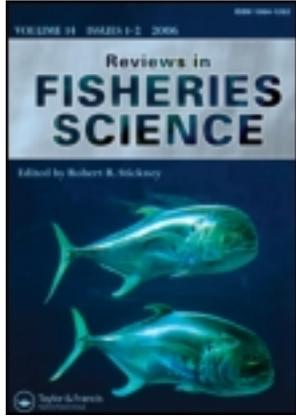


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Southern and Northern Great Plains (United States) Paddlefish Stocks Within Frameworks of Acipenseriform Life History and the Metabolic Theory of Ecology

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*Sampling conducted in 2008–2010 on a southern Great Plains stock of paddlefish *Polyodon spathula* inhabiting the Neosho River, Spring River, and Grand Lake, Oklahoma, is characterized (1) in terms of the Acipenseriform life history framework outlined for the Yellowstone–Sakakawea stock of the Northern Plains and (2) in relation to the framework metabolic theory of ecology and associated latitudinal and environmental correlations with lifespan. In the Grand Lake stock, male fish typically mature at ages 6–7, and females mature at ages 8–9. The five stages of the lifespan (immature, maturing, growth and reproduction, prime reproduction, senescence to death) are compressed into a period of 15–20 years; the prime reproduction period occurs from ages 12 to 16 years for females. This lifespan compares to one of 40–50 years (and occasionally longer), and a prime reproduction period for females from ages 25 to 40 years, for the Yellowstone–Sakakawea stock. The more compressed lifespan of the Grand Lake stock and lower energy storage, as indicated by weights of gonadal fat bodies, are consistent with the framework metabolic theory of ecology. Over the course of a year, fish in Grand Lake are under a much higher metabolic demand than those in Lake Sakakawea. The distinct differences detailed between these two stocks from the southern and northern plains may exist between other paddlefish stocks, other Acipenseriform species, and other fish taxa separated by large latitudinal and climatic differences. The results have specific implications for harvest management and effects of climate change on Acipenseriform life histories and lifespan.*

Keywords paddlefish, Polyodontidae, Oklahoma, Neosho River, metabolism, life history

INTRODUCTION

It is not time as such, but the tempo of life that best measures the rate of aging of an organism. (MacArthur and Baillie, 1929, p. 267; studying *Daphnia*)

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The rate of metabolism sets the pace of life, including the life history schedule. (Brown et al., 2004, p. 1776)

Life had been fast. Death had come young. (Willard Motley, American Novelist (1912–1965) describing Nick Romano and his fate in *Knock on Any Door* [1947, p. 501])

The paddlefish *Polyodon spathula*, an ancient zooplanktivorous Acipenseriform fish (Grande and Bemis, 1991) of North America's large rivers and reservoirs (Gengerke, 1986), has a

broad latitudinal distribution in North America (Jennings and Ziegler, 2009). Reproducing populations are known as far north as the Missouri River in the northern Great Plains of Montana southeastward to Texas and the lower Mississippi River of Louisiana (Russell, 1986; Bettoli et al., 2009). Although the species has been studied in various aspects and localities for more than a century (Dillard et al., 1986), many fundamental questions on its life history and ecology remain unanswered (Jennings and Ziegler, 2009; Paukert and Scholten, 2009).

In a recent work on northern Great Plains paddlefish, the Yellowstone–Sakakawea stock of western North Dakota and eastern Montana (Scarnecchia et al., 2007), the lifespan of 50 or more years was described as having five stages: (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 pre-spawning 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 pre-spawning 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.” (p. 211)

It was hypothesized in that article that these five distinct stages of a paddlefish’s lifespan were more protracted and thus more obvious in longer-lived northern stocks and more compressed and thus less obvious in shorter-lived southern stocks. Past reviews of life history studies have concluded that paddlefish in more northerly stocks tend to mature at an older age and live longer than fish in more southerly stocks (Russell, 1986; Paukert and Fisher, 2001). Factors behind such differences have been suggested for Great Plains fishes (e.g., Braaten and Guy, 2002), including growing season, water temperatures, and growth rates.

More comprehensive evaluations of relations among latitude, temperature, metabolic rate, and life histories (including lifespan) of organisms have been conducted among and within

diverse ectothermic taxa. Munch and Salinas (2009) tied latitudinal variation and animal lifespan within a range of ectothermic species to the metabolic theory of ecology. Brown et al. (2004) effectively outlined a framework for this theory, linking a range of population, community, and ecosystem processes to metabolic rate, which they identified as *the* fundamental biological rate. For ectotherms, temperature strongly influences their metabolic rates, rates of physical activity, and lifespans, described as the “Rate of Living Theory” (Sohal and Allen, 1986). Higher ambient temperatures result in higher metabolic demands, such that ectotherms in lower latitudes, longer periods of warmer ambient conditions, and longer growing seasons, would typically have shorter lifespans than organisms at higher latitudes, cooler ambient conditions, and shorter growing seasons. For walleye, *Sander vitreus*, for example, Beverton (1987) plotted data from Colby and Nepszy (1981) to show strong inverse correlations among stocks between ambient air temperatures and both age at maturity and maximum lifespan (summarized in Finch, 1990). According to Finch (1990), no histological or physiological data were available to evaluate “the extent of senescence at different temperatures or in relation to the lifespan” (p. 500).

At water temperatures of 22°C, the paddlefish is reported to be in continuous motion and an obligate ram ventilator, with a metabolic rate of about twice that of the resting metabolic rate of other Acipenseriformes, none of which are obligate ram ventilators, although some may be capable of ram ventilation (Burggren and Bemis, 1992). It has been observed that paddlefish of all sizes (3–4 cm in length through 40-kg adults) at 20°C are in continuous motion, as they ram ventilate and seek food through particulate feeding (primarily age 0 fish; Fredericks, 1994) or, most commonly, filter-feeding (Rosen and Hales, 1981; Michaletz et al., 1982; Burggren and Bemis, 1992). Fish stationary in rivers position themselves in places where water can flow actively across their gills. Such a species may be especially susceptible to temperature impacts on metabolism. For paddlefish, more information is needed on the relations among stocks regarding their sex-specific life history characteristics, such as age at maturity, size dimorphism, longevity, specific energetic, and physiological characteristics, and their behaviors in relation to rearing environments, especially if understanding of paddlefish lifespan is to be extended beyond straightforward observations of latitudinal patterns of longevity. With the global warming projected for this century (e.g., Meehl et al., 2005), it would also be beneficial to understand and predict effects of potential climate changes on life histories and lifespan of paddlefish, other Acipenseriform species, and other fish taxa (Matthews and Zimmerman, 1990; Regier and Meisner, 1990; Carpenter et al., 1992).

The most detailed data available for understanding these relationships can come from well-monitored fisheries. The Oklahoma Department of Wildlife Conservation (ODWC) has historically managed an important fishery for paddlefish on the Neosho River–Spring River–Grand Lake Reservoir system in the northeastern corner of the state (Branson, 1967; Combs,

1982, 1986; Ambler, 1987). A year-round recreational snag fishery is most active in spring (March–April) in the upper portions of the reservoir (the Gray’s Ranch area) and up the Neosho and Spring Rivers (Figure 1). Estimated angler (snag fishery) harvests in Oklahoma in the past two decades have ranged from more than 11,175 fish in 2009 to just under 3,000 fish in 2002 (Gordon, 2006; B. Gordon, unpublished data).

Although the Grand Lake stock has been the most studied of Oklahoma’s paddlefish (Combs, 1982; Ambler, 1987, 1994; Gordon, 2006), information available prior to 2008 was confined mainly to extensive length information of gill-netted (ODWC-caught and commercial) and recreationally caught fish. Small samples of fish were aged with dentaries (lower jaw bones) by Combs (1982), and additional dentaries were collected by the ODWC in 2004. In 2008, however, the ODWC initiated a roe donation program for recreationally caught fish from the Neosho River, Spring River, and Grand Lake. Under the program, anglers could bring any freshly harvested fish to a central research and processing center (RPC; located at Twin Bridges State Park near the confluence of the two rivers and the reservoir headwaters) for free cleaning in exchange for a donation of the roe, which is processed into caviar under ODWC supervision and sold, with proceeds used to support agency fisheries research, management, and enforcement. In the first three years of the roe donation program (2008–2010), an intensive sampling protocol was implemented to collect detailed biological data from every paddlefish brought into the RPC. Data from the Grand Lake stock were collected in a form consistent with data collected at roe donation stations for the Yellowstone–Sakakawea stock in the upper Great Plains (Montana and North Dakota; Scarnecchia et al., 2007, 2008, 2009). As a result, these two Great Plains stocks have detailed, stock-specific data that allow this study to (1) describe in detail the life history of the Grand Lake Stock, (2) compare the life history of the Grand Lake stock from the southern Great Plains with the Yellowstone–Sakakawea stock of the

northern Great Plains in terms of the Acipenseriform life history framework (i.e., the five stages) outlined by Scarnecchia et al. (2007); and (3) characterize the Grand Lake stock in relation to the framework metabolic theory of ecology of Brown et al. (2004) and associated latitudinal and environmental correlations with lifespan outlined by Munch and Salinas (2009).

MATERIALS AND METHODS

Fish Sampling

Data were collected from Grand Lake stock paddlefish at the RPC from 23 February through 28 April in 2008 ($N = 4,092$ fish with biological data), 13 February through 29 April in 2009 ($N = 7,430$ fish), and 2 March through 1 May in 2010 ($N = 3,945$ fish). During these periods, fish brought into the RPC were assigned a unique number, measured to the nearest mm for body length (BL; front of eye to fork of caudal fin; Ruelle and Hudson, 1977), and weighed to the nearest 0.1 kg. Dentaries for age determination (Adams, 1942; Scarnecchia et al. 2006) were removed from each fish and placed into manila envelopes to dry. Sex of fish was determined at the beginning of the cleaning process, and one of six maturation stages of females (two immature stages, mature, pre-ovulation [i.e., caviar] stage, ovulated, spawned out, and reabsorbed-developing [“salt and pepper”]) was assigned based on visual observation (Bruch et al., 2001). From a subsample of male fish (2008: $N = 2,261$, or 94.8% of all male fish; 2009: $N = 936$, or 22% of all male fish; 2010: $N = 1,128$, or 46.7% of all male fish), testes weight and gonadal fat body (GFB) weight were estimated to the nearest gram. GFBs are discrete clumps of fatty tissue attached to the gonads (Scarnecchia et al., 2007). GFBs were separated from the testes and weighed. For female fish (2008: $N = 1,442$, or 85.4% of all female fish; 2009: $N = 455$, or 14% of all female fish; 2010: $N = 560$, or 36.6% of all female fish), both raw egg weight and GFB weight were obtained in grams.

Age Determination

In 2004, four years before the RPC began, lengths, weights, and dentaries from 147 fish (55 males, 37 females, 55 of unknown sex) were collected by the ODWC from upper Grand Lake and the river systems from netting and creel census work. Eighty of the 92 dentaries (87%) from known-sex fish were taken with gill nets in the Gray’s Ranch area of the upper reservoir. In contrast, the dentaries from 44 of 55 unknown-sex fish (80%) were taken from angler-harvested fish caught in the Neosho River up to the town of Miami.

In 2008, ages were determined for 4,073 fish (2,385 males and 1,688 females), or 99.5% of the fish brought to the RPC. In 2009, ages were determined for 2,419 fish (1,435 males and 984 females), or 33% of fish brought to the RPC. In 2010, ages were determined for 3,945 fish (2,415 males and 1,530 females), or

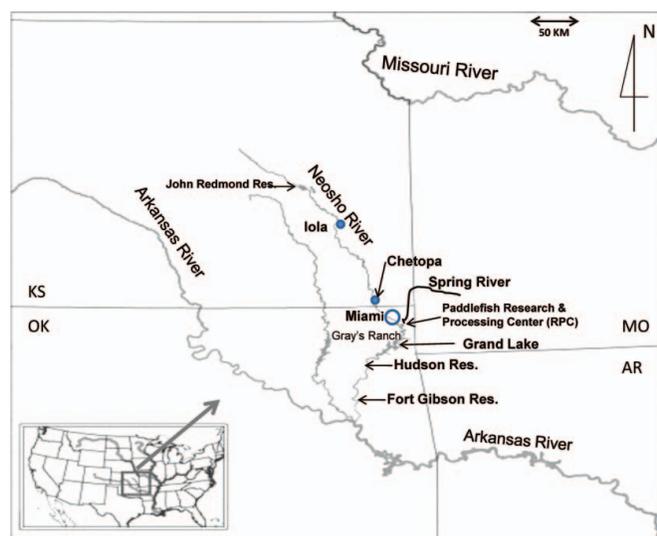


Figure 1 The Neosho River basin, Spring River, and Grand Lake (Oklahoma, Kansas, and Missouri, USA, respectively) (color figure available online).

99.9% of fish brought to the RPC. Prior to 2010, age determination was conducted using the optical pattern recognition system (OPRS) as described in Scarnecchia et al. (2006). In 2010, a new system was used, consisting of an Olympus BX41 compound stereo microscope, an Olympus DP25 high-resolution digital video camera, and a desktop computer connected to the video camera. Two high-resolution (1,920 × 1,080 pixel) widescreen flat-panel monitors viewed camera images. Two image acquisition and processing software suites—Image-Pro Plus software and CellSens Entry software—aided interpretation and archiving of images.

A double-blind aging protocol was used, where fish were aged independently by two readers. Sections with age disagreement were re-aged independently a second time. If disagreement remained, the section was interpreted by both readers together. Validation of paddlefish ages has occurred for the Yellowstone–Sakakawea stock (Scarnecchia et al. 2006); however, ages for the Grand Lake stock could not be validated because no fish of known age were available at the time of the study. Verification (precision) was described as percent agreement (exact age) upon first and second independent readings. Final ages assigned to each fish allowed individual fish to be placed into a brood year class. Because of the importance of accurate age estimates in interpreting life histories, representative reference photographic plates of dentary sections from fish of a range of ages were prepared in lieu of validation.

Growth Rates

Growth of male and female paddlefish was described with a von Bertalanffy growth function (three parameter), expressed as $L = L_{\infty} e^{(1 - K(t - t_0))}$, where L is length, L_{∞} is the asymptotic length, K is the Brody growth coefficient, and t_0 is the initial condition parameter (Ricker, 1975; Moreau, 1987; Chen et al., 1992). For the 2004 data, a two-parameter model was fit to length data (i.e., the curves forced through origin; $t_0 = 0$) to provide insight into the age at which growth of males and females diverged. Weight-converted von Bertalanffy (three-parameter) equations were also calculated, expressed in terms of L as $W = aL^b$, where W is the weight and a and b are parameters.

Weights of fish of a specific year class (1999) were compared within males and within females among 2008, 2009, and 2010 for significant differences with an analysis of variance (ANOVA) model. When significant differences among yearly means were found, pairs of years were compared with a Student-Neuman-Keuls test. A P -value of 0.05 or less was required for significance.

Gonadal Development

Gonadal weight was expressed as a distinct variable, as well as converted into the gonadosomatic index (GSI), i.e., gonad weight as a percentage of fish weight (DeVlaming et al., 1982; Crim and Glebe, 1990). GFB weight was expressed as a distinct

variable, as well as GFB/fish weight and GFB weight/gonad weight. These variables were evaluated in relation to the age of the fish as described in Scarnecchia et al. (2007) for the Yellowstone–Sakakawea stock.

Comparison with Yellowstone–Sakakawea Stock

In analyses of GSI and GFBs by age, data from the Grand Lake stock for the years 2008–2010 were combined. For the Yellowstone–Sakakawea stock, life history attributes, including age at maturity, lifespan, GSI, and GFB variables, were quantified based on validated ages (Scarnecchia et al., 2006), as detailed in Scarnecchia et al. (2007); the approaches were exactly the same as outlined above for the Grand Lake Stock. Data used for growth, GSI, and GFB analyses were combined for the years 2005–2009. Most data for the Yellowstone–Sakakawea stock were analyzed separately by North Dakota and Montana components of the stock, because past studies (Scarnecchia et al., 2007) had shown that fish harvested in Montana are typically a younger and smaller (in size) component of the stock, resulting in incomplete mixing of the fish for life history evaluations.

Reservoir Water Temperature Data

Water temperature data for Grand Lake were obtained from unpublished records of the State of Oklahoma Water Resources Board. Intermittent data were available over the period 1995–2009. Data used were averages at 1.0 m depth for sites 1, 8, and 13, which were located in the upper, middle, and lower reservoir, respectively (Oklahoma Water Resources Board, n.d.). Data were averaged for all three stations. Daily water temperature data from the discharge of Pensacola Dam, which impounds Grand Lake, were also used to characterize annual temperature regimes. Years of data used were 2006–2010.

For Lake Sakakawea, water temperature data used were taken from records of the U.S. Army Corps of Engineers over the period 2005–2009 (U. S. Army Corps of Engineers, 2010). Data used were water temperatures for the Missouri River at Williston, North Dakota near the reservoir headwaters, and from outflows of Garrison Dam, which impounds Lake Sakakawea. Not all daily records were available each year, so mean daily water temperatures, calculated to depict overall mean conditions encountered by paddlefish, were not necessarily based on the same numbers of data points (i.e., years).

RESULTS

Grand Lake Stock

Age Structure

Overall, age structure results indicated a typical lifespan of 15–20 years. In 2004, fish ($N = 147$) ranged in age from 4–22 years (Figure 2). Males ($N = 55$) ranged in age from 4–18 years.

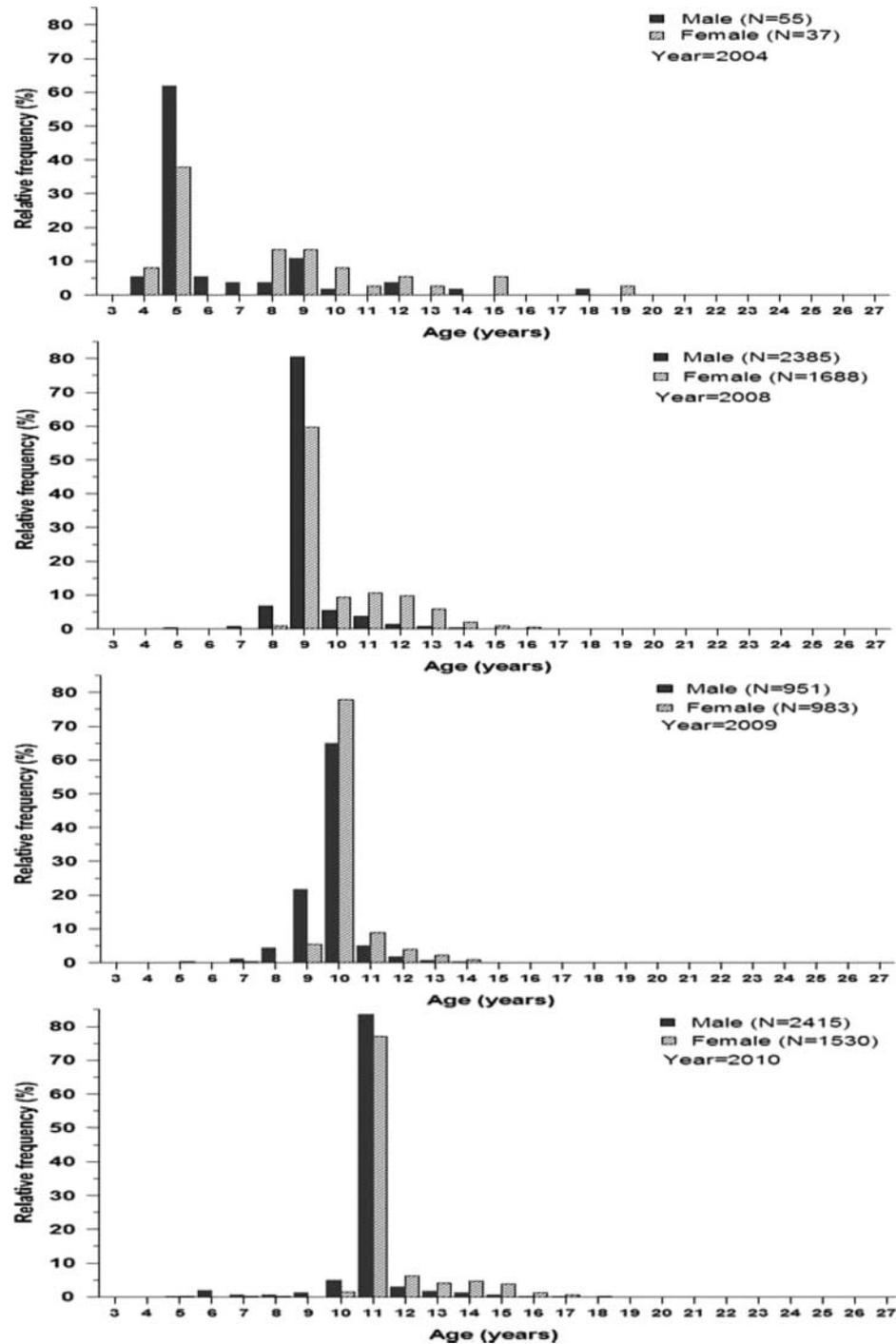


Figure 2 Age-frequency histograms for the Neosho River Grand Lake paddlefish in 2004, 2008, 2009, and 2010, showing the strong 1999 year class.

Age 5 males (1999 year class) constituted 62% of the sample (Plate 1) and age 9 fish 11% of the sample. Only one male fish exceeded age 15 (1.8%). Females ($N = 37$) ranged in age from 4–19. Age 5 females constituted 38% of the sample and ages 8 and 9 females each 14% of the sample. Only one female exceeded age 15 (2.7%). Fish of unknown sex ($N = 55$), nearly all sampled from angler-caught fish from the river, ranged in age from 4–22 years. The most common ages were 8 years (22% of

sample) and 9 years (20% of sample). Three fish of unknown sex exceeded age 15 (5.5%; Figure 2).

In 2008, ages for males ($N = 2,385$) ranged from 3–15 years and averaged 9.1 years (Figure 2). No males were older than age 15. Females ($N = 1,688$) ranged from 8–27 years and averaged 10.1 years. Only 15 age 8 females (< 1% of all females) were found. Less than 1% of all females were older than age 15 (Figure 2). The sample (sexes combined) was

dominated by fish of the 1999 year class (age 9 fish; 80.6% of all males and 59.7% of all females; Plate 2). Overall, males could be distinguished from females by their smaller size, seen both in the length and weight frequency distributions (Figures 3A,B). In general, older fish were longer and heavier for both sexes, although considerable variation in length and weight was possible for males and females of a given age (Figures 4A,B).

In 2009, ages for males ranged from 5–21 years and averaged 9.8 years (Figure 2). Only one male fish exceeded age 14. Females ranged in age from 5–18 and averaged 10.2 years. Only two female fish exceeded age 15 (Figure 2). The sample was dominated by age 10 fish of the 1999 year class (68% of all males and 78% of all females; Plate 3).

In 2010, ages for males ranged from 5–21 years and averaged 10.9 years (Figure 2). Females ranged from 5–21 years and averaged 11.5 years. Few age 9 and younger females were found (< 1% of all females), although 44 age 6 males (1.2% of the total fish; Plate 4) were found. Older females aged 12–17 were more abundant than males of those year classes. Less than 1% of all fish (both sexes) exceeded age 15 (Figure 2; Plate 5). The sample was dominated by age 11 fish of the 1999 year class (83.5% of all males and 77% of all females; Figure 2; Plate 6).

Agreement between readers (first reading) for age estimates was 71% in 2008, 63% in 2008, and 84% in 2010. Agreement between readers (second reading) for age estimates was 69% in 2008, 80% in 2008, and 88% in 2010. Estimates that differed between readers typically did so by one year.

Length-at-Age, Weight-at-Age, and Growth

Grand Lake paddlefish showed distinct sexual size dimorphism. Both length and weight at age were higher for females than males for fish age 8 and older (Figures 4A,B). Two-parameter equations for the 2004 fish suggested that growth of males and females was similar up to age 5 when males began maturing and growing more slowly than females. (Figures 4C,D)

Maturation and Gonadal Energy Storage (GFBs)

Over the years 2008–2010, nearly all of the males and females brought to the RPC for processing were sexually mature; only a few of the youngest males and females were immature. GSI for males increased from 0.6 to 1.3% of body weight from ages 4–8, remained at about 1.3% of body weight for ages 8–10, and then decreased (Figure 5A). For GFB weight as a percentage of fish weight, mean and median values for males fluctuated mostly from 2.5 to 3.5% of fish weight for fish aged 5–16, peaking at ages 8–10 (Figure 5B). The ratio of GFB weight/testes weight was highest for the youngest recruited fish (ages 4 and 5, most of which were immature) but in the range of 2.5:1 to 3.5:1 for ages 6–14 (Figure 5C). A few of the oldest fish with undeveloped testes had larger GFBs (Figure 5C).

For females, GSI was about 15% or less of body weight before age 10 and increased to a peak of nearly 24% at ages 12–16 (Figure 6A). The maturity of females was clearly seen from the presence of black eggs, pre-ovulated in nearly all fish

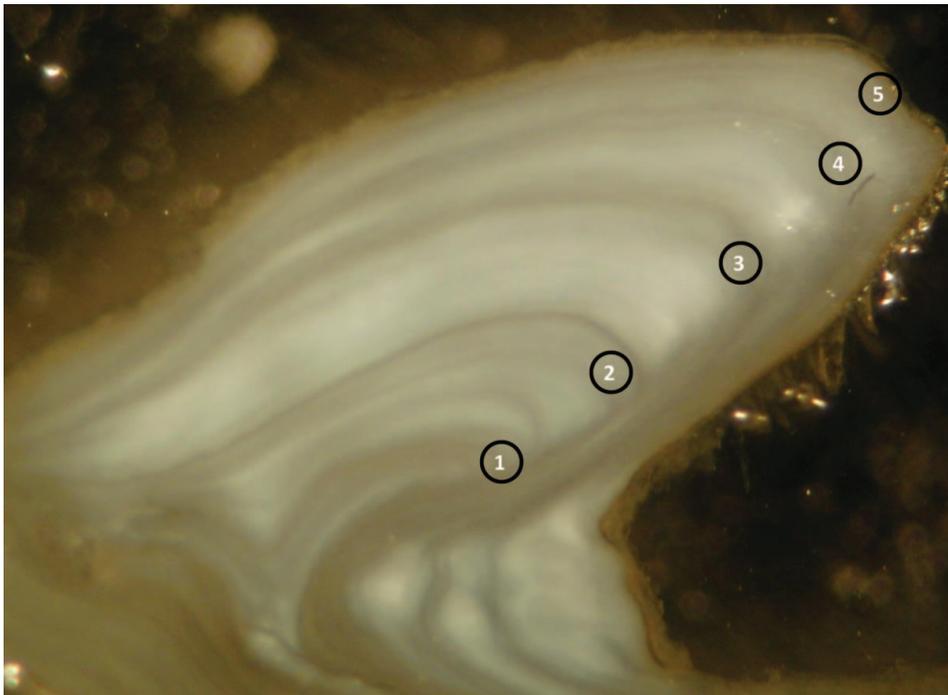


Plate 1 Putative age 5 fish sampled from Grand Lake in 2004 (female, BL = 818 mm, weight = 7.35 kg) (color figure available online).



Plate 2 Putative age 9 fish sampled at the RPC in 2008 (male, BL = 975 mm, weight = 13.7 kg) (color figure available online).

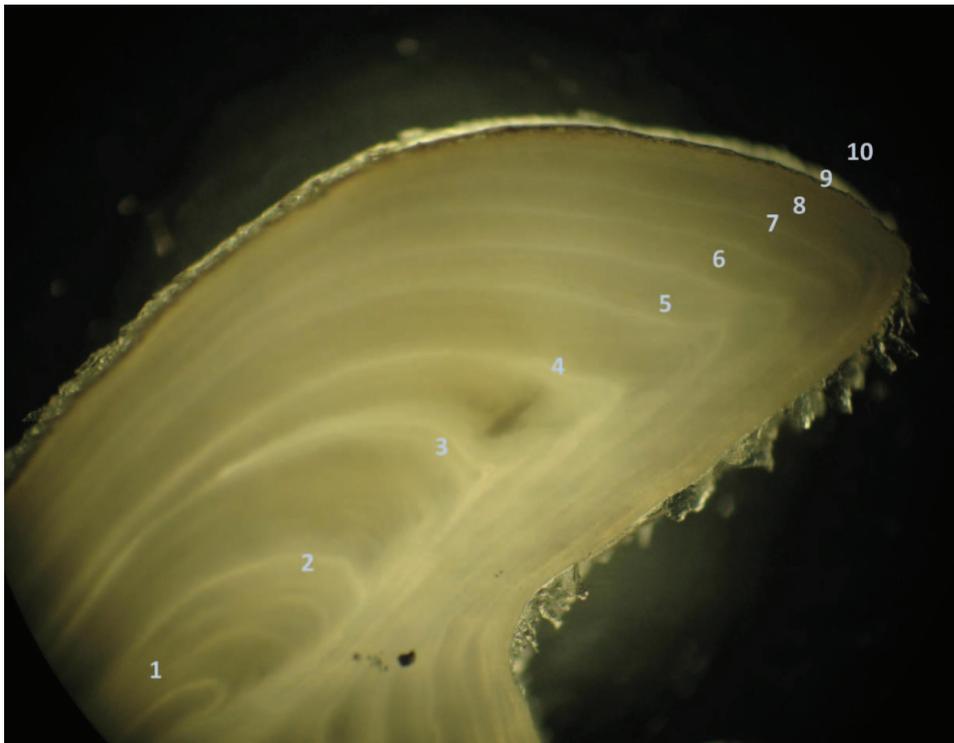


Plate 3 Putative age 10 fish sampled at the RPC in 2009 (female, BL = 991 mm, weight = 18.55 kg) (color figure available online).

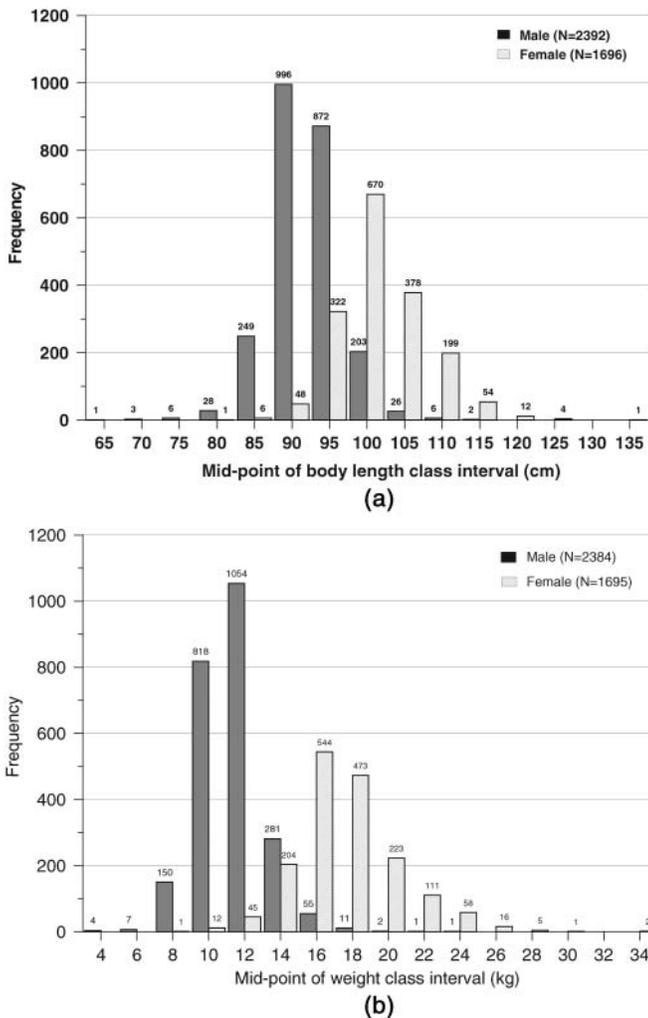


Figure 3 Frequency histograms for Grand Lake paddlefish, 2008 only: (A) male and female body length and (B) male and female weight.

but ovulated and spawned out in a few fish later in the fishing season. For females, average GFB weight/fish weight ratios for fish peaked at the youngest ages (i.e., for immature fish before age 8) and declined steadily thereafter following maturation (Figure 6B). The ratio of GFB weight/egg weight for females also peaked at age 9 and declined as the fish aged (Figure 6C).

The Strong 1999 Year Class

The strength of the 1999 year class was evident from its early contribution to the net catches in 2004 and fishery contributions in 2008–2010. The year class was strong in 2004 (as age 5 fish netted in the reservoir in 2004 but not yet in recruits to the river fisheries of 2004) and dominant through its continuing contributions in 2008 (age 9 fish), 2009 (age 10 fish), and 2010 (age 11 fish; Figure 2). For males of this dominant 1999 year class, there was a significant difference in weight among 2008–2010 (ANOVA, $F = 96.22$, $P < 0.0001$), with all three means significantly different from each other (Student-Newman-Keuls test,

$P < 0.05$; Figure 7A). Mean weight decreased significantly from 2009 to 2010. There was concurrently a decrease in GSI (Figure 7B) and a decrease in the ratio of GFB weight/fish weight (Figure 7C). Females of the 1999 year class, in contrast, showed a significant difference among weights from 2008 to 2010 (ANOVA, $F = 36.62$, $P < 0.0001$) but not a significant difference between 2009 and 2010 (Student-Newman-Keuls test, $P > 0.05$; Figure 7A). For females, there was an increase in mean GSI from 2008 to 2010 (Figure 7D), while mean GFB weight/fish weight decreased from just over 1% in 2008 to about 0.44% by 2010 (Figure 7E).

DISCUSSION

Grand Lake Paddlefish in an Acipenseriform Life History Framework

Life history results for the Grand Lake stock 2004 and 2008–2010 can be summarized in terms of five stages of the Acipenseriform life history framework outlined in Scarnecchia et al. (2007).

Stage 1 (Immature)

After fish spawn in riverine habitat in spring (exact locations unknown), young fish hatch and move down into Grand Lake for a rearing period of several years.

Stage 2 (Maturing)

Growth of males and females appears to remain similar until about age 5 (Figures 4C,D), when most males initiate the sexual maturation process. Most males are mature at age 6 or 7. Most females begin to mature at 6–7 and mature at age 8 or 9 (Figure 2). By ages 6 and 7, male growth has slowed substantially, whereas growth of females continues at a higher rate until 2–3 year later, when their maturation process also results in a slower growth rate. By this time they are larger in length and weight than males of the same cohort (Figures 4A,B).

Samples collected near Gray's Ranch in the upper reservoir in 2004 were a mixture of immature and mature fish as indicated by their age structure (Figure 2). Numerous age 5 males (1999 year class) and a lower proportion of age 5 females were found in this sample. In contrast, the sample of fish of unknown sex in 2004 from the creel census in the river consisted primarily of mature fish; age 5 fish were not dominant in this sample because most of that year class was immature and fish were mostly still in the reservoir and not yet migrating upriver to spawn.

Stage 3 (Somatic Growth and Reproduction)

During this period, somatic growth continues (Figures 4A,B), but an increasing proportion of energy is routed into

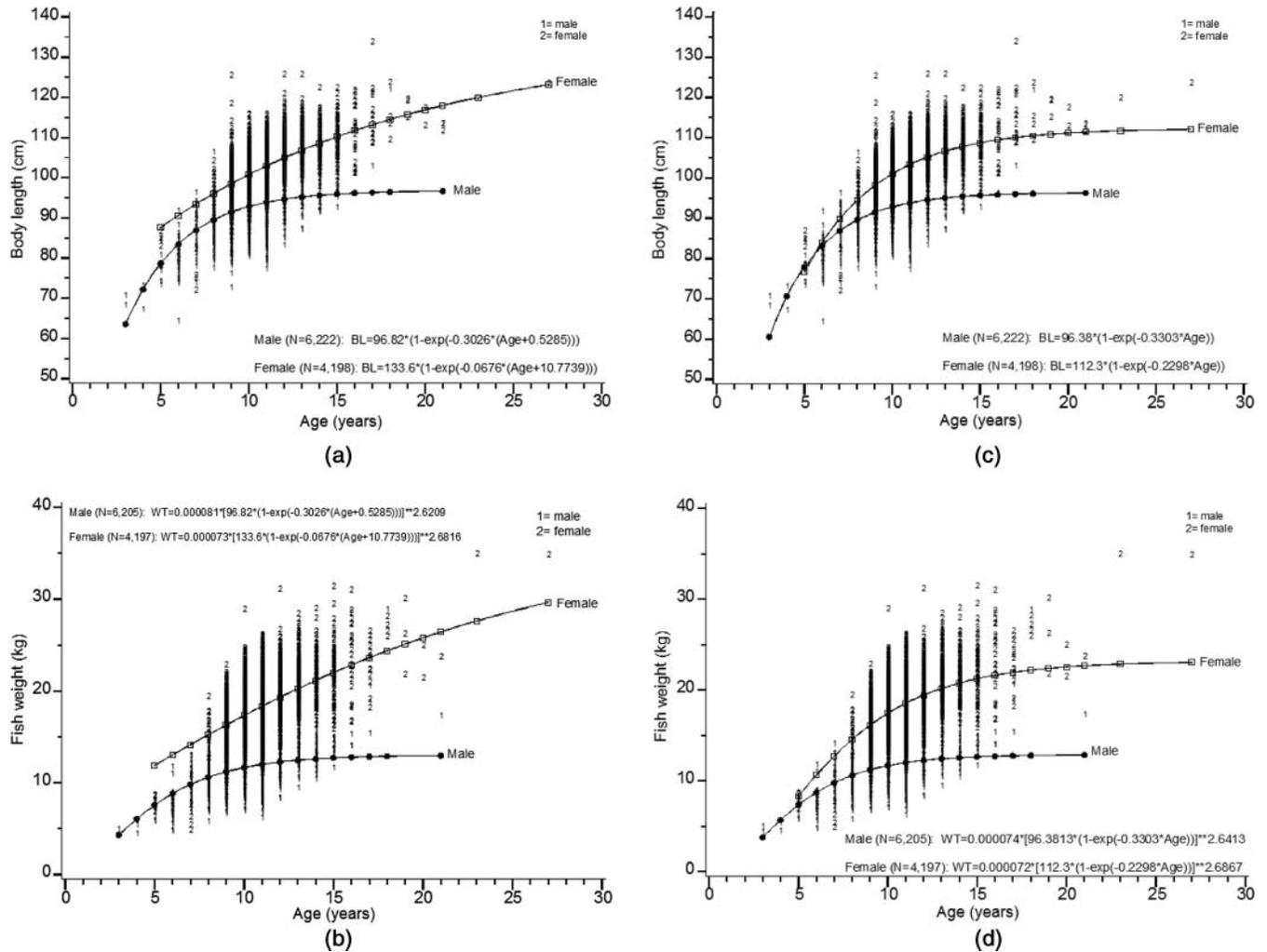


Figure 4 von Bertalanffy growth curves for Grand Lake paddlefish: (A) three-parameter male and female paddlefish lengths, (B) three-parameter male and female weights, (C) two-parameter male and female lengths, and (D) two-parameter male and female weights, based on data from 2008–2010.

reproduction. GSI is increasing (males; ages 5–8; Figure 5A); females ages 8–12; Figures 6A). GFBs for males are stable (Figures 5B,C) but, in females, begin to decrease between age 10 and 11 (Figures 6B,C). Upon sexual maturation, they migrate upriver to spawn and, thereafter, make repeated spawning migrations upriver. The periodicity of migrations is currently being studied by ODWC with telemetry and analysis of tag returns.

Stage 4 (Prime Reproduction)

As of 2010, male fish of the 1999 year class of the Grand Lake stock were in the period of prime reproduction, as described in Scarnecchia et al. (2007). The mean weights of age 11 males had declined (Figure 7A) from the previous year, as had the GSI (Figure 7B) and the GFB weight /fish weight (Figure 7C). For age 11 females of the 1999 cohort, GSI was increasing (Figure 7D), and GFB weight/fish weight was de-

creasing to below 0.5% (Figure 7E). By age 12, age structure, GSI, and GFB values strongly suggest the period of prime reproduction had been reached. This period of prime reproduction of Grand Lake stock paddlefish exists for only about five years (ages 12–16).

Stage 5 (Senescence to Death)

Survival of fish after age 15 is low. Of 10,437 fish assessed for age in 2008–2010, only 59 (0.57%) were found to be older than age 15 and only 6 fish (0.06%) older than age 20. After age 16, GSI decreases slightly (Figure 6A), GFBs are nearly depleted (Figure 6B), and the number of living fish declines greatly (Figure 2). The near absence of older fish may be a result of a combination of fishing mortality and natural mortality. These results along with GFB depletion are consistent with the lifespan of the Grand Lake fish typically not exceeding 20 years.

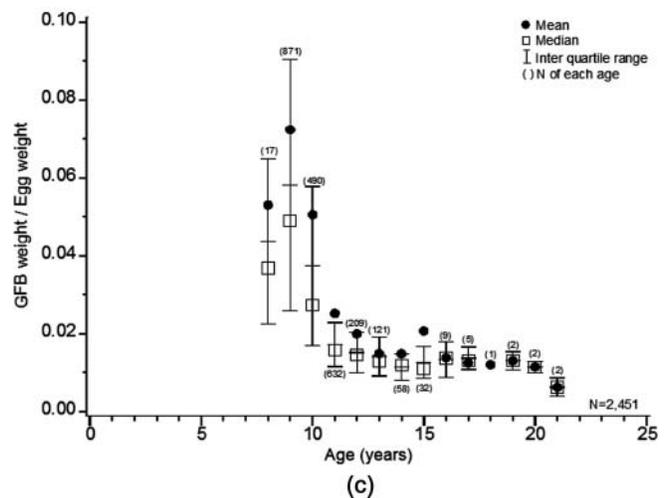
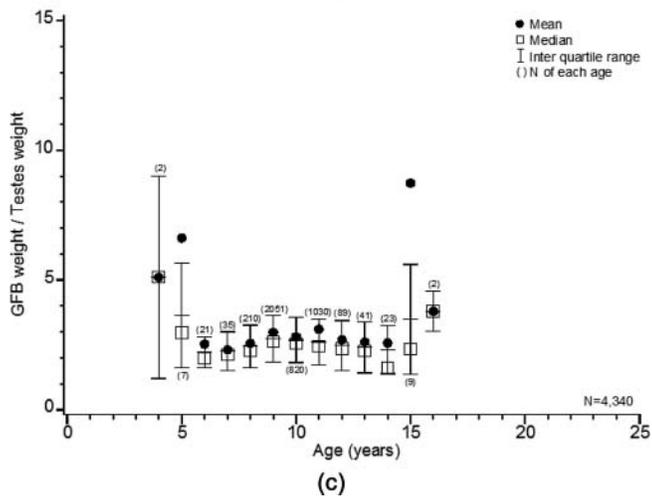
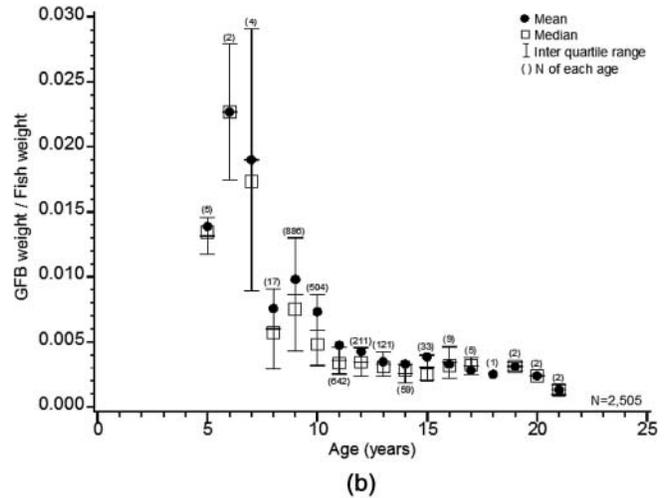
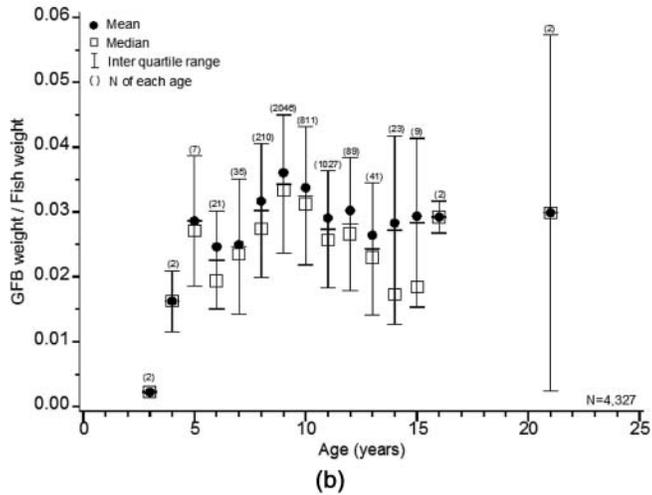
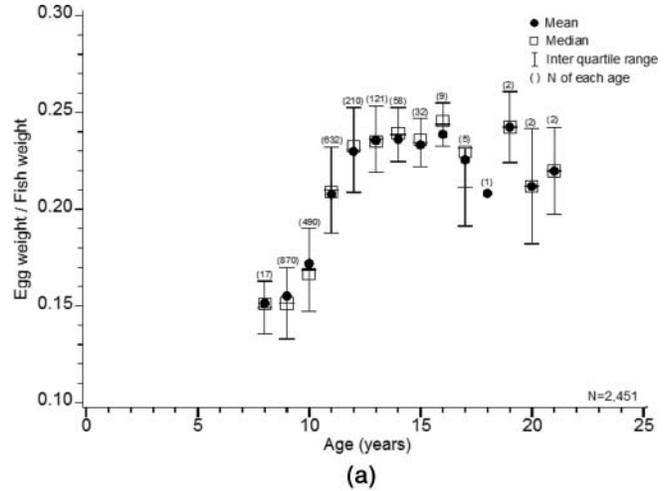
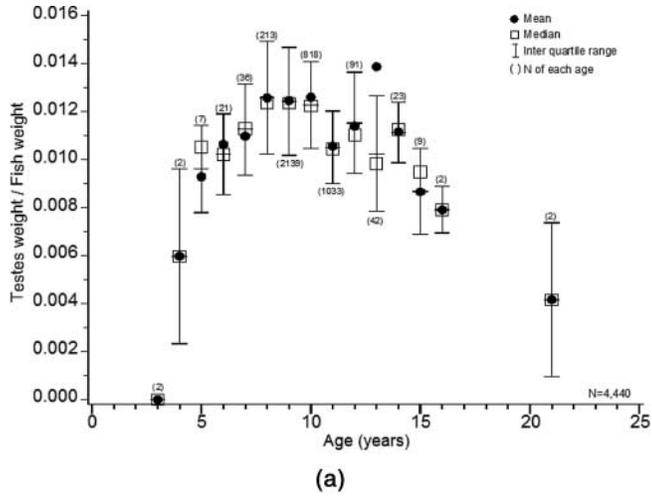


Figure 5 Male paddlefish age in relation to: (A) GSI, (B) GFB weight/fish weight, and (C) GFB weight/testes weight.

Figure 6 Female paddlefish age in relation to: (A) GSI, (B) GFB weight/fish weight, and (C) GFB weight/egg weight.

Life History Similarities and Differences: The Grand Lake (Southern Great Plains) Stock Versus Yellowstone-Sakakawea (Northern Great Plains) Stock

The life histories of the two stocks are similar in that males mature younger than females (Grand Lake: males, ages 6–7, Fig-

ure 8A; females, ages 8–9, Figure 8B; Yellowstone-Sakakawea: males, ages 9–12, Figure 8A; females, ages 16–19, Figure 8B; Scarnecchia et al., 2007) and typically remain smaller size than females through their lives (Grand Lake: males, $L_{\infty} = 96.8$ cm,

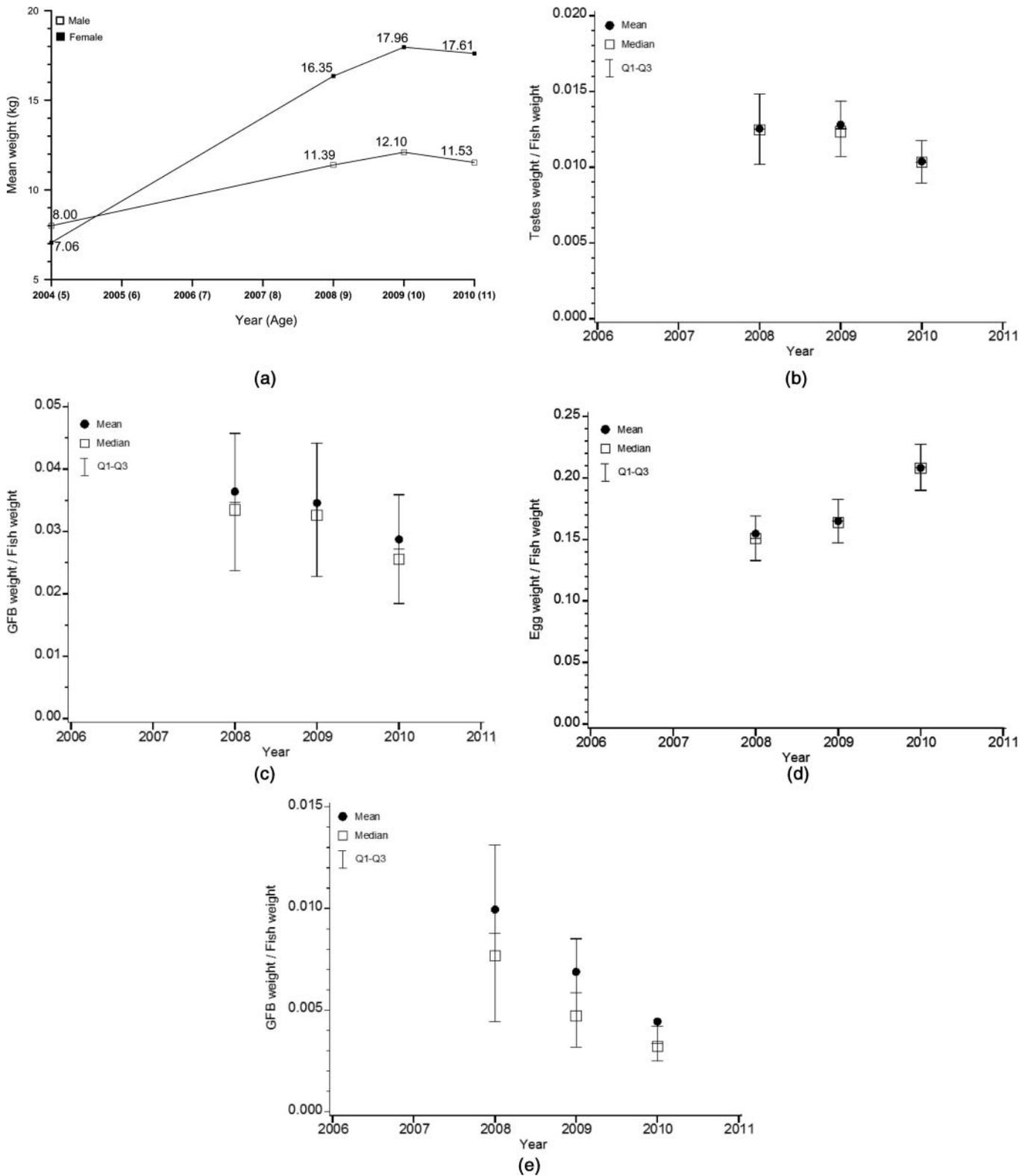


Figure 7 (A) Mean weight of male and female Grand Lake paddlefish of the 1999 cohort and their mean, median, and inter-quartile ranges for: (B) testes weight/fish weight, (C) male GFB weight/fish weight, (D) egg weight/fish weight, and (E) female GFB weight/fish weight in 2008, 2009, and 2010.

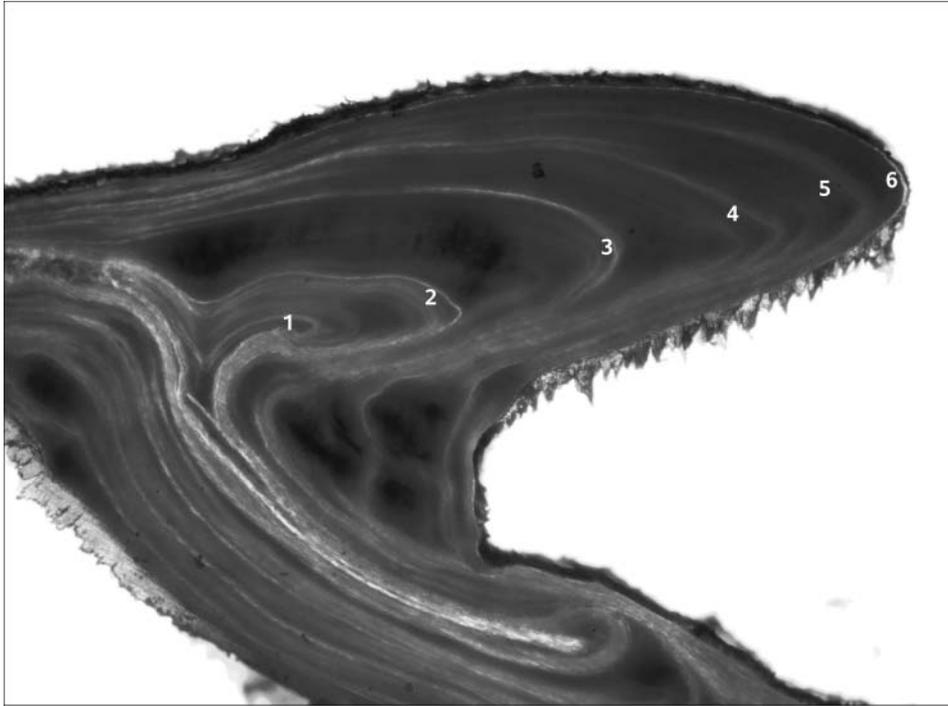


Plate 4 Putative age-6 male paddlefish sampled at the RPC in 2010 (male, BL = 790 mm, weight = 6.8 kg).

Figures 4A,B; females, $L_{\infty} = 133.6$ cm, Figures 4A,B; Yellowstone–Sakakawea (North Dakota harvest): males, $L_{\infty} = 101.1$ cm; females, $L_{\infty} = 124.6$; Scarnecchia et al., 2007). Fish from both stocks that migrate upriver in spring from reservoir habitats are nearly all sexually mature pre-spawners. Once mature, growth rates of both sexes are slow, as is most clearly seen in data from the 1999 year class of Grand Lake (Figures 7A) and from jaw tag recoveries from the Yellowstone–Sakakawea stock (Scarnecchia et al., 2007).

Several distinct differences exist in their life histories, however. First, differential weights of prime male and female spawners are less for the Grand Lake stock than for the Yellowstone–Sakakawea stock. In the Yellowstone–Sakakawea stock, females in their prime reproduction period can weigh three to four times more than males (Scarnecchia et al., 2007), whereas weight differences between the sexes in the Grand Lake stock fish in 2008–2010 were typically less (Figure 7A). Second, the difference in age at recruitment between the sexes is only 2–3 years for the Grand Lake stock versus 7–10 years for the Yellowstone–Sakakawea stock (Figures 8A,B). Third, the GSI values at prime spawning are slightly higher for Grand Lake female paddlefish, averaging about 24% (Figure 6A), whereas GSI for Yellowstone–Sakakawea paddlefish averages only 20–22% (Figure 8B). Fourth, the lower survival rate of Grand Lake paddlefish after 15 years (almost no fish remaining; Figure 2) contrasts sharply with a higher survival rate of Yellowstone–Sakakawea fish upon reaching sexual maturity and fully recruiting to the fishery (Scarnecchia et al., 2007, their Figure 13).

Understanding Paddlefish Life History Within the Framework Metabolic Theory of Ecology

Comparative Life Histories

Overall, the life history *pattern* outlined above (including trends in growth rate, GSI, and GFBs as individual fish age) for the Grand Lake stock is consistent with that outlined by Scarnecchia et al. (2007) for the Yellowstone–Sakakawea stock. The *duration* of the life history stages and the total lifespan differ greatly, however. In the Grand Lake stock, the period of prime reproduction occurs at about ages 7–13 for males and 12–16 for females; in the Yellowstone–Sakakawea stock, prime reproduction occurs at an older age and over a longer period, at ages 15–30 for males and ages 25–40 for females (Scarnecchia et al., 2007). GSI values for Grand Lake stock males and females rise and fall over a period of no more than 20 years, whereas the same pattern for the Yellowstone–Sakakawea stock occurs over 40–50 years (Figures 8A,B). For GFBs, Grand Lake stock males show a decline from ages 10–15 (the range where sample sizes were adequate to assess; Figure 5B) that is similar to declines shown for the Yellowstone–Sakakawea stock from ages 13–40 (Figure 9A). GFBs for Grand Lake stock females show the same pattern of depletion from ages 6–11 as in the Yellowstone–Sakakawea stock from about ages 18–45 (Figure 9B). In the Yellowstone–Sakakawea stock, the five paddlefish life history stages outlined in Scarnecchia et al. (2007) are protracted over a period of 40–50 years (and occasionally longer), whereas in the Grand Lake stock, the same five stages of the lifespan are compressed into a period of 15–20 years.

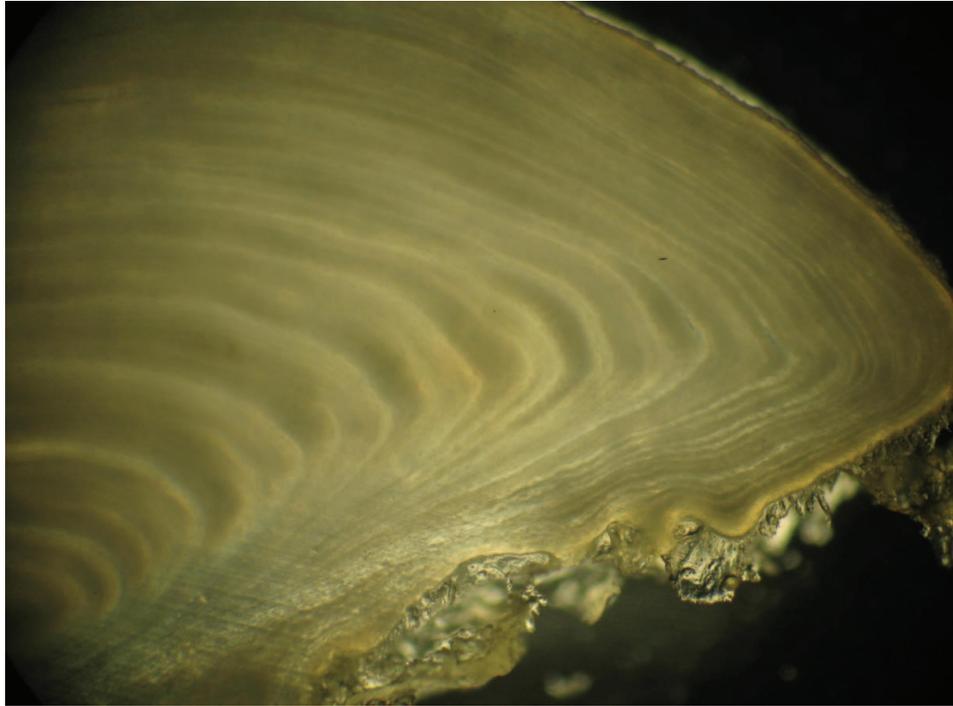


Plate 5 Putative older (age 21) paddlefish of the Grand Lake Stock (male, BL = 1,131 mm, weight = 23.05 kg) (color figure available online).

The more compressed individual life stages and shorter overall lifespan of the Grand Lake stock is consistent with observations of later age at maturity and longer paddlefish lifespans in northern latitudes than in more southerly latitudes (Russell, 1986; Paukert and Fisher, 2001). Braaten and Guy (2002) investigated the longevity of five species of Great Plains fishes (sicklefin chub, Cyprinidae: *Hybopsis meeki*; emerald shiner Cyprinidae: *Notropis atherinoides*; river carpsucker, Catostomidae: *Carpionodes carpio*; sauger, Percidae: *Sander canadensis*; and freshwater drum Sciaenidae: *Aplodinotus grunniens*) and found significantly positive correlations with latitude for all except the freshwater drum. They associated the latitudinal pattern with the number of degree days (daily water temperature minus minimum growth temperature for that species) and number of days in the growing season, which were greater for more southerly latitudes.

Life History and Metabolic Demand

In a larger scale analysis, Munch and Salinas (2009) attributed latitudinal trends in lifespan over a wide range of taxa to metabolic theory of ecology outlined by Brown et al. (2004). Based on their results from 30 species under laboratory conditions and 67 free-living species (1,081 populations), Munch and Salinas (2009) concluded that variations in lifespan both among and within taxa “can be primarily explained by temperature in a manner remarkably consistent with the MTE [metabolic theory of ecology]” (p. 13862).

In a thorough review and synthesis, Brown et al. (2004) associated a wide range of individual, population, and community

attributes to the metabolic rate, linking it in ectotherms of a large range of sizes principally to body size and temperature as

$$I = i_0 M^{3/4} e^{-E/kT},$$

where I is the whole-organism metabolic rate, M is body size (mass), E is the activation energy, k is Boltzmann’s constant, T is the absolute temperature (°K), and i_0 is a normalization constant independent of body size (Brown et al., 2004). A review of sizes of adult paddlefish shows that large paddlefish exceeding 1,200 mm BL and 40 kg have been found in both northerly and southerly latitudes (Russell, 1986; Paukert and Fisher, 2001). Although ultimate maximum sizes of fish may relate to local differences in food availability and size at maturation, the overall range of adult paddlefish sizes across the species’ distribution is well below an order of magnitude, and M can effectively be considered a constant. This elimination of mass for adult fish as an important consideration here results in an inverse semi-log relation between temperature and metabolic rate.

Environmental Effects on Metabolic Demand

Evidence for higher metabolic demands (I) on the Grand Lake stock fish compared to the Yellowstone–Sakakawea stock fish may be approximated by comparing the annual water temperatures (T) of the two respective reservoirs, Grand Lake and Lake Sakakawea, in relation to optimal temperature preferences for paddlefish. Comparisons can only be approximate because the precise habitat use of paddlefish in the reservoirs according to temperature and depth variations is not well understood, and thermal stratification occurs seasonally. Crance (1987)

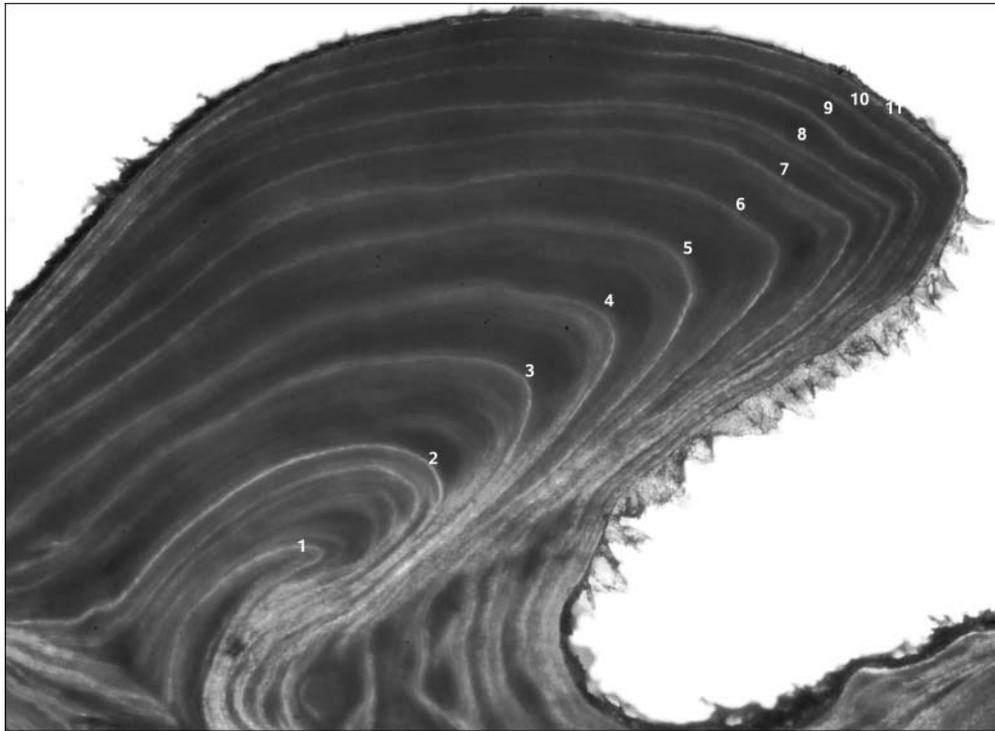


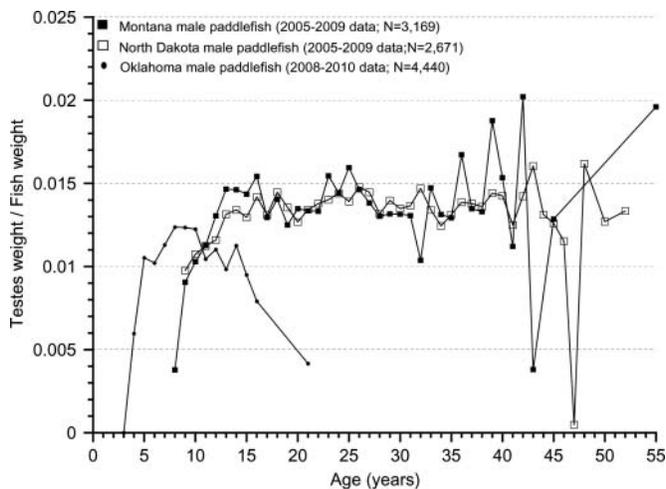
Plate 6 Putative age 11 fish sampled at the RPC in 2010 (female, BL = 1,046 mm, weight = 18.1 kg).

outlined temperature preferences for advanced juvenile and adult paddlefish using the Delphi technique; the optimal temperature range was 12–24°C, with sub-optimal ranges extending from 0°C to about 34°C. Rosen and Hales (1981) identified temperatures of paddlefish habitat as ranging from 0–28°C, with optimal temperatures ranging from 7–20°C. In relation to the optimal temperature range of paddlefish identified by Rosen and Hales (1981), Pensacola Dam water releases from Grand Lake are within the optimal range for 156 days, above the optimal range for 134 days, and below the optimal range for 75 days. Water temperatures do not drop below 4°C at any time during the year (Figure 10A). In contrast, Lake Sakakawea water releases are within the optimal range for 185 days, above the optimal range for 0 days, and below the optimal range by 180 days (Figure 10A). Water temperatures of releases are below 4°C for about 5.5 months per year. Metabolic demands based on surface temperatures are higher; data for Grand Lake and the Missouri River at Williston show the same overall pattern, with maximum temperatures in Grand Lake exceeding 26°C (Figure 10B). Use of Crance's (1987) higher estimated optimal temperature range rather than the lower range of Rosen and Hales (1981) results in fewer periods of high temperature extremes. Total degree days experienced by Grand Lake paddlefish would be higher for each three-month period of the year based on dam discharge data or river and reservoir data (Figures 11A,B). No matter which optimal temperature range is used (7–20°C or 12–24°C), when water temperatures of the reservoirs are outside the optimal temperature range, Grand Lake temperatures are typically super-optimal with greater metabolic

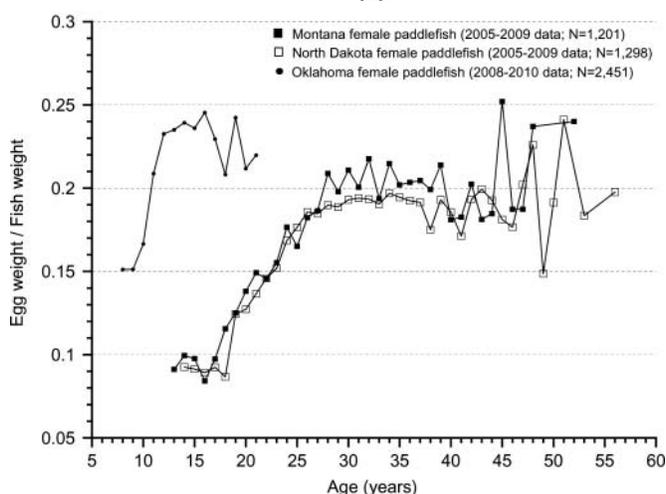
demands, whereas Lake Sakakawea temperatures are typically sub-optimal with less metabolic demands (Figures 10A,B).

Temperature, Metabolic Demand, and Fish Behavior

Observations by the authors in Oklahoma (Grand Lake and the Neosho River), Montana (Yellowstone and Missouri Rivers), and North Dakota (Yellowstone and Missouri rivers in and above Lake Sakakawea) indicate that paddlefish behaviors and their levels of physical activity differ greatly in sub-optimal versus super-optimal temperatures. At low temperatures, movements of actively swimming, freshly gillnetted or snagged paddlefish are much slower (Tomjanovich et al., 1977). Underwater video observations of Yellowstone–Sakakawea paddlefish below Fort Peck Dam in winter, when water temperatures are typically 1–3°C and dissolved oxygen is 6–8 mg/l (U.S. Army Corps of Engineers, 2010), confirms that fish are drifting, slowly drawing water through their nearly closed mouths, rather than more actively swimming (Randy Miller, Williston, ND, personal communication and unpublished video). At these low temperatures, the fish's oxygen demand is lower. Over winter, Yellowstone–Sakakawea paddlefish may benefit from even the modest flows of deep pools in rivers over conditions in reservoirs; numerous fish have been found to overwinter prior to the next year's spawning migration in the Missouri River below its confluence with the Yellowstone (D. Scarnecchia and F. Ryckman, unpublished data). As water temperatures (T) increase, however, a fish's need to obtain more oxygen is associated with more rapid movements and clearly obligatory



(a)



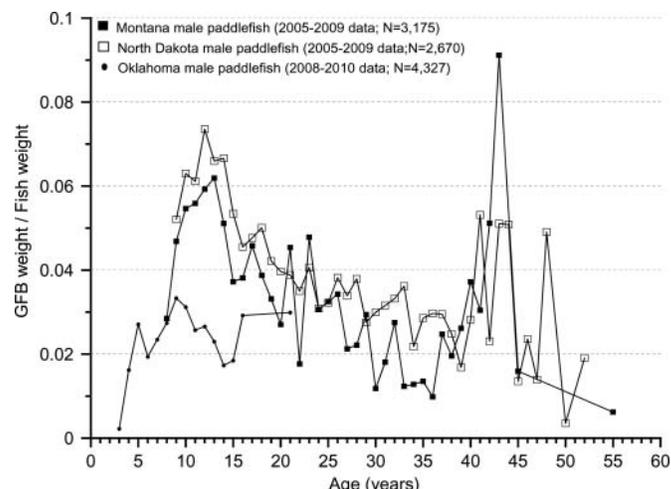
(b)

Figure 8 Median GSI values (gonad weight/fish weight) by age for: (A) male and (B) female paddlefish from Grand Lake stock (2008–2010) and the Yellowstone–Sakakawea stock, Montana and North Dakota harvest components separately (2005–2009).

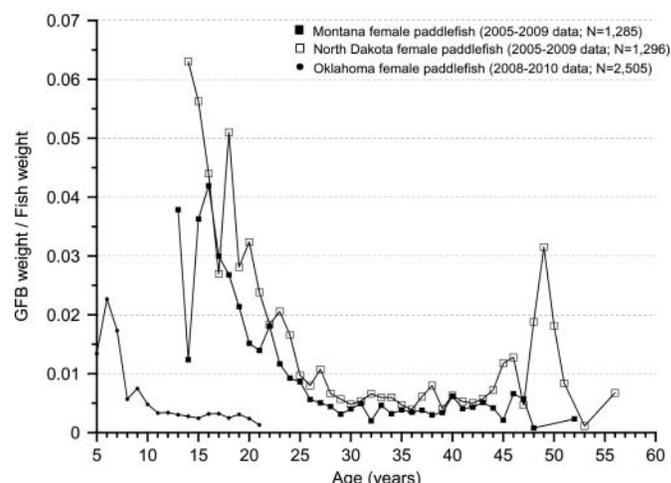
ram ventilation. During the summer growing season, rearing in reservoirs and backwaters, where zooplanktivorous food is more abundant, predominates over river and main channel residency. It was observed that when paddlefish are confined in 20°C water in tanks too small for the fish to actively swim or turn (thus preventing continuous forward movement and ram ventilation), the fish will list after less than a minute, consistent with results of Burggren and Bemis (1992) of obligatory ram ventilation at 22°C. No specific information has been found on the necessity of ram ventilation at water temperatures near freezing.

Metabolic Demand, Energy Allocation, the Cost of Reproduction, and Lifespan

Over the course of a year, fish in Grand Lake would thus be under a much higher metabolic demand than fish in Lake



(a)



(b)

Figure 9 Median GFB weight/fish weight values by age for: (A) male and (B) female paddlefish from Grand Lake stock (2008–2010) and the Yellowstone–Sakakawea stock, Montana and North Dakota harvest components separately (2005–2009).

Sakakawea because of a higher value for T (Figures 10A,B). How this metabolic demand and the associated cost of maintenance compares with the fish's rate of food consumption will strongly influence the size at maturation, the weight adult fish reach, how much accumulation of GFBs (an indicator of energy storage) occurs on average in a given stock, how fast the GFBs and other energy reserves are depleted with successive spawns, how frequently a given fish spawns, how much effort is put into reproduction per event, and lifespan. The differences in metabolic demand thus have important consequences for their entire life histories.

Patterns of weight gains, GSI values, and GFBs provide clues to the role of metabolic demand in affecting life history and lifespan. The accumulation of large GFBs in both stocks is highest per unit fish weight and per gonad weight in young recruits (Figure 9A,B), suggesting that once the fish grow large enough to escape predation (Parken and Scarnecchia, 2002), significant

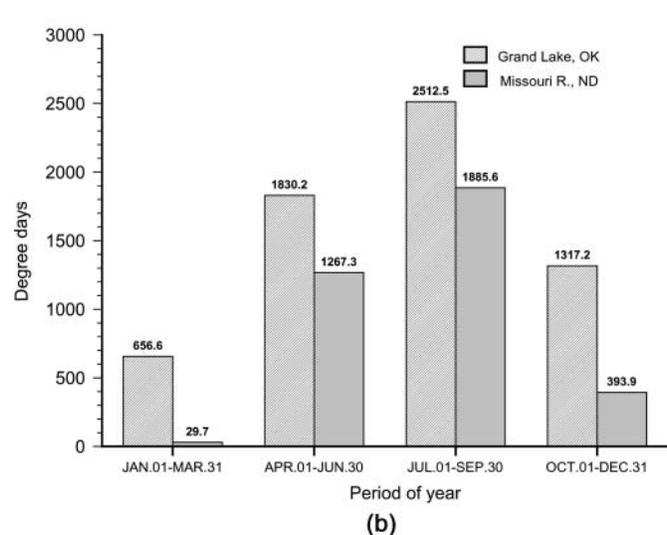
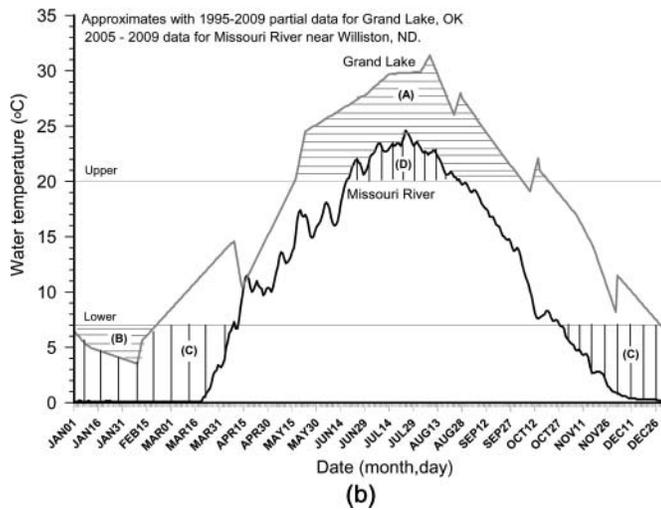
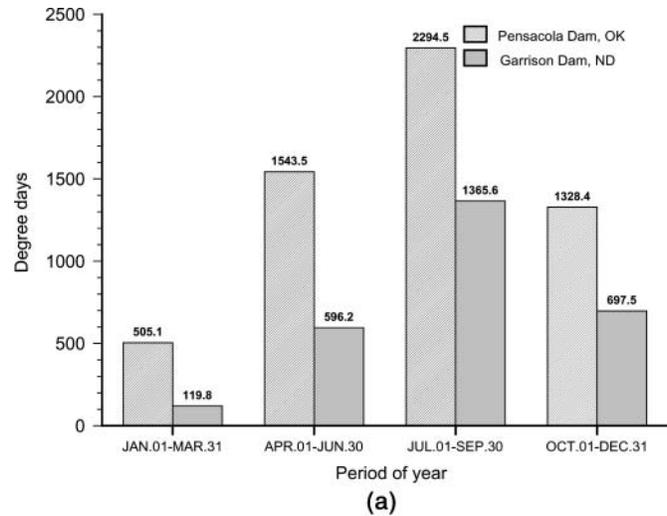
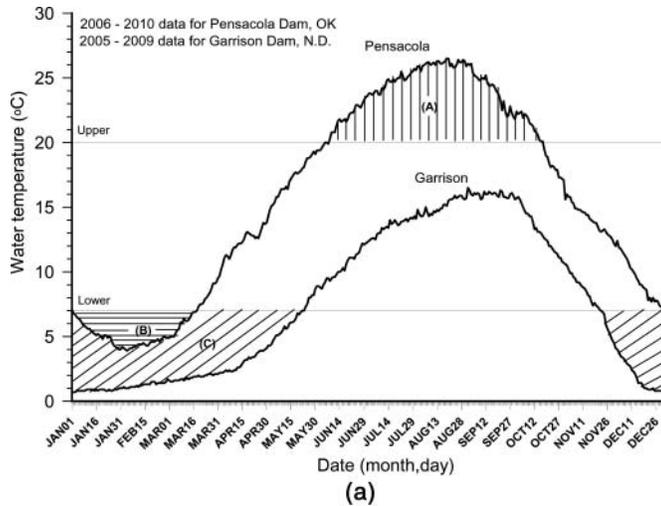


Figure 10 Mean daily water temperatures: (A) water releases from Pensacola Dam (Grand Lake) and Garrison Dam (Lake Sakakawea) and (B) Grand Lake at surface and Missouri River near Williston, ND. Hatching and capital letters indicate where temperatures are above (A) or below (B) the 7–20°C optimal range of Rosen and Hales (1981) for Grand Lake and below (C) or above (D) the optimal range for Lake Sakakawea.

Figure 11 Sum of degree days in three month intervals for: (A) Pensacola Dam (Grand Lake) discharges and Garrison Dam (Lake Sakakawea) discharges and (B) Grand Lake and Missouri River near Williston.

GFB storage becomes an even more adaptive strategy than earlier in life in trophically productive situations where large GFB accumulation is possible. Scarnecchia et al. (2009) showed that both fish weight gain and GFB accumulation were greater in Yellowstone–Sakakawea stock paddlefish during years of higher reservoir levels and associated higher zooplankton abundance in the headwater region of Lake Sakakawea. Lower reservoir levels resulted in lower reservoir productivity, lower zooplankton density, smaller fish at age 9, and smaller GFBs in absolute weight and as a percentage of fish weight. Unpublished data also indicate that Yellowstone–Sakakawea stock fish rearing in the Dredge Cuts, (colder, less productive borrow pits below Fort Peck Dam) remain much smaller throughout life and accumulate smaller GFBs than fish rearing in the main reservoir. Southern stocks can also show great differences in GFB accumulations. Observations by the senior author of paddlefish

weights and GFBs from Table Rock Lake, Missouri, showed larger fish with much larger GFBs than in Grand Lake. The size of fish, size of GFBs, and weight of GFBs per weight of fish are thus closely linked with feeding conditions encountered by the paddlefish, which can be favorable or unfavorable in both northern and southern localities, depending on the ecology and seasonal productivity of rearing habitat.

The storage of lipids, whether in GFBs in paddlefish or other fish species, is widely observed in fishes inhabiting cold water habitats (e.g., Atlantic silverside *Menidia menidia*; Schultz and Conover, 1997), and is seen as having adaptive advantages for use during periods when food supplies are scarce (Thompson et al., 1991). In the Grand Lake stock, however, consistently higher demands for maintenance and somatic growth under existing thermal regime (Figures 10A,B) and the existing ecological conditions prevent GFB weights for males and females from reaching the high values seen in young recruits of the

Yellowstone–Sakakawea stock (Figures 9A,B). In Grand Lake, GFB storage may be more of a luxury, occurring only where available food rations are much higher than typically found over the past decade. With the high abundance of the 1999 year class in Grand Lake, fish density may also play a role in keeping fish weight and GFB accumulation low. This possibility can be evaluated in future years as the abundance of paddlefish fluctuates.

The rate of depletion in GFBs is also linked to metabolic rates. Grand Lake stock females depleted their GFBs more rapidly (from 2% to 0.5% in three years) than Yellowstone–Sakakawea stock fish (the same rate of depletion over seven years; Figure 9b). Depletion of male GFBs by 50% took only 5 years for the Grand Lake stock (ages 9–14), whereas a similar decline took about 12 years for the Yellowstone–Sakakawea stock (Figure 9A).

Some evidence was also found that reproductive investment (Bell, 1980) is higher for fish of the Grand Lake stock than the Yellowstone–Sakakawea stock. The more rapid depletion of GFBs in females than in males is consistent with the higher reproductive investment of females in a given spawning event (Bell, 1980; Jobling et al., 1998). Mean GSI values of prime spawners were higher for the Grand Lake stock (nearly 24%) than the Yellowstone–Sakakawea stock (20–22%), suggesting that more energy is put into fewer spawning events for Grand Lake stock fish (Figure 8B). In Grand Lake, female fish accelerate both their maturation and their spawning effort while storing less GFBs and spawning fewer times. In the Lake Sakakawea stock, female paddlefish exhibit especially long delays in maturation over their male counterparts because of the larger reproductive cost and investment of females relative to males. Yellowstone–Sakakawea stock females will deplete GFBs more slowly, have lower fecundity per unit weight per spawn, and spawn more times over their lifespan. Leggett and Carlscadden (1978) reported a similar occurrence for American shad *Alosa sapidissima*; shad in northern latitudes (New Brunswick) had lower fecundities than those in the St. Johns River, Florida, but had a higher incidence of repeat spawning. For Grand Lake stock fish, higher metabolic demands and the higher investment in eggs per spawn (Figure 8B) suggests that the total annual cost of reproduction (as in Bell, 1980) is much higher than for Yellowstone–Sakakawea stock fish.

Metabolic Limits to Life Histories in Acipenseriformes

The compressed life history for Grand Lake stock paddlefish is similar to that reported for Louisiana paddlefish by Reed et al. (1992), where high natural mortality resulted in maximum ages being less than 15 years. Other southern populations show similarly short lifespans (Paukert and Fisher, 2001). Similar results have been reported for other Acipenseriformes. In an essay on sturgeon life histories, Sulak and Randall (2002) presented evidence to dispel the myth of longevity of several species and stocks of sturgeon. In particular, studies of the Gulf sturgeon *Acipenser oxyrinchus desotoi* clearly indicated that the window

between sexual maturation and death for this, our most southerly Acipenseriform fish, was very narrow, and that “it is highly probable that most females will spawn only 1–2 times before succumbing to natural mortality.” (p. 524). They presented several other examples of a shorter than previously thought lifespan for Acipenseriform species worldwide, the most convincing for stocks from more southerly latitudes. They also noted that Gulf sturgeon and many other Acipenseriform fishes (both northern and southern stocks) feed seasonally, often fasting for long periods each year.

Results of this study on the Grand Lake stock support the conclusions of Sulak and Randall (2002) on lifespan for situations where metabolic demands on Acipenseriformes are high. Paddlefish and other Acipenseriformes, fossil and living, are essentially north temperate fishes and absent from tropical rivers. Bemis and Kynard (1997) suggested that “the absence of Acipenseriformes from tropical rivers is probably related to thermal requirements for maturation and early development.” (p. 169). A review of Acipenseriformes suggests that nearly all species reach a large size (past various threshold sizes to avoid predation), and those species that remain smaller are often highly armored (e.g., shovelnose sturgeon *Scaphirhynchus platorynchus*). The window between the time when fish are large enough to survive to reach maturation and when metabolic demands lead to high natural mortality becomes narrower as their southern distribution limit is approached. During prime reproduction, GFBs are typically nearly depleted in female fish of both stocks in favor of a large number of eggs in the body cavity; the depletion of energy reserves and other physiological changes associated with aging (Sohal and Allen, 1986) may present more problems to paddlefish in areas where metabolic rates are higher. The smaller GFBs and greater rates of GFB depletion in Grand Lake stock fish can be attributed to higher costs of both maintenance and reproduction. Life-cycle compression and a shortened lifespan result. For Grand Lake stock paddlefish, metabolism is high, life is fast, and death comes young compared to their conspecifics on the Northern Plains. Similar results have been found for other fish taxa (e.g., *Lepomis gibbosus*; Dembski et al., 2006). Comparative life history analyses among Acipenseriformes beyond the Gulf sturgeon (Sulak and Randall, 2002) might benefit from similar analyses as conducted in this article. In species where GFBs are less conspicuous, lipid analysis of other parts of the fish may prove useful.

Conservation and Management Implications

Results of this study have several specific conservation and management implications for paddlefish.

Harvest Management

In Grand Lake, 2004, the strong 1999 year class could be easily seen in the harvest as large numbers of age 5 fish, mostly males (Figure 2). As of 2010, there is some indication that

age 6 males may be beginning to recruit to the fishery (Figure 2; Plate 4), but no subsequent high peak in numbers of young fish is obvious (Figure 2), suggesting that recruitment from years 2000–2005 is not strong. Given the short lifespan of these fish (typically < 20 years), it is imperative that significant recruitment of new year classes occurs within the next three to four years. Annual harvest of the strong 1999 year class must be apportioned out until another strong year class is produced.

Harvest management for the Grand Lake stock must be designed to deal with a comparatively short lifespan and highly variable recruitment. A strong year classes in Grand Lake does not provide as long term of a buffer against overharvest as in the Yellowstone–Sakakawea, with its much longer prime reproductive lifespan. In the Yellowstone–Sakakawea stock, recruited fish can be counted on for harvest and for spawning for two or more decades as long as harvest rates are kept low. In the Grand Lake stock, the earlier, more sudden natural death of fish after age 15 suggests that less benefit will result from delaying harvest. Optimal harvest management strategies will thus be different for paddlefish stocks in the northern and southern latitudes.

The much less extreme differences in age at recruitment between the sexes for the Grand Lake stock (2–3 years; Figure 2) compared to the Yellowstone–Sakakawea stock (7–10 years) has major significance for run size forecasting. For run size forecasting of females of a brood year to a river fishery based on male recruits (Scarnecchia et al., 2008), the Yellowstone–Sakakawea stock gives managers a 7–10 year lead time; for the Grand Lake stock, managers have only a 2–3 year lead time. This difference requires a more rapidly responsive harvest management of the Grand Lake stock.

As of 2010, the comparatively small fish in the Grand Lake stock relative to the Yellowstone–Sakakawea stock results in less sexual size dimorphism (Figure 3A,B) and provides less incentive to high-grade to larger (typically female) fish (for flesh or angler status). Whereas high-grading to larger females is prohibited by regulation for Yellowstone–Sakakawea stock fish, such a regulation may be less critical for the Grand Lake stock.

From analysis of the data, it is predicted that over the period from 2011–2015, the strong 1999 year class (Figure 2) will rapidly decline in numbers and, by 2015, will experience high natural mortality as most fish that are not harvested will have lived out their natural lifespans. Future monitoring of the strong 1999 year class in the next decade will clarify if this conclusion is accurate and how much the near absence of older fish (> 15 years) is a result of harvest. Several studies at mid-latitudes of the paddlefish's range have reported what they believed to be truncated age distributions associated with high harvest rates (Watts Bar Reservoir, Tennessee: Alexander et al., 1985; Kentucky Lake: Hoffnagle and Timmons, 1989, Timmons and Hughbanks, 2000). Such harvest may exacerbate the natural life history compression of southern stocks such as observed in this study.

Paddlefish Growth and Stock Size

Results of this study confirm the small size and slow growth of fish in the Grand Lake stock compared to historical sizes documented (Ambler, 1987) for Grand Lake and other Oklahoma paddlefish (Houser and Bross, 1959). As of 2010, few fish of either sex exceeded 25 kg. An assessment of the very limited historical records from Grand Lake indicates that fish in past years have often reached weights twice that of the typical fish caught in 2008–2010. It is not yet known whether the fish caught in 2008–2010 are small because of changes in specific environmental factors or some density-dependent growth, perhaps associated with the very strong year class in 1999 (Figure 2). The role of density in affecting size and maturation period of Grand Lake stock paddlefish will be clarified in future years as more data on growth rates and stock size become available. The potential for non-native Asian carps, which have entered Grand Lake, also deserves monitoring because of potential effects on paddlefish food supply (Schrank et al., 2003).

Paddlefish Life History and Climate Change

Most specific effects of climate change on paddlefish, other fish species, and myriad aspects of their habitats are difficult to forecast, so the assessment is restricted to effects on general life history and lifespan outlined in this article. If climate warms in the Northern Plains and elsewhere throughout the species range, both the more protracted Yellowstone–Sakakawea stock life history and the more compressed Grand Lake stock life history can be expected to become even more compressed. Similar trends might also be anticipated for other paddlefish stocks, other Acipenseriform species, and other fish taxa. Such compression may present fewer problems for the Yellowstone–Sakakawea stock, which, provided other habitat conditions (including river discharge and turbidity) permit it, would shift toward a life history more similar to that of more productive mid-latitude stocks. However, strong year classes would have to become much more frequent than they are at present. As of 2010, the 1995 year class is dominating the population and the harvest (Scarnecchia et al., 2009), and recruitment of subsequent year classes is thought to be poor. For the Grand Lake stock, higher metabolic demands as the fish experience even warmer waters has the potential to push the species' life history flexibility to its limits, close to where the Gulf sturgeon now exists (Sulak and Randall, 2001). Depending on the extent of warming and available food supplies, energy demands for maintenance and growth may so compress the life history that at first the fishery, then the life history itself, becomes non-viable.

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