

Chapter 5

Factors Affecting Recruitment of Paddlefish: Hypotheses and Comparisons with Sturgeons

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Abstract.—Inadequate recruitment is a concern in many stocks of Paddlefish *Polyodon spathula*. Despite the importance of maintaining adequate recruitment, little understanding exists of specific recruitment factors and mechanisms. In this chapter we review and synthesize the results of the relatively few studies and observations of Paddlefish reproduction and recruitment and the factors potentially responsible for observed variations. Comparisons are made with studies on sturgeons. Although Paddlefish and sturgeon show many anatomical, life history, and behavioral similarities, some key features of Paddlefish differing from other Acipenseriform species are lifelong zooplanktivory, filter feeding, midwater foraging behaviors, and lack of armoring. Data from both sturgeon and Paddlefish show higher reproductive success associated with higher river discharge; greater Paddlefish reproductive success in some adfluvial populations has also been linked to increasing and high reservoir levels. Whereas several sturgeon studies suggest that recruitment (and year-class strength) are determined within 2–3 months of hatching, results from Paddlefish suggest that year-class strength may be determined later in their first year or in their second year. Observations and field results lead to the hypothesis that young Paddlefish must grow fast in their first and early second years of life to reach a size where they can successfully overwinter, avoid predation from piscivorous fishes and birds, and recruit. Support for this grow-fast-or-be-eaten hypothesis comes from several sources, both indirect (e.g., the relation between fish length and rostrum length) and direct (higher survival of larger fish released and higher lipids in age-0 fish in years of good recruitment). However, more research is needed to adequately test this hypothesis. Paddlefish rearing habitat changes include river-backwater and side-channel sedimentation, reservoir sedimentation and aging, and threats from increased native and nonnative predator populations. Managers of Paddlefish will need a more detailed understanding of the habitat conditions needed for successful recruitment in the wild.

Introduction

Adequate recruitment is a critical requirement for sustainable management of fisheries, and a limitation for many fish stocks (Jakobsen et al. 2009). Recruitment is the addition of new fish to a potentially harvestable population by growth from smaller sizes (Ricker 1975). Trippel and Chambers

(1997) define recruitment more comprehensively as “survival to a reference time in the life cycle” (p. xxii). The time of recruitment in the life cycle can vary with context; a common benchmark (and the one used here) is the time at which additions of fish available to a fishery can be predicted with reasonable certainty (i.e., preharvest survival rates are typically high and predictable). Recruit-

ment thus typically requires both successful reproduction followed by sufficient growth and survival to reach a specified size (Houde 1987; Parsley et al. 1993; Jakobsen et al. 2009). This distinction between reproduction and recruitment is critical to evaluating ecological impacts on recruitment. Highly successful *reproduction* in a year may eventually result in highly successful *recruitment* of that cohort, but not necessarily. Similarly, recruitment failure can occur even in the presence of continued reproduction (e.g., White Sturgeon *Acipenser transmontanus*; Hildebrand et al. 2016). Ecological factors and mechanisms causing mortality between reproduction and recruitment may act in overt, convulsive ways, with direct, sudden causes (e.g., starvation, disease), or in very subtle ways (e.g., growth-influenced mortality rates). Variable and often subtle events leading up to recruitment success or failure can make the understanding of recruitment mechanisms difficult without detailed, long-term study (Houde 1987). Recruitment synchrony (or asynchrony) among stocks can provide a valuable means to identify causes and the spatial scale and distribution of their effects in relation to climatic, hydrologic, and other landscape-level factors (e.g., Scarnecchia 1984; Myers 1998). Understanding factors affecting recruitment variation can be a special challenge in altered habitats; in many cases anthropogenic causes of recruitment decline (e.g., habitat degradation) may differ from natural factors that lead to recruitment variation.

One group of fish where recruitment and habitat alterations are both major concerns is in Acipenseriform fishes—sturgeons and paddlefishes. Inadequate recruitment is a major problem for many stocks of Paddlefish *Polyodon spathula* (Scarnecchia et al. 2014) and sturgeons (Nilo et al. 1997; McAdam 2015; Bahr and Peterson 2016). Despite the importance of adequate recruitment for sustainable management of Paddlefish and stur-

geon, little understanding exists of specific recruitment factors and mechanisms. Many Paddlefish stocks have suffered decreased recruitment resulting from degradation of their large river habitats (Sparrowe 1986; Gerken and Paukert 2009). Scarnecchia et al. (2007, 2014) demonstrated the vital importance of Paddlefish recruiting adequately to a northern Great Plains stock, showing that low subsequent natural mortality rates and adequately controlled harvest fisheries will result in reliable yields for decades. Hindcasting of past recruitment based on current age structure can provide a valuable source of long term recruitment analysis (McAdam et al. 2005; McAdam 2015), and aid in identifying potential drivers of recruitment, although such correlations may or may not be useful in predicting future recruitment success as environmental conditions change (Myers 1998). For a long-lived species such as Paddlefish, strongly negative human-caused effects on recruitment in most localities (Sparrowe 1986) accentuates the need to understand how ecological effects act to reduce recruitment and how to reverse them.

This chapter reviews and synthesizes the results of the relatively few studies and observations of Paddlefish reproduction and recruitment and the factors potentially responsible for observed variations. We update current literature and use a comparative approach with sturgeon in considering a conceptual model of factors that affect Paddlefish recruitment.

The Complexity of Acipenseriform Recruitment

A range of processes needs to be considered for understanding Paddlefish recruitment. Parsley et al. (1993) presented a generalized conceptual diagram for White Sturgeon that provides a useful starting point (Figure 1). Their figure depicts recruitment

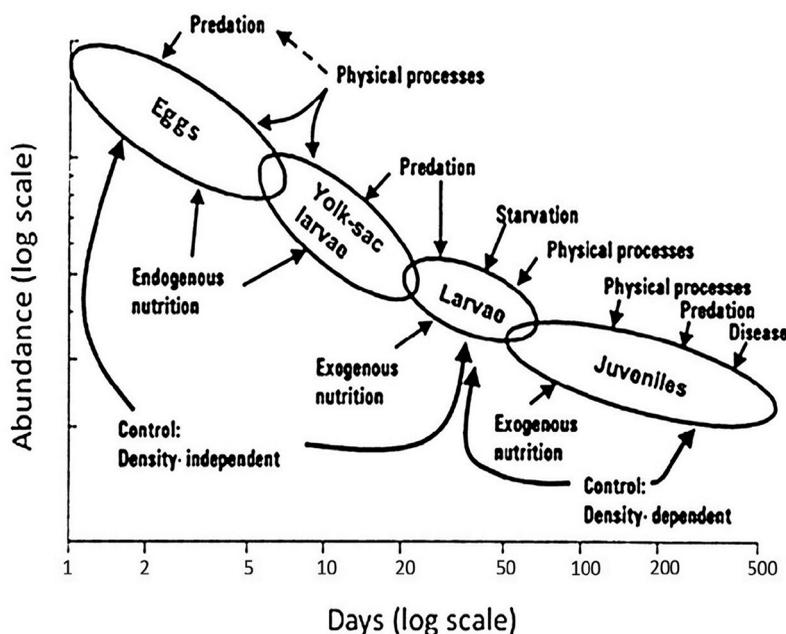


FIGURE 1. Conceptualization of the recruitment process adapted from Houde (1987) showing probable sources of death, nutrition, and mechanism of control for the early life history stages. Negative slopes in abundance throughout each life stage are an approximation, not a measurement of the degree of mortality that could be expected (from Parsley et al. 2002).

as potentially occurring at any time over a period of more than one year after hatching. Factors affecting recruitment may include physical processes related to water flow, turbidity, sediment, and temperature, as well as food web effects such as available nutrition (endogenous and exogenous), prey species abundance and composition, competing species, and predatory species. Issues of initiation of exogenous feeding (i.e., avoiding starvation) and adequate growth in size to avoid predation can play major roles and may be mediated by fish density. In any year, a complex sequence of factors, episodic or subtle and gradual (Houde 1987), may lead to conditions resulting in recruitment. Considering the ecological and economic importance of Acipenseriform species, few studies have been conducted to fill in the details of the conceptual diagram of Figure 1 for either Paddlefish or sturgeon.

Sturgeon Recruitment

When compared to Paddlefish, more effort at understanding recruitment has been expended on sturgeon species, including Lake Sturgeon *Acipenser fulvescens* (Nilo et al. 1997), Pallid Sturgeon *Scaphirhynchus albus* (e.g., Wildhaber 2007; Guy et al. 2015; DeLonay et al. 2016a, 2016b) and White Sturgeon (Hildebrand et al. 2016). Some studies have focused on anthropogenic causes of and contributors to recruitment failure in highly altered systems whereas other studies have focused on natural recruitment drivers in less-altered systems. White Sturgeon and Pallid Sturgeon have received focused attention because of recruitment failure that affects multiple populations (Hildebrand et al. 2016; DeLonay et al. 2016a, 2016b). Spatially variable recruitment success has been observed. For example, White Sturgeon

populations show recruitment intensity ranging from regular and annual, to intermittent, to long-term recruitment collapse (Parsley et al. 1993; McAdam 2015; Hildebrand et al. 2016).

Overall, the studies suggest that the key factors affecting recruitment, and the exact stage of the life cycle when year-class strength is set, may differ among sturgeon populations. Some studies implicate conditions for spawning and larval rearing as limiting to recruitment. For example, findings from multiple studies of White Sturgeon identify increased sedimentation in spawning habitat as a critical impact of upstream flow regulation (McAdam et al. 2005; Paragamian et al. 2009; McAdam 2011, 2015). In addition, the changes in physical processes have led to microhabitat changes and altered food webs, potentially affecting early growth and survival. For example, McAdam et al. (2005) reported that more porous substrates led to more rapid interstitial hiding and less drift in white sturgeon larvae. Studies on the endangered Pallid Sturgeon have identified factors affecting larval drift as likely causes of recruitment failure. Dam construction and blockage of migrations may limit the ability of larval fish to undergo long distance drift without drifting into unfavorable reservoir habitat. Guy et al. (2015) reported that anoxic conditions in flocculent bottom sediments in transitional riverine-reservoir zones create conditions lethal to Pallid Sturgeon larvae. Research is designed and conducted to evaluate the hypothesis that opportunities for longer larval drift in riverine habitat and higher larval survival will lead to improved recruitment (Guy et al. 2015; DeLonay et al. 2016a, 2016b).

The idea that recruitment is determined early in life, within the first 2–3 months, is consistent with correlations between spring freshet discharge and recruitment identified for Lake Sturgeon and White Sturgeon (Kohlhorst et al. 1991). For Lake Sturgeon,

Nilo et al. (1997) found that year classes were stronger in the St. Lawrence River during years of higher May–June water temperatures, and during years of higher mean June discharge in the Des Prairies River, a major spawning tributary. They concluded that “year-class strength is determined during the first few months of life ... during which larvae drift from the spawning grounds and exogenous feeding begins” (p. 774). This result is consistent with finding of Caroffino et al. (2010), who reported almost no predation on age-0 juvenile stage Lake Sturgeon. Similarly, for White Sturgeon, Parsley et al. (1993) sampled early life stages and concluded that year-class strength in the Lower Columbia River was determined during the first 2–3 months after spawning. They further noted that as the fish grow, “Losses of juvenile(s): to predation are probably slight because of the protective scutes, benthic habits, and fast growth” (p. 62). Findings regarding the ontogenetic age of sturgeon recruitment are also supported by the high survival reported for hatchery releases; survival is higher, however, for larger fish (Beamesderfer et al. 2014; Hildebrand et al. 2016). Although the exact mechanisms driving differences in early survival are not precisely known, both abiotic and biotic factors may be implicated. In addition to abiotic factors such as discharge, sediment, and water temperature, biotic factors such as predation may play a role. Laboratory studies on White Sturgeon have indicated that age-0 sturgeon are potentially preyed upon by sculpins *Cottus* spp., Northern Pikeminnow *Ptychocheilus oregonensis*, and other species in their early rearing habitats (Gadonski and Parsley 2005a, 2005b), so predation may be playing a role in affecting recruitment, despite earlier tentative conclusions to the contrary (Parsley et al. 1993). In the wild, abiotic stressors (e.g., loss of habitat for feeding and cover) may also amplify the effects of biotic factors such as predation.

Paddlefish Recruitment

Only a few studies document Paddlefish recruitment, its variations, and what influences those variations. Transect counts conducted in Lake Sakakawea, North Dakota, in July and August for more than two decades show that reproduction, as indicated by an age-0 index of counts of fish (typically 150–300 mm FL; Figure 2) has been recorded in all but 2 years over the period 1992–2014 (Figure 3). Recruitment, however, is much less frequent, with a few strong year classes (episodic recruitment; Figure 4; Scarnecchia et al. 2014). This episodic recruitment is evident in the ages of fish recruited to the snag fisheries; most year classes have few recruits (Figure 5). The 1995-year-class has been dominant. Episodic recruitment has also been documented in Grand Lake, Oklahoma Paddlefish, where the 1999-year-class has been dominant in the harvest over the period 2008–2016 (Figure 6; Scarnecchia et

al. 2011; Unpublished data, Oklahoma Department of Wildlife Conservation). Studies in other localities often suggest more regular and consistent recruitment, although a cautious interpretation is required in that migrations of fish of different stocks may mask irregular recruitment at a specific location. While Paddlefish and sturgeon are both expected to show ‘periodic’ recruitment strategies (Winemiller and Rose 1992), the presence of numerous years with near-zero recruitment is a concern that complicates harvest management (Scarnecchia et al. 2014) and warrants further investigation.

Paddlefish and Sturgeon Similarities in Recruitment

Paddlefish and sturgeon share a wide range of anatomical, life history and ecological attributes (Bemis et al. 1997), such as electroreceptors in the rostral and opercular regions, a long lifespan, delayed maturity,



FIGURE 2. Successful reproduction and early survival (left) and probable recruitment (right) in Lake Sakakawea, North Dakota. (Photo: North Dakota Game and Fish Department).

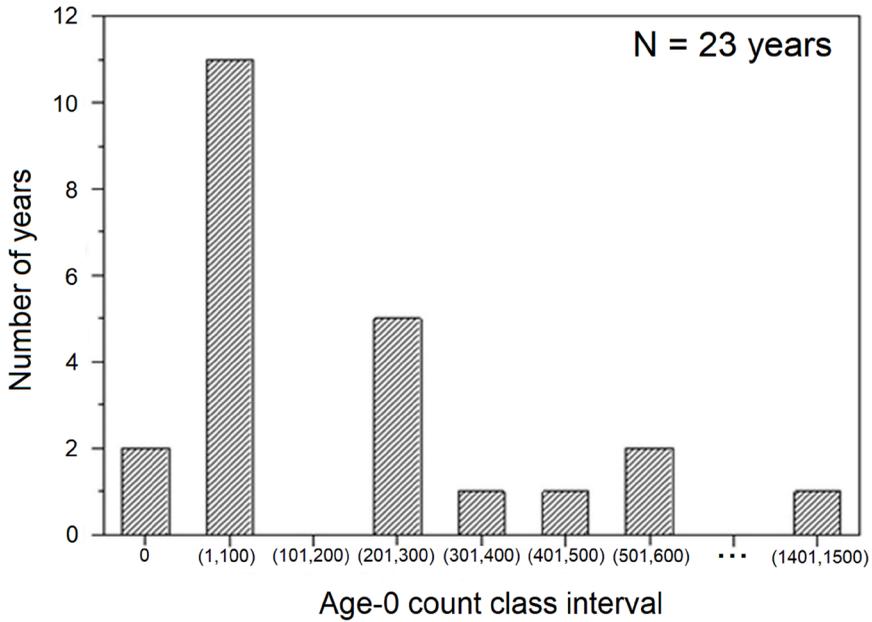


FIGURE 3. Number of years with counts of age-0 Paddlefish within specific intervals, 1992–2014.

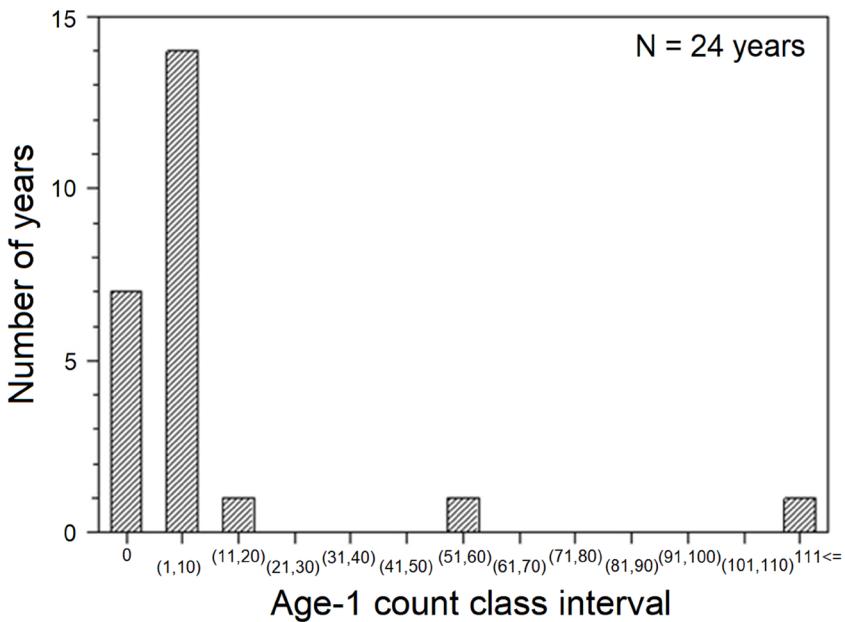


FIGURE 4. Number of years with counts of age-1 Paddlefish within specific intervals.

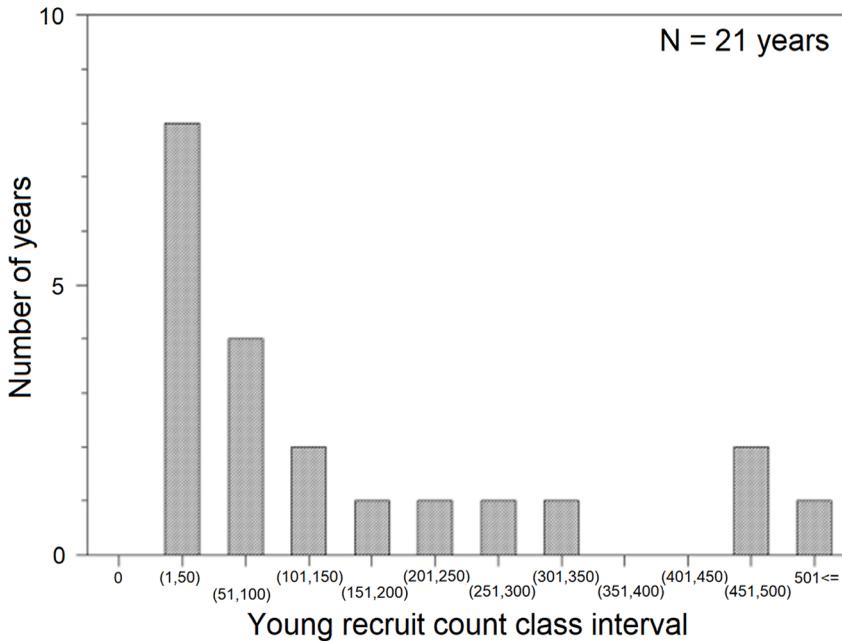


FIGURE 5. Number of years with counts of young mature recruits within specific intervals, 1985–2005 brood years.

demersal, riverine spawning, prespawning migratory behavior (Bemis and Kynard 1997), and vulnerability to river regulation and overharvest (Boreman 1997). It might therefore be assumed that they should also share many factors affecting their recruitment success. As with sturgeon, higher flows during spring have been commonly associated with successful Paddlefish recruitment (North Dakota: Scarnecchia et al. 2009; Oklahoma: Schooley and Neely 2018; Figure 7). Preliminary investigations have implicated higher river discharges in spring and higher reservoir levels as providing more favorable recruitment conditions. High river discharges have the potential to affect multiple habitat attributes ranging from riverine spawning habitats to reservoir productivity. In Oklahoma, for example, widespread flooding throughout the state in 2015 resulted in finding age-0 Paddlefish in nontypical places, including Zink Low Water Dam in Tulsa. Winter netting in 2016 also encountered many age-1 recruits (J.D.

Schooley, personal communication). Higher flows have also generally been associated with higher numbers of age-0 Paddlefish counted in Lake Sakakawea, North Dakota (Scarnecchia et al. 2009).

Paddlefish and sturgeon also show strong similarities in reproductive migration and in some aspects of habitat use (Bemis and Kynard 1997). Paddlefish spawning is preceded by an upstream riverine migration (Firehammer and Scarnecchia 2007; Miller and Scarnecchia 2008) and due to the ubiquity of impoundments, this behavior commonly leads to spawning downstream of dams. Selected spawning habitats are generally gravel and coarse substrate (Jennings and Zigler 2009), although, as with sturgeon, assessing preferred (as opposed to selected) habitats in altered systems can present challenges (Hildebrand et al. 2016). Paddlefish and sturgeon both have adhesive eggs (Russell 1986), and immediately after hatching, larvae drift downstream, shifting to benthic habitats once feeding is initiated (Parsley et

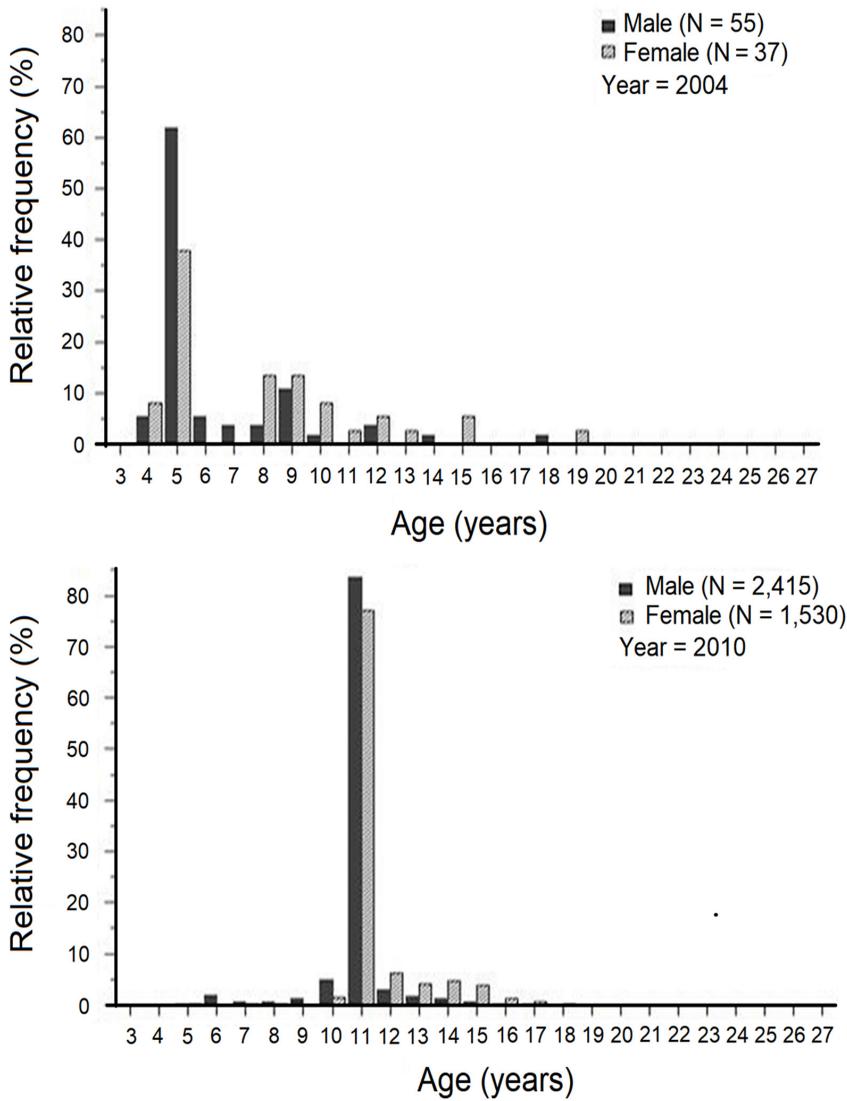


FIGURE 6. Episodic recruitment in the Grand Lake, Oklahoma seen as a strong year class (1999) dominating the harvest. (Scarnecchia et al. 2011). Data are unavailable for 2005–2007.

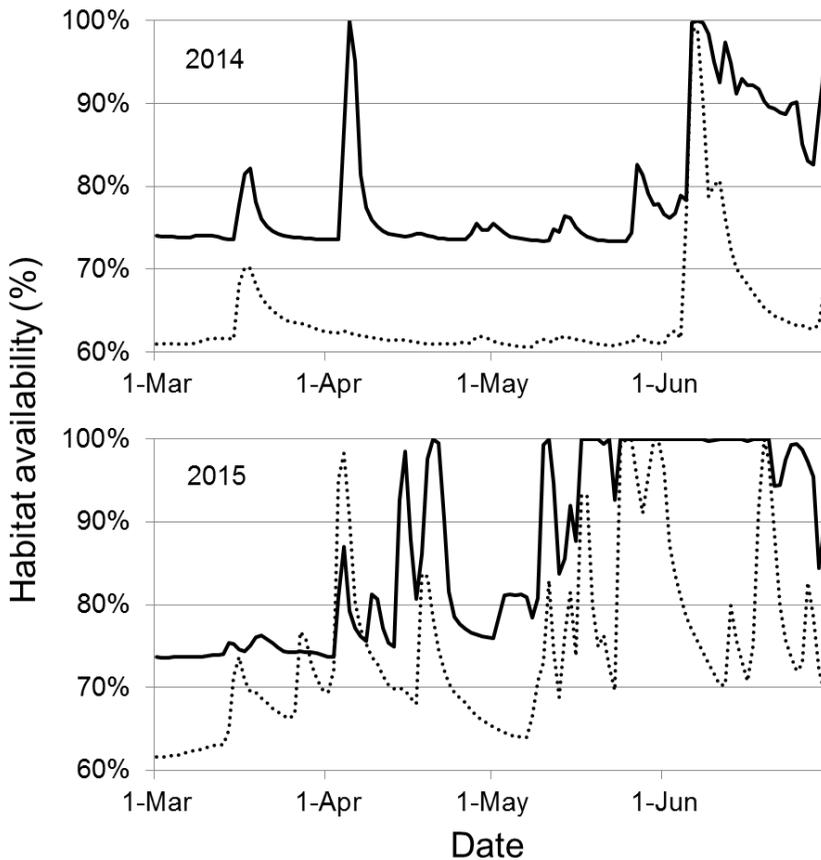


FIGURE 7. Habitat availability in years with successful and unsuccessful recruitment differ greatly; springtime estimates of proportional spawning habitat availability for Neosho (solid line) and Spring (dotted line) rivers, Oklahoma in years with successful recruitment (2015) and unsuccessful recruitment (2014). Schooley and Neely (2018).

al. 1993; Jennings and Zigler 2009). Such numerous similarities would suggest that factors affecting recruitment might also be similar.

Paddlefish: A Special Case of Acipenseriformes?

Despite many similarities between Paddlefish and sturgeon, the North American Paddlefish demonstrates a unique evolutionary development (as compared to other ancestral paddlefishes and sturgeons; Grande and Bemis 1991) as a midwater zooplantivore

well adapted to rearing in river backwaters, lakes and reservoirs (Russell 1986; Jennings and Zigler 2009). It may not be coincidence that despite widespread habitat loss and degradation (Sparrowe 1986), this species, as opposed to nearly all other Acipenseriformes, still supports recreational and commercial fisheries in many states (Quinn 2009; Scholten 2009). The species has also successfully colonized habitats in Europe and Asia (Jelkić and Opačak 2013; Jarić et al. 2018). The study of factors limiting Paddlefish recruitment must therefore consider relevant sturgeon studies but not be limited by them.

Some key features of *Polyodon spathula* differing from other Acipenseriform species are its lifelong zooplanktivory, its filter feeding and midwater foraging behaviors, and its lack of armoring. In the impounded systems which constitute most current Paddlefish habitat, the species uses a progression of habitats in their first and second years, from free-flowing river to reservoir headwaters to pelagic reservoir (or pelagic backwaters in more natural systems). The rapid onset of feeding in Paddlefish, and therefore the cessation of drift (3 d posthatch according to Ji et al. 2012) may reduce the potential negative effects of drifting too early into reservoirs. The ecological and behavioral differences between age-0 Paddlefish and sturgeon may also result in differential responses to reservoir formation and conditions. Unlike sturgeon, young Paddlefish do not remain on the bottom for the duration of their first year. As the rostrum and gill rakers develop, the Paddlefish rapidly transitions from a typical bottom-dwelling Acipenseriform species similar in appearance (although distinguishable; Wallus et al. 1990) and behavior to sturgeon to a midwater zooplanktivore, with a long, flat rostrum, long gill rakers, and no armoring to protect them from predation. In Lake Sakakawea, North Dakota, this transition typically occurs by July following a spring hatch (Fredericks 1994; Scarnecchia et al. 1997; Figure 2). Feeding in the water columns of backwaters, lakes, and reservoirs is based on electrosensory detection (Wilkins et al. 2002) and targeting of individual prey organisms through much of the first year (Fredericks 1994). Feeding typically transitions to filter feeding within a year, or sooner, as gill rakers develop fully. These difference in life history, including the common use of pelagic habitats by age-0 and age-1 Paddlefish, raises the possibility of them having different factors limiting recruitment than other Acipenseriformes. Even though other Acipenseriform species, which are bottom-oriented and armored, may

have their year-class strength determined 2–3 months after hatching, the highly vulnerable, pelagic, nonarmored Paddlefish might not recruit until late age-0 to age-1 (Figure 3; Scarnecchia et al. 2009; 2014), i.e., 300–500 d after hatching, as depicted at the far right of Figure 1.

Factors Affecting Paddlefish Recruitment—Evidence and Speculations

Ecology of age-0 and age-1 Paddlefish

An older age and larger size at recruitment for Paddlefish than for sturgeons is hypothesized because patterns of Paddlefish recruitment have often not followed reproduction and early life stage survival (i.e., growth through their first few months; Figures 2–5), and also because of the distinct ecology of age-0 and age-1 Paddlefish compared to sturgeons. In Lake Sakakawea, North Dakota, age-0 Paddlefish can be observed, collected, and indexed for abundance along transects in late July through September as they swim near the surface ahead of slow-moving motorboats (Fredericks and Scarnecchia 1997; Scarnecchia et al. 1997). As a fish reaches 150–200 mm FL, the rostrum increases in size and breadth. When alarmed by an approaching boat, a fish's increasingly large rostrum commonly results in more sustained swimming near the surface as the fish flee, and its presence at the surface is more evident. In the turbid waters of Lake Sakakawea, age-0 fish below 250 mm FL are translucent to transparent when held up to light; blood can be seen flowing through the fish. Hatchery fish or fish in clearer waters, in contrast, are darker (Figure 8). Foraging of the age-0 fish occurs in loosely aggregated patches (Fredericks and Scarnecchia 1997; Scarnecchia et al. 2007; 2008). The translucency of the age-

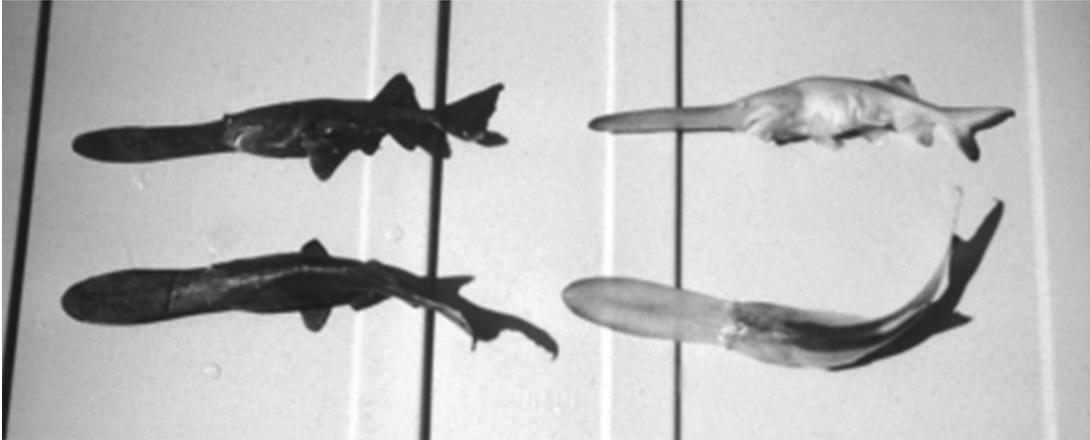


FIGURE 8. Translucent wild Paddlefish (right; approximately 210 mm FL) sampled from turbid headwaters of Lake Sakakawea next to darker Paddlefish reared in clearer ponds of Garrison Dam National Fish hatchery, North Dakota.

0 Paddlefish in turbid reservoir headwaters and their movements in loose aggregations (as opposed to schools) may make them less conspicuous to predators. The large, predaceous cladoceran *Leptodora kindtii* (Figure 9a) is a preferred food item at this prefiltering stage (Figure 9b), when young Paddlefish are seeking individual prey items. Other large invertebrate prey and larval fishes may also be consumed (Lake Sakakawea: Fredericks 1994; Fort Peck Reservoir, Montana: Kozfkay and Scarnecchia 2002; Bowersox et al. 2014). A switch from particulate feeding to filter-feeding can evidently occur in either the first or second year, depending on fish size and gill raker development (Michaletz et al. 1982; Fredericks 1994).

Grow-Fast-or-Be Eaten Hypothesis

During their first year, it is hypothesized that fish are emphasizing growth in length to reach a size where they are less susceptible to predation. The hypothesis that predation is a major factor at this stage is supported by field evidence (Mero et al. 1995). Parken and Scarnecchia (2002) reported Paddlefish in the stomachs of piscivores, including Wall-

eye *Sander vitreus* (Figure 10a), Sauger *S. canadensis*, and Northern Pike *Esox lucius*. They also found that the larger the Walleye and Sauger, the more apt they are to have eaten a Paddlefish (Figure 10b). Age-0 Paddlefish are not elusive. Unlike any other fish species in the lake, individuals are readily observed and dip-netted in open water at the reservoir surface (Scarnecchia et al. 1997). Several hundred have been caught in one day among three boats (D. L. Scarnecchia, unpublished data). This lack of elusiveness also makes them comparatively easy prey during their first summer and fall for piscivorous fish and birds (Parken and Scarnecchia 2002). Avian predation on age-0 Paddlefish has been visually observed on numerous occasions during years of high age-0 Paddlefish abundance.

Observations and field results lead to the hypothesis that young Paddlefish must grow fast in their first year, successfully overwinter, and reach a size in their second year where they can avoid predation from piscivorous fishes and birds, and recruit. Support for this grow-fast-or-be-eaten hypothesis comes from several sources, both indirect and direct. Early indirect evidence comes from Thomp-

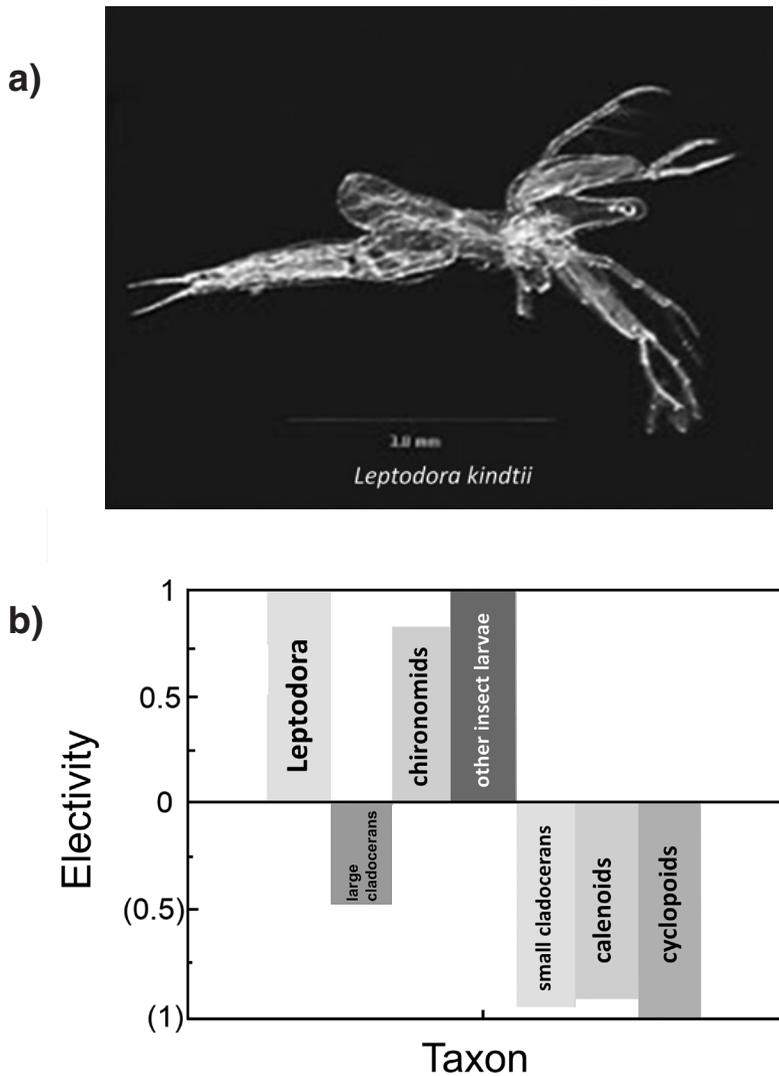


FIGURE 9. a) *Leptodora kindtii*, a preferred food b) of age-0 Paddlefish in Lake Sakakawea, North Dakota. Fredericks 1994).

son (1934), who plotted rostrum length as a percentage of total length and found it to be greatest during this age-0 through age-1 period (Figure 11). At this critically dangerous period in its life, the fish may thus appear larger to predators at a low energetic cost, (i.e., emphasizing growth of the long rostrum instead of more costly growth in the rest of the fish; Hemingway and Scarnecchia 2016). Once they reach a larger size, the ratio of rostrum length to total fish length decreases,

consistent with the idea that the benefits of a longer rostrum are reduced. The rostrum can then primarily serve its coevolved primary electrosensory and hydrodynamic functions (Wilkins et al. 1997; Allen and Riveros 2013). The large size of the rostrum in relation to the total length at age-0 and age-1 (Thompson 1934), presenting a larger apparent size to predators, is consistent with the growth and predation tradeoffs often found in fishes and with the benefits of rapid growth during this



a)

b)

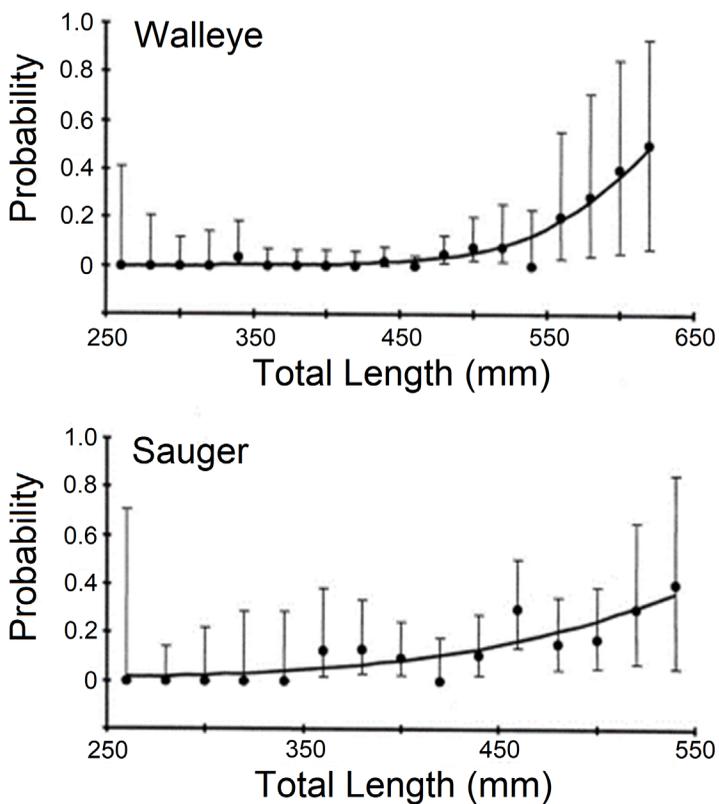


FIGURE 10. a) Age-0 Paddlefish are preyed upon by Walleye and Sauger in Lake Sakakawea, b) with larger predators more likely to have consumed a Paddlefish (Parken and Scarnecchia 2002).

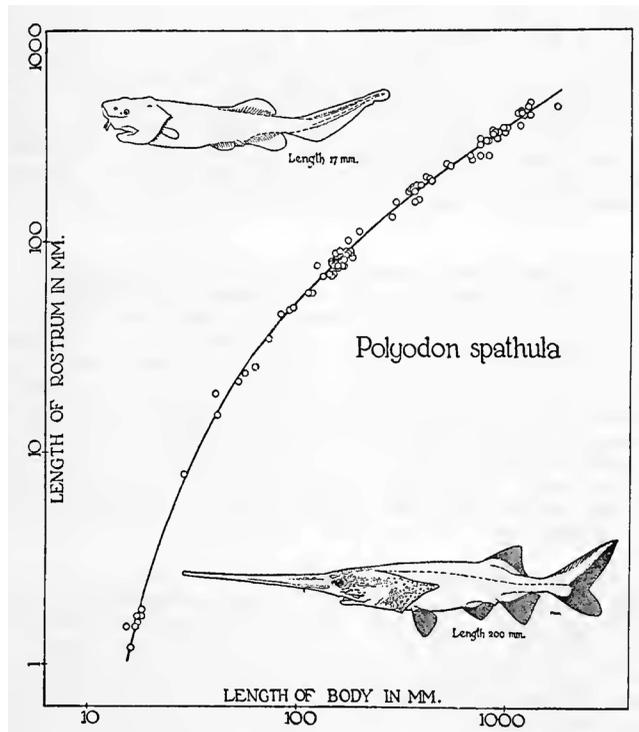


FIGURE 11. Paddlefish rostrum length (mm) versus fish length (mm) (Thompson 1934).

vulnerable period (Jørgensen et al. 2014). It is also consistent with the idea that the changes in the phenotypic characteristic of a fish, such as a Paddlefish's rostrum, even over short periods of time and small size differences, may affect recruitment variability through differential survival (Johnson et al. 2014).

Direct support for the grow-fast-or-beaten hypothesis comes from Scarnecchia et al. (2009), who reviewed factors affecting Paddlefish recruitment in Lake Sakakawea. Age determination studies point to numerous strong year classes following initial reservoir filling and trophic upsurge over a 13-year period. These responses are consistent with trophic upsurge, typically characterized by increased habitat, increased nutrient loading from flooded soils and vegetation, increased availability of detritus, and higher primary production, secondary production, and fish production. The largest upsurge and the larg-

est population increase occurred upon initial filling from 1953 to 1966, when predator populations had not yet become fully established in Lake Sakakawea (Scarnecchia et al. 1996). A smaller upsurge and population increase occurred upon refilling from 1993 to 1995, when excess water in the Mississippi River basin (Lott 1993) necessitated holding back water and re-filling Lake Sakakawea and other upriver reservoirs. Indices of zooplankton also suggested that increased zooplankton abundance followed upsurge. Counts of age-0 Paddlefish along standard transects were also highest in years of higher water levels. The five highest annual count indices occurred from 1996 to 2000, four of which were years of high water levels. For weights, the significantly heaviest fish were found in 1996, 1998 and 1999 (high water years) and the lightest weight fish in 2000, 2002, 2003 and 2005 (lower water years).

An early fast-growth trajectory carried well into the future. Weights of age-10 male recruits that had reared in several high reservoir years immediately prior to capture were 2–3 kg heavier than fish that had reared in low reservoir conditions (Scarnecchia et al. 2009). Recruitment index and catch data also identify two strong year classes since 1992, one in 1995 and one in 2011 (Figure 12). The year 2011 was a record spring flood year on the Yellowstone. Both strong year classes also occurred after a series of rising reservoir levels in the previous three years, resulting in a smaller upsurge (Scarnecchia et al. 2009). In contrast, low and declining water levels will result in decreased production (primary, secondary, and fish) in most cases. Low and declining water levels have been associated with weaker year classes, slower growth of

immature and mature fish, poorer condition, and less energy storage in Paddlefish (Scarnecchia et al. 2009). Reservoir drawdowns are also commonly associated with increasing availability of forage for piscivorous fish (Heman et al. 1969; Noble 1981). More focused studies need to be conducted on how changes in river inflows and reservoir levels, which can lead to trophic upsurge, affect the food web and Paddlefish recruitment.

Additional direct support for the grow-fast-or-be-eaten hypothesis comes from experimental hatchery releases. Based on coded-wire tagging of both hatchery-reared and wild age-0 fish in Lake Sakakawea, larger tagged age-0 fish show higher survival (Table 1). For example, of the two release groups of Paddlefish in the 1990s, both of which were released into the reservoir at times of high

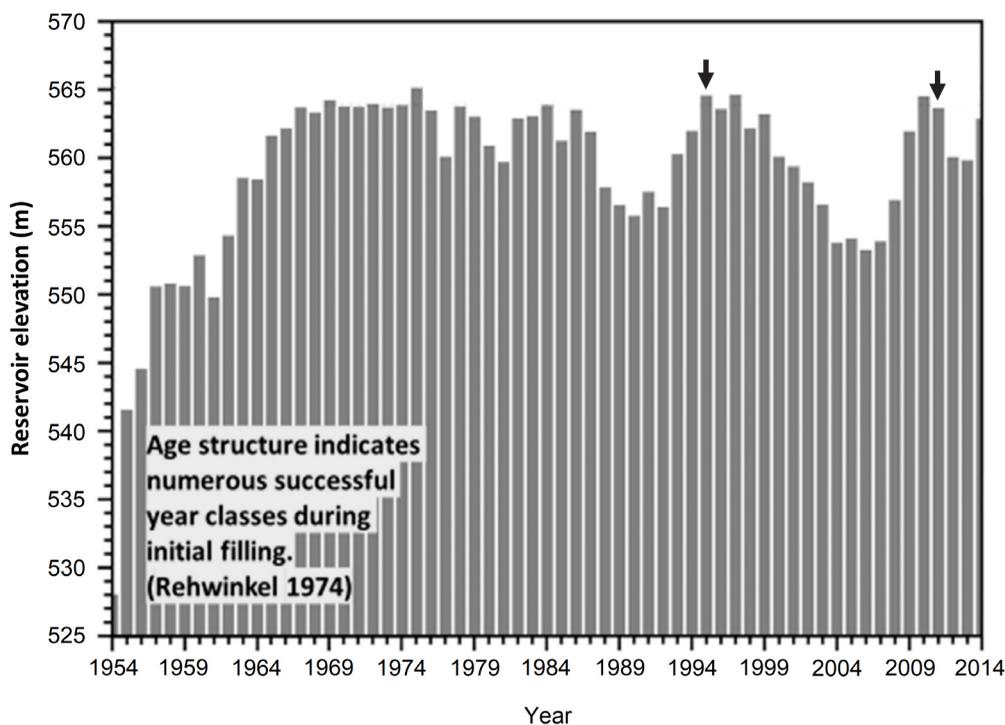


FIGURE 12. Strong year classes of Paddlefish in Lake Sakakawea (left portion of figure, and arrows) have been associated with rising reservoir levels and trophic upsurge. Numerous strong year classes were found during the years of initial filling as inferred from age structure. (Rehwinkel 1974; Scarnecchia et al. 1996, 2009, 2014).

TABLE 1. Wild and hatchery releases and recoveries, 1995–2015. Highest returns of coded-wire tagged fish from 1995 and 2007 are associated with larger fish size at tagging and release. Smaller wild fish have returned to the harvest at much lower rates than larger hatchery fish.

Hatchery-reared				
Year	N Released	Mean Wt (g)	N Recovered	Reservoir Elev.
1995	9,093	84	347	High
1997	9,994	38	0	High
2007	23,956	76	4	Low
2011	32,242	57–70	0	High
Wild				
Year	N Released	Mean Wt (g)	N Recovered	Reservoir Elev.
1996–2008	22,815	approx. 20–35	3	variable

water elevations (1995 and 1997), returns from the larger-sized group (1995) exceeded 3.5% as of 2015, whereas no returns have resulted from the smaller-sized (1997) releases. Only three recoveries of smaller wild fish have been made from more than 22,000 fish caught with dipnets, tagged, and released (Table 1). More recent releases of larger fish in 2007 have also showed promising early returns (Table 1).

We have observed that growth of age-0 Paddlefish in high reservoir elevation years is more rapid than in intermediate and low reservoir elevation years. In high reservoir elevation years, fish reached 250 mm fork length by December whereas they did not reach that length in low reservoir years such as 2008 (Figure 13). In 2008, 7,098 age-0 fish were dipnetted and tagged, the highest counts on record, but mean length remained low (columns in Figure 13) and subsequent recruitment was poor. Large size entering the first winter is evidently highly advantageous for successful recruitment.

Hemingway and Scarnecchia (2016) looked at lipids in age-0 and age-1 Paddle-

fish from Lake Sakakawea, Fort Peck reservoir, and Garrison Dam Hatchery (GDH) between a strong year-class (2011) and a weak year-class (2012) to investigate more explicitly how energy reserves in age-0 and age-1 Paddlefish relate to year-class strength as it relates to fish growth and size. They observed a bi-modal distribution of lipids in 2011 (strong year-class) in age-0 fish, (i.e., two groups). In one group, high lipid fish showed increasing lipid as length increased; in the other group, low lipid fish did not show this pattern. When they divided the same information by stock into three separate panels, the only group that showed a significant linear relationship was the high lipid hatchery fish from GDH (Figure 14a: open triangles). The two-group situation, however, was found in all three stocks (Figure 14a). In contrast, the weak year-class from 2012 showed no significant relationship between length and lipids (Figure 14b). These initial results suggest that in the strong year-class, some of the fish grow well and store more lipids, as might be expected for successfully surviving a long winter. These fish would be

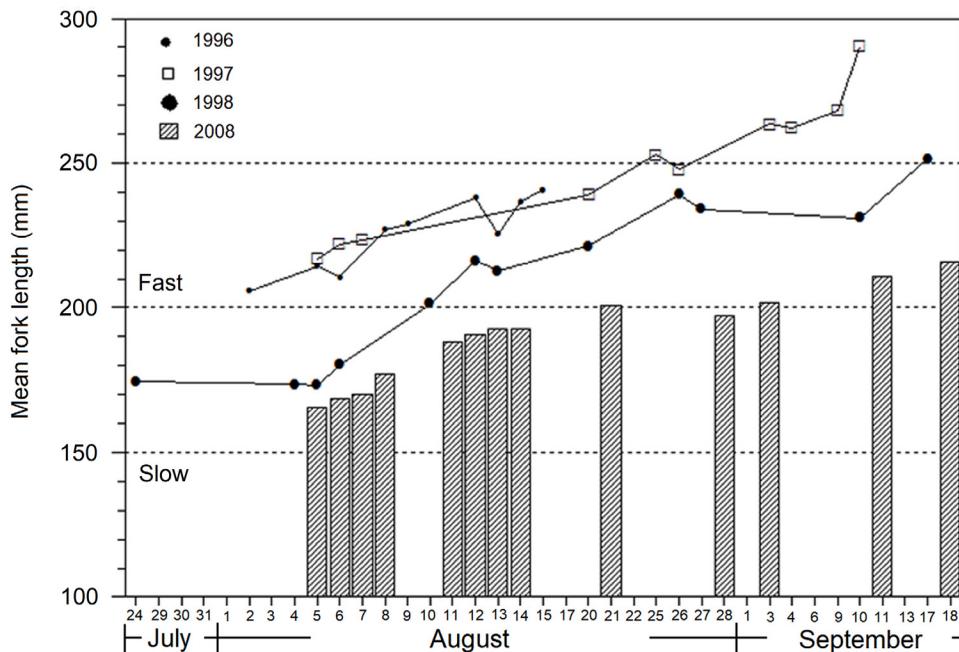


FIGURE 13. Comparison of mean fork length of age-0 Paddlefish by date for 1996, 1997, 1998, and 2008. Growth of larval Paddlefish in higher water years in Lake Sakakawea led to fish reaching 250 mm in length by September. In 2008, a year of low recruitment, 7,098 age-0 fish were dipnetted and tagged, the highest counts on record, but mean length remained low (columns).

expected to be the potential recruits. No such fast-growth group occurred in 2012, a year of low recruitment. We have observational evidence of dead young Paddlefish in winter under the ice in bays; surviving the first winter may be key to recruitment in this stock. In northern latitudes, a combination of rapid growth to avoid predation and to acquire adequate energy for overwinter survival may be needed for successful recruitment.

Studies and observations in the past three decades (Fredericks and Scarnecchia 1997; Scarnecchia et al. 2009; 2014) have provided clues about which factors may affect recruitment, and which hypotheses deserve more thorough evaluation. The limited results available support the hypothesis that young Paddlefish, as their high metabolism (higher than sturgeon) and perpetual motion (Burggren and Bemis 1992) would indicate,

are in a race to grow large enough and obtain sufficient energy reserves to get through the first winter (in northern latitudes) and to reach a size in all locations where predation rates decrease to low levels. Successful recruitment may depend on how many fish in an annual cohort can grow to a size at which they can escape predation and recruit; i.e., from age-0 (Figure 3), to age-1 or age-2 (Figures 4 and 5). Once recruited, they have few predators except humans (boat propeller mortality Bettoli et al. 2019, Chapter 7 this volume), entrainment at dams (Hoover et al. 2019, Chapter 4 this volume), and harvest. They can live out their lifespans of up to 40–50 years with low natural mortality rates in northerly latitudes (North Dakota and Montana: Scarnecchia et al. 2007) and up to 25 years in more southerly localities (Oklahoma: Scarnecchia et al. 2011).

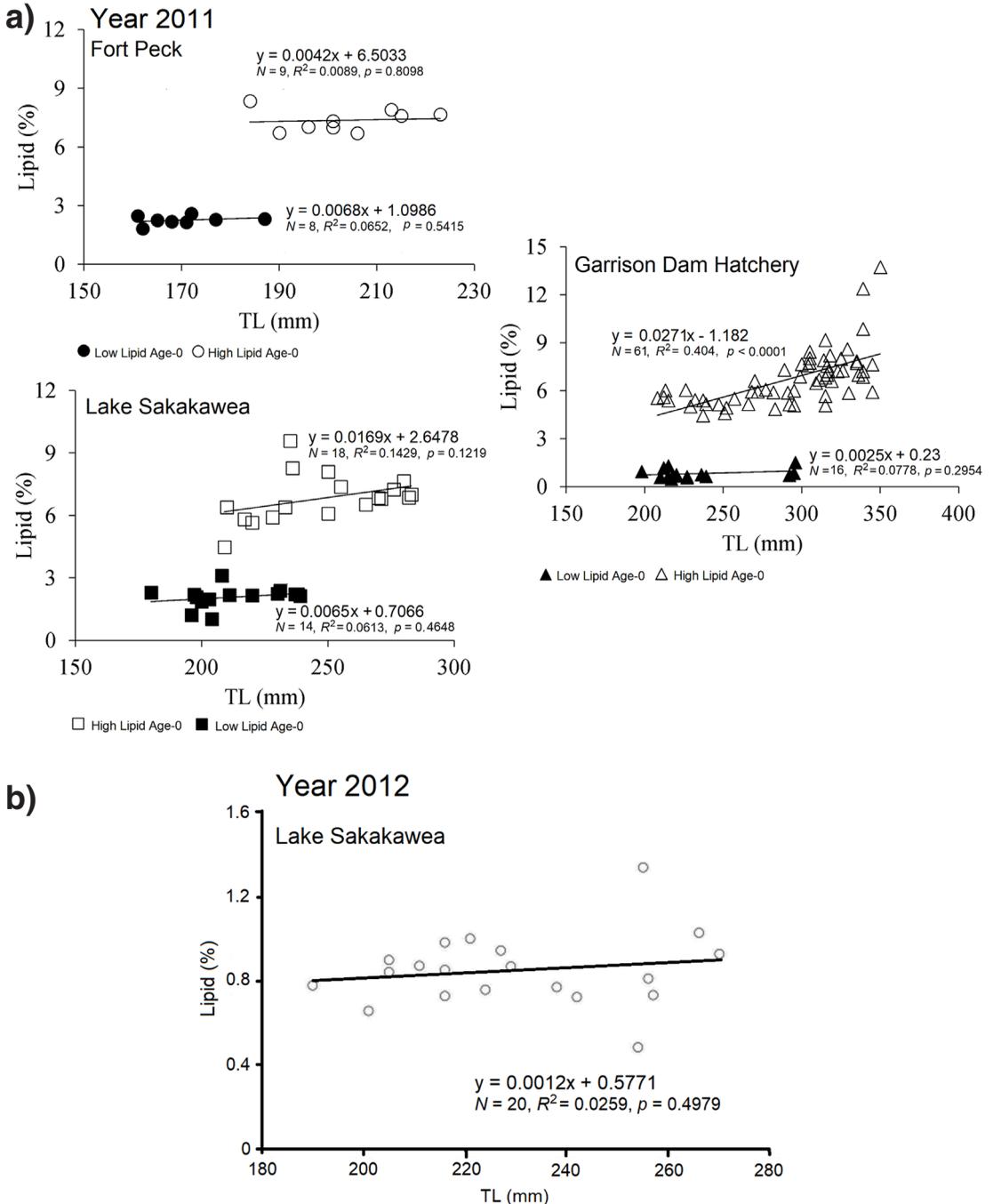


FIGURE 14. Percent lipids in age-0 Paddlefish from Fort Peck Reservoir, Montana (FP), Lake Sakakawea, North Dakota (SAK) and Garrison Dam National Fish Hatchery, North Dakota (GD), 2011. In a documented year of recruitment (a: 2011), age-0 fish separated into two groups, with one group growing faster and accumulating more lipids, the other group growing more slowly and accumulating less lipids. In a poor recruitment year (b: 2012), there was only one group, slow-growing with low lipids in SAK, and no relation between percent lipids and fish length. (Hemingway and Scarnecchia 2016).

Recommendations

Moving forward, more detailed, hypothesis-driven field investigations are needed to supplement the information reviewed in this chapter. Available information is scarce in most localities, as age-0 and age-1 fish are not typically observed or sampled in large numbers. For the long-lived, highly fecund Paddlefish (Russell 1986; Jennings and Ziegler 2009), poor to no survival from hatching to recruitment may be the norm; even in strong recruitment years, a tiny minority of fish reproduced will eventually recruit. These rare survivors can grow, spawn, and support fisheries for years in the south or decades northward (Scarnecchia et al. 2014). As most of the Paddlefish rearing habitats change this century, with river backwater and side channel sedimentation, reservoir sedimentation and aging (e.g., Scarnecchia et al. 2009; Guy et al. 2015), and increased native and non-native predator populations, maintaining and improving natural recruitment is vital. Managers will need a more complete understanding of the conditions needed for successful Paddlefish recruitment. The dearth of detailed studies limits our ability to evaluate other recruitment hypotheses. A combination of studies of wild populations along with selected, well-designed and monitored studies with hatchery-reared fish both kept in captivity and released into the wild can aid in advancing our understanding of recruitment. Recruitment research remains perhaps the highest priority in efforts to manage wild Acipenseriform fishes for long-term sustainability.

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References

- Allen, J. B., and G. Riveros. 2013. Hydrodynamic characterization of the *Polyodon spathula* rostrum using CFD. *Journal of Applied Mathematics* 2013(346173):1–8.
- Bahr, D. L., and D. L. Peterson. 2016. Recruitment of juvenile Atlantic Sturgeon in the Savannah River, Georgia. *Transactions of the American Fisheries Society* 145:1171–1178.
- Beamesderfer, R., T. Garrison, and P. Anders. 2014. Release numbers, movements, growth, condition, survival, & abundance of hatchery-reared, juvenile sturgeon in the Kootenai River. Report to the Kootenai Tribe of Idaho by Cramer Fish Sciences, Gresham, Oregon.
- 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 B. Kynard. 1997. Sturgeon rivers: an introduction to acipenseriform biogeography and life history. *Environmental Biology of Fishes* 48:167–183.
- Boreman, J. 1997. Sensitivity of North American sturgeon and paddlefish to fishing mortality. *Environmental Biology of Fishes* 48:399–405.
- Bettoli, P. W., G. D. Scholten, and E. Ganus. 2019. Cryptic mortality of Paddlefish. Pages 151–162 in J. D. Schooley and D. L. Scarnecchia, editors. *Paddlefish: ecological, aquacultural, and regulatory challenges of managing a global resource*. American Fisheries Society, Symposium 88, Bethesda, Maryland.
- Bowersox, B. J., D. L. Scarnecchia and S., E. Miller. 2014. Distribution, abundance and

- vertical migration of *Leptodora kindtii* in the mainstem Missouri River, Montana. *Journal of Freshwater Ecology* 29:171–186.
- Burggren, W. W., and W. E. Bemis. 1992. Metabolism and ram ventilation in juvenile Paddlefish, *Polyodon spathula* (Chondrostei: Polyodontidae). *Physiological Zoology* 65:515–539.
- Caroffino, D. C., T. M. Sutton, R. F. Elliott, and M. C. Donofrio. 2010. Predation on early life stages of Lake Sturgeon in the Peshtigo River, Wisconsin. *Transactions of the American Fisheries Society* 139:1846–1856.
- DeLonay, A. J., K. A. Chojnacki, R. B. Jacobson, P. J. Braaten, K. J. Buhl, C. M. Elliott, S. O. Erwin, J. D. A. Faulkner, J. S. Candrl, D. B. Fuller, K. M. Backes, T. M. Haddix, M. L. Rugg, C. J. Wesolek, B. L. Eder, and G. E. Mestl. 2016a. Ecological requirements for Pallid Sturgeon reproduction and recruitment in the Missouri River—Annual Report 2014. U.S. Geological Survey Missouri River Recovery Program—Integrated Science Program Open-File Report 2016–1013. Reston, Virginia
- DeLonay, A. J., K. A. Chojnacki, R. B. Jacobson, J. L. Albers, P. J. Braaten, E. A. Bulliner, C. M. Elliott, S. O. Erwin, D. B. Fuller, and J. D. Haas. 2016b. Ecological requirements for Pallid Sturgeon reproduction and recruitment in the Missouri River—A synthesis of science, 2005 to 2012. U. S., Geological Survey, Scientific Investigations Report 2015–5145. Columbia, Missouri.
- Firehammer, J. A., and D. L. Scarnecchia. 2007. The influence of discharge on duration, ascent distance, and fidelity of the spawning migration for Paddlefish of the Yellowstone-Sakakawea stock, Montana and North Dakota, USA. *Environmental Biology of Fishes* 78:23–36.
- Fredericks, J. P. 1994. Distribution, abundance, and feeding ecology of Paddlefish in Upper Lake Sakakawea, North Dakota. Master's thesis, University of Idaho, Moscow.
- Fredericks, J. P., and D. L. Scarnecchia. 1997. Use of surface visual counts for estimating relative abundance of age-0 Paddlefish in Lake Sakakawea. *North American Journal of Fisheries Management* 17:1014–1018.
- Gadonski, D. M., and M. J. Parsley. 2005a. Laboratory studies on the vulnerability of young White Sturgeon to predation. *North American Journal of Fisheries Management* 25:667–674.
- Gadonski, D. M., and M. J. Parsley. 2005b. Vulnerability of young White Sturgeon, *Acipenser transmontanus*, to predation in the presence of alternative prey *Environmental Biology of Fishes* 74:389–396.
- Gerken, J. E., and C. P. Paukert. 2009. Threats to Paddlefish habitat: implications for conservation. Pages 173–183 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.
- 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 Paleontology* 11, Supplement to No. 1.
- Guy, C. S., H. B. Treanor, K. M. Kappenman, E. A. Scholl, J. E. Ilgen, and M. A. Webb. 2015. Broadening the regulated-river management paradigm: a case study of the forgotten dead zone hindering pallid sturgeon recovery. *Fisheries* 40:6–14.
- Heman, M. L., R. S. Campbell, and L. C. Redmond. 1969. Manipulation of fish populations through reservoir drawdown. *Transactions of the American Fisheries Society* 98:293–304.
- Hemingway, R. J., and D. L. Scarnecchia. 2016. Energy acquisition and retention by age-0 and age-1 Paddlefish *Polyodon spathula* (Walbaum 1792) in relation to size, growth, and rearing conditions in two Great Plains reservoirs and hatchery ponds. *Journal of Applied Ichthyology* 33:3–12.
- Hildebrand, L., A. Drauch-Schreier, K. Lepla, S. O. McAdam, J. McLellan, M. Parsley, V. Paragamian, and S. P. Young. 2016. Status of White Sturgeon (*Acipenser transmontanus* Richardson, 1863) throughout the species range, threats to survival, and prognosis for the future. *Journal of Applied Ichthyology* 32 (S1), 261–312.

- Hoover, J. J., P. Bailey, S. R. Januchowski-Hartley, J. Lyons, B. Pracheil, and S. Zigler. 2019. Anthropogenic obstructions to Paddlefish movement and migration. Pages 67–101 in J. D. Schooley and D. L. Scarnecchia, editors. Paddlefish: ecological, aquacultural, and regulatory challenges of managing a global resource. American Fisheries Society, Symposium 88, Bethesda, Maryland.
- Houde, E. D. 1987. Fish early life dynamics and recruitment variability. Pages 17–29 in R. D. Hoyt, editor. 10th annual larval conference. American Fisheries Society, Symposium 2, Bethesda, Maryland.
- Jakobsen, T., M. J. Fogarty, B. A. Megrey, and E. Moksness. 2009. Introduction. Pages 1–10 in T. Jakobsen, M. J. Fogarty, B. A. Megrey, and E. Moksness, editors. Fish reproductive biology. Implications for assessment and management. Wiley, New York.
- Jarić, I., P. Bronzi, G. Cvijanović, M. Lenhardt, M. Smederevac-Lalić, and J. Gessner. 2018. Paddlefish (*Polyodon spathula*) in Europe: an aquaculture species and a potential invader. *Journal of Applied Ichthyology* DOI:10.1111/jai.13672.
- Jelkić, D., and A. Opačak. 2013. A record of the North American Paddlefish (*Polyodon spathula* Walbaum, 1792) in Croatia. *Journal of Applied Ichthyology* 29:1152–1153.
- Jennings, C. A., and S. J. Zigler. 2009. Biology and life history of Paddlefish in North America: an update. Pages 1–22 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.
- Ji, H., H. Sun, J. Tian, and L. Qiu. 2012. Digestive enzyme activity during early larval development of the Paddlefish *Polyodon spathula*. *Acta Hydrobiologica Sinica* 36:457–465.
- Johnson, D. W., K. Grorud-Colvert, S. Sponaugle, and B. X. Semmens. 2014. Phenotypic variation and selective mortality as major drivers of recruitment variability in fishes. *Ecology Letters* 17:743–755.
- Jørgensen, C., A. F. Opdal, and Ø. Fiksen. 2014. Can behavioral ecology unite hypotheses for fish recruitment? *ICES Journal of Marine Science* 71:909–917.
- Kohlhorst, D. W. L. W. Botsford, J. S. Brennan, and G. M. Cailliet. 1991. Aspects of the structure and dynamics of an exploited central California population of White Sturgeon (*Acipenser transmontanus*). Pages 277–293 in P. Williot, editor. Actes du Premier colloque international sur l'esturgeon. Bordeaux, 3–6 October 1989. Cemagref, Groupement de Bordeaux, France.
- Kozfkay, J. R., and D. L. Scarnecchia. 2002. Year-class strength and feeding ecology of age-0 and age-1 Paddlefish (*Polyodon spathula*) in Fort Peck Lake, Montana, USA. *Journal of Applied Ichthyology* 18:601–607.
- Lott, N. 1993. The summer of 1993: flooding in the midwest and drought in the southeast. National Climatic Data Center Technical Report 93–04. Asheville, North Carolina.
- McAdam, S. O. 2011. Effects of substrate condition on habitat use and survival by White Sturgeon (*Acipenser transmontanus*) larvae and potential implications for recruitment. *Canadian Journal of Fisheries and Aquatic Sciences* 68:812–822.
- McAdam, D. S. O. 2015. Retrospective weight-of-evidence analysis identifies substrate change as the apparent cause of recruitment failure in the Upper Columbia River White Sturgeon (*Acipenser transmontanus*). *Canadian Journal of Fisheries and Aquatic Sciences* 72:1208–1220.
- McAdam, S. O., C. J. Walters, and C. Nistor. 2005. Linkages between White Sturgeon recruitment and altered bed substrates in the Nechako River, Canada. *Transactions of the American Fisheries Society* 134:1448–1456.
- Mero, S. W., D. W. Willis, and G. J. Power. 1995. Walleye and Sauger predation on Paddlefish in Lake Sakakawea, North Dakota. *North American Journal of Fisheries Management* 14:226–227.
- 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.

- Miller, S. E., and D. L. Scarnecchia. 2008. Adult paddlefish migrations in relation to spring river conditions of the Yellowstone and Missouri Rivers, Montana and North Dakota, USA. *Journal of Applied Ichthyology* 24:221–228.
- Myers, R. A. 1998. When do environment–recruitment correlations work? *Reviews in Fish Biology and Fisheries* 8:285–305.
- Nilo, P., P. Dumont, and R. Fortin. 1997. Climatic and hydrologic determinants of year-class strength of St. Lawrence River Lake Sturgeon (*Acipenser fulvescens*). *Canadian Journal of Fisheries and Aquatic Sciences* 54:774–780.
- Noble, R. L. 1981. Management of forage fishes in impoundments of the southern United States. *Transactions of the American Fisheries Society* 110:738–750.
- Paragamian, V. L., R. McDonald, G. J. Nelson, and G. Barton. 2009. Kootenai River velocities, depth, and White Sturgeon spawning site selection—a mystery unraveled? *Journal of Applied Ichthyology* 25:640–646.
- Parken, C., and D. L. Scarnecchia. 2002. Predation on age-0 Paddlefish by Walleye and Sauger in a Great Plains reservoir. *North American Journal of Fisheries Management* 22:750–759.
- Parsley, M. J., P. J. Anders, A. I. Miller, L. G. Beckman, and G. T. McCabe, Jr. 1993. Factors affecting spawning and recruitment of White Sturgeon in the Columbia River downstream from McNary Dam. Pages 61–79 in R. C. Beamesderfer and A. A. Nigro, editors. Status and habitat requirements of the White Sturgeon population in the Columbia River downstream from McNary Dam. Volume 1, Bonneville Power Administration, Portland, Oregon.
- Quinn, J. W. 2009. Harvest of Paddlefish in North America. Pages 203–221 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.
- Rehwinkel, B. J. 1978. The fishery for Paddlefish at Intake, Montana during 1973 and 1974. *Transactions of the American Fisheries Society* 107:263–268.
- Ricker, W. E. 1975. Computation and interpretation of biological statistics of fish populations. *Fisheries Research Board of Canada Bulletin* 191. Ottawa, Ontario, Canada.
- Russell, T. R. 1986. Biology and life history of the Paddlefish—a review. Pages 2–20 in J. G. Dillard, L. K. Graham, and T. R. Russell, editor. *The Paddlefish: status, propagation and management*. American Fisheries Society, North Central Division, Special Publication 7, Bethesda, Maryland.
- Scarnecchia, D. L. 1984. Climatic and oceanic variations affecting yield of Icelandic stocks of Atlantic Salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences* 41:917–935.
- Scarnecchia, D. L., P. A. Stewart, and G. J. Power. 1996. Age structure of the Yellowstone-Sakawewa Paddlefish stock, 1963–1993, in relation to reservoir history. *Transactions of the American Fisheries Society* 125:291–299.
- Scarnecchia, D. L., L. F. Ryckman, and J. Lee. 1997. Capturing and tagging of wild age-0 and age-1 Paddlefish in a Great Plains Reservoir. *North American Journal of Fisheries Management* 17:800–802.
- Scarnecchia, D. L., L. F. Ryckman, Y. Lim, G. J. Power, B. J. Schmitz, and J. A. Firehammer. 2007. Life history and the costs of reproduction in Northern Great Plains Paddlefish (*Polyodon spathula*) as a potential framework for other Acipenseriform fishes. *Reviews in Fisheries Science* 15:211–263.
- Scarnecchia, D. L., L. F. Ryckman, B. J. Schmitz, S. Gangl, W. Wiedenheft, L. L. Leslie, and Y. Lim. 2008. Management plan for North Dakota and Montana Paddlefish stocks and fisheries. North Dakota Game and Fish Department and Montana Department of Fish, Wildlife and Parks. Bismarck, North Dakota and Helena, Montana
- Scarnecchia, D. L., L. F. Ryckman, Y. Lim, S. E. Miller, B. J. Schmitz, G. J. Power, and S. A. Shefstad. 2009. Riverine and reservoir influences on year class strength and growth of upper Great Plains Paddlefish. *Reviews in Fisheries Science* 17:241–266.

- Scarnecchia, D. L., B. D. Gordon, J. D. Schooley, L. F. Ryckman, B. J. Schmitz, S. E. Miller, and Y. Lim. 2011. Southern and northern Great Plains (United States) Paddlefish stocks within frameworks of Acipenseriform life history and the metabolic theory of ecology. *Reviews in Fisheries Science* 19:279–298.
- Scarnecchia, D. L., Y. Lim, L. F. Ryckman, K. M. Backes, S. E. Miller, R. S. Gangl, and B. J. Schmitz. 2014. Virtual population analysis, episodic recruitment, and harvest management of paddlefish with application to other Acipenseriform fishes. *Reviews in Fisheries Science and Aquaculture* 22:16–35.
- Scholten, G. D. 2009. Management of commercial paddlefish fisheries in the United States. Pages 291–306 in C. P. Paukert and G. B. 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.
- Schooley, J. D., and B. C. Neely. 2018. Estimation of Paddlefish (*Polyodon spathula* Walbaum, 1792) spawning habitat availability with consumer-grade sonar. *Journal of Applied Ichthyology* 34:364–372.
- Sparrowe, 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.
- Thompson, D. H. 1934. Relative growth in *Polyodon*. Illinois Natural History Survey Biological Notes. Number 2. Champaign-Urbana.
- Trippel, E. A. and R. C. Chambers. 1997. The early life history of fishes and its role in recruitment processes. Pages xxi–xxxii in R. C. Chambers and E. A. Trippel, editors. *Early life history and recruitment in fish populations*. Chapman and Hall, London, England.
- Wallus, R., T. P. Simon, and B. L. Yeager. 1990. Reproductive biology and early life history of fishes in the Ohio River drainage. Volume 1: Acipenseridae through Esocidae. Tennessee Valley Authority, Chattanooga, Tennessee.
- Wildhaber, M. L.; Geological Survey (U.S.) 2007. A conceptual life-history model for Pallid and Shovelnose Sturgeon. U.S. Geological Survey, Reston, Virginia.
- Wilkins, L. A., D. F. Russell, X. Pei, and C. Gurgens. 1997. The Paddlefish rostrum functions as an electrosensory antenna in plankton feeding. *Proceedings of the Royal Society of London*, B 264:1723–1729.
- Wilkins, L. A., M. H. Hofmann, and W. Wojtenek. 2002. The electric sense of the paddlefish: a passive system for the detection of zooplankton prey. *Journal of Physiology, Paris* 96:363–377.
- Winemiller, K. O., and K. A. Rose. 1992. Patterns of life-history diversification in North American fishes: implications for population regulation. *Canadian Journal of Fisheries and Aquatic Sciences* 49:2196–2218.