAE = walleye) present in both Branched Oak and Pawnee reservoirs, Nebraska during 2006 and 2007102
- Figure 5-1. Seasonal stable isotope signatures for memorable-length (M) white crappie (WHC; top panel) and preferred-length (P) hybrid striped bass (HSB; bottom panel) in Branched Oak Lake, Nebraska103
- Figure 5-2. Seasonal stable isotope signatures for preferred- to memorable-length (P-M) white bass (WHB; top panel) and preferred- to memorable-length (P-M) and memorable-length (M) sauger (SAU; bottom panel) in Pawnee Lake, Nebraska.....104

Figure 5-3. Stable isotope signatures for predators (open circles) and prey (solid squares) in Branched Oak Lake, Nebraska. All stock-length fishes were considered predators, except white perch. Predators captured were largemouth bass (LMB), white crappie (WHC), black crappie (BLC), channel catfish (CHC), flathead catfish (FHC), hybrid striped bass (HSB) and walleye (WAE). Predator size categories were stock to quality length (S-Q), quality to preferred length (Q-P), preferred to memorable length (P-M), preferred length (P) and memorable length (M). Prey captured were bluegill (BLG), black crappie (BLC), white crappie (WHC), gizzard shad (GZD) and white perch (WHP). Prey size categories were 80-99 mm and >99 mm for all prey, except white perch. Prey size categories for white perch were 100-129 mm, stock to quality length (S-Q) and quality to preferred length (Q-P).....105

Figure 5-4. Stable isotope signatures for predators (open circles) and prey (solid squares) in Pawnee Lake, Nebraska. All stock-length fishes were considered predators, except white perch. Predators captured were white crappie (WHC), black crappie (BLC), channel catfish (CHC), white bass (WHB), sauger (SAU) and walleye (WAE). Predator size categories were stock to quality length (S-Q), quality to preferred length (Q-P), preferred to memorable length (P-M) and memorable length (M). Prey captured were bluegill (BLG), white perch (WHP) and walleye (WAE). Prey size categories were 60-79 mm, >99 mm and 100-249 mm for all prey, except white perch. Prey size categories for white perch were 100-129 mm, stock to quality length (S-Q) and quality to preferred length (Q-P).....106

List of Appendices

Appendix A. A complete summary of food habits (O_i = frequency of occurrence, $\%V_i$ = percent composition of volume displaced and MSF_i = mean stomach fullness) for white perch by season in Branched Oak (BO) and Pawnee (PA) reservoirs, Nebraska during 2006 and 2007107

Appendix B. A complete summary of food habits (O_i = frequency of occurrence, $\%V_i$ = percent composition of volume displaced and MSF_i = mean stomach fullness) for largemouth bass (LMB), white crappie (WHC), black crappie (BLC), channel catfish (CHC), flathead catfish (FHC), hybrid striped bass (HSB) and walleye (WAE) by season in Branched Oak Lake, Nebraska during 2006 and 2007. Species with fewer than 10 individuals containing prey items per season were not reported because sample size was insufficient to reliably describe food habits.....111

Appendix C. A complete summary of food habits (O_i = frequency of occurrence, $\%V_i$ = percent composition of volume displaced and MSF_i = mean stomach fullness) for largemouth bass (LMB), channel catfish (CHC), flathead catfish (FHC), white bass (WHB), sauger (SAU) and walleye (WAE) by season in Pawnee Lake, Nebraska during 2006 and 2007. Species with fewer than 10 individuals containing prey items per season were not reported because sample size was insufficient to reliably describe food habits.....118

Appendix D. Stomach capacities of six freshwater fishes.....122

Appendix E. A summary of the percentage of empty stomachs (PES) by predator species during spring, summer and autumn in Branched Oak and Pawnee reservoirs,

Nebraska. Predator species with fewer than 10 individuals that contained prey items were not reported because sample size was insufficient to reliably determine

PES.....130

Chapter 1. Introduction

Fishes acquire energy for life processes through the consumption of food, which depends on a predator's ability to locate, capture, handle, ingest and digest prey items (Kestemont and Baras 2001). Consumers are generally categorized as detritivores, herbivores, carnivores and omnivores. Consumers can also be further classified as euryphagous, stenophagous or monophagous, with most fishes classified as euryphagous carnivores (Moyle and Cech 2004). Euryphagous carnivores typically swallow prey items whole; therefore, prey size (e.g., length and depth) and predator size (e.g., length and gape) are two important factors affecting food intake. Piscivorous fishes are capable of consuming prey up to half of their length, but typically consume prey between 20 to 30% of their length (Hoogland et al. 1956; Lawrence 1958; Gillen et al. 1981; Hoyle and Keast 1987; Hambright 1991). Additionally, numerous studies have found that piscivorous fishes typically consume prey with much smaller body depths than the maximum body depth possible for their given gape (Lawrence 1958; Gillen et al. 1981; Hoyle and Keast 1987; Hambright 1991; Juanes 1992; Nilsson and Bronmark 2000) because the probability of successfully capturing and handling smaller prey is likely greater than larger prey even though these predators are capable of consuming larger prey.

Food intake is also affected by the biotic community (e.g., which fishes are present in a waterbody). Invasive species, for example, can drastically change biotic communities, predator-prey dynamics and, subsequently, food intake. Invading species can alter biotic communities through competition, predation and habitat modification,

which can change community structure affecting feeding habits and ultimately survival and growth rates of native fishes (Christie 1972; Burr et al. 1996; Li and Moyle 1999). Frequently, these invading species alter biotic communities as a result of differing physiological tolerances, feeding habits and reproductive habits compared to resident fishes (Taylor et al. 1984).

Though nonnative to Nebraska, the Nebraska Game and Parks Commission (NGPC) stocked white perch, *Morone americana*, in several Nebraska Sandhills' lakes in 1964 (Hergenrader and Bliss 1971). The NGPC believed that this species would flourish in the highly alkaline lakes (McCarrher 1971). Unfortunately, white perch were also inadvertently stocked into Wagon Train Reservoir in southeastern Nebraska in 1964 with largemouth bass (*Micropterus salmoides*) fry (Hergenrader and Bliss 1971). This species then spread to Salt Creek, the Platte River and the Missouri River (Bliss and Schainost 1974). White perch also established self-sustaining populations in Branched Oak and Pawnee reservoirs. The current Branched Oak Lake white perch population is stunted (i.e., high density of slow growing individuals that have a reduced size at maturity and reduced maximum size), whereas the Pawnee white perch population is not stunted (Chizinski 2007).

White perch tend to overpopulate and stunt in freshwater systems (Scott and Crossman 1973). An ability to reproduce during their first year of life and withstand a wide range of environmental conditions allows quick establishment of this species and potential domination of fish communities (Ballinger and Peters 1978; Hodkin 2001). White perch will also consume eggs of other fishes, such as walleye (*Sander vitreus*) and white bass (*Morone chrysops*), which could negatively affect recruitment (e.g., result in

missing or weak year classes) of those species (Schaeffer and Margraf 1987; Hodkin 2001). Furthermore, white perch may also negatively affect fishes that feed on invertebrates (e.g., bluegill and crappie) through competition for food (Ballinger and Peters 1978). Mansueti (1961) suggested that white perch have the potential to reduce the abundance of invertebrates and alter the composition of the invertebrate community. This effect on the invertebrate community could also affect piscivorous fishes that rely on invertebrates during earlier ontogenetic stages (e.g., walleye). In Branched Oak Lake, walleye have not had a strong year class since 1992, despite annual stockings by NGPC (Jackson 1999). Similarly, white perch may have caused the decline in walleye abundance in the Bay of Quinte (Hurley and Christie 1977) and the decline in white bass recruitment in Lake Erie (Madenjian et al. 2000).

Declining sportfish populations in Branched Oak and Pawnee reservoirs lead to drastic management suggestions such as partial and complete chemical renovations to control or eradicate white perch populations (Vrtiska et al. 2001). However, chemical renovation is expensive, difficult to successfully complete and frequently has negative social and political ramifications. All alternatives to chemical renovation should be investigated before taking such extreme measures. Therefore, the objectives of this study were to:

1. investigate potential differences among predator-prey interactions in a fish community with a stunted white perch population and a fish community with a non-stunted white perch population,

2. document white perch food habits to investigate potential negative effects of white perch on other fishes through competition for food and predation on eggs and larvae,
3. document food habits of potential predators of white perch to investigate predation as a potential mechanism for biological control of white perch in Branched Oak and Pawnee reservoirs, and
4. determine trophic position and to trace diets of fishes in Branched Oak and Pawnee reservoirs using stable isotope analysis.

Study Area

Branched Oak Lake

Branched Oak Lake, located in Lancaster County, Nebraska, is a 728-hectare, hypereutrophic flood-control reservoir that was completed in 1967 and filled to conservation pool by 1973 (Vrtiska et al. 2001). This reservoir does not permanently stratify (Hergenrader 1980a). Branched Oak Lake is the largest waterbody in eastern Nebraska and provides recreational opportunity to more than half of the population of the state (Winter 1994). However, lake usage has declined drastically. From 1983 until 1992, average annual angler trips to the reservoir declined by 61% (Winter 1994). The fish community at Branched Oak Lake consists of walleye, hybrid striped bass (*M. saxatilis* x *M. chrysops*), largemouth bass, bluegill (*Lepomis macrochirus*), black crappie (*Pomoxis nigromaculatus*), white crappie (*P. annularis*), common carp (*Cyprinus carpio*), blue catfish (*Ictalurus furcatus*), channel catfish (*I. punctatus*), flathead catfish (*Pylodictis olivaris*), gizzard shad (*Dorosoma cepedianum*), brook silverside (*Labidesthes sicculus*) and white perch. Early in the life of this reservoir, littoral fishes, such as

largemouth bass, bluegill and crappie, comprised the majority of angler catches. However, the sportfish community is now dominated by more pelagic fishes, such as walleye and hybrid striped bass, due to a loss in littoral habitat caused by sedimentation and erosion. Currently, Branched Oak Lake has restrictive harvest regulations (i.e., catch-and-release fishing for hybrid striped bass and flathead catfish, a daily bag limit of 1 walleye longer than 56 cm and a 25-cm minimum length limit for crappie).

Pawnee Lake

Pawnee Lake, located in Lancaster County, Nebraska, is a 299-hectare, hypereutrophic flood-control reservoir that was completed in 1964 (Jackson 2008). Pawnee Lake is located 14 km south of Branched Oak Lake. Like Branched Oak Lake, this lake does not thermally stratify (Hergenrader 1980a). The fish community at Pawnee Lake consists of walleye, sauger (*Sander canadensis*), white bass, largemouth bass, black crappie, white crappie, channel catfish, flathead catfish, freshwater drum (*Aplodinotus grunniens*), common carp and white perch. Currently, Pawnee Lake has less restrictive harvest regulations compared to Branched Oak Lake (i.e., daily bag limit of 10 panfish).

Chapter 2. Predator-Prey Size Relations in a Fish Community with a Stunted White Perch Population and a Fish Community with a Non-stunted White Perch Population

Optimal foraging theory has long suggested that predators should select prey in a way that maximizes energy gain (i.e., caloric intake) and minimizes energy expenditures (Emlen 1966; Stephens and Krebs 1986). A relatively large prey item will likely have a large caloric value; however, the predator must be able to successfully capture that prey item. Smaller prey might be more easily captured; however, that prey item must provide the necessary calories to complete required biological processes (e.g., maintenance, growth and reproduction). Therefore, several factors determine whether a prey item is ingested by a predator. First, the prey item must be available to the predator. Second, the predator must be able to detect the prey item. Third, the predator must be able to successfully capture the prey item upon detection (i.e., the prey must be vulnerable to predation) without expending excessive energy.

Prey vulnerability is an important component of predator-prey interactions in any aquatic system. One of the many factors affecting prey vulnerability is the body size of a predator in relation to its prey because most piscivores are gape-limited (i.e., can only consume prey that can be swallowed whole). Typically, larger piscivorous fishes consume larger prey (Parsons 1971; Knight et al. 1984; Mittelbach and Persson 1998). Mittelbach and Persson (1998) found that piscivore body size explained most of the variation in size of prey consumed. Piscivores can consume prey up to half of their length, though piscivores usually consume prey between 20 to 30% of their length

(Hoogland et al. 1956; Lawrence 1958; Gillen et al. 1981; Hoyle and Keast 1987; Hambright 1991). However, the length of prey is likely not the characteristic that determines whether it is ingestible by a gape-limited predator. Rather prey body depth in relation to predator mouth size (i.e., gape) dictates whether or not a prey item is ingestible (Lawrence 1958; Werner 1977; Tonn and Paszkowski 1986; Hambright 1991).

The white perch (*Morone americana*) populations in Branched Oak and Pawnee reservoirs are markedly different. Chizinski (2007) investigated differences in life-history traits between the stunted white perch population in Branched Oak Lake and the non-stunted white perch population in Pawnee Lake. He concluded that both males and females had a smaller mean and maximum size in the stunted population. White perch in the stunted population also experienced slower growth and an annual survival rate almost twice that of white perch in the non-stunted population. Furthermore, males and females reached sexual maturity at ages 1 and 2, respectively, in the stunted population and ages 2 and 4, respectively, in the non-stunted population. Therefore, the objective of this study was to investigate predator-prey interactions between two fish communities with markedly different white perch populations. I expected the size of prey consumed to increase with predator size within each reservoir for predator size-prey size regression analyses. I expected predators to consume smaller white perch in the stunted Branched Oak Lake population. I also expected larger white perch predators in Branched Oak Lake because harvest regulations for sportfishes are more stringent in Branched Oak Lake than in Pawnee Lake.

Methods

Food habits of piscivorous fishes (largemouth bass [*Micropterus salmoides*], white crappie [*Pomoxis annularis*], black crappie [*P. nigromaculatus*], channel catfish [*Ictalurus punctatus*], flathead catfish [*Pylodictis olivaris*], white bass [*Morone chrysops*], hybrid striped bass [*M. saxatilis* x *M. chrysops*], sauger [*Sander canadensis*] and walleye [*S. vitreus*]) were investigated during the ice-free period (approximately March through November) of 2006 and 2007 in Branched Oak and Pawnee reservoirs. Each reservoir was sampled twice weekly from one hour before to two hours after sunrise and from sunset to three hours after sunset because catchability of fishes is maximized during crepuscular periods (Witt and Campbell 1959). Also, some fishes feed more actively during the day, whereas other fishes feed more actively during the night.

Fishes were captured with a boat-mounted electrofisher (pulsed DC). These individuals were then measured for total length (mm). Gape size was measured as the width (mm) from the outside edge of each maxillary bone with the mouth closed (Hambright 1991). Stomach contents of captured fishes were removed using pulsed gastric lavage (Light et al. 1983; Kamler and Pope 2001) and preserved in a 10% buffered-formalin solution. After the stomach was flushed with water, an appropriately sized clear plastic tube was inserted into the digestive tract and used as a gastroscope to ensure that all stomach contents were removed. Fish were released unharmed after stomach contents were removed.

In the laboratory, all stomach contents were identified to species for fishes and to order for invertebrates using dichotomous keys provided by Scott and Crossman (1973) and Thorp and Covich (1991). Stomach contents were grouped by taxa and measured

volumetrically using water displacement in graduated cylinders. Prey fishes removed from stomachs were measured for standard length (mm) and body depth (mm) when possible.

I used several statistical methods to assess the data. Simple linear regression was used to predict mouth gapes of predators captured during 2006 based on total length because mouth gape measurement was not implemented until 2007. Only significant regressions with an r^2 of at least 0.90 and a sample size of at least 15 were used to predict gape size.

A Kolmogorov-Smirnov test was used to determine if differences existed between the length-frequency distributions of consumed white perch from Branched Oak and Pawnee reservoirs. I also compared length frequency distributions of consumed white perch to length frequency distributions of white perch sampled during Nebraska Game and Parks Commission (NGPC) annual autumn standardized fish sampling using a Kolmogorov-Smirnov test. For comparison purposes, I converted standard lengths of consumed white perch to total length using a conversion factor (total length = standard length \cdot 1.24; Carlander 1997) because NGPC measured total length during standardized fish sampling.

Simple linear regression was used to determine if positive relations existed between prey length and predator length and between prey body depth and predator mouth gape in Branched Oak and Pawnee reservoirs. Minimum sample size for prey length-predator length and prey body depth-predator mouth gape regressions was set at 5 individuals that contained measurable prey. Analysis of covariance (ANCOVA) was used to determine if regression lines differed (i.e., slopes or intercepts if slopes were

similar) between predators in Branched Oak and Pawnee reservoirs. Quantile regression was used to further investigate prey size-predator size relations within and between reservoirs by fitting a line to a particular quantile of the dependent variable (prey size) given the independent variable (predator size). Simple linear regression fits a regression line to the entire prey size-predator size distribution; however, quantile regression fits a regression line to select portions (e.g., the 90th percentile of prey size consumed) of a prey size-predator size distribution. Thus, simple linear regression may not result in a significant relation; however, certain quantiles of that distribution may have significant relations. Quantiles selected were 0.1, 0.5 and 0.9 as a means to effectively characterize the median (0.5) as well as the upper (0.9) and lower (0.1) bounds of prey sizes consumed (Chipps and Garvey 2007). I investigated differences in quantile regression slopes between lakes (i.e., 0.1 quantile regression slope in Branched Oak Lake compared to the 0.1 quantile regression slope in Pawnee Lake) by looking at the 95% confidence intervals for the parameter estimate of the interaction term (predator length by reservoir). If the range of the 95% confidence intervals excluded 0, then the slopes were considered different.

Results

There was no noticeable difference between the mean ratios of length of white perch consumed to the length of predator consuming that particular white perch between reservoirs; in contrast, there was a noticeable difference when using white perch depth to predator gape (Figure 2-1). Length-frequency distributions of consumed white perch were different ($KSa = 1.9$, $P = 0.001$) between reservoirs (Figure 2-2). However, contrary to my *a priori* expectation, larger white perch were consumed in Branched Oak

Lake compared to Pawnee Lake. Furthermore, I sampled noticeably larger predators in Branched Oak Lake compared to Pawnee Lake, which was consistent with my *a priori* expectation. There were also differences in the ages (as determined by Chizinski [2007]) of consumed white perch between reservoirs. In Branched Oak Lake, 42% of consumed white perch were age 1 or older, where as only 1% of consumed white perch were age 1 or older in Pawnee Lake (Figure 2-2). Length-frequency distributions between consumed white perch and NGPC standardized fish sampling surveys overlapped much more in Branched Oak Lake than in Pawnee Lake (Figure 2-3). In Pawnee Lake, predators consumed greater numbers of small white perch compared to the lengths of white perch sampled by NGPC (Figure 2-3).

Largemouth bass, flathead catfish, hybrid striped bass and walleye were the only species with gape width-length regressions that had an r^2 of at least 0.90 and a sample size of at least 15 individuals (Figure 2-4). Therefore, I only predicted gape sizes for these four species during 2006. Gape size for white crappie, channel catfish, white bass and sauger was too variable (i.e., $r^2 < 0.90$) to reliably predict gape size for these fishes captured during 2006.

Positive relations existed between length of white perch consumed and predator length in Branched Oak and Pawnee reservoirs; however, no relation existed between length of gizzard shad consumed and predator length in Branched Oak Lake (Figure 2-5). Additionally, there was no difference between slopes (ANCOVA, $F = 0.60$, $P = 0.44$) or intercepts (ANCOVA, $F=1.64$, $P = 0.10$) for white perch length-predator length regressions among Branched Oak and Pawnee reservoirs. When investigating prey depth-predator gape relations within each reservoir, no relations existed between gizzard

shad or white perch and predators in Branched Oak Lake; however, there was a relation between depth of white perch and predator gape width in Pawnee Lake (Figure 2-5). Additionally, there was a difference between slopes (ANCOVA, $F = 5.63$, $P = 0.02$) for white perch depth-predator gape regressions from Branched Oak and Pawnee reservoirs. Using quantile regression, the slope and the intercept usually increased with increasing quantile (Figure 2-6). Typically, the 0.1 quantile did not have a slope different from zero, whereas the slopes for the 0.5 and 0.9 quantiles were usually greater than zero (Figure 2-6). There were no differences in slopes between lakes for any quantile (i.e., the range of all confidence intervals included 0) using prey length and predator length (Table 2-1). Using prey depth and predator gape width, the slopes for the 0.9 quantile were different between reservoirs with a greater slope in Pawnee Lake, whereas 0.1 and 0.5 slopes were not different between reservoirs (Table 2-1).

Sample size was an issue when investigating white perch-predator size relations by predator species within each reservoir. Only largemouth bass, flathead catfish, hybrid striped bass and walleye had at least 5 individuals during both years combined that contained prey that could be measured for length and depth in Branched Oak Lake. In Pawnee Lake, only white bass, sauger and walleye had at least 5 individuals during both years combined that contained prey that could be measured for length and depth. Only largemouth bass in Branched Oak Lake and walleye in Branched Oak and Pawnee reservoirs had relations between white perch length and predator length (Figure 2-7). Similarly, only largemouth bass in Branched Oak Lake and walleye in Branched Oak Lake and Pawnee Lake had relations between white perch depth and predator gape (Figure 2-7). Furthermore, r^2 values for prey length-predator length and prey depth-

predator gape width regressions were similar for all predators in both reservoirs, except for walleye in Pawnee Lake (Figure 2-7; Figure 2-8). Walleye was the only species that had relations in Branched Oak and Pawnee reservoirs for both white perch length-predator length and white perch depth-predator gape regressions. There was no difference between slopes (ANCOVA, $F = 0.72$, $P = 0.40$) for white perch length-walleye length regressions in Branched Oak and Pawnee reservoirs; however, the Branched Oak Lake intercept was greater than Pawnee Lake (ANCOVA, $F = 6.07$, $P = 0.008$). Additionally, there was no difference between slopes (ANCOVA, $F = 2.16$, $P = 0.15$) or intercepts (ANCOVA, $F = 2.87$, $P = 0.09$) for white perch depth-walleye gape regressions in Branched Oak and Pawnee reservoirs.

Discussion

Piscivores in Branched Oak and Pawnee reservoirs consumed smaller prey in relation to predator length (~17% of predator length in Branched Oak Lake and ~18% of predator length in Pawnee Lake [Figure 2-1]) than the typical 20 to 30% of predator length consumed in other studies (Hoogland et al. 1956; Lawrence 1958; Gillen et al. 1981; Hoyle and Keast 1987; Hambright 1991). When comparing sizes of white perch consumed from the stunted population (Branched Oak Lake) with sizes of white perch consumed from the non-stunted population (Pawnee Lake), I obtained a counterintuitive result of larger white perch consumed from the stunted population. I expected larger white perch would be consumed in the reservoir where larger white perch were present (i.e., Pawnee Lake). However, predator size was greater in Branched Oak Lake compared to Pawnee Lake and larger predators should be able to consume larger prey items. White perch grow much faster in Pawnee Lake (Chizinski 2007); perhaps white

perch quickly reach a size refuge from most predators in Pawnee Lake. In Branched Oak Lake, predators consumed the entire size range of white perch sampled by NGPC. In contrast, predators in Pawnee Lake consumed only smaller individuals of the size range of white perch sampled by NGPC. Many white perch in the 160- to 250-mm size range were collected during standardized fish sampling by NGPC; however, no white perch in this size range were removed from the stomachs of predators in this reservoir.

Furthermore, predators in Pawnee Lake were not only consuming smaller white perch, but younger white perch as well. Predators almost exclusively consumed age-0 white perch in Pawnee Lake, whereas predators in Branched Oak Lake consumed a much wider range of ages. This is likely exacerbating the white perch stunting situation in Branched Oak Lake. Removal of larger white perch (via predation) from this population without sufficient predation on smaller, younger white perch likely promotes stunting much like implementing a minimum length limit regulation on a high-density largemouth bass population. Perhaps white perch would be better controlled by a predator community comprised of a high density of smaller-bodied predators instead of the current predator community comprised mainly of a few large-bodied predators. Additionally, the presence of larger white perch may also be important for control of this species in reservoirs. Fishes become increasingly important to white perch diets as white perch grow (Scott and Crossman 1973; Weisberg and Janicki 1990). Perhaps larger white perch can help control or regulate their population abundance via intraspecific predation (i.e., cannibalism).

Differences in white perch age at maturity existed between Branched Oak and Pawnee reservoirs that could be responsible for differences in population structure

between white perch populations within these reservoirs. White perch reached sexual maturity at ages 2 and 4 for males and females, respectively, in Pawnee Lake, whereas males and females reached sexual maturity at ages 1 and 2, respectively, in Branched Oak Lake (Chizinski 2007). Thus, the consumption of smaller, younger white perch in Pawnee Lake is likely the reason white perch were not stunted in this reservoir. White perch in Branched Oak Lake may potentially spawn several times before being consumed, whereas white perch in Pawnee Lake are more likely to be consumed before reaching sexually maturity. Perhaps predators in Pawnee Lake are preventing stunting by exerting sufficient predation pressure on the smaller, younger white perch in this reservoir. Chizinski (2007) suggested that increasing the mortality of smaller, younger white perch (i.e., ages 2 and 3) was important to prevent white perch stunting. Additionally, non-stunted white perch of all ages in Pawnee Lake experienced a mortality rate almost twice that observed in the stunted Branched Oak Lake population further suggesting that predation could be the mechanism preventing stunting in this reservoir (Chizinski 2007).

When controlling for predator length between the two reservoirs (ANCOVA with predator length as the covariate), there was no difference between the slopes or intercepts for white perch length-predator length regressions in Branched Oak or Pawnee reservoirs suggesting that the trends in length of white perch consumed increased similarly with predator length in both reservoirs. Furthermore, when investigating the ratio of length of white perch consumed to predator length, there was little difference between Branched Oak and Pawnee reservoirs suggesting that similarly-sized white perch are being consumed in relation to predator length. In contrast, when controlling for predator gape

between reservoirs (ANCOVA with predator gape as a covariate), there was a difference between slopes for white perch depth-predator gape regressions in Branched Oak and Pawnee reservoirs. Thus, depth of white perch consumed by predators in Pawnee Lake increased at a greater rate for an increase in predator gape than for a similar increase in predator gape in Branched Oak Lake. Quantile regression further clarifies the relation between predator gape and white perch depth; the upper bound for depth of white perch consumed was greater in Branched Oak Lake for predators with a gape < 35 mm, whereas the upper bound for depth of white perch consumed was greater in Pawnee Lake for predators with a gape > 35 mm (Figure 2-6). This interaction likely is caused by differences in morphology of white perch between reservoirs, with body depths of white perch for a given length being greater in Pawnee Lake compared to Branched Oak Lake (Chizinski 2007).

Prey size-predator size relations between the two reservoirs may be different for a given predator species because available sizes of white perch (prey) differed between reservoirs and size structure for the given predator species potentially differed between reservoirs. Walleye was the only species with prey size-predator size relations for either length or gape in both reservoirs. When controlling for walleye length between reservoirs, there was no difference between slopes in Branched Oak and Pawnee reservoirs; however, there was a difference between the intercepts. This suggests that length of white perch consumed by predators increases similarly between reservoirs but consumed white perch are consistently longer in Branched Oak Lake. When controlling for walleye gape between reservoirs, there was no difference in slope or intercept between reservoirs suggesting that the depth of white perch consumed increases similarly

between reservoirs. Chizinsik (2007) documented major morphological differences between stunted (Branched Oak Lake) and non-stunted (Pawnee Lake) white perch and hypothesized that these morphological differences are a result of disparities in allocation of energy towards growth. Non-stunted white perch had smaller heads relative to their body, whereas stunted white perch had shallower and shorter midsections. Thus, white perch with similar body depths were longer in Branched Oak Lake compared to Pawnee Lake.

In general, prey length-predator length regressions yielded more relations (five compared to four) and usually had greater r^2 values than prey depth-predator gape regressions. Thus, my results contradict previous suggestions that prey depth and predator gape are more appropriate for investigating prey size-predator size relations than prey length and predator length (Lawrence 1958; Werner 1977; Tonn and Paszkowski 1986; Hambright 1991). However, measuring gape according to the methods described by Hambright (1991) may not be the best option for all gape-limited piscivores. I only found strong relations (i.e., $r^2 \geq 0.90$) between predator gape and predator length for four of the eight species investigated. Furthermore, one of those four species with strong relations was largemouth bass (the species Hambright used for his research). Therefore, perhaps a different method for measuring predator gape should be used for those species without strong relations between gape and length (i.e., white crappie, channel catfish, and white bass). Sauger did not have a strong relation; however, this is likely a function of the small size range of sauger present in Pawnee Lake. The sauger population in Pawnee Lake is not self-sustaining (i.e., little to no recruitment) and NGPC ceased stocking

sauger in this reservoir (last stocking occurred during 2000); thus, only small numbers of similarly-sized, large sauger were present in this reservoir.

Overall, simple linear regression analyses suggested that larger predators consumed larger prey items. This is not surprising and supports previous findings (Parsons 1971; Knight et al. 1984; Mittelbach and Persson 1998). Quantile regression further supported the finding of larger predators consuming larger prey; however, this regression technique also demonstrated that large predators consume small prey items as well. Slopes and intercepts typically increased with increasing quantile. For example, the 0.1 quantile was usually flat compared to the other quantiles suggesting that all predator sizes consumed small prey items. Although not surprising, these findings are important. Just because a larger predator is physically capable of consuming larger prey items does not mean that it will always do so. Being physically capable is only one of the requirements necessary to consume larger prey. Larger prey must also be available to a predator and that predator must be able to successfully detect and capture the prey item. Optimal foraging theory typically suggests that large prey result in greater foraging efficiency (Werner and Hall 1974); however, optimal foraging models usually predict prey sizes much larger than the sizes actually consumed by predators (Juanes 1994). This overestimation of optimal prey size is likely a function of small prey remaining highly vulnerable to predators and large prey being more difficult for predators to handle. Furthermore, finding that large predators consume large and small prey could be particularly important to predator-prey interactions in Pawnee Lake where white perch have not stunted considering the aforementioned discussion involving the ages of white perch consumed in this reservoir.

Chapter 3. Food Habits of Stunted and Non-stunted White Perch

The white perch (*Morone americana*) is native to the east coast of North America naturally occurring from South Carolina, USA north to Quebec, Canada (Scott and Crossman 1973). In its native range, the white perch is a valuable commercial fish and sportfish (Ballinger and Peters 1978). In Nebraska, however, the white perch is an invasive species with little commercial or recreational value. This invasive species tends to overpopulate in inland waterbodies outside of its native range resulting in fish communities dominated by stunted individuals. White perch were inadvertently stocked into Wagon Train Reservoir, Nebraska during 1964 and dominated the fish community in this reservoir by 1967 (Hergenrader and Bliss 1971). White perch were also discovered in nearby Stagecoach Reservoir two years later with the same result; white perch dominated the fish community in this reservoir three years after first being discovered (Hergenrader 1980b). The NGPC renovated and restocked both of these reservoirs; however, white perch still remained in the Salt Creek drainage and spread as far as 200 km from Wagon Train Reservoir (Ballinger and Peters 1978).

White perch were discovered in Branched Oak Lake, Nebraska during the 1987 NGPC annual gillnet survey (personnel communication, M. T. Porath, NGPC). Within a few years, white perch dominated the biomass of the fish community in Branched Oak Lake. The current white perch population in Branched Oak Lake is stunted. In nearby Pawnee Lake, white perch were discovered in 2001 (Jackson 2008). Similar to Branched Oak Lake, white perch dominated the fish community shortly after discovery in Pawnee Lake; however, white perch are not stunted in this reservoir. Thus, the objective of this

study was to compare food habits of white perch from a stunted population with white perch from a non-stunted population. This information will help identify possible negative effects of white perch on other fishes through competition for food and predation on eggs and larvae.

Methods

Food habits of white perch were investigated during the ice-free period (approximately March through November) of 2006 and 2007 in Branched Oak and Pawnee reservoirs. White perch were captured with a boat-mounted electrofisher (pulsed DC). Each lake was sampled monthly and target sample size was 25 individuals. Captured white perch were euthanized with a lethal dose (1 g/L) of MS-222 and preserved in a 10% buffered-formalin solution. These individuals were weighed to the nearest 0.1 g and measured to the nearest 1 mm. Stomachs were removed via dissection. Individual stomachs were cut open lengthwise and contents were removed. Stomach contents were identified to species for fishes and to order for invertebrates using dichotomous keys provided by Scott and Crossman (1973) and Thorp and Covich (1991), and grouped by taxa. Grouped contents were measured volumetrically using water displacement in graduated cylinders.

Four approaches were used to quantitatively describe seasonal (spring = March-May, summer = June-August, autumn = September-November) diets of white perch: 1) percent empty stomachs; 2) frequency of occurrence; 3) percent composition of volume displaced; and 4) mean stomach fullness. Prey taxa with less than 5% frequency of occurrence and less than 5% percent composition of volume displaced are not presented in summary graphs herein (see Appendix A for a complete summary). Percent empty

stomachs (PES) is the percentage of stomachs of a particular species that are empty and is quantified as:

$$PES = \frac{NumE}{NumT} \times 100$$

where NumE is the number of white perch with empty stomachs and NumT is the total number of a white perch sampled. Empty is defined as a stomach containing no measurable organic material (Arrington et al. 2002). Frequency of occurrence (O_i) is the percentage of stomachs that contain at least one item for a given prey type (Bowen 1996) and is quantified as:

$$O_i = \frac{J_i}{P} \times 100$$

where J_i is the number of white perch containing prey item i and P is the total number of white perch containing prey items in their stomach (i.e., fish with empty stomachs were not included in this assessment). Percent composition of volume displaced is the percentage of volume displaced ($\%V_i$) by a particular prey item in relation to volume displaced by all prey items found in white perch and is quantified as:

$$\%V_i = \frac{V_i}{\sum_{i=1}^Q V_i} \times 100$$

where i is prey type, Q is number of prey categories, V_i is the volume (ml) displaced by prey type i . Mean stomach fullness (MSF_i) is the percentage of maximum stomach capacity for each prey category (Pope et al. 2001) and is quantified as:

$$MSF_i = \frac{1}{P} \sum_{j=i}^P \left(\frac{V_{ij}}{C_j} \times 100 \right)$$

where P is the number of white perch with food in their stomach, j is the individual fish, i is the prey type, V_i is the volume (ml) of food category i and C_j is the stomach capacity of fish j .

I determined stomach capacity for white perch by constructing a stomach capacity-length equation according to the methods of Knight and Margraf (1982). White perch were divided into 10-mm length groups; length groups with fewer than 10 individuals were excluded from analysis. Maximum total volume found in each length group was plotted as a function of the midpoint of each length group. Stomach capacity increases with fish length; thus, length groups for which the plotted stomach capacity was less than the previous two length groups were removed because it was evident that no fish within that length group contained full (or nearly so) stomachs. Remaining data points were used to develop an exponential regression equation relating stomach capacity (ml) of white perch to total length (mm) (Knight and Margraf 1982) (Figure 3-1). Statistical analysis was performed with Curvfit software (Version 2.10-O, Shareware, Thomas S. Cox) and significance was set at $\alpha = 0.05$.

Scattergrams were constructed with the proportion (by volume) of fish prey in stomachs plotted as a function of white perch total length (mm). Logistic regression was used to determine if there was a relation between presence of fish in white perch diets and total length of white perch. White perch with empty stomachs were excluded from this analysis.

Results

In Branched Oak Lake, I captured 173 white perch during 2006; 161 contained prey items. During 2007, I captured 197 white perch in Branched Oak Lake; 146

contained prey items. During both years, cladocerans and dipterans were the most important prey items for white perch with relatively large O_i , $\%V_i$ and MSF_i values during all seasons of 2006 and 2007 (Figures 3-2 and 3-3). Fish (i.e., white perch or unidentifiable fish) were somewhat important ($\%V_i > 15.0\%$ and $MSF_i > 2.5\%$) prey items during the summer of both years and during the autumn of 2007; however, only ~5% of white perch that contained prey items consumed fishes. Fish eggs had a relatively high O_i during the spring of 2007; however, they accounted for very little of the $\%V_i$ and MSF_i (Figure 3-3).

In Pawnee Lake, I captured 162 white perch during 2006; 156 contained prey items. During 2007, I captured 223 white perch in Pawnee Lake; 143 contained prey items. Similar to Branched Oak Lake, cladocerans and dipterans were important prey items during all seasons of 2006 and 2007 (Figures 3-4 and 3-5). Fish eggs and trichopterans were also important prey items during the spring of 2007 (Figure 3-5). Fish were marginally important ($5.0\% < \%V_i < 20.0\%$ and $0.5\% < MSF_i < 1.5\%$) during the summer of 2006 and the autumn of 2007. Similar to Branched Oak Lake, only ~5% of white perch that contained prey items consumed fishes.

Consistent with *a priori* expectations, larger white perch were captured in Pawnee Lake compared to Branched Oak Lake (Figure 3-6). In Branched Oak Lake, white perch did not start consuming fishes until reaching ~120-mm total length (Figure 3-7). There was no relation ($\chi^2 = 0.09$, $P = 0.76$) between presence of prey fish in diets and total length of white perch in Branched Oak Lake. In contrast, white perch did not start consuming fishes in until reaching ~160-mm total length in Pawnee Lake (Figure 3-7).

There was a relation ($\chi^2 = 5.8$, $P = 0.02$) between presence of prey fish in diets and total length of white perch in Pawnee Lake.

Discussion

Food habits of white perch were remarkably similar for the stunted population (i.e., Branched Oak Lake) and non-stunted population (Pawnee Lake). Cladocerans and dipterans were consistently important prey items for both populations during all seasons. This similarity in food habits provides evidence that preventing the stunting of white perch may not benefit other species. Even if the white perch population is shifted to a non-stunted state, assumed competition between white perch and young sportfishes will likely continue because large white perch also relied heavily on invertebrates.

I expected major differences in white perch food habits between reservoirs because the two populations are markedly different. The stunted population is characterized by small, slow-growing individuals that experience much higher survival rates and reach sexual maturity at a much younger age (Chizinski 2007). I only observed two noticeable differences between the food habits of the two populations. First, the importance of fishes in white perch diets was different between reservoirs. I expected fish to be much less important to white perch diets in Branched Oak Lake because individuals do not grow as large in this population. Contrary to my *a priori* expectation, fish were actually slightly more important in the diet of white perch from the stunted population; fish were somewhat important to white perch diets during the summer of 2006 (Figure 3-2) and during the summer and autumn of 2007 (Figure 3-3) in Branched Oak Lake, whereas fish were only somewhat important during the autumn of 2007 in Pawnee Lake (Figure 3-5). Second, I observed differences in the size in which white

perch started consuming fishes. White perch started consuming fishes at ~120-mm total length in Branched Oak Lake (Figure 3-7); however, the length of white perch did not have any effect on the presence of fish in diets. In Maryland, fish were not important in diets until white perch exceeded 200-mm total length (Weisberg and Janicki 1990) and white perch rarely reach 200-mm total length in Branched Oak Lake (Figure 3-6). In Pawnee Lake, fishes became important in white perch diets at ~160-mm total length and the presence of fish in the diet did increase with increasing white perch length. However, the vast majority of white perch, even large white perch (i.e., >200-mm total length) did not consume any fishes in Pawnee Lake (Figure 3-7). Instead, they consumed large quantities of invertebrates.

The observed differences in length in which white perch started consuming fishes between reservoirs could be a function of different prey fishes available within each reservoir. In Branched Oak Lake, white perch and gizzard shad (*Dorosoma cepedianum*) were the major prey fishes available, whereas white perch are the only major prey fish available in Pawnee Lake. Although no gizzard shad were identified, over half of the prey fish found in white perch stomachs were unidentifiable fish. Furthermore, these unidentifiable fish were mainly consumed during summer with a few also being consumed during the autumn. Large numbers of small gizzard were available for consumption by white perch during the summer. Thus, it is possible that many of these unidentifiable fish were gizzard shad. Gizzard shad have a much slenderer morphology compared to white perch and, subsequently, may be susceptible to predation at shorter lengths than white perch.

In Branched Oak Lake, my results were similar to a white perch food habits study conducted during 1999 and 2000 (Hodkin 2001). In this study, white perch mainly consumed cladocerans, copepods, dipterans, fish eggs and fish. I expected no difference in findings between studies because the population of white perch was stunted in 1999-2000. The only difference between the two studies was that copepods and fish eggs were much more frequently observed during 1999 and 2000 than during 2006 and 2007.

As for white perch effects on other species, white perch are likely in direct competition for food resources (assuming food resources are limited) with young sportfishes in both reservoirs. The importance of invertebrates to the diet of white perch in both reservoirs demonstrates that white perch may create a bottleneck for sportfishes before they become piscivorous. Young sportfishes in these two reservoirs are dependent on invertebrates. Walleye (*Sander vitreus*) and sauger (*S. canadensis*) rely heavily on invertebrates until reaching 280-mm total length (Priegal 1963). Flathead catfish (*Pylodictis olivaris*) shift from invertebrates to fishes between 250- and 360-mm total length (Brown and Dendy 1961; Holz 1969; Roell and Orth 1993). Largemouth bass (*Micropterus salmoides*), white crappie (*Pomoxis annularis*), black crappie (*P. nigromaculatus*) and hybrid striped bass (*M. saxatilis* x *M. chrysops*) mainly consume invertebrates until reaching 100- to 200-mm total length (Applegate et al. 1967; Scott and Crossman 1973; Ellison 1984; Hodson 1989). Mansueti (1961) suggested that white perch could drastically affect other fishes by reducing the abundance of invertebrates. Furthermore, walleye have not had a strong year class since 1992 in Branched Oak Lake, despite annual stockings by NGPC (Jackson 1999). The NGPC stocked walleye in various combinations from fry to advanced 200- to 250-mm fingerlings with little

success. Thus, it appears that white perch are capable of out-competing young sportfishes for food before the onset of piscivory.

Competition for food resources is not the only concern regarding white perch and other fishes. White perch may negatively affect other fishes through egg predation, though no study has been able to determine if white perch egg predation has caused significant effects on the recruitment of other fishes. In both reservoirs, fish eggs constituted only a small portion of white perch diets during 2006. However, fish eggs were much more important to white perch diets during 2007 in both reservoirs. In Branched Oak Lake, egg predation was important during the spring of 2007 when eggs were present in 28% of white perch stomachs that contained prey items; however, eggs only accounted for about 7% of the volume displaced. In Pawnee Lake during the spring of 2007, fish eggs were the most important prey item (eggs were present in 24% of fish stomachs while also having the greatest values for $\%V_i$ and MSF_i for that season). Hodkin (2001) concluded that fish eggs were frequently consumed by white perch (present in 40% of stomachs) when abundant during spring 1999 and 2000 in Branched Oak Lake. In Ohio, fish eggs mixed with detritus comprised almost 100% of white perch diets during the spring of 1981 (Schaeffer and Margraf 1987). Madenjian et al. (2000) suggested that egg predation on white bass by white perch was a possible mechanism causing declines in white bass recruitment in Lake Erie. Similarly, white perch may have negatively affected walleye abundance in the Bay of Quinte through egg predation (Hurley and Christie 1977). Thus, even if individual white perch only consume few fish eggs, white perch may still drastically affect other fishes because of the large number of white perch present in both reservoirs. Furthermore, fish eggs are likely an important

prey item for white perch because eggs are rich in calories from a high lipid content (Chotkowski and Marsden 1999).

Chapter 4. Predation as a Potential Mechanism for Biological Control

Fishery biologists face many challenges while attempting to maximize fishing opportunities for anglers. One major challenge for managers is the control (i.e., reduction or elimination) of undesirable fishes. Numerous criteria are used to determine if a species is undesirable including lack of recreational value to anglers and negative affects on native, endangered or popular sportfish populations (Wydoski and Wiley 1999). If a species meets these criteria, fishery managers have a number of options to control undesirable fishes, which are broadly categorized as chemical, mechanical and biological control. Despite prior widespread use of chemicals to control undesirable fishes, this method is losing popularity among fishery agencies (Bettoli and Maceina 1996). Numerous economic, social and political ramifications are involved when conducting chemical lake renovation. Mechanical removal can be successful, but is labor-intensive and usually only a short-term solution (Wydoski and Wiley 1999). Biological control of undesirable fishes, however, is an attractive option to fishery managers. The stocking of piscivores to control undesirable fishes is particularly attractive (Wydoski and Wiley 1999). If successful, this option simultaneously provides increased recreational opportunity (i.e., more predators for anglers to catch) and reduces undesirable fish populations without the use of chemicals or labor-intensive gears. The objective of this study was to evaluate predation as a potential mechanism for biological control of white perch in Branched Oak and Pawnee reservoirs.

Methods

Food habits of piscivorous fishes (largemouth bass [*Micropterus salmoides*], white crappie [*Pomoxis annularis*], black crappie [*P. nigromaculatus*], channel catfish [*Ictalurus punctatus*], flathead catfish [*Pylodictis olivaris*], white bass [*Morone chrysops*], hybrid striped bass [*M. saxatilis* x *M. chrysops*], sauger [*Sander canadensis*] and walleye [*S. vitreus*]) were investigated during the ice-free period (approximately March through November) of 2006 and 2007 in Branched Oak and Pawnee reservoirs. Fishes were captured with a boat-mounted electrofisher (pulsed DC). Each reservoir was sampled biweekly from one hour before to two hours after sunrise and from sunset to three hours after sunset because catchability of fishes is maximized during crepuscular periods (Witt and Campbell 1959). Also, some fishes feed more actively during the day, whereas other fishes feed more actively during the night. Target sample size was 25 stock-length (Gabelhouse 1984; Quinn 1991) individuals per species per month. Captured individuals were weighed to the nearest 1 g and measured (standard and total length) to the nearest 1 mm. Stomach contents of captured fishes were removed using pulsed gastric lavage (Light et al. 1983; Kamler and Pope 2001) and contents were preserved in a 10% buffered-formalin solution. After the stomach was flushed with water, an appropriately-sized clear plastic tube was inserted into the digestive tract and used as a gastroscope to ensure that all stomach contents were removed. Fish were released unharmed after stomach contents were removed.

In the laboratory, all stomach contents were identified to species for fishes and to order for invertebrates using dichotomous keys provided by Scott and Crossman (1973) and Thorp and Covich (1991). Stomach contents were grouped by taxa and measured

volumetrically using water displacement in graduated cylinders. Prey fishes removed from stomachs were measured for standard length (mm) and body depth (mm) when possible.

Four approaches were utilized to quantitatively describe fish diets: 1) percent empty stomachs; 2) frequency of occurrence; 3) percent composition of volume displaced; and 4) mean stomach fullness. Within each season (spring = March-May, summer = June-August, autumn = September-November), species with fewer than 10 individuals that contained prey items were excluded from analyses. Percent empty stomachs (PES) is the percentage of stomachs of a particular species that are empty and is quantified as:

$$\text{PES} = \frac{\text{NumE}}{\text{NumT}} \times 100$$

where NumE is the number of a particular species with empty stomachs and NumT is the total number of a particular species. Empty is defined as a stomach containing no measurable organic material (Arrington et al. 2002). Frequency of occurrence (O_i) is the percentage of stomachs that contain at least one item for a given prey type (Bowen 1996) and is quantified as:

$$O_i = \frac{J_i}{P} \times 100$$

where J_i is the number of a particular species containing prey item i and P is the total number of a particular species containing prey items in their stomach (i.e., fish with empty stomachs were not included in this assessment). Percent composition of volume displaced ($\%V_i$) is the percentage of volume displaced by a particular prey item in

relation to volume displaced by all prey items found in a particular species and is quantified as:

$$\% V_i = \frac{V_i}{\sum_{i=1}^Q V_i} \times 100$$

where i is prey type, Q is number of prey categories, V_i is the volume (ml) displaced by prey type i . Mean stomach fullness (MSF_i) is the percentage of maximum stomach capacity for each prey category (Pope et al. 2001) and is quantified as:

$$MSF_i = \frac{1}{P} \sum_{j=1}^P \left(\frac{V_{ij}}{C_j} \times 100 \right)$$

where P is the number of fish with food in their stomach, j is the individual fish, i is the prey type, V_i is the volume (ml) of food category i and C_j is the stomach capacity of fish j . Stomach capacity equations exist for largemouth bass, white crappie, black crappie, channel catfish and white bass (Table 4-1). The equation for walleye was also used to estimate stomach capacity for sauger. Mean stomach fullness could not be calculated for flathead catfish because no estimate is available for stomach capacity and I collected insufficient data to determine stomach capacity for this species. I developed a stomach capacity equation for hybrid striped bass, as described below.

I determined stomach capacity for hybrid striped bass by constructing a stomach capacity-length equation according to the methods of Knight and Margraf (1982). When determining stomach capacity, hybrid striped bass were divided into 20-mm length groups. Length groups with fewer than 10 individuals were excluded from analysis. Maximum total volume found in each length group was plotted as a function of the midpoint of each length group. Stomach capacity increases with fish length; thus, length

groups for which the plotted stomach capacity was less than the previous two length groups were removed because it was evident that no fish within that length group contained full (or nearly so) stomachs. Remaining data points were used to develop an exponential regression equation relating stomach capacity (ml) to total length (mm) (Knight and Margraf 1982) (Figure 4-1). The PROC NLIN procedure of SAS software (SAS Institute, Cary, North Carolina) was used to obtain species-specific parameters and their associated standard errors for the regression models. Statistical significance was set at $\alpha = 0.05$.

In addition to the aforementioned methods used to quantitatively describe fish diets, foraging success was also used to determine the effect of each predator on white perch and gizzard shad. Foraging success (FS) is the volume of a prey item consumed per kg of a particular predator and is quantified as:

$$FS = \frac{V_i}{W_j}$$

where V_i is the volume (ml) of prey item i (either white perch or gizzard shad) in the stomach of predator j and W_j is the weight (kg) of predator j . Theoretically, foraging success values can range from 0 to infinity, however, in practice, foraging success values generally ranged from 0 to 90 and displayed a highly right-skewed distribution. Foraging success was assessed by year instead of season to increase sample size. I included gizzard shad in this analysis because this species is the other major prey fish available to piscivorous predators in Branched Oak Lake.

A Kruskal-Wallis non-parametric ANOVA was used to detect differences in foraging success on white perch among predators and Dunn's multiple comparison procedure was used for all pairwise comparisons. Species with fewer than 10 individuals

that contained prey items were excluded from analyses. A Kolmogorov-Smirnov test was used to detect differences between foraging success distributions on white perch and gizzard shad for each predator in Branched Oak Lake.

Foraging success is assessed on a per-kg basis (i.e., this method determines the most efficient white perch predators assuming equal biomass for all predators species). Thus, to better understand the effect of each predator species on white perch populations within each reservoir, I used data collected by NGPC to roughly estimate predator biomass by species. Obtaining biomass estimates is difficult. Toxicants are typically used to obtain these estimates (Bettoli and Maceina 1996); however, this was not an option for this study. Therefore, a combination of fish sampling and creel surveys conducted by NGPC was the best alternative available because NGPC standardized fish sampling gives a reasonable estimate of size structure and creel survey data provides a reasonable estimate of abundance. I used the most recent NGPC data in which standardized fish sampling and creel surveys were conducted during the same year (i.e., 2002 data for Pawnee Lake and 2006 data for Branched Oak Lake). I constructed species-specific length-frequency distributions (10-mm length groups) for predator species from the annual standardized fish sampling surveys (i.e., gillnets and trapnets). I then used creel survey data from the same year to calculate a scaling factor (i.e., total number of a particular predator species captured during the creel survey divided by the total number captured during standard fish sampling) that was multiplied by the number of fish in each length category. The resulting abundance estimates for each length group were summed within each species to provide a rough estimate of relative predator abundance. Unfortunately, only a small number of individuals were weighed during

NGPC surveys; therefore, simple linear regressions on my data (log transformed) were used to determine length-weight relations for each predator species within each reservoir. I used the regression equation to estimate the weight of a fish within each length group by using the midpoint of each length group as the independent variable. The estimated weight of a fish of midpoint length for that length group was multiplied by the total number of fish in the length group providing a biomass estimate for the entire length group. Finally, I summed the biomasses for all length groups yielding a biomass estimate for that predator species. For this estimate, black and white crappie were lumped into one group (crappie) because NGPC creel surveys did not distinguish between species. I was unable to calculate biomass for largemouth bass or flathead catfish because no individuals were sampled during the standardized survey in either reservoir. Therefore, I estimated biomass for these two species relative to the other species based on personal observation from my sampling efforts.

Using the biomass estimates and mean foraging success for each predator species, I calculated the total amount of white perch consumed by predator species in a given year. Mean foraging success was determined by combining data from 2006 and 2007 so that I only had one foraging success value for each predator species within each reservoir. I multiplied the mean foraging success times the estimated biomass, which yielded the estimated consumption of white perch for that particular predator species.

Results

Seasonal Quantitative Description of Diets

During 2006, I captured 767 potential white perch predators in Branched Oak Lake; 506 of these predators contained at least one prey item. In Pawnee Lake, I

captured 559 potential white perch predators; 275 of these predators contained stomach samples. I did not capture sufficient numbers of white or black crappie that contained prey items in Pawnee Lake during any season for the seasonal quantitative description of diets during 2006.

During 2007, I captured 702 potential white perch predators in Branched Oak Lake; 376 of these predators contained at least one prey item. I did not capture sufficient numbers of largemouth bass, black crappie or channel catfish containing prey items in Branched Oak Lake during any season for the seasonal quantitative description of diets during 2007. In Pawnee Lake, I captured 310 potential white perch predators; 172 of these predators contained stomach samples. I did not capture sufficient numbers of largemouth bass, white crappie, black crappie, channel catfish or flathead catfish containing prey items in Pawnee Lake during any season for the seasonal quantitative description of diets during 2007.

White perch were consumed during both 2006 and 2007 in Branched Oak Lake with relatively large values for O_i , $\%V_i$ and MSF_i for most of the investigated predators (Appendix B). During 2006, white perch were the most frequent prey item and accounted for the greatest $\%V_i$ and MSF_i values for largemouth bass during autumn, hybrid striped bass during spring and walleye during spring and summer. Furthermore, white perch were the most frequent prey item and accounted for the greatest $\%V_i$ for flathead catfish during summer. Similarly during 2007, white perch were the most frequent prey item and accounted for the greatest $\%V_i$ and MSF_i values for hybrid striped bass during spring and walleye during spring and summer. However, gizzard shad (*Dorosoma cepedianum*) also had relatively large values for O_i , $\%V_i$ and MSF_i for most

of the investigated predators (Appendix B). During 2006, gizzard shad were the most frequent prey item and accounted for the greatest % V_i and MSF_i values for white crappie, hybrid striped bass and walleye during autumn. Similarly during 2007, gizzard shad were the most frequent prey item and accounted for the greatest % V_i and MSF_i values for white crappie during summer and autumn, hybrid striped bass during summer and autumn and walleye during autumn. Most of the gizzard shad consumption occurred later in the year. A major prey shift from white perch to gizzard shad occurred for most of the predators during the late summer or early autumn (Appendix B).

In Pawnee Lake, white perch were heavily preyed on during both 2006 and 2007 with relatively large values for O_i , % V_i and MSF_i for most of the investigated predators (appendix C). During 2006, white perch were the most frequent prey item and accounted for the greatest % V_i and MSF_i values for largemouth bass during all three seasons, white bass during summer, sauger during all three seasons and walleye during summer and autumn. Similarly during 2007, white perch were the most frequent prey item and accounted for the greatest % V_i and MSF_i values for white bass during summer, sauger during summer and walleye during all three seasons. Consumption of other prey fishes was rare in Pawnee Lake.

Foraging Success on White Perch

During 2006, foraging success was different for predators in both Branched Oak and Pawnee reservoirs (Figure 4-2). In Branched Oak Lake, largemouth bass foraging success on white perch was greater than all other predators (Table 4-2). Similarly, walleye foraging success on white perch was greater than all other predators, except largemouth bass and flathead catfish (Table 4-2). In Pawnee Lake, walleye foraging

success on white perch was greater than all other predators, except sauger (Table 4-3). Similarly, largemouth bass and sauger foraging successes were greater than all other predators, except walleye (Table 4-3).

During 2007, foraging success was different for predators in both Branched Oak and Pawnee reservoirs (Figure 4-3). In Branched Oak Lake, walleye foraging success on white perch was greater (~ three times) than any other predator (Table 4-4). Flathead catfish foraging success was less than any other predator (Table 4-4). In Pawnee Lake, walleye and sauger foraging success on white perch was greater than all other predators (Table 4-5). Similar to Branched Oak Lake, flathead catfish foraging success on white perch was the least for all predators although not statistically less than white bass (Table 4-5).

Foraging Success on White Perch and Gizzard Shad

In Branched Oak Lake, foraging success cumulative frequency distributions on white perch compared to gizzard shad were different for largemouth bass, white crappie, flathead catfish, hybrid striped bass and walleye, but not for black crappie and channel catfish (Figure 4-4). Largemouth bass, flathead catfish, and walleye had more individuals with relatively high foraging success values on white perch than gizzard shad. Conversely, white crappie and hybrid striped bass had more individuals with relatively high foraging success values on gizzard shad than white perch.

Largemouth bass, flathead catfish and walleye consumed greater amounts of white perch than gizzard shad on a per-kg basis; therefore, I also investigated differences in foraging success cumulative frequency distributions on white perch among these three predators. Only walleye and flathead catfish had different (KSa = 2.22, $P < 0.0001$)

foraging success cumulative frequency distributions on white perch in Branched Oak Lake (Figure 4-5). Cumulative frequency distributions on white perch were not different when comparing largemouth bass and flathead catfish ($KSa = 1.25$, $P = 0.09$) or largemouth bass and walleye ($KSa = 0.66$, $P = 0.78$) (Figure 4-5).

Predators Present in Both Reservoirs

I also investigated differences in foraging success cumulative frequency distributions on white perch by reservoir for predators present in both reservoirs. For example, I compared largemouth bass foraging success on white perch in Branched Oak Lake to largemouth bass foraging success on white perch in Pawnee Lake. Walleye had different foraging success cumulative-frequency distributions on white perch between reservoirs with greater foraging success values in Pawnee Lake (Figure 4-6). In contrast, largemouth bass, channel catfish and flathead catfish foraging success cumulative-frequency distributions were not different between reservoirs (Figure 4-6).

Estimates of Biomass and Consumption of White Perch

In Branched Oak Lake, channel catfish had the greatest estimated biomass followed closely by crappie and walleye (Table 4-6). Hybrid striped bass had much less estimated biomass than the other predators in Branched Oak Lake (Table 4-6). Largemouth bass were the rarest predator species sampled; thus, I estimated biomass of largemouth bass to be approximately 10% of the next rarest predator species sampled (hybrid striped bass); I estimated flathead catfish biomass to be equal to walleye biomass in this reservoir (Table 4-6). In Pawnee Lake, crappie and walleye had the greatest estimated biomass followed closely by channel catfish (Table 4-6). White bass and sauger each had a much less estimated biomass than the other predators in Pawnee Lake

(Table 4-6). In Pawnee Lake, I estimated largemouth bass biomass to be equal to sauger biomass and flathead catfish biomass to be equal to channel catfish biomass (Table 4-6). The amount of white perch consumed by walleye was dramatically greater than any of the other predators in Branched Oak Lake (Table 4-6). In contrast, the amount of white perch consumed by largemouth bass was dramatically less than any other predator species in this reservoir (Table 4-6). Similarly, in Pawnee Lake, the amount of white perch consumed by walleye was dramatically greater than any of the other predators and the amount of white perch consumed by largemouth bass and sauger was dramatically less than any other predator species (Table 4-6).

Discussion

White perch are heavily preyed on in both reservoirs. In Branched Oak, most predators consume large quantities of white perch during the spring and then shift to consuming large quantities of gizzard shad during mid- to late-summer and throughout autumn. This is not surprising considering the life history characteristics of gizzard shad in this region. Gizzard shad are vulnerable to winter mortality in the Midwest (Willis 1987). There are numerous examples of large overwinter die-offs of gizzard shad in waterbodies near the northern edge of its range (Walburg 1964; Bodola 1955; Mayhew 1975; White 1986; June 1987; Ward 2005; Porath 2006a). Limited winter survival can even lead to extirpation of gizzard shad from a waterbody (Eichner and Ellison 1983). In Lake Mitchell, South Dakota gizzard shad were extirpated during the winter of 1992-1993 (Ward 2005). In southeast Nebraska, gizzard shad were extirpated from seven flood-control reservoirs during the winter of 2000-2001, including Pawnee Lake (Porath 2006a). Porath (2006b) also found that although not extirpated, gizzard shad numbers

were drastically reduced in Branched Oak Lake. Thus, it is not unusual for a large portion of the gizzard population to succumb to harsh conditions during winter leaving few individuals to spawn and repopulate the reservoir the following spring. In Branched Oak Lake during 2006 and 2007, small numbers of large gizzard shad were available to predators during spring. However, after gizzard shad spawned, large numbers of age-0 shad were available to predators beginning mid-summer and continuing throughout autumn.

In Pawnee Lake, most predators consumed large quantities of white perch throughout the ice-free period. This is not surprising because, unlike Branched Oak Lake, the white perch was the only major prey base available to piscivores in Pawnee. White perch tend to overpopulate and stunt in freshwater systems (Scott and Crossman 1973). The lack of another major prey base (i.e., absence of gizzard shad) in Pawnee may be the reason that white perch are not stunted in this reservoir; that is, predators are likely consuming sufficient quantities of white perch to offset their production and prevent stunting of this species. White perch also have a lower annual adult survival rate in Pawnee (0.39) compared to Branched Oak (0.68) suggesting that predation pressure on white perch is greater in Pawnee (Chizinski 2007). Thus, if predator densities are at least maintained at current levels in Pawnee Lake, stunting of white perch should be prevented in this reservoir. However, catch rates for most of the predators in Pawnee Lake declined (in some cases dramatically) during the last year or two while the catch rate for white perch drastically increased (Jackson 2008). Furthermore, of the predators present in both Branched Oak and Pawnee reservoirs, only walleye had greater foraging success values on white perch in Pawnee Lake compared to Branched Oak Lake. Perhaps foraging

success on white perch is not correlated with of white perch mortality in these waterbodies because biomass of predators is not equal among reservoirs.

Largemouth bass and *Sander* species were the most efficient white perch predators, assuming equal biomass among predators, in Branched Oak and Pawnee reservoirs (i.e., these predators had the greatest foraging success on white perch). However, predator biomass is not equal. Based on my relative estimates of the amount of white perch consumed (a function of predator biomass and foraging success), walleye and channel catfish are having the greatest effect on the Branched Oak Lake white perch population. In contrast, flathead catfish, hybrid striped bass and largemouth bass are having little overall effect on the white perch population in this reservoir. However, flathead catfish abundance may have been underestimated in the creel survey because creel surveys occur during the day and flatheads are commonly targeted by anglers at night. Furthermore, flathead catfish consumed greater amounts of white perch than gizzard shad in Branched Oak Lake on a per-kg basis (Figure 4-4), although flathead catfish are likely having little effect on white perch because flathead catfish consumed relatively small amounts of white perch compared to other predators (Figures 4-2 and 4-3). In Pawnee Lake, walleye are having a drastically greater effect on white perch than any of the other predators, whereas largemouth bass and sauger are having little effect because of low population biomass. My estimates of relative biomass should be used with extreme caution for several reasons. First, there is obvious gear bias associated with standardized fish sampling surveys (i.e., largemouth bass and flathead catfish were not sampled). Second, some species may be underrepresented in creel surveys (e.g., flathead catfish). Third, creel surveys were conducted infrequently in Pawnee Lake (i.e., 2002

was the most recent year with creel and standardized fish sampling data) and fish populations in reservoirs are dynamic. Thus, my estimates may not be accurate. For example, crappie were unlikely to have the greatest biomass in Pawnee Lake during 2006 and 2007 as my estimate indicates. During both of my field seasons, I captured small numbers of crappie relative to other species. Furthermore, catch rates for crappie during 2006 and 2007 were drastically lower than catches from the previous 11 years (Jackson 2008).

If the primary management objective for Branched Oak and Pawnee reservoirs is control of white perch populations, fishery biologists should manage these reservoirs by attempting to shift predator biomass toward walleye and largemouth bass. This recommendation presents major challenges for the biologists of Branched Oak and Pawnee reservoirs. First, largemouth bass were present in extremely small numbers in both reservoirs. In fact, largemouth bass were almost nonexistent during 2007. Prior to spring 2007, both reservoirs lacked suitable littoral habitat for largemouth bass. Both reservoirs were dominated by open-water turbid areas with some areas of rock habitat. In Branched Oak Lake, water levels were down between 2001 and 2006 because biologists lowered water levels approximately 1.5 m for boat ramp maintenance and drought conditions prevented refilling of the reservoir. During the low-water period, terrestrial vegetation was established on the exposed shorelines. Over 70% of the shoreline consisted of small trees and saplings (NGPC, unpublished data). Heavy spring rains during 2007 raised water levels to conservation pool. Now the littoral zone of Branched Oak Lake is dominated by flooded trees and saplings. This newly available habitat prompted fishery biologists to stock largemouth bass into Branched Oak Lake. The

effects of this stocking on the white perch population, if any, will likely not be evident for several years. However, even if the stocking is successful and the largemouth bass have an effect on white perch, this will likely be a temporary solution because the abundance of new littoral habitat is not permanent. Second, walleye recruitment is poor in Branched Oak and Pawnee reservoirs. In Branched Oak Lake, walleye have not had a strong year class since 1992, despite annual stockings by NGPC (Jackson 1999). Managers have attempted walleye stockings from fry to advanced 200- to 250-mm fingerlings in various densities with little success (personnel communication, M. T. Porath, NGPC). It is possible that white perch are out-competing these stocked walleye for food. Previous research suggests that white perch may negatively affect fishes that feed on invertebrates through competition for food (Ballinger and Peters 1978). Mansueti (1961) suggested that white perch have the potential to reduce the abundance of invertebrates and alter the composition of the invertebrate community. This effect on the invertebrate community could affect piscivorous fishes that rely on invertebrates during early life history (i.e., stocked walleye). In Lake Erie, the invasion of white perch likely increased mortality of white bass during their early life history causing declines in white bass recruitment (Madenjian et al. 2000).

The presence of gizzard shad is another major challenge to the success of biological control via predation in Branched Oak. My results indicate the gizzard shad, in addition to white perch, are also heavily consumed in this reservoir. During 2006 and 2007 both hybrid striped bass and white crappie consumed greater amounts of gizzard shad than white perch. Piscivores will generally select soft-rayed fishes (e.g., gizzard shad) over spiny-rayed fishes (e.g., white perch) when given the choice (Beyerle and

Williams 1968; Mauck and Coble 1971; Wahl and Stein 1988; Knight and Vondracek 1993). Furthermore, gizzard shad had a greater caloric density than any of the other investigated freshwater fishes (Miranda and Muncy 1989), including white perch; therefore, piscivores may also select gizzard shad over white perch. Thus, the presence of another major prey fish likely reduces predation pressure on white perch in Branched Oak Lake. Even if the predators of Branched Oak Lake could effectively reduce white perch populations, predators would likely shift to gizzard shad once white perch became more difficult to capture due to lower abundance. This would likely allow the white perch population to rebound shortly after the prey shift. Model simulations investigating white perch removal suggest that a one-time reduction will not be sufficient to keep a white perch population from returning to preremoval stunted conditions (Chizinski 2007).

Predation as a biological control has experienced some success in previous studies. Flathead catfish have successfully controlled stunted or undesirable fishes in small hatchery ponds (Hackney 1966; Swingle 1967; Crowell 1976). Bamberg (1975) concluded that flathead catfish successfully controlled stunted centrarchids in a 259-hectare reservoir in Texas. However, predation as a biological control is often unsuccessful. Largemouth bass and walleye were ineffective in controlling yellow bass (*Morone mississippiensis*), a closely related species to the white perch, in Twelve Mile Lake, Iowa because these predators selected bluegill (Sobotka 2005). Largemouth bass were also ineffective in controlling yellow bass in Viking Lake, Iowa because this predator selected other prey items over this moronid (Larson and Boucher 2005). Furthermore, stocking of sportfishes to control other fishes was the least successful

control method in a review of fish control projects (Meronek et al. 1996); this method was only successful 21% of the time.

Predation as a biological control is likely not a viable option in Branched Oak and Pawnee reservoirs. Managing for the most effective predators (i.e., largemouth bass and walleye) is extremely difficult in these two reservoirs. If managers are unable to increase biomass of largemouth bass and walleye, then white perch will probably not experience sufficient predation pressure. Low success rates for predator biological control projects and the presence of another major prey fish (i.e., gizzard shad) in Branched Oak Lake provide additional evidence against the feasibility of successful biological control of white perch using predation. Furthermore, Chizinski (2007) concluded that only extreme declines in white perch biomass (i.e., $\geq 90\%$) would alter white perch from the stunted state in Branched Oak Lake. Not only are extreme declines in biomass necessary, but increased predation pressure is also necessary to change the ecological conditions causing white perch to stunt (Chizinski 2007). Using predation in combination with other control methods is a possible option. Meronek (1996) found that stocking fishes to control other fishes after chemical or physical treatments was more successful than using chemical treatments, physical treatments, or stocking alone. Furthermore, using a combination of chemical and physical treatments resulted in the greatest success rate (66%). However, sample size was extremely low for this control method; only six control projects using a combination of chemical and physical treatments were found in their literature review.

In the future, the use of genetic modification (i.e., autocidal technology) has the potential to be an effective control technique for invasive species. For example, geneticists could use a gender distortion approach resulting in either all male or all female

offspring eventually resulting in the prevention of future generations. A thorough review of genetic methods for the control of invasive species is provided by Thresher (2008). In summary, the author suggested that genetic control of invasive species could be an extremely appealing method for the following reasons: an ability to target a particular species, sex, or life-history stage, an ability to reverse the effects of genetic modification, and an ability to easily adapt the gene to act on a new target species. However, there are some downsides to the genetic approach. First, successful control of the targeted invasive species will likely be a slow process usually taking at least 10 generations. However, this could also be considered an advantage because it allows the system to slowly adjust and gives scientists time to fine-tune the approach if unexpected problems or complications occur. Second, high stocking rates (up to 5% of natural recruitment) over a long period will likely be necessary, which means hatcheries may not be able to handle such high demand. Third, the general public may not approve of the genetic modification technique. Fourth, there is uncertainty regarding which agency should regulate the use of genetically modified fish as it currently does not fall under the guise of any agency. Fifth, this technique is developing slowly because of a lack of funding and slow generation times. Thus, genetic modification has potential for control of invasive species such as white perch; however, it will likely not be a viable option in the immediate future.

One potentially important factor that I did not investigate was the effect of predator hunting mode on white perch and its effect on predator-prey dynamics and ultimately the fish community. Animals are usually classified as either ambush (i.e., waits for prey) or cruise (i.e., actively searches for prey) predators (Greene 1983). An

ambush predator such as largemouth bass (Helfman 1981) could potentially alter prey behavior, and hence food habits of a highly mobile species such as white perch more so than a cruise predator such as a white bass. For example, Schmitz (2008) investigated the effect of spider hunting mode (ambush versus active-searching) on an herbivorous grasshopper. Different hunting modes had drastically different effects on grasshopper behavior and, subsequently, indirectly affected plant community composition. Therefore, future research on hunting mode may be important to predicting predator effects on ecosystems (Schmitz 2007, 2008). For example, shifting predator biomasses (e.g., increasing biomass of one species while decreasing biomass of another) and, subsequently, hunting modes in a reservoir such as Branched Oak Lake could have cascading effects on white perch and other organisms in the food web (Preisser et al. 2005).

Chapter 5. Using Stable Isotopes to Determine Trophic Position and Complement Traditional Food Habits Methods for Piscivores

Stable isotope analysis is a relatively new technique in determining food habits of fishes. This method provides a relatively easy and inexpensive way to complement traditional stomach contents analysis; however, it should not be substituted in place of traditional techniques (Rounick and Winterbourn 1986). Traditional techniques can sometimes misrepresent true energy flows in aquatic systems and may only give a short-term view of fish diets (Rounick and Winterbourn 1986; Herwig et al. 2004). Stable isotopes, however, provide relatively long-term information regarding which prey items have been assimilated into the consumer's muscle tissue and allow determination of trophic position for a given species within a waterbody (Peterson and Fry 1987).

Stable isotope ratios of $^{13}\text{C}:^{12}\text{C}$ ($\delta^{13}\text{C}$) can be used to investigate if the prey fish observed in predators' stomachs have similar ratios to the predators. Similar $\delta^{13}\text{C}$ ratios suggest long-term consumption of a particular prey fish. Stable isotope ratios of $^{15}\text{N}:^{14}\text{N}$ ($\delta^{15}\text{N}$) can be used to investigate if predators are in a similar trophic position. Similar $\delta^{15}\text{N}$ ratios suggest similar predator trophic position. Enrichments of 0-1‰ and 3-5‰ in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, respectively, typically occur in predatory organisms relative to their prey (Fry and Sherr 1984; Peterson and Fry 1987). These enrichments occur because organisms expel lighter isotopes (i.e., ^{12}C and ^{14}N) quicker than heavier isotopes (i.e., ^{13}C and ^{15}N) (Peterson and Fry 1987). Thus, stable isotopes ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) were used to complement traditional food habits techniques by tracing diets of piscivores and determining trophic position of fishes in Branched Oak and Pawnee reservoirs.

Methods

Stable isotope analysis was conducted according to the methods described in Olson (2004) and Olson et al. (2007). Five prey fish from each size category (40-59 mm, 60-79 mm, 80-99 mm and ≥ 100 mm) and five predators from each length category (S-Q = stock to quality length, Q-P = quality to preferred length, P-M = preferred to memorable length, M = memorable length [P-M and M were combined into a single length group (P = preferred length) for hybrid striped bass (*Morone saxatilis* x *M. chrysops*)] [Gabelhouse 1984]) were collected for stable isotope analysis. White perch (*M. americana*) were the dominant prey fish available to predators in Pawnee Lake and white perch and gizzard shad (*Dorosoma cepedianum*) were the dominant prey fishes available to predators in Branched Oak Lake. Therefore, white perch and gizzard shad were considered prey species regardless of size. Furthermore, fish less than stock length were also considered prey species for this analysis (e.g., 80-99 mm white crappie [*Pomoxis annularis*]). All stock-length fish, except white perch, were considered predators.

Most fishes were captured in conjunction with annual autumn gillnet surveys conducted by the Nebraska Game and Parks Commission (NGPC). However, I had to conduct supplemental sampling during the following spring and summer to obtain some fishes. Therefore, seasonal variability was assessed in isotopic signatures for species captured during different seasons because tissue replacement can affect isotopic signatures. This affect on isotopic signatures is a function of growth (Hesslein 1993; Vander Zanden et al. 1998; Maruyama et al. 2001) and metabolic rates (Herzka et al. 2001; Logan et al. 2006) of fishes. Only prey species found in predator stomachs were

used for the stable isotope analysis. I removed approximately 10 g of dorsal muscle tissue from a side of the large fish and froze the tissue. Fish that were too small to fillet were frozen whole and the intestinal tract was removed. For the smallest fishes, a composite sample of two individuals was required to obtain a sufficient amount of muscle tissue for analysis. Samples were dried at 65°C and ground to powder with a mortar and pestle. Isotopic signatures for ^{15}N and ^{13}C were determined at the Plant Science Department at South Dakota State University, Brookings, South Dakota. Isotope ratios were determined using the following formula:

$$\delta X(\text{‰}) = \left\{ \left(\frac{R_{\text{sample}}}{R_{\text{standard}}} \right) - 1 \right\} \times 1000$$

where X is ^{13}C or ^{15}N , R is $^{13}\text{C}:^{12}\text{C}$ or $^{15}\text{N}:^{14}\text{N}$, and standard is the Pee Dee Belemnite limestone for carbon or atmospheric nitrogen for nitrogen.

Results

Isotopic signatures were similar for white crappie captured in Branched Oak Lake during different seasons (Figure 5-1 A). However, hybrid striped bass isotopic signatures were noticeably different by season (Figure 5-1 B). In Pawnee Lake, white bass (*M. chrysops*) (Figure 5-2 A) and sauger (Figure 5-2 B) had little seasonal variation in isotopic signatures. Thus, season had little effect on isotopic signatures for species collected during different seasons, except for hybrid striped bass. Therefore, I combined samples collected during different seasons for analysis.

In Branched Oak Lake, I was unable to capture sufficient numbers of all predators and all length categories sampled during the food habits analysis. For predators captured in sufficient numbers, I found similar values of $\delta^{13}\text{C}$ for all predators, except channel catfish (*Ictalurus punctatus*), and all possible prey fishes, except for 100 to 129-mm

white perch (Figure 5-3). Gizzard shad were less enriched in ^{13}C compared to most of the predators; however, $\delta^{13}\text{C}$ values for this species were highly variable (Figure 5-3). I found greater $\delta^{15}\text{N}$ values for all stock-length predators compared to potential prey fishes; however, some predators (stock- to quality-length and quality- to preferred-length flathead catfish [*Pylodictis olivaris*], preferred- to memorable-length white crappie and preferred- to memorable-length walleye [*Sander vitreus*]) had noticeably greater $\delta^{15}\text{N}$ values compared to other predators (Figure 5-3). Further, many predators (stock- to quality-length and quality- to preferred-length channel catfish and stock- to quality-length walleye) had only slightly greater $\delta^{15}\text{N}$ values compared to most of the possible prey fishes sampled, excluding gizzard shad (Figure 5-3). Gizzard shad had noticeably lesser $\delta^{15}\text{N}$ values compared to all other fishes sampled (Figure 5-3).

Similar to Branched Oak Lake, I was also unable to capture sufficient numbers of all predators and all length categories sampled during the food habits analysis in Pawnee Lake. For predators captured in sufficient numbers, I found similar $\delta^{13}\text{C}$ values for all predators and potential prey fishes except for small, 100 to 249-mm walleye (Figure 5-4). Stock- to quality-length white perch were noticeably more enriched in ^{13}C than quality to preferred-length white perch (Figure 5-4). I found greater $\delta^{15}\text{N}$ values for all stock-length predators compared to 60 to 79-mm bluegill (*Lepomis macrochirus*) and stock- to quality-length white perch (Figure 5-4). Some predators (preferred- to memorable-length and memorable-length sauger [*S. canadensis*] and quality- to preferred-length walleye) had noticeably greater $\delta^{15}\text{N}$ values compared to other predators (Figure 5-4). Further, many predators (quality- to preferred-length channel catfish, stock- to quality-length walleye and quality- to preferred-length white crappie) had only slightly greater $\delta^{15}\text{N}$

values compared to quality to preferred-length white perch and these predators actually had lesser $\delta^{15}\text{N}$ values compared to some prey fishes (bluegill >99 mm and walleye 100 to 249-mm) (Figure 5-4).

Discussion

In Branched Oak Lake, $\delta^{15}\text{N}$ values make trophic position determination among fishes difficult at best. It appears that there may be just two functional trophic positions among fishes in this reservoir with only gizzard shad occupying the lower trophic position. One could argue that flathead catfish, preferred- to memorable-length walleye and preferred- to memorable-length white crappie occupied a higher trophic position than the other predators. However, this is counterintuitive because one of the other predators was memorable-length white crappie; it seems illogical to place memorable-length white crappie in a lower trophic position than preferred- to memorable-length white crappie.

Time of fish collection is a potential source of variability for isotopic signatures. I collected most fishes for stable isotope analysis in conjunction with annual autumn gillnet surveys conducted by NGPC. However, I had to conduct supplemental sampling during the following spring and summer. Thus, the turnover rate of dorsal muscle tissue within and among fishes collected during different seasons could have affected my results. Isotopic turnover rates in fishes are usually attributed to growth (i.e., faster growing fishes have a faster turnover rate) (Hesslein 1993; Vander Zanden et al. 1998; Maruyama et al. 2001); although, metabolic activity can also significantly affect isotopic turnover rate in fishes (Herzka et al. 2001; Logan et al. 2006). Fishes may have isotopic tissue turnover rates spanning months to years, depending on growth rates (Hesslein et al. 1993); however, muscle tissue turnover rate is usually slower compared to other tissues

(e.g., liver tissue) (Jackim and LaRoche 1973; Fauconneau and Arnal 1985; Perga and Gerdeaux 2005; Logan et al. 2006). Whitefish (*Coregonus nasus*) muscle tissue took over a year to accurately display a diet shift using ^{13}C and ^{34}S signatures (Hesslein et al. 1993). MacAvoy et al. (2001) determined that blue catfish (*I. furcatus*) ^{13}C , ^{15}N and ^{34}S isotopic turnover rates, including dorsal muscle tissue, were slow and that isotopic determination of a prey shift after three months was not possible. Migratory goby (*Rhinogobius* sp.) ^{15}N signatures decreased rapidly after a prey shift ($\sim 3\%$) during the first three months of the study (i.e., a period of rapid growth) and only decreased $\sim 0.9\%$ during the following nine months of the study demonstrating the variability of isotopic signatures due to muscle tissue turnover rate (Maruyama et al. 2001). Therefore, I examined the isotopic ratios and associated variances by season for fishes collected during different seasons (sauger and white bass in Pawnee Lake and hybrid striped bass and white crappie in Branched Oak Lake) to assess the potential effect of muscle tissue turnover rate. For all species collected in different seasons, except hybrid striped bass, there was no seasonal effect on isotopic signatures of C or N. The observed difference for hybrid striped bass could be a function of rapid growth by hybrid striped bass resulting in faster turnover rates of muscle tissue for this species. As for the consumption of particular prey items in Branched Oak Lake, the $\delta^{13}\text{C}$ values suggest that channel catfish consumed smaller white perch (100-129 mm and stock to quality length), whereas all other predators consumed larger white perch (quality to preferred length). The $\delta^{13}\text{C}$ values of predators relative to the $\delta^{13}\text{C}$ values of stock- to quality-length white perch and >99 mm gizzard shad suggest that these prey fishes were consumed by all of the predators. Especially when factoring the standard errors, these $\delta^{13}\text{C}$ values are well

within typical enrichment of 0-1‰ expected between predators and their prey.

Interestingly, white perch removed from predator stomachs that were measurable were usually much smaller (Chapter 2) than the size classes of white perch that appear assimilated into predator muscle tissue.

Similar to Branched Oak Lake, trophic position determination using $\delta^{15}\text{N}$ values was difficult in Pawnee Lake. Preferred- to memorable-length and memorable-length sauger and quality- to preferred-length walleye occupied the highest trophic positions and bluegill 60-70 mm, stock- to quality-length and quality- to preferred-length black crappie, stock- to quality-length white crappie and stock- to quality-length white perch occupied the lowest trophic positions. Further, the other fishes investigated may have comprised their own intermediate trophic position or may have fallen into the previously aforementioned highest and lowest trophic positions. Like Branched Oak Lake, time of fish collection was also a source of variability for stable isotope analysis for Pawnee Lake. As for the consumption of particular prey items in Pawnee Lake, the $\delta^{13}\text{C}$ values suggest that all predators consume white perch, which was observed in the food habits study (Appendix C). This is not surprising because white perch are the dominant forage fish in Pawnee Lake. However, predators had more similar $\delta^{13}\text{C}$ values compared to smaller white perch (S-Q) than larger white perch (Q-P) suggesting that predators may be more effective at capturing smaller white perch in Pawnee Lake. Most of the white perch found in predator stomachs that were measurable (i.e., not highly digested) were much smaller (Chapter 2) than the size classes of white perch that appear assimilated into predator muscle tissue. However, I did not capture any white perch smaller than stock-

length in Pawnee Lake for stable isotope analysis; thus, perhaps these smaller white perch would have shown similar $\delta^{13}\text{C}$ values to predators.

Overall stable isotope analysis supported the findings from the traditional food habits assessment. White perch are heavily consumed in both reservoirs and gizzard shad are also an important prey item in Branched Oak Lake. The only noticeable difference between the stable isotope analysis and the traditional food habits was some discrepancy between sizes of white perch consumed. However, an inability to capture white perch less than stock length and, subsequently, an inability to conduct isotope analysis on this size range could explain the discrepancy. Furthermore, an ability to capture all fishes at the same time (i.e., during autumn) would have reduced uncertainty and improved my stable isotope results. However, that was not possible. For example, flathead catfish were not captured in NGPC's autumn gillnets and they are not effectively electroshocked until the late spring or early summer. Additionally, an ability to capture all species observed in the food habits study would have provided more information. However, this was difficult considering the erratic nature of reservoir fish populations. For example, largemouth bass all but disappeared during my sampling efforts in both reservoirs after I decided to conduct stable isotope analysis.

Chapter 6. Future Management and Research

Research reported herein was applied in nature and initiated because concerns existed with regard to changes in fish communities after the establishment of white perch (*Morone americana*), an estuary species that has become established in Midwest waterbodies. Thus, it is logical to provide guidance for future management and research. Below are recommendations for consideration.

Using information gained from my research, I conclude that a predator community consisting of a low density of large-bodied individuals in combination with the presence of another major prey base (e.g., gizzard shad [*Dorosoma cepedianum*]) likely promotes stunting of white perch. As such, the current predator population in Branched Oak Lake has reinforced the stunted nature of the white perch population despite finding that all of the predators present in this reservoir consume white perch. Much like northern pike (*Esox lucius*) target the largest yellow perch (*Perca flavescens*) in natural lakes resulting in a decreased size structure of yellow perch (Margenau 1995; Paukert and Willis 2003), the large-bodied predators in Branched Oak Lake, when not consuming gizzard shad, target the largest and oldest white perch resulting in a decreased size structure of white perch. In contrast, the current predator population in Pawnee Lake has likely slowed or prevented the transition of the white perch population to a stunted state because the smaller-bodied predators target smaller and younger white perch throughout the year. Furthermore, no other major prey base currently exists for piscivores in Pawnee Lake. I determined that smaller-bodied predators in Pawnee Lake consumed smaller, younger (i.e., 99% of consumed white perch were age 0) white perch

before these white perch had an opportunity to spawn. White perch spawn at ages 2 and 4 for males and females, respectively, in Pawnee Lake (Chizinski 2007), whereas large-bodied predators in Branched Oak Lake consumed larger, older (42% of consumed white perch were age 1 or older) white perch that generally had at least one opportunity to spawn. White perch spawn at ages 1 and 2 for males and females, respectively, in Branched Oak Lake (Chizinski 2007). These differences in predation patterns on white perch will result in differences in population dynamics and resulting age and size structures, as were observed in Branched Oak and Pawnee reservoirs.

Branched Oak Lake is currently a trophy fishery, which has been second in the state of Nebraska in total number of Master Angler Awards during recent years (personnel communication, D. L. Bauer, NGPC). Given my conclusion above, biologists and the general public must realize that if the management objective is to restructure the white perch population via predation then the current trophy fishery at Branched Oak Lake will have to be sacrificed and replaced with a high-density of small-bodied predators. The addition of small-bodied predators to the large-bodied predator community currently present will not relieve predation on the larger, older white perch and is unlikely to establish a sufficient density of predators to exert adequate predation to offset the reproductive capability of white perch. Fisheries management principles dictate that a biologist cannot have a predator population consisting of trophy-sized individuals in high density. Thus, just as managers and anglers must make choices between few large fish or many small fish, a decision must be made between maintaining the current trophy fishery with a stunted white perch population in Branched Oak Lake or

establishing a high-density predator population capable of restructuring the white perch population.

Pawnee Lake is currently a popular fishery that attracts a variety of anglers; yet, the abundance of white perch has increased exponentially and growth rates of individual fish have slowed (likely a density-dependent mechanism) causing concern that the fish community may be transitioning to a state similar to that in Branched Oak Lake (personnel communication, J. Jackson, NGPC). Given my conclusion above, Pawnee Lake is a prime candidate for a manipulation of the predator community in an effort to establish a high-density of small-bodied predators that would feed heavily on small, young white perch. Chizinski (2007) modeled population dynamics of white perch and suggested that increasing the mortality of smaller, younger white perch was important to prevent white perch stunting. I believe that it is feasible to create a high-density community of predators capable of controlling white perch in Pawnee Lake because the food web is simple with white perch being the only major prey base available to piscivores. I recommend the continuation of walleye stocking and the addition of largemouth bass (*Micropterus salmoides*) and white bass (*Morone chrysops*) stocking in Pawnee Lake. Further, I recommend the continuation of a 38-cm (15-in) minimum length limit for walleye and largemouth bass, the implementation of a 25-cm (10-in) minimum length limit on white crappie and a 35-cm (14-in) minimum length limit on all moronids. The objective behind these recommendations is to increase the density of small-bodied predators, minimize the density of large-bodied predators and avoid removal of large white perch by piscivores and anglers alike. I anticipate that harvest would be intense on large-bodied predators given current levels of angling pressure. The

key for success to these length limits is consistent recruitment of these predators. Further research is needed to document the success of these management actions to (1) increase density of small-bodied predators and (2) increase mortality and growth rates of white perch and their subsequent size structure. If these measures successfully increase the size structure of white perch in Pawnee Lake, then lessons learned from this future research could be applied to the more difficult environment in Branched Oak Lake. Further, modeling analyses indicate that only drastic reductions in white perch biomass (i.e., biomass reductions $\geq 90\%$) would be sufficient to drastically alter the white perch population in Branched Oak Lake (Chizinski 2007). Achieving white perch biomass reductions $\geq 90\%$ may not be possible with predation as the only mechanism used to remove white perch from this reservoir. Thus, mechanisms in addition to predation, such as mechanical or chemical removal, may be necessary to restructure the Branched Oak Lake white perch population.

References

- Applegate, R. L., J. W. Mullan, and D. I. Morais. 1967. Food and growth of six centrarchids from shoreline areas of Bull Shoals Reservoir. Proceedings of the Annual Conference of the Southeastern Association of Game and Fish Commissioners 20:469-482.
- Arrington, D. A., K. O. Winemiller, W. F. Loftus, and S. Akin. 2002. How often do fishes "run on empty"? Ecology 83:2145-2151.
- Ballinger, R. E., and E. J. Peters. 1978. Impact of an introduced fish species (*Morone Americana*) on the fisheries resource of Nebraska. Partial Technical Completion Report and Annual Progress Report, University of Nebraska-Lincoln.
- Bamberg, R. M. 1975. Experimental management of Lake Sweetwater. Texas Parks and Wildlife Department, Federal Aid Project F-31-R-1, Final Report, Austin.
- Bettoli, P. W., and M. J. Maceina. 1996. Sampling with toxicants. Pages 303-333 in B. R. Murphy and D. W. Willis, editors. Fisheries techniques, 2nd edition. American Fisheries Society, Bethesda, Maryland.
- Beyerle, G. B., and J. E. Williams. 1968. Some observations of food selectivity by northern pike in aquaria. Transactions of the American Fisheries Society 97:28-31.
- Bliss, Q., and S. Schainost. 1974. Middle Platte Basin stream inventory report. Nebraska Game and Parks Commission, Aquatic Wildlife Division, Bureau of Wildlife Services, Lincoln.

- Bodola, A. 1955. The life history of the gizzard shad, *Dorosoma cepedianum* (Lesueur), in western Lake Erie. Doctoral dissertation. The Ohio State University, Columbus.
- Bowen, S. H. 1996. Quantitative description of the diet. Pages 513-529 in B. R. Murphy and D. W. Willis, editors. Fisheries techniques, 2nd edition. American Fisheries Society, Bethesda, Maryland.
- Brown, B. E., and H. S. Dendy. 1961. Observations on the food habits of the flathead and blue catfish in Alabama. Proceedings of the Annual Conference of the Southeastern Association of Game and Fish Commissioners 15:219-222.
- Burr, B. M., D. J. Eisenhour, K. M. Cook, C. A. Taylor, G. L. Seegert, R. W. Sauer, and E. R. Atwood. 1996. Nonnative fishes in Illinois waters: what do the records reveal? Transactions of the Illinois Academy of Science 89:73-91.
- Carlander, K. D. 1997. Handbook of freshwater fish biology, volume 3. Iowa State University Press, Ames.
- Chipps, S. R., and J. E. Garvey. 2007. Assessment of diets and feeding patterns. Pages 473-514 in C. S. Guy and M. L. Brown, editors. Analysis and interpretation of freshwater fisheries data. American Fisheries Society, Bethesda, Maryland.
- Chizinski, C. J. 2007. Variation in life-history traits and morphology of stunted and non-stunted fish. Doctoral dissertation. Texas Tech University, Lubbock.
- Chotkowski, M. A., and J. E. Marsden. 1999. Round goby and mottled sculpin predation on lake trout eggs and fry: field predictions from laboratory experiments. Journal of Great Lakes Research 25:26-35.

- Christie, W. J. 1972. Lake Ontario: effects of exploitation, introductions, and eutrophication on the salmonid community. *Journal of the Fisheries Research Board of Canada* 29:913-929.
- Crowell, T. E. 1976. Effectiveness of flathead catfish as an auxiliary predator. North Carolina Wildlife Resources Commission, Federal Aid Project F-21-5, Final Report, Raleigh.
- Eichner, D., and D. G. Ellison. 1983. Lake McConaughy fishery investigations. Nebraska Game and Parks Commission, Federal Aid in Fish Restoration, Project F-51-R-5, Performance Report, Study 6, Lincoln.
- Ellison, D. G. 1984. Trophic dynamics of a Nebraska black crappie and white crappie population. *North American Journal of Fisheries Management* 4:355-364.
- Emlen, J. M. 1966. The role of time and energy in food preference. *American Naturalist* 100:611-617.
- Fauconneau, B., and M. Arnal. 1985. In vivo protein synthesis in different tissues and the whole body of rainbow trout (*Salmo gairdnerii* R.). Influence of environmental temperature. *Comparative Biochemistry and Physiology A-Physiology* 82:179-187.
- Fry, B., and E. B. Sherr. 1984. $\delta^{13}\text{C}$ measurements as indicators of carbon flow in marine and freshwater ecosystems. *Contributions in Marine Science* 27:13-47.
- Gabelhouse, D. W., Jr. 1984. A length-categorization system to assess fish stocks. *North American Journal of Fisheries Management* 4:273-285.

- Gillen, A. L., R. A. Stein, and R. F. Carline. 1981. Predation by pellet-reared tiger muskellunge on minnows and bluegills in experimental systems. *Transactions of the American Fisheries Society* 110:197-209.
- Greene, C. H. 1983. Selective predation in freshwater zooplankton communities. *Internationale Revue der Gesamten Hydrobiologie* 68:297-315.
- Hackney, P. A. 1966. Predator-prey relationships of the flathead catfish in ponds under selected forage fish conditions. *Proceedings of the Annual Conference Southeastern Association Game and Fish Commissioners* 19:217-222.
- Hambright, K. D. 1991. Experimental analysis of prey selection by largemouth bass: role of predator mouth width and prey body depth. *Transactions of the American Fisheries Society* 120:500-508.
- Helfman, G. S. 1981. Twilight activities and temporal structure in a freshwater fish community. *Canadian Journal of Fisheries and Aquatic Sciences* 38:1405-1420.
- Hergenrader, G. L. 1980a. Eutrophication of the Salt Valley reservoirs, 1968-73. I. The effects of eutrophication on standing crop and composition of phytoplankton. *Hydrobiologia* 71:61-82.
- Hergenrader, G. L. 1980b. Current distribution and potential for dispersal of white perch (*Morone americana*) in Nebraska and adjacent waters. *American Midland Naturalist* 103:404-406.
- Hergenrader, G. L., and Q. P. Bliss. 1971. The white perch in Nebraska. *Transactions of the American Fisheries Society* 100:734-738.

- Herwig, B. R., D. A. Soluk, J. M. Dettmers, and D. H. Wahl. 2004. Trophic structure and energy flow in backwater lakes of two large floodplain rivers assessed using stable isotopes. *Canadian Journal of Fisheries and Aquatic Sciences* 61:12-22.
- Herzka, S. Z., S. A. Holt, and G. J. Holt. 2001. Documenting the settlement history of individual fish larvae using stable isotope ratios: model development and validation. *Journal of Experimental Marine Biology and Ecology* 265:49-74.
- Hesslein, R. H., K. A. Hallard, and P. Ramlal. 1993. Replacement of sulfur, carbon, and nitrogen in tissue of growing broad whitefish (*Coregonus nasus*) in response to a change in diet traced by $\delta^{34}\text{S}$, $\delta^{13}\text{C}$, and $\delta^{15}\text{N}$. *Canadian Journal of Fisheries and Aquatic Sciences* 50:2071-2076.
- Hodkin, C. E. 2001. Population characteristics and food habits of white perch (*Morone americana*) in Branched Oak Lake, Nebraska. Master's thesis, University of Nebraska-Lincoln, Lincoln.
- Hodson, R. G. 1989. Hybrid striped bass biology and life history. Southern Regional Aquaculture Center, Publication 300, Raleigh, North Carolina.
- Holz, D. D. 1969. The ecology of the unchannelized and channelized Missouri River, Nebraska, with emphasis on the life history of the flathead catfish. Master's thesis, University of Missouri, Columbia.
- Hoogland, R., D. Morris, and N. Tinbergen. 1956. The spines of sticklebacks (*Gasterosteus* and *Pygosteus*) as means of defence against predators (*Perca* and *Esox*). *Behaviour* 10:205-236.

- Hoyle, J. A., and A. Keast. 1987. The effect of prey morphology and size on handling time in a piscivore, the largemouth bass (*Micropterus salmoides*). *Canadian Journal of Zoology* 65:1972-1977.
- Hurley, D. A., and W. J. Christie. 1977. Depreciation of the warm-water fish community in the Bay of Quinte, Lake Ontario. *Journal of the Fisheries Research Board of Canada* 34:1849-1860.
- Jackim, E., and G. LaRoche. 1973. Protein synthesis in *Fundulus heteroclitus* muscle. *Comparative Biochemistry and Physiology A-Physiology* 44:851-866.
- Jackson, J. 1999. Branched Oak white perch control plan. Nebraska Game and Parks Commission, Lincoln.
- Jackson, J. 2008. Pawnee reservoir management plan. Nebraska Game and Parks Commission, Lincoln.
- Juanes, F. 1992. The advantages of advection: recruitment, piscivory, growth, and consumption of young-of-the-year bluefish (*Pomatomus saltatrix*). Doctoral dissertation. State University of New York, Stony Brook.
- Juanes, F. 1994. What determines prey size selectivity in piscivorous fishes? Pages 79-100 in D. J. Stouder, K. L. Fresh, and R. J. Feller, editors. *Theory and application in fish feeding ecology*. University of South Carolina Press, Columbia.
- June, F. C. 1987. Early life history and winter mortality of gizzard shad in Lake Sharpe, South Dakota. Pages 75-83 in *Limnological and fishery studies on Lake Sharpe, a main-stem Missouri River reservoir, 1964-1975*. U.S. Fish and Wildlife Service, Fish and Wildlife Technical Report 8, Washington, D.C.

- Kamler, J. F., and K. L. Pope. 2001. Nonlethal methods of examining fish stomach contents. *Reviews in Fisheries Science* 9:1-11.
- Kestemont, P., and E. Baras. 2001. Environmental factors and feed intake: mechanisms and interactions. Pages 131-156 *in* D. Houlihan, T. Boujard, and M. Jobling, editors. *Food intake in fish*. Iowa State University Press, Ames.
- Knight, R. L., and B. Vondracek. 1993. Changes in prey fish populations in western Lake Erie, 1969-88, as related to walleye, *Stizostedion vitreum*, predation. *Canadian Journal of Fisheries and Aquatic Sciences* 50:1289-1298.
- Knight, R. L., and F. J. Margraf. 1982. Estimating stomach fullness in fishes. *North American Journal of Fisheries Management* 2:413-414.
- Knight, R. L., F. J. Margraf, and R. F. Carline. 1984. Piscivory by walleyes and yellow perch in western Lake Erie. *Transactions of the American Fisheries Society* 113:677-693.
- Larson, C., and M. Boucher. 2005. Stocking walleye as an experimental method of controlling yellow bass in Viking Lake. Fisheries management section completion reports, Iowa Department of Natural Resources, Des Moines.
- Lawrence, J. M. 1958. Estimated sizes of various forage fishes largemouth bass can swallow. *Proceedings of the Annual Conference of the Southeastern Fish and Wildlife Commissioners* 11:220-225.
- Light, R. W., P. H. Alder, and D. E. Arnold. 1983. Evaluation of gastric lavage for stomach analysis. *North American Journal of Fisheries Management* 3:81-85.

- Li, H. W., and P. B. Moyle. 1999. Management of introduced fishes. Pages 345-374 in C. C. Kohler and W. A. Hubert, editors. Inland fisheries management in North America, 2nd edition. American Fisheries Society, Bethesda, Maryland.
- Logan, J., H. Haas, L. Deegan, and E. Gaines. 2006. Turnover rates of nitrogen stable isotopes in the saltwater marsh mummichog, *Fundulus heteroclitus*, following a laboratory diet switch. *Oecologia* 147:391-395.
- MacAvoy, S. E., S. A. Macko, and G. C. Garman. 2001. Isotopic turnover in aquatic predators: quantifying the exploitation of migratory prey. *Canadian Journal of Fisheries and Aquatic Sciences* 58:923-932.
- Madenjian, C. P., R. L. Knight, M. T. Bur, and J. L. Forney. 2000. Reduction in recruitment of white bass in Lake Erie after invasion of white perch. *Transactions of the American Fisheries Society* 129:1340-1353.
- Mansueti, R. J. 1961. Movements, reproduction, and mortality of the white perch, *Roccus americanus*, in the Patuxent estuary, Maryland. *Chesapeake Science* 2:142-205.
- Margenau, T. L. 1995. Stunted northern pike: a case history of community manipulations and field transfer. Wisconsin Department of Natural Resources Report 169.
- Maruyama, A., Y. Yamada, B. Rusuwa, and M. Yuma. 2001. Change in stable nitrogen isotope ratio in the muscle tissue of a migratory goby, *Rhinogobius* sp., in a natural setting. *Canadian Journal of Fisheries and Aquatic Sciences* 58:2125-2128.

- Mauck, W. L., and D. W. Coble. 1971. Vulnerability of some fishes to northern pike (*Esox lucius*) predation. *Journal of the Fisheries Research Board of Canada* 28:957-969.
- Mayhew, J. 1975. Abundance, distribution, mortality, and production of 0-age fish. Iowa Conservation Commission, Federal Aid in Fish Restoration, Project F-88-R-1, Performance Report Jobs 1, 3, Des Moines, Iowa.
- Miranda, L. E., and R. J. Muncy. 1991. Bioenergetic values of shads and sunfishes as prey for largemouth bass. *Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies* 43(1989):153-163.
- Mittelbach, G. G., and L. Persson. 1998. The ontogeny of piscivory and its ecological consequences. *Canadian Journal of Fisheries and Aquatic Sciences* 55:1454-1465.
- Moyle, P. B., and J. J. Cech, Jr. 2004. *Fishes: an introduction to ichthyology*, 5th edition. Prentice-Hall, Inc., Upper Saddle River, New Jersey.
- Nilsson, P. A., and C. Brönmark. 2000. Prey vulnerability to a gape-size limited predator: behavioural and morphological impacts on northern pike piscivory. *Oikos* 88:539-546.
- Olson, N. W. 2004. Interactions among hybrid striped bass, white bass, and walleye in Harlan County Reservoir. Master's thesis, Montana State University, Bozeman.
- Olson, N. W., C. S. Guy, and K. D. Koupal. 2007. Interactions among three top-level predators in a ploymictic Great Plains reservoir. *North American Journal of Fisheries Management* 27:268-278.

- Parsons, J. W. 1971. Selective food preferences of walleyes of the 1959 year class in Lake Erie. *Transactions of the American Fisheries Society* 100:474-485.
- Paukert, C. P., and D. W. Willis. 2003. Population characteristics and ecological role of northern pike in shallow natural lakes in Nebraska. *North American Journal of Fisheries Management* 23:313-322.
- Perga, M. E., and D. Gerdeaux. 2005. 'Are fish what they eat' year round? *Oecologia* 144:598-606.
- Peterson, B. J., and B. Fry. 1987. Stable isotopes in ecosystem studies. *Annual Review of Ecology and Systematics* 18:293-320.
- Pope, K. L., M. L. Brown, W. G. Duffy, and P. H. Michaletz. 2001. A caloric-based evaluation of diet indices for largemouth bass. *Environmental Biology of Fishes* 61:329-339.
- Porath, M. T. 2006a. Climate and habitat factors related to a localized extirpation of gizzard shad (*Dorosoma cepedianum*). *Great Plains Research* 16:127-135.
- Preisser, E. L., D. I. Bolinick, and M. F. Benard. 2005. Scared to death? The effects of intimidation and consumption in predator-prey interactions. *Ecology* 86:501-509.
- Priegel, G. R. 1963. Food of walleye and sauger in Lake Winnebago, Wisconsin. *Transactions of the American Fisheries Society* 92:312-313.
- Quinn, S. P. 1991. Evaluation of a length-categorization system for flathead catfish. *Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies* 43(1989):146-152.

- Roell, M. J., and D. J. Orth. 1993. Trophic basis of production of stream-dwelling smallmouth bass, rock bass and flathead catfish in relation to invertebrate bait harvest. *Transactions of the American Fisheries Society* 122:46-62.
- Rounick, J. S., and M. J. Winterbourn. 1986. Stable carbon isotopes and carbon flow in ecosystems. *BioScience* 36:171-177.
- Scott, W. B., and E. J. Crossman. 1973. *Freshwater fishes of Canada*. Fisheries Research Board of Canada, Bulletin 184, Ottawa.
- Schaeffer, J. S., and F. J. Margraf. 1987. Predation on fish eggs by white perch, *Morone americana*, in western Lake Erie. *Environmental Biology of Fishes* 18:77-80.
- Schmitz, O. J. 2007. Predator diversity and trophic interactions. *Ecology* 88:2415-2426.
- Schmitz, O. J. 2008. Effects of predator hunting mode on grassland ecosystem function. *Science* 319:952-954.
- Sobotka, G. L. 2005. Evaluation of walleye and largemouth bass in controlling yellow bass at Twelve Mile Lake. Fisheries management section completion reports. Iowa Department of Natural Resources, Des Moines, Iowa.
- Stephens, D. W., and J. R. Krebs. 1986. *Foraging theory*. Princeton University Press, Princeton, New Jersey.
- Swingle, H. S. 1967. Experiments with the flathead catfish ("Pylodictis olivaris") in ponds. *Proceedings of the Annual Conference of the Southeastern Association of Game and Fish Commissioners* 18:303-308.

- Taylor, J. N., W. R. Courtenay, Jr., and J. A. McCann. 1984. Known impacts of exotic fishes in the continental United States. Pages 322-373 in W. R. Courtenay, Jr. and J. R. Stauffer, Jr., editors. Distribution, biology, and management of exotic fishes. The John Hopkins University Press, Baltimore, Maryland.
- Thorp, J. H., and A. P. Covich. 1991. Ecology and classification of North American freshwater invertebrates. Academic Press, Inc, San Diego, California.
- Thresher, R. E. 2008. Autocidal technology for the control of invasive fish. Fisheries 33:114-121.
- Tonn, W. M., and C. A. Paszkowski. 1986. Size-limited predation, winterkill, and the organization of *Umbra-Perca* fish assemblages. Canadian Journal of Fisheries and Aquatic Sciences 43:194-202.
- Trautman, M. B. 1957. The fishes of Ohio. Ohio State University Press, Columbus.
- Vander Zanden, M. J., M. Hulshof, M. S. Ridgway, and J. B. Rasmussen. 1998. Applications of stable isotope techniques to trophic studies of age-0 smallmouth bass. Transactions of the American Fisheries Society 127:729-739.
- Vrtiska, L., C. E. Hodkin, A. Severn, E. J. Peters, and K. D. Hoagland. 2001. Branched Oak Reservoir project final report. Federal Aid Project F-133-R, Nebraska Game and Parks Commission, Lincoln.
- Wahl, D. H., and R. A. Stein. 1988. Selective predation by three esocids: the role of prey behavior and morphology. Transactions of the American Fisheries Society 117:142-151.
- Walburg, C. H. 1964. Fish population studies, Lewis and Clark Lake, Missouri River, 1956 to 1962. U.S. Fish and Wildlife Service, Special Scientific Report-

Fisheries No. 482, Washington, D.C.

- Ward, M. J. 2005. Gizzard shad reproductive biology and predator-prey relations with walleyes in western South Dakota reservoirs. Master's thesis, South Dakota State University, Brookings.
- Weisberg, S. B., and A. J. Janicki. 1990. Summer feeding patterns of white perch, channel catfish, and yellow perch in the Susquehanna River, Maryland. *Journal of Freshwater Ecology* 5:391-405.
- Werner, E. E. 1977. Species packing and the niche complementarity in three sunfishes. *American Naturalist* 111:553-578.
- Werner, E. E., and D. J. Hall. 1974. Optimal foraging and the size selection of prey by the bluegill sunfish (*Lepomis macrochirus*). *Ecology* 55:1042-1052.
- White, A. M., F. D. Moore, N. A. Alldridge, and D. M. Loucks. 1986. The effects of natural winter stresses on the mortality of the eastern gizzard shad, *Dorosoma cepedianum*, in Lake Erie. John Carroll University, Report 78, University Heights, Ohio.
- Willis, D. W. 1987. Reproduction and recruitment of gizzard shad in Kansas reservoirs. *North American Journal of Fisheries Management* 7:71-80.
- Winter, R. L. 1994. Environmental assessment: Branched Oak reservoir fisheries restoration. Federal Aid Project F-107-D, Nebraska Game and Parks Commission, Lincoln.
- Witt, A., Jr., and R. S. Campbell. 1959. Refinements of equipment and procedures in electrofishing. *Transactions of the American Fisheries Society* 88:33-35.

Wydoski, R. S., and R. W. Wiley. 1999. Management of undesirable fish species. Pages 403-430 *in* C. C. Kohler and W. A. Hubert, editors. Inland fisheries management in North America, 2nd edition. American Fisheries Society, Bethesda, Maryland.

Table 2-1. Upper and lower 95% confidence limits (CL) for the interactions (length * reservoir or gape * reservoir) for quantile (0.1, 0.5 and 0.9) regressions between prey standard length and predator total length and between prey body depth and predator gape width in Branched Oak and Pawnee reservoirs, Nebraska during 2006 and 2007. Slopes of quantile regressions between reservoirs were not different if the confidence interval included zero.

Quantile	Regression	Lower 95% CL	Upper 95% CL
0.1	Prey length-predator length	-0.12	0.14
0.5		-0.08	0.02
0.9		-0.14	0.05
0.1	Prey depth-predator gape width	-0.16	0.46
0.5		-0.55	0.22
0.9		-1.12	-0.13

Table 4-1. Equations used to predict maximum stomach capacity (V; ml) of fish as a function of their total length (L, mm).

Species	Equation	Reference
Largemouth bass	$V = 2.409 \times 10^{-7} L^{3.248}$	Pope et al. (2001)
White crappie	$V = 1.734 \times 10^{-7} L^{3.207}$	Appendix D
Black crappie	$V = 6.640 \times 10^{-6} L^{2.439}$	Appendix D
Channel catfish	$V = 7.230 \times 10^{-13} L^{5.006}$	Appendix D
White bass	$V = 7.821 \times 10^{-7} L^{2.926}$	Appendix D
Walleye	$V = 5.580 \times 10^{-6} L^{2.560}$	Knight and Margraf (1982)

Table 4-2. Pairwise comparisons for foraging success on white perch between predators (LMB = largemouth bass, WHC = white crappie, BLC = black crappie, CHC = channel catfish, FHC = flathead catfish, HSB = hybrid striped bass, WAE = walleye) using Dunn's multiple comparison procedure in Branched Oak Lake, Nebraska during 2006. An "*" indicates statistically significant comparisons ($\alpha = 0.05$) and "—" indicates non-significant comparisons.

	LMB	WHC	BLC	CHC	FHC	HSB	WAE
LMB							
WHC	*						
BLC	*	—					
CHC	*	—	*				
FHC	*	*	*	*			
HSB	*	*	—	*	*		
WAE	*	*	*	*	—	*	

Table 4-3. Pairwise comparisons for foraging success on white perch between predators (LMB = largemouth bass, CHC = channel catfish, FHC = flathead catfish, WHB = white bass, SAU = sauger, WAE = walleye) using Dunn's multiple comparison procedure in Pawnee Lake, Nebraska during 2006. An "*" indicates statistically significant comparisons ($\alpha = 0.05$) and "—" indicates non-significant comparisons.

	LMB	CHC	FHC	WHB	SAU	WAE
LMB						
CHC	*					
FHC	*	*				
WHB	*	*	*			
SAU	*	*	*	*		
WAE	*	*	*	*	—	

Table 4-4. Pairwise comparisons for foraging success on white perch between predators (WHC = white crappie, FHC = flathead catfish, HSB = hybrid striped bass bass, WAE = walleye) using Dunn's multiple comparison procedure in Branched Oak Lake, Nebraska during 2007. An "*" indicates statistically significant comparisons ($\alpha = 0.05$) and "--" indicates non-significant comparisons.

	WHC	FHC	HSB	WAE
WHC				
FHC	*			
HSB	*	*		
WAE	*	*	*	

Table 4-5. Pairwise comparisons for foraging success on white perch between predators (FHC = flathead catfish, WHB = white bass, SAU = sauger, WAE = walleye) using Dunn's multiple comparison procedure in Pawnee Lake, Nebraska during 2007. An "*" indicates statistically significant comparisons ($\alpha = 0.05$) and "—" indicates non-significant comparisons.

	FHC	WHB	SAU	WAE
FHC				
WHB	—			
SAU	*	*		
WAE	*	*	—	

Table 4-6. Estimated relative biomass of predators in Branched Oak (BO) and Pawnee (PA) reservoirs, Nebraska and their associated consumption of white perch based on calculated rates of foraging success.

Reservoir	Predator species	Biomass (kg)	Foraging success on white perch (ml/kg)	White perch consumed (ml)
BO	Largemouth bass	78.1	4.91	383.5
	Crappie	3872.0	1.70	6582.4
	Channel catfish	5749.9	1.94	11154.8
	Flathead catfish	2729.0	2.18	5949.2
	Hybrid striped bass	781.0	2.37	1851.0
	Walleye	2729.0	5.93	16183.0
PA	Largemouth bass	93.2	8.13	757.7
	Crappie	4021.9	5.61	22562.9
	Channel catfish	2389.8	0.46	1099.3
	Flathead catfish	2389.8	1.67	3991.0
	White bass	256.5	4.43	1136.3
	Sauger	93.2	8.01	746.5
	Walleye	3622.8	9.76	35358.5

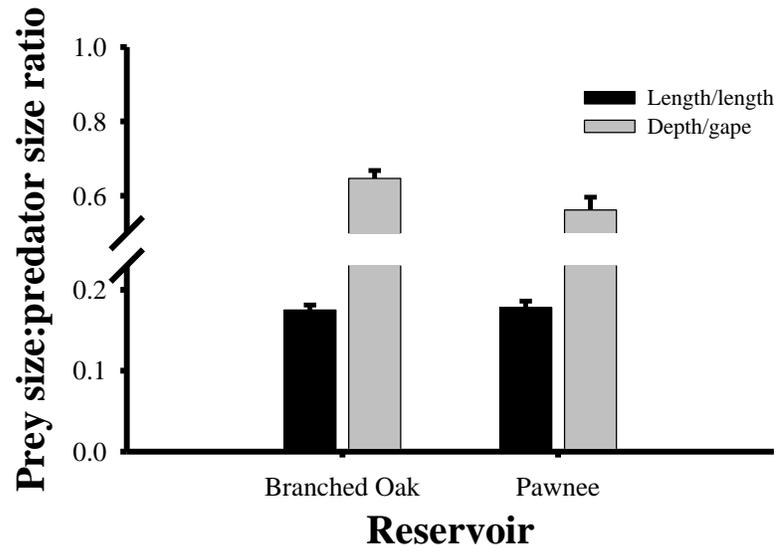


Figure 2-1. Mean \pm SE predator size:prey size ratio in Branched Oak and Pawnee reservoirs, Nebraska during 2006 and 2007.

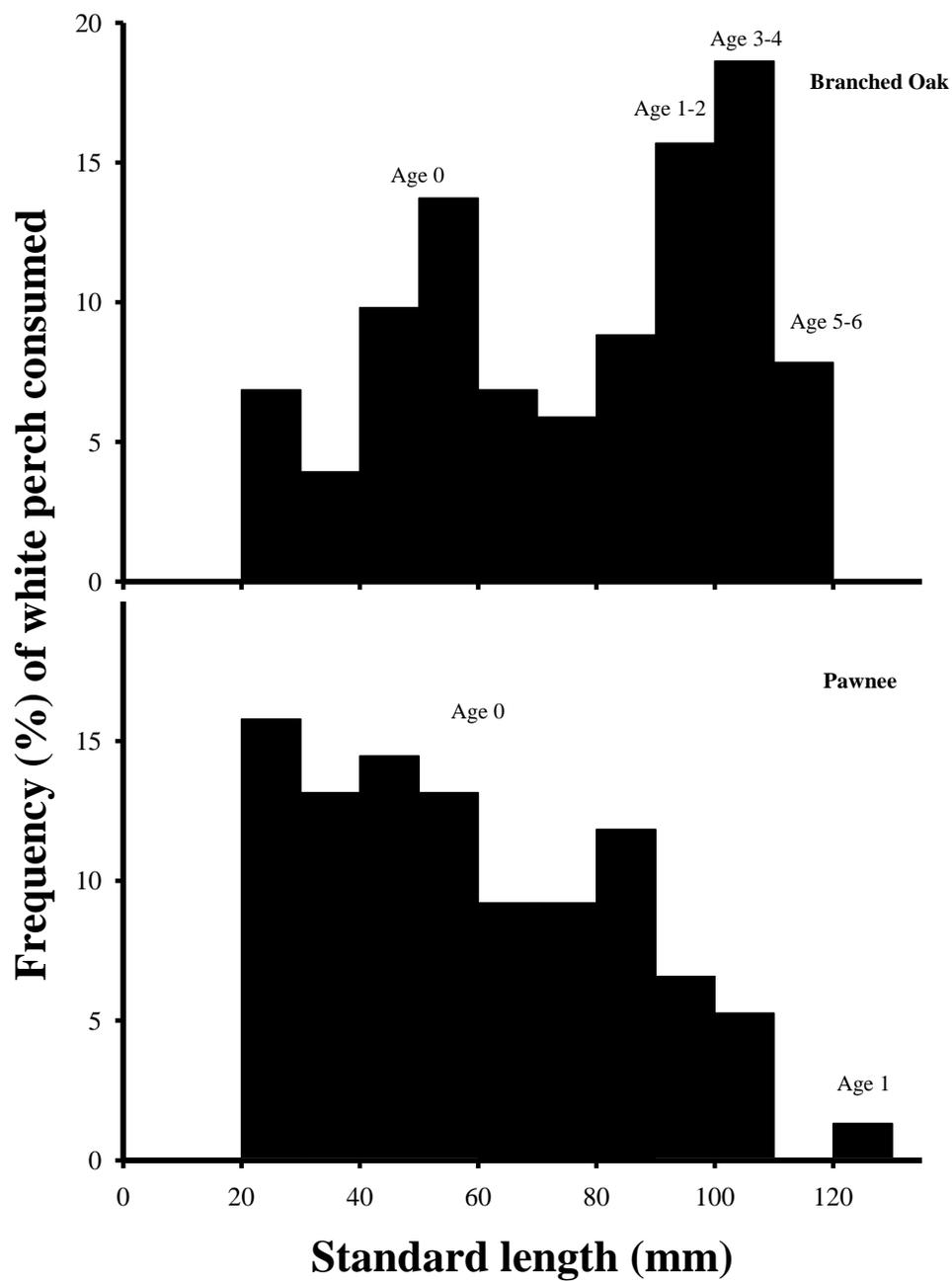


Figure 2-2. Length-frequency distributions of white perch consumed by predators in Branched Oak and Pawnee reservoirs, Nebraska. Ages were determined from Chizinski (2007).

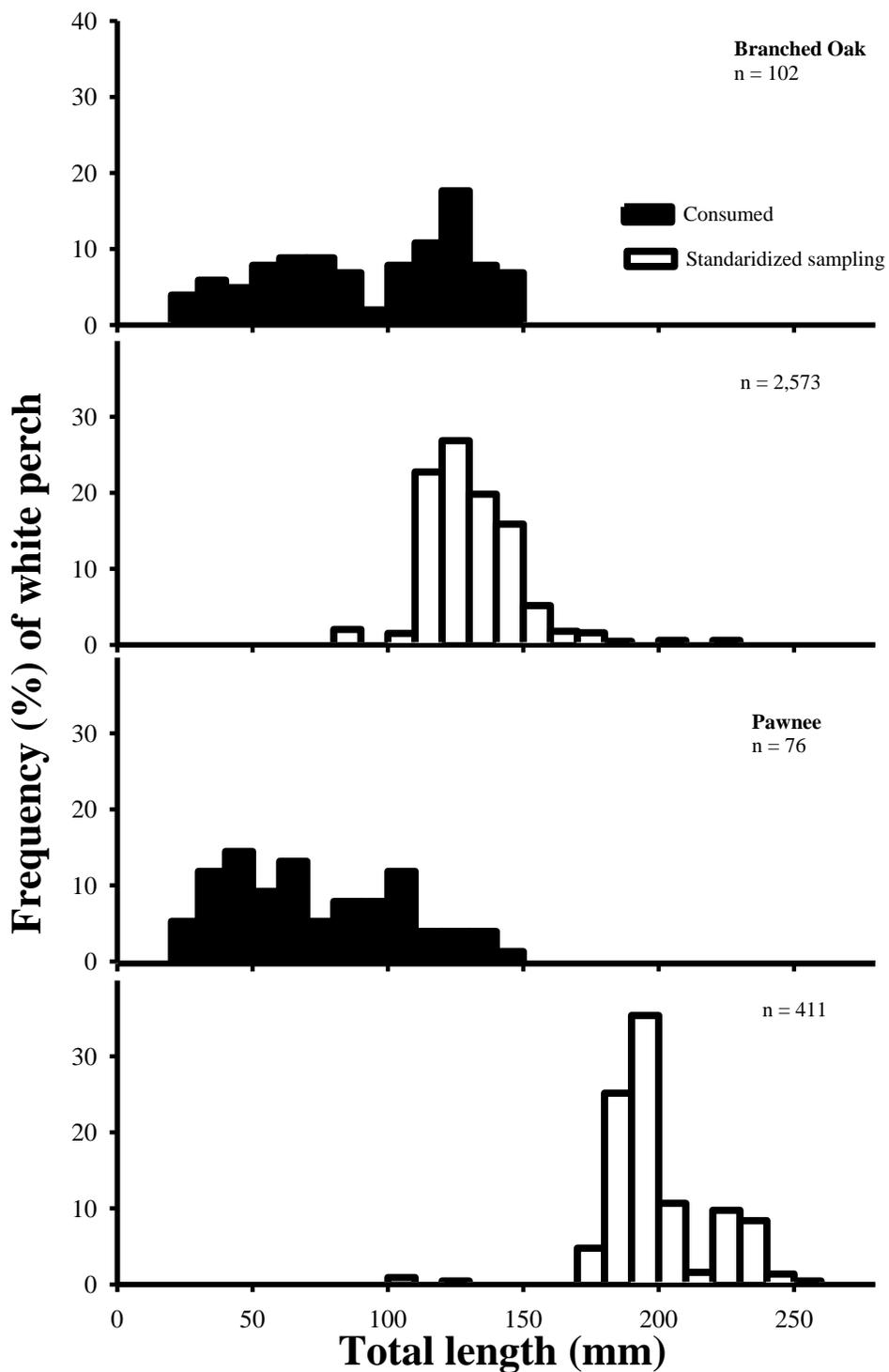


Figure 2-3. Length-frequency distributions of white perch consumed by predators (black fill) and white perch captured by the Nebraska Game and Park Commission (white fill) during annual autumn standardized sampling in Branched Oak (top 2 panels) and Pawnee reservoirs (bottom two panels), Nebraska.

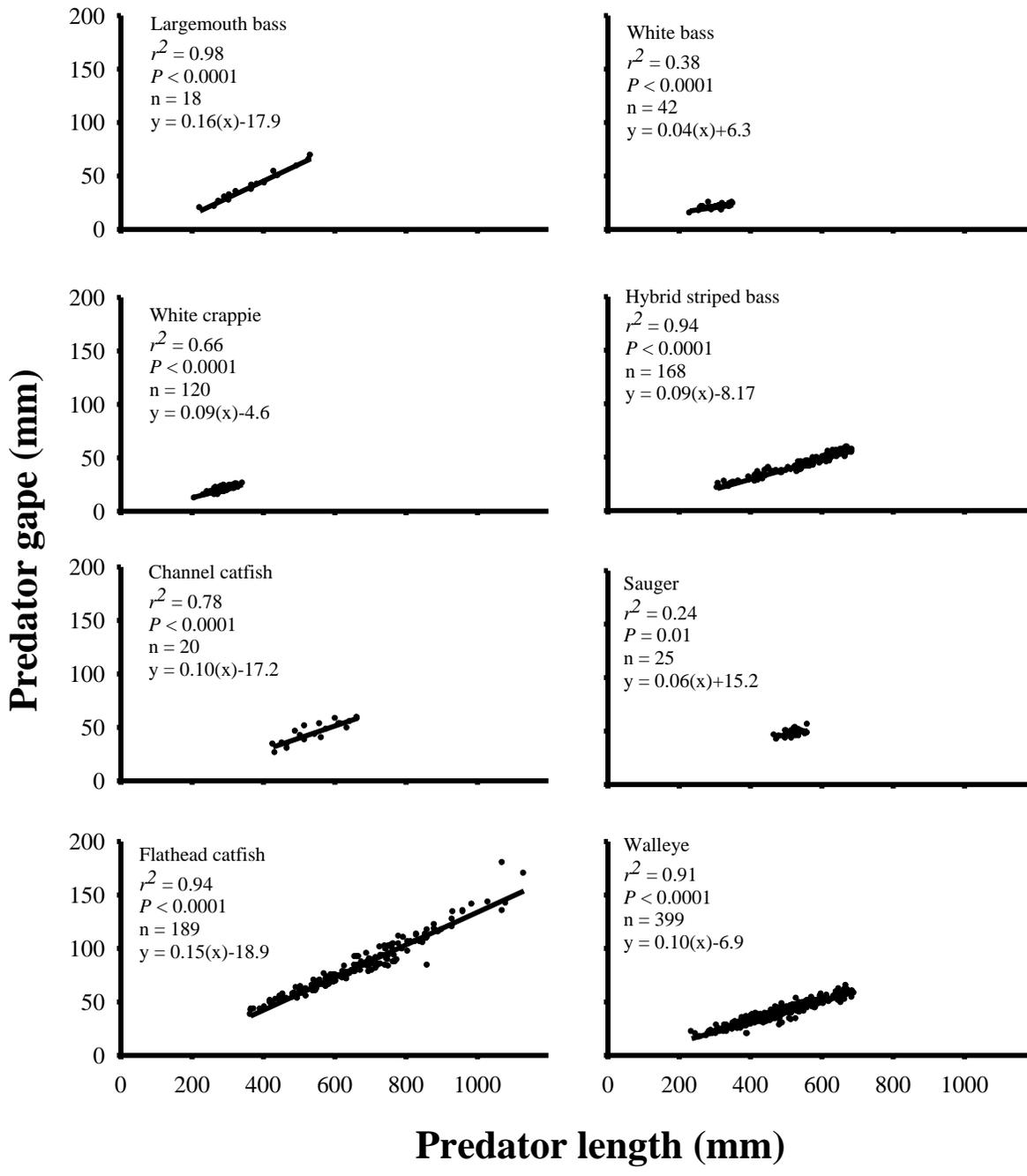


Figure 2-4. Relations between predator gape width and total length for fishes captured in Branched Oak and Pawnee reservoirs, Nebraska during 2007.

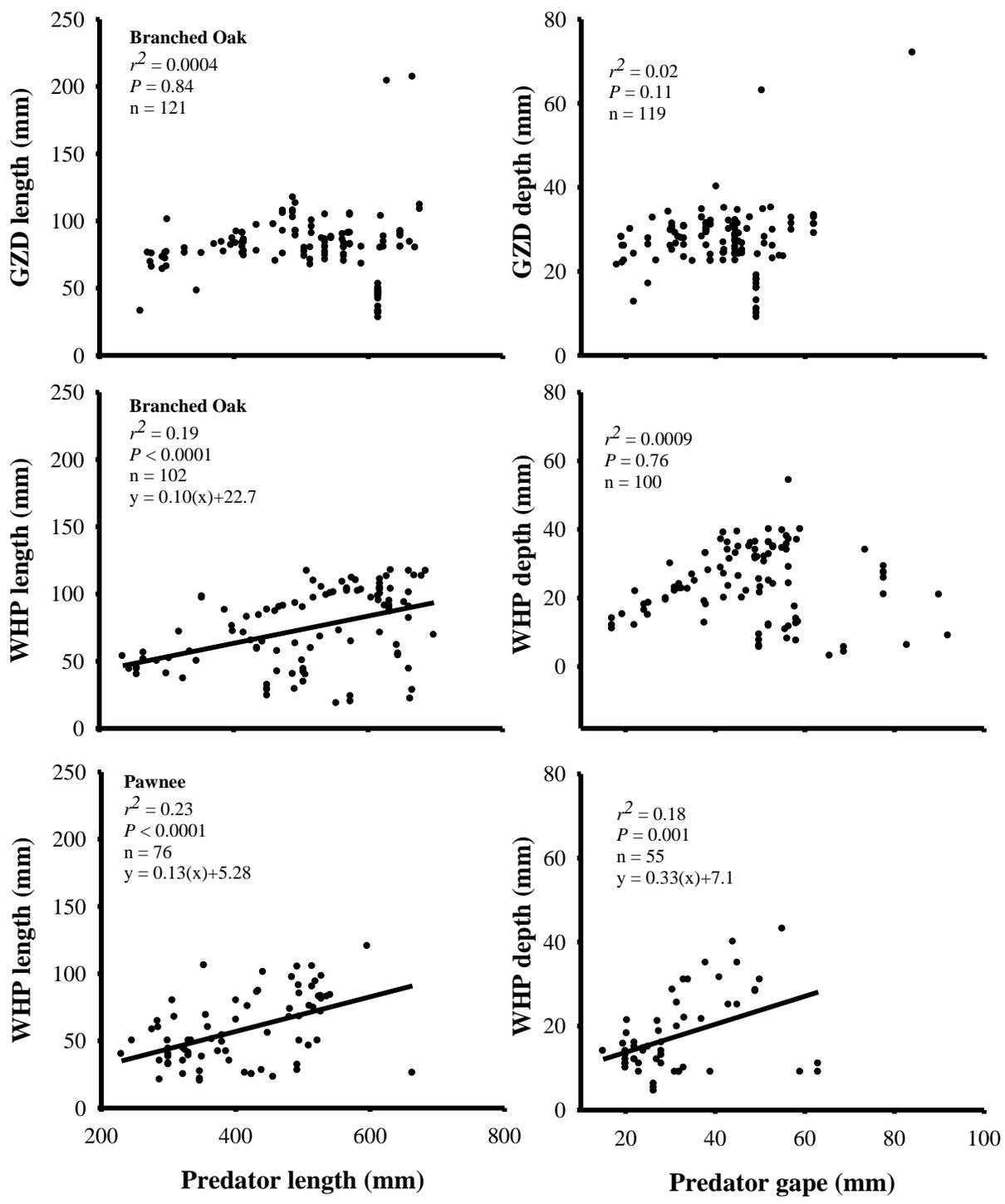


Figure 2-5. Relations between prey standard length (GZD = gizzard shad, WHP = white perch) and predator total length (left panels) and prey body depth and predator gape width (right panels) in Branched Oak (top and middle panels, respectively) and Pawnee (bottom panels) reservoirs, Nebraska during 2006 and 2007.

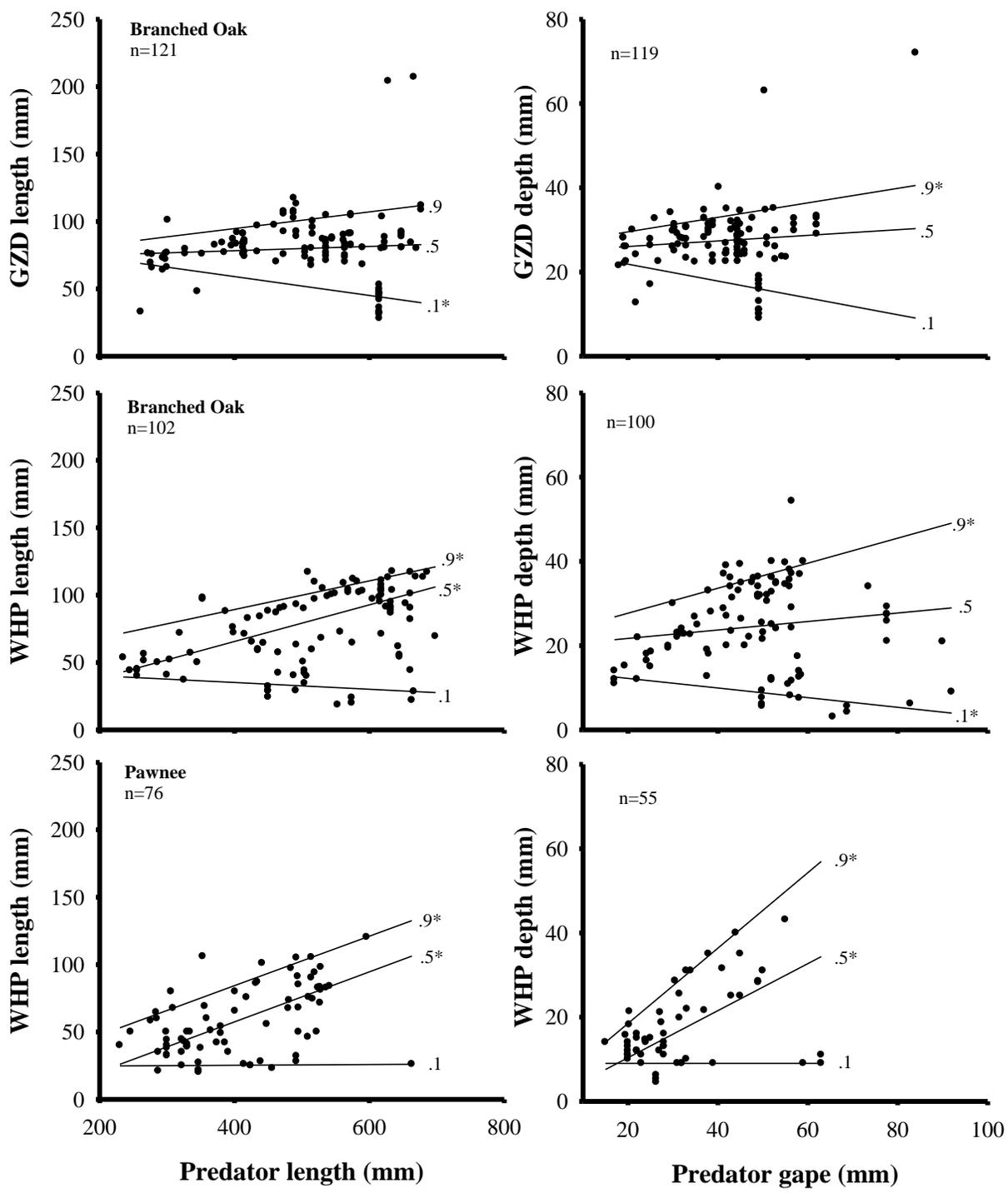


Figure 2-6. Quantile (0.1, 0.5 and 0.9) regressions between prey standard length (GZD = gizzard shad, WHP = white perch) and predator total length and prey body depth and predator gape width in Branched Oak and Pawnee reservoirs, Nebraska during 2006 and 2007(* indicates slope significantly different from zero).

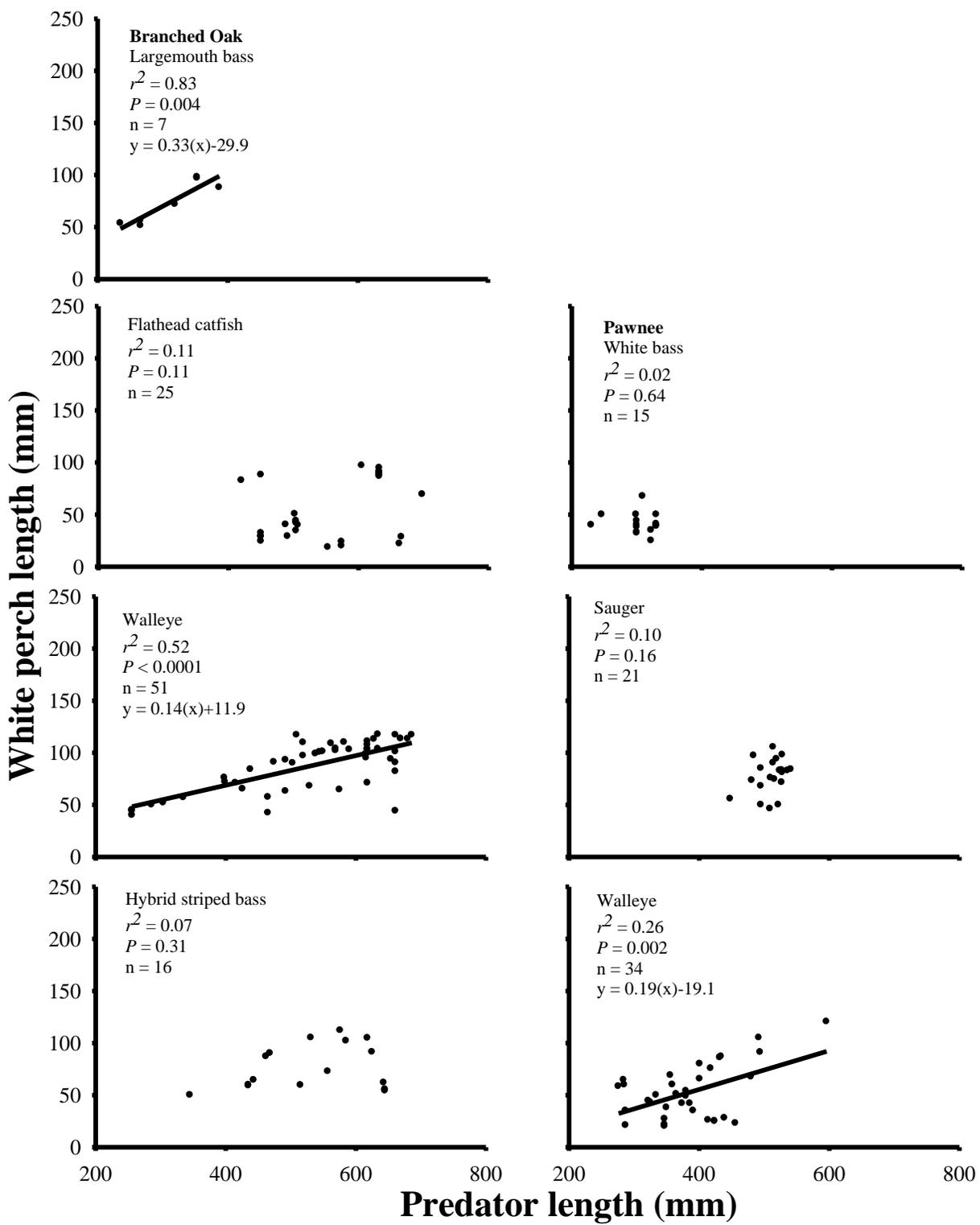


Figure 2-7. Relation between white perch (prey) standard length and predator total length for species in which a minimum of 5 individuals were captured containing at least one measurable white perch in their stomach contents in Branched and Pawnee reservoirs, Nebraska during 2006 and 2007.

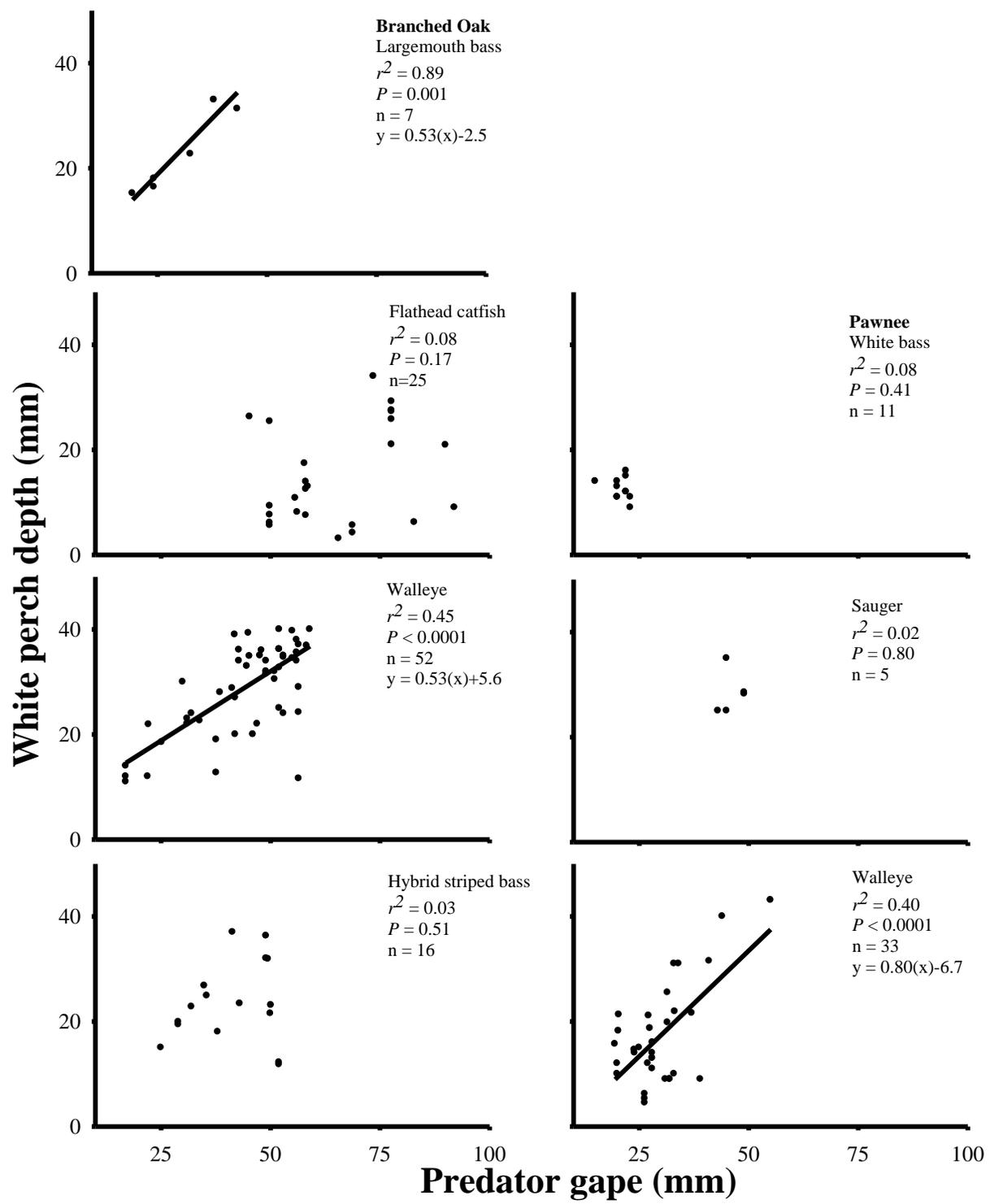


Figure 2-8. Relation between white perch (prey) body depth and predator gape width for species in which a minimum of 5 individuals were captured containing at least one measurable white perch in their stomach contents in Branched and Pawnee reservoirs, Nebraska during 2006 and 2007.

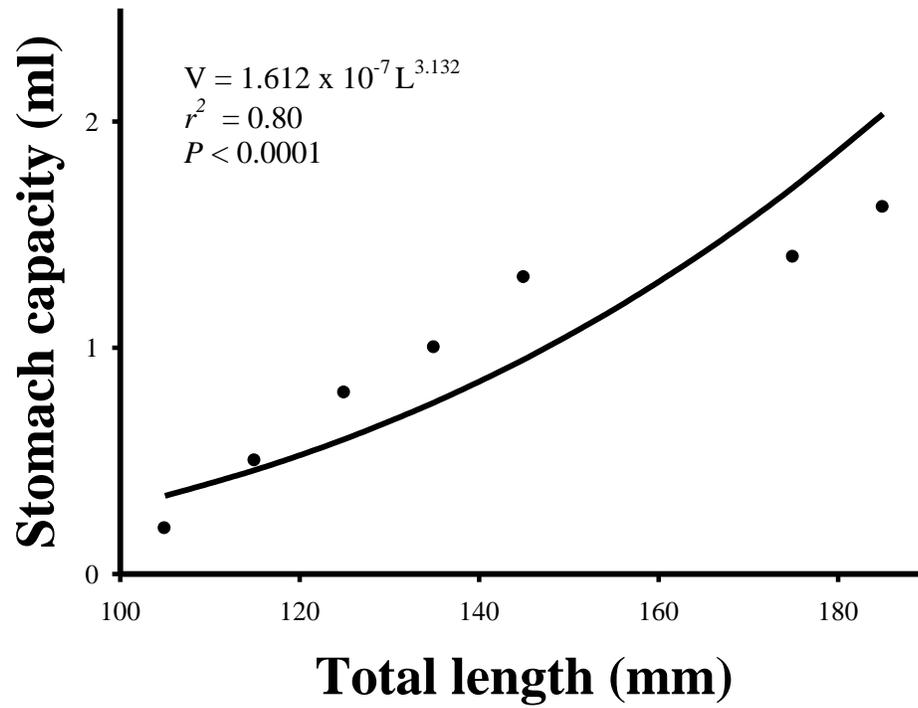


Figure 3-1. Relation between maximum stomach capacity (V) and total length (L) of white perch. A point represents the maximum total volume of prey observed in an individual stomach plotted as the midpoint for each length group.

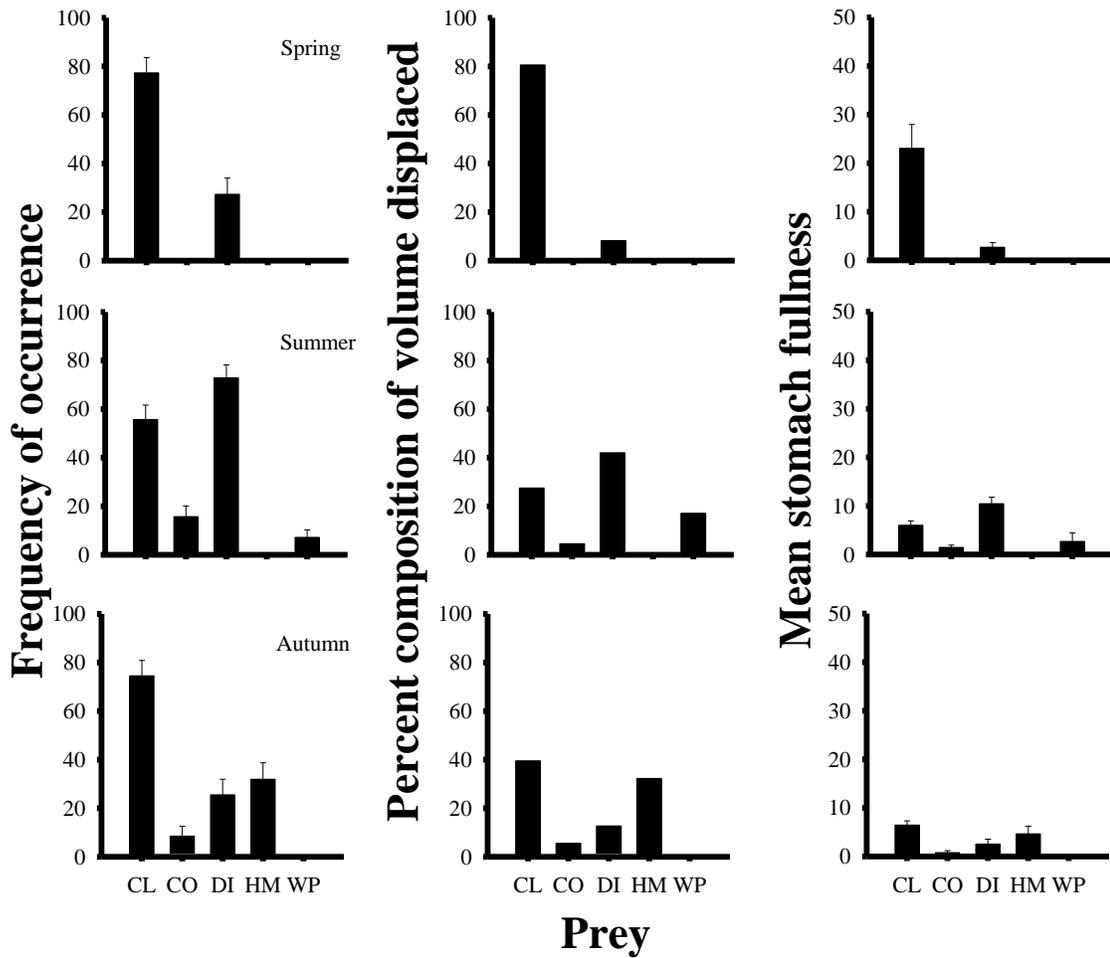


Figure 3-2. Frequency of occurrence \pm SE (left panels), percent composition of volume displaced (middle panels) and mean stomach fullness \pm SE (right panels) for prey consumed (CL = cladocera, CO = coleoptera, DI = diptera, HM = hemiptera, WP = white perch) by white perch during spring (top panels), summer (middle panels) and autumn (bottom panels) 2006 in Branched Oak Lake, Nebraska.

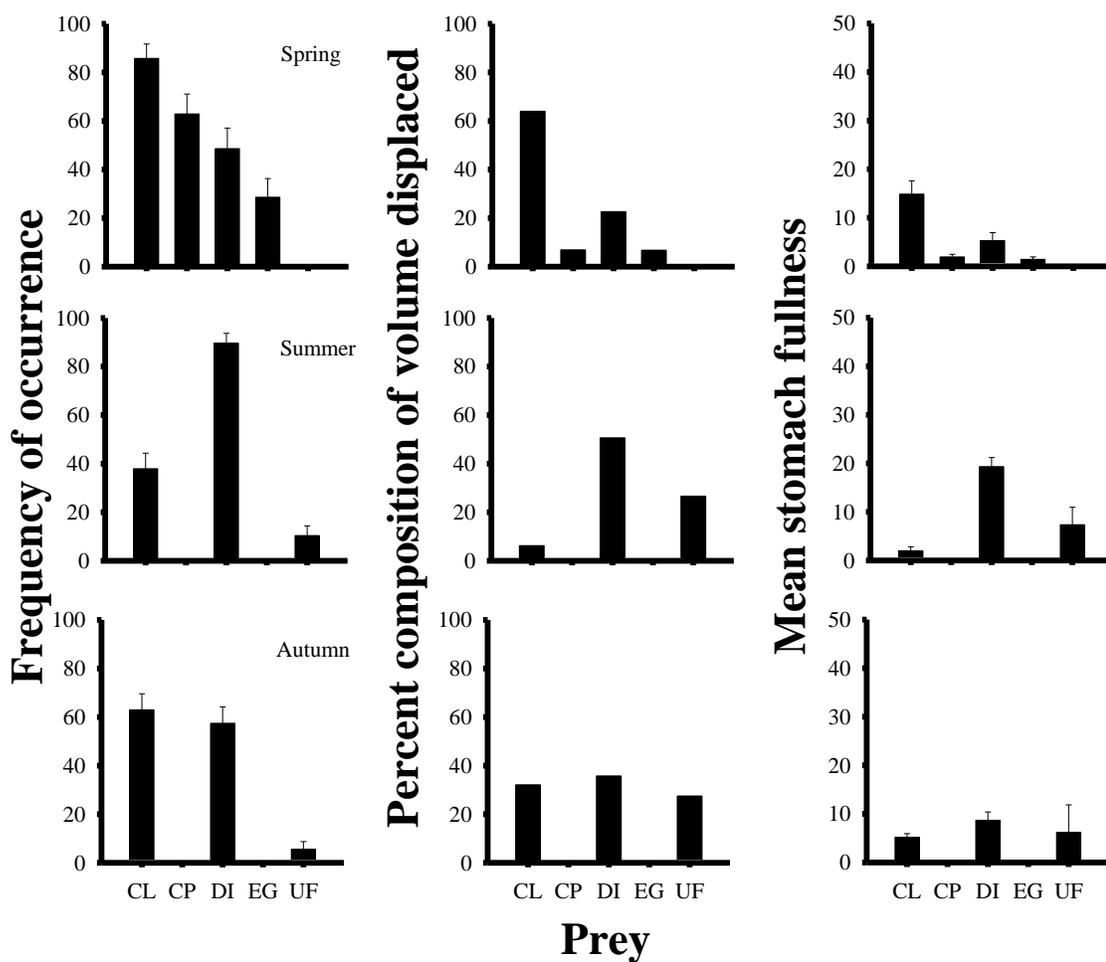


Figure 3-3. Frequency of occurrence \pm SE (left panels), percent composition of volume displaced (middle panels) and mean stomach fullness \pm SE (right panels) for prey consumed (CL = cladocera, CP = copepoda, DI = diptera, EG = fish eggs, UF = unidentifiable fish) by white perch during spring (top panels), summer (middle panels) and autumn (bottom panels) 2007 in Branched Oak Lake, Nebraska.

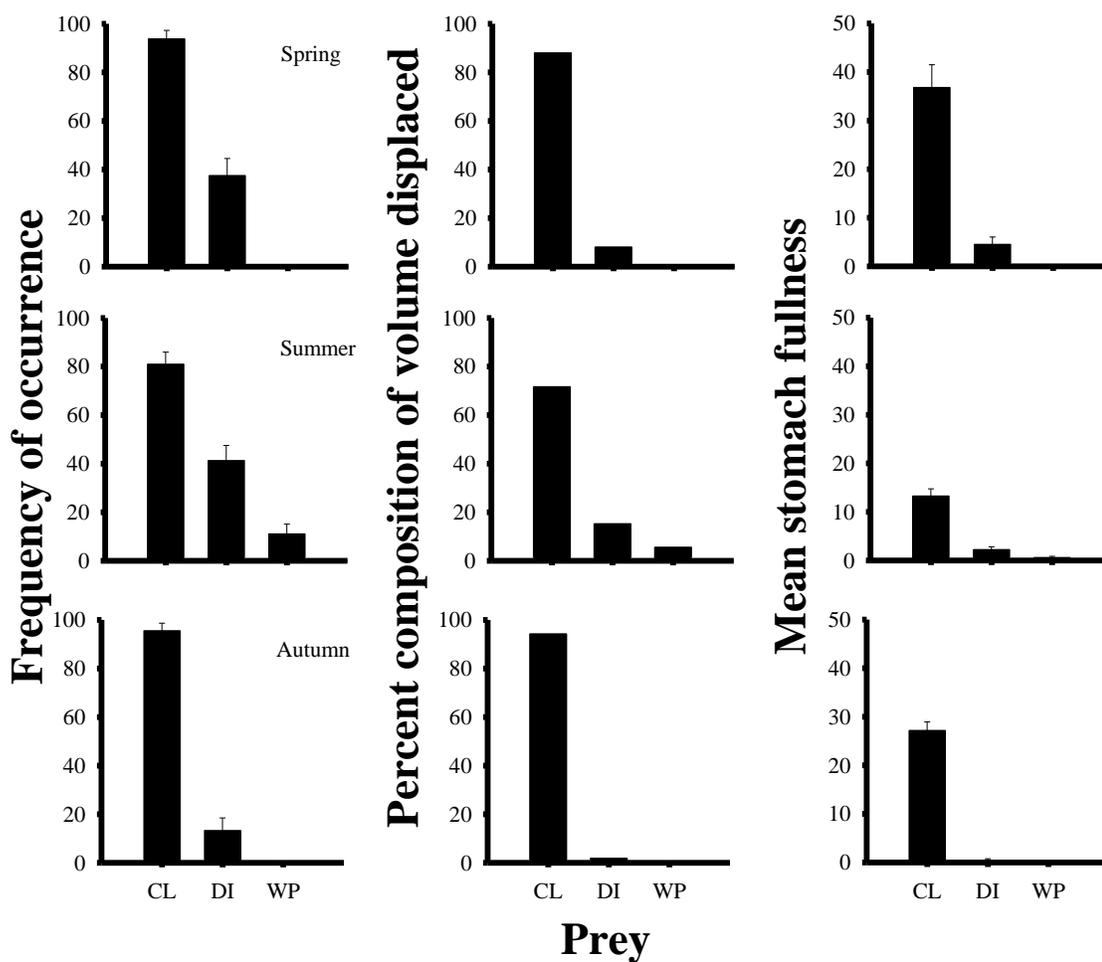


Figure 3-4. Frequency of occurrence \pm SE (left panels), percent composition of volume displaced (middle panels) and mean stomach fullness \pm SE (right panels) for prey consumed (CL = cladocera, DI = diptera, WP = white perch) by white perch during spring (top panels), summer (middle panels) and autumn (bottom panels) 2006 in Pawnee Lake, Nebraska.

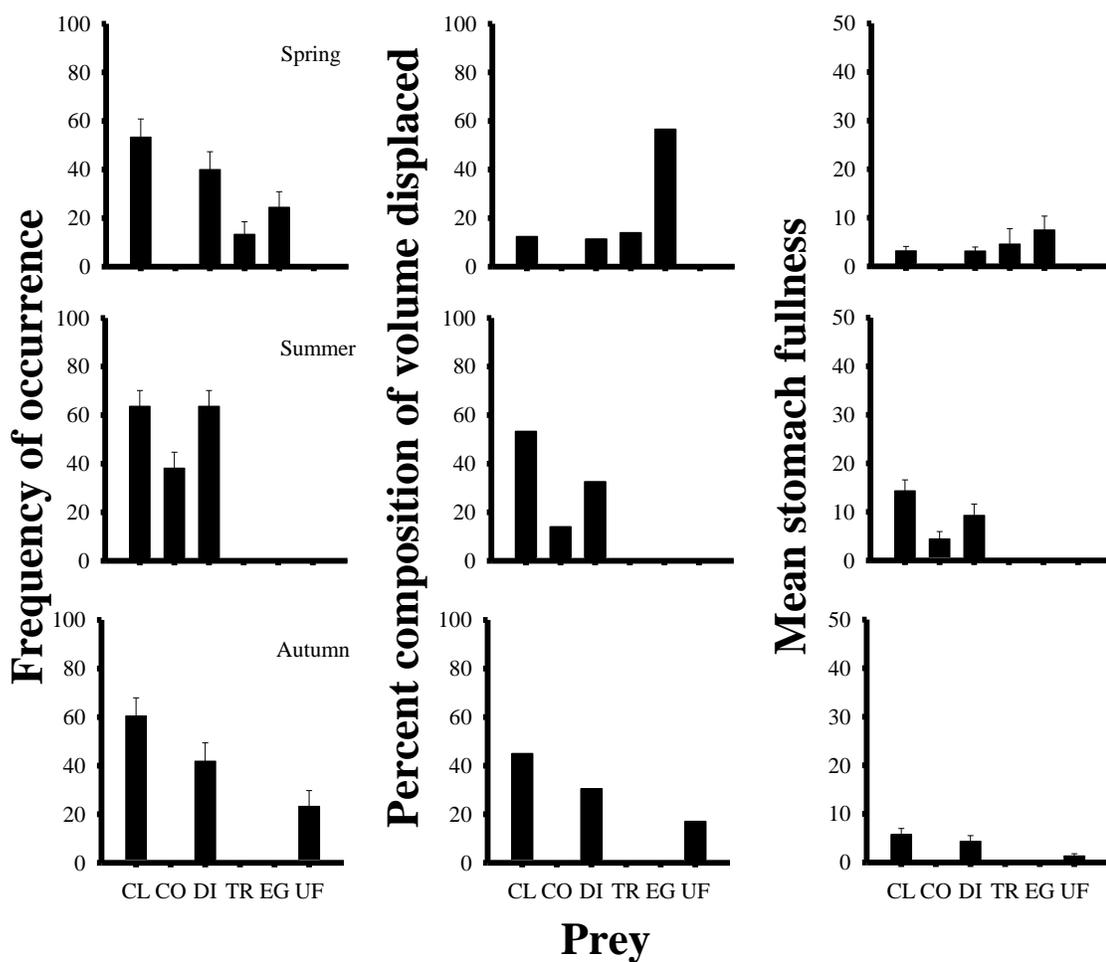


Figure 3-5. Frequency of occurrence \pm SE (left panels), percent composition of volume displaced (middle panels) and mean stomach fullness \pm SE (right panels) for prey consumed (CL = cladocera, CO = coleoptera, DI = diptera, TR = trichoptera, EG = fish eggs, UF = unidentifiable fish) by white perch during spring (top panels), summer (middle panels) and autumn (bottom panels) 2007 in Pawnee Lake, Nebraska.

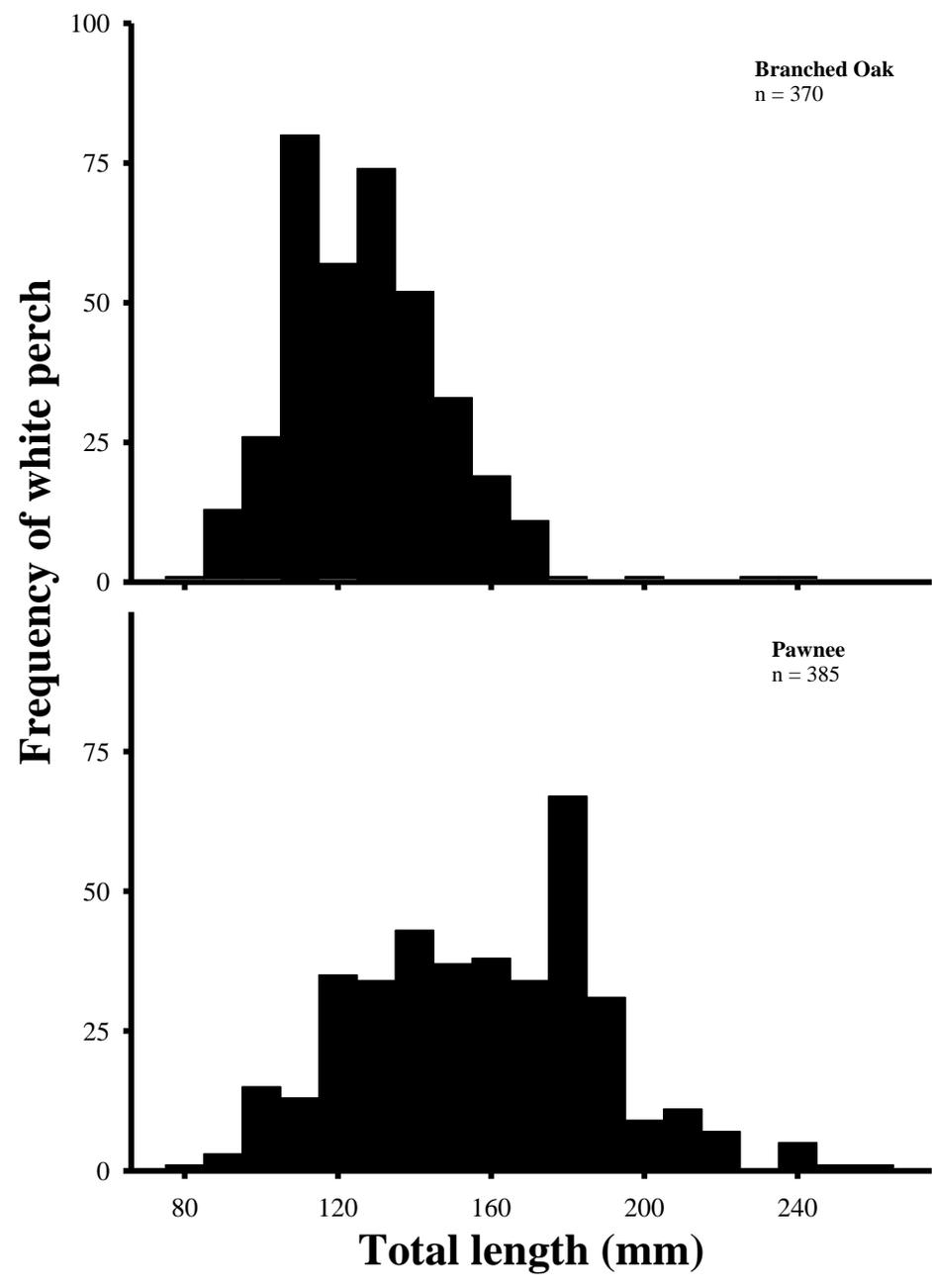


Figure 3-6. Length-frequency distributions of white perch captured in Branched Oak and Pawnee reservoirs, Nebraska.

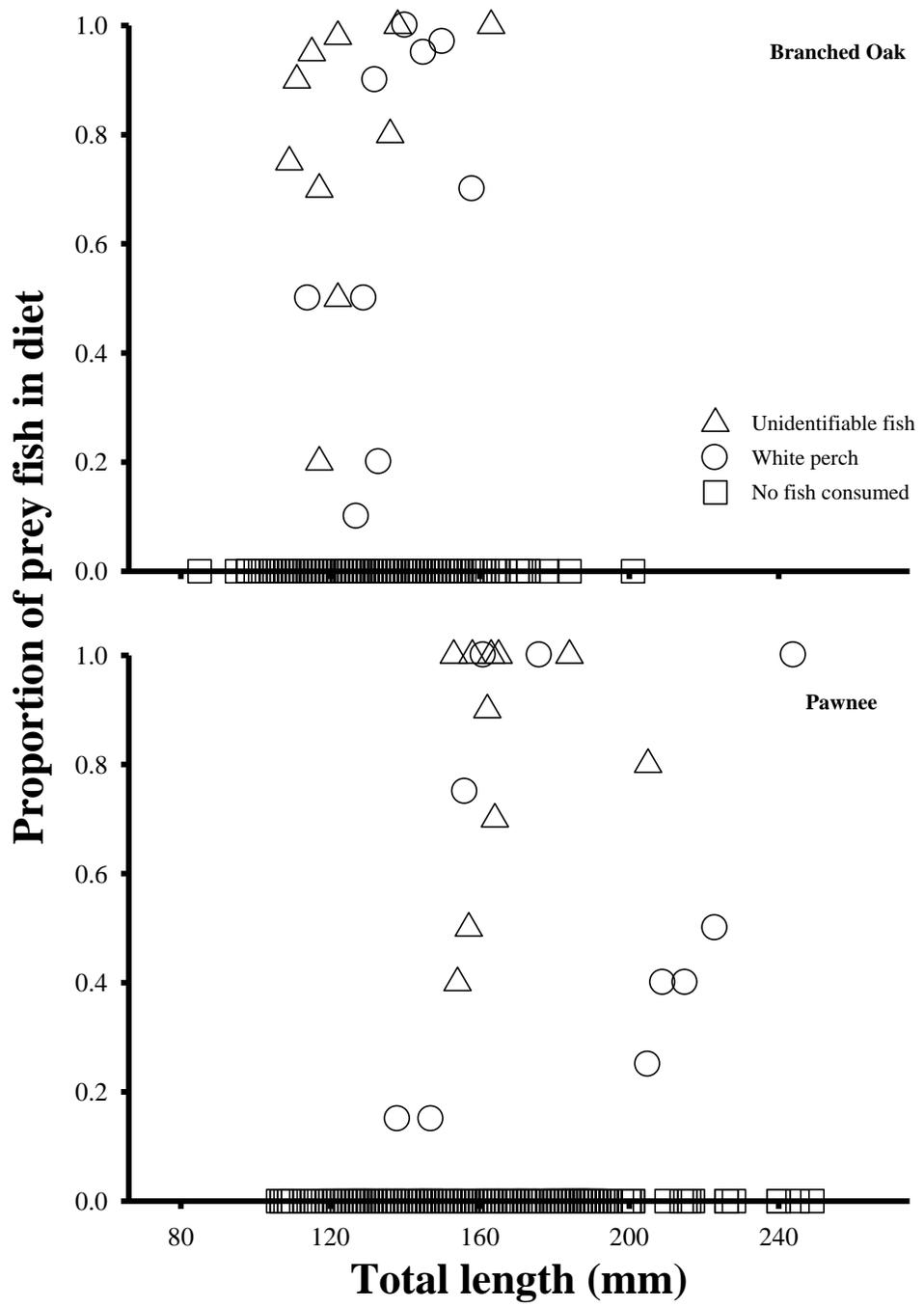


Figure 3-7. Scattergrams of the proportion (by volume) of fish prey in the stomachs of individual white perch plotted as a function of white perch total length for Branched Oak and Pawnee reservoirs, Nebraska.

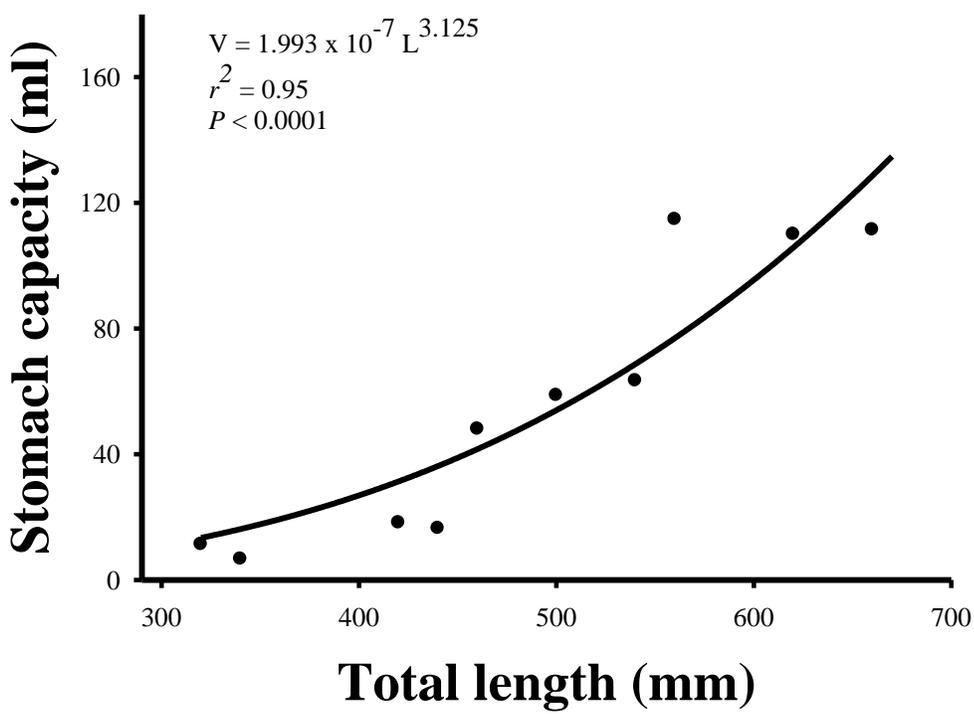


Figure 4-1. Relation between maximum stomach capacity (V) and total length (L) of hybrid striped bass. A point represents the maximum total volume of prey observed in an individual stomach plotted as the midpoint for each length group.

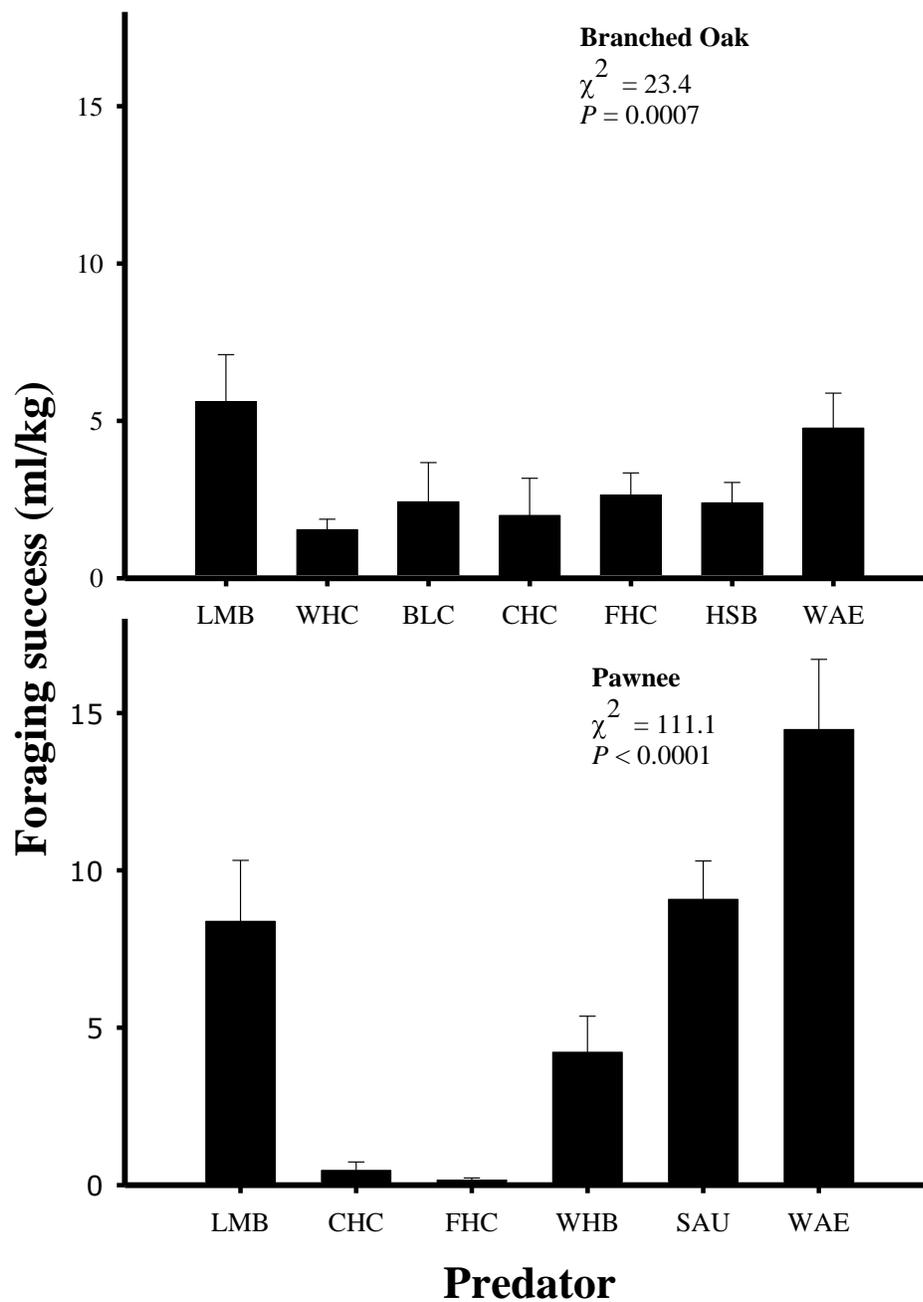


Figure 4-2. Foraging success \pm SE on white perch for predators (LMB = largemouth bass, WHC = white crappie, BLC = black crappie, CHC = channel catfish, FHC = flathead catfish, WHB = white bass, HSB = hybrid striped bass, SAU = sauger, WAE = walleye) captured in Branched Oak and Pawnee reservoirs, Nebraska during 2006.

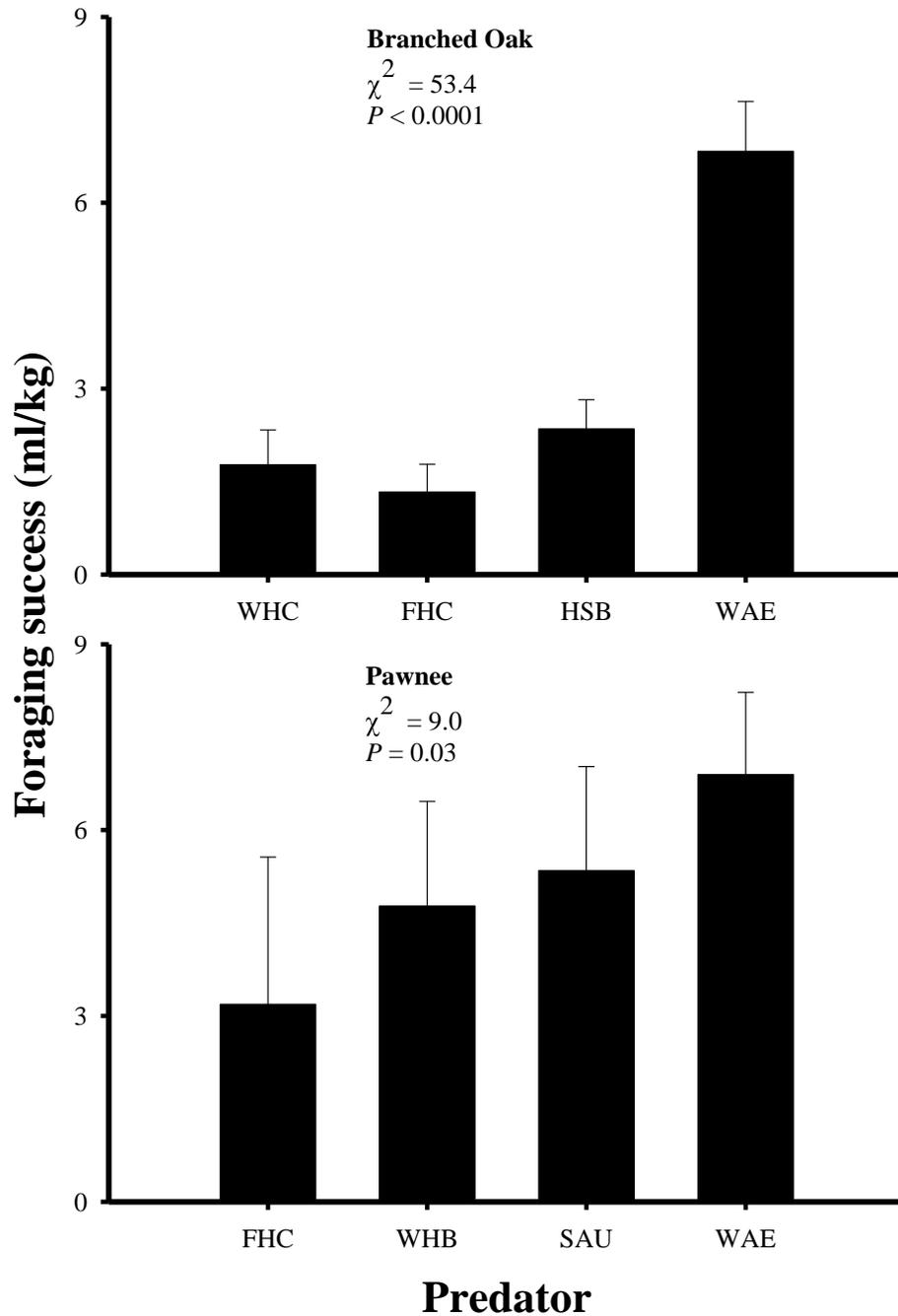


Figure 4-3. Foraging success \pm SE on white perch for predators (WHC = white crappie, FHC = flathead catfish, WHB = white bass, HSB = hybrid striped bass, SAU = sauger, WAE = walleye) captured in Branched Oak and Pawnee reservoirs, Nebraska during 2007.

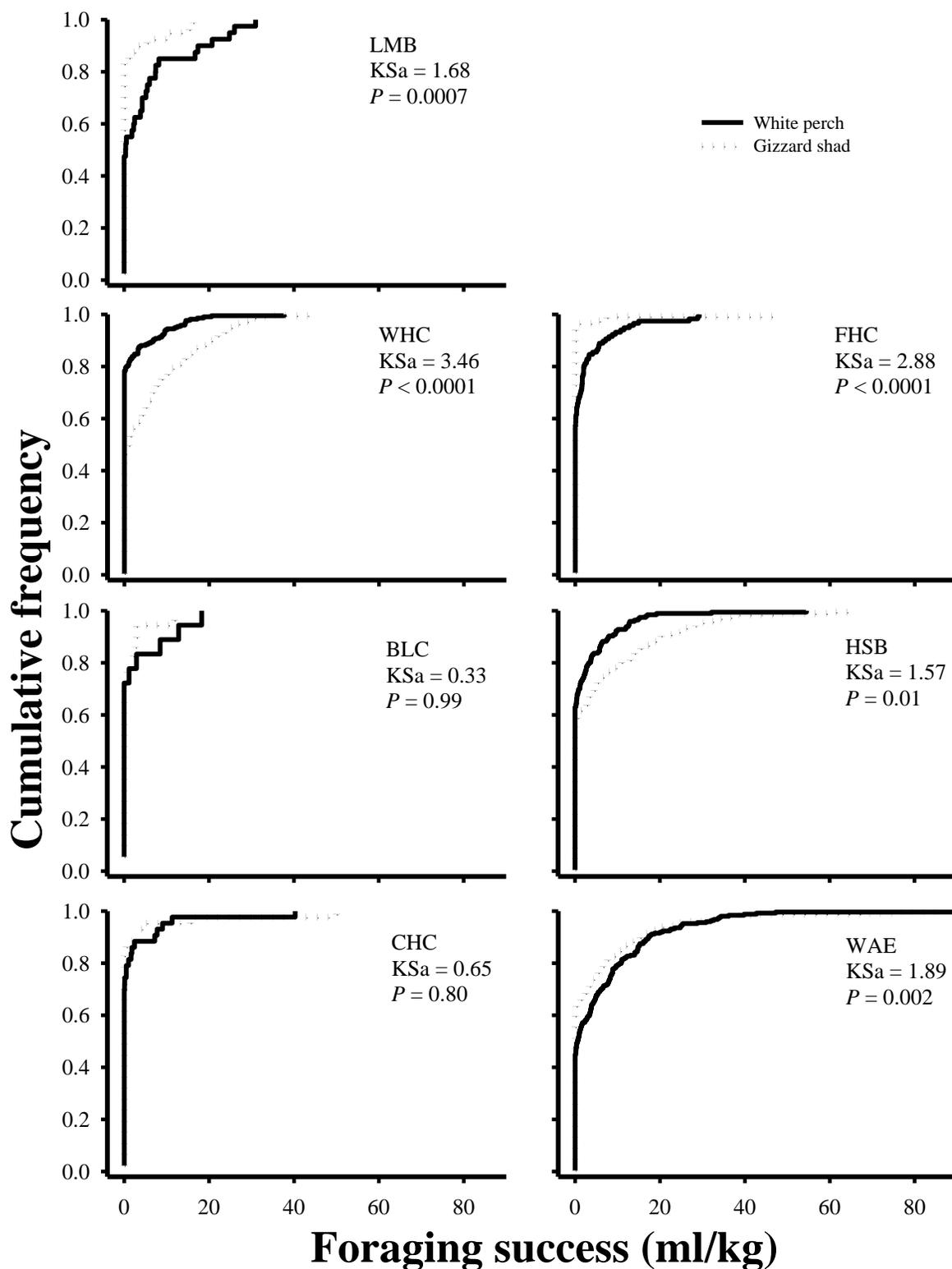


Figure 4-4. Cumulative-frequency distributions of foraging success (ml/kg) on white perch (solid line) and gizzard shad (dotted line) for predators (LMB = largemouth bass, WHC = white crappie, BLC = black crappie, CHC = channel catfish, FHC = flathead catfish, HSB = hybrid striped bass, WAE = walleye) captured in Branched Oak Lake, Nebraska during 2006 and 2007.

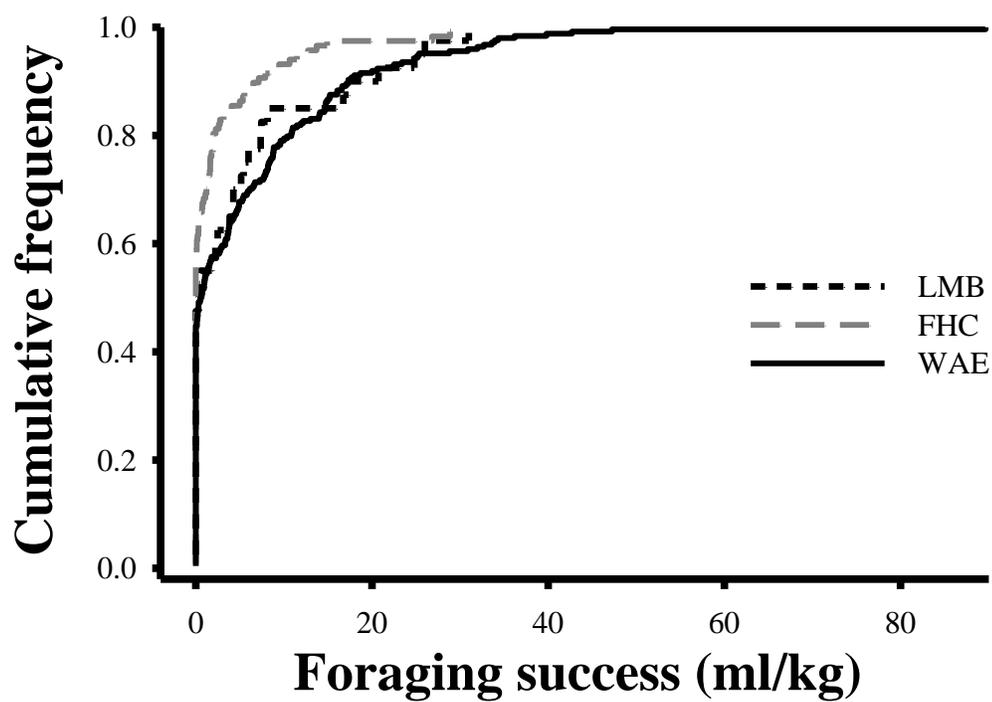


Figure 4-5. Cumulative-frequency distributions of foraging success (ml/kg) on white perch for largemouth bass (LMB), flathead catfish (FHC) and walleye (WAE) in Branched Oak Lake, Nebraska during 2006 and 2007.

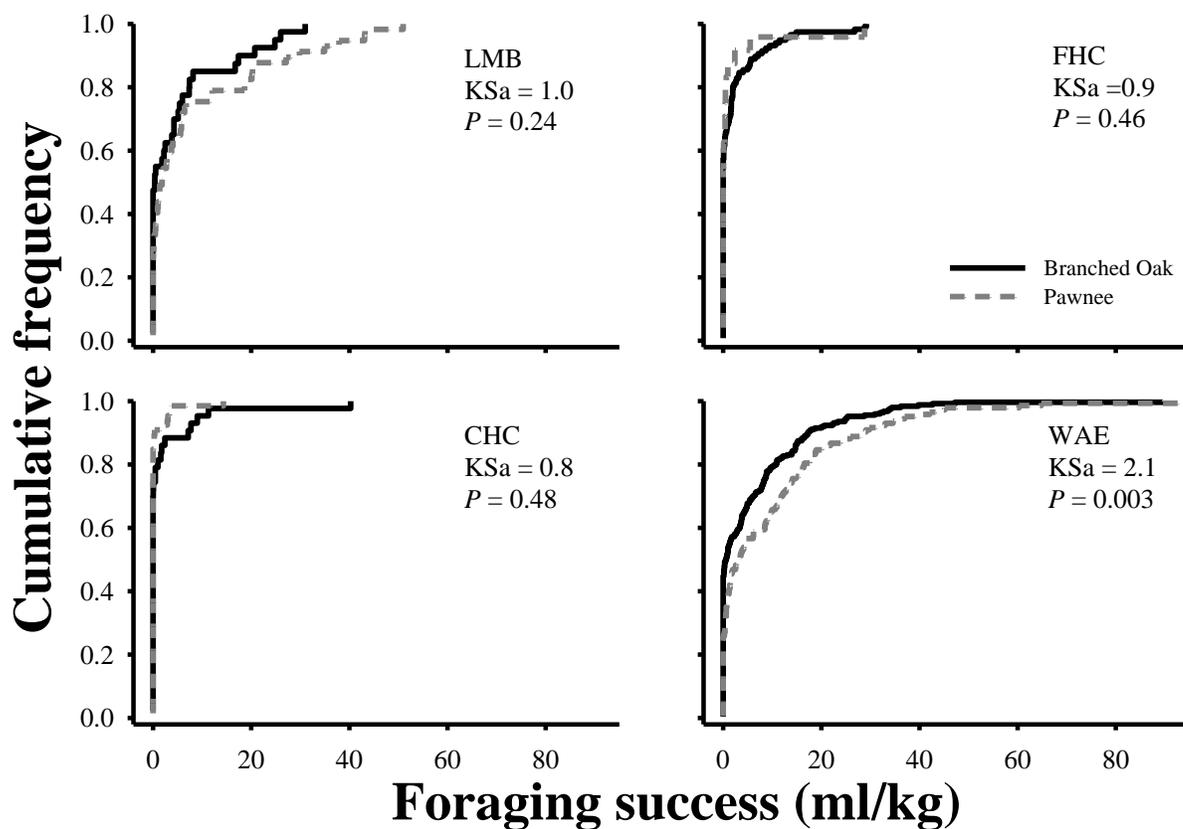


Figure 4-6. Cumulative-frequency distributions of foraging success (ml/kg) on white perch for predators (LMB = largemouth bass, CHC = channel catfish, FHC = flathead catfish, WAE = walleye) present in both Branched Oak and Pawnee reservoirs, Nebraska during 2006 and 2007.

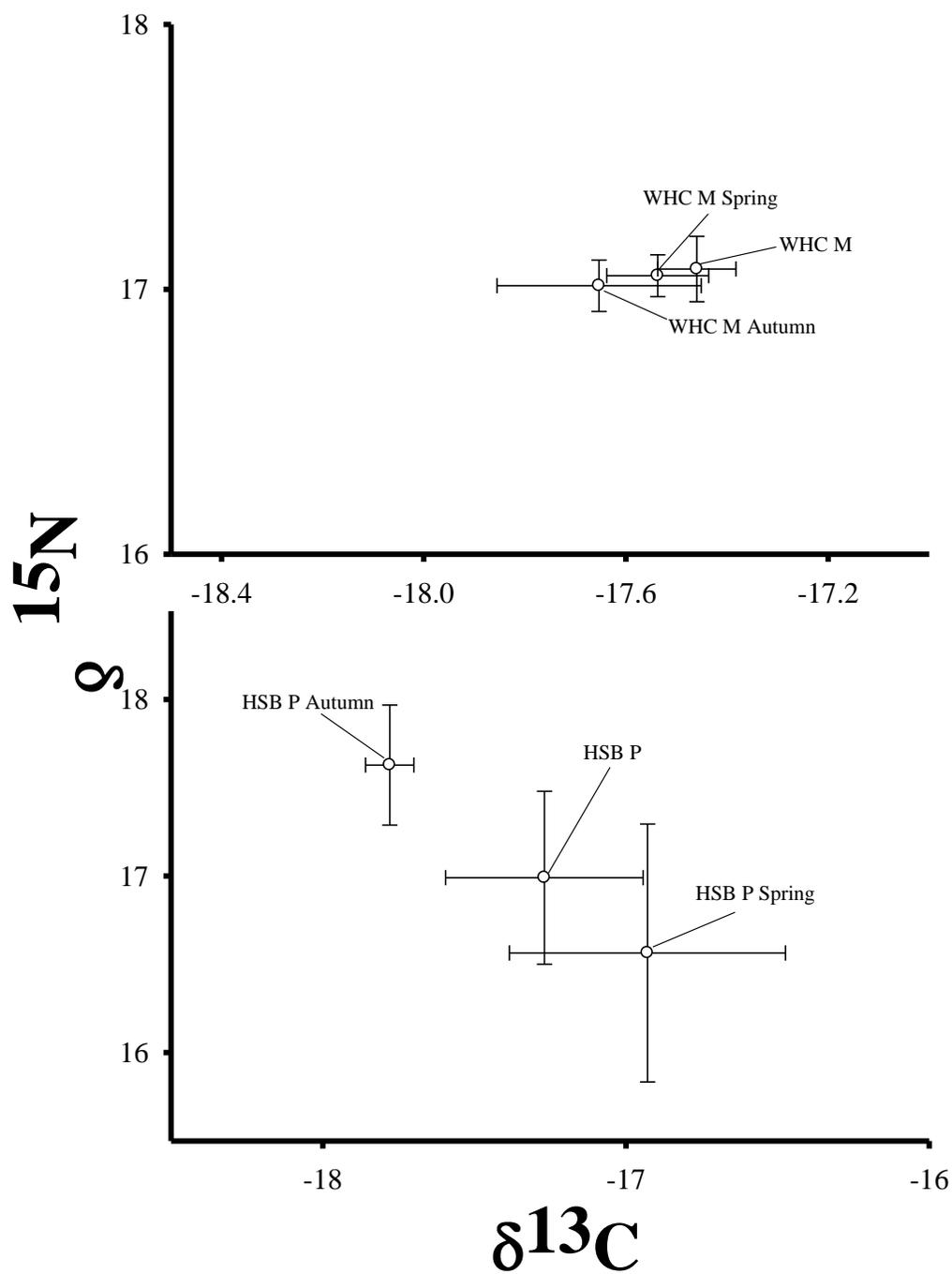


Figure 5-1. Seasonal stable isotope signatures for memorable-length (M) white crappie (WHC; top panel) and preferred-length (P) hybrid striped bass (HSB; bottom panel) in Branched Oak Lake, Nebraska.

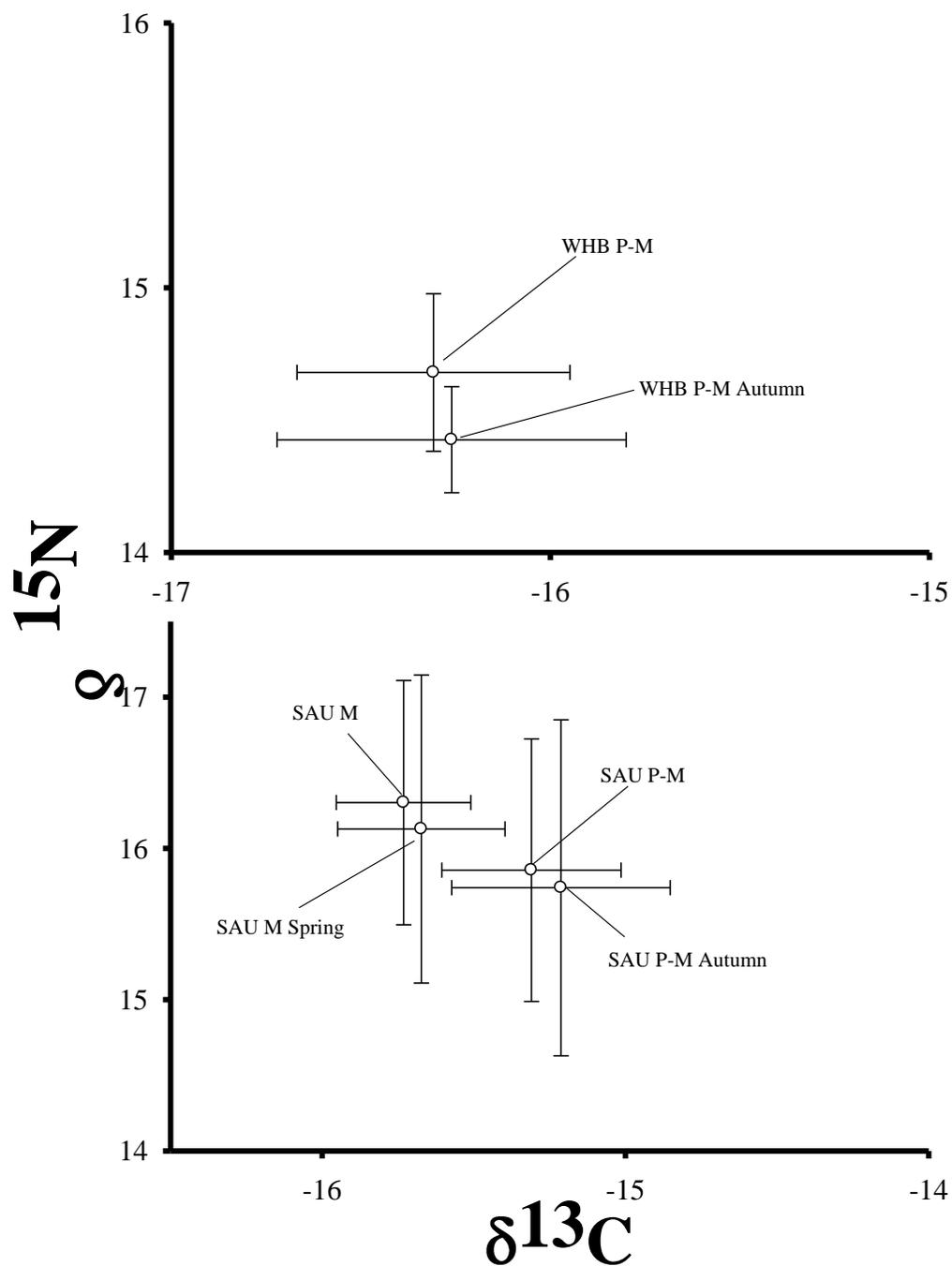


Figure 5-2. Seasonal stable isotope signatures for preferred- to memorable-length (P-M) white bass (WHB; top panel) and preferred- to memorable-length (P-M) and memorable-length (M) sauger (SAU; bottom panel) in Pawnee Lake, Nebraska.

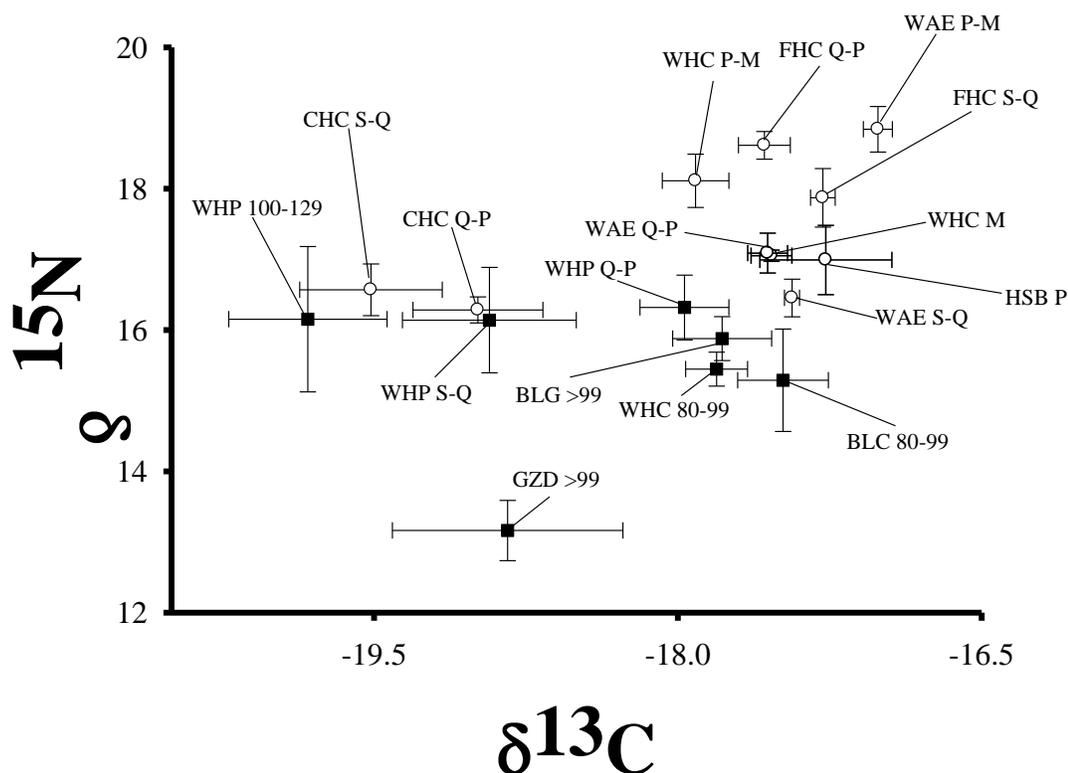


Figure 5-3. Stable isotope signatures for predators (open circles) and prey (solid squares) in Branched Oak Lake, Nebraska. All stock-length fishes were considered predators, except white perch. Predators captured were largemouth bass (LMB), white crappie (WHC), black crappie (BLC), channel catfish (CHC), flathead catfish (FHC), hybrid striped bass (HSB) and walleye (WAE). Predator size categories were stock to quality length (S-Q), quality to preferred length (Q-P), preferred to memorable length (P-M), preferred length (P) and memorable length (M). Prey captured were bluegill (BLG), black crappie (BLC), white crappie (WHC), gizzard shad (GZD) and white perch (WHP). Prey size categories were 80-99 mm and >99 mm for all prey, except white perch. Prey size categories for white perch were 100-129 mm, stock to quality length (S-Q) and quality to preferred length (Q-P).

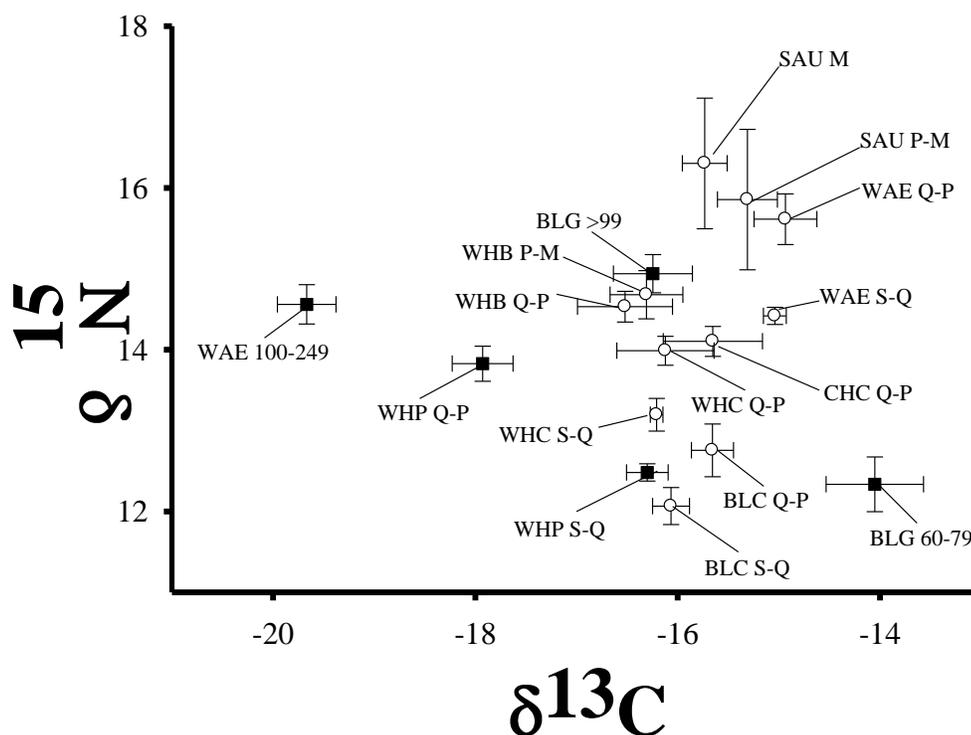


Figure 5-4. Stable isotope signatures for predators (open circles) and prey (solid squares) in Pawnee Lake, Nebraska. All stock-length fishes were considered predators, except white perch. Predators captured were white crappie (WHC), black crappie (BLC), channel catfish (CHC), white bass (WHB), sauger (SAU) and walleye (WAE). Predator size categories were stock to quality length (S-Q), quality to preferred length (Q-P), preferred to memorable length (P-M) and memorable length (M). Prey captured were bluegill (BLG), white perch (WHP) and walleye (WAE). Prey size categories were 60-79 mm, >99 mm and 100-249 mm for all prey, except white perch. Prey size categories for white perch were 100-129 mm, stock to quality length (S-Q) and quality to preferred length (Q-P).

Appendix A. A complete summary of food habits (O_i = frequency of occurrence, % V_i = percent composition of volume displaced and MSF_i = mean stomach fullness) for white perch by season in Branched Oak (BO) and Pawnee (PA) reservoirs, Nebraska during 2006 and 2007.

Year	Season	Reservoir	Prey item	O_i (\pm SE)	% V_i	MSF_i (\pm SE)
2006	spring	BO	cladocera	77.3 (\pm 6.3)	80.4	23.0 (\pm 4.9)
			coleoptera	4.6 (\pm 3.1)	1.6	0.3 (\pm 0.2)
			diptera	27.3 (\pm 6.7)	8.1	2.7 (\pm 1.0)
			rock	6.8 (\pm 3.8)	3.7	2.3 (\pm 2.0)
			unidentifiable fish	11.3 (\pm 4.8)	4.8	1.1 (\pm 0.5)
			unidentifiable plant	9.1 (\pm 4.3)	1.5	0.2 (\pm 0.2)
	summer	algae	2.9 (\pm 2.0)	1.7	0.5 (\pm 0.3)	
		annelida	1.4 (\pm 1.4)	0.02	0.005 (\pm 0.005)	
		araneae	1.4 (\pm 1.4)	0.05	0.01 (\pm 0.01)	
		cladocera	55.7 (\pm 5.9)	27.4	6.0 (\pm 0.9)	
		coleoptera	15.7 (\pm 4.3)	4.5	1.4 (\pm 0.5)	
		diptera	72.9 (\pm 5.3)	41.9	10.4 (\pm 1.3)	
		fish eggs	4.3 (\pm 2.4)	1.5	0.3 (\pm 0.2)	
		hemiptera	14.3 (\pm 4.2)	3.5	1.0 (\pm 0.4)	
		hymenoptera	1.4 (\pm 1.4)	0.3	0.1 (\pm 0.1)	
		trichoptera	1.4 (\pm 1.4)	0.5	0.2 (\pm 0.2)	
		unidentifiable plant	1.4 (\pm 1.4)	1.7	0.4 (\pm 0.4)	
		autumn	white perch	7.1 (\pm 3.1)	16.9	2.7 (\pm 1.7)
	algae		2.1 (\pm 2.1)	2.9	0.5 (\pm 0.5)	
	amphipoda		4.3 (\pm 2.9)	2.9	0.4 (\pm 0.3)	
	araneae		2.1 (\pm 2.1)	0.1	0.02 (\pm 0.02)	
	cladocera		74.5 (\pm 6.4)	39.4	6.5 (\pm 0.8)	
	coleoptera		8.5 (\pm 4.1)	5.4	0.8 (\pm 0.4)	
	diptera		25.5 (\pm 6.4)	12.5	2.6 (\pm 1.0)	
hemiptera	31.9 (\pm 6.8)		32.1	4.7 (\pm 1.6)		
rock	2.1 (\pm 2.1)		0.07	0.01 (\pm 0.01)		
unidentifiable plant	12.8 (\pm 4.9)		4.6	1.9 (\pm 0.7)		

Appendix A. Continued.

Year	Season	Reservoir	Prey item	$O_i (\pm SE)$	$\% V_i$	$MSF_i (\pm SE)$
2006	spring	PA	cladocera	93.8 (± 3.5)	87.9	36.8 (± 4.6)
			coleoptera	2.1 (± 2.1)	0.01	0.007 (± 0.007)
			diptera	37.5 (± 7.0)	8.0	4.5 (± 1.5)
			hemiptera	2.1 (± 2.1)	0.3	0.1 (± 0.1)
			white perch	4.2 (± 2.9)	3.7	0.4 (± 0.4)
	summer		algae	1.6 (± 1.6)	1.6	0.3 (± 0.3)
			cladocera	81.0 (± 4.9)	71.6	13.3 (± 1.5)
			coleoptera	4.8 (± 2.7)	1.0	0.2 (± 0.1)
			diptera	41.2 (± 6.2)	15.2	2.3 (± 0.6)
			hemiptera	6.3 (± 3.1)	0.9	0.1 (± 0.07)
			rock	1.6 (± 1.6)	3.8	0.7 (± 0.7)
			trichoptera	1.6 (± 1.6)	0.5	0.04 (± 0.04)
	autumn		white perch	11.1 (± 4.0)	5.5	0.6 (± 0.2)
			annelid	4.4 (± 3.1)	0.4	0.1 (± 0.01)
			cladocera	95.6 (± 3.1)	94.2	27.2 (± 1.7)
			coleoptera	4.4 (± 3.1)	0.3	0.09 (± 0.06)
			diptera	13.3 (± 5.1)	1.8	0.5 (± 0.2)
			hemiptera	6.7 (± 3.7)	1.7	0.5 (± 0.3)
hymenoptera		2.2 (± 2.2)	1.2	0.4 (± 0.4)		
white perch		2.2 (± 2.2)	0.4	0.1 (± 0.1)		
2007	spring	BO	amphipoda	2.9 (± 2.8)	0.08	0.02 (± 0.02)
			cladocera	85.7 (± 5.9)	63.8	14.8 (± 2.8)
			copepoda	62.9 (± 8.2)	6.7	1.9 (± 0.5)
			diptera	48.6 (± 8.4)	22.5	5.3 (± 1.6)
			fish eggs	28.6 (± 7.6)	6.7	1.4 (± 0.5)
	summer		trichoptera	2.9 (± 2.8)	0.2	0.1 (± 0.1)
			amphipoda	12.1 (± 4.3)	3.8	1.4 (± 0.6)
			cladocera	37.9 (± 6.4)	6.1	2.0 (± 0.9)

Appendix A. Continued.

Year	Season	Reservoir	Prey item	$O_i (\pm SE)$	% V_i	$MSF_i (\pm SE)$	
2007	summer	BO	coleoptera	1.7 (\pm 1.7)	3.8	0.1 (\pm 0.1)	
			copepoda	13.8 (\pm 4.5)	6.1	1.4 (\pm 0.7)	
			decapoda	1.7 (\pm 1.7)	1.1	0.1 (\pm 0.1)	
			diptera	89.7 (\pm 4.0)	4.0	19.3 (\pm 1.9)	
			ephemeroptera	1.7 (\pm 1.7)	0.2	1.6 (\pm 1.6)	
			plecoptera	3.4 (\pm 2.4)	50.5	0.7 (\pm 0.7)	
			trichoptera	1.5 (\pm 1.6)	4.8	0.1 (\pm 0.1)	
			unidentifiable fish	10.3 (\pm 4.0)	2.1	7.4 (\pm 3.6)	
			unidentifiable plant	3.4 (\pm 2.4)	0.5	0.1 (\pm 0.1)	
			autumn	cladocera	63.0 (\pm 6.6)	32.0	5.2 (\pm 0.7)
				coleoptera	9.3 (\pm 3.9)	2.6	0.6 (\pm 0.3)
				diptera	57.4 (\pm 6.7)	35.6	8.7 (\pm 1.7)
				hemiptera	7.4 (\pm 3.6)	2.4	0.6 (\pm 0.4)
			spring	PA	unidentifiable fish	5.6 (\pm 3.1)	27.3
	amphipoda	2.2 (\pm 2.2)			0.04	0.02 (\pm 0.02)	
	cladocera	53.3 (\pm 7.4)			12.3	3.2 (\pm 0.9)	
	copepoda	20.0 (\pm 6.0)			1.1	0.4 (\pm 0.2)	
	diptera	40.0 (\pm 7.3)			11.3	3.1 (\pm 0.8)	
	fish eggs	24.4 (\pm 6.4)			56.5	7.5 (\pm 2.8)	
	trichoptera	13.3 (\pm 5.1)			13.9	4.6 (\pm 3.2)	
	unidentifiable invertebrate	4.4 (\pm 3.1)			2.2	0.3 (\pm 0.2)	
	unidentifiable plant	8.9 (\pm 4.2)			2.6	0.3 (\pm 0.2)	
	summer	amphipoda			1.8 (\pm 1.8)	0.3	0.09 (\pm 0.09)
		cladocera			63.6 (\pm 6.5)	53.2	14.3 (\pm 2.2)
		copepoda			38.2 (\pm 6.6)	13.9	4.5 (\pm 1.5)
		diptera			63.6 (\pm 6.5)	32.5	9.3 (\pm 2.3)
	autumn	cladocera			60.5 (\pm 7.5)	44.9	5.7 (\pm 1.3)
		diptera	41.9 (\pm 7.5)	30.4	4.4 (\pm 1.2)		

Appendix A. Continued.

Year	Season	Reservoir	Prey item	$O_i (\pm SE)$	$\% V_i$	$MSF_i (\pm SE)$
2007	autumn	PA	hirudinea	2.3 (\pm 2.3)	3.7	0.3 (\pm 0.3)
			unidentifiable fish	23.3 (\pm 6.4)	16.9	1.4 (\pm 0.4)
			unidentifiable plant	2.3 (\pm 2.3)	4.1	0.4 (\pm 0.4)

Appendix B. A complete summary of food habits (O_i = frequency of occurrence, $\%V_i$ = percent composition of volume displaced and MSF_i = mean stomach fullness) for largemouth bass (LMB), white crappie (WHC), black crappie (BLC), channel catfish (CHC), flathead catfish (FHC), hybrid striped bass (HSB) and walleye (WAE) by season in Branched Oak Lake, Nebraska during 2006 and 2007. Species with fewer than 10 individuals containing prey items per season were not reported because sample size was insufficient to reliably describe food habits.

Species	Year	Season	Prey item	O_i (\pm SE)	$\%V_i$	MSF_i (\pm SE)
LMB	2006	autumn	bluegill	4.8 (\pm 4.7)	2.7	0.3 (\pm 0.3)
			coleoptera	4.8 (\pm 4.7)	0.03	0.02 (\pm 0.02)
			decapoda	23.8 (\pm 9.3)	12.0	1.4 (\pm 1.0)
			gizzard shad	14.3 (\pm 7.6)	7.7	2.4 (\pm 1.4)
			goldfish	4.8 (\pm 4.7)	13.3	1.4 (\pm 1.4)
			green sunfish	4.8 (\pm 4.7)	22.7	1.6 (\pm 1.6)
			unidentifiable fish	9.5 (\pm 6.4)	1.7	0.1 (\pm 0.1)
WHC	2006	spring	white perch	57.1 (\pm 10.8)	39.9	10.0 (\pm 3.8)
			amphipoda	4.0 (\pm 2.8)	0.2	0.03 (\pm 0.02)
			cladocera	22.0 (\pm 5.6)	1.3	0.2 (\pm 0.08)
			cyclopoida	4.0 (\pm 2.8)	0.2	0.02 (\pm 0.02)
			diptera	64.0 (\pm 6.8)	10.9	1.4 (\pm 0.4)
			ephemeroptera	2.0 (\pm 2.0)	0.03	0.003 (\pm 0.003)
			gizzard shad	48.0 (\pm 7.1)	73.9	11.8 (\pm 2.6)
		hirudinea	2.0 (\pm 2.0)	0.1	0.01 (\pm 0.01)	
		unidentifiable fish	12.0 (\pm 4.6)	4.2	0.6 (\pm 0.3)	
		unidentifiable invertebrate	2.0 (\pm 2.0)	0.09	0.009 (\pm 0.009)	
		unidentifiable plant	4.0 (\pm 2.8)	0.1	0.01 (\pm 0.01)	
		white perch	8.0 (\pm 3.8)	8.9	1.0 (\pm 0.8)	
		summer	cladocera	2.5 (\pm 2.5)	0.08	0.01 (\pm 0.01)
			decapoda	5.0 (\pm 3.4)	0.06	0.01 (\pm 0.01)
			diptera	15.0 (\pm 5.6)	0.8	0.1 (\pm 0.08)
			gizzard shad	47.5 (\pm 7.9)	60.6	12.5 (\pm 3.1)
			heteroptera	2.5 (\pm 2.5)	0.2	0.05 (\pm 0.05)
unidentifiable fish	5.0 (\pm 2.5)		1.9	0.4 (\pm 0.3)		

Appendix B. Continued.

Species	Year	Season	Prey item	O _i (± SE)	% V _i	MSF _i (± SE)		
WHC	2006	summer	unidentifiable plant	12.5 (± 5.2)	0.8	0.1 (± 0.07)		
			white perch	52.5 (± 7.9)	35.5	5.4 (± 1.5)		
		autumn	algae	3.0 (± 3.0)	1.1	0.3 (± 0.3)		
			decapoda	3.0 (± 3.0)	0.2	0.05 (± 0.05)		
			diptera	12.1 (± 5.7)	0.8	0.2 (± 0.1)		
			gizzard shad	57.6 (± 8.6)	71.0	14.1 (± 4.2)		
			unidentifiable fish	3.0 (± 3.0)	0.01	0.002 (± 0.002)		
			white perch	36.4 (± 8.4)	26.9	6.5 (± 2.3)		
			BLC	spring	acariformes	16.7 (± 10.7)	0.04	0.01 (± 0.01)
					cladocera	33.3 (± 13.6)	1.1	0.3 (± 0.2)
cyclopoida	25.0 (± 10.9)	0.3			0.1 (± 0.05)			
decapoda	8.3 (± 8.0)	18.4			5.5 (± 5.5)			
diptera	66.7 (± 13.6)	13.7			3.4 (± 1.3)			
gizzard shad	25.0 (± 10.9)	32.2			7.2 (± 5.2)			
unidentifiable fish	25.0 (± 10.9)	2.2			0.6 (± 0.5)			
unidentifiable invertebrate	8.3 (± 8.0)	0.3			0.07 (± 0.07)			
unidentifiable plant	25.0 (± 10.9)	1.9			0.6 (± 0.6)			
white perch	25.0 (± 10.9)	29.8			6.6 (± 6.6)			
CHC		algae	38.5 (± 9.5)	34.5	92.1 (± 32.7)			
		amphipoda	3.8 (± 3.7)	0.03	0.1 (± 0.1)			
		coleoptera	7.7 (± 5.2)	0.07	0.1 (± 0.09)			
		decapoda	15.4 (± 7.0)	5.6	3.6 (± 2.2)			
		diptera	15.4 (± 7.0)	0.1	0.6 (± 0.5)			
		fish eggs	11.5 (± 6.1)	3.9	15.5 (± 11.8)			
		ephemeroptera	3.8 (± 3.7)	0.04	0.08 (± 0.08)			
		gizzard shad	23.1 (± 8.3)	9.1	26.8 (± 18.4)			
		hirudinea	3.8 (± 3.7)	0.06	0.1 (± 0.1)			

Appendix B. Continued.

Species	Year	Season	Prey item	$O_i (\pm SE)$	$\% V_i$	$MSF_i (\pm SE)$
CHC	2006	spring	unidentifiable fish	26.9 (± 8.7)	28.1	99.5 (± 54.6)
			unidentifiable plant	15.4 (± 7.0)	4.6	10.1 (± 6.9)
			white perch	30.8 (± 9.1)	13.9	23.7 (± 13.3)
FHC		summer	coleoptera	1.5 (± 1.5)	0.01	N/A
			decapoda	21.5 (± 5.1)	10.5	N/A
			diptera	6.1 (± 2.9)	0.03	N/A
			fish eggs	1.5 (± 1.5)	1.0	N/A
			gizzard shad	3.1 (± 2.1)	0.3	N/A
			rock	6.1 (± 2.9)	1.5	N/A
			unidentifiable fish	1.5 (± 1.5)	0.02	N/A
			unidentifiable invertebrate	16.9 (± 4.5)	0.7	N/A
			unidentifiable plant	1.5 (± 1.5)	2.3	N/A
			white perch	52.3 (± 6.2)	83.6	N/A
HSB		spring	decapoda	19.4 (± 7.0)	13.0	1.2 (± 0.8)
			diptera	3.2 (± 3.1)	0.02	0.02 (± 0.02)
			gizzard shad	6.5 (± 4.3)	34.1	6.2 (± 4.3)
			rock	3.2 (± 3.1)	0.03	0.01 (± 0.01)
			unidentifiable fish	22.6 (± 7.5)	12.3	2.1 (± 1.1)
			unidentifiable plant	16.1 (± 6.6)	0.4	0.06 (± 0.03)
			white perch	54.8 (± 9.0)	40.2	7.5 (± 2.3)
		summer	algae	2.3 (± 2.1)	0.07	0.01 (± 0.01)
			decapoda	22.7 (± 6.4)	24.6	2.4 (± 1.0)
			diptera	9.1 (± 4.4)	0.07	0.01 (± 0.007)
			gizzard shad	27.3 (± 6.8)	40.3	7.8 (± 2.9)
			hirudinea	2.3 (± 2.1)	0.1	0.06 (± 0.06)
			unidentifiable fish	15.9 (± 5.6)	1.5	0.5 (± 0.3)
			unidentifiable plant	4.5 (± 3.0)	0.06	0.005 (± 0.004)
			white perch	34.1 (± 7.2)	33.3	8.4 (± 2.9)

Appendix B. Continued.

Species	Year	Season	Prey item	$O_i (\pm SE)$	$\% V_i$	$MSF_i (\pm SE)$
HSB	2006	autumn	decapoda	5.7 (\pm 3.6)	2.7	0.93 (\pm 0.7)
			gizzard shad	85.7 (\pm 6.4)	90.4	38.2 (\pm 6.7)
			rock	2.9 (\pm 2.8)	0.09	0.02 (\pm 0.02)
			unidentifiable fish	8.6 (\pm 4.7)	0.6	0.3 (\pm 0.2)
			white perch	17.1 (\pm 6.3)	6.2	1.9 (\pm 0.9)
WAE	spring		algae	5.3 (\pm 3.5)	0.4	0.06 (\pm 0.06)
			ephemeroptera	2.6 (\pm 2.6)	0.04	0.01 (\pm 0.01)
			gizzard shad	31.6 (\pm 7.5)	19.8	5.6 (\pm 2.0)
			unidentifiable fish	15.8 (\pm 5.8)	2.7	0.9 (\pm 0.5)
			unidentifiable plant	5.3 (\pm 3.5)	0.3	0.04 (\pm 0.04)
			white perch	63.2 (\pm 7.8)	76.7	18.5 (\pm 5.0)
	summer		common carp	3.7 (\pm 3.6)	16.7	2.2 (\pm 2.2)
			diptera	3.7 (\pm 3.6)	0.02	0.002 (\pm 0.002)
			gizzard shad	29.6 (\pm 8.8)	22.6	9.5 (\pm 3.6)
			unidentifiable fish	22.2 (\pm 8.0)	1.5	0.3 (\pm 3.6)
			white perch	63.0 (\pm 9.3)	59.2	15.9 (\pm 3.6)
			gizzard shad	100.0 (\pm 0.0)	90.3	27.6 (\pm 3.7)
			unidentifiable fish	7.0 (\pm 3.9)	0.4	0.1 (\pm 0.1)
autumn		white perch	27.9 (\pm 6.8)	9.2	2.1 (\pm 1.1)	
		gizzard shad	27.9 (\pm 6.8)	9.2	2.1 (\pm 1.1)	
WHC	2007	spring	algae	2.9 (\pm 2.9)	0.09	0.02 (\pm 0.02)
			cladocera	5.9 (\pm 4.0)	0.3	0.05 (\pm 0.04)
			copepoda	5.9 (\pm 4.0)	0.1	0.02 (\pm 0.02)
			crappie	2.9 (\pm 2.9)	6.4	1.1 (\pm 1.1)
			diptera	50.0 (\pm 8.6)	7.6	1.5 (\pm 0.7)
			ephemeroptera	5.9 (\pm 4.0)	0.2	0.04 (\pm 0.03)
			gizzard shad	23.5 (\pm 7.3)	29.3	4.5 (\pm 2.3)
			trichoptera	26.5 (\pm 7.6)	0.8	0.1 (\pm 0.04)
			unidentifiable fish	38.2 (\pm 8.3)	3.0	0.6 (\pm 0.2)

Appendix B. Continued.

Species	Year	Season	Prey item	$O_i (\pm SE)$	$\% V_i$	$MSF_i (\pm SE)$	
WHC	2007	spring	unidentifiable plant	26.5 (\pm 7.6)	1.9	0.4 (\pm 0.2)	
			white perch	29.4 (\pm 7.8)	50.2	7.9 (\pm 2.6)	
		summer	brook silversides	6.3 (\pm 6.1)	8.8	4.3 (\pm 4.3)	
			diptera	25.0 (\pm 10.8)	0.6	0.4 (\pm 0.2)	
			gizzard shad	62.5 (\pm 12.1)	56.2	26.9 (\pm 6.6)	
			unidentifiable invertebrate	6.3 (\pm 6.1)	0.1	0.09 (\pm 0.09)	
			unidentifiable plant	12.5 (\pm 8.3)	0.3	0.2 (\pm 0.1)	
			white perch	12.5 (\pm 8.3)	42.8	5.0 (\pm 3.4)	
		autumn	cladocera	4.5 (\pm 3.1)	0.2	0.05 (\pm 0.03)	
			decapoda	2.3 (\pm 2.2)	0.7	0.2 (\pm 0.2)	
			diptera	6.8 (\pm 3.8)	0.1	0.05 (\pm 0.04)	
			gizzard shad	88.6 (\pm 4.8)	95.8	28.6 (\pm 4.3)	
			hirudinea	2.3 (\pm 2.2)	0.1	0.04 (\pm 0.04)	
			unidentifiable plant	2.3 (\pm 2.2)	0.05	0.02 (\pm 0.02)	
			white perch	6.8 (\pm 3.8)	3.1	0.9 (\pm 0.5)	
		FHC	spring	decapoda	9.1 (\pm 8.7)	3.8	N/A
				gizzard shad	9.1 (\pm 8.7)	65.7	N/A
unidentifiable fish	36.4 (\pm 14.5)			0.8	N/A		
white perch	45.5 (\pm 15.0)			29.7	N/A		
summer	decapoda		46.4 (\pm 9.4)	47.6	N/A		
	larval fish		17.9 (\pm 7.2)	0.7	N/A		
	unidentifiable fish		10.7 (\pm 5.8)	0.3	N/A		
	unidentifiable plant		7.1 (\pm 4.9)	0.8	N/A		
	white perch		32.1 (\pm 8.8)	50.6	N/A		
HSB	spring	decapoda	6.3 (\pm 6.1)	5.0	0.2 (\pm 0.2)		
		diptera	6.3 (\pm 6.1)	0.2	0.09 (\pm 0.09)		
		gizzard shad	6.3 (\pm 6.1)	0.8	0.05 (\pm 0.05)		
		unidentifiable fish	25.0 (\pm 10.8)	5.5	0.8 (\pm 0.6)		

Appendix B. Continued.

Species	Year	Season	Prey item	O _i (± SE)	% V _i	MSF _i (± SE)		
HSB	2007	spring	white perch	62.5 (± 12.1)	88.5	6.5 (± 2.0)		
			summer	brook silverside	4.8 (± 4.6)	0.5	0.09 (± 0.09)	
			decapoda	4.8 (± 4.6)	0.2	0.2 (± 0.2)		
			diptera	4.8 (± 4.6)	0.003	0.001 (± 0.001)		
			gizzard shad	66.7 (± 10.3)	88.4	19.9 (± 4.8)		
			largemouth bass	4.8 (± 4.6)	0.5	0.6 (± 0.6)		
			larval fish	4.8 (± 4.6)	0.05	0.04 (± 0.04)		
			unidentifiable fish	4.8 (± 4.6)	0.7	0.1 (± 0.1)		
			unidentifiable plant	9.5 (± 6.4)	0.1	0.03 (± 0.3)		
			autumn	white perch	19.0 (± 8.6)	9.4	2.7 (± 1.3)	
				algae	2.0 (± 2.0)	0.01	0.002 (± 0.002)	
				decapoda	2.0 (± 2.0)	0.02	0.004 (± 0.004)	
				gizzard shad	59.2 (± 7.0)	78.9	24.7 (± 6.3)	
				hemiptera	2.0 (± 2.0)	0.01	0.002 (± 0.002)	
				isopoda	2.0 (± 2.0)	0.02	0.003 (± 0.003)	
				unidentifiable plant	4.1 (± 2.8)	0.03	0.006 (± 0.004)	
				white perch	42.9 (± 7.1)	21.0	8.9 (± 2.3)	
				spring	algae	2.3 (± 2.2)	0.04	0.01 (± 0.01)
					gizzard shad	15.9 (± 5.5)	1.8	0.6 (± 0.4)
			unidentifiable fish		20.5 (± 6.1)	5.6	1.7 (± 0.8)	
	unidentifiable plant	4.5 (± 3.1)	0.04		0.008 (± 0.008)			
	summer	white perch	65.9 (± 7.1)		92.6	21.8 (± 4.2)		
		diptera	2.4 (± 2.4)		0.01	0.004 (± 0.004)		
		gizzard shad	7.3 (± 4.1)		1.8	0.9 (± 0.6)		
		unidentifiable fish	4.9 (± 3.4)		0.8	0.2 (± 0.2)		
	unidentifiable plant	4.9 (± 3.4)	0.06	0.04 (± 0.4)				
	walleye	2.4 (± 2.4)	4.4	3.9 (± 3.9)				
	white perch	80.5 (± 6.2)	93.0	28.1 (± 5.8)				

Appendix B. Continued.

Species	Year	Season	Prey item	$O_i (\pm SE)$	$\% V_i$	$MSF_i (\pm SE)$
WAE	2007	autumn	brook silverside	1.8 (\pm 1.8)	1.2	1.2 (\pm 1.2)
			gizzard shad	60.0 (\pm 6.6)	52.4	24.7 (\pm 5.1)
			rock	1.8 (\pm 1.8)	0.04	0.02 (\pm 0.02)
			unidentifiable plant	3.6 (\pm 2.5)	0.05	0.01 (\pm 0.01)
			white perch	45.5 (\pm 6.7)	46.3	13.2 (\pm 3.1)

Appendix C. A complete summary of food habits (O_i = frequency of occurrence, $\%V_i$ = percent composition of volume displaced and MSF_i = mean stomach fullness) for largemouth bass (LMB), channel catfish (CHC), flathead catfish (FHC), white bass (WHB), sauger (SAU) and walleye (WAE) by season in Pawnee Lake, Nebraska during 2006 and 2007. Species with fewer than 10 individuals containing prey items per season were not reported because sample size was insufficient to reliably describe food habits.

Species	Year	Season	Prey item	O_i (\pm SE)	$\%V_i$	MSF_i (\pm SE)		
LMB	2006	spring	common carp	5.9 (\pm 5.7)	0.1	0.04 (\pm 0.04)		
			decapoda	11.8 (\pm 7.8)	1.0	0.3 (\pm 0.2)		
			unidentifiable fish	17.6 (\pm 9.2)	2.5	0.1 (\pm 0.7)		
			unidentifiable plant	5.9 (\pm 5.7)	0.1	0.02 (\pm 0.02)		
			walleye	5.9 (\pm 5.7)	11.4	1.5 (\pm 1.5)		
		summer	white perch	58.8 (\pm 11.9)	84.8	19.7 (\pm 7.0)		
			crappie	7.7 (\pm 7.4)	28.3	5.2 (\pm 5.2)		
			hemiptera	7.7 (\pm 7.4)	0.04	0.01 (\pm 0.01)		
			unidentifiable fish	38.5 (\pm 13.5)	2.1	0.6 (\pm 0.5)		
			white perch	69.2 (\pm 12.8)	69.6	9.5 (\pm 4.8)		
		autumn	caudata	5.3 (\pm 5.1)	16.2	3.0 (\pm 3.0)		
			decapoda	36.8 (\pm 11.1)	32.8	6.5 (\pm 2.5)		
			unidentifiable fish	5.3 (\pm 5.1)	0.06	0.01 (\pm 0.01)		
			walleye	5.3 (\pm 5.1)	16.2	1.1 (\pm 1.1)		
			white perch	57.9 (\pm 11.3)	34.7	9.4 (\pm 3.3)		
			CHC	spring	acariformes	2.8 (\pm 2.7)	0.002	0.008 (\pm 0.008)
					algae	80.6 (\pm 6.6)	95.3	86.0 (\pm 15.2)
cladocera	2.8 (\pm 2.7)	0.002			0.008 (\pm 0.008)			
decapoda	2.8 (\pm 2.7)	0.1			0.09 (\pm 0.09)			
diptera	8.3 (\pm 4.6)	0.01			0.02 (\pm 0.02)			
hirudinea	2.8 (\pm 2.7)	0.1			0.07 (\pm 0.07)			
unidentifiable fish	8.3 (\pm 4.6)	1.9			3.1 (\pm 2.8)			
unidentifiable plant	11.1 (\pm 5.2)	1.0			0.2 (\pm 0.1)			
white perch	2.8 (\pm 2.7)	1.6			0.9 (\pm 0.6)			
summer	algae	69.2 (\pm 12.8)			92.9	31.7 (\pm 11.7)		

Appendix C. Continued.

Species	Year	Season	Prey item	$O_i (\pm SE)$	$\% V_i$	$MSF_i (\pm SE)$
CHC	2006	summer	decapoda	15.4 (± 10.0)	5.6	1.4 (± 1.3)
			diptera	7.7 (± 7.4)	0.02	0.006 (± 0.006)
			ephemeroptera	7.7 (± 7.4)	0.06	0.01 (± 0.01)
			hirudinea	7.7 (± 7.4)	0.1	0.02 (± 0.02)
			hemiptera	7.7 (± 7.4)	0.06	0.01 (± 0.01)
			rock	7.7 (± 7.4)	0.1	0.05 (± 0.05)
			unidentifiable fish	7.7 (± 7.4)	0.1	0.1 (± 0.1)
			unidentifiable plant	7.7 (± 7.4)	1.7	0.4 (± 0.4)
FHC			bluegill	9.1 (± 8.7)	91.4	N/A
			decapoda	9.1 (± 8.7)	7.1	N/A
			diptera	9.1 (± 8.7)	0.04	N/A
			hirudinea	9.1 (± 8.7)	0.4	N/A
			hemiptera	9.1 (± 8.7)	0.1	N/A
			pulmonata	9.1 (± 8.7)	0.2	N/A
			unidentifiable fish	9.1 (± 8.7)	0.2	N/A
			unionoida	9.1 (± 8.7)	0.3	N/A
			unidentifiable plant	9.1 (± 8.7)	0.1	N/A
			white perch	45.5 (± 15.0)	7.8	N/A
WHB		spring	cladocera	50.0 (± 11.8)	9.7	0.7 (± 0.3)
			coleoptera	11.1 (± 7.4)	5.8	0.3 (± 0.3)
			diptera	38.9 (± 11.5)	2.6	0.1 (± 0.05)
			hirudinea	5.6 (± 5.4)	0.6	0.1 (± 0.1)
			hemiptera	16.7 (± 8.7)	2.7	0.04 (± 0.03)
			hymenoptera	5.6 (± 5.4)	0.3	0.02 (± 0.02)
			megaloptera	5.6 (± 5.4)	0.05	0.003 (± 0.003)
			unidentifiable fish	5.6 (± 5.4)	74.6	3.8 (± 3.8)
			unidentifiable invertebrate	5.6 (± 5.4)	0.1	0.008 (± 0.008)

Appendix C. Continued.

Species	Year	Season	Prey item	O _i (± SE)	% V _i	MSF _i (± SE)		
WHB	2006	spring	unidentifiable plant	22.2 (± 9.8)	2.9	0.1 (± 0.08)		
			white perch	5.6 (± 5.4)	0.7	0.05 (± 0.05)		
		summer	common carp	4.8 (± 4.6)	30.6	4.3 (± 4.3)		
			diptera	4.8 (± 4.6)	0.9	0.1 (± 0.1)		
			ephemeroptera	4.8 (± 4.6)	0.7	0.06 (± 0.06)		
			larval fish	19.0 (± 8.6)	10.7	1.7 (± 1.0)		
			unidentifiable fish	19.0 (± 8.6)	1.9	0.3 (± 0.2)		
			unidentifiable plant	4.8 (± 4.6)	0.1	0.01 (± 0.01)		
		SAU		spring	white perch	57.1 (± 10.8)	54.9	7.0 (± 2.9)
					unidentifiable fish	5.9 (± 5.7)	1.8	0.7 (± 0.7)
summer	white perch			94.1 (± 5.7)	98.2	36.5 (± 6.9)		
	unidentifiable fish			36.4 (± 14.5)	5.4	0.5 (± 0.2)		
	white perch			72.7 (± 13.4)	94.6	8.7 (± 2.7)		
autumn	largemouth bass			4.2 (± 4.1)	0.7	0.2 (± 0.2)		
	walleye			4.2 (± 4.1)	0.5	0.1 (± 0.1)		
	white perch			95.8 (± 4.1)	98.8	23.0 (± 4.4)		
WAE		summer	megaloptera	3.4 (± 3.4)	0.06	0.01 (± 0.01)		
			platyhelminthes	3.4 (± 3.4)	0.2	0.02 (± 0.02)		
			unidentifiable fish	6.9 (± 4.7)	2.2	0.5 (± 0.5)		
			white perch	86.2 (± 6.4)	97.6	31.4 (± 6.2)		
		autumn	diptera	6.3 (± 6.1)	0.02	0.01 (± 0.01)		
			fathead minnow	6.3 (± 6.1)	2.3	1.4 (± 1.4)		
			white perch	100.0 (± 0.0)	97.7	32.9 (± 8.3)		
WHB	2007	spring	annelida	7.7 (± 7.4)	1.9	0.05 (± 0.05)		
			diptera	38.5 (± 13.5)	4.9	0.1 (± 0.07)		
			hemiptera	30.8 (± 12.8)	8.7	0.3 (± 0.1)		
			trichoptera	23.1 (± 11.7)	4.1	0.1 (± 0.09)		
			unidentifiable plant	61.5 (± 13.5)	11.9	0.3 (± 0.1)		

Appendix C. Continued.

Species	Year	Season	Prey item	$O_i (\pm SE)$	$\% V_i$	$MSF_i (\pm SE)$	
WHB	2007	spring	white perch	7.7 (± 7.4)	68.6	2.0 (± 2.0)	
			summer	decapoda	9.1 (± 8.7)	0.7	0.2 (± 0.2)
		summer	larval fish	9.1 (± 8.7)	0.3	0.07 (± 0.07)	
			unidentifiable fish	36.4 (± 14.5)	6.4	2.1 (± 1.2)	
SAU		spring	white perch	63.6 (± 14.5)	92.7	23.8 (± 8.3)	
			unidentifiable fish	10.0 (± 9.5)	0.1	0.02 (± 0.02)	
			unidentifiable plant	10.0 (± 9.5)	1.0	0.08 (± 0.08)	
			white perch	90.0 (± 9.5)	98.9	10.1 (± 3.7)	
WAE			algae	2.8 (± 2.7)	0.07	0.007 (± 0.007)	
			annelida	8.3 (± 4.6)	0.7	0.09 (± 0.07)	
			hirudinea	2.8 (± 2.7)	0.5	0.06 (± 0.06)	
			trichoptera	5.6 (± 3.8)	0.03	0.02 (± 0.02)	
			unidentifiable fish	44.4 (± 8.3)	12.1	2.3 (± 1.3)	
			unidentifiable plant	5.6 (± 3.8)	0.08	0.02 (± 0.01)	
			summer	white perch	41.7 (± 8.2)	86.5	12.1 (± 3.4)
				bluegill	2.7 (± 2.7)	35.1	4.2 (± 4.2)
				fathead minnow	2.7 (± 2.7)	1.4	0.5 (± 0.5)
				larval fish	8.1 (± 4.5)	0.3	0.08 (± 0.07)
				unidentifiable fish	13.5 (± 5.6)	0.8	0.4 (± 0.3)
				unidentifiable plant	2.7 (± 2.7)	0.06	0.02 (± 0.02)
			autumn	white perch	75.7 (± 7.1)	62.3	18.1 (± 6.9)
white perch	100.0 (± 0.0)	100.0		22.6 (± 4.6)			

Appendix D. Stomach capacities of six freshwater fishes

Energy acquisition, through the consumption of food, is a requirement for survival and growth of fishes. The importance of predator gape size to food consumption has received much attention (Hambright 1991; Nilsson and Brönmark 2000; Husky and Turingan 2001). In many situations, fishes are gape limited because they lack the ability to disassemble and masticate their food (i.e., they swallow their food whole). However, there exist many situations in which fishes are not gape limited. For example, adult largemouth bass, *Micropterus salmoides* Lacepède, are generally not gape limited when consuming small bluegill, *Lepomis macrochirus* Rafinesque, in a lake containing a stunted (i.e., high density of slow growing individuals) bluegill population. Further, previous research suggests that fishes often select prey much smaller than the maximum size ingestible (Paszkowski and Tonn 1994; Nilsson and Brönmark 2000; Truemper and Lauer 2005).

When fishes are not gape limited or prefer to prey on smaller items, rate of digestion and stomach size limit food consumption. Thus, stomach capacity plays an important role in the consumption of food and, subsequently, predator-prey interactions in aquatic systems. Herein, relationships of stomach capacity with length are reported for bluegill, spotted bass, *M. punctulatus* Rafinesque, white crappie, *Pomoxis annularis* Rafinesque, black crappie, *P. nigromaculatus* Lesueur, channel catfish, *Ictalurus punctatus* Rafinesque, and white bass, *Morone chrysops* Rafinesque. We specifically were interested in whether fish stomachs grew allometrically with fish length.

Methods

We collected bluegill and channel catfish in Blind Pony Lake and Macon Lake, Missouri, during 1998-2000 and spotted bass, white crappie, black crappie, and white bass in Pomme de Terre Lake and Stockton Lake, Missouri, during 1987-1991. Detailed descriptions of reservoir characteristics and sampling methodology are provided by Michaletz (1997, 2006). In summary, bluegill and channel catfish were collected monthly primarily by daytime electrofishing during May-October. Spotted bass were collected monthly by nighttime electrofishing, white and black crappie were collected monthly by overnight trapnetting and white bass were collected monthly by overnight gillnetting during April-October. Captured fishes were identified and measured (nearest 1 mm; total length). Stomach contents were then removed using clear plexiglass tubes for all fishes and preserved, except stomach contents were removed via dissection for bluegill. Stomach contents were weighed to the nearest 0.01 g (bluegill and channel catfish) or measured volumetrically using volume displacement (spotted bass, white crappie, black crappie and white bass). Weight of stomach contents for bluegill and channel catfish were converted to volume by assuming a specific density of one for all stomach contents because the majority of aquatic organisms have a specific density slightly greater than one (Lampert and Sommer 1997).

Species-specific assessments were completed. All fishes were divided into 10-mm length groups, except bluegill were divided into 5-mm length groups. Length groups with fewer than 10 individuals were excluded from analysis. The maximum total volume of stomach contents found in each length group was plotted as a function of the midpoint of each length group. Three obvious outliers were removed (one each for bluegill,

spotted bass and channel catfish) and the next greatest stomach volume was used for the respective length group. Stomach capacity theoretically increases with length; thus, length groups whose maximum total volume of stomach contents was less than each of the two previous length groups were removed because it was likely that no fish captured within those length groups had full (or nearly full) stomachs. Remaining data points were used to develop an exponential regression equation

$$V = aL^b$$

relating stomach capacity (V , ml) to total length (L , mm) (Knight and Margraf 1982).

The PROC NLIN procedure of SAS software (SAS Institute, Cary, North Carolina) was used to obtain species-specific parameters and their associated standard errors for the regression models. Statistical significance was set at $\alpha = 0.05$. The 95% confidence intervals for the exponent (b) were examined to determine if it encompassed (possible isometric growth) or excluded (allometric growth) 1 ($H_0: b = 1$; $H_a: b \neq 1$).

Results

We collected 719 bluegill and 663 channel catfish in Blind Pony Lake and Macon Lake, and 649 spotted bass, 2,563 white crappie, 788 black crappie, and 1,333 white bass in Pomme de Terre Lake and Stockton Lake. A significant exponential relationship existed between stomach capacity and length for each species investigated (Figure D-1). Parameter estimates for b for each investigated species ranged from 1.8 for bluegill to 5.0 for channel catfish. We failed to reject our null hypothesis that $b = 1$ for black crappie, whereas we rejected our null hypothesis for bluegill, spotted bass, white crappie, channel

catfish and white bass (Figure D-1) and concluded that stomachs grew allometrically with length for these five species.

Discussion

Stomach capacity is important for understanding predator-prey interactions in aquatic systems. When predators are not gape-limited, the next logical limitation on food consumption is how much the stomach can hold (i.e., stomach volume or capacity) (Truemper and Lauer 2005). Stomach capacity and size of prey relative to predator should provide important insight into ecological roles of fish. For example, large yellow perch, *Perca flavescens* Mitchill, were able to consume a constant biomass of fathead minnows regardless of available sizes of fathead minnows, whereas small yellow perch consumed less biomass when only large fathead minnows were available (Paszkowski and Tonn 1994). Therefore, fish with larger stomach capacities have more plastic diets by being able to consume a wider range of prey sizes, particularly when they already have prey present in their stomach, compared to fish with smaller stomach capacities. Stomach capacities for bluegill, spotted bass, white crappie, channel catfish and white bass grow allometrically with fish length (i.e., $b \neq 1$). In contrast, there was not strong evidence of allometric growth of stomach capacity with length for black crappie. Other species for which stomach capacity has been related to length include largemouth bass ($b = 3.2$ [Pope et al. 2001]), walleye, *Sander vitreus* Mitchill, ($b = 2.6$ [Knight and Margraf 1982]) and yellow perch ($b = 2.96$ [Phelps et al. 2007]), though no measure of variance was provided for b . For species with $b > 1$, the rate of increase in stomach capacity for a given change in length is greater for large individuals of that species than small

individuals. Further, the rate of change in stomach capacity for a given change in fish length is greater for species with greater b values. Thus, spotted bass and channel catfish experience the greatest rates of increase in stomach capacity with increasing length. These differences are likely a function of different feeding strategies exhibited by these species. For example, piscivory becomes increasingly important for spotted bass (Smith and Page 1969) and channel catfish (Hubert 2000) as they grow and, thus, larger stomachs relative to length might be beneficial to the handling of prey fishes.

We discussed the importance of stomach capacities and presented stomach capacity information for six fishes. This brief investigation of stomach capacities of fishes provides insight for the development of several hypotheses. Within a species, we predict that differences in b exist between sexes and life-history stages (e.g., juveniles versus adults), among habitats within a waterbody and among waterbodies with different prey communities. Among species, we predict that differences in b exist between trophic levels, feeding strategies (e.g., piscivory versus planktivory) and hunting modes (e.g., ambush versus active search).

References

- Hambright, K. D. 1991. Experimental analysis of prey selection by largemouth bass: role of predator mouth width and prey body depth. *Transactions of the American Fisheries Society* 120:500-508.
- Hubert, W. A. 2000. Biology and management of channel catfish. Pages 3-22 in E.R. Irwin, W.A. Hubert, C.F. Rabeni, H.L. Schramm, Jr., and T. Coon, editors. *Catfish 2000*. American Fisheries Society, Bethesda, Maryland.
- Husky, S. H., and R. G. Turingan. 2001. Variation in prey-resource utilization and oral jaw gape between two populations of largemouth bass, *Micropterus salmoides*. *Environmental Biology of Fishes* 61:185-194.
- Knight, R. L., and F. J. Margraf. 1982. Estimating stomach fullness in fishes. *North American Journal of Fisheries Management* 2:413-414.
- Lampert, W., and U. Sommer. 1997. *Limnoecology: the ecology of lakes and streams*. Oxford University Press, New York.
- Michaletz, P. H. 1997. Influence of abundance and size of age-0 gizzard shad on predator diets, diet overlap, and growth. *Transactions of the American Fisheries Society* 126:101-111.
- Michaletz, P. H. 2006. Prey resource use by bluegill and channel catfish in small impoundments. *Fisheries Management and Ecology* 13:347-354.
- Nilsson, P.A., and C. Brönmark. 2000. Prey vulnerability to a gape-size limited predator: behavioural and morphological impacts on northern pike piscivory. *Oikos* 88:539-546.

- Paskowski, C. A., and W. M. Tonn. 1994. Effects of prey size, abundance, and population structure on piscivory by yellow perch. *Transactions of the American Fisheries Society* 123:855-865.
- Phelps, Q. E., K. A. Powell, S. R. Chipps, and D. W. Willis. 2007. A method for determining stomach fullness for planktivorous fishes. *North American Journal of Fisheries Management* 27:932-935.
- Pope, K. L., M. L. Brown, W. G. Duffy, and P. H. Michaletz. 2001. A caloric-based evaluation of diet indices for largemouth bass. *Environmental Biology of Fishes* 61:329-339.
- Scott, W. B., and Crossman, E. J. 1973. *Freshwater fishes of Canada*. Fisheries Research Board of Canada, Bulletin 184, Ottawa.
- Smith, P. W., and L. M. Page. 1969. The food of spotted bass in streams of the Wabash River drainage. *Transactions of the American Fisheries Society* 98:647-651.
- Truemper, H.A., and T. E. Lauer. 2005. Gape limitation and piscine prey size-selection by yellow perch in the extreme southern area of Lake Michigan, with emphasis on two exotic prey items. *Journal of Fish Biology* 66:135-149.

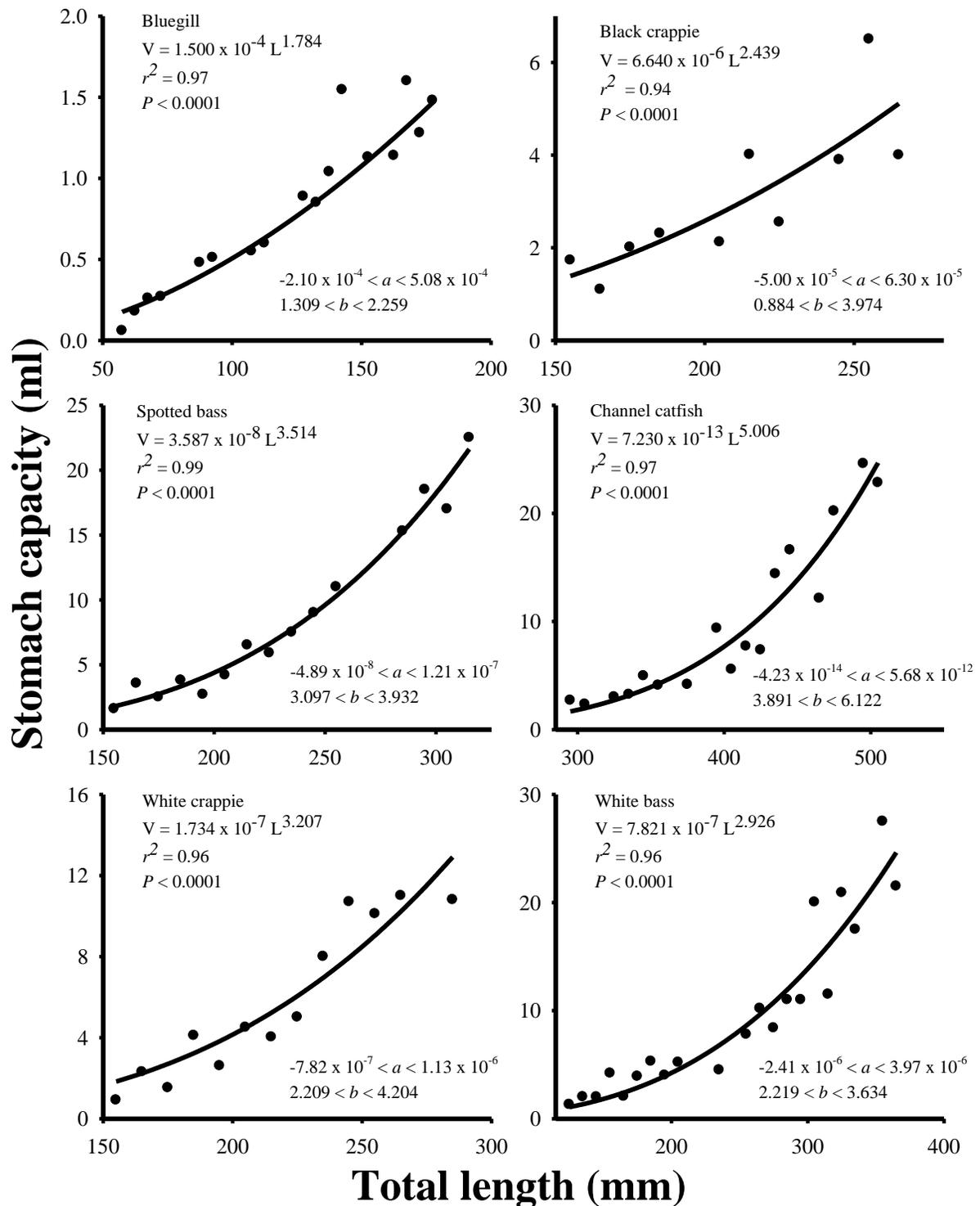


Figure D-1. Relations between maximum stomach capacity (V) and total length (L) for six freshwater fishes collected from Missouri reservoirs. A point represents the maximum total volume of prey observed in an individual stomach plotted as the midpoint for each length group. Correlation coefficient and probability level for each exponential regression equation (capacity = $a \cdot \text{Length}^b$) are provided along with upper and lower 95% confidence limits for parameter estimates a and b .

Appendix E. A summary of the percentage of empty stomachs (PES) by predator species during spring, summer and autumn in Branched Oak and Pawnee reservoirs, Nebraska. Predator species with fewer than 10 individuals that contained prey items were not reported because sample size was insufficient to reliably determine PES.

Species	Year	Season	Reservoir	N	PES (\pm SE)
Largemouth bass	2006	autumn	Branched Oak	31	32.3 (\pm 8.4)
White crappie		spring		61	18.0 (\pm 4.9)
		summer		47	14.9 (\pm 5.2)
		autumn		45	26.7 (\pm 6.7)
Black crappie		spring		19	38.6 (\pm 11.9)
Channel catfish				28	7.1 (\pm 4.8)
Flathead catfish		summer		151	56.9 (\pm 4.0)
Hybrid striped bass		spring		40	22.5 (\pm 6.5)
		summer		67	34.3 (\pm 5.8)
		autumn		46	23.9 (\pm 6.3)
Walleye		spring		70	45.7 (\pm 6.0)
		summer		46	41.3 (\pm 7.3)
		autumn		53	18.9 (\pm 5.4)
Largemouth bass		2007		spring	Pawnee
	summer		20	35.0 (\pm 10.7)	
	autumn		32	40.6 (\pm 8.7)	
Channel catfish	spring		40	10.0 (\pm 4.7)	
	summer		25	48.0 (\pm 10.0)	
Flathead catfish			37	70.3 (\pm 7.5)	
White bass	spring		55	67.3 (\pm 3.3)	
	summer		52	59.6 (\pm 6.8)	
Sauger	spring		21	19.0 (\pm 8.6)	
	summer		38	71.1 (\pm 7.4)	
	autumn		32	25.0 (\pm 7.7)	
Walleye	summer		57	49.1 (\pm 6.1)	
	autumn		28	39.3 (\pm 9.2)	
White crappie	2007		spring	Branched Oak	

Appendix E. Continued.

Species	Year	Season	Reservoir	N	PES (\pm SE)
White crappie	2007	summer	Branched Oak	20	20.0 (\pm 8.9)
		autumn		60	26.7 (\pm 5.7)
Flathead catfish		spring		16	31.3 (\pm 11.6)
		summer		124	77.4 (\pm 3.8)
Hybrid striped bass		spring		25	36.0 (\pm 10.3)
		summer		52	59.6 (\pm 6.8)
Walleye		autumn		98	50.0 (\pm 5.1)
		spring		97	54.6 (\pm 5.1)
		summer		75	45.3 (\pm 5.7)
White bass		autumn	Pawnee	67	17.9 (\pm 4.6)
		spring		20	35.0 (\pm 10.6)
Sauger		summer		17	35.3 (\pm 11.6)
Walleye		spring		13	23.3 (\pm 11.7)
				81	55.6 (\pm 5.5)
		summer		60	38.3 (\pm 6.3)
		autumn		28	42.9 (\pm 9.4)