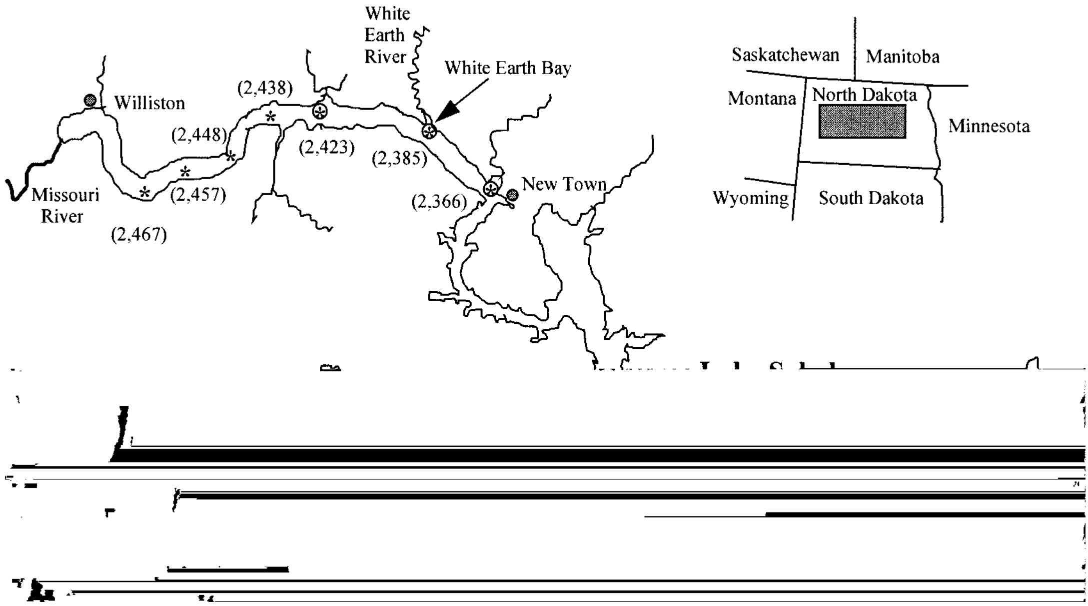

FIGURE 1.—Location of fish predator sampling sites and community monitoring sites within Lake Sakakawea, North Dakota.

of paddlefish stocked at 6–8 mm TL in 1970 (Graham 1986), but more fish survived when larger paddlefish (250–300 mm TL) were stocked. In Lake Sakakawea, North Dakota, Mero et al. (1994) observed wild paddlefish (170–255 mm TL) in the stomachs of walleyes *Stizostedion vitreum* and saugers *S. canadense* during September and October 1991, but not from May to August.

Knowledge of size-related susceptibility of paddlefish to predation by fishes is valuable for fisheries biologists seeking to maximize the survival of wild and hatchery-reared paddlefish. For wild paddlefish, it is important to identify key predators so that, where possible, management of the predator species can be made compatible with the needs for paddlefish recruitment. Hatchery-reared paddlefish production and releases are increasing throughout the species' range (Dillard et al. 1986; Tidwell and Mims 1990; Pitman and Isaac 1995; Scarnecchia et al. 1995; Guy et al. 1996; Hoxmeier and DeVries 1996). Although paddlefish are thought to experience reduced vulnerability to predation from fishes after they exceed 250 mm TL (Graham 1986; Tidwell and Mims 1990; Mero et al. 1994), definitive studies have not been done. Information on the lengths of paddlefish eaten by fishes will benefit hatchery programs and management plans for wild stocks.

Our objectives in this study were to (1) evaluate the potential piscivorous predators of age-0 paddlefish, (2) assess the spatial and temporal variation in predation on age-0 paddlefish, (3) evaluate the size of wild age-0 paddlefish eaten by other fishes, (4) evaluate the susceptibility of large, hatchery-reared paddlefish to predation from other fishes, and (5) describe the condition of paddlefish in stomachs and identify the structures resistant to digestion.

Study Site

Lake Sakakawea, a main-stem Missouri River impoundment in westcentral North Dakota (Figure 1), was formed after the completion of Garrison Dam in 1953 and filled gradually until 1967. The reservoir was developed by the U.S. Army Corps of Engineers for flood control, navigation, irrigation, water supply, hydroelectric power, water quality control, and recreation. The full pool is at an elevation of 565 m and has a surface area of 156,058 ha, a total storage capacity of 30.1 km^3, a maximum depth of 57 m, a length of 322 km, a shoreline of 2,574 km, and an average width of 4.8 km (Berard 1989).

The reservoir has a diverse fish community of at least 53 species (Berard 1989). The more abundant native species include walleye, sauger, northern pike *Esox lucius*, channel catfish, paddlefish, white bass *Morone chrysops*, goldeye *Hiodon alosoides*, freshwater drum *Aplodinotus grunniens*, yellow perch *tostomus commersoni*, burbot *Lota lota*, shorthead redhorse *Moxostoma macrolepidotum*, and river carpsucker *Carpiodes carpio*. Several nonnative fishes are also present; the most abundant species are rainbow smelt *Osmerus mordax*, common carp *Cyprinus carpio*, chinook salmon *Oncorhynchus tshawytscha*, and rainbow trout *Oncorhynchus mykiss*. The study site was the upper portion of Lake Sakakawea between river kilometer (RKM) 2,385 from the confluence with the Mississippi River and RKM 2,467, which encompassed the transitional area from a river to reservoir environment. This site was chosen because it was a known age-0 paddlefish rearing area (Fredericks 1994; Fredericks and Scarnecchia 1997; Scarnecchia et al. 1997) where fish predation on age-0 paddlefish was previously documented (Mero et al. 1994).

Methods

Data collection.—Seven sample sites were chosen that included areas of known age-0 paddlefish relative abundance (Fredericks 1994) and that the state management agency monitored annually for fish community status (Figure 1; Berard 1989; Parken 1996). At each site in 1994 and 1995, predators were collected from July to October with two monofilament experimental gill nets (76 3 1.8 m composed of five equal-length panels with mesh sizes of 19, 25, 38, 51, and 64 mm bar measure) set on the bottom perpendicular to shore and in similar aquatic habitat. Nets were set overnight in 3–5 m of water when catch rates of walleye or sauger were low (, 0.50 fish/net-hour) or during the day when catch rates were high (≥0.50 fish/net-hour). Nets were checked frequently (every 2–4 h) during high catch rates to reduce the effects of digestion on stomach contents and mortality and stress on the bycatch.

Walleyes, saugers, northern pike, channel catfish, white bass, chinook salmon, and rainbow trout were measured for total length. Stomach contents were examined for walleyes and saugers greater than 270 mm, northern pike greater than 320 mm, and channel catfish greater than 360 mm. These sizes were based on the lengths of fish of these species known to have eaten paddlefish in other studies (Tidwell and Mims 1990; Mero et al. 1994). Also, stomach contents were examined for white bass greater than 300 mm and all chinook salmon and rainbow trout, but too few were sampled for inferences.

Predator stomachs were excised and preserved in 15% formalin for 3 d, then transferred to 40% ethanol until examined. Stomach contents were identified to species when possible based on characteristics described in Pflieger (1975) and Oates et al. (1993). Other structures resistant to digestion, such as Bridge's bone for paddlefish (Allis 1903), were also used. Body lengths (in millimeters from front of eye to fork of caudal fin; Ruelle and Hudson 1977) were obtained from age-0 paddlefish eaten by predators. Few total lengths of paddlefish were measured because rostrums were digested quickly.

Statistical analysis.—To determine whether the proportions of species preying on paddlefish were equal, a chi-square test of homogeneity was used. To determine whether predator size influenced predation on paddlefish, the length distributions of predators that did and did not consume paddlefish were compared with a Mann–Whitney *U*-test. Conditional probabilities were calculated as the number of predators containing paddlefish divided by the total number of predators of that length. Exact 95% confidence limits (Zar 1984) were calculated for the proportions of predators in 20-mm groups that ate paddlefish. The effect of predator size on the probability of a predator consuming a paddlefish was assessed with logistic regression (Menard 1995).

The proportions of walleyes and saugers containing paddlefish were compared between sites and months, between sites, and between months with chi-square tests of homogeneity. Assuming no spatial–temporal interaction for comparisons between sites, each site was pooled over the 4 months to obtain larger sample sizes and permit better detection of spatial differences. For similar reasons, comparisons between months were pooled over the seven sites. When the chi-square test assumptions of expected cell frequency size were not met, bootstrapping was used (Mooney and Duval 1993).

To determine whether walleyes and saugers preyed on similar-sized paddlefish, the size distributions were illustrated with Tukey box plots and compared with a Mann–Whitney *U*-test. Data on the size of paddlefish eaten by predators were combined among all sites for stronger inferences. Size-selectivity of predators for age-0 paddlefish was not determined because paddlefish in the reservoir were too sparse in 1995 to be captured effectively with our sampling gear (dip nets; Scarnecchia et al. 1997).

To determine the ratio of age-0 paddlefish total length to predator total length, paddlefish body lengths were converted to total lengths with linear regression. Total length was compared with body

TABLE 1.—The number of predators sampled for food habits and the number, percent, and total length (TL) of those found to have consumed paddlefish in Lake Sakakawea in 1994 and after hatchery-reared paddlefish were released in White Earth Bay, Lake Sakakawea, in 1995.

	Number
Predator	Number sampled

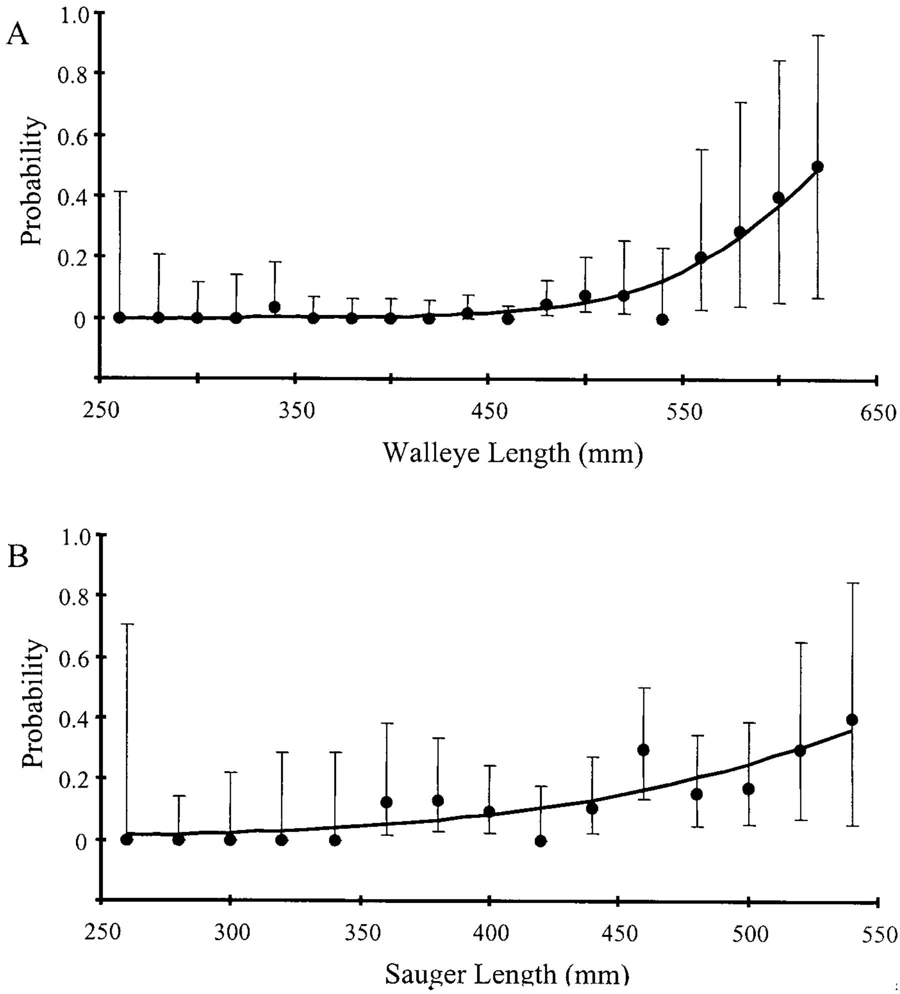

FIGURE 2.—The probability of an **(A)** walleye or **(B)** sauger in Lake Sakakawea, North Dakota, consuming paddlefish, by total length of the predator. Error bars indicate 95% confidence limits.

Whitney U 5 2,188.5, P , 0.001). The probability of a sauger consuming a paddlefish was also significantly related to sauger length (logit[y] 5 0.0132[x] 2 7.68, r^2 5 0.78; G_M 5 19.040, P , 0.001; Figure 2b).

TABLE 2.—The number of walleye and sauger stomachs with identifiable prey that contained paddlefish, rainbow smelt, freshwater drum, and white bass in Lake Sakakawea, 1995.

	Number (and percent) of prey eaten			
Predator	Paddlefish	Rainbow smelt	Freshwater drum	White bass
Walleye	20 (3)	549 (79)	33 (5)	67 (10)
Sauger	32 (12)	91 (33)	73 (27)	57 (21)

Few walleye or sauger stomachs contained wild age-0 paddlefish compared with the other common prey taxa (Table 2). Nevertheless, 31% of walleye ate paddlefish in September at RKM 2,424 and 38% of sauger ate them in July at RKM 2,448 (Figure 3). The proportion of walleyes consuming paddlefish varied for individual site by month measurements (χ^2 5 105.3, bootstrapped P , 0.001). When pooling months, the proportion of walleyes consuming paddlefish varied among sites (χ^2 5 27.7, bootstrapped P , 0.001), and when pooling sites, the proportion varied among months (χ^2 5 13.66, bootstrapped P , 0.002). The proportion of saugers consuming paddlefish varied for individual site by month measurements (χ^2 5 37.36, bootstrapped P , 0.050). When pooling months,

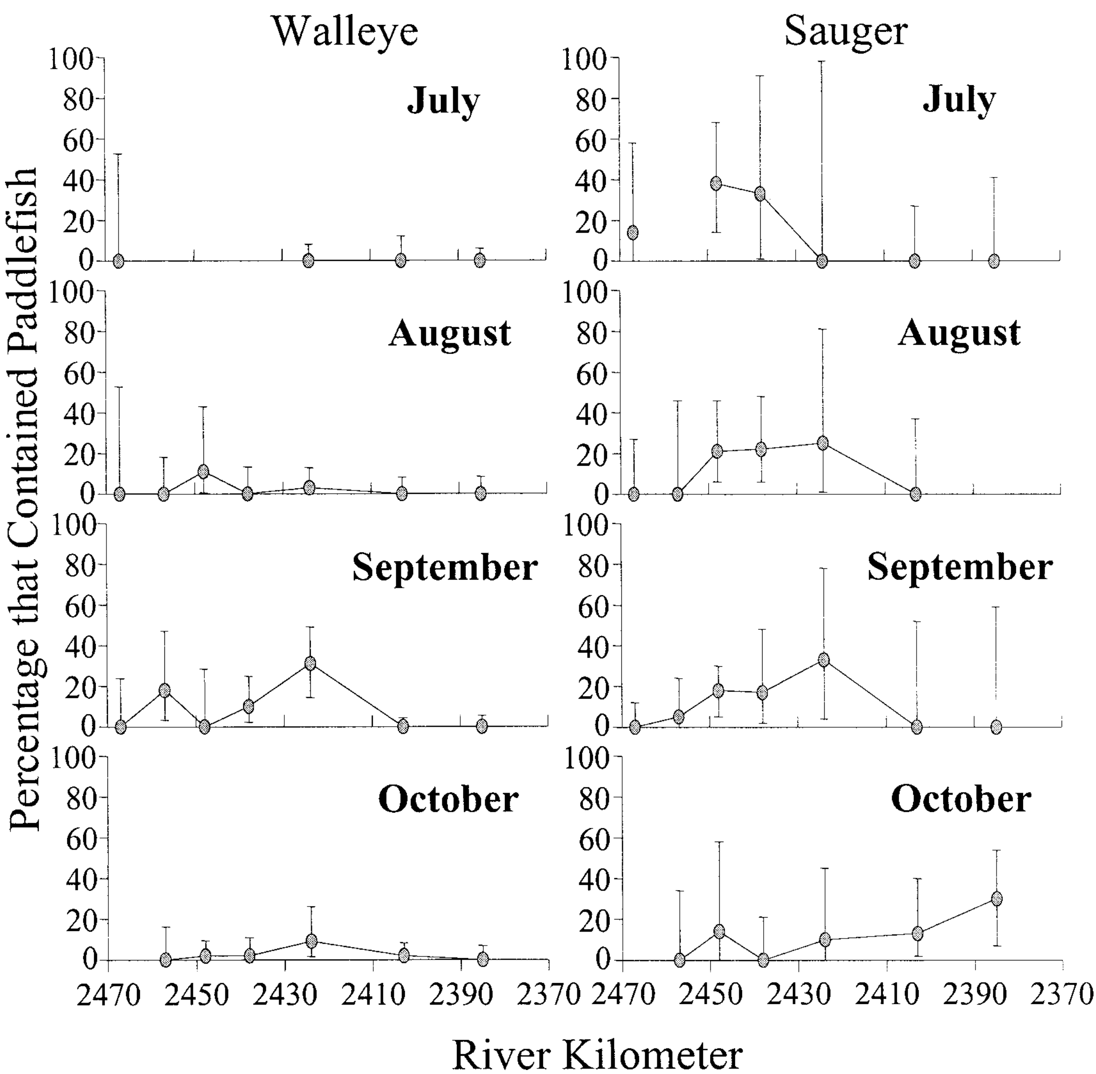

FIGURE 3.—Spatial–temporal patterns of predation on paddlefish by walleyes and saugers in Lake Sakakawea, North Dakota, from July to October, 1995. Error bars indicate 95% confidence limits of percentages.

the proportion of sauger consuming paddlefish varied among sites ($\chi^2 = 17.78$, bootstrapped $P < 0.006$), but when pooling sites, the proportions were similar among months ($\chi^2 = 1.77$, $P < 0.619$).

Wild age-0 paddlefish preyed on by walleyes (range, 71–167 mm BL; mean, 112 mm) were larger than those preyed on by sauger (range, 38–145 mm BL; mean, 83 mm; Mann–Whitney $U = 85.5$, $P < 0.0033$; Figure 4). A 142-mm-BL (269-mm-

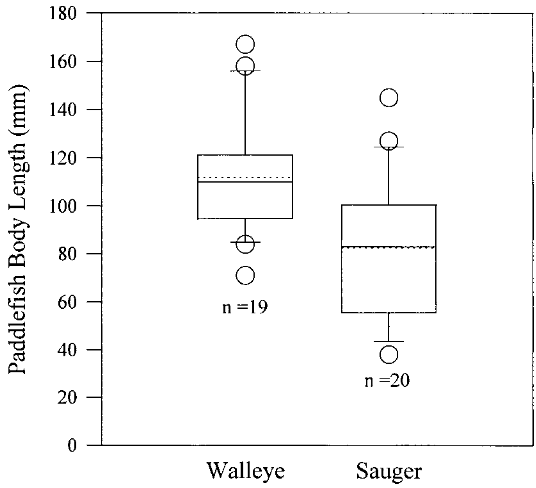

FIGURE 4.—Size distribution of paddlefish consumed by walleyes and saugers in Lake Sakakawea, North Dakota. Each Tukey box plot presents the median (solid line), mean (dashed line), upper and lower quartiles (upper and lower box boundaries), 10th and 90th percentiles (error bars), and outliers (circles).

hatchery-reared paddlefish (175 and 220 mm BL) were found in 2 of 17 northern pike (680 and 600 mm TL) with identifiable prey.

A variety of distinguishing characteristics identified paddlefish in predator stomachs. Small paddlefish were consumed head-first, whereas larger paddlefish were consumed caudal fin-first. The least digested paddlefish had complete rostrums that were progressively digested from the edges toward Bridge's bone, which was semiresistant to digestion. The rostrum was commonly separated

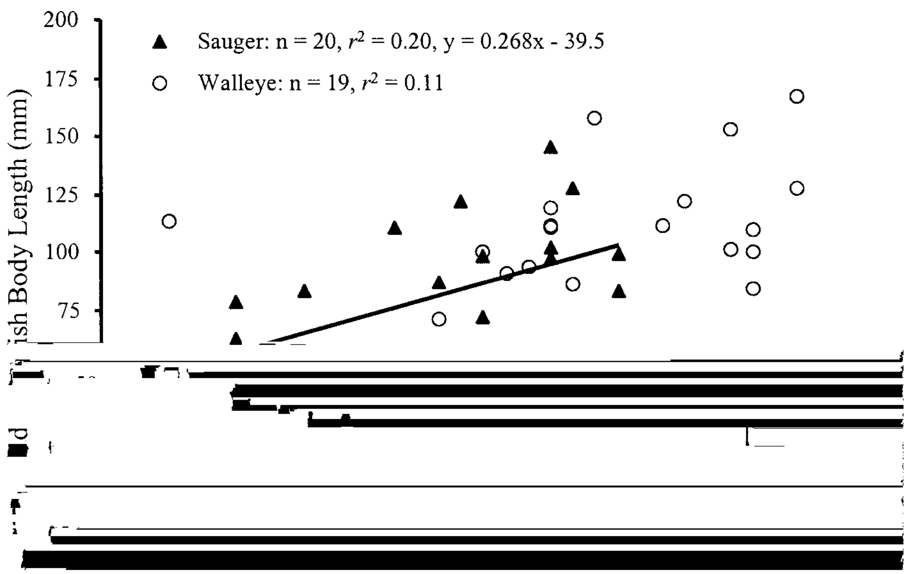

FIGURE 5.—Comparison between the lengths of paddlefish in stomachs and those of the walleyes and saugers that ate them, Lake Sakakawea, North Dakota.

tion on paddlefish is overlap in habitat use. Walleyes and saugers occupy a broad range of habitats (Swenson and Smith 1976; McMahon et al. 1984; Johnson et al. 1988; Hubert and O'Shea 1992), including the pelagic areas frequented by age-0 paddlefish (Fredericks 1994).

Channel catfish predation on paddlefish may have been rare because the species use different habitats and may therefore seldom encounter each other. Channel catfish are benthic feeders closely associated with the substrate (Scott and Crossman 1973; Pflieger 1975; Hubert and O'Shea 1992). In contrast, age-0 paddlefish from 74 to 175 mm BL are evidently pelagic feeders (Fredericks 1994), and they may not be readily available to channel catfish in the wild. In hatchery ponds, channel catfish predation may be a result of shallow depths and high densities of both species.

Similarly, the absence of wild paddlefish in northern pike diets may be related to differences in habitat use. Northern pike are littoral feeders (Savino and Stein 1989a; Hinch et al. 1991), frequenting the vegetation-water interface (Chapman and Mackay 1984). They are substrate-oriented and often select the vegetated shallows (Diana et al. 1977; Chapman and Mackay 1984; Cook and Bergersen 1988) and cover to ambush prey (Inskip 1982; Craig and Babaluk 1989; Savino and Stein 1989a, 1989b). They consequently consume prey associated with shallow, vegetated areas (Chapman and Mackay 1984, 1990; Chapman et al. 1989). In Lake Sakakawea, northern pike may only rarely encounter wild age-0 paddlefish because northern pike rarely use pelagic habitats (Chapman and Mackay 1984; Cook and Bergersen 1988).

The percentage of walleyes containing paddlefish varied spatially and temporally, whereas the percentage of saugers containing paddlefish varied only spatially. The spatial–temporal pattern of predation by saugers resembled the spatial–temporal distribution of wild age-0 paddlefish described by Fredericks (1994). In 1993, age-0 paddlefish were concentrated in the most upstream area of Lake Sakakawea during late August and became more evenly distributed as they dispersed down-reservoir away from the natal area. Saugers appeared to opportunistically eat age-0 paddlefish relative to their abundance. Walleyes, however, were selective, and suitable conditions for eating paddlefish may have been spatially and temporally limited.

The absence of paddlefish from predator diets in 1994 may reflect the lower abundance of age-0 paddlefish compared with 1995. Year-class estimates and forecasting methods indicated that age-0 paddlefish were scarce in 1994, probably because of low Yellowstone River discharge and minimal spawning success. Predator feeding ecology and prey consumption are often affected by prey abundance and, accordingly, prey encounter rates (Swenson and Smith 1976; Swenson 1977; Begon et al. 1990).

In this study, the length of wild paddlefish preyed on by walleyes, saugers, and channel catfish was greater than reported elsewhere. Paddlefish up to 167 mm BL (305 mm TL) were conreared paddlefish were stocked in a bay with abundant littoral habitat, the habitat favored by pike (Cook and Bergersen 1988; Savino and Stein 1989a; Hinch et al. 1991). Stocking paddlefish in unconfined areas with minimal littoral habitat may reduce predation from northern pike.

In this study, the sizes of wild paddlefish consumed by walleyes and saugers (, 167 mm BL or 305 mm TL) were within the size range recommended by other authors for stocking hatchery-reared paddlefish. Mero et al. (1994) found paddlefish greater than 255 mm TL were not preyed on by percids and recommended age-0 paddlefish be at least 250 mm TL before stocking. Tidwell and Mims (1990), Graham et al. (1986) and Graham (1986) recommended paddlefish be 250–300 mm TL when stocked for polyculture with channel catfish or in lakes with piscivorous fishes. To recover populations in east Texas rivers, Pitman (1992, cited in Pitman and Isaac 1995) recommended that paddlefish be 203–254 mm TL when stocked. Because we found that walleyes and saugers were capable of eating wild paddlefish up to 167 mm BL (305 mm TL), we believe that many stocked fish may be susceptible to predation. Nevertheless, it is unknown whether this predation adversely effects survival and population establishment or recovery. State agencies should consider stocking larger paddlefish where high densities of saugers or large (. 490 mm TL) walleyes are present.

Acknowledgments

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