

Egg lipid and thiamine vary between early and late spawning lake sturgeon

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Summary

Nutritional deficiency associated with reduced thiamine (vitamin B1) and reduced natural reproduction of salmonid species in the Great Lake Region is well established. The negative relationship between egg thiamine and lipid concentration to post-hatch larval growth and survival in teleost species, coupled with the limited research of egg thiamine in Acipenseriform species of conservation concern, including lake sturgeon, indicates that study of thiamine concentrations lake sturgeon eggs is warranted. Eggs were collected from females ($N = 12$) during the early and late portion of the spawning run in 2007 in a wild population from Black Lake, MI. Concentrations of thiamine, lipid and fatty acid concentration were measured along with female biological information (body size and egg size) and characteristics of larvae at hatch. Significant differences in egg thiamine concentrations were observed between early- and late-spawning females (mean \pm SD: $2.36 \text{ nmol}\cdot\text{g}^{-1} \pm 1.09$ vs. $0.73 \pm 0.25 \text{ nmol}\cdot\text{g}^{-1}$, $W = 0.05$, $p < .01$). No significant relationships were observed between female body size or egg size and egg lipid or thiamine concentration. Differences in lipid and thiamine concentrations were not predictive of larval body size or yolk sac volume at hatch. Total and phosphorylated thiamine were correlated with n-3 polyunsaturated fatty acids, suggesting that dietary items were likely partially responsible for provisioning of essential compounds. Given the negative effects of low egg thiamine concentration on larval survival in other fish species globally, results indicate that further research in areas of nutrient acquisition and thiamine effects on larval survival, natural recruitment, and hatchery feeding strategies is warranted for lake sturgeon.

1 | INTRODUCTION

Trait adaptation, specifically, the development of suites of morphological, behavioral, physiological, and life history traits tied to environmental conditions at the time of reproduction can have far-reaching consequences at individual and population levels (Hendry & Day, 2005). There is strong selection for adults to breed at times and in locations that are conducive to the survival of offspring. Embryonic and larval developmental time varies as a function of environmental factors (e.g., temperature, stream discharge,

etc., Gillooly et al., 2002; Jaworski & Kamler, 2002; Jay et al., 2020; O'Connor et al., 2007). Therefore, maternal effects, including female resource expenditures and provisioning of eggs conditional on environments experienced prior to and at the time and location of spawning can significantly influence offspring phenotypic traits (Mousseau & Fox, 1998), and can collectively contribute to embryonic and larval development (Einum & Fleming, 2000; Jaworski & Kamler, 2002) and dispersal (Edwards et al., 2007).

Maternal reproductive investments including egg size (Bernardo, 1996; Trippel & Neil, 2004), lipids (Einum & Fleming, 2000)

and essential vitamins (e.g., thiamine, Fisher et al., 1998; Fitzsimons et al., 2007) are largely dictated by the physiological condition of females during gametogenesis (McCormick, 1998). Few studies have addressed questions regarding variation in maternal provisioning of eggs related to the timing of spawning. Specifically, understanding of how the timing of reproduction affects individual ovary quality and reproductive success is limited (Lowerre-Barbieri et al., 2011).

Maternal effects associated with the provisioning of eggs with essential nutrients can significantly affect offspring growth and survival during early ontogenetic stages (Berkeley et al., 2004; Einum & Fleming, 2000; Fuiman & Ojanguren, 2011; Green, 2008; Tocher, 2003). Thiamine (vitamin B₁) plays important physiological roles in fishes and is essential for enzymes involved in carbohydrate metabolism (Amcoff et al., 1998). The implications of thiamine deficiency, commonly referred to as thiamine deficiency complex (TDC, review in Harder et al., 2018) are well established (Brown et al., 2005; Fitzsimons & Brown, 1999). In Acipenseriforms, increases in thiamine concentration are associated with increased larval weight and length (Ghiasi et al., 2017). Additionally, thiamine deficient Sterlet sturgeon (*Acipenser ruthenus*) demonstrated disease symptoms including yolk-sac deformation, loss of equilibrium and erratic swimming behavior (Ghiasi et al., 2017). Fishes that are susceptible to thiamine deficiency obtain thiamine from dietary items from lower trophic levels. Thiamine injections increase free thiamine, thiamine pyrophosphate and total thiamine in sturgeon broodstock (Ghiasi et al., 2014). There is evidence of microbial gut synthesis in fish, but its availability to the host fish is not known (Ji et al., 1998; Kraft & Angert, 2017).

Fatty acids, particularly polyunsaturated fatty acids (PUFAs) are important building blocks during egg and embryonic development (Ahmadi et al., 2011). In many fish, synthesis of PUFAs varies temporally (Madenjian et al., 2000; McKinley et al., 1993). A reduction in hatch success (Leray et al., 1985; Watanabe et al., 1984), egg quantity, size (Leray et al., 1985; Moodie et al., 1989), and larval survival (Czesny et al., 1999; Moodie et al., 1989) have all been reported in fishes with a reduced concentration of n-3 high unsaturated fatty acids (HUFA) during embryonic and larval development. In lake trout (*Salvelinus namaycush*), *cis*-7-hexadecenoic acid in both neutral lipids (NL) and polar lipids (PL) was correlated with pre-hatch mortality, as was docosapentaenoic acid in PL and docosahexaenoic acid in NL (Czesny et al., 2009). Further, total lipids, like thiamine pyrophosphate, were correlated with the frequency of early mortality syndrome in lake trout (Czesny et al., 2009, 2012). Fatty acid transfer to the egg during vitellogenesis is associated with female nutritional status (Frémont et al., 1984; Navas et al., 1998), suggesting that variability in HUFA's and other PUFAs during vitellogenesis, may have lasting fitness consequences. This is particularly evident during embryogenesis, ontogenesis, and in the critical period immediately following hatch (Bruce et al., 1999), influencing reproductive success, and ultimately recruitment.

Lake sturgeon (*Acipenser fulvescens*) are a long-lived, iteroparous, lithophilic spawning species (Bruch et al., 2016; Peterson et al., 2007), that is characterized by delayed sexual maturity and prolonged inter-spawning intervals (Forsythe, et al., 2012). Natural

recruitment remains low (Holey et al., 2000) and has been attributed to compensatory effects of low spawner abundance (Dammerman et al., 2019), but also potentially to female provisioning of eggs (Wassink et al., 2019, 2020). Knowledge of physiological processes and characteristics of eggs and associations with essential nutrients, environmental conditions experienced during embryogenesis, survival during embryogenesis, and early post-hatch periods would greatly aid efforts to predict population-wide natural recruitment and to direct supplementation programs. Information is lacking regarding maternal effects in lake sturgeon associated with egg provisioning, and the utilization of essential nutrient reserves deposited in yolks such as lipids and antioxidant vitamins in relation to environmental regimes associated with the timing of reproduction. In situations when spawning may occur over a protracted period, as has been characterized in this sturgeon population from Black Lake, MI (Forsythe, Crossman, et al., 2012), variation in levels of female provisioning can be considerable (Wassink et al., 2020).

Our objectives were to quantify lipid and thiamine concentrations in eggs of female lake sturgeon, determine whether these nutrient and vitamin concentrations varied as a function of the timing of spawning, female body size or egg size, and whether concentrations were associated with larval phenotype and yolk sac area at hatch.

2 | MATERIALS AND METHODS

2.1 | Study location

The research was conducted on a well-studied population from the upper Black River, a shallow and wadable fourth-order stream and primary tributary of Black Lake, MI (Dammerman et al., 2016; Wassink et al., 2019). The population is closed to immigration and dams restrict movement to just Black Lake (~4,000 ha) and the upper Black River (UBR). Each year, groups of adults enter the UBR and arrive at spawning areas several km up-stream from the lake over a period of 28–43 days (Forsythe, Crossman, et al., 2012; Forsythe, Scribner, et al., 2012), typically in 2 or more groups that generally correspond to “early” and “late” (Crossman et al., 2011; Dammerman et al., 2019; Duong et al., 2011; Forsythe, Crossman, et al., 2012; Forsythe, Scribner, et al., 2012) times in the spawning period (see Forsythe, Crossman, et al., 2012, figure 2 for characterizations of the 2007 chronology of spawning). These two periods are characterized by different temperature and flow regimes, with temperatures cooler and flows higher during earlier spawning periods. Most spawning adults can be captured using long-handed dip nets over ~2 km of stream each year during migration in the river or while in the act of spawning (Duong et al., 2011; Forsythe, Scribner, et al., 2012).

2.2 | Field sampling

Unfertilized eggs were collected from females ($N = 12$) in the act of spawning over the period from 26 April to 11 May 2007 using

methods described in Crossman et al. (2011). Eggs were placed into sealed plastic ziplock bags in the field and retained for less than 12 hr in coolers containing stream water maintained at ambient stream temperatures while in the field. Following sampling, eggs were frozen in the field with dry ice, transported to the laboratory, photographed and measured, and stored at -80°C until analyses were performed (Ghiasi et al., 2014, 2017). Females were categorized into early and late spawning groups based on long-term capture-recapture data on date of spawning and stream temperature (Dammerman et al., 2019; Duong et al., 2011; Forsythe, Crossman, et al., 2012) and interval between spawning episodes (Figure 1). Each individual was measured for total length (cm), fork length (cm), weight (kg), and girth (cm) at the time of capture.

2.3 | Laboratory analyses

2.3.1 | Characterization of egg and larval traits

Estimates of mean egg size (diameter in mm) were measured from 30 randomly selected eggs per female prior to freezing at -80°C . Randomly selected eggs were collected from the totality of eggs that could be extracted from a female lake sturgeon during an active spawning attempt (150–300 ml of eggs per female at 52 eggs ml^{-1} , Michigan State University, unpublished data). Estimates of total length (mm), body area (mm^2), and yolk sac area (YSA, mm^2) were averaged from 30 randomly selected larvae from each female at

hatch (Bauman et al., 2015, 2016). Randomly selected eggs fertilized to measure larval characteristics were collected from the totality of eggs that could be extracted from a female lake sturgeon during an active spawning attempt. Measurements of eggs and larval traits were made using a 6.0 megapixel digital camera and a mm ruler to scale the photo for Image J analysis software (Version 1.34, free-ware) as described by Crossman et al. (2014).

2.3.2 | Thiamine, lipid, and fatty acid analysis

High performance liquid chromatography (HPLC) analysis was used for free thiamine and its phosphated derivatives (mono- and di-phosphate) (Brown et al., 1998) in the sturgeon eggs. The HPLC system consisted of a delivery system pump (110B, Beckman Instruments Inc.) equipped with an FP-920 intelligent fluorescence detector (JASCO Co.). The thiamine-HCL, thiamine-monophosphate, and thiamine diphosphate were identified and quantified using external standards supplied from Sigma-Aldrich.

For thiamine analysis, Waters Spherisorb® 5 μm NH₂ (4.6×250 mm) column coupled with a NH₂ packed guard column was used on set at 375 nm for excitation and 430 nm for emission slightly modified from Brown et al. (1998). Briefly, 600 μl of 2% TCA extraction solution was added to tissue samples and gently homogenized for 30 s. The homogenized samples were placed into a boiling water bath for five min and then cooled on ice for 10 min. After cooling, the samples were supplemented by 600 μl of ice-cold 10% TCA

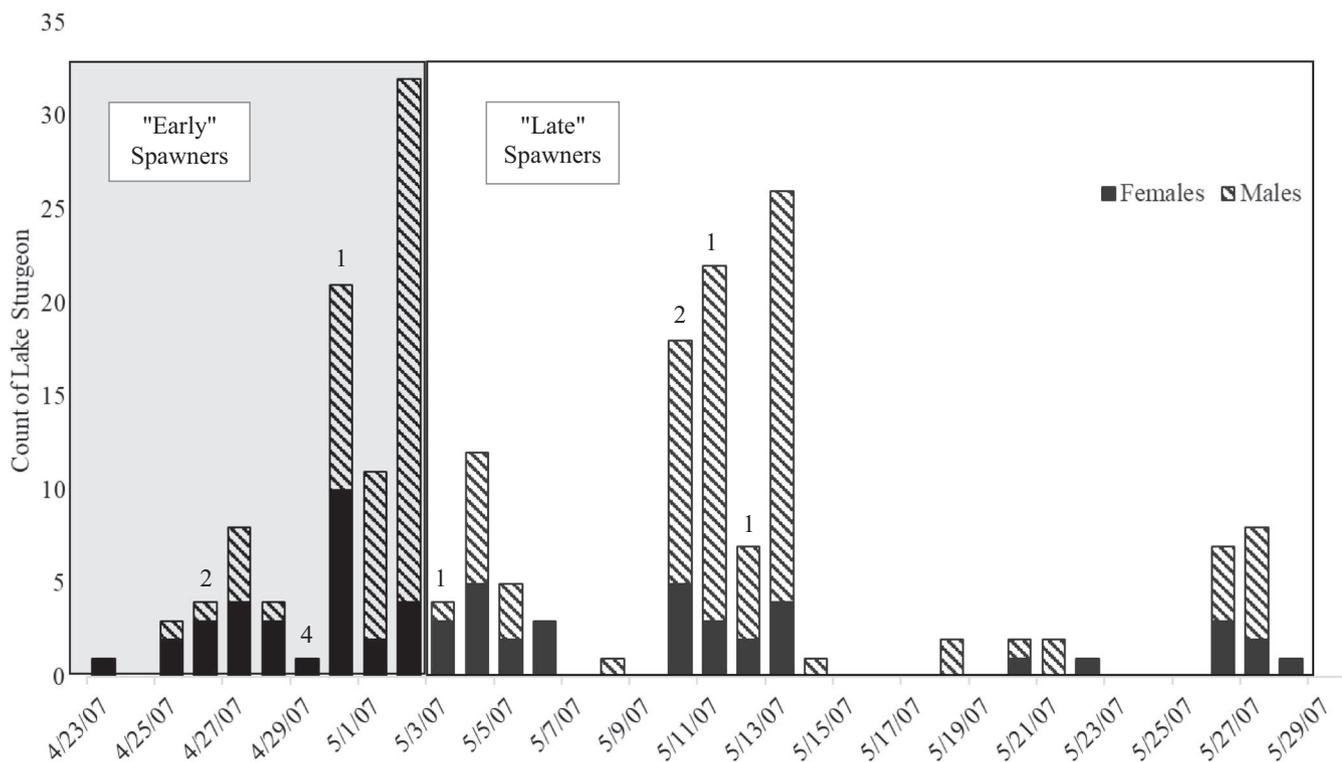


FIGURE 1 Temporal distribution of "early" and "late" spawning male and female lake sturgeon (see Forsythe, Crossman, et al., 2012) arriving in the upper Black River during the 2007 spawning season. The number of females from which eggs were collected on a given day is noted above each day

solution. Then, the samples were centrifuged at 14,000g for 15 min at 4°C. The clear supernatants (1 ml) were transferred into glass test tubes (10 ml capacity). To remove TCA and lipids, the sample extracts in the test tubes were washed with 4 volumes of ethyl acetate-hexane solution (v/v, 3/2). The washed sample (0.5 ml) was oxidized to thiochrome by adding 25 µl of 30 mM $K_3Fe(CN)_6$ and 25 µl of 0.8 M NaOH. Then, the oxidized sample extracts were vortexed and filtered before injection into HPLC system. The mobile phase consisted of KH_2PO_4 (pH 7.5, 85 mM) with acetonitrile (v/v, 65/35).

2.3.3 | Lipid and fatty acids analysis

Total lipid (TL) of sturgeon eggs were extracted according to the method described by Folch et al. (1957). Extracted lipids were separated into neutral (NL) and polar (PL) lipids using Sep-Pak silica cartridges, 690 mg, 55–105 µm, (Waters). NL was extracted using 20 ml chloroform, and then PL was eluted using 20 ml methanol (Juaneda & Rocquelin, 1985). The lipid content and the proportion of each lipid class were measured gravimetrically.

Lipids were converted to fatty acid methyl esters (FAME) by the method of Metcalfe and Schmitz (1961). The internal standard nonadecanoic acid (C19:0, Nu-Check-Prep, Inc.) was added to the samples prior to transmethylation as reference standard for quantification. FAME were analyzed with a gas chromatography (Varian 3900 GC, Varian, Inc.) equipped with a flame ionization detector, a capillary column (WCOT fused silica 100 m × 0.25 mm coating CPSIL 88 for FAME, $df = 0.2$) and an auto-injector (CP-8410 Autoinjector, Varian, Inc.). Helium was used as a carrier gas at a flow rate of 30 ml min^{-1} . The injector and detector temperatures were 270 and 300°C, respectively. The initial temperature of the oven was 175°C for 26 min, which increased to 205°C by increments of 2°C min^{-1} , then held at 205°C for 24 min. The individual fatty acid (FA) was identified by comparing to their retention times with a standard mix (Nu-Check-Prep, Inc.).

2.4 | Statistical analysis

Differences in female body size (fork length, FL) and egg size between females spawning during early and late periods (Dammerman et al., 2019; Duong et al., 2011; Forsythe, Crossman, et al., 2012; Forsythe, Scribner, et al., 2012) were quantified using Wilcoxon-Mann-Whitney tests (WMW, Siegel & Castellan, 1988). Relationships between female body size and egg lipids and thiamine concentration were investigated using regression analysis. Differences in thiamine and lipid concentration in eggs of early and late spawning females were also conducted using a Wilcoxon-Mann-Whitney test. Analyses of relationships between egg thiamine and lipid concentration and larval phenotypic traits were conducted using regression analysis. Relationships between standardized spawning day and female body size, egg size, thiamine concentration, lipid concentration, and larval phenotypic traits were included to demonstrate that

grouping of fish by spawning run was consistent with evaluating variables across the 2007 spawning run in totality. All assumptions of normality were tested using Shapiro-Wilk tests. Total thiamine, thiamine monophosphate, thiamine pyrophosphate and free thiamine concentrations required log transformation (Figure S5a-d) to achieve normality. Analyses were conducted in R (4.0.2, www.r-project.org).

3 | RESULTS

Adults ($N = 208$) were collected during the 2007 spawning period, which extended from 24 April through 1 June. We collected eggs from 12 of 64 females captured (18.8%) including seven females during the early spawning period (April 26–29) and five females spawning later in the season (May 10–12). Water temperatures during the period of collection of eggs from early and late spawning female were 11–14 and 15–18°C, respectively.

No significant difference (mean ± SD) in female body size (FL, 153.7 ± 12.7 cm vs. 160.4 ± 8.8 cm; $W = 12.5$, $p = .46$) was observed between individuals from early and late spawning groups. Mean ± SD egg size did not differ significantly between early and late spawning females (3.8 ± 0.23 vs. 3.6 ± 0.24; $W = 27$, $p = .15$). Egg size was not significantly associated with standardized day of capture ($R^2 = .14$, $F = 1.62$, $df_{1,10}$, $p = .23$, Figure S1a). Female body size was not significantly associated with egg lipid concentration ($F = 0.28$, $df_{1,10}$, $p = .61$) or concentrations of egg thiamine ($F = 0.03$, $df_{1,10}$, $p = .85$) (Table 1). At the time of hatch, larvae from early and late females did not differ significantly in total length (mean ± SD: 12.29 ± 0.42 mm vs. 11.31 ± 1.10 mm, $W = 27$, $p = .14$), but larval size at hatch did decrease as a function of standardized day of capture ($R^2 = .42$, $F = 7.19$, $df_{1,10}$, $p = .02$, Figure S1b). An increase of one unit of standardized day of capture decreased total length at hatch by 3.56 mm. Larvae from early and late females did not differ in body area (mean ± SD: 19.25 ± 1.80 vs. 17.77 ± 2.32 mm²; $W = 25$, $p = .25$), nor was larval body area significantly associated with standardized day of capture ($R^2 = .12$, $F = 1.39$, $df_{1,10}$, $p = .27$, Figure S1c). Larvae from early and late females did not differ in yolk-sac area (mean ± SD: 9.95 ± 0.65 vs. 9.35 ± 1.20 mm²; $W = 25$, $p = .25$) (Table 1), nor was larval yolk-sac area significantly associated with standardized day of capture ($R^2 = .12$, $F = 1.37$, $df_{1,10}$, $p = .27$, Figure S1d).

Concentration of total, neutral, and polar lipids (Table S1) were moderately but not significantly higher in eggs from early relative to late spawning females (Table 1). Total lipids did not differ significantly between eggs collected from females collected during different spawning periods (mean ± SD, early: 11.91% ± 3.33% of wet weight, late: 11.32% ± 4.87% of wet weight, $W = 20$, $p = .76$) (Table 1). Total lipids was not associated with standardized day of capture ($R^2 = .02$, $F = 0.249$, $df_{1,10}$, $p = .86$, Figure S2a). Neither neutral lipids (mean ± SD; early: 10.20% ± 1.37% of wet weight, late: 7.54% ± 4.02% of wet weight, $W = 28$, $p = .11$) nor polar lipids (mean ± SD; early: 2.91% ± 0.53% of wet weight, late: 2.12% ± 1.21% of wet weight, $W = 28$, $p = .11$) differed significantly from eggs collected from females spawning in different spawning periods

TABLE 1 Comparison of mean (standard deviation) female, egg, and larval traits for early and late spawning female lake sturgeon captured at spawning areas during April and May 2007

| Trait | Spawning time | | MannU (<i>p</i> -value, 10 <i>df</i>) |
|--|-----------------------|----------------------|---|
| | Early (<i>N</i> = 7) | Late (<i>N</i> = 5) | |
| Egg characteristics | | | |
| Total lipids (nmol g ⁻¹) | 11.91 (3.33) | 11.32 (4.87) | <i>W</i> = 20 (0.76) |
| Neutral lipids (nmol g ⁻¹) | 10.20 (1.37) | 7.54 (4.02) | <i>W</i> = 28, (0.11) |
| Polar lipids (nmol g ⁻¹) | 2.91 (0.53) | 2.12 (1.21) | <i>W</i> = 28, (0.11) |
| Total thiamine (nmol g ⁻¹) | 2.36 (1.09) | 0.73 (0.25) | <i>W</i> = 0.05 (<0.01)* |
| Free thiamine (nmol g ⁻¹) | 0.05 (0.04) | 0.09 (0.11) | <i>W</i> = 13 (0.53) |
| Thiamine monophosphate (nmol g ⁻¹) | 0.16 (0.08) | 0.07 (0.03) | <i>W</i> = 31 (0.03)* |
| Thiamine pyrophosphate (nmol g ⁻¹) | 2.14 (1.00) | 0.57 (0.31) | <i>W</i> = 34 (<0.01)* |
| Characteristics of larvae at hatch | | | |
| Total length (mm) | 12.29 (0.42) | 11.31 (1.10) | <i>W</i> = 27 (0.14) |
| Body area (mm ²) | 19.25 (1.80) | 17.77 (2.32) | <i>W</i> = 25 (0.25) |
| Yolk sac area (mm ²) | 9.95 (0.65) | 9.31 (1.20) | <i>W</i> = 25 (0.25) |
| Adult female characteristics | | | |
| Fork length (cm) | 153.7 (12.7) | 160.9 (8.8) | <i>W</i> = 12.5 (0.46) |
| Egg size (diameter, mm) | 3.9 (0.2) | 3.7 (0.2) | <i>W</i> = 27 (0.15) |

*Denotes *p*-values less than .05.

(Table 1). Additionally, neither neutral lipids ($R^2 = .10$, $F = 1.15$, $df_{1,10}$, $p = .31$, Figure S2b), nor polar lipids ($R^2 = .10$, $F = 1.07$, $df_{1,10}$, $p = .33$, Figure S2c) were associated with standardized day of capture.

Total thiamine was significantly higher for eggs that were collected from females during the early spawning run (mean \pm SD: $2.36 \text{ nmol}\cdot\text{g}^{-1} \pm 1.09$ vs. $0.73 \pm 0.25 \text{ nmol}\cdot\text{g}^{-1}$, $W = 0.05$, $p < .01$). Log total thiamine decreased as a function of standardized capture day during the spawning season ($R^2 = .33$, $F = 11.1$, $df_{1,22}$, $p < .01$, Figure S3a). An increase of 1 unit of standardized spawning day decreased total thiamine by $3.5 \text{ nmol}\cdot\text{g}^{-1}$. Thiamine monophosphate (TMP) was slightly but significantly higher in eggs collected from females in the early spawning run (mean \pm SD: early: $0.16 \pm 0.08 \text{ nmol}\cdot\text{g}^{-1}$, late: $0.07 \pm 0.03 \text{ nmol}\cdot\text{g}^{-1}$, respectively; $W = 31$, $p = .03$). Log TMP decreased as a function of standardized capture day during the spawning season ($R^2 = .35$, $F = 11.7$, $df_{1,22}$, $p < .01$, Figure S3b). An increase of 1 unit of standardized spawning day decreased TMP by $3.0 \text{ nmol}\cdot\text{g}^{-1}$. Additionally, Thiamine pyrophosphate (TPP) was significantly higher in early spawning run eggs (mean \pm SD: 2.14 ± 1.00 vs. $0.57 \pm 0.31 \text{ nmol}\cdot\text{g}^{-1}$, respectively; $W = 31$, $p < .01$). Log TPP decreased as a function of standardized capture day during the spawning season ($R^2 = .33$, $F = 11$, $df_{1,22}$, $p < .01$, Figure S3c). An increase of 1 unit of standardized spawning day decreased TPP by $4.3 \text{ nmol}\cdot\text{g}^{-1}$. Free thiamine did not differ between eggs collected during the early (mean \pm SD: $0.05 \pm 0.04 \text{ nmol}\cdot\text{g}^{-1}$) and late (mean \pm SD: $0.069 \pm 0.11 \text{ nmol}\cdot\text{g}^{-1}$) spawning runs ($W = 13$, $p = .53$) (Table 1). Log free thiamine was not significantly associated with standardized day of capture ($R^2 = .11$, $F = 0.249$, $df_{1,22}$, $p = .62$, Figure S3d).

Polyunsaturated fatty acids (n-3; neutral lipid) were strongly associated with the concentration of total thiamine in lake sturgeon eggs ($R^2 = .65$, $F = 18.86$, $df_{1,10}$, $p < .01$; Figure S4a). Additionally, both TMP ($R^2 = .76$, $F = 32.32$, $df_{1,10}$, $p < .01$, Figure S4b) and TPP

($R^2 = .63$, $F = 16.84$, $df_{1,10}$, $p < .01$, Figure S4c) were strongly associated with the content of n-3 PUFAs in lake sturgeon eggs. Conversely, free thiamine ($R^2 = .01$, $F = 0.02$, $df_{1,10}$, $p = .90$, Figure S4d) was not associated with neutral lipids.

ω -3 PUFAs (polar lipid) were associated with the concentration of total thiamine ($R^2 = .46$, $F = 8.16$, $df_{1,10}$, $p = .01$, Figure S5a), and TPP ($R^2 = .44$, $F = 7.75$, $df_{1,10}$, $p = .02$, Figure S5c) in lake sturgeon eggs. Additionally, TMP ($R^2 = .61$, $F = 15.62$, $df_{1,10}$, $p < .01$, Figure S5b) was strongly associated with the content of ω -3 PUFAs in lake sturgeon eggs. Again, free thiamine ($R^2 < .01$, $F < 0.01$, $df_{1,10}$, $p = .98$, Figure S5d) was not associated with polar lipids.

4 | DISCUSSION

Factors related to fatty acid and vitamin provisioning of eggs were investigated in early- and late-spawning groups of lake sturgeon. Thiamine concentrations were significantly higher in females spawning early in the season relative to later spawning females. Thiamine concentration of the late spawning females were below the critical concentration associated with early mortality syndrome (EMS) in Great Lakes salmonids (1.0 nmol g^{-1} total thiamine, Fisher et al., 1995; Fisher et al., 1996; Hill & Nellbring, 1999), though a critical threshold for egg thiamine in sturgeon has not been established. Differences in lipid and thiamine concentrations were not related to female body size or egg size, though egg size was slightly lower in early-spawning females compared to late-spawning females. Lipid concentration (T-MP and T-PP) in sturgeon eggs were moderately but not significantly lower in females spawning late in the run relative to eggs collected from females spawning earlier in the spawning season (Table 1).

While only a small portion of females from each spawning group were sampled in this one study year, maternal effects associated with egg provisioning related to the timing of reproduction remains uncertain and understudied for sturgeons. For some species, older, larger females spawn earlier (Wright & Trippel, 2009) and produce larger, higher quality eggs and larvae than smaller females (Esteve, 2005; Schreck et al., 2001). Data for lake sturgeon in the Black Lake population show no evidence of similar relationships (see also Dammerman et al., 2020). Regardless, the repeatability of spawning times for individuals in the Black Lake population (Forsythe, Crossman, et al., 2012) suggests further studies into factors influencing early life stage survival and ultimately recruitment are warranted.

In fish, synthesis of PUFAs varies temporally (Bergström, 1989; McKinley et al., 1993; Schwalme et al., 1993). Vitamins and PUFAs directly affect reproduction and embryonic development by modulating maturation (Sturmey et al. 2009, McKeegan & Sturmey, 2012). The ratios of n-3 PUFAs on reproduction and embryo/progeny performance were addressed in fish as well as non-teleost vertebrates (Abayasekara & Wathes, 1999). Different metabolic efficiencies associated with differences in incubation temperature can have profound effects on developmental processes that in turn strongly effect larval traits at hatch and through critical early life-history stages. Physiological processes related to egg provisioning represents an important focus for further research. Importantly, metabolic elongation and desaturation of fatty acids is associated with differences in gametogenesis (Carboni et al., 2013; Dupont et al., 2014) and along with embryo incubation temperature, can have profound effects on developmental processes that in turn have been shown to effect larval traits at hatch and through critical early life-history stages in lake sturgeon (Dammerman et al., 2016).

Low concentrations of thiamine in eggs of lake sturgeon may be linked to diet which has been discussed as a major contributor to variation in egg quality in other Great Lakes fishes (Tillit et al., 2009). While dietary information specific to Black Lake lake sturgeon is not available, sturgeon are opportunistic bottom feeders that forage principally on invertebrates within lake substrate. A portion of the lake sturgeon diet includes dreissenid mussels, *Dreissena bugensis* and *D. polymorpha* (Karatajev et al., 2014) that have been shown to have high thiaminase activity (Tillit et al., 2009). Consumption of dreissenids, in conjunction with low thiamine content of lake sturgeon eggs are separate lines of evidence which indicate that lake sturgeon may suffer from thiamine deficiency. Dietary effects may be important to lake sturgeon thiamine concentration but are not likely to completely reconcile egg thiamine concentration in females spawning two weeks apart. Food consumption during the 2-week period that separated the early and late spawning groups (late April vs. mid-May) is unlikely to affect thiamine provisioning of eggs that were fully developed and ovulated (Dettlaff et al., 1993).

Thiamine is an essential element required in biochemical reactions of all organisms. Because free thiamine is scarce in natural environments, organisms have evolved various means of acquisition, in large part associated with dietary consumption (Bettendorff, 2007, review in Kraft & Angert, 2017). Microbes are widely believed to be

involved with production (Fitzpatrick & Thore, 2014; Ji et al., 1998) or degradation by production of thiaminase including the bacterial taxa implicated in other fish species: *Clostridium sporogenes*, *Burkholderia pseudomallei*, *B. thailandensis*, and *Paenibacillus* spp. (Kraft & Angert, 2017). Microbial communities in the sediment and in dietary items consumed by sturgeon are likely to be more abundant and taxonomically different during the later (warmer) period when late-spawning females are present (Abdul Razak et al., 2019; Bucci et al., 2014; Hullar et al., 2006). DNA metabarcoding (e.g., Abdul Razak et al., 2019) could be a profitable avenue of research along with quantitative PCR to ascertain changes in dietary microbial community composition and taxonomic abundance in directions consistent with microbial taxa known to produce or degrade thiamine.

Larval body size (total length, body area, yolk sac area) at hatch was significantly greater in offspring from early spawning females compared to late spawning females (Table 1). Larval size in poikilothermic vertebrates has been widely documented to vary as a function of rearing temperature (Atkinson, 1995) as observed in our data. However, larval size was not significantly associated with thiamine or lipid concentration in this study.

Lake sturgeon abundance and distribution in the Great Lakes has declined precipitously over the past decades (Bruch et al., 2016; Hay-Chmielewski & Whelan, 1997). Understanding the mechanisms associated with declines in abundance is an important research area for fisheries managers, and planning is underway to implement basin-wide restoration activities. Results on lipid and vitamin concentration in lake sturgeon represent the first evidence quantifying differences between different groups of lake sturgeon that spawn at different times in the reproductive season. These data also provide a preliminary evaluation of the importance of main effects and interactions of these nutrients to larval traits at hatch. Perhaps most important, these data provide evidence of decreasing thiamine concentration across a spawning season, which may fill knowledge gaps in the current understanding of female egg provisioning in migratory fish species.

Preliminary data on thiamine-fatty acid interaction in lake sturgeon suggest further research on vitamin and antioxidant interactions is needed. Great Lakes scientists recommended intensification of the studies into natural reproduction and early life history of lake sturgeon (Holey et al., 2000). Given the negative effects of low egg thiamine concentration to salmonid (Czesny et al., 2009, 2012; Fisher et al., 1995, 1996; Hill & Nellbring, 1999) and percid larval survival (Rincharde et al., 2011), and given the findings of this study, further research is warranted for lake sturgeon hatcheries involved in stocking programs. Additional field research could facilitate development of feed formulations that enhance egg, hatch, and larval quality and survival. Other work should specifically evaluate the post-hatch larval survival of lake sturgeon for which egg thiamine approaches the critical level described in salmonids (1.0 nmol g^{-1} , Fisher et al., 1995; Fisher et al., 1996; Hill & Nellbring, 1999). Black Lake was the system where the thiamine deficiency was first documented in lake sturgeon and other Great Lakes tributaries even though there is no present connectivity.

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CONFLICT OF INTEREST

The authors listed above certify that they have no affiliations with or involvement in any organization or entity with any financial or non-financial interest in the subject matter or materials discussed in this manuscript.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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