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Thiamin dynamics during the adult life cycle of Atlantic salmon (*Salmo salar*)

Vittoria Todisco[1] | **Emil Fridolfsson**[1] | **Charlotte Axén**[2] | **Elin Dahlgren**[3] | **Maciej J. Ejsmond**[1,4] | **Marc M. Hauber**[1] | **Kjetil Hindar**[5] | **Petter Tibblin**[1] | **Markus Zöttl**[1] | **Linda Söderberg**[3] | **Samuel Hylander**[1]

[1]Centre for Ecology and Evolution in Microbial Model Systems (EEMiS), Linnaeus University, Kalmar, Sweden

[2]Section for Fish, National Veterinary Institute (SVA), Uppsala, Sweden

[3]Institution of Aquatic Resources, Swedish University of Agricultural Sciences (SLU), Uppsala, Sweden

[4]Institute of Environmental Science, Jagiellonian University, Cracow, Poland

[5]Norwegian Institute for Nature Research (NINA), Trondheim, Norway

Correspondence
Vittoria Todisco, Centre for Ecology and Evolution in Microbial Model Systems (EEMiS), Linnaeus University, Kalmar, Sweden.
Email: vittoria.todisco@lnu.se

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Abstract

Thiamin is an essential water-soluble B vitamin known for its wide range of metabolic functions and antioxidant properties. Over the past decades, reproductive failures induced by thiamin deficiency have been observed in several salmonid species worldwide, but it is unclear why this micronutrient deficiency arises. Few studies have compared thiamin concentrations in systems of salmonid populations with or without documented thiamin deficiency. Moreover, it is not well known whether and how thiamin concentration changes during the marine feeding phase and the spawning migration. Therefore, samples of Atlantic salmon (*Salmo salar*) were collected when actively feeding in the open Baltic Sea, after the sea migration to natal rivers, after river migration, and during the spawning period. To compare populations of Baltic salmon with systems without documented thiamin deficiency, a population of landlocked salmon located in Lake Vänern (Sweden) was sampled as well as salmon from Norwegian rivers draining into the North Atlantic Ocean. Results showed the highest mean thiamin concentrations in Lake Vänern salmon, followed by North Atlantic, and the lowest in Baltic populations. Therefore, salmon in the Baltic Sea seem to be consistently more constrained by thiamin than those in other systems. Condition factor and body length had little to no effect on thiamin concentrations in all systems, suggesting that there is no relation between the body condition of salmon and thiamin deficiency. In our large spatiotemporal comparison of salmon populations, thiamin concentrations declined toward spawning in all studied systems, suggesting that the reduction in thiamin concentration arises as a natural consequence of starvation rather than to be related to thiamin deficiency in the system. These results suggest that factors affecting accumulation during the marine feeding phase are key for understanding the thiamin deficiency in salmonids.

KEYWORDS

Atlantic salmon, Baltic Sea, M74 syndrome, Salmon life cycle, Thiamin, Thiamin deficiency

1 | INTRODUCTION

Several groups of organisms such as invertebrates, birds, and fish have been suggested to suffer from a periodic deficiency in a key vitamin called thiamin, also known as vitamin B_1 or thiamine (Balk et al., 2016; Brown et al., 2005b; Karlsson et al., 1999; Lonsdale, 2006; Mörner et al., 2017). Salmonid species appear the most sensitive to thiamin deficiency, which is suggested to cause population declines across the Northern Hemisphere (Sutherland et al., 2018). This deficiency is known to be a source of health impairment, causing behavioral and physiological abnormalities, as well as decreased survival in offspring (Bylund & Lerche, 1995; Fitzsimons, 1995; Ketola et al., 2000; Brown et al., 2005b). The reduced recruitment that derives from low levels of thiamin in early life stages and adults was initially documented in salmonid species from the North America Great Lakes region (early mortality syndrome, EMS; Fitzsimons et al. [1999]) and has later been observed in Atlantic salmon (*Salmo salar*) populations in the New York Finger Lake (Cayuga syndrome; Fisher et al. [1995]) and the Baltic Sea (M74; Börjeson et al. [1999]). More recently, adverse effects of thiamin deficiency in offspring have also been detected in Chinook salmon (*Oncorhynchus tshawytscha*) in California's Central Valley (Mantua et al., 2021).

Fish are thiamin auxotrophs; therefore they cannot synthesize thiamin but need to acquire it through their diet (Harder et al., 2018). Thiamin uptake is essential for aerobic metabolism given its role, for example, in the citric acid cycle (Krebs cycle) as a cofactor of enzymes (Manzetti et al., 2014; Sañudo-Wilhelmy et al., 2014; Kraft & Angert, 2017) and its role in other metabolic processes due to its antioxidant properties (Lukienko et al., 2000). In aquatic ecosystems, thiamin is produced by certain species of prokaryotes, phytoplankton, and fungi (Croft et al., 2006; Paerl et al., 2018). The rate of thiamin production is affected by biotic and abiotic factors, and this vitamin reaches higher trophic levels through grazing and predation (Fridolfsson et al., 2020; Fridolfsson et al., 2023; Majaneva et al., 2020; Sylvander et al., 2013). The food web model described by Ejsmond et al. (2019) showed that the thiamin flow up to planktivorous fish can be constrained under low abundance of zooplankton and prevalence of small species among the primary producers, such as picophytoplankton. Therefore, there is a growing body of literature investigating how thiamin is transferred through the food web levels, but still little is known about possible bottleneck mechanisms regulating the final transfer to predatory fish, such as Atlantic salmon.

The Baltic salmon, a subgroup of Atlantic salmon and hereafter referred to as salmon, is the focus of this study. This species acquires thiamin during its 1–4 years long sea feeding period in the southern Baltic Sea (Karlsson & Karlström, 1994; Ejsmond et al., 2019). When spawning migration begins (4–6 months prior to spawning), salmon reduce their feeding, and it is assumed that feeding stops completely once salmon reach spawning rivers (Vuorinen et al., 2014). Therefore, thiamin acquisition from the diet is limited during the final period leading up to spawning. Several factors have been hypothesized to limit thiamin uptake throughout the life cycle of salmon. Apart from a constrained flow of thiamin in the food web, another factor that may contribute to a reduced uptake in fish is a thiamin-degrading enzyme called thiaminase I. The potential connection between prey items containing thiaminase and thiamin deficiency in salmon has been demonstrated in the region of the Great Lakes in North America (Fisher et al., 1996; Honeyfield et al., 2005a; Richter et al., 2023). In the Baltic Sea populations of herring (*Clupea harengus*) and sprat (*Sprattus sprattus*), the thiaminase activity varies among and within species and depends on the geographic area (Wistbacka et al., 2002; Wistbacka & Bylund, 2008). Another factor that has been suggested to reduce the availability of thiamin to the offspring is the degradation of thiamin when used as an antioxidant during fat metabolism in adult salmon (Keinänen et al., 2012; Lukienko et al., 2000; Vuorinen et al., 2020). Overall, the causes of thiamin deficiency are still debated, and there is a need for more studies on thiamin dynamics that compare the feeding, migrating, and spawning salmon from systems with different thiamin deficiency status. These studies would constitute a baseline understanding on how thiamin concentration varies in salmon throughout its life cycle and if these variations could possibly lead to thiamin deficiency.

The aim of this study was therefore to determine how thiamin varies in gonad and muscle tissues during the salmon life cycle, from open water feeding individuals, during their migration to the natal rivers and at spawning. This study also compares salmon populations from the Baltic Sea system sampled in 2020 and 2021 and salmon from two systems where thiamin deficiency has not been demonstrated or investigated, that is, the North Atlantic Ocean and a landlocked population in Lake Vänern sampled in 2021. We hypothesize that thiamin concentration in muscle and gonad tissues varies during the life cycle of salmon, and in relation to length, sex, body condition as well as the geographic location of the sampled populations, and thus previous feeding history.

2 | MATERIALS AND METHODS

2.1 | Salmon sampling design

Salmon were captured during four adult life stages, that is, during the marine feeding phase (only in the Baltic Sea, brackish water system) in spring, upon arrival to their natal river (river mouths) and after initial migration in the river in summer, and at the reproduction site in fall (Table 1). In 2020, salmon were caught at the river mouths and upstream sites in Torneälven and Umeälven rivers. In 2021, salmon were caught at three sites in the open Baltic Sea representing the feeding and migration areas for salmon, as well as in Torneälven, Luleälven, and Umeälven river mouths and then 15–20 km upstream in the same rivers on their way to the spawning grounds (Figure 1; Table 1). Samples were also collected from rivers draining into the North Atlantic Ocean (full salinity marine system) in Ätran, Driva, Drammen, and Enningdalselva river mouths and upstream sites. One landlocked salmon population was sampled in Lake Vänern (freshwater system) and at an upstream location in the River Klarälven. Five of the upstream locations were sampled both

TABLE 1 Summary of each sampling session.

System	Area	Site	Catching method	Date of sampling (mm/dd/yy)	Life stage
Baltic Populations	Southern Baltic Sea (1)		Trolling	March–May 2021	Actively feeding
	Kalmar—Blekinge regions (2)			May–June 2021	
	Åland Sea (3)			5/29–30/2021	
	Torne River	River mouth (4a)	Trap	7/13/2020 6/17/2021	After sea migration
		Upstream (4b)	Drift net	7/14/2020 6/19/2021	After river migration
	Ume River	River mouth (6a)	Drift net	7/8/2021	After sea migration
		Upstream (6b)	Fish stop (fish ladder)	7/7/2021	After river migration
				10/19/2021	Actively spawning
	Lule River	River mouth (5a)	Trap	7/5/2021	After sea migration
		Upstream (5b)	Fish stop	7/6/2021	After river migration
				10/18/2021	Actively spawning
Lake Vänern Population	Lake Vänern	Open lake (7a)	Trap	7/13/2021	After lake migration
		Upstream (7b)	Fish stop	7/12/2021	After river migration
North Atlantic Populations	Ätran River	Upstream (8)	Trap	5/20/2021	After river migration
				9/30/2021	Actively spawning
	Drammen River	River mouth (10a) Oslo Fjord area	Bag net	6/21/2021	After sea migration
		Upstream (10b)	Fish stop	6/28/2021	After river migration
				11/4/2021	Actively spawning
	Driva River	River mouth (11a) Tingvoll Fjord area	Bag net	7/13/2021	After sea migration
		Upstream (11b)	Fish stop	7/12/2021	After river migration
				9/27/2021	Actively spawning
	Enningdal River	Upstream (9)	Rod	5/23–28/2021	After river migration

Note: The sampled salmon populations are divided into three systems (Baltic, Lake Vänern, and North Atlantic) and the river, lake, or open sea locations where they were caught are indicated in the "Area" column. The "Site" column indicates the specific part of the river where the fish were caught and sampled. The numbers in brackets next to the different areas or sites indicate the reference geographic locations reported in Figure 1; the date of sampling is displayed as the month, day, and year (mm/dd/yy).

during spawning migration in summer and during the reproduction period in the fall (Table 1). The sampling during reproduction was possible because the sampling sites were located at restocking facilities, where migrating salmon are caught and kept for restocking each year. Therefore, the samples obtained represent a wide range of conditions in terms of different populations, adult life stages, and systems. At each sampling occasion, we sampled from 3 to 20 individuals with the target set to 20 individuals, which was also met at most of the sampling occasions. The details of the different sampling locations, including fishing method, number of individuals sampled, sex ratio, and life stages, are summarized in Tables 1 and 2.

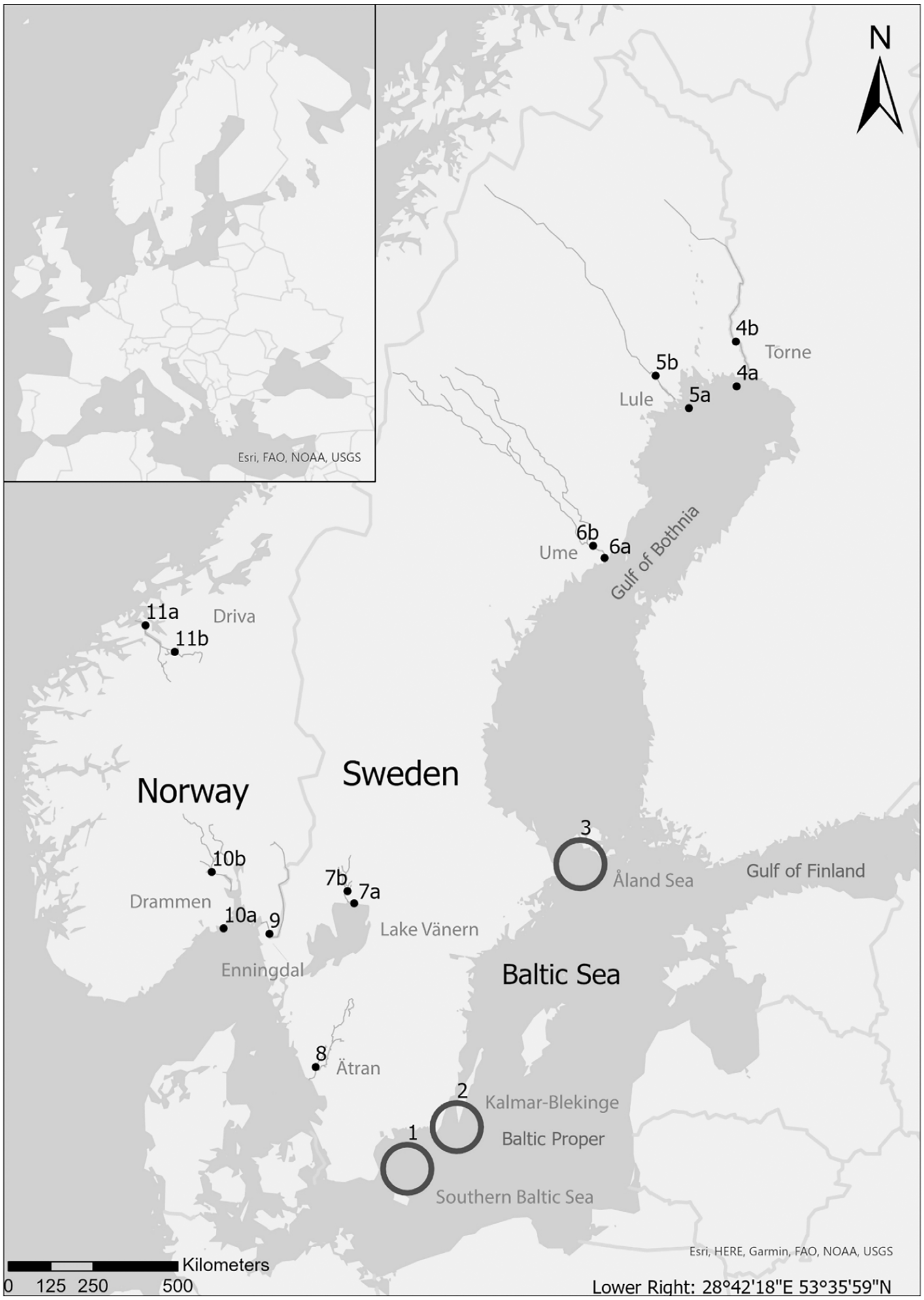

FIGURE 1 Map showing the sites where salmon was sampled during 2021. The numbers 1, 2, and 3 represent the three sampling areas in the open Baltic Sea: southern Baltic Sea, Kalmar–Blekinge regions, and Åland Sea, respectively. Swedish sampling sites are numbered from 4 to 8 (in order Torne, Lule, Ume rivers, Lake Vänern, Ätran River); Norwegian sites are numbered from 9 to 11 (in order Enningdal, Drammen, Driva rivers). Letters a and b indicate river mouths and upstream sites, respectively. The map was created in ArcGIS software by Esri (ArcGIS Pro 2.7.1 https://arcgis.com/).

2.2 | Ethics statement

All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. This study was granted approval (Dnr 2713-2020) by the Swedish Agency for Marine and Water Management (HaV) in Göteborg, Sweden, for sampling wild salmon in the Baltic Sea. Ethical permission for sampling in the Baltic Sea was granted as well (Dnr 16867-2018) by the Ethical Committee of Animal Experiments of the Swedish Board of Agriculture (Jordbruksverket) in Linköping. Ethical permission for sampling in Swedish rivers was granted (Dnr 5.8.18-06256/2019) by the Ethical Committee of Animal Experiments of the Swedish Board of Agriculture (Jordbruksverket) in Uppsala. Permissions to fish for sampling in the Swedish river systems were granted by HaV (Torneälven, Dnr 1876-2021 and 1892-2021) and the county boards of Västerbotten (Umeälven, Dnr 621-6241-2021), Värmland (Klarälven, Dnr 621-5715-2021), and Halland (Ätran, Dnr 623-4420-2021). As the sampling activity at the mouth of Luleälven was conducted within the designated fishing window, no fishing permit was required. Vattenfall, which holds the fishing rights at the restocking facility in our upstream sampling site, authorized us to fish in this area. Permissions to catch, kill, and sample salmon from Enningdalselva, Drammen, and Driva

TABLE 2 Means of weight in kg and total length in cm, and GSI and HSI (expressed in %) for every sampling occasion in 2021.

System	Area	Site	Sex	Number of individuals	Weight (mean ± S.D.)	Total length (mean ± S.D.)	GSI (mean % ± S.D.)	HSI (mean % ± S.D.)
Baltic populations	Southern Baltic Sea		Female	13	4.10 ± 1.56	75.50 ± 9.54	0.84 ± 0.43	1.42 ± 0.38
			Male	1	3.40	77.00	0.23	1.47
	Kalmar–Blekinge regions		Female	11	6.97 ± 0.99	87.67 ± 1.34	1.05 ± 0.29	1.36 ± 0.13
			Male	1	6.30	85.00	0.33	-
	Åland Sea		Female	2	7.80 ± 1.61	89.25 ± 8.37	1.34 ± 0.09	1.43 ± 0.01
			Male	1	6.20	88.00	0.84	1.93
	Torne River	River mouth	Female	13	8.37 ± 2.69	91.96 ± 8.61	2.00 ± 0.84	1.51 ± 0.20
			Male	7	11.19 ± 5.15	99.23 ± 16.11	0.69 ± 0.31	1.15 ± 0.18
		Upstream	Female	17	7.07 ± 2.83	89.18 ± 10.49	2.12 ± 0.84	1.16 ± 0.12
			Male	3	12.01 ± 5.01	103.00 ± 14.78	0.41 ± 0.11	1.01 ± 0.08
	Ume River	River mouth	Female	3	6.24 ± 0.65	87.67 ± 3.14	2.34 ± 0.34	1.18 ± 0.13
			Male	-	-	-	-	-
		Upstream (summer)	Female	17	7.67 ± 1.97	92.62 ± 8.02	2.42 ± 0.92	1.31 ± 0.31
			Male	3	8.27 ± 3.84	94.00 ± 17.32	0.49 ± 0.11	1.07 ± 0.32
		Upstream (fall)	Female	20	5.66 ± 0.99	89.95 ± 3.86	24.14 ± 3.65	1.62 ± 0.28
			Male	-	-	-	-	-
	Lule River	River mouth	Female	16	8.22 ± 1.83	92.75 ± 7.08	2.03 ± 0.58	1.64 ± 0.25
			Male	4	7.30 ± 1.12	89.00 ± 4.21	0.52 ± 0.28	1.49 ± 0.32
		Upstream (summer)	Female	15	8.74 ± 2.02	92.90 ± 5.36	2.56 ± 1.02	1.10 ± 0.13
			Male	5	9.09 ± 2.58	93.60 ± 8.42	1.15 ± 0.47	0.99 ± 0.10
		Upstream (fall)	Female	15	7.12 ± 1.42	92.47 ± 6.01	24.31 ± 3.60	1.39 ± 0.28
			Male	5	7.57 ± 2.74	96.50 ± 13.05	2.96 ± 0.93	1.04 ± 0.31
Lake Vänern population	Lake Vänern	Open lake	Female	14	4.64 ± 1.19	72.14 ± 5.48	2.26 ± 0.53	1.41 ± 0.37
			Male	4	6.04 ± 1.79	82.50 ± 11.48	1.23 ± 0.77	1.10 ± 0.27
		Upstream	Female	15	4.58 ± 1.49	74.37 ± 7.24	2.62 ± 1.08	0.80 ± 0.11
			Male	5	5.38 ± 2.35	78.00 ± 9.19	0.26 ± 0.06	0.87 ± 0.07
North Atlantic populations	Ätran River	Upstream (summer)	Female	12	4.17 ± 0.56	76.04 ± 3.70	0.97 ± 0.23	1.04 ± 0.15
			Male	-	-	-	-	-
		Upstream (fall)	Female	2	2.15 ± 0.40	68.5 ± 8.48	22.54 ± 1.91	1.77 ± 0.28
			Male	6	2.00 ± 0.40	75.50 ± 4.44	4.16 ± 0.72	1.13 ± 0.61
	Drammen River	River mouth	Female	11	5.20 ± 0.85	80.59 ± 4.06	1.72 ± 0.24	1.29 ± 0.33
			Male	7	5.36 ± 0.68	80.90 ± 4.26	0.19 ± 0.05	1.08 ± 0.25
		Upstream (summer)	Female	8	7.23 ± 2.22	89.87 ± 7.96	2.14 ± 0.57	1.00 ± 0.14
			Male	1	1.60	56.00	0.13	0.87
		Upstream (fall)	Female	8	4.54 ± 0.71	82.37 ± 3.39	18.41 ± 6.66	1.19 ± 0.38
			Male	12	2.53 ± 1.02	69.03 ± 8.31	2.93 ± 0.46	1.07 ± 0.21
	Driva River	River mouth	Female	13	4.60 ± 1.96	79.23 ± 8.54	2.75 ± 0.89	1.23 ± 0.23
			Male	7	3.68 ± 1.60	70.93 ± 11.61	0.91 ± 0.65	1.04 ± 0.15
		Upstream (summer)	Female	12	6.23 ± 2.96	88.75 ± 8.03	4.00 ± 1.27	1.13 ± 0.17
			Male	8	2.98 ± 1.78	68.38 ± 13.34	1.35 ± 1.04	1.04 ± 0.14
		Upstream (fall)	Female	5	3.95 ± 0.76	77.80 ± 5.05	14.06 ± 2.46	2.24 ± 0.24
			Male	17	2.52 ± 1.99	65.06 ± 12.53	3.89 ± 1.18	1.11 ± 0.26
	Enningdal River	Upstream	Female	9	7.71 ± 0.45	91.72 ± 3.37	1.50 ± 0.31	1.11 ± 0.35
			Male	6	8.99 ± 2.42	94.08 ± 10.14	0.28 ± 0.11	0.93 ± 0.10

Note: Standard deviation (S.D.) is also reported.

Abbreviations: GSI, gonado-somatic index; HSI, hepato-somatic index.

rivers were granted by the county officers of Oslo and Viken, Møre and Romsdal, and Vestfold and Telemark (Refs. 2021/8912, 2021/3310, 2021/4432).

2.3 | Sample collection

Fish were stunned by a blow to the head followed by exsanguination immediately after lifting them out of the water. Then the fish were photographed to document the external status (e.g., possible hemorrhages, wounds, parasites), followed by measurement of total length (cm) and weight (kg). Mean total length and weight are summarized in Table 2. Fulton's condition factor (CF) was calculated as 100 × weight (kg) × (total length [cm])$^{-3}$. For DNA analysis, small pieces of adipose fin from wild fish or fin clips from the anal fin of restocked fish (adipose fin was removed before release) were sampled and stored in Eppendorf vials with 96% ethanol at room temperature. At least 20 g of proximal dorsal muscle was dissected and sampled. Salmon were then opened, and weights of whole liver and gonads were measured for calculating the hepato-somatic index (HSI; HSI (%) $=$ weight$_{\text{liver}}$ (g) × 100/weight$_{\text{body}}$ (g)) and gonado-somatic index (GSI; GSI (%) $=$ weight$_{\text{gonad}}$ (g) × 100/weight$_{\text{body}}$ (g)), respectively. A subsample (~20 g) of gonads was collected, and the samples were vacuum packed separately and immediately placed in dry ice or in a portable freezer (−80°C, Stirling Ultracold ULT25NEU). Gonads in females included both eggs and small amounts of gonadal tissues in all life stages. The samples were transported to the lab and then stored at −80°C until further analysis.

2.4 | Thiamin quantification analysis

Thiamin was analysed according to Brown et al. (1998), with method modifications according to Vuorinen et al. (2002), Futia et al. (2017), Futia and Rinchard (2019). Approximately 0.5 g of frozen gonad and muscle tissues were weighed and placed in 15-mL Falcon tubes (using one technical replicate per tissue and individual fish). Mechanical homogenization was achieved by adding 3 mL of ice-cold 2% trichloroacetic acid (TCA) and five stainless steel balls (Steelball Lysing Matrix) and using the lysing system FastPrep-24 5G (MP Biomedicals) for 1 min repeated thrice at a speed of 6.5 m s^{-1}. Lysing matrices were removed from the tubes. The tubes were incubated in a water bath at 100°C for 10 min and then placed on ice for additional 10 min. One and a half mL of 10% TCA was added, and samples were centrifuged at 14,000 × g for 15 min using the high-speed centrifuge Beckman Avanti J-HC. The supernatants (1 mL) were washed four times with an equal volume of ethyl acetate:hexane (3:2 volume ratio), by removing the upper phase. A volume of 850 μL of the lower phase was mixed with 150 μL of freshly made 0.1% $K_3Fe(CN)_6$ solubilized in a 1.2 M NaOH solution. The mix was filtered through 0.45 μm PTFE/PP filters into sample glass vials. Standard solutions for the three vitamers of thiamin (free thiamin [TF], thiamin monophosphate [TMP], and thiamin diphosphate [TDP]) were subjected to the same procedure as the tissue samples except for the homogenization and the centrifugation steps and prepared in 0.1 M HCl solution and aliquoted in a five-points standard series. Samples were analysed with a Hitachi Chromaster HPLC system using a Hamilton PRP-1 column (5 μm particle size, 4.1 mm [I.D.] × 150 mm) protected by a guard column (10 μm particle size, 2.1 mm [I.D.] × 2.1 mm), and a fluorescence detector (excitation wavelength 375 nm, emission wavelength 433 nm). The injection volume was 100 μL (flow rate 1 mL/min) with a runtime of 25 min. The mobile phase consisted of 25 mM potassium phosphate buffer (pH 8.4) and *N*, *N*-dimethylformamide (DMF) at changing ratios over time (Table S1). The analyses were conducted at 4°C in the autosampler and 30°C in the column oven. The chromatograms were integrated using the software OpenLab (Agilent Technologies) with baselines drawn automatically and inspected manually. In this way, the three vitamers of thiamin, TF, TMP, and TDP, were quantified in muscle and gonads, and the amounts were summed and normalized by wet weight to total thiamin (Ttot) using the unit nmol g^{-1} wet weight. A subset of 77 female gonad samples from Torneälven, Luleälven, Umeälven, Driva, and Drammen rivers after sea migration and actively spawning life stages were freeze-dried to estimate dry weights. These latter were used to normalize the total thiamin concentrations by dry weight.

2.5 | DNA analysis

To determine the river of origin of fish caught during the marine feeding phase and after the sea migration, the total DNA was extracted from scales or fin clips of 70 salmon females from the open Baltic sampling, as well as from Torneälven, Luleälven, and Umeälven river mouths. A chelex-method (Walsh et al., 1991) was used for the DNA extraction, followed by PCR and genotyping of 18 polymorphic microsatellite markers: Ssa407 (Cairney et al., 2000); SSsp3016 (Gilbey et al., 2004); SSaD157 (King et al., 2005); Ssa14, Ssa289 (McConnell et al., 1995); Ssa85, Ssa171, Ssa197, Ssa202 (O'Reilly et al., 1996); SSsp1605, SSsp2201, SSsp2210, SSsp2216, SSspG7 (Paterson et al., 2004); SsOsl85, SsOsl311, SsOsl417, and SsOsl438 (Slettan et al., 1995). Each PCR reaction contained approximately 100 ng DNA template, 4.5 μL of Type-it Multiplex PCR Master Mix (Qiagen); the concentration of each primer pair was balanced to achieve uniform signal intensity during fragment analysis. PCR was run with an initial step of 5 min at 95°C followed by 25 cycles of 30 s at 95°C, 90 s at 56°C, 30 s at 72°C, and a final step of 15 min at 60°C. Electrophoresis was performed on an ABI 3500 with LIZ 500 size standard, and allele sizes were determined using GeneMapper5 software. An individual assignment was then conducted with ONCOR (Kalinowski et al., 2008) using a baseline dataset for 17 DNA microsatellite markers for 39 Baltic salmon stocks, totaling 7227 individuals. SsOsl311 was missing on several populations and was therefore excluded from the statistical analysis. The assignment needed to have a 0.95 probability for it to be considered a true match.

2.6 | Statistical analysis

Statistical analysis and graphics were performed using R, version 4.2.1 (R Core Team, 2021). We studied the effect of several variables on thiamin concentrations in salmon caught in 2021 with linear mixed modeling using the function *lmer* from the package "lme4" (Bates et al., 2014). The AIC was used to distinguish among the best models describing the relationship between total thiamin and sex, tissue, system, adult life stage, and potential fitness variables (z-score transformed CF and z-scored transformed total length of fish). To analyse the change in thiamin levels in different adult life stages of salmon, the best-fit model (model1), carrying 99% of the cumulative model weight and having the lowest AIC, included all the parameters mentioned earlier together with all the biologically meaningful interactions as fixed effects. The only random effect variable included in the model was the "Fish ID." To investigate differences in thiamin concentration between sexes, the best-fit model (model2) was similar to the previously described one except that the "life stage" and "system" parameters were included as random variables together with "Fish ID." Finally, model3 was used to explore general population differences. Its structure was similar to the previous ones, but it included "sex" and "life stage" as random effects together with "Fish ID." The three models are summarized in Table S2.

3 | RESULTS

3.1 | Thiamin concentrations across systems and yearly variation

Thiamin concentrations in gonads and muscle differed significantly among systems, as indicated by the predictor value for the variable "system" in Figure 2. The highest average concentration was found in the Lake Vänern population, intermediate concentrations in the North Atlantic populations, and the lowest concentrations in the Baltic populations (Figures 2 and 3). Thiamin concentration in the muscle of the Baltic populations ranged from 1.0 to 22.0 nmol g^{-1}, whereas in the muscle of the North Atlantic populations the concentrations ranged from 4.4 to 16.1 nmol g^{-1}. In Lake Vänern, thiamin concentrations in the muscle ranged from 9.7 to 23.1 nmol g^{-1}. In the gonads, the variation in thiamin concentration among individuals was higher in the Baltic populations ranging from 0.6 to 30.9 nmol g^{-1}, whereas in the North Atlantic populations, it ranged from 2.1 to 21.6 nmol g^{-1} and in the Lake Vänern population from 6.0 to 34.1 nmol g^{-1}. The differences among systems were also present when females and males were analysed separately (Figure S1). The analysis of microsatellite DNA of salmon that were caught in the open Baltic Sea and at Torneälven and Luleälven river mouth sites allowed us to determine the thiamin concentration in relation to the river of origin (Figure 4). Eight rivers of origin were identified among the samples (Figure 4): Iijoki, Kalix, Lödgeälven, Luleälven, Simojoki, Torneälven, Torneälven–Kalix river bifurcation, Umeälven–Vindel river bifurcation. Here we focus on female individuals from Torneälven and Luleälven as they were the most common among the sampled fish. There was no difference in the mean thiamin concentrations when comparing individuals caught in the Southern Baltic Sea that originated from two different rivers, Luleälven and Torneälven–Kalix river bifurcation (two-sample t-test, t [26] $= -0.59$, $p = 0.560$). There was also no difference in the mean thiamin concentrations between individuals caught at the Luleälven and Torneälven river mouths and originated, respectively, in the Luleälven River and Torneälven–Kalix river bifurcation (Welch's two-sample t-test, t [41.86] $= -1.39$, $p = 0.172$). This suggests that thiamin levels did not seem to be affected by the river of origin (Figure 4). Salmon from Umeälven and Torneälven rivers were sampled both in 2020 and 2021 during summer (Figure 5). In general, individuals from populations that were sampled in different years showed significant differences in thiamin concentrations between years (one-way ANOVA, $F_{1,291} = 28.33$, $p < 0.0001$), with the samples from year 2020 having lower thiamin concentrations when compared to 2021 samples (t value $= -2.759$). To further investigate the differences in thiamin concentration between the years in different tissues (Figure 5), two separate two-way ANOVAs were conducted for gonad and muscle. In the gonad, total thiamin concentrations were affected by year ($F_{1,134} = 172.4$, $p = 0.002$), river location ($F_{3,134} = 540.6$, $p < 0.001$), and their interaction ($F_{3,134} = 430.0$, $p < 0.001$). However, in the muscle, total thiamin concentrations were affected only by year ($F_{1,143} = 431.8$, $p < 0.001$).

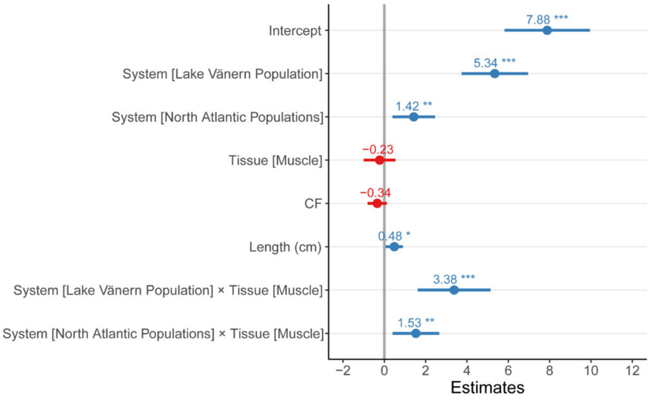

FIGURE 2 Summary of linear mixed modeling (model3) with 95% C.I., showing the effects of the predictors included in the model on total thiamin. The intercept represents the reference level (system = Baltic populations, tissue = gonad). The vertical gray line indicates no effect. Positive (blue) and negative (red) values denote positive and negative relationships, respectively. Statistically significant effects are indicated by asterisks where ***$p < 0.001$.

3.2 | Sex-specific thiamin concentrations and effect of length and condition factor

Thiamin concentrations in gonads were significantly lower in males than in females when comparing all individuals regardless of life stage in one-way comparisons (Figure 6; Table 3). The same pattern was observed for thiamin concentrations in the muscle of North Atlantic

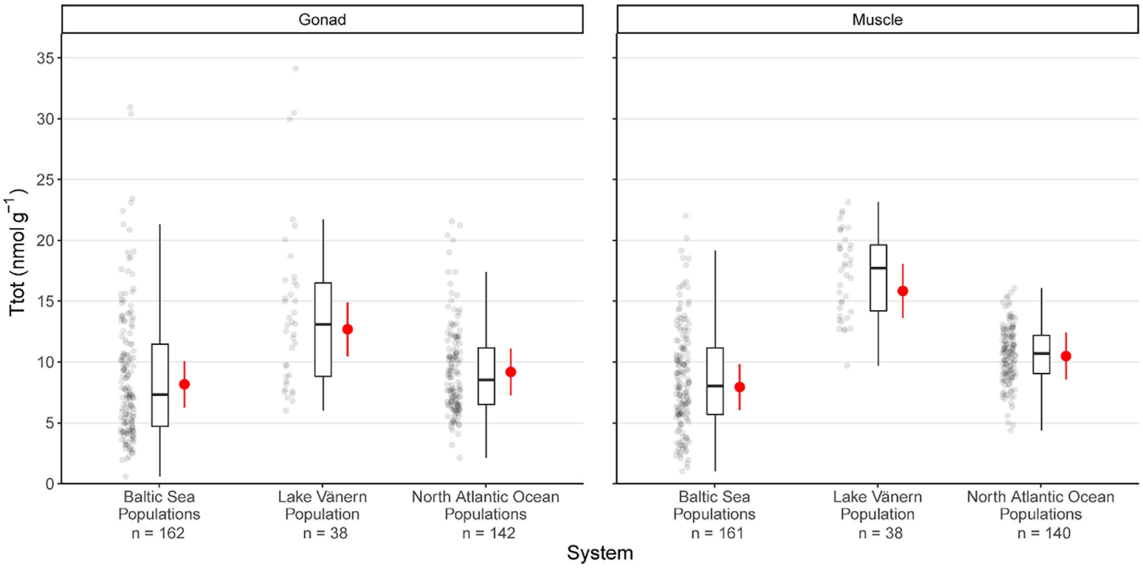

FIGURE 3 Total thiamin content (Ttot) expressed in nmol gram of tissue analysed, comparing the three different systems included in the study (Baltic, Lake Vänern, and North Atlantic populations). The dots represent the raw data, and the numbers (*n*) show the number of individuals analysed for each population. The box delimits the second and third quartiles, with the median as a bold horizontal line; whiskers represent the first and the fourth quartiles. The red dots show the predictions from linear mixed modeling (model3) with 95% C.I.

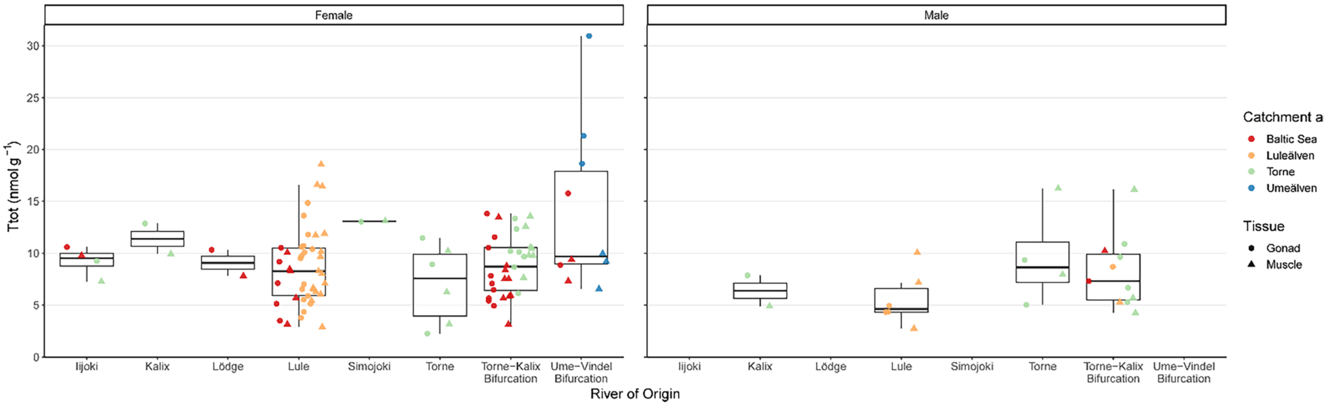

FIGURE 4 Total thiamin concentration (Ttot) expressed in nmol gram of tissue analysed comparing different rivers of salmon origin that drain in the Baltic Sea. Different colors indicate where the salmon was caught during the sampling sessions. The box delimits the second and third quartiles, with the median as a bold horizontal line; whiskers represent the first and the fourth quartiles.

individuals, but not for female and male muscle concentrations of the Baltic and Lake Vänern populations (Table 3). However, modeling life stage and system as random variables (model2) showed that sex alone did not have a statistically significant effect on total thiamin concentrations (Figure 7). As indicated by the predictor value for sex though, female thiamin concentrations were slightly higher than those of males. There was also a significant interaction between sex and tissue likely driven by higher concentrations in gonads in females compared to males but no difference when comparing concentrations in muscle of females and males (Figure 7). Moreover, there was no significant main or interaction effect of sex and length or condition factor on thiamin concentrations (Figure 7). Salmon sampled in the open Baltic Sea, which were actively feeding, tended to be smaller than the ones sampled after the sea migration at the river mouths of Torneälven, Luleälven, and Umeälven rivers. For males, there were no differences in length between salmon caught in the open Baltic Sea and the ones at the river mouths (one-way ANOVAs, $p > 0.05$); for females these differences in length comparing salmon caught in the open Baltic Sea and individuals at the river mouths were significant (one-way ANOVAs, $p < 0.05$) except for individuals caught in Umeälven river mouth (one-way ANOVA, $F_{1,25} = 0.74$, $p = 0.399$). Although smaller and in some cases significantly, salmon caught in the open Baltic were probably ready to migrate towards their natal rivers given their GSI values (Table 2) higher than GSI threshold for the onset of maturation in Atlantic salmon of 0.06 and 0.3% defined by previous studies (Peterson & Harmon, 2005; Davidson et al., 2016; Martinez, Balseiro,

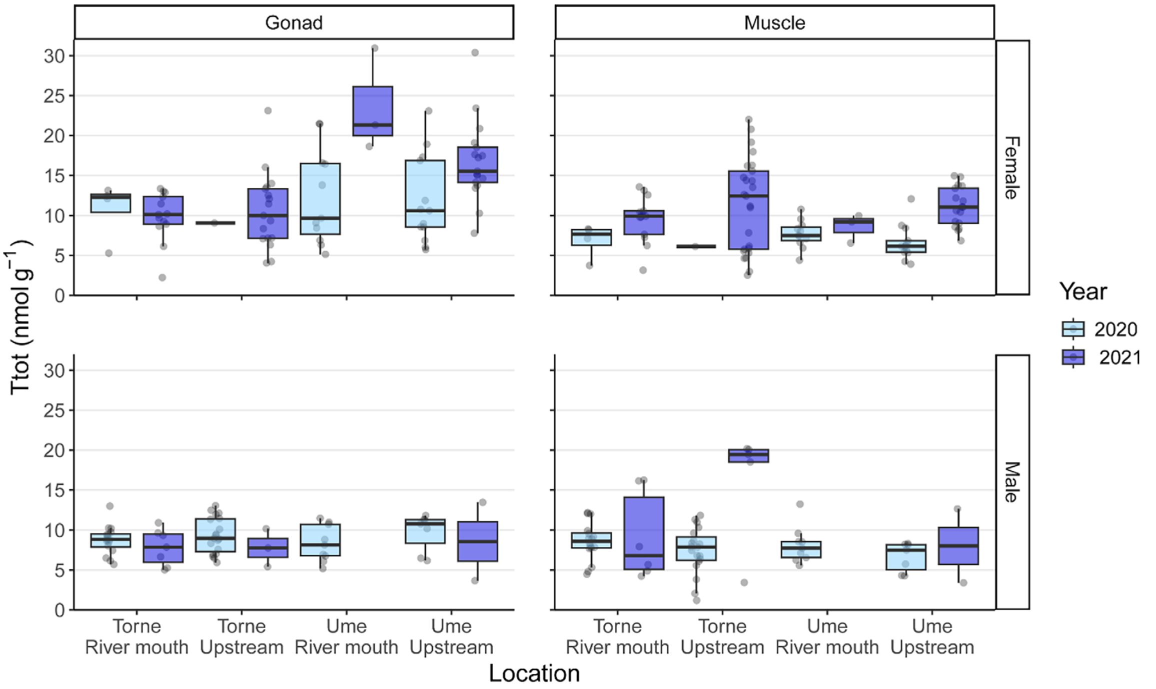

FIGURE 5 Total thiamin concentration (Ttot) expressed in nmol g^{-1} of tissue analysed in salmon sampled in Ume and Torne rivers. The different colors indicate a different sampling year. Fainted gray dots represent raw data; the box delimits the second and third quartiles, with the median as a bold horizontal line; whiskers represent the first and the fourth quartiles.

Fleming, et al., 2023; Martinez, Balseiro, Stefansson, et al., 2023). Length of the fish also tended to vary somewhat between sampling occasions in each river but not significantly (one-way ANOVAs, $p > 0.05$), except for females in Drammen (one-way ANOVA, $F_{2,24} = 6.94$, $p = 0.004$) and Driva rivers (one-way ANOVA, $F_{1,15} = 7.41$, $p = 0.016$). Total thiamin concentrations were negatively correlated with all the fitness variables except for CF and total weight, but the relationships were weak (Figure S2). Therefore, thiamin concentration in this study did not seem to be strongly related to length or any of the fitness indexes (Figure S2).

3.3 | Thiamin concentrations during the life cycle of salmon

Temporal changes in thiamin concentration were studied throughout four different adult life stages of salmon as they spend time in the marine feeding grounds, migrate toward the rivers, migrate upstream, and at spawning (Figure 8). Fewer individuals were sampled in Lake Vänern and only during two adult life stages; therefore the following analyses are exclusively based on data from the Baltic and North Atlantic populations. Throughout the four adult life stages, there were stable or slightly increasing thiamin concentrations in individuals during the migration phases from sea to upstream locations whereas the concentrations decreased toward spawning, especially in gonads (Figure 8; Table S2). The decline in thiamin levels through subsequent stages differed between tissues, which resulted in a significant tissue by life stage interaction (Figure 9; Table S2). In fact, thiamin levels during the actively spawning life stage were almost 5-fold lower than those during the actively feeding stage, which represents the reference predictor level for the main effect of life stage (Figure 9; Table S2). This decreasing pattern of thiamin concentration toward spawning was observed in both Baltic and North Atlantic populations (Figure 8). Moreover, gonad thiamin concentrations were less variable among individuals when they were ready to spawn than among individuals in the other adult life stages in both Baltic and North Atlantic populations (Figures 8 and 9; Table S2). Levels of thiamin in the gonads tended to be higher in females than in males—although not significantly—when including life stages in the statistical model, based on the main effect of sex and tissue (Figure 9; Table S2). There was a significant sex by system interaction likely driven by smaller differences between males and females in the Baltic populations when compared to the North Atlantic ones (Figures 6, 8 and 9; Table S2). Thiamin concentrations of only females followed a similar pattern with higher thiamin concentration in the North Atlantic populations compared to the Baltic, and declining concentrations in the gonads toward spawning were present (Figure S3). Thiamin concentrations expressed in nmol gram wet weight in gonads decreased toward spawning (Figures 8 and 9), and the same patterns were observed when normalizing the concentration values by dry weight in a subset of data where dry weights were available (Figure 10). This indicates that dilution due to increased water content in eggs is not the reason for reductions in thiamin concentrations when comparing salmon after sea migration with actively spawning individuals.

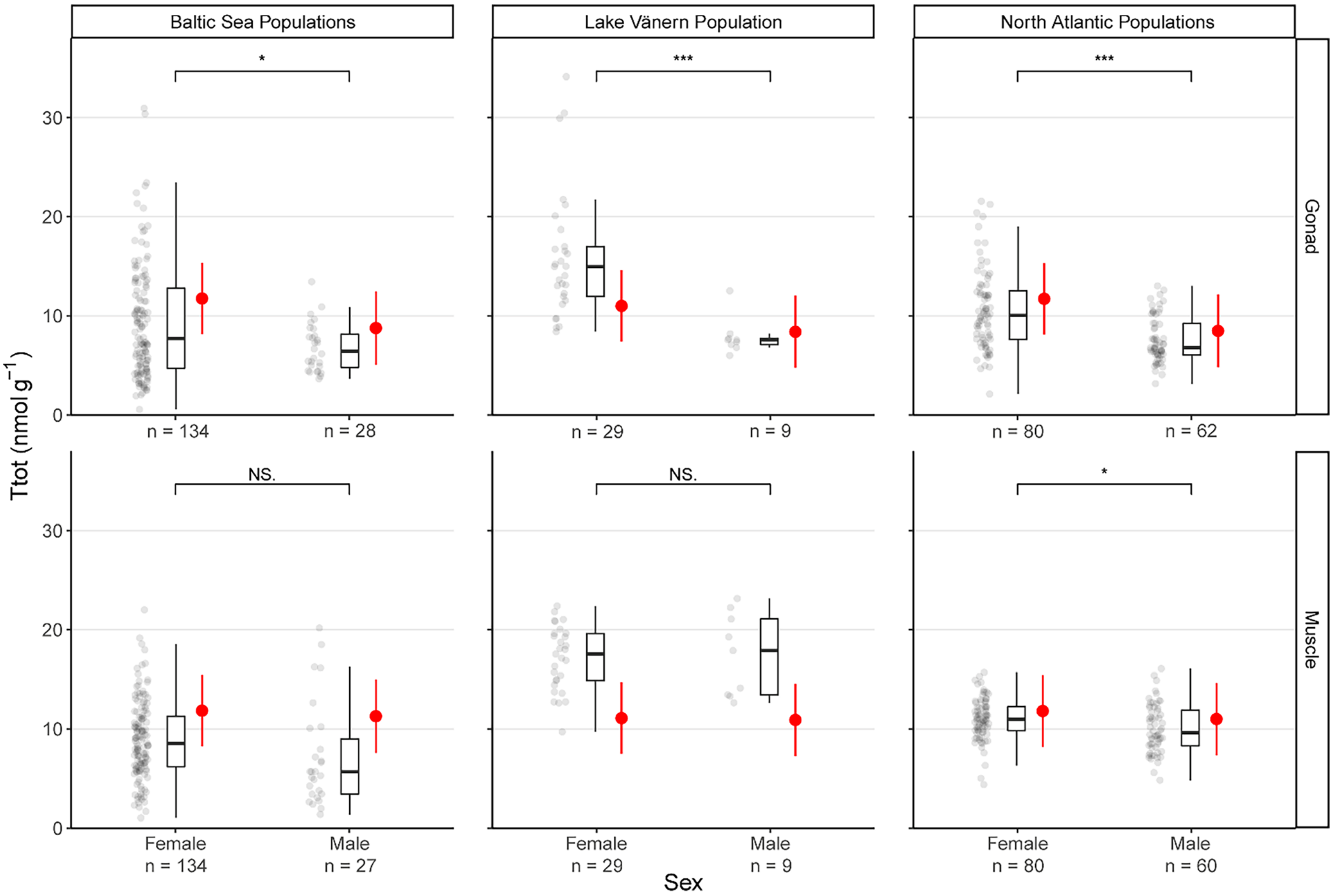

FIGURE 6 Total thiamin concentration (Ttot) expressed in nmol gram of tissue analysed, comparing females and males from different populations. Fainted gray dots represent raw data, and the numbers (n) show the number of individuals analysed for each population, sex, and tissue. The box delimits the second and third quartiles, with the median as a bold horizontal line; whiskers represent the first and the fourth quartile. Statistically significant differences are indicated by asterisks (****p* < 0.001). The red points show the predictions of linear mixed modeling (model2) with 95% C.I.

TABLE 3 Results from Tukey's post-hoc test for differences in total thiamin concentrations (nmol g^{-1}) between females and males within populations.

			Ttot (nmol g^{-1})	
Tissue	**System**	**Sex**	***t* value**	**Sig. level**
Gonad	Baltic Sea populations	Male–female	−2.461	*
	North Atlantic populations	Male–female	−3.021	***
	Lake Vänern population	Male–female	−8.098	***
Muscle	Baltic Sea populations	Male–female	−1.741	
	North Atlantic populations	Male–female	0.339	
	Lake Vänern population	Male–female	−0.992	*

**p* < 0.05; ***p* < 0.01; ****p* < 0.001.

4 | DISCUSSION

Thiamin concentrations varied significantly among salmon populations coming from the three different systems included in the study, that is, the Baltic Sea, North Atlantic Ocean, and Lake Vänern. The highest mean concentrations were found in Lake Vänern followed by the North Atlantic and finally lowest in Baltic salmon. Therefore, salmon in the Baltic Sea seem to have systematically lower concentrations of thiamin compared to those in other systems (Figure 2). Temporal patterns of thiamin concentrations during different adult life stages were similar among systems: concentrations were stable or slightly increasing throughout the feeding and migratory life stages, whereas these concentrations decreased during spawning, especially in gonads (Figure 8). The differences at a system level mentioned earlier were consistent during the different life stages of salmon as well.

4.1 | Thiamin concentration decreases toward spawning

As salmon migrate from their feeding grounds to their natal rivers, they start a fasting period lasting approximately 4 to 6 months until the actual spawning begins (Vuorinen et al., 2014). Vuorinen et al. (2020) suggested that thiamin is consumed during this migration before arriving at the river. We found no evidence of such reduction in thiamin in muscle and gonad tissues comparing actively feeding individuals in the Southern Baltic to individuals arriving after migration at the river mouth or just after migration further upstream into the river. However, after the summer migration and when they approached the actual spawning period in late October–November, we did find lower concentrations in gonads, suggesting that thiamin supply is constrained in the development of the offspring. This pattern occurred in the North Atlantic populations as well, where thiamin deficiency is generally not observed. Reductions in thiamin concentrations in gonads do not seem to be related to changes in water content, because concentrations normalized to dry weights showed the same patterns as when normalized to wet weights. Therefore, this reduction in thiamin concentrations toward reproduction could be part of the natural consequence of thiamin decay related to its short half-life and associated with starvation and lipid catabolism in preparation for spawning. Thus, this reduction might not be associated with thiamin deficiency. The possible mechanism behind this could be that the thiamin pool in muscle and gonads is used as an antioxidant reservoir to prevent damage to cell structures due to oxidative stress (Depeint et al., 2006; Gibson & Zhang, 2002; Keinänen et al., 2017; Lukienko et al., 2000; Lundström et al., 1999; Pickova et al., 1998). Considering the same life stages in salmon from the two systems, North Atlantic salmon still had overall higher average thiamin concentrations in muscle and gonads. This indicates a generally lower thiamin status in the Baltic Sea throughout all the adult life stages from the feeding to the spawning grounds.

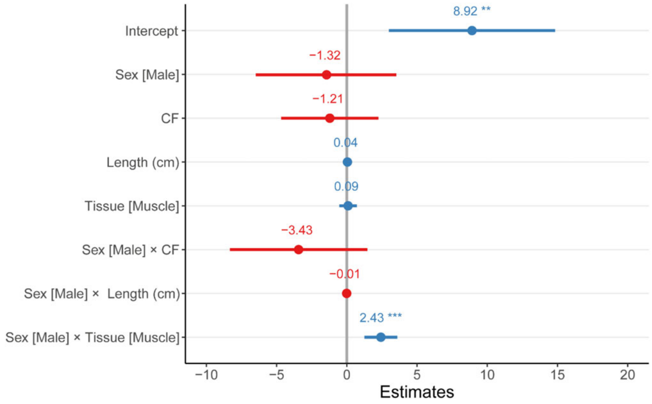

FIGURE 7 Summary of linear mixed modeling (model2) with 95% C.I., showing the effects of the predictors included in the model on total thiamin. The intercept represents the reference value (sex = female, tissue = gonad). The vertical gray line indicates no effect. Positive (blue) and negative (red) values denote positive and negative relationships, respectively. Statistically significant effects are indicated by asterisks where ***$p < 0.001$.

4.2 | Baltic populations have systematically lower thiamin concentrations

Only a few studies have compared thiamin in salmon stocks from different systems, and to date, there is no systemic comparison between

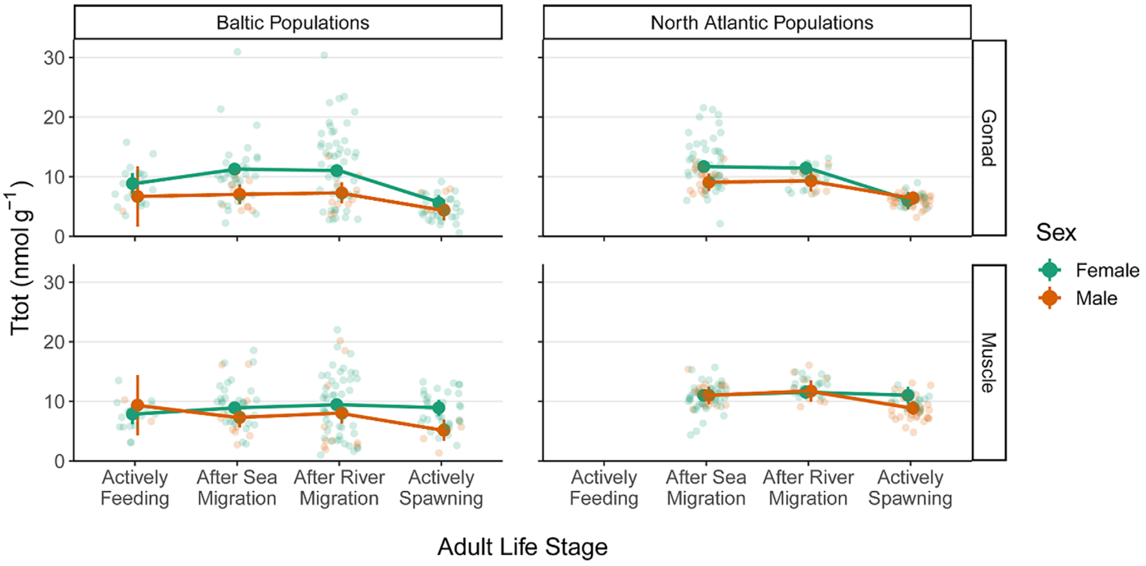

FIGURE 8 Temporal changes in total thiamin (Ttot) through four adult life stages of salmon. Fainted dots represent raw data for females and males (color-coded). Bold points show the predicted values from linear mixed modeling (model1) with 95% C.I. Bold points were slightly jittered to avoid overlapping.

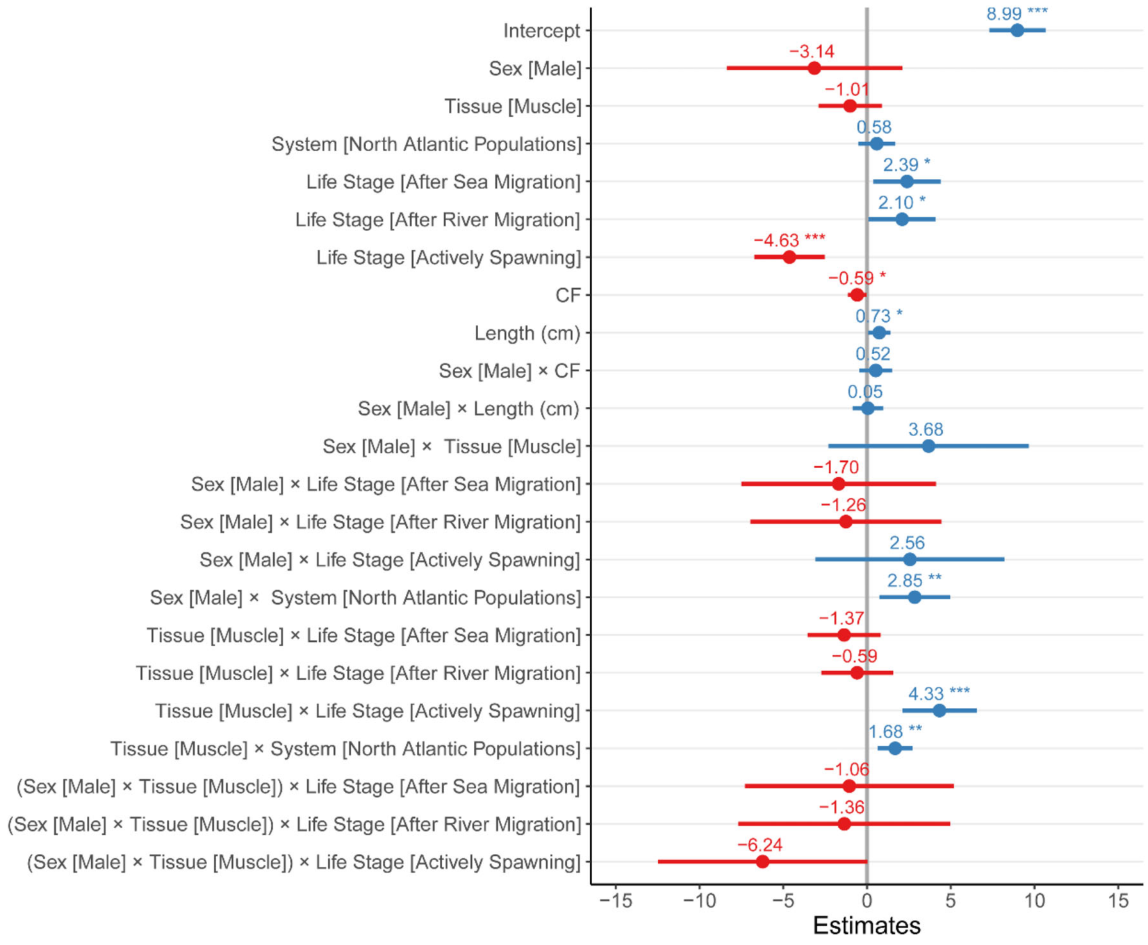

FIGURE 9 Summary of linear mixed modeling (model1) with 95% C.I., showing the effects of the predictors included in the model on total thiamin. The intercept represents the reference level (sex = female, tissue = gonad, system = Baltic populations, life stage = actively feeding). The vertical gray line indicates no effect. Positive and negative values denote positive and negative relationships, respectively. Statistically significant effects are indicated by asterisks where *** = *p* value <0.001.

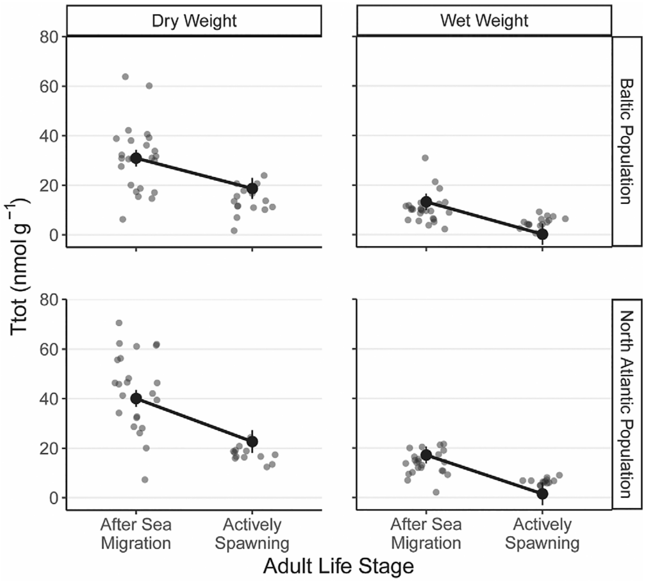

FIGURE 10 Total thiamin (Ttot) normalized per dry weight (left panels) and wet weight (right panels) in female gonads. Fainted dots represent raw data, and bold points show the predicted values from linear mixed modeling with 95% C.I.

the North Atlantic and Baltic salmon. This is surprising as thiamin deficiency has been repeatedly reported for Baltic salmon whereas few or no reports of this disorder exist for the North Atlantic populations (Hylander et al., 2020). Few estimates of thiamin in North Atlantic salmon are available from one river that drains in the Arctic Ocean and from one on the Swedish west coast, and these indicate approximately the same concentrations as in this study, although the sampling size was small and quantification method was different (Amcoff et al., 1999; Balk et al., 2016; Koski et al., 2001). To the best of our knowledge thiamin concentrations have been measured only once in the landlocked salmon population located in Lake Vänern (Amcoff et al., 1999). Although the study included only four females from Lake Vänern, the thiamin concentration in fertilized eggs was higher when compared to fertilized eggs from other Swedish rivers (Amcoff et al., 1999), and this is in line with our results as well. Thiamin concentrations in other populations of Atlantic salmon ranged from 0.5 to 13.6 nmol g^{-1} in muscle which is approximately within the same range as our data (Amcoff et al., 1999; Balk et al., 2016; Koski et al., 2001; Vuorinen et al., 2020). With this study, we can start developing an understanding of thiamin ranges that occur naturally in different systems and will help future monitoring of thiamin concentration reductions that may indicate that these populations are facing periods of thiamin deficiency.

4.3 | Variation in thiamin concentrations among years and rivers

When making comparisons among years, there were lower concentrations in individuals caught in 2020 in Torneälven and Umeälven rivers compared to 2021. Fluctuations in salmon thiamin over the years and the resulting incidence of M74 have been documented previously (Keinänen et al., 2012; Keinänen et al., 2017; Mikkonen et al., 2011). It has been demonstrated that M74 incidence is positively correlated to sprat population size (Karlsson et al., 1999; Mikkonen et al., 2011). However, these variations in M74 incidence also correlate with other large-scale changes in the food web including changes in several abiotic factors and all trophic levels ranging from phytoplankton and zooplankton to fish (Majaneva et al., 2020). This suggests that yearly variation in salmon thiamin concentrations is due to changes in the food web of the marine feeding area. We found no differences in thiamin concentrations comparing salmon originating in different rivers, suggesting the use of the same feeding grounds regardless of the natal river. Jacobson et al. (2020) showed that the most northerly salmon populations of the Baltic Sea system reached the southern feeding grounds during their marine life phase approximately at the same latitude, supporting this conclusion. Other studies have also concluded that most of the Baltic salmon populations use the Southern Baltic Sea as their main marine feeding ground, although some individuals stay in the Gulf of Bothnia to some extent (Jacobson et al., 2020; Jutila et al., 2003; Kallio-Nyberg et al., 2015; Kallio-Nyberg & Ikonen, 1992; McKinnell & Lundqvist, 1998; Torniainen et al., 2014). Interestingly, there was a significant variation among individuals within populations suggesting that different fish had experienced different availability of thiamin before reaching the natal rivers. In all, this emphasizes the importance of understanding the factors affecting thiamin availability for salmon when they share common marine feeding grounds.

4.4 | Different feeding grounds lead to different thiamin availability, fatty acid composition, and thiaminase activity in salmon diet

The salmon populations from the three systems studied here do not share the same feeding grounds. Whereas the diet of salmon in the Southern Baltic Sea is dominated by sprat and herring (Hansson et al., 2001; Karlsson et al., 1999), the main prey items of salmon in the North Atlantic Ocean are herring, sand eels, capelin, crustaceans (mostly krill), and pelagic amphipods (Hansen & Pethon, 1985; Haugland et al., 2006; Jacobsen & Hansen, 2000). Thiamin concentrations in amphipods are not well known, but other crustaceans such as mesozooplankton have in order of five times higher concentrations compared to small fish such as herring (Hylander et al., in prep., Fridolfsson et al. [2018]; Fridolfsson et al. [2019]; Fridolfsson et al. [2020]). Therefore, the absolute thiamin concentration of a mixed crustacean and fish diet would be higher than a diet with only fish, and this could potentially explain the differences in thiamin status between Baltic and North Atlantic salmon populations observed here. Other studies have also suggested that a variable diet promotes higher thiamin concentrations in predators (Futia et al., 2019). The diet of the salmon stock in Lake Vänern is mainly dominated by European smelt (*Osmerus eperlanus*) and vendace (*Coregonus albula*) (Nyquist, 2022). Measurements of thiamin concentrations in these prey fish are not available, but Lake Vänern salmon had the highest concentrations, suggesting that a diet dominated by these small fish species can still sustain a high thiamin concentration in the predator, as observed in this study. However, apart from absolute thiamin concentrations and the food web transfer, other factors, including insufficient availability of thiamin in relation to lipids, or activity of thiamin degrading enzymes, could affect the thiamin concentrations in top predators.

A lipid-rich diet with a high proportion of polyunsaturated fatty acids (PUFAs) has been suggested to cause thiamin deficiency (Keinänen et al., 2012; Keinänen et al., 2017; Keinänen et al., 2018; Vuorinen et al., 2020). This suggested mechanism relies on the assumption that thiamin requirements increase if the organisms feed on high-energy diets. The mechanism of thiamin reduction is proposed to be related to lipid peroxidation and its usage as an antioxidant (Keinänen et al., 2012; Keinänen et al., 2017; Keinänen et al., 2018; Lukienko et al., 2000; Vuorinen et al., 2020). Negative correlations between the proportion of PUFAs and thiamin concentrations have been demonstrated in several salmonids including Atlantic salmon (Czesny et al., 2009; Czesny et al., 2012; Keinänen et al., 2018; Futia & Rinchard, 2019) although other studies have not found such negative correlations (Brown et al., 2005a). To the best of our knowledge no studies exist comparing the PUFAs of North Atlantic, Baltic, and Lake Vänern salmon. For this reason, it is difficult to determine if Baltic salmon are more susceptible to thiamin loss through this oxidative stress defense mechanism than the other two populations, which in turn would explain the lower thiamin concentrations in these populations. It is possible that thiamin deficiency is caused by other factors, and that low thiamin concentration, in turn, leads to oxidative stress and lipid peroxidation, and not the other way around. For example, other factors that may influence thiamin status in various geographical regions of the Baltic Sea are environmental conditions, such as variations in temperature (Olsvik et al., 2013), or occurrence of environmental contaminants (Asplund et al., 1999). As the fish are exposed to increasing temperature or toxins that induce oxidative stress, draining of antioxidants may ultimately affect available pools of thiamin.

Another potential cause of thiamin deficiency in salmonids is the presence of the thiamin-degrading enzyme, thiaminase, in their diets. Relatively few studies have focused on investigating the presence and activity of this enzyme in the prey items of salmon in the Baltic Sea and Lake Vänern populations (Hirn & Pekkanen, 1975; Wistbacka et al., 2002; Wistbacka & Bylund, 2008), and to the best of our knowledge, there are no reports from North Atlantic salmon. Instead, this has been extensively studied in salmonids from the Great Lakes region (Fitzsimons et al., 2005; Honeyfield et al., 2005b; Honeyfield et al., 2012; Houde et al., 2015; Tillitt et al., 2005). Through feeding experiments, it has been demonstrated that a diet dominated by alewife (*Alosa pseudoharengus*), a non-native species in the Great Lakes that is known to have high thiaminase activity, is related to a reduction in thiamin concentrations in eggs and muscle of salmonid females (Honeyfield et al., 2005b; Houde et al., 2015). However, the source of thiaminase activity remains elusive (Richter et al., 2012), and it is not known if thiamin degradation by thiaminase is the main mechanism that leads to thiamin deficiency observed in nature. In the Baltic Sea, both sprat and herring showed thiaminase activity and, in some comparisons, herring had higher thiaminase activity than sprat (Wistbacka & Bylund, 2008). In Lake Vänern, zero to low thiaminase activity has been detected in European smelt and vendace (Hirn & Pekkanen, 1975). The data from this study indicate that a system-specific factor causes thiamin constraints in Baltic Sea salmon compared to Lake Vänern and North Atlantic populations. However, further research is necessary to determine if thiamin-degrading enzymes are a plausible explanation for the observed thiamin deficiencies and for the lower thiamin concentrations in the Baltic Sea salmon compared to the other examined systems.

4.5 | Little to no effect of length, fitness variables, and sex on thiamin concentrations

Thiamin concentrations in salmon were overall weakly correlated to length or fitness variables (CF, GSI, and HSI). There was also little to no evidence of relationships between condition factor and thiamin in any of the studied systems. Other studies on Baltic salmon have suggested the opposite with a positive correlation between the incidence of thiamin deficiency syndromes such as M74 and condition factor (Mikkonen et al., 2011). The mechanism suggested for this relationship would be an unbalanced high-fat diet in M74-producing females (Mikkonen et al., 2011). When modeling, we did not find such evidence of length or condition factor affecting the thiamin concentrations studied here in any significant way. In addition, sex did not have a major effect on thiamin concentrations in muscle, but there were significant differences between females and males when comparing concentrations in gonads. Besides genetically, males do not contribute to the allocation of resources into the eggs and thus to offspring, suggesting that they probably do not invest energy in having a large gonadal thiamin pool as females do.

4.6 | How the results relate to literature thresholds and thiamin deficiency

Balk et al. (2016) suggested a thiamin deficiency threshold for sublethal negative effects at 17–19 nmol g^{-1} in muscle. About 96% of the Baltic salmon sampled in 2021 had thiamin concentration in the muscle below 17 nmol g^{-1}, suggesting that sublethal thiamin deficiency is widespread in these populations. However, the incidence of M74 that year was 5% indicating that many of the individuals with sublethal thiamin concentrations could still reproduce. Approximately 45% of Lake Vänern salmon and all North Atlantic salmon were also below the threshold suggested by Balk et al. (2016). This suggests that sublethal thiamin deficiency may also exist in other systems, albeit at a lower incidence in Lake Vänern. However, it is important to note that the suggested threshold for sublethal thiamin deficiency should be used with some caution, given that all the individuals sampled in the North Atlantic populations were below this threshold, although there is no documented history of thiamin deficiency in this system. Regarding thiamin concentration in eggs, several studies have investigated thiamin thresholds in relation to mortality in the offspring (Amcoff et al., 1999; Balk et al., 2016; Fitzsimons et al., 2013; Riley et al., 2011). Harder et al. (2020) recently demonstrated that the effective thiamin concentration in eggs required for 50% survival of Atlantic salmon fry is 5.5 nmol g^{-1}. In our study, around 69% and 20% of the females that were ready for spawning from Baltic and North Atlantic populations, respectively, had lower thiamin concentrations in gonads than the threshold for 50% mortality (Harder et al., 2020). Therefore, sublethal thiamin deficiency may be widespread in salmon populations. Although a threshold for negative sublethal effects has been suggested, it may still need more development before being used on a broad scale comparing different populations.

5 | CONCLUSIONS

In conclusion, this study provides a novel overview of thiamin concentrations in salmon populations across different systems. The findings suggest that Baltic Sea salmon consistently have lower thiamin concentrations than those from other systems, indicating a potential constraint in thiamin availability in this region. The results shed light on the importance of dietary diversity among systems as well as the variation in thiamin reaching higher trophic levels. This variation can be influenced by thiamin availability, a fatty acid signature indicative of oxidative stress, the presence of thiamin-degrading enzymes, or other unknown environmental factors. Furthermore, the decline in thiamin concentrations toward spawning appears to be a natural phenomenon during pre-spawning fasting occurring in all systems, rather than being related to thiamin deficiency. This highlights the need for a more comprehensive monitoring of thiamin levels in salmon populations with different previous feeding histories.

AUTHOR CONTRIBUTIONS

Vittoria Todisco and Samuel Hylander conceived and designed the study and led the writing of the first manuscript drafts. Vittoria Todisco collected and analysed the samples for thiamin quantification, analysed the data, and led the interpretation of the results. Emil Fridolfsson provided support in the study design, methodology, sample collection in 2020, data analysis, and interpretation of results. Charlotte Axén, Kjetil Hindar, and Petter Tibblin contributed to the sampling design, collection of samples, and interpretation of results. Elin Dahlgren, Maciej J. Ejsmond, Marc M. Hauber, Markus Zöttl, and Linda Söderberg actively participated in interpreting results and editing and reviewing the manuscript drafts. Linda Söderberg and Elin Dahlgren analysed the samples for the DNA analysis. All authors read and approved the final version of the manuscript.

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ORCID

Vittoria Todisco https://orcid.org/0009-0006-0327-9547

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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