

## ARTICLE

## Patterns and Scaling of Reproductive Output in Paddlefish *Polyodon spathula* and Its Conservation Implications

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### Abstract

We used a large, three-state data set to investigate if larger female Paddlefish *Polyodon spathula* reproduce disproportionately more than smaller females. The approach was to assess the relation between fecundity  $F$ , expressed as raw egg weight, and fish weight  $W$ , in the expression  $F = aW^b$ . We compared results among three fisheries for Paddlefish harvested in the three states and between two stocks and compared results between total fish weight and total raw egg weight with results across taxa presented in other studies. Paddlefish from all three state-managed fisheries (Montana, North Dakota, and Oklahoma) showed hyperallometric increases in fecundity, expressed as raw egg weight, with fish weight (i.e.,  $b > 1$ ). For Montana females, hyperallometry was greatest ( $b = 1.75$ ;  $n = 8,487$ ), followed by North Dakota ( $b = 1.61$ ;  $n = 9,549$ ) and Oklahoma ( $b = 1.47$ ;  $n = 14,294$ ). Paddlefish from Montana and North Dakota in general allocated a lower percentage of their total weight to egg weight (asymptotic gonadosomatic index [ $GSI_{\infty}$ ]) than did Oklahoma Paddlefish (Montana: 21.46%; North Dakota: 20.01%; and Oklahoma: 24.22%). The hyperallometric increases in raw egg weight with fish weight reported here depict only one of several conservation benefits associated with maintaining larger and older fish in the populations. Conclusions about weight–fecundity relationships for a particular species should be considered with an adequate understanding of the complete life history and factors which would affect somatic growth versus fecundity tradeoffs.

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In the past two decades, greater recognition has been given to the importance of maintaining age and size structure of harvested fish stocks to mimic that of the unharvested stocks (Birkeland and Dayton 2005; Francis et al. 2007). Increasingly, fisheries scientists recommend avoiding complete removal of all of the largest, most fecund female fish and avoiding truncation of the age and size structure typically characteristic of harvested species and stocks (Hixon et al. 2014). With persistent size-selective harvest, a long-lived species may shift into a shorter-lived species through genetic changes and responses to environment (Kuparinen and Merilä 2007). In most fish species, the largest fish and oldest fish removed are also predominantly females (e.g., Scarnecchia and Schooley 2020) except for species where males compete strongly for females in paired courtship (Bell 1980).

Additional support for the importance of maintaining large, fecund females in fish stocks has been provided in other studies. Barneche et al. (2018) compared female weight (mass) versus fecundity (number of eggs per female) for 177 species of fish from studies around the world and found that overall scaling of fecundity ( $F$ : number of eggs) versus female mass ( $W$  in grams) was a power function  $F = aW^b$  given by  $F = 2.93W^{1.18}$ . One-hundred forty of the 177 species considered (79.1%) showed hyperallometric scaling, i.e., with the power function exponent  $b > 1.0$ . Further analyses of relations between female mass and egg volume, and between egg volume and egg energy, led to their conclusion that larger females reproduced disproportionately more than smaller females in fecundity and in total reproductive energy. The value of  $b$  and reproductive output constitute only one consideration that might lead to the need to protect large females. Other considerations might be diverse genetic and phenotypic factors, such as threat of size-selective predation and other intra- and interspecies interactions favoring large females. It is important to examine the hyperallometry ( $b > 1$ ), isometry ( $b = 1$ ), or hypoallometry ( $b < 1$ ) of various individual fish species and stocks (King 1998). Reproductive output as measured by  $b$  remains an important and quantifiable characteristic of the stock, and its value above, at, or below 1.0 has harvest regulation implications.

The Paddlefish *Polyodon spathula*, an ancient species and a source of valuable caviar, supports recreational and commercial fisheries in numerous states throughout the Mississippi and Missouri River basins (Mestl et al. 2019; Rider et al. 2019). The species is strongly sexually size dimorphic, especially in more northerly stocks, with the largest fish being females (Scarnecchia et al. 2011). Some fisheries, especially commercial ones seeking large, roe-laden female fish, harvest in ways that truncate size and age structure and selectively remove the largest, oldest females (Rider et al. 2019). In contrast, some recreational Paddlefish fisheries have been managed with mandatory

retention and other regulations to balance sex ratios of harvest. Carefully-managed fisheries can result in the intentional maintenance of large females in the population and maintenance of old fish of both sexes (Scarnecchia et al. 2014).

In the states of Montana, North Dakota, and Oklahoma, nonprofit Paddlefish roe donation programs (Brown 2014; Schooley et al. 2014; Scarnecchia et al. 2021) provide biologists with information on raw egg weight (i.e., weight or mass of eggs attached to the membrane with gonadal fat deposits removed but before processing into caviar) and fish weight from all female Paddlefish voluntarily brought into fish cleaning stations. The fisheries in Montana and North Dakota both harvest the Yellowstone–Sakakawea stock (Scarnecchia et al. 2007); the fishery in Oklahoma targets the Grand Lake O' the Cherokees (Grand Lake) stock (Scarnecchia et al. 2011). Here, we investigate allometry in Paddlefish by comparing the relationship between fecundity, expressed as raw egg weight, and fish weight for Paddlefish harvested in the three states, compare results among the three fisheries and between the two stocks, and compare results between total fish weight and total raw egg weight with results across taxa. We also compare raw egg weight with fish age and discuss its life history significance and conservation implications.

## METHODS

Paddlefish weights and raw egg weights were obtained from fish cleaning stations in the three states associated with recreational harvest fisheries: (1) at Intake, Montana, on the Yellowstone River; (2) at the confluence of the Missouri and Yellowstone rivers near Buford, North Dakota; and (3) at the Paddlefish Research Center (PRC) near Miami, Oklahoma, associated with the Neosho River and Grand Lake (Schooley et al. 2014). A small fraction (<1%) of fish brought to the PRC fish cleaning station come from other Oklahoma fisheries, primarily Fort Gibson Reservoir, located downriver from Grand Lake; these fish may also be Grand Lake stock. Data from Montana and North Dakota both came from the Yellowstone–Sakakawea stock, although not the same age distribution of the stock (Scarnecchia et al. 2007), each year over the period 1994–2019. Data from Oklahoma came from each year over the period 2008–2019. Data from all fish for which data were available were used. Fish were measured for length and weighed (to the nearest 0.45 kg in Montana and North Dakota; to the nearest 0.045 kg in Oklahoma), and dentary (lower jaw) samples were taken from harvested fish for age estimation. Ages of fish were estimated from counting annuli on thin cross sections of dentaries according to established methods (Scarnecchia et al. 2006, 2011; Faust and Scholten 2017). Validation of younger

ages of Paddlefish has occurred for the Montana and North Dakota fish (age 10: Scarnecchia et al. 2006), and annuli on sections have been consistent with known-age fish up to age 25. Age validation has not yet been formally conducted for the Oklahoma fish.

Raw egg weights were obtained from fish cleaning stations as stage-4 caviar-grade roe was removed from the body cavity and trimmed of gonadal fat deposits immediately prior to processing for caviar production. Raw egg weights were obtained to the nearest 4.54 g. Only slight variation in egg size is found. For example, in another study in Oklahoma at the PRC, 900 total eggs from 30 individuals (30 eggs per fish) were measured for egg volume, egg width, and egg length. Mean egg volume was 7.632  $\mu\text{L}$  (95% CI: 7.549–7.716). Mean egg width was 2.360 mm (95% CI: 2.350–2.369), and mean egg length was 2.597 mm (95% CI: 2.586–2.609; J. D. Schooley, unpublished data). No information was available on egg energy density. All total raw egg weights corresponded to pre-ovulated eggs suitable for caviar production. Fish having ovulated roe (i. e., separated and loose from the membrane), completely or in part, were excluded from analyses. Allometry (hyperallometry, isometry, or hypoallometry) of female fish weight and fecundity, the latter expressed as raw egg weight, was evaluated by plotting weight ( $W$ :  $x$ -axis) versus raw egg weight ( $F$ :  $y$ -axis) and fitting a power function to the data of the form  $F = aW^b$ . In hyperallometry,  $b > 1$ ; in isometry,  $b = 1$ ; and in hypoallometry,  $b < 1$ . Ninety-five percent confidence intervals were also calculated using the Wald-base expression:

$$\hat{\beta}_i \pm \text{stderr}_i \times t(n - p, 1 - \alpha/2),$$

where  $\hat{\beta}_i$  is the  $i$ th parameter estimate,  $\text{stderr}_i$  is its estimated approximate standard error,  $t(n - p, 1 - \alpha/2)$  is a  $t$ -statistic with  $n - p$  degrees of freedom,  $n$  is the number of observations, and  $p$  is the number of parameters. The confidence intervals are only asymptotically valid, and  $p < 0.05$  is required for significance.

To assess the weight-specific fecundity of fish by age from Montana, North Dakota, and Oklahoma, the percentage of the total fish weight consisting of raw roe weight (gonadosomatic index [GSI]) was calculated by age for fish from the three states. The relations between GSI and fish age ( $t$ ) were fitted with a Gompertz curve expressed as:

$$\text{GSI}_t = (\text{GSI}_\infty) \left\{ e^{-e^{-k(t-T_i)}} \right\},$$

where  $\text{GSI}_\infty$  is the asymptotic percentage of fish weight consisting of raw egg weight,  $k$  is the growth rate parameter, and  $T_i$  is the time of inflection parameter. This model has a long history of usefulness in characterizing

biological growth rates (Tjørve and Tjørve 2017) and was appropriate here because the model fits data where the slope on the left side of an inflection point is greater than on the right side (Franses 1994), the situation observed here where the Paddlefish fecundity increase among younger females far exceeds that of older females (Scarnecchia et al. 2011).

## RESULTS

Fish from both stocks and from all three fisheries (Montana, North Dakota, and Oklahoma) showed hyperallometric increases in fecundity, expressed as raw egg weight, with fish weight (i.e.,  $b > 1$ ). For Montana females, hyperallometry was greatest ( $b = 1.75$ ,  $n = 8,487$ ; Figure 1A), followed by North Dakota ( $b = 1.61$ ,  $n = 9,549$ ; Figure 1B). The larger females of these stocks often weighed 40–50 kg. For the stock as a whole (i.e., Montana and North Dakota combined),  $b = 1.71$  ( $n = 18,036$ ). Data showed a marked increase in raw egg weight with increasing weight of fish, such that a 22.5-kg Paddlefish from North Dakota, for example, would have on average 3,007 g of eggs, whereas a Paddlefish twice that heavy (45 kg) would have 9,208 g of eggs, or over three times the weight in eggs. Similar calculations for the other two states indicate similar trends. Notably, in North Dakota, which had the largest and oldest fish, the few fish above 50 kg in weight displayed a fecundity in nearly all instances below, rather than above, the fitted power function, indicating a relative decline in relative fecundity among the very largest fish (Figure 1B). For Oklahoma, where the largest females weighed less than in the Yellowstone–Sakakawea stock (commonly 25–30 kg), hyperallometric increase in fecundity was less but still pronounced ( $b = 1.47$ ,  $n = 14,294$ ; Figure 1C). No decline in relative fecundity among the very largest fish was observed in Oklahoma Paddlefish (Figure 1C).

Paddlefish from Montana and North Dakota had much lower fecundities through ages 10–25 (Figure 2A), even though mean weights of females were comparable in Montana, North Dakota, and Oklahoma fish through ages 10–25 (Figure 2B). Throughout their lives, at each age, Montana and North Dakota Paddlefish allocated a lower percentage of their total weight to egg weight (Figure 2C) and ultimately reached a lower  $\text{GSI}_\infty$  than did Oklahoma Paddlefish. The  $\text{GSI}_\infty$  was 21.46% for Montana fish (Figure 3A), 20.01% for North Dakota fish (Figure 3B), 20.49% for combined Montana and North Dakota fish, and 24.22% for Oklahoma fish (Figure 3C). Although Montana and North Dakota stocks had many fish older (30–60 years) than the oldest Oklahoma fish (29 years), in all samples, GSI remained high in the older fish in each group; in nearly all instances, large, older females continued to produce eggs throughout their adult lives, even if

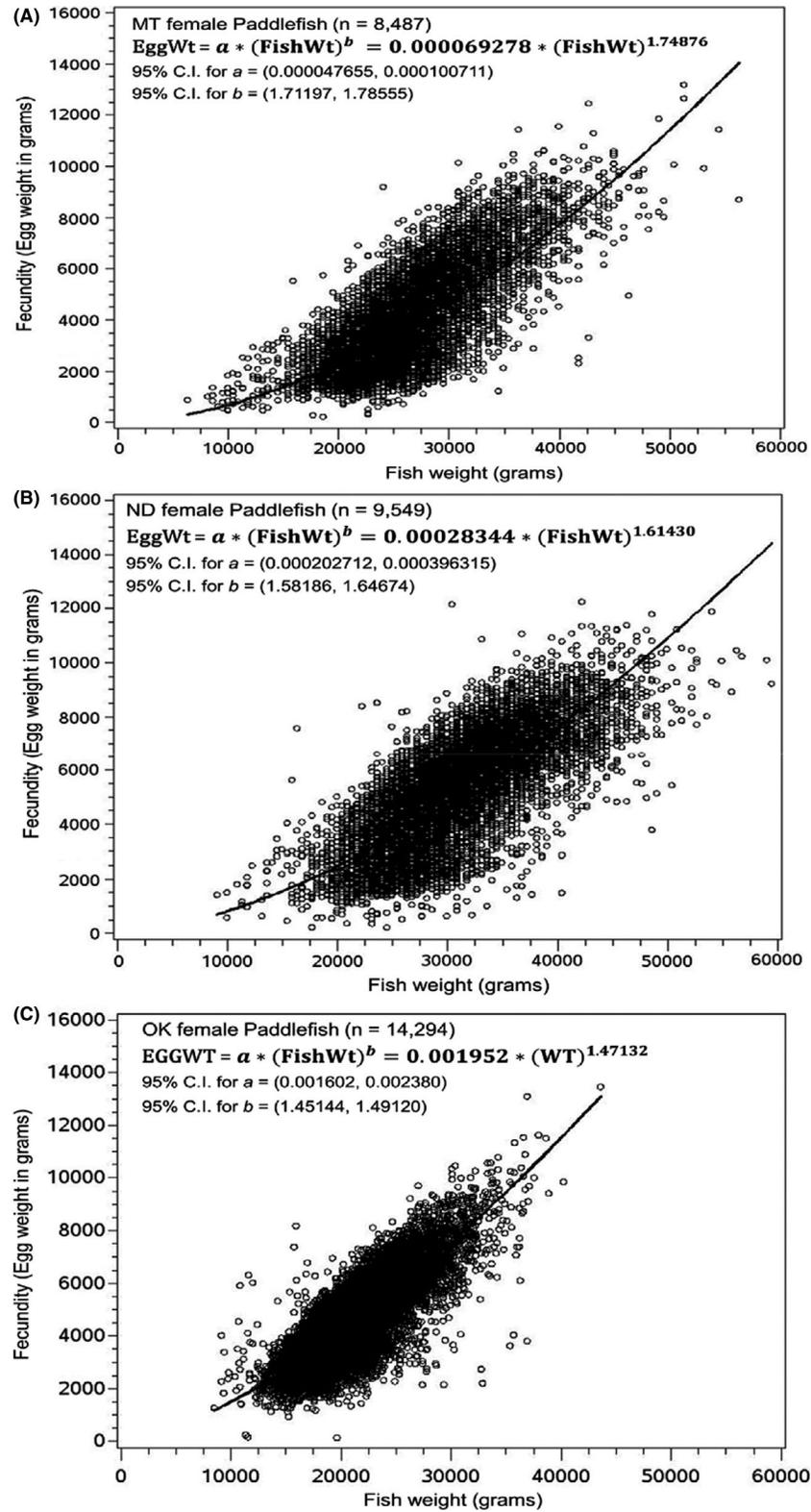


FIGURE 1. Paddlefish raw egg weight versus fish weight for (A) Montana, 1994–2019; (B) North Dakota, 1994–2019; and (C) Oklahoma, 2008–2019.

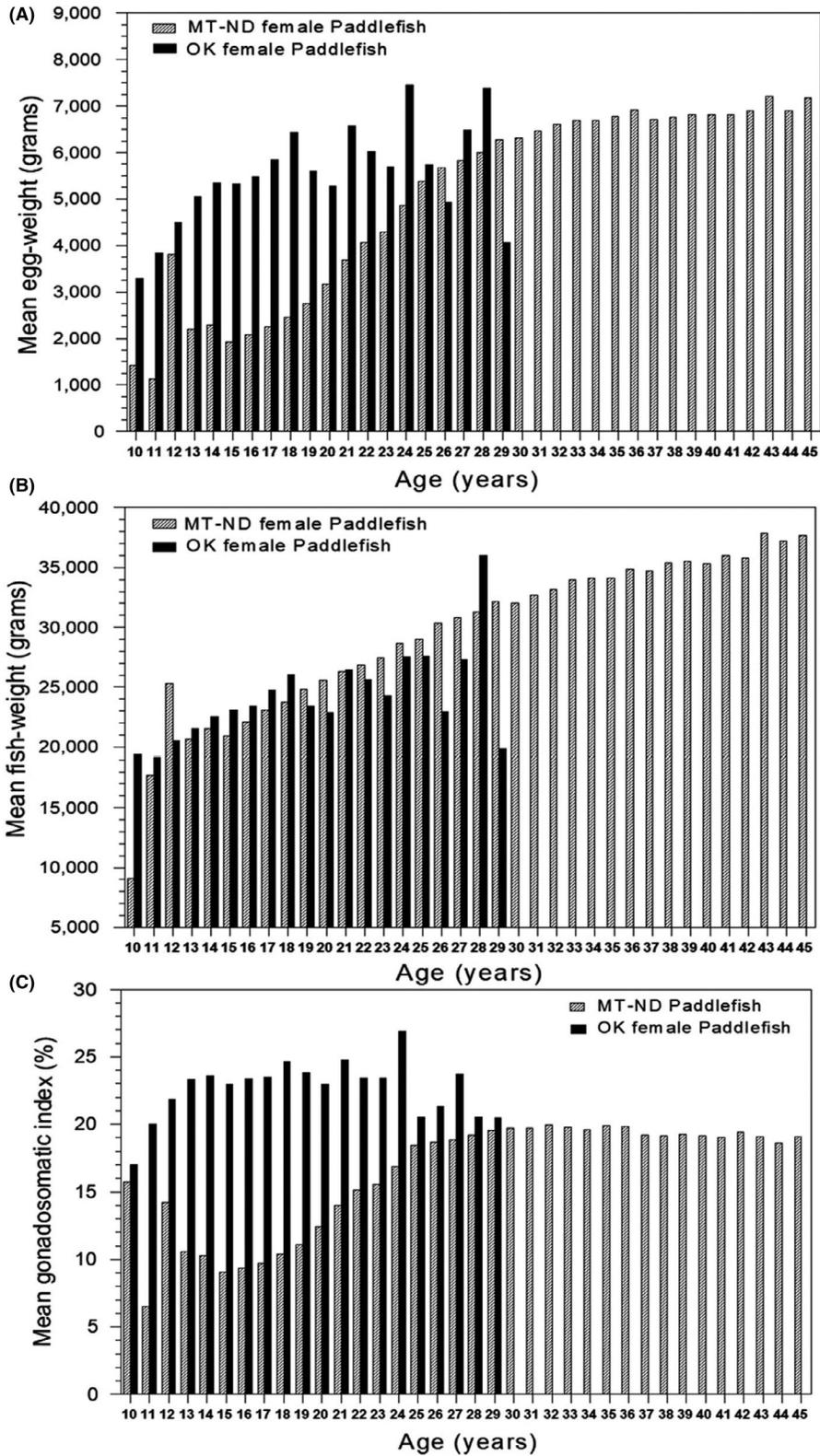


FIGURE 2. Estimated age of female Paddlefish in relation to (A) mean egg weight, (B) mean fish weight, and (C) gonadosomatic index for Montana and North Dakota, 1994–2019, and Oklahoma, 2008–2019.

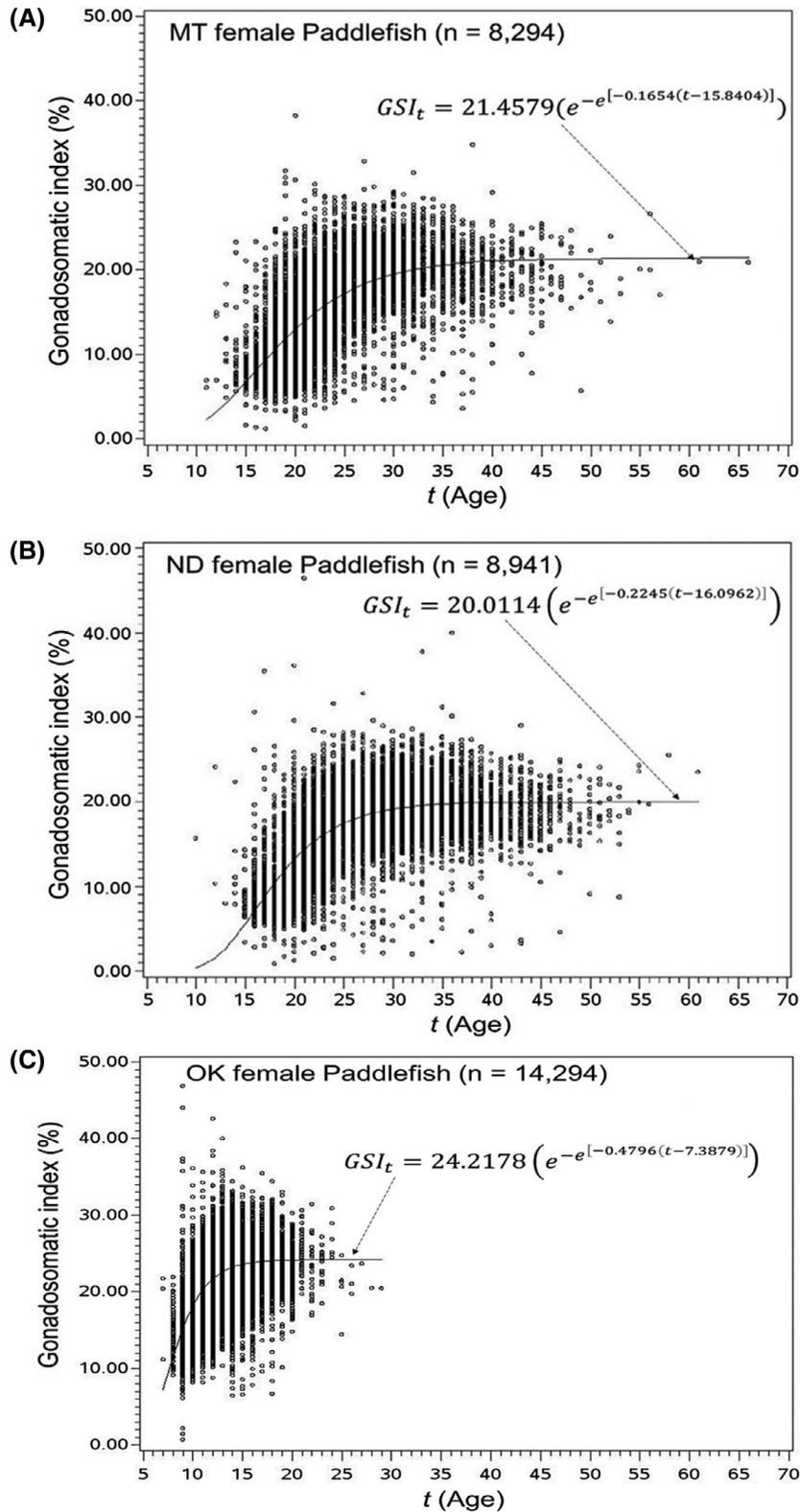


FIGURE 3. Gompertz growth function fitted to gonadosomatic index (GSI) values for Paddlefish from (A) Montana, 1994–2019; (B) North Dakota, 1994–2019; and (C) Oklahoma, 2008–2019.

in some instances (e.g., North Dakota) fecundities declined among the oldest fish.

## DISCUSSION

The hyperallometry shown here in the large sample sizes from the three states and two Paddlefish stocks is consistent with the most common worldwide findings summarized by Barneche et al. (2018) that larger females reproduce disproportionately more than smaller females. In cases involving more modest sample sizes (e.g., Das 1977; Pathani 1981; King 1998), it may be difficult to determine if a power function or a linear function best reflects the overall biological realities or just an interpretation of too little or scattered data. In Paddlefish, the scattered data available from other stocks have not been systematically evaluated. Fish weight and fecundity (number of eggs) for 11 Paddlefish in Pool 13 of the upper Mississippi River (Gengerke 1978) were sufficiently variable that ascertaining hyperallometry, isometry, or hypoallometry was not possible. When data from these 11 fish were fitted with a linear model, the fit was not close ( $r^2 = 0.61$ ;  $p = 0.05$ ). For Paddlefish in the lower Mississippi River of Arkansas, weight–fecundity (number of eggs) relations for 55 gravid females were assumed by investigators to be linear, and 76% of the variation in fecundity was explained by fish weight (Risley et al. 2017). Other studies having fecundity data were more concerned with length–fecundity (egg count) relations as they affected reproductive potential under different harvest strategies, especially minimum length limits (Colvin et al. 2013; Hupfeld et al. 2016). Weight–fecundity relations were not expressed in a way suitable for comparison with our study. Populations were also subjected to substantial size-selective harvest. To address the allometry question for Paddlefish and other species as accurately as possible, we recommend obtaining many more samples than the minimum statistically valid sample size and having samples spread over a wide range of fish weights and ages, as we have used here. Such sampling is best conducted on ongoing sustainable fisheries rather than by sacrificing fish for research data. In many harvested stocks of fish of different species, however, serious weight and age truncation may already have occurred at the time of sampling, which would reduce the range of fish weights from which to obtain weight–fecundity data. This limitation would further challenge efforts to accurately identify isometry versus allometry of weight and fecundity.

We might expect that hyperallometry would be favored for Paddlefish, for which sexually maturing females would have little reason for allocating energy to larger fish size for reasons other than the benefits to fecundity. Paddlefish have no one-on-one paired spawning (Purkett 1961) and no parental care (Russell 1986), and females may allocate

as much as 30% or more of their adult weight to raw egg weight in the form of large numbers of small, low-volume, unmaintained eggs for dispersal. In a large species such as Paddlefish, mature females of any weight typically have very low natural mortality and suffer minimal predation from other fishes (Scarnecchia et al. 2007, 2019). Many of these life history characteristics may apply to many of the marine teleost fishes; it is therefore not unexpected to us that most species show hyperallometry in weight–fecundity relationships (Barneche et al. 2018).

Several factors may lead to isometry or hypoallometry, as opposed to hyperallometry, in particular situations, however. Large size among mature females may confer other advantages besides fecundity to individual fish, such as success in defending territories (Silva et al. 2020), avoidance of predation (especially in smaller species), and positive outcomes of other intra- or interspecies interactions. Other factors may include the demands of uniparental care (rare in externally fertilizing species such as Paddlefish but more common in internally fertilizing species; Gross and Sargent 1985) or benefits of larger maternal size on resulting larval and juvenile growth and mortality (Beldade et al. 2012). In such situations, hyperallometry in weight–fecundity may be less valuable evolutionarily than, for example, isometry or hypoallometry combined with a large body size and emphasis on somatic growth. This situation would still ultimately lead large females to have greater success in spawning and recruiting offspring. In such a case, large females may still need to be retained in the stock but not solely, or even primarily, for fecundity reasons per se. For these reasons, interpretations about weight–fecundity relationships for a particular species should be made with an adequate understanding of the complete life history of the species in question. Fish weight–fecundity relationships might benefit from a detailed evaluation of their published relations with reference to specific life histories and species ecologies as they affect somatic growth versus fecundity tradeoffs. Weight–fecundity relationships classified by reproductive diversity (Smith and Wootton 2016) or mode (e.g., demersal, pelagic, scatterer, and mouthbrooder/internal, or some more detailed classification, such as Balon 1975) may be good starting points.

The results showing the percentage of weight associated with eggs (GSI) remaining stable throughout most of the older portion of life ( $GSI_{\infty}$ ) are also consistent with the concept of a *prime spawner* previously developed in studies of Yellowstone–Sakakawea Paddlefish in Montana and North Dakota. The prime spawner was associated with depletion of stored gonadal fat reserves (i.e., little fat attached to the egg skeins, unlike first-time spawners; Scarnecchia et al. 2007), a minimized period of gonadal recrudescence (i.e., the fewest years between successive spawns), little or no increase in somatic growth in weight

other than eggs, and shorter spawning migrations compared to young female spawners (Scarnecchia et al. 2007, 2019). In fish from the three states investigated here, larger fish remain prime spawners and maintain their reproductive capability. In North Dakota fish, for example, it is only in a few fish over about 45 years of age and a few of the largest fish over 50 kg that declines in fecundity and GSI can be detected. Declines are less frequent in Montana and Oklahoma fish. That lower fecundity can be attributed either to senescence manifested as a reproductive slowing or, in some old Paddlefish, as an increase in gonadal fat attached to the gonads in the body cavity (Scarnecchia et al. 2007) or both. The diminution of reproduction is only minor, however, even in the Yellowstone–Sakakawea stock where mandatory retention and harvest caps, combined with low natural mortality rates, have allowed the persistence of old female fish in the population. Senescence does not seem to be a potential concern with protecting large, frequently old females having low natural mortality rates, consistent with classic theoretical analyses by Williams (1957). These findings are actively incorporated directly into Paddlefish harvest regulations in Montana and North Dakota. Prime spawners are harvested but are buffered from excessive or selective harvest with the mandatory retention requirement of the snag fisheries, where all mature fish must be kept, with no optional catch and release, under a one-fish-per-snagger annual bag limit and an overall harvest cap (Scarnecchia et al. 2021). This general approach of protecting some females from harvest, which has been recommended for Paddlefish for at least 30 years (Scarnecchia et al. 1989), has helped to keep older fish (age 50 or older) in the population after more than a half-century of harvest. Although Oklahoma does not use harvest caps or mandatory retention (this state has a two-fish annual limit; Schooley et al. 2014), the duration and structure of the fishery have provided a relatively stable, balanced sex ratio in the harvest.

Although high fecundity is associated with all Paddlefish in this study and elsewhere (Russell 1986), the higher  $GSI_{\infty}$  for the Oklahoma fish than the Montana and North Dakota fish is also consistent with the shorter life span and higher metabolic demands of the Oklahoma Paddlefish than the Montana–North Dakota Paddlefish (Scarnecchia et al. 2019). The Oklahoma Paddlefish put more effort into each reproductive event and also have a shorter period of gonadal recrudescence (1–2 years versus 2–3 years; Scarnecchia et al. 2007, 2019). These general results conform with findings from other migratory species, such as American Shad *Alosa sapidissima* and the salmon species (Salmonidae), where a higher investment in reproduction (migration plus fecundity) is associated with a reduced tendency for repeat spawning, even to the extent of the evolution of semelparity in some species (Glebe and Leggett 1981).

The hyperallometric increases in raw egg weight with fish weight found here depict only one of several benefits associated with maintaining some larger and older females in the populations (Hixon et al. 2014; Scarnecchia et al. 2014; Rider et al. 2019). The demonstrable benefits are unfortunately not consistent with most of the harvest regulations for the species rangewide, where only minimum size limits are often applied. While the minimum size limits can, and generally do, have considerable conservation value (Hupfeld et al. 2016), they are not by themselves adequate in the long term for managing large, long-lived species such as the Paddlefish. Under high harvest rates, size and age truncation is the common result. Harvest slots or other regulations designed to reduce harvest of larger, older fish are needed (Scarnecchia et al. 1989, 2014). The implication for Paddlefish is that sustainable long-term harvest of the species, like many other freshwater and marine species, requires a re-thinking of our historical approaches to regulations. Future efforts to maintain larger, older fish in the stocks will require more carefully thought out and finely tuned regulatory and monitoring approaches than exist in most Paddlefish fisheries.

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