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Propagation and Culture of Paddlefish

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Abstract.—Paddlefish *Polyodon spathula* populations in North America have long been exploited commercially for meat and roe; however, the history of paddlefish propagation and culture is more recent. Early efforts to artificially propagate and culture paddlefish were motivated by conservation following the construction of dams and destruction of spawning habitat on major rivers of the central United States. From these beginnings, paddlefish propagation and the species itself have spread from native U.S. waters to other countries, including Russia and China. In the United States, conservation is still an important aspect of paddlefish culture, although sport fishing and aquaculture production have been added to the mix. However, in those countries where paddlefish have been introduced, the motivation has been the perceived potential for producing food for domestic consumption and valuable products for export, including one of the most exotic and expensive food products in today's world—caviar. The collective efforts of state and federal hatchery personnel in the United States, along with university researchers from the United States and worldwide have resulted in a more complete body of information on paddlefish propagation and culture. Included in this collection are methods for handling broodstock, induced spawning, and nursery stages of production, along with cryopreservation of milt and manipulation of sex ratios in the hatchery to produce a preponderance of female fish. We have assembled this collection here to provide a single source reference and have added information concerning hatchery design, regulations, and the grow-out stages of aquaculture food fish production.

Historical Overview

Domestic Culture

Propagation and culture of paddlefish *Polyodon spathula* had its roots and early development in efforts of the Missouri Department of Conservation during the early1960s. The efforts to culture paddlefish in Missouri were stimulated by concern over the perceived adverse effects of environmental perturbations, in particular the rapid development of reservoirs, on the native populations and fisheries (Sparrow 1986). Purkett (1961, 1963a) reported key information on the natural reproductive biology and the sport fishery in Missouri, and he initiated studies on artificial propagation (Purkett 1963b). Needham (1965) used pituitary injections to success-

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fully induce spawning of paddlefish. Russell (1973) continued to develop artificial propagation, including pond nursery techniques; the program in Missouri was oriented primarily to the maintenance of the sport fishery (Graham 1986).

Other research on paddlefish developed in the 1970s within Tennessee Valley Authority (TVA) relative to populations in the TVA reservoir system (Pasch et al. 1980) and at Auburn University, Alabama (Semmens 1982). Paddlefish have been an important food fish in the United States, but the populations have vacillated under variable spates of commercial overharvest for meat and roe (Carlson and Bonislawsky 1981; Jennings and Zigler 2000). Efforts to apply culture techniques at Auburn University were focused on aquaculture rather than restoration. Information on paddlefish as a cultured food fish was reported by Semmens and Shelton (1986). They also demonstrated that luteinizing hormone-releasing hormone analog (LHRH*a*) would induce ovulation and spermiation as described by Doroshov et al. (1983) for white sturgeon *Acipenser transmontanus* (Semmens 1986). This modification in artificial propagation was important in facilitating commercial development, as it eliminated the reliance on pituitary material for induced spawning. The refinement of artificial propagation is also important to restoration programs and, reciprocally, food fish production has similar positive influences on conservation through the reduction in reliance on exploitive fishing (Billard and Lecointre 2001).

From the mid-1980s to the present, most of the research in the United States to enhance and refine techniques for culture of paddlefish as a food fish has occurred at Kentucky State University (KSU), Aquaculture Research Center, Frankfort, Kentucky. Much of the orientation has been toward improvements in nursery techniques. Mims et al. (1991, 1993b, 1995a, 1995b) developed organic and inorganic fertilization schedules and the inoculation of *Daphnia* sp. to promote high survival (50–80%) and growth rates (2 cm/week) in nursery ponds for paddlefish fingerlings. Production strategies such as Phase-I and Phase-II fingerling (see definitions, Phase-I and Phase-II Fingerling Culture section) production using prepared diets (Onders et al. 2005; Onders et al. 2008), reservoir ranching (Onders et al. 2001; Mims and Onders 2006), and integrated pond culture with catfish (Mims et al. 1999; Mims and Shelton 2005; Mims and Onders 2006) have been under continuing development.

Systems development to increase the preponderance of females in cultured populations relate to the importance of caviar as a market commodity. A program to produce female offspring through direct gynogenesis and a more involved breeding program to use sexually manipulated broodstock have been investigated (Mims and Shelton 1998a). Cryopreservation of sperm is an important tool in the management of broodstock and artificial propagation, especially relative to selected lines and for extension of unique stocks (Brown and Mims 1999; Mims et al. 2000; Hóvath et al. 2006).

Processing and marketing studies have been conducted at KSU on paddlefish meat and caviar to increase potential for national and international commerce. Investigations have included testing refrigerated and frozen meat stability (Lou et al. 2000a), value-added products such as smoked paddlefish and surimi (Mims et al. 1999; Lou et al. 2000b), and consumer acceptability of paddlefish products (Wang et al. 1995; Mims et al. 1999).

Currently, nine state and federal hatcheries and three private fish farms in the United States and Kentucky State University, Frankfort, USA are propagating and culturing paddlefish; protocols are described in Table 1. The primary objectives

Table 1. Summary of propagation and culture protocols for 10 hatcheries in the United States collected through mail and telephone surveys in 2007–2008. (MIST = minimally invasive surgical technique; TL = total length; na = not applicable or unknown)

	Kentucky	**Louisiana**	**Louisiana**
Facility	Kentucky State University, Aquaculture Research Center	Department of Wildlife & Fisheries Booker Fowler Fish Hatchery	U.S. Fish and Wildlife Natchitoches National Fish Hatchery
Purpose	Aquaculture/conservation/recovery	Educational	Restoration
Broodstock; source	Wild/domestic F_2; Ohio River; private lakes	Wild; Mermentare River	Wild; Red River
Holding tanks	2.5–4 m diameter	2 m diameter	2.4 m diameter
Induction	LHRH*a*	LHRH*a*	LHRH*a*
Injection	♀ two series (90:10) 100 μg/kg ♂ one injection 50 μg/kg	♀ two series (90:10) 100 μg/kg ♂ one injection 10 μg/kg	♀ two series (90:10) 100 μg/kg ♂ one injection 10 μg/kg
HATCHERY			
Egg collection	MIST/modified MIST	MIST	MIST
Milt collection	Syringe with tubing; refrig in	In bowls vials	Syringe with tubing; refrig in Nalgene bottles
Fertilization	20–30 mL/L water to 1 L of eggs	No set ratio	3 mL milt/150 mL water; eggs divided into three (3) pans
Water	De-chlorinated tap water	Combine groundwater and Indian River	De-chlorinated tap water
Flow; temperature	4–6 L/min; 18°C	4–6 L/min; 18–19°C	4–6 L/min; 18–19°C
PRODUCTION			
Phase I , <7.5 cm			
Unit and size	Circular tanks; 4 and 20 m diameter	Circular tanks; 3,500 L	Raceways; 30,000 L
Diet	Zooplankton first 30 d until fish are more than 7.5 cm	Automatic feeders; trout #00–#02 with zooplankton	Automatic belt feeder; trout #00–#02 manually feed three times per day and add zooplankton
Stocking rate; survival	0.05–0.5 fry/L; ≥50%	5.7 fry/L; n/a	n/a
Phase II, >7.5 cm			
Unit	1-ha ponds; 1 million liter circular tanks	3,500 L	Raceways
Stocking rate	25,000/22,000 fish ≥ 7.5 cm 1.5–4.6 mm floating; 36% to 45%	n/a	n/a
Diet	Protein	Automatic feeder; trout #02–#4	Automatic feeder; 1.5 and 3.5 mm floating diet
Harvest size	≥35 cm TL	20–27 cm TL	≥20 cm TL
Survival	80–90%	5–10%	5–10%
Cost per fish	$0.65	$1.67	n/a

Table 1. Continued.

	Oklahoma	**Pennsylvania**	**South Dakota**
Facility	U.S. Fish & Wildlife Service Tishomongo National Fish Hatchery	Fish & Boat Commission Linesville Hatchery	U.S. Fish & Wildlife Service Gavins Point National Fish Hatchery
Purpose	Recovery	Recovery	Conservation/recovery
Broodstock; source	Wild; Red, Neosho, and Verdigris rivers	Fertilized eggs from KY and WV (125,000); Ohio, White, and Niotira rivers	Wild; White and Niobara rivers
Holding tanks	8 m diameter	n/a	3 m diameter
Induction	LHRH*a*	n/a	LHRA*a*
Injection	♀ 2 series (90:10) 100μg /kg ♂ 1 injection 30μg /kg	n/a	♀ 2 series (90:10)100μg/kg ♂ 1 injection 50 μg/kg
HATCHERY			
Egg collection	Caesarean section	n/a	MIST
Milt collection	Syringe w/ tubing; refrig in vials	n/a	Syringe with tubing
Fertilization	No set ratio	n/a	No set ratio
Water	Aerated groundwater	UV filtered water	Aerated groundwater
Flow; temperature	4 to 6 L/min; 18.5°C	1 to 2L/min;18°C	2 to 4L/min;13°C
PRODUCTION			
Phase I , <7.5cm			
Unit and size	Raceways; 3 × 0.6 × 0.4 m	Raceways; 30 × 305 × 1.2m	n/a
Diet	Automatic feeder diets (#00–#02) w/ zooplankton	Automatic feeders; trout #00–#02 w/ zooplankton	n/a
Stocking rate; survival	55 fry/L; n/a	1 fry/L; n/a	n/a
Phase II, >7.5cm			
Unit	Circular tanks	Raceways	Four ponds (0.53 ha)
Stocking rate	n/a	n/a	Stock 25,000 larvae/pond
Diet	Floating diet; 36–45% protein	Automatic feeder; trout #03 semi-sinking	Automatic feeder; 1.5 and 4.6 mm floating diet combined with zooplankton-rich water
Harvest size	≥35 cm TL	≥25 cm TL	25–30 cm and 40–51 cm TL
Survival	80–90%	20%	80–90%
Cost/fish	$0.65	$8.01	$4.51

Table 1. Continued.

	Mississippi	Missouri	New York
Facility	U.S. Fish & Wildlife Service, Private John Allen Fish Hatchery	Department of Conservation, Blind Pony Hatchery	Dept. of Environmental Conservation, Oneida Fish Hatchery
Purpose	Conservation/recovery	Sportfishing	Recovery
Broodstock; source	Wild; Tennessee-Tombigbee River	Domestic F_2; Table Rock Lake	Fertilized eggs from KY (10,000 fry)
Holding tanks	3–4 m diameter	3 m diameter	n/a
Induction	LHRA*a*	LHRH*a*	n/a
Injection	♀ 2 series (90:10) 100 μg/kg ♂ 1 injection 100 μg/kg	♀ 2 series (90:10)100 μg/kg ♂ 1 injection 10 μg/kg	n/a
HATCHERY			
Egg collection	MIST	Caesarean section	n/a
Milt collection	Syringe with tubing	Syringe with tubing; refrig in plastic bags	n/a
Fertilization	10–15 mL/400 mL water to eggs	No set ratio	n/a
Water	Aerated well	Reservoir water	Scriba Creek
Flow; temperature	4 L/min; 18°C	4 L/min; 17–18°C	4 to 6L/min; 18°C
PRODUCTION			
Phase I, <7.5 cm			
Unit and size	Recirculating; 10.5 m diameter	n/a	Raceways; 3.5 × 3.5 × 1.2 m
Diet	Prepared #00–#02 diet; zooplankton first 28 d	n/a	Automatic feeders; trout diets #00–#02
Stocking rate; survival	0.2 fry/L; 10%	n/a	0.7 fry/L; n/a
Phase II, >7.5 cm			
Unit	Raceways and ponds	Ponds	Raceways
Stocking rate	Based on survival in Phase 1	25,000 fry/ha	n/a
Diet	Belt feeder with zooplankton-rich water; 1.5 to 4.6 mm floating (36–45% protein)	Organic fertilizer for zooplankton. At >7.5 cm, add 1.5–4.5 mm floating diets	Automatic feeders; trout diets #03–#04
Harvest size	25–30 cm and 40–51 cm TL	25–30 cm TL	≥33 cm TL
Survival	80–90%	30–35%	5–10%
Cost/fish	$4.51	$1.23–$6.85	$4.75

Table 1. Continued.

	West Virginia
Facility	Department of Natural Resources Palestine Hatchery
Purpose	Conservation/recovery
Broodstock; source	Wild; Ohio River
Holding tanks	3 m diameter
Induction	LHRH*a*
Injection	♀ 2 series (90:10) 100 μg/kg ♂ 1 injection 50 μg/kg
HATCHERY	
Egg collection	Traditional stripping
Milt collection	Syringe with tubing; refrig in vials
Fertilization	Add 2 mL/300 mL water to eggs
Water	Little Kanawha River
Flow; temperature	4 L/min; 18–21°C
PRODUCTION	
Phase I , <7.5 cm	
Unit and size	n/a
Diet	n/a
Stocking rate; survival	n/a
Phase II, >7.5 cm	
Unit	Two ponds; (0.2 and 0.6 ha)
Stocking rate	25,000 larvae/ha
Diet	Organic fertilizer of alfalfa and soybean meal at 250 kg/ha; then add #00 diet for zooplankton. When fish are >7.5, add 1.5 to 4.5 mm floating diets
Harvest size	25–30 cm TL
Survival	30–35%
Cost/fish	$1.23–$6.85

of the public hatcheries are raising paddlefish for sport fishing, conservation, and/or restoration programs in their states, whereas the objectives of KSU and three private hatcheries are developing paddlefish for meat and caviar.

International Culture

Paddlefish have been widely dispersed in various other countries (Vedrasco et al. 2001). The early introductions into eastern Europe in 1974 and 1977 as part of a cooperative scientific agreement between the U.S. Fish and Wildlife Service and the Soviet Union Acclimatization Department of the All-Union Research Institute of Pond Fisheries are documented by Simonović et al. (2006). The imported fertilized eggs, which originated from the state of Missouri, USA, were successfully raised at the Goryachi Klyouch Experimental Fish Breeding Plant in the Krasnodar region near the Black Sea. Dr. Evgeniy Melchenkov (All-Russian Research Institute of Freshwater Fish Culture, Rybnoe, Moscow Province, Russia, personal communication) reported that two hatcheries conducted artificial propagation of paddlefish in the south of Russia (Astrakhan and Rostov regions) in 2008. Several million fertilized eggs from this production and fry have been sold annually to private producers in Russia and abroad. Paddlefish production in Russia has been primarily in pond polyculture with common carp *Cyprinus carpio*, or various sturgeon species, and in reservoir ranching (see later section on this topic). Paddlefish have been distributed from Russia to other eastern European countries, including Bulgaria, Czech Republic, Hungary, Moldavia, Romania, and Ukraine for food fish culture (Simonović et al. 2006).

Long-term traditions of sturgeon culture and high demand for fish meat and premium caviar have facilitated acceptance of paddlefish in the current aquaculture industry of eastern Europe. Culture of the paddlefish outside of its native range currently has the greatest practicable potential. Opposition to the culture of nonnative species is common (Casal 2006); however, the fact that 13–17% of the world's freshwater finfish protein production of more than 45 million metric tons is based on nonnative species is evidence of the importance of using these resources (Shelton and Rothbard 2006). Only one species each of *Polyodon* and *Psephurus* are extant, and interfertility with sturgeons has not been demonstrated (Mims et al. 1997), and therefore, hybridization has been limited or nonextistent.

Some countries have now developed their own broodstock and established hatchery paddlefish propagation. Food habits of the American paddlefish are very similar to that of bighead carp *Hypophthalmichthys nobilis*, which is one of the primary components of the Chinese style of polyculture (FAO 1983; Shelton and Smitherman 1984). Because of the excellent food quality of paddlefish, it is frequently being used in polyculture in place of bighead carp. Two established farms in Ukraine have stocked paddlefish in their polyculture systems instead of bighead carp. In 2006, Ukraine produced 12 metric tons (mt) of paddlefish, with about 8 mt sold for meat and the rest carried over for broodstock development and caviar production (V. Belk, Institute of Fisheries, Kiev, Ukraine, personal communication). By 2012, production in Ukraine is predicted to be between 300 and 400 mt/year

In China, fertilized paddlefish eggs and fry that originated from a private hatchery in Missouri were first introduced in the mid- to late 1980s. Since then, several million fertilized eggs and fry have been imported into China each year from hatcheries in Russia as well as from the United States (H. Ji, Northwest Science-Technical University of Agriculture and Forestry, Yangling, Shaanxi, China, personal com-

munication). There have been no culture techniques developed for the endangered Chinese paddlefish *Psephurus gladius* (Grande and Bemis 1991), and the species probably will be further decimated by the Three-Gorges project on the Yangtze River, which was completed in 2008. Further, the Chinese paddlefish is a piscivore and thus less suitable for food fish culture than the American paddlefish (Mims et al. 1993a; Waldman 1995). China recently reported artificial propagation of the American paddlefish in Hubei Province in China. In Xianto City, close to Wuhan, American paddlefish have been artificially propagated and juveniles grown to 1 kg in floating net pens ($5 \times 4 \times 2.5$ m). Paddlefish are well accepted in high-end restaurants in large Chinese cities. Fish for caviar production are not presently known to be available, but there can be little doubt that paddlefish caviar will be a future high-dollar export from China.

Regulations and Permitting

Paddlefish, like all sturgeon species worldwide, are listed under the provisions of CITES (Convention on International Trade in Endangered Species of Wild Fauna and Flora, United Nations). 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. In 1989, the U.S. Fish and Wildlife Service (USFWS) was petitioned to include paddlefish on the list of threatened and endangered species under the provisions of the Endangered Species Act of 1973. After collecting supplemental data on paddlefish populations from the 22 states within its natural range in the Mississippi River and Mobile River drainages, the USFWS agreed that the listing of paddlefish as threatened was not justified. However, because of the uncertainty of the status of paddlefish in some areas of its range, the USFWS recommended a reclassification from category 3C ("abundant and not subject to threat") to category 2 ("potential endangered or threatened species, but needs more data to be conclusive"). Subsequently, paddlefish were added to the CITES Appendix II in 1992, which requires that an exporting country must have a CITES 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, whether native or introduced, it is considered to be verification that the export will not be detrimental to the species survival in the wild and that it was legally acquired.

Regulations for the propagation, culture, and transport of paddlefish as a food fish vary from state to state within the United States. Culturists should check with their natural resource conservation agency for proper permits and regulations before developing plans to farm paddlefish. In general, most broodstock must be captured from wild populations, which will require a license or special permit; also, some legal documentation might be needed if captured fish are purchased from commercial fishermen. Only six states (Arkansas, Indiana, Illinois, Kentucky, Missouri, and Tennessee) permitted commercial harvest in the period 1983–1994, down from 11 (Graham 1997; Bettoli et al. 2009, this volume). Currently, there are seven states (Arkansas, Illinois, Indiana, Kentucky, Mississippi, Missouri, and Tennessee) that permit restricted commercial harvest of paddlefish (see Bettoli et al. 2009).

Concern over gene pool contamination is essentially a nonissue relative to stocking in the United States. While the Mobile Bay drainage paddlefish population has some genetic divergence from the Mississippi River populations, paddlefish exhibit lower levels of allelic and haplotypic diversity than other freshwater fishes (Epifanio

et al. 1996; Heist and Mustapha 2008). Hybridization with related species is also not a potential problem. While hybridization among sturgeons is common (Billard and Lecointre 2001), paddlefish × sturgeon hybrids are unknown. Heterologous spermatozoa are purposefully used to activate egg development for gynogenic induction, and in induction studies for both paddlefish and shovelnose sturgeon *Scaphirhynchus platorynchus*, no viable hybrids were produced in control groups (paddlefish ♀ × sturgeon ♂ or sturgeon ♀ × paddlefish ♂) the only diploid offspring were gynogenotes from the heat-shock-treated eggs (Mims et al. 1997; Mims and Shelton 1998b).

Hatchery Facilities

Water Supply and Quality

A sustainable supply of good quality water is necessary for successful paddlefish hatchery and nursery operations. Groundwater is recommended, but surface water sources such as ponds, reservoirs, or streams can be acceptable. Groundwater tends to have a relatively minor seasonal temperature change but varies regionally.

Groundwater temperatures in the United States range from about 26°C in southern Florida to 3°C in northern Minnesota (Soderburg 1994). For paddlefish, water temperature for egg incubation should be 15–20°C, and 20–24°C for tank rearing. Groundwater typically contains few pathogens but may be low in dissolved oxygen, while other gases such as carbon dioxide, nitrogen, or argon can be supersaturated; therefore, groundwater might need to be treated. Other water quality characteristics such as alkalinity, hardness, and dissolved minerals (total dissolved solids [TDS]) should be tested since these characteristics can be very different from surface water. Water with hardness and alkalinity in the range of 100–300 mg/L as $CaCO_3$ range is preferable. Paddlefish commonly inhabit water with low TDS, for example within the Mobile Bay drainage of Alabama (W. Shelton, University of Oklahoma, Norman, personal observation). Calcium hydroxide can be added to groundwater to increase pH and alkalinity for making it more suited for fish culture and also to eliminate carbon dioxide.

Holding Tanks

Under most circumstances, circular tanks are best for holding broodstock and for fingerling production because continuous swimming is facilitated in tanks with no corners. Paddlefish swim continuously to aerate their gills (see ram ventilation in Mims and Shelton 2005). Paddlefish have a low capacity for branchial pump action (Bemis et al. 1997) and cannot efficiently respire without movement of water past their gills. This respiratory behavior is quite distinct from active filter-feeding which is triggered by detection of food in the water, followed by circling, flaring of the opercula and gaping of the mouth (Figure 1; W. Shelton, University of Oklahoma, Norman, personal observation). Broodstock must be held in tanks that have a diameter of $\geq$2.4 m so as to have sufficient swimming area.

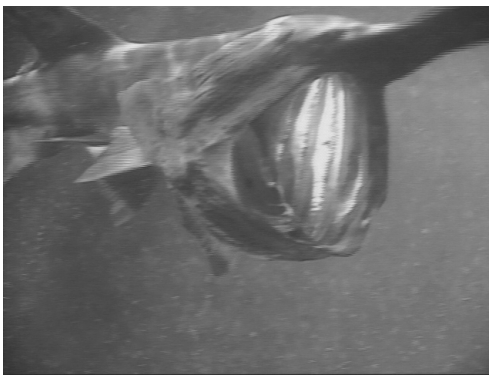

Figure 1. Photo illustrating the ability of paddlefish to filter feed by flaring of opercula, wide open mouth, and elongated gill rakers for capturing zooplankton from the water (Mims and Durborow 1998).

Tanks should be covered with netting fastened around the perimeter to prevent fish from escaping. Fingerlings also should be raised in circular tanks with diameters greater than 1.5 m. Water exchange of 25% of the tank volume per day is recommended. Tanks should have a smooth internal surface to prevent physical abrasions to the fish during their confinement. Fiberglass or plastic circular tanks are recommended, though painted metal stock tanks can be used. In the fingerling operation, circular tanks with conical-shape bottoms are beneficial because of the "vortex effect" by which excrement and excess feed move toward the drain and thus facilitate removal with a swimming pool vacuum system. Stainless steel or aluminum screens are recommended for the drain; mesh size should be about 1.5 mm (1/32 in) for newly hatched fry and up to 6-mm mesh for 12-cm and larger fish.

Broodstock

Paddlefish mature at a large size, and consequently broodstock management requires special considerations. If captive fish are to be retained from one year to the next, either large, fertile culture ponds are needed for year-round maintenance or, alternatively adults can be stocked in private watershed ponds or lakes. Semmens (1986) demonstrated that broodstock can be held in watershed ponds, and that egg development is not different from fish captured in riverine habitats. Broodstock that have been retained under pond conditions, produce mature eggs which are viable and have fertility equivalent to those of wild-caught females. In several instances a single female has developed mature eggs on consecutive years. Further, egg development is normal under conditions of low TDS, and incubation does not appear to be affected (W. Shelton, University of Oklahoma, unpublished data).

Initially, broodstock must be obtained from public waters (Mims et al. 1999). Some states classify paddlefish as a sport fish, and thus, special permits must be obtained in order to capture adults for artificial propagation. Licensed commercial fishermen can be a source of broodstock; however, special permission might be required in addition to their normal license in order to obtain stock for propagation. Fish are captured in gill nets with 15-cm or larger bar-mesh webbing; nets are set in rivers or lakes in late winter or early spring when water temperatures are less than 16°C (see harvest section in Mims and Shelton 2005). A broodstock registry has been established for paddlefish (Kincaid et al. 1999). This resource provides a mechanism to collect, analyze, and interpret diverse biological information needed by fishery managers and aquaculturists.

Males are generally smaller and can be identified by minute tubercles on their head and opercular flaps during the spawning season (O'Keefe and Jackson 2009, this volume), although this is not entirely dependable as not all males are tuberculate and some females may have some tuberculation. Females mature at sizes larger than 9–15 kg (107–140 cm) and males larger than 7–9 kg (Mims et al. 1999; Jennings and Zigler 2000). Paddlefish mature at a somewhat smaller size in the Mobile River drainage (females > 7–10 kg or 82–90 cm; males < 7 kg or 72–75 cm [Hoxmeier and DeVries 1997; Lein and DeVries 1998]). A gravid female will have an enlarged abdomen and the gonopore area may be distended and reddish.

Broodstock can be transported to hatchery facilities in transport tanks that have dimensions sufficient to accommodate the fish length. A loading rate of about 0.25 kg/L, supplemental oxygen, and the addition of sodium chloride (2.5–5.0 g/L) are highly recommended. Paddlefish respond to confinement by becoming lethargic and

unresponsive. As soon as they are loaded in transport tanks, they float belly up moving infrequently and they have weak operculation. They appear to be in a state of extreme physiologic stress; however, plasma levels of stress indicators increase less in paddlefish than for most teleosts (Barton et al. 1998). Paddlefish survive surprisingly well despite this behavior and their poor capacity to operculate by branchial pumping (Bemis et al. 1997; Mims and Shelton 2005). Upon arrival at the destination, fish recover and will swim normally with some stimulation, such as sharply slapping the caudal fin and pushing them through the water until they resume swimming on their own.

Induced Spawning

Some of the techniques used to propagate paddlefish have been modified from those developed for sturgeon (Conte et al. 1988; Dettlaff et al. 1993). A dependable supply of seed stock through artificial propagation is a vital component for aquaculture, but similarly, it is just as important to hatchery programs aligned with stocking for resource management. Further, commercial production can have a positive effect on conservation efforts, as the products supplied for the market reduce fishing pressure on wild populations of paddlefish and sturgeons (Billard and Lecointre 2001).

Broodstock Selection

Unlike most teleosts, the oviduct branches of paddlefish and sturgeons open dorsally into the body cavity rather than being attached directly to the ovaries. Consequently, unovulated oocytes cannot be directly sampled via oviductal catheterization (see Predicting Ovulation in Shelton 1989). However, paddlefish broodstock can be evaluated by ova staging to determine gamete maturity as has been done for sturgeon (Kazanskii et al. 1978; Doroshov et al. 1983). Intraovarian ova are sampled through a small (0.5 cm) abdominal incision (Shelton and Mims 1995). For paddlefish, distribution of ova pigmentation and the position of the germinal vesicle can be used to judge progress toward final maturation (Figure 2). Oocytes that have been sampled from the ovary are placed in a vial with a small amount of water, then boiled for 2–5 min until the yolk is hardened. With a sharp blade, several eggs are cut in half passing through the polar axes. The position of the nucleus (germinal vesicle [GV]) indicates the status of progression toward final maturation; the GV moves toward the animal pole (germinal vesicle migration [GVM]) from a central location embedded in the yolk. If the GV is centrally located at sampling, the effect of hormonal injection (see below) will be uncertain; however, if GV has been displaced toward the animal pole under the influence of endogenous hormones, then ovulation probably can be stimulated by hormone injection. Upon reaching the animal pole, the nuclear membrane disintegrates (germinal vesicle breakdown [GVBD]); this transformation signals the resumption of meiosis and produces the first meiotic polar body.

Injection Protocol

Common carp *Cyprinus carpio* pituitaries are commercially available and have been used as a standard means of artificial propagation for many species. Clemens and Sneed (1962) reported the efficacy of various pituitary donor–recipient relationships. However, Semmens (1986) found that common carp pituitary had a lower stimulating effectiveness than a homoplastic injection for paddlefish; consequently, until other gonadotropic materials were subsequently developed, propagation depended on collecting pituitaries from mature paddlefish during the prespawning period. The early conventional practice for artificial propagation of paddlefish was to induce ovula-

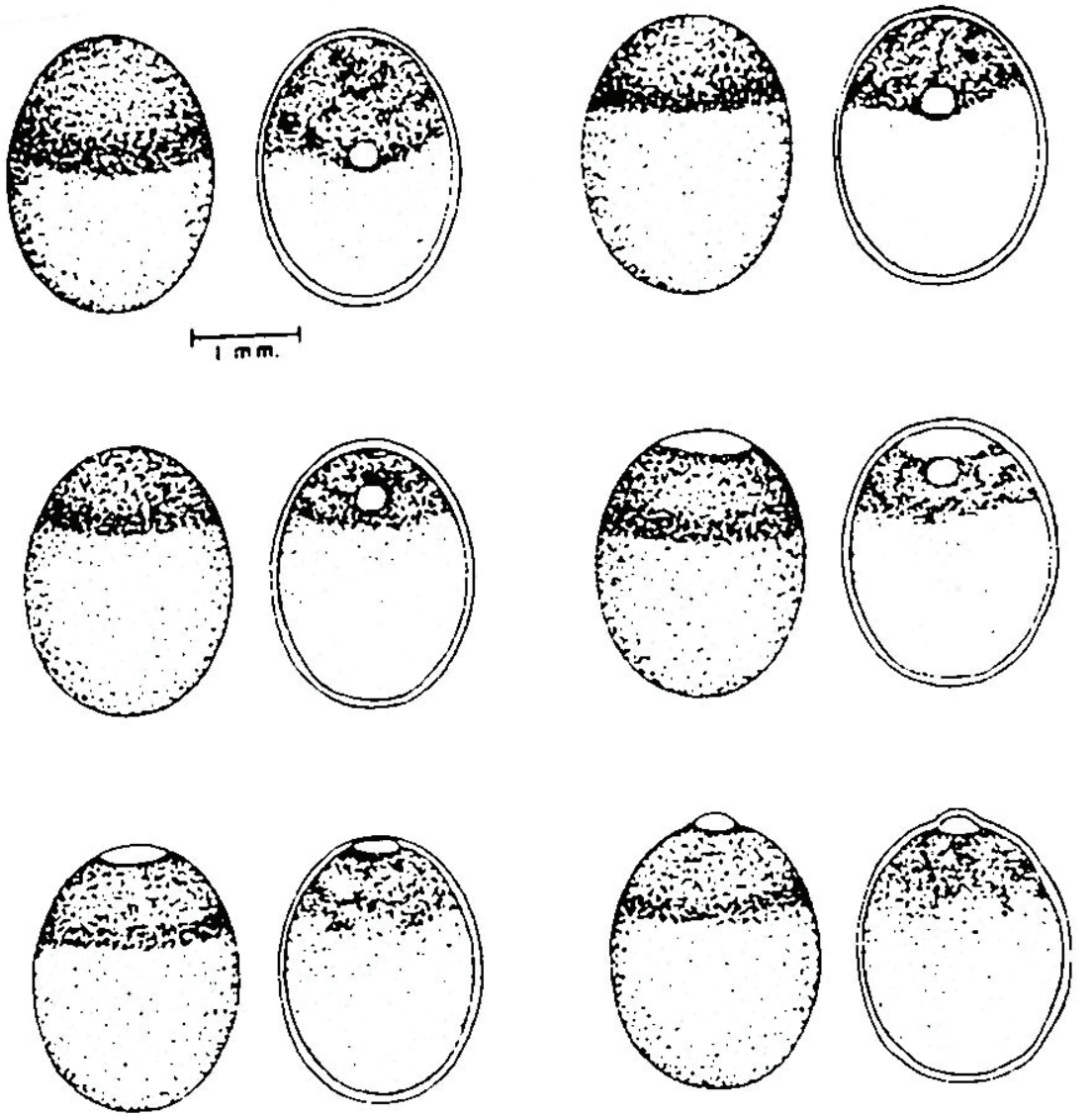

Figure 2. Paddlefish oocytes stages; left illustration of each pair is representative of the surface pigmentation and the right illustration of each pair is of bisected oocytes showing yolk distribution and germinal vesicle position (Shelton and Mims 1995).

tion with a homoplastic injection of freshly collected paddlefish pituitaries; the glands were collected and frozen until they were thawed and injected. Dose for females was a single injection of two glands from equivalent weight donors (Graham et al. 1986). The latent period for females injected early in the spawning season is 30–36 h, but after18–24 h, later in the season. Dose rate for males is not as critical; generally one-half the female dose is adequate to stimulate good milt flow.

Contemporary treatment for gamete maturation is to induce with intraperitoneal injections of LHRH*a*) of des-Gly 10(D-Ala6) ethylamide (Mims et al. 1997, 1999). In the

United States, use of this hormone is not yet approved for paddlefish. To use LHRH*a*, an investigational new animal drug permit is required; it is administered by the U.S. Fish and Wildlife Service.

Both Graham et al. (1986) and Semmens (1986) report that latency for females injected with LHRH*a* is somewhat shorter than for females injected with pituitaries. Females are given a total dose of 100 μg/kg body weight administered in two injections, 12 h apart; the priming injection is 10 μg/kg and the resolving injection is 90 μg/kg. Ovulation is expected in 12–24 h at 17°C. Males are given a single dose of 50 μg/kg when the females receive the priming injection. They will spermiate within 24 h and continue for 3–4 d. Unlike injection with pituitary, which primarily increases milt volume rather than stimulating spermatogenesis (Shelton 1989), injecting males with LHRH*a* does significantly increase the numbers of spermatozoon (Linhart et al. 2000). Late in the spawning season, particularly if broodstock are recently captured, females might ovulate after receiving only the priming dose. As the gonadotropin effects maturation, the GVM proceeds toward the animal pole, and upon reaching the polar area, GVBD signals the resumption of meiosis and the pending formation of the first polar body.

Females should be checked periodically during the latency period for behavioral or physical signs of pending ovulation; some jumping or increased swimming speed frequently precedes ovulation. Slight pressure on the abdomen will express a few eggs, verifying that ovulation has occurred, or occasionally some eggs may be seen adhering to the bottom of the holding tank. If eggs are to be stripped without further intervention, then collection can begin, but if one of the surgical techniques is to be used, a delay of an hour or so will ensure a more complete ovulation.

Gamete Collection

Eggs are ovulated into the peritoneal cavity, and to be spawned, they must enter the dorsally attached oviducts via mid-anteriad openings. This morphological feature is the reason ovarian egg sampling via catherization cannot be done (Shelton 1989). After ovulation, conventional egg collection has been through multiple strippings of a few hundred milliliters of eggs at 30– 60-min intervals over a 12–24-h period (Graham et al. 1986). More recently, ovulated eggs have been scooped from the abdominal cavity through a long ventral incision as practiced in artificial propagation of sturgeons (Conte et al. 1988). Surgical removal accelerates the collection of eggs compared to the labor-intensive and lengthy stripping procedure; however, in our experience, most females die if exposed to extended and frequent stripping or to surgical egg removal. If an incision is made, it is subsequently closed with sutures or staples, but unlike sturgeon, the closure is usually disrupted because sutures or staples pull through the flesh of paddlefish leaving an unprotected wound. The continuous swimming action of the paddlefish might put more stress on the incision compared to the more sedentary behavior of sturgeon.

Stéch et al. (1999) demonstrated a minimally invasive surgical technique (MIST) that provides free-flowing eggs via a small incision (ca. 1.0 cm) through the common oviduct near the urogenital opening (Figure 3). A direct opening into the body cavity is thus developed, which permits free-flow stripping of ovulated eggs; the procedure requires only 10–15 min to collect the eggs and the fish can be returned to the water with minimal stress. This procedure has not resulted in either short-term or delayed mortality of fish. Second-time MIST spawners have been successfully ovulated in subsequent years (Mims et al. 2004). Recently, S. D. Mims (unpublished data) has demon-

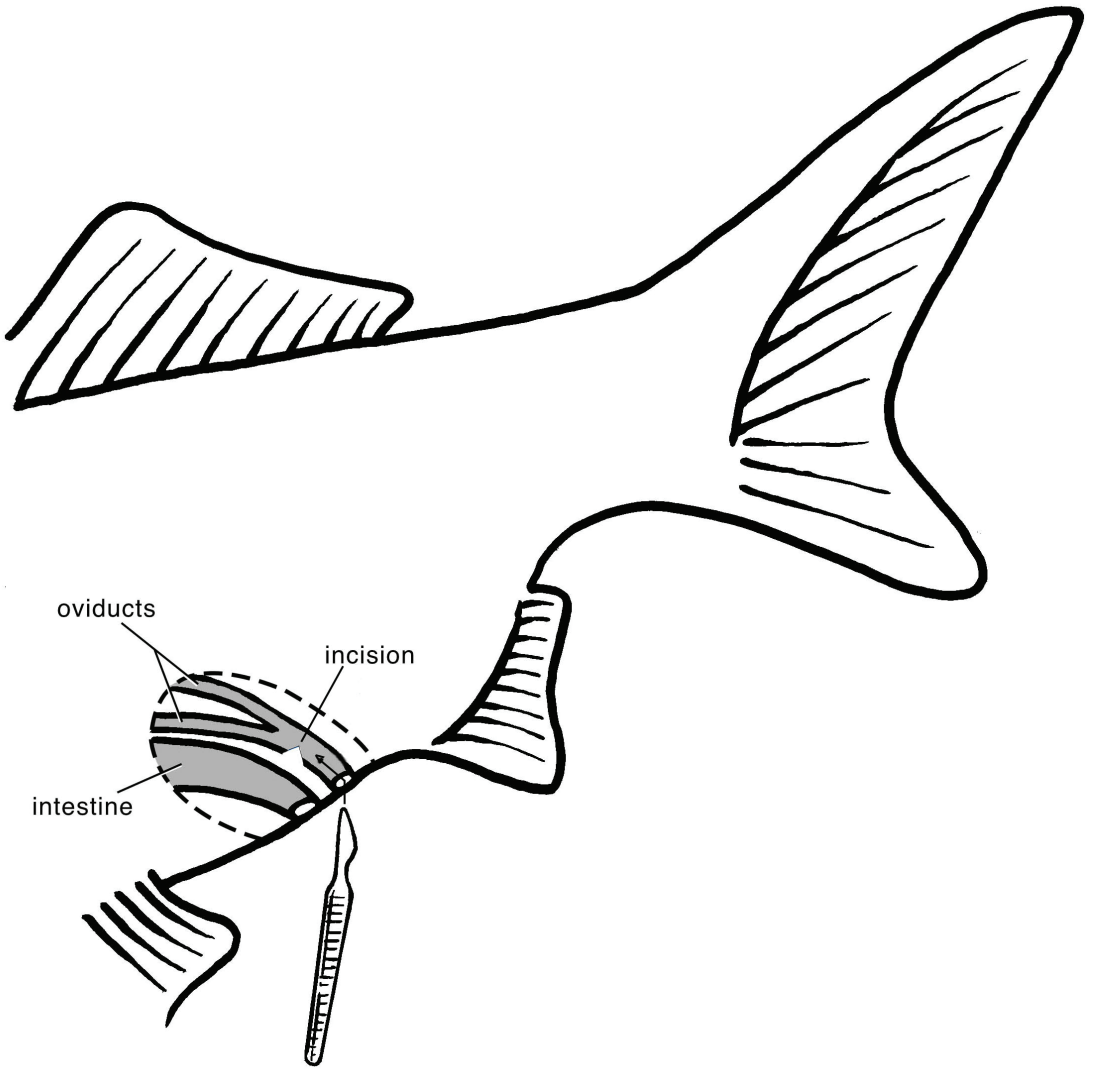

Figure 3. Schematic illustration of minimally invasive surgical technique for removal of ovulated eggs from paddlefish (Mims and Shelton 2005).

strated a modification of the MIST where a small incision (1.0 cm) is made externally through the relatively thin body wall, either to the left or the right of the gonopore. The eggs can be removed by stripping in less than 10 min, and a single suture or stainless steel staple is suitable for closing the incision. This procedure has demonstrated minimal complications and nearly 100% of the fish have survived.

The total number of ovulated eggs varies with fish size. Mims et al. (1999) reported that 9–36-kg females will release 70,000–300,000 eggs while Graham et al. (1986) reported that 20–30 kg-females (10–13 years old) have 300,000–400,000 eggs (ca. 15,000–20,000/kg). Total fecundity for paddlefish from the Mobile Bay drainage is 15,000–23,000 eggs/kg of body weight (Lein and DeVries 1998), but ovulation range is about 8,000–11,000 eggs/kg of body weight (Semmens 1986).

Spermiating males can provide large volumes of milt (i.e., >500 mL) over a 96-h period (Linhart et al. 2000). Milt is collected by inserting a short segment of plastic tubing attached to a syringe into the urogential opening and applying light suction to fill the syringe. The concentration of spermatozoa can be estimated in a square, 10-mm pathway cuvette placed in a spectrophotometer at a wavelength of 450 nm. Linhart et al. (2000) reported a linear regression relationship for sperm concentration: sperm concentration $\times 10^9$/mL = $1.3244 \times X^{-0.9969}$, where X is the percentage of light transmittance. A considerable range in milt volume is produced, which affects the spermatozoan concentration. Paddlefish milt has a range of 0.3–1.7 $\times 10^9$ spermatozoa/mL (Linhart et al. 2000). Milt samples can be chilled on "wet" ice (ice held at room temperature until ice surface is wet) or held undiluted in a refrigerator (1–4°C) for short-term storage of 12–24 h.

Cryopreservation

Cryopreservation of paddlefish milt is useful in the domestication of broodstock either for commercial culture or for conservation efforts. Cryopreservation of paddlefish milt was first reported by Brown and Mims (1999) using a cryoprotectant medium with dimethyl sulfoxide (DMSO). The volume of milt to medium was 3:1 with a final concentration of 0.6 M DMSO or about 4%. The mixture was frozen in 5-mL straws on dry ice for 15 min and stored in liquid nitrogen. Hatching rate of fry was 16 ± 2% using post-thawed milt compared to 90 ± 3% using fresh sperm. Hórvath et al. (2006) reported a method using methanol as a safer and more reliable cryoprotectant than DMSO for freezing paddlefish milt in liquid nitrogen vapors. Post-thaw sperm were viable and provided fertilization and hatch rates comparable to fresh sperm. Milt was diluted 1:1 in a modified Tsvetkova's extender containing 30 mM tris, 23.4 mM sucrose, 0.25 mM KCl, pH 8.0, and osmolality of 82 mOsmol/kg, as described by Glogowski et al. (2002) for extending sturgeon milt. Methanol at 5% or 10% (V/V, final concentration) was used as a cryoprotectant. The milt samples were loaded into 0.5-mL French straws, which were distributed horizontally on a Styrofoam frame and frozen in the vapor of liquid nitrogen in an insulated box and plunged into liquid nitrogen after 3 min in the vapors. With modified Tsvetkova's extender and 5% methanol, thawed milt gave hatching rate of fry as high as 79 ± 5% compared to 88 ± 6% with fresh milt (control). There was no significant difference found in fertilization or hatching rate when either 5% or 10% methanol was used as a cryoprotectant (Hórvath et al. 2006).

Fertilization and Egg Incubation

Motility of spermatozoa should be checked microscopically for viability in egg fertilization. Milt is diluted in water (1:100–200) just prior to adding to the eggs to prevent polyspermy (Ginzburg 1972; Dettlaff et al. 1993); acipenserids have multiple micropyles (Cherr and Clark 1985) increasing the probability of polyspermy. Twenty to thirty milliliters of milt are added to 2–4 L of water, then added to 1–2 L of eggs and stirred for about 1 min. The number of fertilized eggs can be estimated by assuming volumetric displacement of about 50,000/L (Mims and Shelton 1999).

Fertilized eggs are adhesive and demersal (Purkett 1961, 1963a; Yeager and Wallus 1982). The outer membranes react causing adhesiveness as described for sturgeon by Cherr and Clark (1985) and Markov (1978). If incubation is to be in a flow-through jar, they must be treated to prevent clumping. Conventional treatment of sturgeon eggs has been to coat them with river silt (Doroshov 1985; Conte et al. 1988; Dettlaff et al. 1993) or with a suspension of Fuller's

earth at about 50–75 g/L; the latter has been the most widely applied to counter the adhesiveness of paddlefish eggs (Graham et al. 1986; Mims and Shelton 1998a). A Fuller's earth suspension is added to the fertilized eggs and stirred continuously for 20 min, usually with one change of fresh suspension during this interval. The eggs are rinsed in freshwater prior to loading in the hatching jars. Kowtal et al. (1986) reported an alternative treatment with urea/salt/tannic acid that would remove the adhesiveness of white sturgeon *Acipenser transmontanus* eggs. The hatch rate was comparable to silt treatment. Although this technique is widely used for common carp eggs, it is more complicated than direct coating of the adhesive eggs and is not recommended.

Water for incubating fertilized eggs should be one time through, not recirculated, in order to maintain optimal water quality and minimize diseases. The most reliable means of incubation is with upwelling, flow-through hatching jars such as the McDonald hatching jar, commonly use for sturgeon and striped bass. The incubation jars are 8-L capacity, round bottom cylinders, 46 cm tall and 16 cm in diameter, and are made from an acrylic plastic that allows direct observation of the eggs and water flow patterns. The water enters the jar through a 2.5-cm-diameter acrylic tube that has three wings attached to the bottom of the tube; a screen at the top holds the tube firmly in place. This design provides adequate control of water flow and movement of the eggs, which fosters egg development and limits mortality from environmental stress and bacterial or fungal development. Each jar can be loaded with 50,000–70,000 eggs (Graham et al. 1986; Mims et al. 1999). Water flow is supplied at about 4–6 L/min in order to introduce aerated water, remove metabolic wastes, and maintain a gentle motion of the eggs.

Time to first cleavage ranges from 148 to 215 min inversely within the temperature range of 14–20°C or about 2.5 times the interval between subsequent synchronous mitotic divisions (τ_0), 48–84 min, respectively (Rubinshtein et al. 1997; Shelton et al. 1997). The mitotic interval or developmental duration (τ_o) for paddlefish in the range of 16–20°C is between 75 and 50 min, respectively, which is longer than that of the shovelnose sturgeon *Scaphirhynchus platorynchus* (Shelton et al. 1997) and for four species of Russian sturgeons: Russian sturgeon *Acipenser gueldenstaedti*, stellate sturgeon (sevryuga) *A. stellatus*, sterlet *A. ruthenus*, and beluga *Huso huso* (Dettlaff et al. 1993). Paddlefish and sturgeon embryogeny are comparable but atypical of teleostean development. Cleavage is intermediate holoblastic, and at 14°C, the early blastula is formed in 24 h, gastrulation is initiated by 32 h, and neuralization, including optic vesicle formation, is evident in 90 h, although little increase in size of the eye occurs between 4 and 21 d (Ballard and Needham 1964). During day 6 (121–144 h), the tail bud is free from the yolk surface and active movement begins.

Fry Hatching and Development

Incubation period to hatching takes about 5–12 d (155–166 h) inversely within the temperature range of 11–19°C. Time to hatching is 10–12 d at 11–12°C, 7–8 d at about 16°C, or 5–6 d at 18–19°C (Graham et al. 1986; Melchenkov et al. 1996; Bemis and Grande 1992; Mims and Shelton 2005). Earliest hatching may begin significantly sooner than the time of peak hatching, and total hatching period may last 2–3 d. As the fry begin to hatch and swim-up, the jar should be positioned to permit the fry to swim into a catchment container such as an aquarium with a screened drain or into screen baskets floating in a tank. Dur-

ing early posthatching, yolk sac fry are about 9–10 mm and they swim vertically in the water column, then sink passively. Swimming behavior changes as the swim bladder develops and yolk absorption proceeds; fry swim continuously for the next 2–3 d near the water surface in erratic circular patterns.

Yolk absorption is complete by about 5–6 d posthatch at 18°C and at 17–18 mm; during this interval, the foregut forms and perforates the oral plate to develop the mouth and barbels begin to form as the rostrum elongates. The mouth opening has developed by about 8–9 mm and the jaw becomes functional between 13 and 17 mm; incisor-like teeth form in the upper and lower jaws and barbels can be easily seen as they are disproportionately large compared to the minute structures in adults. Between 21–34 mm, fins assume their definitive shape, including the heterocercal caudal fin (Yeager and Wallus 1990).

Fry

Shipment and Transport

Fry can be shipped in plastic bags filled with water and oxygen, placed in a Styrofoam container and then into a cardboard box. The following technique has been satisfactory for air transport of 48–60 h (Mims, unpublished data). The plastic bags should be 38 × 38 × 56 cm, 75-μ-thick square-bottom bags. The Styrofoam container and cardboard box should be 43 × 43 × 25 cm. Two plastic bags should be used to avoid loss in the event of a puncture. About 10 L (one-third filled) of good quality water (well aerated, neutral pH, low ammonia and nitrite levels) should be added to the inner bag. Fry should be stocked at 0.5 fry/mL of water. Then the remaining air volume is displaced with oxygen by injecting through a flexible tube, which is inserted through a narrow opening of the inner bag formed around the flexible tube in the palm of the hand. The upper portion of the inflated bag is twisted and folded, then sealed with a strong rubber band. The outer bag is similarly closed and secured. Water temperature during shipping should remain between 12°C and 15°C; gel cold packs (400 g) can be taped to the inside lid of the Styrofoam container to reduce warming. Mortality will be generally less than 10% within 48 h. Carbon dioxide accumulation ranging from 6 to 8 mg/L after 48 h has been found to be the main factor causing higher mortality rates (Mims, unpublished data).

Pond Nursing

Pond nursing is the traditional method of raising paddlefish to fingerlings but is dependent on managing for large cladocerans as the food of choice (Ruelle and Hudson 1977; Rosen and Hales 1981; Michaletz et al. 1982; Webster et al. 1991; Mims et al. 1995a). When fry begin to feed exogenously, they can be stocked into earthen ponds. First feeding coincides with the appearance of darkly pigmented material in the gut and in the spiral valve. Pond preparation should begin about 2 weeks before stocking.

Organic fertilizers have been the most effective in stimulating cladoceran populations (Michaletz et al. 1982; Graham et al. 1986; Mims et al. 1991; Mims et al. 1995a, 1995b, 1999). A combination of rice bran and inorganic fertilizer has given best results in Kentucky (Table 2). Ponds should be filled from a groundwater source and organic fertilizer distributed over the surface of the pond. Until fish are stocked, continuous aeration will ensure oxygen saturation and help to disperse fertilizers. After pond fertilization, the pond should be inoculated with *Daphnia* spp. (i.e., *D. pulex* and *D. magna*) at a rate of at least one organism per 4-L pond volume. Fertilized ponds should stand for about 2 weeks to permit expansion of cladoceran populations and then, fish fry stocked at a rate of 62,000/ha. Fry

Table 2. Quantities and application schedules for rice bran and inorganic fertilizer in paddlefish nursery ponds (Mims et al. 1991).

Week	Rice bran[a] kg/ha	Inorganic fertilizer[b] L/ha
0[c]	1,410	37.0
1	310	4.6
2	160	9.3
3	160	9.3
4[d]	160	9.3

[a] Other organic fertilizers can be used based on a total application of 45 kg/ha of nitrogen.
[b] Inorganic fertilizer 10–34–0.
[c] Fertilizers were applied to filled ponds three times per week during a 2-week period before stocking.
[d] Fish should be offered extruded diet of 1.5 mm during week 4.

should be transported to nursery ponds before dawn; stocking rate in plastic bags with an atmosphere of oxygen can be up to 500–600/L of water. Transient time can be up to 36 h (Graham et al. 1986; Mims and Durborow 1998).

Variation in water temperature in late spring can greatly affect the numbers of large cladocera and therefore result in variable fish growth and survival. An insufficient supply of cladocera is a particular problem during the 3–4 weeks before fish have been trained to a floating diet. Other zooplankton such as rotifers, copepods, and ostracods are either too small or too fast to be a suitable food for paddlefish. Ponds should be aerated, but small-mesh (6 mm) screen should surround the impellers to prevent contact with fish. Dissolved oxygen should be maintained at greater than 30% oxygen saturation (i.e., 3–4 mg/L).

Another problem with pond culture is bird predation. The surface orientation of fry/fingerlings and their swimming behavior make them extremely vulnerable to birds such as cormorants and herons. Covering ponds ($\leq$400 m^2) with netting has reduced losses but may not be practical or cost-effective on large ponds. Survival in uncovered nursery ponds is highly variable with reported ranging from about 30–80% (Michaletz et al. 1982; Mims et al. 1991, 1995a).

With intensive systems such as tanks and raceways, early training to prepared larval diets is critical to survival and growth. Selection of the optimum prepared diet is important for proper nutrition, energetics, and palatability. Paddlefish fry readily accept trout and salmon prepared diets (40–50% protein and 8–10% fat), especially those made by Rangen, Inc. (Kroll et al. 1994; Mims and Shelton 1998; Onders et al. 2005). Suggested feed sizes and durations are as follows: #00 fed for week 1, #01 fed for week 2, #02 fed for weeks 3 and 4, and 1.5-mm extruded diet thereafter, once fish are more than 7 cm total length (TL). Each increase in diet size per week should include a mixture of 25% of the smaller diets for smaller fish in the population for a 2–3-d transition period. Water temperatures between 22°C and 24°C are necessary for prepared diets to be digested and to provide essential nutrients for growth of the fish (Kroll et al. 1992; Melchenkov et al. 1996). The first week is most critical in training the fish to prepared diets and is often when most mortality occurs.

Automatic belt feeders are best suited for continuous feeding over a 24-h period. The fish will only eat feed floating on the surface or as it sinks through the water column. Feed that has accumulated on the bottom will not be eaten and should

be vacuumed once or twice daily so as not to affect water quality (Onders et al. 2005). Increased vertical water movement slows the feed settling, which results in more efficient utilization and thus better growth and survival (Mims, unpublished observations). Indications that the fry are not ingesting enough feed will be the nipping of the caudal fin or even cannibalism. Survival should range from 10% to 20%.

When fish reach more than 12.5 cm TL or more than 20 g and are trained on 1.5-mm extruded pellets, they can be stocked in tanks or ponds for further grow-out (Onders et al. 2005, 2008). As the rostrum develops, it becomes an impediment to ingesting prepared floating diets; when fish rise to the surface to feed, they must rotate partially on their side to be able to take the pellets into their mouth.

A recent study in Kentucky (Mims, unpublished data) has demonstrated fry having higher survival and better growth using live *Daphnia* in circular tanks the first 4–5 weeks than those fed prepared diets from swim-up. Massive quantities of *Daphnia* were obtained from secondary wastewater treatment tanks (Mims et al. 2007, 2008). Fry fed 270 *Daphnia*/L twice daily in a static system had about 80% survival and were then easily trained to extruded 1.5-mm pellets after 4–5 weeks. Tank cleaning was reduced to twice weekly when live food was used as compared to twice daily with prepared diets.

In Texas, stocking rate in tanks or raceways at about two fish/L for the first 2 weeks (to size of 5 cm) has been successful; then, to maintain good growth, stocking rate was reduced at biweekly intervals by about half. Survival of 20–30% can be expected (J. Isaac, A.E. Woods Hatchery, personal communication). In Russia, Melchenkov et al. (1996) have reported using higher densities (10/L) of paddlefish fry when fed prepared diets and raised in flow-through circular tanks to produce 2–4 g fish that were ca. 7.5–10 cm TL (Table 3). Other fry production protocols are indicated in Table 1.

Phase-I and -II Fingerling Culture

Phase-I paddlefish fingerlings are defined as fish averaging 2–4 g and 7.5–10 cm TL; this size fish can readily consume a 1.5-mm extruded pellet. Phase-II fingerlings (sometime called armlings) are defined as fish at least 150 g and 35 cm TL; stocking fish of this size reduces predation (Onders et al. 2005).

Tanks

The culture of Phase-I to Phase-II fish in tanks has not been published, but some information and observations will be provided. Paddlefish do not tolerate crowding and will compete for space (Gershanovich 1983) relative to their type of respiration and competition for feed. As the paddlefish increase in size, they frequently collide under crowded conditions. When this condition occurs, a feeding hierarchy develops and results in differential growth. Under these conditions, even feeding to satiation will not rectify the continuation of this disparate growth. Larger fish can be transferred from the tank to reduce competition on the smaller fish. A complete diet with a minimum of 32% protein, 4.5% lipid, and

Table 3. Density of paddlefish juveniles nursed in raceway flow-through system relative to weight and water flow [modified from Melchenkov et al. (1996)].

Weight (mg)	Density (fish/L)	Water flow (L/min)
20–50	30–35/L	12–15
51–100	20–25/L	12–15
101–500	10–12/L	15–17
501–2,000	2–3/L	20–25
2,001–4,000	<1/L	20–25

a maximum of 5% fiber should be fed. Diets made for channel catfish *Ictalurus punctatus*, hybrid striped bass (female white bass *Morone chrysops* × male striped bass *M. saxatilis*), and trout have been observed to provide adequate nutrition for good growth and survival (Onders et al. 2005).

Initially, Phase-I fish will take a floating 1.5-mm pellet for the first 3 weeks. Thereafter, fish that are larger than 15 cm (about 20 g) can use a larger pellet of 3.2 mm, but feed should be mixed with smaller pellets until all fish can eat the larger size. Fish greater than 25 cm (about 50 g) can take a pellet size of 5 mm. Fish should be fed 5–10% of body weight daily unless water quality begins to deteriorate. Low dissolved oxygen and elevated nitrites are two most frequent water quality problems in tank culture. Surface aeration can be used to maintain adequate dissolved oxygen levels (i.e., 40% of saturation). In tanks deeper than 2 m, forced air diffusion should be used in addition to surface aeration so as to provide vertical water movement. Nitrite levels that may cause methemoglobinemia (brown blood disease) in paddlefish have not been studied. However, as a precaution, application of salt should be made using a similar protocol to that recommended for channel catfish; use 20:1 (chloride:nitrite) or milligrams Cl^-/L to milligrams NO^{-2}-N/L sodium chloride (noniodized salt) for treatment (Tucker et al. 1989). The chloride blocks the transport of nitrite via the gills to the blood and prevents the condition. Phase-I and –II paddlefish fingerlings grown in 1.2 million liter tanks in Kentucky showed no ill-effects at nitrite levels as high as 7.4 mg/L NO^{-2}-N when treated with 150 mg/L of chlorides (Mims, unpublished data).

Ponds

Phase-I fish greater than 20 g can be stocked in ponds covered with bird netting at densities up to 25,000/ha to obtain Phase-II fish during a 100-d growing period (Onders et al. 2008). Survival, relative growth, and feed conversion ratio were reported to average 90%, 5.45, and 1.5, respectively. Higher stocking density can be considered, but in order to obtain high numbers of Phase-II fish, reducing the population size or extending the growing period might be required. Onders et al. (2005) reported paddlefish can be fed a commercial catfish diet containing 32% protein and 4.5% lipid without adverse effects on survival and growth, but significantly lower production cost when compared to fish fed a commercial trout diet containing 45% protein and 16% lipid. After initial pond stocking, fish should be fed about 10% of their body weight per day. Thereafter, fish should be sampled every 2 weeks and their feeding rate adjusted for satiation (Onders et al. 2008).

Grow-Out Production

Cage Culture

Confining fish in floating cages or pens is an attractive alternative in some culture situations, such as ponds that cannot be drained, reservoirs, and lakes (Stickney 2000). This production system has been recently practiced with paddlefish in reservoirs in central China. Cages (5 × 4 × 2.5 m) or 50 m^3 were constructed with 5-cm polyvinyl chloride pipe covered with 1.5-cm knotless mesh. Paddlefish (15 cm TL or about 20 g) were stocked at 10–20 fish/m^3 and fed a 35% protein extruded diet for 150–180 d. Fish were harvested at an average weight of 0.7 kg and were marketed live to high-end restaurants (C. Wang, Kentucky State University, Frankfort).

A circular-designed cage (6 m in diameter by 2.5 m in depth constructed with knotless mesh) is being tested for paddlefish in some Indiana reservoirs. The advantage of this type of cage is that there are no corners and therefore permits continuous swimming, which is important for paddle-

fish growth and survival. A disadvantage has been predation by river otters, which has been corrected by using metal mesh for the top of the cage and around the outer edge. If cage culture is proven to be suitable, it will permit more bodies of water to be used for paddlefish culture as fish could be fed to a larger size before being released (see Reservoir Ranching).

Polyculture with Channel Catfish

Growing paddlefish (2–3 kg) with channel catfish over a 12-month period is an aquaculture strategy that targets meat production. However, this culture system could also be used by governmental facilities to grow larger fish so as to reduce bird and fish predation when stocking rivers and reservoirs. Since paddlefish are filter feeders and feed primarily on zooplankton, the carrying capacity of a system will be higher than if only catfish are stocked. Currently, there is not a bioenergetics model to predict the optimal number of paddlefish to be stocked relative to biomass potential; however, based on some preliminary research, pond type and stocking rate can be estimated.

Ponds that are more than 5 years old typically have an established food base favorable to paddlefish; newer ponds (less than 5 years) should be assessed for zooplankton abundance before stocking. In Kentucky studies, average survival was about 30% in new ponds (i.e., less than 2 years old) compared to 75% in ponds that were 6 years or older (Mims and Onders 2006). Newer ponds can be seeded with zooplankton to increase and diversify its natural population. Stocking rate will depend on the target-size fish for the market or for further grow-out. About 250 Phase-II paddlefish/ha can be stocked in polyculture with channel catfish (i.e., fed a commercial diet). After one growing season (about 12 months), assuming 75% survival, about 350–500 kg/ha of 1.9- to 2.7-kg size fish can be harvested (Mims and Onders 2006). Paddlefish can be removed using the same net or seine used to harvest catfish. Seines should be large enough to encircle the entire area of the pond. In the middle of the seine, there is a "sock" attachment, which is 3–5 m long and allows the fish to be crowded. Socks are of different mesh sizes to passively grade fish by allowing small fish to escape into the pond and larger fish to be retained. During this grading process, paddlefish can be easily removed by hand-sorting. The fish are relatively docile and the rostrum permits easy capture. In addition, the paddlefish tend to congregate around the perimeter of the sock and at the surface. Paddlefish should not be grown in catfish ponds longer than 1 year, and catfish culture ponds are not considered suitable for growing fish for caviar production. Frequent handling during partial sequential harvest of catfish or during periods of warm water (above 20°C) and low dissolved oxygen (2 mg/L) could result in catastrophic losses, particularly of mature fish.

A modified polyculture system that has been used with paddlefish and catfish was developed in Arkansas by a private fish farmer (K. Semmens, University of West Virginia, personal communication). Catfish and paddlefish were stocked in separate ponds, but the enriched water from the catfish ponds was allowed to flow into the paddlefish ponds, either by gravity or with air-lift pumps. With this approach, catfish were fed and harvested without handling the paddlefish. Another modified polyculture system using channel catfish and paddlefish being tested in Alabama is known as "in-pond raceways," in which the catfish are intensively raised in raceways built in the pond using flow-through pond water. Effluent water is returned to the open pond for biofiltration partially managed with paddlefish in the

open pond (J. Chappel, Auburn University, personal communication).

Reservoir Ranching

This production system is an extensive, sustainable, nonpolluting operation in which Phase-II fish are stocked into lakes or reservoirs, public or private waters, and allowed to freely forage on zooplankton until they reach a harvestable size and age (Onders et al. 2001). Several states stock paddlefish and permit harvesting by angling as a sport fish (Graham 1997). Whether the end user is an angler or a commercial fisherman, the open-system management is essentially the same. However, in public waters, conflicts invariably develop between sportfishermen and commercial fishermen. Although many countries use reservoir ranching to produce food fishes, most freshwater reservoirs in the United States are used solely for sport angling and recreation. Recently, the Kentucky Department of Fish and Wildlife Resources passed a series of regulations (i.e., 301KAR1:115 propagation of aquatic organisms) providing for permits to stock water-supply reservoirs owned by small municipalities, presenting the option to grow mature female paddlefish for caviar (Mims et al. 2006).

In general, Phase-II paddlefish can be stocked in lakes and reservoirs that are managed for sport fishes such as largemouth bass *Micropterus salmoides*, hybrid striped bass, or walleye *Sander vitreus*. However, they should not be stocked in reservoirs managed for large predators such as striped bass, tiger muskellunge (muskellunge *Esox masquinongy* × northern pike *E. lucius*), or northern pike that could prey on the stocked paddlefish or later could be entangled in gill nets during harvest. Paddlefish can be stocked at 25–50 fish/ha and with an expected survival of at least 50% after 2 years, some of the fish can be removed for meat, while others are permitted to grow to maturity for 7–12 years depending on latitude (Jennings and Zigler 2000). Carrying capacity will vary by reservoir; however, production of 100–300 kg/ha is feasible. To harvest meat fish, a 12.5-cm-bar-mesh gill net will capture 5 kg or larger paddlefish. Research in Kentucky has demonstrated that less than 1% of the fish caught in 11.25-cm-bar-mesh gill nets are sport fishes (T. Crowell, Kentucky Department of Fish and Wildlife Resources, personal communication). To harvest mature female paddlefish of greater than 15 kg, 15-cm-bar-mesh nets are best suited. Gill nets should be 50 m or longer and 6–8 m deep and be set perpendicular to the shore and left overnight if the water temperature is below 10°C. When water temperatures are above 10°C, nets need to be checked every couple of hours to prevent fish mortality. Fish with roe must be harvested alive in order to process and market high-quality caviar. This system is economical for mature paddlefish production, whether for caviar production or broodstock development.

Conclusions

Paddlefish have had a variable history as a commercial and sport fish. More recently, interest has increased through value-added meat products and the demand for caviar placing considerable stress on wild populations. This chapter summarizes the progress in improved artificial propagation methods, intensive nursery production, and pond and tank culture options. Culture in the United States may develop as a component of the catfish industry, but some form of reservoir ranching and cage culture is more likely to be the system that develops.

The conditions for rapid expansion of paddlefish culture already exist in China and Russia. Mixed species culture in the expansive system of reservoirs in China can immediately utilize a new component

in that niche, and the meat will have immediate acceptance in food markets. This eventuality only awaits the application of artificial propagation techniques into their repertoire. Adoption of paddlefish culture is already well advanced in Russia; propagation and production facilities are already in operation. With the supply of Caspian Sea sturgeon caviar plummeting and under restricted marketing, the Russians will logically opt for caviar production and export. Since the United States is one of the largest importers and consumers of caviar, this will lead to U.S. importers purchasing paddlefish caviar produced overseas, thereby adding to the list of native North American species (e.g., rainbow trout *Oncorhynchus mykiss*, salmon *Oncorhynchus* sp., and channel catfish) now being produced in other countries and exported to the United States. It is important that federal and state agencies and the aquaculture industry work together to develop farm-raised paddlefish in the United States in order to provide a reliable supply of caviar and meat for commerce, thereby reducing the balance of trade deficit.

More research is needed in nutrition and disease management to maintain healthy, fast-growing fish. Also, research is needed in bioenergetics modeling for predicting stocking rates in water bodies, in molecular biology for stock identification, and in implementation of milt cryobiology for stock enhancement and domestication.

References

Ballard, W. W., and R. G. Needham. 1964. Normal embryonic states of *Polyodon spathula*. Journal of Morphology 114:465–477.

Barton, B. A., A. B. Rahn, G. Feist, H. Bollig, and C. B. Schreck. 1998. Physiological stress response of the freshwater chondrostean paddlefish (*Polyodon spathula*) to acute physical disturbances. Comparative Biochemistry and Physiology A 120:355–363.

Bemis, W. E., E. K. Findeis, and L. Grande. 1997. An overview of Acipenseriformes. Environmental Biology of Fishes 48:25–71.

Bemis, W. E., and L. Grande. 1992. Early development of the Actinoperygian head. I. External development and staging of the paddlefish *Polyodon spathuloa*. Jounal of Morphology 2132:47–83.

Bettoli, P. W., J. A. Kerns, and G. D. Scholten. 2009. Status of paddlefish in the United States. Pages 23–37 *in* C. Paukert and G. Scholten, editors. Paddlefish management, propagation, and conservation in the 21st century: building from 20 years of research and management. American Fisheries Society, Symposium 66, Bethesda, Maryland.

Billard, R., and G. Lecointre. 2001. Biology and conservation of sturgeon and paddlefish. Reviews in Fish Biology and Fisheries 10:355–392.

Brown, G. G., and S. D. Mims. 1999. Cryopreservation of paddlefish *Polyodon spathula* milt. Journal of the World Aquaculture Society 30:245–249.

Carlson, D. M., and P. S. Bonislawsky. 1981. The paddlefish fisheries of the Midwest United States. Fisheries 6(2):17–27.

Casal, C. M. V. 2006. Global documentation of fish introductions: the growing crisis and recommendations for action. Biological Invasions 8:3–11.

Cherr, G. N. and W. H. Clark, Jr. 1985. Gamete interaction in the white sturgeon *Acipenser transmontanus*: a morphological and physiological review. Pages 11–22 *in* F. P. Binkowski and S. I. Dorosov, editors. North American sturgeons: biology and aquaculture potential. Dr. W. Junk Publishers, Boston.

Clemens, H. P. and K. E. Sneed. 1962. Bioassay and use of pituitary materials to spawn warmwater fishes. U.S. Fish and Wildlife Research Report 61, Washington, D.C.

Conte, F. S., S. I. Doroshov, P. B. Lutes and E. M. Strange. 1988. Hatchery manual for the white sturgeon *Acipenser transmontanus* Richardson with application to other North American Acipenserids. University of California, Cooperative Extension Publication 3322, Oakland.

Dettlaff, T. A., A. S. Ginsburg and O.I. Schmalhausen. 1993. Sturgeon fishes, develop-

mental biology and aquaculture. Springer-Verlag, New York.

Doroshov, S. I. 1985. Biology and culture of sturgeon, Acipenseriformes. Pages 251–274 *in* J. F. Muir and R. J. Roberts, editors. Recent advances in aquaculture, volume 2. Croom Helm, Sydney.

Doroshov, S. I., W. H. Clark, P. B. Lutes, R. L. Swallow, K. E. Beer, A. B. McGuire, and M. D. Cochran. 1983. Artificial propagation of the white sturgeon, *Acipenser transmontanus* Richardson. Aquaculture 32:93–104.

Epifanio, J. M., J. B. Koppelman, M. A. Nedbal, and D. P. Philipp. 1996. Geographic variation of paddlefish allozymes and mitochondrial DNA. Transactions of the American Fisheries Society 125:546–561.

FAO (Food and Agriculture Organization). 1983. Freshwater aquaculture development in China. FAO Fisheries Technical Paper 215.

Gershanovich, A. D. 1983. Factors determining variations in growth rate and size distribution in groups of young paddlefish, *Polyodon spathula* (Polyodontidae). Journal of Ichthyology 23:56–61.

Ginzburg, A. S. 1972. Fertilization in fishes and the problem of polyspermy. T. A. Detlaff, editor. D. A. Detlaff, editor. Israel Program for Scientific Translations, Jerusalem.

Glogowski, J., R. Kolman, M. Szczepkowski, Á. Hórvath, B. Urbányi, P. Sieczynski, A. Rzemieniecki, J. Domagala, W. Demianowicz, R. Kowalski, and A. Ciereszko. 2002. Fertilization rate of Siberian sturgeon (*Acipenser baeri*, Brandt) milt cryopreserved with methanol. Aquaculture 211:367–373.

Graham, L. K. 1986. Establishing and maintaining paddlefish populations by stocking. Pages 96–104 *in* J. G. Dillard, L. K. Graham, and T. R. Russell, editors. The paddlefish: status, management and propagation. American Fisheries Society, North Central Division, Special Publication 7, Bethesda, Maryland.

Graham, L. K., E. J. Hamilton, T. R. Russell, and C. E. Hicks. 1986. The culture of paddlefish: a review of methods. Pages 78–94 *in* J. G. Dillard, L. K. Graham, and T. R. Russell, editors. The paddlefish: status, management and propagation. American Fisheries Society, North Central Division, Special Publication 7, Bethesda, Maryland.

Graham, K. 1997. Contemporary status of the North American paddlefish, *Polyodon spathula*. Environmental Biology of Fishes 48:279–289.

Grande, L., and W. E. Bemis. 1991. Osteology and phylogenetic relationships of fossil and recent paddlefishes (Polyodontidae) with comments on the interrelationships of Acipenseriformes. Journal of Vertebrate Paleoecology II, supplement 1:1–121.

Heist, E., and A. Mustapha. 2008. Rangewide genetic structure in paddlefish inferred from DNA microsatellite loci. Transactions of the American Fisheries Society 137:909–915.

Hórvath, Á., B. Urbányi, S.D. Mims, W.B. Bean, B. Gomelsky, and T. R. Tiersch. 2006. Improved cryopreservation of sperm of paddlefish (*Polyodon spathula*). Journal of the World Aquaculture Society 37:356–362.

Hoxmeier, R. J. H., and D. R. DeVries. 1997. Habitat use, diet, and population structure of adult and juvenile paddlefish in the lower Alabama River. Transactions of the American Fisheries Society 126:288–301.

Jennings, C. A., and S. J. Zigler. 2000. Ecology and biology of paddlefish in North America: historical perspectives, management approaches, and research priorities. Reviews in Fish Biology and Fisheries 10:167–181.

Kazanskii, B. N., Y. A. Feklov, S. B. Podushka and A. N. Molodtsov. 1978. Quick method for the determination of gonad maturity in the sturgeon. Pages 217–219 *in* T. A. Dettlaff, A. S. Ginsburg, and O. I. Schmalhausen. Sturgeon fishes, developmental biology and aquaculture. Springer-Verlag, New York.

Kincaid, H. L., L. J. Mengel, M. J. Gray, and S. Brimm. 1999. National fish strain registry-paddlefish and sturgeon, species tables of reported populations. U.S. Fish and Wildlife Service Resource Publication, Washington, D.C.

Kowtal, G. V., W. H. Clark, Jr., and G. N. Cherr. 1986. Elimination of adhesiveness in eggs from the white sturgeon, *Acipenser transmontanus*: chemical treatment of fertilized eggs. Aquaculture 55:139–143.

Kroll, J. K., J. P. Van Eenennaam, S. I. Doroshov, J. E. Hamilton, and T. R. Russell. 1992. Effect of water temperature and formulated diets on growth and survival of larval pad-

dlefish. Transactions of American Fisheries Society 121:538–543.

Kroll, J. K., J. P. Van Eenennaam, S. I. Doroshov, J. Linares, E. J. Hamilton, and T. R. Russell. 1994. Growth and survival of paddlefish fry raised in the laboratory on natural and artificial diets. Progressive Fish-Culturist 56:169–174.

Lein, G. M., and D. R. DeVries. 1998. Paddlefish in the Alabama River drainage: population characteristics and adult spawning migration. Transactions of the American Fisheries Society 127:441–454.

Linhart, O., S. D. Mims, B. Gomelsky, A. E. Hiott, W. L. Shelton, J. Cosson, M. Rodina, and D. Gela. 2000. Spermiation of paddlefish (*Polyodon spathula*, Acipenseriformes) stimulated with injection of LHRH analogue and carp pituitary powder Aquatic Living Resources 13(2000):1–6.

Lou, X., C. Wang, Y. L. Wang, and S. D. Mims. 2000a. Physical and chemical stability of paddlefish (*Polyodon spathula*) meat under refrigerated and frozen storage. Journal of Aquatic Food Product Technology 9(4):27–39.

Lou, X., C. Wang, Y. L. Xiong, B. Wang, and S. D. Mims. 2000b. Gelation characteristics of paddlefish surimi under different heating conditions. Journal of Food Science 65:394–398.

Markov, K. P. 1978. Adhesiveness of egg membranes in sturgeons (family Acipenseridae). Journal of Ichthyology 18(3):437–446.

Melchenkov, E. A., V. K. Vinogradov, L. V. Erohina, V. G. Chertihin, V. A. Ilyasova, M. V. Bredenko, O. V. Sitnova, V. E. Chrisanfov, T. A. Kanidyeva, E. V. Bubunetz, and O. B. Harzin. 1996. In-country experience in propagation and rearing of paddlefish. All-Russian Institute of Information in Fisheries, Review Information, series Aquaculture, Number 1, Moscow. [In Russian]

Michaletz, P. H., C. F. Rabeni, W. W. Taylor, and T. R. Russell. 1982. Feeding ecology and growth of young-of-the-year paddlefish in hatchery ponds. Transactions of the American Fisheries Society 111:700–709.

Mims, S. D., J. A. Clark, and J. H. Tidwell. 1991. Evaluation of three organic fertilizers for paddlefish, *Polyodon spathula*, production in nursery ponds. Aquaculture 99:69–82.

Mims, S. D., T. A. Georgi, and L. Chen-Han. 1993a. The Chinese paddlefish, *Psephurus gladius*: biology, life history, and potential for cultivation. World Aquaculture 24(1):46–48.

Mims, S. D., J. A. Clark, J. C. Williams, and D. B. Rouse. 1993b. Comparison of two by-products and a prepared diet as organic fertilizers on growth and survival of larval paddlefish, *Polyodon spathula*, in earthen ponds. Journal of Applied Aquaculture 2(3/4):171–187.

Mims, S. D., J. A. Clark, J.C. William, and L. L. Lovshin. 1995a. Food selection by larval paddlefish, *Polyodon spathula*, supplied with rice bran to promote production of live foods, with prepared diets or with their combination in earthen ponds. Journal of World Aquaculture Society 26:438–446.

Mims, S. D., J. A. Clark, J.C. Williams, and D. R. Bayne. 1995b. Factors influencing zooplankton production in organically fertilized ponds for culture of paddlefish, *Polyodon spathula*. Journal of Applied Aquaculture 5(1):29–43.

Mims, S. D., W. L. Shelton, O. Linhart, and C. Wang. 1997. Induced meiotic gynogenesis of paddlefish *Polyodon spathula*. Journal of the World Aquaculture Society 28:334–343.

Mims, S. D. and R. M. Durborow, producers. 1998. Propagation and culture of the American paddlefish *Polyodon spathula*. Video. Kentucky State University, Land Grant Program, Frankfort, Kentucky.

Mims, S. D., and W. L. Shelton. 1998a. Monosex culture of paddlefish and shovelnose sturgeon. Pages 67–76 *in* D. F. Williamson, G. W. Benz, and C. M. Hoover, editors. Proceedings of the symposium on harvest, trade and conservation of North American paddlefish and sturgeon. TRAFFIC North America/ World Wildlife Fund, Washington, D.C.

Mims, S. D., and W. L. Shelton. 1998b. Induced meiotic gynogenesis in shovelnose sturgeon. Aquaculture International 6:323–329.

Mims, S. D., W. L. Shelton, F. S. Wynne, and R. J. Onders. 1999. Production of paddlefish. Southern Regional Aquaculture Center (SRAC) Publication 437. Available: http://agpublications.tamu.edu (January 2000).

Mims, S. D., L. I. Tsvetkova, G. G. Brown, and B. Gomelsky. 2000. Cryopreservation of

sperm of sturgeon and paddlefish. Pages 123–129 *in* T. A. Tiersch and P. M. Mazik, editors. Cryopreservation in aquatic species. Advances in world aquaculture, volume 7. World Aquaculture Society, Baton Rouge, Louisiana.

Mims, S. D., R. J. Onders, B. Gomelsky, and W. L. Shelton. 2004. Effectiveness of the minimally invasive surgical technique (MIST) for removal of ovulated eggs from first-time and second-time MIST spawned paddlefish. North American Journal of Aquaculture 66:70–72.

Mims, S. D., and W. L. Shelton. 2005. Paddlefish. Pages 227–249 *in* A. M. Kelly and J. Silverstein, editors. Aquaculture in the 21st century, American Fisheries Society, Symposium 46, Bethesda, Maryland.

Mims, S. D., and R. J. Onders. 2006. Polyculture and reservoir ranching: sustainable aquaculture strategies for paddlefish (*Polyodon spathula*) production. SARE Agricultural Innovations. Available: www.sare.org/publications/factsheet/0705.htm (November 2006).

Mims, S., R. Onders, T. Parrott, and J. Stickney. 2006. Caviar from paddlefish in water supply lakes. Waterproof 8(4):12–13.

Mims, S. D., R. J. Onders, and T. Parrott. 2007. Culturing paddlefish fingerlings at Kentucky wastewater treatment plant. Hatchery International (July–August 2007):28–29.

Mims, S. D., R. J. Onders, W. Scalf, and B. T. Parrott. 2008. Paddlefish shown to thrive in treated sewage water. Fish Farming International May: 34–35.

Needham, R. G. 1965. Spawning of paddlefish induced by means of pituitary material. Progressive Fish-Culturist 27:13–19.

O'Keefe, D. M., and D. C. Jackson. 2009. Population characteristics of paddlefish in two Tennessee-Tombigbee Waterway habitats. Pages 83–101 *in* C. P. Paukert and G. D. Scholten, editors. Paddlefish management, propagation, and conservation in the 21st century: building from 20 years of research and management. American Fisheries Society, Symposium 66, Bethesda, Maryland.

Onders, R. J., S. D. Mims, C. Wang, and W. D. Pearson. 2001. Reservoir ranching of the paddlefish *Polyodon spathula*. North American Journal of Aquaculture 63:179–190.

Onders, R. J., S. D. Mims, B.A. Wilhelm, and J. D. Robinson. 2005. Growth, survival and fillet composition of paddlefish, *Polyodon spathula* (Walbaum) fed commercial trout or catfish feeds. Aquaculture Research 36:1–9.

Onders, R. J., S. D. Mims, and S. Dasgupta. 2008. Growth, condition and size distribution of paddlefish *Polyodon spathula* juveniles reared in ponds at three densities. Journal of World Aquaculture Society 39:565–571.

Pasch, R. W., P. A. Hackney, and J. A. Holbrook. 1980. Ecology of paddlefish in Old Hickory Reservoir, Tennessee, with emphasis on first-year life history. Transactions of the American Society 109:157–167.

Purkett, C. A. 1961. Reproduction and early development of paddllefish. Transactions of the American Fisheries Society 90:125–129.

Purkett, C. A. 1963a. The paddlefish fishery of the Osage River and the Lake of the Ozarks, Missouri. Transactions of the American Fisheries Society 92:239–244.

Purkett, C. A. 1963b. Artificial propagation of paddlefish. Progressive Fish-Culturist 25:31–33.

Rosen, R. A., and D. C. Hales. 1981. Feeding of paddlefish, *Polyodon spathula*. Copeia 1981:441–455.

Ruelle, R., and P. L. Hudson. 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.

Rubinshtein, I., S. Rothbard, and W. L. Shelton. 1997. Relationships between embryological age, cytokinesis-1 and the timing of ploidy manipulations in fish. Israeli Journal of Aquaculture-Bamidgeh 49:99–110.

Russell, T. R. 1973. A study of artificial propagation of the paddlefish. Missouri Department of Conservation, Dingell-Johnson Project F-1-R-21, Study S-5, Job Numbers 1 and 2, Jefferson City.

Semmens, K. J. 1982. Production of fingerling paddlefish (*Polyodon spathula*) in earthen ponds. Master's thesis. Auburn University, Auburn, Alabama.

Semmens, K. J. 1986. Evaluation of paddlefish hypophysis, carp hypophysis, and LHRH

analogue to induce ovulation in paddlefish, *Polyodon spathula*. Doctoral dissertation. Auburn University, Auburn, Alabama.

Semmens, K. J., and W. L. Shelton. 1986. Opportunities in paddlefish aquaculture. Pages 106–113 *in* J. G. Dillard, L. K. Graham, and T. R. Russell, editors. The paddlefish: status, management, and propagation. American Fisheries Society, North Central Division, Special Publication 7, Bethesda, Maryland.

Shelton, W. L., and R. O. Smitherman. 1984. Exotic fishes in warmwater aquaculture. Pages 262–301 *in* W. R. Courtenay and J. R. Stauffer, editors. Distribution, biology, and management of exotic fishes. John Hopkins University Press, Baltimore, Maryland.

Shelton, W. L. 1989. Management of finfish reproduction for aquaculture. CRC Critical Reviews in Aquatic Sciences 1(3):497–535.

Shelton, W. L., and S. D. Mims. 1995. Oocyte staging in paddlefish, *Polyodon spathula*. Transactions of the Kentucky Academy of Science 56 (1–2):22–27.

Shelton, W. L., S. D. Mims, J. A. Clark, A. E. Hiott, and C. Wang. 1997. A temperature-dependent index of mitotic interval (τ_0) for chromosome manipulation in paddlefish and shovelnose sturgeon. Progressive Fish-Culturist 59:229–234.

Shelton, W. L., and S. Rothbard. 2006. Exotic species in global aquaculture: review. Israeli Journal of Aquaculture-Bamidgeh 58:3–28.

Simonović, P, S. Marić, and V. Nikolić. 2006. Occurrence of paddlefish *Polyodon spathula* (Walbaum, 1792) in the Serbian part of the lower River Danube. Aquatic Invasions 1(3):183–185.

Soderburg, R.W. 1994. Flowing water fish culture. Lewis Publication, Boca Raton, Florida.

Sparrow, R. D. 1986. Threats to paddlefish habitat. Pages 36–45 *in* J. G. Dillard, L. K. Graham and T. R. Russell, editors. The paddlefish: status, management, and propagation. American Fisheries Society, North Central Division, Special Publication 7, Bethesda, Maryland.

Stéch, L., O. Linhart, W. L. Shelton, and S. D. Mims. 1999. Minimally invasive surgical removal of ovulated eggs from paddlefish. Aquaculture International 7:129–133.

Stickney, R. R. 2000. Encyclopedia of Aquaculture. Wiley, New York.

Tucker, C. S., R. Francis-Floyd, and M. H. Beleau. 1989. Nitrite-induced anemia in channel catfish, *Ictalurus punctatus* Rafinesque. Bulletin of Environmental Contamination and Toxicology 43:295–301.

Vedrasco, A., V. Lobchenko and R. Billard. 2001. Introduction of the paddlefish *Polyodon spathula* in Europe. Aquatic Living Resources 14:383–390. [In French, English summary]

Waldman, J. R. 1995. Sturgeons and paddlefishes: a convergence of biology, politics and greed. Fisheries 20(9):20- 21:49.

Wang, C., S. D. Mims, and Y. L. Xiong. 1995. Consumer acceptability of paddlefish, a potential aquaculture species. Meat Focus International 4(1):8–9.

Webster, C. D., S. D. Mims, J. H. Tidwell, and D. H. Yancey. 1991. Comparison of live food organisms and prepared diets as first food for paddlefish, *Polyodon spathula* (Walbaum), fry, Aquaculture and Fisheries Management 22:155–163.

Yeager, B. L., and R. Wallus. 1982 Development of larval *Polyodon spathula* (Walbaum) from the Cumberland River in Tennessee. Pages 73–77 *in* C. F. Bryan, J. V. Conner, and F. M. Truesdale, editors. Proceedings of the 5th annual larval fish conference. Louisiana State University, Baton Rouge.

Yeager, B. L., and R. Wallus. 1990. Paddlefish *Polyodon spathula* (Walbaum). Pages 50–56 *in* Reproductive biology and early life history of fishes in the Ohio River Drainage, volume 1. Tennessee Valley Authority, Chattanooga.