Sex-, growth- and size-related differences in radionuclide bioaccumulation in perch (*Perca fluviatilis*)

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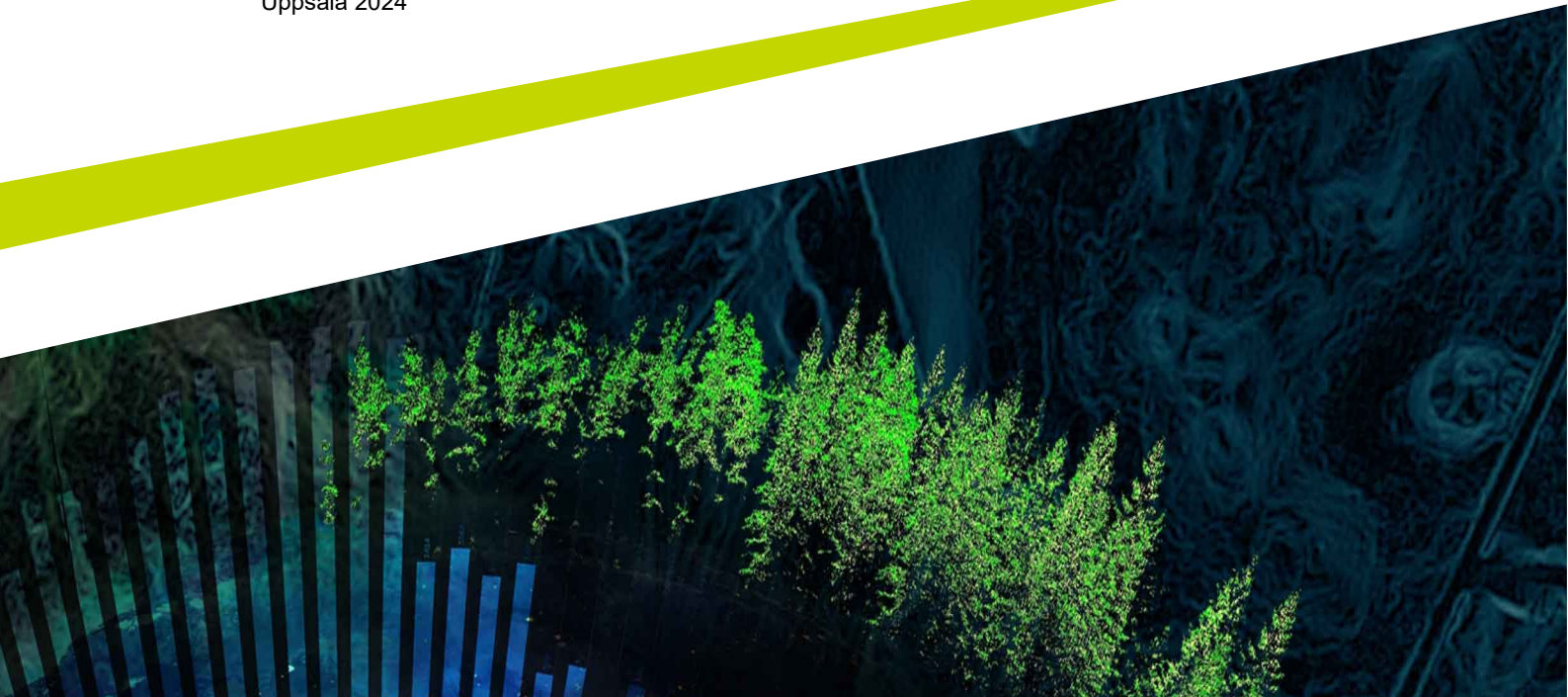

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Abstract

Bioaccumulation is a process that occurs when an organism's assimilation of a substance, through diet or passive uptake, outweighs its elimination. As organisms consume each other in a food web, the concentrations of substrates may increase with increasing trophic levels, a process called biomagnification. The underlying mechanisms of bioaccumulation involve factors like diet, metabolism and energy allocation, and as organisms grow in size, bioaccumulation increases. In teleost fish, female biased sexual size dimorphism (SSD) is well documented, with females generally growing faster and larger than males due to differences in metabolism and energy allocation. By recognizing that the drivers of both SSD and bioaccumulation overlap, this study investigate potential influences of sex, size and growth on the bioaccumulation of the radionuclide ^{137}Cesium(^{137}Cs) in Eurasian perch (*Perca fluviatilis*). Using a small sample of perch from an artificially heated and enclosed coastal ecosystem in the Baltic Sea, ^{137}Cs concentrations were measured in female and male perch of two size groups. Results revealed a significant increase in ^{137}Cs concentration with body size, confirming biomagnification patterns reported in previous studies. Furthermore, sex differences in the bioaccumulation of ^{137}Cs were found when controlling for growth, where males had a significantly higher increase of the radionuclide than females in relation to a proxy for the accumulated growth. These findings suggest that the underlying differences in processes, such as metabolism, energy allocation and growth patterns could influence radionuclide bioaccumulation in perch. Results from this study highlights the importance of considering both sex and growth in bioaccumulation models, as size alone may not fully capture the variation in contaminant concentrations in fish. Although the small sample size used in this study limits the generalizability of these results, they provide valuable preliminary insights for future research on sex-specific bioaccumulation patterns in fish.

Keywords: Bioaccumulation, Biomagnification, ^{137}Cs, Biotest lake, Eurasian Perch, *Perca fluviatilis*, sex, growth.

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1. Introduction

Aquatic environments, especially coastal areas, often contain elevated concentrations of hazardous substances. Heavy metals from industries, polycarbonate biphenyls (PCBs) from airfields and radioactive forms of elements, e.g. radionuclides, from nuclear power plants tend to concentrate in these environments due to transport through rivers and runoff (Montuori et al. 2014; Sanada et al. 2021; Mok et al. 2023). These substances can subsequently bioaccumulate in organisms inhabiting the polluted areas, a process that occurs when the assimilation of substances is greater than their elimination (Ali & Khan 2019). The rate of bioaccumulation is influenced by various biotic and abiotic factors. Abiotic factors include nutrient availability, pH, temperature, and the nature of the substance itself (Streit 1992; Schäfer et al. 2015; Woolway et al. 2022; Wu et al. 2023). Biotic factors encompass diet, growth rate, body size, and sex (Kryshev & Ryabov 2000; Rennie et al. 2008; Doi et al. 2012).

As organisms consume each other within a food web, accumulated substances are transferred between them. Additionally, fish can assimilate substances directly from the water through respiration, though this process generally has a minor impact compared to dietary uptake (Yamamoto et al. 2015). This transfer can lead to these substances further accumulating resulting in a higher concentration in organisms at higher trophic levels, a process called biomagnification (Ali & Khan 2019). In contrast to biomagnification lies biodilution, where concentrations of substances decrease with increasing trophic level, which occurs when the elimination of substances outweighs the assimilation (Watanabe et al. 2008; Ali & Khan 2019). Studies made on the bioaccumulation of the radionuclide ^{137}Cesium (^{137}Cs) in fish have shown that predatory species like the Eurasian perch (*Perca fluviatilis)* accumulate higher concentrations than their prey, indicating biomagnification due to increased accumulation at higher trophic levels (Doi et al. 2012; Kaglyan et al. 2015). Furthermore, perch have been shown to be sensitive to radiation, which can lead to delayed maturation and underdeveloped phenotypes as a result of prolonged exposure to ^{137}Cs (Lerebours et al. 2018).

Feeding, leading to the transfer and biomagnification of substances, often depends on body size. This is particularly evident in piscivorous fish species, where body

size often correlates with gape size, which in turn can determine the prey an individual fish can consume (Keppeler et al. 2020). Besides influencing diet, size also affects fish metabolism. Larger and older fish tend to have lower metabolic rates per unit biomass compared to younger and smaller individuals of the same species (Doi et al. 2012; Lindmark et al. 2022). Because metabolic rate determines the rate of several physiological processes, this can lead to reduced rates of both assimilation and elimination of hazardous substances (Doi et al. 2012). This corresponds to the findings by Ishii et al. (2023) that ^{137}Cs concentrations in food webs rise along trophic positions, with higher levels found in predatory and larger-bodied fish species, highlighting the influence of species' body size on ^{137}Cs bioaccumulation.

In addition to differences in metabolic rate with body size, metabolic rate has been found to differ between sexes in fish. Males of percid species, such as the Walleye (*Sander vitreus*) and Yellow perch (*Perca flavescens*), exhibit lower food consumption and metabolic costs compared to females, coupled with lower food conversion efficiency (conversion of ingested food to body mass). (Rennie et al. 2008). Moreover, studies suggest that females might shift to a piscivorous diet at a smaller size than males (Ulićević et al. 2017). Studies on Walleye have found that males have higher concentrations of PCBs and mercury compared to similarly sized females (Henderson et al. 2003; Madenjian et al. 2016b). A possible explanation for this could be that, due to female-biased sexual size dimorphism, males take a longer time to reach a comparable size and therefore accumulate substances over a longer period (Madenjian et al. 2016b).

An often-overlooked variable in studies regarding bioaccumulation, which further could explain the elevated concentrations of PCBs and mercury in males, is growth rate and its diluting effect. Growth dilution occurs when rapid growth reduces the concentration of accumulated substances due to increased body mass, not due to actual elimination of the substance (Madenjian et al. 2016a). Increased growth has been seen to negatively affect the biological half-life (the time it takes for the concentration of a substance to decrease by half) and steady-state concentration (constant concentration) of ^{137}Cs in fish (Niizeki et al. 2020). While previous research has documented sex-based differences in the accumulation of hazardous substances like PCBs and mercury (Henderson et al. 2003, Madenjian et al. 2016), it is unknown whether similar difference between sexes exists for radionuclides, e.g. ^{137}Cs. Understanding the mechanisms behind sex-based differences in bioaccumulation, such as growth, size, and metabolism, could provide important insights into how radionuclides vary in aquatic ecosystems.

1.1 Aims and objectives

The aim of this study was to test whether radionuclide concentration (^{137}Cs, Bq/kg) differs depending on sex and whether ^{137}Cs concentrations are affected by individual growth rates in fish. To address this, I use the Eurasian Perch (*Perca fluviatilis*), a predatory species which exhibits a strong female-biased sexual size dimorphism (Skovrind et al. 2023). Perch is common in coastal areas of the Baltic Sea (HELCOM 2023), which is the most contaminated marine system globally concerning ^{137}Cs (Kotilainen et al. 2021). I specifically test (1) if there is a difference in ^{137}Cs concentrations between the sexes within the same size class, hypothesizing that males have higher concentrations due to slower size-specific growth rates; (2) if there is a larger difference in ^{137}Cs concentration between the sexes in large versus small perch, as continuous variations in metabolism and energy allocation could amplify these differences as perch grow; and (3) if fast growth correlates with lower concentrations of ^{137}Cs due to growth dilution.

2. Materials and methods

2.1 Study area

To conduct this study, I selected the Biotest Lake, an artificially enclosed coastal ecosystem constructed in 1977 to serve as a cooling water outlet for the Forsmark nuclear power plant (Figure 1). This controlled environment, which has been used for decades as a scientific monitoring system, allows researchers to study the effects of increased water temperatures on local ecosystems (Huss et al. 2019; van Dorst et al. 2024). Moreover, the lake is situated in a region impacted by historical ^{137}Cs fallout from the Chernobyl disaster, which makes it an ideal location for investigating radionuclide bioaccumulation (Kotilainen et al. 2021).

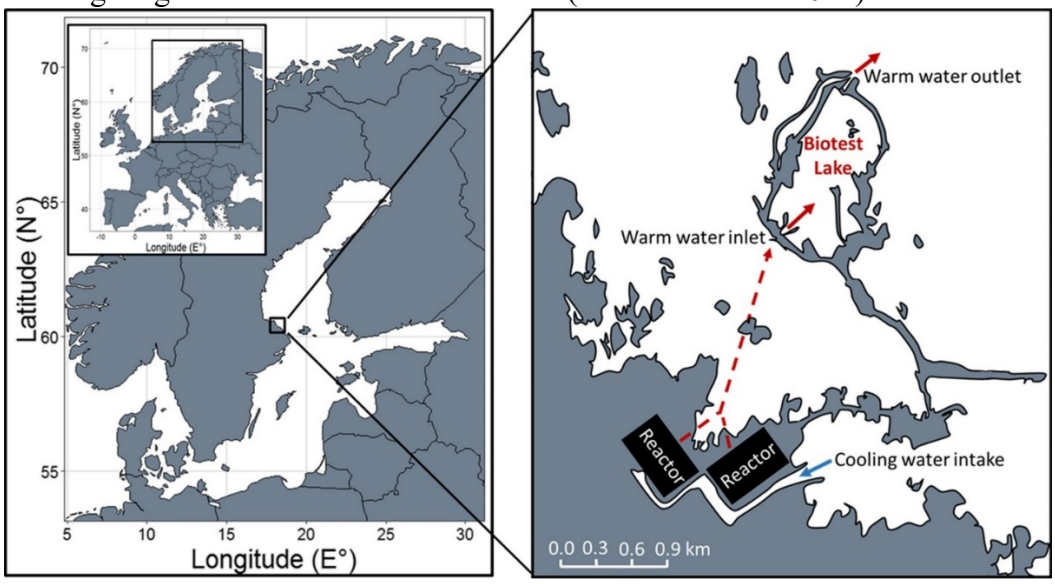

***Figure 1**. Location (left) and map (right) of the enclosed Biotest Lake, modified from Huss et al. 2019.*

2.2 Sampling

Perch were collected in the Biotest Lake using standard Nordic coastal multi-mesh gillnets consisting of nine different mesh sizes (10-60 mm), each section being 5 meters for a total net length of 45 meters and a depth of 1.8 meters (HELCOM 2015). Sampling occurred in May 2024, with nets set at approximately 15:00 and retrieved at 07:30 the following morning, resulting in a soak time of approximately 16.5 hours. Captured perch were recorded for sex, length (measured to the nearest millimeter), gonad weight, and somatic weight (both measured in grams to two decimal places). Gut contents were removed to avoid daily fluctuations caused by undigested food and ^{137}Cs content of prey in the guts to influence the measurements of ^{137}Cs accumulated by perch. Additionally, opercular bones and otoliths were extracted for age determination and growth measurements.

For further growth analysis, 22 perch that met a specific criterion for size and sex (see below) were randomly selected from the total catch. Of the 22 perch that underwent growth assessments, 12 were selected for radiological analyses. This number is due to limited radiological laboratory availability. The criteria for selected fish were two size groups: smaller fish (16–20.9 cm) and larger fish (26–30.9 cm), with three males and three females in each group. The size groups were chosen to exclude sexually immature individuals, avoid overlap and to ensure captures of both sexes. The fish were then individually prepared by cutting, weighing in pre-weighed aluminum trays, and drying at 80°C for 7 days in a Memmert drying oven. After drying, the fish were weighed again, ashed in a Nabertherm muffle furnace at a maximum of 430°C for 49 hours (see Table A1 for detailed ashing program), and then weighed post-ashing. All weighing was done in grams to two decimal places. Finally, the samples were ground to a fine powder using a pestle and mortar, cleaned between each individual grounding, before undergoing radiological analysis.

2.3 Growth Assessments

Opercular bones and otoliths from the 22 chosen individuals were examined using a Leica MZ6 stereo microscope with substage illumination at 6.3x magnification. Otoliths were burned and split laterally to read annual rings and determine age whereas growth between years was measured by the distance between each annual growth ring on the opercular bones, which were boiled and cleaned beforehand. Operculum growth during the first growth season was measured as the radius from the growth point to the first growth ring. The radius was measured with a Mitutoyo digital caliper (absolute digimatic) and the length at age was then back-calculated,

to the nearest millimeter, using the radius and age data with the following formula (Lindmark et al. 2022):

$$L_a = L_s(\frac{r_a}{r})^{0.861}$$

Where L_a is the length at age, L_s is the length at catch, r_a is the radius at age, and r is the total radius, with 0.861 being a constant specific to perch (Thoresson 1996).

To verify varying growth curves between the sexes, Von Bertalanffy growth models (Appendix Figure A2) were fitted in RStudio (Hart & Chute 2009):

$$L(t) = L_{inf} * (1 - e^{-k(t-t_0)})$$

where $L(t)$ is the length at age t, t is the age of the perch, t_0 is the theoretical age for when the fish is 0 mm, k is the rate at which the individual approaches L_{inf} ("growth rate") and L_{inf} is the asymptotic length (Appendix Figure A1).

To investigate the effect of growth on ^{137}Cs concentrations, a proxy for accumulated growth for each perch until their length when caught was derived by calculating the area under each individual growth curve using integrals, performed with the pracma package in RStudio. Growth curves were based on age-specific growth to ensure a consistent starting point across individuals, avoiding the bias in the growth proxy that could arise from using length-specific growth curves. This approach allowed for a more nuanced analysis by considering back-calculated differences in growth patterns between individuals (Appendix Figure A2). A higher value of the growth proxy equals faster growth during their first year or/and growth spurts without equally matched growth declines.

2.4 Radiological Analysis

The concentrations of ^{137}Cs in the 12 perch selected for radionuclide analyses were determined using detectors at the radiological lab at the Forsmark nuclear power plant and expressed in Becquerels per kilogram (Bq/kg). The detectors used for radiological analysis were HPGe detectors with a relative measurement efficiency of 50%, models GC4018 CANBERRA. The detectors were placed in lead shielding (CANBERRA 767 Lead Shield) to minimize radiation contribution from the surroundings. The ashed powder was placed into the detectors and analyzed using

the software APEX v1.4.1, Genie 2000, which provides the results with uncertainty parameters in the operative system VDM 3.3.1 (Virtual Data Manager). All samples were analyzed with an uncertainty of less than 8%.

2.5 Statistical Analyses

All statistical analyses were performed in R (R Core Team 2022) with the software RStudio 2023.03.0 build 386 (Posit Team 2023).

To determine whether to use parametric or non-parametric models, residuals were inspected and Shapiro-Wilk test and Levene's test were used to determine normality and equality of variances respectively. To test my first two hypotheses, I fitted a full linear regression model (lm) to see how size groups and sex, as well as their interaction, influenced the concentration of ^{137}Cs. I tested for a significance level of each term at p=0.05. When significant interactions were found in the linear model, two-sample t-tests were conducted as post hoc tests to determine if there was a difference in ^{137}Cs concentrations between the sexes within each size group.

There was high collinearity (0.97) between the growth proxy and age. I therefore analyzed how growth influenced the concentration of ^{137}Cs separately for the two distinct age groups found in the two size groups (three and five years old respectively). To do this, I fitted a linear regression model with ^{137}Cs as the response variable and the proxy for accumulated growth as the explanatory variable and sex as an interaction term to account for the potential effect of sex on this relationship.

3. Results

3.1 Effect of sex and size

Large perch had significantly higher concentrations of ^{137}Cs than smaller perch and there was a tendency for smaller male perch to have higher ^{137}Cs concentrations (table 1, figure 2). However, there were no general differences between the sexes, nor interaction between sex and size.

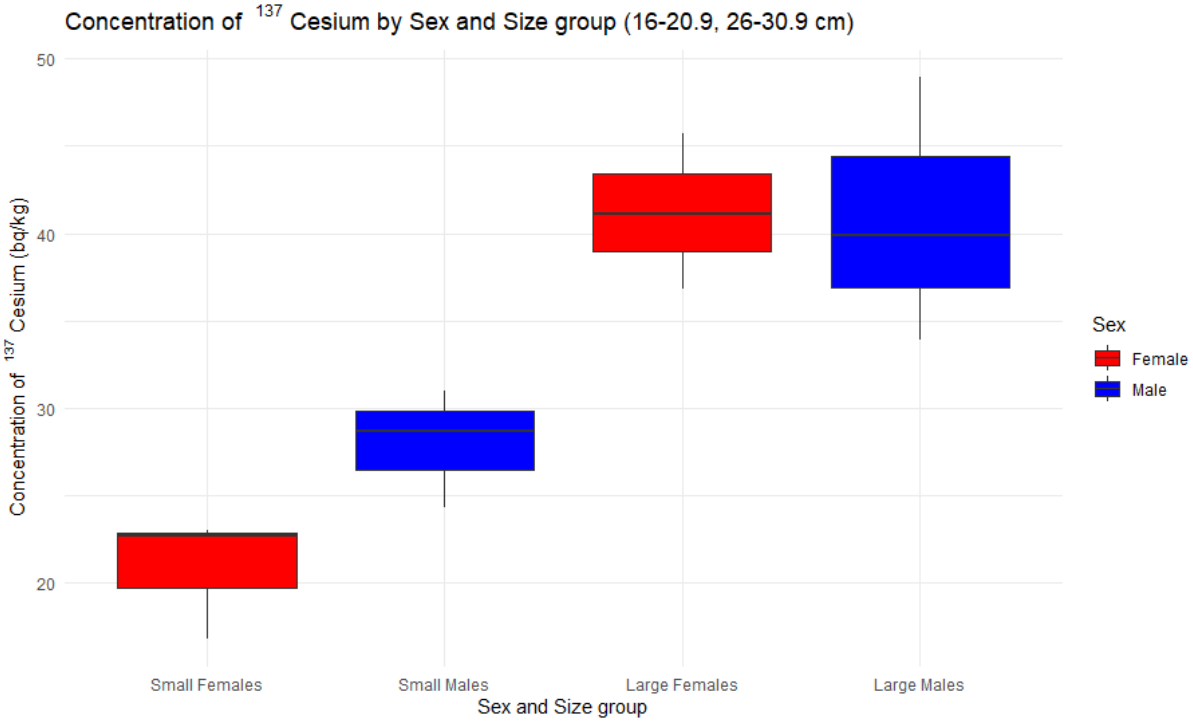

Figure 2. *Boxplots of ^{137}Cs concentrations (Bq/kg) between female (red) and male (blue) perch of different size groups (Size groups, 16-20.9 cm and 26-30.9 cm.). The boxplots display the median (line within box), first and third quartiles (boundaries of the box) and whiskers extending to the minimum and maximum values.*

***Table 1**. Results from individual t-test of ^{137}Cs concentrations within the two size groups and linear regression with both size groups included. *=significant at p<0.05*

Test	Explanatory Variables	Estimate	SE	t	p
Linear regression (lm)	Intercept	-9.717	8.442	-1.151	0.283
	Sex	18.367	11.939	1.538	0.16253
	SizeGroup	10.183	2.048	4.973	0.00109*
	Sex:SizeGroup	-3.733	2.896	-1.289	0.23334
Post hoc T-test	Small size group			-2.5437	0.06377
	Large size group			0.059289	0.9562

lm: Adjusted r-squared: 0.7504; F-stat: 12.02 on 3 and 8 DF (p = 0.002472)
Post hoc T-test: Mean Bq/kg in female and male in small and large: 20.8, 28.0 and 41.2, 40.9

3.2 Effect of growth and age

Using the proxy for accumulated growth instead of body size revealed a difference in concentration of ^{137}Cs between the sexes in the older and larger perch, where males had significantly increased ^{137}Cs concentration with an increasing growth proxy, than equally old females (table 2: figure 3). Additionally, the interaction between the growth proxy and sex was significant, showing that the relationship between growth and ^{137}Cs concentration varied depending on the sex of the fish in this age group. However, there was no general effect of growth alone in either age group.

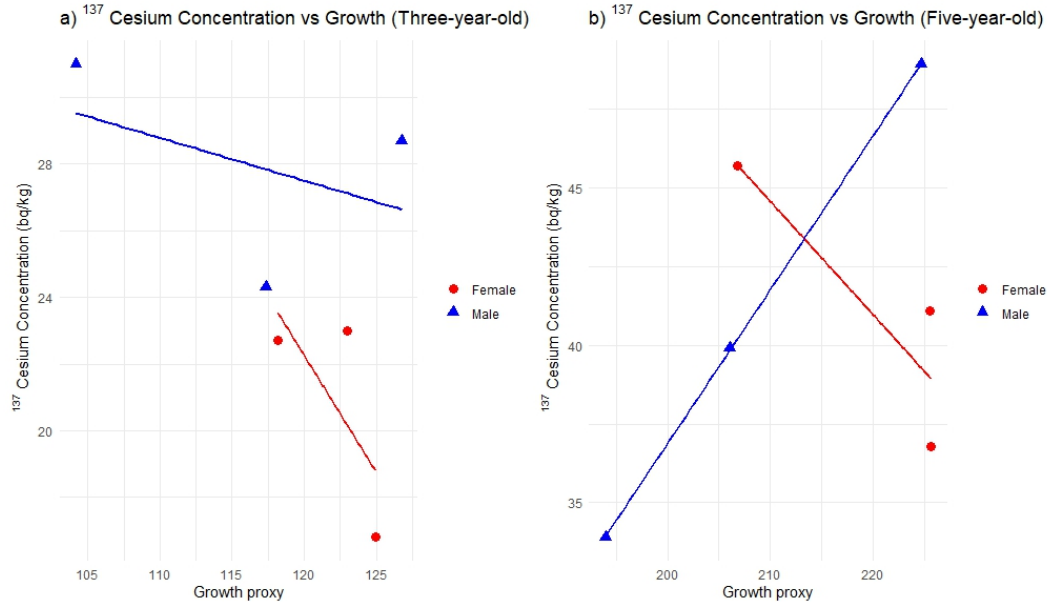

Figure 3. *Effect of growth and sex on ^{137}Cs concentrations in (a) three-year-old perch and (b) five-year-old perch.*

Table 2. *Results from linear regression on ^{137}Cs concentrations in the two separate age groups, *=significant at p<0.05.*

Age group	Explanatory Variables	Estimate	SE	t	p
3	Intercept	106.3229	98.6726	1.078	0.394
	GrowthProxy	-0.7005	0.8083	-0.867	0.478
	Sex	-63.4436	102.7986	-0.617	0.600
	GrowthProxy:Sex	0.5724	0.8454	0.677	0.568
5	Intercept	119.9925	30.5390	3.929	0.0591
	GrowthProxy	-0.3592	0.1391	-2.582	0.1229
	Sex	-180.5483	36.7009	-4.919	0.0389*
	GrowthProxy:Sex	0.8464	0.1699	4.981	0.0380*

Age group 3: adjusted r-squared: 0.3673; F-stat: 1.968 on 3 and 2 DF (p = 0.3545)

Age group 5: adjusted r-squared: 0.8513; F-stat: 10.54 on 3 and 2 DF (p = 0.0879)

4. Discussion

This study revealed that perches exhibit significantly higher concentrations of ^{137}Cs as they grow in size. However, sex differences in ^{137}Cs concentrations were also observed in older fish when controlling for growth differences, but not when controlling for size alone. This suggests that while body size may indicate some level of ^{137}Cs accumulation, it is the underlying growth dynamics that better explain sex-specific bioaccumulation patterns. Due to the limited number of individuals analyzed, the potential three-way interaction between sex, the growth proxy, and age could not be thoroughly tested. As a result, these findings should be interpreted with caution.

The finding that larger perch accumulate more contaminants is consistent with previous research on biomagnification, where larger predators tend to show higher concentrations of many contaminants, including ^{137}Cs (Rowan et al. 1998; Henderson et al. 2003; Ali & Khan 2019). The observed sex difference in older perch, when growth is considered, is novel in the context of radionuclides and has not, to my knowledge, previously been documented. This means that my findings that suggest growth-driven bioaccumulation processes differ significantly between the sexes in perch is a factor not yet accounted for in biomagnification models. The stronger increase in ^{137}Cs concentrations with the growth proxy in old males compared to in females of the same age suggests that differences in growth rates and energy allocation strategies between the sexes could influence bioaccumulation patterns also of ^{137}Cs, as earlier found for e.g. Hg (Rennie et al. 2008). While males showed a positive correlation between growth and ^{137}Cs concentration, females exhibited a tendency of the opposite trend. This observation, while not statistically robust due to the small sample size, suggests that sex-specific factors, such as metabolic and reproductive demands, could play an important role in how ^{137}Cs accumulate.

4.1 Metabolism and Elimination rates

The increase in ^{137}Cs concentration with body size (i.e. the biomagnification) may be attributed to metabolic rates and resulting elimination processes. Larger

individuals tend to have lower metabolic rates relative to their body size, which can impact the rate at which they process and eliminate contaminants (Doi et al. 2012). This slower elimination may result in larger perch retaining ^{137}Cs for a longer period, leading to the higher concentrations. However, the tendency observed, where smaller males have higher concentrations of the radionuclide than equally sized females, must be credited to other processes. One process that may be relevant is the effect of maturity. Once maturity is reached more energy is spent on reproduction rather than growth, and growth dilution may thus be less. Male perch have been shown to mature earlier, typically between the first and second year of life, while females typically mature between their second and third year (Ceccuzzi et al. 2011). Concentrations of ^{137}Cs have also been seen to increase after maturation in walleye and yellow perch which share the same family as the Eurasian perch (Rowan et al. 1998). However, this cannot explain the observed tendency of higher concentration of ^{137}Cs in males among small individuals, because these were all of the same body size.

4.2 Growth dilution & sexual size dimorphism

The observation that larger males exhibited increased ^{137}Cs concentrations opposed to females when considering growth cannot be explained by biomagnification alone, as the groups were of equal size and age. By the same logic, neither can growth dilution explain this result. Important to remember is that the effect of the growth proxy alone did not impact the accumulation of ^{137}Cs, only with the interaction of sex. One additional explanation to why 137Cs could differ between males and females could be sexual size dimorphism (SSD) and its implication on a sex-specific elimination process, namely spawning. Female and male perch have a gonadosomatic index of approximately 20-25% and 5-10%, respectively (Ceccuzzi et al. 2011). This index is similar to that of lake trout, which have been found to release as much as 5-11% of their ^{137}Cs burdens during spawning through the release of eggs and sperm (Rowan et al. 1998). This means that, in every spawning season, females get rid of a larger proportion of their ^{137}Cs concentration in relation to males. This, however, does not explain the relationship between growth and increasing concentrations of the radionuclide in male perch in relation to equally sized and aged females. This suggests that other mechanisms, possibly related to diet, growth patterns or metabolic differences between the sexes, may contribute to the observed increase in ^{137}Cs concentrations in males

It is important to highlight that the perch used in my study were all caught from an artificially created, enclosed and heated area and therefore reference values from previous studies should be compared with caution. Previous studies on perch in the

Biotest Lake found that males and females exhibit typical female-biased growth, where males and females length-at-age are similar only during their first two years due to faster growth in females (van Dorst et al. 2024). It is worth noting that the data used by van Dorst et al. (2024) to evaluate perch growth was collected between 1977 and 1990, and growth dynamics in the Biotest Lake may have shifted since then. Especially when considering that the perch in my study did not follow this pattern. In the smaller size group (16–20.9 cm), both males and females were 3 years old, which could be expected given the small size. Surprisingly, all perch in the larger size group (26–30.9 cm) were 5 years old, contradicting my expectations that larger males would be older than females. Alternatively, it is also likely that the small sample size in my study may not be representative samples of the population, and a more robust sampling could reveal generalized age differences between the sexes that were not detected here.

4.3 Implications and Conclusion

The results of this study suggest that sex-specific growth patterns do influence ^{137}Cs bioaccumulation in perch, particularly in older individuals. This observation underscores the importance of incorporating both sex and growth factors into future studies regarding the bioaccumulation of ^{137}Cs. Given that female fish tend to allocate more energy to reproduction and mature later than males, the patterns observed in this study may reflect broader trends in teleost species where sexual size dimorphism drives differential bioaccumulation (Rennie et al. 2008; Estlander et al. 2017). Furthermore, the relationship between sex-specific growth and ^{137}Cs concentrations may have broader implications for other contaminants that share similar bioaccumulation pathways, such as primarily binding to muscle tissue and accumulating through dietary sources (Arai 2014; Yamamoto et al. 2015).

Despite the limited sample size, which affected the statistical power of the analysis, these findings could contribute valuable preliminary insights into the interaction between sex, size, and growth in radionuclide bioaccumulation. This pilot study provides a foundation for future research on sex- and growth-specific bioaccumulation processes in fish and underscores the importance of considering sex as a factor in bioaccumulation models, a factor often overlooked in ecological studies focused on contaminants.

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Popular science summary

When we think of radioactive contamination, we often imagine disasters like Chernobyl or Hiroshima. Radioactive substances can however also build up slowly in organisms, a process called bioaccumulation. This happens when organisms take up more contaminants than they can get rid of, and when they are eaten by others, these contaminants transfer to other organisms. This can result in higher concentrations in predators than prey - a process called biomagnification. For example, fish often contain more contaminants than their invertebrate prey. Concentration of radioactive substances in fish therefore depends on their diet, as well as their body size and thus growth. However, fish do not always grow at the same rate. In many species, including perch, females grow faster and larger than males due to differences in how they allocate energy. Could these growth patterns affect how males and females accumulate cesium?

To find out, I studied perch from an artificially heated coastal ecosystem in Sweden exposed to radioactive cesium (Cs^{137}) from the Chernobyl fallout in 1986. I measured radiocesium levels, size and annual body growth in perch from different size groups consisting of both males and females. I found that larger perches had higher cesium concentrations, following the well-known biomagnification pattern. However, I also found that males, especially older ones, accumulated more cesium relative to their growth compared to females. This suggests that differences in growth and energy use may cause males to retain more cesium than females.

My findings highlight the importance of considering both sex and growth, not only size, in understanding how contaminants accumulate in fish.

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Appendix

Table A1*: Ashing program.*

T1: RPM1= 2°C/min, T.SP1= 160°C, DWELL1= 4h 1h20min, 160 °C, 4h
T2: RPM2= 1°C/min, T.SP1= 220°C, DWELL1= 10h 220-160=60 1h, 220 °C, 10h
T3: RPM3= 1°C/min, T.SP1= 250°C, DWELL1= 10h 250-220=30 30 min, 250 °C, 10h
T4: RPM4= 1°C/min, T.SP1= 350°C, DWELL1= 10h 350-250=100 1h40min, 350 °C, 10h
T5: RPM5= 1°C/min, T.SP1= 400°C, DWELL1= 5h 400-350=50 50min, 400 °C, 5h
T6: RPM6= 1°C/min, T.SP1= 430°C, DWELL1= 10h 430-400=30 30min, 430 °C, 10h

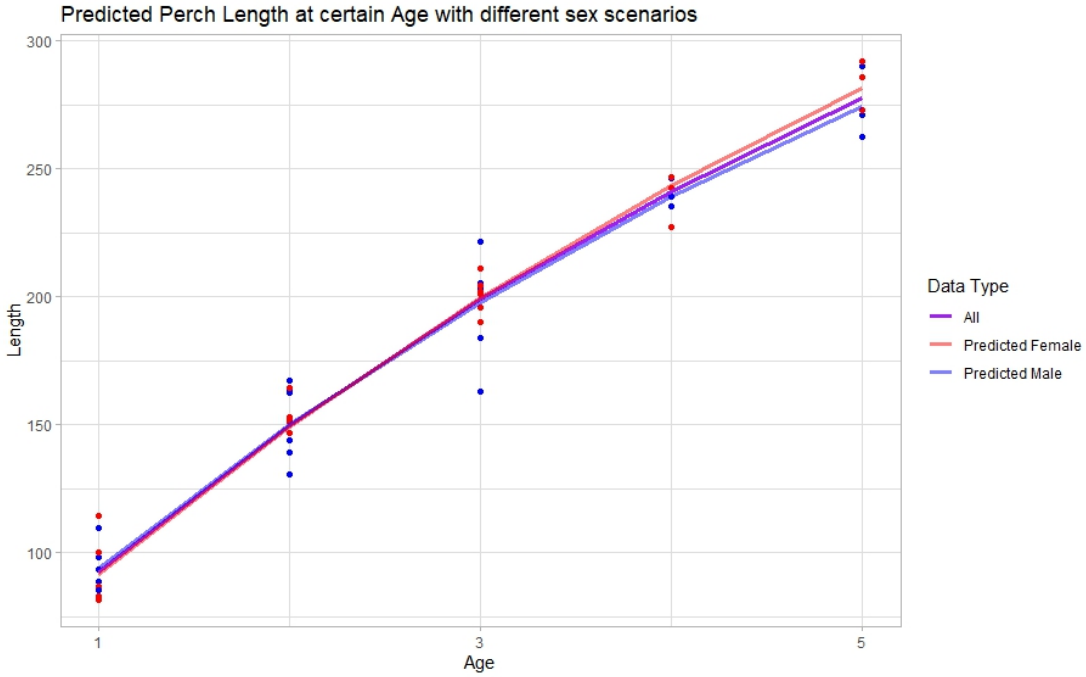

***Figure A1**: Predicted Von Bertalanffy body growth curve, estimated for all 12 perch individuals (purple), females only (red) or males only (blue). For all individuals, the parameters t_0, linf and k were estimated as 0, 400 and 0.3 respectively. Through the function SSE in RStudio the sum of squared deviations was calculated between observed lengths and predicted lengths based on estimated parameters. The nlm function was then used to change the estimated parameters to minimize SSE and provide a better fit for the Von Bertalanffy model for each sex. The estimated growth values were for females and males respectively: Linf: 545 and 490 mm, k: 0,136 and 0,159 and t_0: -0,353 and -0,400.*

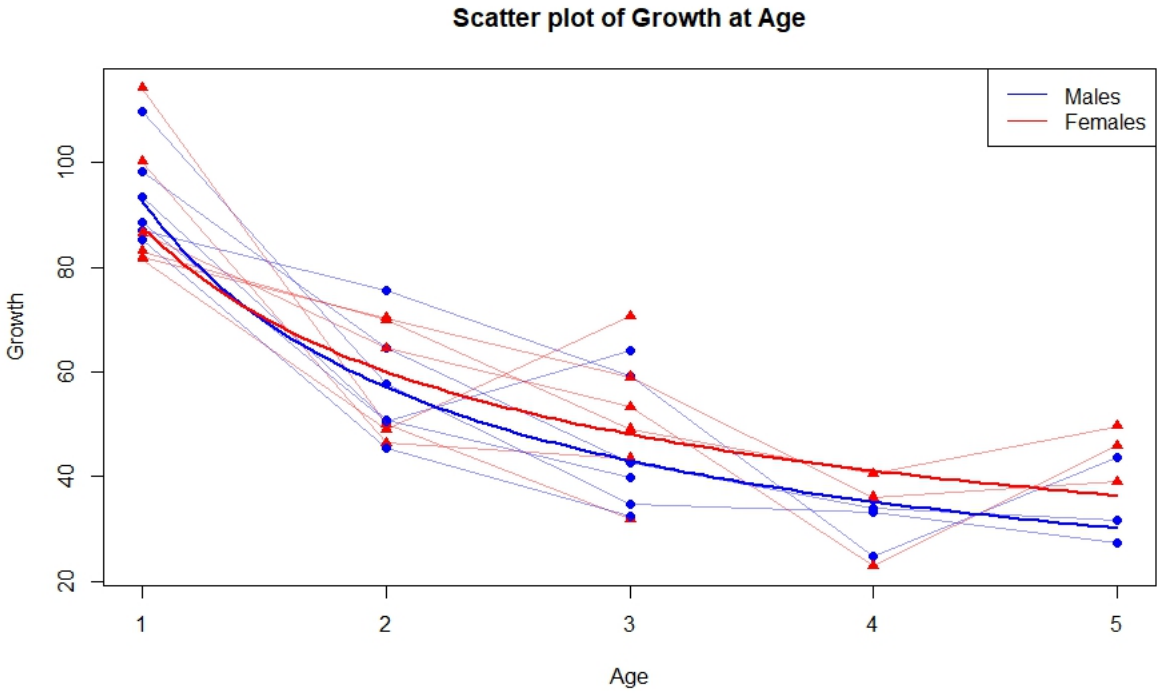

***Figure A2**: Individual annual growth increments (females: red triangles, males: blue circle) that the integrals were calculated from.*

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