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Thiamine and Fatty Acid Content of Walleye Tissue from Three Southern U.S. Reservoirs

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[Article]

Thiamine and Fatty Acid Content of Walleye Tissue from Three Southern U.S. Reservoirs

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Abstract.—We determined the thiamine concentration in egg, muscle, and liver tissues of walleyes *Sander vitreus* and the fatty acid content of walleye eggs from three southern U.S. reservoirs. In two Tennessee reservoirs (Dale Hollow and Center Hill), in which there were alewives *Alosa pseudoharengus* in the forage base, natural recruitment of walleyes was not occurring; by contrast in Lake James Reservoir, North Carolina, where there were no alewives, the walleye population was sustained via natural recruitment. Female walleye tissues were collected and assayed for thiamine (vitamin B_1) and fatty acid content. Thiamine pyrophosphate was found to be the predominant form of thiamine in walleye eggs. In 2000, mean total egg thiamine concentrations were similar among Center Hill, Dale Hollow, and Lake James reservoirs (2.13, 3.14, and 2.77 nmol thiamine/g, respectively). Egg thiamine concentration increased as maternal muscle ($r^2 = 0.73$) and liver ($r^2 = 0.68$) thiamine concentration increased. Walleye egg thiamine does not appear to be connected to poor natural reproduction in Tennessee walleyes. Threadfin shad *Dorosoma petenense*, which are found in all three reservoirs, had higher thiaminase activity than alewives. Six fatty acids differed among the walleye eggs for the three reservoirs. Two were physiologically important fatty acids, arachidonic acid (20:4[n-6]) and docosahexaenoic acid (22:6[n-3]), which are important eicosanoid precursors involved in the regulation of biological functions, such as immune response and reproduction.

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Thiamine is an essential vitamin necessary for normal energy metabolism within the Krebs cycle, synthesis of ribose in the pentose phosphate shunt (transketolase), and neurological function in vertebrates, including fish (Halver 1989). Thiamine pyrophosphate is the active cofactor in thiamine-requiring enzymes. Salmonid reproductive failure in the Great Lakes and New York's Finger Lakes has been linked to thiamine deficiency caused by the consumption of nonnative species, such as alewife *Alosa pseudoharengus* (Brown et al. 2005). Several freshwater fish and marine species, including alewives, contain a vitamin-destroying enzyme, thiaminase (Neilands 1947; Greig and Gnaedinger 1971; Ji and Adelman 1998). Thiaminase catalyzes a base substitution reaction (Evans 1975). In the reaction, thiazole moiety is cleaved from the thiamine molecule and an organic base (Lewis base) is substituted for thiazole. The resulting molecule typically cannot be phosphorylated or function as a cofactor (thiamine pyrophosphate) in thiamine-requiring enzymes, thus leading to thiamine deficiency and fry mortality.

Other deficiencies of essential nutrients may also contribute to recruitment failure. Deficiencies in essential fatty acids have been shown to impair larval behavior (Bell et al. 1995; Masuda et al. 1998; Ishizaki et al. 2001). Normal behavior is critical to feral fish survival. More is known about the role of essential

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fatty acids in immune function and disease resistance of finfishes (reviewed by Balfry and Higgs 2001) than reproduction. For additional information on the biochemistry of lipids and fatty acids in freshwater fish, see Henderson and Tocher (1987). There is limited evidence that fatty acids may be important in the reproduction process of walleye *Sander vitreus* (Czesny and Dabrowski 1998). The composition of the food web is important, and it is well established that maternal diet influences fatty acid profiles in eggs and, thus, can influence egg quality (Fernandez-Palacios et al. 1995; Rodrigues et al. 1998; Pickova et al. 2003). In the reproductive failure of Baltic salmonids, Pickova et al. (2003) reported a difference in fatty acid profiles among fish affected with M74, another thiamine-responsive syndrome.

Natural reproduction of walleyes in many Tennessee reservoirs has become a concern. Before the construction of flood control and hydroelectric dams on the Cumberland and Tennessee rivers in the 1940s, walleye populations were sustained via natural reproduction (Hackney and Holbrook 1978). After the construction of Dale Hollow Reservoir in the Cumberland River drainage, the walleye population in the reservoir initially thrived but declined shortly thereafter (Hackney and Holbrook 1978). The factor(s) leading to poor recruitment was never identified. A similar decline in the walleye population occurred in Center Hill Reservoir, a tributary impoundment in the Cumberland River drainage that was impounded in 1948.

Self-sustaining walleye populations in Dale Hollow Reservoir and Center Hill Reservoir were subsequently reestablished with progeny from Great Lakes walleye stocks in the 1960s (Libbey 1969); those populations persisted through the early 1980s (Schultz 1992). Subsequent recruitment failure by walleye in Dale Hollow Reservoir was noted in the late 1970s after the introduction of alewives as an additional forage species (Vandergoot and Bettoli 2003). Beginning in the mid-1980s, the walleye fishery in Dale Hollow Reservoir could only be maintained by stocking walleye fry and fingerlings. A walleye stocking program was also initiated at Center Hill Reservoir in 2001 after routine sampling by the Tennessee Wildlife Resources Agency (TWRA) revealed declining walleye recruitment and the presence of a self-sustaining population of alewives that arose from an illegal or accidental introduction (T. Churchill, TWRA, personal communication).

Walleye forage species in some Tennessee reservoirs have also changed over time. Gizzard shad *Dorosoma cepedianum*, which are native to the lower reaches of the Cumberland River (Etnier and Starnes 1993), initially flourished in Dale Hollow Reservoir and Center Hill Reservoir. Later, threadfin shad *D. petenense* were stocked to provide pelagic forage for walleyes, black bass *Micropterus* spp., and crappies *Pomoxis* spp. (Netsch and Turner 1964; Range 1971). The last known introduced species, alewife, was first stocked in the 1970s into Dale Hollow Reservoir, as noted above.

Natural recruitment failure of native freshwater fishes in North American lakes and reservoirs has been associated with the presence of alewives and rainbow smelt *Osmerus mordax* (Crowder 1980; Ketola et al. 2000). In reservoirs outside of the Great Lakes, alewife and rainbow smelt were introduced into freshwater environments either intentionally or by accident (Van Oosten 1937; Miller 1957; Ketola et al. 2000). As the burgeoning Great Lakes populations of alewife grew, natural reproduction of lake trout *Salvelinus namaycush* (Holey et al. 1995), cisco *Coregonus artedi* (Eck and Wells 1987; Hrabik et al. 1998), lake whitefish *C. clupeaformis* (Hoagman 1974), yellow perch *Perca flavescens* (Brandt et al. 1987; Hrabik et al. 1998), and walleye (Johnson and Goettl 1999) plummeted. Although competition and predation by these nonnative fishes have been suggested as causative factors in the decline of native fish populations (Crowder 1980; Brandt et al. 1987; Hrabik et al. 1998), the evidence has usually been indirect or circumstantial. In laboratory studies, Honeyfield et al. (2005) documented that low egg thiamine in lake trout fed either alewife or experimental diets containing bacterial thiaminase produced low egg thiamine that led to high fry mortality. Those findings were consistent with observations from feral fish (Fitzsimons et al. 1995; Marcquenski and Brown 1997; McDonald et al. 1998; Fitzsimons and Brown 1999; Hill and Nellbring 1999).

For this study, we measured walleye tissue concentrations of thiamine and fatty acids. Walleyes were evaluated from two reservoirs containing alewife with limited or no natural walleye recruitment and from one reservoir with natural walleye reproduction with no alewife. The objectives were to (1) measure the concentration of thiamine and fatty acid content of walleye eggs from those three southern U.S. reservoirs; (2) determine major body stores of thiamine in female walleye muscle and liver; and (3) report thiaminase activity of alewife and threadfin shad in the Tennessee reservoirs.

Methods

Broodfish collection.—In March 1999, eggs from 10 walleyes were collected at or near known spawning areas in Dale Hollow Reservoir and from 15 walleyes in Center Hill Reservoir to ascertain egg thiamine

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status. Although two methods of collecting eggs were used in this study, no difference in egg thiamine was found in lake trout eggs that had ovulated (free flowing) or were unovulated up to 21 d before expected spawning (D.C.H., unpublished data). Thus, different egg collection methods were assumed to be inconsequential to the outcome of the study. In March 2000, adult female walleyes ($n = 12$–13) were collected from two Tennessee reservoirs with horizontal gill nets (50-mm-bar mesh) and DC electrofishing gear. Fish were transported in an aerated hauling tank (1,140 L) to the Tennessee Cooperative Fishery Research Unit laboratory in Cookeville. Females were held at 8–10°C in 2,014-L tanks supplied with recirculated water treated by biofilters. Maximum fish density was 7 kg/m^3. Fish were held from 6 h to a maximum of 7 d. Spawning readiness was checked twice daily by gently squeezing the abdomen of females to determine the presence of free-flowing eggs. Walleyes that failed to ovulate within the first 24 h of capture were injected intraperitoneally with 1 mL Chorulon (human chorionic gonadotropin [HCG]), and every 72 h thereafter until ovulation occurred. Fish were anesthetized with tricaine methanesulfonate (MS-222; 50–100 mg/L) by immersion before the HCG injections and spawning. After they ovulated, fish were subsequently euthanized by effecting cervical dislocation via a blow to the head and closely observing them to ensure all gill and muscle movement ceased. Egg, muscle, and liver tissue samples were immediately taken for thiamine analysis. Similar samples were collected in 2000 from 12 walleyes captured in Lake James Reservoir, North Carolina. We sampled 10 g (each) of eggs, liver, and muscle from each fish. Tissue samples were immediately placed on dry ice and stored at −80°C until analyzed. Adult fish were measured for total length (TL; mm) and weighed (g). Sagittal otoliths were removed for age determination (Erickson 1983).

Thiamine and fatty acid analysis.—Commercially available authentic standards were used to identify chromatographic peaks. Data reported are from duplicate analyses of each sample with less than 10% difference in value. Walleye egg, liver, and muscle thiamine content was quantified with the high-performance liquid chromatography method described by Brown et al. (1998). The method separates and measures the concentration of the three forms of thiamine: thiamine pyrophosphate (TPP), thiamine monophosphate (TMP), and free thiamine. Fatty acid profiles of walleye eggs were determined by fatty acid methyl ester analyses, which consisted of three steps: extraction, derivatization, and quantification with a gas chromatograph. Briefly, samples were extracted in a 2:1 chloroform : methanol solution (Bligh and Dyer 1959). Methyl ester derivatives of the fatty acids were prepared with BF3-methanol (10% by weight) and quantified with gas chromatography as described by Watkins et al. (1997).

Clupeid collections and thiaminase activity.—Clupeids were collected with vertical gill nets in Center Hill and Dale Hollow reservoirs during July–August 1999 and in Lake James during August 2000. Vertical gill nets (bar measures 13 and 19 mm) were constructed of nylon mesh; each net was 3.7 m wide × 36 m deep. Three transects were established on each reservoir; generally, transects were located near the dam, mid reservoir, and below the headwaters. Nets were deployed at dusk (1700–1900 hours) and retrieved the following morning (0800–1000 hours). At time of collection, fish length (mm) and weight (g) were recorded before freezing. Fish were frozen on dry ice and stored at −80°C until analyzed. Thiaminolytic activity (nmol thiamine destroyed·g^{-1}·min^{-1}) for fish collected from the two Tennessee reservoirs was determined following the methods of Zajicek et al. (2005). As a result of not maintaining the samples frozen during transport, quantitative values for thiaminolytic activity in Lake James clupeids were deemed unacceptable for reporting.

Statistical analysis.—Mean TLs, weights, and ages of female walleyes collected from Center Hill Reservoir, Dale Hollow Reservoir, and Lake James were evaluated with one-way analysis of variance (ANOVA) and Duncan's multiple-comparison procedure. Similarly, the variance in mean thiamine concentration in egg, liver, and muscle samples was tested with ANOVA. Relationships between thiamine concentrations in different tissues were conducted with simple linear regression models. Mean TLs, weights, and thiaminase activity in clupeids also were compared with ANOVA. All statistical analyses were performed with Statistical Analysis System (SAS) software (SAS 2003).

Results

Broodfish Characteristics

Mean ± SE walleye TL ($P = 0.2153$), weight ($P = 0.1797$), and age ($P = 0.4986$) in 2000 were similar among the three reservoirs: Center Hill (565 ± 10.5 mm, 1,927 ± 149 g, 4.0 ± 0.11 years), Dale Hollow (556 ± 15.4 mm, 1,950 ± 170 g, 4.0 ± 0.77 years), and Lake James (528 ± 19.4 mm, 1,561 ± 166 g, 5.0 ± 0.38 years).

Thiamine Content of Eggs and Somatic Tissues

Mean walleye egg TPP ($P = 0.0017$), TMP ($P = 0.0016$), and total thiamine ($P = 0.0043$) concentrations differed between Center Hill Reservoir and Dale

TABLE 1.—Mean (SE) thiamine pyrophosphate (TPP), thiamine monophosphate (TMP), free or unphosphorylated thiamine (T), and total thiamine (total T) concentrations (nmol/g) in egg, muscle, and liver tissues of walleyes collected from two Tennessee reservoirs (Center Hill and Dale Hollow) and a North Carolina reservoir (Lake James), 1999 and 2000. Within columns, values with different letters are significantly different ($P < 0.05$).

Reservoir	*N*	TPP	TMP	T	Total T
			Eggs, 1999[a]		
Center Hill	10	1.27 (0.12)	0.13 (0.02)	0.01 (0.009)	1.41 (0.14)
Dale Hollow	15	3.15 (0.42)	0.50 (0.08)	0.21 (0.129)	3.86 (0.62)
			Eggs, 2000		
Center Hill	13	1.81 (0.26)	0.30 (0.04)	0.02 (0.005)	2.13 (0.31)
Dale Hollow	12	2.65 (0.35)	0.46 (0.07)	0.03 (0.009)	3.14 (0.43)
Lake James	12	2.28 (0.40)	0.46 (0.08)	0.03 (0.012)	2.77 (0.48)
			Muscle		
Center Hill	13	0.204 (0.04)	0.029 (0.01)	0.008 (0.001) y	0.241 (0.05)
Dale Hollow	12	0.447 (0.12)	0.070 (0.02)	0.004 (0.001) y	0.520 (0.14)
Lake James	12	0.565 (0.15)	0.061 (0.02)	0.014 (0.002) z	0.640 (0.17)
			Liver		
Center Hill	13	1.39 (0.42) y	0.26 (0.05)	0.01 (0.002) y	1.66 (0.28) y
Dale Hollow	12	2.29 (0.42) zy	0.39 (0.07)	0.02 (0.009) y	2.69 (0.50) zy
Lake James	12	3.01 (0.55) z	0.52 (0.10)	0.05 (0.010) z	3.57 (0.65) z

[a] The differences between reservoirs were significant for TPP ($P = 0.0017$), TMP ($P = 0.0016$), and total T ($P = 0.0043$) but not for T ($P = 0.2149$).

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Hollow Reservoir in 1999, but there was no difference in free thiamine ($P = 0.2149$; Table 1). Egg total thiamine concentrations in 2000 were similar among the three walleye populations (Table 1). Furthermore, mean egg total thiamine concentrations were similar in Tennessee walleyes between 1999 and 2000: TPP ($P = 0.5037$), TMP ($P = 0.7589$), free thiamine ($P = 0.1608$), and total thiamine ($P = 0.5025$).

All forms of thiamine (i.e., TPP, TMP, and free thiamine) were present at higher concentrations in the eggs and livers of walleyes than in their muscle tissue (Table 1). The predominant form of thiamine in walleye eggs was TPP (84–88%). In 2000, mean total thiamine concentrations in muscle were higher in Lake James walleyes than in fish from the two Tennessee reservoirs (Table 1). All other thiamine concentrations in muscle tissue and eggs were similar. Liver thiamine concentrations varied more and were higher in walleyes from Lake James than in walleyes from Center Hill Reservoir (Table 1). Within the 2000 data, a strong positive relationship in total thiamine concentrations existed between eggs and liver tissue (combined data; $R^2 = 0.73$) and between eggs and muscle tissue (combined data; $R^2 = 0.68$). The relationship between egg total thiamine concentration and tissue concentration was stronger when evaluated by state for liver (Tennessee: $R^2 = 0.79$, $P < 0.0001$; North Carolina: $R^2 = 0.66$, $P = 0.0012$; Figure 1) and muscle (Tennessee: $R^2 = 0.85$, $P < 0.0001$; North Carolina: $R^2 = 0.76$, $P = 0.0002$; Figure 2). A positive relationship between maternal age and total egg thiamine existed only in Lake James walleyes ($R^2 = 0.56$).

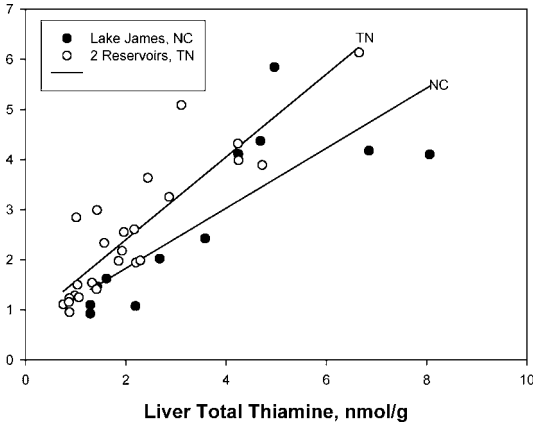

FIGURE 1.—Relationship between total thiamine in walleye liver and egg samples from fish collected in Center Hill and Dale Hollow reservoirs, Tennessee (intercept = 0.746, slope = 0.826; $R^2 = 0.79$) and Lake James, North Carolina (intercept = 0.627, slope = 0.600; $R^2 = 0.66$), 1999 and 2000.

Clupeid Catches and Thiaminase Activity

Threadfin shad represented most (≥95%) of the shad captured in vertical gill nets in Center Hill Reservoir and Lake James and all of the shad collected in Dale Hollow Reservoir (i.e., no gizzard shad were collected in Dale Hollow Reservoir). Alewives were collected in Center Hill and Dale Hollow reservoirs. No alewives were found in Lake James. Alewife TL and weight (mean ± SE) were greater in fish from Center Hill (158 ± 2.0

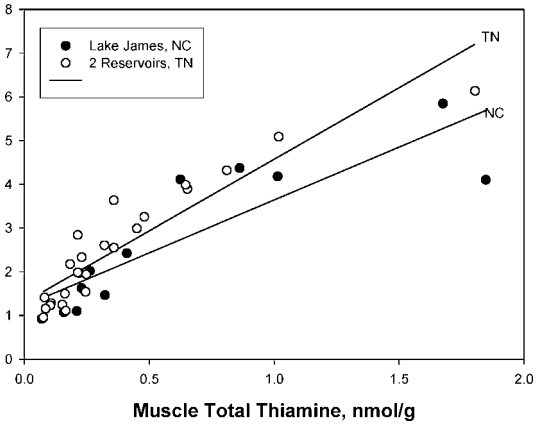

FIGURE 2.—Relationship between total thiamine in walleye muscle and egg samples from fish collected in Center Hill and Dale Hollow reservoirs, Tennessee (intercept = 1.298, slope = 3.274; $R^2 = 0.85$) and Lake James, North Carolina (intercept = 1.223, slope = 2.417; $R^2 = 0.76$), 1999 and 2000.

mm, 34 ± 1.1 g; $n = 10$) than in those from Dale Hollow (116 ± 1.5 mm, 12 ± 0.4 g; $n = 10$). There were no differences in the mean TL or weight of threadfin shad from Center Hill (100 ± 1.8 mm, 8 ± 0.4 g; $n = 20$) and Dale Hollow (97 ± 1.3 mm, 7 ± 0.3 g; $n = 10$). Average thiaminase activity was higher in 30 threadfin shad (11.25 ± 0.61 nmol thiamine destroyed·g^{-1}·min^{-1}) than in Tennessee alewives (3.3 ± 0.32 nmol thiamine destroyed·g^{-1}·min^{-1}; $n = 20$). Mean thiaminase activity in alewives was similar in Center Hill Reservoir (3.8 ± 0.50 nmol·g^{-1}·min^{-1}) and Dale Hollow Reservoir (2.8 ± 0.41 nmol·g^{-1}·min^{-1}). Similarly, there was no difference in mean thiaminase activity in threadfin shad from Center Hill Reservoir (11.5 ± 0.93 nmol·g^{-1}·min^{-1}) and Dale Hollow Reservoir (11.0 ± 0.50 nmol·g^{-1}·min^{-1}).

Egg Fatty Acids

Six fatty acids in walleye eggs were found to differ between the two Tennessee reservoirs and North Carolina's Lake James: myristic acid (14:0), palmitic acid (16:0), erucic acid (20:1[n-9]), arachidonic acid (20:4[n-6]; ARA), eicosatetraenoic acid (22:4[n-6]), and docosahexaenoic acid (22:6[n-3]; DHA); Table 2).[1] Two polyunsaturated fatty acids (PUFAs) that are precursors of longer-chained essential fatty acids differed in eggs from Center Hill Reservoir and Lake James: linoleic acid (18:2[n-6]) and stearidonic acid (18:4[n-3]). Two essential omega-3 fatty acid precursors of DHA—α-linolenic acid (18:3[n-3]; ALA) and eicosapentaenoic acid (20:5[n-3])—and one omega-6 fatty acid precursor—γ-linolenic acid (18:3[n-6]) of ARA were similar among fish from the three sites. Differences among egg fatty acid content from the three locations in essential PUFAs existed for ARA ($P < 0.0001$) and DHA ($P < 0.0001$). The sum of omega-3 PUFA fatty acids ($P = 0.0402$) and the ratio of omega-6 to omega-3 fatty acids ($P = 0.0075$) differed among the three locations.

Discussion

Compared with salmonid data, walleye egg thiamine is low and within the range in which fry mortality has been documented (McDonald et al. 1998). The interesting thing is that Lake James walleyes are reproducing with low egg thiamine, whereas Tennessee walleyes were not reproducing. Although we found differences in walleye egg thiamine collected from two Tennessee reservoirs in 1999, egg thiamine values were in the lower end of the salmonid range. Lake trout egg thiamine has been reported to average 30 nmol/g in fish without thiaminase in the diet, and individual egg lots can be as high as 60–100 nmol/g (Honeyfield et al. 1998b). The mean egg thiamine concentration of walleyes collected in southern U.S. waters in the present study is comparable to that for walleyes collected in the St. Mary's River, Michigan (3.81 nmol/g; G. Wright, Chippewa–Ottawa Tribal Fishery Management Association, personal communication) and in several of New York's Finger Lakes (individual lake means ranged from 2.4 to 4.3 nmol/g; G. Ketola, U.S. Geological Survey, personal communication). Thiaminase-positive prey are present in all of these waters.

Thiaminase activity for threadfin shad has not been reported in the literature. Threadfin shad thiaminase activity was found to be higher than alewife and lower than that reported for gizzard shad (Tillitt et al. 2005). Thiaminase activity of threadfin shad from Lake Griffin, Florida (J. P. Ross, University of Florida, personal communication), was similar to data in this study. Clupeids are the predominate forage of walleyes in many southern reservoirs (Muench 1966; Kohler and Ney 1982; Ney et al. 1982). Thiaminase activity in Tennessee reservoir alewives was comparable with thiaminase activity of New York's Finger Lakes alewives (mean, 3.4 nmol thiamine destroyed·g^{-1}·min^{-1}; range, 1.6–5.3; Fitzsimons et al. 2005) and Lake Michigan alewives (4.28 nmol·g^{-1}·min^{-1}; Tillitt et al. 2005). There is little doubt that thiaminase in the forage base affects thiamine stores, but because

[1] In this fatty acid notation, the number to the left of the colon is the number of carbon atoms in the compound, the number immediately to the right of the colon is the number of double bonds, and the number after the hyphen indicates the position of the first double bond from the methyl end.

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TABLE 2.—Mean (SE) walleye (expressed as a percentage of total fatty acids in walleye egg lipid) egg fatty acid content from two Tennessee reservoirs (Center Hill and Dale Hollow) with little or no natural reproduction and one reservoir in North Carolina (Lake James) with natural reproduction, 1999 and 2000. Within rows, means with different letters are significantly different ($P < 0.05$).

Fatty acid					
Molecular formula	Common name	Center Hill	Dale Hollow	Lake James	P[a]
14:0	Myristic acid	2.84 (0.072) z	3.02 (0.110) z	2.49 (0.154) y	0.0085
15:0	Pentadecanoic acid	1.51 (0.035)	1.57 (0.061)	1.51 (0.105)	0.7900
16:0	Palmitic acid	9.57 (0.176) y	9.50 (0.140) y	10.27 (0.193) z	0.0068
16:1(n-7)t	trans-Palmitoleic acid	1.79 (0.045) y	2.19 (0.125) z	1.63 (0.093) y	0.0005
16:1(n-7)c	cis-Palmitoleic acid	10.51 (0.415) y	8.46 (0.409) z	9.56 (0.337) z	0.0028
16:2(n-4)	Hexadecadienoic acid	0.42 (0.032)	0.36 (0.059)	0.30 (0.024)	0.1600
16:3(n-4)	Hexadecatrienoic acid	0.61 (0.111) y	1.19 (0.021) z	1.34 (0.079) z	<0.0001
17:0	Heptadecanoic acid	6.69 (0.201)	6.96 (0.241)	7.05 (0.294)	0.5500
18:0	Stearic acid	1.65 (0.029)	1.58 (0.039)	1.72 (0.064)	0.1120
18:1(n-9)	Oleic acid	12.21 (0.168) y	14.31 (0.500) z	11.99 (0.346) y	<0.0001
18:1(n-7)	cis-Vaccenic acid	2.41 (0.048) z	2.15 (0.048) y	2.54 (0.103) z	0.0014
18:2(n-6)t	Linolelaidic acid	0.19 (0.008)	0.26 (0.009)	0.24 (0.028)	0.3330
18:2(n-6)	Linoleic acid	4.41 (0.069) z	4.24 (0.094) zy	4.07 (0.118) y	0.0516
18:3(n-6)	γ-linolenic acid	0.52 (0.012)	0.53 (0.012)	0.54 (0.030)	0.6800
18:3(n-3)	α-Linolenic acid	5.76 (0.184)	4.85 (0.413)	5.07 (0.365)	0.1250
18:3(n-4)		1.44 (0.048)	1.33 (0.054)	1.48 (0.071)	0.1920
18:4(n-3)	Stearidonic acid	1.67 (0.084) y	1.98 (0.099) zy	2.12 (0.157) z	0.0240
20:1(n-9)	Erucic acid	0.25 (0.008) y	0.27 (0.013) y	0.35 (0.024) z	0.0003
20:2(n-6)	cis-ll, 14-Eicosadienoic acid	0.17 (0.007) y	0.20 (0.005) z	0.20 (0.009) z	0.0036
20:3(n-3)	Eicosatrienoic acid (ETA)	0.24 (0.020)	0.23 (0.004)	0.22 (0.011)	0.7000
20:3(n-6)	Homo-γ-linolenic acid	0.24 (0.006) z	0.22 (0.005) y	0.25 (0.015) z	0.0130
20:4(n-3)	ω-3 arachidonic acid	0.88 (0.028) y	0.98 (0.027) z	0.81 (0.044) y	0.0038
20:4(n-6)	Arachidonic acid	2.94 (0.082) x	3.31 (0.075) y	3.61 (0.096) z	<0.0001
20:5(n-3)	Eicosapentaenoic acid (EPA)	0.34 (0.010)	0.31 (0.010)	0.33 (0.020)	0.1800
22:4(n-6)	cis-7, 10, 13, 16-Eicosatetraenoic acid	0.40 (0.029) y	0.42 (0.022) y	0.68 (0.056) z	<0.0001
22:5(n-6)	ω-6 Docosapentaenoic acid	2.26 (0.120) y	2.79 (0.091) z	2.34 (0.140) y	0.0064
22:5(n-3)	Docosapentaenoic acid	1.76 (0.059) z	1.54 (0.036) y	1.96 (0.107) z	0.0010
22:6(n-3)	Docosahexaenoic acid	15.51 (0.241) y	17.25 (0.327) z	14.21 (0.598) x	<0.0001
	All saturated fatty acids	22.27 (0.141)	22.63 (0.194)	23.04 (0.314)	0.0590
	All monounsaturated fatty acids	27.41 (0.471)	27.42 (0.503)	26.08 (0.567)	0.1300
	All omega-6 polyunsaturated fatty acids	10.99 (0.229) y	11.82 (0.147) z	11.83 (0.265) z	0.0118
	All omega-3 polyunsaturated fatty acids	30.83 (0.298) zy	31.02 (0.445) z	29.22 (0.764) y	0.0402
	Ratio of all omega-6 to all omega-3 fatty acids	0.36 (0.008) y	0.38 (0.007) zy	0.41 (0.017) z	0.0075

[a] P-value from analysis of variance.

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this study did not examine a walleye population without a thiaminase-positive forage base, it is not possible to state with certainty what egg, muscle, and liver thiamine concentrations would be in walleyes without dietary thiaminase. Lake James walleyes are reproducing (Besler 2004) with low egg thiamine as are walleyes in Greer's Ferry Reservoir, which harbors threadfin and gizzard shad in its prey base (T. Bly, Arkansas Game and Fish Commission, personal communication). The difference between Tennessee walleyes with poor reproduction (Vandergoot and Bettoli 2001, 2003) and these other two populations of walleyes is the presence of alewives in Tennessee reservoirs. The influence of alewives on walleye reproduction is unclear and warrants further investigation.

Another difference between salmonids and walleyes is the predominant form of thiamine. In salmonid eggs, thiamine is free or nonphosphorylated (McDonald et al. 1998), while thiamine pyrophosphate is the predominant form in walleye eggs. Thiamine pyrophosphate is the metabolic active cofactor of thiamine-requiring enzymes (Phillips 1988). If consideration is given to the difference in egg development between the two species, the time interval between fertilization and hatch is relatively short for walleyes (10–21 d) compared with lake trout (2–4 months; Scott and Crossman 1973; Balon 1980). Thus, the difference in form of thiamine would appear to mirror the immediate metabolic requirement of thiamine pyrophosphate in walleyes, whereas in salmonids, a longer incubation time would allow for the translation of RNA and synthesis of the kinase involved in phosphorylation of thiamine. In lake trout, thiamine pyrophosphate begins to increase around the fourth week in eggs incubated at 9°C (D.C.H., unpublished data).

Fisher et al. (1995, 1996) and Fitzsimons and Brown (1998) reported that liver and muscle samples could be used as a surrogate measure of egg thiamine in lake trout and Atlantic salmon *Salmo salar*. Walleye muscle

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and liver are lower in thiamine concentration than in several salmonid species (Marcquenski and Brown 1997; Amcoff et al. 1998; Honeyfield et al. 1998a; Fitzsimons et al. 1999). The significance of this is not known, but walleyes may rely less on metabolic pathways requiring thiamine than salmonid species. A positive relationship between walleye age and egg thiamine was observed only in Lake James walleyes. In contrast, lake trout egg thiamine has been reported to decline in older fish (Fitzsimons and Brown 1998).

In this study, we found a difference in egg fatty acid composition among the two Tennessee walleye populations and the Lake James, North Carolina, population. In this study, saturated fatty acids and monounsaturated fatty acids differed from that reported for northern latitude walleye populations (Moodie et al. 1989; Czesny and Dabrowski 1998; Wiegand et al. 2004). The higher level of saturated fatty acids and a lower level of monounsaturated fatty acids found in walleyes from three southern reservoirs is probably an adaptation to water temperatures. Fatty acid composition of fish from more southern ranges has been reported to contain more saturated fatty acids than fish of the same species from colder, more northern latitudes (Glemet et al. 1997). Alternatively, higher saturated fatty acids may indicate a greater reliance on bacterial sources of fatty acids in the food web (Arts and Wainman 1998).

Fish have a metabolic requirement for PUFAs such as ALA, eicosapentaenoic acid (20:5[n-3]; EPA), DHA, and ARA (NRC 1993). These fatty acids play a crucial role in physiology and reproduction of fish and zooplankton in both marine and freshwater ecosystems (Arts 1997, 1998; Arts et al. 2001). Czesny and Dabrowski (1998) suggested that a deficiency of omega-3 fatty acids reduces walleye reproduction. In this study, Dale Hollow walleye eggs had higher levels of omega-3 PUFAs than fish from Lake James, suggesting that a deficiency of omega-3 fatty acids was not involved. We did observe differences in important fatty acids (ARA and DHA) among the three walleye populations (Table 2). Both fatty acids are precursors to separate families of eicosanoids (Kinsella et al. 1990) and may have biological significance, especially in the ratio of their relative amounts. In walleye eggs from Dale Hollow and Center Hill, the ARA : DHA ratio was lower (0.19) than in eggs from Lake James (0.25). The Lake James value is closer to that observed in walleye eggs (0.28) from Greer's Ferry Reservoir, Arkansas (Wiegand et al. 2004). Ling et al. (2006) found a significant impact of these fatty acids on the reproduction of green swordtail *Xiphophorus hellerii*. Although promising, our present knowledge is inadequate to suggest a role for these two fatty acids or their eicosanoid metabolite in walleye reproduction. Further investigations would be enlightening.

Alternately, differences in egg fatty acids may be a reflection of the food web for the three populations. Palmitoleic acid (16:1[n-7]) is associated with diatoms, some cyanobacteria and some sulfate-reducing bacteria, whereas the sum of pentadecanoic acid (15:0), heptadecanoic acid (17:0), cis-11-heptadecanoic acid (17:1) and oleic acid (18:1[n-9]) provide an index of the bacterial sources of fatty acids (Napolitano 1999). Diatoms are a good source of EPA, but not generally of DHA. Cryptophytes depending on species are rich in EPA (Weers and Gulati 1997; von Elert and Stampel 2000). Dinoflagellates are often associated with DHA (Napolitano 1999). In addition, alewives have been reported to affect the food web by their foraging activity (Wells 1970). The presence of alewives as forage in the Tennessee reservoirs but not in Lake James could also be reflected in the walleye egg fatty acid profiles. Fatty acids are being successfully used to understand prey consumption in aquatic species (Iverson et al. 2004). One thing is certain, our understanding of lipids and sources of fatty acids in freshwater systems lag behind knowledge of saltwater food webs (Arts and Wainman 1998).

In summary, walleye egg thiamine does not appear to be the reason for poor natural reproduction in Tennessee walleyes. Threadfin shad thiaminase activity is higher than that reported for alewives and less than that reported in gizzard shad. Finally, many questions concerning the differences observed in walleye egg fatty acids remain unanswered.

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