Predation on Age-0 Paddlefish by Walleye and Sauger in a Great Plains Reservoir

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Abstract.—From July to October 1994 and 1995, the food habits of walleye Stizostedion vitreum, sauger S. canadense, northern pike Esox lucius, and channel catfish Ictalurus punctatus were studied in Lake Sakakawea, a Missouri River main-stem reservoir in North Dakota. In 1994, no paddlefish Polyodon spathula were found in stomachs of these predators. In 1995, 3% of the walleyes, 12% of the saugers, and 1% of the channel catfish with identifiable prey ate wild age-0 paddlefish. Walleyes ate paddlefish from August to October, with the highest proportions in September, whereas saugers ate paddlefish from July to October in equal proportions. Walleye and sauger stomachs contained wild age-0 paddlefish as large as 167 mm body length (BL; 305 mm total length, TL), and one channel catfish stomach contained a 142-mm-BL (269-mm-TL) paddlefish. Predators were also sampled after 8,000 hatchery-reared, age-0 paddlefish (mean BL = 189 mm) were released in White Earth Bay, Lake Sakakawea. Hatchery-reared paddlefish were absent from stomachs of 47 walleyes, 3 saugers, 9 channel catfish, and 3 white bass Morone chrysops with identifiable prey. However, two hatchery-reared paddlefish (175 and 220 mm BL) were found in 2 of 17 northern pike with identifiable prey. Because we found that walleyes and saugers were capable of eating paddlefish of at least 167 mm BL (305 mm TL), many stocked paddlefish may be susceptible to predation. State agencies should consider stocking larger paddlefish where high densities of sauger or large walleyes (>490 mm TL) are present.

The paddlefish Polyodon spathula, an ancient zooplanktivorous fish native to large rivers of the Mississippi River and adjacent Gulf Slope drainages (Gengerke 1986), seasonally inhabits areas of free-flowing rivers such as main channels, side channels, backwaters, and oxbow lakes (Russell 1986; Hoxmeier and DeVries 1997). Throughout much of the paddlefish's range the construction of dams and navigation channels has eliminated spawning habitat and reduced abundance (Dillard et al. 1986; Hoxmeier and DeVries 1996). In states with naturally reproducing stocks supporting fisheries, maintenance of wild stocks is considered paramount (Scarnecchia et al. 1995). In states with reduced paddlefish abundance, agencies often use hatchery-reared paddlefish to establish or supplement populations (Dillard et al. 1986; Pitman and Isaac 1995; Guy et al. 1996; Hoxmeier and DeVries 1996). In both cases, knowledge of factors affecting the abundance and survival of age-0 paddlefish is essential.

The vulnerability of age-0 paddlefish to predation is not well understood. Graham (1986), however, suggested the size of paddlefish selected for stocking affected their vulnerability to predators. Most of the available information on predation of age-0 paddlefish comes from observations in hatchery ponds. Graham et al. (1986) reported that paddlefish in outdoor ponds at Blind Pony Hatchery, Missouri, were eaten by a variety of predators and that their susceptibility to predation was related to length. Paddlefish fry 6–8 mm total length (TL) were eaten by water boatmen (Corixidae), backswimmers (Notonectidae), whirligig beetles (Gyrinidae), and water scorpions (Nepidae). Herons Larus argentatus and great black terns Chlidonias niger ate paddlefish less than 76 mm TL and belted kingfishers Ceryle alcyon, green herons Butorides virescens, and great blue herons Ardea herodias preyed on paddlefish ranging from 76 to 152 mm TL (Graham et al. 1986). Turtles, bull frogs, water snakes, muskrats Ondatra zibethicus, and mink Mustela vison were also observed feeding on small paddlefish. In hatchery polyculture, channel catfish Ictalurus punctatus ate paddlefish 90–150 mm TL (Tidwell and Mims 1990).

Less information exists on predation of age-0 paddlefish in natural environments. The scarcity of wild age-0 paddlefish in many of their habitats may account for the shortage of information. In Table Rock Lake, Missouri, predacious fishes were believed to have eliminated the entire year-class...
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 *Perca flavescens*, white sucker *Ca-
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 × 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 Pfieger (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.

<table>
<thead>
<tr>
<th>Predator</th>
<th>Number sampled</th>
<th>Number with identifiable prey</th>
<th>Consumed paddlefish</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Number</td>
<td>Percent</td>
<td>TL (mm)</td>
</tr>
<tr>
<td></td>
<td>with</td>
<td></td>
<td>range</td>
</tr>
<tr>
<td></td>
<td>identifiable</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>prey</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1994: Lake Sakakawea</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Walleye</td>
<td>713</td>
<td>284</td>
<td>0</td>
</tr>
<tr>
<td>Sauger</td>
<td>650</td>
<td>220</td>
<td>0</td>
</tr>
<tr>
<td>Northern pike</td>
<td>142</td>
<td>51</td>
<td>0</td>
</tr>
<tr>
<td>Channel catfish</td>
<td>287</td>
<td>161</td>
<td>0</td>
</tr>
<tr>
<td>1995: Lake Sakakawea</td>
<td>1,511</td>
<td>695</td>
<td>20</td>
</tr>
<tr>
<td>Walleye</td>
<td>710</td>
<td>275</td>
<td>32</td>
</tr>
<tr>
<td>Sauger</td>
<td>355</td>
<td>104</td>
<td>0</td>
</tr>
<tr>
<td>Northern pike</td>
<td>232</td>
<td>128</td>
<td>1</td>
</tr>
<tr>
<td>Channel catfish</td>
<td>88</td>
<td>47</td>
<td>0</td>
</tr>
<tr>
<td>Northern pike</td>
<td>10</td>
<td>3</td>
<td>0</td>
</tr>
<tr>
<td>Channel catfish</td>
<td>27</td>
<td>17</td>
<td>2</td>
</tr>
<tr>
<td>White bass</td>
<td>10</td>
<td>9</td>
<td>0</td>
</tr>
<tr>
<td>White bass</td>
<td>4</td>
<td>3</td>
<td>0</td>
</tr>
</tbody>
</table>

Results

In 1994, no wild age-0 paddlefish were found in stomachs of any walleye, sauger, northern pike, or channel catfish with identifiable prey, so all further results refer to sampling conducted in 1995. In 1995, wild age-0 paddlefish were found in 3% of walleye, 12% of sauger, and 1% of channel catfish stomachs containing identifiable prey (Table 1). No wild age-0 paddlefish were found in any northern pike with identifiable prey. The proportions of walleye, sauger, and channel catfish that consumed paddlefish differed ($\chi^2 = 38.06, P < 0.001$); saugers consumed paddlefish most frequently and channel catfish least frequently.

Walleyes that consumed paddlefish (range, 330–610 mm; mean, 520 mm) were larger than those that did not consume them (range, 260–710 mm; mean, 420 mm; Mann–Whitney $U = 1,942.5, P < 0.001$). The probability of a walleye consuming a paddlefish was significantly related to walleye length ($\text{logit}[y] = 0.0235[x] - 14.6, r^2 = 0.95, G_M = 41.465, P < 0.001$; Figure 2a) and increased sharply after a size threshold of approximately 490 mm. Two walleyes, lengths 630 and 710 mm, were considered outliers and excluded from the calculation because conditional probabilities could not be calculated ($N = 1$). Saugers that consumed paddlefish (range, 360–530 mm; mean, 450 mm) were also larger than those that did not consume them (range, 260–540 mm; mean, 400 mm; Mann–
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 ($\chi^2 = 105.3$, bootstrapped $P < 0.001$). When pooling months, the proportion of walleyes consuming paddlefish varied among sites ($\chi^2 = 27.7$, bootstrapped $P < 0.001$), and when pooling sites, the proportion varied among months ($\chi^2 = 13.66$, bootstrapped $P < 0.002$). The proportion of saugers consuming paddlefish varied for individual site by month measurements ($\chi^2 = 37.36$, bootstrapped $P < 0.050$). When pooling months,
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-TL) paddlefish was found in a 410-mm channel catfish. Walleyes from 330 to 610 mm ate wild paddlefish as large as 305 mm TL, which represented 25–62% of the walleye’s total length. Saugers from 360 to 530 mm ate wild paddlefish as large as 264 mm TL, representing up to 53% of the sauger’s total length. The relationships between the size of age-0 paddlefish in stomachs and predator size differed among walleyes and saugers (analysis of covariance [ANCOVA]: $F = 8.49$, $P < 0.001$; Figure 5) and showed a weak positive relation with sauger size ($F = 4.40$, $P < 0.05$), but none with walleye size ($F = 2.02$, $P < 0.17$).

Little predation was detected on hatchery-reared paddlefish released in White Earth Bay (Table 1). Hatchery-reared paddlefish were absent from stomachs of 47 walleyes, 3 saugers, 9 channel catfish, and 3 white bass with identifiable prey. Two
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 at its base from the paddlefish’s body. The paddlefish’s caudal fin structure and large stomach, with respect to other prey taxa, were slightly more resistant to digestion. Dentary bones and gill arches with many long, fine gill rakers were characteristics identified on paddlefish in further stages of digestion. In advanced stages of digestion lacking the head and stomach, identification was aided by the absence of bony structures (common in other fishes) and vertebra and the presence of the notochord. In the most advanced stages of digestion we identified paddlefish by their notochord, which remained after the flesh was digested.

Discussion

In 1995, wild age-0 paddlefish were frequently found in the stomachs of walleyes and saugers, rarely found in channel catfish, and never found in northern pike. Mero et al. (1994) also found paddlefish in the stomachs of walleyes and saugers in Lake Sakakawea, but they did not examine other predators. Although channel catfish predation on paddlefish in the wild has not been reported, Tidwell and Mims (1990) reported that channel catfish consumed them in hatchery ponds.

One explanation for walleye and sauger preda-
tion on paddlefish is overlap in habitat use. Wall-
eyes 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 
behave 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; Pfieger 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 cat-
fish 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), fre-
quenting 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 (Chap-
man 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 paddle-
fish varied spatially and temporally, whereas the 
percentage of saugers containing paddlefish varied 
only spatially. The spatial–temporal pattern of pre-
dation 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-reser-
voir away from the natal area. Saugers appeared 
to opportunistically eat age-0 paddlefish relative 
to their abundance. Walleyes, however, were se-
lective, and suitable conditions for eating paddle-
fish may have been spatially and temporally lim-
ited.

The absence of paddlefish from predator diets 
in 1994 may reflect the lower abundance of age-
0 paddlefish compared with 1995. Year-class es-
timates 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 ec-
ology 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 cat-
fish was greater than reported elsewhere. Paddle-
fish up to 167 mm BL (305 mm TL) were con-
sumed by walleyes and those up to 145 mm BL 
(264 mm TL) by saugers. By comparison, Mero 
et al. (1994) found that paddlefish smaller than 255 
mm TL were consumed by percids. In our study, 
the average length of paddlefish eaten by saugers 
was less than that of those eaten by walleyes, pos-
sibly because saugers were generally smaller than 
walleyes. Also, saugers were found to consume 
paddlefish in July, whereas walleyes were not 
found to consume paddlefish until August. A 410-
mm channel catfish ate a large paddlefish of 269 
mm TL (142 mm BL), whereas in hatchery ponds, 
channel catfish (>380 mm) ate paddlefish from 90 
to 150 mm TL (Tidwell and Mims 1990). Thus, 
age-0 paddlefish remain susceptible to predation 
for a longer time than previously indicated.

The ratio of age-0 paddlefish total length to 
predator total length was high compared with that 
reported for other prey, a result similar to that of 
Mero et al. (1994). In this study, paddlefish length 
was as much as 62% of walleye and 53% of sauger 
lengths. Lake Erie walleyes collected from May 
through November of 1959 and 1960 consumed 
prey up to 44% of their length (Parsons 1971), and 
in August 1981 prey ranged up to 40% of walleye 
length (Knight et al. 1984). In laboratory experi-
ments, Campbell (1998) reported that small wall-
eyes (159–239 mm TL) consumed yellow perch 
up to about 50% of their length. The ability of 
walleyes to consume relatively large paddlefish 
may be explained by the length of the paddlefish’s 
rostrum, which represented up to 50% of the total 
length for age-0 fish (D. L. Scarnecchia, unpub-
lished data).

We found that large hatchery-reared paddlefish 
(mean BL = 189 mm) were not preyed upon by 
walleyes, saugers, or channel catfish; however, 
large northern pike (≥600 mm) did consume hatchery-reared paddlefish in White Earth Bay, but 
no wild fish in the reservoir were consumed. The 
difference may have been a result of the high den-
sity of stocking in a confined area. Also, hatchery-
reared 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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