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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

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Summary

The objective of this study was to investigate lipid accumulation and storage in age-0 and age-1 paddlefish *Polyodon spathula* (Walbaum, 1792) in relation to age, stock, year, and growth. Juvenile paddlefish were collected from three locations in North Dakota and Montana, USA, during July and August of 2011 and 2012 and proximate analysis was used to determine lipid content. RNA/DNA ratios were used as an index of growth rates. Differences in age-based lipid accumulation and storage in juvenile paddlefish suggest a split allocation between growth and lipid storage, with growth being the highest initial priority and emphasis on energy storage occurring at a larger size, later in life. Differences in lipid allocation between stocks indicate that allocation is influenced by hatchery/wild rearing conditions. Differences within and between year-classes are consistent with field evidence observed in 2012 of a strong 2011 year-class, and indicate that during productive times, paddlefish may allocate energy to both body growth and lipid reserves, and that allocation differs among years. The lack of a relationship between RNA/DNA ratio and lipid does not support a physiologically exclusive allocation strategy between growth and lipid. Evidence from this and other studies suggests rather that an emphasis on growth, some energy storage, and a large rostrum size in relation to overall fish length in age-0 and age-1 fish, may be adaptive in avoiding predation while accruing necessary energy reserves for overwintering. Although this study also provides reference information regarding proximate composition of wild and hatchery origin juvenile paddlefish, much more study is needed into the relationships among growth, low and high lipid groups, lipid allocation in juvenile paddlefish as well as the existence and timing of allocation changes between growth and storage. To aid in understanding paddlefish survival and year-class strengths, these relationships also need to be linked to inter-annual differences in early rearing environments for age-0 and age-1 fish.

1 | INTRODUCTION

Characterization of energy acquisition and use in a fish species or stock is fundamental to understanding its life history, recruitment, and population dynamics. Energy acquisition and use (primarily in the form of lipids) differ with age and condition, as well as with external environmental conditions and selective pressures (Adams, 1999; Olsen, 1999). As individual fish develop from exogenous feeding through senescence, energy is allocated differentially into maintenance, somatic growth, storage, maturation, and reproduction (Adams, 1999; Hilton, Poortenaar, & Sewell, 2008; Scarnecchia et al., 2007). In the early stages of life, larval fish are highly susceptible to starvation and predation (Esteves, Pina, Chícharo, & Andrade, 2000; Hunter, 1981; Osse, van den Boogaart, van Snik, & van der Sluys, 1997). After the larval stage, energy is allocated to growth of tissues such as bone, cartilage, and muscle (Craig, Kenley, & Talling, 1978) in order to increase size and speed, thus avoiding predation (Biro, Post, & Abrahams, 2005; Post & Parkinson, 2001; Wuenschel, Jugovich, & Hare, 2006). Little energy is stored as lipids (Sogard & Spencer, 2004). Later in ontogeny, in response to seasonal variations in environmental conditions, energy can be stored as lipid, and also with sexual maturation, utilized in gonadal maturity. After a period of prime reproduction (Scarnecchia et al., 2007), senescence can lead to an additional reallocation of energy to storage and maintenance (Tedesco, Benito, & Garcia-Berthou, 2008). Energy allocation is regulated by food availability, growth, and energy acquisition, and is likely a driver of many life history events (Jørgensen & Fiksen, 2006; Scarnecchia et al., 2007). The timing of these events is dependent on age-specific environmental stressors and selection pressures.

Energy storage may be useful at various life stages in order to supplement metabolic needs during periods of low metabolism or reduced food availability (Biro et al., 2005; Jacobs, Breck, & Höök, 2012). Long term energy storage primarily involves accumulation of lipids at various locations within the body, including white muscle (Adams, 1999), red muscle, and within the abdomen (Sheridan, 1988). Reliance on stored energy reserves tends to increase in northern climates, where fish are adapted to lower temperatures and longer periods of reduced food availability (Anthony, Roby, & Turco, 2000; Schultz & Conover, 1997; Tocher, 2003).

Inter-annual differences in age-0 fish survival and recruitment may also be affected by inter-annual differences in their energy accumulation and storage. In particular, overwinter survival may be related to late-summer growth and energy reserves going into winter (Adams, 1999; Post & Parkinson, 2001; Thompson, Bergersen, Carlson, & Kaeding, 1991), including seasonal changes in allocation (Jacobs et al., 2012). Because lipid contains roughly twice the energy per unit mass as protein, it is the most efficient form of energy, and the most energetically valuable form that can be stored by small, young fish. However, in terms of first-year survival and recruitment success, energy storage at a young age involves a potentially critical trade-off with growth. Storing energy may come at the expense of a smaller total length and potentially increased susceptibility to predation (Wuenschel et al., 2006). How fish manage this trade-off in different populations may be indicative of selection pressures limiting recruitment that are geographically specific. Because tradeoffs between growth and energy acquisition can take place over relatively short periods of time, changes in short term growth rates may reflect the onset of such changes.

In evaluating energy storage and growth tradeoffs, two potentially useful approaches are proximate analysis for energy storage and RNA/DNA ratios (Bulow, 1987) for short term growth in fish. Proximate analysis in lipid, protein, water, and carbohydrate has been used globally as an indicator of relative nutritional quality of fish feeds, forage species (Rand, Lantry, O'Gorman, Owens, & Stewart, 1994), fish tissues (Hendry, Dittman, & Hardy, 2000), and fish products (Decker, Crum, Mims, & Tidwell, 1991). Because fish from different locations may have different hatch dates, traditional measures of growth such as length may be insufficient for comparing juvenile fish. Nucleic acid quantitation techniques such as RNA/DNA ratio have been used extensively for assessing recent larval and juvenile fish growth (Buckley & Bulow, 1987).

Little is known about energy allocation or the selection pressures that drive it in juvenile paddlefish *Polyodon spathula* (Walbaum, 1792). This ancient species (Grande & Bemis, 1991) has been impacted by alteration of much of its large river habitat through impoundment and channelization (Gerken & Paukert, 2009; Sparrowe, 1986). In addition, loss of spawning habitat and an altered flow regime have reduced reproductive success and recruitment in many populations. Some northern and southern stocks have been shown to exhibit highly episodic recruitment (Scarnecchia et al., 2011). The causes of the highly differential success in year-class strength are thought to be related to river discharges and reservoir levels (higher water levels and trophic upsurge; Scarnecchia et al., 2009, 2014).

From a physiological perspective, differences in annual paddlefish reproductive success and recruitment may be affected by inter-annual differences in energy accumulation and storage. Understanding energy use, allocation, and storage in paddlefish may provide insight into early (age-0 and age-1) life history and survival and can be useful in the prediction of year-class strength, evaluation of optimal hatchery stocking practices, and evaluation of reservoir productivity (e.g. higher paddlefish lipid storage in more productive reservoir conditions (Scarnecchia et al., 2009)). Paddlefish stocks associated with Lake Sakakawea, North Dakota (the SAK stock), and Fort Peck Lake, Montana (the FP stock), two Missouri River, USA main stem reservoirs, show variable and often weak recruitment. Although wild stock management is still promulgated, hatchery-rearing of fish to advanced age-0 stage has been conducted at Garrison Dam National Fish Hatchery (GD) as a contingency management tool. Little information is available on the relation between energy density and juvenile growth in wild paddlefish. Information on energy reserves in relation to growth rates (as indicated by RNA/DNA ratios) would be useful as baseline data to compare with other stocks and species or reservoir productivity changes caused by reservoir aging (Scarnecchia et al., 2009) and climate change. For effective management of these two stocks and others, the underlying factors that lead to differential age-0 survival and recruitment, perhaps involving energy acquisition, use, and associated food web factors (e.g. competition, predation; Scarnecchia et al., 2014), need to be much better understood.

The objective of this study was to investigate lipid accumulation and storage in age-0 and age-1 paddlefish in relation to age, stock, year, and growth. This study describes and compares lipid content in paddlefish from three different sources (SAK wild stock, FP wild stock, and Garrison Dam Hatchery-reared fish of SAK stock [GD]). Depending on availability of fish of each source and age, four questions were posed: (i) Do lipid values differ between age-0 and age-1 fish?; (ii) Do lipid values differ among fish of different stocks?; (iii) Is there a difference in lipids between brood years of age-0 fish?; and (iv) Is there a significantly negative trend between growth rate and whole body lipids, indicating a potential energy tradeoff, that can be detected with RNA/DNA ratios? Hypotheses were that there would be differences in tissue lipid storage by age, stock, and year, and that fish with higher RNA/DNA ratios would have lower lipid levels.

2 | MATERIALS AND METHODS

2.1 | Study site and source populations

We obtained juvenile paddlefish from three distinct locations during July and August of 2011 and 2012: the wild FP stock of the Missouri River upriver of Fort Peck Dam, the wild SAK stock of eastern Montana and western North Dakota, and hatchery-reared paddlefish raised in ponds at Garrison Dam National Fish Hatchery (GD) located in North Dakota, just downriver of Lake Sakakawea (Fig. 1). Garrison Dam National fish hatchery periodically produces paddlefish marked with coded wire tags (CWT) used to supplement natural production and provide management information for the SAK stock (Scarnecchia et al., 2008).

The FP stock rears in Fort Peck Reservoir, which was created in 1940, with the completion of Fort Peck Dam which to provide flood control, hydropower, and irrigation. After a 10-year filling process (1937–1947), the reservoir inundated approx. 215 km of the upper Missouri River basin, for an area of 97,100 ha, and a shoreline of 2,575 km (West et al., 1987). Since the mid-1960s (the period for which extant age-classes of paddlefish exist), the reservoir pool has varied between 670 m above sea level (asl) and 686 m asl (with full pool at 685 m asl), and tends to be drawn down in the autumn and winter (Bowersox, 2004). With the construction of Fort Peck Reservoir, fish that historically migrated large distances between rearing and spawning areas (Wilson & McKinley, 2004) have since been restricted to the reservoir and river above the dam.

The SAK stock rears in Lake Sakakawea, a reservoir on the Missouri River, located in the western half of North Dakota, Garrison Dam was completed in December 1953, impounding the reservoir. A 13-year filling period, inundated approx. 286 km of river. At an elevation of 554 m asl, the area covered by the reservoir is 124,239 ha, with an approx. shoreline of 2,120 km. The reservoir level has fluctuated by as much as 8 m since filling, depending on drought and flood conditions (Scarnecchia et al., 2014).

Garrison Dam National Fish Hatchery fish are the result of broodstock obtained by gillnetting in spring from the Yellowstone and

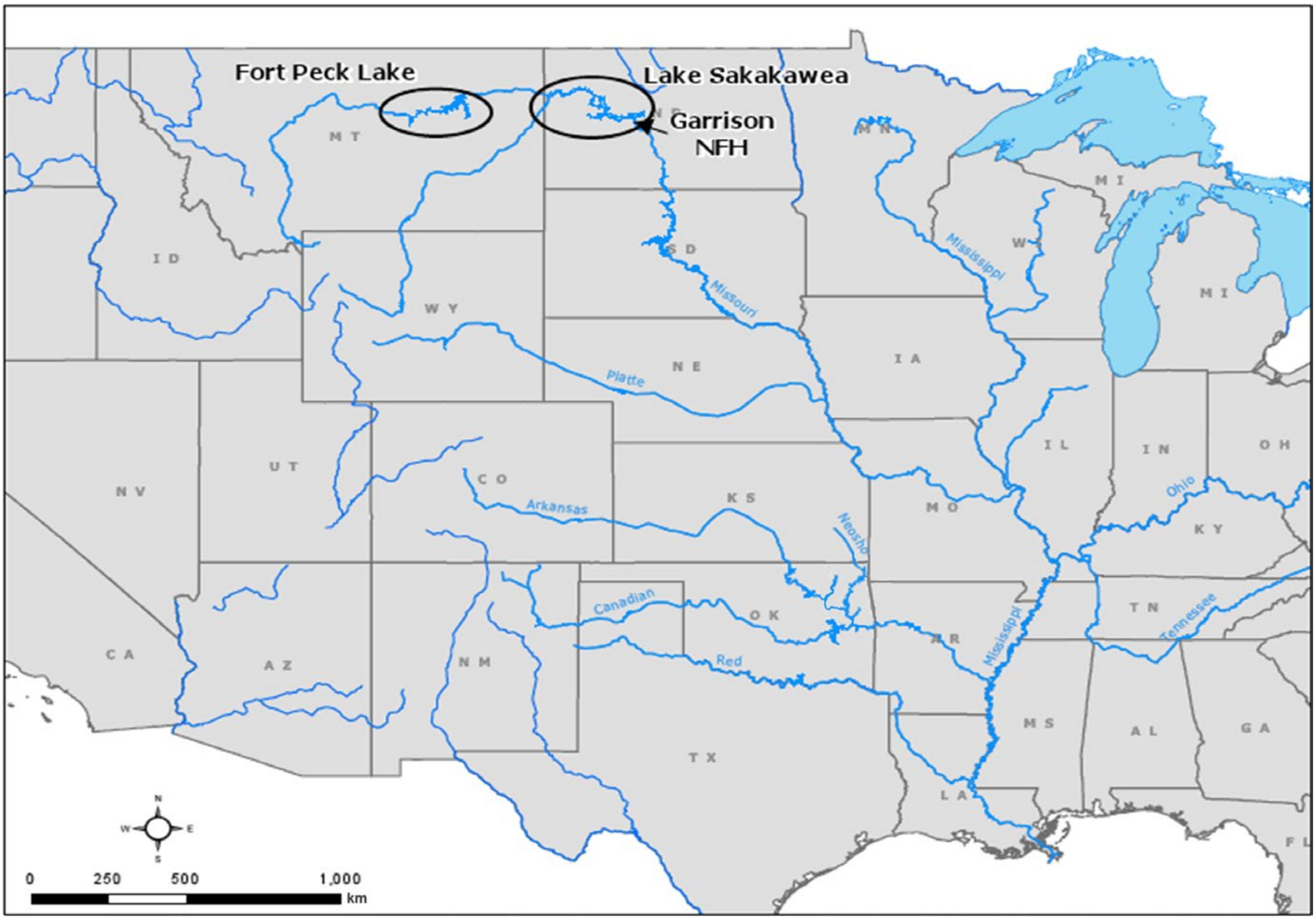

FIGURE 1 Origins of paddlefish *Polyodon spathula* used in this study

Missouri rivers above Lake Sakakawea. Broodstock are spawned, and young hatched and reared in ponds at the hatchery, which is located directly below Garrison Dam, near the town of Riverdale, North Dakota. Fish are stocked in September into Lake Sakakawea.

The SAK and FP stocks of Montana and North Dakota can be characterized as long-lived (commonly 30–40 years), with extended periods of low metabolic activity during winter months (Scarnecchia et al., 2011). Immature paddlefish of the FP and SAK stocks and those between spawns rely almost exclusively on reservoir feeding, and exhibit a life history that is adfluvial, with rearing in lentic (reservoir) habitats and spawning in riverine habitat upriver of the reservoirs.

2.2 | Sample and data collection

Although target sample sizes were set for each stock and year, actual sample sizes obtained were constrained by availability for the wild fish from the SAK and FP stocks, which are difficult to locate and capture. We collected age-0 and age-1 paddlefish from Fort Peck Reservoir (FP stock) and Lake Sakakawea (SAK stock) from late July through mid-August in 2011 and 2012 as part of annual abundance and distribution surveys. Fish were collected with long-handled dip nets during random searches following the methods described by Fredericks and Scarnecchia (1997).

We collected 250 juvenile paddlefish during 2011 and 2012: FP 2011 age-0 (*N* = 33), FP 2012 age-1 (*N* = 3), SAK 2011 age-0 (*N* = 73), SAK 2012 age-0 (*N* = 29), SAK 2012 age-1 (*N* = 21). We also obtained samples from 2011 age-0 hatchery-reared fish (*N* = 91) that had been hatched and reared at GD (SAK origin) for release into Lake Sakakawea (Table 1).

All fish were euthanized with a lethal dose of tricaine methanesulfonate (MS-222), and measured (TL, mm) and weighed (g) in the field.

2.3 | Proximate analysis

Standard methods (AOAC International, 2000, AOCS 2005) for proximate analysis were used. Fish were dried for 21 hr at 70°C to determine moisture content, and ash was determined on dried material by loss on ignition after 4 hr at 550°C in a muffle furnace. We used ANKOM lipid extraction instrument (model XT-15; Macedon, NY) to extract lipid at the University of Idaho Fish Culture Experiment Station in Hagerman, Idaho. Lipid extraction was performed following established protocols (AOCS 2005), and fish were processed for total energy (in calories) using a Parr Instruments calorimeter (model 6300; Moline, Illinois). We reprocessed calorimetry samples if duplicates differed by 100 calories. The calorimeter was calibrated at the beginning of each day with benzoic acid tablets, with a required relative standard deviation of 0.2% between days of operation. Subtraction (Hendry et al., 2000) was used to estimate protein. All samples were analyzed in duplicate, and mean difference between lipid duplicates was 0.012 (±0.17 *SD*). Inter-assay coefficients of variation between batches were calculated using a control sample of dry animal feed and were 0.05 for moisture, 0.06 for lipid, and 0.13 for ash.

Fish size and procedural difficulties affected whether a particular fish was able to undergo all procedures associated with proximate analysis. A minimum amount of tissue was required to perform all analyses, an amount that corresponded to fish approx. 170 mm TL. In small fish, as well as when procedures needed to be repeated to maintain quality control, there was sometimes not enough sample left to complete all the steps of proximate analysis. Therefore, there was sometimes a discrepancy between samples collected and sample sizes used for analyses (Tables 1, 2). In all, 224 (183 whole body, 39 eviscerated) of 250 fish samples collected underwent all proximate procedures (Table 2).

Group	Total collected	Whole collected	Whole lipid	Evisc collected	Evisc lipid
FP11-0	33	20	17	13	11
FP12-1	3	3	3	0	0
GD11-0	91	86	77	4	4
SAK11-0	73	69	47	4	4
SAK12-0	29	20	20	9	9
SAK12-1	21	20	19	1	1

TABLE 1 Total number of 2011 and 2012 FP, GD, and SAK age-0 and age-1 paddlefish *Polyodon spathula* samples collected (by total and tissue types; whole body [Whole] and eviscerated carcasses [Evisc]) and measured for lipids and available for analyses. Collected = number of fish collected; lipid = number of samples of that type processed for proximate constituents

TABLE 2 Proximate composition (% ±*SD*) of age-0 and age-1 whole body paddlefish *Polyodon spathula* from FP, GD, and SAK stocks collected in 2011 and 2012 and processed for proximate constituents. Categories denoted by Stock/Year-age

Stock, year, and age	*N*	Lipid % (*SD*)	Water % (*SD*)	Ash % (*SD*)	Protein % (*SD*)	Cal (*SD*)
FP/11-0	17	4.96 (2.66)	87.37 (.76)	0.110 (.001)	6.18 (1.39)	5313.85 (143.27)
FP/12-1	3	2.36 (1.31)	85.50 (1.66)	0.132 (.017)	11.70 (.17)	4939.38 (374.78)
GD/11-0	77	5.51 (2.86)	86.94 (2.18)	0.128 (.018)	7.43 (1.77)	4792.14 (291.17)
SAK/11-0	47	4.03 (2.39)	86.68 (1.46)	0.104 (.026)	9.60 (2.06)	4790.36 (214.27)
SAK/12-0	20	0.85 (.17)	88.45 (.57)	0.137 (.009)	10.65 (.48)	4613.49 (93.0)
SAK/12-1	19	2.60 (1.28)	84.68 (1.80)	0.128 (.017)	12.62 (1.14)	4978.25 (298.19)

2.4 | Growth

We euthanized 29 age-0 SAK fish, 21 age-1 SAK fish, and three age-0 FP fish in 2012, and removed a 5 mm muscle plug to estimate RNA/DNA ratios. The plug was placed in a 2.0 ml vial of RNAlater® (Qiagen, Inc) and stored on ice until it could be frozen at −80°C. Individual fish were placed in labeled sealable bags, and stored in a cooler on wet ice until a −20°C freezer was available. Sample plugs were frozen as soon as possible, and shipped on dry ice to the Ted Stevens Marine Research Institute in Juneau, Alaska, for RNA/DNA quantification (Buckley & Bulow, 1987). We calculated RNA/DNA ratios of white muscle from juvenile fish (Buckley & Bulow, 1987; Bulow, 1971) using a flourometric protocol described in Caldarone, Wagner, St. Onge-Burns, and Buckley (2001). This technique extracts RNA and DNA from tissues and quantifies the amount of each with a fluorescence microplate reader. Because RNA level in cells fluctuates with protein synthesis, but DNA levels remain constant, the ratio between them can be used as an index of growth rate (Thorgaard & Disney, 1990).

2.5 | Statistical analysis

A Wilcoxon test compared lipid values of fish between ages 0 and 1 of 2012 SAK fish, which was the only group for which there were sufficient sample sizes for a within-year comparison. We used a Kruskal–Wallace test of ranks of lipid values, followed by a *post hoc* Tukey–Kramer test of individual mean ranks to evaluate differences among stocks (FP, SAK, and GD). Non-parametric tests were used because lipid values were not normally distributed.

A Wilcoxon test was applied to compare lipid levels in age-0 SAK fish collected in 2011 ($N = 47$) and 2012 ($N = 20$). This comparison was limited to SAK fish because it was the only stock from which age-0 fish were collected during both years of the study.

In addition, a linear regression was used to evaluate the relationship between RNA/DNA ratio and lipid content of 29 2012 age-0 and 20 age-1 fish from SAK. In order to further explore the significance of an observed bimodal distribution of lipid in age-0 fish, fish were divided into high lipid (>4%) and low lipid (<4%) groups and additional analysis was performed, including linear regression of lipid and total length for 2011 age-0 fish, and 2012 age-0 and age-1 fish. Statistical analyses were completed using SAS (SAS 2013) and Excel (Microsoft 2007). All statistical tests were evaluated for significance at α = 0.05.

3 | RESULTS

Lipid values for all groups of 2011 age-0 fish were bi-modally distributed with a break at approx. 4%. SAK 2012 age-0 fish did not exhibit this bimodal distribution, however their lipid values were very low, with no fish over four percent (Table 2).

Lipids differed significantly by age for 2012 SAK paddlefish (Wilcoxon test, $Z = 4.538$, $p < .001$). Age-0 fish had significantly lower levels of lipid than age-1 fish (Fig. 2). Lipid values of 2011 age-0 fish differed significantly by stock with fish from GD having significantly higher lipid than SAK fish, but not FP fish (Kruskal–Wallis test, $\chi^2 = 20.719$, $p = .049$). (Fig. 3).

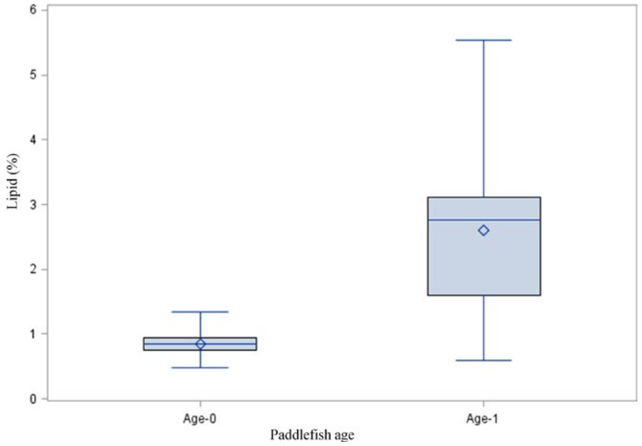

FIGURE 2 Distribution of lipid (%) (including mean [diamond] median [line], interquartile range [box], outliers, and minimum and maximum values) of 2012 Sakakawea age-0 ($N = 20$) and age-1 ($N = 19$) paddlefish *Polyodon spathula* ($p < .001$)

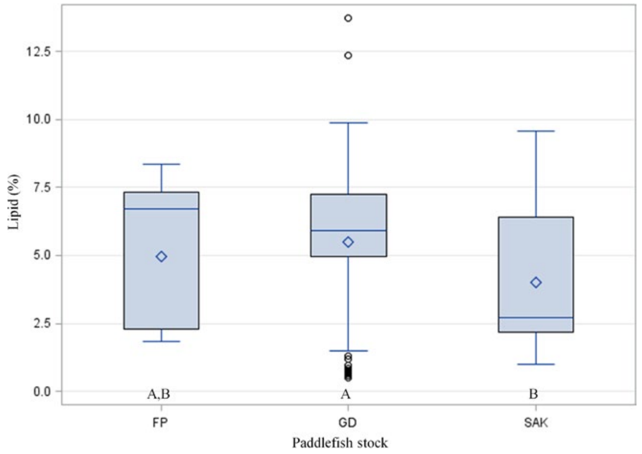

FIGURE 3 Box plot distribution of lipid (%) (including mean [diamond] median [line], interquartile range [box], outliers, and minimum and maximum values) in 2011 age-0 paddlefish *Polyodon spathula* from Fort Peck (FP; $N = 17$) Garrison Dam National Fish Hatchery (GD; $N = 77$), and Sakakawea (SAK; $N = 47$; $p = .049$). Comparisons significant at the α = 0.05 level indicated by different letters

Lipid values of age-0 SAK fish were significantly different by year (Wilcoxon test, $Z = 109.44$, $p < .001$). Lipid values of 2011 SAK age-0 fish were much higher than lipid values of the 2012 age-0 fish (Fig. 4).

RNA/DNA ratios did not relate significantly to lipid values for any of the groups tested ($R^2 < .17$, $p > .53$). In addition, no significant difference was found between RNA/DNA ratios of SAK age-0 and age-1 fish in 2012 (Wilcoxon test, $Z = 5.2$, $p = .65$).

The relationships between length and lipid were not significant for 2011 age-0 fish sorted into high and low lipid categories, with the exception of GD high lipid fish ($R^2 = .404$, $p < .001$; Fig. 5). The 2011 age-0 fish displayed a similar trend as that of 2012 age-0 fish,

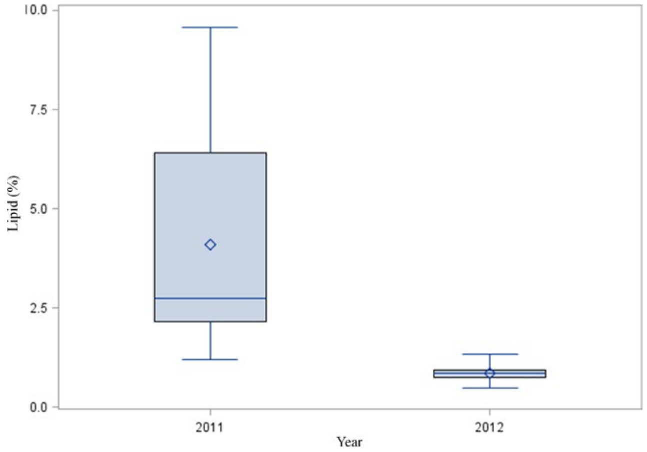

FIGURE 4 Box plot distribution of lipid (%) (including mean [diamond] median [line], interquartile range [box], outliers, and minimum and maximum values) in 2011 Sakakawea (N = 47) and 2012 Sakakawea age-0 (N = 20) whole body paddlefish *Polyodon spathula* by year. Groups are by year. (p < .001)

which did not show a significant relationship between length and lipid (R^2 = .026, p = .498). The strongest relationship between length and lipid was for 2012 age-1 SAK fish, which displayed a strong positive trend between the two variables (R^2 = .504, p = .001; Table 3). However, when low and high groups were combined between stocks the relationships were much stronger, with larger fish in each group showing more or less lipid, respectively (Fig. 6).

4 | DISCUSSION

The modest objectives of this study, i.e. comparing lipid values between age-0 and age-1 fish, among fish of different stocks and brood years, and comparing growth rate and lipids with RNA/DNA ratios, should be viewed as only an initial step in understanding the role of lipids in paddlefish life history. It is also an initial step in developing metrics useful in understanding the causes of variations in annual survival and year-class strengths of paddlefish. This understanding is critical

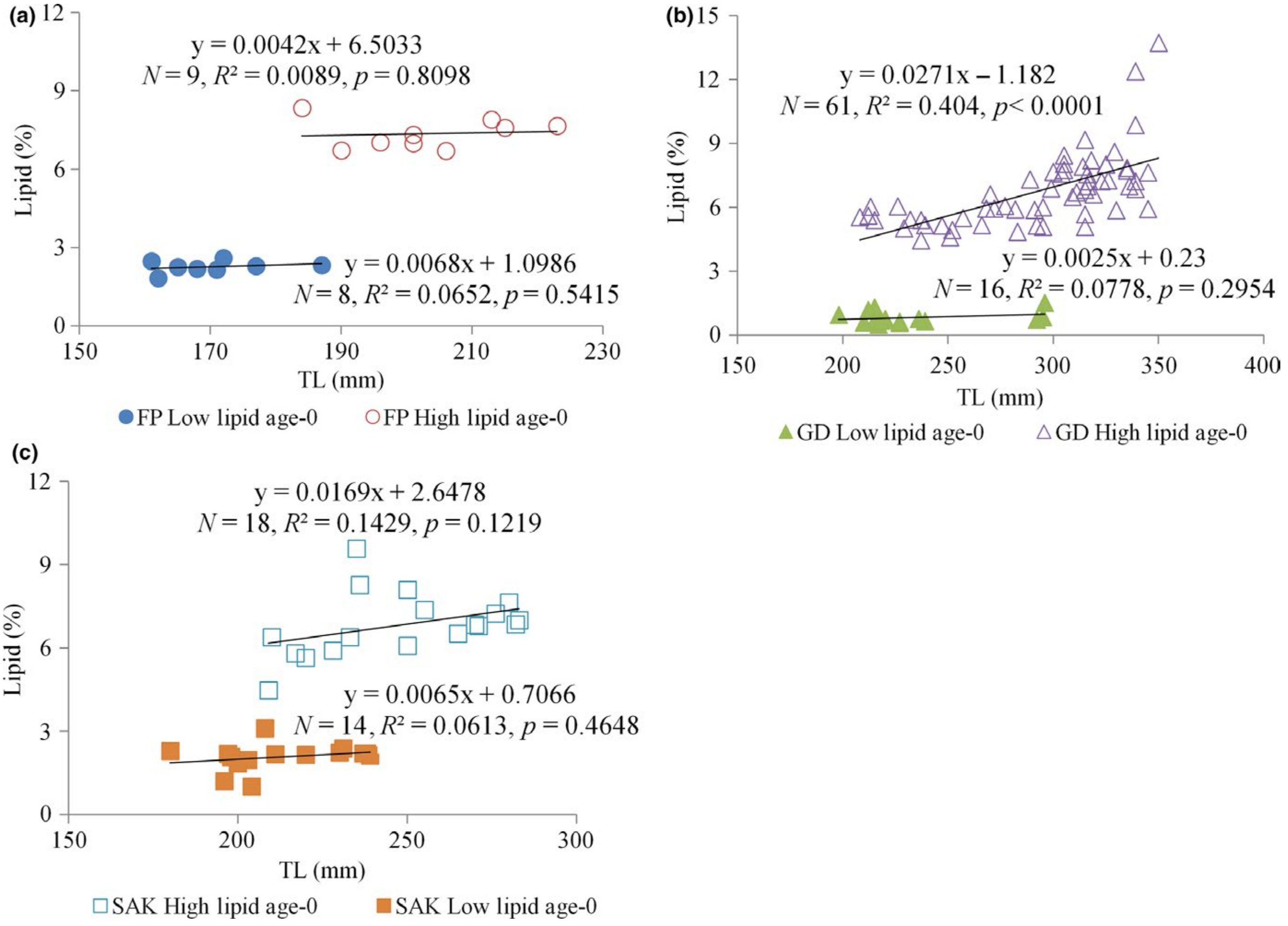

FIGURE 5 Relationships of lipid (%) with total length (TL) of Sakakawea (SAK), Fort Peck (FP), and Garrison Dam National Fish Hatchery (GD) 2011 age-0 paddlefish *Polyodon spathula* classified into low lipid (<4%) and high lipid (>4%) groups. Panels are (a) FP low and high lipid fish, (b) GD low and high lipid fish, (c) SAK low and high lipid fish

TABLE 3 Parameter estimates for high and low lipid groups in 2011 from age-0 fish from FP, GD, and SAK

Group	N	Length	Intercept	R^2	p
FP low	8	0.0068	1.0986	.0652	.5414
FP high	9	0.0042	6.5033	.0089	.8098
GD low	16	0.0025	0.23	.0778	.2954
GD high	61	0.0271	−1.182	.404	<.0001
SAK low	14	0.0044	1.2125	.0453	.4648
SAK high	18	0.0169	2.6478	.1412	.1219

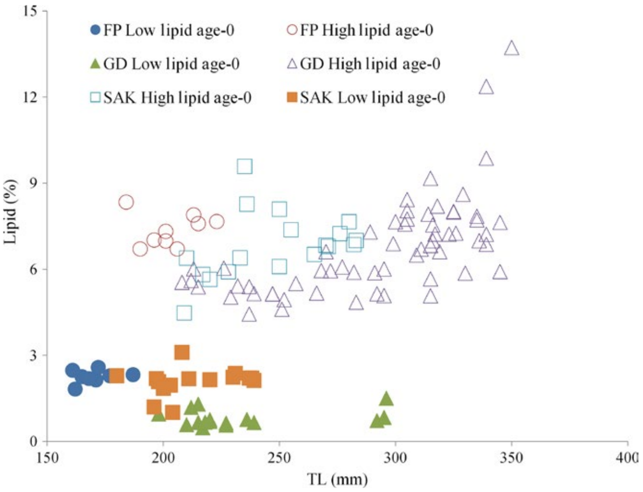

FIGURE 6 Overall plot of relationships of lipid (%) with total length (TL) of Sakakawea (SAK), Fort Peck (FP), and Garrison Dam National Fish Hatchery (GD) 2011 age-0 paddlefish *Polyodon spathula* classified into low lipid (<4%) and high lipid (>4%) groups

because paddlefish exhibit highly irregular, episodic recruitment in several instances where it has been investigated; understanding its causes is critical for effective management (Scarnecchia et al., 2014). At this stage, interpretation of the data toward this understanding remains largely speculative; little other data on this topic are available for paddlefish. For more fully understanding the relations among lipids, survival, and year-class strengths of populations hypothesized in this paper, more comprehensive sampling will need to be continued over a period of years. However, the results in this paper are in nearly all cases consistent with studies on other fish species linking environmental conditions, lipids, survival, and year-class strengths.

The significantly higher lipid content in SAK age-0 paddlefish in 2011 than in 2012 (Fig. 4, Table 2) provides evidence of substantial inter-annual differences in lipid storage during the first summer of rearing, prior to winter. These differences may influence overwinter survival. Hurst and Conover (2003) linked inter-annual variation in fish size and lipid content to overwinter survival of age-0 striped bass *Morone saxatilis* (Walbaum, 1792). Thompson et al. (1991) reported that both fish length and lipid level influenced over-winter survival of age-0 Colorado pikeminnow *Ptychocheilus lucius* Girard, 1856. Overwinter survival may also depend on inter-specific interactions. Miranda and Hubbard (1994) found that age-0 largemouth bass *Micropterus salmoides* (Lacepède, 1802) that were smaller, with lower energy values, suffered greater overwinter mortality only in the presence of predation.

In explaining these inter-annual differences in lipid content of age-0 paddlefish (Fig. 4), the role of variations in inter-annual ecological conditions, and their potential effects on recruitment, should not be overlooked. In 2011, the year of higher lipid levels, spring and summer discharge in the Yellowstone River were at record highs and reservoir levels were also as high as could be maintained in an effort to reduce downriver flooding (Maximuk & Nadolski, 2012). Higher river discharges, as well as reservoir water levels and associated trophic upsurge, have been implicated as influencing growth and year-class strength in paddlefish in general (Alexander & McDonough, 1983; Russell, 1986) and the SAK stock in particular (Scarnecchia, Stewart, & Power, 1996; Scarnecchia et al., 2009). Strong recruitment success (i.e. survival to at least age-1) in the SAK stock has been characterized as episodic, and was documented in only 2 years since 1990: in 1995 and 2011, both high flow and high reservoir level years (Scarnecchia et al., 2014). During 2012, age-1 fish were also abundant at Fort Peck, also indicating a strong 2011 year-class in that reservoir. Conversely, age-0 fish were nearly absent during index counts in both Lake Sakakawea and Fort Peck reservoir in 2012. The few age-0 fish found in Lake Sakakawea had low lipids, and results of transect sampling from 2013 indicated few age-1 fish compared to age-2 fish. Lower lipid levels seen in age-0 fish in 2012 (Table 1), and their comparatively low numbers, could reflect poor condition from a number of possible causes beyond the scope of this study, including lower reservoir productivity or density-dependent foraging competition due to habitat saturation from the large 2011 year-class.

The higher lipids in age-0 SAK fish in 2011 than in 2012 indicated that paddlefish allocated energy to both body growth and lipid reserves, and allocation differed between years. A split allocation between growth and lipids is what would be expected to be selected for in a strongly temperate climate, where some overwinter reserves may be adaptive (Hurst, 2007). For example, Mogensen and Post (2012) found that overwinter survival of age-0 rainbow trout *Oncorhychus mykiss* (Walbaum, 1792) in British Columbia was dependent upon environmentally driven allocation between growth and lipid storage.

The lower lipid reserves in age-1 fish late in their second summer than in age-0 of that year-class for the previous year (Table 2) was consistent with the idea that, at least after their first winter, rapid growth in length also remains a highly adaptive use of energy for age-1 fish. The hypothesis of growth prioritization over lipid storage gains support from Thompson (1934), who evaluated relative growth proportions between the paddlefish body and rostrum. Thompson found that fish approx. 200–500 mm total length have the longest rostrum length relative to total length, with rostrum length often exceeding the length of the rest of the fish. Thompson's (1934) data on rostrum length as a percentage of total length demonstrates that the proportional rostrum length of the paddlefish increases from hatching through approx. 400 mm (which corresponded with the dividing line between age-0 and age-1 fish in this study), and then decreases proportionately throughout life (Fig. 7). This relationship supports the notion that for

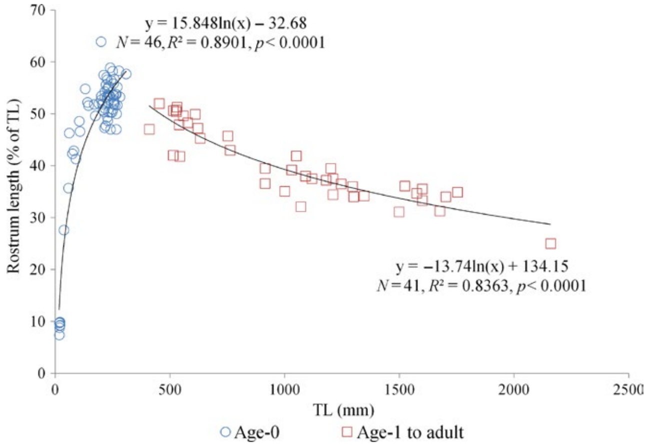

FIGURE 7 Relationship between rostrum length (% of TL) and total length (mm) of paddlefish *Polyodon spathula* from Thompson (1934) (*N* = 87) divided into two groups (Thompson Age-0 fish, Thompson Age-1 to adult fish)

age-0 fish and into age-1, the highest priority is growth, including growth of a relatively large rostrum. From an evolutionary perspective, this prioritization favors fish that reach a large length, and thereby appear as large as possible, as soon as possible, to discourage potential predation. One cost and outcome of this prioritization is reduced lipid storage. Energy storage can occur prior to winter in years when habitat conditions allow it, as in 2011 (Table 2).

Predation may be one important reason why the age-0 and age-1 paddlefish in this study allocated energy to growth in length. In Lake Sakakawea, age-0 paddlefish, and even some age-1 fish, have been shown to be highly vulnerable to predation from walleye *Sander vitreus* (Mitchill, 1818), sauger *Sander canadensis* (Griffith and Smith, 1834), and other species (Mero, Willis, & Power, 1995; Parken & Scarnecchia, 2002). The presence of these large predators may create a situation where overcoming predator gape limit by growing larger as rapidly as possible is beneficial within the constraints of overwinter survival their first year. Decker et al. (1991) reported extremely low levels of lipid in captive paddlefish that are comparable to values for age-1 fish in this study. Both SAK and FP age-1 fish are from the brood year 2011, when a 1000-year flood event (Driscoll, Southard, Koenig, Bender, & Holmes, 2014) resulted in an uncharacteristically strong year-class, even for Acipenseriform fish. Age-1 fish were also abundant relative to age-0 fish in Fort Peck reservoir (D. Scarnecchia, unpubl. data). All age-1 fish that we collected in both reservoirs appeared to be healthy and vigorous, thus lower lipids in age-1 fish may be normal, and may reflect evolutionary prioritization of growth over storage during this stage of paddlefish development. Miranda and Hubbard (1994) reported that age-0 largemouth bass *M. salmoides* overwinter survival was only lipid- and size-dependent under conditions of predation. If this relationship also applies to age-0 and age-1 paddlefish, then predation may be the factor that drives evolutionary prioritization patterns in allocation for both age 0 and age-1 fish. More substantial energy storage must wait for later in life, when the predation threat is reduced.

A second hypothesis, not readily testable, is that the low lipids in age-1 fish were the outcome of intra-specific competition from the strong 2011 year-class, the strongest recorded since 1995 (Scarnecchia et al., 2014). In order to fully understand this potential tradeoff, lipids should be monitored consistently in age-0 fish in relation to growth and year-class strength. More years of data will be needed to adequately assess effects of density on lipid reserves and energy allocation.

The overall significantly higher lipid levels of GD fish than in SAK fish are consistent with the idea that the hatchery fish generally experience greater food availability, and expend less energy foraging. Sogard and Spencer (2004) reported that hatchery sablefish *Anaplopoma fimbria* (Pallas, 1814) had much higher lipids than wild fish, and suggested that part of the reason was the higher energy requirement of foraging under wild conditions. GD fish were reared in artificially fertilized ponds, whereas FP and SAK fish consumed live feed and had to forage widely for it. In addition, GD fish were raised to a larger size in a comparable period of time. The lack of both size and lipid differences in FP and SAK fish support the idea that greater length was a factor in higher GD lipid levels. It is unknown if this hatchery-reared versus wild difference occurs consistently, as this is beyond the scope of the current study. It would be advantageous to conduct additional studies to include other juvenile paddlefish populations.

The failure of RNA/DNA ratios to predict lipids lends no support to the hypothesis that lipid accumulation in juvenile paddlefish is related to the rate of protein synthesis. If the physiological ability to grow or to store lipids is exclusive, fish with higher lipid would show lower RNA/DNA, because fish would have to allocate energy to either growth or storage. Under this scenario, high growth rates would reflect less emphasis on lipid storage. This was not the case with age-0 and age-1 fish, despite a significant difference in lipid between the two groups. The inability of RNA/DNA ratio to detect a difference in growth rate could be due to several factors. One is that the technique measures protein synthesis only over a short time period (up to 1 week) prior to sampling. Existence and timing of a possible abrupt decision to store lipid in preparation to winter in juvenile paddlefish is unknown, and fish were only sampled once. It is possible that onset of a change in storage allocation from growth to storage does happen in age-0 fish, but occurs outside the window reflected in this sampling and analysis. The lack of differences in RNA/DNA among reservoirs in 2012, and the lack of a relationship between RNA/DNA and lipid indicate that differences in lipid storage between age-0 and age-1 fish are not a result of exclusive energy partitioning between growth and storage in larger fish. This may, however, be the case in smaller fish, as well as in years when resources are limited. Sogard and Spencer (2004) reported that although juvenile sablefish fed low rations exhibited a negative relationship between growth and lipid storage (indicating an energetic trade-off), fish fed higher rations stored more lipid as they became larger. In this situation, larger fish under prime conditions have the ability to allocate to either storage or growth, but are able to capitalize on abundant energy and allocate successfully to both growth and storage concurrently. This idea is consistent with a cautious interpretation of the trends observed in 2011 age-0 high lipid fish. Although a positive relationship between lipid and length did not quite reach significance ($p = .1219$), age-0 SAK fish appeared to be intermediate between the responses observed in smaller FP fish and larger GD fish. The smallest fish, FP, showed no trend; the intermediate size fish, SAK, showed a trend just missing significance. The largest fish, GD, showed a positive trend (Figs 5 and 6). The trend toward a positive relationship between total length and percent lipids in high lipid groups as length increases, and no relationship between total length and lipids in low lipid groups as length increases, may reflect a tendency toward concurrent storage and growth as length increases (Fig. 6). The high SAK age-0 lipid group in 2011, the record high water year, is on a positive track toward larger size and higher lipids; prioritization of lipid storage and growth may not be mutually exclusive, but larger fish may instead be more adept at both growth and storage. In contrast, the low lipid fish of 2011, and all of the age-0 fish in the 2012 group, the lower water year, are trading off and can store lipids only at a potentially fatal cost of slow growth. The high lipid groups in 2011 would result in stronger year-classes of larger individual fish, the low lipid group in 2012 in smaller year-classes of smaller individual fish. A strongly positive feedback involving growth and adequate energy storage would thus be an optimal approach for survival in temperate areas, and that response would be selected for. The individual fish response, either a strongly positive feedback or a strongly negative feedback, might also explain the boom or bust episodic recruitment observed in this species (Scarnecchia et al., 2014). In this scenario, for a strong cohort of recruits, there must be ecological conditions, including upsurge (Scarnecchia et al., 2009) leading to a higher-than-typical number of positive feedback age-0 fish. A satisfactory confirmation of this pattern of positive feedback, as well as the exact mechanism for a potentially positive vs. negative feedback cannot be made clear unless fish are followed through a wider range of sizes from small age-0 to large age-1. Further study is needed concerning the relationships among growth, low and high lipid groups, lipid allocation in juvenile paddlefish, as well as the existence and timing of allocation changes between growth and storage. To aid in understanding paddlefish survival and year-class strengths, these relationships also need to be linked to inter-annual differences in early rearing environments for age-0 and age 1 fish.

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