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How May the Increase in Pink Salmon (*Oncorhynchus gorbucsha*) Cause the Populations of the Atlantic Salmon (*Salmo salar*) to Decline?

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Abstract

Atlantic salmon (*Salmo salar*) populations in the Arctic River Teno (Tana) and other North Atlantic rivers have declined at the same time as pink salmon (*Oncorhynchus gorbuscha*) have begun to spawn extensively in these rivers in odd-numbered years. In the River Teno, especially, the number of one-sea-year Atlantic salmon ascendants has decreased. In this short review, we assess, based on current information, how the abundance of pink salmon may weaken the survival of Atlantic salmon. Our hypothesis is based on recent evidence from Atlantic salmon in the Baltic Sea showing that the high marine lipid content in the diet of Atlantic salmon post-smolts impairs their growth and survival and is manifested in low numbers of ascendants and in poor thiamine (vitamin B1) status in both juvenile and spawning Baltic salmon. The high energy density of lipids increases the need for thiamine in the metabolism, and the high content of highly unsaturated fatty acids (*n*–3 HUFAs), like docosahexaenoic acid (DHA, 22:6*n*–3), in marine fish lipids increases the rate of lipid peroxidation, which consumes thiamine as it acts as an antioxidant against lipid peroxidation. The review presents information that could be used in planning possible future research on the topic.

Keywords: Atlantic salmon (*Salmo salar*); early developmental phases; eggs; dietary energy density; lipid content; *n*–3 HUFAs; pink salmon (*Oncorhynchus gorbuscha*); post-smolt survival; River Teno; thiamine deficiency

Key Contribution: The hypothesis is based on the cause and mechanism of the decline of Atlantic salmon populations demonstrated in the Baltic Sea, as well as experimental studies and field observations of pink salmon and Atlantic salmon. We present how the eggs, alevins/smolts, and post-smolts of abundant pink salmon may affect the physiology, growth, and survival of Atlantic salmon in rivers and the sea.

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1. Background

1.1. Invasive Species Pink Salmon Spreads in the North Atlantic

The salmonines of the genus *Oncorhynchus* are native to the northwestern and northeastern Pacific Ocean and spawn in rivers of these areas. Their spawning rivers are on

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the coasts from Canada to California in the United States and from Arctic Russia to North Korea. Pink salmon (*Oncorhynchus gorbuscha*) is the most abundant and economically most important *Oncorhynchus* species caught in the open sea fisheries in its native range [1,2].

Pink salmon was introduced into the rivers of the Kola Peninsula draining to the White Sea in the late 1950s [2,3], and after the initial introductions failed, reintroductions in 1985–1999 led to the formation of self-sustaining populations [4]. Because the life cycle of pink salmon lasts exactly two years, the gene pools of populations in even-numbered and odd-numbered years are different [5]. Populations that spawn in odd-numbered years survived and thrived in the Kola Peninsula area, while even-year populations remained insignificantly small [4].

Pink salmon have been observed in rivers in northern Norway since 1960 [6], and recently, in 2023, eDNA samples showed that the pink salmon has spread south to some rivers on the west coast of Sweden [7]. The temporal and spatial distribution history of pink salmon is presented in detail with maps in Diaz-Pauli et al. [4]. The numbers of pink salmon ascending rivers across the North Atlantic coast, such as the River Teno (Tana in Norwegian), have increased dramatically in 2017 and since [2,6]. In the early 2000s, a few dozen or hundreds of pink salmon ascended the River Teno, but in 2017 there were around 5000, and in 2019 at least as many, while in 2021 there were 50,000 pink salmon ascending and in 2023 already 150,000 [8]. Although the pink salmon is an invasive species in the River Teno, it is not on the list of invasive alien species in Finland or the European Union. In Norway, it is on the Norwegian Biodiversity Information Centre's Black List of alien species, in the "high risk" category.

1.2. The Decline of Atlantic Salmon and the Increase in Pink Salmon Coincide

The River Teno (Figure 1) has been the most important Atlantic salmon (*Salmo salar*) river flowing into the Barents Sea, with an estimated annual production of 1–2 million smolts [9]. The total catch of Atlantic salmon in the River Teno has varied from 32,000 to 250,000 kg in 1974–2020 [10], which means that the number of ascending Atlantic salmon exceeded 125,000 individuals in the record year 2001. However, the populations of the native Atlantic salmon, i.e., the number of spawning individuals in the spawning grounds, have declined alarmingly in the River Teno since 2019 [11]. This is two years after the major increase in the number of spawning pink salmon in 2017. The decline has been particularly evident in one-sea-winter (1-SW) Atlantic salmon, i.e., those returning after their first winter at sea. The 1-SW Atlantic salmon that entered the river in 2019 have had the opportunity to eat the eggs, alevins, and smolts of pink salmon that spawned in the fall of 2017 and the post-smolts that migrated to the sea in the spring of 2018. The number of 1-SW Atlantic salmon was very low in 2024, approximately 11% of the number in 2014–2018, despite a relatively large number of smolts in 2023 [11].

In the mouth of the River Utsjoki (Figure 1), a large tributary of the River Teno, the number of ascending Atlantic salmon, according to the video counting, has been below 2000 individuals since 2019 [11]. In 2024, the number of ascendants decreased to 500, while the long-term (2002–2024) average in the River Utsjoki is approximately 3100 ascendants [11].

Due to the dramatic decrease in its spawning populations, fishing of Atlantic salmon on the River Teno was prohibited in 2021, and the ban has continued annually until this year, 2025. In 2023, and especially in 2025, the ascent of pink salmon into the River Teno and dozens of other rivers has been prevented in Norway by building dams and removing pink salmon below the dams, as well as by intensive fishing for them downriver [12].

There is no information on the annual numbers of Atlantic salmon smolts in the River Teno, but in electrofishing, the densities of $\geq$1+ parr in the main River Teno and the tributary

Utsjoki have been lower since 2018, with 7.3 and 10.3 parr per 100 m^2, respectively, than the long-term (1979–2024) average, of 12.6 and 16.3 parr per 100 m^2, respectively [11]. In 2024, the numbers of Atlantic salmon aged 0+ were again high, more than twice the long-term average, in the tributaries Utsjoki and Inarijoki. This observation, however, remains to be ascertained, as water temperatures were higher in 2024 than usual and the water levels were lower compared to normal. The Atlantic salmon fishing ban and measures taken to prevent pink salmon ascent may have enabled more Atlantic salmon to spawn in 2023 [11], which may explain the higher number of Atlantic salmon aged 0+ in 2024.

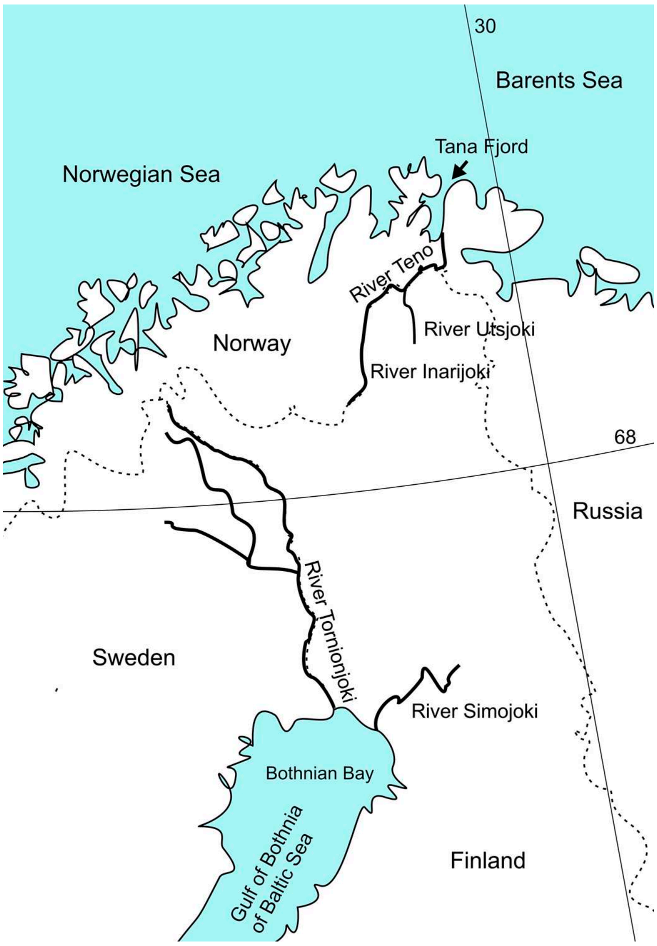


Figure 1. The location of the River Teno that flows into the Barents Sea (only the main stem, with its two largest tributaries, the River Utsjoki and the River Inarijoki, indicated). The locations of the River Tornionjoki and the River Simojoki of the Baltic Sea, which flow into the Bothnian Bay of the Gulf of Bothnia, are also shown.

1.3. The Prey Fauna of Salmon Is Much Wider in the North Atlantic than in the Baltic Sea

The main differences between the Arctic Ocean and the Baltic Sea are that the Baltic Sea is a eutrophic brackish water environment that periodically receives oxygenated and salty seawater from the Atlantic Ocean through the narrow Danish Straits. The surface salinity gradient varies from approximately 0.8% in the southern Baltic Sea to approximately 0.2% in the Bothnian Bay of the Gulf of Bothnia in the summer [13]. Also, in the fjords of northern Norway, surface water is often stratified and less salty than deep water. The Baltic Sea has been severely polluted by environmental toxicants, especially in recent decades [14,15], but, for example, dioxin concentrations in Baltic salmon have more than halved since the 1970s [16,17]. Bottom trawling is used in fishing in both the Baltic Sea and the North Atlantic off the coast of Norway [18]. It is the most extensive source of human-induced physical disturbance to seabed habitats [18,19]. Bottom trawling weakens ecosystems and reduces biodiversity, and it has been proposed to be restricted at least in nature reserves [18,20].

The Baltic Sea, contrary to the northern Atlantic Ocean is still severely eutrophicated, so that large areas of the seabed in the main basin of the Baltic Sea, the Baltic Proper, are anoxic and devoid of benthic fauna [21]. The Baltic Proper is the main feeding area of Atlantic salmon of the Baltic Sea (hereafter referred to as Baltic salmon). Post-smolts from rivers in the Bothnian Bay of the Gulf of Bothnia (Figure 1), such as the River Tornionjoki, migrate through the Bothnian Sea to feed in the Baltic Proper and some, especially those that are reared, remain to feed in the Bothnian Sea [22]. The condition of the seabed in the Bothnian Sea has also deteriorated somewhat, near the coast [23]. Due to the underwater sills, the anoxic bottoms do not extend to the Bothnian Sea, where the deep bottoms are oxygenated and the benthic fauna is diverse [23].

Sprat (*Sprattus sprattus*) and herring (*Clupea harengus*) are the most abundant fish species in the Baltic Proper, and herring is the dominant fish species in the Gulf of Bothnia. A few sprat in the Gulf of Bothnia originate from the Baltic Proper. The scarcity or absence of benthic fauna in the Baltic Proper weakens the bottom ecosystem and the survival opportunities of fish species dependent on it, such as cod (*Gadus morhua*) and, to some extent, herring. This has an increasing effect on the sprat population, which feeds exclusively on plankton and whose main predator is cod, and a decreasing effect on herring populations in the Baltic Proper. The scarcity of Baltic species is decisively reflected in the differences in prey species composition between Arctic Atlantic salmon and Baltic salmon, as shown by studies of their stomach contents [24,25]. The diet of Baltic salmon consists mainly of two pelagic prey fish species and, to a lesser extent, of a third, while invertebrates are practically non-existent [24]. In the North Atlantic, about a third of the salmon diet consists of various invertebrates, and there are several species of prey fish [25], e.g., herring, mackerel (*Scomber scombrus*), and capelin (*Mallotus villosus*) [26].

1.4. The Survival of Atlantic Salmon Depends on the Diet of Post-Smolts—A High-Lipid Fish Diet Reduces Survival

The number of Atlantic salmon returning to the rivers in both North Atlantic and the Baltic Sea is related to their survival in their first year at sea [27,28], i.e., as post-smolts [29,30]. Both the slow growth rate and low survival rate of Baltic salmon were associated with the high lipid content of post-smolt prey fish [22,28]. The number of ascended salmon depended strongly on the ratio of 0-year-old herring and youngish sprat, the dominant prey species for Baltic salmon, in the available prey fish of suitable length when the post-smolts arrive at the feeding areas [28]. When there was a low number of 0-year-old herring and a high number of fattier, youngish sprat upon the arrival of post-smolts of Baltic salmon to their feeding grounds of the Baltic Proper, the growth rate and survival of post-smolts had been weaker than in years when there was an abundance of 0-year-old herring [22,28,31].

Since there are very few suitable invertebrates for Baltic salmon post-smolts to prey on in the Baltic Proper, they feed almost exclusively on pelagic sprat and herring, and to a lesser extent, three-spined stickleback (*Gasterosteus aculeatus*), all of which are fatty species [32]. However, the lipid percentage of sprat is on average twice that of smallish herring, which are suitable for salmon as prey, and the youngest sprat are the fattiest of the Baltic salmon's prey fish, especially in the fall [32–35]. Due to the high lipid content of sprat [22,28], the protein-to-lipid ratio of the diet was also lower than considered optimal (1.88 [36]) for Atlantic salmon post-smolts in years of low survival of post-smolts from the Rivers Tornionjoki and Simojoki. Post-smolts from the Bothnian Bay rivers of the Gulf of Bothnia, which constitute the majority of Baltic salmon, arrive in the Baltic Proper in the fall, when sprat especially are at their fattiest [35].

1.5. A Diet Rich in Fish-Based Marine Lipids Causes Thiamine Deficiency

Lipids in marine fish are the major storage site for metabolic energy, and are used in the form of ATP through the β-oxidation of fatty acids for both maintaining vital functions, such as respiration and growth, and for physical activity, such as predation and predator avoidance [37]. The fatty acids of marine fish consist largely of long-chain, highly unsaturated fatty acids of *n–3* series (*n–3* HUFAs), which play a particularly important role in animal nutrition, including fish and human nutrition [37]. The ability of salmonines to synthesize *n–3* HUFAs docosahexaenoic acid (DHA, 22:6*n–3*), eicosapentaenoic acid (EPA, 20:5*n–3*), and docosapentaenoic acid (DPA, 22:5*n–3*) is very low [37,38]. Consequently, they accumulate lipids, and these fatty acids very efficiently by eating fish [32,37,39,40], and the content of *n–3* HUFAs, especially DHA, increases with increasing dietary and body lipid content of salmonines [22,32,39,41,42]. According to Tocher [37], HUFAs, also called long-chain PUFAs (LC-PUFAs), include fatty acids with at least a length of 20 carbon atoms and 3 ethylenic bonds, and the term PUFA is used for the fatty acids with at least 18 carbon atoms and 2 ethylenic bonds. A one-sided fish diet rich in these marine lipids easily leads to thiamine (vitamin B1) deficiency in fatty predatory fish, such as different salmonine species and river lamprey (*Lampetra fluviatilis*) [35,39,43,44].

The nutritional requirement of thiamine for both salmon and humans depends on the energy content of the diet, i.e., its calorie content [45,46], and the requirement increases as the energy content of the diet increases [45,46]. The thiamine requirement for growth in salmon has been proposed to be 0.36 nmol/kJ [45], which does not appear to take into account the consumption of thiamine in lipid peroxidation [28]. The physiological fuel equivalent, i.e., the net energy value of lipids is more than twice that of protein [47]. Therefore, the more lipid a predatory fish obtains from the diet, the greater its requirement for thiamine [45–47], as the proportion of carbohydrates in fish is negligible.

Thiamine, as thiamine pyrophosphate derivative (TPP), is an essential cofactor for the key enzymes of energy metabolism [48]. Its availability with magnesium therefore determines whether and how much ATP is produced [46,48,49]. It also plays an important role in sustaining cellular reducing power by regulating NAD/NADH and NADP/NADPH balances and regulates fatty acid and lipid metabolism [50,51]. As thiamine is vital for energy and fatty acid metabolisms [48,51,52], its deficiency overall slows metabolism, impairs growth and swimming activity, and can lead to death [22,28,32,53]. As thiamine triphosphate derivative (TTP), thiamine regulates chloride channels by acting as a phosphate donor and modifies especially sodium transport, thus affecting nervous functioning [51]. Therefore, thiamine deficiency could adversely affect smoltification, or at least the survival of smolts in salty seawater.

Another, and even more important, cause of thiamine deficiency in fatty fish is the susceptibility of highly unsaturated HUFAs to peroxidation [32,47], against which thiamine acts as an antioxidant and is destroyed in these reactions [32,35,50,51,54,55]. DHA, which has the highest number of double bonds [47], is the most abundant HUFA in both Baltic salmon and its prey fish sprat and herring, and also in Atlantic salmon from the River Teno [22,56].

1.6. The Lipid Peroxidation of n–3 PUFAs Produces Toxic Malondialdehyde

The thiamine status of salmonines is impaired mainly due to the peroxidation of *n–3* PUFAs, especially DHA, while the effect of total lipid content alone was smaller [32,55]. The principal peroxidation product of *n–3* PUFAs is malondialdehyde (MDA), which, therefore, has been used as an indicator of an increased rate of lipid peroxidation [57,58]. MDA is a highly toxic molecule, which reacts with DNA, forming adducts that can lead to mutations, and with proteins, leading to damage in cellular structures [58]. MDA also depresses mitochondrial potential, and dose-dependently inhibits mitochondrial respiration; it also increases reactive oxygen species that further increase cellular damages [57,59]. Another toxic molecule, 4-hydroxynonenal, is also formed in lipid peroxidation in brain tissue and leads to neuronal cell deaths [50]. The hepatic concentration of MDA increased exponentially with increasing body *n–3* PUFA or merely DHA concentration in juvenile salmon [32] and doubled during the pre-spawning fast of adult salmon [55]. On the other hand, a decrease in the concentration of hepatic total thiamine, a sensitive indicator of thiamine status in fish, was associated with an increase in the MDA concentration and an increase in body *n–3* PUFA and DHA contents [32]. A decrease in the body's thiamine concentration in itself causes oxidative stress [51]. This is most clearly observed during fasting, and can lead to rapid depletion of thiamine and other antioxidants in a vicious cycle [35,55].

1.7. Invertebrates Are Lower in n–3 HUFAs than Marine Fish

The thiamine status of salmonines and river lampreys is poorer, the higher the body lipid content, and, especially, the higher the *n–3* HUFA and DHA content [32,39,44,55]. The majority of thiamine is located in the soft tissues, especially in muscles [48], and most of the thiamine in muscle is in the form of TPP [50], which is the biochemically active form of thiamine acting as a cofactor for metabolic enzymes [48]. Therefore, the thiamine status is not clearly reflected in the total thiamine concentration of muscle and does not vary greatly with the lipid content of salmon [32,55]. However, in both juvenile and spawning Baltic salmon, the proportion of TPP in muscle was higher, the higher the body lipid or *n–3* PUFA or DHA content alone [32,55]. In contrast, the concentration and proportion of the unbound or free thiamine (THIAM), which is available for additional metabolic needs, is very low overall in the muscle [32,39,55]. The concentration of THIAM and its proportion of the total thiamine in the muscle of salmon decreases with increasing body lipid content, but also with increasing *n–3* PUFA content and, most clearly, with increasing DHA content alone (both in concentration and proportion) [32].

Mortality due to thiamine deficiency caused by a lipid-rich fish-based diet has been known primarily in the yolk-sac fry (free embryo, eleutheroembryo [60]) of several salmonine species, whose reserve food, yolk, received from the female, has been too low in thiamine. In the Baltic Sea, in addition to salmon, brown trout (*S. trutta*) and river lampreys have also suffered from thiamine deficiency, called the M74 syndrome, in the Baltic Sea region [35,44,61]. The lipid content of river lampreys is as high as that of Atlantic salmon [62], and they have an even longer pre-spawning fast than Atlantic salmon. In North America, several salmonine species have suffered from thiamine deficiency (called Thiamine Deficiency Complex, TDC) due to diets high in fatty fish [39,43]. In the worst cases, adult salmonine have died of thiamine deficiency before spawning, as have river lampreys, which have suffered mass deaths due to thiamine deficiency in the early spring before spawning, with only a few hatched larvae surviving [44,53]. As brown trout are leaner and utilize a more diverse diet on the coasts, thiamine deficiency has been less severe than in Baltic salmon [53].

Because adult Atlantic salmon in the North Atlantic eat considerable amounts of invertebrates in addition to fish [25,63], unlike Baltic salmon, River Teno ascendants have not been found to be thiamine deficient [22]. For example, in 1997, when the mean (±SE) THIAM concentration in the eggs of River Simojoki salmon was 2.0 ± 0.3 nmol·g^{-1}, and the M74 mortality of their offspring was 12%, the thiamine concentration in the eggs of River Teno salmon was more than three times higher, 6.8 ± 0.4 nmol·g^{-1} [22,53]. A good thiamine status is also reflected in the intense orange–red color of eggs from River Teno salmon [22]. Oxidative stress caused by thiamine deficiency depletes carotenoids [53,55], as they act as antioxidants against general oxidative stress [64]. Salmonids obtain carotenoids, the most abundant of which is astaxanthin, from their insect diet, especially crustaceans [65]. Lipid content is lower in most invertebrates than in prey fish of Atlantic salmon, such as herring, capelin, and mackerel [22,63,66], and, especially, the concentrations of *n–3* HUFAs and DHA are also lower in invertebrates. Eating invertebrates does not therefore cause the accumulation of *n–3* HUFAs in Atlantic salmon as much as eating fatty pelagic fish, of which herring accounted for approximately 8%, mackerel for 2%, and capelin for 2% on a mass basis of the stomach content [26].

Poor survival at sea of reared, stocked Atlantic salmon smolts was also found to be associated with their high whole-body lipid content [67]. Slower growth of Atlantic salmon post-smolts during the first growing season on a high-lipid fish diet has been observed not only in nature, but also experimentally, to be reflected in the following year's growth in a similar direction [22,68]. A lipid-rich fish diet was also reflected in post-smolts as a poorer thiamine status, measured as a total hepatic thiamine concentration [68]. The growth-impairing effect of an excessively fatty fish diet was still at the spawning time visible in the length of Atlantic salmon that had been on a feeding migration for two years (2-SW salmon) [22].

1.8. Studies on the Effects of Pink Salmon Have Focused on Other *Oncorhynchus* Species

To date, studies on the effects of pink salmon have focused mainly on competition between pink salmon and other *Oncorhynchus* species for food, and in particular, on the effects of pink salmon on the growth and survival of sockeye salmon (*O. nerka*), as this Pacific salmon species has the greatest dietary overlap with pink salmon [1]. In the Gulf of Alaska and the Bering Sea, pink salmon showed competitive dominance over sockeye salmon, and the growth of second sea-year sockeye salmon decreased by 7–14% in years when pink salmon was abundant compared to years of low presence of pink salmon [69].

The marine survival of released Chinook salmon (*O. tshawytscha*) decreased in even-numbered years, when there were large numbers of pink salmon in the sea, compared to odd-numbered years, when there were no pink salmon [70]. Regarding the studies on the effects of pink salmon on the genus *Salmo* species, there are observations that some Atlantic salmon and brown trout parr have eaten large quantities of pink salmon eggs [3,6,71]. The abundant available energy and marine nutrients from eggs and carcasses of dead pink salmon have been concluded to improve the survival of Atlantic salmon fry over the winter [71]. Atlantic salmon smolts were also found to eat pink salmon alevins and smolts [3,6].

The decline of Atlantic salmon returning to the River Teno to spawn, and especially the decline of 1-SW salmon, appears to coincide with the increase in the abundance of pink salmon ascendants two years earlier [2,11]. This suggests that the decline of Atlantic salmon in the River Teno and other Atlantic rivers may be caused by the increase in the abundance of pink salmon. This brief review examines the potential impacts of pink salmon on the decline of Atlantic salmon in the River Teno and other North Atlantic rivers. Presenting this knowledge may help to understand the cause of the decline in Arctic Atlantic salmon and to conserve the stocks.

We use the following terminology for the developmental phases of salmonines (Figure 2): the yolk-sac fry (free embryo, eleutheroembryo [60]) hatches from an egg in the gravel and relies on yolk; the alevin, a short developmental phase, emerges from the gravel, with a little yolk left and begins external feeding [60]; and the Atlantic salmon parr lives in the river and is called a smolt after smoltification [60]. After reaching the sea, the smolt is called a post-smolt [29,30]. However, the terms fry and juvenile are used in citing the literature when it is not clear what developmental phase the author intended. The alevins of pink salmon begin their migration towards the sea, and pink salmon, like Atlantic salmon, are called smolts in the river during their downstream migration and post-smolts once they reach the estuary. Nutrients can be transferred in the river to different life phases of Atlantic salmon, from different life phases of pink salmon, from the spawning of pink salmon to the smolt phase of its offspring, and in the estuary from smaller pink salmon post-smolts to larger Atlantic salmon post-smolts (Figure 3).

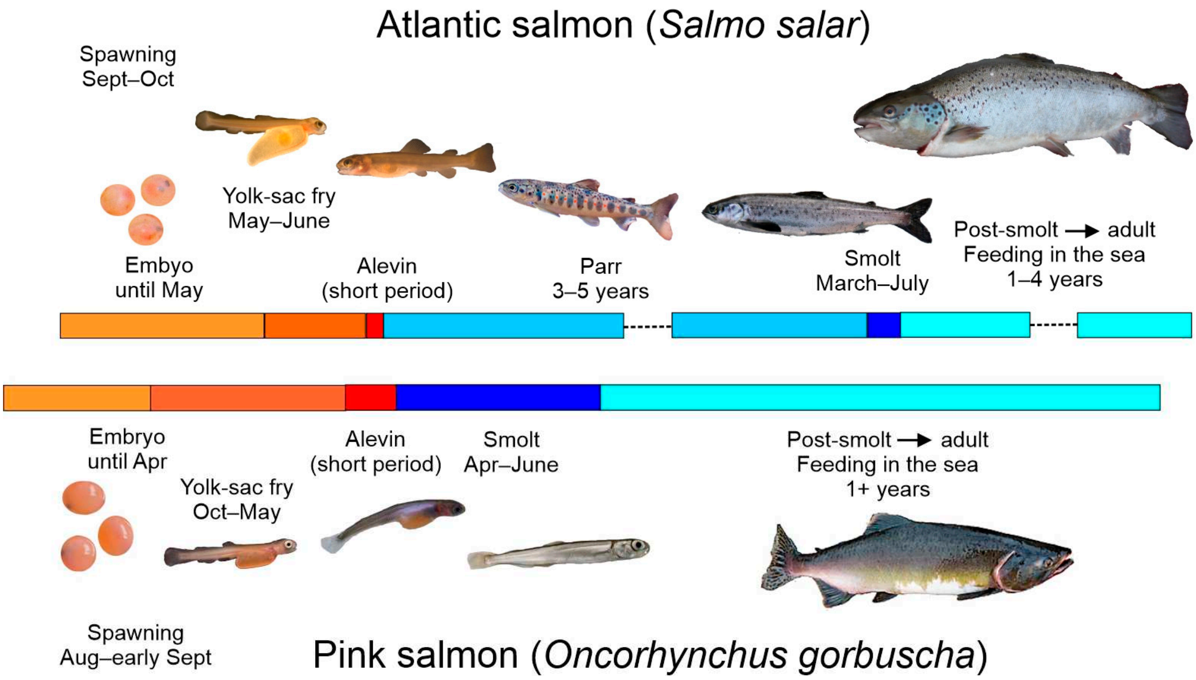


Figure 2. The life cycle of Atlantic salmon and pink salmon from spawning and embryonic phase in a river to adult feeding in the sea. The colors on the horizontal bars represent the duration of the different developmental phases as follows: embryo 🟧; yolk-sac fry 🟧; alevin 🟥; parr 🟦; smolt 🟦; post-smolt 🟦. The parr phase of Atlantic salmon, which lasts for several years in the river, is absent in pink salmon. The feeding migration of Atlantic salmon from post-smolt to adult in the sea can take several years, but the feeding migration of pink salmon from post-smolt to adult takes a little over a year. The total life cycle of a salmon is 4–10 years and that of pink salmon is 2 years. (Photos: Mikko Kytökorpi, Ari Savikko, Ville Vähä, and Pekka J. Vuorinen).

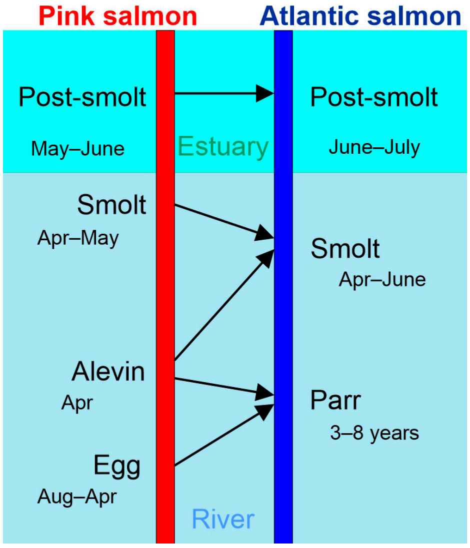


Figure 3. Diagram showing the transfer of nutrients (arrows) from pink salmon (*Oncorhynchus gorbuscha*) to Atlantic salmon (*Salmo salar*) during their different life phases.

2. The Life Cycles of Atlantic Salmon and Pink Salmon Differ

2.1. Atlantic Salmon

Atlantic salmon ascend the River Teno in June–August (Figure 4) and spawn in September–October (Table 1, Figure 2). In 2023, approximately 18,700 salmon ascended the River Teno [72]. This means that approximately 43 million eggs were spawned, assuming that Atlantic salmon female spawn approximately 1150 eggs per kg body mass [73] and that the average female mass is 4 kg. Yolk-sac fry hatch in the gravel in May, and after consuming most of the yolk within 4–6 weeks, they emerge from the gravel as alevins, a short phase during which they begin external feeding while consuming the rest of the yolk. As parr, they live in the River Teno for three to eight years, most often three to five years [74], feeding mostly on various invertebrates (Table 1).

Figure 4. Atlantic salmon (*Salmo salar*) in the River Teno. (Photo: Mikko Kytökorpi).

After these freshwater growing years, Atlantic salmon parr smoltify during the spring. The adequate size of the parr, the photoperiod, and the change in water temperature trigger smoltification, which involves major physiological, morphological, and behavioral changes that enable them to live in the sea [67,75]. After smoltification is complete, the smolts migrate to the sea. According to Thorstad et al. [30], Atlantic salmon smolts moving downstream in the river may feed. Their stomachs have contained larvae of various species of insects (Table 1) [76]. There are also observations that smolts eat pink salmon alevins or smolts when available [3,6]. Atlantic salmon smolts reach the sea in June–July [74].

Table 1. The timing and duration of the different life phases of Atlantic salmon and pink salmon, as well as their main diet and lipid content of post-smolts and adults. It is also indicated which life phases of Atlantic salmon use some life phases (and which) of pink salmon as their food.

Life Phase	Atlantic Salmon	Pink Salmon	References
In the river			
Ascending	June–Aug	July–Aug	[74]
Spawning	Sept–Oct	Aug–early Sept	[74,77]
Embryo	Sept/Oct–May	Aug/early Sept–Oct/Apr	[74,77]
Hatching	May	Oct–Apr	[74,77]
Yolk-sac fry	May–June	Oct–Apr	[74,77]
Alevin	May–June	Apr	
Parr	3–8 years	–	[74]
Parr food	Chironomid and Ephemeroptera larvae (pink salmon eggs)		[8]
Smolt migration	June–July	Apr–June	[74,78]
Smolt food	Trichoptera, Plecoptera and Ephemeroptera larvae (pink salmon alevins/smolts)	Chironomid, Plecoptera and Ephemeroptera larvae	[8,76,78]
In the sea			
Post-smolts in the estuary	A couple of weeks	At least four weeks	[8,30]
Post-smolt food in the estuary	Fish fry, Euphausiids, (pink salmon smolts)	Copepods, Euphausiids, amphipods, fish fry	[79,80]
Post-smolt, lipid content, %	1.3; 1.4	0.6–2.1	[81–83]
Adult, open sea residence period	1–4 years	1+ year	[74,84]
Adult food			
Adult, lipid content, %	2.1–22	1.2–7.6	[82,83,85–88]

Atlantic salmon feed for one or more years at sea before returning to spawn. The majority (>50%) of Atlantic salmon originating from the River Teno feed for one year at sea (1-SW salmon). The numbers of 3-SW and 4-SW ascendants has decreased since the 1970s [89], which is likely related to the large-scale decline in Atlantic salmon around the Atlantic Ocean [26,89,90]. As an iteroparous species, Atlantic salmon can spawn several times, and in the River Teno, the number of individuals that spawned two or more times was 0–19% in the period between 1973 and 2006 [9].

2.2. Pink Salmon

The life cycle of pink salmon from fertilization to spawning adults lasts two years (Table 1 and Figure 2), and after spawning they soon die in the river. Pink salmon is the smallest of the *Oncorhynchus* species, with an average adult mass of 1.5 kg [6], typically 45–55 cm in length [91]. In 2021, the pink salmon that ascended the River Indera on the Kola Peninsula were 42–53 cm in length, and their mass was 0.6–1.7 kg [92]. A female spawns, on average, 1550 eggs [71]. There are two distinct populations of pink salmon: one spawns in even-numbered years and the other in odd-numbered years [4]. Those spawning in odd-numbered years are the dominant populations in their native regions and, likewise, in the North Atlantic [6].

A significant number of pink salmon was observed in the River Teno in 2017, when it was estimated to have reached the 5000–individuals mark, and a similar number ascended in 2019 [8]. In the River Teno, pink salmon spawn in early August–September (Table 1 and Figure 5). Although yolk-sac fry may hatch as early as in October [77], they remain in the gravel until the yolk is almost consumed. In the rivers of northern Norway, pink salmon yolk-sac fry had assimilated their yolk by early April, while they were still in the gravel [6]. The alevins emerge from the gravel in the rivers flowing to the Sea of Okhotsk in April, when the water temperature reaches 2.5–4 °C [78], and according to Diaz-Pauli [4], in Norwegian rivers in March–May. Pink salmon alevins/smolts were present in the spawning grounds in the River Teno from April to mid-May in 2022 [8].

Pink salmon is a unique salmonine, in that the alevins begin to move downstream as soon as they emerge from the gravel [6,93,94]. They begin feeding in the river, and the proportion of alevins that have started external feeding increases towards the sea, especially if the water level is lower than normal [78]. At the same time, they smoltify as their hypo-osmoregulatory ability, determined by an increase in gill Na^+/K^+-ATPase activity, increases as the yolk is absorbed while they are still in freshwater [93]. However, observations from rivers in northern Norway and in the rivers flowing to the Sea of Okhotsk showed that pink salmon smolts may stay and feed in the river for weeks or even months after hatching before they reach the estuary [6,78]. Their food in the river consists of various insect larvae, especially chironomids (Table 1). Pink salmon post-smolts may spend up to months in the estuary before migrating further out to sea [6]. In the estuary, they feed mainly on small crustaceans, especially calanoid copepods, and fish larvae (Table 1). In the River Teno, pink salmon smolts feed for six weeks on their way to the estuary, where they stay for approximately four weeks from mid-May to early June [8]. Thus, pink salmon have already been feeding in the Tana Fjord for approximately a month when Atlantic salmon smolts reach the estuary, before migrating as post-smolts farther into the sea [74]. The growth of pink salmon is slow for the first eight months at sea, but after that they grow rapidly and their mass increases fivefold by the time they reach the spawning river [1].

Figure 5. Pink salmon (*Oncorhynchus gorbuscha*) at spawning time in the River Teno. (Photo: Mikko Kytökorpi).

3. Possible Impacts of Pink Salmon on Atlantic Salmon

3.1. Pink Salmon Spawn Earlier than Atlantic Salmon

Although Atlantic salmon and pink salmon ascend the river at the same time, in June–August, pink salmon spawn earlier, in early August–September, than Atlantic salmon, which spawn in September–October (Table 1). Because there is some overlap in their spawning only in September in the River Teno [77], the ascending or spawning of pink salmon is unlikely to affect the spawning of Atlantic salmon and their spawning success.

Pink salmon nourishes the environment of its spawning rivers by ascending in large numbers and laying lots of energy-rich eggs [71], and by dying and decomposing soon after spawning. This is likely to dramatically change the water quality, especially in Arctic rivers, and to increase the growth of algae and plants. As a result, for example, the oxygen content of the water may decrease due to the decomposition of plant waste. However, pink salmon carcasses provide food for various invertebrates, which in turn are food for

Atlantic salmon and brown trout parr and pink salmon alevins and smolts, as well as other fish [6,71,95]. For example, age-1 coho salmon (*O. kisutch*) parr grew longer and heavier in 2021 when pink salmon spawned in Montana Creek compared to 2022, when there were no pink salmon spawning [95].

In the river, pink salmon alevins/smolts eat the same food as Atlantic salmon and brown trout parr [8], thereby increasing food competition. Large numbers of pink salmon offspring can also take over favorable foraging sites in the river and push other species into less favorable foraging conditions [6]. However, the potential increase in invertebrate abundance in Arctic oligotrophic rivers due to increased productivity caused by the decomposition of pink salmon, could, over time, moderate competition for food between pink salmon alevins/smolts and Atlantic salmon parr.

3.2. Pink Salmon Eggs Are Energy-Rich Food for Atlantic Salmon Parr

Water temperature is higher during the earlier spawning of pink salmon than during the spawning of Atlantic salmon. Because the food intake of poikilothermic fish decreases when the waters cool, predation on pink salmon eggs is more likely than on Atlantic salmon eggs. When the number of pink salmon ascending the River Teno was the highest, in 2023, at 150,000 [8], they laid approximately 116 million eggs [71]. In the same year, 18,700 Atlantic salmon ascended the River Teno [72], and they were estimated to have laid 43 million eggs. This means that in 2023 there were three times as many pink salmon eggs in the River Teno as Atlantic salmon eggs.

During pink salmon spawning, larger Atlantic salmon parr (Figure 6) may eat pink salmon eggs, as has been observed in rivers of the Kola Peninsula [3]. Similarly, in the River Vesterelva in northern Norway, Atlantic salmon parr > 83 mm in length have been observed to eat pink salmon eggs [71]. The energy density of salmonine eggs, 7–12 kJ/g (in fresh mass, *ww*), is much higher than that of the natural diet of the parr, i.e., aquatic invertebrates, which is 3–5 kJ/g (*ww*) [71] (Figure 7). The approximate mean energy content of salmonine eggs was reported to be (*ww*) 10–11 $kJ{\cdot}g^{-1}$ for pink salmon (Figure 7), 7 and 9 $kJ{\cdot}g^{-1}$ for Atlantic salmon, 8–11 $kJ{\cdot}g^{-1}$ for sockeye salmon, and 11 $kJ{\cdot}g^{-1}$ for chinook salmon [71,96,97].

Figure 6. Atlantic salmon (*Salmo salar*) parr in the River Teno. (Photo: Mikko Kytökorpi).

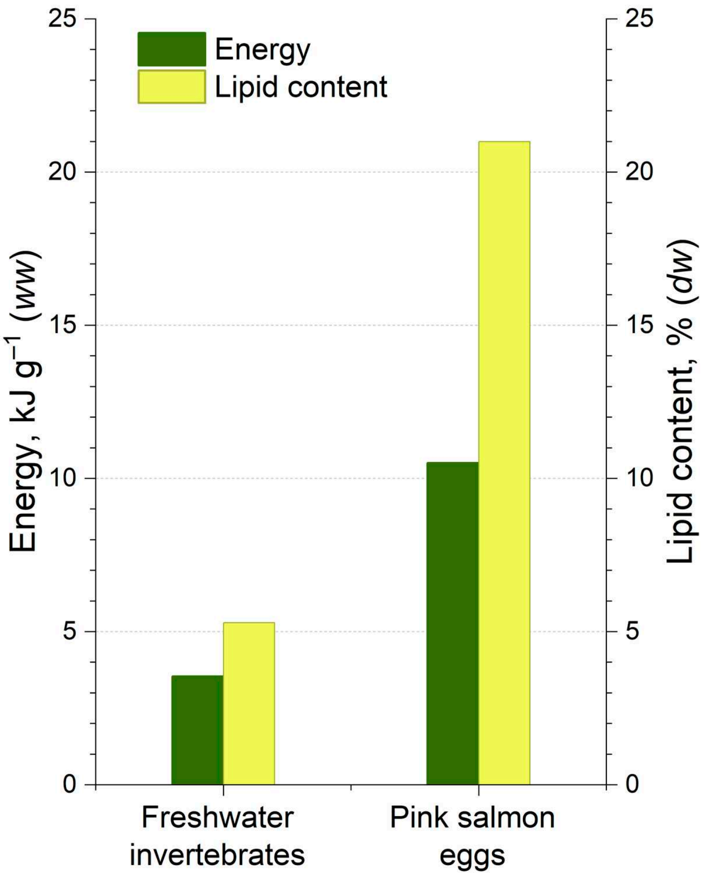


Figure 7. Energy density and total lipid content (*dw*) in typical river invertebrate (cf. Figure 8) diet of Atlantic salmon (*Salmo salar*) and in pink salmon (*Oncorhynchus gorbuscha*) eggs. Data for invertebrate energy are from Dunlop et al. [71] and for lipid from Meier et al. [98] and Dvorak et al. [99]; for pink salmon energy they are from Armstrong [97] and for lipid from Murzina et al. [100].

For comparison, Baltic sprat in the fall provided an average of 7.7 kJ·g^{-1} (*ww*) of energy for Baltic salmon post-smolts and juveniles [28]. Thus, Atlantic salmon parr obtain clearly more energy per unit from pink salmon eggs than Baltic salmon post-smolts and juveniles obtain from sprat. Although pink salmon eggs are only available for six weeks, their consumption may be able to shift the fatty acid composition of Atlantic salmon parr to a more marine one. The energy of pink salmon eggs comes from marine lipids, as does the energy of sprat, the abundant consumption of which slowed the growth and impaired survival of Baltic salmon post-smolts, and was manifested as thiamine deficiency in the returned salmon [22,28,35]. In addition, it is presumably easier for Atlantic salmon parr to pick up stationary eggs than to catch invertebrates, and it is easier than for Baltic salmon post-smolts to forage sprat in the sea, even though sprat have been abundant.

The difference in energy density between the invertebrate diet naturally consumed by Atlantic salmon parr and that of pink salmon eggs is largely due to differences in lipid content. Pink salmon eggs contains three times more energy and up to four times more lipids compared to a diet consisting of invertebrates (Figure 7). The eggs of River Teno salmon contained 11% lipids (*ww*) [22], and an even higher percentage, 11–15% (*ww*), was found in the eggs of pink salmon [101]. Thus, although adult pink salmon are smaller and leaner, the lipid content of their eggs appears to be in the same range as in Atlantic salmon eggs, or even higher, similar to the energy density of eggs [97].

The lipid content of eggs does not correlate with the lipid content of the muscle of salmonines [22], which varies greatly between species and according to the feeding area and lipid content of prey [32,102]. It increases with size and age [15,40], and decreases before spawning, as lipids are hydrolyzed and fatty acids catabolized for energy and are also transferred to the oocytes [55]. For example, in the 1990s, when thiamine deficiency M74 was severe in Baltic salmon [34,53,56], the average annual lipid percentage in their muscle during spawning was high, at 12–31% (*ww*), and in years when the M74 syndrome was moderate, the annual averages of muscle lipid content varied between 3.3 and 5.9% (*ww*) [53]. In Baltic salmon caught from the sea in the fall in years when the strength of annual M74 varied from mild to moderate, the average lipid content of muscle was 7–17% (*ww*), varying by sea areas [15,32,55]. The muscle lipid content of Atlantic salmon caught in the Atlantic Ocean has been lower on average than that of Baltic salmon, ranging from 2.1 to 22% at spawning [83,103]. In the muscle of pink salmon, 36–48 cm in length, caught from several sea areas, the North Pacific, Prince William Sound, the Gulf of Alaska, and the Bering Sea, the lipid content averaged 2.6–7.6% (*ww*) in the spring and the summer [82,86,87], and in pink salmon ascending the River Indera on the Kola Peninsula, the muscle lipid content was 1.2–2.9% (*ww*) [92].

Unlike muscle, the lipid content of eggs is less variable. During spawning in 2014–2017, the lipid content in the eggs of Baltic salmon that had been feeding in different sea areas was on average 8–9.5% (*ww*) [22]. The lipid percentage and thiamine concentration of the eggs of 2-SW spawners from the River Simojoki in 2014 were higher than those of spawners in 2016 and 2017, whose prey fish in the Baltic Proper consisted mainly of small sprat with high-lipid and *n*–*3* HUFA content [22]. Correspondingly, the lipid percentage and thiamine concentration in the eggs of salmon from the River Teno were higher than those in the eggs of Baltic salmon in 2016 and 2017 [22]. River Teno salmon had presumably been feeding on a lower lipid diet in the Arctic Ocean [22] than Baltic salmon.

3.3. Pink Salmon Eggs and Alevins Provide Atlantic Salmon Parr and Smolts with an Excess of Marine Lipids

In addition to eggs, the free-swimming alevins of pink salmon, which still have some maternal lipid reserves at that phase [6,8,104], also provide a potential food source for Atlantic salmon parr and smolts. Pink salmon alevins switch from assimilating yolk reserves to external feeding while migrating in the river towards the sea [8]. They feed in the river for longer, the weaker the spring floods are [8,78]. There are observations that Atlantic salmon and brown trout parr eat pink salmon eggs [71], and that Atlantic salmon smolts eat juvenile pink salmon in the river [3]. Such observations were also made in a Norwegian river during electrofishing Atlantic salmon and brown trout smolts [6]: one Atlantic salmon smolt regurgitated several pink salmon fry, and, in addition, many individuals of both Atlantic salmon and brown trout had extended stomachs, indicating they had very likely fed on pink salmon [6].

Because salmonines efficiently accumulate lipids from their diet [22,32,42,105], the lipid, *n*–*3* HUFA, and DHA content of Atlantic salmon parr/smolts increase when they consume pink salmon eggs or alevins instead of invertebrates such as chironomids. Consequently, their lipid and DHA content will be higher than under natural conditions on an invertebrate diet. The lipid content of the chironomid larvae has varied from less than 5% to 5.8% (*dw*), depending on the environment [99,106]; this is very much lower than in pink salmon eggs or alevins, on average 21% (*dw*) in both [100] (Figure 8a).

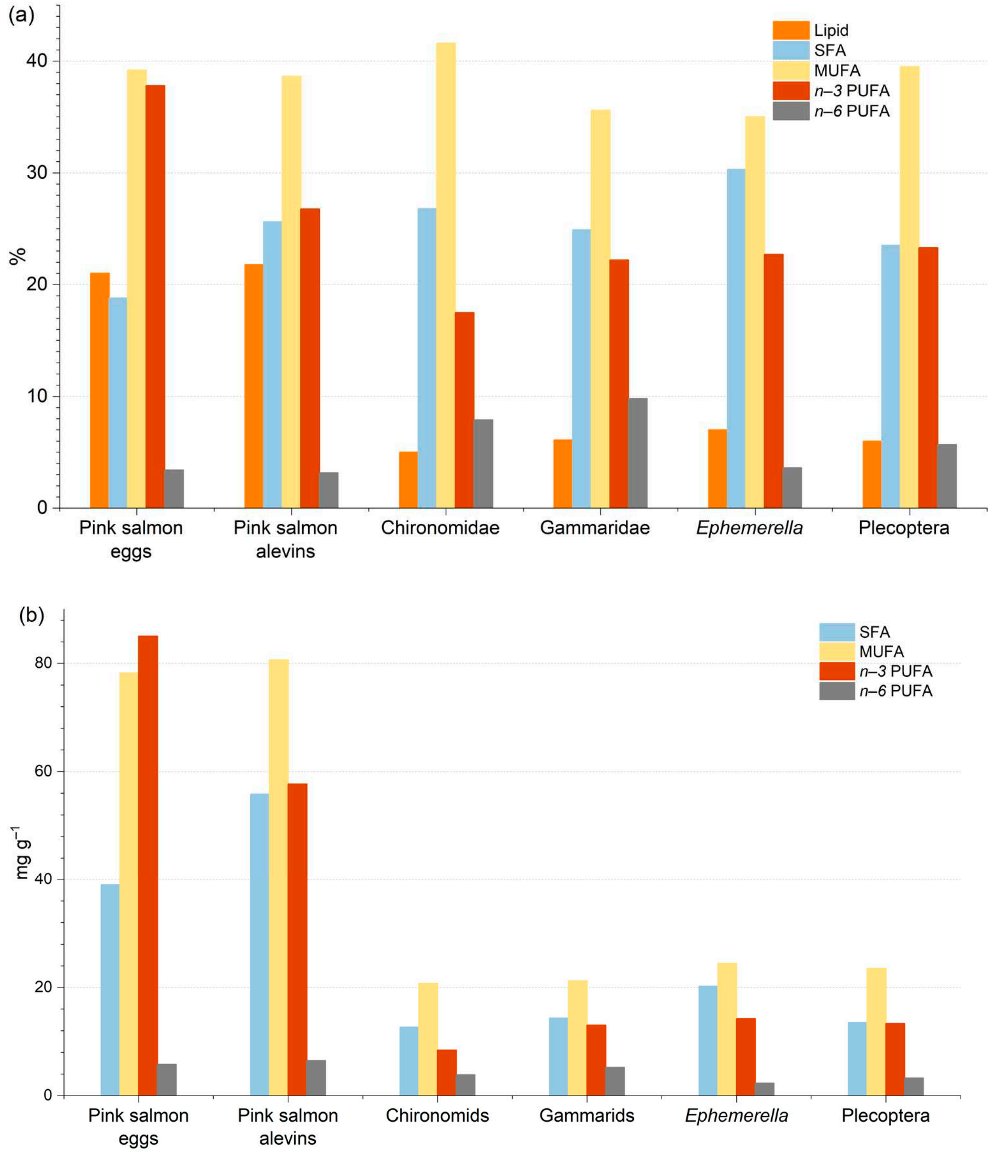


Figure 8. Lipid percentage (*dw*) and the proportions (**a**) and concentrations (**b**) of different fatty acid groups, saturated (SFAs), monounsaturated (MUFAs) and *n–3* and *n–6* polyunsaturated fatty acids (PUFAs) in pink salmon (*Oncorhynchus gorbuscha*) eggs and alevins and various freshwater invertebrates in the typical diet of Atlantic salmon (*Salmo salar*) parr and smolts. Data are from Bell et al. [107], Dvorak et al. [99], Kaivarainen et al. [104], Meier et al. [98], and Murzina et al. [100].

The lipid content in pink salmon eggs is 3–4 times higher than in the freshwater invertebrate groups that Atlantic salmon naturally feed on in the river (Figures 7 and 8a). In addition, the fatty acid composition of pink salmon eggs and alevins is completely different from the natural invertebrate diet of Atlantic salmon parr and smolts. The proportion of *n–3* PUFAs is clearly higher in pink salmon eggs than in any invertebrate group, and the proportion of saturated fatty acids (SFAs) is lower (Figure 8a). There are some differences in fatty acid composition between the invertebrate groups, and the proportion of *n–3* PUFAs is lowest in Chironomidae. Thus, among the invertebrate groups, chironomids differ most from pink salmon eggs in terms of *n–3* PUFA content (Figure 8).

Because both the lipid content and the proportion of *n–3* PUFAs in fatty acids are higher in pink salmon eggs than in freshwater invertebrates, the concentration of *n–3* PUFAs is many times higher in pink salmon eggs (Figure 8b). In pink salmon alevins, the proportion and concentration of *n–3* PUFAs in this data appear to be slightly lower than in pink salmon eggs, but still clearly higher than in freshwater invertebrates. Due to the higher lipid content, the concentrations of MUFAs and SFAs are also higher in pink salmon eggs and alevins than in freshwater invertebrates (Figure 8b). Although the proportion of *n–6* PUFAs typical of the freshwater food chain is higher in freshwater invertebrates than in pink salmon eggs or alevins (Figure 8a), their concentration is not (Figure 8b).

The proportions of marine fatty acids, i.e., *n–3* HUFAs, and especially DHA, which causes the most peroxidation and thiamine depletion [32], are much higher in pink salmon eggs than in aquatic invertebrates (Figure 9), and the difference in the concentrations of these fatty acids is even greater between invertebrates and eggs, due to the higher lipid content of the eggs. Thiamine depletion due to lipid peroxidation can potentially be expressed as the unsaturation index (UI), which indicates the degree of unsaturation in fatty acids and is calculated from the fatty acid profile and lipid content of tissues [108]. IU takes into account the number of double bonds of each fatty acid, which is highest in DHA, and determines their potential lipid peroxidation strength and thus the amount of thiamine needed as its specific antioxidant. As thiamine is also known to act as an antioxidant against the oxidation of the most common MUFA, oleic acid (18:1 *n–9*) [50], it is relevant that the double bonds of MUFAs are also taken into account when calculating UI (Figure 9). Because thiamine deficiency causes oxidative stress, lipid peroxidation of PUFAs, especially during fasting, can deplete thiamine as well as other antioxidants in a downward spiral [50,51]. During fasting, when fatty acids hydrolyzed from lipid stores are used as an energy source [37], the proportion of *n–3* PUFAs, especially DHA, increases [56], and thiamine status becomes poorer when no replacement thiamine is supplied from the diet [55,109,110].

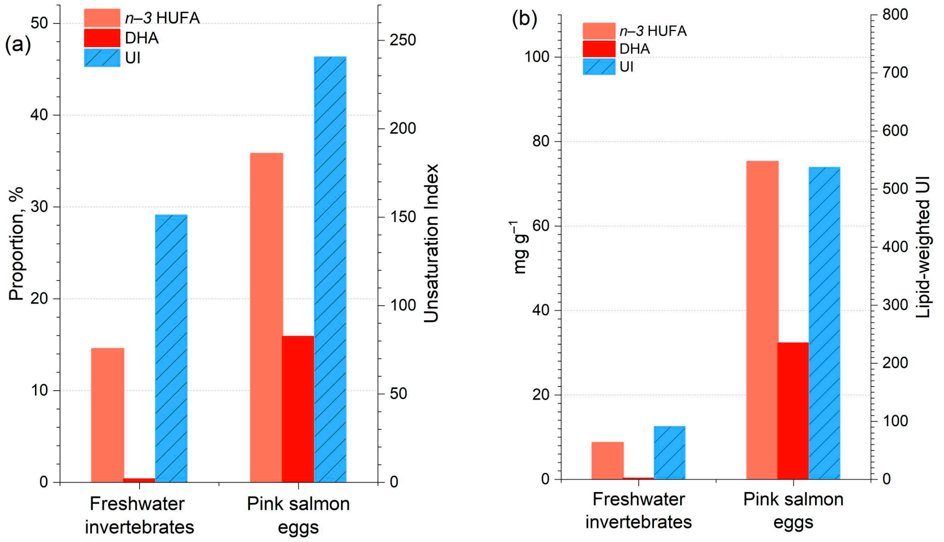


Figure 9. The proportions (**a**) and concentrations (**b**) of long-chain, highly unsaturated *n–3* fatty acids (*n–3* HUFAs) and DHA, and the unsaturation index (UI) (**a**) and the lipid-weighted UI (**b**) in the typical freshwater invertebrate diet (cf. Figure 8) of Atlantic salmon (*Salmo salar*) parr and smolts, as well as in pink salmon (*Oncorhynchus gorbuscha*) eggs. Data are from Bell et al. [107], Dvorak et al. [99], Meier et al. [99] and Murzina et al. [100].

When considering the fatty acid profiles of the freshwater diet of Atlantic salmon parr and smolts (Figure 10a), it is noteworthy that 18:1*n–9* is the most common fatty acid in both pink salmon eggs and alevins, followed by palmitic acid (16:0) and then DHA, which is, especially in Baltic salmon, but also in River Teno Atlantic salmon, more common than palmitic acid [22]. The proportion of EPA is high compared to both Baltic salmon and River Teno Atlantic salmon [22]. In freshwater invertebrates, the proportions of palmitoleic acid (16:1*n-7*), but also its elongation product vaccenic acid (18:1*n-7*), and alpha-linolenic acid (ALA, 18:3*n–3*), are clearly higher than in pink salmon eggs or alevins. Although the proportion of EPA is even higher in invertebrates than in alevins, the proportion of DHA in invertebrates is negligible. The fatty acids in salmon parr reflect the consumption of invertebrate food, with DHA and 18:1*n-9* proportions being lower than in pink salmon eggs or alevins, but with 18:3*n–3*, 16:1*n-7*, 18:1*n-7*, and linoleic acid (LNA, 18:2*n–6*) proportions being higher (Figure 10a).

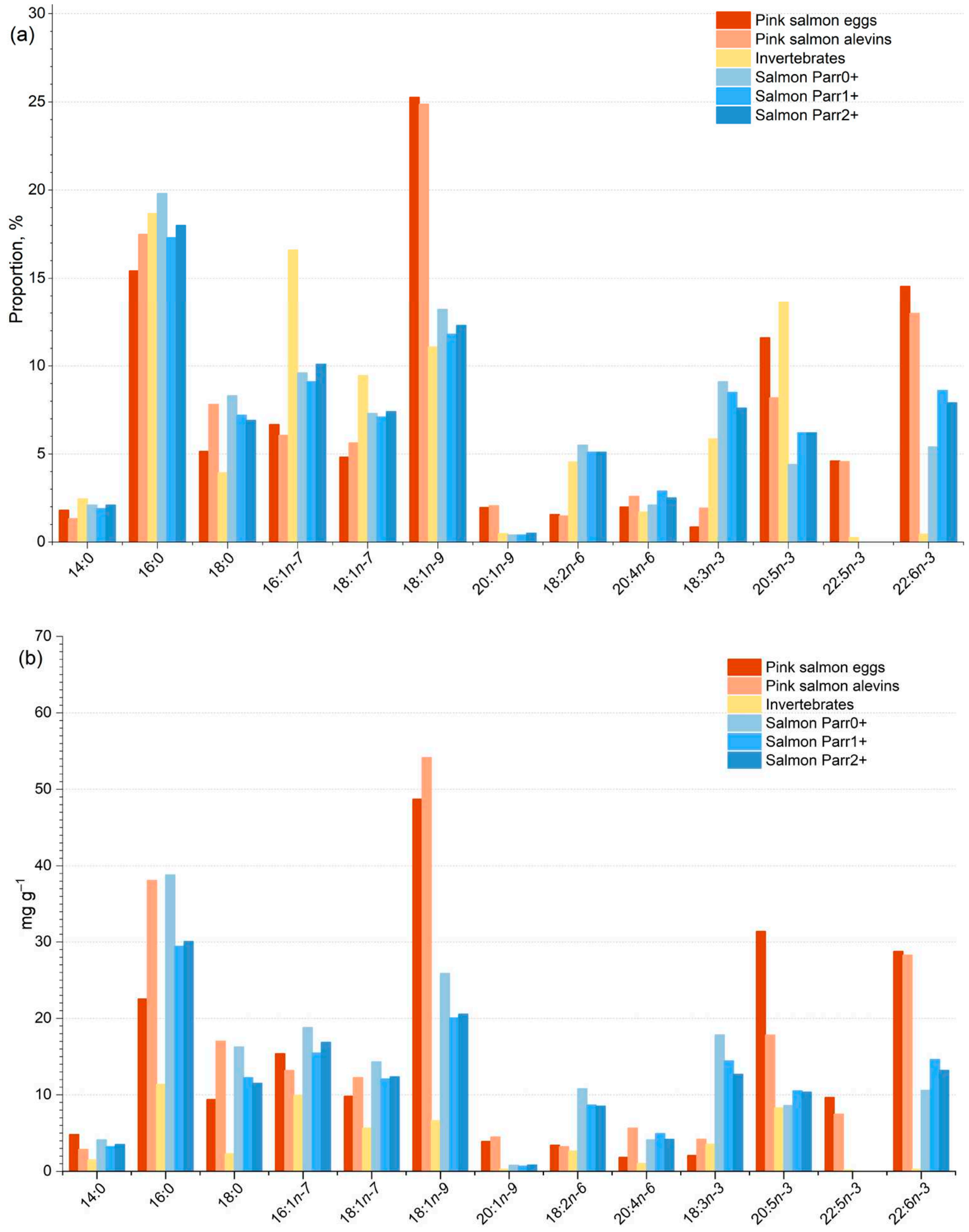


Figure 10. Fatty acid proportions (**a**) and concentrations (**b**) in pink salmon (*Oncorhynchus gorbuscha*) eggs, alevins, and the typical freshwater invertebrate diet (see Figure 8) of Atlantic salmon (*Salmo salar*) parr and smolts. Parr data are from the River Varzuga [111]. Other data are from Bell et al. [107], Dvorak et al. [99], Kaivarainen et al. [104], and Murzina et al. [100].

In terms of concentrations (Figure 10b), the concentrations of almost all fatty acids are lower in freshwater invertebrates than in pink salmon eggs and alevins. In particular, the concentration of DHA is negligible in invertebrates. The concentrations of 18:1*n-9*, DHA, and EPA in pink salmon eggs and alevins are higher than in Atlantic salmon parr, in which the concentrations of 18:3*n–3* and 18:2*n–6* are higher, indicating feeding on invertebrates.

Because the lipids of pink salmon eggs and newly emerged pink salmon alevins are maternal, they originate from the marine environment and are rich in *n–3* HUFAs [37]. Therefore, pink salmon eggs and alevins/smolts are not optimal food for Atlantic salmon parr or smolts. If larger Atlantic salmon parr partially replace their invertebrate diet with more energy-dense pink salmon eggs in this way, their lipid percentage likely increases and their fatty acid composition changes from terrestrial to more marine. This means that the requirement for thiamine increases in parr, and high *n–3* HUFA content additionally predisposes them to thiamine depletion. If such parr smoltify the next spring, their smoltification may be impaired due to altered fatty acid composition [112]. Consistently, the dietary fatty acid composition of Atlantic salmon parr and smolt, which more closely resembled that of freshwater invertebrates than marine fish, was concluded to be beneficial for smoltification and for smolts' acclimatization to seawater, as well as growth, development, and prevention of pathologies [107,113]. Thus, premature transition to a fish diet rich in marine fatty acids by eating pink salmon eggs and alevins/smolts may impair survival in several ways.

For example, the massive stocking of chum salmon (*O. keta*) fry of 4.5–6.7 cm in length in three Japanese rivers led to the fattening of native juvenile brown trout, as they ate chum salmon fry [114]. The condition factor of brown trout, representing lipid accumulation, and the triglyceride and DHA concentration of muscle increased clearly with the time span of feeding on chum salmon fry. The DHA concentration in the muscle of brown trout was higher in all the rivers where chum salmon fry were introduced compared to brown trout in the control rivers [114]. No data were available on the lipid content of chum salmon alevins or smolts in the river, but, according to Murzina [100], pink salmon alevins contain lipids 21% (*dw*), which may be even higher than that of chum salmon alevins and smolts. At least, the average lipid content of the muscle of juveniles in the spring after the first sea-winter may be higher in pink salmon than in chum salmon (as a range of mean values): 0.8–6.2% and 0.8–3.8% (*ww*), respectively [40,86,87,102,115].

For comparison, the total fatty acid and DHA content in the muscle of white-spotted charr (*Salvelinus leucomaenis*) increased during feeding on introduced hatchery-reared masu salmon (*O. masou*) fry of 4.6–4.7 cm in length in three tributaries of the Japanese Shiribetsu River system, compared to tributaries with no introductions [42]. There was no information on the lipid content of the masu salmon fry, but the total muscle lipid content of masu salmon parr was on average 1.0–4.9% (*ww*), depending on sex and season [116].

Both chum salmon and masu salmon have higher lipid and DHA content than aquatic insects, which was manifested as fattening and increased DHA content in brown trout and white-spotted charr. As the feeding on chum salmon fry has caused fattening and accumulation of DHA in brown trout [114] and the feeding on masu salmon fry increased the total fatty acid and DHA content of white-spotted charr [42], the same is likely to happen to Atlantic salmon parr and smolts when they eat pink salmon alevins or smolts instead of aquatic insects, especially, because Atlantic salmon naturally accumulate dietary lipids more efficiently than leaner brown trout [117].

In an experiment using high- and low-lipid diets, Atlantic salmon smolts that had become fattier (6% muscle lipid, *ww*) during 6 months of freshwater feeding, grew less after being transferred to seawater than leaner smolts (2% muscle lipid, *ww*) [112]. Because post-smolts used their endogenous energy stores for metabolic needs during the first 3–6 week of 14 weeks of seawater rearing, their muscle lipid content decreased, and they lost mass, despite being fed. However, by the end of the seawater period, muscle lipid content had increased to 6% and 8% (*ww*) in the low- and high-lipid groups, respectively, and the slower growth rate on the high-lipid diet during the freshwater period was still evident at week 14 [112].

If the offspring of Atlantic salmon become too fatty by eating pink salmon eggs and alevins in the river, their development and smoltification, as well as growth and survival in the sea, may be impaired, as can be concluded from the experiments [68,113,118]. Thus, among hatchery-reared Atlantic salmon smolts, the fattiest survived the worst, and of the several parameters measured, only the total lipid content of the smolts was associated with poorer survival [67]. In the reared smolts, the average whole-body lipid content ranged from 8 to 9% (*ww*), while in wild smolts it was 2% [67]. Apparently, the poorer survival of reared Atlantic salmon smolts in the Baltic Sea than wild smolts, as observed by Kallio-Nyberg et al. [31], has also been due to their high lipid content.

An excessive fish-based diet with a high energy density, high lipid content, and high DHA and total *n–3* HUFA concentration is challenging for the growth and survival of fatty predatory fish. It may provide insufficient protein-to-lipid ratio and insufficient thiamine to meet the requirements of energy metabolism, and the high marine fatty acid content exposes fish tissues to lipid peroxidation and thiamine depletion, due to its functioning as a site-specific antioxidant [32,51].

3.4. Due to the Short River Period, a Large Proportion of Pink Salmon Fry Survive Until the Sea

The offspring of Atlantic salmon spend several years in the river and are exposed to both predation and interspecific and intraspecific competition for food, as they are territorial foragers. As a result, their numbers are decreasing year by year. Since pink salmon only stay in the River Teno for about a month and a half after emerging from gravel, a much larger proportion of them survive to the sea, relative to the number of eggs laid, than do Atlantic salmon. When Atlantic salmon smolts descend to the estuary in the Tana Fjord in June–July, in even-numbered years there are varying numbers of pink salmon post-smolts that have descended earlier, from mid-May, and have been feeding there for a month or two [8].

The number of pink salmon post-smolts in the Tana Fjord, which is approximately 45 km in length and 11 km wide, varies depending on the number of pink salmon that ascended the river the previous summer. According to Erkinaro et al. [8], approximately 50,000 pink salmon ascended the River Teno for spawning in 2021, and 150,000 pink salmon in 2023. If a pink salmon female lays 1550 eggs on average [71], if approximately 98% of them hatch into alevins [77], and if 80% of the hatched offspring then reach the estuary of the Tana Fjord, there will have been approximately 30 million pink salmon post-smolts in the Tana Fjord in 2022 and 91 million in 2024, while the River Teno would have normally produced 1–2 million Atlantic salmon post-smolts [9]. In those years, the number of pink salmon post-smolts has, therefore, been dozens of times larger than the number of Atlantic salmon post-smolts.

3.5. Pink Salmon Post-Smolts Are of a Suitable Size as Prey for Atlantic Salmon Post-Smolts

Pink salmon arrive in the estuary in the Tana Fjord, which is a relatively small area compared to the open seacoast. The estimated 30 million pink salmon smolts in 2022 reached the estuary of the River Teno from mid-May by the end of June. Apparently, they spread rapidly into the fjord, as there were no more pink salmon post-smolts at the sampling point close to the river mouth by the end of June in 2022 [8]. In the estuary of Prince William Sound of Alaska, pink salmon post-smolts typically first feed on large zooplanktonic calanoid copepods, which are rich in lipids (Figure 11) and thus also rich in energy [119,120]. However, copepod lipids are predominantly composed of MUFAs, unlike the herring fry lipids, which are mostly *n–3* PUFAs. Arthropods, benthic animals, have clearly higher proportions of *n–3* PUFAs than copepods, but much lower than herring fry. The most obvious difference in terms of concentrations between these food items is the very high MUFA concentration and the highest SFA concentration of copepods. Of the food items, herring fry have the highest *n–3* PUFA concentration, and the lowest MUFA and SFA concentrations.

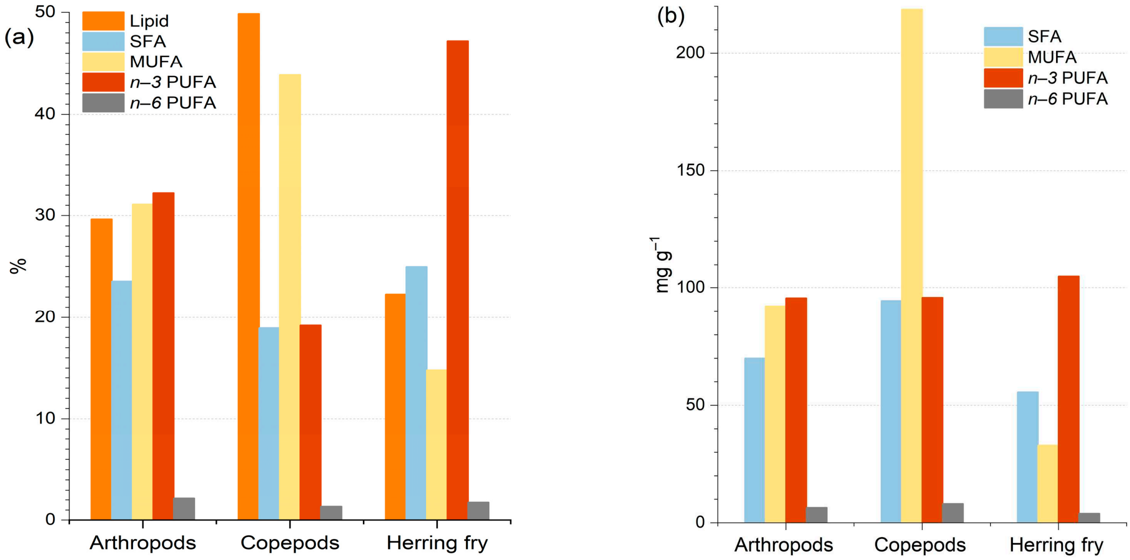


Figure 11. Lipid percentage (*dw*) and proportions (**a**) and concentrations (**b**) of different fatty acid groups, saturated (SFAs), monounsaturated (MUFAs), and *n–3* and *n–6* polyunsaturated fatty acids (PUFAs) in arthropods, copepods, and herring (*Clupea harengus*) fry. Data are from Auel et al. [121], Iverson et al. [82], Lee et al. [122], and Utne et al. [83].

Once in the sea, Atlantic salmon post-smolts shift from a river-phase diet, which under natural conditions is based almost entirely on insects, to a diet containing juvenile fish and invertebrates such as crustaceans [30]. Closer to the estuary, insects are also an important part of the diet [63,80]. According to Andreassen et al. [80], in the Trondheim Fjord in 1997, the diet of Atlantic salmon post-smolts gradually changed as they moved further offshore, and although adult insects were a high component of the diet in all areas, the proportion of small fish in addition to large *Calanus* sp. and crustaceans increased as post-smolts moved further offshore. During the feeding migration in the Norwegian Sea in 1991–2003, the stomach contents of Atlantic salmon post-smolts consisted, on average, of 36% by mass of invertebrates, almost all of which were crustaceans (*Themisto* sp.), and fish constituted 64% of the stomach contents [63].

The proportion of *n–3* HUFAs, especially DHA, are lower in marine invertebrates (crustaceans) than in fish such as herring fry (Figure 12a). UI is also higher in lipids of herring fry than in invertebrates, on average. Due to the high proportion and concentration of MUFAs in copepods (Figure 11), the lipid-weighted UI is at least as high in invertebrates as in herring fry (Figure 12b). However, the DHA concentration is considerable higher in herring fry than in invertebrates, on average, and the *n–3* HUFA concentration is also higher (Figure 12b). For example, in Atlantic shrimp (*Pandalus* sp.), the DHA concentration (1.2 $mg{\cdot}g^{-1}$) was only one-tenth that of sprat (10 $mg{\cdot}g^{-1}$) and a sixth that of herring (6.4 $mg{\cdot}g^{-1}$) (see [22,33,123]), and the total lipid content of shrimp was 1.7% (*ww*) [66]. In krill species, which accounted for about 4% of the mass of the stomach contents of Atlantic salmon [25], the total lipid content was 1.5% (*ww*) [66]. Since the proportion of *n–3* HUFAs, and especially DHA, in the fatty acids of marine fish is higher than in freshwater fish [37] and especially higher than in invertebrates (Figure 11) [66], their proportion and concentration increase in post-smolts as they become more piscivorous.

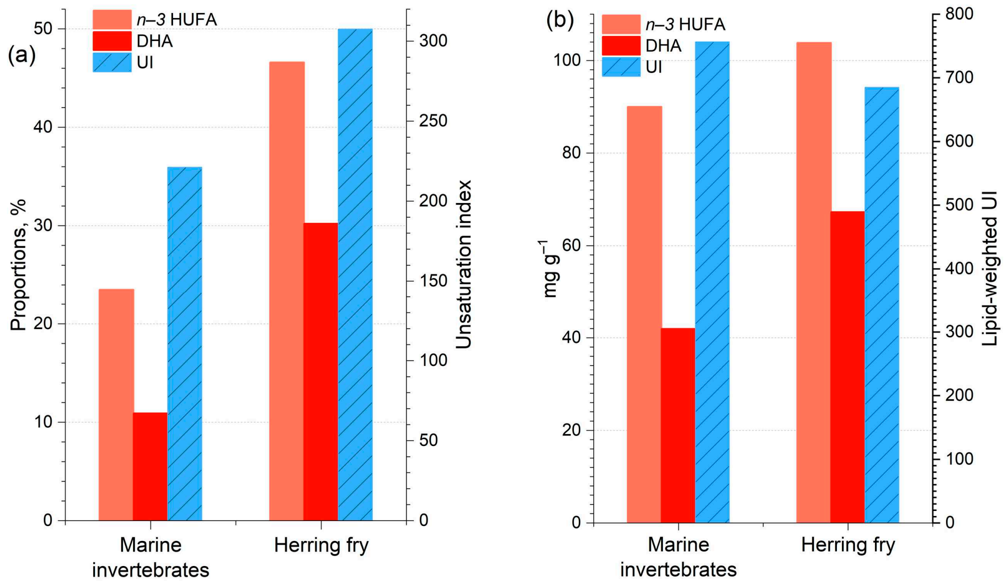


Figure 12. The proportions (**a**) and concentrations (**b**) of long-chain, highly unsaturated *n–3* fatty acids (*n–3* HUFAs) and DHA, and the unsaturation index (UI) (**a**) and the lipid-weighted UI (**b**) in marine invertebrates and herring (*Clupea harengus*) fry. Data are from Auel et al. [121], Iverson et al. [82], Lee et al. [122], and Utne et al. [83].

The high proportion and concentration of MUFA in copepods is mainly due to 22:1*n–11*, which is hardly present in herring, but also gondoic acid (20:1*n–9*). In contrast, the concentration of 18:1*n–9* in copepods is of the same order as in herring, but higher in arthropods. Although the lipid content of copepods is high [119], due to the abundance of certain MUFAs, both the proportion and concentration of DHA are higher in herring fry (Figure 13).

Pink salmon post-smolts from the River Teno are much smaller, approximately 4 cm in June after reaching the estuary [8], than Atlantic salmon smolts (14–17 cm) upon their arrival. From the River Indera, pink salmon smolts were 2.8–3.3 cm in length [124]. As the size of Atlantic salmon prey depends on both the size of salmon and the size of the available prey (i.e., size-dependent prey availability) [125,126], Atlantic salmon post-smolts feed on prey that is less than 30% of their body length [30,126]. On this basis, they can eat prey items up to approximately 5 cm in length [126] when they arrive in the Tana Fjord. Pink salmon post-smolts are therefore of a suitable size to be prey for Atlantic salmon post-smolts in the Tana Fjord.

The diet of Atlantic salmon post-smolts in four Norwegian fjords was studied in two years [127]: in 2018, the stomach contents of post-smolts in the Alta Fjord were almost exclusively fish fry (99% of the mass), which could not be identified with certainty, but were thought to be sand eels (*Ammodytes* ssp.), capelin, and herring. In 2019, invertebrates made up 47% of the diet and fish fry 53%. The majority of invertebrates were crustaceans (*Themisto* species). In 2018, there have also been pink salmon post-smolts in the Alta Fjord, because a small number of pink salmon ascended the River Alta in 2017 [6]. However, because only 32 pink salmon had ascended the River Alta in that year, pink salmon post-smolts, even if the Atlantic salmon post-smolts had eaten them, would not have been important in the diet of Atlantic salmon post-smolts in the Alta Fjord. It was estimated that 5000 pink salmon ascended the River Teno in 2017 [26], so there would have been many more pink salmon post-smolts in the Teno Fjord (ca. 3 million) than in the Alta Fjord in 2018.

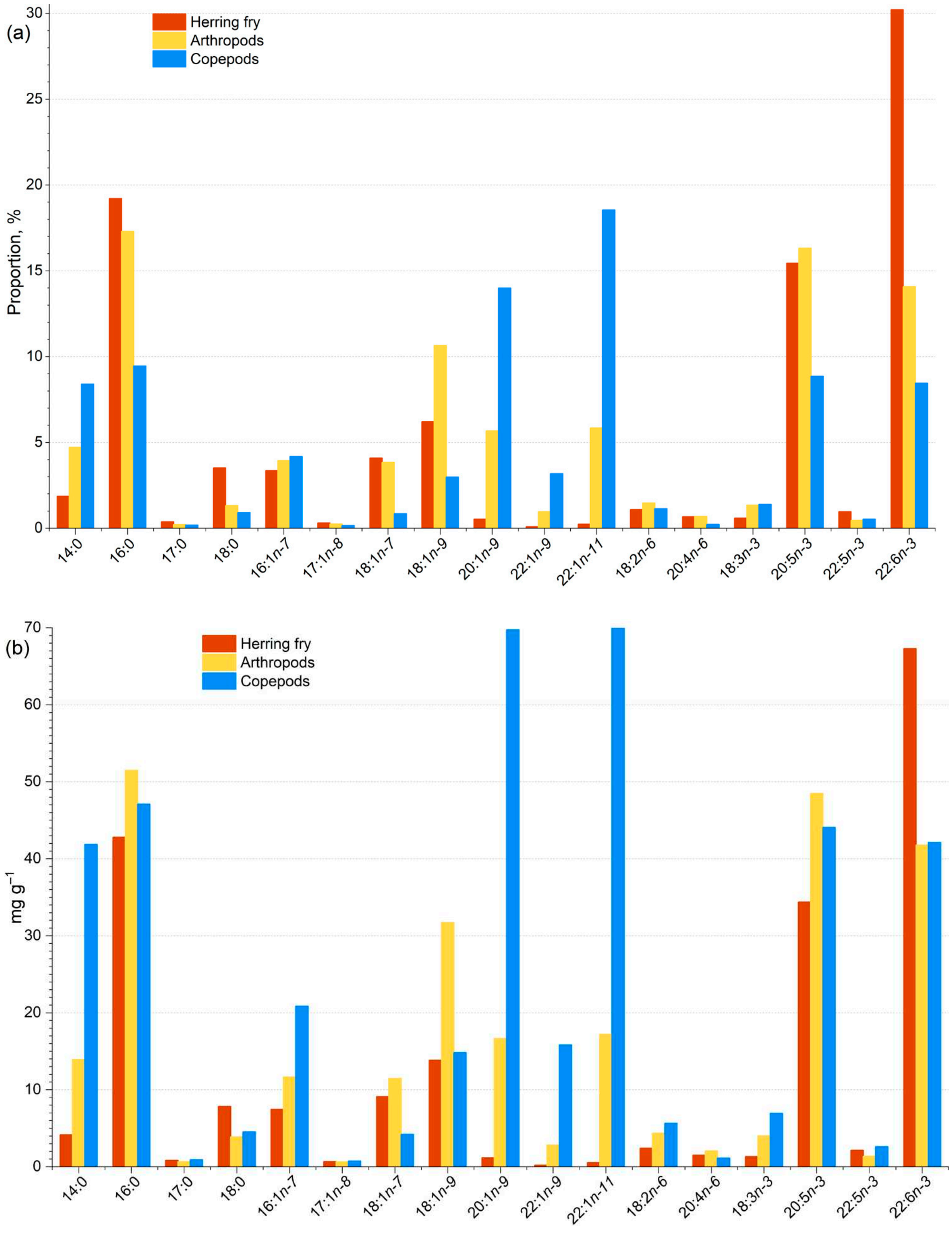


Figure 13. Fatty acid proportions (**a**) and concentrations (**b**) in herring (*Clupea harengus*) fry, arthropods, and copepods. Data are from Auel et al. [121], Iverson et al. [82], Lee et al. [122], and Utne et al. [83].

3.6. Post-Smolts Need Protein to Grow

Atlantic salmon can exploit a variety of prey animals [30], depending on their presence and size [126]. It is therefore likely that Atlantic salmon post-smolts eat pink salmon post-smolts in the Tana Fjord if the latter are abundant and if the Atlantic salmon have survived through smoltification and their first weeks at sea. Before Atlantic salmon smolts arrive in the estuary and begin feeding in the fjord, pink salmon post-smolts have been feeding there for about a month, and have had time to accumulate lipids from copepods. During this time, their fatty acid composition has probably already changed, as stable isotope analyses of pink salmon smolts descending the River Teno showed a shift from a parental marine diet to active invertebrate feeding within two months [8], and in a feeding experiment, the fatty acid composition of the muscle of young Atlantic salmon changed almost completely to that of the new diet within 12 weeks [128]. The total lipid content in large arctic copepods varies from 30% to 60% (*dw*) [119], which is higher than the lipid content of post-smolt feed prepared from sprat in the experiment by Salminen [68]. Such food leads to the accumulation of lipids, as has been observed in the Baltic Sea in Baltic salmon prey species, specifically younger age groups of sprat, which feed solely on zooplankton [33,35].

Although pink salmon post-smolts are not very fatty, they contain approximately over twice more total *n–3* PUFAs and at least twice more DHA than copepods [100,122]. If invertebrates have been partially replaced by pink salmon post-smolts in the diet of Atlantic salmon post-smolts, the protein content of the diet may be too low relative to lipids, and the *n–3* HUFA content may be too high, as in young sprat [22,28,33]. Thiamine requirement may in this case exceed intake, due to its excessive depletion in lipid peroxidation, which may lead to impaired growth and survival of post-smolts. Such food is not optimal for the growth and survival of post-smolts [28,36].

Atlantic salmon post-smolts require sufficient protein for growth, especially for muscle formation. The growth of adult salmon is known to be determined by available food during the first months after post-smolts have entered the sea [22,31,129]. High-energy food, which in fish means high lipid content, can deplete thiamine [28,35], and a decrease in thiamine itself reduces appetite and growth [48]. To achieve a proper growth rate, an optimal protein-to-lipid ratio is essential to enhance protein utilization and lipid retention [36,130,131]. On the other hand, the degree of lipid peroxidation and its adverse effects due to increased MDA concentration and decreased thiamine concentration are also more pronounced the more *n–3* HUFAs are present in the diet [32,55].

The optimal protein-to-lipid ratio for Atlantic salmon post-smolts in rearing experiments was determined to be 1.88 from a diet with 49% protein and 26% lipid (*dw*) [36]. In a feeding experiment, after the first growing season in seawater, the total body mass of Atlantic salmon post-smolts fed a high-lipid diet (31% *dw*) was lower than that of post-smolts fed a diet containing 21% lipids, and the difference increased over the following years [68]. Even in spawning Baltic salmon, the high lipid content and low protein-to-lipid ratio of prey fish during their first sea-year was reflected in lower length and mass, as well as higher muscle lipid content [22].

In the Baltic Proper, the protein-to-lipid ratio of sprat is much lower than optimal, at only 1.02, while in 0-year-old herring it is slightly higher than optimal, at 2.26 [28]. Thus, when in the post-smolt year of Baltic salmon from the Gulf of Bothnia rivers there were plenty of sprat and a low number of 0-year-old herring, in the Baltic Proper, the number of 2-SW salmon returning two years later was low [28], and the length and mass of the ascendants were lower than those that had more 0-year-old herring available as post-smolts [22]. Thus, the optimal nutritional quality of the Atlantic salmon diet and the fast growth rate during the first feeding year are reflected in faster growth in the subsequent feeding years [22,31,132].

In the Baltic Sea, the lipid percentage and more pronouncedly DHA content of the smallest herring, especially sprat, have been higher than in larger individuals [33]. Zooplanktivorous sprat are twice as fatty as small herring, which also start to consume benthic invertebrates as they grow, and already earlier in the winter (see [33]). The high energy density and abundance of *n–3* HUFAs in the diet of Baltic salmon post-smolts, which consists largely of the youngest sprat, has exposed them to an increased need for, and consumption of, thiamine [28,35]. Chinook salmon feeding off the California coast have, apparently due to changes in the ecosystem, also consumed large amounts of fatty northern anchovies (*Engraulis mordax*) in recent years, leading to thiamine deficiency [43,133].

This concerns also the Atlantic salmon post-smolts of the North Atlantic if the invertebrates in their diet are partly replaced by pink salmon post-smolts, and may be more likely if they have eaten pink salmon eggs as parr and alevins as smolts in the river. The diet of Baltic salmon post-smolts from the Bothnian Bay rivers in the sea initially, when they migrate through the low-salinity Gulf of Bothnia, consists largely of surface insects [134]. Such a diet, being low in lipids and thus low in energy, seemed to be a safe diet for the post-smolts [28]. At a total length of 24–32 cm, post-smolts migrate from the Gulf of Bothnia to the Baltic Proper and change from mixed diet to exclusive fish diet in the absence of suitable invertebrate prey [134]. Their diet in the Baltic Proper consists mainly of pelagic sprat and 0-year-old herring [28,34]. If the lipid content of the diet in the Baltic Proper, consisting of abundant young fatty sprat, is too high, post-smolts do not survive [28]. Therefore, prey fish that are unilaterally high in lipids are a risk because the protein content is too low for growth, the intake of thiamine relative to energy is reduced, and the intake of *n–3* HUFAs, which exposes tissues to lipid peroxidation, is increased [28].

The natural diet of Atlantic salmon post-smolts consisting of small fish and crustaceans leads to a growth spurt [30]. However, if they have eaten pink salmon eggs the previous fall and pink salmon alevins and smolts in the river, their *n–3* HUFA and DHA content may have increased and thiamine concentration decreased, leading to slower growth and impaired survival, as observed in the Baltic Sea and in feeding experiments [22,28,67,68,113,135]. In the eggs of Atlantic salmon which ascended the River Teno, the total thiamine concentration averaged 6.8 nmol$\cdot$g^{-1} [22]. Thus, in their eggs there was 0.6–0.9 nmol thiamine per kJ energy from marine nutrients, calculated using the energy values of Atlantic salmon eggs obtained from Armstrong [97]. Approximately the same thiamine content of Baltic sprat, 0.8 per kJ energy, was not sufficient to ensure the growth and survival of Baltic salmon post-smolts [28] or to save 2-SW Baltic salmon from thiamine deficiency [32,35]. In fact, the thiamine content per energy unit was higher, as the Baltic salmon diet also included herring. The proposed thiamine requirement of 0.36 nmol per kJ of energy [45] for growth of Atlantic salmon smolts [28] does not seem to take into account the consumption of thiamine in lipid peroxidation, the importance of which is probably even greater than that of energy.

3.7. Post-Smolts of Pink Salmon and Atlantic Salmon Do Not Compete for the Same Food

Since pink salmon post-smolts are much smaller than Atlantic salmon post-smolts, they prefer prey of different sizes [126]. Competition for food between the post-smolts of pink salmon and Atlantic salmon in the Northeast Atlantic and Barents Sea is therefore low in even-numbered years, i.e., in years when pink salmon descend to the sea. Once in the sea, pink salmon post-smolts feed on plankton [1], unlike Atlantic salmon, which eat small fish and crustaceans, as well as insects [30,63,80]. It is therefore unlikely that the two species would compete for the same food before the Atlantic salmon's second feeding season at sea, when the size of pink salmon will be closer to that of Atlantic salmon.

It has also been shown that pink salmon and Chinook salmon do not compete for the same food until during the second marine feeding season of Chinook salmon, because by then the pink salmon have grown larger [1]. Chinook salmon are comparable to Atlantic salmon, due to their potentially multi-year marine feeding migration, large size, and high lipid content, which predisposes them both to thiamine deficiency [32,43,133]. The survival of introduced Chinook salmon decreased in Salish Sea Region in even-numbered years when there were large numbers of pink salmon from natural spawning, compared to odd-numbered years with low numbers of pink salmon [70]. Similarly, after the notable spawning of pink salmon in the River Teno in 2017 and the subsequent odd-numbered years, the number of 1-SW Atlantic salmon continued to collapse after two years, and successively [11,136].

During the second year in the sea, pink salmon and Atlantic salmon may, to some extent, compete for the same food resources. The diet of pink salmon juveniles living in the Norwegian Sea consisted of various fish between 29 and 92% by mass, as well as crustaceans like Euphausiids (krill) and amphipods such as *Themisto* sp. [4]. The main prey varied depending on the feeding area. In the North Atlantic in the 1990s, the diet of even adult Atlantic salmon has largely consisted of invertebrates (32% in mass percent), mainly crustaceans, in addition to small fish (>50% in mass percent) during 1992–1995 [25]. Since the diet of juvenile and adult Atlantic salmon in the North Atlantic has largely consisted of invertebrates in addition to small fish, unlike Baltic salmon (see [22]), they might compete with larger pink salmon for the same food. However, during the period of pink salmon abundance, the decrease has occurred specifically in the number of 1-SW Atlantic salmon ascendants, not in the number of older ascendants [11].

However, competition between Atlantic salmon post-smolts and pink salmon post-smolts could be indirect. When pink salmon post-smolts descend to the sea in large numbers in the late spring, they deplete oceanic food resources and have a large top-down impact on food webs [1]. This could reduce the food supply of invertebrates and small prey fish of Atlantic salmon post-smolts, which could indirectly affect their survival. However, the small prey fish for Atlantic salmon post-smolts would be replaced by pink salmon post-smolts of approximately the same size. As pink salmon numbers increase, intraspecific competition for food or predation of small pink salmon post-smolts by larger pink salmon may cause the observed large variation in pink salmon abundance.

It is known that for both the Atlantic salmon in the Atlantic Ocean and Baltic salmon, the first year at sea is the most critical for survival [27,28,31]. When the diet of post-smolts of Baltic salmon is one-sided and consists of fish with a high lipid content, their growth is impaired, and not all of them survive until the second growing season [28]. The impaired growth, in turn, is reflected in a smaller length, at least until after the next growing season [22,68]. It seems possible that the decline in the number of Atlantic salmon ascending the River Teno since 2019 has been due to poor survival of post-smolts, as the number of 1-SW salmon has collapsed at the same time as the number of pink salmon has increased. Now that the salmon fishing ban was extended to the coastal fishery in large areas of Northern Norway in the summer of 2025, more Atlantic salmon have returned to the River Teno in 2025. The increase in Atlantic salmon ascendants was mainly due to an increase in the number of 1-SW specimens [72].

4. Conclusions and Suggestions

4.1. General

The decline in the number of Atlantic salmon ascending the River Teno began in 2019, two years after the first numerous pink salmon ascending in 2017, which suggests that the high number of pink salmon has weakened the survival of Atlantic salmon. Since the number of 1-SW Atlantic salmon entering the river has decreased, the detrimental effect of pink salmon must have occurred by the end of the first feeding year, at the latest. Already in the fall, during the spawning season of pink salmon, their eggs provide the largest Atlantic salmon parr with high-energy food rich in *n–3* HUFAs, especially DHA, which are highly susceptible to lipid peroxidation. These marine lipids, when used for metabolic needs during the winter, may have weakened the thiamine status of parr because thiamine, which acts as an antioxidant against lipid peroxidation, is destroyed in these reactions. According to observations, during and after their smoltification, Atlantic salmon eat pink salmon alevins, which have approximately the same lipid content and fatty acid composition as pink salmon eggs, and pink salmon smolts in the river, thereby accumulating more *n–3* HUFAs. When the natural invertebrate diet of Atlantic salmon offspring has in this way been replaced too early by a fish-based diet containing an excess of marine fatty acids, their acclimatization to seawater may have failed. In addition, their growth and development may have slowed, and their survival may have been impaired. For example, in the spring of 2022, dozens of times more pink salmon smolts left the River Teno than the number that the river would normally produce of Atlantic salmon smolts. When pink salmon post-smolts descend to the sea and feed on lipid-rich plankton for several weeks before the arrival of Atlantic salmon post-smolts, Atlantic salmon post-smolts have an abundance of marine fish to eat, if they have even acclimatized to seawater. However, this diet may not be optimal for them, due to the unfavorable protein-to-lipid ratio and high *n–3* HUFA content, and their growth is slowed and survival is impaired. Pink salmon and Atlantic salmon post-smolts do not initially compete for the same food, as pink salmon are much smaller. However, pink salmon can also deplete lower marine food webs, for example the number or abundance of plankton species, which can impair the growth and survival of prey for Atlantic salmon post-smolts, whose diets typically consist of one-third of invertebrates. One measure that would help preserve the natural diet of Atlantic salmon in the sea is to restrict or stop bottom trawling, which affects the entire ecosystem by weakening benthic life in many ways, such as reducing populations and biodiversity [19,137].

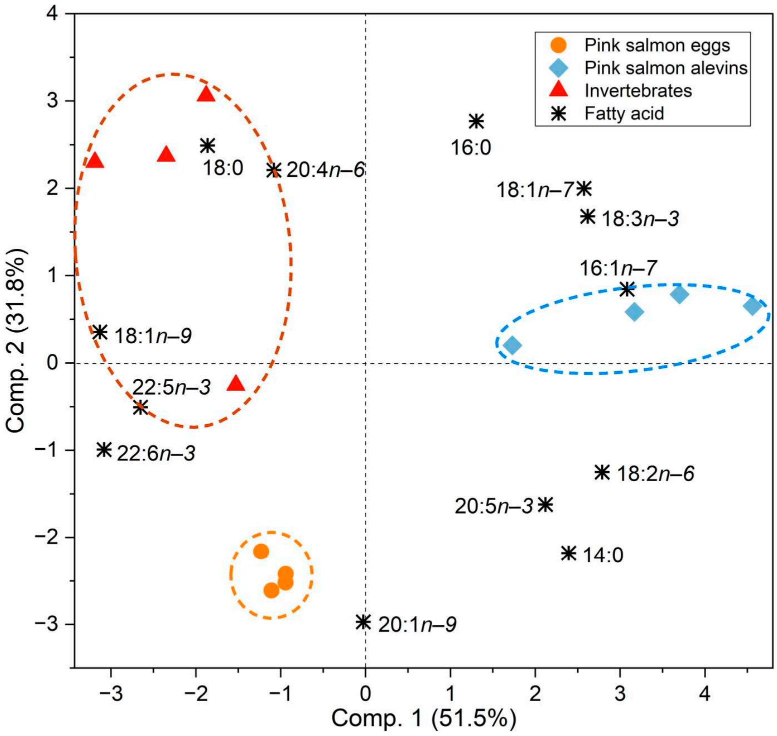
Although there are several knowledge gaps on the topic, and the existing information is fragmentary and incomplete, it appears that preventing pink salmon from entering the River Teno has been a good decision for the protection of Atlantic salmon stocks. At the same time, it makes studying the effects of pink salmon on Atlantic salmon in the River Teno difficult. This could be done by comparing Atlantic salmon smolts and post-smolts in the river and estuary and returning 1-SW salmon in even and odd years.

4.2. Research to Further Assess the Hypothesis Presented

Because pink salmon ascend the river to spawn in odd years, even-year Atlantic salmon smolts are those that have had the opportunity to consume pink salmon as food in the river, first pink salmon eggs as parr, then pink salmon alevins and smolts as smolts, and possibly pink salmon post-smolts as post-smolts in the sea. Atlantic salmon smolts and post-smolts in river and estuarine should be compared in even and odd years by measuring their muscle lipid percentage and fatty acid composition and comparing these with those of a natural freshwater invertebrate diet and pink salmon. For this purpose, similar, more thorough and systematic data are needed, especially for pink salmon. By comparing these in odd and even years, it can be concluded to what extent the consumption of pink salmon has possibly changed the natural fatty acid composition of Atlantic salmon, and whether they have become too fatty. A higher proportion of DHA and *n–3* HUFAs in an even year than in an odd year indicates that the parr/smolts have eaten pink salmon eggs and/or alevins/smolts. Below, we present eight avenues for further research.

1. In the preliminary PCA biplot depicting the fatty acid profiles of the potential diet of Atlantic salmon parr/smolts, all food groups, freshwater invertebrates, pink salmon eggs and pink salmon alevins, differ significantly from each other (Figure 14). The principal components 1 and 2 explained 83.3% of the variation. The PCA biplot shows that the *n–3* HUFAs DHA and DPA and the most common MUFA, 18:1*n–9*, which is typical for sprat in the Baltic Sea [33], and the oxidation of which is also prevented by thiamine, are associated with approximately the same strength with pink salmon eggs and alevins. The fatty acid stearic acid (18:0), the precursor of which is the most common SFA, palmitic acid (16:0), is clearly associated with alevins, and 20:1*n–9* with eggs. The *n–6* fatty acids, such as 18:2*n–6*, which is associated with invertebrates, are typical of freshwater organisms, and 18:2*n–6* is a precursor of arachidonic acid (ARA, 20:4*n–6*). The deviation of the fatty acid composition of pink salmon alevins from the fatty acid composition of eggs, so that ARA and 18:0 are typical of alevins, indicates that they have used up their stored energy. In Baltic salmon, 18:0 was strongly associated with Gulf of Finland salmon, which were the leanest. MUFA

18:1*n*–*7* and its precursor 16:1*n*–*7* are typical of freshwater invertebrates, and also indicate feeding on benthic animals in the sea, so that herring consumes more benthic animals as it grows [33].

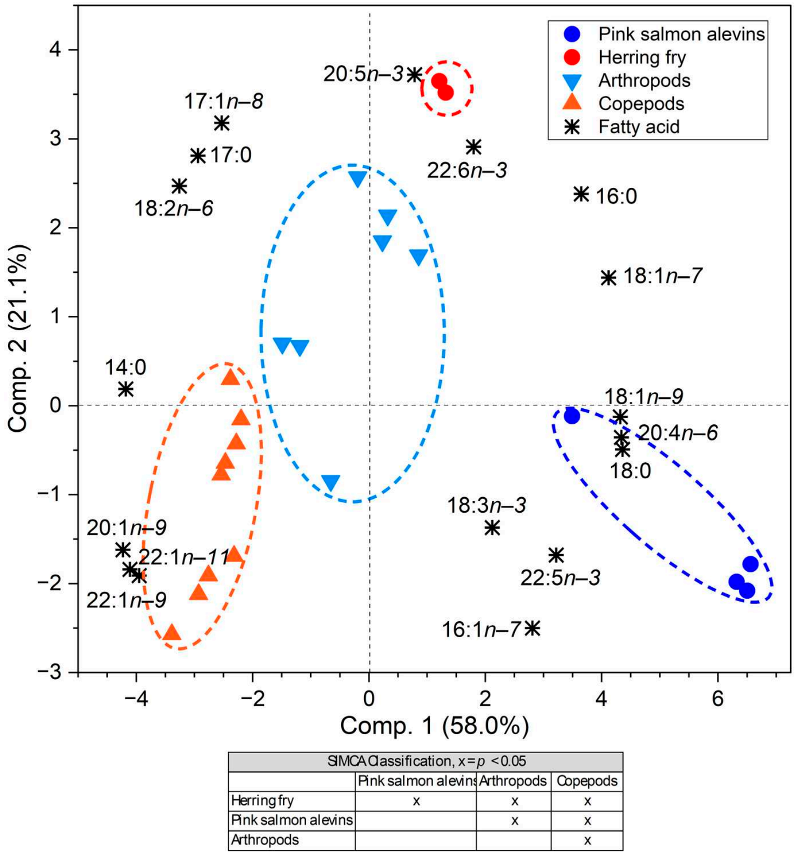


SIMCA Classification, x = $p < 0.01$		
	Pink salmon eggs	Invertebrates
Pink salmon alevins	x	x
Pink salmon eggs		x

Figure 14. Biplot from the PCA model, with principal components 1 and 2, for the food of Atlantic salmon (*Salmo salar*) parr and smolts in the river: freshwater invertebrates, pink salmon (*Oncorhynchus gorbuscha*) eggs and alevins. Data are from Bell et al. [107], Kaivarainen et al. [104], and Murzina et al. [100].

Since pink salmon smolts apparently feed on freshwater invertebrates as they migrate towards the sea, their fatty acid composition may have changed upon arrival in the estuary to resemble somewhat more the fatty acid composition of freshwater invertebrates than the fatty acid composition of pink salmon eggs and alevins originally resembled [8], or, if they have eaten sparingly and even partially fasted, this is likely to be reflected more strongly, for example, as an increase in the proportion of ARA.

In the PCA biplot depicting Atlantic salmon and pink salmon fatty acid profiles of all food groups, copepods, arthropods, herring fry (representing juvenile fish) and pink salmon alevins (representing pink salmon post-smolts, as no data were found on their fatty acids), differ significantly from each other (Figure 15). The principal components 1 and 2 explained 79.1% of the variation. EPA is strongly associated with herring fry, as is DHA, which is also associated with arthropods, although there is variation between arthropods, perhaps related to species differences. The MUFA 20:1*n*–*9* and two other MUFAs are associated with copepods. Also, SFA 14:0, which is also associated with arthropods, was associated with the saltier southern Baltic Sea [56]. The *n*–*3* HUFA DPA, as well as the *n*–*3* PUFA 18:3*n*–*3*, is associated with pink salmon alevins.



SIMCA Classification, x = $p < 0.05$			
	Pink salmon alevins	Arthropods	Copepods
Herring fry	x	x	x
Pink salmon alevins		x	x
Arthropods			x

Figure 15. Biplot from the PCA model, with principal components 1 and 2, for marine invertebrates copepods and arthropods, as well as herring (*Clupea harengus*), and for pink salmon (*Oncorhynchus gorbuscha*) alevins, as no fatty acid data on pink salmon smolts and post-smolts was found. Data are from Auel et al. [121], Iverson et al. [82], Lee et al. [122], and Utne et al. [83].

2. Atlantic salmon smolts are naturally low in lipids; i.e., their lipid percentage should be around 2%. If the percentage of lipids is too high, smoltification and post-smolt survival are impaired. The most important thing to study is the percentage of muscle lipids in salmon parr, smolts, and post-smolts (and possibly adults), and the whole-body lipid content of pink salmon at the different life phases as a salmon food. Post-smolts need protein and micronutrients to grow, and therefore the protein–lipid ratio of the diet must not be too low. In addition to the proportions of DHA and *n–3* HUFAs, the fatty acid profile should also examine their concentrations, since their amount is crucial for lipid peroxidation. The higher their proportions and the higher the lipid percentage, the greater the lipid peroxidation potential.

3. Because if the food of smolts and post-smolts of Atlantic salmon contain an excess of lipids and marine fatty acids and, as a result their own excessive lipid content and exposure to peroxidation, their growth and survival are impaired, and because the slowed growth of survivors is still visible in ascendants' size, these parameters of Atlantic salmon returning to the river to spawn should be examined and compared between years and at different time periods, before and after the abundance of pink salmon. Also, for Atlantic salmon caught from the sea, the change in the size over a longer period of time could be examined, as well as in relation to the abundance of pink salmon and its post-molts in the sea, as a potential food source for Atlantic salmon.

4. The high percentage of lipids in the diet and the body, and the high content of *n–3* HUFAs and DHA consume thiamine in energy metabolism and lipid peroxidation as an antioxidant. The thiamine status of salmon can best be measured as total hepatic

thiamine concentration [32,55], but also from unfertilized eggs [53] for sparing the fish. However, if the survival of smolts as post-smolts in the sea has been impaired due to their fattiness, and the food eaten in the sea has not been too fatty, the thiamine status of returning salmon could be good. On the other hand, if there are many small pink salmon post-smolts in the sea and the salmon eat them, the thiamine status would probably be impaired.

5. Invertebrates are an important part of the diet of Atlantic salmon post-smolts and juveniles in the sea, and there is reason to be concerned about their sufficient abundance. Since pink salmon can compete in the sea for the same zooplankton food, e.g., copepods, as small fish and invertebrates that Atlantic salmon use for food, their abundance should be examined. Because bottom trawling can also reduce the abundance of benthic animals and have a negative impact on the entire aquatic ecosystem, its effects must also be taken into account, and adverse effects prevented. According to Hiddink et al. [19], the number of individuals and the biomass of the whole community are the most appropriate indicators of the impacts of bottom trawling.

6. The maintenance of a sufficient invertebrate diet for Atlantic salmon parr and smolts when pink salmon are abundant in the river should be examined. Although pink salmon eggs and alevins/smolts provide abundant energy for Atlantic salmon parr and smolts in the river, switching a freshwater diet to a pink salmon-derived diet is detrimental to Atlantic salmon smoltification and post-smolt success in the sea.

7. Atlantic salmon (and pink salmon) sampled can be measured for length and weight, and stomach contents can be examined in the traditional way or possibly by also measuring the lipid content of the stomach contents. A higher-than-normal condition factor of Atlantic salmon can indicate either fatness or good muscle growth [22], and it should be compared with the lipid percentage of the fish.

8. The external characteristics of Atlantic salmon smolt are not completely reliable in describing their readiness to migrate in seawater [67]. Smoltification is associated with several physiological and structural changes in the gills, kidney and intestine. Although these changes are regulated by photoperiod, the most important factor affecting the speed of physiological changes, and thus the timing of the peak of migratory readiness, is temperature. How quickly a fish smoltifies maximally depends on the water temperature. Despite silvering, smolts may lack the characteristic ability to maintain the salt and water balance of their tissues at seawater salinity. The success of smoltification can be studied by saltwater exposure.

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Abbreviations

1-SW	one-sea-winter Atlantic salmon; i.e., those which return after their first sea-winter
2-SW	two-sea-winter Atlantic salmon; i.e., those which return after their second sea-winter
3-SW	three-sea-winter Atlantic salmon; i.e., those which return after their third sea-winter
4-SW	four-sea-winter Atlantic salmon; i.e., those which return after their fourth sea-winter
ALA	alpha-linolenic acid, 18:3*n–3*
ARA	arachidonic acid, 20:4*n–6*
ATP	adenosine triphosphate
DHA	docosahexaenoic acid, 22:6*n–3*
DPA	docosapentaenoic acid, 22:5*n–3*
eDNA	environmental DNA, referring to genetic material shed by organisms
EPA	eicosapentaenoic acid, 20:5*n–3*
HUFA	highly unsaturated long–chain fatty acid
LNA	linoleic acid, 18:2*n*–6
M74 syndrome	thiamine deficiency in fish called in the Baltic Sea region
MDA	malondialdehyde
MUFA	monounsaturated fatty acid
n–3 HUFA	long-chain, highly unsaturated fatty acid of *n–3* series
n–3 PUFA	polyunsaturated fatty acid of *n–3* series
Na^+/K^+-ATPase	Na^+/K^+-adenosine triphosphatase
NAD/NADH	nicotinamide adenine dinucleotide/nicotinamide adenine dinucleotide hydrogen
NADP/NADPH	nicotinamide adenine dinucleotide phosphate/nicotinamide adenine dinucleotide phosphate hydrogen
PCA	Principal Component Analysis
PUFA	polyunsaturated fatty acid
SFA	saturated fatty acid
TDC	Thiamine Deficiency Complex, thiamine deficiency in fish called in North America
THIAM	unbound or free thiamine
TPP	thiamine pyrophosphate derivative of thiamine
TTP	thiamine triphosphate derivative of thiamine
UI	unsaturation index, the sum of double bonds in fatty acids

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