

Chapter 1

Introduction

William L. Shelton and Steven D. Mims

1.1 INTRODUCTION

The paddlefish *Polyodon spathula* (Walbaum 1792) is a large, long-lived, late maturing fish that retains many non-derived anatomical characteristics and possesses several special biological features. Its appearance alone stimulates interest, but many other attributes of this unique fish add to its attractiveness. Native distribution is limited to North America and it is one of the only two extant members of the family Polyodontidae. The family is included in the order Acipenseriformes, superorder Chondrostei, subclass Actinopterygii, class Osteichthyes.

The other surviving member of the family, the Chinese paddlefish *Psephurus gladius* (Martens 1861), is endemic to the Yangtze River of mainland China (Chenhan & Yongjun 1988; Rochard *et al.* 1991; Birstein 1993). Our discussion in this book will focus on the culture of the American paddlefish, but reference to the Chinese paddlefish will be specified when appropriate, and we will include more detailed information on the Southeast Asian species in Chapter 5.

A symposium on paddlefish biology and culture was organized and convened in the mid-1980s; the published proceedings was a milestone in collating and integrating important information, and providing an extensive bibliography (Dillard *et al.* 1986). An updated collection of literature citations was subsequently published (Georgi & Dingerkus 2001). In 1998, a symposium on exploitation and conservation of North American paddlefish and sturgeons was convened, and the proceedings were published (Williamson *et al.* 1999). Many other symposia and proceedings have focused on sturgeons and some of these have included material on paddlefish, for example, LeBreton *et al.* (2004). A comprehensive book was recently published on paddlefish biology (Paukert & Scholten 2009).

In the present volume, detailed information on the life history of the American paddlefish will be discussed in Chapter 2; however, some of the more unusual anatomical and physiological characteristics are worthy of mention by way of introduction (Coker 1923). The paddle-shaped rostrum has been the object of much conjecture. It has been speculated to play a mechanical role in feeding. Jordan and Evermann (1896) stated that “They

feed chiefly on mud and minute organisms contained in it, stirring it up with the spatulate snout..." (Alexander 1914). Although an interesting thesis, this putative digging function would logically damage the delicate sensory elements that are now known to be a part of this structure. Alternatively, their swimming movement suggests another benefit of the flattened snout that has not been studied nor widely discussed. The paddlefish swim continuously, and as the snout passes through water in alternating side-to-side arcs, some upward force is obviously generated, which probably supplements the buoyancy afforded by the swim bladder. The swim bladder of paddlefish is relatively smaller than most other fishes, and does not appear to produce neutral buoyancy. The rostrum is vulnerable to damage and even loss, which probably has an adverse effect on swimming, but it also presents some potential problems for measurements of length. Thus, Ruelle and Hudson (1977) suggested reporting eye-fork length (body length) rather than the more conventional total length (TL) or standard length (SL).

Some less obvious morphological characteristics of paddlefish, but worthy of note, are the fins. The paired pectoral and pelvic fins, unlike most teleosts, are relatively fixed and inflexible, functioning during forward motion primarily as hydrodynamic maneuvering structures; they provide minimal maneuverability for backing or sculling. The dorsal and anal fins also have a rather rigid structural base. The caudal fin retains a primitive heterocercal morphology, in contrast to the more flexible homocercal tail fin of higher teleosts. The operculum projects backward in an extended flap and there is a functional spiracle behind each eye. The body surface generally lacks scales, except for a few bony rhomboid-shaped scales on, and partially embedded on either side of the caudal peduncle and under the opercular flap. A single pair of minute barbels are located just in front of the mouth on the ventral surface of the snout.

Internally, similarly primitive features in the digestive system include a large, fan-shaped pyloric cecum and a spiral valve in the hind gut. The reproductive organs are of an unusual type among fishes. The paired ovaries are described as gymnovarian, where the mature eggs rupture through the ovarian wall at ovulation and are shed into the body cavity instead of collecting in a central ovarian cavity. From the coelomic cavity, the eggs must enter into dorsally attached oviducts that adhere to the caudad portion of the ovaries. During spawning, the eggs must enter one of the dorsally located open funnels of the paired oviducts (Müllerian ducts). Spermatozoa pass from the testes through the kidneys via vasa deferentia, which are directly attached to the gonads, even though males retain vestigial Müllerian ducts and funnels. Mature ova are highly pigmented; consequently, these dark eggs are quite valuable in the caviar trade, and thus providing the impetus for heavy fishing exploitation. Paddlefish eggs are equivalent to sturgeon caviar in appearance, texture, and taste. Further, like other acipenserids, the eggs have multiple micropyles; paddlefish eggs have an average of about eight, but range from 3 to 20 (Linhart & Kudo 1997; Debus *et al.* 2002).

1.2 HISTORICAL FISHERY OVERVIEW

Generally, paddlefish inhabit large rivers, but they also occur in natural lakes, and frequently maintain populations that thrive in large impoundments, particularly if inflowing tributaries have conditions that will support reproduction. The natural historical range of the paddlefish included 26 states within the Mississippi River and Mobile Bay basins, and other Gulf of Mexico drainages westward to tributaries of Galveston Bay, Texas, but not eastward to the Apalachicola River system (Figure 1.1) (Smith-Vaniz 1968;

Lee *et al.* 1980; Gengerke 1986; Hocutt & Wiley 1986; Pitman & Parks 1994; Jennings & Zigler 2009). Some other older records include the Great Lakes within the range (Hubbs & Lagler 1958).

Despite some decline at the extremes of their range and extirpation from four states – Maryland, New York, North Carolina, and Pennsylvania – all declines are in the north-eastern portion; paddlefish populations currently in 22 states are considered by most resource agencies to be generally in good condition – increasing in three states, stable in 14 states, unknown in three states, and declining in only two states (Graham 1997; Jennings & Zigler 2009). Between 1994 and 2006, despite continued vacillation, there has been no basin-wide collapse in stocks as was earlier predicted (Bettoli *et al.* 2009). However, there have been recent efforts to re-establish paddlefish in some extirpated areas and restore former levels through supplemental stocking in others (Argent *et al.* 2009; Bettoli *et al.* 2009; Grady & Elkington 2009). Reintroduction has proceeded in New York, Pennsylvania, West Virginia, and in select Oklahoma reservoirs. A 10-year stocking program (1990–99) was conducted in Texas, including several rivers within the previous range (Sabine and Trinity Rivers systems). Viable reservoir populations have been reproducing for decades in Lake of the Cherokees on the Grand/Neosho River but restocking efforts have occurred in that watershed in Kansas, and populations have been re-established within Keystone Reservoir on the Arkansas River, Oologah Reservoir on the Verdigris River, Eufaula Reservoir on the North and South Canadian Rivers, and in Lake Texoma on the Red River (Figure 1.1) (Patterson 2009; ODWC 2010).

Production and population dynamics are vital to managing and harvesting only surplus yield, and thus factors that affect individual growth can impact population yields. Growth varies in different bodies of water in relation to the abundance of food. Consequently, weight-length relations may vary considerably based on population differences. Sexual dimorphism in adults is minimal, but males are generally thinner than the more rotund condition of females; the contrast is much more evident in fish from rivers compared to one from reservoirs or ponds.

Paddlefish exploitation has varied from spates of elevated intense harvest, to intervals of low fishing pressure. For example, the harvest was high in the 1890s, reaching about 1000 metric tonnes (MT) in 1899, then rapidly declined in the early 1900s (Coker 1923), only to escalate more recently in the 1970s and 1980s (Carlson & Bonislavsky 1981). The periods of heavy harvest were stimulated by demand for caviar in conjunction with shortfalls from Caspian Sea production; the recent fishing pressure was also related to trade in this product, much of which was illicit (Waldman & Secor 1999; W.L. Shelton, Chair, ad hoc committee on paddlefish, 1981–83, unpublished data, Southern Division, American Fisheries Society). Because paddlefish are long-lived and late maturing, and are quite vulnerable to netting, populations are easily and rapidly overexploited. As periods of heavy fishing pressure occur, catch-per-effort deteriorates, and the fishery is usually abandoned soon after. With reduced fishing pressure, after a few years the population once again recovers. However, under environmentally stressed conditions, population recovery can be protracted, or may not occur at all if conditions are unsuitable for natural recruitment.

Habitat destruction and river modifications have affected distribution and abundance, as well as reducing the capacity for populations to rebound, particularly at the periphery of their range. Construction and operation of dams have altered water flow and quality, and often eliminated traditional spawning areas or interfered with access to these habitats (Sparrowe

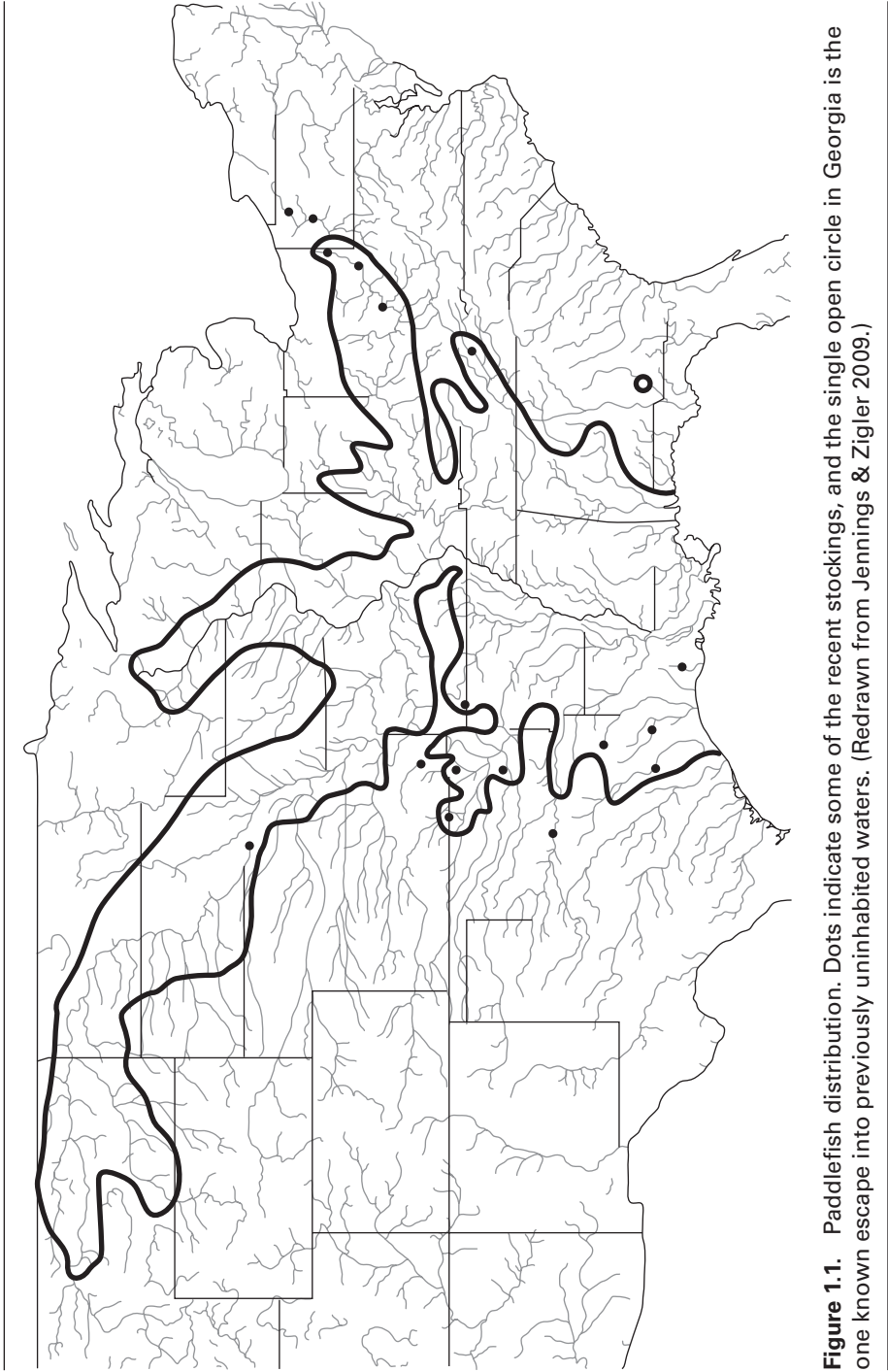


Figure 1.1. Paddlefish distribution. Dots indicate some of the recent stockings, and the single open circle is the one known escape into previously uninhabited waters. (Redrawn from Jennings & Zigler 2009.)

1986; Unkenholtz 1986; Boreman 1997; Graham 1997). Further, other anthropogenic habitat alterations, such as environmental contamination, have adversely affected paddlefish populations (Pflieger 1975; Carlson & Bonislawsky 1981; Pasch & Alexander 1986). The wide distribution of paddlefish complicates status verification, not to mention management strategies. The populations are dispersed over many jurisdictional interstate boundaries, consequently concern over conflicts stimulated the organization of MICRA (Mississippi Interstate Cooperative Resource Association) in 1997, which consisted of multiple states and the US Fish and Wildlife Service (Graham 1997; Graham & Rasmussen 1999).

In 1983, commercial harvest of paddlefish was permitted in 11 states, but by 1994, only six states continued to allow non-sportfish exploitation (Graham 1997; Bettoli *et al.* 2009). Fourteen states currently manage angler harvest. Although recent commercial harvest has been about 10 times that removed by sport fishermen, angler harvest can be significant and periodically heavy. For the period of 2000–06, the annual average commercial harvest was about 47,000 fish for a total annual average of nearly 500MT (Quinn 2009), while a single sport fishery in Oklahoma removed between 25,000 and 34,000 fish per year in one peak period (Gordon 2009). It is likely that commercial fisheries will continue to dwindle as exploitive fisheries are subject to the tragedy of the commons syndrome, and when commercial and sport interests are in conflict, the former invariably loses. Several factors come into play in this dichotomous demand: sport fishing interests are much more broadly based, funded by user fees (Wallop-Breaux and Dingell-Johnson taxes), and exploitive uses of natural resources generally are less supported by public opinion and agency commitment.

1.3 OVERVIEW OF NATURAL REPRODUCTION

Population stability obviously depends on successful reproduction and recruitment, whether it is natural or hatchery dependent. Little knowledge of paddlefish reproduction was known until Purkett (1961) reported on observations of natural spawning. Paddlefish move upstream after the water temperature has warmed to about 10–11°C and under the impetus of increased flow during spring flooding. They spawn over gravel substrate in the main current when water temperatures reach 13–16°C (Pasch *et al.* 1980; Wallus 1986). The eggs are adhesive, oval and heavily pigmented with melanophores (Ballard & Needham 1964; Shelton & Mims 1995). Eggs swell slightly in water and after fertilization; they are demersal and adhesive, sticking to gravel (Purkett 1961, 1963).

Hatchery production can facilitate restocking of depleted natural populations, or as a primary component of aquaculture (Graham 1986; Graham *et al.* 1986). Early development of artificial propagation was initiated in Missouri, primarily because of the following factors. Important details of paddlefish life history were initially described in the 1960s by Missouri biologists, where the paddlefish provided an important sport-fishery (Russell 1986). The development of large impoundments, one in particular on the Osage River, inundated the primary spawning area in central Missouri (Sparrowe 1986). Together these factors stimulated the development of artificial propagation techniques in order to perpetuate and maintain this valuable fishery (Graham *et al.* 1986).

1.4 INTERNATIONAL REGULATING FACTORS

In 1989, the US Fish and Wildlife Service was petitioned to include paddlefish on the list of Threatened and Endangered Species under the provisions of the endangered Species Act of 1973. This request for a “threatened” status was subsequently determined to be

unjustified, but in 1992 paddlefish were added to the CITES Appendix-II listing (United Nations Convention on International Trade of Endangered Species of Wild Fauna and Flora). A CITES listing requires that the exporting country must have an export permit for international trade of paddlefish and their parts such as meat, caviar, and so forth. When an exporting country issues a permit for an Appendix-II listed species, it purports that the species was legally acquired and has not impacted wild populations. All sturgeons worldwide are currently listed under the provisions of CITES (Khodorevskaya *et al.* 1997; Pikitch *et al.* 2005). In general, CITES provides an international mechanism for the maintenance of biodiversity by protecting listed species of wildlife and plants from overexploitation through international trade. Paddlefish have been included in this system, in part to attempt to regulate illegal trade in caviar. Paddlefish and sturgeon roe are similar and differential identification can present an enforcement enigma. Further, paddlefish possession, transport, propagation, and culture are independently regulated by state laws. Therefore, legal considerations should be checked before committing to paddlefish culture.

1.5 WHY CULTURE PADDLEFISH?

Paddlefish are native to more than half the United States and well suited for temperate climates. They are filter feeders and are therefore ecologically efficient; they demonstrate rapid growth (2–4 kg/year) in water abundant in zooplankton. Reproduction and culture techniques are well developed for producing paddlefish stock, whether for mitigation or food production. Interest in culture in the United States is stimulated by conservation motivation as well as managing populations for the sport fisheries. Propagation to support culture for food will probably have its greatest potential in fish-growing areas outside the United States, particularly in areas where polyculture is practiced and where the importance of paddlefish as a commodity is greater than a perceived recreational value. Paddlefish have boneless white meat and their grey to black roe is processed into caviar; both are valuable products and permit entry into diverse global marketplaces.

These various components of paddlefish culture will be developed in more detail in subsequent chapters. Some preliminary discussion of fish culture will be included in Chapter 2, but more detailed discussion of important components of culture will be detailed in other chapters, including artificial propagation, special techniques for reproductive manipulation, nursing, and grow-out. In addition, preparation of specialty products will be elaborated.

REFERENCES

- Alexander, M.L. (1914) The paddle-fish (*Polyodon spathula*). (Commonly called spoonbill catfish). *Transactions of the American Fisheries Society* 44:73–78.
- Argent, D.G., Lorson, R., McKeown, P., Carlson, D.M., & Clancy, M. (2009) Paddlefish restoration to the upper Ohio and Allegheny River Systems. In: *Paddlefish Management, Propagation, and Conservation in the 21st Century* (eds C.P. Paukert & G.D. Scholten), pp. 397–409. American Fisheries Society Symposium 66, Bethesda, MD.
- Ballard, W.W. & Needham, R.G. (1964) Normal embryonic states of *Polyodon spathula*. *Journal of Morphology* 114:465–477.
- Bettoli, P.W., Kerns, J.A., & Scholten, G.D. (2009) Status of paddlefish in the United States. In: *Paddlefish Management, Propagation, and Conservation in the 21st Century* (eds C.P. Paukert & G.D. Scholten), pp. 23–38. American Fisheries Society Symposium 66, Bethesda, MD.

- Birstein, V.J. (1993) Sturgeons and paddlefishes: Threatened fishes in need of conservation. *Conservation Biology* 7:773–787.
- Boreman, J. (1997) Sensitivity of North American sturgeon and paddlefish to fishing mortality. *Environmental Biology of Fishes* 48:399–405.
- Carlson, D.M. & Bonislawsky, P.S. (1981) The paddlefish (*Polyodon spathula*) fisheries of the Midwestern United States. *Fisheries* 6:17–27.
- Chenhan, L. & Yongjun, Z. (1988) Notes on the Chinese paddlefish, *Psephurus gladius* (Martens). *Copeia* 1988:482–484.
- Coker, R.E. (1923) Methuselah of the Mississippi. *The Scientific Monthly* 16:89–103.
- Debus, L., Winkler, M., & Billard, R. (2002) Structure of micropyle surface on oocytes and caviar grains in sturgeons. *International Review of Hydrobiology* 87:585–603.
- Dillard, J.G., Graham, L.K., & Russell, T.R. (1986) *The Paddlefish: Status, Management and Propagation*. North Central Division, Americana Fisheries Society, Special Publication 7, Columbia, MO.
- Gengerke, T.W. (1986) Distribution and abundance of paddlefish in the United States. In: *The Paddlefish: Status, Management and Propagation* (eds J.G. Dillard, L.K. Graham, & T.R. Russell), pp. 22–35. American Fisheries Society, North Central Division, Special Publication 7, Bethesda, MD.
- Georgi, T.A. & Dingerkus, G. (2001) *Paddlefish Bibliography*. Doane College, Crete, Nebraska.
- Gordon, B. (2009) Paddlefish harvest. In: *Paddlefish Management, Propagation, and Conservation in the 21st Century* (eds C.P. Paukert & G.D. Scholten), pp. 223–233. American Fisheries Society Symposium 66, Bethesda, MD.
- Grady, J.M. & Elkington, B.S. (2009) Establishing and maintaining paddlefish populations by stocking. In: *Paddlefish Management, Propagation, and Conservation in the 21st Century* (eds C.P. Paukert & G.D. Scholten), pp. 385–396. American Fisheries Society Symposium 66, Bethesda, MD.
- Graham, L.K. (1986) Establishing and maintaining paddlefish populations by stocking. In: *The Paddlefish: Status, Management and Propagation* (eds J.G. Dillard, L.K. Graham, & T.R. Russell), pp. 96–104. American Fisheries Society, North Central Division, Special Publication 7, Bethesda, MD.
- Graham, K. (1997) Contemporary status of the North American paddlefish, *Polyodon spathula*. *Environmental Biology of Fishes* 48:279–289.
- Graham, L.K. & Rasmussen, J.L. (1999) A MICRA perspective on closing paddlefish and sturgeon commercial fisheries. In: *Symposium on the Harvest, Trade and Conservation of North American Paddlefish and Sturgeon* (eds D.F. Williamson, G.W. Benz, & C.M. Hoover), pp. 130–142. TRAFFIC North America, World Wildlife Fund, Washington, DC.
- Graham, L.K., Hamilton, E.J., Russell, T.R., & Hicks, C.E. (1986) The culture of paddlefish – A review of methods. In: *The Paddlefish: Status, Management and Propagation* (eds J.G. Dillard, L.K. Graham, & T.R. Russell), pp. 78–94. American Fisheries Society, North Central Division, Special Publication 7, Bethesda, MD.
- Hocutt, C.H. & Wiley, E.O. (eds) (1986) *Zoogeography of North American Freshwater Fishes*. John Wiley & Sons, Inc., New York.
- Hubbs, C.L. & Lagler, K.F. (1958) *Fishes of the Great Lakes Region*. Publication no. 26, Cranbrook Institute of Science.
- Jennings, C.A. & Zigler, S.J. (2009) Biology and life history of paddlefish in North America: an update. In: *Paddlefish Management, Propagation, and Conservation in the 21st Century* (eds C.P. Paukert & G.D. Scholten), pp. 1–22. American Fisheries Society, Symposium 66, Bethesda, MD.
- Jordan, D.S. & Evermann, B.W. (1896) *The Fishes of North and Middle America: A Descriptive Catalogue of the Species of Fish-like Vertebrates Found in the Waters of North America, North of the Isthmus of Panama*. Reprinted in 1963 as Bulletin of the Smithsonian Institution, U.S. National Museum, number 12, vol. 1, Washington, DC.

- Khodorevskaya, R.P., Dovgopol, G.F., Zhuravleva, O.L., & Vlasenko, A.D. (1997) Present status of commercial stocks of sturgeon in the Caspian Sea basin. *Environmental Biology of Fishes* 48:209–219.
- LeBreton, G.T.O., Beamish, F.W.H., & McKinley, R.S. (2004) *Sturgeons and Paddlefish of North America*. Kluwer Academic Publishers, New York.
- Lee, D.S., Gilbert, C.R., Hocutt, C.H., Jenkins, R.E., McAllister, D.E., & Stauffer, J.R. (1980) *Atlas of North American Freshwater Fishes*. North Carolina Biological Survey, North Carolina State Museum of Natural History, Raleigh, NC.
- Linhart, O. & Kudo, S. (1997) Surface ultrastructure of paddlefish eggs before and after fertilization. *Journal of Fish Biology* 51:573–582.
- Martens, E. von (1861) Über einen neuen Polyodon (*P. gladius*) aus dem Yantsekiang und über die Sogenannten Glaspolypen. *Monatsberichte der Deutschen Akademie der Wissenschaften zu Berlin* 1861:476–479.
- ODWC (Oklahoma Department of Wildlife Conservation) (2010) Website. Available at: <http://www.wildlifedepartment.com/>
- Pasch, R.W. & Alexander, C.M. (1986) Effects of commercial fishing on paddlefish populations. In: *The Paddlefish: Status, Management and Propagation* (eds J.G. Dillard, L.K. Graham, & T.R. Russell), pp. 46–53. American Fisheries Society, North Central Division, Special Publication 7, Bethesda, MD.
- Pasch, R.W., Hackney, P.W., & Holbrook, J.A. (1980) Ecology of the paddlefish in Old Hickory Reservoir, Tennessee, with emphasis on first-year life history. *Transactions of the American Fisheries Society* 109:157–167.
- Patterson, C.P. (2009) Ecology of a reintroduced population of paddlefish, *Polyodon spathula*, in Lake Texoma. Master's thesis, Oklahoma State University, Stillwater.
- Paukert, C.P. & Scholten, G.D. (eds) (2009) *Paddlefish Management, Propagation, and Conservation in the 21st Century; Building from 20 years of Research and Management*. American Fisheries Society, Symposium 66, Bethesda, MD.
- Pfielger, W.L. (1975) *The Fishes of Missouri*. Missouri Department of Conservation. Jefferson City, MO.
- Pikitch, E.K., Doukakis, P., Lauck, L., Chakrabarty, P., & Erickson, D.L. (2005) Status, trends and management of sturgeon and paddlefish fisheries. *Fish and Fisheries* 6:233–265.
- Pitman, V.M. & Parks, J.O. (1994) Habitat use and movement of young paddlefish (*Polyodon spathula*). *Journal of Freshwater Ecology* 9:181–189.
- Purkett, C.A. (1961) Reproduction and early development of paddlefish. *Transactions of the American Fisheries Society* 90:125–129.
- Purkett, C.A. (1963) The paddlefish fishery of the Osage River and the Lake of the Ozarks, Missouri. *Transactions of the American Fisheries Society* 92:239–244.
- Quinn, J.W. (2009) Harvest of paddlefish in North America. In: *Paddlefish Management, Propagation, and Conservation in the 21st Century* (eds C.P. Paukert & G.D. Scholten), pp. 203–221. American Fisheries Society, Symposium 66, Bethesda, MD.
- Quinn, J.W., Posey, W.R., Leone, F.J., & Limbird, R.L. (2009) Management of the Arkansas River Commercial paddlefish fishery with check stations and special seasons. In: *Paddlefish Management, Propagation, and Conservation in the 21st Century* (eds C.P. Paukert & G.D. Scholten), pp. 235–275. American Fisheries Society, Symposium 66, Bethesda, MD.
- Rochard, E., Williot, P., Castelnaud, G., & Lepage, M. (1991) *Éléments de systématique et de biologie des populations sauvages d'esturgeons*. In: *Acipenser* (ed. P. Williot), pp. 475–507. Cemagref, Bordeaux, France.
- Ruelle, R. & Hudson, P.L. (1977) Paddlefish (*Polyodon spathula*): Growth and food of young of the year and a suggested technique for measuring length. *Transactions of the American Fisheries Society* 106:609–613.

- Russell, T.R. (1986) Biology and life history of the paddlefish – a review. In: *The Paddlefish: Status, Management and Propagation* (eds J.G. Dillard, L.K. Graham, & T.R. Russell), pp. 2–20. American Fisheries Society, North-Central Division, Special Publication 7, Bethesda, MD.
- Shelton, W.L. & Mims, S.D. (1995) Oocyte staging in paddlefish, *Polyodon spathula*. *Transactions of the Kentucky Academy of Science* 56:22–27.
- Smith-Vaniz, W.F. (1968) *Freshwater Fishes of Alabama*. Auburn University, Agricultural Experiment Station, AL.
- Sparrowe, R.D. (1986) Threats to paddlefish habitat. In: *The Paddlefish: Status, Management and Propagation* (eds J.G. Dillard, L.K. Graham, & T.R. Russell), pp. 36–45. American Fisheries Society, North Central Division, Special Publication 7, Bethesda, MD.
- Unkenholtz, D.G. (1986) Effects of dams and other habitat alterations on paddlefish sportfisheries. In: *The Paddlefish: Status, Management and Propagation* (eds J.G. Dillard, L.K. Graham, & T.R. Russell), pp. 54–61. American Fisheries Society, North Central Division, Special Publication 7, Bethesda, MD.
- Walbaum, J.J. (1792) Petri artem renovati, bibliotheca et philosophia ichthyologica. *Ichthyologicae* pars 3, Grypsewaldiae.
- Waldman, J.R. & Secor, D.H. (1999) Caviar trade in North America: an historical perspective. In: *Proceedings of the Symposium on Harvest, Trade and Conservation of North American Paddlefish and Sturgeon* (eds D.F. Williamson, G.W. Benz, & C.M. Hoover), pp. 77–89. TRAFFIC North America/World Wildlife Fund, Washington, DC.
- Wallus, R. (1986) Paddlefish reproduction in the Cumberland River and Tennessee River systems. *Transactions of the American Fisheries Society* 115:424–428.
- Williamson, D.F., Benz, G.W., & Hoover, C.M. (eds) (1999) *Proceedings of the Symposium on the Harvest, Trade and Conservation of North American Paddlefish and Sturgeon*. TRAFFIC North America/World Wildlife Fund, Washington, DC.

