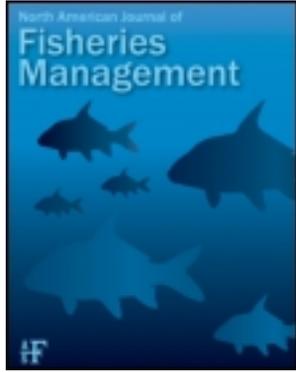


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North American Journal of Fisheries Management

Publication details, including instructions for authors and subscription information:

<http://www.tandfonline.com/loi/ujfm20>

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Version of record first published: 19 Dec 2011.

To cite this article: Stephen C. Riley, Jacques Rinchar, Dale C. Honeyfield, Allison N. Evans & Linda Begnoche (2011): Increasing Thiamine Concentrations in Lake Trout Eggs from Lakes Huron and Michigan Coincide with Low Alewife Abundance, North American Journal of Fisheries Management, 31:6, 1052-1064

To link to this article: <http://dx.doi.org/10.1080/02755947.2011.641066>

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ARTICLE

Increasing Thiamine Concentrations in Lake Trout Eggs from Lakes Huron and Michigan Coincide with Low Alewife Abundance

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Abstract

Lake trout *Salvelinus namaycush* in the Laurentian Great Lakes suffer from thiamine deficiency as a result of adult lake trout consuming prey containing thiaminase, a thiamine-degrading enzyme. Sufficiently low egg thiamine concentrations result in direct mortality of or sublethal effects on newly hatched lake trout fry. To determine the prevalence and severity of low thiamine in lake trout eggs, we monitored thiamine concentrations in lake trout eggs from 15 sites in Lakes Huron and Michigan from 2001 to 2009. Lake trout egg thiamine concentrations at most sites in both lakes were initially low and increased over time at 11 of 15 sites, and the proportion of females with egg thiamine concentrations lower than the recommended management objective of 4 nmol/g decreased over time at eight sites. Egg thiamine concentrations at five of six sites in Lakes Huron and Michigan were significantly inversely related to site-specific estimates of mean abundance of alewives *Alosa pseudoharengus*, and successful natural reproduction of lake trout has been observed in Lake Huron since the alewife population crashed. These results support the hypothesis that low egg thiamine in Great Lakes lake trout is associated with increased alewife abundance and that low alewife abundance may currently be a prerequisite for successful reproduction by lake trout in the Great Lakes.

Lake trout *Salvelinus namaycush* are native to but were virtually extirpated from the Laurentian Great Lakes exclusive of Lake Superior by the 1950s due to a combination of overfishing and predation by sea lampreys *Petromyzon marinus* (Hansen 1999). Sea lamprey control and stocking programs to restore

lake trout populations in the Great Lakes have been underway since the 1960s, but there has been little evidence of sustained natural reproduction of lake trout outside Lake Superior since these efforts began (Krueger et al. 1995a; Eshenroder et al. 1999; Krueger and Ebener 2004). There are many potential

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Received January 4, 2011; accepted July 20, 2011

reasons for a lack of natural reproduction (Bronte et al. 2003), which include insufficient numbers of adults, inappropriate stocking practices, and poor survival of early life stages (Holey et al. 1995; Bronte et al. 2007, 2008). Poor early life stage survival likely results from at least two mechanisms: predation on lake trout embryos and juveniles, and a thiamine (vitamin B₁) deficiency that causes lake trout embryo mortality (Brown et al. 2005a; Strakosh and Krueger 2005; Bronte et al. 2008).

Thiamine deficiency complex (TDC; also known as early mortality syndrome) results in early life stage mortality of salmonines in the Great Lakes and may also decrease the performance or survival of adults (Brown et al. 2005a, 2005b; Fitzsimons et al. 2005a; Ketola et al. 2009a). Thiamine deficiency complex results from low thiamine concentrations that are thought to be caused by thiaminase (a thiaminolytic enzyme) in the diet of adult lake trout (Honeyfield et al. 2005; Tillitt et al. 2005). Invasive alewives *Alosa pseudoharengus* in the Great Lakes contain high thiaminase activity (Ji and Adelman 1998; Fitzsimons et al. 2005b; Tillitt et al. 2005), and the ingestion of alewives by adult female lake trout is thought to lower their whole-body thiamine content, resulting in too little thiamine to allocate to eggs (Brown et al. 2005a).

The egg thiamine concentration associated with 20% fry mortality (ED20) for lake trout has been estimated to be 2.63 nmol/g (95% confidence interval [CI] = 1.27–4.84 nmol/g; Fitzsimons et al. 2007), whereas sublethal effects (i.e., 20–50% reductions in foraging and growth rates) of low thiamine on lake trout fry occur when thiamine concentrations are less than approximately 3–8 nmol/g (Fitzsimons et al. 2009). Thiamine deficiency complex may be a significant impediment to natural reproduction by lake trout in the Great Lakes and may be an obstacle to restoration of this native species (Brown et al. 2005a), and egg thiamine concentrations greater than 4 nmol/g have been recommended by Great Lakes fishery managers for successful lake trout reproduction (Bronte et al. 2008).

Long-term monitoring provides valuable information upon which to evaluate management objectives. In 2001, the U.S. Geological Survey (USGS) began cooperating with natural resource agencies in the Great Lakes to conduct a monitoring program in Lakes Michigan and Huron to assess the status of lake trout populations relative to the management objective of 4 nmol/g of thiamine in lake trout eggs. This paper represents the first analysis of long-term trends in lake trout egg thiamine resulting from this collaborative effort. Herein we report the results of lake trout egg thiamine monitoring at 15 sites in Lakes Huron and Michigan. The objectives of our analyses were to (1) determine whether lake trout egg thiamine concentrations have changed over time and whether those changes differed by site and lake, (2) determine whether the proportion of females with egg thiamine lower than 4 nmol/g has changed over time and whether the change differed by site and lake, and (3) determine whether lake trout egg thiamine concentrations were related to alewife abundance.

METHODS

Sample collection.—Mature female lake trout were collected using gill nets during annual assessment surveys at 15 sites in Lakes Huron and Michigan during the spawning season (October–November) during 2001–2009 (Figure 1). At some sites, females were collected from more than one spawning reef. Five to ten grams of eggs were sampled from each lake trout and were immediately frozen and shipped to the USGS Northern Appalachian Research Center (2001–2005) or to the USGS Great Lakes Science Center (GLSC; 2006–2009) for analysis. Egg samples arrived frozen and were stored at –80°C until processing, which occurred within 6 months. Eggs were collected from 1,449 females over 9 years at 15 sites.

Egg thiamine quantification.—From 2001 to 2005, thiamine concentrations in lake trout eggs were determined using high-performance liquid chromatography (HPLC) as described by Brown et al. (1998b). From 2006 to 2009, egg thiamine was determined using the rapid solid-phase extraction fluorometric method (RSPE; Zajicek et al. 2005) because RSPE is more cost-effective than HPLC. To compare results from the two methods, 42 egg samples were analyzed using both methods in 2006 and a linear regression relationship was used to develop a correction factor that was applied to the RSPE values. Results from the two methods were highly correlated (by linear regression; $F_{1,40} = 89.44$, $P < 0.0001$, $r^2 = 0.873$), as previously reported by Zajicek et al. (2005). Results from the RSPE method were adjusted to be comparable to the HPLC results using the relationship

$$\text{Total thiamine} = T_R - 2.0825,$$

where T_R is total thiamine estimated by RSPE (slope of the relationship was equal to 1). Thiamine concentrations in lake trout eggs were expressed as nanomoles per gram (nmol/g) of total thiamine, which includes free thiamine, thiamine monophosphate, and thiamine pyrophosphate. We also calculated the proportion of females having egg thiamine concentrations below the management objective of 4 nmol/g at each site.

Data analysis.—Preliminary analyses, including analysis of variance and linear regression, were conducted to determine whether the relationship between egg thiamine and time varied by site (i.e., whether a site-by-year interaction existed) and whether a linear model was a good approximation of the relationship. These analyses revealed that a site-by-year interaction was significant and that the relationship between egg thiamine and time was not linear at some sites, which aligned with graphical inspection of the data. The presence of a site-by-year interaction indicated that analyses should be conducted at each site rather than for each lake. Therefore, a rank-based correlation method was adopted and analysis of the relationship between egg thiamine concentration and time (year) was conducted separately for each site. For each site, the Spearman's rank correlation coefficient was calculated, and a 95% CI for the correlation coefficient was constructed using the Fisher transformation.

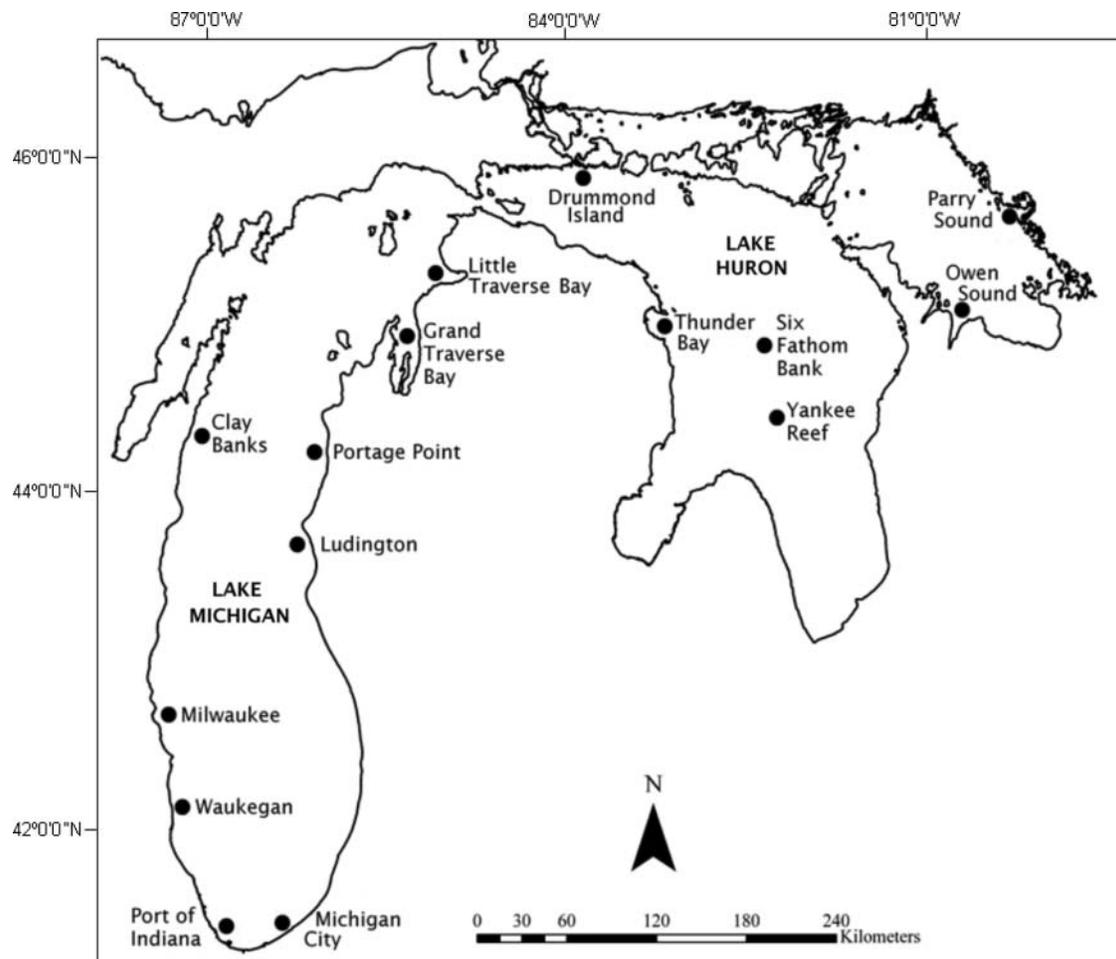


FIGURE 1. Sites in Lakes Huron and Michigan where female lake trout were collected during October and November 2001–2009.

We also examined changes over time in the proportion of females with egg thiamine concentrations less than the management objective of 4 nmol/g. We began with binomial logistic regression, but model fits were poor owing to nonlinear relationships. Graphical inspection and preliminary logistic regression models indicated that a site-by-year interaction existed and that a linear fit was poor at some sites. Therefore, we adopted a similar rank-based approach as above and conducted separate analyses for each site. We assigned the egg thiamine concentration of each individual lake trout to one of two categories: (1) less than 4 nmol/g or (2) greater than or equal to 4 nmol/g. For each site, we conducted a rank biserial correlation to determine whether a correlation existed between the category and year. This correlation technique is nonparametric and accommodates nonlinear relationships.

We also determined whether the correlations between egg thiamine concentration and time differed between Lakes Michigan and Huron. We conducted a rank-sum analysis using the 12 sites with significant rank correlation coefficients to determine if the coefficients differed between the two lakes. A continuity

correction was used given the small sample sizes, and an exact P -value was calculated. We repeated this analysis with the eight significant correlation coefficients from Table 1 to determine whether the correlations between the proportions of females with egg thiamine concentrations less than 4 nmol/g and time differed between Lakes Michigan and Huron.

Because we examined trends in egg thiamine over time, the potential for temporal autocorrelation exists. Traditional methods of assessing autocorrelation require that no data are missing in the time series; none of the sites satisfied this requirement. In addition, the 9-year time series is relatively short, precluding a meaningful evaluation. If temporal autocorrelation existed, the relationship between time and any response would not change, but the evaluation of the significance of the relationship would differ (i.e., the P -value would increase). Therefore, temporal autocorrelation can be accounted for by interpreting P -values in a conservative manner. (Specifically, we considered models with $P < 0.01$ to provide convincing evidence of a significant relationship and those with $0.01 < P < 0.05$ to provide suggestive evidence.)

TABLE 1. Yearly proportions of female lake trout with egg thiamine concentrations less than 4 nmol/g and a summary of correlation coefficients between proportion and sampling year for Lakes Huron and Michigan.

Site	Rank biserial correlation coefficient	<i>P</i> -value	Proportion of females with egg thiamine < 4 nmol/g for sampling year:								
			2001	2002	2003	2004	2005	2006	2007	2008	2009
Lake Huron											
Drummond Island	−0.741	<0.001		0.69	0.69	0.74		0.64	0.10	0.04	0.00
Owen Sound	−0.263	0.053	0.17	0.28	0.83				0.17	0.17	0.05
Parry Sound	−0.090	0.404	0.66					0.27	0.60	0.41	0.40
Six Fathom Bank	−0.501	<0.001	0.50	0.89		0.75		0.27	0.19		
Thunder Bay	−0.802	<0.001		0.53			0.00	0.09	0.00	0.00	0.00
Yankee Reef	−0.789	<0.001	0.57	1.00		0.50		0.00		0.00	
Lake Michigan											
Clay Banks	−0.296	0.010	0.76	0.73	0.64	0.60	0.80	0.90	1.00		0.05
Grand Traverse Bay	−0.413	<0.001	1.00			1.00	0.30	0.47		0.71	0.17
Little Traverse Bay	−0.482	<0.001	1.00			0.67	0.42	0.50	0.46	0.14	
Ludington	−0.216	0.022				0.52	0.52	0.71	0.13	0.57	0.21
Michigan City	−0.179	0.405					0.00	0.10	0.40		0.00
Milwaukee	−0.339	0.001				0.44		0.72	0.47	0.77	0.03
Port of Indiana	−0.049	0.802		0.50			0.29	0.14	0.46	0.20	
Portage Point	−0.545	<0.001					0.67	0.75	0.83	0.57	0.11
Waukegan	−0.250	0.018				1.00	0.37	0.57	0.43	0.57	0.27

We related egg thiamine concentrations in lake trout eggs to the abundance of alewives at six sites in Lakes Huron and Michigan during 2001–2009. We used site-specific alewife abundance data from the USGS annual fall bottom trawl survey, which were expressed as the mean biomass (g/ha) of all depths sampled at each site (for further details of trawl sampling, see Riley et al. 2008, 2010; Madenjian et al. 2010). To evaluate the relationship between egg thiamine and alewife abundance, we performed linear regression analysis using \log_e transformed egg thiamine concentrations as the response. As the predictor, we used the mean of the site-specific, \log_e transformed biomass of yearling and older alewives for the year of egg thiamine sampling and the previous year, as lake trout may need to feed on prey items containing thiaminase for more than a year before low thiamine concentrations occur (Honeyfield et al. 2005). The full model also included site and was specified as

$$\log_e(\text{egg thiamine}) = \text{intercept} + \log_e(\text{biomass}) + \text{site} \\ + [\log_e(\text{biomass}) \times \text{site}].$$

An extra-sum-of-squares *F*-test was used to compare the full model with reduced models. The full model had a significant site-by-year interaction, indicating that slopes varied by site, so we analyzed the relationships at each site separately using linear regression of \log_e transformed data.

RESULTS

Relationships between lake trout egg thiamine and year varied by site (Table 2; Figures 2, 3). Nine of the fifteen sites sampled showed a significant positive relationship between egg thiamine concentration and year (Table 2; $P < 0.001$ in all cases), including five of the six sites in Lake Huron (Drummond Island, Owen Sound, Six Fathom Bank, Thunder Bay, and Yankee Reef) and four of the nine sites in Lake Michigan (Grand Traverse Bay, Little Traverse Bay, Milwaukee, and Portage Point). In Lake Huron, Parry Sound was the only site that showed no relationship (Figure 2; Table 2; $P > 0.20$). In Lake Michigan, two sites (Clay Banks and Ludington) showed suggestive evidence of a relationship between egg thiamine concentration and year (Figure 3; Table 2; $0.01 < P < 0.05$), and three sites (Michigan City, the Port of Indiana, and Waukegan) showed no significant relationship (Figure 3; Table 2; $P > 0.05$). Sites in Lake Huron had higher correlation coefficients for these relationships than sites in Lake Michigan (rank-sum analysis: $P = 0.0173$), suggesting that sites in Lake Huron had stronger associations between egg thiamine and time.

Eight sites (Drummond Island, Six Fathom Bank, Thunder Bay, and Yankee Reef in Lake Huron; Grand Traverse Bay, Little Traverse Bay, Milwaukee, and Portage Point in Lake Michigan) showed a significant decline over time in the proportion of females with egg thiamine below 4 nmol/g (Table 1; Figure 4; all $P \leq 0.001$). In Lake Huron, Owen Sound showed inconclusive evidence of a decline (Table 1; Figure 4; $P = 0.053$) and Parry Sound showed no change ($P = 0.40$). In Lake Michigan,

TABLE 2. Mean (SE in parentheses) egg thiamine concentration in female lake trout from Lake Huron and Lake Michigan sites during each sampling year and a summary of correlation coefficients (95% confidence interval [CI] in parentheses) between egg thiamine concentration and sampling year.

Site	Correlation coefficient (95% CI)	Rank correlation <i>P</i> -value	Mean egg thiamine concentration (nmol/g) for sampling year:								
			2001	2002	2003	2004	2005	2006	2007	2008	2009
Lake Huron											
Drummond Island	0.744 (0.664–0.807)	<0.001		4.02 (0.84)	3.49 (0.74)	4.01 (0.86)		4.48 (0.70)	7.83 (0.67)	11.20 (0.85)	20.83 (1.83)
Owen Sound	0.420 (0.220–0.587)	<0.001	7.37 (1.14)	7.10 (1.11)	2.42 (0.82)				13.60 (1.91)	10.98 (2.14)	13.13 (1.34)
Parry Sound	0.085 (–0.101 to 0.265)	0.20 < <i>P</i> < 0.50	3.91 (0.37)					6.76 (0.88)	4.35 (0.90)	7.72 (1.30)	7.52 (3.13)
Six Fathom Bank	0.434 (0.212–0.613)	<0.001	3.72 (0.65)	2.47 (1.27)		3.33 (0.70)		7.56 (1.95)	10.23 (1.80)		
Thunder Bay	0.566 (0.414–0.687)	<0.001		4.72 (1.10)			10.43 (1.30)	10.60 (1.20)	12.19 (1.20)	12.20 (0.79)	22.08 (2.26)
Yankee Reef	0.763 (0.634–0.851)	<0.001	3.98 (0.79)	1.65 (0.29)		5.36 (1.27)		7.61 (1.65)		13.63 (0.77)	
Lake Michigan											
Clay Banks	0.187 (0.023–0.341)	0.02 < <i>P</i> < 0.05	2.54 (0.50)	2.96 (0.88)	3.42 (1.12)	3.86 (1.69)	2.77 (0.45)	1.34 (0.32)	0.95 (0.45)		15.03 (1.64)
Grand Traverse Bay	0.387 (0.197–0.549)	<0.001	1.00 (0.20)			0.73 (0.16)	8.89 (2.34)	6.29 (1.02)		6.38 (2.76)	9.25 (1.04)
Little Traverse Bay	0.392 (0.244–0.523)	<0.001	1.61 (0.25)			3.50 (0.81)	8.53 (1.53)	4.30 (0.65)	5.36 (1.10)	12.10 (1.30)	
Ludington	0.212 (0.048–0.365)	0.01 < <i>P</i> < 0.02				6.15 (1.48)	7.16 (1.32)	4.14 (1.14)	8.03 (1.29)	5.68 (1.45)	10.84 (1.77)
Michigan City	0.166 (–0.183 to 0.477)	0.20 < <i>P</i> < 0.50					9.28 (2.31)	10.49 (1.61)	3.74 (1.42)		13.36 (1.93)
Milwaukee	0.390 (0.227–0.531)	<0.001				6.32 (1.21)		3.14 (1.08)	6.68 (1.07)	3.38 (0.52)	14.26 (1.58)
Port of Indiana	–0.175 (–0.458 to 0.141)	0.20 < <i>P</i> < 0.50		13.05 (6.10)			8.42 (2.45)	11.42 (2.64)	5.38 (1.32)	5.90 (0.78)	
Portage Point	0.516 (0.359–0.645)	<0.001					4.54 (2.00)	3.20 (0.97)	2.38 (1.50)	5.65 (0.83)	10.71 (1.43)
Waukegan	0.184 (–0.006 to 0.362)	0.05 < <i>P</i> < 0.10				2.03 (0.09)	8.26 (1.29)	4.32 (0.90)	5.49 (1.59)	4.17 (0.54)	7.81 (0.94)

suggestive evidence of a decline in the proportion of females with egg thiamine lower than 4 nmol/g existed at Clay Banks, Ludington, and Waukegan (Table 1; Figure 4; $0.01 < P < 0.02$), and Michigan City and the Port of Indiana showed no change (Table 1; Figure 4; $P > 0.40$). Sites in Lake Huron had higher correlation coefficients than sites in Lake Michigan for these relationships (rank-sum analysis: $P = 0.057$), indicating that sites in Lake Huron had stronger associations between the proportion of females with low thiamine and time.

Egg thiamine concentrations at five of six sites in Lakes Huron and Michigan were significantly negatively related to site-specific estimates of alewife abundance (Table 3; Figure 5). Waukegan was the only site where a significant relationship did not exist (by linear regression: $F_{1,101} = 0.09$, $P = 0.7689$).

DISCUSSION

Lake trout egg thiamine concentrations increased at 9 of 15 sites in Lakes Huron and Michigan from 2001 to 2009, and showed suggestive evidence of an increase at two sites. The inability of linear models to adequately represent increases in egg thiamine at these sites suggests that these changes did not occur steadily over time. Our results provide geographically widespread evidence of increasing egg thiamine concentrations from 2001 to 2009 but also indicate that an increasing trend in egg thiamine over time was not universal at all sites in Lakes Huron and Michigan. Egg thiamine concentrations in Lake Ontario coho salmon *Oncorhynchus kisutch* decreased between 2003 and 2006 (Ketola et al. 2009b), however, and larval mortality of Pacific salmon *Oncorhynchus* spp. remains high in Lake Michigan (G. Whelan, Michigan Department of Natural

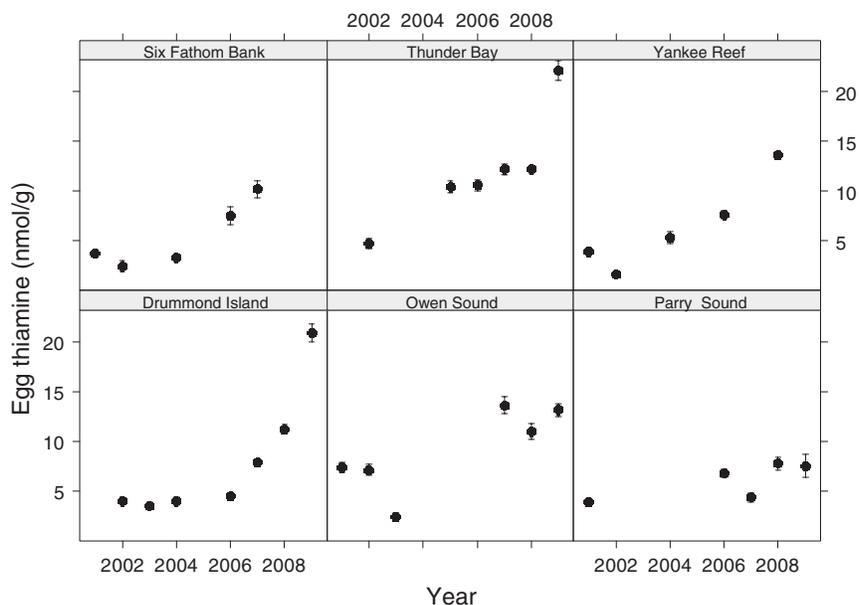


FIGURE 2. Mean egg thiamine concentrations for female lake trout sampled from sites in Lake Huron, 2001–2009. Error bars represent 95% confidence intervals; where error bars are not visible, they are obscured by the symbols.

Resources [DNR], unpublished data), suggesting that egg thiamine concentrations in salmonines remain low for some species in some areas of the Great Lakes.

All sites in Lake Huron except Parry Sound showed an increase in egg thiamine over time. The dramatic increase in egg

thiamine in Lake Huron resulted in average annual egg thiamine concentrations exceeding 20 nmol/g at Drummond Island and Thunder Bay, similar to those in areas where TDC was not reported to occur (Brown et al. 1998a; Fitzsimons and Brown 1998). The lack of increase in egg thiamine at Parry Sound

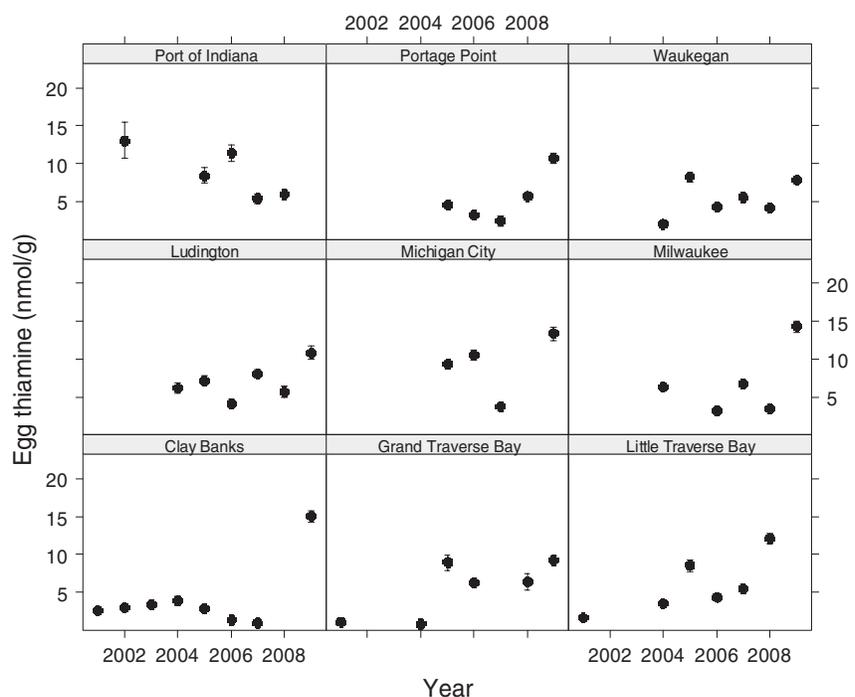


FIGURE 3. Mean egg thiamine concentrations for female lake trout sampled from sites in Lake Michigan, 2001–2009. Error bars represent 95% confidence intervals; where error bars are not visible, they are obscured by the symbols.

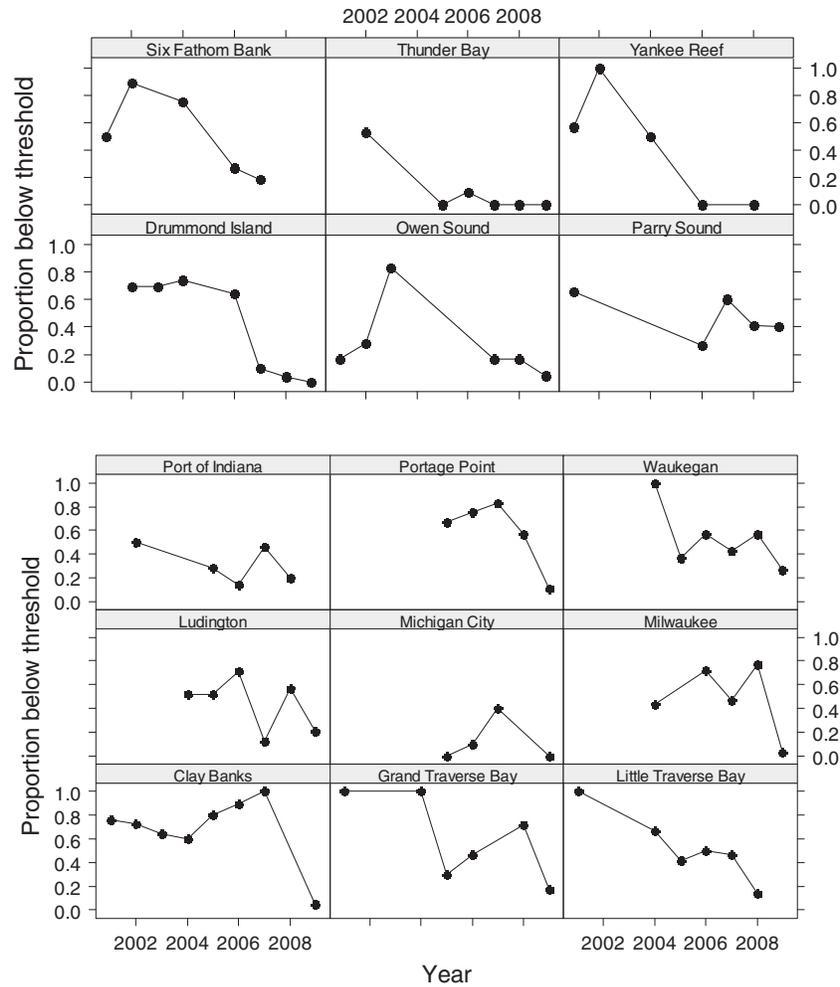


FIGURE 4. Proportion of female lake trout sampled from Lake Huron (top panel) or Lake Michigan (bottom panel) that had egg thiamine levels less than the recommended management target (4 nmol/g).

may be due to a lack of samples early in the time series, when thiamine concentrations were low at most sites. Parry Sound supports a remnant stock of lake trout that has exhibited successful natural reproduction for years (Reid et al. 2001), and

mean egg thiamine concentrations were at or above 4 nmol/g in every year since 2006 (Table 2). Fitzsimons et al. (2010) reported an increase in lake trout egg thiamine concentrations between 2001 and 2005 at one spawning reef in Parry Sound,

TABLE 3. Summary of linear regression relationships between lake trout egg thiamine concentration during the sampling year and the estimated abundance of alewives near Lake Huron and Lake Michigan sites during the egg sampling year and the previous year.

Site	Slope (SE)	Intercept (SE)	<i>F</i>	<i>P</i>	<i>n</i>	<i>R</i> ²
Lake Huron						
Drummond Island	-0.171 (0.029)	2.572 (0.151)	35.51	<0.0001	151	0.1900
Thunder Bay	-0.153 (0.023)	2.545 (0.087)	43.94	<0.0001	95	0.3200
Lake Michigan						
Clay Banks	-0.452 (0.166)	4.392 (1.450)	7.43	0.0072	139	0.0500
Ludington	-0.521 (0.217)	5.534 (1.720)	5.77	0.0177	137	0.0400
Portage Point	-0.576 (0.126)	3.985 (0.706)	20.88	<0.0001	100	0.1800
Waukegan	-0.035 (0.853)	1.254 (0.853)	0.09	0.7689	104	0.0009

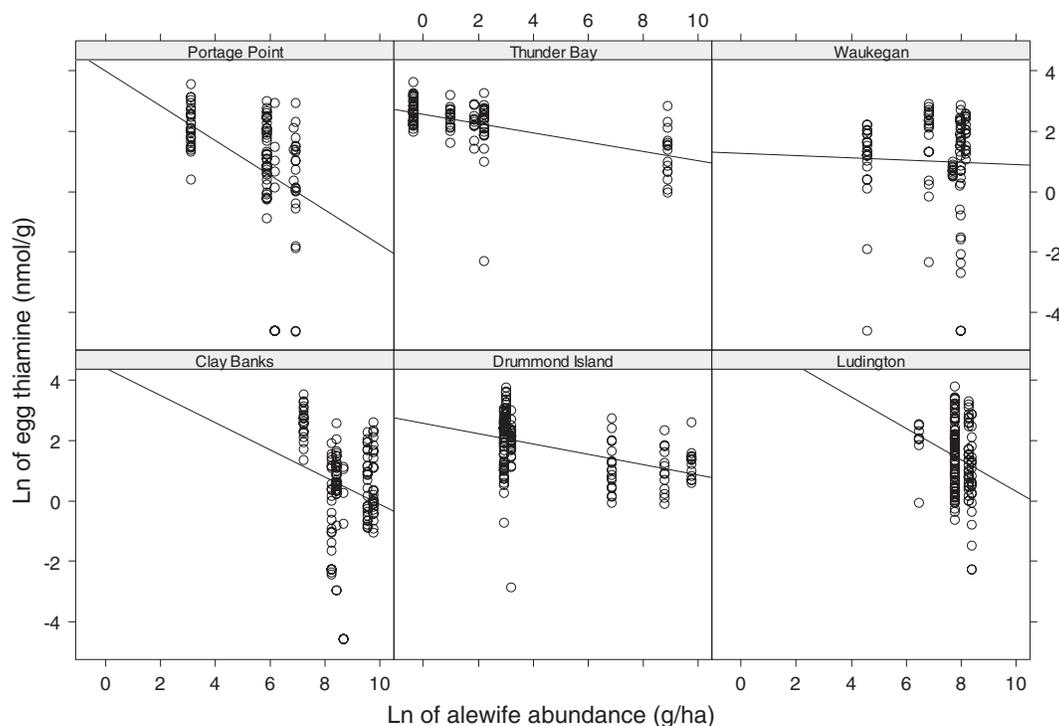


FIGURE 5. Lake trout egg thiamine concentration at sites in Lakes Huron and Michigan as a function of estimated mean abundance of yearling and older alewives for the egg sampling year and the previous year. The lines represent the least-squares regression lines fitted to \log_e transformed variables (see text).

but in the context of a longer time series it appears that no significant increase occurred.

A significant increase in egg thiamine concentration was observed at four of the nine sites in Lake Michigan, and Clay Banks and Ludington showed suggestive evidence of an increase. At Clay Banks, egg thiamine concentrations markedly increased in 2009, while at Ludington egg thiamine increased with a more steady trend. The three sites in Lake Michigan at which egg thiamine concentrations did not increase (Michigan City, the Port of Indiana, and Waukegan) were the southernmost sites in the lake. For two of these sites (Michigan City and Waukegan), data collection did not begin until 2004 or 2005, and only 1 year was sampled prior to 2005 in Indiana (Table 4). Thus, the lack of increase in egg thiamine concentrations over time could result from a difference in the factors contributing to decreased egg thiamine at these sites or a lack of egg thiamine data in the early part of the time series.

Evidence of a decrease in the proportion of females with mean egg thiamine concentrations lower than 4 nmol/g over time existed at approximately half of the sites. In Lake Huron, five of the six sites showed evidence of a decrease, and each also showed an increase in mean egg thiamine over time, but no trend was detected at Parry Sound. In Lake Michigan, the four sites which showed convincing evidence of a significant decrease in the proportion of females with mean egg thiamine concentrations lower than 4 nmol/g also showed an increase in mean egg thiamine concentrations. Three more sites (Clay

Banks, Ludington, and Waukegan) showed suggestive evidence of a decrease, and Clay Banks and Ludington also showed suggestive evidence of an increase in egg thiamine concentration over time. At Clay Banks, the decrease in the proportion of females below the management objective is attributable to a sharp decline in 2009, while at Ludington the trend occurred more steadily. Waukegan was the only site in which the proportion of females with egg thiamine lower than the management objective showed evidence of a decrease but the mean egg thiamine concentration did not increase, which may be due to the unusually high proportion of females (100%) that were below the management objective in the first year of sampling.

Alewife abundance crashed in Lake Huron in 2003 (Riley et al. 2008) and has remained at very low levels since (Riley et al. 2010). In Lake Michigan, alewife abundance declined in 2004 and has also remained relatively low (Madenjian et al. 2010), but abundance is not as low as in Lake Huron. This may explain why a higher proportion of sites in Lake Huron showed increasing egg thiamine concentrations and why sites in Lake Huron had stronger associations between egg thiamine and time. Further monitoring will be necessary to determine if egg thiamine concentrations in these lakes will continue to increase.

Egg thiamine concentrations were inversely related to the abundance of alewives at five of six sites in Lakes Huron and Michigan. This finding is consistent with previous research (Fitzsimons and Brown 1998) and provides additional

TABLE 4. Number of female lake trout from which eggs were collected at 15 sites in Lakes Huron and Michigan between 2001 and 2009.

Site	2001	2002	2003	2004	2005	2006	2007	2008	2009	Total N for site
Lake Huron										
Drummond Island	0	13	13	19	0	25	30	27	24	151
Owen Sound	12	18	6	0	0	0	12	6	22	76
Parry Sound	29	0	0	0	0	30	30	17	5	111
Six Fathom Bank	6	9	0	20	0	11	16	0	0	62
Thunder Bay	0	15	0	0	11	22	15	22	10	95
Yankee Reef	7	12	0	14	0	3	0	23	0	59
Lake Huron subtotal	54	67	19	53	11	91	103	95	61	554
Lake Michigan										
Clay Banks	21	11	14	5	30	29	8	0	21	139
Grand Traverse Bay	6	0	0	4	10	32	0	7	29	88
Little Traverse Bay	11	0	0	21	24	20	28	36	0	140
Ludington	0	0	0	25	31	21	8	23	29	137
Michigan City	0	0	0	0	3	10	5	0	13	31
Milwaukee	0	0	0	16	0	18	32	22	30	118
Port of Indiana	0	6	0	7	7	13	5	5	0	38
Portage Point	0	0	0	0	3	20	12	37	28	100
Waukegan	0	0	0	12	19	28	7	23	15	104
Lake Michigan subtotal	38	17	14	83	127	185	113	153	165	895
Total N for year	92	84	33	136	138	276	216	248	226	1,449

field-based evidence implicating a diet of alewives, which are high in thiaminase (Ji and Adelman 1998; Tillitt et al. 2005), as the cause of TDC in lake trout (Honeyfield et al. 2005). Our results provide further support that a diet of alewives is associated with TDC in Great Lakes lake trout, as thiamine concentrations in lake trout eggs have generally increased in Lakes Huron and Michigan during 2001–2009 and the increase was coincident with a decline in alewife abundance in both lakes (Riley et al. 2008; Madenjian et al. 2010). Similarly, Werner et al. (2011) reported that egg thiamine concentrations of Atlantic salmon *Salmo salar* from the St. Marys River, which were likely feeding in northern Lake Huron, were higher in 2005 and 2007 than in 2003. These results suggest that low alewife abundance may currently be a prerequisite for high egg thiamine concentrations and subsequent successful reproduction by lake trout in the Great Lakes.

Lake trout in Lakes Huron and Michigan no longer feed primarily on alewives, as is expected for an opportunistic feeder (Eschmeyer 1964; Vander Zanden et al. 2000) given the current low abundance of alewives in both lakes. Alewives were the primary prey of lake trout in Lake Huron during 1983–1986, although rainbow smelt *Osmerus mordax* were also important (Diana 1990), and alewives accounted for 75–90% of the diet of lake trout from offshore reefs in Lake Huron during 1998–2003 (Madenjian et al. 2006a). Recent (2004–2010) unpublished diet data, however, suggest that alewives are much less important in the diet of lake trout in Lake Huron, which now consume mostly

round goby *Neogobius melanostomus* and rainbow smelt (J. He, Michigan DNR, Alpena, unpublished data; E. Roseman, USGS, Ann Arbor, Michigan, unpublished data). Alewives were the primary prey item of lake trout during the period 1973–1995 in Lake Michigan, particularly for larger, mature fish (Eck and Wells 1986; Jude et al. 1987; Miller and Holey 1992; Madenjian et al. 1998), but alewives made up only approximately 8% of the diet of large (>600-mm) lake trout from northern Lake Michigan in 2006–2008, the majority of the diet being rainbow smelt (Jacobs et al. 2010). Large lake trout continue to consume alewives in some parts of Lake Michigan (USGS–GLSC, unpublished data), however, which may explain why decreases in egg thiamine concentration were more significant in Lake Huron and why some sites in Lake Michigan showed no decrease.

Low alewife abundance and increasing thiamine concentrations in lake trout eggs in Lake Huron after 2003 coincided with widespread catches of wild juvenile lake trout in trawl surveys (Riley et al. 2007), and wild adult lake trout are now appearing in assessment catches throughout the main basin (A. Cottrill, Ontario Ministry of Natural Resources, personal communication; M. Ebener, Chippewa Ottawa Resource Authority, personal communication; J. He, personal communication; S. Koproski, U.S. Fish and Wildlife Service, personal communication). This provides further circumstantial evidence that alewives have a negative effect on lake trout reproduction, as successful natural recruitment of lake trout is now occurring after alewife abundance was reduced. However, alewives may also limit successful

lake trout reproduction in the Great Lakes by predation on eggs or fry (Krueger et al. 1995b). Fitzsimons et al. (2010) suggested that the successful reproduction by lake trout in Lake Huron was related to increasing thiamine concentrations rather than relief from alewife predation. Although our results support an increase in egg thiamine concentrations, we do not feel that currently available data contain sufficient evidence to address the potential effects of reduced predation due to declining alewife abundance.

Fitzsimons et al. (2007) reported the opposite relationship between lake trout egg thiamine concentrations and alewife abundance in Lake Ontario, which predicted lower egg thiamine values at low alewife abundance. The difference between their results and ours could be explained by several factors. First, the alewife abundance data used by Fitzsimons et al. (2007) were collected at transects distant from the site of egg collection, whereas our alewife abundance data were collected at the same locations where eggs were collected. Moreover, our alewife abundance estimates were based on mean alewife biomass for the year of egg collection and the previous year, whereas Fitzsimons et al. (2007) used estimates for the year of egg collection only. Laboratory studies indicate that more than 1 year of feeding on alewives is required to induce thiamine deficiency in lake trout (Honeyfield et al. 2005), and our alewife abundance estimates may be a more realistic indicator of total alewife biomass available to lake trout at specific sites over the time required to induce thiamine deficiency.

Ketola et al. (2009b) did not find a relationship between alewife abundance and thiamine content of eggs of coho salmon in Lake Ontario, but their analysis was limited to four alewife abundance estimates (one in each of 4 years) and to a relatively limited range of egg thiamine concentrations (1.5–2.5 nmol/g). We sampled over a greater number of years and achieved a greater contrast in both alewife abundance and egg thiamine concentrations. Karlsson et al. (1999) found a significant relationship between the prevalence of thiamine deficiency in Atlantic salmon in the Baltic Sea and the abundance of a thiaminase-containing prey fish, the European sprat *Sprattus sprattus*. Thus, while there is evidence of a relationship between thiamine deficiency and the abundance of thiaminase-containing prey, not all studies are in agreement.

Relationships between egg thiamine concentration and alewife abundance at individual sites were significant but explained little of the variation in thiamine concentration. Several explanations for the relatively low R^2 -values exist. Egg thiamine concentrations reflect dietary intake of thiaminase by adult females over the course of several years (Honeyfield et al. 2005), and the annual fall alewife abundance data we used are unlikely to capture the total annual alewife abundance at a particular site, as alewife abundance may be highly variable seasonally in the Great Lakes (Wells 1968; Hatch et al. 1981). Also, both alewives and lake trout move throughout the lakes, and lake trout collected at a specific spawning site were potentially exposed to variable alewife densities. The extent to which lake trout feed

on alewives will depend on the sizes of both species, the relative abundance of other predators and prey, the degree of selectivity of lake trout for alewives, and other factors. In addition, thiaminase activity might be affected by factors such as temperature or physiology of thiaminase-containing fish. Such effects may result in different thiaminase burdens for a particular amount of alewives consumed, potentially causing additional variation.

Thiamine deficiency complex has not always caused lake trout fry mortality in the Great Lakes, as wild lake trout fry from various sites in Lake Michigan showed good survival from the late 1980s through the early 1990s (Mac and Edsall 1991; Holely et al. 1995), when alewives were at moderate levels of abundance (Madenjian et al. 2010). This suggests that recent changes to Great Lakes ecosystems may have affected the prevalence of TDC. It is difficult to determine exactly when TDC began significantly affecting lake trout in the Great Lakes. Unexplained mortality of coho salmon fry was observed as early as the 1960s in Great Lakes hatcheries but increased dramatically in the early 1990s, and this was the impetus for the identification of the cause of TDC (Marcquenski and Brown 1997; Brown et al. 2005a). Hatchery lake trout in the Great Lakes are reared from eggs of captive broodstock, however, and similar long-term wild fry survival data for lake trout are not available. Previous researchers (Mac et al. 1985; Mac and Edsall 1991) noted very poor survival of lake trout fry from Lake Michigan (but not Lake Huron or Lake Superior) reared in 1978–1981 from eggs of feral fish, but although the fish showed symptoms of thiamine deficiency the authors did not attribute the mortality to TDC, as it had not yet been identified.

Survival of naturally produced lake trout fry has reportedly been very low in some instances in the Great Lakes at various times (Fitzsimons et al. 1995, 2007; Fisher et al. 1996; Brown et al. 1998a), particularly since the mid-1990s, and we suggest that the importance of TDC as an impediment to lake trout reproduction may be variable (depending on the ecosystem context) and may be associated with additional factors that are not understood. Lakes Huron and Michigan have recently undergone drastic changes in food web structure, including changes in abundance and community structure of phytoplankton (Fahnenstiel et al. 2010; Barbiero et al. 2011), zooplankton (Barbiero and Tuchman 2004; Barbiero et al. 2009a, 2009b), benthos (Nalepa et al. 2007, 2009), and fish (Riley et al. 2008); these food web alterations have led to changes in the diets of many species, including alewives (Pothoven and Vanderploeg 2004; Hondorp et al. 2005). Changes in alewife diet have led to reduced growth and energy density (Hondorp et al. 2005; Madenjian et al. 2006b; Pothoven and Madenjian 2008), and we speculate that these changes could result in alterations to alewife physiology that have affected the concentration or availability of thiaminase. Thiaminase activity in alewives is highly spatially and temporally variable (Tillitt et al. 2005), and the factors associated with this variability and the actual source of thiaminase are not understood (Lepak et al. 2008; Riley and Evans 2008), although thiaminase levels in alewives may be related to fatty

acids in the diet (Honeyfield et al. 2010). Thus, recent consumption of alewives may have a different effect on salmonine egg thiamine concentrations than previously, and it is possible that recent lower food web changes have cascaded through alewives to salmonines and are causing reproductive failure, as suggested by Ahlgren et al. (2005) for the Baltic Sea.

To our knowledge, this is the first large-scale, long-term effort to monitor thiamine concentrations in any wild animal species. Thiamine concentrations in lake trout eggs from Lakes Huron and Michigan were variable over time and space and increased at many sites. Many individual female lake trout had mean egg thiamine concentrations that were low enough to cause larval mortality or sublethal effects. Our results indicate that the large-scale reproductive failure of lake trout in the Great Lakes may be partly attributable to low egg thiamine concentrations, which in turn may be related to the presence of the alewife, an exotic marine species. Thiamine deficiency has also been demonstrated in a variety of other feral animal species, including the rainbow smelt (Chalupnicki et al. 2010), Atlantic salmon (Werner et al. 2006), coho salmon, Chinook salmon *Oncorhynchus tshawytscha* (Fitzsimons et al. 2007), walleye *Sander vitreus* (Rincharde et al. 2010), fishes in the Baltic Sea (Breitholtz et al. 2001), and the American alligator *Alligator mississippiensis* (Honeyfield et al. 2008), and has been recently implicated in widespread mortalities of several species of wild birds in Europe (Balk et al. 2009), suggesting that thiamine deficiency is a widespread problem. Further monitoring of thiamine concentrations in other species and systems will be required to determine the full extent to which thiamine deficiency affects the reproduction and performance of wild animals.

ACKNOWLEDGMENTS

We thank the many individuals that collected eggs for thiamine monitoring, including Steve Robillard and Dan Makauskas (Illinois DNR); Brian Breidert and Randy Brindza (Indiana DNR); Tom Burzynski and Bradley Eggold (Wisconsin DNR); Steve Lenart (Little Traverse Bay Band of Ottawa Indians); Erik Olsen (Grand Traverse Bay Band of Ottawa and Chippewa Indians); Archie Martell (Little River Band of Ottawa Indians); Sergiusz Czesny (Illinois Natural History Survey); Dale Hanson, Mark Holey, Scott Koproski, Adam Kowalski, and Aaron Woldt (U.S. Fish and Wildlife Service); Ji He and James Johnson (Michigan DNR); Mark Ebener, Amanda Handziak, and Greg Wright (Chippewa Ottawa Resource Authority); and Adam Cottrill, David Reid, and Jeff Speers (Ontario Ministry of Natural Resources). Courtenay Vining, Michael Gabor, Kimberly Smith, Christina Accardi, Blake Snyder, and Robert Gerroux provided technical assistance during sample analysis. Clifford Kraft, Don Tillitt, David Warner, and two anonymous reviewers provided comments that improved the manuscript. John Van Sickle (U.S. Environmental Protection Agency, Corvallis, Oregon) provided helpful statistical advice. D. Bunnell provided alewife abundance data for Lake Michigan.

This work was funded by the USGS–GLSC, the USGS Leetown Science Center, the Great Lakes Fishery Commission's Fishery Research Program, and the Great Lakes Fishery Trust. This is Contribution 1638 of the USGS–GLSC. Reference to trade names does not imply endorsement by the U.S. Government.

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