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Biology and Life History of Paddlefish in North America: An Update

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Abstract.—Paddlefish *Polyodon spathula* are among the largest and longest lived of the freshwater fishes (e.g., more than 2.2 m long; 72 kg; 30 years old) and can be distinguished by the presence of a large mouth and a long, paddle-shaped snout. Smooth skin, small eyes, a large, tapering operculum flap, bluish-gray to black coloration dorsally, and a deeply forked heterocercal caudal fin all serve to distinguish paddlefish from other species. Paddlefish become sexually mature and spawn at a later age than many other freshwater fishes; males mature at an earlier age than females, but maturity varies by latitude. Male paddlefish typically spawn each year, but spawning periodicity may be variable for females. Paddlefish spawn over gravel or other hard surfaces and require specific photoperiod, water temperature, and water flow for successful spawning. Paddlefish are relatively fecund (9,000–26,000 eggs per kilogram of body weight); mature eggs range from about 2.0–4.0 mm in diameter, and time from egg fertilization to hatching is directly related to water temperature. Optimum temperature for hatching is about 18°C. Newly hatched larvae average about 8.5 mm total length (TL) and are passive drifters until they are about 17 mm long when the yolk sac has been absorbed and the larvae begin active feeding on zooplankton and insects. Paddlefish complete fin ray development at 145–160 mm TL; at this size, they are considered juveniles and are similar in appearance to adults. Few paddlefish reach the maximum known age; instead, the median age for most populations is 5–8 years and maximum age is 14–18 years. Paddlefish growth seems to be directly related to the length of the growing season and food abundance. Generally, paddlefish length increases rapidly for about the first 5 years. After 5 years, paddlefish weight increases rapidly and may double during this time. Paddlefish feed primarily on zooplankton but occasionally consume small insects, insect larvae, and small fish. Traditionally, paddlefish inhabited slow-moving waters of side channels and river-lakes. In regulated rivers, paddlefish congregate where current velocities are reduced. In large rivers, paddlefish tend to congregate in the deep waters,

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usually selecting areas with depths greater than 3 m and current velocities less than 0.5 m/s. Further, paddlefish are highly mobile and make extensive movements within a system. Most of this movement is random, but paddlefish also make extensive nonrandom movements in spring during upstream migration to spawning areas. Some aspects of paddlefish life history and biology make them highly vulnerable to human activities. High prices for paddlefish roe or flesh periodically have stimulated fishing pressure and overexploitation followed by rapid declines in some populations. Dredging, flow manipulation, and the construction of dams have altered much of the traditional paddlefish habitat. Increasing levels of recreational and commercial boat traffic may also contribute to the mortality of paddlefish. Understanding and considering paddlefish biology and ecology can contribute to scientifically sound stewardship of all paddlefish populations, whether management is for conserving healthy populations or restoring decimated stocks.

Introduction

Paddlefish *Polyodon spathula* (Polyodontidae) are large, mostly riverine fish that once were abundant in medium and large river systems throughout much of the central United States (Burr 1980). Concern for paddlefish populations has grown from a regional fisheries issue to one of national importance for the United States. The number of states listing paddlefish as endangered, threatened, or species of special concern increased from five states in 1983 to 11 states in 1994 (Graham 1997). As a result, the Mississippi Interstate Cooperative Resource Association (MICRA), composed of members from 28 states and the U.S. Fish and Wildlife Service, was formed, in part, because of concern for interjurisdictional paddlefish populations in the Mississippi River basin (Rasmussen 1991). Much research has been conducted on paddlefish life history, biology, ecology, and management since MICRA's formation more than a decade ago and since the original paddlefish book (see Dillard et al. 1986a) was published in 1986. Our intentions here are to update the understanding of paddlefish life history and biology. The current update is based in part on our synthetic review of the literature on paddlefish in North America[1] (see Jennings and Zigler 2000).

Taxonomy

Paddlefish are among the most ancient of the freshwater fishes with fossil records dating their first appearance in the early Cretaceous about 135 million years before the present (Grande et al. 2002). Paddlefish belong to the family Polyodontidae (Bond 1979), which contains only one other extant species, the Chinese paddlefish *Psephurus gladius*, native to the Yangtze-Kiang River (Pflieger 1975). Paddlefish are close relatives of the sturgeons (family, Acipenseridae) (Dingerkus and Howell 1976), and both families comprise the order Acipenseriformes of the class Actinoptergyii (ray-finned fishes; Helfman et al. 1997). However, recent genetic evidence suggests an early divergence (i.e., basal phylogeny) of Polyodontidae from Acipenseridae (Krieger et al. 2000, 2006). Grande and Bemis (1991) and Bemis et al. (1997) provide thorough overviews of the taxonomic relationships among paddlefishes specifically and the Acipenseriformes in general.

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[1] Portions of Jennings and Zigler 2000 are reprinted here with permission from *Reviews in Fish Biology and Fisheries*.

Morphology

The unusual morphology of the paddlefish was a source of amazement to early European explorers of the mid-1600s (McKinley 1984). The first scientific account of paddlefish morphology was published by Mauduit (1774, cited in McKinley 1984). Since then, many accounts of paddlefish morphology have been published in conjunction with inventories of local fish fauna (e.g., Eddy and Underhill 1974; Pflieger 1975; Becker 1983; Boschung et al. 1983).

Paddlefish can be distinguished by the presence of a very large mouth and a long, paddle-shaped snout that is about one-third the length of the body (Figure 1). The unusual morphology has resulted in considerable confusion of length measurements (i.e., total length, fork length, standard length, and body length) used in various studies. In this review, we used Pasch et al.'s (1980) conversion equation to convert adult paddlefish total length measurements to eye-to-fork length (EFL), which is defined as the distance from the anterior of the eye to the fork of the tail. Measuring EFL is advantageous because it eliminates errors associated with damaged or missing rostrums, frayed caudal fins (Ruelle and Hudson 1977), and negative allometric growth of rostrums (Hoover et al. 2000). Small eyes, numerous slender gill rakers, and a large, tapering operculum flap that extends to the pelvic fins also serve to distinguish this species from others. Paddlefish are dull-colored and often are mottled; color ranges from bluish-gray to black dorsally and grades to lighter on the sides and white ventrally. The skin is smooth except for a small patch of rhomboid scales on the deeply forked abbreviate heterocercal caudal fin (Lagler et al. 1977). Paddlefish are among the largest of the freshwater fishes, attaining a size of more than 2.2 m (USOFR 1992) and weighing up to 72 kg (Epifanio et al. 1996).

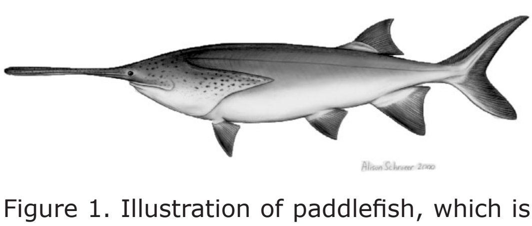

Figure 1. Illustration of paddlefish, which is native to the Mississippi River drainage of North America and can reach a maximum length (including rostrum) of 2.2 m and weight up to 72 kg.

Distribution and Legal Status

Paddlefish are known from large rivers and associated lakes throughout much of the Mississippi River drainage and adjacent gulf slope drainages in North America (Figure 2), from the Missouri and Yellowstone rivers in the northwest to the Ohio and Allegheny rivers of the Northeast, from the headwaters of the Mississippi River south to its mouth, from the San Jacinto River in the southwest to the Tombigbee and Alabama rivers of the Southeast. Paddlefish were reported in the Great Lakes around the turn of the century, but these fish were thought to be strays that entered through canals (Becker 1983); they were never common in Canada (Reid et al. 2007). Paddlefish still occur over much of their historic range, although populations in four states along the northeastern periphery of that range were extirpated by the mid-1980s (Gengerke 1986).

Paddlefish were common components of the fish assemblage of the Mississippi River until the late 1800s (Carlander 1954). The importance of paddlefish as the major domestic source of eggs for caviar increased during the late 1800s with the depletion of the lake sturgeon *Acipenser fulvescens* stocks (Carlson and Bonislawsky 1981). In the ensuing years, commercial paddlefish landings from the Mississippi River declined from overharvest; moreover, the declines in paddlefish abundance were greatest in the northern reaches of the river (Carland-

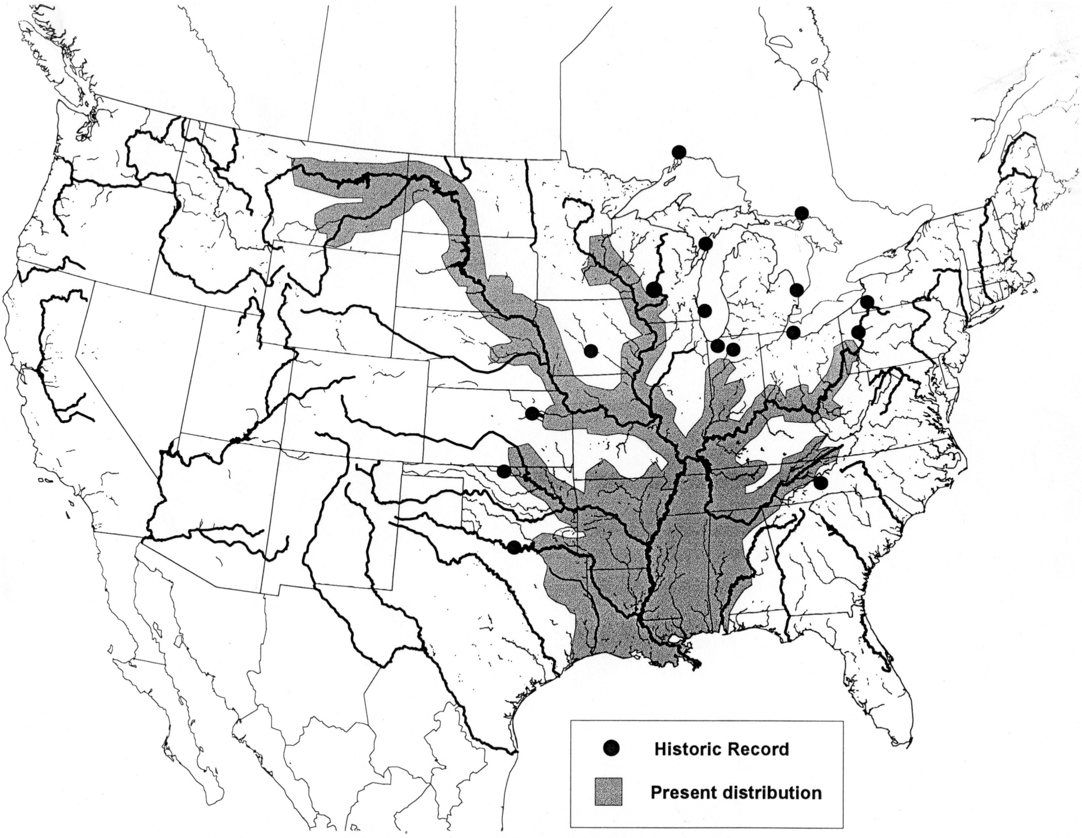

Figure 2. Distribution of paddlefish in North America (adapted from Carlson and Bonislawsky 1981). The shaded portion shows the current distribution. Markers (•) indicate locations of early, historic records of capture without recent confirmation and represent loss in species range.

er 1954). During the 1970s and 1980s, some localized paddlefish populations supported commercial or recreational fisheries, but most were marginal and existed well below historic levels (Carlson and Bonislawsky 1981; Runstrom 1996). Since then, the general status of paddlefish stocks range-wide has improved, and some states have changed the legal status and harvests regulation accordingly (see Bettoli et al. 2009, this volume).

In 1989, the U.S. Fish and Wildlife Service (USFWS) was petitioned to list paddlefish as a federally threatened species under the Endangered Species Act. The petition was not granted because most fishery biologists in the fish's historic range thought that although several population segments probably were not self-sustaining, the remaining populations in most states with extant populations were at least stable at low levels (USOFR 1992). In fact, empirical data on paddlefish population size, age structure, growth, or harvest rates across the present 22-state range were almost completely absent (USOFR 1992). Consequently, paddlefish were reclassified in 1992 as a species of special concern (formerly "category 2") under the Endangered Species Act, which indicated that the data needed to assess the status of the species were lacking (USOFR 1992). Currently, paddlefish do not receive any federal consideration because, as of 1996, the USFWS discontinued the use of the list of species of special concern.

Concern for paddlefish populations prompted the USFWS to recommend that paddlefish be protected through the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES). The addition of paddlefish to Appendix II of CITES, which was approved in March 1992, provides a mechanism to curtail illegal trade in paddlefish and paddlefish products (USOFR 1992) and supports a variety of conservation plans (see Epifanio et al. 1996). This listing has resulted in improved monitoring of the international trade of paddlefish (Raymakers 2002).

Life History and Ecology

Paddlefish have been studied widely since the species was formally brought to the attention of the scientific community by Mauduit (1774, cited in McKinley 1984). One indexed bibliography of paddlefish literature (Graham 1986a) listed more than 550 titles (mostly unpublished agency reports) that pertain to limited aspects of the biology and management of the species. Prior to the turn of the century, much of the literature on paddlefish pertained to systematics and phylogeny (McKinley 1984). After the turn of the century, research focused on understanding the life history of the species (e.g., Stockard 1907; Wagner 1908; Allen 1911; Hussakof 1911; Alexander 1915; Adams 1942). Despite this attention, paddlefish remained a scientific enigma until about 45 years ago, when detailed life history studies were published (e.g., Houser and Bross 1959; Meyer 1960; Purkett 1961, 1963a, 1963b). Although research aimed at resolving questions about paddlefish life history and status has been ongoing (see Dillard et al. 1986a), significant information needs continue to the present (National Paddlefish and Sturgeon Steering Committee 1993; Graham 1997; Conover and Grady 2000; Jennings and Zigler 2000; Grady et al. 2005).

Reproduction

Paddlefish require a longer period of time to become sexually mature and spawn than many other freshwater fishes, with males maturing at an earlier age than females (Adams 1942; Larimore 1950). Moreover, age and size at maturity varies greatly with latitude (Carlson and Bonislawsky 1981; Reed et al. 1992). In the southern and central portion of its range, male paddlefish mature as early as age 4 and all males are mature by age 9; females mature as early as age 6 and all females are mature by age 12 (Adams 1942; Gengerke 1978; Carlson and Bonislawsky 1981; Reed 1989; Timmons and Hughbanks 2000; Scholten and Bettoli 2005). The slowest maturing populations have been reported from Montana where the average age at maturity is 14 years (Carlson and Bonislawsky 1981). In Missouri, mature males usually weigh at least 6.8 kg, whereas females weigh at least 13.6 kg (Russell 1986). Purkett (1961) gave the average weight at maturity for paddlefish populations in the central United States as 12.7 kg for males and 18.7 kg for females.

Male paddlefish are able to spawn each year, but several studies suggest that spawning periodicity may be variable for female paddlefish. In some central or southern systems, some or all females may spawn annually (Lein and DeVries 1998; Scholten and Bettoli 2005). In other systems, females may require 2–5 years to develop mature ova. Analyses of annuli spacing on paddlefish dentary bones led Meyer (1960) to conclude that female paddlefish in the Mississippi River spawn every 4–7 years. Female paddlefish in Missouri may make spawning runs only every 2–3 years (Russell 1986). Other studies have shown that adult females sampled during and after the spring spawning season frequently contain ovaries with immature eggs (e.g., Alexander and Peterson 1982; Rosen et al. 1982; S. J. Zigler and C. A. Jennings, unpublished data). Russell (1986) suggested that the long interval between spawnings may result from the need to acquire and mobilize the energy required to produce the large egg masses of female paddlefish, which can comprise up to 25% of the body weight (Purkett 1961).

Attempts to document paddlefish reproduction and collect eggs and larvae date back to the early 1900s (Stockard 1907; Allen 1911; Alexander 1915). Observations of ripe adults were commonplace, but locations of spawning areas were unknown (Stockard 1907; Allen 1911; Alexander 1915) and collection of larval paddlefish was rare (e.g., Barbour 1911; Danforth 1911; Thompson 1933). The first authentic account of the timing and location of paddlefish reproduction was given by Purkett (1961), who observed paddlefish spawning over gravel bars in the Osage River, Missouri and then collected eggs and larvae. Since that time, paddlefish larvae have been collected from below dams on the Missouri River (Ruelle and Hudson 1977) and below dams on the Cumberland and Tennessee River systems (Pasch et al. 1980; Wallus 1986). Eggs or larvae also have been collected in unchannelized, unimpounded reaches of several systems that contain suspected spawning areas of gravel or coarser substrates (Unkenholz 1982; Hesse and Mestl 1993; Zigler et al. 2004; Firehammer et al. 2006). Nonetheless, specific spawning areas for most paddlefish populations remain unknown.

Photoperiod, water temperature, and water flow are the most important factors controlling paddlefish spawning, and the timing of their occurrence has to be precise for successful reproduction to occur (Russell 1986). Photoperiod and water temperature regulate the development and maturation of gametes, but an increase in water flow is the stimulus necessary to trigger spawning; if any of these three conditions are not satisfied, the females resorb their eggs (Russell 1986). Spawning has been documented over gravel (Purkett 1961) and is suspected to occur over other hard surfaces such as rock in areas with enough current to keep the eggs free from silt (Alexander 1915; Ruelle and Hudson 1977; Pasch et al. 1980; Wallus 1986).

Generally, spawning is preceded by an upstream migration to the vicinity of the spawning areas where the fish may congregate in deep waters (Purkett 1961; Pasch et al. 1980; Russell 1986). Migrating paddlefish often exhibit fidelity to particular tributary rivers and spawning sites (Lein and DeVries 1998; Stancill et al. 2002; Firehammer and Scarnecchia 2007), but water flows may override site fidelity (Paukert and Fisher 2001; Firehammer and Scarnecchia 2007). Spawning populations may aggregate in only a few areas in some systems with limited spawning habitat or where migrations are impeded by dams (Russell 1986; Stancill et al. 2002), but populations may be dispersed among many spawning sites in other systems with numerous areas of suitable spawning habitat (Zigler et al. 2003; Firehammer and Scarnecchia 2006b). Upstream spawning migration begins during spring as water temperature approaches 10°C, and upstream movement increases as the water warms (Purkett 1961; Russell 1986; Lein and DeVries 1998), with males migrating to spawning areas before females (Stancill et al. 2002). Paddlefish movements can be directionally synchronized (i.e., upstream and downstream) with flow and associated suspended sediment loads (Firehammer and Scarnecchia 2007). Flow may influence directional movement more than water temperature once sufficient spring temperatures are reached (Firehammer and Scarnecchia 2006b), and migrations may be aborted or not attempted during years without substantial flows during spring

(Paukert and Fisher 2001). Large increases in river flow trigger paddlefish to move into the nearby spawning areas and spawn (Purkett 1961; Gengerke 1978; Pasch et al. 1980; Russell 1986). Changes in the flow rate can cause cessation and resumption of spawning activity until the fish are spent (Purkett 1961). Spawning typically occurs from late March in the southern rivers to late June in northern rivers (Purkett 1961; Pasch et al. 1980; Russell 1986; Lein and DeVries 1998; Firehammer et al. 2006). Optimum spawning temperatures have not been reported in the literature, but spawning occurs at water temperatures ranging from about 10°C to 20°C (Purkett 1961; Pasch et al. 1980; Russell 1986; Lein and DeVries 1998; Firehammer et al. 2006).

Early Life Stages

Eggs.—Paddlefish produce large numbers of eggs, but variation exists in the number of eggs produced by similarly sized individuals (Russell 1986; Reed et al. 1992; Scholten and Bettoli 2005). For example, Reed et al. (1992) indicated that paddlefish from Lake Pontchartrain, Louisiana produced fewer eggs per kg of body mass (mean = 9,484 eggs/kg; SE = 696) than paddlefish from Iowa (mean = 19,900 eggs/kg) and Missouri (mean = 26,000 eggs/kg). However, total and weight-specific fecundity of paddlefish from the Alabama River drainage were similar to those of paddlefish from more northern latitudes (Lein and DeVries 1998). These differences between Reed et al.'s (1992) observations and Lein and DeVries'(1998) suggest variability among local populations rather than latitudinal variations in total and weight-specific fecundity. Mean weight-specific fecundity for paddlefish ranges from about 9,000 to 26,000 eggs per kilogram of body weight (Gengerke 1978; Reed et al. 1992; Lein and DeVries 1998; Scholten and Bettoli 2005).

Immature paddlefish eggs are white and generally are attached to large fat deposits (Larimore 1950; Russell 1986). Developing ovaries become granular and enlarged and change from white to gray; developed ovaries usually have very little attached fat and are grayish-black (Larimore 1950; Russell 1986). Unfertilized eggs are nonadhesive and demersal but become adhesive and stick singularly at first contact after fertilization (Purkett 1961; Yeager and Wallus 1982). Anecdotal observations from hatchery operations indicate that unfertilized eggs may become adhesive upon contact with water (B. Reed, Louisiana Department of Wildlife and Fisheries, personal communication). Mature eggs range from about 2.0 to 4.0 mm in diameter (Larimore 1950; Purkett 1961; Rosen 1976; Yeager and Wallus 1982). Time from egg fertilization to hatching is directly related to water temperature. At warmer temperatures (18–21°C), hatching occurs 6–7 d after fertilization (Purkett 1961; Yeager and Wallus 1982), whereas 12–14 d are required at cooler temperatures (11–14°C); optimum temperature for hatching success is about 18°C (Graham et al. 1986). Eggs attached to substrates hatch sooner and survive better than unattached eggs (Purkett 1961). A precise account of gametogenesis in paddlefish was given by Larimore (1950), and descriptions of the embryonic developmental stages were given by Ballard and Needham (1964) and by Yeager and Wallus (1982).

Larvae.—Newly hatched larvae average about 8.5 mm total length (TL; Purkett 1961; Pasch et al. 1980; Yeager and Wallus 1982). Almost immediately after hatching, larval paddlefish begin erratic swimming toward the surface, only resting occasionally (Purkett 1961; Yeager and Wallus 1982). The immediate upward swimming motion is thought to position the larvae so they can be swept away from the temporarily inundated spawning areas before the water recedes (Purkett 1961). Although capable of the erratic swimming to move into the water column from the substrate, field samples of yolk sac larvae suggest that they are passive drifters because their fins and musculature are not sufficiently developed to allow the larvae to select water column position or avoid downstream displacement. Further, spatial and temporal changes in vertical water column position between yolk and post-yolk-sac larvae suggest that ontogenetic habitat shifts occur between these two life stages. Lateral distribution of paddlefish larvae is uniform across river channels for all sizes (Wallus 1986), but post-yolk-sac larvae tend to concentrate on the bottom of the river channel during the day (Allen 1911; Ruelle and Hudson 1977) and move near the surface at night (Allen 1911; Wallus 1986). Smaller larvae (i.e., <25 mm TL) held in aquaria mostly stay near the surface, whereas larger larvae remain deeper (Yeager and Wallus 1982).

At about 17 mm TL, larval paddlefish absorb the yolk sac and begin active feeding on zooplankton and insects (Ruelle and Hudson 1977; Yeager and Wallus 1982). Larval paddlefish actively select larger zooplankters (Ruelle and Hudson 1977; Rosen and Hales 1981; Michaletz et al. 1982). Active feeding on individual prey organisms continues until the fish are 120–250 mm TL and the gill rakers are sufficiently developed to be used as a filter (Rosen and Hales 1981; Michaletz et al. 1982). Diet items of larval paddlefish include zooplankton such as *Daphnia* spp., *Cyclops* spp., and *Diaptomus* spp., as well as all stages of aquatic insects such as *Hexagenia* spp. (Ruelle and Hudson 1977; Rosen and Hales 1981). Larval paddlefish reared under laboratory conditions readily accepted natural prey items (live and frozen) as well as commercially prepared powdered diets; some instances of cannibalism have been noted in the laboratory (Yeager and Wallus 1982). However, growth and survival of larvae fed live prey items was higher than larvae fed nonliving diets (Webster et al. 1991).

Juvenile.—Sexually immature paddlefish more than 160 mm TL are considered juveniles (complete development of fin rays at 145–160 mm TL signals entry into the juvenile life stage [Yeager and Wallus 1982, 1990]). Juveniles are similar in appearance to adults, although in smaller individuals (about 200–600 mm TL), the length of the rostrum is greater than one-third the total length (Yeager and Wallus 1990). The rostrum, head and opercular flaps of juvenile paddlefish contain tens of thousands of ampullae of Lorenzini, which function to passively detect electric fields generated by individual or concentrations of plankton prey (Wilkens et al. 1997; Russell et al. 1999; Wilkens et al. 2001). Juvenile paddlefish rely primarily on this electrosensory system for active particulate feeding rather than visual, chemical, or hydraulic sensory cues (Wilkens et al. 2001). When their gill rakers are developed sufficiently, they begin ram suspension filtering for prey, which occurs between 120 and 250 mm TL (Rosen and Hales 1981). Juvenile paddlefish can switch between active particulate feeding and filter feeding depending on prey size and availability (Michaletz et al. 1982). If large zooplankton are abundant, juvenile paddlefish may delay filter feeding until they reach EFL 300 mm (Kozfkay and Scarnecchia 2002).

Little information exists on the spatial and temporal distribution of juvenile paddlefish. Some studies have suggested that small juvenile paddlefish form large schools and remain suspended near the bottom of main channel areas of rivers (Ruelle and Hudson 1977) or large reservoirs (Hevel 1983). However, surface trawling and visual observations of age-0 and age-1 paddlefish indicate use of surficial waters in lentic portions of some reservoirs during late summer to early fall (Fredericks and Scarnecchia 1997; Kozfkay and Scarnecchia 2002). Generally, habitat choice and movement patterns of larger juvenile paddlefish appear similar to that of adults (Pitman and Parks 1994; Hoxmeier and DeVries 1997; Roush et al. 2003).

Adults

Age and growth.—Paddlefish age has been estimated with varying degrees of success by counting the number of annuli present in cleared sections of hard body parts such as fin rays, otoliths, and dentary bones (Adams 1942; Meyer 1960). Fin rays are inadequate for determining the age of paddlefish because adjacent fin rays do not always have the same number of annuli (Meyer 1960). Otoliths provide precise ages, but crowding of the annuli past the six or seventh year restricts the use of this method to young fish (Adams 1942; Meyer 1960). The dentary bone is the most common structure for aging paddlefish because of reduced false annuli compared to otoliths and comparatively large interannular distances for older fish (Adams 1942; Meyer 1960). However, most studies of paddlefish age and growth have not validated paddlefish ages, and the accuracy of ages determined from dentary bones may be poor (Alexander et al. 1985). In the few instances where age validation has been attempted, there was relatively high precision between estimated and observed ages, although the ease with which dentary sections can be read and interpreted varies locally (Scarnecchia et al. 2006). High variability in dentary bone morphology among paddlefish was thought to produce unreliable back-calculated lengths at age (Meyer 1960). However, useful back-calculated lengths at age have been reported in some studies (Reed et al. 1992; Scarnecchia et al. 1996a; Scarnecchia et al. 2006), and methods that use sections of the mesial arm of the dentary bone may be especially reliable (Scarnecchia et al. 2006).

Paddlefish can live for 30 or more years (Purkett 1963b; Scarnecchia et al. 1996a) and grow to at least 2 m EFL (Nichols 1916). Few paddlefish reach such sizes as most populations have a median age ranging from 5 to 8 years and a maximum age ranging from about 14–18 years (Adams 1942; Meyer 1960; Gengerke 1978; Reed 1989; Runstrom et al. 2001; Scholten and Bettoli 2005). Generally, maximum age among paddlefish populations increases with latitude. For example, maximum ages reported for paddlefish population in southern states (e.g., Louisiana, Oklahoma, and Tennessee) rarely exceeded 16 years (but see Timmons and Hughbanks 2000), whereas reported maximum ages for paddlefish populations in northern states (e.g., North Dakota, South Dakota, and Montana) have been at least 20 years (see page 639 in Paukert and Fisher 2001).

Growth of paddlefish seems to be directly related to the length of the growing season and food availability. For example, at the end of the first-year growing season, the mean length of age-1 paddlefish from Fort Gibson Reservoir in Oklahoma was 502 mm EFL (Houser and Bross 1959), and age-1 paddlefish from three different populations in Louisiana ranged from 411 to 455 mm EFL (Reed et al. 1992). By contrast, the mean length of age-1 paddlefish from Lewis and Clark Reservoir (Missouri River) on the Nebraska–South Dakota border was 192 mm EFL (Ruelle and Hudson 1977). Rapid increase in length occurs for about the first 5 years (Adams 1942; Russell 1986) and then slows. However, rapid weight gain occurs after the first 5 years, and paddlefish may double their weight during this time (Russell 1986). In instances where introduced planktivores (e.g., bighead carp *Hypophthalmichthys nobilis* in the upper Mississippi River) compete with paddlefish, growth of age-0 paddlefish can be much reduced; this potential was demonstrated in an experimental mesocosm (Schrank et al. 2003), but field observations suggested minimal overlap between adult paddlefish and bighead carp (Sampson et al. 2008). Females usually grow faster in length and weigh more at sexually maturity than males (Rosen et al. 1982; Hageman et al. 1986; Russell 1986). Growth of paddlefish in reservoirs and river-lakes (e.g., Lake Pepin in the upper Mississippi River) is faster than in riverine habitats and may reflect increased food abundance and availability (Stockard 1907; Rosen 1976; Russell 1986; Paukert and Fisher 2001) and reduced metabolic cost of a reduced current or current-free environment.

Food habits and feeding.—There has been much speculation about how the paddlefish rostrum is used for feeding. Some early investigators hypothesized that paddlefish used the rostrum to dig food items from the substate (Forbes 1878; Jordan and Evermann 1896) or to dislodge them from vegetation (Beach 1902; Norris 1923). These hypotheses were revised when paddlefish were confirmed to be primarily planktivores (Stockard 1907; Wagner 1908). Moreover, paddlefish with missing or severely damaged rostrums had conditions that were similar to those of paddlefish with healthy, intact rostrums (Stockard 1907). The discovery of electrical receptors in paddlefish rostrum led to speculation that it was used detect zooplankton (Grande and Bemis 1991). Wilkens et al. (1997) demonstrated that electrosensory receptors in paddlefish rostrum can detect weak electrical fields and then confirmed (Wilkens et al. 2001) that paddlefish can use their rostrum to selectively detect zooplankton from among other similarly sized inert particles.

Paddlefish feed primarily on zooplankton (Meyer 1960; Ruelle and Hudson 1977; Rosen and Hales 1981; Michaletz et al. 1982; Blackwell et al. 1995) and occasionally consume small insects, insect larvae, and small fish (Wagner 1908; Meyer 1960; Ruelle and Hudson 1977; Rosen and Hales 1981). Adult paddlefish are ram-suspension filter feeders (Sanderson et al. 1994) that usually consume zooplankton larger than 100 μ wide regardless of fish size (Rosen and Hales 1981). Although paddlefish are capable of moderate changes in gill raker spacing (Rosen and Hales 1981), smaller, more mobile zooplankton such as copepods are ingested less frequently than larger taxa because they are detected less readily by paddlefish and often can elude capture (Rosen and Hales 1981; Michaletz et al. 1982). Insects and insect larvae usually are consumed during periods of peak abundance such as the hatching of mayfly *Hexagenia* spp. nymphs (Wagner 1908; Meyer 1960).

Habitats and movements.—Slow-moving waters of side channels and river-lakes were the traditional habitat of paddlefish (Stockard 1907). Much of these traditional habitats have been lost to inundation as most of the major rivers have been channelized and dammed (Russell 1986). In regulated rivers, paddlefish congregate in small areas below structures such as sandbars, protected bays, dikes, bridge supports, and eddies in the tailwaters below dams where current velocities are below 0.3 m/s (Rosen 1976; Southall and Hubert 1984; Moen et al. 1992; Zigler et al. 2003). When these structures are not available for refuge from high current velocities, paddlefish select the nearshore habitats with low current velocities (Rosen 1976). In reservoirs, paddlefish tend to congregate in the deep waters (Zigler et al. 1999, 2003; Paukert and Fisher 2001; Stancill et al. 2002), usually selecting areas with depths greater than 3 m and current velocities less than 0.5 m/s (Rosen et al. 1982; Zigler et al. 2003).

Paddlefish use a wide variety of habitats, but habitat use varies seasonally and annually. In highly regulated rivers such as the upper Mississippi and Missouri rivers, paddlefish strongly selected the tailwaters of dams during spring and summer, although this habitat comprised less than 10% of the available habitat (Southall and Hubert 1984; Moen et al. 1992; Stancill et al. 2002). In part, tailwater use may be related to impeded upstream movement during spring spawning season. During winter, paddlefish congregate at the downstream portions of reservoirs (Paukert and Fisher 2001; Stancill et al. 2002) or deeper areas of backwaters in large rivers (Zigler et al. 2003). In the lower Alabama River, paddlefish inhabit backwater areas during summer and fall but shift to main channel habitats during winter and spring (Hoxmeier and DeVries 1997). Habitat use by paddlefish in the upper Mississippi River also varies among years, presumably in response to differences in river discharges and temperatures (Southall and Hubert 1984; Moen et al. 1992; Zigler et al. 2003; Firehammer and Scarnecchia 2006, 2007). At high discharges, paddlefish often used backwater sloughs, whereas at low discharges, paddlefish used main channel border habitats (Rehwinkel 1978; Southall and Hubert 1984; Moen et al. 1992).

Paddlefish are highly mobile and make extensive movements within a system (Wagner 1908; Rosen et al. 1982; Southall and Hubert 1984; Russell 1986; Moen 1989; Zigler et al. 1999, 2003; Firehammer and Scarnecchia 2006, 2007). Within a year of being of being tagged, paddlefish in an unchannelized section of the Missouri River traveled upstream an average net distance of 20 km to the tailwaters of a dam; some fish traveled more than 50 km to reach the dam (Rosen et al. 1982). However, downstream movement during the same time period was considerably larger. The average net downstream distance traveled was 147 km; some fish had traveled more than 200 km downstream. After the termination of the study, one tagged fish was recaptured nearly 2,000 km downstream. In another example, a single paddlefish moved 1,900 river kilometers from South Dakota to Kentucky and passed over five dams en route (Stancill et al. 2002). Rosen et al. (1982) hypothesized that paddlefish may have evolved patterns of long-distance migrations because the lentic waters that are best for growth may be widely separated from suitable spawning areas.

The most extensive nonrandom movements occur in the spring as paddlefish move upstream towards spawning areas (Purkett 1961; Rehwinkel 1978; Southall and Hubert 1984; Lein and DeVries 1998; Paukert and Fisher 2001; Stancill et al. 2002; Firehammer and Scarnecchia 2006), with the largest movements often occurring at night (Zigler et al. 1999). Spawning migrations of more than 333 km upstream were common in the Osage River, Missouri (Russell 1986). On rare occasions, paddlefish make their spawning migration in large aggregations (Stockard 1907; Meyer 1960). During the spring of 1959, Meyer (1960) observed an aggregation of paddlefish in Navigation Pool 19 of the upper Mississippi River near Burlington, Iowa. All ages and sizes of fish were represented in this aggregation, and the sex ratio was even. Meyer (1960) suggested that this was a feeding aggregation in response to a concentration of food organisms (e.g., spring hatch of *Hexagenia* spp.) and not to concentration of fish at a spawning area as evidenced by the absence of sexually ripe individuals.

Dams are substantial barriers to upstream movements of paddlefish (Southall 1982; Russell 1986; Moen et al. 1992). However, paddlefish move upstream over the low-head navigation dams in the upper Mississippi River under certain conditions. Specifically, upstream movement over some low-head dams is possible during periods of high river discharge (Southall and Hubert 1984; Zigler et al. 2003) when low dam head results in reduced velocities in the gate bays (Zigler et al. 2004). However, such conditions rarely occur at many upper Mississippi River dams (Wlosinski and Hill 1995). Generally, upstream movement pass dams happens more frequently during the summer than in any other season, gradually diminishes through summer and fall, and does not occur during winter (Zigler et al. 2003). However, Moen et al. (1992) did not observe upstream interpool movement of radio-tagged paddlefish inhabiting tailwaters in the upper Mississippi River, even when dam gates were completely open. Paddlefish can move downstream through partially open roller gates without experiencing major injury (Gengerke 1978; Southall and Hubert 1984; Moen et al. 1992; Zigler et al. 2003). In other rivers, paddlefish may be incapable of moving upstream through some dams because of high head or dam design (Russell 1986; Zigler et al. 2003).

Although the pools formed by dams can isolate and confine paddlefish (Russell 1986), extensive within-pool movements still occur (Rosen et al. 1982; Southall 1982; Moen 1989; Zigler et al. 1999, 2003; Paukert and Fisher 2001; Stancill et al. 2002). In some circumstances, paddlefish move farther (0.78 km/h) at night than during the day (0.35 km/h); maximum movements (~4 km/h) occur at night (Paukert and Fisher 2000; Roush et al. 2003). Some paddlefish will swim back and forth between the locks and dams on both ends of the pool (Moen 1989). Others seem to establish home ranges or have preferred areas and usually remain in the same general vicinity for many consecutive days (Southall 1982; Stancill et al. 2002; Zigler et al. 2003; Firehammer and Scarnecchia 2007). Some fish make occasional, directed movements from the preferred area but quickly return; during these excursions, paddlefish swam at speeds ranging from 1.3 to 5.2 km/h (Southall 1982; Moen 1989). Generally, within-pool movements seem to be influenced more by season (Stancill et al. 2002) and discharge (Firehammer and Scarnecchia 2007) than by river temperature (Firehammer and Scarnecchia 2006). However, temperature may influence movement under certain conditions (Roush et al. 2003).

Mechanisms Leading to Declines

Overharvest

Both sport and commercial harvest of paddlefish can influence populations throughout the species range and are discussed in detail in Hansen and Paukert (2009, this volume), Quinn (2009, this volume), and Scholten (2009, this volume). Paddlefish were abundant in the commercial fishing harvest in the large rivers of the Mississippi River drainage prior to 1900. The commercial harvest of paddlefish peaked at about 1.1 million kilograms in 1899 (Coker 1929). Initially, paddlefish were sought primarily for their flesh. However, demand for paddlefish roe for domestic caviar increased dramatically after lake sturgeon stocks were depleted (Hussakof 1911; Carlson and Bonislawsky 1981). By the 1920s, several paddlefish stocks were depleted (Stockard 1907; Alexander 1914; Coker 1929; Pasch and Alexander 1986), and biologists became concerned that some paddlefish populations could be extirpated (Alexander 1914). Following the initial peak, commercial harvest continued to decline because of reduced and erratic demand for roe and depleted populations in lakes and reservoirs (Pasch and Alexander 1986). Population declines related to habitat alterations caused by construction of dams (Carlson and Bonislawsky 1981) also may have contributed to the decline in the commercial catch.

High prices for paddlefish roe or flesh periodically have stimulated fishing pressure and overexploitation followed by rapid declines in some populations. For example, paddlefish harvest in Guntersville, Wheeler, and Pickwick reservoirs in Alabama declined from 323 metric tons in 1942 to 48 metric tons in 1952 despite regulations enacted to permit liberalized capture methods in 1946 (Pasch and Alexander 1986). In that case, high demand was caused by reduced imports of sturgeon eggs into the United States. Since the 1960s, high prices for paddlefish roe led to increased legal and illegal commercial harvest in several rivers and reservoirs in the south and central United States. The increased harvest resulted in overexploited populations as evidenced by drastic reductions in paddlefish catch and mean weight, young age structure, and high mortality rates of populations (e.g., Pasch and Alexander 1986; Hoffnagle and Timmons 1989; Hoxmeier and DeVries 1997).

Paddlefish are particularly susceptible to overharvest because of their behavior and life history (Boreman 1997). Paddlefish are easily captured with several fishing gears, including large-mesh gill nets and trammel nets, seines, and snag lines (Larimore 1950; Alexander and Peterson 1982; Graham et al. 1986; Pasch and Alexander 1986; Betolli and Scholten 2006; Scholten and Bettoli 2007). Commercial and sport fishers can take advantage of the predictable spring spawning runs of paddlefish, especially in systems where paddlefish are concentrated in tailwaters below dams (Pasch and Alexander 1986).

Although there is no evidence of a population being extirpated solely because of illegal harvest in states that protect paddlefish, the increasing value of paddlefish roe for caviar, which can command prices in excess of up to US$1,100/ kg (USOFR 1992; Timmons and Hughbanks 2000; Pikitch et al. 2005; Scholten and Bettoli 2005), provides substantial incentive for illegal harvest (Pasch and Alexander 1986; Graham 1997). Moreover, paddlefish do not exhibit sexual dimorphism, and both males and females are sacrificed in the quest for roe. Bycatch mortality of males can be as high as 92% (Scholten and Bettoli 2007), often because gear such as gill nets are nonselective (Scholten and Bettoli 2007). As a result, spawners and nonspawners (i.e., immature males and females) are lost from the population. Overharvested populations may take decades to recover because paddlefish reach sexual maturity at a later age than most other freshwater fishes (Pasch and Alexander 1986) and may not spawn each year. Illegal harvest has been and continues to be a significant threat to paddlefish populations (Graham 1997; Pikitch et al. 2005) and has the potential to eliminate this species from much of its historic range. The illegal harvest of paddlefish for the domestic and international market led to the 1998 listing of the species under CITES, which resulted in better monitoring and control of the international trade in paddlefish (Raymakers 2002). Continued concern for the fate of paddlefish and subsequent research on the effects of commercial harvest has led to improved documentation of how stocks respond to fishing pressure (Timmons and Hughbanks 2000; Scholten and Bettoli 2005; Bettoli and Scholten 2006). These efforts sometimes result in legislative initiatives that provide paddlefish stocks a modicum of protection (e.g., Bettoli and Scholten 2006).

There are several sport fisheries for paddlefish throughout the species' range (Graham 1997; Hansen and Paukert 2009). These fisheries developed after the construction of dams on large rivers and usually are located in the tailwaters immediately below dams or other such areas where paddlefish congregate and become vulnerable to snagging (Carlson and Bonislawsky 1981). Direct angling mortality and indirect mortality (e.g., related to handling stress, hooking wounds, and secondary bacterial infections) related to catch-and-release fishing (Scarnecchia et al. 1996b; Scarnecchia and Stewart 1997) contribute to the negative effects of legal harvests. Additional information about how harvesting may affect paddlefish populations are given in Sections 2 and 3 of this volume.

Waterway Development

Beginning around 1930, nearly all of the large rivers within the native range of paddlefish were modified for hydropower, navigation, and flood control. Dredging, flow manipulation, and the construction of dams on the large river systems in the United States altered much of the traditional paddlefish habitat (Sparrowe 1986). Paddlefish populations may have benefited from some aspects of the modifications (e.g., reservoirs increase food abundance); however, the resulting changes in river hydrology and morphometry significantly reduced paddlefish habitat (Sparrowe 1986).

Increasing levels of recreational and commercial boat traffic on highly used rivers may contribute to mortality of paddlefish. Wounds from boat collisions and motor propellers are common in some areas (Rosen and Hales 1980; Lyons 1993; Runstrom et al. 2001). Commercial navigation may increase the mortality of larval paddlefish as a result of propeller-associated shear stress (Killgore et al. 2001) and stranding related to vessel-induced drawdown (Adams et al. 1999).

Dams have had several negative effects on paddlefish recruitment. Construction of dams reduce spawning habitat through inundation and increased siltation (Sparrowe 1986; Unkenholz 1986). Regulation of river flows by dams during spring can disrupt paddlefish spawning by altering river temperatures and discharge necessary to trigger spawning (Unkenholz 1986; Hesse and Mestl 1993). Dams can impede normal upstream migration during spring spawning runs and reduce access to spawning areas (Sparrowe 1986; Unkenholz 1986; Zigler et al. 2003, 2004). Obstruction of paddlefish movement combined with habitat degradation can have severe consequences for paddlefish populations. For example, paddlefish are extirpated in the Wisconsin River above the dam at Prairie du Sac, Wisconsin because they cannot access spawning areas above the dam; however, they remain abundant in the tailwaters below the dam (Lyons 1993; Runstrom et al. 2001).

Concern for paddlefish populations has played a role in deauthorizing several proposed dam projects (Elser 1986; Sparrowe 1986). In some cases, operation of existing dams can be improved to reduce threats to paddlefish. For example, flow releases of the Fort Randall Dam on the Missouri River were modified to reduce daily fluctuations (peaking) to protect paddlefish and other spawning fish during spring (Elser 1986). Hesse and Mestl (1993) suggested that discharge of some dams on the Missouri River could be manipulated to better resemble the natural spring hydrograph and stimulate paddlefish spawning. However, the biological and political issues of flow modification are often complex (Petts et al. 1989).

Preservation of existing spawning areas is difficult because most remain unknown. Destruction of unidentified spawning areas is one of the most serious threats to remaining paddlefish populations (Dillard et al. 1986b). Other proactive management options include construction of fish passage facilities to allow movement of paddlefish through dams and improve access to spawning areas, construction or rehabilitation of spawning areas, and programs to improve water quality. The utility of passage facilities may be limited because construction costs are high, especially for high-head dams, and the efficacy of facility designs for movement of paddlefish remains unproven.

Pollution and Contaminants

Increased pollution and siltation are substantial problems in the large rivers that contain paddlefish (Sparks 1984; Turner and Rablais 1991; Holland-Bartels 1992; Schmulbach et al. 1992). These decreases in water quality are thought to adversely affect paddlefish populations, but the data to evaluate the effects currently are lacking. Increased sediment loads and sedimentation rates caused by reservoir aging and continued erosion that have occurred in large river systems can reduce survival of fish embryos (Muncy et al. 1979). Fish species such as paddlefish that require deposition of eggs onto clean, well oxygenated substrates such as gravel may be particularly vulnerable to increased sedimentation. Moreover, high turbidity can reduce feeding success and survival of larval fish (Muncy et al. 1979).

Contaminants and their affects on fish health have become an increasing concern for many states (USOFR 1992). High levels of dioxin, polychlorinated biphenols, chlordane, and heavy metals in paddlefish eggs and fillets have caused some state fish and game agencies to issue consumption advisories or consider closing certain river reaches to fishing (USOFR 1992). Gundersen and Pearson (1992) and Gundersen et al. (1998) documented high levels of polychlorinated biphenols (PCBs) and chlordane in paddlefish fillets and gonads from the Ohio River. Some of their estimates of PCBs (4.0 μg/g wet weight during 1992) and chlordane (0.3 ppm during 1998) in mature ovaries of paddlefish from the Ohio River greatly exceeded the U.S. Food and Drug Administration's (FDA) action limit of 2.0 μg/g wet weight. However, PCB levels in paddlefish from the Ohio River appear to be declining (Gundersen et al. 2000). Histological and blood plasma analyses of Ohio River paddlefish suggest that contaminant loads are resulting in reduced fish health, including immunosuppression, hepatic metabolic disorders, and altered neuroendicrine function (Gundersen et al. 2000). Gundersen and Pearson (1992) expressed concern for the reproductive success of paddlefish in the Ohio River because the levels of PCBs in paddlefish roe were higher than those reported to cause high egg mortality in other fishes (Monod 1985). However, Gundersen et al. (2000) were unable to experimentally substantiate such an effect. Dasgupta et al. (2004) documented increasing methlymercury concentrations in flesh with age of wild and cultured paddlefish in Kentucky waters. Concentrations in all Kentucky paddlefish were below the 1.0 ppm FDA action limit for seafood, but concentrations in older Cumberland Lake and Ohio River paddlefish ranged up to 0.5 ppm.

Summary

Paddlefish are among the most ancient and largest members of the freshwater fish fauna on North America. These long-lived, late maturing filter feeders inhabit medium to large rivers and associated habitats in the central United States; they also have specific spawning requirements and may not spawn annually. Paddlefish are prized for their roe, which is used to make caviar. Overfishing during the early 1900s decimated many paddlefish populations and may have contributed to the extinction of many local populations at the periphery of the species range. Habitat alteration such as dam construction, flow regulation, and siltation further contributed to the decline in many paddlefish populations. Today, some paddlefish populations remain imperiled and are afforded some legal protection; others are healthy and support commercial or recreational fisheries. Understanding and considering paddlefish biology and ecology can contribute to scientifically sound stewardship of all paddlefish populations, whether management is for healthy populations or restoring and enhancing decimated stocks.

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