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[Article]

Interactions among Three Top-Level Predators in a Polymictic Great Plains Reservoir

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Abstract.—After the introduction of hybrid striped bass (white bass *Morone chrysops* × striped bass *M. saxatilis*) into Harlan County Reservoir, Nebraska, gill-net catch per unit effort (CPUE) of walleyes *Sander vitreus* appeared to decline while that of white bass remained stable. This result prompted the question of whether these three species can be managed collectively in reservoir ecosystems. However, despite the frequency with which these three popular sport fishes coexist in Great Plains reservoirs, we are unaware of any studies that evaluate resource overlap among them. Therefore, we compared their diets, diet overlap, isotopic composition, vertical distribution, and vertical overlap in Harlan County Reservoir from June to September 2002 and 2003. All three species consumed similar prey (i.e., gizzard shad *Dorosoma cepedianum* and Chironomidae), and diet overlap was high (i.e., Pianka's index > 40) during all months. On no occasion did all three predators consume the same sizes of gizzard shad. Hybrid striped bass consumed larger gizzard shad than white bass did in September 2002 and 2003, whereas white bass consumed smaller gizzard shad than walleyes and hybrid striped bass did in August 2002 and 2003. Stable isotope analysis corroborated the diet analysis and indicated that all three species occupied the same trophic level and that each predator derived carbon from a similar prey source. White bass were consistently located within the upper 3 m of water, whereas the vertical distribution of hybrid striped bass and walleyes varied from the surface to 10 m deep. Spatial overlap was therefore not as high as dietary overlap and was variable among species and months. Although diet overlap was high, resource partitioning (i.e., different feeding locations and different sizes of gizzard shad eaten) reduced the negative interactions among the three predators. Therefore, we conclude that concurrent management of these three sport fishes is feasible in highly productive reservoirs similar to the one in this study.

Hybrid striped bass (white bass *Morone chrysops* × striped bass *M. saxatilis*) were first produced in 1965 and proved superior to striped bass in growth and survival in reservoirs (Bishop 1968; Logan 1968; Williams 1971), which led to large-scale introductions of hybrid striped bass into these systems. By 1978, 26 hybrid striped bass fisheries had been established in reservoirs in the southern United States (Axon and Whitehurst 1985). As has occurred in many other states, the Nebraska Game and Parks Commission (NGPC) stocked hybrid striped bass in many reservoirs to increase angling opportunities and to reduce prey fish density (e.g., gizzard shad *Dorosoma cepedianum*; D. Bauer, NGPC, personal communication). Many of these reservoirs already contained established fisheries for white bass and walleyes *Sander vitreus*. One such example is Harlan County Reservoir, where the introduction of hybrid striped bass in 1988 resulted in an angler catch rate of up to 0.56 hybrid striped bass/h (NGPC 2002b). Despite the success of hybrid striped bass stocking, walleye catch per unit effort (CPUE) in gill nets decreased fivefold over 10 years (NGPC 2002c). Such a decline was not observed in another top-level predator, the white bass.

Although several abiotic mechanisms may be associated with the decline in the walleye population (e.g., spring storage ratios, temperature, and spring water levels; Quist et al. 2003), competition with other species is also possible. Gizzard shad have exhibited the ability to reduce zooplankton abundance, thus reducing the resources available for larval walleyes (Dettmers and Stein 1992). Quist et al. (2003) found walleye recruitment in Kansas reservoirs to be negatively related to abundance of white crappies *Pomoxis annularis*, primarily because of their ability to prey on larval walleyes. Several studies have found that hybrid striped bass posed no threat to existing

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predatory fishes (Gilliland and Clady 1984; Ebert et al. 1988; Jahn et al. 1987; Phalen et al. 1989). However, in a small North Carolina impoundment devoid of shads *Dorosoma* spp., the condition (relative weight [W_r]) of largemouth bass *Micropterus salmoides* declined because hybrid striped bass preyed on centrarchids, the primary prey of largemouth bass (Neal et al. 1999).

Although negative impacts of hybrid striped bass on white bass have not been observed (Gilliland and Clady 1984), no study has evaluated the interactions between walleyes and hybrid striped bass or among all three of these species collectively in a nonstratifying reservoir. These species are commonly found in reservoirs throughout the Great Plains; thus, an understanding of the interaction among these predators is critical to the successful management of these reservoirs. Therefore, the objectives of this study were to (1) evaluate diet overlap and size of gizzard shad consumed by hybrid striped bass, white bass, and walleyes; (2) document the trophic interactions among the three predators; (3) determine the extent of spatial overlap among the three species; and (4) to determine whether hybrid striped bass consumed walleyes. Based on our understanding of the natural history of these species, we predicted high dietary and trophic overlap among the three predators and that gizzard shad would constitute the primary diet item. In addition, we predicted that hybrid striped bass would exhibit spatial overlap with white bass but not with walleyes. Finally, we predicted that hybrid striped bass would eat few walleyes and that, given abundant prey resources, these two species could coexist and provide excellent recreational opportunities.

Study Site

Harlan County Reservoir was built by the U.S. Army Corps of Engineers (USACE) in 1952. Located on the Republican River in south-central Nebraska, it is the second-largest water body in Nebraska (area = 5,362 ha). The reservoir has a mean depth of 4 m and a maximum depth of 18 m and does not thermally stratify (USACE 2001). Water levels are variable throughout the year; filling occurs from fall to spring and lowering occurs throughout the summer from irrigation releases.

Walleyes and white bass were first stocked into Harlan County Reservoir in 1953 and became the most sought-after species in the reservoir (NGPC 2002a, 2002b). Supplemental stockings of fry and fingerling walleyes continue, whereas the white bass population is sustained by natural reproduction. The annual number of stocked walleyes is variable and dependent upon availability. The number of hybrid striped bass stocked is also variable among years, but stockings were suspended after 2000 until their effect on walleyes could be evaluated. Other common fish species in Harlan County Reservoir are black bullheads *Ameiurus melas*, bluegills *Lepomis macrochirus*, black crappies *Pomoxis nigromaculatus*, channel catfish *Ictalurus punctatus*, common carp *Cyprinus carpio*, flathead catfish *Pylodictis olivaris*, freshwater drum *Aplodinotus grunniens*, gizzard shad, golden shiners *Notemigonus crysoleucas*, largemouth bass, northern pike *Esox lucius*, river carpsuckers *Carpiodes carpio*, and white crappies.

Methods

Hybrid striped bass, walleyes, and white bass were sampled monthly from June to September of 2002 and 2003 with 45- × 2.5-m monofilament experimental gill nets. The 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 downstream end (i.e., near the dam) of the reservoir 1 h before sunset and were checked every hour until 4 h after sunset. Hybrid striped bass, walleyes, and white bass feed most actively during this time (Voigtlander and Wissing 1974; Kelso 1978; Prophet et al. 1991). Sampling was concentrated in the downstream section of the reservoir because data collected by NGPC employees indicated that the habitat (i.e., dissolved oxygen [DO], temperature, and depth) was more suitable than other sections for the three species targeted. In addition, sampling efforts in the upstream section yielded few fish. To obtain a variety of fish sizes, an attempt was made to collect 20 fish/month from each of four length categories (Gabelhouse 1984): stock–quality (S–Q), quality–preferred (Q–P), preferred–memorable (P–M), and memorable–trophy (M–T).

Hybrid striped bass, white bass, and walleyes were weighed (nearest 1.0 g) and measured (total length [TL]; nearest 1.0 mm), and their stomach contents were removed by means of gastric lavage. Stomach contents were preserved in 15% formalin. Diet items were identified to family or order for invertebrates and to species for fish. Wet weights (nearest 0.01 g) of prey items by taxonomic group were recorded for each fish. Frequency of occurrence and percent composition by wet weight was determined for each taxon (Bowen 1996).

Pianka's (1973) index of niche overlap was used to determine the amount of diet overlap among hybrid striped bass, white bass, and walleyes 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} = Pianka's measure of overlap, p_{ij} = the proportional contribution of diet item i to species j's total resources, p_{ik} = the proportional contribution of diet item i to species k's total resources, and n = the total number of diet items. The value of this index varies from 0 (no overlap) to 1.0 (complete overlap); a value exceeding 0.75 indicates high overlap, and values less than 0.40 indicate low overlap (Matthews and Hill 1980; Matthews et al. 1982; Ross 1986). Pianka's index values were based on weight of prey and were bootstrapped 5,000 times to obtain an estimate of variability. The mean index value and its SE were calculated (Smith 1985; Olson 2004). Because of low sample sizes in some length categories, we pooled all fish from a single species and calculated a single diet overlap value.

The standard lengths (SLs) of gizzard shad were measured (nearest 1.0 mm) when possible. The SL of consumed gizzard shad was related to predator TL using a weighted least-squares regression for each predator species. One-way analysis of variance (ANOVA) on the weighted mean SL (mm) of gizzard shad consumed by each predator was conducted for each month to determine whether predators were consuming different-sized gizzard shad. The weights used in the analysis were the number of gizzard shad consumed by each individual (e.g., if a hybrid striped bass consumed five gizzard shad, the gizzard shad length received a weight of 5). Multiple comparisons were made using Tukey's 95% simultaneous confidence intervals.

Stable isotopes are used to conduct long-term diet analyses and to assess overlap within or among species. Thus, stable isotopes were used in 2002 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 that the predators were occupying a similar trophic level). Only prey fish (i.e., gizzard shad, freshwater drum, and white bass) observed in the diets were sampled for stable isotopes.

Five prey fish from each of four length-groups (40–59, 60–79, 80–99, and greater than 120 mm), and five hybrid striped bass, five white bass, and five walleyes from the S–Q, Q–P, P–M, and M–T length categories were included in the analyses. All fish were collected during July–September in 2002 using gill nets and seines. For large fish, approximately 10 g of muscle tissue was removed from the left side and frozen. Small fish were frozen whole, and their intestinal tracts were removed before analysis. Small gizzard shad (40–59 mm) and white bass (60–79 mm) samples were a composite of two individuals. Samples were dried at 65°C 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, by use of a Europa ANCA-GSL 20–20 isotope ratio mass spectrometer. Isotope ratios were determined by means of the formula provided by Fry (1991); the standards were Pee Dee Belemnite limestone for carbon and atmospheric nitrogen for nitrogen. 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) was used to compare the isotope signatures of the predators and prey.

Hybrid striped bass, white bass, and walleyes were sampled monthly during June through August of 2002 and 2003 by use of 14-m-deep × 2.5-m-wide vertical gill nets marked at 1-m intervals. Each used one 3.81-cm-diameter, sealed polyvinyl chloride (PVC) pipe as the float bar and one 1.27-cm-diameter, sand-filled PVC pipe as the weight bar. Vertical gill nets were set in two groups of three for at least five net-nights (a total of 10 net-nights). Each group consisted of one net with 6.35-cm bar measure mesh, one with 3.81-cm mesh, and one with 2.54-cm mesh. The groups were randomly set in the downstream end (i.e., near the dam) of the reservoir each evening in similar water depths. The vertical distribution of gizzard shad was also evaluated with a vertical gill net (0.64-cm bar measure mesh; 2.5-m wide) set in 9 m of water for one night on July 16, 2003. Temperature (±0.1°C) and DO (±0.3 mg/L) profiles were measured at 1-m intervals near each group of nets using a Yellow Springs Instrument (YSI) model 85 electronic probe. One measurement was taken in the evening before the nets were set, and another was taken the next morning before the nets were pulled; these two measurements were averaged. All captured fish were separated by vertical location in the net (nearest 1 m). Similar to diet overlap, vertical overlap among the three predators by month was assessed using Pianka's (1973) index of niche overlap for which depth was the resource. Values were bootstrapped 5,000 times, and the mean index value and SE were calculated (Smith 1985; Olson 2004).

Results

Diet

The 2 years of sampling yielded 237 walleyes (231–726 mm), 498 white bass (155–386 mm), and 315 hybrid striped bass (315–720 mm) used for diet content analyses. During both years, invertebrates (i.e., Chironomidae and Chaoboridae) were important prey for all predators in June, but gizzard shad were the primary prey item from July to September (Figure 1). Freshwater drum were also an abundant prey of walleyes and hybrid striped bass in June 2002 and July and September 2003 (Figure 1). Other material found in the diets consisted primarily of unidentified matter, but white bass and common carp were also consumed. Although more than 200,000 walleye fingerlings (80–100 mm) were stocked in late June 2003, no walleyes were found in any of the hybrid striped bass diets. The only walleye consumed was found in the diet of another walleye in September 2003.

Overall, diet overlap was high among all predators each month in both years because predators consumed only a few prey species (Table 1). Only three overlap values were less than 0.75 (Table 1). Overlap was lowest in June 2002 (Table 1), when a large percentage of the weight consumed by white bass consisted of Chironomidae (Figure 1). However, higher diet overlap between walleyes and hybrid striped bass resulted because a large amount of the total weight consumed by both species was made up of freshwater drum (Figure 1).

Predator length was weakly related to the length of gizzard shad consumed (Table 2). Of the 18 relationships evaluated, only five were significant ($P < 0.05$); the highest r^2 value was 0.48 (Table 2). However, mean lengths of gizzard shad consumed by walleyes, white bass, and hybrid striped bass differed (Table 3). For example, hybrid striped bass consumed gizzard shad that were about 14 mm larger than those consumed by white bass in September 2002 and 2003 (Table 3). Similarly, white bass consumed smaller gizzard shad than did walleyes and hybrid striped bass in August 2002 and 2003. White bass and hybrid striped bass consumed larger gizzard shad than did walleyes in July 2002, but hybrid striped bass consumed smaller gizzard shad than did walleyes and white bass in July 2003 (Table 3).

Stable Isotope Analysis

Predators had higher δ^{15}N values than possible prey items in 2002, but δ^{15}N and δ^{13}C values were similar among predators (Figure 2). Values of δ^{13}C were similar between predators and 60–79-mm gizzard shad, 40–59-mm freshwater drum, and 60–79-mm freshwater drum (Figure 2). The 40–59-mm gizzard shad and those greater than 120 mm appeared to be less enriched in ^{13}C relative to predator species and other prey (Figure 2). The δ^{13}C values of freshwater drum larger than 120 mm were variable and overlapped with δ^{13}C values of a majority of other prey, but overlap with predator δ^{13}C values was minimal (Figure 2).

Spatial Overlap

Harlan County Reservoir did not develop a thermocline during 2002 and 2003 (Figure 3). During both years, water temperature increased from June to August and DO declined throughout the water column (Figure 3). From June to August, 130 white bass, 58 hybrid striped bass, and 37 walleyes were sampled in 2002, and 202 white bass, 41 hybrid striped bass, and 28 walleyes were sampled in 2003. Although surface water temperatures in 2003 increased by almost 6°C from June to August, walleyes were still abundant near the surface (i.e., depth = 1–3 m; Figure 3). Hybrid striped bass were commonly abundant at depths of 3–5 m in 2002 (Figure 3), whereas hybrid striped bass distribution in 2003 was more variable, extending from 2 to 7 m (Figure 3). White bass generally occupied surface waters during all months except June 2002 and August 2003, when they were abundant in 4–6 m of water (Figure 3). Sampling conducted in July 2003 revealed that 68 of 77 age-0 gizzard shad caught (88%) were located within the first 3 m of water.

Spatial overlap among predators was less than diet overlap. Only 2 of 16 values were greater than 0.75 (Table 1). Spatial overlap values were highest between white bass and hybrid striped bass except during July 2003 (Table 1), when overlap was highest between white bass and walleyes (0.92) because they were both located primarily within 1 m of the surface (Table 1; Figure 3). Hybrid striped bass were located at greater depths than white bass and walleyes in July 2003, resulting in low degrees of overlap between hybrid striped bass and the other two predators (Table 1; Figure 3). Too few hybrid striped bass ($n = 3$) were sampled in August 2003 to determine their overlap with the other two predators (Table 1)

Discussion

Walleyes, white bass, and hybrid striped bass of all sizes consumed similar prey. Invertebrates were the primary diet component in June of both years, but gizzard shad were the primary prey for all three predators from July to September. This led to high diet overlap among the three predator species. High diet overlap existed between age-0 walleyes and white bass in July in Lake Poinsett, South Dakota (Beck et al. 1998). Germann and Bunch (1987) found that diet overlap was also high between hybrid striped bass and white bass in Clarks Hill Reservoir, Georgia–South Carolina. Gizzard shad were the primary diet item of walleyes and hybrid striped bass in other reservoirs (Ebert et al. 1988; Jahn et al. 1987; Quist et al. 2002); thus, diet overlap is likely between these two top-level predators in systems where they coexist.

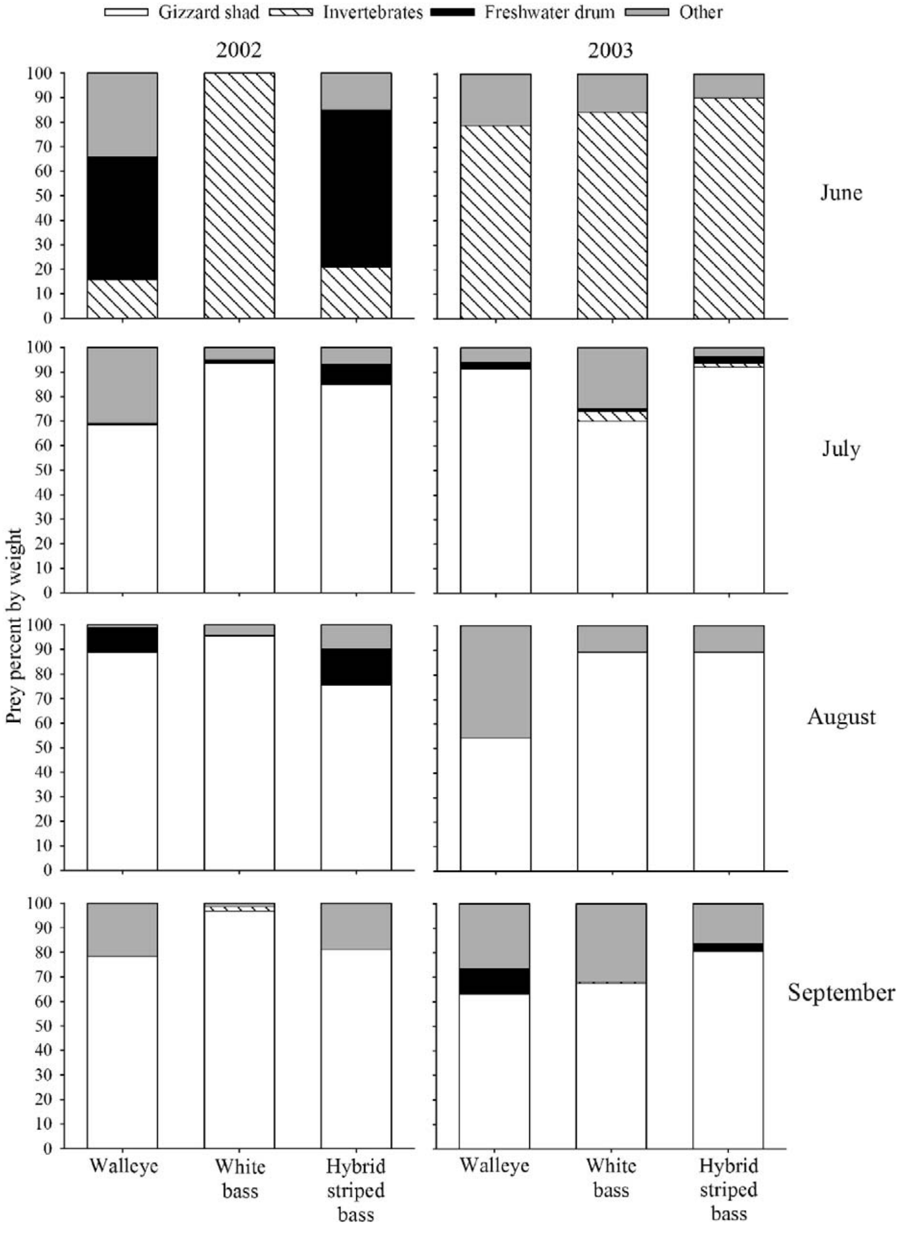

FIGURE 1.—Percentage (by weight) of common prey items found in the diets of walleyes, white bass, and hybrid striped bass sampled from Harlan County Reservoir, Nebraska, from June to September 2002 and 2003. The "other" category consisted primarily of unidentified material, common carp, and white bass.

Although high diet overlap existed among the predators, they consumed different sizes of gizzard shad. For example, in September of both years, hybrid striped bass consumed gizzard shad that were more than 14 mm longer than those consumed by white bass. These differences might be the result of size differences among the predators, but we found weak relationships between predator and prey size, indicating that these results were not attributable to predator size. Despite high overlap, the three predators appeared to partition food resources based on size.

The limited time frame during which we sampled diets prompted the need for a more long-term evaluation of the prey consumption and diet overlap

TABLE 1.—Mean Pianka's overlap values measured for diet and vertical depth of walleyes (WAE), white bass (WHB), and hybrid striped bass (HSB) sampled during June–September 2002 and 2003 in Harlan County Reservoir, Nebraska.

		Mean (SE)	
Year and month	Predator	Diet overlap	Vertical depth overlap
2002			
Jun	WAE–WHB	0.26 (0.16)	0.39 (0.18)
	WHB–HSB	0.37 (0.31)	0.57 (0.15)
	WAE–HSB	0.67 (0.29)	0.09 (0.11)
Jul	WAE–WHB	0.84 (0.22)	0.32 (0.14)
	WHB–HSB	0.99 (0.02)	0.67 (0.13)
	WAE–HSB	0.82 (0.23)	0.53 (0.17)
Aug	WAE–WHB	0.99 (0.02)	0.43 (0.13)
	WHB–HSB	0.95 (0.06)	0.64 (0.12)
	WAE–HSB	0.97 (0.06)	0.24 (0.11)
Sep	WAE–WHB	0.94 (0.11)	
	WHB–HSB	0.98 (0.01)	
	WAE–HSB	0.94 (0.10)	
2003			
Jun	WAE–WHB	0.92 (0.09)	0.69 (0.16)
	WHB–HSB	0.88 (0.11)	0.80 (0.12)
	WAE–HSB	0.85 (0.12)	0.61 (0.20)
Jul	WAE–WHB	0.95 (0.07)	0.92 (0.06)
	WHB–HSB	0.95 (0.07)	0.27 (0.09)
	WAE–HSB	0.99 (0.01)	0.13 (0.09)
Aug	WAE–WHB	0.78 (0.23)	0.69 (0.14)
	WHB–HSB	0.99 (0.01)	[a]
	WAE–HSB	0.76 (0.24)	[a]
Sep	WAE–WHB	0.84 (0.12)	
	WHB–HSB	0.94 (0.08)	
	WAE–HSB	0.91 (0.09)	

[a] Insufficient HSB sample size to calculate values.

TABLE 3.—Mean standard length (SE) and degrees of freedom (df) of gizzard shad consumed by walleyes (WAE), white bass (WHB), and hybrid striped bass (HSB) during July–September 2002 and 2003 in Harlan County Reservoir, Nebraska. Lengths followed by letters in common were not significantly different based on one-way ANOVA and Tukey's 95% confidence intervals.

Year	Month	Predator	df	Mean standard length (SE)
2002	Jul	WAE	164	16.87 (2.041) z
		WHB		22.32 (1.080) y
		HSB		22.52 (0.871) y
	Aug	WAE	184	44.47 (1.443) z
		WHB		31.84 (1.354) y
		HSB		36.79 (0.766) x
	Sep	WAE	231	51.44 (3.467) zy
		WHB		45.48 (1.914) z
		HSB		59.66 (0.638) y
2003	Jul	WAE	159	42.15 (3.642) z
		WHB		34.60 (1.316) z
		HSB		30.75 (0.682) y
	Aug	WAE	113	61.15 (2.925) z
		WHB		48.46 (0.949) y
		HSB		54.21 (1.501) z
	Sep	WAE	62	57.10 (1.607) zy
		WHB		46.70 (3.837) z
		HSB		60.79 (2.617) y

of walleyes, white bass, and hybrid striped bass. The stable isotope analysis of the three predators and their potential prey provided us with this information and corroborated the diet and diet overlap analyses. The predator species of all length categories were enriched in ^{15}N relative to the potential prey items. However, within the predators, no single species was enriched in

TABLE 2.—Number of predators (walleye [WAE], white bass [WHB], and hybrid striped bass [HSB]) sampled for diet analysis, number of gizzard shad prey measured, P-value, r^2, intercept (SE), and slope (SE) results from weighted regressions of prey standard length versus predator TL for July–September 2002 and 2003 in Harlan County Reservoir, Nebraska.

Year and month	Predator	Predator n	Prey n	P	r^2	Intercept	Slope
2002							
Jul	WAE	5	18	0.962	0.00	18.2 (27.8)	−0.0047 (0.0979)
	WHB	19	53	0.000	0.26	−4.7 (6.5)	0.0918 (0.0218)
	HSB	29	94	0.000	0.15	44.5 (5.5)	−0.0500 (0.0125)
Aug	WAE	16	41	0.099	0.07	66.5 (13.1)	−0.0488 (0.0289)
	WHB	16	41	0.385	0.02	20.5 (13.0)	0.0323 (0.0368)
	HSB	24	103	0.211	0.02	27.1 (7.7)	0.0222 (0.0177)
Sep	WAE	9	15	0.339	0.07	28.8 (23.1)	0.0584 (0.0588)
	WHB	23	46	0.944	0.00	44.9 (8.1)	0.0019 (0.0267)
	HSB	33	171	0.063	0.02	74.9 (8.2)	−0.0334 (0.0179)
2003							
Jul	WAE	9	14	0.507	0.04	25.3 (24.9)	0.0577 (0.0844)
	WHB	15	43	0.000	0.34	−48.3 (18.1)	0.2368 (0.0516)
	HSB	24	103	0.930	0.00	30.0 (9.0)	0.0016 (0.0186)
Aug	WAE	6	10	0.026	0.48	−16.8 (28.7)	0.2101 (0.0768)
	WHB	42	76	0.115	0.03	32.0 (10.4)	0.0487 (0.0305)
	HSB	13	28	0.856	0.00	51.8 (13.3)	0.0050 (0.0274)
Sep	WAE	18	38	0.028	0.13	26.5 (13.5)	0.0790 (0.0346)
	WHB	5	8	0.877	0.00	59.4 (79.1)	−0.0362 (0.2248)
	HSB	8	17	0.469	0.04	101.1 (54.3)	−0.0842 (0.1132)

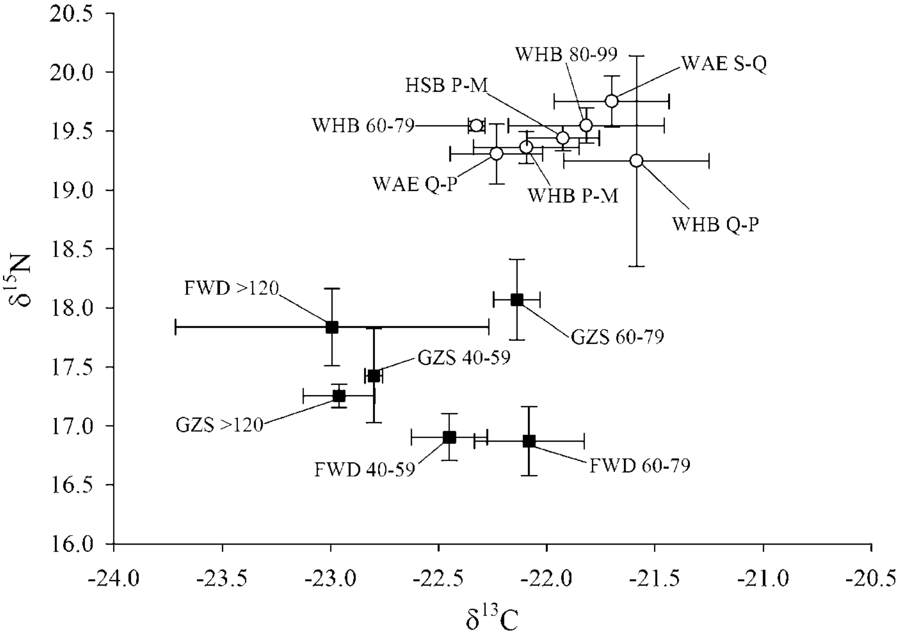

FIGURE 2.—Stable isotope signatures (SE) of predators (open circles) and potential prey (solid squares) collected during July–September 2002 from Harlan County Reservoir, Nebraska. Predator species sampled were walleyes (WAE), white bass (WHB), and hybrid striped bass (HSB); predator length categories are 60–79 mm TL, 80–99 mm TL, stock–quality (S–Q), quality–preferred (Q–P), and preferred–memorable (P–M). Prey species sampled were freshwater drum (FWD) and gizzard shad (GZS); prey length categories are 40–59, 60–79, 80–99, and over 120 mm SL.

^{15}N, suggesting that all three predators were feeding at the same trophic level. Based on overlapping δ^{13}C values, predators appeared to be deriving some of their carbon from 60–79-mm gizzard shad and 40–59-, 60–79-, and 80–100-mm freshwater drum. Because of the long-term assimilation of stable isotopes in the muscle, these predators probably exhibited diet similarity beyond the time of our sampling (Peterson and Fry 1987).

Due to a lack of thermal stratification in Harlan County Reservoir, hybrid striped bass and walleyes were distributed more evenly throughout the water column in this reservoir than in reservoirs studied elsewhere. The lack of thermal stratification (polymictic) in Harlan County Reservoir is caused by continuous circulation of the water related to shallow depths and prevailing winds. Radio telemetry studies have indicated that hybrid striped bass are typically located near the thermocline when present (Austin and Hurley 1987; Douglas and Jahn 1987). Walleyes in Laurel River Lake, Kentucky, were located at a depth of 4.2–7.6 m at approximately 23°C during thermal stratification (Williams 1997). In contrast, white bass distribution observed during our study was similar to that seen in other studies. Irrespective of thermal stratification, white bass have been documented as occupying the top 5 m (Borges 1950; Colvin 1993). We suspect that the white bass, walleyes, and hybrid striped bass would have shown more spatial overlap if Harlan County Reservoir experienced thermal stratification.

The vertical overlap we observed was probably related to the distribution of gizzard shad. Vertical gillnetting of age-0 gizzard shad in July 2003 indicated that they primarily occupied depths of 0–3 m and that all predators occupied these depths at some time. Age-0 gizzard shad are also primarily located near the surface in other reservoirs during April to August (Netsch et al. 1971; Downey and Toetz 1983; Van Den Avyle et al. 1995). White bass and walleye vertical distributions are related to prey distributions in Lake of the Ozarks, Missouri (Borges 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; Craig and Babaluk 1993; Sellers et al. 1998), these variables appeared to have little effect on fish distribution in Harlan County Reservoir. Despite water temperatures increasing from June to August, white bass and hybrid striped bass were commonly found within the upper 4

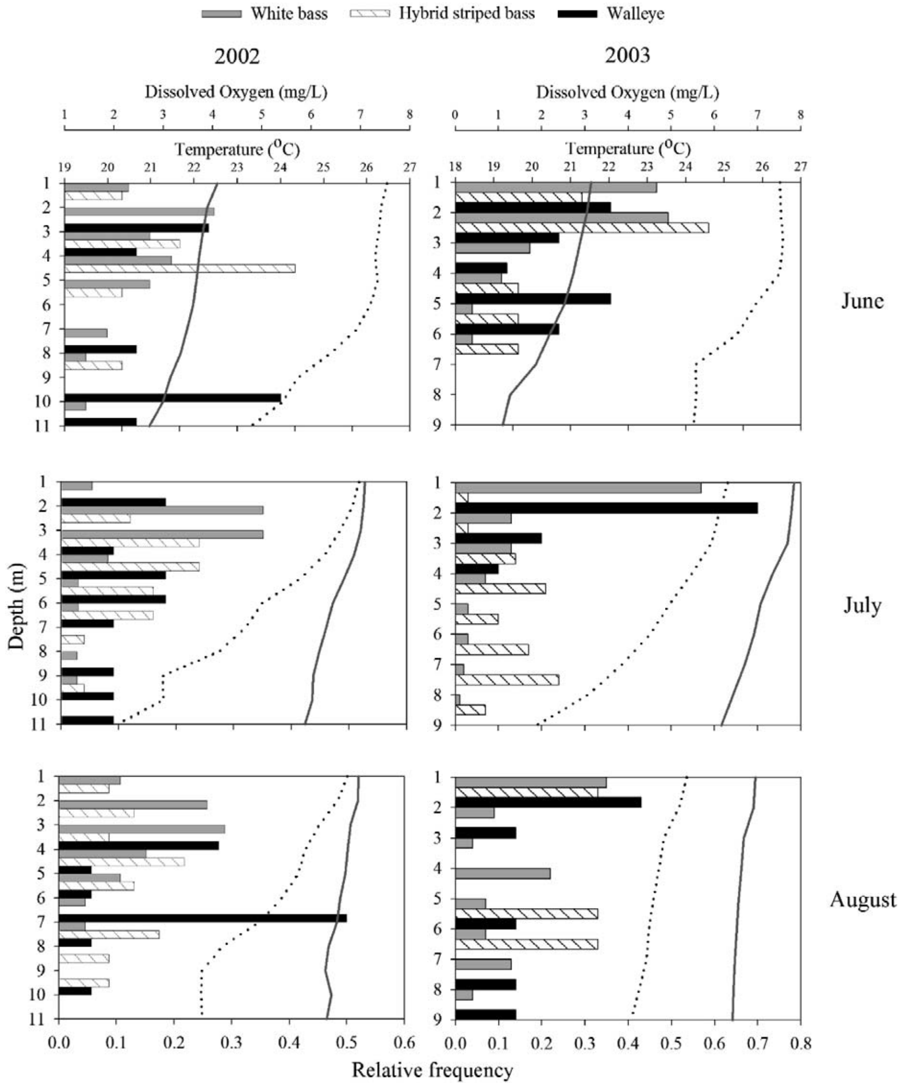

FIGURE 3.—Vertical (depth) distribution (m) of walleyes, white bass, and hybrid striped bass in relation to water temperature (°C; solid line) and dissolved oxygen (mg/L; dotted line) in Harlan County Reservoir, Nebraska, during June–August 2002 and 2003.

m of the water column and walleyes were abundant in the top 2 m in June and July 2003.

Despite the 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). 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 (Crowder 1990). In our study, similar prey (i.e., gizzard shad) and space (i.e., depth) were used by all predators. However, each predator species appeared to consume different sizes of gizzard shad (i.e., resource partitioning), which may allow these species to coexist. Although 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 of these predators is near or above the statewide average (Hurley 2001).

It appears unlikely that the introduction of hybrid striped bass into Harlan County Reservoir is negatively affecting the walleye or white bass population. Nonetheless, managers should be aware of the possibility for competition to occur if prey resources (e.g., gizzard shad) become limiting (Matthews et al. 1992). In addition, predator use of resources before the hybrid striped bass introduction is unknown. It is possible that the introduction of hybrid striped bass may have caused the other predators to shift their diets or vertical distribution. However, studies evaluating the diets and vertical position of white bass and walleyes in other reservoirs devoid of hybrid striped bass have found similar results to those observed in our study (Eley et al. 1967; Hover 1976; Johnson et al. 1988; Williams 1997; Cox et al. 2001; Quist et al. 2002). Therefore, introduction of hybrid striped bass into Harlan County Reservoir probably did not alter the diets or vertical distribution of white bass or walleyes.

Several alternative hypotheses may explain the decline in the walleye population in Harlan County Reservoir. Gizzard shad can reduce zooplankton densities and compete for prey resources with larval walleyes in Great Plains reservoirs, causing a bottleneck for walleyes that rely on zooplankton during the spring (Dettmers and Stein 1992). Quist et al. (2003) found that walleye recruitment in four Kansas reservoirs was positively related to spring storage ratio and air temperature but negatively related with spring water level and abundance of 130–190-mm white crappies. Mesocosm experiments showed that white crappies have the ability to prey on larval walleyes and that the abundance of white crappies had a predominating effect on walleye recruitment despite abiotic conditions (Quist et al. 2003). We believe that these are more logical hypotheses for the decline in walleye abundance, and we suggest the testing of hypotheses concerning the effects of reservoir abiotic factors, gizzard shad competition, and white crappie abundance on walleye early life history. We conclude that hybrid striped bass have little direct or indirect impact on the walleye population in Harlan County Reservoir and are a viable management option for highly productive Great Plains reservoirs that contain walleyes and white bass.

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