American Fisheries Society Symposium 21:160–171, 1998

Reduced Egg Thiamine Levels in Inland and Great Lakes Lake Trout and Their Relationship with Diet[1]

JOHN D. FITZSIMONS
Bayfield Institute, Department of Fisheries and Oceans
Burlington, Ontario L7R 5R9, Canada

SCOTT B. BROWN[2]
Freshwater Institute, Department of Fisheries and Oceans
Winnipeg, Manitoba R3T 2N6, Canada

Abstract.—Lake trout *Salvelinus namaycush* eggs were collected from 18 separate locations in the Great Lakes and inland lakes to evaluate the relationship between diet and egg thiamine content. Thiamine concentrations in the eggs of lake trout whose diet consisted primarily of rainbow smelt *Osmerus mordax* and alewife *Alosa pseudoharengus* were one-ninth to one-seventeenth those of eggs of lake trout whose diet lacked either of these two species and was composed of lake herring *Coregonus artedi*, yellow perch *Perca flavescens*, cyprinids, or invertebrates. Within the Great Lakes, concentrations of thiamine in the eggs of lake trout increased in the order Ontario, Erie, Michigan, Huron $<$ Superior and reflected the proportion of smelt, alewives, or both in the diet. Of the three forms of thiamine found in eggs, free thiamine was the most important and the form most affected by a diet of alewives or smelt. Collections from inland lakes were similar in terms of thiamine content and its relationship to diet composition. Average free thiamine concentrations in lake trout from Lakes Ontario, Erie, Michigan, and Huron were 1.5 to 4 times a threshold of 0.8 nmol/g that has been associated with the development of a thiamine-responsive early mortality syndrome. In contrast, the concentration of free thiamine in Lake Superior lake trout eggs was 26 times the threshold. We concluded that the reduction in egg thiamine concentrations in lake trout whose diet was primarily smelt or alewives was the result of their high thiaminase content, because published thiamine contents could not explain the patterns observed. Egg thiamine concentrations in lake trout were unaffected by maternal age.

Fisher et al. (1996) reported that levels of thiamine in the eggs of lake trout *Salvelinus namaycush* from Lakes Ontario and Erie were much lower than those found in hatchery fish. These low thiamine levels are of concern because they have been associated with a swim-up mortality syndrome in lake trout (Fitzsimons 1995; Fitzsimons et al. 1995; Fisher et al. 1996; Fitzsimons and Brown 1996; Brown et al. 1998b, this volume) for which thiamine has a therapeutic effect (Fitzsimons 1995). This syndrome, which is associated with anorexia, ataxia, hyperexcitability, and loss of equilibrium, affects larval lake trout around the swim-up stage. The clinical signs and timing of the syndrome are consistent with a deficiency of thiamine, an essential vitamin that is important, particularly in its phosphorylated forms, for normal carbohydrate metabolism and nerve function (Combs 1992). Thiamine concentrations decline by approximately 50% between fertilization and swim-up (Sato et al. 1987; Brown et al. 1998b).

Lake trout in Lakes Ontario and Erie feed almost exclusively on alewives *Alosa pseudoharengus* and rainbow smelt *Osmerus mordax* (Rand and Stewart, in press; F. Cornelius, New York Department of Environmental Conservation [NYDEC], personal communication). Because these species have high thiaminase levels (Nielands 1947; Gnaedinger 1964; Ji and Adelman 1998, this volume), Fisher et al. (1996) speculated that the low egg thiamine concentrations measured in lake trout from Lakes Ontario and Erie might reflect thiamine degradation by thiaminase in the gut, with the result that less thiamine was available for deposition into the eggs. Alewives and smelt also constitute an important part of the diet of lake trout in Lake Michigan (Miller and Holey 1992; Madenjian et al. 1998) and Lake Huron (Diana 1990; J. Johnson, Michigan Department of Natural Resources [MDNR], personal communication) but a smaller proportion in Lake Superior (Fisher and Swanson 1996; M. Gallinat, Red Cliff Band of Lake Superior Chippewa Indians, personal communication). Consequently, egg thiamine levels in lake trout from these lakes may also be affected. Other

---

[1] Portions of this publication were presented at the Second Workshop on Reproductive Disturbances in Fish, Stockholm, Sweden (1995).

[2] Current address: Environment Canada, Canada Center for Inland Waters, 867 Lakeshore Road, Box 5050, Burlington, Ontario L7R 4A6, Canada.

TABLE 1.— Summary of diet information for lake trout from the Great Lakes and inland lakes where eggs were collected for thiamine analysis, based on the percentage composition by weight in summer diets of adults. Abbreviations for species or groups: LH, lake herring; WF, lake whitefish; BC, bloater chub; CY, cyprinids; INV, invertebrates (includes *Mysis*, *Hyallela*, or zooplankton); YP, yellow perch; AW, alewife; RS, rainbow smelt. The presence of a species in unknown proportions is indicated with x.

				Species or group						
Lake	Site abbreviation	Region	Period	LH (WF)	BC (CY)	INV	YP	AW	RS	Source
				Great Lakes						
Ontario	LO	Southern	1993					90	5	Rand and Stewart, in press
Erie	LE	Eastern	1990–1993						95	F. Cornelius, NYDEC, personal communication
Huron	LH	Western	1994					44	46	J. Johnson, MDNR, personal communication
	LH	Eastern	1992		x			29	67	R. Payne, OMNR, personal communication
Michigan	LM	Southwestern	1994–1995		3			95		Madenjian et al. 1998
	LM	Offshore	1994–1995		19			80		Madenjian et al. 1998
Superior	LSP	Southwest	1994	58					24	M. Gallinat, Red Cliff Band of Lake Superior Chippewa Indians, personal communication
	LSP	Southwest[a]	1993	70–95						Fisher and Swanson 1996
				Inland lakes						
382	382				(x)	x				S. B. Brown, DOE, personal communication
Roddy	RL			(x)	(x)		x			S. B. Brown, DOE, personal communication
Opeongo	OL			80			20			Matuszek et al. 1990
Manitou	LU								x	D. Anderson, OMNR, personal communication
Simcoe	LS		1983	64					14	M. McMurtry, OMNR, personal communication
Seneca	SL							80–90		D. Kosowski, NYDEC, personal communication
Big Rideau	BR			x				80–90		J. Hoyle, OMNR, personal communication
Charleston	CL		1983					67–75		B. Kryshka, OMNR, personal communication

[a] Siscowet lake trout.

factors may be involved as well, such as contaminant effects on either the use or storage of thiamine (Yagi 1979), differences in the thiamine content of prey species (Fitzsimons et al. 1998, this volume), or changes in biological productivity, because thiamine is obtained through the diet from bacterial and algal production (Carlucci and Bowes 1972; Nishijima and Hata 1977).

Our objective was to collate information to assess the possible relationship between the diet of adult lake trout and egg thiamine concentrations. We were specifically interested in comparing egg thiamine levels of lake trout whose diets were composed of smelt or alewives, two marine invaders that are the major component of contemporary diets of lake trout in Lakes Michigan, Huron, Erie, and Ontario (Miller and Holey 1992; Madenjian et al. 1998; Rand and Stewart, in press; J. Johnson, personal communication; F. Cornelius, personal communication), with those of lake trout whose diets lacked these two species. The native coregonids, particularly lake herring *Coregonus artedi*, were historically important in the diet of lake trout throughout the Great Lakes and in some inland lakes (Scott and Crossman 1973). Of all the native coregonids in the Great Lakes, the lake herring is now the only significant dietary component of lake trout, and that only in Lake Superior (Fisher and Swanson 1996; M. Gallinat, personal communication). Bloater chub *Coregonus hoyi* are present in the diet of lake trout from parts of Lake Michigan (Madenjian et al. 1998). Samples were also collected from inland lakes, where lake trout also feed on smelt and alewives but where alternative diet items include lake herring, yellow perch *Perca flavescens*, cyprinids, and invertebrates.

Methods

Fish Collections

Fish were collected from 18 locations (Figure 1, Table 1) in 1994 and 1995 using gill nets and trap nets. All lake trout were of the lean variety (see Krueger and Ihssen 1995) with the exception of those from Isle Royale in Lake Superior, where siscowets, a fat variety, were collected. At the time of collection, the length of all females was determined, but only some of the fish were weighed. Age determinations based on coded wire tag data (1994 western Lake Ontario), fin clips (1994 Lake Simcoe), or otoliths (1995 Isle Royale) were used to assess the potential relationship between maternal age and egg thiamine content. Samples of ripe or ovulated eggs, which were collected from live females that had been killed by a blow to the head, were frozen (−20°C) until the time of analysis.

Thiamine Analysis

Thiamine was analyzed according to the methods of Brown et al. (1998a, this volume). All data were corrected for recoveries of each of the three forms: thiamine pyrophosphate, thiamine monophosphate, and free thiamine. Concentrations of the three forms were summed on a molar basis and expressed as nanomoles per gram wet weight. Thiamine data were included from Fisher et al. (1996) for Lake Erie lake trout to facilitate a broader comparison of thiamine levels and dietary linkages in the Great Lakes. Analysis of total thiamine for the Lake Erie samples was by the thiochrome method (AOAC International 1990).

Adult Lake Trout Diets

Information on diet obtained from published and unpublished sources was used to establish the major dietary items for lake trout at each of the collection locations (Table 1). Only the most recent data were used, and this information was verified by local fisheries personnel to ensure that it reflected current conditions. The presence or absence of smelt or alewives in a lake was also verified by local fisheries personnel. Where annual data were available, only information from the summer was used, because this is the period (e.g., July–October) when the greatest change in egg weight occurs (Martin 1970) and the greatest thiamine transfer to the egg occurs (J. Fitzsimons, Department of Fisheries and Oceans, unpublished observations), so it likely represents the period of greatest thiamine requirement by the parent. Moreover, Ji et al. (1998, this volume) estimated a thiamine turnover rate of 40 d for lake trout muscle, the largest repository of thiamine in the body of this species (estimated at 70%; S. Brown, Department of the Environment [DOE], unpublished observations). As a consequence, thiamine deposition during oogenesis, a process that lasts about 180 d, would presumably be strongly dependent on dietary intake.

Statistical Analysis

The linear relationship between adult age and egg thiamine concentration was evaluated using regression analysis. Differences within lakes were tested by means of *t*-tests, and differences between years and between group means of fish collected in each lake were tested by analysis of variance (ANOVA) computed using the Systat statistical package (Wilkinson 1992).

The analysis represents a lakewide overview of egg thiamine levels and combines like data from both inland and Great Lakes. Because of the variation in known diets from each of the lakes sampled (see Table 1), the data for each lake were placed in one of four general categories: (1) >50% alewives in the diet; (2) <50% of alewives in the diet, with the remainder composed mainly of smelt; (3) a low proportion of smelt in the diet, along with other items that did not include alewives; and (4) no smelt or alewives in the diet.

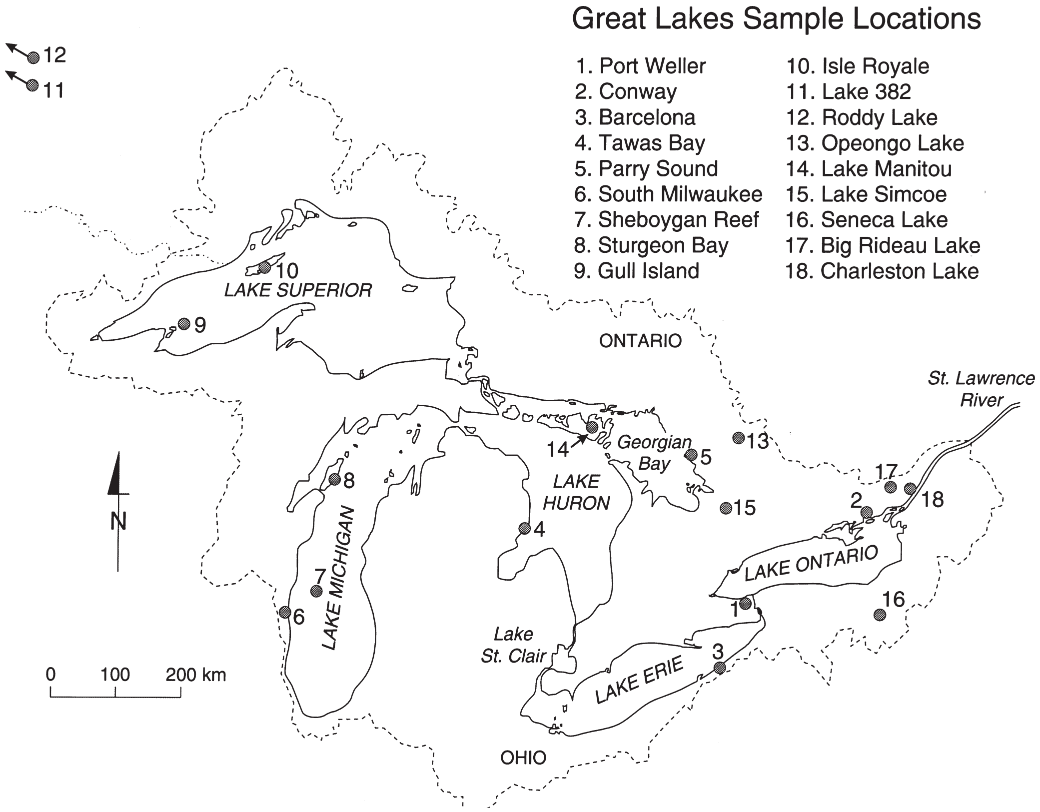

FIGURE 1.—Map showing sampling locations in the Great Lakes and inland lakes where lake trout eggs were collected from 1992 to 1995. The dotted line shows the limit of the Great Lakes drainage basin.

Independent variables used in each category were the mean parameter values calculated for each lake. The Bartlett or the Hartley test was used to test for homogeneity of variance, and, where necessary, data were log-transformed to obtain more uniform variances. Pairwise comparisons were conducted by applying the least-significant-difference test to the least-squares means produced by the ANOVAs. A P-value ≤ 0.05 was considered significant. For clarity of presentation, arithmetic means with standard errors were used in the figures.

Results

General Observations

Data for the 21 collections from 18 locations (Figure 1) shown in Table 2 indicate a variability of greater than 40 times in mean total thiamine concentrations. On the basis of the individual forms (thiamine pyrophosphate, thiamine monophosphate, and free thiamine) in lean lake trout, the variability in concentration was 6, 9, and 291 times, respectively, indicating that most of the between site difference was attributable to free thiamine, the major form of thiamine in eggs at spawning time. This was true for the Great Lakes and inland lakes (Figure 2). Because thiamine can be converted from one form to another (Gubler 1991) and all of the forms may be involved in the expression of early mortality syndrome, we have chosen to limit all further comparisons to total thiamine, the sum of all three forms.

Age Effect

Maternal age had no effect on egg thiamine levels for stocks exhibiting low (Lake Ontario, Port Weller), intermediate (Lake Simcoe), or high (Lake Superior, Isle Royale) average levels of thiamine. There was no relationship between maternal age and total thiamine content in egg samples from western Lake Ontario (Port Weller) during 1994 and 1995 (Figure 3; $F = 1.83$, $r^2 = 0.05$, $P =$

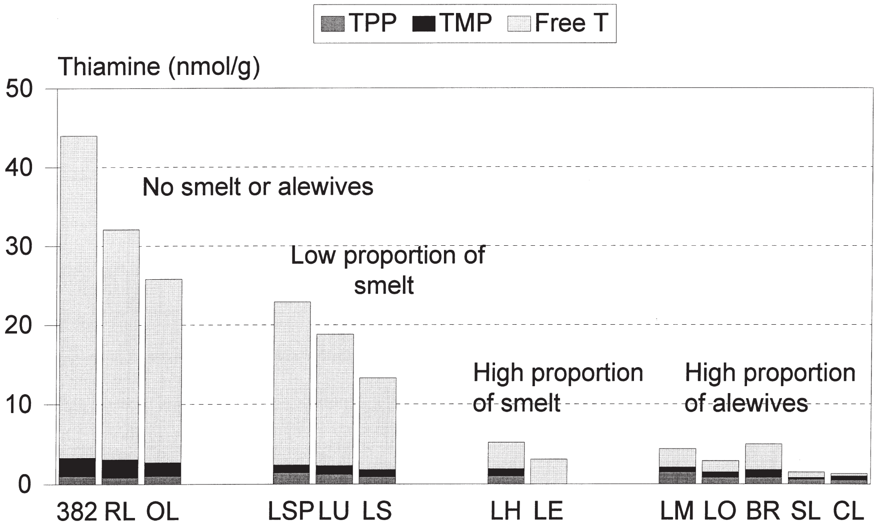

FIGURE 2.—Mean concentrations of thiamine pyrophosphate (TPP), thiamine monophosphate (TMP), and free thiamine (Free T) in lake trout eggs from the Great Lakes and inland lakes combined. Means represent whole lake means. Labels above bars indicate relative proportions of smelt or alewives in the diet. Definitions of site abbreviations are given in Table 1. Data for Lake Erie are from Fisher et al. (1996) and represent total thiamine.

0.19; age range, 5–14 years; mean age, 8.6 years; $N = 42$). This was also the case in Lake Simcoe ($F = 0.23$, $r^2 = 0.02$, $P = 0.64$; age range, 6–15 years; mean age, 9.6 years; $N = 12$) and at Isle Royale ($F = 2.09$, $r^2 = 0.23$, $P = 0.19$; age range, 13–18 years; mean age, 15.3 years; $N = 9$). Given the lack of an age effect, all further comparisons were based on mean thiamine concentration without consideration of age.

Year to Year Variation

Using a two-way analysis of variance on three lakes sampled in 1994 and 1995 (Lake Ontario [Port Weller], Charleston Lake, and Lake Manitou), no significant ($F = 1.5$, $P = 0.217$) year to year variation was evident. As a result, data were pooled across the 2 years for each of the three lakes to derive the mean values used in between lake comparisons.

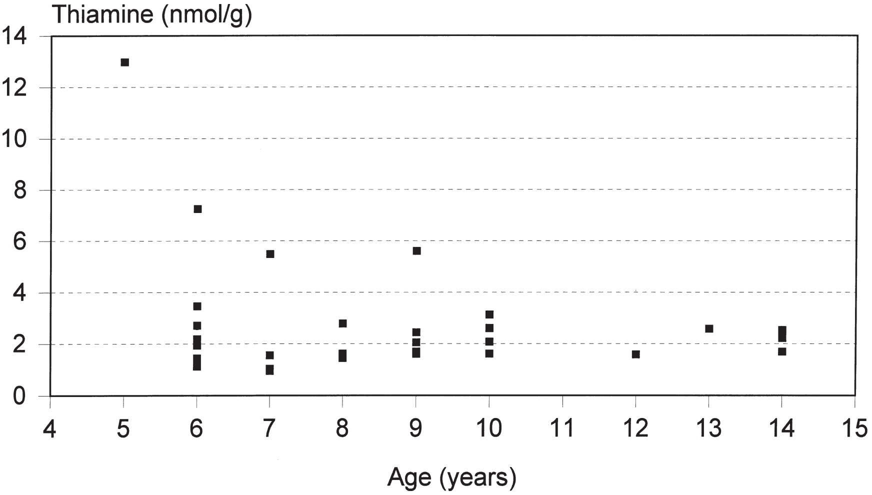

FIGURE 3.—Relationship between the total egg thiamine concentration and maternal age for lake trout collected at Port Weller during the fall of 1994 and 1995.

TABLE 2.—Summary of concentrations (nmol/g) of thiamine pyrophosphate (TPP), thiamine monophosphate (TMP), free thiamine (FT), and total thiamine in lake trout eggs from various Great Lakes and inland lakes. Values shown are means ± SE (N).

Lake	Location	Date	TPP	TMP	FT	Total thiamine
		Great Lakes				
Ontario	Port Weller	25 October–14 November 1994	0.9 ± 0.0 (30)	0.5 ± 0.1 (30)	1.2 ± 0.4 (30)	2.6 ± 0.4 (30)
	Port Weller	2 November 1995	0.8 ± 0.0 (12)	0.4 ± 0.0 (12)	1.5 ± 0.5 (12)	2.7 ± 0.5 (12)
	Conway	2 November 1995	0.4 ± 0.1 (11)	1.4 ± 0.2 (11)	2.2 ± 1.0 (11)	4.0 ± 1.1 (11)
Erie[a]	Barcelona	10 November 1992				3.1 ± 0.3 (5)
Huron	Tawas Bay	October 1994	1.0 ± 0.2 (11)	0.8 ± 0.1 (11)	3.4 ± 1.1 (11)	5.2 ± 1.3 (11)
	Parry Sound	October 1994	0.8 ± 0.2 (6)	1.0 ± 0.1 (6)	3.2 ± 0.7 (6)	4.9 ± 0.9 (6)
Michigan	South Milwaukee	18 October 1994	1.3 ± 0.3 (8)	0.6 ± 0.2 (8)	3.0 ± 1.7 (6)	4.9 ± 2.1 (8)
	Sheboygan Reef	17 October 1994	2.0 ± 0.2 (12)	0.8 ± 0.1 (12)	2.1 ± 0.7 (12)	5.0 ± 0.9 (12)
	Sturgeon Bay	26 October 1994	0.9 ± 0.1 (10)	0.4 ± 0.1 (10)	2.0 ± 0.8 (10)	3.3 ± 0.9 (10)
Superior	Gull Island	14 October 1994	1.4 ± 0.1 (8)	1.0 ± 0.1 (8)	20.5 ± 3.2 (8)	22.9 ± 3.2 (8)
	Isle Royale[b]	20–26 June 1995	0.1 ± 0.0 (9)	1.6 ± 0.3 (9)	24.1 ± 2.1 (9)	25.8 ± 2.1 (9)
		Inland lakes				
382		21–24 September 1994	1.0 ± 0.1 (3)	2.3 ± 0.2 (3)	40.7 ± 4.5 (3)	43.9 ± 4.7 (3)
Roddy		25–27 September 1994	0.8 ± 0.2 (5)	2.3 ± 0.2 (5)	29.0 ± 2.6 (5)	32.1 ± 2.6 (5)
Opeongo		13–23 October 1995	1.0 ± 0.2 (6)	1.7 ± 0.3 (6)	23.1 ± 2.0 (6)	25.8 ± 2.2 (6)
Manitou		17–18 October 1994	1.2 ± 0.1 (18)	1.2 ± 0.2 (18)	17.0 ± 1.0 (18)	19.4 ± 1.1 (18)
Manitou		23 October 1995	1.3 ± 0.1 (6)	1.0 ± 0.1 (6)	14.9 ± 2.1 (6)	17.2 ± 2.3 (6)
Simcoe	North Georgina Island	25–31 October 1994	0.9 ± 0.1 (12)	0.9 ± 0.1 (12)	11.5 ± 1.2 (12)	13.4 ± 1.3 (12)
Seneca		17–18 October 1995	0.6 ± 0.1 (11)	0.2 ± 0.0 (11)	0.7 ± 0.1 (11)	1.5 ± 0.1 (11)
Big Rideau		1995	0.4 ± 0.1 (10)	0.9 ± 0.1 (10)	0.9 ± 0.3 (10)	2.1 ± 0.4 (10)
Charleston		1994	0.3 ± 0.0 (13)	0.8 ± 0.1 (13)	0.4 ± 0.1 (13)	1.5 ± 0.1 (13)
Charleston		8–10 November 1995	0.7 ± 0.1 (11)	0.2 ± 0.0 (11)	0.1 ± 0.0 (11)	1.0 ± 0.1 (11)

[a] From Fisher et al. 1996.

[b] Siscowet lake trout.

Within Lake Variation

Samples collected from locations within Lakes Superior, Michigan, Huron, and Ontario did not indicate any significant within lake variation despite some variation in the relative proportions of smelt and alewives in the diet. In southwestern Lake Superior, the mean thiamine concentration in eggs of lean lake trout from Gull Island (22.9 ± 3.2 nmol/g) did not differ ($t = -0.78$, $P = 0.45$) from that of eggs of siscowet lake trout from offshore at Isle Royale (25.8 ± 2.1 nmol/g). The diet of lake trout from southwestern Lake Superior was composed of 24% smelt during the summer months (M. Gallinat, personal communication), whereas the proportion of smelt was negligible for the offshore siscowet lake trout (Fisher and Swanson 1996). Similarly, no site to site variation was evident among three sites evaluated in western Lake Michigan ($F = 0.04$, $P = 0.97$). The mean thiamine concentration in Lake Michigan at Sheboygan reef (5.0 ± 0.9 nmol/g), where 80% of the adult lake trout diet consisted of alewives, did not differ from concentrations in either South Milwaukee (4.9 ± 2.1 nmol/g) or Sturgeon Bay (3.3 ± 0.9 nmol/g), where 95% of the diet was composed of alewives (Madenjian et al. 1998). The mean thiamine level in lake trout eggs from Tawas Bay (5.2 ± 1.3 nmol/g) on western Lake Huron did not differ from that in lake trout from Parry Sound (4.9 ± 0.9 nmol/g) on eastern Lake Huron, despite some variation in the relative proportions of smelt and alewives in the diet of lake trout from western (44:46%; J.

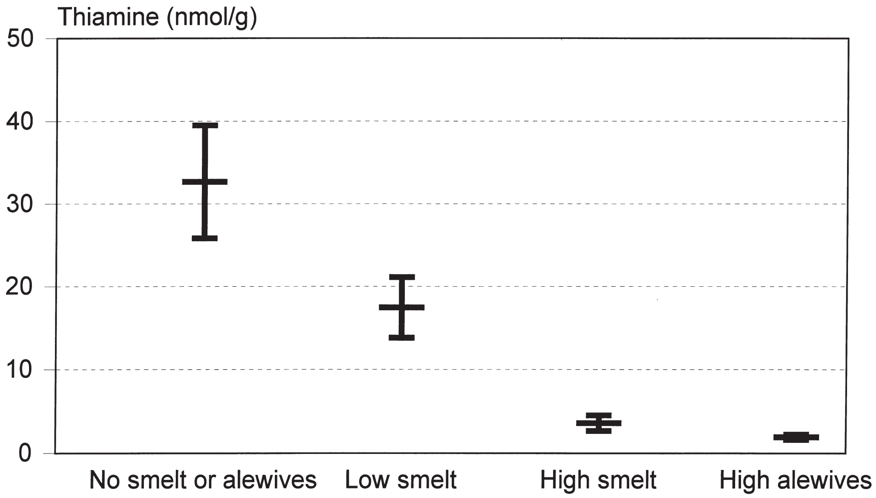

FIGURE 4.—Mean concentrations (±SE) of total thiamine for groups of lakes where lake trout diets had no smelt or alewives, a low proportion of smelt, a high proportion of smelt and some alewives, or a high proportion of alewives.

Johnson, personal communication) and eastern (67:29%; R. Payne, Ontario Ministry of Natural Resources [OMNR], personal communication) Lake Huron. The mean thiamine concentration in eggs of lake trout collected at Port Weller in western Lake Ontario in 1995 (2.7 ± 0.5 nmol/g) did not differ from that in lake trout eggs collected at Conway in eastern Lake Ontario (4.0 ± 1.1 nmol/g). The proportion of alewives in the diet of lake trout in Lake Ontario was 90% (Rand and Stewart, in press).

Lake to Lake Variation

When lakes were grouped according to the relative proportion of smelt and alewives in lake trout diets for each lake and compared, diet had a significant effect ($F = 58.17$, $P < 0.001$, $r^2 = 0.95$) on between lake variation in egg thiamine concentrations (Figure 4). For Lake 382, Opeongo Lake, and Roddy Lake, where neither smelt nor alewives are present in lake trout diets, the average egg thiamine level was highest overall (32.7 nmol/g). Where smelt composed a small percentage of the diet and there were no alewives in the diet, as in Lakes Superior, Manitou, and Simcoe, the mean egg thiamine concentration (17.2 nmol/g) exhibited a significant ($P = 0.05$) decline of almost 50% compared with that in lakes where both smelt and alewives were absent from the diet. Where smelt was a major component of the diet and alewives constituted a small proportion of the diet, as in Lakes Erie and Huron, there was a further significant ($P = 0.001$) decline in mean egg thiamine concentration (3.6 nmol/g) of almost fivefold from that in lakes where alewives were absent and smelt composed a small percentage of the diet. Moreover, compared with those lakes where both smelt and alewives were absent from the diet, this level represented an almost 10 times decline in the mean egg thiamine concentration. Finally, in those lakes where alewives composed a major portion of the diet, as in Big Rideau, Seneca, and Charleston lakes and Lakes Ontario and Michigan, the mean egg thiamine concentration (1.9 nmol/g) was lowest overall and exhibited a further significant ($P = 0.044$) decline of almost 50% from that in lakes where alewives were a minor component of the diet. Overall, this represented a 17 times decline in average egg thiamine concentration from that in lakes where both smelt and alewives were absent from the diet.

Discussion

This synopsis supports the hypotheses of Fitzsimons (1995) and Fisher et al. (1996) that salmonid diets containing either smelt or alewives are associated with low egg thiamine concentrations, although the exact relationship between the actual proportion of these two species in the diet and reductions in egg thiamine levels remains unclear. Stocks with a high proportion of alewives in the diet were found to have the lowest egg thiamine concentrations relative to those whose diet contained neither smelt nor alewives, whose mean egg thiamine concentrations were much higher.

For those stocks in which smelt composed the highest proportion of the diet but with alewives also present, egg thiamine concentrations were still depressed, but not to the same extent as for those stocks in which alewives dominated the diet. Moreover, as the diet became more diverse and other species such as herring were included in higher proportions, the mean egg thiamine concentration showed the smallest difference relative to stocks in which smelt and alewives were absent from the diet.

The variation in mean egg thiamine levels for stocks eating either mostly smelt or mostly alewives may be related to the ecological characteristics of these two schooling pelagic species. With a temperature preferenda of 17°C, alewives would tend to occur above the thermocline during the summer months, whereas smelt, which have a thermal preferenda of 7°C, would occur below the thermocline, where they could co-occur with lake herring, which have a thermal preferenda of 12°C (Wismer and Christie 1987). As a result, lake trout may alternate between the two species, leading to considerable variation in thiamine levels depending on the actual amount of smelt consumed. Compensation of body stores of thiamine may also occur during the consumption of lake herring, particularly at low levels of smelt consumption.

It is only in Lakes Ontario and Erie (Fisher et al. 1996) and Seneca and Charleston lakes (Fitzsimons, unpublished observations) that thiamine levels have been associated with a swim-up mortality syndrome and thus represent a deficiency. Nevertheless, thiamine concentrations in lake trout eggs from Lakes Michigan and Huron were also low relative to those in eggs from Lake Superior by a factor of fivefold and were just above a tentative egg thiamine threshold concentration for early mortality syndrome that lies between 1.4 and 3.0 nmol/g total thiamine, based on Lake Ontario lake trout eggs (Brown et al. 1998b). Early mortality syndrome is the only effect of the thiamine deficiency identified so far. Its absence in Lakes Michigan and Huron in recent years (C. Edsall, U.S. Geological Survey, personal communication) is consistent with the thiamine levels measured in this study that were above the threshold concentration. The threshold for sublethal effects may be higher, however; mortality is a relatively crude indicator of a thiamine deficiency (Halver 1989), and for other end points lake trout from lakes other than Lakes Erie and Ontario may also be thiamine deficient. For example, Fisher et al. (1996) reported decreased yolk conversion efficiency and bradycardia in thiamine-deficient larval Atlantic salmon *Salmo salar*, Halver (1957) reported poor appetite and muscle atrophy in thiamine-deficient larval chinook salmon *Oncorhynchus tshawytscha*, and Spannhof et al. (1978) noted reduced hemoglobin and hematocrit in thiamine-deficient juvenile rainbow trout *O. mykiss*.

The low thiamine concentrations in the eggs of lake trout that feed predominantly on either smelt or alewives are consistent with the high thiaminase contents of these two species (Ji and Adelman 1998a) and the hypothesis that elevated thiaminase in the diet results in the destruction of thiamine in the gut of the lake trout. Thiaminase activity in the gut of a predator such as lake trout is consistent with reported activities (Krampitz and Wooley 1944; Melnick et al. 1945) and the temperature (Krampitz and Wooley 1944) and pH requirements (Deolalkar and Sohonie 1954) for thiaminase. Ji and Adelman (1998) reported similar levels of thiaminase in smelt and alewives from the Great Lakes. These data are in contrast to data from an earlier report by Gnaedinger (1964) that indicated far higher levels of thiaminase in alewives, a difference Ji and Adelman (1998) attributed to interlake variation. In contrast to the similar thiaminase contents of smelt and alewives, Fitzsimons et al. (1998), working with samples from Lakes Michigan and Ontario, found that alewives had approximately six times more thiamine in their muscle than smelt. Based on the average thiaminase activity reported by Ji and Adelman (1998) of 360 pmol of thiamine destroyed per gram of tissue per minute and a thiamine concentration of 10,000 pmol/g in alewives (Fitzsimons et al. 1998), it would take 27 min to completely destroy the thiamine in an alewife under these conditions. Similarly, for smelt with the same thiaminase activity as alewives but lower thiamine content (1,700 pmol/g; Fitzsimons et al. 1998), it would take only 5 min to completely destroy the thiamine. Although it is not known how well the conditions of the assay used by Ji and Adelman (1998) actually reflect conditions in the gut of a predator, these intervals are well within the reported 3- to 6-d digestion times for fish meals (Vonk 1929; Karpevitch and Bokoff 1937), which suggests that the potential for destruction of thiamine within the gut of a predator is high. Other results also support the proposed relevance of thiaminase activity in prey, rather than their thiamine content, in the determination of lake trout egg thiamine concentrations. Fitzsimons et al. (1998) reported that the thiamine content of alewives was 1.5 times higher than that of the coregonids bloater chub and lake herring, yet the mean egg thiamine concentration of Lake

Superior lake trout that fed predominantly on lake herring was 5–8 times higher than that of lake trout eggs from Lakes Michigan and Ontario.

The two to ninefold variation in egg thiamine concentrations noted between lake trout consuming smelt and those consuming alewives was similar to the results reported for thiamine-deficient Atlantic salmon from the Finger Lakes of New York State (Fisher et al. 1996). These authors found that the mean egg thiamine concentration of Atlantic salmon from Cayuga Lake that fed on alewives was approximately one-fifth that of Atlantic salmon from Little Clear Pond, a control lake where resident Atlantic salmon fed on smelt. These authors attributed the differences to an earlier reported difference in the thiaminase content of smelt and alewives (Gnaedinger 1964; Gnaedinger and Krzeczkowski 1966). However, based on the pattern of thiamine levels and diet in this study and the findings of Ji and Adelman (1998) that indicated a similar thiaminase content of smelt and alewives, the observations of Fisher et al. (1996) likely represent differences in the proportions of the two species in the diets of Atlantic salmon from the two locations. Differences in the thiamine content of the two prey species may also be involved (Fitzsimons et al. 1998). Fisher et al. (1996) had also speculated that the lack of significant reproductive problems in lake trout from Seneca Lake, in contrast to Atlantic salmon from this same lake, was the result of a more diverse diet that presumably contained some prey items lacking thiaminase. Based on the present study, however, the eggs of lake trout from Seneca Lake had thiamine concentrations that were one-third to one-half those of lake trout from Lakes Michigan and Ontario. Because lake trout in Lakes Michigan and Ontario feed predominantly on alewives, it seems reasonable to conclude, based on the low egg thiamine concentrations in lake trout from Seneca Lake, that they, like Atlantic salmon, are also feeding heavily on alewives.

The pattern of free thiamine representing the major form of thiamine in the eggs of lake trout with no thiaminase in the diet and being the form most affected by a diet high in thiaminase is consistent with findings in hatchery fish fed a thiamine antagonist, amprolium, in their food. Honeyfield et al. (1998a, this volume) reported that free thiamine accounted for more than 98% of the thiamine found in eggs of lake trout reared on a thiamine-replete diet. When amprolium was added to the diet at the rate of 0.05%, however, these authors observed a 93% decrease in free thiamine but no significant change in either thiamine monophosphate or thiamine pyrophosphate. Free thiamine was also the predominant form in lake trout plasma (Brown et al. 1998a), although thiamine pyrophosphate, the biologically active form, predominated in the red blood cells, liver, muscle, and kidney of this species. Thiamine pyrophosphate does not become an important constituent of the total thiamine concentration of lake trout eggs until hatch, when most of the free thiamine appears to be converted to thiamine pyrophosphate (Brown et al. 1998b).

The declines in egg thiamine concentrations noted in this study appear to represent a unique sensitivity of the ovary, relative to other tissues, to the effects of decreased thiamine uptake by the parent. Honeyfield et al. (1998a) observed a 31 and 53% decline in liver and muscle thiamine pyrophosphate, the major form in these tissues, when the diet of hatchery fish contained 0.05% amprolium relative to an amprolium-free control diet. In contrast, these same authors noted a 93% decline in the free thiamine concentration in the ovaries of the group fed amprolium. Similarly, Brown et al. (1998a) compared the amount of thiamine in the bodies of non-thiamine-deficient and thiamine-deficient lake trout and noted a 94% decline in the egg free thiamine concentration in the thiamine-deficient group yet only 40 and 63% declines in the thiamine pyrophosphate concentrations in the livers and kidneys of the thiamine-deficient group.

For the ranges in age and thiamine concentration that we evaluated, age differences cannot account for the observed variation in thiamine egg content among lakes. For lake trout from Lakes Ontario, Simcoe, and Superior, where relative egg thiamine concentrations were low, intermediate, and high, respectively, no significant relationships were evident between egg thiamine content and maternal age. Age-related differences in egg thiamine concentration, however, may occur in younger fish. Size-dependent changes in the diet of juvenile lake trout have been reported for Lakes Superior (Dryer et al. 1965; Fisher and Swanson 1996), Michigan (Jude et al. 1987), and Ontario (Elrod and O'Gorman 1991), where they were related to a transition from either an invertebrate to a piscine diet or from a benthic to a pelagic piscine diet. Both of these changes could potentially affect egg thiamine concentrations. Invertebrates have thiamine concentrations that are intermediate to those of prey fish (Fitzsimons et al. 1998), whereas benthic fish such as sculpin appear to lack thiaminase (Nielands 1947) and have high thiamine concentrations in their muscle (Fitzsimons et al. 1998).

Some of the lakes sampled, such as Lakes Michigan and Ontario, have high burdens of organic contaminants (Baumann and Whittle 1988), which have been associated with reduced thiamine levels in rats (Yagi 1979). It seems unlikely, however, that such contaminants played a major role in the observed lake to lake differences in egg thiamine concentrations. Lake trout from Charleston, Seneca, and Big Rideau lakes, which feed on alewives and are relatively uncontaminated with organic compounds (Fisher et al. 1996; W. Scheider, Ministry of Environment and Energy, unpublished data), all had lower egg thiamine concentrations than lake trout from Lake Ontario, which also feed on alewives but in contrast are heavily contaminated with chlorinated hydrocarbons (Ontario 1995; Heustis et al. 1996).

Our findings indicate a strong association between a diet high in thiaminase, dominated by the two marine invaders smelt and alewives, and reduced egg thiamine concentrations in lake trout to the extent that concentrations in some locations are deficient (Fisher et al. 1996; Brown et al. 1998b). Such a diet has been speculated to contribute to reduced egg thiamine concentrations and associated thiamine-responsive early mortality syndromes in the eggs of Lake Michigan coho salmon *Oncorhynchus kisutch* and chinook salmon (Honeyfield et al. 1998b, this volume) as well as Baltic salmon (Amcoff et al. 1998, this volume). All of these species are salmonids, which tend to have higher dietary requirements for thiamine (Halver 1989), and so may be especially sensitive. Nevertheless, other nonsalmonid species in the Great Lakes may also be affected. Smelt and alewives are also important in the diets of walleye *Stizostedion vitreum*, burbot *Lota lota*, yellow perch, American eel *Anguilla rostrata*, and northern pike *Esox lucius* (Scott and Crossman 1973).

The documentation of the negative effects of smelt and alewives on salmonid nutriture, which in turn can affect reproduction, is but one more negative effect associated with these two species. Their effects on thiamine can be added to predation on the larval stages of several fish species, including lake whitefish *Coregonus clupeaformis*, lake trout, emerald shiner *Notropis atherinoides*, yellow perch, deepwater cisco *Coregonus johannae*, and deepwater sculpin *Myoxocephalus thompsoni* (Smith 1970; Crowder 1980; Jude and Tesar 1985; Eck and Wells 1987; Evans and Loftus 1987; Krueger et al. 1995). If our hypothesis regarding the effect of a smelt or alewife diet on egg thiamine concentrations is correct, it is unlikely that full restoration of lake trout can occur if smelt or alewives are a major part of their diet. Moreover, restoration of Atlantic salmon, another species whose thiamine levels are affected by diet (Fisher et al. 1996; Fynn-Aikins et al., in press), may be similarly affected if smelt or alewives are a major part of their diet.

Acknowledgments

We are greatly indebted to L. Vandenbyllaardt, who did all of the thiamine analyses. We also thank R. Allan, C. Bronte, G. Cholwek, F. Cornelius, C. Edsall, B. Henderson, B. Kryshka, M. Keir, M. Keniry, S. Marcquenski, E. McIntyre, P. Mettner, K. Osika, V. Palace, J. Radford, S. Schram, B. Timmins, M. Toneys, D. Walsh, and B. Williston, whose assistance with the collection of these samples contributed enormously to the scope of this study. We also thank Victor Cairns, Arthur Niimi, Michael Hornung, and an anonymous reviewer, who provided valuable comments on an earlier draft.

References

Amcoff, P., H. Börjeson, J. Lindeberg, and L. Norrgren. 1998. Thiamine concentrations in feral Baltic salmon exhibiting the M74 syndrome. Pages 82–89 *in* McDonald et al. (1998).

AOAC (Association of Official Analytical Chemists) International. 1990. Official methods of analysis, 15th edition, volume 2. AOAC International, Arlington, Virginia.

Baumann, P. C., and D. M. Whittle. 1988. The status of selected organics in the Laurentian Great Lakes: an overview of DDT, PCBs, dioxins, furans, and aromatic hydrocarbons. Journal of Aquatic Toxicology 11:241–257.

Brown, S. B., D. C. Honeyfield, and L. Vandenbyllaardt. 1998a. Thiamine analysis in fish tissues. Pages 73–81 *in* McDonald et al. (1998).

Brown, S. B., J. D. Fitzsimons, V. P. Palace, and L. Vandenbyllaardt. 1998b. Thiamine and early mortality syndrome in lake trout. Pages 18–25 *in* McDonald et al. (1998).

Carlucci, A. F., and P. M. Bowes. 1972. Determination of vitamin B12, thiamine, and biotin in Lake Tahoe waters using modified marine bioassay techniques. Limnology and Oceanography 17:774–776.

Combs, G. F. 1992. The vitamins. Academic Press, San Diego, California.

Crowder, L. B. 1980. Alewife, rainbow smelt and native fishes in Lake Michigan: competition or predation? Environmental Biology of Fishes 5:225–233.

Deolalkar, S. T., and K. Sohonie. 1954. Thiaminase from fresh-water, brackish-water and salt-water fish. Nature 4402:489–490.

Diana, J. S. 1990. Food habits of angler-caught salmonines in western Lake Huron. Journal of Great Lakes Research 16:271–278.

Dryer, W. R., L. F. Erkkila, and C. L. Tetzloff. 1965. Food of lake trout in Lake Superior. Transactions of the American Fisheries Society 94:169–176.

Eck, G. W., and L. Wells. 1987. Recent changes in Lake Michigan's fish community and their probable causes, with emphasis on the role of alewife (*Alosa pseudoharengus*). Canadian Journal of Fisheries and Aquatic Sciences 44(Supplement 2):53–60.

Elrod, J. H., and R. O'Gorman. 1991. Diet of juvenile lake trout in southern Lake Ontario in relation to abundance and size of prey fishes, 1979–1987. Transactions of the American Fisheries Society 120:290–302.

Evans, D. O., and D. H. Loftus. 1987. Colonization of inland lakes in the Great Lakes region by rainbow smelt, *Osmerus mordax*: their freshwater niche and effects on indigenous fishes. Canadian Journal of Fisheries and Aquatic Sciences 44(Supplement 2):249–266.

Fisher, J. P., J. D. Fitzsimons, G. F. Combs, Jr., and J. M. Spitsbergen. 1996. Naturally occurring thiamine deficiency causing reproductive failure in Finger Lakes Atlantic salmon and Great Lakes lake trout. Transactions of the American Fisheries Society 125:167–178.

Fisher, S. J., and B. L. Swanson. 1996. Diets of siscowet lake trout from the Apostle Islands region of Lake Superior, 1993. Journal of Great Lakes Research 22 (Supplement 2):463–468.

Fitzsimons, J. D. 1995. The effect of B-vitamins on a swim-up syndrome in Lake Ontario lake trout. Journal of Great Lakes Research 21(Supplement 1):286–289.

Fitzsimons, J. D., and S. B. Brown. 1996. Effect of diet on thiamine levels in Great Lakes lake trout and relationship with early mortality syndrome. Pages 76–78 *in* B.-E. Bengtsson, C. Hill, and S. Nellbring, editors. Report from the second workshop on reproduction disturbances in fish. Swedish Environmental Protection Agency Report 4534, Stockholm.

Fitzsimons, J. D., S. B. Brown, and L. Vandenbyllaardt. 1998. Thiamine levels in food chains of the Great Lakes. Pages 90–98 *in* McDonald et al. (1998).

Fitzsimons, J. D., S. Huestis, and B. Williston. 1995. Occurrence of a swim-up syndrome in Lake Ontario lake trout in relation to contaminants and cultural practices. Journal of Great Lakes Research 21(Supplement 1):277–285.

Fynn-Aikins, K., D. C. Honeyfield, P. Bowser, and J. D. Fitzsimons. In press. Early mortality syndrome in Atlantic salmon fry from fish fed dietary amprolium. Transactions of the American Fisheries Society.

Gnaedinger, R. H. 1964. Thiaminase activity in fish: an improved assay method. Fishery Industrial Research 2:55–59.

Gnaedinger, R. H., and R. A. Krzeczkowski. 1966. Heat inactivation of thiaminase in whole fish. Commercial Fisheries Review 28(8):11–14.

Gubler, C. J. 1991. Thiamin. Pages 234–281 *in* L. J. Machlin, editor. Handbook of vitamins, second edition. Marcel Dekker, New York.

Halver, J. E. 1957. Nutrition of salmonid fishes. III. Water-soluble vitamin requirements of chinook salmon. Journal of Nutrition 62:225–243.

Halver, J. E. 1989. Fish nutrition, second edition. Academic Press, New York.

Heustis, S. Y., M. R. Servos, D. M. Whittle, and D. G. Dixon. 1996. Temporal and age-related trends in levels of polychlorinated biphenyl congeners and organochlorine contaminants in Lake Ontario lake trout (*Salvelinus namaycush*). Journal of Great Lakes Research 22:310–330.

Honeyfield, D. C., K. Fynn-Aikins, J. D. Fitzsimons, and J. A. Mota. 1998a. Effect of dietary amprolium on egg and tissue thiamine concentrations in lake trout. Pages 172–177 *in* McDonald et al. (1998).

Honeyfield, D. C., J. G. Hnath, J. Copeland, K. Dabrowski, and J. H. Blom. 1998b. Correlation of nutrients and environmental contaminants in Lake Michigan coho salmon with incidence of early mortality syndrome. Pages 135–145 *in* McDonald et al. (1998).

Ji, Y. Q., and I. R. Adelman. 1998. Thiaminase activity in alewives and smelt in Lakes Huron, Michigan, and Superior. Pages 154–159 *in* McDonald et al. (1998).

Ji, Y. Q., J. J. Warthesen, and I. R. Adelman. 1998. Thiamine nutrition, synthesis, and retention in relation to lake trout reproduction in the Great Lakes. Pages 99–111 *in* McDonald et al. (1998).

Jude, D. J., and F. J. Tesar. 1985. Recent changes in the inshore forage fish of Lake Michigan. Canadian Journal of Fisheries and Aquatic Sciences 42:1154–1157.

Jude, D. J., F. J. Tesar, S. F. Deboe, and T. J. Miller. 1987. Diet and selection of major prey species by Lake Michigan salmonines, 1973–1982. Transactions of the American Fisheries Society 116:677–691.

Karpevitch, A., and E. Bokoff. 1937. The rate of digestion in marine fishes. Zoologicheskii Zhurnal 16:28–44. (Russian; English summary.)

Krampitz, L. O., and D. W. Wooley. 1944. The manner of inactivation of thiamine by fish tissue. Journal of Biological Chemistry 152:9–17.

Krueger, C. C., and P. E. Ihssen. 1995. Review of genetics of lake trout in the Great Lakes: history, molecular genetics, physiology, strain comparisons, and restoration management. Journal of Great Lakes Research 21(Supplement 1):348–363.

Krueger, C. C., D. L. Perkins, E. L. Mills, and J. E. Marsden. 1995. Predation by alewives on lake trout fry in Lake Ontario: role of an exotic species in preventing restoration of a native species. Journal of Great Lakes Research 21(Supplement 1):458–469.

Madenjian, C. P., T. J. DeSourcie, and R. M. Stedman. 1998. Ontogenetic and spatial patterns in diet and growth of lake trout in Lake Michigan. Transactions of the American Fisheries Society 127:236–252.

Martin, N. V. 1970. Long-term effects of diet on the biology of the lake trout and the fishery in Lake Opeongo, Ontario. Journal of the Fisheries Research Board of Canada 27:125–146.

Matuszek, J. E., B. J. Shuter, and J. M. Casselman. 1990. Changes in lake trout growth and abundance after introduction of cisco into Lake Opeongo, Ontario. Transactions of the American Fisheries Society 119:718–729.

McDonald, G., J. D. Fitzsimons, and D. C. Honeyfield, editors. 1998. Early life stage mortality syndrome in fishes of the Great Lakes and Baltic Sea. American Fisheries Society, Symposium 21, Bethesda, Maryland.

Melnick, D., M. Hochberg, and B. L. Oser. 1945. Physiological availability of the vitamins. II. The effect of dietary thiaminase in fish products. Journal of Nutrition 30:81–88.

Miller, M. A., and M. E. Holey. 1992. Diets of lake trout inhabiting nearshore and offshore Lake Michigan environments. Journal of Great Lakes Research 18(Supplement 1):51–60.

Nielands, J. B. 1947. Thiaminase in aquatic animals of Nova Scotia. Journal of the Fisheries Research Board of Canada 7:94–99.

Nishijima, T., and Y. Hata. 1977. Distribution of thiamine, biotin, and vitamin B12 in Lake Kojima. I. Distribution in lake water. Bulletin of the Japanese Society of Scientific Fisheries 44:815–818.

Ontario. 1995. Guide to eating Ontario sport fish. 1995–1996. Queen's Printer for Ontario, Toronto.

Rand, P. S., and D. S. Stewart. In press. Dynamics of salmonine diets and foraging in Lake Ontario 1983–1993: a test of a bioenergetic model prediction. Canadian Journal of Fisheries and Aquatic Sciences.

Sato, M., R. Yoshinaka, R. Kuroshima, H. Morimoto, and S. Ikeda. 1987. Changes in water soluble vitamin contents and transaminase activity of rainbow trout egg during development. Nippon Suisan Gakkiaishi 53:795–799.

Scott, W. B., and E. J. Crossman. 1973. Freshwater fishes of Canada. Bulletin of the Fisheries Research Board of Canada 184.

Smith, S. H. 1970. Species interactions of the alewife in the Great Lakes. Transactions of the American Fisheries Society 99:754–765.

Spannhof, S. L., K. P. Hase, M. Mehl, and A. Plantikow. 1978. Wirkung gleichzeitigen thiamine- und sauerstoffmangels auf den physiologichen zustand von forellensetzlingen. Fischerei-Forschung Wissenschaftliche Schriftenreihe 16:21–24.

Vonk, H. J. 1929. Das pepsin verschiedener vertebraten. Zeitschrift fur Vergleichende Physiologie 5:685–702.

Wilkinson, L. 1992. Systat: the system for statistics. Systat, Inc., Evanston, Illinois.

Wismer, D. A., and A. E. Christie. 1987. Temperature relationships of Great Lakes fishes: a data compilation. Great Lakes Fishery Commission Special Publication 87-3, Ann Arbor, Michigan.

Yagi, N. 1979. Effects of PCB, DDT and other organochloride compounds on thiamine metabolism in rat. Journal of the Japanese Society of Food and Nutrition 32:55–60.