INTERACTIONS AMONG HYBRID STRIPED BASS, WHITE BASS, AND WALLEYE IN HARLAN COUNTY RESERVOIR

by

Nathan William Olson

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APPROVAL

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Nathan William Olson

This thesis has been read by each member of the thesis committee and has been found to be satisfactory regarding content, English usage, format, citations, bibliographic style, and consistency, and is ready for submission to the College of Graduate Studies.

Christopher S. Guy

Approved for the Department of Ecology

Scott Creel

Approved for the College of Graduate Studies

Bruce R. McLeod

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Nathan William Olson

June 8, 2004

This thesis is dedicated to my parents, who always provided support and motivation throughout my education, and especially to my father, who always had time to take me fishing.

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF TABLES - CONTINUED

LIST OF FIGURES

LIST OF FIGURES - CONTINUED

ABSTRACT

Walleye *Sander vitreus*, white bass *Morone chrysops*, and hybrid striped bass *M. chrysops* x *M. saxatilis* are common top-level predators in Midwestern reservoirs. However, the ecology and interactions among these species are not well understood. Therefore, I compared the food habits, diet breadth, diet overlap, isotopic composition, vertical distribution, and vertical overlap of these species in Harlan County Reservoir, Nebraska, during the months of June through September 2002 and 2003. In addition, prey selection of hybrid striped bass for walleye and golden shiner *Notemigonus crysoleucas* was evaluated using feeding experiments. All three species consumed similar prey (i.e., gizzard shad *Dorosoma cepedianum*), and diet overlap was high during all months in both years. No species was found to have consistently higher diet breadth. Vertical distribution was similar and spatial overlap was high for white bass and hybrid striped bass in 2002, and between white bass and walleye in 2003. Stable isotope analysis indicated that all three species occupied the same trophic level, and that each predator was deriving carbon from a similar prey source. Few hybrid striped bass consumed prey during feeding experiments, thus definitive selection by hybrid striped bass for walleye and golden shiner could not be determined. This study provides the first comprehensive evaluation of these three top-level predators in a reservoir system. Although resource overlap was high among these predators, competition is not suggested or expected because resources do not appear to be limited in Harlan County Reservoir.

INTRODUCTION

Most natural lakes are the product of glacial activity and the fish species have co-evolved for 10,000 years (Noble 1986; Hayes et al. 1999). This has created "well-balanced" systems, especially among the fish species that inhabit them (Noble 1986). However, fish introductions can have negative effects on these native species assemblages. Introduced species can occupy similar niches as native species, resulting in resource overlap or native species declines from predation. For example, Hrabik et al. (2001) found that the native yellow perch *Perca flavescens* population in Crystal Lake, Wisconsin, declined because non-native rainbow smelt *Osmerus mordax* fed on the same food items as the yellow perch. Similarly, Ruzycki et al. (2001) documented introduced lake trout *Salvelinus namaycush* in Bear Lake, Utah-Idaho, excluded endemic Bonneville cutthroat trout *Oncorhynchus clarki utah* from predation on Bear Lake sculpin *Cottus extensus*, thus reducing the condition of Bonneville cutthroat trout.

Unlike natural lakes, reservoirs do not have a long evolutionary history (most are less than 100 years old) and are characterized as being environmentally unstable systems (Wetzel 1990; Hayes et al. 1999). However, species introduced into reservoirs can impact existing species through predation or competition. For example, predators (e.g., walleye *Sander vitreus*, smallmouth bass *M. dolemieui*, and northern pike *Esox lucius*) introduced into western reservoirs can cause large declines in salmonid populations due to direct predation (Gray and Rondorf 1986; McMahon and Bennett 1996). Saugeye *S. vitreus* x *S. canadensis* introduced into Thunderbird Reservoir, Oklahoma, had high diet overlap with existing largemouth bass (Horton and Gilliland 1990). In addition, Matthews et al. (1992) found high diet and spatial overlap between introduced juvenile striped bass *Morone saxatilis* and existing juvenile populations of white bass *M. chrysops* in Lake Texoma, Oklahoma-Texas.

Hybrid striped bass *Morone saxatilis* x *M. chrysops* were first created in 1965, and proved superior to striped bass in growth, survival, and palatability (Bishop 1967; Logan 1967; Williams 1971). These favorable characteristics lead to large-scale introductions of hybrid striped bass into many reservoirs. By 1978, 26 hybrid striped bass fisheries had been established in reservoirs in the southern United States (Axon and Whitehurst 1985).

A majority of these hybrid striped bass introductions were conducted without prior evaluation of their possible effects on existing fish communities. Therefore, studies were undertaken to investigate the interactions among hybrid striped bass and other predatory fish species subsequent to introduction. Several studies found that hybrid striped bass posed no threat to existing predatory fishes because of their strong selection of clupeids (*Dorosoma* spp.) as prey and limited spatial overlap with other fish species (Gilliland and Clady 1981; Ebert et al. 1987; Jahn et al. 1987; Phalen et al. 1988). However, Neal et al. (1999) found that age-0 (120-170 mm total length) and age-1 (240-350 mm total length) hybrid striped bass stocked into a small North Carolina impoundment without clupeids primarily consumed larval sunfish *Lepomis* spp. and black crappies *Pomoxis nigromaculatus*, which reduced prey density and caused a subsequent decrease in largemouth bass *Micropterus salmoides* condition (relative weight [W_r]).

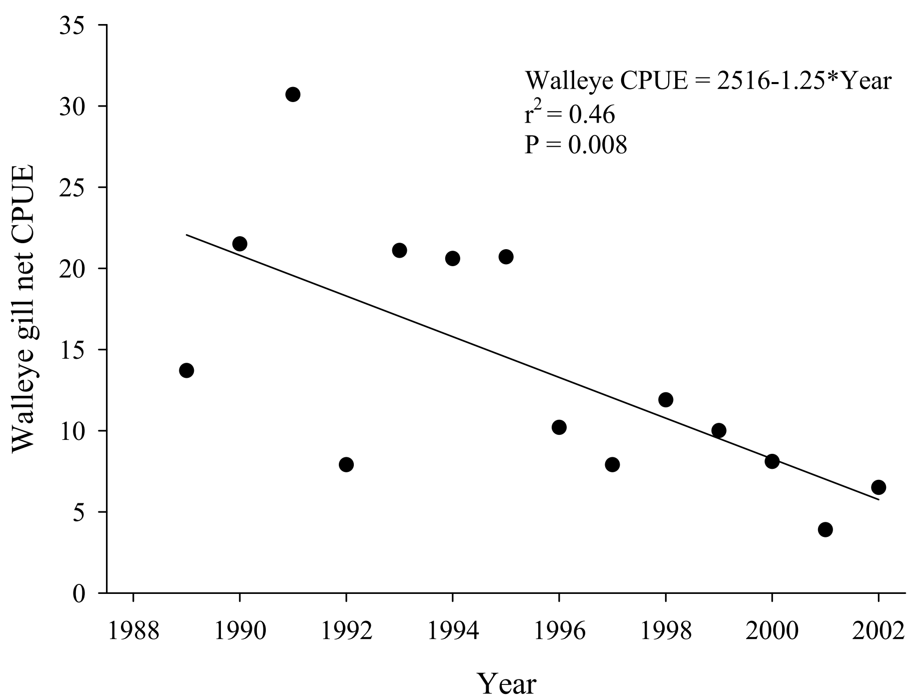
The Nebraska Game and Parks Commission (NGPC) has stocked hybrid striped bass in many reservoirs to increase angling opportunities and to reduce prey fish density (i.e., gizzard shad *D. cepedianum*; Daryl Bauer, NGPC, personal communication). Many of these reservoirs contained populations of walleye and white bass, which are top-level predators in these systems. However, no information exists on the interactions among these species collectively, despite the possibility of their negative associations. Germann and Bunch (1985) concluded that hybrid striped bass and white bass exhibit diet overlap, and that increased stocking rates of hybrid striped bass may result in competition with white bass. Similarly, diet overlap between walleye and white bass may exist (Beck et al. 1998), and walleye have been found to consume white bass (Slipke and Duffy 1997). Moreover, gizzard shad is a selected prey item for both walleye and hybrid striped bass (Knight et al. 1984; Momot et al. 1977; Johnson et al. 1988) and walleye growth has been linked to gizzard shad abundance in Lake Erie (Hartman and Margraf 1992).

Hybrid striped bass, white bass, and walleye may also exhibit spatial overlap. Hybrid striped bass and white bass have been found near the surface (McNaught and Hasler 1961; Hamilton and Nelson 1984; Austin and Hurley 1987). Although no study has evaluated the spatial overlap of hybrid striped bass and walleye, Phalen et al. (1988) found that hybrid striped bass in Mississippi often occupied depths of 4-7 m, and avoided depths of 0.3-2 m. Similarly, walleye have been found to select depths of 5-10 m (Kelso 1978), 4.5-7.1 m (Williams 1997), and 6.5 m (Summers 1979).

Harlan County Reservoir, Nebraska, does not thermally stratify and thus is a unique type of irrigation reservoir. It was first stocked with walleye and white bass in

1953 and since then these species have become the most sought after species in the reservoir (NGPC 2002a; NGPC 2002b). Supplemental stocking of fry and fingerling walleye continues, whereas the white bass population is sustained by natural reproduction. The density of stocked walleye is primarily variable and dependent upon availability. Striped bass were stocked from 1972-1978 in an attempt to increase angling opportunities, but low survival resulted in stocking hybrid striped bass in 1988 (NGPC 2002a). Similar to walleye stockings, the number of hybrid striped bass stocked is variable among years. These stockings have provided an angler catch rate as high as 0.56 per hour (NGPC 2002b).

Figure 1. Walleye gill net catch per unit effort (CPUE) in Harlan County Reservoir, Nebraska, from 1989 to 2002. Hybrid striped bass were initially stocked in 1988.

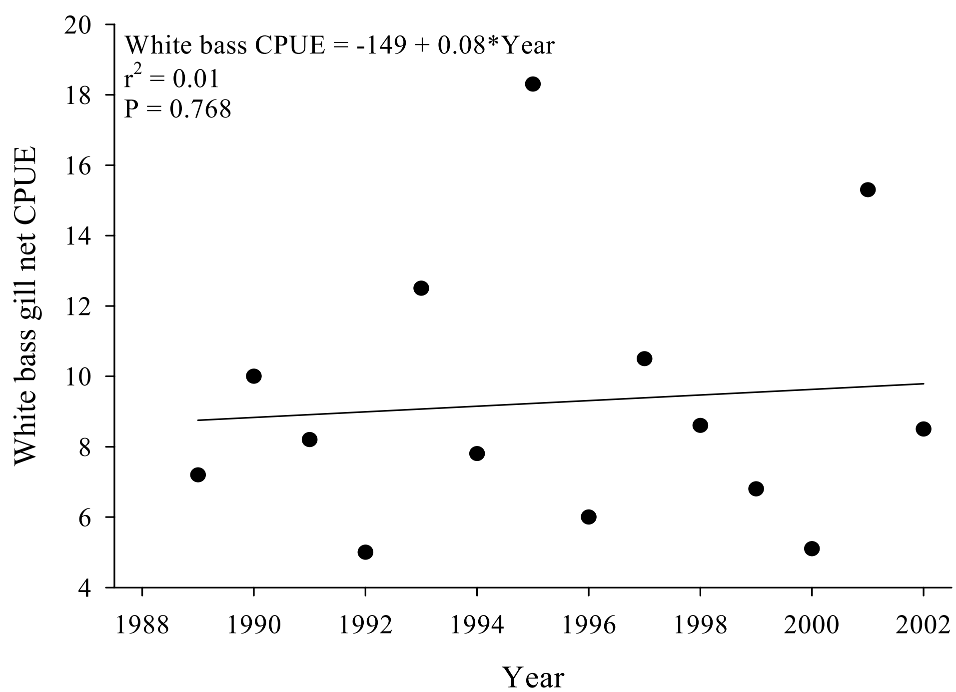


Unlike the success of the hybrid striped bass, walleye gill net catch per unit effort (CPUE) in Harlan County Reservoir showed a decline after hybrid striped bass stockings (Figure 1). However, walleye populations in similar reservoirs without hybrid striped bass have not shown a decline (Table 1). Moreover, the white bass population in Harlan County Reservoir has shown no declining trend since hybrid striped bass were introduced (Figure 2).

Table 1. Slope standard errors (SE), r-squared (r^2), sample size (N), and p-values of linear models for walleye gill net catch per unit effort from 1988-2002 regressed on time in years for Merritt, Pawnee, and Sherman Reservoirs, Nebraska. All three reservoirs do not contain hybrid striped bass.

Reservoir	Area (ha)	Model	Slope SE	r^2	N	P-value
Merritt	1174	-1021+0.529*Year	0.7742	0.35	15	0.506
Pawnee	300	153-0.074*Year	0.2726	0.01	15	0.789
Sherman	1151	-1256+0.638*Year	0.3842	0.20	13	0.125

Figure 2. White bass gill net catch per unit effort (CPUE) in Harlan County Reservoir, Nebraska, from 1988 to 2002. Hybrid striped bass were initially stocked in 1988.



Thus, it appears hybrid striped bass may be influencing walleye, but not white bass in Harlan County Reservoir. In order to better understand the interactions among these three predators and to evaluate the extent of hybrid striped bass predation on walleye, the objectives of this study were to i) document and compare the food habits, diet breadth, diet overlap, and size of gizzard shad consumed among hybrid striped bass, white bass, and walleye, ii) use stable isotope analysis to document the trophic interactions among hybrid striped bass, white bass, and walleye, iii) use vertical gill nets to determine the vertical distribution and spatial overlap among hybrid striped bass, white bass, and walleye, and iv) use experimental manipulations to determine the extent of prey selection by hybrid striped bass on walleye and golden shiner *Notemigonous crysoleucas*. I hypothesized that there would be high resource overlap among all three predators, with gizzard shad being the primary diet item and few walleyes consumed by hybrid striped bass. In addition, hybrid striped bass would exhibit spatial overlap with white bass and walleye, but minimal overlap would exist between white bass and walleye. Finally, hybrid striped bass would select golden shiners over walleye in the experimental trials.

STUDY AREA

Harlan County Reservoir was built by the United States Army Corps of Engineers (COE) in 1952. It is located on the Republican River in south-central Nebraska and is the second largest water body in Nebraska with an area of 5,362 ha. The reservoir has a mean depth of 4 m, a maximum depth of 18 m, and does not thermally stratify (COE 2001). It has a drainage area of 18,550 km^2 and provides irrigation for 9,308 ha of farmland in Nebraska and 4,856 ha of farmland in Kansas (COE 1999).

Water levels are variable throughout the year, with filling occurring from fall to spring and lowering occurring throughout the summer from irrigation releases. Aquatic vegetation is sparse, but reservoir filling may inundate terrestrial vegetation. Surrounding land use is primarily row-crop farming, with terrestrial vegetation consisting of annual herbaceous species, shrubs, timber stands, and mixed-grass prairie. Topography surrounding the reservoir is gently rolling, with some drainages being steeply sloped (COE 2001).

Other common fish species sampled by NGPC include black bullhead *Ameirus melas*, bluegill *Lepomis macrochirus*, black crappie, channel catfish *Ictalurus punctatus*, common carp *Cyprinus carpio*, flathead catfish *Pylodictis olivaris*, freshwater drum *Aplodinotus grunniens*, gizzard shad, golden shiner, largemouth bass, northern pike, river carpsucker *Carpiodes carpio*, and white crappie *P. annularis*.

Prey selection experiments were completed at the Calamus State Fish Hatchery located on the Calamus River near Burwell, Nebraska. Water sources for the hatchery consisted of an underground well and water from Calamus Reservoir. The hatchery is owned by the Bureau of Reclamation, and operated by the NGPC. Hybrid striped bass used for the prey selection experiments were collected from Calamus Reservoir, Nebraska, by angling and short-term gill netting.

METHODS

Food Habits, Niche Breadth, and Diet Overlap

Hybrid striped bass, walleye, and white bass were sampled monthly from June-September, 2002 and 2003 with 45-m x 2.5-m monofilament experimental gill nets. The experimental gill nets consisted of six, 18-m panels of 10.16, 7.62, 6.35, 5.08, 3.81, and 2.54-cm bar measure mesh. Gill nets were randomly set in the lower half of the reservoir one hour before sunset and checked every hour until four hours past sunset. During this time hybrid striped bass, walleye, and white bass are most actively feeding (Kelso 1973; Voigtlander and Wissing 1974; Prophet et al. 1991). To obtain a variety of fish sizes, an attempt was made to collect twenty fish from the stock-quality (S-Q), quality-preferred (Q-P), preferred-memorable (P-M), and memorable-trophy (M-T) length categories for each species. These categories were 250-379 mm, 380-509 mm, 510-629 mm, and 630-760 mm for walleye; 150-229 mm, 230-299 mm, 300-379 mm, and 380-460 mm for white bass; and 200-299 mm, 300-379 mm, 380-509 mm, and 510-630 mm for hybrid striped bass (Gabelhouse 1984).

Hybrid striped bass, white bass, and walleye were weighed (nearest 1.0 g), measured (total length; nearest 1.0 mm), and stomach contents removed using gastric lavage. Gastric lavage has been used on many species, including yellow perch, largemouth bass, white perch *Morone americana* (Hartleb and Moring 1995), walleye (Seaburg 1957), and hybrid striped bass (Dettmers et al. 1996). Stomach contents were preserved in 15% formalin.

Diet items were identified to family or order for invertebrates and to species for fish. Numbers and wet weights (nearest 0.01 g) of prey items by taxonomic group were recorded for each fish. In addition, when possible, the standard length (SL) of gizzard shad was measured (nearest 1.0 mm). If gizzard shad were abundant, only 10 individuals per fish were measured. Frequency of occurrence, percent composition by number, and percent composition by wet weight was determined for each taxon (Bowen 1996).

Niche breadth of each predator species was calculated by month using Levins (1968) index,

$$B = \frac{1}{\sum p_j^2},$$

with a standardization proposed by Hurlbert (1978) to express values on a scale from 0 to 1.0,

$$B_A = \frac{B-1}{n-1},$$

where B is Levins measure of niche breadth, p_j is the fraction of items in the diet that are of food category j, B_A is Levin's standardized niche breadth, and n is the number of possible resource states. Values of 0 indicate an organism has specialized food habits (i.e., it is only consuming a select number of prey species) and values of 1.0 indicate an organism is more generalistic (i.e., consuming a variety of possible prey species). Pianka's (1973) index of niche overlap was used to determine the amount of diet overlap among hybrid striped bass, white bass, and walleye by month. It is defined as:

$$O_{jk} = \frac{\sum_{i}^{n} p_{ij} p_{ik}}{\sqrt{\sum_{i}^{n} p_{ij}^{2} \sum_{i}^{n} p_{ik}^{2}}},$$

where O_{jk} is Pianka's measure of overlap, p_{ij} is the proportion diet item i is of the total resources used by species j, p_{ik} is the proportion diet item i is of the total resources used by species k, and n is the total number of diet items. The values of this index vary from 0 (no overlap) to 1.0 (complete overlap) with 0.75 indicating high overlap and values less than 0.4 indicating low overlap (Matthews and Hill 1980; Matthews et al. 1982; Ross 1986). Both indices were calculated based on weight of prey consumed and number of prey consumed. All Pianka and standardized Levin's index values were bootstrapped 5,000 times (Appendix A; Efron and Tibshirani 1993) because bootstrapping can reduce bias and provide estimates of variability for niche overlap values (Mueller and Altenberg 1985). The mean index value and its standard deviation (SD) were calculated using the method described by Smith (1985). Low sample sizes in some length categories resulted in all fish of one species being pooled and a single niche breadth and diet overlap value calculated. One-way analysis of variance (ANOVA) on the weighted mean standard length (mm) of gizzard shad consumed was conducted by month to determine whether each predator was consuming different-sized gizzard shad. Multiple comparisons were made using Tukey 95% simultaneous confidence intervals. Similarly, the SL of consumed gizzard shad was related to total length of walleye, white bass, and hybrid striped bass using weighted least-squares regression.

Stable Isotope Analysis

Stable isotopes were used to determine whether prey fish seen in the predator diets had similar ratios of ^{13}C:^{12}C ($\delta^{13}C$) as the predator species (which would indicate consumption of that prey by the predator), and to determine whether all three predator species had similar ratios of ^{15}N:^{14}N ($\delta^{15}N$; which would indicate the predators were occupying a similar trophic level). Only prey fish observed in the diets were sampled for stable isotopes. For example, in 2002 prey fish sampled included gizzard shad, freshwater drum, and white bass, whereas in 2003 prey fish sampled included gizzard shad, common carp, white bass, and walleye. Although freshwater drum was consumed in 2003, attempts to collect them for stable isotopes were unsuccessful.

Targeted sample sizes to include in the analyses were five prey fish in each of the 40-59 mm, 60-79 mm, 80-99 mm, and >120 mm length groups, and five hybrid striped bass, white bass, and walleye from the S-Q, Q-P, P-M, and M-T length categories. All fish were collected during July-September in 2002 and June-September 2003 using gill nets and seines. For large fish, approximately 10 g of muscle tissue was removed from the left side and frozen. Fish that were too small for a fillet to be removed were frozen whole. Small gizzard shad (40-59 mm) and white bass (60-79 mm) samples were a composite of two individuals. Samples were dried at 65ºC and ground into a powder using a mortar and pestle.

The $\delta^{15}N$ and $\delta^{13}C$ values were determined at the Plant Science Department of South Dakota State University, Brookings, South Dakota, with a Europa ANCA-GSL 20-

20 IRMS mass spectrometer. Isotope ratios were determined using the following formula:

$$\delta X(‰) = \left(\frac{R_{sample}}{R_{standard}} - 1 \right) \text{x } 1{,}000,$$

where X = ^{13}C or ^{15}N, R = ^{13}C:^{12}C or ^{15}N:^{14}N, and the standard is Pee Dee Belemnite limestone for carbon and atmospheric nitrogen for nitrogen. I used a dual-isotope approach (i.e., $\delta^{15}N$ values for an indication of trophic level and $\delta^{13}C$ values as a dietary tracer; Fry 1991) to compare the isotope signatures of the predators and prey.

Vertical Distribution and Overlap

Hybrid striped bass, white bass, and walleye were sampled monthly from June through August, 2002 and 2003 with 14-m deep x 2.5-m wide vertical gill nets marked in 1-m intervals. Vertical gill nets have been used to assess the vertical distribution of many fishes, including cisco *Coregonus artedi* (Aku et al. 1997), hybrid striped bass (Austin and Hurley 1987), kokanee salmon *Oncorynchus nerka*, lake trout (Sellers et al. 1998), rainbow trout *Oncorynchus mykiss*, striped bass (Lewis 1983), walleye and white bass (Boaze 1972), and yellow perch (Horak and Tanner 1964). Each vertical gill net consisted of one 3.81-cm diameter sealed polyvinylchloride (PVC) pipe as the float bar and one 1.27-cm diameter sand-filled PVC pipe as the weight bar. To minimize net twisting, an anchor was attached to the float bar with a 15-m rope and placed to the side of the net in line with the float bar.

A complement included three vertical gill nets set in a group. Each complement consisted of one net with 6.35-cm, one with 3.81-cm, and one with 2.54-cm bar measure mesh. Two complements were randomly set in the lower half of the reservoir each evening in similar water depth. Temperature (± 0.1°C) and dissolved oxygen (DO; ± 0.3 mg/L) profiles were measured in 1-m intervals near each complement using a Yellow Springs Instrument (YSI) model 85. One measurement was taken in the evening before the complements were set and again the following morning before the complements were pulled, the two measurements were averaged. All fish captured were weighed (± 1 g), measured (total length; ± 1 mm), and separated by mesh size and vertical location in the net (nearest 1 m). Finally, because the vertical distribution of fish can be affected by light intensity (Scherer 1975; Kelso 1978; Vigg and Hassler 1982), Secchi depth was measured every two weeks at several stations throughout the reservoir in 2003.

Similar to diet overlap, vertical overlap among the three species by month was assessed using Pianka's (1973) index of niche overlap, with depth as the resource. These values were bootstrapped 5,000 times (Appendix A; Efron and Tibshirani 1993) and the mean index value and SD were calculated using the method described by Smith (1985).

Prey Selection Experiments

Prey selection experiments were used to assess whether hybrid striped bass would select a walleye over a soft-rayed prey fish. Experiments were conducted in 2.3-m x 2.4-m x 0.9-m (50.97 m^3) raceway compartments. The compartments had a mean water temperature of 24.8 (± 0.04)°C and a mean dissolved oxygen concentration of 7.60 (±0.04) mg/L. Each raceway compartment contained a single hybrid striped bass (mean length ± standard error, 481±8 mm), 10 golden shiners (76±0.7 mm), and 10 walleyes

(109±0.5 mm). Golden shiners were selected as the alternate prey source because gizzard shad are difficult to handle in the laboratory. Hybrid striped bass were acclimated and starved in raceway compartments for 24 h. After this 24-h period, the golden shiners and walleye were added and the hybrid striped bass were allowed to feed for 15 h in order to minimize digestion of consumed prey. The experiment had 16 replications, with each replication consisting of a different hybrid striped bass. Sixteen experimental controls were used that consisted of ten individuals of each prey species. The number of walleye and golden shiners left at the end of the 15-h period was recorded and the consumption of prey items was confirmed by removing the stomachs from the hybrid striped bass.

Prey selection experiments were also conducted in circular tanks inside a building at the Calamus State Fish Hatchery. Two hybrid striped bass were placed in 0.8 m^3 circular tanks and the remaining six were placed in 1.1 m^3 circular tanks. Mean water temperature (6.98±0.1°C) and dissolved oxygen (24.56±0.3 mg/L) in the tanks were similar to the water temperature and dissolved oxygen concentration of the outside raceway compartments. Hybrid striped bass were allowed to acclimate inside the circular tanks for 24 hours, then 10 golden shiners and 10 walleye were placed inside the tank. Hybrid striped bass were then allowed to feed for seven days. Because the experiments were conducted inside, where no other predators had access to the prey items, no controls were conducted and all missing prey fish were recorded as consumed by the hybrid striped bass. Stomachs were also excised in order to evaluate whether prey were still present or digested.

RESULTS

Food Habits

In 2002, 117 walleye (231-726 mm), 222 white bass (155-386 mm), and 142 hybrid striped bass (315-720 mm) were sampled for food habits (Appendix B). In June, the primary prey items of all three predators were invertebrates (i.e., Chironomidae and Chaoboridae), but based on percent by weight, freshwater drum was also an abundant prey item in walleye and hybrid striped bass food habits (Figure 3). From July through September, gizzard shad was the most abundant prey item numerically and by weight for all predators (Figure 3). A large number of Chironomidae was also eaten, but contributed little to the overall weight of prey consumed. Besides unidentified fish, freshwater drum was the second most abundant prey item based on prey weight in July and August, whereas white bass was the second most abundant prey item based on prey weight in September (Figure 3).

In 2003, 120 walleye (241-711 mm), 276 white bass (250-264 mm), and 173 hybrid striped bass (376-625 mm) were sampled for food habits (Appendix B). Similar to 2002, 2003 food habits primarily consisted of invertebrates (i.e., Chironomidae and Chaoboridae) in June and gizzard shad from July through September (Figure 4). However, in contrast to June 2002, freshwater drum was not found in any of the predator diets in June 2003. In July 2003, the second most abundant prey items by weight were freshwater drum in walleye and hybrid striped bass diets, and common carp in white bass diets (Figure 4). White bass was the second most abundant prey species by weight in walleye and white bass diets in August, and freshwater drum made up a large percentage of the prey weight consumed by walleye and hybrid striped bass in September (Figure 4). In addition, although only one walleye was consumed by walleye in September, it was the second most abundant prey item by weight.

Figure 3. Percent by weight of common prey items found in the diets of walleye, white bass, and hybrid striped bass sampled from Harlan County Reservoir, Nebraska, from June to September 2002.

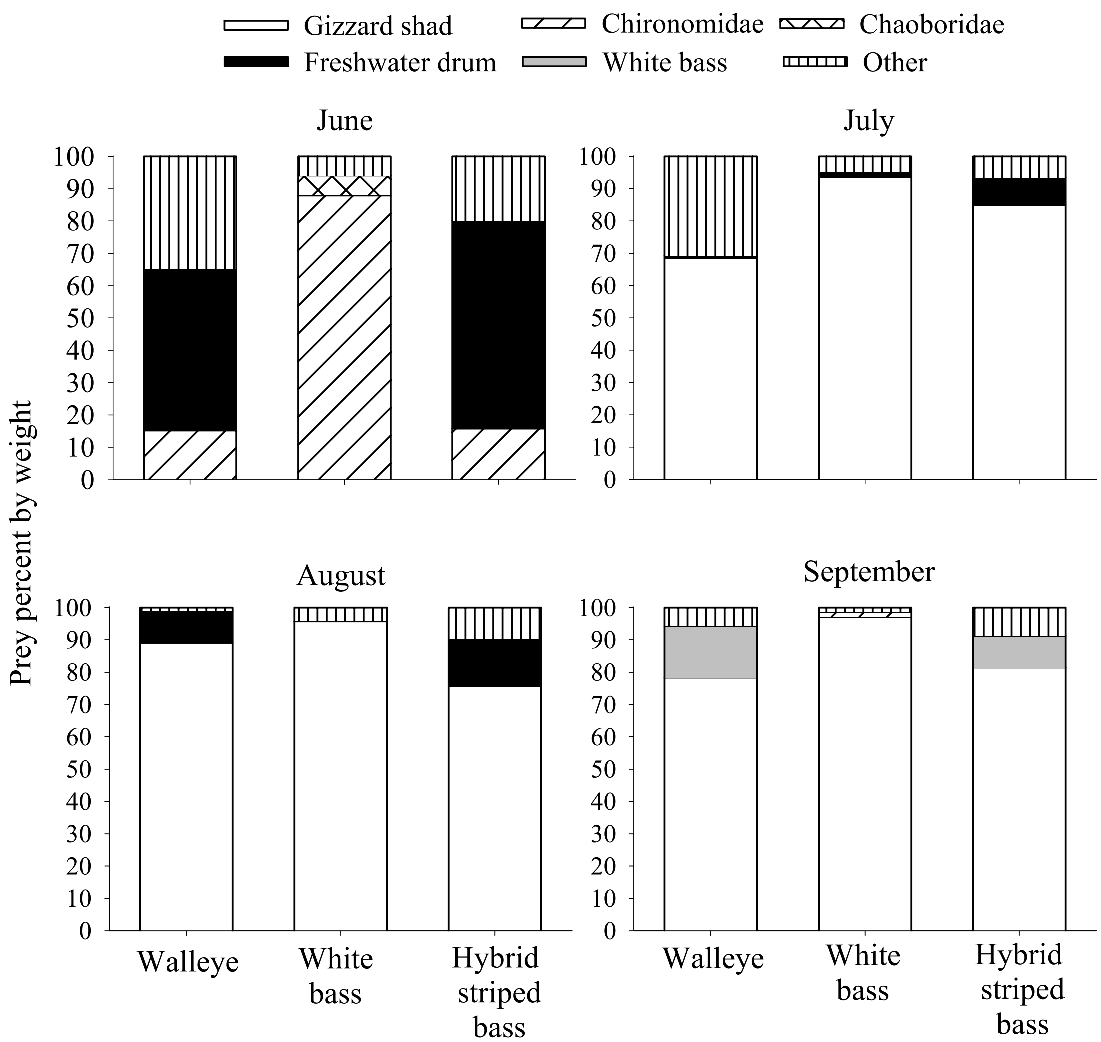
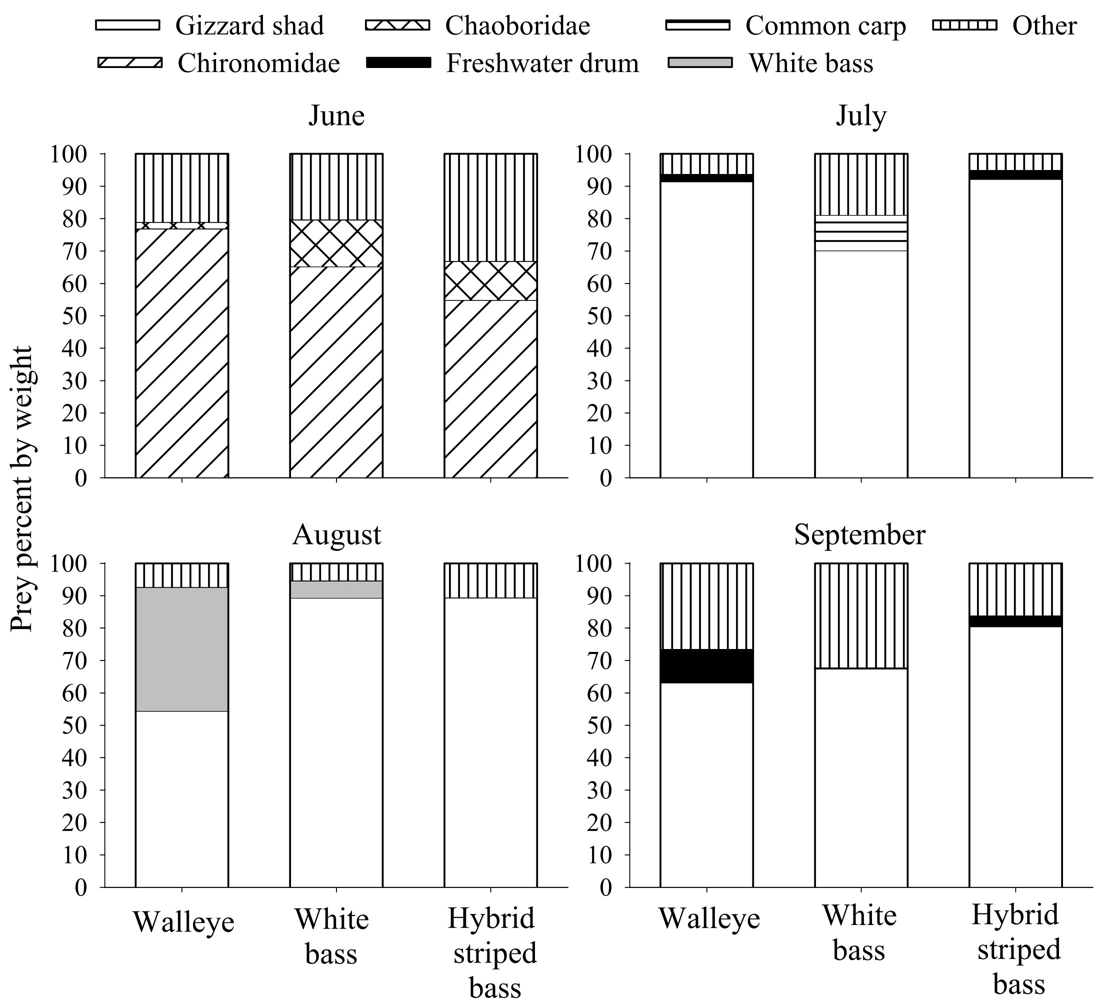


Figure 4. Percent by weight of common prey items found in the diets of walleye, white bass, and hybrid striped bass sampled from Harlan County Reservoir, Nebraska, from June to September 2003.



Diet Breadth

In general, predator diet breadth was low during each month (Table 2). In June and July 2002, white bass and hybrid striped bass had the highest diet breadth based on number of prey, but from weight of prey walleye had the highest diet breadth (Table 2). Similarly, walleye exhibited the highest diet breadth based on number of prey in August, but from weight of prey hybrid striped bass had the highest diet breadth (Table 2). In addition, in September, diet breadth was higher for white bass based on number of prey but walleye had the highest diet breadth from weight of prey (Table 2).

Table 2. Mean standardized Levins index (SD) of diet breadth for walleye, white bass, and hybrid striped bass sampled during June-September 2002 and 2003 from Harlan County Reservoir, Nebraska.

			Mean (SD)	
Year	Month	Predator	Number of prey	Weight of prey
2002	June	Walleye	0.02 (0.01)	0.07 (0.03)
		White bass	0.04 (0.01)	0.02 (0.00)
		Hybrid striped bass	0.04 (0.02)	0.06 (0.03)
	July	Walleye	0.06 (0.05)	0.05 (0.03)
		White bass	0.14 (0.04)	0.02 (0.01)
		Hybrid striped bass	0.11 (0.03)	0.03 (0.02)
	August	Walleye	0.11 (0.05)	0.03 (0.02)
		White bass	0.08 (0.04)	0.01 (0.01)
		Hybrid striped bass	0.04 (0.02)	0.07 (0.04)
	September	Walleye	0.13 (0.07)	0.08 (0.06)
		White bass	0.15 (0.03)	0.01 (0.00)
		Hybrid striped bass	0.03 (0.01)	0.07 (0.03)
2003	June	Walleye	0.03 (0.02)	0.04 (0.03)
		White bass	0.08 (0.00)	0.08 (0.03)
		Hybrid striped bass	0.08 (0.00)	0.11 (0.04)
	July	Walleye	0.13 (0.03)	0.02 (0.01)
		White bass	0.19 (0.05)	0.07 (0.04)
		Hybrid striped bass	0.11 (0.03)	0.01 (0.00)
	August	Walleye	0.18 (0.08)	0.16 (0.09)
		White bass	0.09 (0.03)	0.05 (0.03)
		Hybrid striped bass	0.09 (0.04)	0.05 (0.03)
	September	Walleye	0.18 (0.05)	0.20 (0.09)
		White bass	0.23 (0.05)	0.13 (0.03)
		Hybrid striped bass	0.16 (0.03)	0.09 (0.05)

In contrast to 2002 diet breadth, 2003 diet breadth values based on number of prey and weight of prey were more consistent. For example, in June 2003 hybrid striped bass had the highest diet breadth based on number prey and from weight of prey (Table

2). White bass had the highest diet breadth in July, and walleye had the highest diet breadth in August (Table 2). The only exception was September, when white bass had the highest diet breadth based on number of prey, but walleye had the highest diet breadth from weight of prey (Table 2).

Diet Overlap

Predators primarily consumed only a few prey species and thus diet overlap was high among all predators during each month for both years (Table 3). For example, of all of the diet overlap values calculated, only five were less than 0.75 (Table 3). The lowest amount of diet overlap observed was based on weight of prey in June 2002 (Table 3).

Table 3. Mean Pianka diet overlap values (SD) for walleye, white bass, and hybrid striped bass sampled during June-September 2002 and 2003, from Harlan County Reservoir, Nebraska.

			Mean (SD)	
Year	Month	Predator	Number of prey	Weight of prey
2002	June	Walleye-white bass	0.96 (0.03)	0.26 (0.16)
		White bass-hybrid striped bass	0.98 (0.02)	0.37 (0.31)
		Walleye-hybrid striped bass	0.98 (0.03)	0.67 (0.29)
	July	Walleye-white bass	0.91 (0.07)	0.84 (0.22)
		White bass-hybrid striped bass	0.95 (0.03)	0.99 (0.02)
		Walleye-hybrid striped bass	0.92 (0.05)	0.82 (0.23)
	August	Walleye-white bass	0.97 (0.09)	0.99 (0.02)
		White bass-hybrid striped bass	0.98 (0.02)	0.95 (0.06)
		Walleye-hybrid striped bass	0.97 (0.03)	0.97 (0.06)
	September	Walleye-white bass	0.89 (0.08)	0.94 (0.11)
		White bass-hybrid striped bass	0.85 (0.09)	0.98 (0.01)
		Walleye-hybrid striped bass	0.94 (0.08)	0.94 (0.10)
2003	June	Walleye-white bass	0.76 (0.12)	0.92 (0.09)
		White bass-hybrid striped bass	0.99 (0.02)	0.88 (0.11)
		Walleye-hybrid striped bass	0.76 (0.11)	0.85 (0.12)
	July	Walleye-white bass	0.73 (0.14)	0.95 (0.07)
		White bass-hybrid striped bass	0.88 (0.08)	0.95 (0.07)
		Walleye-hybrid striped bass	0.71 (0.15)	0.99 (0.01)

Table 3. Continued.

August	Walleye-white bass	0.88 (0.14)	0.78 (0.23)
	White bass-hybrid striped bass	0.99 (0.02)	0.99 (0.01)
	Walleye-hybrid striped bass	0.89 (0.13)	0.76 (0.24)
September	Walleye-white bass	0.82 (0.12)	0.84 (0.12)
	White bass-hybrid striped bass	0.93 (0.07)	0.94 (0.08)
	Walleye-hybrid striped bass	0.82 (0.13)	0.91 (0.09)

Diet overlap between white bass and walleye and white bass and hybrid striped bass during this month was low (<0.40; Table 3) primarily because a large percentage of the weight consumed by white bass was Chironomidae (Figure 3). Diet overlap between walleye and hybrid striped bass was higher, however, because a large amount of the total weight consumed by both species was freshwater drum (Figure 3). However, because only one hybrid striped bass had consumed a freshwater drum, diet overlap from weight of prey was not as high as diet overlap from number of prey (Figure 3 and Table 3).

Length of Consumed Gizzard Shad

Most of the relationships between gizzard shad length and predator length were not significant within species (Table 4). Thus, predator length did not have a significant influence on length of prey consumed for a given species. However, length of gizzard shad consumed by walleye, white bass, and hybrid striped bass differed among predators (Table 5). For example, in September 2002 and 2003, hybrid striped bass were found to consume gizzard shad that were approximately 14 mm larger than gizzard shad consumed by white bass (Table 5). Similarly, white bass were found to consume smaller gizzard

Table 4. Number of gizzard shad measured (N), number of predator species (n), p-value (P), r-squared value (r^2), and slope (standard error) results from weighted regressions of prey length and walleye, white bass, or hybrid striped bass (H.S.B.) total length for July-September 2002 and 2003 in Harlan County Reservoir, Nebraska.

Year	Month	Predator	n	N	P	r^2	Slope
2002	July	Walleye	5	18	0.962	0.000	-0.0047 (0.0979)
		White bass	19	53	0.000	0.258	0.0918 (0.0218)
		H.S.B.	29	94	0.000	0.149	-0.0500 (0.0125)
	August	Walleye	16	41	0.099	0.068	-0.0488 (0.0289)
		White bass	16	41	0.385	0.019	0.0323 (0.0368)
		H.S.B.	24	103	0.211	0.015	0.0222 (0.0177)
	September	Walleye	9	15	0.339	0.070	0.0584 (0.0588)
		White bass	23	46	0.944	0.000	0.0019 (0.0267)
		H.S.B.	33	171	0.063	0.020	-0.0334 (0.0179)
2003	July	Walleye	9	14	0.507	0.037	0.0577 (0.0844)
		White bass	15	43	0.000	0.340	0.2368 (0.0516)
		H.S.B.	24	103	0.930	0.000	0.0016 (0.0186)
	August	Walleye	6	10	0.026	0.483	0.2101 (0.0768)
		White bass	42	76	0.115	0.033	0.0487 (0.0305)
		H.S.B.	13	28	0.856	0.001	0.0050 (0.0274)
	September	Walleye	18	38	0.028	0.127	0.0790 (0.0346)
		White bass	5	8	0.877	0.004	-0.0362 (0.2248)
		H.S.B.	8	17	0.469	0.036	-0.0842 (0.1132)

shad than walleye and hybrid striped bass in August 2002 and 2003. In addition, in July 2002, white bass and hybrid striped bass consumed larger gizzard shad than walleye, but in July 2003, hybrid striped bass consumed smaller gizzard shad than walleye and white bass (Table 5).

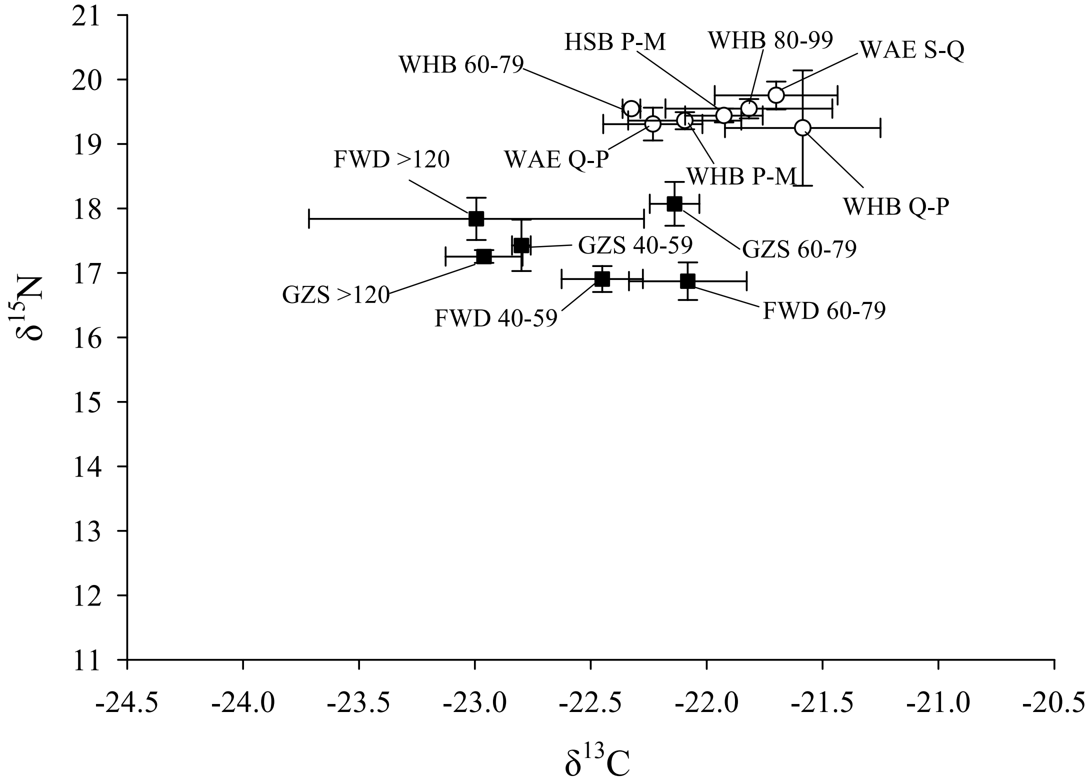
Table 5. Mean length of gizzard shad consumed by walleye, white bass, and hybrid striped bass (H.S.B.) during July-September 2002 and 2003 in Harlan County Reservoir, Nebraska (standard error). Lengths with the same superscript(s) were not significantly different based on one-way ANOVA and 95% Tukey confidence intervals.

Year	Month	Predator	Mean length (standard error)
2002	July	Walleye	16.87 (2.041)^{A}
		White bass	22.32 (1.080)^{B}
		H.S.B.	22.52 (0.871)^{B}
	August	Walleye	44.47 (1.443)^{A}
		White bass	31.84 (1.354)^{B}
		H.S.B.	36.79 (0.766)^{C}
	September	Walleye	51.44 (3.467)^{AB}
		White bass	45.48 (1.914)^{A}
		H.S.B.	59.66 (0.638)^{B}
2003	July	Walleye	42.15 (3.642)^{A}
		White bass	34.60 (1.316)^{A}
		H.S.B.	30.75 (0.682)^{B}
	August	Walleye	61.15 (2.925)^{A}
		White bass	48.46 (0.949)^{B}
		H.S.B.	54.21 (1.501)^{A}
	September	Walleye	57.10 (1.607)^{AB}
		White bass	46.70 (3.837)^{A}
		H.S.B.	60.79 (2.617)^{B}

Stable Isotope Analysis

Predators sampled for stable isotopes in 2002 had higher $\delta^{15}N$ values compared to possible prey items, but among predators, $\delta^{15}N$ and $\delta^{13}C$ values were similar (Figure 5). Values of $\delta^{13}C$ were similar between predators and gizzard shad 60-79 mm, freshwater drum 40-59 mm, and freshwater drum 60-79 mm (Figure 5). Gizzard shad 40-59 mm and >120 mm appeared to be less enriched in ^{13}C compared to predator species and other prey (Figure 5), whereas $\delta^{13}C$ values of freshwater drum >120 mm were variable and overlapped $\delta^{13}C$ values of a majority of other prey, but overlap with predators was minimal (Figure 5).

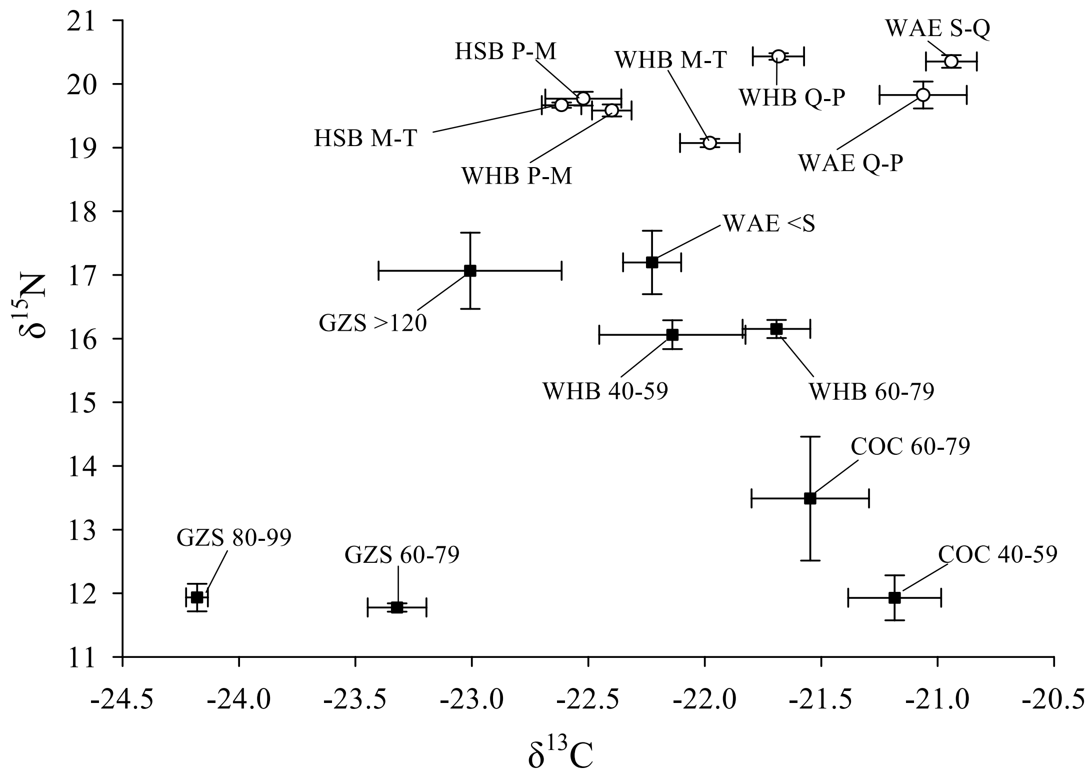
Figure 5. Stable isotope signatures of predators (open circles) and potential prey (solid squares) collected during July-September 2002 from Harlan County Reservoir, Nebraska. Fish species sampled were walleye (WAE), white bass (WHB), hybrid striped bass (HSB), freshwater drum (FWD), and gizzard shad (GZS), and length categories are stock to quality (S-Q), quality to preferred (Q-P), preferred to memorable (P-M), 40-59 mm, 60-79 mm, 80-99 mm, and greater than 120 mm (>120).



Predators sampled for stable isotopes were also enriched in ^{15}N compared to possible prey in 2003 (Figure 6). However, although all predators had similar $\delta^{15}N$ values, $\delta^{13}C$ values were only similar among white bass P-M, hybrid striped bass P-M, and hybrid striped bass M-T, and overlapped the $\delta^{13}C$ values of gizzard shad >120 mm, white bass 40-59 mm, and walleye <S (Figure 6). Values of $\delta^{13}C$ were also similar between walleye S-Q and walleye Q-P, and overlapped the $\delta^{13}C$ values of common carp of both sizes (Figure 6). In addition, white bass M-T $\delta^{13}C$ values overlapped that of

walleye <S and white bass 40-59 mm, whereas $\delta^{13}C$ values of white bass Q-P overlapped that of white bass 60-79 (Figure 6). No predator $\delta^{13}C$ values were overlapped with the $\delta^{13}C$ values of gizzard 60-79 mm or 80-99 mm (Figure 6).

Figure 6. Stable isotope signatures of predators (open circles) and potential prey (solid squares) collected during June-September 2003 from Harlan County Reservoir, Nebraska. Fish species sampled were walleye (WAE), white bass (WHB), hybrid striped bass (HSB), common carp (COC), and gizzard shad (GZS), and length categories are less than stock (<S), stock to quality (S-Q), quality to preferred (Q-P), preferred to memorable (P-M), memorable to trophy (M-T), 40-59 mm, 60-79 mm, 80-99 mm, and greater than 120 mm (>120).



Vertical Distribution and Overlap

Harlan County Reservoir did not develop a thermocline during 2002 and 2003 (Figures 7 and 8). During both years, water temperature increased from June to August and dissolved oxygen declined throughout the water column (Figures 7 and 8). Although surface water temperatures in 2003 increased by almost 6°C from June to August, walleye were still abundant near the surface (i.e., 1-3 m; Figure 8). In 2002 hybrid striped bass were commonly abundant in 3-5 m of water (Figure 7), whereas hybrid striped bass distribution in 2003 was more variable, extending from 2-7 m (Figure 8). White bass were generally distributed close to the surface during all months, with the exception of June 2002 and August 2003 when white bass were abundant in 4-6 m of water (Figures 7 and 8). Mean Secchi depth (cm) in 2003 showed an increasing trend from June to the middle of July, then declined through the month of August (Figure 9).

The amount of vertical overlap among predators was not as great as diet overlap. Of the 16 overlap values calculated, only two were greater than 0.75 (Table 6). Vertical overlap values were highest between white bass and hybrid striped bass except during July of 2003 (Table 6). In July 2003, vertical overlap was highest between white bass and walleye (0.92), which were located primarily within the first meter of the surface (Table 6; Figure 8). Hybrid striped bass were at deeper depths than white bass and walleye in July 2003, resulting in low amounts of vertical overlap between hybrid striped bass and the other two predators (Table 6; Figure 8). Unfortunately, only three hybrid striped bass were sampled in August 2003, which was insufficient to determine the amount of vertical overlap occurring with the other two predators (Table 6).

Figure 7. Vertical distribution (m) of walleye, white bass, and hybrid striped bass in relation to water temperature (°C; solid line) and dissolved oxygen (mg/L; dotted line) during June-August 2002 in Harlan County Reservoir, Nebraska.

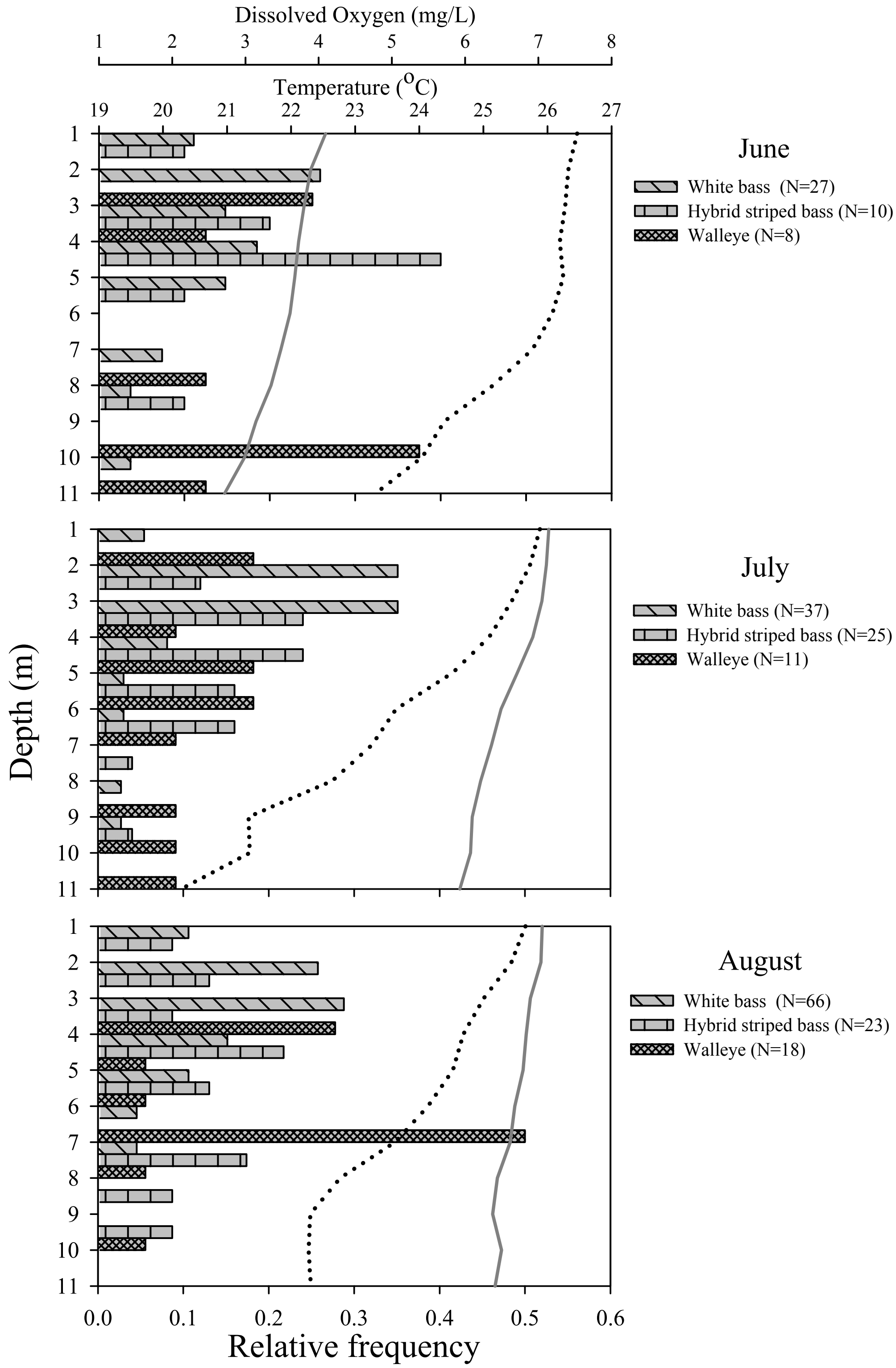


Figure 8. Vertical distribution (m) of walleye, white bass, and hybrid striped bass in relation to water temperature (°C; solid line) and dissolved oxygen (mg/L; dotted line) during June-August 2003 in Harlan County Reservoir, Nebraska.

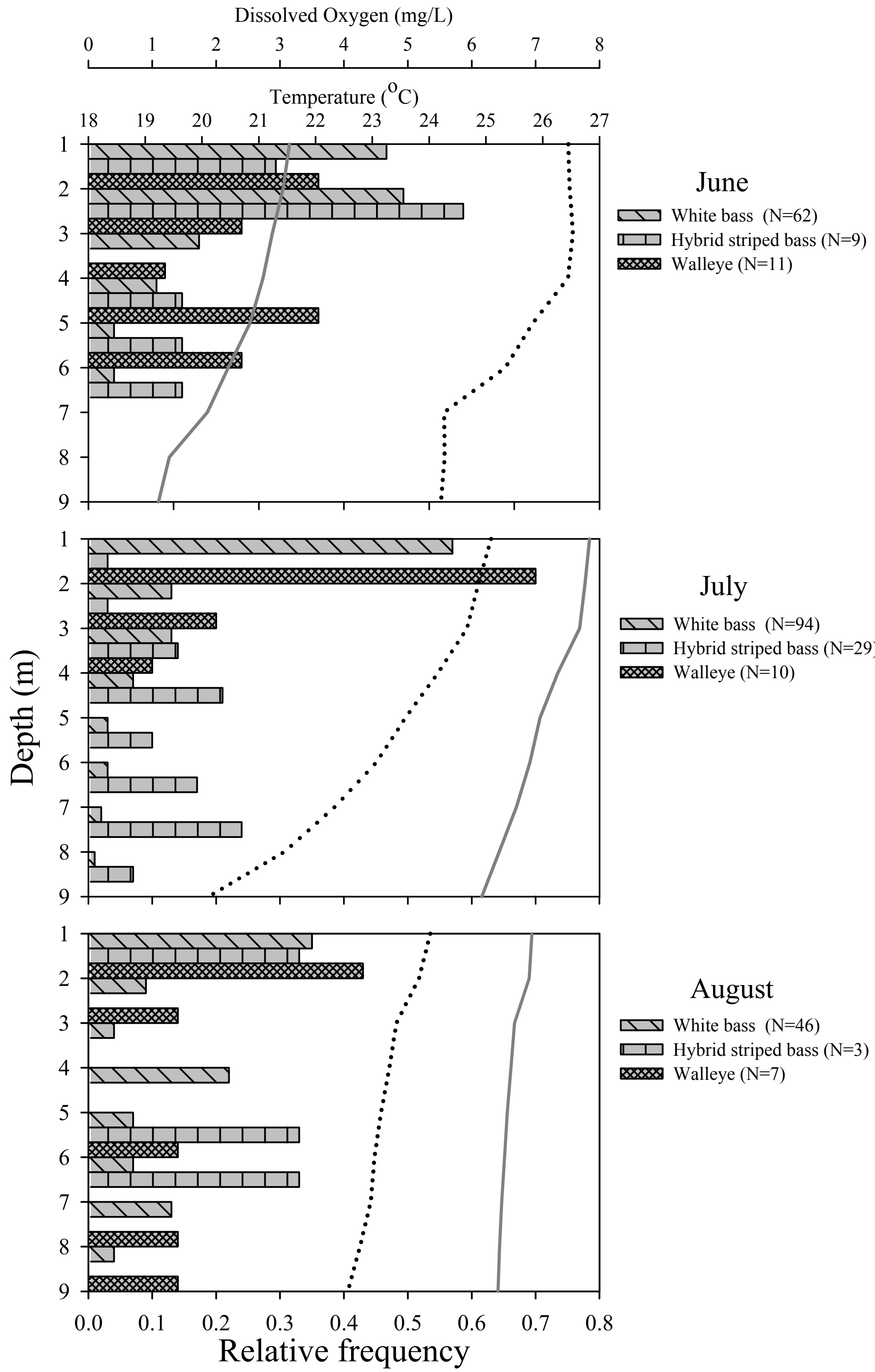


Figure 9. Mean Secchi depth (cm; standard error) and mean depth (m; standard error) of walleye, white bass, and hybrid striped bass in Harlan County Reservoir, Nebraska, June-August 2003.

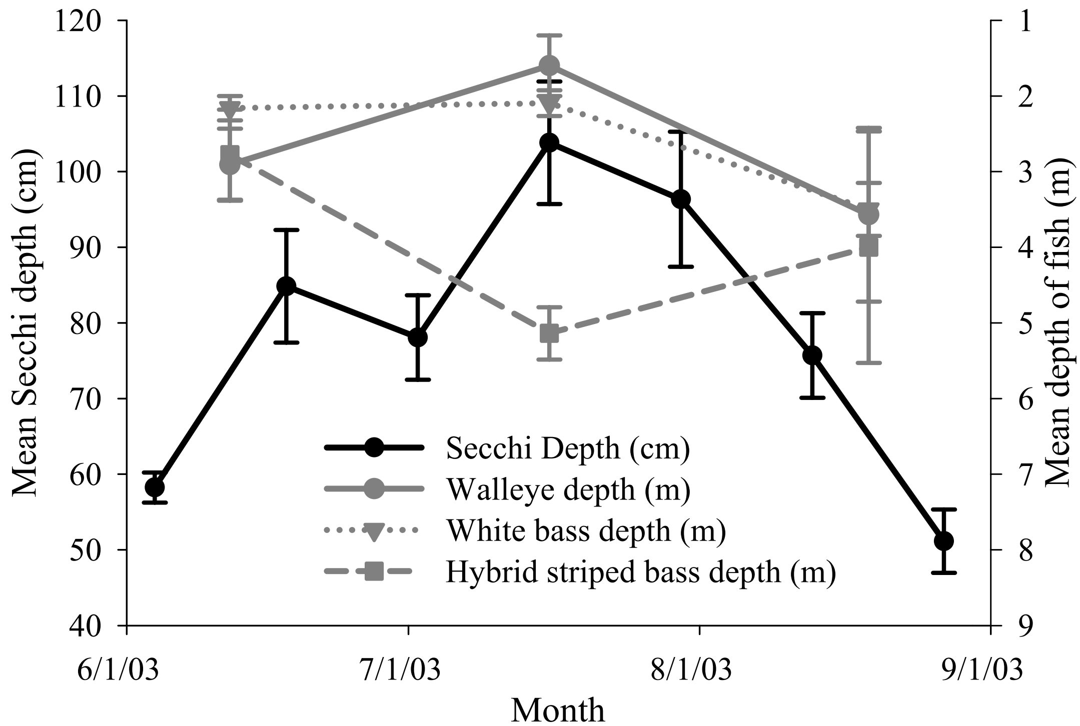


Table 6. Mean Pianka overlap values (SD) for vertical distribution of walleye, white bass, and hybrid striped bass sampled during June-August 2002 and 2003 from Harlan County Reservoir, Nebraska.

Year	Month	Predator combination	Mean (SD) vertical overlap
2002	June	Walleye-white bass	0.39 (0.18)
		White bass-hybrid striped bass	0.57 (0.15)
		Walleye-hybrid striped bass	0.09 (0.11)
	July	Walleye-white bass	0.32 (0.14)
		White bass-hybrid striped bass	0.67 (0.13)
		Walleye-hybrid striped bass	0.53 (0.17)
	August	Walleye-white bass	0.43 (0.13)
		White bass-hybrid striped bass	0.64 (0.12)
		Walleye-hybrid striped bass	0.24 (0.11)
2003	June	Walleye-white bass	0.69 (0.16)
		White bass-hybrid striped bass	0.80 (0.12)
		Walleye-hybrid striped bass	0.61 (0.20)
	July	Walleye-white bass	0.92 (0.06)
		White bass-hybrid striped bass	0.27 (0.09)

Table 6. Continued.

	Walleye-hybrid striped bass	0.13 (0.09)
August	Walleye-white bass	0.69 (0.14)
	White bass-hybrid striped bass	[a]
	Walleye-hybrid striped bass	[a]

[a]Insufficient sample size of hybrid striped bass to calculate values.

Prey Selection Experiments

Eleven of the 16 hybrid striped bass used in the outdoor raceways survived the entire 15 hours. After the 15 hours, no golden shiners or walleye were missing from the 16 controls, but four of the raceway compartments containing a hybrid striped bass had at least one golden shiner missing and only one raceway compartment containing a hybrid striped bass had a walleye missing (Table 7). However, all hybrid striped bass had empty stomachs, and no confirmed feeding was reported. Therefore, the missing prey could not be attributed to predation and statistical analyses were not conducted.

During the seven-day indoor tank experiments, two of the eight hybrid striped bass did not survive. Of the remaining six hybrid striped bass, three had at least one golden shiner missing and only one had a walleye missing (Table 7). In addition, one hybrid striped bass did contain a golden shiner in its stomach.

Table 7. Size of hybrid striped bass (H.S.B) placed in outdoor raceways or indoor tanks at Calamus State Fish Hatchery, Nebraska, for prey selection experiments and the number of golden shiners (GOS) or walleye (WAE) missing out of 10 available of each species.

		Number missing	
Enclosure	H.S.B. length (mm)	GOS	WAE
Outdoor raceway	475	1	0
	495	0	0
	460	0	0
	510	0	0
	490	2	1

Table 7. Continued.

	460	0	0
	440	1	0
	480	0	0
	450	2	0
	526	0	0
	501	0	0
Indoor tank	486	0	0
	349	1	0
	343	0	0
	540	0	0
	367	2	0
	350	3	1

DISCUSSION

The food habits of walleye, white bass, and hybrid striped bass in Harlan County Reservoir, Nebraska, were similar to other systems. For example, walleye food habits in Glen Elder Reservoir, Kansas were found to consist primarily of gizzard shad, Chironomidae, and freshwater drum (Quist et al. 2002). White bass food habits in Fall River Reservoir, Kansas, consisted primarily of invertebrates (i.e., Ephemeroptera and Chironomidae) during the spring and age-0 gizzard shad from July to January (Cox et al. 2001). Germann and Bunch (1985) also reported white bass food habits in Clarks Hill Reservoir, Georgia-South Carolina, consisted primarily of insects (i.e., dipteran larvae) during the spring, but threadfin shad (*D. petenense*) dominated the diets in the summer, fall, and winter; despite gizzard shad being available, they were not found in any of the white bass diets. Similar to white bass, hybrid striped bass diets primarily consisted of threadfin shad in Clarks Hill Reservoir (Germann and Bunch 1985), but in reservoirs without threadfin shad, gizzard shad have been found to be the primary diet item of hybrid striped bass (Ebert et al. 1987; Jahn et al. 1987).

Diet breadth for a specific predator from number of prey was typically greater than diet breadth from weight of prey when a prey item was numerically abundant in the diet but contributed little to the overall weight consumed by a predator. For example, white bass food habits in July 2002 based on percent by number primarily consisted of gizzard shad, Chironomidae, and unidentified fish, and diet breadth based on number of prey was 0.14. However, based on percent by weight, gizzard shad made up 93.7% of the total weight consumed by white bass, and diet breadth was much lower (0.02).

Although less frequent, the opposite was true, with a prey item being numerically small but contributing a large amount of weight to the total weight consumed by the predator. In June 2003, the diet of hybrid striped bass based on percent by number was 43.6% Chironomidae and 54.4% Chaoboridae, and diet breadth from number of prey was 0.08. However, based on percent by weight, the diet of hybrid striped bass consisted of 54.9% Chironomidae, 12.0% Chaoboridae, 21.3% Scarabaeidae, and 10.0% unidentified fish, and diet breadth from weight of prey was 0.11. Despite these analytical differences within species, predators primarily preyed on a few prey items, diet breadth for each predator was low during all months, and no single predator species appeared to have consistently higher diet breadth.

Diet overlap among walleye, white bass, and hybrid striped bass in Harlan County Reservoir, Nebraska, was high from June to September. Although this is the first study that has evaluated the diet overlap among these species, several studies have evaluated the diet overlap of a combination of these species. High diet overlap existed between age-0 walleye and white bass in July in Lake Poinsett, South Dakota (Beck et al. 1998). Germann and Bunch (1985) found diet overlap was also high between hybrid striped bass and white bass in Clarks Hill Reservoir, Georgia-South Carolina. No study has directly evaluated the diet overlap between walleye and hybrid striped bass. However, gizzard shad were the primary diet item of walleye and hybrid striped bass in other reservoirs (Ebert et al. 1987; Jahn et al. 1987; Quist et al. 2002), thus the possibility of diet overlap occurring between these two top-level predators in other systems where they coexist is highly likely.

Although diet analysis and overlap indices are a common method used to look at the impacts of species introductions, stable isotope analysis has recently given researchers a way to view the diet and diet overlap among predators. An enrichment of 3-5‰ in ^{15}N and 0-1‰ in ^{13}C (Fry and Sherr 1984) occurs in predatory organisms compared to their prey because the heavier isotopes ^{15}N and ^{13}C are eliminated in smaller amounts than the lighter isotopes ^{14}N and ^{12}C (Peterson and Fry 1987). The large enrichment of ^{15}N in predators enables this isotope to be used as a good indicator of trophic position (Peterson and Fry 1987; Fry 1988), whereas the small enrichment of ^{13}C between predator and prey enables this isotope to be used as an indicator of predator consumption of certain prey items (Peterson and Fry 1987). The stable isotope analysis in 2002 of walleye, white bass, hybrid striped bass, and potential prey in Harlan County Reservoir revealed similar results to the food habits and diet overlap analyses. The predator species (i.e., walleye, white bass, and hybrid striped bass) of all length categories were enriched in ^{15}N compared to the potential prey items. However, within the predators, no one species was enriched in ^{15}N, suggesting all three predators were feeding at the same trophic level. Based on overlapping $\delta^{13}C$ values, predators appeared to be deriving some of their carbon from gizzard shad 60-79 mm and freshwater drum of 40-59 mm, 60-79 mm, and 80-100 mm. It could not be concluded that these were the only prey items used as a carbon source for the predators because not all possible prey items were collected and analyzed for stable isotope analysis,. Nonetheless, similar to the stable isotope analysis, food habits did show gizzard shad and freshwater drum to be primary diet items in 2002.

In contrast to 2002, stable isotope analysis in 2003 only marginally agreed with the food habits analysis. For example, compared to the large predators, walleye less than stock length had lower $\delta^{15}N$ values but similar $\delta^{13}C$ values. This suggests large predators are deriving a portion of their carbon from walleye less than stock length, but only one walleye less than stock length was found in the large predator food habits. In addition, $\delta^{13}C$ values of small gizzard shad (60-99 mm) were not similar to large predators, despite food habits of large predators consisting primarily of gizzard shad this size. These discrepancies may be a result of changes in fish diet or temporal sampling differences. Gizzard shad are omnivores and are known to consume zooplankton, detritus, or phytoplankton (Kutkuhn 1958; Pierce et al. 1981), thus diet switching may have influenced their isotope signature in Harlan County Reservoir. Isotope signatures may vary seasonally (Yoshioka et al. 1994) and the amount of time required for an isotope signature to be incorporated into the tissue of another organism may be 6.4 to 47.5 days, depending on the type of tissue used (Tieszen et al. 1983). In this study, a majority of the large predators were sampled for stable isotopes in early June of 2003, when their diets consisted primarily of invertebrates, whereas small gizzard shad were sampled for stable isotopes in July 2003. Despite these differences, values of $\delta^{15}N$ for walleye, white bass, and hybrid striped bass in 2003 were similar, indicating each predator was feeding at the same trophic level and $\delta^{13}C$ signatures were overlapping in some instances, suggesting diet overlap among predators for some unknown prey item(s).

Hybrid striped bass and walleye were distributed more evenly throughout the water column in Harlan County Reservoir than in other reservoirs. The reason for the difference is probably a lack of thermal stratification in Harlan County Reservoir. Douglas and Jahn (1987) found radio-tagged hybrid striped bass were located near the thermocline, primarily in 3-4 m of water where dissolved oxygen was above 2 mg/L and water temperatures were approximately 25°C in Spring Lake, Illinois. Hybrid striped bass in East Fork Lake, Ohio, were also located near the thermocline in 0-4 m of water in temperatures up to 27.8°C (Austin and Hurley 1987). Walleye in Laurel River Lake, Kentucky, were located in 4.2-7.6-m water and approximately 23°C water during thermal stratification (Williams 1997). In contrast, white bass distribution observed during this study is similar to other studies. Irrespective of thermal stratification, white bass have been found to be abundant in the top 5 m of water (Borges 1950; Colvin 1993).

The vertical distribution and overlap of white bass, walleye, and hybrid striped bass observed in this study may be related to the distribution of gizzard shad. Age-0 gizzard shad commonly occupy depths of 0-3 m (Netsch et al. 1971), all predators were found to occupy these depths at some time, and predator food habits primarily consisted of gizzard shad. White bass and walleye vertical distributions have also been related to prey distribution in Lake of the Ozarks, Missouri (Boges 1950), Keystone Reservoir, Oklahoma (Eley et al. 1967), and Claytor Lake, Virginia (Boaze 1972). Although the vertical distribution of fishes can also be affected by water temperature and turbidity (Vigg and Hassler 1982; Sellers et al. 1998; Craig and Babaluk 1993), they appeared to have little effect on fish distribution. Despite water temperatures increasing from June to August, white bass and hybrid striped bass were commonly found within the first 4 m of the water column and walleye were abundant in the top 2 m of the water column in June and July 2003. In addition, mean Secchi depth (cm) was greatest from the middle of June through the beginning of August, corresponding to the time when walleye and white bass were close to the surface.

The use of experiments can also aid researchers in assessing the effects of species introductions. Matthews et al. (1992) used experiments to determine whether juvenile largemouth bass would change food habits in the presence of juvenile striped bass, which are commonly stocked in many reservoirs. However, no change in the diet of juvenile largemouth bass in the presence of juvenile striped bass was found. Similarly, Michaelson et al. (2001) used experiments to determine whether largemouth bass would prey on stocked age-0 striped bass. Although few striped bass were consumed when other prey was available (i.e., alewives), striped bass consumption by the largemouth bass increased when alewives were absent. In addition, Schrank et al. (2003) found introduced age-0 bighead carp have the ability to reduce age-0 paddlefish growth in experimental ponds. Unfortunately, the results from the experiments in this study were not as definitive. A greater number of golden shiners appeared to be consumed during the indoor circular tank experiments, but I presumed that with such a small sample size, definite conclusions on the prey selection of hybrid striped bass would be weak (at best) and statistical analysis was not attempted. However, with the small number of walleye assumed to be consumed during the experiments and the lack of walleye in any of the diets of hybrid striped bass from Harlan County Reservoir, it appears walleye are not a common prey item for hybrid striped bass when soft-rayed fishes are available.

Despite the high amount of resource overlap among these top-level predators, competition cannot be inferred. Overlap only indicates that resources are being used by each species similarly (Matthews et al. 1992). According to Crowder (1990), three conditions must be met in order for competition to be present: (1) the same resource must be used by the organisms, (2) the resource must be in limited supply, and (3) the resource use, growth, or any other measure related to the fitness of an individual must decline. In this study, similar prey (i.e., gizzard shad) and space (i.e., depth) are being utilized by each predator species. However, each predator species appeared to consume different sizes of gizzard shad, which may allow each of these species to utilize them as prey. Although all three predators had vertical overlap during some period of the study, I was unable to determine whether each species was present at the same depth at the same time. It is possible that these three predators are feeding at the same depth, but during different times. Finally, though not specifically tested in this study, the similarly used resources do not appear to be limiting in Harlan County Reservoir. Gizzard shad abundance appears to be sufficient to support all three predators because growth and condition is near or above the statewide average (Hurley 2001).

Although there is little evidence of competition among these predators, managers should be aware of the possibility for competition to occur if resources (e.g., gizzard shad) were to become limiting (Matthews 1992). Reservoirs are dynamic systems (Wetzel 1990) and commonly experience dramatic fluctuations in water levels. As of July 2003, Harlan County Reservoir was at its lowest level (580 m above sea level) since 1952. Low water levels may negatively affect the abundance of age-0 gizzard shad

(Michaletz 1997), a primary prey item of all three predators in this study, and an important prey item for predators in other reservoirs (Noble 1981). Thus, monitoring of gizzard shad populations should be implemented in reservoirs where these three predators coexist.

It appears unlikely that predation by hybrid striped bass is the cause of the declining walleye population in Harlan County Reservoir. Only one walleye was found in any of the predator diets, and it occurred in another walleye. Although in less abundance, white bass did appear in the diets of hybrid striped bass, but they also appeared in the diets of walleye and white bass. Similarly, few game fishes have been found in the diets of hybrid striped bass from Spring Lake, Illinois (Jahn et al. 1987) and Clarks Hill Reservoir, Georgia (Germann 1982). Several alternative hypotheses exist for the decline in the walleye population in Harlan County Reservoir. Gizzard shad may reduce zooplankton density, possibly causing a juvenile bottleneck for other larval fishes (such as walleye) that rely on zooplankton during the spring (Dettmers and Stein 1992). Similarly, the abundance of white crappie *P. annularis* (which are present in Harlan County Reservoir) can limit the survival of larval walleye. Quist et al. (2003) found that the abundance of 130-199-mm white crappie was negatively related to walleye recruitment in several Kansas reservoirs, and that predation by white crappies in experiments caused over 90% mortality in larval walleye. There is little empirical evidence that predation by hybrid striped bass is a factor in the decline of walleye abundance in Harlan County Reservoir.

MANAGEMENT IMPLICATIONS

Hybrid striped bass are popular sport fish and contribute much to the fishery in Harlan County Reservoir. As found by this study and others in Arkansas (Ebert et al. 1987), Florida (Borkowski and Snyder 1982), Illinois (Jahn et al. 1987), Oklahoma (Gilliland and Clady 1981), Oregon (Gestring 1991), Texas (Farquhar 1981), and South Carolina (Williams 1971), hybrid striped bass appear to be having no direct negative affect on other game fish species in Harlan County Reservoir. The only game species consumed by hybrid striped bass were white bass, and these occurred in small amounts. Walleye and white bass also were found to consume white bass. The only walleye consumed during the entire study was found in the diet of another walleye. In addition, although more than 200,000 walleye (≈ 8 cm) were stocked from June 23 to June 25, 2003, no walleye were found in hybrid striped bass diets. Thus, the continued stocking of hybrid striped bass in Harlan County Reservoir will not be detrimental to the walleye population. However, since each of these top-level predators in Harlan County Reservoir appears to be linked with the gizzard shad population, assessing its abundance annually should be conducted.

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APPENDICES

APPENDIX A

BOOTSTRAP METHODOLOGY

The bootstrapping method used to calculate the Pianka index values for diet and spatial overlap consisted of randomly selecting individuals with replacement from one species, randomly selecting individuals with replacement from another species, and using these data to calculate the overlap value. The number of individuals sampled with replacement from each species is equal to the total number of individuals sampled of one species (e.g., if 20 individuals of one species were sampled for food habits, a sample of 20 individuals with replacement is taken). This process was repeated 5,000 times and the mean index and its SD were calculated. To facilitate the process, bootstrapping was conducted using R-software version 1.8. The code used was:

```
index=rep(0,5000)
for (i in 1:5000){
samp1=X[sample(1:nX,replace=T),]
samp2=Y[sample(1:nY,replace=T),]
nvec1=apply(samp1,2,sum)/TRX
nvec2=apply(samp2,2,sum)/TRY
index[i]=sum(nvec1*nvec2)/(sqrt(sum(nvec1^2)*sum(nvec2^2)))}
```

where the bolded text represents places were data must be inputted and are defined as X = data matrix of resources used by different individuals of species X, Y = data matrix of resources used by different individuals of species Y, n_X = number of individuals of species X sampled, n_Y = number of individuals of species Y sampled, TR_X = total amount of all resources used by all individuals of species X, and TR_Y = total amount of all resources used by all individuals of species Y.

A similar method was used to calculate bootstrapped estimates of the standardized Levin's index. For one species, individuals were randomly selected with replacement and the index calculated. This process was repeated 5,000 times and the mean index and SD were calculated. The code used for this process was:

```
index.X=rep(0,5000)
for (i in 1:5000){
samp1=X[sample(1:nX,replace=T),]
nvec1=apply(samp1,2,sum)
index[i]=((sum(nvec1)^2/sum(nvec1^2))-1)/(RX-1)}
```

where X = data matrix of resources used by different individuals of species X, n_X = number of individuals of species X sampled, and R_X = the number of resources used by species X.

To further illustrate this method, an example of is shown below where 2 species (walleye = wae and white bass = whb) are evaluated for diet overlap based on number of prey. The number of walleye sampled was 26 and the number of white bass sampled was 55. A total of 194 prey items were found in the 26 walleyes and a total of 1532 prey items were found in the 55 white bass. The code used to bootstrap this index 5,000 times is thus:

```
waewhbindex=rep(0,5000)
for (i in 1:5000){
samp1=wae[sample(1:26,replace=T),]
samp2=whb[sample(1:55,replace=T),]
nvec1=apply(samp1,2,sum)/194
nvec2=apply(samp2,2,sum)/1532
waewhbindex[i]=sum(nvec1*nvec2) / (sqrt(sum(nvec1^2)*sum(nvec2^2)))}
```

and the mean index can be retrieved by typing summary(waewhbindex) and the SD can be calculated by simply taking the square root of the variance which is given by typing var(waewhbindex). To find the bootstrapped Levin's index value of the walleye based on number of prey the code is:

```
index.wae=rep(0,5000)
for (i in 1:5000){
samp1=wae[sample(1:26,replace=T),]
nvec1=apply(samp1,2,sum)
index.wae[i]=((sum(nvec1)^2/sum(nvec1^2))-1)/(16-1)}
```

where the 16 used in the last line represents 16 different resource categories used by the walleye. Efron and Tibshirani (1993) provide additional information about bootstrapping and its methodology.

APPENDIX B

FOOD HABITS DATA

Table 8. Number of fish sampled (N), number of fish with food, prey frequency of occurrence (FO; percent), prey percent by number, and prey percent by weight sampled from three predator species during June-September, 2002, from Harlan County Reservoir, Nebraska. H.S.B represents hybrid striped bass.

Month	Predator	N	Number with food	Prey	FO	Percent by Number	Percent by Weight
June	Walleye	34	26	Chironomidae	69.23	88.14	15.19
				Chaoboridae	11.54	3.61	0.46
				Freshwater drum	19.23	2.58	50.07
				Hydrachnellae	15.38	5.15	0.14
				Unidentified Fish	3.85	0.52	34.14
	White bass	66	55	Chironomidae	90.91	75.72	87.90
				Chaoboridae	45.45	20.76	6.19
				Coccinellidae	3.64	0.26	0.66
				Carabidae	5.45	0.33	0.65
				Scarabaeidae	3.64	0.13	0.57
				Staphylinidae	1.82	0.07	0.24
				Corixidae	20.0	1.24	0.95
				Ephemeridae	7.27	0.39	0.43
				Hydrachnellae	1.82	0.13	0.05
				Formicidae	3.64	0.13	0.05
				Lepidoptera	1.82	0.07	0.51
				Odonata	1.82	0.07	1.09
				Hydropsychidae	7.27	0.46	0.28
				Araneae	7.27	0.26	0.43
	H.S.B.	23	20	Chironomidae	90.00	80.00	15.76
				Chaoboridae	30.00	10.45	1.72
				Carabidae	5.00	0.45	0.13
				Scarabaeidae	5.00	0.45	1.31
				Corixidae	15.00	3.18	0.24
				Freshwater drum	5.00	0.45	64.32
				Hydrachnellae	5.00	0.45	0.09
				Lepidoptera	5.00	0.45	0.71
				Hydropsychidae	15.00	3.64	0.92
				Unidentified fish	5.00	0.45	14.79
July	Walleye	22	9	Gizzard shad	55.56	81.08	68.53
				Chaoboridae	11.11	2.70	0.03
				Corixidae	11.11	2.70	0.06
				Freshwater drum	11.11	2.70	0.78
				Hydrachnellae	11.11	2.70	0.01
				Unidentified fish	22.22	5.41	30.50
				Unidentified material	11.11	2.70	0.09
	White Bass	44	38	Gizzard shad	63.16	56.30	93.65

Table 8. Continued

				Chironomidae	44.74	17.23	0.69
				Chaoboridae	10.53	9.24	0.07
				Corixidae	2.63	0.42	0.01
				Ephemeridae	2.63	0.42	0.11
				Freshwater drum	5.26	0.84	1.50
				Unidentified fish	23.68	11.76	3.76
				Unidentified material	13.16	3.36	0.14
				Ictaluridae	2.63	0.42	0.07
	H.S.B.	50	41	Gizzard shad	80.49	61.00	85.00
				Chironomidae	53.66	20.75	0.58
				Carabidae	2.44	0.41	0.12
				Scarabaeidae	2.44	0.41	1.20
				Ephemeridae	9.76	4.15	2.16
				Freshwater drum	4.88	0.83	8.34
				Hydrachnellae	2.44	0.41	0.01
				Hydropsychidae	2.44	0.41	0.01
				Unidentified fish	12.20	4.56	2.35
				Unidentified material	14.63	7.05	0.25
August	Walleye	40	24	Gizzard shad	66.67	70.49	89.12
				Chironomidae	20.83	14.75	0.07
				Freshwater drum	12.50	6.56	9.82
				Unidentified fish	8.33	3.28	0.17
				Unidentified material	8.33	3.28	0.12
				Lumbricidae	4.17	1.64	0.69
	White bass	42	26	Gizzard shad	69.23	75.32	95.74
				Chironomidae	23.08	11.69	0.08
				Hydrachnellae	3.85	1.30	0.01
				Formicidae	3.85	2.60	0.02
				Unidentified fish	19.23	7.79	4.14
				Unidentified material	3.85	1.30	0.01
	H.S.B.	28	27	Gizzard shad	88.89	86.21	75.73
				Chironomidae	22.22	6.21	0.06
				Ephemeridae	7.41	1.38	0.13
				Freshwater drum	3.70	3.45	14.48
				Unidentified fish	7.41	1.38	2.59
				Unidentified material	3.70	0.69	0.01
				Golden shiner	3.70	0.69	7.00
September	Walleye	21	14	Gizzard shad	71.43	69.57	78.32
				Chironomidae	7.14	13.04	0.16
				Unidentified fish	21.43	13.04	5.56
				White bass	7.14	4.35	15.96
	White bass	70	43	Gizzard shad	74.42	59.00	97.10
				Chironomidae	37.21	36.00	1.58

Table 8. Continued

				Chrysomelidae	2.33	1.00	0.01
				Unidentified fish	9.30	4.00	1.31
	H.S.B.	41	38	Gizzard shad	84.62	91.37	81.47
				Chironomidae	2.56	0.51	<0.01
				Freshwater drum	5.13	1.02	7.43
				Unidentified fish	15.38	3.05	1.26
				Unidentified material	5.13	1.02	0.12
				White bass	10.26	2.54	9.72
				Acrididae	2.56	0.51	0.02

Table 9. Number of fish sampled (N), number of fish with food, prey frequency of occurrence (FO; percent), prey percent by number, and prey percent by weight sampled from three predator species during June-September, 2003, from Harlan County Reservoir, Nebraska. H.S.B. represents hybrid striped bass.

						Percent by	
Month	Predator	N	Number with food	Prey	FO	Number	Weight
June	Walleye	15	9	Chironomidae	88.89	86.79	76.91
				Chaoboridae	11.11	11.95	2.09
				Unidentified fish	11.11	0.63	20.72
				Unidentified material	11.11	0.63	0.28
	White bass	59	45	Chironomidae	95.56	46.14	65.27
				Chaoboridae	82.22	52.19	14.44
				Coccinellidae	6.67	0.18	0.28
				Scarabaeidae	2.22	0.06	0.95
				Corixidae	11.11	0.65	0.50
				Unidentified insects	6.67	0.71	2.96
				Unidentified fish	2.22	0.06	15.59
	H.S.B.	64	57	Chironomidae	98.25	43.58	54.91
				Chaoboridae	54.39	54.35	11.98
				Coccinellidae	5.26	0.15	0.41
				Carabidae	3.51	0.07	0.10
				Scarabaeidae	8.77	0.59	21.28
				Chrysomelidae	5.26	0.22	0.25
				Staphylinidae	1.75	0.04	0.02
				Corixidae	8.77	0.30	0.28
				Talitridae	3.51	0.07	0.09
				Hydropsychidae	1.75	0.04	0.04
				Araneae	3.51	0.15	0.12
				Unidentified insects	5.26	0.37	0.56
				Unidentified fish	1.75	0.04	9.95
				Unidentified material	1.75	0.04	0.03

Table 9. Continued.

July	Walleye	35	22	Gizzard shad	50.00	40.00	91.53
				Chironomidae	9.09	7.50	0.15
				Freshwater drum	13.64	7.50	2.30
				Unidentified insects	4.55	10.00	0.28
				Unidentified fish	31.82	35.00	5.74
	White Bass	53	31	Gizzard shad	58.06	40.41	70.23
				Chrironomidae	35.48	20.55	0.49
				Chaoboridae	6.45	14.38	0.13
				Carabidae	9.68	2.05	0.20
				Ephemeridae	3.23	0.68	0.13
				Freshwater drum	3.23	0.68	1.04
				White bass	3.23	0.68	6.87
				Common carp	3.23	1.37	10.99
				Acrididae	3.23	4.11	3.06
				Unidentified fish	19.35	10.96	6.68
				Unidentified material	9.68	4.11	0.18
	H.S.B.	50	40	Gizzard shad	72.50	51.70	92.24
				Chironomidae	57.50	31.70	1.04
				Chaoboridae	2.50	2.64	0.02
				Carabidae	2.50	0.38	0.01
				Scarabaeidae	2.50	0.38	0.20
				Gyrinidae	5.00	0.75	0.15
				Corixidae	12.50	2.26	0.05
				Freshwater drum	7.50	1.51	2.73
				Halictidae	2.50	0.38	0.02
				Unidentified insects	2.50	3.40	0.11
				Unidentified fish	15.00	4.53	3.39
				Unidentified material	2.50	0.38	0.03
August	Walleye	20	9	Gizzard shad	66.67	58.82	54.50
				White bass	11.11	5.88	38.23
				Unidentified fish	22.22	35.29	7.27
	White bass	114	65	Gizzard shad	87.69	81.10	89.38
				Cerambycidae	1.54	0.79	0.12
				White bass	1.54	0.79	5.31
				Unidentified insects	1.54	0.79	0.02
				Unidentified fish	13.85	15.75	5.14
				Unidentified material	1.54	0.79	0.02
	H.S.B.	22	15	Gizzard shad	86.67	80.43	89.48
				Unidentified fish	40.00	19.57	10.52
September	Walleye	50	32	Gizzard shad	62.50	63.51	63.23
				Freshwater drum	15.63	8.11	10.42
				Walleye	3.13	1.35	16.09
				Unidentified fish	43.75	25.68	6.15

Table 9. Continued.

			White bass	3.13	1.35	4.10
White bass	50	20	Gizzard shad	50.00	38.30	67.55
			Chironomidae	25.00	10.64	0.29
			Ephemeridae	5.00	2.13	0.33
			Unidentified fish	60.00	48.94	31.83
H.S.B.	37	20	Gizzard shad	60.00	40.35	80.58
			Freshwater drum	5.00	1.75	3.41
			Unidentified fish	55.00	57.89	16.01