fishes

MDPI

Article

Reduced Numbers of Returning Atlantic Salmon (*Salmo salar*) and Thiamine Deficiency Are Both Associated with the Consumption of High-Lipid Prey Fish

Marja Keinänen [1], Jari Raitaniemi [2], Jukka Pönni [1], Tiina Ritvanen [3], Timo Myllylä [2] and Pekka J. Vuorinen [1,4,5,*]

[1] Natural Resources, Fisheries and Fish Resources, Natural Resources Institute Finland (Luke), P.O. Box 2, FI-00791 Helsinki, Finland; m.e.keinanen@gmail.com (M.K.); jukka.ponni@luke.fi (J.P.)
[2] Natural Resources, Fisheries and Fish Resources, Natural Resources Institute Finland (Luke), Itäinen Pitkäkatu 4 A, FI-20520 Turku, Finland; jari.raitaniemi@luke.fi (J.R.); timo.myllyla@luke.fi (T.M.)
[3] Chemistry Unit, Laboratory and Research Division, Finnish Food Authority (Ruokavirasto), P.O. Box 200, FI-00027 Helsinki, Finland; tiina.ritvanen@ruokavirasto.fi
[4] Faculty of Biological and Environmental Sciences, University of Helsinki, P.O. Box 65, FI-00014 Helsinki, Finland
[5] Department of Biological and Environmental Science, University of Jyväskylä, P.O. Box 35, FI-40014 Jyväskylä, Finland
* Correspondence: pekka.vuorinen@helsinki.fi or pekka.vuorinen@gmail.com or pekka.j.vuorinen@jyu.fi; Tel.: +358-40-577-7323

Abstract: In 2023, exceptionally few salmon (*Salmo salar*) ascended from the Baltic Sea to spawn in the Rivers Tornionjoki and Simojoki, regardless of the proper number of smolts descending to the sea in preceding years. We investigated how the numbers of age-0 and young herring (*Clupea harengus*) and sprat (*Sprattus sprattus*), which are the principal prey species of salmon in the Baltic Proper, the main feeding area of these salmon, as well as the amount of lipid obtained from them and their protein-to-lipid ratio, correlated with the number of returning salmon and the thiamine (vitamin B1) status of spawning salmon. The fewer the 0-year-old herring were and the more abundant were the youngish sprat in the Baltic Proper when the post-smolts arrived there, and the greater the lipid content and lower the protein-to-lipid ratio of the prey fish, the fewer salmon returned to the Rivers Tornionjoki and Simojoki to spawn two years later. The number of returning salmon was lowest with a high ratio of youngish sprat, 1–3 years old, regarding the River Tornionjoki and 1–2 years old regarding the River Simojoki post-smolts, to 0-year-old herring, which were of a suitable size to be the prey for the post-smolts upon their arrival in the Baltic Proper. In 2021, the ratios were lowest due to the record-low number of 0-year-old herring. The poor thiamine status of spawning salmon was also associated with the high lipid content of available prey fish and with the abundance of youngish sprat, which have twice the lipid content of age-0 herring. Our findings parallel the observations in the early 1990s when post-smolt survival declined concurrently with the outbreak of thiamine deficiency, M74. We conclude that consuming high-lipid marine fish reduces the survival of post-smolts and, thus, the number of returning salmon, in addition to causing thiamine deficiency.

Keywords: Atlantic salmon (*Salmo salar*); Baltic Sea; herring (*Clupea harengus*); lipid content; M74 syndrome; post-smolt; protein-to-lipid ratio; sprat (*Sprattus sprattus*); thiamine (vitamin B1); thiamine deficiency

Academic Editor: Bror Jonsson

Received: 4 November 2024
Revised: 24 December 2024
Accepted: 25 December 2024
Published: 31 December 2024

Citation: Keinänen, M.; Raitaniemi, J.; Pönni, J.; Ritvanen, T.; Myllylä, T.; Vuorinen, P.J. Reduced Numbers of Returning Atlantic Salmon (*Salmo salar*) and Thiamine Deficiency Are Both Associated with the Consumption of High-Lipid Prey Fish. *Fishes* **2025**, *10*, 16. https://doi.org/10.3390/fishes10010016

Key Contribution: Salmon, during their first feeding year, are sensitive to excessively fatty marine prey fish with too much lipid relative to protein and, thus, too much energy relative to thiamine. Such food reduces the survival of post-smolts during their first year of foraging and, therefore, largely determines how many of these salmon return for spawning.

1. Introduction

The River Tornionjoki (hereafter Tornionjoki) has been the most important spawning river of Atlantic salmon (*Salmo salar*) foraging in the Baltic Sea (hereafter Baltic salmon or salmon) since the damming of the largest river of the northern Baltic Sea, the River Kemijoki, in 1948 (Figure 1). In all, 80% of the salmon rivers of the Gulf of Bothnia have been dammed or spoiled by other treatments so that they have lost their salmon stocks like the River Kemijoki, or the stocks are maintained by producing offspring by hatchery rearing and smolt releases. As the border river between Finland and Sweden, Tornionjoki has remained undammed and produces the most wild salmon in the Baltic Sea. The River Simojoki (hereafter Simojoki) is the other undammed river on the Finnish side of the Bothnian Bay in the Gulf of Bothnia (Figure 1), in which salmon reproduce naturally. It is considerably smaller than Tornionjoki, and its salmon production capacity is a fraction of that of Tornionjoki [1].

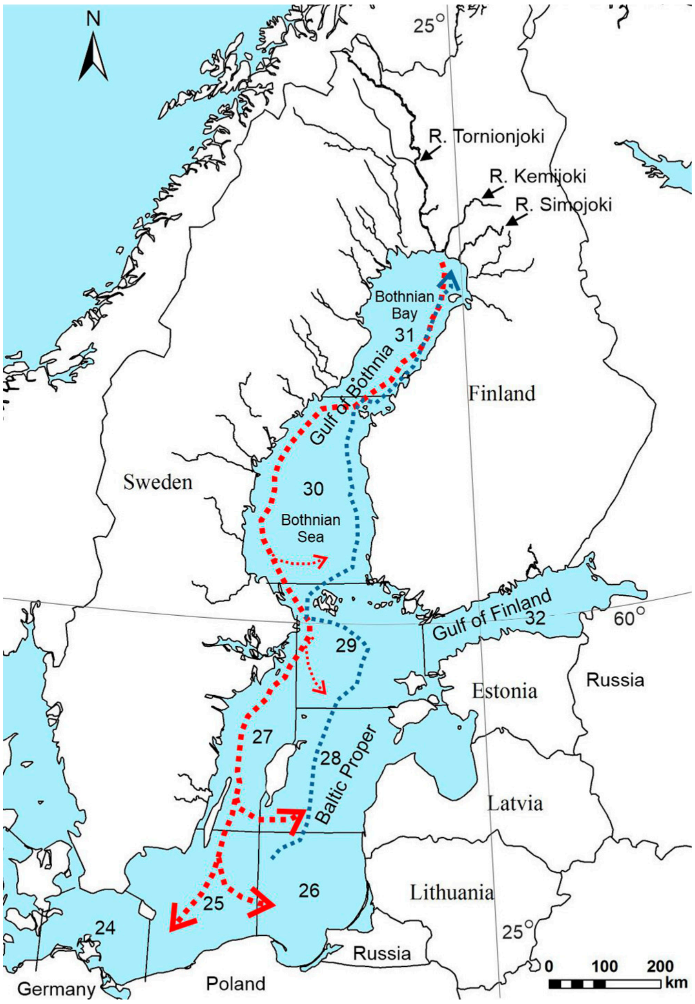

Figure 1. Baltic Sea with the subareas and location of the principal Finnish salmon (*Salmo salar*) rivers the River Tornionjoki and the River Simojoki, as well as the dammed River Kemijoki, are indicated.

The major routes for the migration of the post-smolt from the Bothnian Bay rivers (red) to sea areas and salmon ascending for spawning (blue) into rivers are also indicated. The subdivisions (SD) of the International Council for the Exploration of the Sea (ICES, origin of the map, ICES Spatial Facility, ICES, Copenhagen) are also presented. Post-smolts from the Bothnian Bay rivers [2], whether from natural reproduction or from introductions, migrate towards the south largely along the east coast of the Bothnian Bay. After reaching the Quark halfway into the bay, they mainly swim according to the currents along the west coast of the Gulf of Bothnia to the Baltic Proper [3,4].

According to the hydroacoustic counting of Natural Resources Institute Finland (Luke), salmon ascend Tornionjoki and Simojoki (Figure 1) mainly in June–July, and the timing and progression of the run varies between years [5]. In 2023, a dramatically lower number of salmon than on average in the previous five to ten years ascended both rivers for spawning [5]. This was unexpected and remained unexplained, as no major changes were observed in the numbers of salmon smolts these rivers produced in preceding years [1]. A decrease in the numbers of salmon returners was also detected in the Swedish rivers Kalixälven and Råneälven in the Bothnian Bay [1]. However, the survival of salmon post-smolts had begun to decline from the early 1990s, and the decline continued into the 2000s, though it has stabilized since 2005 [1,6]. The decline in post-smolt survival appeared to have begun concurrently with the violent outbreak of lipid-related thiamine (vitamin B1) deficiency, called the M74 syndrome in the Baltic Sea region, at the turn of the 1980s and 1990s [7,8]. The question arose as to whether they could have a common cause.

The salmon stocks of Tornionjoki and Simojoki, like other salmon stocks in the Baltic Sea, were on the verge of disappearing due to M74 in the 1990s. M74 has manifested as the death of salmon offspring as yolk-sac fry [free embryo or eleutheroembryo [9], most of which died in several years in the early and mid-1990s. Since then, the mortality rate has varied from year to year [10,11]. Some or all of the yolk-sac fry of females with a free thiamine (THIAM) concentration of <0.71 nmol g^{-1} in unfertilized eggs (M74 females) die of M74 [8]. In the worst M74 years, some brood salmon have also died of M74 before spawning after ascending the river [8]. However, the salmon's thiamine status was already weakened during the feeding migration in the sea area where prey fish were fattiest and the juvenile salmon themselves were also fattiest [12].

Poor thiamine status or thiamine deficiency in fatty predatory fish results from an unbalanced diet abundant in fatty marine prey fish, which are rich in peroxidation-prone polyunsaturated fatty acids of the *n–3* family (*n–3* PUFAs) [12,13]. In the Baltic Sea region, thiamine deficiency has mainly affected salmon and to a lesser extent sea trout (*S. trutta*) [14,15], and M74 has also recently been found to impair the reproduction of the lamprey (*Lampetra fluviatilis*) [16]. In North America, lipid-related thiamine deficiency is called Thiamine Deficiency Complex (TDC), and there it has affected several salmonine species, especially the fattiest, Chinook (*Oncorhynchus tshawytscha*), coho (*O. kisutch*), and Atlantic salmon and steelhead trout (*O. mykiss*) in the Great Lakes [17,18], Atlantic salmon in the Finger Lakes [19], and Chinook salmon off the central coast of California [20–22].

The requirement for thiamine increases as the energy content of the diet increases [13,23] because thiamine is needed as a coenzyme in all enzymatic reactions that produce energy for cells in the form of ATP (adenosine triphosphate) [24] and in fatty acid metabolism [25,26]. Both a lower-than-optimal thiamine-to-energy and protein-to-lipid ratio in the diet have been reported to weaken the growth of fish [11,23,27,28]. In addition, marine fish lipids are characterized by very long-chain *n–3* PUFAs, docosahexaenoic acid (DHA, 22:6*n–3*), eicosapentaenoic acid (EPA, 20:5*n–3*), and docosapentaenoic acid (DPA, 22:5*n–3*), which are sensitive to peroxidation [29,30]. Acting as an antioxidant against the peroxidation of PUFAs, thiamine is destroyed in these reactions [8,12,13,31–34].

Most of the salmon feeding in the Baltic Sea return to their home rivers to spawn after two years, but some do so after a few more years of feeding migration, and as an iteroparous species, some individuals may spawn several times [35]. According to Pardo et al. [36], the variation in the number of returners of the North Atlantic salmon populations in eastern Canada was mostly explained by their survival during the first feeding year in the sea. In the mark–recapture surveys of Bothnian Bay salmon stocks, the survival of post-smolts of Simojoki salmon was found to increase in the Baltic Proper of the Baltic Sea (Figure 1) in the years when a strong year-class of herring (*Clupea harengus*) hatched there [37]. Thus far, no information is available about whether and how the survival of salmon post-smolts is related to the number of sprat (*Sprattus sprattus*), nor about whether the strong new year-class of herring affects the number of salmon returning to Tornionjoki to spawn. It is also unknown why the abundance of age-0 herring increases survival, or whether the outbreak of M74 in the early 1990s and the decline in post-smolt survival shared a common factor.

Thiamine deficiency in salmon females feeding in the Baltic Proper and the resulting M74 mortality in yolk-sac fry both in the 1990s and later were caused by the abundance of young sprat in the diet [10,11,13,38]. The reason for the sudden multiplication of the sprat stock at the turn of the 1980s and 1990s was mainly the collapse of the cod (*Gadus morhua*) population due to overfishing, which enabled the sprat population to increase quickly [38,39], because cod is the principal predator of sprat [40]. Cod stocks have remained weak [41,42], and since the beginning of the 1990s, the spawning stock of sprat has been stronger than before [41]. Herring is the other important prey species of salmon in the Baltic Proper. However, the average lipid content of sprat is twice that of small herring—that is, those that are of a suitable size as prey for salmon—in the same areas of the Baltic Sea [12,13,43,44]. Youngish sprat in the fall are the fattiest prey fish, whereby the supply of thiamine per energy unit is lower from them than from herring and lower than from older sprat [13]. Lipid peroxidation already reduces the thiamine status of the fattiest juvenile salmon during the feeding migration [12] because the fatty acids of lipids, especially in marine fish, are the source of energy needed for swimming and metabolism, for example [30]. Apparently for the same reason, while the youngest age groups of sprat and herring contain more n–3 PUFAs than the older age groups, thiamine concentration has also been lower in them than in older individuals [43,45].

After descending from the river to the sea and seawater adaptation in the spring, salmon post-smolts from the Bothnian Bay rivers, whether from natural reproduction or from introductions, migrate all the way to the southern Baltic Sea, the Baltic Proper (Figure 1) [3,4]. Most leave the Gulf of Bothnia in August–September [46], but some remain to feed there [11,35,37,46,47]. The proportion of salmon remaining there increases in years when a strong new year-class of herring, the dominant prey species of salmon in the Gulf of Bothnia, hatches there [11,37]. In the sea, salmon post-smolts at first eat invertebrates in addition to small fish [48] and become solely piscivorous at a length of 24–32 cm [46,49]. At this size, most salmon post-smolts from the rivers of the Bothnian Bay move from the Gulf of Bothnia to the Baltic Proper and feed in the sea for two years, attaining a total body length of 73–76 cm and mass of 3–7 kg [35,50].

Based on stomach analyses and fatty acid signature analyses (FASA) of adult salmon, sprat is known to have been quantitatively the most important prey for salmon in the Baltic Proper in recent decades [10,11,43,51–53]. The proportions of sprat and herring in the total prey biomass of all salmon in the Baltic Proper have varied on a large scale, depending mainly on the abundance of sprat [38]. Especially in the southernmost Baltic Proper, herring quickly grow larger than the size appropriate for salmon prey [38]. Only the very youngest herring are therefore of a suitable size for salmon during their first growing year at sea—that is, during their post-smolt phase [2]. Instead, sprat is slow-growing and does not usually grow longer than 15 cm, making sprat of all ages suitable prey for at least most salmon [38,54].

The size of fish preyed by salmon depends on both the size of salmon and the availability of prey of a suitable size, (i.e., size-dependent prey availability [54]), and somewhat differs, depending on the status of prey fish stocks and the feeding area in the Baltic Proper [38,54]. The youngest salmon can only eat the smallest fish due to the salmon's relatively small mouth cap [55]. However, even large salmon mainly eat small prey fish if abundant [52,54,55]. For example, salmon post-smolts of 45 cm in length eat prey fish approximately 5–13 cm in length [54].

We hypothesized that the characteristics of available prey fish affected salmon post-smolt survival and thus the number of salmon ascending for spawning. As the feeding migration of most salmon takes two years, the effect of diet on the survival of post-smolts is reflected in the number of salmon ascending their home rivers for spawning two years later. Using the existing data, the aim was to evaluate whether and how the numbers of herring and sprat that hatched annually in the Baltic Proper and were recruited there into the salmon's prey biomass have affected the survival of Tornionjoki and Simojoki salmon post-smolts in recent years. Due to the simultaneous decline in ascending salmon and the sudden increase in the M74 mortality of yolk-sac fry, the possible relationship of reduced post-smolt survival with lipid-related thiamine deficiency was evaluated. To assess these, we compared the numbers of 0-year-old and young herring and sprat in the feeding years of salmon post-smolts with the numbers of salmon ascending these two rivers two years later. We also compared the lipid content and protein-to-lipid ratio in herring and sprat with the number of returners and with the THIAM concentration in the eggs of salmon returning to these rivers for spawning.

2. Materials and Methods

2.1. Salmon Data

The numbers of salmon (*Salmo salar*) that had entered Tornionjoki and Simojoki for spawning in 2012–2023 according to hydroacoustic counting were obtained from the data of the International Council for the Exploration of the Sea (ICES) (cf. Table 3.1.1.2. in [1,56]). The numbers include both females and males that had been on their feeding migration for at least two years—that is, multi-sea-winter (MSW) salmon [2]. The hydroacoustic counting point is located in Tornionjoki, approximately 100 km, and in Simojoki 5 km, from the river mouth [5,57].

Of the thiamine components, the concentration of unphosphorylated, or free, thiamine (THIAM) in both fish muscle and eggs decreases with thiamine deficiency [8,10,16] and thus indicates thiamine status. The annual mean concentration of THIAM in the ovulated unfertilized eggs of salmon females that returned for spawning to Simojoki and Tornionjoki in the falls of 2012–2022 were obtained from Luke's Finnish M74 monitoring data [8]. The salmon sampled for the thiamine analyses were therefore from the same populations as in the hydroacoustic counting. The THIAM concentration of the eggs had been analyzed using the HPLC method with fluorescence detection [8]. The mean THIAM value for the females of the fall of 2016 was excluded as an extreme outlier, because an exceptionally large proportion of the 2016 salmon ascendants had been feeding in the Gulf of Bothnia during 2014–2016 [11] after an exceptionally large new year-class of herring had hatched there in 2014 [58,59]. However, 2016 was included in other calculations because we used the prey fish data of only the Baltic Proper.

In the present study, the post-smolt phase of salmon is considered from entering the sea in May until the end of April in the following year [2].

2.2. Clupeid Data

The numbers of 0-year-old (young-of-the-year or age-0) herring (*Clupea harengus*) hatched annually in the Baltic Proper in 2010–2021 were obtained from the data of the ICES (cf. Table 4.2.11. in [41]). The numbers of 1–3-year-old herring and 1–8-year-old sprat (*Sprattus sprattus*) were from the ICES reports in 2022 (cf. Table 4.2.14. in [60]) and 2024 (cf. Table 7.18. in [41]). The numbers of 0-year-old sprat were calculated (log-transformed data) from the numbers of 1–8-year-old sprat of each year-class.

The total body lipid and energy content and the total body thiamine concentration of herring and sprat were obtained from Vuorinen et al. [45] and Keinänen et al. [13,43]. The total lipid content of herring and sprat samples had been determined by the Schmid–Bondzynski–Ratzlaff method [61], and the energy content was calculated from the lipid content as in Keinänen et al. [13]. From these data, only the values of 1-year-old herring and 1–3-year-old sprat were included in this study. The body mass and lipid data of 0-year-old sprat and herring that were unavailable in the above data were obtained from Vuorinen et al. [62].

2.3. Calculations and Statistics

The numbers of ascendant salmon from 2012 to 2023 were compared with the numbers and quality of prey fish in the Baltic Proper two years earlier, 2010–2021, because most salmon that returned to the rivers for spawning were second sea-year salmon [8] and because the second sea-year salmon had started feeding as post-smolts in the sea two years earlier. The relationship of the annual number of returning salmon to the number of herring and sprat in combinations of different age groups two years earlier and to their lipid content, and protein-to-lipid ratio, was examined using regression models of log-transformed values. The regression model was also applied for the relationships of the THIAM concentration in the eggs of the 2nd sea-year females included in the M74 monitoring to the number of ascending salmon of Tornionjoki and Simojoki, to the number of herring and sprat, to the ratio of the numbers of sprat to herring, and to the lipid content and protein-to-lipid ratio in available and suitable prey fish. For the protein-to-lipid ratio, the protein content was calculated from the lipid content and dry mass of herring and sprat [13,43]. Lipid available in prey fish during the 2nd feeding year of salmon that returned for spawning in 2012–2022 was calculated from the numbers and mean mass in the herring and sprat in the catches [41,60], as well as the estimated lipid content of herring and sprat in 2011–2021.

The normal distribution of total body lipid content, the ratio of protein concentration to the lipid content, and the ratio of total body thiamine concentration to energy density of sprat and herring was tested by the Kolmogorov–Smirnov test. The significance of the similarity of the parameter means was tested by the Wilcoxon test.

The statistical analyses were performed with Statistical Analysis System (SAS Studio, Release: 3.81, 2024 SAS Institute Inc., Cary, NC, USA) software. The figures were drawn with OriginPro 2023 (OriginLab Co., Northampton, MA, USA).

3. Results

3.1. The Number of Returning Salmon Depended Inversely on the Numbers of 0-Year-Old Herring and Youngish Sprat

According to the regression analysis, the number of salmon that returned annually from the feeding migration to spawn in Tornionjoki and Simojoki during 2012–2023 was higher when more herring had hatched in the Baltic Proper two years earlier (Figure 2a,c and Table S1). The number of salmon ascending Tornionjoki was positively and significantly correlated with the number of 0-year-old herring, and the regression model explained 44.5%

of the variation (Figure 2a and Table S1). Regarding Simojoki salmon ascendants, the nearly significant relationship with the number of 0-year-old herring was also positive, and the regression model explained 32.6% of the variation (Figure 2c and Table S1). If herring older than 0 years were included in the calculations, the positive correlation of returners tended only to be significant with 0 plus 1-year-old herring and only for Tornionjoki salmon, but other age combinations of herring were not significantly correlated with the numbers of the ascendants of either river, and the coefficients of determination were very low (Table S1). Similarly, if 0-year-old sprat were included in the calculations, the relationships were not significant.

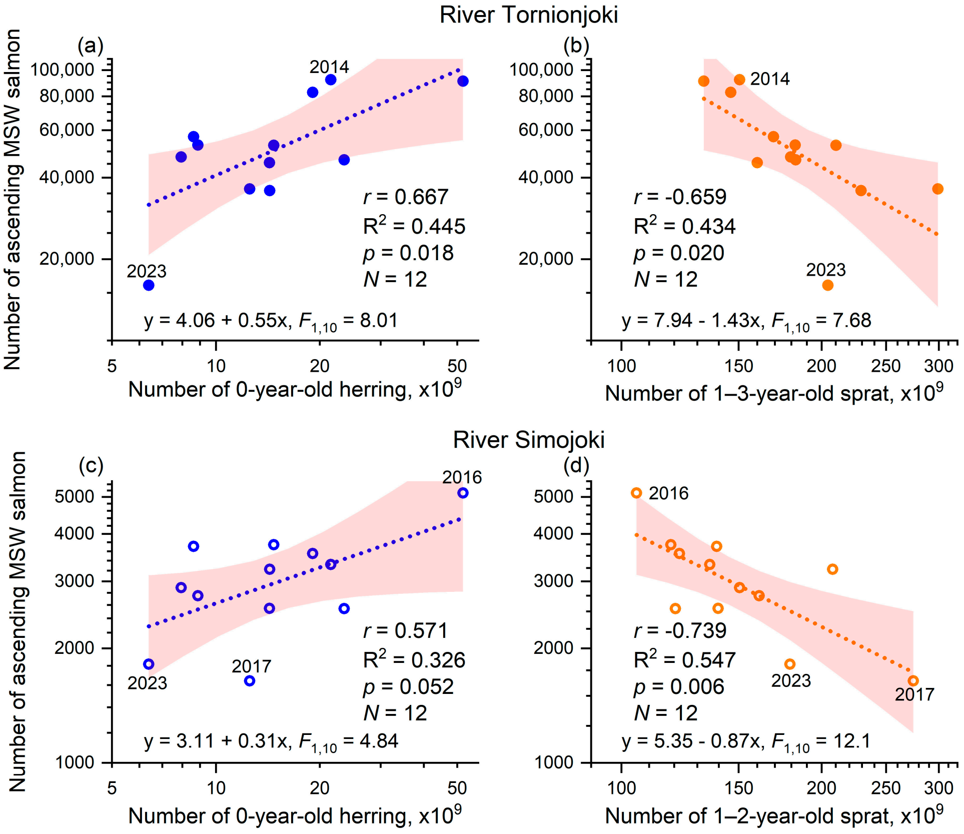

Figure 2. The number of multi-sea-winter (MSW) salmon (*Salmo salar*) ascending the River Tornionjoki in 2012–2023 in relation to the number of (**a**) 0-year-old herring (*Clupea harengus*) and (**b**) 1–3-year-old sprat (*Sprattus sprattus*) two years earlier (2010–2021) in the Baltic Proper, and the River Simojoki in relation to the number of (**c**) 0-year-old herring and (**d**) 1–2-year-old sprat. The values for the Pearson correlation coefficients and the coefficients of determination, *p*-values, and the number of observations (N) for the regression models are shown. Data points for 2023 and the minimum and maximum numbers of ascending salmon are indicated.

In contrast, the number of ascending salmon on both rivers was lower when more youngish sprat were in the Baltic Proper two years earlier—that is, in the 2010–2021 feeding years (Figure 2b,d and Table S1). The number of salmon ascending Tornionjoki or Simojoki had a negative and significant relationship with the number of 1–2-, 1–3-, and 1–4-year-old sprat. The total number of sprat minus the age-0 group was also negatively and significantly correlated with the number of ascending salmon: $r = 0.628$, $p = 0.029$, and $r = 0.688$, $p = 0.013$ for Tornionjoki and Simojoki respectively (Table S1). The negative correlation of Tornionjoki returners was strongest with 1–3-year-old sprat, where the regression model explained 43.4% of the variation, and the negative correlation of Simojoki returners was strongest with 1–2-year-old sprat, with the regression model explaining 54.7% of the variation (Figure 2b,d and Table S1). The regression model deteriorated when more older age groups were included. No correlation with the total number of sprat, including 0-year-olds, was observed (Table S1).

In addition, the numbers of salmon ascendants of both Tornionjoki and Simojoki were also positively and significantly correlated with the number of 0-year-old sprat and the sum of the number of 0-year-old herring and 0-year-old sprat (Table S1).

The number of salmon ascendants had an even stronger and negative relationship with the ratio of the numbers of youngish sprat (1–3-year-old sprat regarding Tornionjoki returners and 1–2-year-old sprat regarding Simojoki returners) to 0-year-old herring (Figure 3). The negative and significant relationship of the ascendants with the ratio of the numbers of youngish sprat to 0-year-old herring was stronger for Tornionjoki salmon than Simojoki salmon. For Tornionjoki salmon, the regression model of the ratio explained 66.7% of the variation, and the model for Simojoki salmon explained 51.9% of the variation (Figure 3a,b).

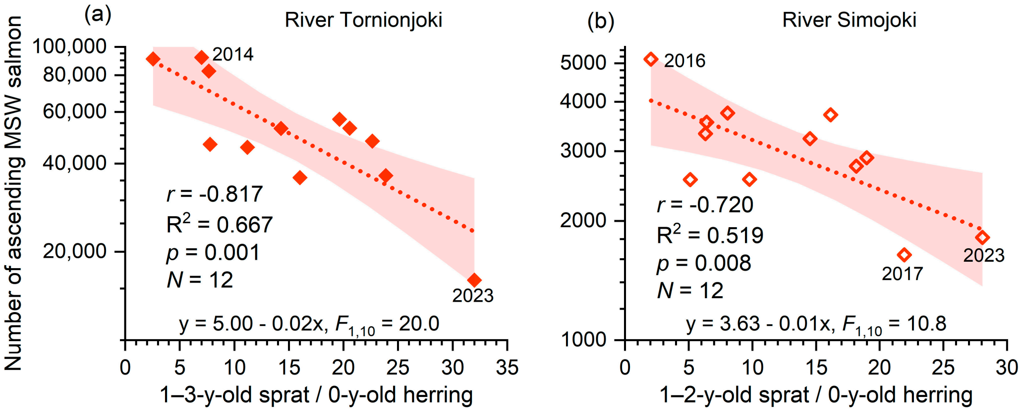

Figure 3. The number of MSW salmon (*Salmo salar*) in relation to the ratio of (**a**) the number of 1–3-year-old sprat (*Sprattus sprattus*) to 0-year-old herring (*Clupea harengus*) for the River Tornionjoki, and (**b**) the number of 1–2-year-old sprat to 0-year-old herring for the River Simojoki. See Figure 2 for other explanations.

The regression models showed significantly that the higher the proportion of 0-year-old herring and the lower the proportion of youngish sprat in the total number of these prey fish in the Baltic Proper, the more salmon returned to spawn to each river, Tornionjoki and Simojoki, two years later. However, the positive relationship between the numbers of age-0 herring and salmon returning two years later was stronger for Tornionjoki than for Simojoki salmon, whereas the negative relationship with the number of youngish sprat was slightly stronger for Simojoki than for Tornionjoki salmon (Figures 2 and 3 and Table S1). Because the number of salmon returning to Tornionjoki had the strongest relationship with the number of 1–3-year-old sprat, and the number of Simojoki returners with the number of 1–2-year-old sprat (Table S1), these combinations of age groups were used in the statistical analyses regarding the relationships of the number, lipid content, and protein-to-lipid ratio of prey fish with the numbers of returning salmon and the concentration of THIAM in salmon eggs. The number of 1–3-year-old sprat was 130–300 billion specimens annually in 2010–2021, which is an average of one-fourth larger than the number of 1–2-year-old sprat, 105–275 billion specimens, and an average of 15 times (2.6–32) larger than the number of 0-year-old herring, 6.4–51.9 billion specimens (Table S2).

The number of salmon returning to Tornionjoki in 2023 was clearly lower, 16,020 specimens, than in other research years (Figure 2a,b and Table S2). This was two years after the number of 0-year-old herring was at its lowest, 6.4 billion specimens, which was in 2021. However, the number of salmon returning to Simojoki was even somewhat lower in 2017, 1642 specimens, than in 2023. This is two years after the number of 1–2-year-old and 1–3-year-old sprat were at their highest, 275 billion and 299 billion specimens, respectively—that is, in 2015 (Table S2). The number of salmon returning to Tornionjoki was the third lowest in 2017, following 2018 and 2023. The highest number of 0-year-old herring in the Baltic Proper, 51.9 billion specimens, was in 2014, when the numbers of 1–2-year-old and 1–3-year-old sprat were near their lowest numbers, 105 billion and 133 billion specimens, respectively (Figure 2 and Table S2). Two years after 2014, the number of Simojoki returners was at its highest, 5125 specimens, but the number of Tornionjoki returners was approximately similar in 2014 (92,167) to 2016, when there were 91,137 specimens (Table S2).

3.2. A High Lipid Content of Available Prey Fish Was Reflected as a Low Number of Returning Salmon

The total body lipid content was significantly larger in sprat than in herring, regardless of age (Figure S1a), despite the small number of observations. In contrast, the total body thiamine concentration per energy density (Figure S1b) tended to be higher in herring than in sprat. Similarly, the protein-to-lipid ratio was higher in herring than in sprat, and the difference was statistically significant, even though the number of observations was small. In sprat, the protein-to-lipid ratio was considerably smaller than the assumed optimal value for the growth of salmon post-smolts, but the mean protein-to-lipid ratio in herring was slightly higher than the optimum (Figure S1c).

The more youngish sprat there were in the Baltic Proper (Figure S2) and the higher the number of youngish sprat in relation to the number of age-0 herring (Figure S3), the larger the amount of available lipid in salmon prey fish. The number of salmon ascending Tornionjoki and Simojoki appeared to be lower when the lipid content in prey fish was higher (Figure S2). Indeed, the number of salmon ascending Tornionjoki had a negative and significant relationship with the sum of the total lipid content in the clupeids of a suitable size for salmon prey—that is, 0-year-old herring and 1–3-year-old sprat—available in the Baltic Proper two years earlier (Figure 4a). The regression model explained 41.8% of the variation. Regarding Simojoki salmon returners, the relationship with the lipid content of proper prey fish, 0-year-old herring and 1–2-year-old sprat, was similarly negative and nearly significant when the model explained 30.9% of the variation (Figure 4b).

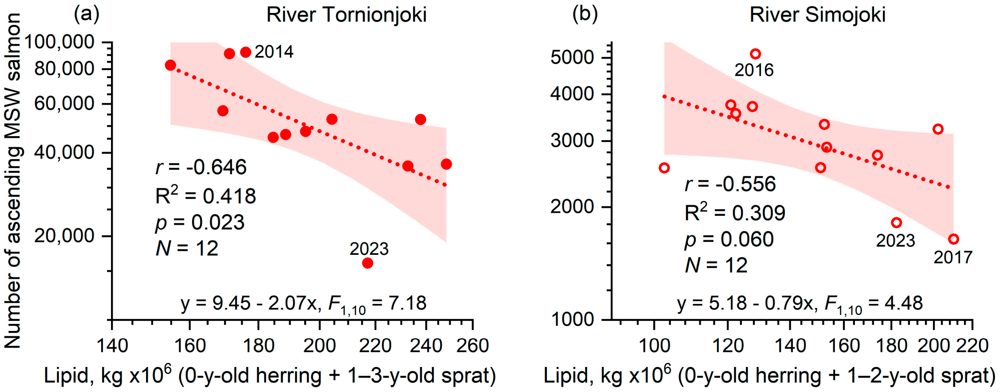

Figure 4. The number of multi-sea-winter (MSW) salmon (*Salmo salar*) returning to their home river in 2012–2023 in relation to the amount of lipid available for (**a**) River Tornionjoki salmon from 0-year-old herring (*Clupea harengus*) plus 1–3-year-old sprat (*Sprattus sprattus*) and (**b**) River Simojoki salmon from 0-year-old herring plus 1–2-year-old sprat in the Baltic Proper when post-smolts arrived there two years earlier (2010–2021). See Figure 2 for other explanations.

3.3. A High Lipid Content of Available Prey Fish Was Reflected as a Low THIAM Concentration in the Eggs of Salmon

The number of salmon returning to either Tornionjoki or Simojoki to spawn in 2012–2022 was positively and significantly correlated with the mean THIAM concentration in the unfertilized eggs of the 2nd sea-year females included in the annual M74 monitoring in the respective years (Figure 5). The coefficient of determination of the regression model was 0.549 for Tornionjoki returners and 0.506 for Simojoki returners, respectively.

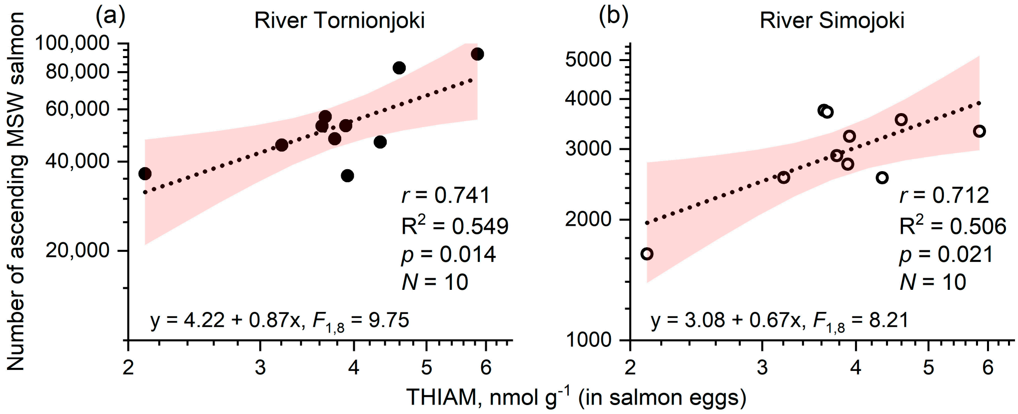

Figure 5. The number of multi-sea-winter (MSW) salmon (*Salmo salar*) returning to their home river in 2012–2022, excluding 2016, in relation to the concentration of mean free thiamine (THIAM) in the eggs of 2nd sea-year salmon included annually in the Finnish M74 monitoring for (**a**) the River Tornionjoki and (**b**) the River Simojoki. See Figure 2 for other explanations.

The mean THIAM concentration in the eggs of the 2nd sea-year salmon was positively, though not significantly, correlated (r = 0.420, N = 10) with the number of 0-year-old herring in the Baltic Proper two years earlier, in 2010–2020, and the regression model had a coefficient of determination of 0.177 (Figure 6a). In contrast, the respective correlation with the number of 1–3-year-old sprat was negative and significant (r = −0.762, N = 10), with a coefficient of determination of 0.581 for the regression model (Figure 6b). As for the number of sprat, the correlation between the THIAM concentration in the eggs of 2nd sea-year salmon and the ratio of the numbers of 1–3-year-old sprat to 0-year-old herring was negative and significant (r = −0.686, N = 10), with a coefficient of determination of 0.471 of the linear model (Figure 6c). The respective correlations of the THIAM concentration of the eggs with the number of 1–2-year-old sprat and the ratio of the numbers of 1–2-year-old sprat to 0-year-old herring were also negative and significant, r = −0.680, p = 0.030, and r = −0.667, p = 0.035, respectively.

The THIAM concentration in the eggs of 2nd sea-year salmon spawners returning to Tornionjoki and Simojoki in 2012–2022 was negatively related to the amount of lipid available in 0-year-old herring plus 1–3-year-old sprat in 2010–2020, when salmon arrived in the Baltic Proper as post-smolts (Figure 7a). The regression model explained 36.7% of the variation, and it was nearly significant. The coefficient of determination of the respective relationships with lipid available in 0-year-old herring plus 1–2-year-old sprat was 0.214, and the Pearson correlation was r = −0.463, p = 0.178. After the post-smolt phase, during the 2nd feeding year of the salmon, in 2011–2021, the similar relationship was also negative and nearly significant, and the regression model explained 36.1% of the variation (Figure 7b).

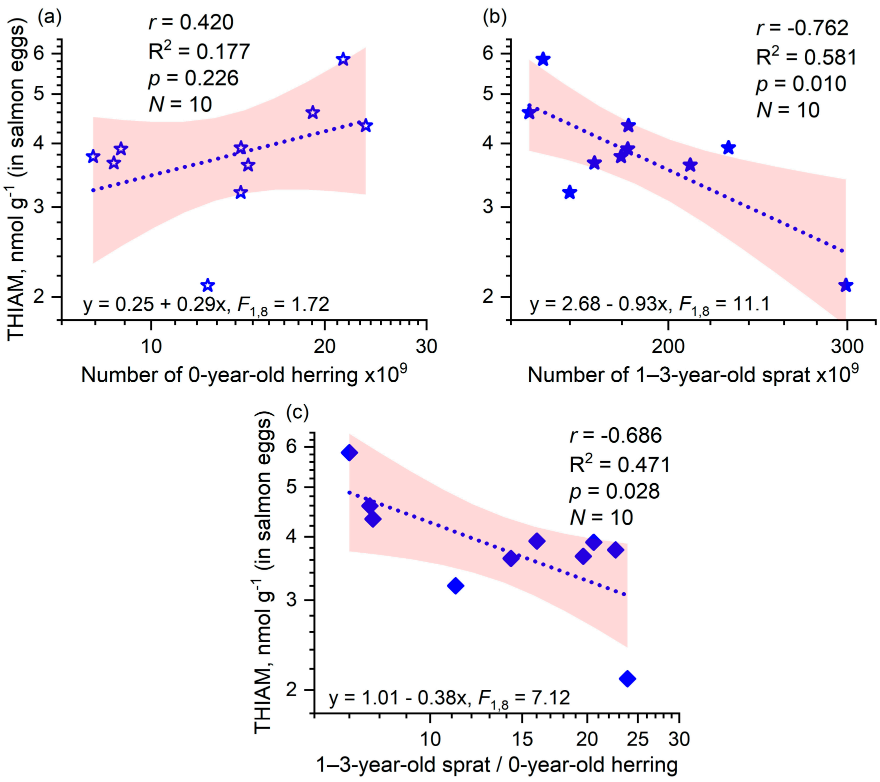

Figure 6. The concentration of free thiamine (THIAM) in the eggs of 2nd sea-year salmon (*Salmo salar*) included in the Finnish M74 monitoring in 2012–2022, excluding 2016, in relation to (**a**) the number of 0-year-old herring (*Clupea harengus*), (**b**) the number of 1–3-year-old sprat (*Sprattus sprattus*), and (**c**) the ratio of the numbers of these herring to sprat in the Baltic Proper. See Figure 2 for other explanations.

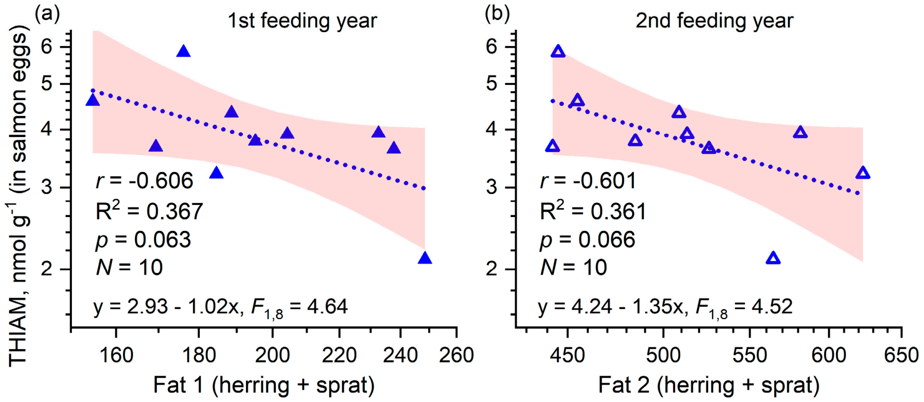

Figure 7. The concentration of free thiamine (THIAM) in the eggs of 2nd sea-year salmon (*Salmo salar*) included in the Finnish M74 monitoring in 2012–2022, excluding 2016, (**a**) in relation to the amount of lipid available in 0-year-old herring (*Clupea harengus*) plus 1–3-year-old sprat (*Sprattus sprattus*) (Fat 1) in the Baltic Proper in the post-smolt arrival years (2010–2020), and (**b**) in relation to the amount of lipid available in 0-year-old herring and 1–3-year-old sprat during the 1st feeding year plus 0–1-year-old herring and 1–3-year-old sprat (Fat 2) in the second feeding year (2011–2021). See Figure 2 for other explanations.

3.4. The Fatness of Prey Fish Was Associated with Both Low Numbers of Returning Salmon and Thiamine Deficiency

The number of salmon returners in 2012–2022 was positively and significantly correlated with the protein-to-lipid ratio of suitable-sized and available prey fish present in the Baltic Proper in the post-smolts' first feeding year—that is, 0-year-old herring plus

1–3-year-old sprat for Tornionjoki salmon and 0-year-old herring plus 1–2-year-old sprat for Simojoki salmon. The correlation was stronger for Simojoki than for Tornionjoki salmon (Figure 8a,b), with the regression models explaining 43.9% and 36.9% of the variation, respectively. The THIAM concentration in the eggs of 2nd sea-year salmon spawners was also positively and significantly correlated with the protein-to-lipid ratio in post-smolts' prey fish—that is, in the 0-year-old herring plus 1–3-year-old sprat of the first feeding year. The regression model explained 50.7% of this variation (Figure 8c). The THIAM concentration of the eggs was also positively correlated with the protein-to-lipid ratio of the prey fish combination, including the first (2010–2020) and second feeding year (2011–2021). The correlation was strongest for the combination of 0-year-old herring plus 1–3-year-old sprat during the first year and 0–1-year-old herring plus 0–4-year-old sprat during the second feeding year, but the correlation was not statistically significant, and the regression model explained 19.6% of the variation (Figure 8d).

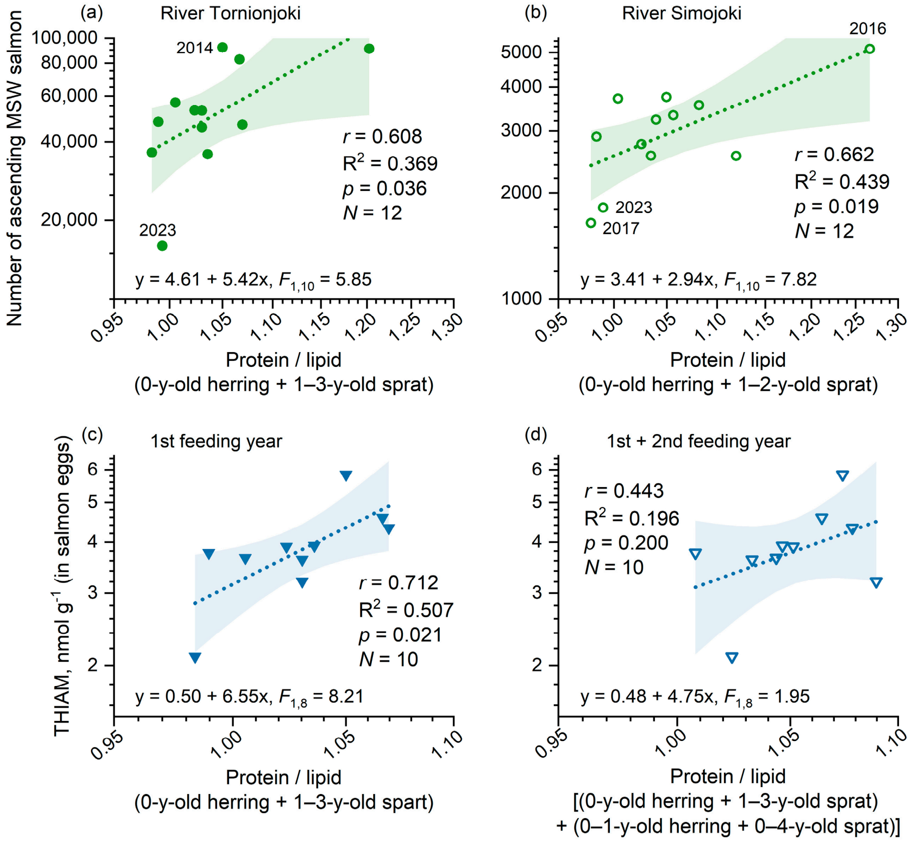

Figure 8. The number of salmon (*Salmo salar*) ascendants in relation to the protein-to-lipid ratio in the combinations of 0-year-old herring (*Clupea harengus*) and (**a**) 1–3-year-old sprat (*Sprattus sprattus*) for River Tornionjoki salmon, and (**b**) 1–2-year-old sprat for River Simojoki salmon, and the free thiamine (THIAM) concentration in the eggs of 2nd sea-year salmon included in the Finnish M74 monitoring in 2012–2022, excluding 2016, in relation to the protein-to-lipid ratio of (**c**) 0-year-old herring plus 1–3-year-old sprat of the first feeding year, and (**d**) 0-year-old herring plus 1–3-year-old sprat of the 1st feeding year plus 0–1-year-old herring plus 0–4-year-old sprat of the 2nd feeding year. See Figure 2 for other explanations.

3.5. A High Number of 0-Year-Old Herring and Sprat Coincided

During 2010–2021, the number of 0-year-old sprat varied from 96 billion to 539 billion and was thus an average of 12.1 (range 8.6–20.1) times higher than the number of age-0 herring (Figure 9a). However, the numbers were significantly and positively correlated, with the regression model explaining 73.4% of the variation (Figure 9b). If 2014, when an extremely strong year-classes of both herring and sprat hatched in the Baltic Proper, was omitted, the correlation was still positive and statistically significant, and the model explained 47.3% of the variation (Figure 9b inset).

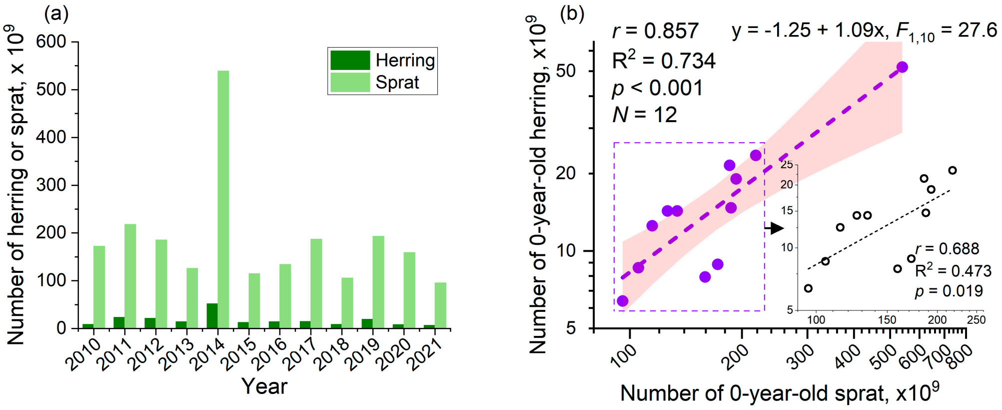

Figure 9. The (**a**) numbers of 0-year-old herring (*Clupea harengus*) and 0-year-old sprat (*Sprattus sprattus*) in the Baltic Proper in 2010–2021 and (**b**) the relationship between them. The inset presents the relationship without the very strong year-class 2014. See Figure 2 for other explanations.

In contrast, the numbers of 0-year-old herring and youngish sprat (1–3-year-olds concerning Tornionjoki salmon and 1–2-year-olds concerning Simojoki salmon) appeared to have negative relationships (Figure 2). The negative correlation of 0-year-old herring with 1–2-year-old sprat was nearly significant, $r = -0.521$ ($p = 0.082$, $N = 12$), and stronger than the negative correlation with 1–3-year-old sprat, $r = -0.466$ ($p = 0.127$, $N = 12$). If sprat from the exceptionally strong year-class of 2014—that is, 1-year-olds—were excluded, the negative correlations between 0-year-old herring and youngish sprat were stronger for 1–2-year-old sprat, $r = -0.673$, $p = 0.023$, and 1–3-year-old sprat, $r = -0.584$, $p = 0.059$.

4. Discussion

The general trend was that the fewer 0-year-old herring and the more youngish sprat there were in the Baltic Proper when the post-smolts arrived at their feeding grounds, the fewer salmon returned to Tornionjoki and Simojoki to spawn two years later (Figure 10). The number of salmon returning to their home rivers had the strongest negative relationship with the high ratio of the numbers of youngish sprat to 0-year-old herring at the arrival of post-smolts in the Baltic Proper: Tornionjoki salmon returned least when the ratio of the numbers of 1–3-year-old sprat to 0-year-old herring was highest, and Simojoki salmon when the ratio of the numbers of 1–2-year-old sprat to 0-year-old herring was highest. The low numbers of returning salmon in both rivers were associated with the high lipid content and low protein-to-lipid ratio in the available prey fish, which indicates that the high number of youngish sprat compared to the number of age-0 herring had provided the post-smolts with fish too fatty for survival (Figure 10). The direct cause of the reduced post-smolt survival is uncertain, although we think that thiamine deficiency is involved in it. The poor thiamine status of the spawning salmon, seen as a low THIAM concentration in the eggs, was also associated with the high lipid content of the available prey fish (Figure 10); around the years when fewer salmon returned to spawn, the thiamine status of the ascendants was also poorer.

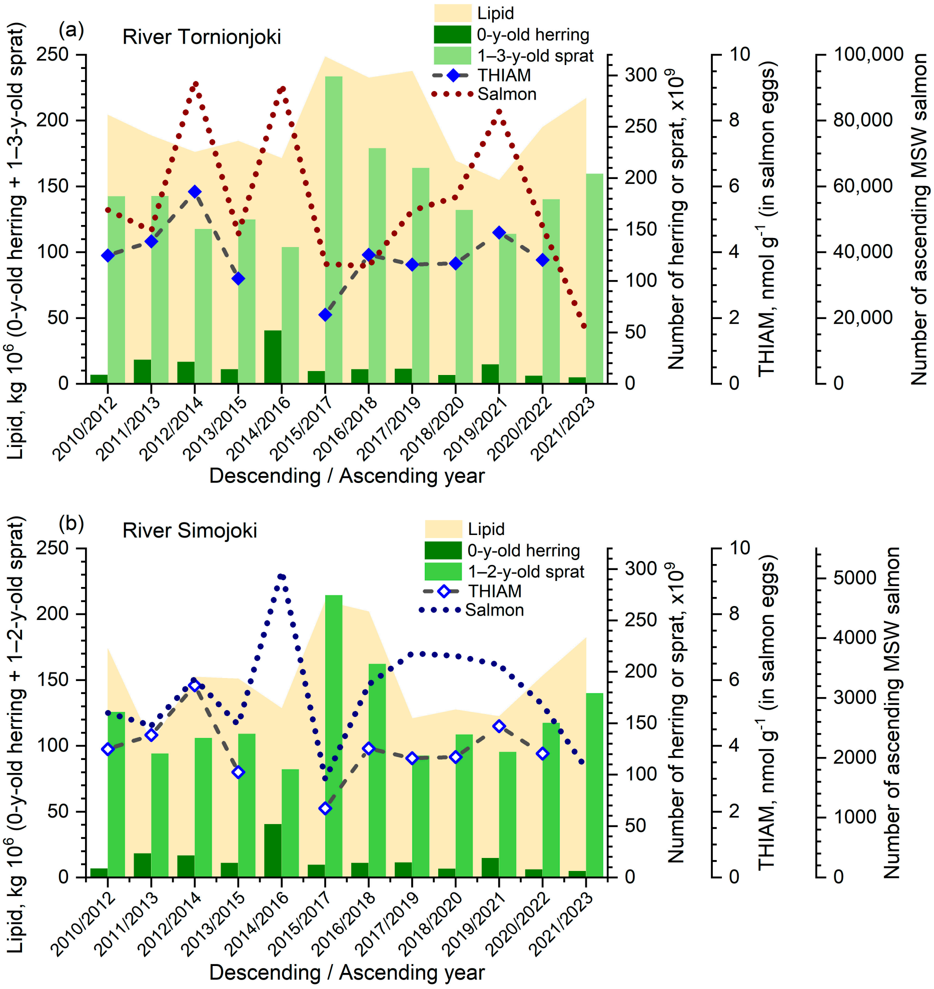

Figure 10. The number of prey fish and the amount of lipid in prey fish in the Baltic Proper in 2010–2021, and the number of multi-sea-winter (MSW) salmon (*Salmo salar*) ascending the rivers, when prey fish two years earlier for the post-smolts of (**a**) the River Tornionjoki had been 0-year-old herring (*Clupea harengus*) and 1–3-year-old sprat (*Sprattus sprattus*), and (**b**) the River Simojoki had been 0-year-old herring and 1–2-year-old sprat, and THIAM concentration (excluding year 2016) in unfertilized eggs of 2nd sea-year ascendants.

4.1. The Number of Salmon Returning to Spawn Depends on the Survival of Post-Smolts

The number of salmon returning to the rivers was explained by the survival of post-smolts. In turn, this depended on the quality of available prey fish of a suitable length at the time of the post-smolts' arrival at the feeding grounds. Similarly, in the western salmon populations of the North Atlantic, the variation in the number of returners was mostly explained by survival during the first feeding year in the sea [36]. A strong new year-class of herring—that is, the abundance of 0-year-olds—in the principal feeding area of salmon in the Baltic Proper increased the survival of salmon post-smolts, thereby increasing the number of ascending salmon two years later. This result is consistent with the result obtained in the mark–recapture studies, which showed that between 1986 and 2006, the survival of Simojoki post-smolts increased in years when larger numbers of herring had hatched in the Baltic Proper [37]. In that study, the survival of Simojoki salmon was determined based on the catches of salmon during their 2nd sea-year by professional fishers in the Baltic Proper. In our study, the numbers of ascendants confirmed the same positive effect of age-0 herring on the survival of not only Simojoki salmon post-smolts [37] but also Tornionjoki salmon post-smolts.

We also found that not only did the number of returners depend on the success of recruitment of young-of-the-year herring as prey, but the abundance of youngish sprat had the opposite effect on the survival of post-smolts, reducing the number of returners. For Tornionjoki salmon, the negative effect of a low number of 0-year-old herring on the number of ascending salmon appeared to be stronger than for Simojoki salmon. By contrast, the abundance of youngish sprat seemed to have a stronger reducing effect on the number of Simojoki ascendants. When the number of 0-year-old herring was at its lowest upon the arrival of post-smolts to the Baltic Proper in 2021 [41], the fewest salmon ascended Tornionjoki in 2023 [1]. Simojoki salmon returned in even smaller relative numbers in 2017, which was two years after the highest number of youngish sprat in the Baltic Proper—that is, in 2015. The large number of youngish sprat was mainly due to the very large 2014 year-class of sprat [41,63].

However, both the abundance of 0-year-old herring and the paucity of youngish sprat had a favorable effect on the numbers of salmon returners of both rivers. The highest number of salmon ascended Simojoki in 2016 [1], which was two years after an exceptionally high number of herring was hatched in the Baltic Proper [41]. At the same time, in the summer of 2014, there was the lowest number of youngish sprat, both 1–2- and 1–3-year-olds. A high number of salmon also returned to Tornionjoki in 2016, but there were also high numbers of returners in 2014 and 2021 [1]. Two years before the spawning year 2014, in the post-smolt year 2012, the number of 0-year-old herring was well above the average, and the numbers of 1–2- and 1–3-year-old sprat were 12% and 20%, respectively, below the average. Correspondingly, in 2019, two years before the spawning year 2021, the number of youngish sprat was considerably low.

Overall, in the study period 2012–2023, the ratios of the numbers of 1–2 and 1–3-year-old sprat to 0-year-old herring were the lowest, 2.0 and 2.6, respectively, in 2014. These lowest ratios were manifested as the highest numbers of returners in 2016, especially for Simojoki salmon. As in 2014, the very small ratios of the numbers of youngish sprat to age-0 herring in 2012 and 2019 were reflected in the large numbers of salmon returning to Tornionjoki to spawn two years later. In contrast, in 2021, when the number of age-0 herring was lowest in absolute terms and in relation to sprat, the ratio of the numbers of 1–3-year-old sprat to 0-year-old herring was 32, while the average for the period was 15. Furthermore, the ratio of the numbers of 1–2-year-old sprat to 0-year-old herring was 28, and the average was 13. These record high sprat-to-herring ratios were reflected in low numbers of ascending salmon in both rivers in 2023. Due to the record low number of 0-year-old herring, the number of salmon ascending Tornionjoki decreased from the average of the previous five years in the fall of 2023 more (71%) than the number of salmon ascending Simojoki (41%) [1]. For both studied rivers, Tornionjoki and Simojoki, it was true that the more youngish sprat there were in the Baltic Proper in relation to 0-year-old herring, the fewer salmon returned to spawn. The ratio of the number of youngish sprat to the number of age-0 herring thus best explained the number of salmon that returned to spawn.

Although in 2014, in addition to herring, an exceptionally large number of sprat also hatched in the Baltic Proper [41,63], these 0-year-old sprat did not reduce the number of ascending salmon in 2016. However, the strong 2014 sprat year-class as youngish sprat negatively affected the salmon over the following couple of years by reducing the number of ascendants and already lowering the thiamine status of the 2015 ascendants. The exceptionally large number of youngish sprat upon the arrival of the 2015 post-smolts in the Baltic Proper was reflected in 2017 as the lowest number of Simojoki ascendants and as the third-lowest number of Tornionjoki ascendants during the study period. The ratio of the number of youngish sprat to the number of age-0 herring was second highest for both rivers in 2015. The ratios were even higher in the diet of the post-smolts of 2021, as a result of which a record few salmon returned to Tornionjoki to spawn in 2023.

The large sprat year-class in 2014 weakened the thiamine status most in the 2016 salmon ascendants, but also did so in the 2017 ascendants [11], which, during their two-year feeding migration, apparently ate abundant youngish sprat, including the 2014 year-class. Based on FASA, 13% of the 2016 and 15% of the 2017 female returners of Simojoki that had been feeding in the Baltic Proper were, therefore, M74 females [11]. The ascendants of 2015 had also apparently fed during their last feeding winter on the abundant sprat of the 2014 year-class because even big salmon eat such small fish [52], but the feeding area of the females of that year was not studied using FASA [11]. Although thiamine deficiency can impair salmon's ability to ascend through the cascades [64], thiamine deficiency was not as severe in the study years as in the early and mid-1990s [8,11]. Salmon for the M74 monitoring are caught from the sea near the river mouth in June. During the study period, only one female in the M74 monitoring, in 2016, died of thiamine deficiency, but only close to spawning, in October.

The effects of the abundance of herring and sprat on the numbers of salmon ascending the rivers to spawn were clear, even though the number of ascendants was not set in proportion to the estimated numbers of smolts descending to the sea from the rivers [1]. On average, 2.1 million (range 0.95–2.9 million) smolts entered the sea from Tornionjoki in 2014–2022. Regarding 2017, when the lowest number of smolts descended into the sea, the number of ascending salmon two years later was only 4% less than the average number of ascendants. Regarding 2021, the number of descending smolts was only 4.5% less than the average, though the number of ascending salmon was the lowest on record in 2023. Thus, the variation in the number of descending smolts does not seem to be a very important factor affecting the number of returning salmon.

Furthermore, it is possible that the relationships between the numbers of salmon ascendants and the numbers of available prey fish would have been even more pronounced if only 2nd sea-year salmon had been included in the calculations instead of the available MSW salmon. In the M74 monitoring data of Finland, most ascending salmon, approximately 78% of the females during 1994–2009, were 2nd sea-year salmon—that is, salmon that had been on the feeding migration in the sea for two years [8]. However, in 2023, salmon aged three sea-years or older accounted for 48% of the river fishery catch of Tornionjoki, which was the highest number between 1974 and 2023 [1]. This was two years after the ratio of the number of youngish sprat to the number of 0-year-old herring was highest, which suggests that the high proportion of salmon older than the 2nd sea-year among the ascending salmon was probably due to the poor survival of post-smolts upon their arrival to the Baltic Proper in 2021. Salmon that had been at sea for three or more years appear to have had better feeding conditions upon their arrival in their feeding grounds, and thus a higher survival rate, than the 2021 post-smolts.

Fishing did not reduce the numbers of ascending salmon in 2023, as a commercial salmon offshore mixed-stock fishery was closed in 2022; longline fishing was markedly reduced in 2021, and driftnet fishing had already stopped in 2008 [1]. The predation effect of the increase in the number of grey seals (*Halichoerus grypus*) in the Baltic Sea in recent decades on salmon post-smolts has also increased, but this does not explain the annual variation in post-smolt survival [65]. Bird predation, mainly by the great cormorant (*Phalarocorax carbo*), may also target post-smolts to some extent [66]. This is unlikely to have changed much during the study period, as cormorant populations have been relatively constant since the mid-2010s [67].

4.2. Prey Fish of Post-Smolts Should Be 0-Year-Old Herring Instead of Youngish Sprat in the Baltic Proper

The salmon post-smolts from the Bothnian Bay rivers move from the Gulf of Bothnia southward to the Baltic Proper in August–September [46,49]. Herring spawn in coastal areas mainly in May–July, where the hatched herring first feed, but later in the summer, they move to the open sea [68], where salmon prey. In the Gulf of Bothnia, in addition to 0-year-old herring, 1-year-old herring are suitably sized food for the largest salmon post-smolts, but they are too large for small post-smolts [69]. In the present study, the number of salmon returning to their home river was specifically related to the diet that prevailed in the Baltic Proper upon the arrival of the post-smolts there. At that time, the abundance of 0-year-old herring had a significantly positive effect on the survival of post-smolts, but the total number of 0-year-old plus 1-year-old herring had no significant relationship with the number of salmon returning to Simojoki. Instead, the largest post-smolts of Tornionjoki salmon were apparently able to eat some 1-year-old herring in addition to 0-year-old herring when they arrived in the Baltic Proper, because their total number had an almost significant positive relationship with the number of returners. However, Simojoki post-smolts had not eaten 1-year-old herring, nor larger 0-year-old herring, based on the weaker positive, almost significant, relationship with age-0 herring.

The differences between Tornionjoki and Simojoki salmon in the effect of the abundance of prey fish species on the number of salmon returning to spawn were probably mainly due to the different sizes of smolts between the rivers. When descending into the sea in the Bothnian Bay, the wild smolts of Tornionjoki were larger (on average 15.5 cm and 28.3 g) than those of Simojoki (14.5 cm and 21.7 g) [35]. The post-smolts from these rivers had grown by their arrival in the Baltic Proper, but based on our results, Tornionjoki salmon were still larger than Simojoki salmon after they reached the Baltic Proper. In the southern Baltic Sea, herring grow so fast [38] that a herring older than age 0 seems, in most cases, to be too big as prey for the post-smolts, and especially for Simojoki post-smolts.

Due to the later spawning and slower growth of sprat than herring [70,71], age-0 sprat do not seem to be large enough to be prey for post-smolts when they arrive in the Baltic Proper. Sprat spawn there in the open sea in June–August [4], and age-0 sprat do not reach the length of 7–8 cm until November in the Bornholm Basin [71]. This is the mean length of the prey fish that post-smolts with a mean size of 45 cm prey upon [54]. Bayesian modeling found no relationship between the abundance of adult sprat and the survival of post-smolts [65]. We found that the number of all sprat, excluding 0-year-olds, was negatively and significantly correlated with the number of ascending salmon, but when 0-year-old sprat were included, there was no correlation. Tornionjoki and Simojoki post-smolts can probably prey on almost all age groups of sprat older than 0 years because sprat do not usually exceed 15 cm in length [43,45], but Simojoki post-smolts especially seem to prey mostly on young age groups.

On the arrival of the post-smolts to the Baltic Proper, the most suitably sized sprat for Tornionjoki post-smolts seemed to be the 1–3-year-olds, and for Simojoki post-smolts, the 1–2-year-olds, because these had the clearest negative effect on their survival. As Tornionjoki post-smolts are larger [35] and possibly arrive in the Baltic Proper earlier than post-smolts from other rivers [72], their most likely alternative prey fish to 0-year-old herring is 1–3-year-old sprat. As the post-smolts of Simojoki are smaller than the post-smolts of Tornionjoki and possibly arrive later in the Baltic Proper, they mainly prey on 1–2-year-old sprat, in addition to herring of approximately the same size—that is, smallish 0-year-olds. Probably because the post-smolts of Simojoki thus ate more youngish sprat in relation to 0-year-old herring than the post-smolts of Tornionjoki, the negative effect of sprat on the number of returning salmon was stronger for Simojoki than Tornionjoki salmon. The negative correlations between the numbers of sprat and ascendants weakened when older age groups of sprat were added to the model. This may also be partly due to the decrease in the number of sprat individuals of each year-class from year to year, making younger individuals more likely prey.

In addition to the different sizes of Tornionjoki and Simojoki post-smolts [35], the differences in the spawning time [4] and growth rate of herring and sprat [70,71] have affected the survival of Tornionjoki and Simojoki post-smolts slightly differently. The feeding migration routes and progression to the feeding areas of the Baltic Proper probably also differ slightly, and Tornionjoki salmon apparently eat further south on average than Simojoki salmon [11,72]. The scarcity of 0-year-old herring, specifically in the southernmost Baltic Proper in 2021, for example [73], may therefore have had a stronger effect on the survival of Tornionjoki than Simojoki post-smolts. Tornionjoki post-smolts also migrate to a greater extent to the Baltic Proper than Simojoki salmon, even when an unusually large year-class of herring hatches in the Gulf of Bothnia [35]. Apparently for these reasons, M74 had already broken out strongly among Tornionjoki salmon in 1990, while M74 was then mild among Simojoki salmon and strengthened in the following year [8]. At that time, the sudden increase in the number of young sprat in the southernmost Baltic Proper could therefore have affected Tornionjoki salmon faster. Around the same time, post-smolt survival also began to decline [6,74,75], but unfortunately, the numbers of ascending salmon were not yet counted at that time.

Salmon do not appear to be selective in terms of prey species; they prey on fish of a suitable size that are available in the open sea. Only a small number of three-spined stickleback (*Gasterosteus aculeatus*) or other pelagic fish like sand eels (*Ammodytes* sp.) are occasionally eaten by salmon in the southern Baltic Sea [51,52]. The number of three-spined stickleback has increased during the 2000s, but this has occurred especially in the Gulf of Bothnia and the northwestern Baltic Proper [76]. Post-smolts from the Bothnian Bay rivers, after descending to the Gulf of Bothnia, initially eat a variety of aerial insects, gammarids, and a few small fish [48] such as vendace (*Coregonus albula*) [68], which are all leaner species than herring [77]. Upon arrival in the Baltic Proper, they become exclusively piscivores [49]. The only significant pelagic species in the Baltic Proper serving as prey for salmon post-smolts are, therefore, suitably sized herring and sprat [52,53], whose relative abundance determines the diet of post-smolts. The relative number of youngish sprat and 0-year-old herring upon the arrival of post-smolts therefore appears to affect how many salmon feeding in the Baltic Proper survive until the 2nd feeding year and, further on, make it to the spawning migration and ascend the Bothnian Bay rivers to spawn.

4.3. Sprat Benefits from the Warming of the Environment and the Reduction in Cod

The Baltic Sea is the coldest region where sprat live [78], and 0-year-old sprat benefit from warmer waters in the archipelago, for example. The optimal water temperatures for growth from the larval to juvenile phases of sprat are 15–22 °C [71], whereas the optimal temperature for herring growth is around 16 °C [79]. High temperatures seemed to contribute to the good reproductive success of both species. The highest number of both species hatched in 2014, which was the second warmest year in the history of temperature measurements, and the summer of 2021 was also exceptionally warm (statistics of the Finnish Meteorological Institute, FMI, accessed 15 June 2024). During these years, a very strong year-class of herring also hatched in the Gulf of Bothnia [41,80]. However, the strength of a year-class does not only depend on the water temperature; many other abiotic and biotic factors are involved [79,81]. The favorable effect of the strong herring year-class of 2014 was reflected in the large number of ascending salmon in 2016, while the negative effect of the abundance of youngish sprat on the number of returners in the next couple of years was apparent.

Salmon also eat in the winter, especially in warm winters, and then they eat sprat in particular [53]. By the winter, at least in the southernmost Baltic Sea, herring probably start to be too large as prey for smaller salmon post-smolts of the same year [38]. Instead, the large sprat year-class of 2014 already offered prey more abundantly than average for salmon post-smolts at the turn of 2014 to 2015 and throughout 2015. This was already seen in the poorer thiamine status of the salmon that had been feeding on abundant sprat during their second feeding year and ascended in 2015 for spawning than in the previous four years, 2011–2014. In these years, the THIAM concentrations in salmon eggs had been the highest since the start of thiamine measurement history in 1994, and no M74 mortalities occurred in yolk-sac fry [8,11]. In these years, the mean THIAM concentration of Simojoki salmon eggs was at a record high, up to 5.85 nmol g^{-1} in 2014 (range 1.52–12.45 nmol g^{-1}) [8]. Even more clearly than in the 2015 ascendants, the abundance of youngish sprat was reflected in the poor thiamine status of the salmon that had been feeding in the Baltic Proper from 2014 to 2016 and returned to the river to spawn in 2016, with a mean THIAM concentration of 1.67 nmol g^{-1} (range 0.19–4.02 nmol g^{-1}) in their eggs [11]. This result is consistent with the M74 research results regarding the 1990s and 2000s, which showed that the THIAM concentration in salmon eggs is at its lowest two years after a large year-class of sprat hatches in the Baltic Proper, and the M74 mortality of their offspring at the yolk-sac phase is, therefore, at its highest in the subsequent spring [13,38].

Regarding the two-year feeding migration of the salmon that returned to the river to spawn in 2023, the last months of 2021, and the year 2022, were warmer than usual (statistics of FMI). Although the number of sprat hatched in 2021 was the lowest during the research period, the number of 0-year-old sprat was 14 times larger than the number of 0-year-old herring, and the total number of 0–3-year-old sprat was then even 45 times larger. With a very high probability since late 2021 and in 2022, which was the 2nd feeding year for the salmon that started their marine feeding as post-smolts in 2021, their prey fish was many times more often a sprat than a herring. This caused the thiamine status of the salmon to decline, and some M74 mortality was observed in Tornionjoki salmon [1], which were included in the M74 monitoring. The M74 situation was apparently not very bad, as there were also plenty of older and leaner sprat in the sea because a relatively large sprat year-class had also hatched in 2020.

A high annual variation in the numbers of young-of-the-year is typical of pelagic clupeids [79]. Between 2010 and 2021, the number of age-0 sprat in the Baltic Proper varied 5.6-fold, from 95.6 billion to 539 billion, but the number of age-0 herring varied even more, 8.3-fold, from 6.4 billion to 51.9 billion specimens. There may be some uncertainty in the estimates of the numbers of 0- and 1-year-olds in particular, possibly because small herring in shallow areas may be unreachable by research vessels or in surface water, where they cannot be detected by sonar, nor can an exact amount corresponding to their abundance be obtained with test trawls. Regarding the youngish sprat, the number of 1–3-year-old sprat varied 2.4-fold, and that of 1–2-year-olds 2.6-fold. However, the proportion of sprat in the sum of 0-year-old herring plus youngish sprat was much higher than the proportion of herring; considering 1–3-year-old sprat in 2010–2021, it was 72–97%, while that of age-0 herring was 3–28%. Because the herring biomass as prey was much lower than the sprat biomass, changes in the relative proportions of sprat and herring in the prey fish biomass of salmon were mainly caused by fluctuations in the abundance of sprat. The abundance of herring and sprat as prey also differs to some extent between different regions of the Baltic Proper [13,54]. When there are plenty of youngish sprat, they seem to spread to all parts of the Baltic Proper and to the Gulf of Finland, but only to some degree to the southern part of the Gulf of Bothnia. At the times of several recent fall research surveys, the highest densities of sprat have been in the northern part of the Baltic Proper, in the Gulf of Finland and in the eastern half of the Baltic Proper, relatively close to the coasts of the Baltic countries [59,80,82].

In the 1980s, when M74 was non-existent, or its incidence was very low [83], herring accounted for a larger proportion of the total prey biomass of salmon in the Baltic Proper than sprat [38]. In contrast, in the 1990s and 2000s [38] and since [41], the proportion of sprat has been larger than the proportion of herring. FASA of the muscle of salmon in their second feeding year and during spawning migration in 2004, and of the muscle and eggs of spawning salmon in 1998, 2014, 2016, and 2017, have also shown that the sprat was the main prey fish of salmon in the Baltic Proper [10–12]. The change in the salmon's diet to one dominated by sprat can be due to overfishing of cod and herring, as well as the effects of eutrophication and anoxic bottoms on fish stocks, but also due to the rise in temperature. The whole Baltic Sea has warmed—the surface water temperature by 0.3–0.4 °C per decade—during the 1950–2020 period [84].

Young herring in the Baltic Proper mainly eat the same zooplankton species as sprat, so they must compete for food with sprat that are solely zooplanktivorous [85,86]. Herring are probably less successful in the competition for food with sprat because sprat are more numerous than young herring. In the Gulf of Bothnia, herring do not need to compete for food with the small numbers of sprat. Apparently, therefore, herring—and the small numbers of sprat—have been fattier in the Gulf of Bothnia than in the Baltic Proper [12,43,87]. The salmon stocks benefit from eating young herring instead of sprat, as in the Baltic Proper, they provide salmon posts-smolts with a leaner diet than sprat. In the Arctic Ocean, the diet of even adult Atlantic salmon has included 30% crustaceans [88], which are considerably leaner than sprat and herring [89]. In the Baltic Sea, crustaceans such as *Monoporeia affinis* are too small to be prey for salmon post-smolts.

Global warming increases eutrophication, because increasing precipitation and snowless winters increase the sea's nutrient load. The eutrophication of the Baltic Sea is particularly harmful to herring, not only in terms of food intake but also because herring spawn in the shallows, where the eggs must stick to their substrate. This can be prevented by the periphyton covering the spawning areas. The bottom areas of the Baltic Proper are largely and increasingly anoxic [90], which further complicates the life of organisms dependent on the benthic communities of the Baltic Sea, such as herring. Herring increasingly feed on benthic invertebrates as they grow, but smaller herring also eat them in the winter [85,86,91]. Eutrophication and the expansion of anoxic areas therefore adversely affect the success of herring populations.

When cod stocks have been strong, cod have effectively thinned out the sprat stock, as was seen in the 1980s [38,40]. The cod stocks, which collapsed due to fishing that was too intensive in previous decades [38,92], have remained low, and cod have suffered from food shortages and liver parasites [93,94]. The anoxic bottom areas of the southern Baltic Sea weaken the life chances of cod because a crustacean *Saduria entomon*, an important food animal for cod juveniles and adults [40], has nearly disappeared from the cod diet since the 1990s in the Baltic Proper [95]. In addition, as sprat and cod spawn in the same open sea areas [4], the strong sprat stock may weaken the recovery of cod stocks because sprat eat cod eggs and young-of-the-year cod compete for food with sprat [39,96].

Although salmon post-smolts specifically need 0-year-old herring instead of youngish sprat, older salmon also need sprat, especially in the southernmost Baltic Sea, where herring quickly grow too large for them [38]. As salmon grow, the average size of their potential prey also increases [54], and older, slightly larger sprat provide them with somewhat leaner food than youngish sprat [13,45]. In particular, a good reproductive success of the herring populations in the southernmost Baltic Proper would be important, so that the number of 0-year-old herring in relation to youngish sprat would be as large as possible in the diet of salmon post-smolts.

4.4. Poor Survival of Post-Smolts and Reduced Growth Are Related to an Excessively Fatty Fish Diet

The high number of 0-year-old herring appeared to have a protective effect on the survival of post-smolts against youngish sprat, which were many times more numerous than age-0 herring. Because sprat are much fattier than herring, and especially young age groups of sprat are fattiest [13,43,45,87], they were too fatty as food for the post-smolts.

An optimal protein-to-lipid ratio is necessary to enhance protein utilization and lipid retention, so that the growth rate can improve [28,97,98]. Overall, the protein-to-lipid ratio is lower in sprat than in herring in the Baltic Proper [11]. In youngish sprat, the protein content in relation to the lipid content is still lower. For 1–3-year-old sprat with a 14.4% lipid content (wet mass), it was 1.02, which is much lower than the suggested optimal value of 1.88 for the growth of salmon post-smolts [28]. Apparently, due to the increased mortality of post-smolts overfed on fatty prey fish, the number of salmon that survived until the spawning migration and returned to the spawning rivers was on average lower in both rivers when more lipids were available from suitable-sized prey fish.

In a feeding experiment [99], in which salmon post-smolts were fed with feeds prepared of sprat or herring, the post-smolts grew faster with herring feed than with sprat feed during the post-smolt phase from May to December. The herring feed contained 21% lipid in dry mass, and the sprat feed 31%, which corresponds to the lipid content of young sprat and herring in this study. According to a mark–recapture study, a high survival rate of post-smolts was associated with the high body mass of recaptured juvenile salmon (Carlin-tagged as smolts) and high recruitment of herring, but when both of these were low, survival collapsed [37]. In the experiment by Salminen [99], the difference in the growth rate increased during the two consecutive years. Similarly, the favorable growing conditions and fast growth rate of Atlantic salmon during the first marine feeding year were reflected in a faster growth rate during the second feeding year [100]. According to Thurow [48], the growth of adult salmon is determined by the food available, even during the first months after post-smolts have entered the sea.

The growth-promoting effect of a leaner fish diet was also observed at the time of spawning, when salmon that had eaten leaner prey fish in the Baltic Proper in 2012–2014 were compared with salmon that had eaten fattier prey fish there in 2014–2016 and 2015–2017 [11]. In 2012–2014, the salmon grew faster with the leaner, more herring-rich, diet than the salmon that were on the feeding migration later, when youngish sprat were abundant [11]. When Simojoki post-smolts arrived in their feeding area in the Baltic Proper in 2012, the number of 0-year-old herring was higher than average, and the number of 1–2-year-old sprat was lower than average. The ratio of the number of young sprat to the number of age-0 herring was 6.3, which is one of the lowest values in the research period. Not only that, the THIAM concentration in the eggs of the salmon that returned to Simojoki to spawn in 2014 was higher, and those salmon were longer and heavier than the salmon that returned in 2016 or 2017 [11].

In addition, the smaller of the 2014 ascending salmon, with higher muscle lipid content and lower, though adequate, egg THIAM concentration than the larger ascendants, had been feeding more on sprat and specifically more on younger sprat due to size-dependent prey availability [54]. The lower muscle lipid content and higher THIAM concentration in the eggs of the larger ascendants of 2014 indicated feeding on average leaner fish—that is, more on herring and older sprat than the smaller salmon. Indeed, the fatty acid composition of the muscle and eggs of these salmon confirmed that the smaller ones had eaten more sprat and less herring than the larger ones [11]. Consistently, in the years of low M74 incidence (e.g., in 1997/1998 and 2004/2005), smaller salmon had a lower average egg THIAM concentration because they had apparently relied more on small sprat in their diet than larger salmon [8,38,101]. In the feeding experiment by Salminen [99], the thiamine status of salmon post-smolts fed with herring feed, expressed as hepatic total thiamine concentration, was somewhat better than those fed with sprat feed and that grew more slowly (unpubl. data). The probable reason for the slower growth rate and poorer thiamine status of post-smolts fed sprat feed was that the protein-to-lipid ratio of the diet was too low [28] and, thus, the lipid content was too high. The different lipid contents of prey fish of different-sized salmon females also explains the observation of Backman [102] that, among wild salmon that ascended Simojoki between 1994 and 2001, there were fewer M74 females among the individuals that were larger, and that ascended first, than among those that ascended later and were smaller.

Poor thiamine status negatively affects growth and physiological conditions because along with magnesium [24,103], thiamine is the most critical cofactor in energy metabolism reactions, and the availability of thiamine determines whether and how much ATP is produced [24,32]. If insufficient ATP is formed, the salmon's physiological functions and swimming ability deteriorate, and thiamine deficiency also negatively affects the functioning of the nervous system [34]. In yolk-sac fry and adult salmon, thiamine deficiency therefore caused swimming disorders and passivity and, eventually, death [8,19,104,105]. Passive swimming-impaired post-smolts easily become prey, fail to catch prey, and may simply die of weakness.

Due to their higher adiposity, M74 females tend to have a higher condition factor than non-M74 females [8]. However, larger but leaner ascendants of 2014 had a higher condition factor due to the faster growth rate [11]. Similarly, when the protein-to-lipid ratio of the diet of Atlantic salmon post-smolts in the experiment by Dessen et al. [97] was higher—that is, more affordable—more muscle mass was formed. As high dietary lipid content slows down growth but increases body lipid, which has been observed in farmed and wild salmon [8,11,38,98,106], it weakens the salmon's energy metabolism and vitality.

Lipid accumulation and thiamine requirement are interconnected, meaning specifically that fatty fish species suffer from thiamine deficiency. Because the requirement for thiamine increases as the energy content of the diet increases [23], and the net energy value of lipid is more than twice that of protein [107], the increase in the lipid content of the diet and, therefore, the fish's own fattiness, largely determines the requirement for thiamine. It has been suggested that the minimum requirement for thiamine in the diet for juvenile salmon's growth is 0.36 nmol kJ^{-1} [23], which was exceeded in both 1–3-year-old sprat and 1-year-old herring but was slightly lower in 0-year-olds. In any case, the mean total thiamine per energy value was 28% less in those sprat than in herring. The intake of thiamine in relation to the energy obtained is, therefore, much lower from youngish sprat than from 0-year-old herring [13]. Apparently, Woodward's [23] recommendation did not take into account the *n–3* PUFA content of the food and the salmon's own lipid and *n–3* PUFA content, which affect the reduction rate of thiamine from the tissues of salmon.

With an abundant fatty-fish-based marine diet rich in *n–3* PUFAs, salmon inevitably accumulate lipid and *n–3* PUFAs in their viscera and muscle tissue and become fattier than on a leaner diet [11,12,38,98,106]. The slowest growth of salmon in the sea was not only associated with the high lipid content of prey fish but also with their high *n–3* PUFA and DHA content [11]. The protein-to-lipid and thiamine-to-energy ratios of the diet and their effects are therefore interconnected, but the quality of the lipids is also important in terms of proper growth and general vitality, as well as the development of thiamine deficiency.

4.5. Fatty Prey Fish Predispose Salmon to Thiamine Deficiency

Consistent with the results of an earlier study [13], the concentration of THIAM in the eggs of the salmon included in this study in 2012–2022 was lower when the amount of lipid available from the prey fish was larger. When a large year-class of sprat hatched in the Baltic Proper in 2014 and plenty of youngish sprat were available as food for the post-smolts of 2014 during their subsequent feeding year, as well as for the post-smolts of the next couple of years, the thiamine status of the salmon that returned to the rivers to spawn in 2016 and 2017 deteriorated [11]. As has been established in previous studies [11,13,38], this study also confirmed that after the hatching of a strong sprat year-class, thiamine deficiency was at its worst in salmon that spawned two years later.

Although the decrease in the number of salmon returning to spawn, apparently due to the death of post-smolts, and the deficiency of thiamine in spawning salmon were related to the same abundant year-class of sprat, they were timed for different years. The decrease in the number of ascending salmon was specifically associated with the ratio of the numbers of youngish sprat to 0-year-old herring on the arrival of post-smolts to their feeding area, but thiamine deficiency in the 2nd sea-year salmon resulted mainly from the abundance of sprat during the two subsequent feeding years of post-smolts. Although the 2014 year-class of sprat was very strong, a record-high number of salmon returned to Simojoki—and the second-highest number to Tornionjoki—in 2016 [1]. The THIAM concentration in the eggs was then low due to the poor thiamine status of these salmon females [8,11]. The abundance of age-0 herring had a greater positive effect on the viability of post-smolts than on the thiamine status of returning salmon, apparently because their number was much lower than that of youngish sprat. However, in the second marine feeding year, the abundance of 0-year-old herring of that year would also help improve the protein-to-lipid ratio of the salmons' diet and improve the thiamine status of the salmon by reducing their requirement for thiamine and lipid peroxidation-related thiamine consumption.

This study showed that the fattiest prey fish, which are youngish 1–3-year-old sprat rich in *n–3* PUFAs [43], were not the optimal food for post-smolts. In general, a high amount of fish-based lipid in the diet of salmonines leads to the accumulation of lipid and *n–3* PUFAs in their viscera and muscle tissue [12,17,98]. Although the proportion of *n–3* PUFAs is even higher in herring than in sprat [43,44], due to the higher lipid content of sprat, the concentration and amount of *n–3* PUFAs are higher in sprat in the same sea area [43]. For the same reason, the supply of thiamine in relation to its requirement is lower from youngish sprat than from young herring [13]. The high proportion and concentration of PUFAs make the tissues susceptible to peroxidation [98,108,109], in which case more thiamine is consumed, the thiamine status deteriorates [26,32], and the fish may not survive. As marine fish in particular use lipids as an energy source for swimming and metabolism and so on [30], more thiamine is consumed in the metabolism of juvenile salmon during feeding migration [12] when they eat fattier youngish sprat instead of leaner herring in the Baltic Proper.

Thiamine deficiency in predatory fish develops from the use of abundant body lipids, containing a high amount of *n–3* PUFAs, as an energy source [13]. The fish species that accumulate most lipids during their feeding period in the Baltic Sea and fast before spawning, salmon and lamprey, are, therefore, the most prone to thiamine deficiency [11,16]. Sea trout, which eat a more varied diet and are leaner than them, with an approximate muscle lipid content of 11.3% before [110] and 1.6–5.5% at spawning time [111], are less prone to thiamine deficiency [14,15]. Juvenile salmon caught during their 2nd feeding year from the Baltic Proper contained 13.4–20.6% lipid in the whole body [12], and mature 2nd sea-year females contained 2.3–10.4% in muscle during the spawning time [11]. The lipid content of lampreys before the pre-spawning fast was of the same order of magnitude and ranged from 12 to 21% [68,77,112,113]. In North America, the fattiest salmonines, such as Chinook salmon, with a whole-body lipid content of up to 18.2% [114,115], have been most susceptible to thiamine deficiency [13,17,21,22,116]. The high total body lipid content of reared salmon smolts, 8–9%, was also found to be the reason for their lower survival rate after release [117]. The lipid content was three times higher than the recommended minimum lipid content and up to four times higher than that of wild smolts [117]. In the sea, they probably had to initially use their body lipids while getting accustomed to natural feeding and searching for food, which consumed their thiamine stores.

The lipid content and composition of fatty predatory fish are naturally determined by the composition of their diet [12,98,109,118]. In the Baltic Proper, the lipid content of 1–3-year-old sprat, ranging between 14.4 and 15.9% (in fresh mass) in the fall, was twice as high as that of the same-aged herring, 6.7–7.1% [12]. As the lipid content of young herring has been higher in the Gulf of Bothnia (7.7–8.8%) than in the Baltic Proper, and the proportion of *n–3* PUFAs in herring is somewhat higher than in sprat [43,44], the average supply of *n–3* PUFAs for salmon in the Gulf of Bothnia has been approximately equal to that obtained from sprat and herring in the Baltic Proper [12]. In any case, the concentration of DHA and *n–3* PUFAs is highest in the youngest individuals and decreases with age in both sprat and herring of a size suitable for salmon as prey [43]. After years such as 2002, 2014, and possibly 2022, when a very large year-class of herring hatched in the Gulf of Bothnia [41,59], salmon, as well as lampreys, when they had been feeding on 0-year-old herring, became thiamine-deficient, so that even all the yolk-sac fry of individual salmon died, and the largest and fattiest female lampreys died during the pre-spawning fast [8,11,16].

Off the coast of California, extensive feeding of Chinook salmon on northern anchovy (*Engraulis mordax*) with an average lipid content of 7.2% and range between 1.7 and 17.6% (in wet mass) in May–June and a high proportion of *n–3* PUFAs also led to thiamine deficiency and impaired reproduction [21,22]. As in anchovy, the lipid content in sprat, 1.2–17.3% [43], and alewife (*Alosa pseudoharengus*) in the Great Lakes, 2–19% [119], has varied widely according to age, season, and feeding area. The dominance of alewife as the diet of Atlantic salmon in the Finger Lakes, and Chinook and coho salmon in the Great Lakes, has been associated with the incidence of TDC [17,18,120,121]. In the second-most-common prey item in these lakes, the rainbow smelt (*Osmerus mordax*) [122,123], which has not been associated with TDC, the lipid content, at 1–6%, has been lower than in Baltic Proper herring [17,119,124].

The quality of the diet of the post-smolts contributes to the fattiness of the salmon returning to spawn and, thus, also to their thiamine status, which was seen in this study. Based on the data from the 1990s and 2000s, the higher the supply of thiamine and lipids in the Baltic Proper, the lower the thiamine status of salmon two years later at the time of spawning [13]. The problem regarding the thiamine deficiency in fatty fish is, therefore, not a result of a low intake of thiamine but its high consumption in predatory fish due to a high-energy fish-based diet and lipid peroxidation. Although the body's thiamine stores are most used during pre-spawning fasting, when replacement thiamine is unavailable [31,116,125], thiamine also decreases due to lipid peroxidation during the feeding phase [12], when the body's *n–3* PUFAs along with other FAs are used for energy. Already during the feeding migration, the thiamine status was the poorest in the fattiest juvenile salmon [12]. The lipids of these salmon contained the largest amounts of *n–3* PUFAs and DHA, which is the most common PUFA in Baltic salmon, as well as in Baltic sprat and herring [10–12,31,43,44].

The predominant source of metabolic energy for salmon during the growth and especially during the pre-spawning fast and formation of eggs is palmitic acid (16:0), which is the most common saturated fatty acid in salmon and its prey fish [10,11,30,31,126]. Monounsaturated fatty acids, the most common of which is oleic acid (18:1*n–9*), are the next most catabolized fatty acid group for energy, and among *n–3* PUFAs, EPA is prior to DHA [10,11,30]. The proportion of oleic acid in fatty acids is higher in sprat than in herring [43,44], which is manifested in its higher proportion in salmon that have been feeding more on sprat than in salmon that have been feeding mainly on herring [10–12].

As Keinänen et al. [13] describe, the pyrophosphate derivative of thiamine (TPP) acts as an essential coenzyme in all reactions of oxidative metabolism to produce energy in the form of ATP [24]. Thiamine also acts as a site-specific antioxidant against lipid peroxidation and the oxidation of oleic acid [26,33,34]. In these various radical and oxidation reactions, thiamine is inactivated, which depletes the thiamine stores [26,34]. The fattiest salmonines, considering both species and individuals such as Chinook salmon [115] and the fattiest Baltic salmon [12], that have fed on abundant marine fatty prey fish, contain the most *n–3* PUFAs [12,17]. When they use the body's lipids for energy, as shown in studies by Honeyfield et al. [116] and Vuorinen et al. [31], thiamine is depleted in a downward spiral due to autocatalytic radical chain reactions of PUFAs and the oxidative stress caused by thiamine deficiency [8,29,34]. If thiamine deficiency in brood salmon is severe, like lampreys, they may die even before spawning [8,14,127,128]. However, salmon yolk-sac fry and post-smolts appear to be more prone to dying due to the high-lipid marine prey fish of salmon: yolk-sac fry mainly die due to low THIAM concentrations in the eggs of thiamine-deficient females, and post-smolts apparently because fish food that is too fatty impairs their growth, vitality, and viability.

The THIAM concentration in the eggs depends on the thiamine status of the salmon, an indicator of which, already before spawning time, is the liver's total thiamine concentration [12,31,129]. This study's results, consistent with the results of previous studies [11–13], showed that an excessively fatty fish diet weakens the thiamine status of salmon [12] and predisposes spawning salmon to thiamine deficiency and yolk-sac fry to M74 mortality. Furthermore, many post-smolts feeding on abundant fatty prey fish have apparently died and have never returned to their home river to spawn.

5. Conclusions

This study shows that post-smolts are sensitive to excessively fatty marine prey fish with too much lipid relative to protein and, thus, much energy relative to thiamine during their first growing season in the sea. This food is associated with the reduced survival of salmon post-smolts. Reduced survival is reflected in fewer salmon returning to their home river to spawn and in their smaller size. The availability of food of suitable quality for post-smolts when they arrive at their feeding grounds, therefore, largely determines how many of these salmon return. In the Baltic Sea, the Baltic Proper is the most important feeding area for salmon from the rivers of the northern part of the Gulf of Bothnia, from which most Baltic salmon originate. Invertebrates in the Baltic Proper, which are leaner than prey fish, are too small prey for post-smolts when they arrive there from Tornionjoki, Simojoki, or the other rivers of the Bothnian Bay. Thus, post-smolts only eat small fish. Age-0 herring and youngish sprat are of a suitable size to be prey for salmon post-smolts, but age-0 sprat are too small. If the number of 0-year-old herring relative to youngish sprat is low when post-smolts arrive to feed there, the food of post-smolts is too fatty. The higher the ratio of smallish sprat to age-0 herring, the worse the viability of salmon post-smolts and, as a result, the fewer salmon return to spawn two years later, as the feeding migration of most returners lasts for two years. Since the proportion of sprat in the number of post-smolts' prey fish is considerably larger than the proportion of herring, it is important that there are enough 0-year-old herring in relation to youngish sprat for the post-smolts to survive. Because younger sprat are fattier than herring and older sprat, and because the number of fish per year-class decreases exponentially year by year, an abundance of youngish sprat is most likely to predispose post-smolts to poor survival and returning salmon to thiamine deficiency. Cod, in addition to the prey fish of salmon, have an indirect impact on salmon stocks. When regulating fish stocks in the Baltic Sea and setting fishing quotas, their impact on the survival of salmon must be taken into account. The salmon stocks may decline due to the smallness of the herring spawning stocks in the Baltic Proper and the low numbers of the new year-classes of herring. However, the abundance of sprat and its large new year-classes, especially when cod stocks are weak, may weaken salmon stocks, first by reducing the survival of post-smolts and, thus, the number of ascending salmon, and second by deteriorating the thiamine status of spawning salmon and thus causing M74 mortality.

Supplementary Materials: The following supporting information can be downloaded at https://www.mdpi.com/article/10.3390/fishes10010016/s1, Table S1: Linear model parameters for the relationships of the numbers of salmon returning to the Rivers Tornionjoki and Simojoki in 2012–2023 and the numbers of prey fish in 2010–2021; Table S2: Numbers of salmon ascendants from 2012 to 2023, the mean concentration of free thiamine in unfertilized eggs of salmon, and the numbers of 0-year-old herring and youngish sprat and their ratios in the Baltic Proper in 2010–2021; Figure S1: Mean total body lipid content of sprat and herring from the Baltic Proper, and the ratio of total thiamine concentration to the unit of energy and ratio of total protein concentration to lipid content in them; Figure S2: Numbers of herring and sprat in the Baltic Proper when salmon post-smolts arrived there in 2010–2021, the number of salmon returned to their home river in 2012–2023, and the amount of lipid available from herring and sprat; Figure S3: Numbers of returning salmon and the ratio of the number of youngish sprat to 0-year-old herring.

Author Contributions: Conceptualization, M.K. and P.J.V.; investigation, M.K. and P.J.V.; resources, M.K., J.P., J.R., T.R., T.M. and P.J.V.; validation, T.R.; formal analysis, P.J.V. and M.K.; data curation, P.J.V., J.R., J.P., T.M. and T.R.; writing—original draft preparation, M.K. and P.J.V.; writing—review and editing, M.K., J.R., J.P., T.M., T.R. and P.J.V.; visualization, P.J.V. and M.K.; project administration, P.J.V. All authors have read and agreed to the published version of the manuscript.

Funding: This research received no external funding.

Institutional Review Board Statement: Not applicable.

Informed Consent Statement: Not applicable.

Data Availability Statement: Data are contained within the article and Supplementary Materials: The datasets used and analyzed during the current study are available as stated in the Materials and Methods Section.

Acknowledgments: Rupert Moreton and Tomás Ó Toghdha revised the English.

Conflicts of Interest: The authors declare no conflicts of interest.

References

1. ICES. Baltic Salmon and Trout Assessment Working Group (WGBAST). *ICES Sci. Rep.* **2024**, *6*, 425. [CrossRef]
2. Salminen, M. Relationships between smolt size, postsmolt growth and sea age at maturity in Atlantic salmon ranched in the Baltic Sea. *J. Appl. Ichthyol.* **1997**, *13*, 121–130. [CrossRef]
3. Ikonen, E. The Role of the Feeding Migration and Diet of Atlantic Salmon (*Salmo salar* L.) in Yolk-Sac Fry Mortality (M74) in the Baltic Sea. Ph.D. Thesis, Department of Biological and Environmental Sciences, Faculty of Biosciences, University of Helsinki, Finland and Finnish Game and Fisheries Research Institute, Helsinki, Finland, 2006.
4. Aro, E. A review of fish migration patterns in the Baltic. *Rap. Proc.-Verb. Re. Cons. Int. Explor. Mer* **1989**, *190*, 72–96.
5. Luke. Tornionjoen Nousulohiseuranta. Available online: https://kalahavainnot.luke.fi/fi/seurannat/tornionjoen-nousulohiseuranta/ (accessed on 24 March 2024).
6. ICES. *Report of the Baltic Salmon and Trout Assessment Working Group (WGBAST), 24–31 March 2009, Oulu, Finland*; ICES CM 2009/ACOM:05; ICES: Copenhagen, Denmark, 2009; 280p.

7. Keinänen, M.; Iivari, J.; Juntunen, E.-P.; Kannel, R.; Heinimaa, P.; Nikonen, S.; Pakarinen, T.; Romakkaniemi, A.; Vuorinen, P.J. Thiamine Deficiency M74 of Salmon Can Be Prevented; *Riista-ja kalatalous—Tutkimuksia ja selvityksiä* 14/2014; Helsinki, Finland, 2014. 41p. Available online: http://jukuri.luke.fi/bitstream/handle/10024/519813/rkts2014_14.pdf?sequence=1 (accessed on 16 September 2024). (In Finnish with Abstract in English)
8. Vuorinen, P.J.; Rokka, M.; Nikonen, S.; Juntunen, E.-P.; Ritvanen, T.; Heinimaa, P.; Keinänen, M. Model for estimating thiamine deficiency-related mortality of Atlantic salmon (*Salmo salar*) offspring and variation in the Baltic salmon M74 syndrome. *Mar. Freshw. Behav. Physiol.* **2021**, *54*, 97–131. [CrossRef]
9. Balon, E.K. Terminology of intervals in fish development. *J. Fish. Res. Board Can.* **1975**, *32*, 1663–1670. [CrossRef]
10. Keinänen, M.; Käkelä, R.; Ritvanen, T.; Pönni, J.; Harjunpää, H.; Myllylä, T.; Vuorinen, P.J. Fatty acid signatures connect thiamine deficiency with the diet of the Atlantic salmon (*Salmo salar*) feeding in the Baltic Sea. *Mar. Biol.* **2018**, *165*, 161. [CrossRef]
11. Vuorinen, P.J.; Käkelä, R.; Pakarinen, T.; Heinimaa, P.; Ritvanen, T.; Nikonen, S.; Rokka, M.; Keinänen, M. Thiamine deficiency M74 developed in salmon (*Salmo salar*) stocks in two Baltic Sea areas after the hatching of large year-classes of two clupeid species—Detected by fatty acid signature analysis. *Fishes* **2024**, *9*, 58. [CrossRef]
12. Keinänen, M.; Nikonen, S.; Käkelä, R.; Ritvanen, T.; Rokka, M.; Myllylä, T.; Pönni, J.; Vuorinen, P.J. High lipid content of prey fish and n-3 PUFA peroxidation impair the thiamine status of feeding-migrating Atlantic salmon (*Salmo salar*) and is reflected in hepatic biochemical indices. *Biomolecules* **2022**, *12*, 526. [CrossRef]
13. Keinänen, M.; Uddström, A.; Mikkonen, J.; Casini, M.; Pönni, J.; Myllylä, T.; Aro, E.; Vuorinen, P.J. The thiamine deficiency syndrome M74, a reproductive disorder of Atlantic salmon (*Salmo salar*) feeding in the Baltic Sea, is related to the fat and thiamine content of prey fish. *ICES J. Mar. Sci.* **2012**, *69*, 516–528. [CrossRef]
14. Amcoff, P.; Börjeson, H.; Landergren, P.; Vallin, L.; Norrgren, L. Thiamine (vitamin B_1) concentrations in salmon (*Salmo salar*), brown trout (*Salmo trutta*) and cod (*Gadus morhua*) from the Baltic sea. *Ambio* **1999**, *28*, 48–54. Available online: https://www.jstor.org/stable/4314848 (accessed on 16 September 2024).
15. Landergren, P.; Vallin, L.; Westin, L.; Amcoff, P.; Börjeson, H.; Ragnarsson, B. Reproductive failure in Baltic sea trout (*Salmo trutta*) compared with the M74 syndrome in Baltic salmon (*Salmo salar*). *Ambio* **1999**, *28*, 87–91. Available online: https://www.jstor.org/stable/4314853 (accessed on 16 September 2024).
16. Vuorinen, P.J.; Juntunen, E.-P.; Iivari, J.; Koski, P.; Nikonen, S.; Rokka, M.; Ritvanen, T.; Pakkala, J.; Heinimaa, P.; Keinänen, M. Lipid-related thiamine deficiency cause mortality of river lampreys (*Lampetra fluviatilis*) during pre-spawning fasting. *Reg. Stud. Mar. Sci.* **2023**, *62*, 14. [CrossRef]
17. Futia, M.H.; Connerton, M.J.; Weidel, B.C.; Rinchard, J. Diet predictions of Lake Ontario salmonines based on fatty acids and correlations between their fat content and thiamine concentrations. *J. Great Lakes Res.* **2019**, *45*, 934–948. [CrossRef]
18. Futia, M.H.; Rinchard, J. Evaluation of adult and offspring thiamine deficiency in salmonine species from Lake Ontario. *J. Great Lakes Res.* **2019**, *45*, 811–820. [CrossRef]
19. Fisher, J.P.; Spitsbergen, J.M.; Iamonte, T.; Little, E.E.; DeLonay, A. Pathological and behavioral manifestations of the “Cayuga syndrome”, a thiamine deficiency in larval landlocked Atlantic salmon. *J. Aquat. Anim. Health* **1995**, *7*, 269–283. [CrossRef]
20. Mantua, N.; Johnson, R.; Field, J.; Lindley, S.; Williams, T.; Todgham, A.; Fangue, N.; Jeffres, C.; Bell, H.; Cocherell, D.; et al. *Mechanisms, Impacts, and Mitigation for Thiamine Deficiency and Early Life Stage Mortality in California's Central Valley Chinook Salmon*; Techninal Report 17; North Pacific Anadromous Fish Commission: Vancouver, BC, Canada, 2021; pp. 92–93.
21. Crozier, L.G.; Siegel, J.E. A comprehensive review of the impacts of climate change on salmon: Strengths and weaknesses of the Literature by life stage. *Fishes* **2023**, *8*, 319. [CrossRef]
22. Ludwig, J.M. Assessing Diets of California Salmonines Using Fatty Acid Signatures and Its Impact on Observed Thiamine Deficiency. Master's Thesis, Department of Environmental Science and Ecology, SUNY Brockport, Brockport, NY, USA, 2024.
23. Woodward, B. Dietary vitamin requirements of cultured young fish, with emphasis on quantitative estimates for salmonids. *Aquaculture* **1994**, *124*, 133–168. [CrossRef]
24. Lonsdale, D.; Marrs, C. *Thiamine Deficiency Disease, Dysautonomia, and High Calorie Malnutrition*; Academic Press: London, UK; San Diego, CA, USA, 2019.
25. Casteels, M.; Sniekers, M.; Fraccascia, P.; Mannaerts, G.P.; VanVeldhoven, P.P. The role of 2-hydroxyacyl-CoA lyase, a thiamin pyrophosphate-dependent enzyme, in the peroxisomal metabolism of 3-methyl-branched fatty acids and 2-hydroxy straight-chain fatty acids. *Biochem. Soc. Trans.* **2007**, *35*, 876–880. [CrossRef]
26. Depeint, F.; Bruce, W.R.; Shangari, N.; Mehta, R.; O'Brien, P.J. Mitochondrial function and toxicity: Role of the B vitamin family on mitochondrial energy metabolism. *Chem. Biol. Interact.* **2006**, *163*, 94–112. [CrossRef]
27. Behbodi, Z.; Bahram, S.; Bahrekazemi, M.; Javadian, S.R.; Bozorgnia, A.; Abdel-Tawwab, M. Effects of dietary thiamin (vitamin B1) on the growth performance, serum biochemical factors, immune response, and antioxidant activity of great sturgeon (*Huso huso*) juveniles. *Vet. Res. Commun.* **2024**, *48*, 485–496. [CrossRef]
28. Grisdale-Helland, B.; Gatlin, D.M.; Helland, S.J. Optimization of dietary macronutrients for Atlantic salmon post-smolts using increasing ration levels. *Aquaculture* **2013**, *408*, 88–94. [CrossRef]

29. Spector, A.A. Lipid metabolism: Essential fatty acids. In *Biochemical and Physiological Aspects of Human Nutrition*; Stipanuk, M.H., Ed.; Saunders/Elsevier: Philadelphia, PA, USA, 2000; pp. 365–383.
30. Tocher, D.R. Metabolism and functions of lipids and fatty acids in teleost fish. *Rev. Fish. Sci.* **2003**, *11*, 107–184. [CrossRef]
31. Vuorinen, P.J.; Rokka, M.; Ritvanen, T.; Käkelä, R.; Nikonen, S.; Pakarinen, T.; Keinänen, M. Changes in thiamine concentrations, fatty acid composition, and some other lipid-related biochemical indices in Baltic Sea Atlantic salmon (*Salmo salar*) during the spawning run and pre-spawning fasting. *Helgol. Mar. Res.* **2020**, *74*, 10. [CrossRef]
32. Combs, G.F., Jr.; McClung, J.P. Thiamin. In *The Vitamins, Fundamental Aspects in Nutrition and Health*, 5th ed.; Academic Press: London, UK; San Diego, CA, USA; Cambridge, UK; Oxford, UK, 2017; pp. 297–314.
33. Lukienko, P.I.; Mel'nichenko, N.G.; Zverinskii, I.V.; Zabrodskaya, S.V. Antioxidant properties of thiamine. *Bull. Exp. Biol. Med.* **2000**, *130*, 874–876. [CrossRef] [PubMed]
34. Gibson, G.E.; Zhang, H. Interactions of oxidative stress with thiamine homeostasis promote neurodegeneration. *Neurochem. Int.* **2002**, *40*, 493–504. [CrossRef]
35. Kallio-Nyberg, I.; Romakkaniemi, A.; Jokikokko, E.; Saloniemi, I.; Jutila, E. Differences between wild and reared *Salmo salar* stocks of two northern Baltic Sea rivers. *Fish. Res.* **2015**, *165*, 85–95. [CrossRef]
36. Pardo, S.A.; Bolstad, G.H.; Dempson, J.B.; April, J.; Jones, R.A.; Raab, D.; Hutchings, J.A. Trends in marine survival of Atlantic salmon populations in eastern Canada. *ICES J. Mar. Sci.* **2021**, *78*, 2460–2473. [CrossRef]
37. Kallio-Nyberg, I.; Saloniemi, I.; Jutila, E.; Jokikokko, E. Effect of hatchery rearing and environmental factors on the survival, growth and migration of Atlantic salmon in the Baltic Sea. *Fish. Res.* **2011**, *109*, 285–294. [CrossRef]
38. Mikkonen, J.; Keinänen, M.; Casini, M.; Pönni, J.; Vuorinen, P.J. Relationships between fish stock changes in the Baltic Sea and the M74 syndrome, a reproductive disorder of Atlantic salmon (*Salmo salar*). *ICES J. Mar. Sci.* **2011**, *68*, 2134–2144. [CrossRef]
39. Casini, M.; Hjelm, J.; Molinero, J.C.; Lovgren, J.; Cardinale, M.; Bartolino, V.; Belgrano, A.; Kornilovs, G. Trophic cascades promote threshold-like shifts in pelagic marine ecosystems. *Proc. Natl. Acad. Sci. USA* **2009**, *106*, 197–202. [CrossRef]
40. Bagge, O.; Thurow, F.; Steffensen, E.; Bay, J. The Baltic cod. *Dana* **1994**, *10*, 1–28.
41. ICES. Baltic Fisheries Assessment Working Group (WGBFAS). *ICES Sci. Rep.* **2024**, *6*, 584. [CrossRef]
42. Bryhn, A.C.; Bergek, S.; Bergström, U.; Casini, M.; Dahlgren, E.; Ek, C.; Hjelm, J.; Königson, S.; Ljungberg, P.; Lundström, K.; et al. Which factors can affect the productivity and dynamics of cod stocks in the Baltic Sea, Kattegat and Skagerrak? *Ocean Coast. Manag.* **2022**, *223*, 106154. [CrossRef]
43. Keinänen, M.; Käkelä, R.; Ritvanen, T.; Myllylä, T.; Pönni, J.; Vuorinen, P.J. Fatty acid composition of sprat (*Sprattus sprattus*) and herring (*Clupea harengus*) in the Baltic Sea as potential prey for salmon (*Salmo salar*). *Helgol. Mar. Res.* **2017**, *71*, 4. [CrossRef]
44. Røjbek, M.C.; Tomkiewicz, J.; Jacobsen, C.; Støttrup, J.G. Forage fish quality: Seasonal lipid dynamics of herring (*Clupea harengus* L.) and sprat (*Sprattus sprattus* L.) in the Baltic Sea. *ICES J. Mar. Sci.* **2014**, *71*, 56–71. [CrossRef]
45. Vuorinen, P.J.; Parmanne, R.; Vartiainen, T.; Keinänen, M.; Kiviranta, H.; Kotovuori, O.; Halling, F. PCDD, PCDF, PCB and thiamine in Baltic herring (C*lupea harengus* L.) and sprat [*Sprattus sprattus* (L.)] as a background to the M74 syndrome of Baltic salmon (*Salmo salar* L.). *ICES J. Mar. Sci.* **2002**, *59*, 480–496. [CrossRef]
46. Salminen, M.; Kuikka, S.; Erkamo, E. Divergence in feeding migration of Baltic salmon (*Salmo salar* L.); the significance of smolt size. *Nord. J. Freshw. Res.* **1994**, *69*, 32–42.
47. Jutila, E.; Jokikokko, E.; Kallio-Nyberg, I.; Saloniemi, I.; Pasanen, P. Differences in sea migration between wild and reared Atlantic salmon (*Salmo salar* L.) in the Baltic Sea. *Fish. Res.* **2003**, *60*, 333–343. [CrossRef]
48. Thurow, F. *On Food, Behaviour and Population Mechanism of Baltic Salmon*; Report 4; Swedish Salmon Research Institute: Älvkarleby, Sweden, 1968; pp. 1–16.
49. Salminen, M.; Erkamo, E.; Salmi, J. Diet of post-smolt and one-sea-winter Atlantic salmon in the Bothnian Sea, northern Baltic. *J. Fish Biol.* **2001**, *58*, 16–35. [CrossRef]
50. Karlsson, L.; Karlström, Ö. The Baltic salmon (*Salmo salar* L.): Its history, present situation and future. *Dana* **1994**, *10*, 61–85.
51. Vuorinen, P.J.; Kiviranta, H.; Koistinen, J.; Pöyhönen, O.; Ikonen, E.; Keinänen, M. Organohalogen concentrations and feeding status in Atlantic salmon (*Salmo salar* L.) of the Baltic Sea during the spawning run. *Sci. Total Environ.* **2014**, *468–469*, 449–456. [CrossRef] [PubMed]
52. Hansson, S.; Karlsson, L.; Ikonen, E.; Christensen, O.; Mitans, A.; Uzars, D.; Petersson, E.; Ragnarsson, B. Stomach analyses of Baltic salmon from 1959-1962 and 1994-1997: Possible relations between diet and yolk-sac-fry mortality (M74). *J. Fish Biol.* **2001**, *58*, 1730–1745. [CrossRef]
53. Karlsson, L.; Ikonen, E.; Mitans, A.; Hansson, S. The diet of salmon (*Salmo salar*) in the Baltic sea and connections with the M74 syndrome. *Ambio* **1999**, *28*, 37–42. Available online: https://www.jstor.org/stable/4314846 (accessed on 16 September 2024).
54. Jacobson, P.; Gårdmark, A.; Östergren, J.; Casini, M.; Huss, M. Size-dependent prey availability affects diet and performance of predatory fish at sea: A case study of Atlantic salmon. *Ecosphere* **2018**, *9*, e02081. [CrossRef]
55. Jacobson, P. Size-Dependent Predator-Prey Interactions, Distribution and Mortality in Salmon: Effects on Individuals and Populations. Ph.D. Thesis, Swedish University of Agricultural Sciences, SLU, Öregrund, Sweden, 2020.

56. ICES. Baltic Salmon and Trout Assessment Working Group (WGBAST). *ICES Sci. Rep.* **2023**, *5*, 465. [CrossRef]
57. Isometsä, K.; Orell, P.; Romakkaniemi, A.; Vähä, V.; Lilja, J. *Tornionjoen Nousulohien Kaikuluotausseurannat Vuosina 2009–2020*; Luonnonvara-ja Biotalouden Tutkimus 9; Luonnonvarakeskus (Luke): Helsinki, Finland, 2021; 32p. (In Finnish)
58. ICES. Baltic fisheries assessment working group (WGBFAS). *ICES Sci. Rep.* **2020**, *2*, 643. [CrossRef]
59. Pönni, J. Silakka. In *Kalakantojen Tila Vuonna 2021 Sekä Ennuste Vuosille 2022 ja 2023*; Raitaniemi, J., Sairanen, S., Eds.; Luonnonvara-ja Biotalouden Tutkimus 72; Luonnonvarakeskus: Helsinki, Finland, 2022; pp. 9–23. (In Finnish)
60. ICES. Baltic Fisheries Assessment Working Group (WGBFAS). *ICES Sci. Rep.* **2022**, *4*, 659. [CrossRef]
61. *ISO 1735:2004/IDF 5:2004*; Cheese and Processed Cheese Products–Determination of Fat Content–Gravimetric Method (Reference Method). ISO: Geneva, Switzerland, 2004; 16p.
62. Vuorinen, P.J.; Myllylä, T.; Ritvanen, T.; Keinänen, M. Lipid and fatty acid contents in three prey species of Baltic salmon (*Salmo salar*) from three areas of the Baltic Sea. *Manuscript for a journal article in preparation.*
63. Pönni, J. Kilohaili. In *Kalakantojen Tila Vuonna 2021 Sekä Ennuste Vuosille 2022 ja 2023*; Raitaniemi, J., Sairanen, S., Eds.; Luonnonvara-ja Biotalouden Tutkimus 72; Luonnonvarakeskus: Helsinki, Finland, 2022; pp. 24–28. (In Finnish)
64. Ketola, H.G.; Chiotti, T.L.; Rathman, R.S.; Fitzsimons, J.D.; Honeyfield, D.C.; Van Dusen, P.J.; Lewis, G.E. Thiamine status of Cayuga Lake rainbow trout and its influence on spawning migration. *N. Am. J. Fish. Manag.* **2005**, *25*, 1281–1287. [CrossRef]
65. Mäntyniemi, S.; Romakkaniemi, A.; Dannewitz, J.; Palm, S.; Pakarinen, T.; Pulkkinen, H.; Gårdmark, A.; Karlsson, O. Both predation and feeding opportunities may explain changes in survival of Baltic salmon post-smolts. *ICES J. Mar. Sci.* **2012**, *69*, 1574–1579. [CrossRef]
66. Säterberg, T.; Jacobson, P.; Ovegård, M.; Rask, J.; Östergren, J.; Jepsen, N.; Florin, A.-B. Species- and origin-specific susceptibility to bird predation among juvenile salmonids. *Ecosphere* **2023**, *14*, e4724. [CrossRef]
67. Heikinheimo, O.; Marjomäki, T.J.; Olin, M.; Rusanen, P. Cormorant predation mortality of perch (*Perca fluviatilis*) in coastal and archipelago areas, northern Baltic Sea. *ICES J. Mar. Sci.* **2022**, *79*, 337–349. [CrossRef]
68. Koli, L. *Suomen Kalat*; Werner Söderström Osakeyhtiö: Porvoo, Finland, 1990. (In Finnish)
69. Salminen, M. *Marine Survival of Atlantic Salmon in the Baltic Sea*; Technical Report No. 4; North Pacific Anadromous Fish Commission: Vancouver, BC, Canada, 2002; pp. 27–29.
70. Arrhenius, F.; Hansson, S. Growth of Baltic Sea young-of-the-year herring *Clupea harengus* is resource limited. *Mar. Ecol.-Prog. Ser.* **1999**, *191*, 295–299. [CrossRef]
71. Peck, M.A.; Baumann, H.; Bernreuther, M.; Clemmesen, C.; Herrmann, J.-P.; Haslob, H.; Huwer, B.; Kanstinger, P.; Köster, F.W.; Petereit, C.; et al. The ecophysiology of *Sprattus sprattus* in the Baltic and North Seas. *Prog. Oceanogr.* **2012**, *103*, 42–57. [CrossRef]
72. Jacobson, P.; Gådmark, A.; Huss, M. Population and size-specific distribution of Atlantic salmon *Salmo salar* in the Baltic Sea over five decades. *J. Fish Biol.* **2020**, *96*, 408–417. [CrossRef]
73. ICES. Working Group on Baltic International Fish Survey (WGBIFS; outputs from 2022 meeting). *ICES Sci. Rep.* **2023**, *05*, 529. [CrossRef]
74. ICES. *Report of the Baltic Salmon and Trout Assessment Working Group (WGBAST), Uppsala, Sweden, 15–23 March 2012*; ICES CM 2012/ACOM:08353p; ICES: Copenhagen, Denmark, 2012; 08353p.
75. Friedland, K.D.; Dannewitz, J.; Romakkaniemi, A.; Palm, S.; Pulkkinen, H.; Pakarinen, T.; Oeberst, R. Post-smolt survival of Baltic salmon in context to changing environmental conditions and predators. *ICES J. Mar. Sci.* **2017**, *74*, 1344–1355. [CrossRef]
76. Olin, A.B.; Olsson, J.; Eklöf, J.S.; Eriksson, B.K.; Kaljuste, O.; Briekmane, L.; Bergström, U. Increases of opportunistic species in response to ecosystem change: The case of the Baltic Sea three-spined stickleback. *ICES J. Mar. Sci.* **2022**, *79*, 1419–1434. [CrossRef]
77. Airaksinen, R.; Jestoi, M.; Keinänen, M.; Kiviranta, H.; Koponen, J.; Mannio, J.; Myllylä, T.; Nieminen, J.; Raitaniemi, J.; Rantakokko, P.; et al. *Changes in the Levels of Environmental Contaminants of Finnish Wild Caught Fish*. Publications of the Government's Analysis, Assessment and Research Activities 51. 2018. 71p. Available online: http://urn.fi/URN:ISBN:978-952-287-600-3 (accessed on 16 September 2024). (In Finnish with Abstract in English)
78. Frisk, C.; Andersen, K.H.; Temming, A.; Herrmann, J.P.; Madsen, K.S.; Kraus, G. Environmental effects on sprat (*Sprattus sprattus*) physiology and growth at the distribution frontier: A bioenergetic modelling approach. *Ecol. Model.* **2015**, *299*, 130–139. [CrossRef]
79. Moyano, M.; Illing, B.; Akimova, A.; Alter, K.; Bartolino, V.; Börner, G.; Clemmesen, C.; Finke, A.; Gröhsler, T.; Kotterba, P.; et al. Caught in the middle: Bottom-up and top-down processes impacting recruitment in a small pelagic fish. *Rev. Fish Biol. Fisher.* **2023**, *33*, 55–84. [CrossRef]
80. Pönni, J. Silakka. In *Kalakantojen Tila Vuonna 2020 Sekä Ennuste Vuosille 2021 ja 2022*; Raitaniemi, J., Sairanen, S., Eds.; Luonnonvara-ja Biotalouden Tutkimus 61; Luonnonvarakeskus: Helsinki, Finland, 2021; pp. 9–23. (In Finnish)
81. Burbank, J.; DeJong, R.A.; Turcotte, F.; Rolland, N. Understanding factors influencing Atlantic herring (*Clupea harengus*) recruitment: From egg deposition to juveniles. *Fish. Oceanogr.* **2023**, *32*, 147–159. [CrossRef]
82. Pönni, J. Silakka. In *Kalakantojen Tila Vuonna 2018 Sekä Ennuste Vuosille 2019 ja 2020*; Sairanen, S., Raitaniemi, J., Eds.; Luonnonvara-ja Biotalouden Tutkimus 48; Luonnonvarakeskus: Helsinki, Finland, 2019; pp. 6–16. (In Finnish)

83. Bengtsson, B.-E.; Hill, C.; Bergman, Å.; Brandt, I.; Johansson, N.; Magnhagen, C.; Södergren, A.; Thulin, J. Reproductive disturbances in Baltic fish: A synopsis of the FiRe project. *Ambio* **1999**, *28*, 2–8. Available online: https://www.jstor.org/stable/4314841 (accessed on 16 September 2024).
84. Stockmayer, V.; Lehmann, A. Variations of temperature, salinity and oxygen of the Baltic Sea for the period 1950 to 2020. *Oceanologia* **2023**, *65*, 466–483. [CrossRef]
85. Casini, M.; Cardinale, M.; Arrhenius, F. Feeding preferences of herring (*Clupea harengus*) and sprat (*Sprattus sprattus*) in the southern Baltic Sea. *ICES J. Mar. Sci.* **2004**, *61*, 1267–1277. [CrossRef]
86. Möllmann, C.; Kornilovs, G.; Fetter, M.; Köster, F.W. Feeding ecology of central Baltic Sea herring and sprat. *J. Fish Biol.* **2004**, *65*, 1563–1581. [CrossRef]
87. Vuorinen, P.J.; Keinänen, M.; Kiviranta, H.; Koistinen, J.; Kiljunen, M.; Myllylä, T.; Pönni, J.; Peltonen, H.; Verta, M.; Karjalainen, J. Biomagnification of organohalogens in Atlantic salmon (*Salmo salar*) from its main prey species in three areas of the Baltic Sea. *Sci. Total Environ.* **2012**, *421–422*, 129–143. [CrossRef]
88. Jacobsen, J.A.; Hansen, L.P. Feeding habits of wild and escaped farmed Atlantic salmon, *Salmo salar* L., in the Northeast Atlantic. *ICES J. Mar. Sci.* **2001**, *58*, 916–933. [CrossRef]
89. Hyvönen, L.; Koivistoinen, P. Fatty acid analysis, TAG equivalents as net fat value, and nutritional attributes of fish and fish products. *J. Food Compos. Anal.* **1994**, *7*, 44–58. [CrossRef]
90. Kouts, M.; Maljutenko, I.; Elken, J.; Liu, Y.; Hansson, M.; Viktorsson, L.; Raudsepp, U. Recent regime of persistent hypoxia in the Baltic Sea. *Environm. Res. Commun.* **2021**, *3*, 075004. [CrossRef]
91. Arrhenius, F.; Hansson, S. Food consumption of larval, young and adult herring and sprat in the Baltic Sea. *Mar. Ecol.-Prog. Ser.* **1993**, *96*, 125–137. [CrossRef]
92. ICES. *Report of the Baltic Fisheries Assessment Working Group (WGBFAS), 18–27 April 2006, Rostock, Germany*; ICES CM 2006/ACFM:24; ICES: Copenhagen, Denmark, 2006; 669p.
93. Ryberg, M.P.; Skov, P.V.; Vendramin, N.; Buchmann, K.; Nielsen, A.; Behrens, J.W. Physiological condition of Eastern Baltic cod, *Gadus morhua*, infected with the parasitic nematode *Contracaecum osculatum*. *Conserv. Physiol.* **2020**, *8*, 14. [CrossRef]
94. Marnis, H.; Kania, P.W.; Syahputra, K.; Zuo, S.; Dirks, R.P.; Buchmann, K. Transcriptomic analysis of Baltic cod (*Gadus morhua*) liver infected with Contracaecum osculatum third stage larvae indicates parasitic effects on growth and immune response. *Fish Shellfish Immun.* **2019**, *93*, 965–976. [CrossRef] [PubMed]
95. Neuenfeldt, S.; Bartolino, V.; Orio, A.; Andersen, K.H.; Andersen, N.G.; Niiranen, S.; Bergström, U.; Ustups, D.; Kulatska, N.; Casini, M. Feeding and growth of Atlantic cod (*Gadus morhua* L.) in the eastern Baltic Sea under environmental change. *ICES J. Mar. Sci.* **2019**, *77*, 624–632. [CrossRef]
96. Köster, F.W.; Möllmann, C.; Hinrichsen, H.-H.; Wieland, K.; Tomkiewicz, J.; Kraus, G.; Voss, R.; Makarchouk, A.; Mackenzie, B.R.; St John, M.A.; et al. Baltic cod recruitment—The impact of climate variability on key processes. *ICES J. Mar. Sci.* **2005**, *62*, 1408–1425. [CrossRef]
97. Dessen, J.E.; Weihe, R.N.; Hatlen, B.; Thomassen, M.S.; Rorvik, K.A. Different growth performance, lipid deposition, and nutrient utilization in in-season (S1) Atlantic salmon post-smolt fed isoenergetic diets differing in protein-to-lipid ratio. *Aquaculture* **2017**, *473*, 345–354. [CrossRef]
98. Gélineau, A.; Corraze, G.; Boujard, T.; Larroquet, L.; Kaushik, S. Relation between dietary lipid level and voluntary feed intake, growth, nutrient gain, lipid deposition and hepatic lipogenesis in rainbow trout. *Reprod. Nutr. Dev.* **2001**, *41*, 487–503. [CrossRef]
99. Salminen, T. Kilohaili- ja Silakkaperäisen Ravinnon Vaikutus Itämeren Lohen (*Salmo salar*) Kasvuun ja Rasvahappokoostumukseen Sekä Yhteydet M74-Oireyhtymään. Master's Thesis, Helsingin Yliospisto, Biotieteellinen Tiedekunta, Bio-ja Ympäristötieteiden Laitos, Helsinki, Finland, 2018. (In Finnish)
100. Power, M.; Thorstad, E.B.; Forseth, T.; Fiske, P. Temporal shifts in the marine feeding of individual Atlantic salmon inferred from scale isotope ratios. *Ecol. Evol.* **2023**, *13*, e10656. [CrossRef]
101. Mikkonen, J. Itämeren Kalakantamuutokset ja Lohen M74-Oireyhtymä. Master's Thesis, Helsingin Yliopisto, Biotieteellinen Tiedekunta, Bio-Ja Ympäristötieteiden Laitos, Akvaattiset Tieteet/Kalataloustiede, Helsinki, Finland, 2008. (In Finnish)
102. Backman, J. Itämeren Hydrologisten Vaihteluiden Sekä Biologisten Tekijöiden Yhteys Lohen M74-Oireyhtymään. Master's Thesis, Helsingin Yliopisto, Bio-ja ympäristötieteiden laitos, Akvaattiset Tieteet/Hydrobiologia, Helsinki, Finland, 2004. (In Finnish)
103. Lee, B.J.; Jaroszewska, M.; Dabrowski, K.; Czesny, S.; Rinchard, J. Effects of dietary vitamin B-1 (thiamine) and magnesium on the survival, growth and histological indicators in lake trout (*Salvelinus namaycush*) juveniles. *Comp. Biochem. Phys. A* **2012**, *162*, 219–226. [CrossRef]
104. Vuorinen, P.J.; Keinänen, M.; Heinimaa, P.; Iivari, J.; Juntunen, E.-P.; Kannel, R.; Pakarinen, T.; Romakkaniemi, A. *M74-Oireyhtymän Seuranta Itämeren Lohikannoissa*; RKTL:n työraportteja 41; Riista-ja Kalatalouden Tutkimuslaitos: Helsinki, Finland, 2014; 24p. (In Finnish)

105. Keinänen, M.; Tolonen, T.; Ikonen, E.; Parmanne, R.; Tigerstedt, C.; Rytilahti, J.; Soivio, A.; Vuorinen, P.J. *Reproduction Disorder of Baltic Salmon–M74*; Kalatutkimuksia–Fiskundersökningar, No 165; Riista-ja Kalatalouden Tutkimuslaitos: Helsinki, Finland, 2000; 38p. Available online: http://urn.fi/URN:ISBN:951-776-255-0 (accessed on 16 September 2024). (In Finnish)
106. Paspatis, M.; Boujard, T. A comparative study of automatic feeding and self-feeding in juvenile Atlantic salmon (*Salmo salar*) fed diets of different energy levels. *Aquaculture* **1996**, *145*, 245–257. [CrossRef]
107. Kriketos, A.D.; Peters, J.C.; Hill, J.O. Cellular and whole-animal energetics. In *Biochemical and Physiological Aspects of Human Nutrition*; Stipanuk, M.H., Ed.; Saunders/Elsevier: Philadelphia, PA, USA, 2000; pp. 411–424.
108. Tacon, A.G.J. Lipid nutritional pathology in farmed fish. *Arch. Anim. Nutr.* **1996**, *49*, 33–39. [CrossRef]
109. Kjær, M.; Todorcevic, M.; Torstensen, B.; Vegusdal, A.; Ruyter, B. Dietary n-3 HUFA affects mitochondrial fatty acid β-oxidation capacity and susceptibility to oxidative stress in Atlantic salmon. *Lipids* **2008**, *43*, 813–827. [CrossRef]
110. Hallikainen, A.; Airaksinen, R.; Rantakokko, P.; Koponen, J.; Mannio, J.; Vuorinen, P.J.; Jääskeläinen, T.; Kiviranta, H. *Environmental Pollutants in Baltic Fish and Other Domestic Fish: PCDD/F, PCB, PBDE, PFC and OT Compounds*; Eviran tutkimuksia, 2. Elintarviketurvallisuusvirasto Evira: Helsinki, Finland, 2011. 106p. Available online: https://urn.fi/URN:ISBN:978-952-225-083-4 (accessed on 16 September 2024). (In Finnish)
111. Vuorinen, P.J.; Paasivirta, J.; Piilola, T.; Surma-Aho, K.; Tarhanen, J. Organochlorine compounds in Baltic salmon and trout. I. Chlorinated hydrocarbons and chlorophenols 1982. *Chemosphere* **1985**, *14*, 1729–1740. [CrossRef]
112. Kumar, E.; Koponen, J.; Rantakokko, P.; Airaksinen, R.; Ruokojärvi, P.; Kiviranta, H.; Vuorinen, P.J.; Myllylä, T.; Keinänen, M.; Raitaniemi, J.; et al. Distribution of perfluoroalkyl acids in fish species from the Baltic Sea and freshwaters in Finland. *Chemosphere* **2022**, *291*, 132688. [CrossRef] [PubMed]
113. Isosaari, P.; Hallikainen, A.; Kiviranta, H.; Vuorinen, P.J.; Parmanne, R.; Koistinen, J.; Vartiainen, T. Polychlorinated dibenzo-*p*-dioxins, dibenzofurans, biphenyls, naphthalenes and polybrominated diphenyl ethers in the edible fish caught from the Baltic Sea and lakes in Finland. *Environ. Pollut.* **2006**, *141*, 213–225. [CrossRef] [PubMed]
114. O'Neill, S.M.; Ylitalo, G.M.; West, J.E. Energy content of Pacific salmon as prey of northern and southern resident killer whales. *Endanger. Species Res.* **2014**, *25*, 265–281. [CrossRef]
115. Lerner, J.E.; Hunt, B.P.V. Seasonal variation in the lipid content of Fraser River Chinook Salmon (*Oncorhynchus tshawytscha*) and its implications for Southern Resident Killer Whale (*Orcinus orca*) prey quality. *Sci. Rep. UK* **2023**, *13*, 2675. [CrossRef]
116. Honeyfield, D.C.; Peters, A.K.; Jones, M.L. Thiamine and Lipid Utilization in Fasting Chinook Salmon. In *Bulletin Number 6: Pacific Salmon and Steelhead Production in a Changing Climate: Past, Present, and Future*; North Pacific Anadromous Fish Commission: Vancouver, BC, Canada, 2016; pp. 13–19. [CrossRef]
117. Pasternack, M.; Salminen, M.; Heinimaa, P. *Physiological Condition and Migratory Readiness of Hatchery-Reared Neva Stock Salmon Smolts in 2007–2009*; Riista-ja Kalatalous Selvityksiä 16; Finnish Game and Fisheries Research Institute: Helsinki, Finland, 2010; 33p. Available online: http://urn.fi/URN:ISBN:978-951-776-788-0 (accessed on 16 September 2024). (In Finnish)
118. Corraze, G.; Kaushik, S. Lipids from marine and freshwater fish, Les lipides des poissons marins et d'eau douce. *OCL* **1999**, *6*, 111–115.
119. Madenjian, C.P.; Elliott, R.F.; DeSorcie, T.J.; Stedman, R.M.; O'Connor, D.V.; Rottiers, D.V. Lipid concentrations in Lake Michigan fishes: Seasonal, spatial, ontogenetic, and long-term trends. *J. Great Lakes Res.* **2000**, *26*, 427–444. [CrossRef]
120. Fisher, J.P.; Fitzsimons, J.D.; Combs, G.F., Jr.; Spitsbergen, J.M. Naturally occurring thiamine deficiency causing reproductive failure in Finger Lakes Atlantic salmon and Great Lakes lake trout. *T. Am. Fish. Soc.* **1996**, *125*, 167–178. [CrossRef]
121. Ketola, H.G.; Rinchard, J.; O'Gorman, R.; Begnoche, L.J.; Bishop, D.L.; Greulich, A.W. Thiamine content of eggs and lengths of coho salmon (*Oncorhynchus kisutch*) in relation to abundance of alewife (*Alosa pseudoharengus*) in eastern Lake Ontario, 2003 to 2006. *J. Freshw. Ecol.* **2009**, *24*, 247–254. [CrossRef]
122. Brandt, S.B. Food of trout and salmon in Lake Ontario. *J. Great Lakes Res.* **1986**, *12*, 200–205. [CrossRef]
123. Jude, D.J.; Tesar, F.J.; DeBoe, S.F.; Miller, T.J. Diet and selection of major prey species by Lake Michigan Salmonines, 1973–1982. *Trans. Am. Fish. Soc.* **1987**, *116*, 677–691. [CrossRef]
124. Happel, A.; Pattridge, R.; Walsh, M.; Rinchard, J. Assessing diet compositions of Lake Ontario predators using fatty acid profiles of prey fishes. *J. Great Lakes Res.* **2017**, *43*, 838–845. [CrossRef]
125. Todisco, V.; Fridolfsson, E.; Axén, C.; Dahlgren, E.; Ejsmond, M.J.; Hauber, M.M.; Hindar, K.; Tibblin, P.; Zöttl, M.; Söderberg, L.; et al. Thiamin dynamics during the adult life cycle of Atlantic salmon (*Salmo salar*). *J. Fish Biol.* **2024**, *104*, 807–824. [CrossRef] [PubMed]
126. McKenzie, D.J.; Higgs, D.A.; Dosanjh, B.S.; Deacon, G.; Randall, D.J. Dietary fatty acid composition influences swimming performance in Atlantic salmon (*Salmo salar*) in seawater. *Fish Physiol. Biochem.* **1998**, *19*, 111–122. [CrossRef]
127. Brown, S.B.; Honeyfield, D.C.; Hnath, J.G.; Wolgamood, M.; Marcquenski, S.V.; Fitzsimons, J.D.; Tillitt, D.E. Thiamine status in adult salmonines in the Great Lakes. *J. Aquat. Anim. Health* **2005**, *17*, 59–64. [CrossRef]

128. Futia, M.H.; Hallenbeck, S.; Noyes, A.D.; Honeyfield, D.C.; Eckerlin, G.E.; Rinchard, J. Thiamine deficiency and the effectiveness of thiamine treatments through broodstock injections and egg immersion on Lake Ontario steelhead trout. *J. Great Lakes Res.* **2017**, *43*, 352–358. [CrossRef]
129. Koski, P.; Soivio, A.; Hartikainen, K.; Hirvi, T.; Myllylä, T. M74 syndrome and thiamine in salmon broodfish and offspring. *Boreal Environ. Res.* **2001**, *6*, 79–92.