Received: 31 December 2016 | Accepted: 20 September 2017

DOI: 10.1111/jai.13580

STURGEON PAPER

WILEY Journal of Applied Ichthyology DWK

Lipid acquisition and retention in tissues of spawning adult paddlefish *Polyodon spathula* (Walbaum, 1792) in relation to extended and compressed life history patterns in two river-reservoir systems

R. J. Hemingway[1] | **D. L. Scarnecchia**[2]

[1]Western Fisheries Research Center, Columbia River Research Laboratory, Cook, WA, USA

[2]Department of Fish and Wildlife Sciences, University of Idaho, Moscow, ID, USA

Correspondence
R. J. Hemingway, Western Fisheries Research Center, Columbia River Research Laboratory, Cook, WA, USA.
Email: rhemingway@usgs.gov

Funding information
Montana Fish Wildlife and Parks; Oklahoma Department of Wildlife Conservation

Summary

Data from recreationally caught adult paddlefish from North Dakota and Oklahoma, USA, was used in an initial attempt to explain variation in lipid content in adult wild paddlefish *Polyodon spathula* (Walbaum, 1792) by stock and by sex. The objectives of this study were to describe the relative importance of three distinct paddlefish tissues [white muscle, red muscle, and gonadal fat body (GFB)] for lipid storage, and compare lipid content of these tissues between stock and sex. It was hypothesized that lipid content of the three tissue types would be related to each other within individual fish; and that, consistent with previously documented life history differences, lipid concentrations for all tissues would be sex- and stock-specific. Paddlefish were sampled in April and May 2012 from the Grand Lake, Oklahoma, USA (GL) and Yellowstone-Sakakawea, North Dakota (SAK) stocks. Three tissue types were collected from SAK fish, including white muscle (N = 137; 83M, 54F), red muscle (N = 74; 36M, 38F), and GFB (N = 164; 105M, 59F). Samples from GL fish included white muscle (N = 60; 36M, 24F), and GFB (N = 42; 41M, 1F). Proximate analysis was used to quantify the percentage of lipid, water, ash, and protein in tissue samples. The lipid component of proximate analysis was completed using the ANKOM method of lipid extraction which uses heated petroleum ether to extract lipid. Also investigated were lipid accumulation and storage in adult paddlefish in relation to tissue type: white muscle, red muscle, gonadal fat bodies (GFB) within individual fish, between the sexes, and between the two different stocks. White muscle was significantly correlated with both red muscle and GFB lipid, but red muscle lipid was not significantly correlated with GFB lipid. White muscle lipid content differed by stock and sex, with the more northerly stock having higher lipid content than the more southerly stock. Females had higher white muscle lipid content (SAK F = 17.18, M = 9.09; GL F = 6.74, M = 4.99) and red muscle (SAK F = 47.72, M = 30.93) than males. In contrast, GFB lipid differed by sex but not stock, with females having lower lipid content (SAK = 79.79, GL = 89.08) than males (SAK = 89.08; GL = 91.72). Life history differences, growing season, and the role of metabolism may help explain the differences in concentrations of lipids observed between stocks and between the sexes for all three tissues. It was

hypothesized that different tissues may be used for different metabolic processes and that although metabolism likely strongly influences muscle tissue lipid, GFB lipid is probably linked more closely to reproductive demands associated with gonad development.

1 | INTRODUCTION

Understanding energy allocation in paddlefish *Polyodon spathula* (Walbaum, 1792) requires consideration of species life history as well as life history differences among and within individual stocks. Among stocks, paddlefish show substantial variation in life history aspects such as growth, age at maturity, and lifespan between populations that are geographically separated or occupy distinctly different habitats (Jennings & Zigler, 2009; Russell, 1986; Scarnecchia et al., 2011). Within stocks, paddlefish are sexually dimorphic, with females exhibiting a greater weight than males, later age at sexual maturity, and often a longer period of gonadal recrudescence (i.e. more time between successive spawns; Scarnecchia et al., 2007). Long term monitoring of stage specific energy density (Wuenschel, Jugovich, & Hare, 2006) in paddlefish may help describe effects of stored energy on life history events. Because energy allocation strategies in juvenile paddlefish may be fundamentally different from those of adults and by sex, (Scarnecchia et al., 2011; Wuenschel et al., 2006), energy density must be described in terms of sex and life-stage.

Five stages of paddlefish life history were identified by Scarnecchia et al. (2007) in a stock inhabiting the Yellowstone River and Lake Sakakawea, Montana and North Dakota: (i) immature, (ii) maturing, (iii) adult- somatic growth and reproduction, (iv) prime reproduction, and (v) senescence to death:

> *"The five periods … occur at different ages for each sex …. 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. In the fourth, reproductive periodicity is typically close to two years for males and three years for female; the rate of gonadal recrudescence is at its maximum. Fish make shorter pre-spawning migrations upriver. In the fifth period (senescence to death), GSI (Gonadosomatic Index) of some of the oldest females decreases; the oldest males have fewer energy reserves and are long and lean." (p. 211)*

The duration of these life stages is more compressed in paddlefish from more southern localities (e.g. Oklahoma) where total lifespan may be 20–25 years than farther north (e.g. Montana and North Dakota), where the lifespan may be 50–60 years (Scarnecchia et al., 2007, 2011). The shorter lifespans were in this case associated with higher metabolic demands and smaller accumulations of perigonadal fat in the more southerly stock (Scarnecchia et al., 2011). The accumulation of perigonadal fat tissue in spawning adult paddlefish was identified and described by Scarnecchia et al. (2007), who labeled the resulting tissue masses gonadal fat bodies (GFBs). Females also deplete their GFBs more rapidly than males, associated with the higher costs of reproduction (Scarnecchia et al., 2007, 2011). Knowledge of the way in which energy is utilized throughout each of the life history phases of paddlefish would be helpful in their conservation.

As a cruising zooplantivore and a ram ventilator (Burggren & Bemis, 1992), paddlefish have white muscle tissue and a considerable amount of red muscle (Decker, Crum, Mims, & Tidwell, 1991; Lou et al., 2000) outside of the white muscle core, next to the integument (D. Scarnecchia, Personal observation). Studies cited by Ackman (1980) indicated that red muscle in other fish species can have up to five times the lipids of white muscle. Paddlefish from different locations, different life stages, sexes, and different opportunities for growth are thus likely to exhibit different strategies for energy allocation. They may also store lipids differently by tissue type.

The Yellowstone-Sakakawea stock of North Dakota and Montana (hereafter SAK), and the Grand Lake stock of Oklahoma (hereafter GL) are widely separated geographically and exhibit the aforementioned life history differences such as age at maturity, lifespan, spawning periodicity, and timing of the five periods of life history (Scarnecchia et al., 2007, 2011). Investigations of lipid by stock, sex, and tissue types (white muscle, red muscle, and gonadal fat body (Scarnecchia et al., 2007) between these two widely separated populations may provide insight into factors that favor life history traits in paddlefish under markedly different environmental conditions and projected environmental changes.

This study uses data from recreationally-caught adult fish in an initial attempt to explain variation in lipid content in male and female paddlefish by stock and by sex. The objectives of this study were to (i) describe the relative importance of three distinct paddlefish tissues (white muscle, red muscle, and GFB) for lipid storage, (ii) compare lipid content of these tissues between stocks. Hypotheses were that the lipid content of the three tissue types would be related to each other within individual fish, and that, consistent with results of Scarnecchia et al. (2007, 2011) of life history differences among stocks, lipid concentrations for all tissues would be sex and stock specific.

2 | MATERIALS AND METHODS

2.1 | Data collection

Samples of white muscle, red muscle, and GFBs were collected during 2012 from adult fish harvested (snagged) by recreational fishermen (N = 213, Age Range = 9–52). Because the fisheries capture almost

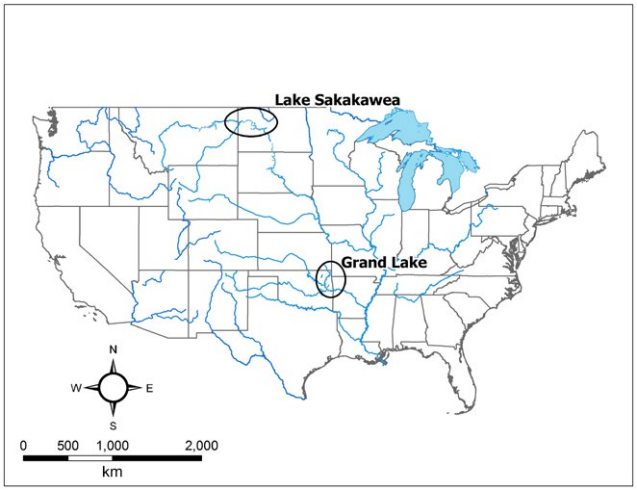

FIGURE 1 Locations of paddlefish, *Polyodon spathula*, used in this study

exclusively adult migratory pre-spawning fish, and not all paddlefish spawn every year, at least in northern stocks (Scarnecchia et al., 2007), only the migratory portion of the adult population was evaluated, and not those fish between spawns remaining in reservoirs. Fish from the SAK stock were sampled for tissue at the fish -cleaning station at the confluence of the Missouri and Yellowstone rivers during May 2012 (Scarnecchia, Ryckman L. F., Wiedenheft S. G. W., & Lim, 2008) (Figure 1). Fish from the GL stock were sampled for tissues at the Paddlefish Research Center associated with the Neosho River and Grand Lake, near Miami, Oklahoma, during April 2012 (Figure 1). These collection times corresponded with the annual upriver spawning migrations for the respective populations. Samples were promptly frozen and transported on ice to freezers (−20°C) at the University of Idaho.

2.2 | Laboratory processing and analysis

In preparation for proximate analysis, frozen tissues of the three types (white muscle, red muscle, and GFB) were homogenized for 30–60 s with a NINJA™ blender, sealed in a centrifuge tube, and stored in a freezer until transport to Hagerman, Idaho. Tissue samples underwent proximate analysis at the University of Idaho, Moscow, and the Fish Culture Experiment Station in Hagerman, Idaho. This procedure separates tissue into four components: lipid, water, ash, and protein. Lipid and water were determined using ANKOM method 5-04 (AOCS 2005). Lipid content of homogenized adult tissues was assessed in duplicate using the ANKOM method (AOCS, 2005). The ANKOM method uses a solvent (heated petroleum ether) to extract lipid, and utilizes gravimetric loss to determine lipid content. In addition to extracting triacylgylcerols (TAGs), which are the primary component of stored energy (Adams, 1999), it most likely also extracts an insignificant fraction of structural lipids (Tocher, 2003). ANKOM is an indirect method that removes and combines the lipid fraction of multiple samples, therefore the remaining lipid fraction was unsuitable for further analysis. Ashing was completed in Moscow using AOAC method 938.08 (AOAC, 2000). Protein was estimated by subtraction (Hendry, Dittman, & Hardy, 2000). All procedures associated with proximate analysis included a control sample of homogenized pet food to evaluate homogeneity of run cycles.

2.3 | Statistical analysis

A non-parametric Kruskal–Wallis test was applied to lipid values, given that they were non-normally distributed for each tissue type via a one-way ANOVA, with a *post hoc* Tukey-Kramer test to identify differences in means due to stock and sex. A Wilcoxon test was used for comparisons for which there were only two groups. We used linear regression to examine relationships between white muscle, red muscle and GFB lipids of individual fish. The program SAS 9.3 (SAS Institute, 2011) was used for all statistical analyses, and all analyses were evaluated for significance at $\alpha = .05$.

3 | RESULTS

White muscle tissue was collected immediately behind the head from 197 fish: 54 females and 83 males from SAK, and 24 females and 36 males from GL. Red muscle was sampled from 38 females and 36 males from the SAK stock only from the outer portion of the fillets by using a fillet knife during fish processing. Samples of GFB tissue were collected during existing GFB collection protocols (Scarnecchia et al., 2007). GFBs were collected from 206 fish: 59 females and 105 males from the SAK stock, and 41 males from the GL stock. Female fish from the GL stock were of nearly uniform age and were primarily prime spawners (Scarnecchia et al., 2007) with too little GFB material for use, thus sample size for GL females was only one fish. Sample sizes and age ranges are given in Table 1. Because some tissues contained up to approximately 90% water, at least 50 g of tissue per sample were collected to ensure an adequately dry sample. Relative percent differences (mean ± SE) for tissue duplicates were calculated for white muscle (1.56 ± 0.11), red muscle (2.93 ± 0.34) and GFB (1.55 ± 0.12). Inter-assay coefficient of variation was .06 for lipid extraction.

3.1 | Proximate analysis

White muscle lipid concentration was the lowest of the three tissues, with GL fish ranging from 4.99% to 6.74%, and SAK fish ranging from 9.09% to 17.18%. Red muscle lipid was higher, with SAK values ranging from 30.93% to 47.72%. Highest lipid concentrations were found in GFBs, with SAK fish ranging from 79.79% to 89.08%, and GL fish ranging from 91.72% to 92.17% (Table 1). All proximate analysis data, including lipid, water, ash, and protein are presented in Table 1.

3.2 | White muscle

Significant relationships were found between lipid values in some of the tissue types in individual fish. There was a significant positive relationship between SAK white muscle lipid and red muscle lipid in individual fish ($R^2 = .40$, df = 66, $p < .001$) (Figure 2). In contrast, there

TABLE 1 Proximate composition (mean % ± SD) of all tissues of 2012 spawning Lake Sakakawea, North Dakota, USA (SAK) and Grand Lake, Oklahoma, USA (GL) paddlefish, *Polyodon spathula*. Groups categorized by stock, sex (M, F, in parentheses), and tissue [WM (white muscle), RM red muscle, and GFB (gonadal fat body)]

Group	*N*	Age	Lipid %	Water %	Ash %	Protein %
SAK (F) WM	54	17–52	17.18 (6.67)	6.49 (0.53)	0.014 (0.005)	76.31 (6.24)
SAK (M) WM	83	14–42	9.09 (4.29)	7.1 (0.35)	0.015 (0.005)	83.78 (3.98)
GL (F) WM	24	13–16	6.74 (2.74)	7.36 (0.27)	0.017 (0.005)	85.86 (2.51)
GL (M) WM	36	9–16	4.99 (1.59)	7.29 (0.17)	0.020 (0.005)	87.69 (1.47)
SAK (F) RM	38	17–45	47.72 (10.19)	4.06 (0.78)	0.044 (.101)	48.20 (9.39)
SAK (M) RM	36	14–42	30.93 (8.54)	5.37 (0.68)	0.065 (.146)	63.39 (7.86)
SAK (F) GFB	59	17–52	79.79 (11.8)	1.66 (1.0)	0.002 (0.001)	18.54 (10.8)
SAK (M) GFB	105	14–42	89.08 (6.6)	0.87 (0.5)	0.001 (0.001)	10.04 (6.11)
GL (F) GFB	1	13	92.17 (na)	0.58 (na)	0.001 (na)	7.25 (na)
GL (M) GFB	41	9–16	91.72 (2.4)	0.61 (0.19)	0.001 (0.008)	7.67 (2.22)

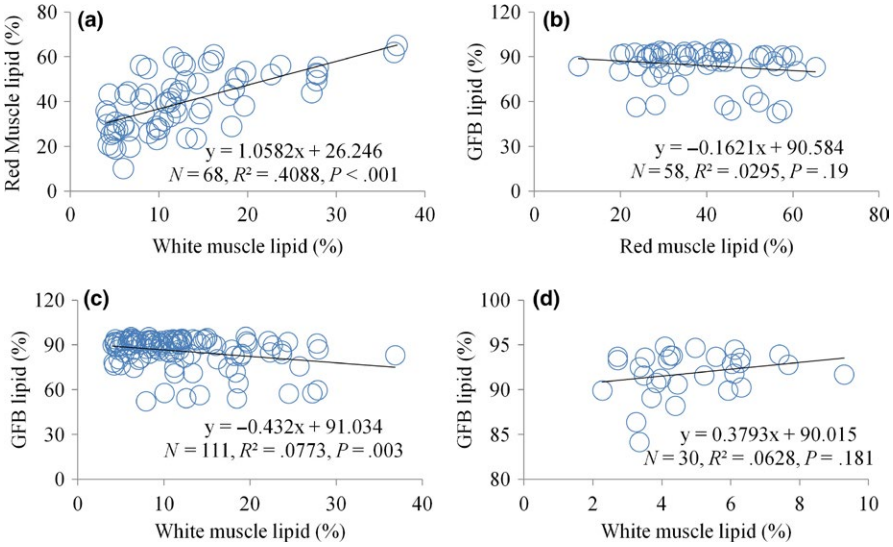

FIGURE 2 Relationships between tissue lipids (% wet weight) within individual 2012 adult Lake Sakakawea, North Dakota, USA (SAK) and Grand Lake, Oklahoma, USA (GL) male and female paddlefish of all size classes sampled. Tissues are white muscle, red muscle and gonadal fat body (GFB). Panel a,b, and c are SAK, and d is GL

was a negative relationship between white muscle lipid and GFB lipid for SAK fish (R^2 = .07, df = 109, p < .003), but not for GL fish (R^2 = .06, df = 28, p = .181), and no trend between SAK red muscle lipid and GFB lipid (R^2 = .02, df = 56, p = .19) (Figure 2). Red muscle comparisons were limited to SAK fish.

Lipid values differed significantly by both location and sex (Kruskal–Wallis test, p < .001). The GL fish had significantly lower levels of white muscle lipid than SAK fish, and female fish from both stocks had significantly higher white muscle lipid than males (Figure 3).

3.3 | Red muscle

Lipid values for SAK red muscle differed significantly by sex (Wilcoxon test, p < .001). Among SAK fish, females had significantly higher red muscle lipids than males (Figure 4).

3.4 | GFB

Lipid values of GFBs in SAK fish were significantly different by sex (Kruskal–Wallis test, p < .0001). Among SAK fish, males had significantly higher GFB lipids than females (Figure 5). GFB lipid values of males did not differ by stock (Wilcoxon test, p < .07).

4 | DISCUSSION

An important outcome of the current study is the establishment of reference data for lipid content in wild paddlefish tissues. Proximate results for white muscle lipid (4.99%–17.18%) were much higher than the few other results reported in the literature for hatchery-reared fish, which ranged from 0.27% in the white muscle (Decker et al., 1991) to 3.96 in the whole fillet (Simeanu, Simeanu, & Pasarin, 2012). The lower reported values in those studies were more likely due to differences in age and geographical origin of the paddlefish used. Regarding age, Decker et al. (1991) reported results for 17-month-old fish, and Simeanu et al. (2012) reported results for paddlefish ages 0–3. Their results are comparable to the lipid concentrations we found (0.85%–5.51%) using juvenile paddlefish of similar ages (0 and 1) (Hemingway & Scarnecchia, 2016). The higher white muscle lipid values observed in larger, adult fish are consistent with other sturgeon

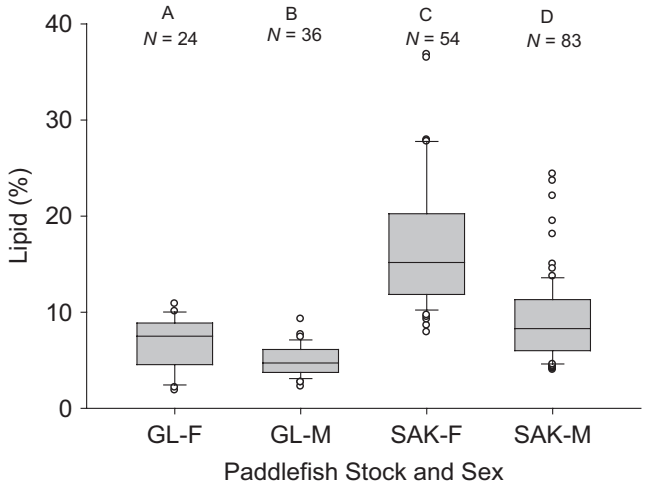

FIGURE 3 Box plot distribution of lipids (%) in 2012 adult Grand Lake, Oklahoma USA (GL) and Lake Sakakawea, North Dakota, USA (SAK) paddlefish white muscle including median (line), interquartile range (box), outliers, and minimum and maximum values. The four groups represented are Grand Lake female (GL-F), Grand Lake male (GL-M)), Sakakawea female (SAK-F), and Sakakawea male (SAK-M) (Kruskal–Wallis test, $p < .001$). Differences significant at $\alpha = .05$ (Tukey-Kramer test) are indicated by different letters

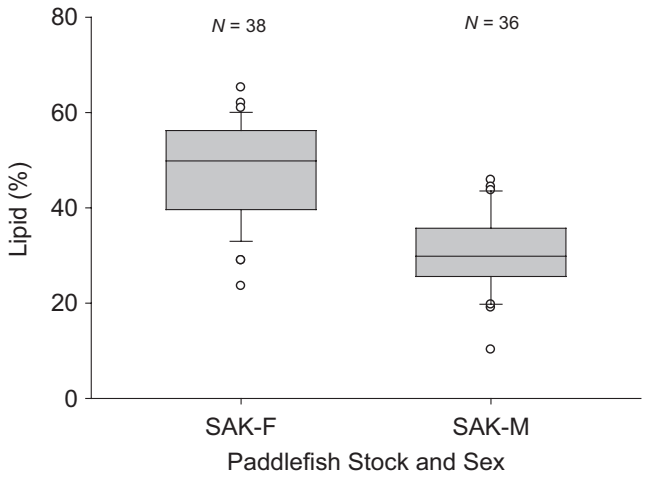

FIGURE 4 Box plot distribution of lipids (%) values for red muscle tissue from 2012 adult Lake Sakakawea, North Dakota, USA (SAK) male and female paddlefish (including median (line), interquartile range (box), outliers, and minimum and maximum values). Groups represented are Sakakawea female (SAK-F), and Sakakawea male (SAK-M), (Wilcoxon test, $p < .001$)

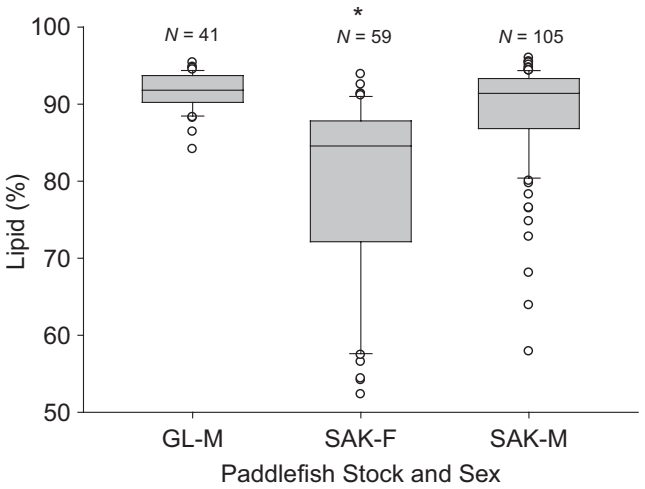

FIGURE 5 Box plot distribution of lipid (%) (including median (line), interquartile range (box), outliers, and minimum and maximum values) in Gonadal Fat Body (GFB) tissue of 2012 Grand Lake, Oklahoma, USA (GL) and Lake Sakakawea, North Dakota, USA (SAK) adult male and female paddlefish. The three groups represented are GL male (GL-M), SAK female (SAK-F), and SAK male (SAK-M), (Kruskal–Wallis test, $p < .001$). Differences significant at $\alpha = .05$ (Tukey-Kramer test) are indicated by *

species (Lebreton & Beamish, 2004). The overall pattern is consistent with the hypothesis that lipid accumulation increases, once fish pass life stages where growth in length and apparent length (as indicated by a long rostrum relative to total length) are vital to escape predation. Lipids can then be useful in preparation for reproduction and related activities.

Proximate results for SAK female red muscle lipid obtained in this study (47.72%) were higher as than those reported by Gundersen and Pearson (1992) in commercially harvested female paddlefish in the Ohio River (22%). However, those fish had white muscle lipid at levels comparable to GL fish used in this study (Ohio 3.2%, GL 4.99%). Decker et al. (1991) reported slight differences between whole fillet and white muscle, and cited Ackman (1980) for red muscle values in other species, which were up to five times the value of white muscle. Therefore, our results regarding the much higher lipid content of red muscle are consistent with other studies. Our proximate lipid results for GFBs were on the high end of those reported by Scarnecchia et al. (2007), where the lower values reported for older fish probably reflected lipid content of collagen-based connective tissue remaining from depleted GFBs; the tissue in the Scarnecchia et al. (2007) study was not specifically excluded from proximate analysis.

The results for adults are also consistent with the idea that geographical location of a stock as it relates to growing season may influence lipid concentrations. Life history adaptations of fish to temperate climates may help explain the higher white muscle lipid content observed in SAK fish than in GL fish. Lou et al. (2000) reported a range of white muscle lipid of approx. 1%–9% for sub-adult and adult fish from Kentucky, with results comparable to those we obtained from GL adults in Oklahoma. In contrast, lipids were significantly higher in the more northerly SAK stock (9.09%–17.18%) (Table 1).

Although effects of fish density cannot be ruled out in explaining the muscle lipid differences between the two stocks, the role of the metabolism should not be overlooked. This is particularly compelling, considering results of investigations in the factors that determine the metabolic rate in paddlefish. Body size, rather than temperature, was the primary factor affecting paddlefish metabolism (Patterson, Mims, & Wright, 2013). Scarnecchia et al. (2007) characterized the size differences of the two stocks in their study and suggested that fish from SAK are larger and have lower metabolic rates than those from GL.

The smaller GL fish have a higher metabolic rate, which demands more energy, leaving less available for storage. It is likely that higher lipids in northerly areas with shorter growing seasons may aid fish maintenance during periods of lower food availability (Scarnecchia et al., 2009). The SAK fish are also subjected to longer periods of low water temperatures (Scarnecchia et al., 2007, 2011) and lower food availability during winter, which is longer and more severe than that experienced by GL fish. In most fishes, white muscle lipid is a good surrogate of whole body lipid (Buckley & Bulow, 1987; Bulow, 1971), thus our results support the idea that environmental factors such as latitude and climate affect lipid storage in paddlefish. Latitudinal differences in growth and condition have been detected in lake sturgeon *Acipenser fulvescens*, (Power & McKinley, 1997), in addition to seasonal variation in lipid content, with the lower lipid values following winter (Beamish, Jebbink, Rossiter, & Noakes, 1996).

Another possible specific mechanism that may explain the relationship between lipid storage and environmental factors relates to the specifics of diet. The primary storage lipid in fish is triacylglycerols (TAGS), which form a specific class of fatty acids that most fishes cannot manufacture (Adams, 1999), but must acquire through their diet (Olsen, 1999). Diets of SAK fish are likely higher in TAGs than that of GL fish, because many zooplankton species in colder climates are richer in TAGS than those in warmer climates (Tocher, 2003).

Life history differences and the role of metabolism may also help explain the differences in concentrations of lipid in females and males that were observed for all three tissues. If higher muscle lipid in females reflects higher overall body lipid, it is likely beneficial for female fish (which are larger than males at age) to store more lipid. Female fish likely have a higher initial reproductive investment than males because of the volume and size of the eggs they produce (Tocher, 2003). Higher lipid levels may help meet the energy demands of producing energy-rich eggs during periods of low food availability. Female paddlefish GSIs are much higher than those of males (Scarnecchia et al., 2007), therefore it is likely that the energy invested in gametes by males is not energetically commensurate with the level of parental investment of the female fish. In addition, the energy that males expend in migration is lost to the fish, whereas in females the majority of invested energy is transferred to the ovaries, with little net whole-body energy loss to the fish until egg deposition. Medford and Mackay (1978) found that mature ovaries in northern pike *Esox lucius* (Linnaeus, 1758) contained more than 10 times the amount of lipid as did mature testes. Large differences in gonad lipid might be reflected by muscle lipids. Sutharshiny, Sivashanthini, and Thulasitha (2013) observed greater increases and decreases in muscle lipids in the female double spotted queenfish *Scomberoides lysan* (Forsskål, 1775) than in their male counterparts just prior to and after spawning.

The energetic demands associated with ram ventilation may help explain observed differences in red muscle lipid between males and females. Because its primary energy source is lipid, and its higher aerobic capacity, red muscle is an important asset for the persistent swimming that a ram-ventilator requires (Sen, 2005). This demand for constant movement may be more energetically costly for larger female fish, which respond by storing more lipid in red muscle. Alternately, at the time that we sampled, males may have expended more of their smaller depot of red muscle energy in migration, because they mature younger (Scarnecchia, Stewart, & Power, 1996), spawn more often (Scarnecchia et al., 2007), and may typically migrate earlier in the season (D. Scarnecchia, Unpublished data).

The temporal aspect of reproductive demands may help explain lower lipids in female GFBs, which may be due to the longer duration of physiological demands associated with reproduction. The theory of natural selection suggests that while overall reproductive energy expenditure in male and female organisms is similar, the investment of that energy is directed into different pathways, with females investing more in gamete production and males investing more in reproductive behavior (Fisher, 1930). If this is the case for paddlefish, the primary energy expenditure of the female fish is likely to be due to the physiological demand of gamete production, in which oocytes are maturing all winter; while in males, the primary expenditure is likely behavioral and condensed into the migration period, which is experienced over a shorter time period in early spring.

Specificity of tissue storage and depletion pathways is another possible explanation for the higher observed GFB lipid values in males than in females. Paddlefish may use lipid from muscle differently than from GFBs. Female bluefin tuna *Thunnus thynnus* (Storer, 1855) utilize lipids from the mesenteric perigonadal fat (the tuna equivalent of paddlefish GFBs) for gamete development, and energy from muscle for locomotion (Mourente, Megina, & Diaz-Salvago, 2002); this pattern is also plausible for the paddlefish, another ram ventilator. McPherson, Slotte, Kvamme, Meier, and Marshall (2011) found evidence for differentiated storage and depletion pathways in muscle vs. mesenteric fat in Atlantic herring *Clupea hurengus* (Linnaeus, 1761). The idea of specific pathways gains support from the different responses of muscle and GFB lipids in individual fish in this study. These observations suggest that lipid in different tissues may be used for different purposes. This study builds upon previous ideas in the literature regarding paddlefish lipid. Scarnecchia et al. (2007) suggested that lipid content was driven by metabolic differences between the SAK and GL stocks. However, the negative relationship between white muscle and GFB lipid in individual fish suggests that although size-induced metabolic rate may be the primary factor in muscle lipid, it may not be the primary driver for GFB lipid. The relationship between tissue-specific lipid content and different metabolic demands in paddlefish is an area deserving further study.

5 | ACKNOWLEGEMENTS

We thank L. Breen, C. Nagel, F. Ryckman, and S. Shefsted for help with fieldwork and data collection. Special thanks are extended to C. J. Reeves, C. Dekker, A. Vincent, and W. Schrader and H. Hemingway for lab and other assistance. C. Hoffman of the University of Idaho Fish Culture Experiment Station assisted with lab procedures and equipment. D. Graden, C. Moffitt, and B. Dennis provided valuable comments. Funding was provided by Montana Fish Wildlife and Parks, Helena, Montana, USA, with logistical support from Oklahoma Department of Wildlife Conservation.

REFERENCES

Ackman, R. G. (1980). Fish lipids I. In J. J. Connell (Ed.), *Advances in fish science and technology* (pp. 87–103). Farnham, United Kingdom: Fishing News Books.

Adams, S. M. (1999). Ecological role of lipids in the health and success of fish populations. In M. T. Arts, & B. C. Wainman (Eds.), *Lipids in freshwater ecosystems* (pp. 133–160). New York: Springer-Verlag.

AOAC (2000). *Official methods of analysis of AOAC international*, 17th ed. Gaithersburg, Maryland, USA: Association of Official Analytical Chemists.

AOCS (2005). *Official methods and recommended practices of the AOCS*, 6th ed. Urbana, IL, USA: American Oil Chemists Society.

Beamish, F. W. H., Jebbink, J.-A., Rossiter, A., & Noakes, D. L. G. (1996). Growth strategy of juvenile lake sturgeon (*Acipenser fulvescens*) in a northern river. *Canadian Journal of Fisheries and Aquatic Sciences*, *53*, 481–489.

Buckley, L. J., & Bulow, F. J. (1987). Techniques for the estimation of RNA, DNA, and protein in fish. In R. C. Summerfelt, & G. E. Hall (Eds.), *Age and growth of fish* (pp. 345–354). Ames: Iowa State University Press.

Bulow, F. J. (1971). Selection of suitable tissues for use in the RNA-DNA ratio technique of assessing recent growth rate of a fish. *Iowa State Journal of Science*, *46*, 71–78.

Burggren, W. W., & Bemis, W. E. (1992). Ram ventilation in the paddlefish, *Polyodon spathula*. *Physiological Zoology*, *65*, 515–539.

Decker, E. A., Crum, D., Mims, S. D., & Tidwell, J. H. (1991). Processing yields and composition of paddlefish *(Polyodon spathula)*, a potential aquaculture species. *Journal of Agriculture and Food Chemistry*, *39*, 686–688.

Fisher, R. A. (1930). *The genetical theory of natural selection*. Oxford, UK: Oxford University Press.

Gundersen, D. T., & Pearson, W. D. (1992). Partitioning of PCB's in the muscle and reproductive tissues of paddlefish, *Polyodon spathula*, at the falls of the Ohio River. *Bulletin Environmental Contaminants and Toxicology*, *49*, 455–462.

Hemingway, R. H., & Scarnecchia, D. L. (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.

Hendry, A. P., Dittman, A. H., & Hardy, R. W. (2000). Proximate composition, reproductive development, and a test for trade-offs in captive sockeye salmon. *Transactions of the American Fisheries Society*, *129*, 1082–1095.

Jennings, C. A., & Zigler, S. J. (2009). Biology and life history of paddlefish in North America: An update. In C. P. Paukert & G. D. Scholten (Eds.), *Paddlefish management, propagation, and conservation in the 21st century: Building from 20 years of research and management* (pp. 1–22). Bethesda, Maryland: American Fisheries Society, Symposium 66.

Lebreton, G. T. O., & Beamish, F. W. H. (2004). Growth, bioenergetics and age. In G. T. O. LeBreton, F. W. H. Beamish, & R. S. McKinley (Eds.), *Sturgeons and paddlefish of North America* (pp. 195–216). Dordrecht, The Netherlands: Kluwer Academic Publishers.

Lou, X., Wang, C., Xiong, Y. L., Wang, B., Lim, G., & Mims, S. D. (2000). Physiochemical stability of paddlefish (*Polyodon spathula*) meat under refrigerated and frozen storage. *Journal of Aquatic Food Product Technology*, *9*, 4.

McPherson, L. R., Slotte, A., Kvamme, C., Meier, S., & Marshall, C. T. (2011). Inconsistencies in measurement of fish condition: A comparison of four indices of fat reserves for Atlantic herring (*Clupea harengus*). *ICES Journal of Marine Science*, *68*, 52–60.

Medford, B. A., & Mackay, W. C. (1978). Protein and lipid content of gonads, liver, and muscle of northern pike (*Esox lucius*) in relation to gonad growth. *Journal Fisheries Research Board of Canada*, *35*, 213–219.

Mourente, G., Megina, C., & Diaz-Salvago, E. (2002). Lipids in female northern bluefin tuna (*Thunnus thynnus* L.) during sexual maturation. *Fish Physiology & Biochemistry*, *24*, 351–363.

Olsen, Y. (1999). Lipids and essential fatty acids in aquatic food web: What can freshwater ecologists learn from mariculture? In M. T. Arts, & B. C. Wainman (Eds.), *Lipids in freshwater ecosystems* (pp. 161–202). New York: Springer-Verlag.

Patterson, J. T., Mims, S. D., & Wright, R. A. (2013). Effects of body mass and water temperature on routine metabolism of American paddlefish *Polyodon spathula*. *Journal of Fish Biology*, *82*, 1269–1280.

Power, M., & McKinley, R. S. (1997). Latitudinal variation in lake sturgeon size as related to the thermal opportunity for growth. *Transactions of the American Fisheries Society*, *126*, 549–558.

Russell, T. R. (1986). Biology and life history of the paddlefish - a review. In J. G. Dillard, L. K. Graham, & T. R. Russell (Eds.), *The paddlefish: Status, management and propagation* (pp. 2–20). Bethesda, Maryland: American Fisheries Society.

SAS (2011). *SAS/STAT users guide, release 9.03 ed*. Cary, North Carolina: SAS Institute.

Scarnecchia, D. L., Gordon, B. D., Schooley, J. D., Ryckman, L. F., Schmitz, B. J., Miller, S. E., & Lim, Y. (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., Ryckman L. F., Schmitz. B. J., Wiedenheft S. G. W., Leslie. L. L., & Lim, Y. (2008). *Management plan for North Dakota and Montana paddlefish stocks and fisheries. A Cooperative Interstate plan*. Helena, Montana and Bismarck, North Dakota: Montana Department of Fish, Wildlife and Parks and North Dakota Game and Fish Department.

Scarnecchia, D. L., Ryckman, L. F., Lim, Y., Miller, S. E., Schmitz, B. J., Power, G. J., & Shefstad, S. A. (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., Ryckman, L. F., Lim, Y., Power, G. J., Schmitz, B. J., & Firehammer, J. A. (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., Stewart, P. A., & Power, G. J. (1996). Age structure of the Yellowstone-Sakakawea paddlefish stock, 1963-1993, in relation to reservoir history. *Transactions of the American Fisheries Society*, *125*, 291–299.

Sen, D. P. (2005). *Advances in fish science and technology*. New Delhi, India: Allied Publishers.

Simeanu, C., Simeanu, D., & Pasarin, B. (2012). Research on physic-chemical indices of the meat of the sturgeon species *Polyodon spathula*. *Lucrari Stiintifice - Universitatea de Stiinte Agricole si Medicina Veterinara Seria Zootehnie*, *57*, 230–233.

Sutharshiny, S., Sivashanthini, K., & Thulasitha, W. S. (2013). Lipid changes in relation to maturation and spawning of tropical double spotted queenfish, *Scomberoides lysan* (Forsskål, 1775). *Asian Journal of Animal and Veterinary Advances*, *8*, 555–570.

Tocher, D. R. (2003). Metabolism and functions of lipids and fatty acids in teleost fish. *Reviews in Fisheries Science*, *11*(2), 107–184.

Wuenschel, M. J., Jugovich, A. R., & Hare, J. A. (2006). Estimating the energy density of fish: The importance of ontogeny. *Transactions of the American Fisheries Society*, *135*, 379–385.

How to cite this article: Hemingway RJ, Scarnecchia DL. Lipid acquisition and retention in tissues of spawning adult paddlefish *Polyodon spathula* (Walbaum, 1792) in relation to extended and compressed life history patterns in two river-reservoir systems. *J Appl Ichthyol*. 2017;00:1–7. https://doi.org/10.1111/jai.13580