American Fisheries Society Symposium 88:1–27, 2019

Chapter 1

Paddlefish Life History: Advances and Applications in Design of Harvest Management Regulations

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Abstract.—In the past decade, advances in our understanding of Paddlefish *Polyodon spathula* life history have provided additional insight into the information needed for sustainable harvest management of this long-lived species. Recovery of known-age fish in some stocks has enabled stock assessment biologists and managers to not only validate ages of individual fish, but to begin to validate the life histories. A framework for potentially recruited Paddlefish life history can be broken into five stages: 1) immature, 2) maturing, 3) somatic growth and reproduction, 4) prime reproduction, and 5) senescence to death. These stages involve measurable changes in growth in length and weight, gonadosomatic index (GSI), gonadal fat storage (GFBs), reproductive periodicity, natural mortality rates, and, in some cases, fish migrations. Stages 2–5 are typically initiated at younger ages for males than for females. Metabolic demands on Paddlefish result in them progressing through these life history stages more rapidly in southern stocks, inhabiting warmer waters, than in northern ones, inhabiting colder waters. Lifespans in most northerly stocks tend to be 2–3 times longer than for southern stocks. Natural mortality is also typically lower in northern stocks. These differences necessitate fundamentally different harvest management strategies among stocks. Regardless of the stock, however, in the prime reproduction stage, somatic growth is slow or negative, as energy is routed more strongly into reproduction, GSI is at a maximum, the period of gonadal recrudescence (i.e., spawning interval) is minimized, and GFBs are largely or completely depleted in females. Consistent with recommendations for other long-lived freshwater and marine species, harvest management strategies should be specifically planned to retain some older, prime spawning females in the population. In addition, sporadic or episodic recruitment in many stocks makes steady-state harvest models unrealistic, necessitating that harvest be appropriately matched to recruitment rates or events.

The Importance of Paddlefish Life History in Effective Management

Life history can be defined as a sequence of the changes through which an organism passes in its development from the first stage to its natural death. In wild fish populations, life history is inseparable from aspects of the ecology and habitat use throughout a fish's lifespan. A thorough understanding of life history also provides a sound foundation needed for effective, sustainable management (Summerfelt 1987; Winemiller 2005)

Understanding the life history of the Paddlefish *Polyodon spathula*, an ancient and distinctive Acipenseriform species of evolutionary and ecological importance, is of both academic and practical interest. It is a fundamental need for effective harvest management of this species, which supports important recreational and commercial fisheries yielding high-quality boneless meat and expensive caviar (Decker et al. 1991; Mims

2001). Knowledge of the relations among sex-specific length, weight, age, growth, maturity, fecundity, reproductive periodicity, mortality, and potential lifespan (i.e., in the absence of harvest) are important for developing models and approaches for sustainable harvest strategies in both recreational and commercial fisheries (Graham 1997; Scarnecchia et al. 2007). This life history knowledge is needed not just at one locality, but throughout the range of this mobile species (Pracheil et al. 2012; Hupfeld et al. 2016), which inhabits 22 states of the USA (Gengerke 1986; Jennings and Zigler 2009) as well as several other countries in Europe and Asia where it has been introduced (Kharin and Cheblukov 2009; Kaczmarczyk et al. 2012; Jelkić and Opačak 2013; Jarić et al. 2018; Ji and Li 2019, Chapter 11 this volume). Although historical records indicate that Paddlefish have often made long riverine migrations (Russell 1986) and continue to do so in accessible waterways (Pracheil et al. 2012), river impoundments in the 20th century (Sparrowe 1986) have limited many movements, resulting in isolated or semi-isolated populations. These isolated and semi-isolated populations, referred to here as stocks (*sensu* Ricker 1972), often have distinct differences in life histories, even within a small geographic area (Russell 1986; Paukert and Fisher 2001; Leone et al. 2012) requiring different management regulations for effective conservation, (e.g., Arkansas River impoundments: Leone et al. 2012). In regulated rivers, Paddlefish may be confined or limited to unidirectional movements, resulting in stock-like units within one state (e.g., Fort Peck stock, Montana), two states (e.g., Yellowstone-Sakakawea stock, Montana and North Dakota) or mixed into larger harvest management units (HMUs) traversing several states (e.g., lower Mississippi River) and other nonstate management entities.

A few early accounts of the species provide observations of aspects of life history, such as fecundity, general habitats occupied by the species (Kofoid 1900; Stockard 1907) and the fisheries (Hussakof 1910). Scientific knowledge of the Paddlefish's life history by the early 20th century was mostly indirectly obtained, as studies centered mainly on the diverse anatomical aspects of the species, including skeletal structure (Bridge 1897a, 1897b) circulatory system, (Allis 1911; Danforth 1912), musculature (Danforth 1913), gill rakers (Imms 1904), and the rostrum (Kistler 1906; Nachtrieb 1910). Before mid-century, however, advances in age estimation, primarily through the use of cross sections of dentaries (Adams 1931, 1942) provided an important foundation on which age- and sex-specific length, weight, growth, maturity, and mortality could be estimated. Several life history studies documenting many of these relationships were conducted in the last half of the century, with data from both recreational snag fisheries and commercial fisheries (e.g., Iowa: Gengerke 1978; Kentucky: Timmons and Hughbanks 2000; Montana: Rehwinkel 1978; Scarnecchia et al. 1996b; Nebraska: Hesse et al. 1991; South Dakota: Friberg 1974). Improved knowledge of habitat usage and requirements (Hubert et al. 1984; Crance 1987), and telemetry studies documenting movements (Southall and Hubert 1984; Moen et al. 1992; Paukert and Fisher 2000; Firehammer and Scarnecchia 2006; Tripp et al. 2019, Chapter 3 this volume), and ecological studies on feeding (Michaletz 1981; Rosen and Hales 1981) and the electrosensory system (Freund et al. 2002; Wilkins et al. 2002; Wilkens and Hoffmann 2007) further advanced our knowledge of the species in the wild.

Much of what was learned about Paddlefish life history through the 20th century has been concisely summarized in two previous symposia focused on conservation of the species. Russell (1986) reviewed biology and life history and included considerable data on length, weight and age of several populations throughout the species range. He also summarized information on anatomy, habitats, movements, spawning, and feeding. Key aspects of the life history were identified, including the recognition of nonannual spawning (specifically for female fish), a shift from particulate feeding to filter feeding and differences in maturity and age structure among stocks. A comprehensive bibliography of all known papers with life history information to that time was also provided. Jennings and Zigler (2009) provided an update to Russell (1986) on these topics based on research in the ensuing two decades. They also discussed advances in our understanding of early life history, mechanisms for overharvest, effects of waterway development, and pollution and contaminants on the species. These informative reviews were not specifically focused toward harvest management considerations. However, other papers in the two symposia addressed harvest (Combs 1986; Elser 1986; Pasch and Alexander 1986; Hansen and Paukert 2009; Scholten 2009). It was also recognized that there was a need for "(1) consistent regulations based on regional characteristics of Paddlefish populations, rather than political boundaries, and (2) an increase in cooperation among states in protecting Paddlefish habitat" (Elser 1986). Although the past studies reviewed in Russell (1986) and Jennings and Zigler (2009) have laid the life history foundation for much-needed twenty-first century efforts at cooperative, interjurisdictional stock assessment and management, such management, while often proposed (Pracheil et al. 2012; Hupfeld et al. 2016), remains only partially implemented three decades later (e.g., Scarnecchia et al. 2008; Mestl and Sorensen 2009).

In this synthesis, we focus primarily on advances in our understanding of key aspects of Paddlefish life history since the last symposium review (Jennings and Zigler 2009). We will also attempt to take the information a step further, by providing some potential approaches to stock assessment through knowledge of life history (King and MacFarlane 2003). Emphasis will be on advances in validating ages, characterizing life histories, and using ecological information in stock assessment and management. We will present a testable framework for characterizing Paddlefish life history and discuss how we might use aspects of that framework and recent life history knowledge advances in more effectively designing and applying harvest management regulations. This linkage between life history and harvest management strategies is needed, not just at the broader level of recognizing r-selected versus k-selected species differences (Adams 1980; King and MacFarlane 2003), or broad patterns such as late maturation and long lifespan of Acipenseriform species (Bemis and Kynard 1997; Billard and Lecointre 2001). It is needed at a more refined, higher resolution level of differences in strategies needed among stocks within a species (Bemis and Kynard 1997; Scarnecchia et al. 2011). Even though overall Paddlefish abundance has decreased in the last century, populations in several states remain stable, and in some cases, have increased (Unkenholz 1986; Bettoli et al. 2009). As a result, the species continues to support important recreational (Hansen and Paukert 2009; Mestl et al. 2019, Chapter 12 this volume) and commercial (Scholten 2009; Rider et al. 2019, Chapter 13 this volume) fisheries. As pressures from increasing numbers of harvesters mount, well-justified harvest strategies that transcend management jurisdictions, yet accommodate local and regional stock differences and harvester preferences, must be developed.

Linking Life History Validation and Harvest Management

In Paddlefish stock assessment and management, an important early step is to initiate efforts toward validation, not just of the age determination method, which is fundamental, but of the entire life history and ecology. For long-lived species such as Paddlefish and sturgeon, the entire process may take decades, as will the successful management of such a long-lived species (Bruch 1999).

Age Validation

The first step, age validation, or confirmation of age accuracy, has long been understood as an important but frequently overlooked step in fisheries stock assessment (Beamish and McFarlane 1983; Campana 2001). As with many species, life history information on Paddlefish has been used in management in many localities even though it has not been formally validated for accuracy. Out of necessity, this usage will continue. Management needs are acute, and validation is not necessarily routine or rapid, especially for long-lived species, and can present challenges in Paddlefish and other Acipenseriform fish.

Age validation efforts can take several forms. The preferred method is to mark known-age fish and count the annual marks (annuli) on a structure from a marked fish recovered by agency-directed fish collection or from sampling the fisheries. Ideally, it is desirable to mark adequate numbers of known age fish, preferably at age-0, so that the entire pattern of annulus development can be followed through the life history stages as marked fish are recovered. In some cases, shortcuts can be taken, where validation of fish of unknown age may be used to assess whether annual marks are deposited annually at some specific interval in the life history (Lake Sturgeon, *Acipenser fulvescens*; Rossiter et al. 1995). In at least one case, quasi-validation has occurred for older Paddlefish by marking fish of known minimum age and recovering the fish many years later, leading to minimum estimates of total age (Scarnecchia et al. 2006). Bomb radio carbon has also been used successfully as a dating tool with older Lake Sturgeon (Bruch et al. 2009).

Sectioned dentaries (lower jaw bones) have been the most widely used structure in Paddlefish age determination; otoliths and fin rays are less reliable and less likely to show distinct annuli among older fish (Jennings and Zigler 2009). Even with dentaries, however, the authors have observed great variations among stocks in the clarity of annuli. As reported by Russell (1986), “annuli on sections of the dentary bone are frequently difficult to identify, especially in older fish, because of crowding and the presence of halo bands” (p. 10). The latter problem is especially great among southerly stocks, where seasonal growth cessation during warm periods can occur. Stocks with dentaries that are more difficult to age will also typically result in less repeatability among readers, i.e., lower precision, in age estimates. Previous reviews of Paddlefish age estimates in Russell (1986) and Jennings and Zigler (2009) showed considerable variability in length at age, weight at age, and longevity among harvested populations. For that reason, validation of Paddlefish ages needs to be conducted in more than one locality, with validation for each stock or HMU as a long-term goal.

The longest effort at validation of Paddlefish dentaries in the published literature has occurred for the Yellowstone-Sakakawea stock of eastern Montana and western North Dakota (Scarnecchia et al. 2006). This validation has occurred for hatchery-reared fish released in 1995 and recaptured over the period 2002–2016. As of 2016, 347 known age fish have been analyzed. Results from the first four years of recaptures (2002–2005) are detailed in Scarnecchia et al. (2006). Annuli in recaptured fish, all of which were males, were identifiable with a high degree of accuracy (25 of 30 aged correctly; the other five mis-aged by one year) and precision (mean coefficient of variation 3.6% for Montana recoveries, 7.1% for North Dakota recoveries; Figure 1). Subsequent recoveries have provided an improved understanding of annuli formation in both sexes. By age 17, annuli have remained well-defined, although they are increasingly crowded together near the outer margin, especially in males (Figure 2a), which can mature at ages 8–10 in this stock (Scarnecchia et al. 2007). In contrast, females, which may not mature until at least ages 16–18, typically show much more uniform spacing of annuli during the first 17 years (Figure 2b). By age 21, the close packing of annuli, especially in males, can in some cases result in underestimates of age, typically by 1–3 years (Figure 3). Scarnecchia et al. (2006) had anticipated that ages of older fish of the Yellowstone-Sakakawea stock appeared to be under-estimates based on long-term recoveries of fish tagged as adults. In such cases, even if validation efforts eventually show weaknesses in the age determination method for old fish, knowledge of biases can lead to adjustments made for older fish as more known-age fish are recaptured from this cohort in future years.

It was fortuitous that this northern stock was investigated for initial validation efforts, as the clarity of annuli, and lack of false annuli or "halo" bands compared to more southerly stocks has greatly facilitated the life history validation process. Observations on dentaries in this northerly stock in comparison with a more southerly stock (Grand Lake, Oklahoma; Scarnecchia et al. 2011) and other southern stocks (Alabama, Arkansas, Missouri, Mississippi, Tennessee; D. Scarnecchia, unpublished data; Figure 4), indicates that validation will present more of a challenge among southern stocks, even though the southern fish are shorter lived.

Figure 1. Validated age-10 Paddlefish from the Yellowstone-Sakakawea stock (Scarnecchia et al. 2006).

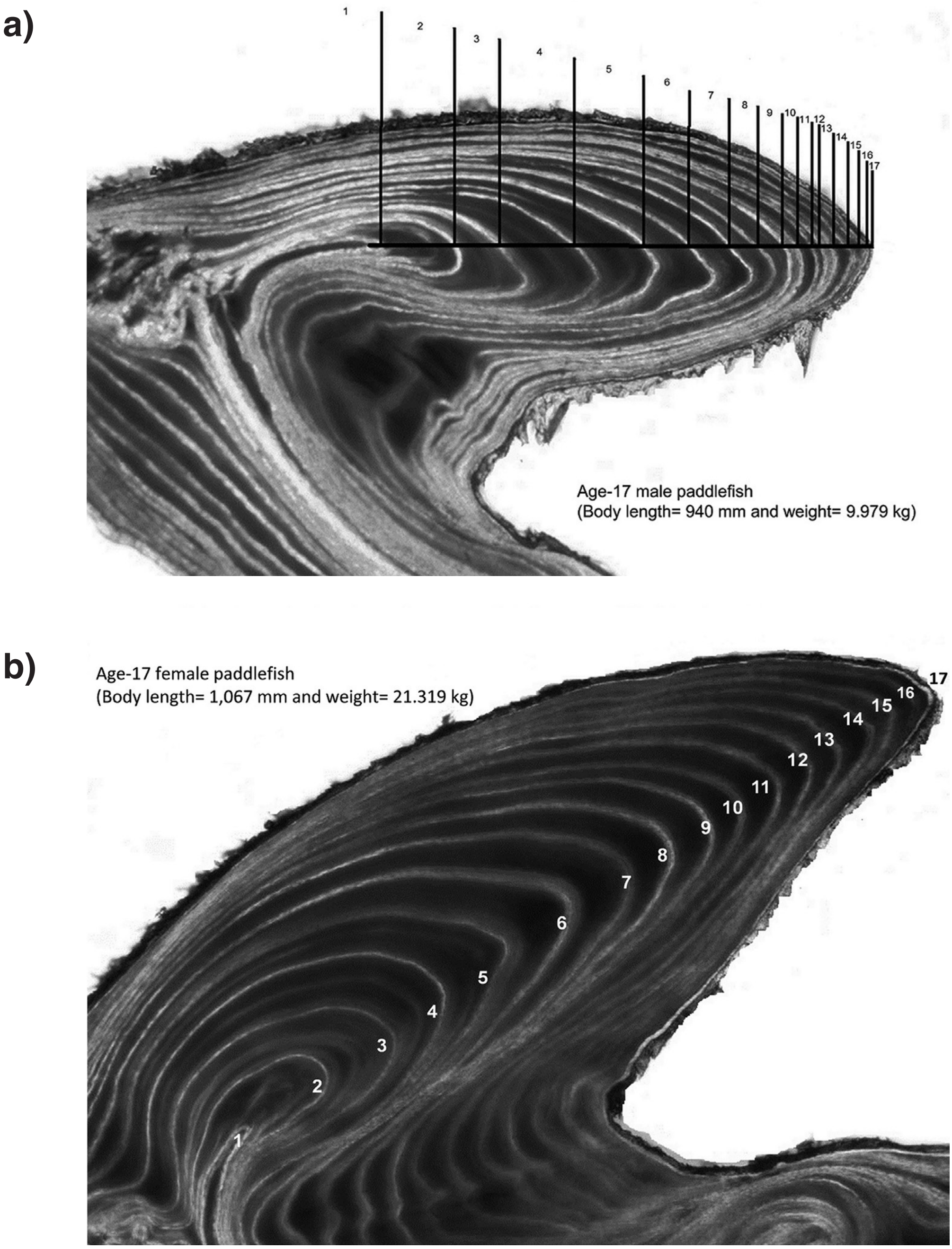


FIGURE 2. Two validated age-17 Paddlefish from the Yellowstone-Sakakawea stock: a) male showing close spacing of last 8 annuli after maturation; b) female showing more even spacing than the male but decreasing spacing of last annuli leading up to maturation and spawning migration.

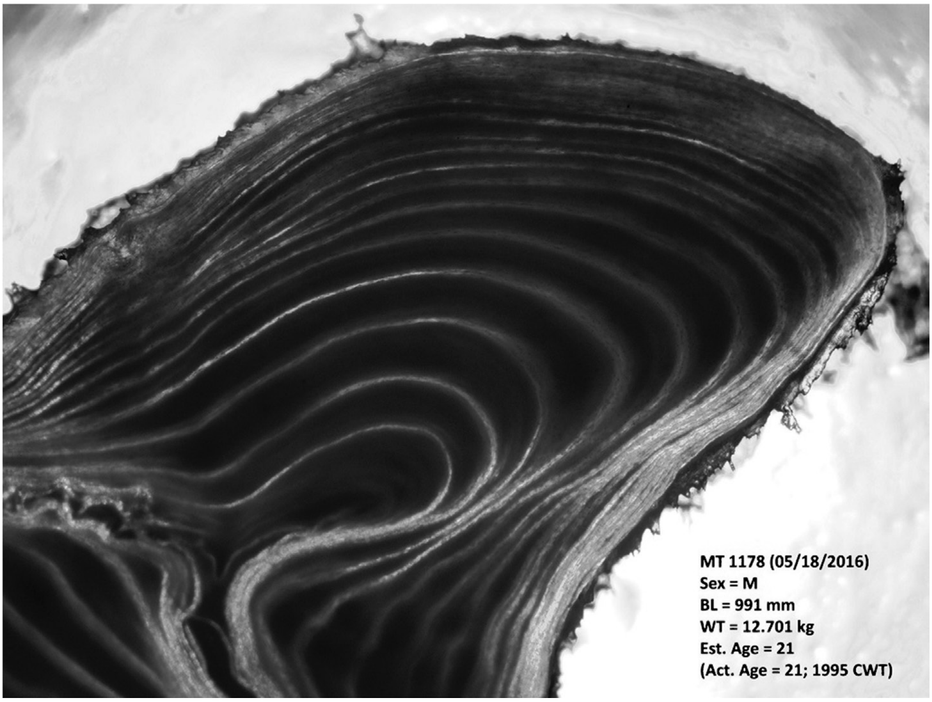
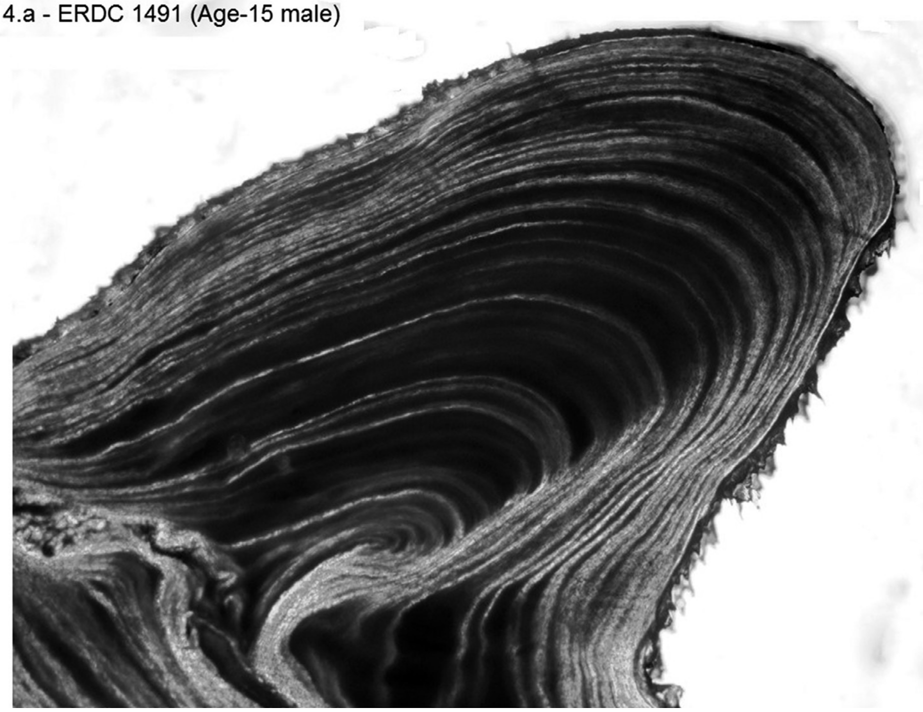


Figure 3. Validated age-21 male Paddlefish from the Yellowstone-Sakakawea stock showing extremely close and overlapping spacing of last 13 annuli after maturation. Although this fish was aged correctly, ages for fish with this pattern are likely to be under-estimated.

Age Validation—Implications for Harvest Management

Accurate knowledge of ages is vital for effective stock assessment. Underestimation of ages results in erroneous estimates of growth, recruitment and mortality, leading to unreliable stock assessments for many species (Beamish and McFarlane 1983; Reeves 2003; Yule et al. 2008). For Paddlefish, there is not widespread agreement on the maximum age of the species nor on the ages commonly reached by fish of a stock. Russell (1986) reviewed data from several states and concluded that Paddlefish may reach 30 years of age, even though most stocks had lower maximum ages. Jennings and Zigler (2009) reviewed available studies and reported that "most populations have a median age of 5–8 years and a maximum age of 14–18 years" (p. 9). Although these conclusions may be accurate in some southern stocks, evidence since then suggests that in northern stocks of Montana and North Dakota, as well as in many unfished stocks elsewhere, previous age estimates and assumptions of maximum age are too low. Fish ages in northern stocks not subjected to high levels of fishing on large fish are now estimated to exceed 60 years in some instances, with ages of 40–50 years common (Scarnecchia et al. 2007). More southerly stocks have lower maximum ages but may also reach 20–30 years in the absence of fishing (Moon Lake, Mississippi; Mississippi Department of Wildlife, Fisheries and Parks, Unpublished data). Most studies have consisted of younger fish from a stock being subjected to size-selective and resulting age-selective harvest at high rates. Stocks subjected to high harvest rates may be still growing upon capture, resulting in separable annuli to the edge of the dentary. In

4.a - ERDC 1491 (Age-15 male)



4.b - ERDC 3317 (Age-22 male)

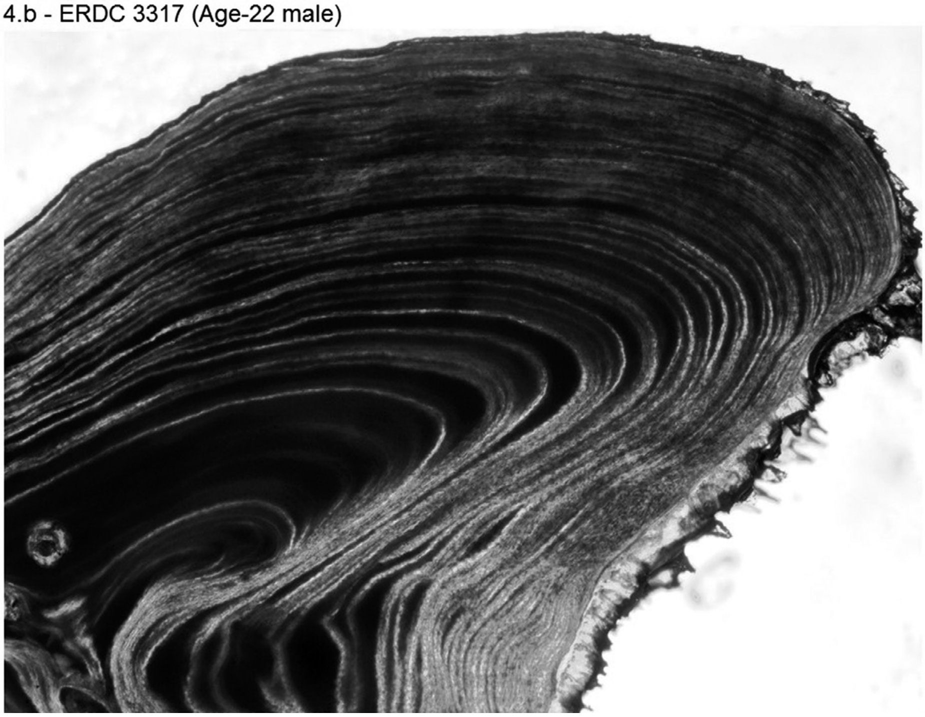


Figure 4. Southern Paddlefish stocks such as these from Mississippi have more false annuli and doublets, making them more difficult to age (courtesy of Darrin Hardesty, Mississippi Department of Wildlife, Fisheries and Parks).

contrast, dentaries from unfished stocks may show very closely packed or overlapping annuli; total age can easily be underestimated (Figure 4b). This overlapping of annuli can be more pronounced in males than in females as their annuli are typically deposited closer together earlier in life than those of females because of the earlier maturation and slower growth thereafter.

Validation of ages will also allow managers to detect strong and weak year classes of fish at their most identifiable recruited age—as they enter the fishery. These fish can then be subsequently followed through the remainder of their life. Fish can then be managed around strong and weak year classes if necessary.

Since the last symposium (Jennings and Zigler 2009), validation of ages has progressed as known-age Paddlefish, mostly hatchery reared and stocked, have been recovered in fisheries in various localities in the Mississippi and Missouri River basins. Validation results from those efforts remain largely unpublished. Although age-0 Paddlefish have been sampled for decades (e.g., Hesse et al. 1991), not all such fishes were marked upon release, and fisheries were not necessarily sampled with the intent of recovering and identifying known age fish. Validation of ages remains a high priority that should be initiated as soon as possible for managed stocks and HMUs. As known age fish are recovered over a period of years, a formal process, as detailed in Campana (2001) and demonstrated for Paddlefish in Scarnecchia et al. (2006), can be conducted each year to evaluate the accuracy of the age estimates assigned by readers. Even if this is not done in detail yearly, age estimates of known age fish should be made in a mixed group of marked and unmarked fish, without knowledge of their ages, results documented and bias in age estimation recorded as the fish become older. In situations where harvest is not occurring, pectoral fin rays have shown promise for aging younger fish (<age-10) and validation of that structure should be pursued (Adams 1942; O'Keefe and Jackson 2009).

Life History Validation—the Need for a Framework.

Because of the challenges associated with effective sampling of Paddlefish and sturgeons, most life history summaries consist of tables of selected life history data, usually temporally incomplete snapshots of a stock, from published studies without a framework or series of reference points for interpreting the significance of the data (e.g., Table 3 in Russell 1986; Tables 2–4 in Billard and Lecointre 2001). A life history framework would provide some perspective for interpreting these data, and for following characteristics of a cohort through their lifespan.

Since Russell (1986) and Jennings and Zigler (2009) presented life history data, an initial effort has been made to validate not just the ages, but the entire life history based on known age fish. Life history validation can be accomplished first by matching known ages of individual fish with other morphological, physiological, and behavioral measures from an individual fish. Such measures can include length, weight, Fulton's condition factor, gonadosomatic index (GSI; gonad weight/fish weight), indices of energy reserves (e.g., gonadal fat body (GFB) weight (Scarnecchia et al. 2007), reproductive periodicity or period of gonadal recrudescence, spawning migration distance and timing, and potentially other morphological, physiological or behavioral measures in existence or in development.

Based on the reliability of validated age estimates, Scarnecchia et al. (2007) matched ages of fish with age-specific somatic growth, GSI, gonadal fat (GFB) weights, spawning interval, and migratory prespawning movements of adult fish (distance upriver) for the Yellowstone-Sakakawea stock. They developed an empirical framework of the life history for this northern stock in relation to the costs of reproduction for that species and potentially for sturgeons, concluding that:

> Nearly all aspects of life histories of males and females differed from each other after the immature period. The five periods in the juvenile and adult life histories for males and females, which occur at different ages for each sex, were 1) immature, 2) maturing, 3) somatic growth and reproduction, 4) prime reproduction and 5) senescence to death. During the first period (immature), fishes exhibit rapid somatic growth as well as accumulation of energy reserves in the form of gonadal fat bodies (GFBs) and other fat deposits. During the second period (maturing), somatic growth slows as production and stored energy reserves are diverted into reproduction. In the third period, fish are allocating energy to both somatic growth and reproduction. Reproductive periodicity is typically close to two years for males and three years for females; gonadal recrudescence is slower than in older fish. The gonadosomatic index (GSI) is increasing and GFBs are depleted over 2–3 spawns in females and reduced more gradually in males. Fish make longer prespawning migrations upriver. In the fourth period (prime reproduction), somatic growth is slow or negative, as energy is routed more strongly into reproduction. GSI is at a maximum; GFBs are completely depleted in females. Reproductive periodicity is typically one year for males and two years for females; the rate of gonadal recrudescence is at its maximum. Fish make shorter prespawning migrations upriver. In the fifth period (senescence to death), GSI of some of the oldest females decreases; the oldest males have few energy reserves and are long and lean. Distinct male-female differences in life histories were consistent with theoretical models and with empirical observations of the lack of direct male competition for females. The framework outlined for this Paddlefish stock may exist among other Acipenseriform fishes and is potentially useful for evaluating their life histories. (Scarnecchia et.al. 2007; Figure 5).

As of 2016, results have validated distinct male-female life history differences in the Paddlefish, with differences greater for northern stocks. Known-age males have been shown to mature as early as age-7, nearly a decade sooner than female maturation, leading to extreme sexual size dimorphism in a northern (Montana–North Dakota) stock, where nearly all mature males are smaller than nearly all mature females (Scarnecchia et al. 2007). Known age fish from the Yellowstone-Sakakawea 1995 cohort have shown the strong sexual size dimorphism in length (Figure 6a) and weight (Figure 6b), previously only inferred (Scarnecchia et al. 2007) from fish with nonvalidated ages. This male-female size dimorphism is less extreme in more southerly stocks (e.g., Grand Lake, Scarnecchia et al. 2011).

As of 2016, the increases in GSI up to prime spawning and depletion of GFBs with age documented in Scarnecchia et al. (2007), while not yet fully observed across all known ages, show initial results consistent with expectations from the life history framework. GSI has continued to increase in young female spawners. Young spawners also frequently have high GFBs, manifested as large clumps of adipocytes attached to gonads and considerable adipocytes interspersed with eggs. At prime spawning, about age-25 on average for females in the Yellowstone-Sakakawea stock, GSI is maximized and remains nearly constant (about 20%) for about 15–20

Paddlefish juvenile and adult life stages

	Somatic growth	GSI	GFB	Spawning interval	Movements
1. Immature	highest	low	increasing	—	reservoir
2. Maturing	moderate	increasing	near maximum	—	reservoir
3. Somatic growth and reproduction	moderate to low	increasing	decreasing	longer	longer upriver migration
4. Prime reproduction	low to negative	high stable	decreasing (♂) depleted (♀)	shorter and minimized	shorter upriver migration
5. Senescence to death	negative	decreasing	decreasing (♂) depleted (♀)	unknown or dysfunctional	shorter upriver migration

FIGURE 5. Paddlefish juvenile and adult life stages relevant to harvest management (Scarnecchia et al. 2007).

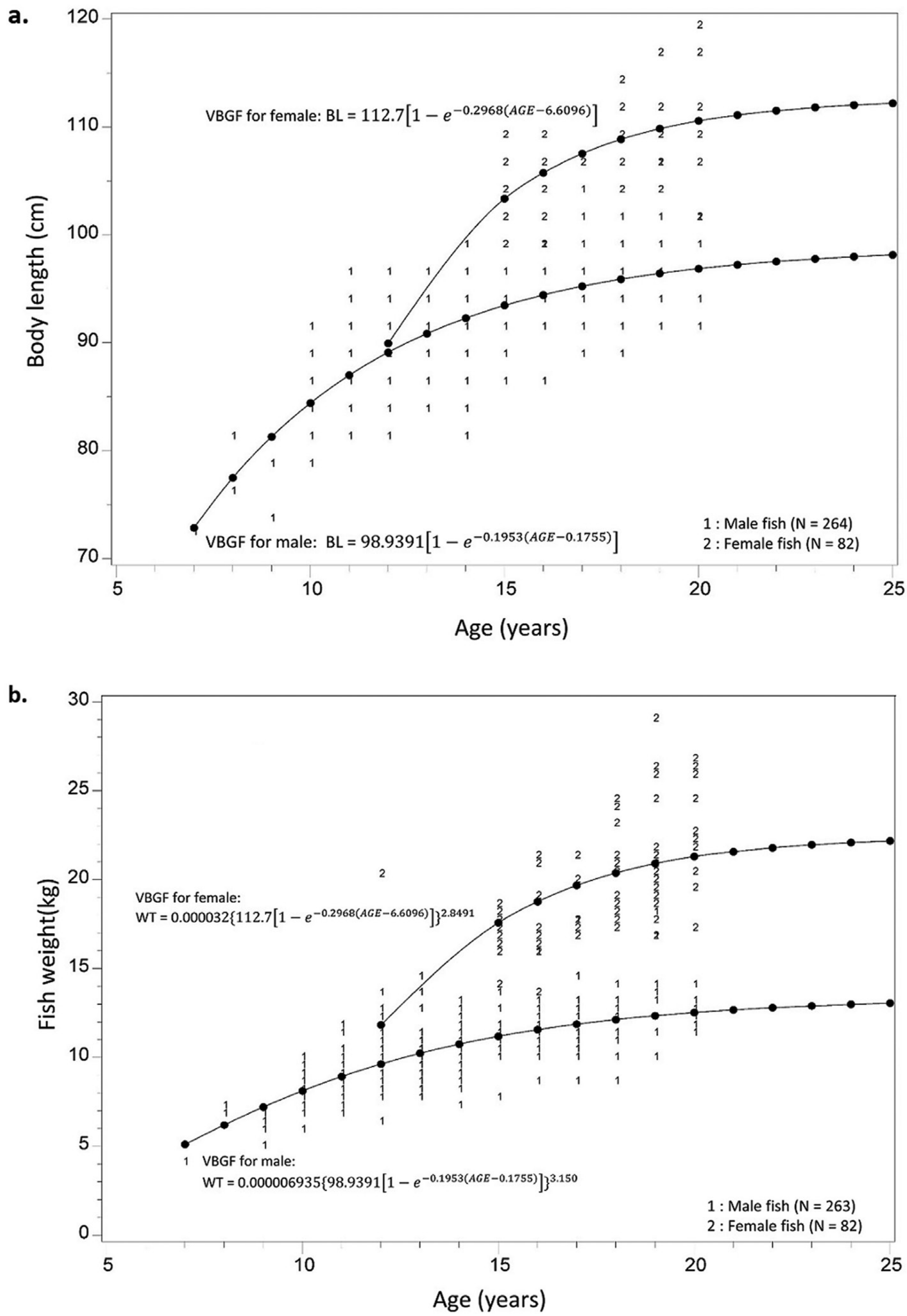


Figure 6. Validated sexual size dimorphism in Yellowstone-Sakakawea Paddlefish for length and weight as shown in von Bertalanffy growth curves. a) body length and fitted VBGF versus age for Montana-and-North Dakota combined 1995-cohort CWT Paddlefish catch (N = 347) from 2002 (age-7) to 2015 (age-20); b) fish weight and fitted VBGF versus age for Montana-and-North Dakota combined 1995-cohort CWT Paddlefish catch (N = 347) from 2002 (age-7) to 2015 (age-20).

years (Figure 7). At prime spawning, GFBs stored during the immature and maturing stages are also largely depleted (Figure 8), as the fish are focused on reproduction, with a minimum period of gonadal recrudescence and minimized spawning movements (Scarnecchia et al. 2007).

Although this five-stage life history framework was suggested to apply to other Paddlefish stocks, it has been evaluated in the past decade only for the Grand Lake stock (Scarnecchia et al. 2011). A key life history difference between more northerly versus more southerly stocks is that the five life history stages are more protracted in time farther north, where fish have a lower metabolic rate, and more compressed in time farther south, where the Paddlefish's metabolism is higher (Scarnecchia et al. 2011). More northerly stocks can also live much longer than more southerly stocks. They also have a lower GSI at prime spawning (Figure 7), suggesting that they invest less energy into a given spawning event, a result consistent with life history theory. Scarnecchia et al. (2011) evaluated (nonvalidated) ages of Grand Lake fish and found that whereas the five life history stages occurred over a period of 40–60 years for the more northerly Yellowstone-Sakakawea stock, the fish in Grand Lake progressed through these phases in 20–25 years (GSI: Figure 7; GFB: Figure 8). This result is consistent with other investigators, who have concluded based on age estimates that lifespans of Paddlefish were greater in more northerly stocks (Paukert and Fisher 2001; Jennings and Zigler 2009).

Life History Validation—Implications for Harvest Management

Linking life history characteristics such as age at maturation, GSIs, GFBs, reproductive periodicity, and migration distance with age and categorizing them into life stages can provide a useful framework for characterizing the status of individual fish and of the stock or HMU. The best harvest management options will vary with the life history and the nature and location of the fishery.

Sexual size dimorphism.—First, harvest managers must be aware of the degree of sexual size dimorphism in their stock or HMU, as it will influence the harvest regulations to be enacted to prevent overharvest of females. This dimorphism may be extreme in more northerly stocks. For example, in the Fort Peck stock of Montana and the Yellowstone-Sakakawea stock of Montana and North Dakota, nearly all mature females are larger than nearly all mature males (Scarnecchia et al. 2007; Figure 9). This extreme difference may require the manager to take steps, such as harvest slot limits (Scarnecchia et al. 1989) or mandatory retention (Scarnecchia et al. 2008), so that the sex ratio of the harvest is not strongly biased toward, or solely focused on, large female fish. The slot limit approach is also used for White Sturgeon *Acipenser transmontanus* on the Columbia River to protect broodstock (Rieman and Beamesderfer 1990). In more southerly localities, such as Grand Lake (Scarnecchia et al. 2011) and the Arkansas River in Arkansas (Leone et al. 2012), the amount of sexual size dimorphism may be much less, and a more equitable sex ratio of fish may naturally be harvested without resorting to mandatory retention, catch-and-release (Scarnecchia et al. 1996a; Scarnecchia and Stewart 1997), or harvest slots.

Stock Forecasting.—Some Paddlefish fisheries target both mature and immature fish in common feeding areas such as reservoir or large-river rearing habitats. In other cases, particularly river-reservoir stocks or HMUs, Paddlefish fisheries are focused on sexually mature, prespawning fish migrating in spring (and sometimes in the fall) from feeding areas into rivers. For example, the Montana recreational snag fisheries in May and June target

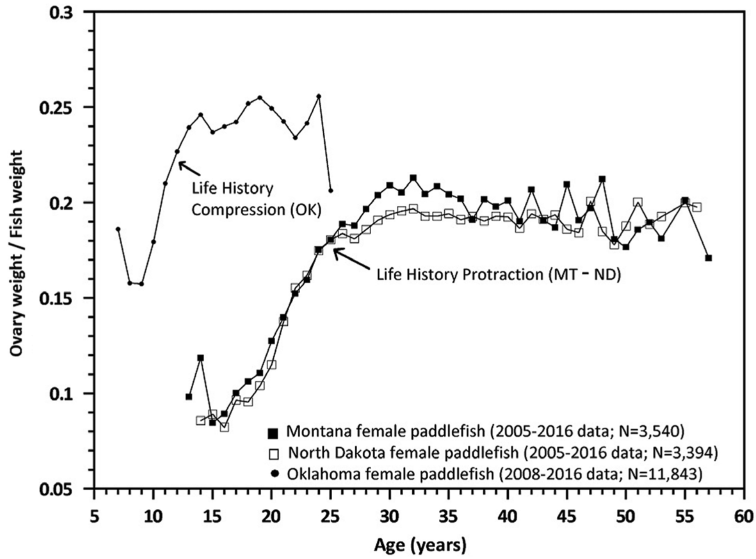


FIGURE 7. Gonadosomatic indices (ovary weight/fish weight) for a northern and southern stock showing the life history stage compression in the southerly stock (Oklahoma) compared to the more northerly stock (Montana–North Dakota). GSI at prime spawning is also higher for the southerly stock, indicating more reproductive effort per spawning event

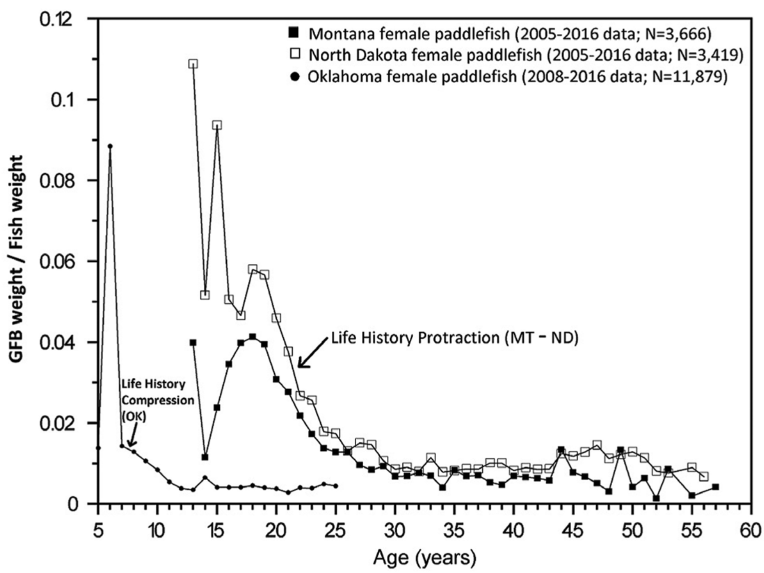


FIGURE 8. Gonadal fat (GFB) weight/fish weight for a northern and southern stock showing the life history stage compression in the southerly stock compared to the more northerly stock (Montana–North Dakota; Scarnecchia et al. 2011). Owing to differences in food availability and conversion, some southern stocks (and individual fish) may have large GFBs, and some northern stocks (and individuals) may have small GFBs. However, the compression of life stages is temperature- and metabolism-mediated and therefore more consistent between northern and southern stocks.

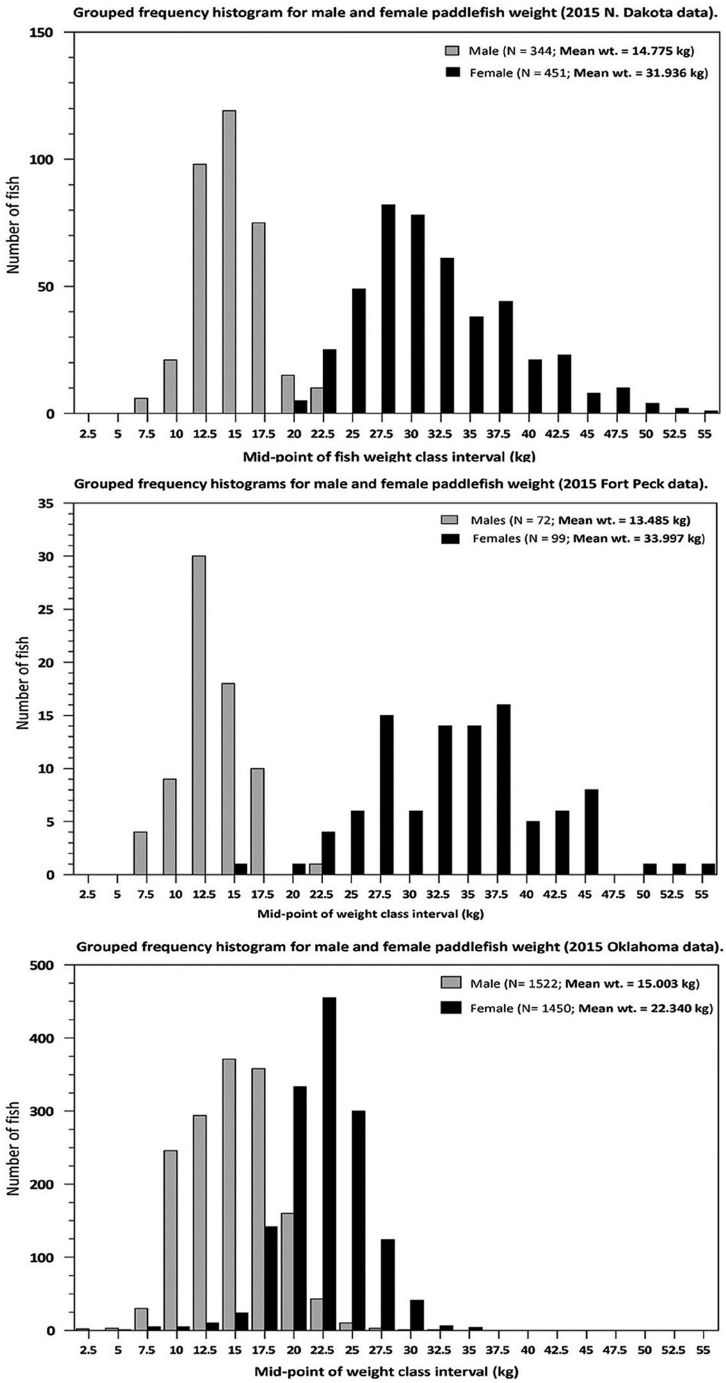


FIGURE 9. The amount of sexual size dimorphism has major implications for harvest management. In stock with more dimorphism (Yellowstone-Sakakawea (North Dakota) and Fort Peck (Montana)), absence of regulation leads to the tendency to harvest the largest fish, all of which are females. More overlap exists for the Grand Lake, Oklahoma Stock, and less difference between mean weights of males and females.

exclusively the mature, prespawning migratory portion of the stocks; immature fish and fish between spawns remain largely in the reservoirs, Lake Sakakawea and Fort Peck Reservoir (Scarnecchia et al. 2008). Males in the Yellowstone-Sakakawea stock mature at ages 8–11, whereas females mature several years later, at 16–18 (Scarnecchia et al. 2007). In this case, the mandatory retention requirement (i.e., all fish snagged must be kept) and the focused, as opposed to dispersed, area of harvest results in a harvest that is representative of the stock's age structure. The harvest of young, mature males ages 8–11 can be used as an index of recruitment success up to 10 or more years before females will be recruited to the fishery (Figure 10). Similar use of young mature males (e.g., a "jack" index) has been long used for Atlantic and Pacific salmon (Peterman 1982; Scarnecchia 1984). Even without mandatory retention, the forecasting approach can be used, as in the Grand Lake stock, where males mature 2–3 years before females and the fishery harvests predominantly mature fish (Scarnecchia et al. 2011). Under conditions of episodic recruitment, sex ratios of the harvested portion of the stock can fluctuate widely as initially the young males are harvested, and then young females dominate the harvest (Figure 10). Managers can use this pattern as a powerful tool to forecast abundance and identify strong year classes of females years before harvest, and to forecast probable sex ratios of the fish susceptible to harvest in each year. In other cases, where both immature and mature fish can intermingle for much of the year, appropriate time-area closures can by implemented

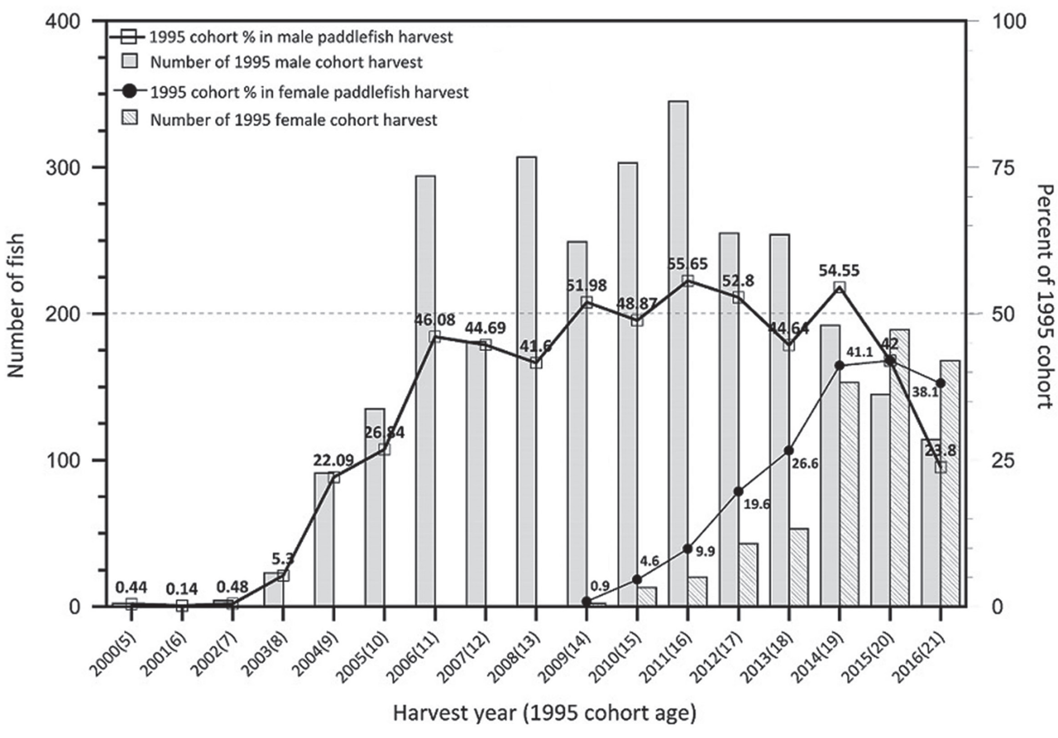


Figure 10. Episodic recruitment combined with major sexual size dimorphism and differences in age at first recruitment can result in males from a cohort entering the fishery several years before females. Percent of 1995 cohorts in male and female harvest in the North Dakota Paddlefish data, 2000–2016.

to minimize the harvest of immature fish, resulting in a fishery focused more heavily on mature fish. In that case, the above approach can be used.

Maintaining all Life History Stages, including older fish.—Whether a stock is viewed as having actual life stages or just as a continuum of ages, the life stage *concept* (Scarnecchia et al. 2007) has importance for stock assessment. It is not the age *per se*, but the life stage, i.e., in relation to growth, maturity, reproduction, that harvest managers must understand for sustainable management of their stock. A 25-year old female Paddlefish is old in the Grand Lake stock but is only entering its prime spawning period in the Yellowstone-Sakakawea stock of Montana and North Dakota. In both localities, however, a critical management need is to maintain older age, prime spawners, not just younger, new spawners, at whatever chronological age those stages occur for a given stock. Under inadequately regulated Paddlefish harvests, prime spawning female fish, as defined in Scarnecchia et al. (2007), may be rare or absent as harvesters target the largest females for caviar. Regulation must prevent the elimination of these prime spawners. In contrast, stocks with little sexual size dimorphism fished at very low rates may retain older female fish, even without protection of large spawners (e.g., Lower Mississippi River, Arkansas; Risley 2012).

The need to maintain larger, older spawners has been increasingly recognized as a vital aspect of sustainable management of fish stocks of many species. For example, Francis et al. (2007) designated the third of ten commandments of ecosystem-based fisheries scientists as the need to maintain old-growth age structure in a population. Hixon et al. (2014) identified the importance of BOFFFFs—big old fat fecund female fish—for fostering stock productivity and stability. Potential benefits of maintaining large, old fecund females in various species, reviewed in Hixon et al. (2014), can include more and larger eggs, faster growing larvae, possible differences in spawning time and location, protection against periods of poor reproductive success (i.e., conditions such as episodic recruitment), and a buffering against stock collapse under variable and unpredictable environmental conditions (Berkeley et al. 2004).

This concept of maintaining large and old fish in a harvested population is recognized and accommodated through regulations in some Paddlefish fisheries. For example, in the snag fisheries for the Yellowstone-Sakakawea stock, the mandatory retention requirement and a harvest cap has resulted in maintenance of not only prime spawners but even some senescent female Paddlefish (typically >40 years old; Scarnecchia et al. 2007). Low harvest rates (partly a result of limited access to fish) and a harvest cap in the Fort Peck stock of Montana has had a similar result (Scarnecchia et al. 2008).

In contrast, size and age truncation has been a pervasive problem in heavily harvested Paddlefish stocks (Alexander et al. 1985; Scholten and Bettoli 2005) as well as sturgeon stocks worldwide (Boreman 1997). Many Paddlefish fisheries are managed based on minimum length limits applied to both sexes (Colvin et al. 2013; Hupfeld and Phelps 2014; Hupfeld et al. 2016), designed to allow spawners an opportunity to spawn at least once, a fundamentally rational approach identified more than a half century ago (Larimore 1950). This approach can be sound if harvest rates on mature fish are not high. Under high harvest rates, additional regulations may also need to be applied, including harvest slots, a combination of mandatory retention and harvest caps (to equalize and limit the harvest of both sexes), protected areas and other options that meet the conservation needs of the stock and the intent of the fishery. In the long term, efforts must be made to maintain an age structure of the recruited fish for all harvested stocks and HMUs as that of an unexploited stock, rather than a truncated catch curve characteristic of overharvest of larger, older fish (Figure 11).

"Validation" of the Ecology and Implications for Harvest Management

Another subsequent benefit to harvest management emanating from the validation of ages and life histories is ecological "validation." This validation requires an accurate understanding of key ecological aspects of the stock, particularly as it relates to the frequency and magnitude of reproduction (age-0 index of abundance) and recruitment (by size and age) to potential harvest (i.e., and index of prerecruits or early recruits; Scarnecchia et al. 2009, 2019, Chapter 5 this volume). For effective harvest management, it is especially important to know whether recruitment typically occurs every year, every few years, or only episodically (e.g., once a decade or a longer interval). Although the same level of accuracy and predictability expected in age and many life history aspects cannot be expected in ecological responses, the ecological factors leading to successful or unsuccessful recruitment should be understood.

Inadequate recruitment is a pervasive problem in Acipenseriform species. Recruitment information is largely lacking for Paddlefish stocks, as it is for many long-lived, migratory fish species, and is a high research priority for Paddlefish. In former, prereservoir times, low recruitment in one location may have been compensated for by high recruitment in another, with fish from large year classes moving freely and opportunistically between areas, repopulating areas where reproductive success was lower. In recently impounded systems, however, recruitment within a particular river section may be dependent on reproduction and early survival occurring within that section and its reservoir or reservoirs, leading to more variable recruitment. Research in these areas deserves high priority.

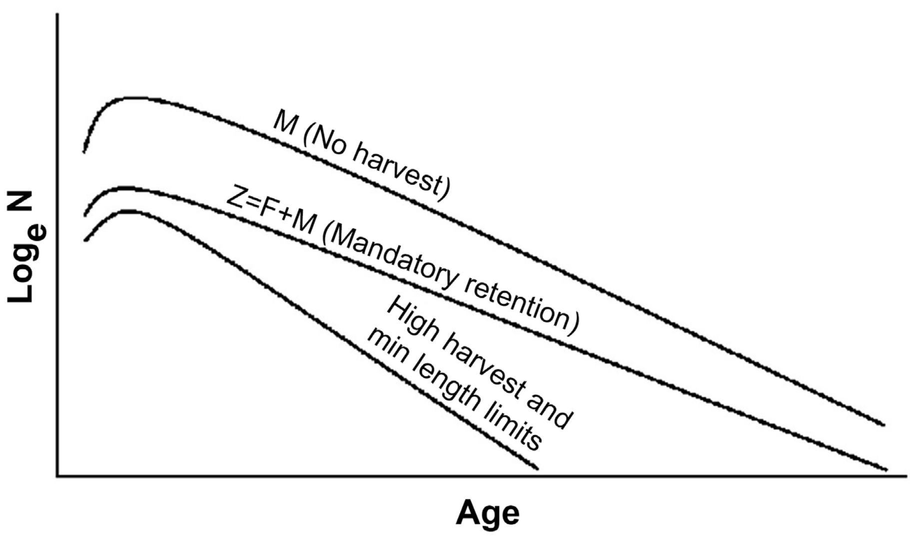


Figure 11. To maintain the age structure of a harvested population, the harvest strategy should seek to mimic the natural, mortality pattern (to curve) with a lower curve of similar slope (middle curve), avoiding the age and size truncation associated with cropping only large, old fish (bottom curve).

Under conditions of relatively reliable annual recruitment, harvest models can be used to balance harvest and natural mortality against annual growth and recruitment. However, under conditions of strongly episodic recruitment, males and females enter the fishery in pulses, with intervening periods of depletion from harvest and natural mortality (Figure 12; Scarnecchia et al. 2014). The natural mortality rate will typically be higher in the southern stocks than the northern ones, associated with higher metabolic demands southward (Scarnecchia et al. 2011). Situations with episodic recruitment may require cessation of harvest during periods of low recruitment, or, as a minimum, require carefully monitored harvest between recruitment events (Scarnecchia et al. 2014). It is also with stocks showing episodic recruitment that the effects of truncating age structure would be most harmful (Longhurst 2002). Under episodic recruitment, effective harvest management may require harvest caps or other restrictions designed to limit annual harvest, as it will appear to the harvesters that stock abundance is high (i.e., more recruited fish to harvest), even though there is poor recruitment of younger aged fish and poor harvest opportunities will follow. In extreme cases, it becomes necessary to manage around these recruitment pulses to maintain adequate spawners, until the next pulse in recruitment (Scarnecchia et al. 2014). In situations with more steady recruitment, more conventional harvest management is possible. Harvest will in any case be highly dependent on the recruitment (Rieman and Beamesderfer 1990).

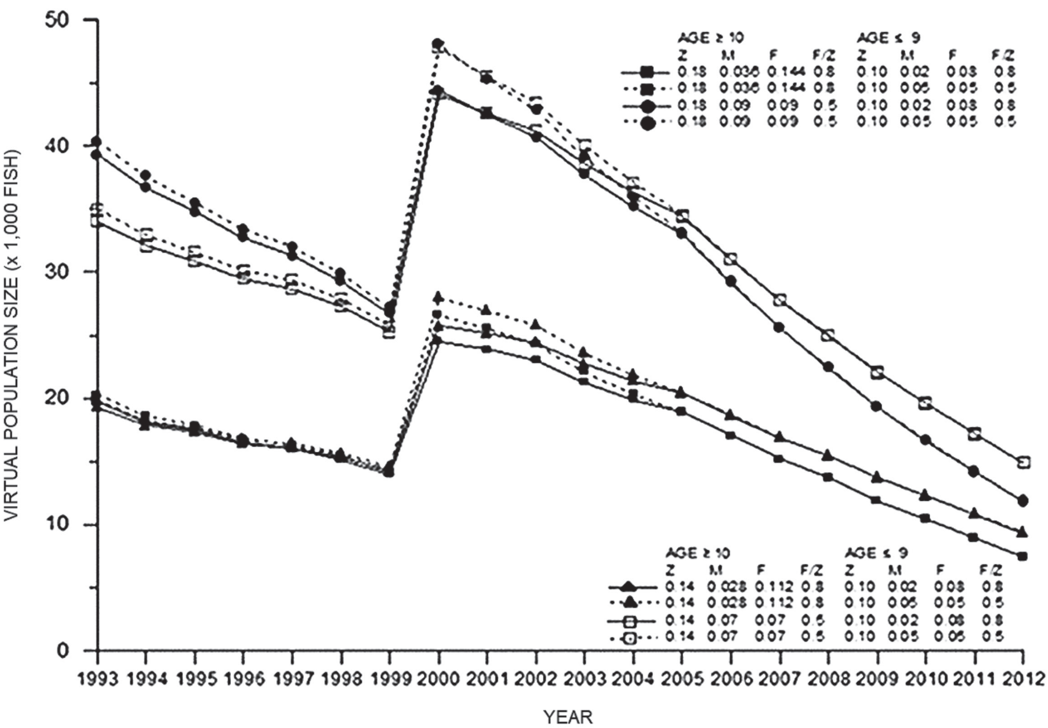


Figure 12. Episodic recruitment in some stocks can result in fish entering the fishery in pulses, with carefully monitored harvest of fish between major recruitment events (Scarnecchia et al. 2014). Managers must understand the recruitment pattern of their stocks and HMUs.

Effective Stock Assessment and Harvest Management—Lessons from Life History

In the next decades, managers can take several steps that link advances in knowledge of the life history of the Paddlefish to effective stock assessment and harvest management. First, genetics (Kaczmarczyk et al. 2012; Schwemm et al. 2014; Schwemm et al. 2019, Chapter 2 this volume), tagging data (Pracheil et al. 2012; Tripp et al. 2019, Chapter 3 this volume) and otolith microchemistry data (Bock et al. 2016; Whitledge et al. 2019, Chapter 6 this volume) need to be effectively used to identify stocks and HMUs. This is not a simple process ecologically or politically, as dams and river modifications have altered historical migration patterns (Sparrowe 1986) and multiple management jurisdictions are involved (Pracheil et al. 2012; Neely et al. 2015).

Second, it is important to obtain accurate, precise, unbiased data (lengths, weights, sex, age, fecundity, and fat reserves (GFBs)) from stocks and HMUs. To reduce the costs of data collection and improve data quality, managers of public fisheries should seek to implement harvest regulations that enhance the quality and the utility of the data needed for management. The fisheries themselves are usually the most cost-effective sources of data if harvest is managed and monitored appropriately. Data collection should be coordinated with adjacent and regional Paddlefish data collection efforts to ensure uniformity of data collection wherever possible (Scarnecchia et al. 2008).

Third, age and life history validation efforts for stocks and HMUs should be continued or initiated. It is important to validate ages of at least the first 10–15 years through either dentaries or fin rays. This effort will result in the ability to detect strong year classes early, and these strong cohorts can be followed as they age, an approach much easier than aging old fish from a mixed-age harvest and attributing them back to a cohort.

Fourth, managers should assess the degree of sexual size dimorphism of the stock or HMU. Distinct differences between male and female Paddlefish (e.g., Larimore 1950; Gengerke 1986; Scarnecchia et al. 1989; 1996) must be identified and accounted for in harvest management regulations.

Fifth, managers should characterize the age specific life stages of the stock, by sex, that is to be managed. It is important to understand the ages at which the five life stages identified (Scarnecchia et al. 2007; 2011) occur in each stock or HMU.

Sixth, regulations should ensure that all life stages remain in a harvested stock, avoiding size or age truncation. Focusing harvest on mature fish is acceptable, recruitment permitting, particularly if caviar is the most highly valued product. However, it is desirable to mimic the natural mortality pattern (Figure 11).

Seventh, harvest caps will go far to ensure that continually changing fisheries still result in a sustainable stock (Combs 1986; Hoffnagle and Timmons 1989; Scarnecchia et al. 2008). Indirect methods such as area closures and fee increases, if monitored appropriately, can have similar but less direct benefits (Timmons and Hughbanks 2000; Schooley et al. 2014).

Finally, managers should understand, monitor, and—if possible—forecast recruitment of the stock or HMU (Scarnecchia et al. 2019, Chapter 5 this volume). In fisheries targeting prespawning migrants, mature males, which mature up to 10 years before females of a cohort, can be used to forecast the number of females. Knowledge of age, growth, and the recruitment pattern will enable agencies to manage proactively under conditions of variable recruitment.

Based on a review of historical Paddlefish investigations and of the two symposia synthesizing historical studies, we suggest that there is an acute need for advances in our knowledge of genetics, movements, life history and ecology to be used more effectively in management of the species. As in most species, Paddlefish management has trailed too far behind acquired knowledge of life history, ecology and habitat use. Future efforts should emphasize improved data collection and mobilization of existing data to advance management efforts within and among jurisdictions.

Acknowledgments

We thank biologists and managers from the many Paddlefish states for useful discussions and information leading to this paper. We are especially grateful to the fisheries managers and technicians who have worked with us throughout more than two decades in collecting information presented in this paper, including, but not limited to, G. Power, S. Gangl, F. Ryckman and S. Shefstad of the North Dakota Game and Fish Department; P. A. Stewart, B. Schmitz, R. Molstad, and D. Skaar of Montana Fish, Wildlife and Parks, and B. Gordon, K. Cunningham, B. Bolton, and B. Brown of the Oklahoma Department of Wildlife Conservation, and S. Miller and J. Vrtelova of the University of Idaho.

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