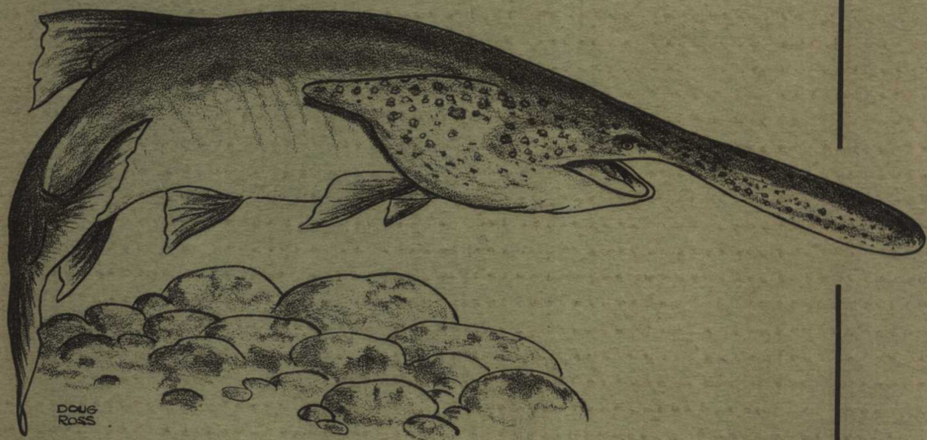
The Paddlefish:

Status, Management And Propagation



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The Paddlefish: Status, Management and Propagation

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Foreword and Acknowledgments

This symposium grew out of a need for more information about the paddlefish, a species which has recently sparked both public and professional interest. Paddlefish habitat, and in some instances paddlefish populations, have been greatly reduced by water resource development projects over several decades. The range of the species has also diminished. Now a new threat has arisen. Within the last few years the demand for paddlefish eggs for caviar has put a severe strain on various populations. In addition, the mystique of this large, freshwater fish with its unusual features and life habits has made it an object of curiosity.

Our basic objectives in this project were to review, synthesize, present and publish the currently available information on paddlefish, especially information on threats to its survival. We were aware when planning the symposium that much was known but not reported.* Therefore, we invited experts on paddlefish biology, resource managers knowledgeable about threats to habitat, and fisheries managers who had tried various strategies, to review and present what has been done and what needs to be done to better manage the paddlefish resources of the United States.

Paddlefish fisheries in the western, midwestern and southern United States have declined in some areas, but have increased and become more important in others. Papers in this proceedings emphasize that the paddlefish is a unique species with great potential value, and that management agencies must choose either to make the best of a limited resource or to just ignore an important segment of their aquatic resources. Specific management plans for this species, along with public awareness and support, are essential to protect critical habitat, regulate harvest and allow us to answer the question that was posed during the symposium ("Paddlefish — A Threatened Resource?") with a "no" rather than a "yes".

A project of this magnitude is obviously not the work of a few, although Tom, Kim and I nurtured it from 30 April 1982 to date. We especially thank the North Central Division of the American Fisheries Society for their approval, support, funding, patience and understanding in a project that took so long to complete. Thanks also to the speakers/authors who graciously gave of their time and talent. Their excellent presentations were the backbone of the symposium's success.

Dr. Larry A. Jahn (IL) and Mr. Larry R. Mitzner (IA), co-chairmen (1983-85) of the North Central Division's Publication Committee, and Mr. Gary Novinger, chairman (1985-86), performed an invaluable service as reviewers of all the manuscripts. Thanks also to the Missouri Department of Conservation, especially Charles A. Purkett, Jr., Assistant Director, for allowing Tom, Kim and me the time, materials, and support staff necessary to complete such a project.

A special thanks to the Fishery Resources Programs of the U.S. Fish and

*Considerable information included in this proceedings was supported by Federal Aid to Fish Restoration Funds, more commonly known as Dingell-Johnson projects.

Wildlife Service, Department of the Interior for partial funding for the printing and distribution of this proceedings.

Although I am listed as co-editor, Tom, Kim and Barb let me assume the lead role in making the tough decisions that always have to be made in publishing a proceedings such as this. From that perspective, I took tremendous liberties in adapting the presentations for this publication, and in doing so I accept full responsibility for any errors and inconsistencies.

Joe G. Dillard
March 1986

Guide for Readers

We generally followed the format conventions, manuscript components and symbols and abbreviations recommended by the managing editor of the American Fisheries Society. Deviations from these guidelines include the following:

References — Because many authors in this proceedings cite the same literature on paddlefish, we coded all of those references into a comprehensive bibliography that makes up the last chapter of this book. Therefore, a citation such as Purkett[410] or (Purkett[410]) refers to publication number 410 on page 145 in the bibliography. Non-paddlefish references such as Anderson 1975 or (Anderson 1975) are listed at the end of the appropriate paper under ***References*** and are not listed in the comprehensive bibliography.

Measurements — Most measurements are in English units except when experimental values were originally reported in metric units. In these instances, the English equivalent is provided in parentheses.

Fish lengths — Fish lengths are reported as total length (TL). For a further discussion of how paddlefish are measured see page 20.

Abbreviations — All units of measure are abbreviated except for units of time.

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Welcome to the Symposium

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Welcome to Missouri, to the Midwest Fish and Wildlife Conference and to the Paddlefish Symposium. I'm pleased to see so many of you here, and I'm sure you will benefit from the excellent program. Obviously you will hear the latest information from those people who are currently working in the field.

My involvement with paddlefish goes back to the mid-1950s, to the Osage River in central Missouri where there were large spawning runs of paddlefish. The catch of these fish was very large, especially in 1957, and a year later Paul Barnickol and John Funk asked me to study the fish and the fishery. At that time I knew only three people who were involved with paddlefish: Ted Shields, then working in South Dakota; Fred Meyer, at Iowa State University and Glenn Chambers, who was doing a special study at Central Missouri State University at Warrensburg, Missouri. Previously there had been a few studies, most of them in Illinois. The most notable of these were by L. A. Adams, Dave Thompson, Paul Barnickol and Weldon Larimore.

Hussakof[259] at the 1910 meeting of the American Fisheries Society presented a paper entitled, "The Spoonbill Fishery of the Lower Mississippi." Following the presentation, Dr. B. W. Evermann, who was in the audience, stated: "The queerest thing about the spoonbill is this, that no one has been able to locate definitely its spawning grounds and to find the young fry. Spoonbills five or six inches long are about as small as anyone has ever reported. I think the smallest I've ever seen were eight inches; but fish five to six inches long have been reported." When I saw this it spurred me on to fill this long-standing void, i.e., to find where the fish spawn and observe their eggs and larvae.

The third year of my study I did observe spawning activity, and on April 24, 1960, following a seven-foot drop in the water level, I found what many had been looking for — paddlefish eggs on rocks of gravel bars and hatching young fish in the adjacent water.

Since then a good many workers have made great progress in researching paddlefish biology, and I'll listen with interest to learn what has transpired. I urge you to attend the entire symposium and participate actively in what I know will be excellent discussions of a unique fish.

Biology and Life History of the Paddlefish — A Review

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Abstract

The paddlefish (*Polyodon spathula*) is a primitive species characterized by a predominantly cartilaginous skeleton, a rostrum or "paddle" nearly one-third of the body length, and a smooth skin. Paddlefish are found mostly in large river systems of the Mississippi River Basin and in some rivers entering the Gulf of Mexico. Populations have developed in some large, man-made impoundments, but paddlefish must have access to large, free-flowing rivers to spawn. Their spawning needs include a water temperature near 60 F, clean gravel substrate for egg attachment, and increased water flow to trigger spawning. Because of these exacting requirements, a precise timing of events is necessary to stimulate migration and ensure successful reproduction.

Paddlefish grow relatively rapidly, reach large sizes, and are long-lived. Individuals heavier than 50 lb. are common, and 90-100 lb. specimens are reported frequently. In older established populations, 15 to 20-year-old fish are common, and some may live 30 years. Most males reach sexual maturity at 7-9 years of age; females at 10-12 years.

Paddlefish frequently occur in large groups. They may be found in a variety of habitats, but spend much of their time feeding in quiet or slow-moving water. They feed primarily on zooplankton and aquatic insect larvae, which they filter from the water. Because they are filter feeders, few are caught by conventional fishing methods. In many areas, substantial numbers of paddlefish are caught by blind snagging with large treble hooks.

Paddlefish have adapted to some environmental alterations such as construction of reservoirs on major rivers. However, because of specialized spawning requirements, they have been adversely affected by those alterations that destroy, permanently flood, or prevent access to limited spawning sites. Impacts are not always immediately recognized because paddlefish are long-lived and highly mobile, and their presence is sometimes construed as an indication that the species has not been adversely affected. Wise and practical management requires an understanding of life history requirements of paddlefish and a knowledge of how environmental factors affect this species.

Paddlefish (*Polyodon spathula*) were once abundant in the large rivers in the Mississippi River drainage (Carlson and Bonislawsky[95]). However, within the last 100 years, the peripheral range of the species has shrunk (Gengerke[196]) and there have been significant declines in paddlefish populations in some of our major rivers (Unkenholz[528]). Habitat alteration and destruction, overexploitation, and pollution have detrimentally affected many paddlefish populations (Pflieger[398]; Carlson and Bonislawsky[95]). Water development projects and their operations (Sparrowe[480]) and potential overharvest for roe (Pasch and Alexander[390]) are major current threats to paddlefish populations.

Because of current problems, threats,

and interest in managing the species, research on paddlefish has increased in the last 25 years. Considerable information has been published on various aspects of the biology and life history of paddlefish, but there has been no general review of this material. Vasetskiy[534] reviewed literature on the family Polyodontidae but emphasized systematics, anatomy, and embryonic development. Carlson and Bonislawsky[95] briefly discussed the life history of paddlefish in their review of commercial and sport harvests of the species.

The purposes of this paper are to review the general biology and life history of paddlefish, to relate this information to the species' needs and requirements, and to provide a source of pertinent information that can be quickly located. Information was obtained from a review of the literature and from personal knowledge gained from 20 years of research on the species.

Description

The paddlefish, frequently called spoonbill or spoonbill cat, is one of the largest freshwater fishes, attaining lengths of more than 6 ft. and weights of more than 100 lb. It is the only species of the family Polyodontidae found in North America.

The paddlefish is a primitive species distinguished from other fishes by an elongated rostrum or "paddle" that is approximately one-third the length of the body. The rostrum is absent in newly hatched young, but it starts growing in 1-2 weeks and within 4-5 weeks it is largely developed.

The function of the rostrum is not precisely known. Fishermen generally believe it is used to dig in the bottom for food. Although this theory was supported by some early investigators (Forbes[176]; Imms[261]; Alexander[10]), most believe that the presence of a large number of sensory receptors (Kistler[287]; Nachtrieb[345]) and electro-receptors (Jorgenson[275]) suggests the rostrum is used to detect concentrations of food. The rostrum is not essential for survival. Paddlefish with portions or all of the rostrum missing are in comparable condition to fish of the same size with an intact rostrum. This suggests that the rostrum may not be functionally important in adult fish.

The skeleton of paddlefish is mostly cartilage. The only bony material is primarily in the jaws. The mouth is large, toothless except in young fish, and located under the head at the caudal end of the rostrum. The eyes are small and vision is reportedly poor (Hussakof[259]). Paddlefish have long, thin, close-set gill rakers, which are used to filter food. Like other primitive fishes, the paddlefish has a spiracle and a spiral valve. The body is smooth and appears scaleless, although small patches of minute scales have been found on the pectoral girdle (Wagner[535]), on the upper lobe of the caudal fin (Nikolskii[382]), and between the lateral line and dorsal fin (Collinge[108]). Coloration varies from bluish-gray to almost black above the lateral line, grading to white on the lower sides and belly.

Numerous anatomical studies of paddlefish have been conducted. Vasetskiy[534] reviewed and summarized these, and they are not included in this paper.

In the 1960s and early 1970s there was considerable interest in the immune response system of paddlefish. Although a primitive fish, the paddlefish was considered a key link in phylogenetic development because it possesses a blood serum complement system similar to mammals (Gewurz et al. 1966; Legler[303]), and because antibodies are vigorously formed in response to antigenic stimulation (Clawson[102]). Medical researchers believed that study of the paddlefish immune system might lead to a better understanding of antibody production, so that the tissue rejection phenomenon associated with human organ transplants could be understood and ultimately prevented. However, I am not aware of anyone currently using paddlefish in medical research.

Habitat

The paddlefish is an open water species. Under the natural, unaltered conditions that existed in the late 1800s and early 1900s, this species inhabited the large, free-flowing rivers of the Mississippi Valley. These river systems, with their braided channels, extensive backwater areas and oxbow lakes, provided ideal habitat and supported large paddlefish populations. Adults were usually found in the slower-moving waters of the rivers and were rarely found in small tributaries (Coker[105]). During spring rises, paddlefish moved quickly into bayous and river-lakes. Most of them remained there as long as connection with the river was maintained (Stockard[489]). Some fish stayed in these river-lakes, and moved back into the river during rises. Paddlefish in the bayous and river-lakes were reported to be in better condition than "river fish" (Stockard[489]) presumably because zooplankton, their primary food, was more abundant in the standing waters.

Most of our major rivers have been channelized or dammed in the last 100 years. These alterations have increased water currents, altered natural flow and temperature regimes, and destroyed spawning areas, backwaters, and other preferred habitat. Paddlefish are still present — sometimes in substantial numbers — in some of the altered but still free-flowing rivers, but in general the habitat throughout the range of the paddlefish is now less favorable.

In large, altered streams with strong current, such as the Missouri and Mississippi rivers, paddlefish concentrate in protected natural areas such as pools below sand bars, near physical features like big islands, or near shore irregularities where the current is deflected and velocity reduced (Rosen[425]). They may also gather near man-made structures like dikes, revetments, and bridge supports, where these structures or associated scour holes reduce current (Southall and Hubert[478]). Individuals or small groups of paddlefish may occasionally be found in backwater chutes or nonflowing tributaries, but these habitats appear to be of lesser importance except as feeding areas. Paddlefish seem to prefer water deeper than 4 ft., and during late fall and winter move to areas where the water is 10 ft. or more deep (Rosen[425]). Little is known about habitat preferences in sluggish rivers, but presumably paddlefish would frequent deep pools where food would be most abundant.

Larger paddlefish populations are now usually found in reservoirs which provide optimal feeding environments. Paddlefish spend most of their time in these reservoirs, but the adults migrate into suitable streams in the spring to spawn. Some fish remain in the upstream riverine habitat year-round (Rehwinkel[419]; Russell[450]) but most return to the reservoirs after spawning. Little is known about habitat preference or behavior of paddlefish in standing waters.

Paddlefish are adaptable to a variety of habitats. However, standing or slowly moving waters are preferred during most of the year, are beneficial to most life stages and support greater numbers of paddlefish because of increased food production.

Movement

Paddlefish are known to be mobile; however, very little information is available on precise movements of the species and most is based upon recapture of tagged fish. Although data from tagged fish represent minimum estimates of movement between two points, they do show that paddlefish make extensive upstream and downstream movements.

Most extensive upstream movements of paddlefish are associated with the spring spawning season (Purkett[407]; Elser[151]; Bonislawsky[55]; Rehwinkel[419]; Berg[42]; Southall[477]). Movements of more than 100 mi. are common in the Yellowstone River, Montana (Rehwinkel[419]), and the Osage River, Missouri (unpublished data, 1983, L. Kim Graham, Fisheries Research Biologist, Missouri Department of Conservation, Columbia, Missouri), and movements of more than 145 mi. occur in the Missouri River above Fort Peck Reservoir, Montana (Berg[42]). Some paddlefish have moved more than 200 mi. up the Osage River (Russell[449]). These spawning movements involve large numbers of sexually mature fish.

Dams are barriers to upstream movements, and reservoirs in series isolate and confine paddlefish populations. However, movements within these systems are often extensive. Upstream movement of paddlefish in Garrison Reservoir on the upper Missouri River, North Dakota, is blocked by Fort Peck Dam on the Missouri River and Intake Dam on the Yellowstone River, Montana. However, paddlefish move more than 200 mi., both upstream and downstream, within this system, frequently within a short period of time (Robinson[423]; Elser[151]; Rehwinkel[419]). Robinson[423] reported that three fish moved 200 mi. in 32-45 days, and Rehwinkel[419] reported three paddlefish moved approximately 100 mi. in 17, 35, and 62 days, respectively.

Paddlefish are not confined to reservoirs and frequently emigrate when floodgates are open. Occasionally fish may even go through turbines unharmed although most are killed. Downstream movement of paddlefish from Harry S. Truman Reservoir into Lake of the Ozarks, Missouri, has been significant. Thirty-three of 140 tagged females (23.6%) released in Truman Reservoir were caught in Lake of the Ozarks. They passed through the floodgates, which were opened for extended periods during spring. Four fish passed through both Truman Reservoir and Lake of the Ozarks, which is almost 100 mi. downstream from Truman Dam (unpublished data, 1983, L. Kim Graham, Fisheries Research Biologist, Missouri Department of Conservation, Columbia, Missouri).

Paddlefish frequently move between the pools created by locks and dams on the Mississippi River (Gengerke[195]; Southall and Hubert[478]). Gengerke[195] reported 14 fish moved one to four pools downstream (mean, 57.6 mi.) and four moved one to four pools upstream (mean, 51.5 mi.). Upstream interpool movement was possible because of the navigation locks.

Greatest point-to-point movement has been in open river systems. Unkenholz[526] reported that 12% of the paddlefish tagged below Gavins Point Dam, South Dakota, the lowermost dam on the Missouri River, were harvested outside the South Dakota border. Several fish moved more than 400 mi. downstream, and the farthest movement was 1,200 mi. downstream. Rosen[425] reported that most of the fish he tagged below Gavins Point Dam moved downstream. He reported downstream movement of 42-48 mi. in 3-8 months.

Paddlefish also move considerable distances daily. Transmitter-equipped paddlefish in Lake of the Ozarks made mean overnight (about 12 hours) movements of between 3.4 and 9.5 mi., and maximum movements of 5 to 28 mi. The average 24-hour movement of males was 4.4 mi. (maximum 25 mi.) and of females 3.5 mi. (maximum 27 mi.) (unpublished data, 1983, L. Kim Graham, Fisheries Research Biologist, Missouri Department of Conservation, Columbia, Missouri). These movements were in March, April and May during the spawning period. Movement patterns during other seasons were not determined.

Paddlefish in Pool 13 of the Mississippi River, Iowa, also exhibited greatest movement during the spawning season (Southall and Hubert[478]). During this period they moved an average of 158 ft./hour (0.30 mi./hour) compared to 38 (0.007 mi./hour), 75 (0.014 mi./hour), and 48 ft./hour (0.009 mi./hour) during the prespawning, post spawning, and summer periods, respectively. During the prespawning period paddlefish responded to increased flows with upstream movements, but during other periods movements were not in direct response to changes in water levels.

Long-range movements, both upstream and downstream, seem to be characteristic of the species and may be important to long-term survival and/or population maintenance in some areas. This may be especially significant in areas where dams prevent migration to traditional spawning areas or where reservoirs have flooded existing spawning areas.

Reproduction

Paddlefish do not reach sexual maturity until they are relatively old, and males mature at a younger age than females. Gengerke[195] reported that 6% of the males in the Mississippi River started to mature at 4 years, and all were mature at 9 years of age. In Missouri, most males are sexually mature between 8-10 years of age. When they first reach maturity, males weigh between 15-20 lb.

Females usually do not reach sexual maturity until at least 10 years of age (Gengerke[195]) and many may not mature until they are 12 (Bonislawsky[55]; unpublished data, 1983, L. Kim Graham, Fisheries Research Biologist, Missouri Department of Conservation, Columbia, Missouri). Adams[5] reported females in the Mississippi River were mature at 8-9 years of age. Gengerke[195] reported that 3% of females as young as 6 years were mature, 50% of females at age 10 were mature, and all females 12 years of age and older were mature. Mature females generally weigh at least 30 lb. The smallest sexually mature female collected in Missouri weighed 29 lb. and was 13 years old.

There are no reliable external characteristics for determining sex of paddlefish. Usually, adult males are more slender and in the spring have more tubercles on the top of the head than females, but these characteristics are not reliable. The only precise method to determine sex is by examination of the gonads. Testes lie along the lateral margin of the dorsal surface of the body cavity in a long wavy band. In all but small, immature males the testes lay along extensive fat bodies and are slightly gray. The histology and spermatogenesis of paddlefish were described by Larimore[301].

Ovaries are highly convoluted organs, white when immature, and generally attached to large fat bodies. As ovaries develop they became granular, and small black ova become visible. Later the eggs enlarge, turn gray, and the fat bodies become small. At maturity, the eggs are gray to black and range from 2.0-2.5 mm (0.08-0.10 in.) in diameter (Robinson[423]; Rosen[429]). Fat bodies are usually absent. The histology of ovaries was described by Larimore[301].

Male paddlefish are capable of spawning yearly, but most females are not. The time required to develop mature eggs is not known, but apparently more than 1 year may be necessary. Adult females are frequently collected in spring with ovaries in various stages of development (personal communication, 1983, Dennis G. Unkenholz, Missouri River Coordinator, South Dakota Department of Game, Fish and Parks, Pierre, South Dakota). Elser[151] also reported that females do not spawn annually and Meyer[328] and Sprague[481] concluded that, because of close spacing of annuli on the dentary bone, females may spawn only once every 4 or 5 years.

In Missouri, we also have indirect evidence that mature females make the spawning run only every 2-3 years. Of 140 females tagged and released after their eggs were collected, only three were recaptured the following year during the spawning run. During subsequent years 21 more were recaptured by anglers during the spring spawning season; 11, 6, and 4 were caught 2, 3, and 4 years, respectively, after release. All were gravid when captured.

These observations suggest that most females require 2 years or more to develop mature ova. Similarly, female lake sturgeon (*Acipenser fulvescens*), which mature at 24-26 years of age, spawn once every 3-5 years (Priegel and Wirth 1971). It seems probable, therefore, that fishes which produce large egg masses require more than 1 year to store and mobilize energy for the production of eggs.

The size of the ovaries of paddlefish is not directly proportional to the weight of the female, but larger females usually have larger egg masses. The ovaries of gravid females may comprise 15-25% of the body weight, and females weighing 25-55 lb. will generally contain ovaries weighing 6-8 lb. (Purkett[407]). Stockard[489] reported "lake fish" contained 10-12 lb. of eggs and "river fish" 3-4 lb. of eggs, which suggests that food may affect the number of eggs produced.

Paddlefish produce large numbers of eggs. Eleven fish from the Mississippi River, weighing between 31-52 lb., produced from 148,000-507,000 eggs each. Mean egg production was about 7,700 eggs per pound of body weight (Gengerke[195]). Egg production was higher for paddlefish in the Osage River-Lake of the Ozarks, Missouri, population. Fecundity estimates from 71 females between 31 and 85 lb. ranged from about 184,000 eggs in a 37-lb. fish to slightly over 1,000,000 eggs in a 79-lb. fish. Mean egg production was about 12,000 for each additional pound of body weight (Russell[449]).

Spawning

Early paddlefish researchers were puzzled that no one knew where the species spawned. In fact, considerable effort was devoted to finding young paddlefish. Stockard[489] spent the springs of 1904 and 1905 searching unsuccessfully in the lower Mississippi River for spawning areas and young paddlefish. The smallest paddlefish ever collected by early investigators were seven specimens ranging from 17-

20 mm (0.68-0.80 in.) long, collected from the Mississippi River by Thompson[504]. He concluded that paddlefish spawned in the swift, turbid river channel, and the young remained there. Prior to his collection the smallest paddlefish collected were 35 mm (1.4 in.) long (Barbour[30]) and 74 mm (3.0 in.) long (Danforth[126]). It wasn't until 1960 that precise information on spawning areas was obtained by Purkett[407]. He observed paddlefish spawning over inundated gravel bars in the Osage River, Missouri, during a spring rise. Most of the information about reproduction and early development of young was obtained largely through subsequent investigations in the Osage River (Ballard and Needham[28]; Russell[437, 438, 450]).

Paddlefish require precise timing of events for successful reproduction. They spawn only in flowing water over a gravel substrate. The three most important factors controlling spawning are photoperiod, water temperature and water flow. Within their range, paddlefish may spawn from late March to late June when the water is in the mid-50 F range. Photoperiod and water temperature control the timing of spawning, but an increase in flow is the triggering stimulus. If all three of these conditions are not satisfactory, females resorb their eggs.

Prior to spawning, when the water is near 50 F, paddlefish congregate in deep pools and start moving upstream. As the water warms, their movement increases. When flows are sufficient, paddlefish move quickly to inundated gravel bars and spawn. In the Osage River, paddlefish spawn when flows are sufficient to produce a river stage of 10 ft. and flows of approximately 12,000 cubic feet per second (cfs). Flows of 24,300 cfs in the Mississippi River (Gengerke[195]) and 10,000-20,000 cfs in the Neosho River, Kansas (Bonislawsky[55]), were reported to be associated with movement and spawning of paddlefish.

Paddlefish are very sensitive to changes in water levels, and move downstream quickly into deep pools when water levels start to recede. At the next rise, they move back onto the bars. When a female has completed spawning, she moves quickly downstream.

Because paddlefish spawn when rivers are high and turbid, the spawning act has not been observed. However, considerable activity generally occurs at the water's surface. It is believed that several males accompany a female, and that a spawning "rush" starts near the bottom and culminates at the surface. Splashing can be heard after dark when many fish are spawning (Purkett[407]). Eggs are released during the spawning rush, and immediately after being fertilized they become adhesive and stick tightly to the first object they touch. Most adhere singly to gravel, although some may become attached to twigs or debris. Clean gravel bars are the most favorable substrate and seem to be a prerequisite for spawning.

The maintenance of high water following spawning is important for successful hatching of paddlefish eggs and dispersal of larvae. When water recedes quickly, eggs and larvae are stranded on gravel bars (Purkett[407]). The eggs hatch in about 7 days when the water temperature is in the low 60 F range, so high water levels must remain for at least that long after spawning to ensure a significant hatch. In large streams, rises that stimulate spawning are usually maintained long enough to keep most of the gravel inundated until the eggs hatch. In smaller streams, however, rises frequently recede quickly and many eggs and larvae perish.

Clean gravel and current are important for survival and hatching of eggs. The adhesive coat of the egg holds it in aerated water, and the current prevents siltation. The attachment of the egg to the gravel aids in hatching because the capsule is secure and allows the young to wriggle free. Young in unattached eggs have difficulty freeing themselves from the capsule and many die. After hatching, the young swim up and are immediately swept downstream. A systematic account of the embryonic stages of paddlefish is given by Ballard and Needham[28].

Newly hatched young swim erratically and vertically due to a large yolk sac. This behavior is important because it keeps them in the water column, where currents can carry them from shallow water into areas where food is available. In 3-5 days most of the yolk is absorbed, the mouthparts develop and the young are ready to feed. The young do not have a rostrum or paired fins at this time and do not resemble the adults. After about 1 week they start developing rapidly, and within 10 days to 2 weeks the rostrum begins to develop. At approximately 1 month of age the young are easily recognized as paddlefish.

Feeding

Although early investigators believed that paddlefish used the rostrum to stir up the bottom and feed on dislodged organisms (Forbes[176]; Imms[261]; Alexander[10]), most studies have shown that paddlefish feed primarily on zooplankton (Forbes[176]; Stockard[489]; Eddy and Simer[143]; Barbour[29]; Ruelle and Hudson[432]; Rosen and Hales[427]). Their long, thin gill rakers enable them to efficiently filter zooplankton and other food organisms from the water. Paddlefish have been reported to consume fish (Meyer[328]; Fitz[172]) and at times considerable numbers of insects (Meyer[328]; Hoopes[251]), but these appear to be isolated instances.

Like adults, young paddlefish feed almost exclusively on zooplankton, but their mode of feeding is different because gill rakers are either absent or nonfunctional when the young fish first start to feed. Young paddlefish are particulate feeders, selecting and capturing individual food items (Rosen and Hales[427]; Michaletz[332]). They feed primarily on large cladocerans and occasionally on small insect larvae, like chironomids. Even when cladocerans are not abundant, young paddlefish select them. Copepods are generally not eaten, probably because they are more difficult to capture than the slower cladocerans.

Gill rakers appear on the gill arch when the fish are approximately 3 in. total length (TL — See Appendix A for a discussion on measuring paddlefish) (Michaletz[332]) to 4¾ in. TL (Rosen and Hales[427]), but they are not functional until the fish are approximately 5 in. TL (Michaletz[332]). Rosen and Hales[427] reported that paddlefish were approximately 16-18 in. TL before their gill rakers were fully functional. However, Michaletz[332] reported that, in aquaria, paddlefish approximately 5 in. TL would switch from particulate to filter feeding depending upon the size of food available. When small food items were introduced, young fish fed by filtering, but switched to particulate feeding when larger cladocerans were added. This is an important adaptation and demonstrates that small fish are capable of filtering with less than fully developed gill rakers. When paddlefish become filter feeders, the growth rate generally increases because of increased food consumption (Michaletz[332]).

Once gill rakers are fully developed, paddlefish feed almost exclusively by filtering, and consume organisms roughly in proportion to their abundance, except for small nauplii and rotifers which are consumed in disproportionately small amounts (Eddy and Simer[143]; Rosen and Hales[427]). Rosen and Hales[427] reported paddlefish in the Missouri River below Lewis and Clark Lake, South Dakota, fed mostly in spring and fall and ceased to feed or fed little from late June to early September. They attributed the lack of summer feeding to an unstable environment caused by increased discharge from an upstream reservoir. Adult paddlefish in the Osage River, Missouri, fed actively during the summer and had an average of 140 ml of food in the gut (unpublished data, 1983, L. Kim Graham, Fisheries Research Biologist, Missouri Department of Conservation, Columbia, Missouri). This probably reflected the lack of flow and resulting increased production of food in the Osage River during the summer. The observations of Rosen and Hales[427] suggest that feeding opportunities are reduced in most rapidly flowing waters. These areas are less productive of zooplankton, so paddlefish numbers and growth rates are undoubtedly less than in standing or slowly moving waters.

Age and Growth

Paddlefish are aged by sectioning the dentary bone of the lower jaw and viewing the sections under magnification. Adams[5] used otoliths and dentary bones but reported that otoliths were satisfactory only for aging young fish. Annuli on sections of the dentary bone are frequently difficult to identify, especially in older fish, because of crowding and the presence of halo bands. These two factors make precise aging difficult (Russell[443]), and undoubtedly account for much variation in ages and growth rates reported in the literature.

Paddlefish are long-lived. Fish up to 30 years of age have been reported (Purkett[409]), and paddlefish older than 15 years are common in many populations. Where fisheries are sustained by sexually mature adults, the majority of fish harvested range from 7-18 years of age (Table 1).

Paddlefish grow rapidly compared to most warmwater species, especially during their first year of life. Where food is unlimited, young paddlefish can reach more than 20 in. TL during the first year. However, most grow at a slower rate. Growth in hatchery ponds has ranged from about 1-5 mm/day (0.04-0.20 in./day). In general, paddlefish reach an average total length of 10 in. in less than 100 days (Kallemeyn[277]; Unkenholz[517]; Michaletz[332]; unpublished data, 1983, L. Kim Graham, Fisheries Research Biologist, Missouri Department of Conservation, Columbia, Missouri). In extensively fertilized ponds, paddlefish have grown from fry to about 28 in. TL in about 110 days (personal communication, 1983, E. Jerry Hamilton, Fisheries Area and Hatchery Manager, Missouri Department of Conservation, Sweet Springs, Missouri). Ruelle and Hudson[432] reported young paddlefish grew at the rate of 2.7 mm/day (0.11 in.) in Lewis and Clark Lake, and were about 12 in. TL by September 30. Fastest growth of young-of-the-year paddlefish was reported from Fort Gibson Reservoir, Oklahoma, where they grew at a rate of 0.17 in./day (4.3 mm/day) and averaged 28.4 in. TL by December (Houser and Bross[253]). This exceptional rate of growth was attributed to an abundant plankton population, which developed following a doubling of the surface area of the reservoir and