Sex ratio of Eurasian Perch (*Perca fluviatilis*) in the Baltic Sea- spatial and temporal gradients along the Swedish Baltic Sea coast

Könsfördelning hos abborre (Perca fluviatilis) i Östersjön- rumsliga och tidsmässiga gradienter längs den svenska Östersjökusten

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Master thesis project· 30 hp
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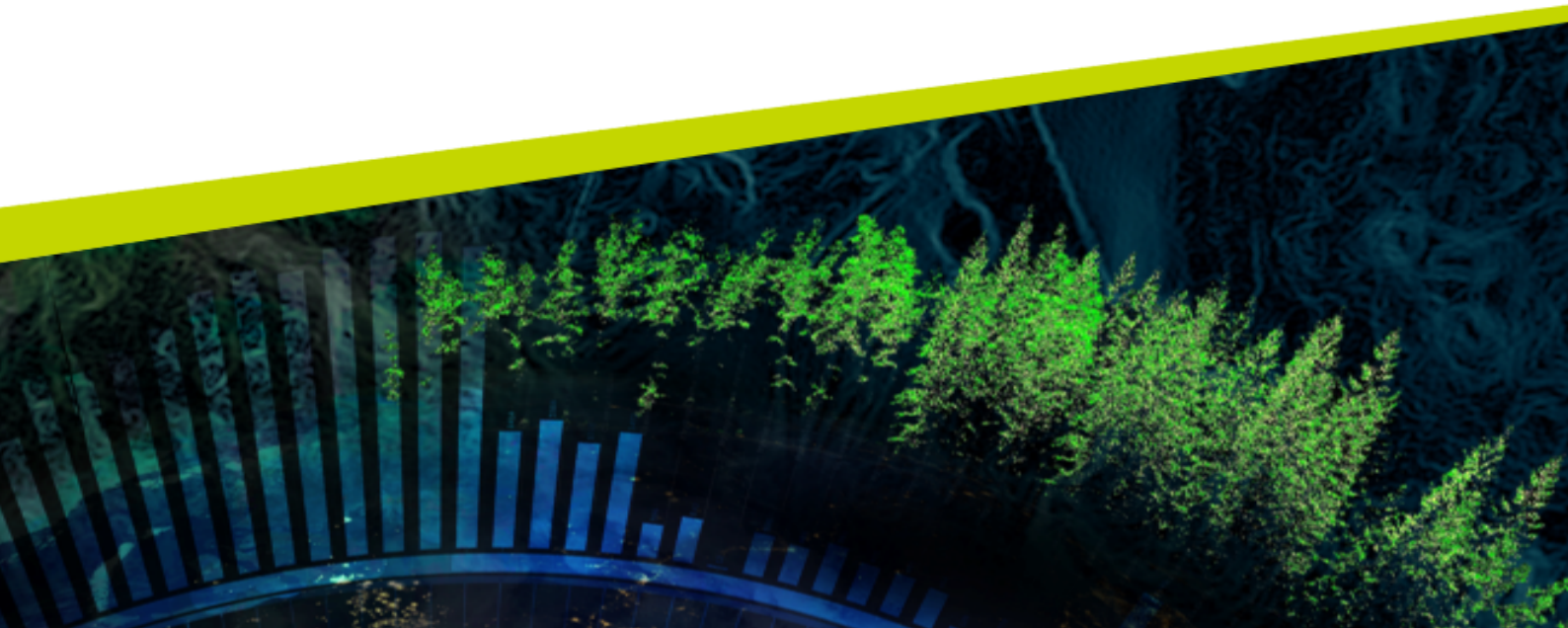
Uppsala, 2026



Project Details

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Credits:	30 credits
Level:	Second cycle, A2E
Course title:	Master thesis in Biology
Course code:	EX0895
Course coordinating dept:	Swedish University of Agricultural Sciences, Department of Aquatic Resources
Place of publication:	Uppsala
Year of publication:	2026
Keywords:	**Baltic Sea, costal area, Eurasian perch, sex ratio**

SLU, Swedish University of Agricultural Sciences
Faculty of Natural Resources and Agricultural Sciences
Department of Aquatic Resources (SLU Aqua)

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Abstract

The sex ratio, or the female proportion in a population, is one of the most basic demographic properties that directly influences reproductive output and population dynamics. Spatial and temporal variation in sex ratio has been largely overlooked in the case of the ecologically important species like Eurasian perch *(Perca fluviatilis)* in the coastal part of the Baltic Sea. In this thesis gillnet monitoring data from up to 14 coastal locations (2007–2024) were analyzed with generalized linear mixed-effects models and principal component analysis to examine the variation in sex ratio across time and space along the Swedish Baltic Sea coast. The main aim was to identify biological and environmental factors that contribute to any potential sex ratio variation.

I found clear size-dependent sexual dimorphism, with a greater proportion of females in the larger size classes and a greater proportion of males in the smaller size classes. Neither latitude nor time had strong predictive power for explaining sex ratio variation observed.

The lack of a latitudinal gradient, the results imply that patterns in sex ratios are more likely driven by local factors, such as population abundance, fishing pressure, habitat quality, and the thermal environment. Moreover, I also found indications of a flattening of the sex ratio curves with size in several locations during the recent sampling years, suggesting that, there is shift towards more balanced sex ratio in most locations along the Swedish Baltic Sea coast.

In all, the results of my thesis suggests that water temperature and perch population abundance might be important local factors affecting the sex ratio variation in perch. This is relevant for fisheries management and monitoring of the ecosystem, since size selective fishing and climate change-induced shifts in growth conditions can indirectly affect the reproductive capacity through changes in the sex ratio.

Keywords European perch *(Perca fluviatilis)*, Baltic Sea, sex ratio, spatial and temporal changes

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1 Introduction

One of the basic parameters in a fish population is the sex ratio (the proportion of females to the total number of fish in a population). It affects the effective population size (Ne; the number of individuals contributing to the next generation genetically), reproductive output, and evolutionary dynamics (Wright, 1931; Luikart et al., 2021). Fisher's principle (Fisher, 1930) predicts that a 1:1 sex ratio is the evolutionarily stable strategy in general (Wishart et al., 2018), but predictable deviations can occur in various ways, due to, for example, sex-biased mortality, the type of mating system, environmental sex determination, local mate competition (Baroiller & D'Cotta, 2001; Ospina-Alvarez & Piferrer, 2008; Geffroy & Wedekind, 2020). Sexual dimorphism in growth, maturation, and survival rates can also lead to spatiotemporal variations in sex ratio in fish populations, especially in species with size-selective fishing mortality, which are more likely to remove larger individuals (typically females; Prchalová et al., 2008).

The widely distributed freshwater fish species, Eurasian perch *(Perca fluviatilis)*, is one of the most common fish species in coastal fish communities in Baltic Sea coastal waters and plays an important role in ecosystem functioning, coastal fisheries, and the recreational sector (Olsson, 2019). Eurasian perch is a highly female-biased sexual size dimorphic species, in which females grow much larger than males of the same age (Prchalova et al., 2022). This dimorphism could impact spatial ecology and trophic interactions, but recent studies indicate that the two sexes do not necessarily segregate in space, despite their size differences (Prchalova et al., 2022). The recruitment, growth, and distribution of perch are closely related to water temperature and other environmental factors (Olsson et al., 2012; Östman et al., 2016; Östman et al., 2017a; Kokkonen et al., 2019). It has been demonstrated that ongoing warming trends have already affected growth rates and body length of perch along latitudinal gradients (Gårdmark & Huss, 2020), and that the perch stock-recruitment relationship can be modified by interactions with other species like pikeperch *(Sander lucioperca)* (Kokkonen et al., 2019).

The Baltic Sea is a semi-enclosed brackish waterbody with large environmental gradients in terms of salinity, temperature, and nutrient concentrations (HELCOM, 2023; Stockmayer & Lehmann, 2023). These gradients create a mosaic of habitats which impact the biology, distribution, and population dynamics of resident fish (Olsson, 2019; Östman et al., 2016; Östman et al., 2017a). Knowledge of the spatial heterogeneity of fish populations and their response to environmental gradients is central to effective fisheries management and conservation in the region (Bartolino et al., 2017). Some fish species in the Baltic Sea exhibit spatial variation in their stock structure (Östman et al., 2017b), as well as differences in body size, growth rates, and maturation patterns across regions (Erlandsson et al., 2017). Olsson et al. (2011) have documented a fine-scaled genetic population structure in perch, along the Swedish Baltic Sea coastline, resulting in isolation-by-distance patterns and possible gene flow barriers between the sub-basins. These spatial trends in growth and genetics are well documented, and similar spatial trends in sex ratio could be predicted along the Baltic coast of Sweden. However, sex ratio patterns along coastal gradients are still poorly documented.

The Swedish Baltic Sea coasts have strong gradients in temperature and salinity, ranging from the warmer and more saline conditions in the south, to cooler and more freshwater like conditions further north (Snickars et al., 2010; Christensen et al., 2020). Spatial and temporal variation in the sex ratios of perch may hence be influenced by these environmental gradients, as well as potentially by fishing pressure, predation, and habitat quality. Such variation must be understood, not only for basic population ecology, but also when assessing the status of a population, as an unbalanced sex ratio can significantly reduce the effective size and reproductive potential of the population.

Despite the ecological significance of sex ratio variation in fish, no studies have explicitly examined how the sex ratio of Eurasian perch varies across space and time in the Baltic Sea. This knowledge gap is particularly relevant in the context of ongoing environmental change with rising water temperatures, high levels of eutrophication, and shifting species interactions, all of which may differentially affect male and female perch.

The aim of this thesis is therefore to investigate spatial and temporal patterns in the sex ratio of Eurasian perch along the Swedish coast of the Baltic Sea and address the following questions:

- How do spatial and temporal patterns in the sex ratio of Eurasian perch vary along the Swedish Baltic Sea coast?
- What environmental or biological factors can potentially be associated with sex ratio variation across coastal areas?

By addressing these questions, this thesis contributes to a more comprehensive understanding of perch population dynamics in the Baltic Sea and provides information relevant to the sustainable management of coastal fish species.

2 Materials and Methods

2.1 Study area

This study covers the Swedish Baltic Sea coast, spanning about 1 500 km coastline from Råneå in the north (65.8°N) to Torhamn in the south (56.1°N; Figure 1).

Figure 1: The study area. The blue dots (Spatial) represent 14 locations that were used in the spatial analysis to examine changes in sex ratio of Eurasian perch across latitude. The red dots (Temporal) represent 11 locations that were used in the temporal analysis to adress the sex ratio trends across years. One green dot (Protected) represents a protected marine area.

There is a significant time imbalance in the monitoring data available, with some locations starting monitoring earlier, some sampling for longer, and some having data covering only a few years (Table 1). Therefore, two partially overlapping subsets of locations were used to answer the first research question, which focused on the variation of the sex ratio of Eurasian perch along the Swedish Baltic Sea coast and the variation over time.
The aim of the spatial analysis was to get a wide geographical representation of the Swedish coast over time, rather than getting a complete temporal representation of the coastline. A set of 14 sites: Seskaröfjärden, Råneå, Kinnbäcksfjärden, Holmön, Norrbyn, Gaviksfjärden, Forsmark, Lagnö, Asköfjärden, Askrikefjärden, Simpevarp, Östra Gotlands marina kustvatten, Kvädöfjärden, and Torhamn/Karlskona Ö skärgård (Figure 1) were used for the years 2020 to 2024. When comparing temporal variation, only locations that were sampled over a common time period with adequate sampling frequency were used. The 2007–2024 time period was the longest time frame over which there were enough geographically spread-out sites to provide data from an annual observation. 11 sites that fulfilled this criterion were: Råneå, Holmön, Gaviksfjärden, Norrbyn, Forsmark, Lagnö, Finbo (Åland), Långvindsfjärden, Asköfjärden, Kvädöfjärden, and Torhamn/Karlskrona Ö skärgård (Figure 1).
Licknevarpefjärden is a protected nature reserve that has been fully cloased for fisheries since the early 2000s (Bergström et al., 2022). As sampling in the area has not been conducted annually (Table 1) it was excluded from the statistical analyses and used only for visual comparison as it represent a no-take area.

Table 1: Summary of monitoring data for Eurasian perch sampled at coastal locations along the Swedish Baltic Sea coast. For each location, the gear type used, the time period over which data were collected, the total number of years sampled, and any missing years within the time series is listed.

Area	Gear	Time period	NO. years	Missing years
Asköfjärden	Nordiska kustöversiktsnät	2005–2024	19	2006
Askrikefjärden	Nordiska kustöversiktsnät	2016–2025	10	–
Finbo, Åland	Nordiska kustöversiktsnät	2007–2024	17	2021
Forsmark	Nordiska kustöversiktsnät	2002–2025	24	–
Gaviksfjärden	Nordiska kustöversiktsnät	2007–2025	19	–
Holmön	Nordiska kustöversiktsnät	2002–2025	24	–
Kinnbäcksfjärden	Nordiska kustöversiktsnät	2004–2025	22	–
Kvädöfjärden	Nordiska kustöversiktsnät	2001–2024	24	–
Licknevarpefjärden	Nordiska kustöversiktsnät	2013; 2018–2024	5	2014–2017; 2021–2022
Lagnö	Nordiska kustöversiktsnät	2004–2025	22	–
Långvindsfjärden	Nordiska kustöversiktsnät	2002–2024	21	2018; 2020
Norrbyn	Nordiska kustöversiktsnät	2002–2025	24	–
Östra Gotlands m kustvatten	Nordiska kustöversiktsnät	2018–2025	8	–
Råneå	Nordiska kustöversiktsnät	2002–2025	24	–
Seskaröfjärden	Nordiska kustöversiktsnät	2020–2025	6	–
Simpevarp	Nordiska kustöversiktsnät	2020–2025	6	–
Torhamn, Karlskrona skärgård	Nordiska kustöversiktsnät	2002–2025	24	–

2.2 Data collection

The data were part of the national coastal fish monitoring programme, which is coordinated by the Department of Aquatic Resources, Swedish University of Agricultural Sciences (SLU Aqua). Scientific fish surveys in coastal waters in Sweden have undergone changes in methodology. In the past, surveys were carried out using trawls and other types of nets, but there was a major change in

gear in the late 1990s and early 2000s, which involved using standardised gillnets for monitoring. (Cardinale & Svedäng, 2011; Naddafi et al., 2022). Nordic-type multi-mesh gillnets have been standardized and used for fish sampling since 2001 along the Swedish Baltic coast. These nets are 45m long and 1.8m high, consisting of nine 5m panels with mesh sizes of 10, 12, 15, 19, 24, 30, 38, 48, and 60 mm (Säterberg & Olsson, 2026).
Sampling is carried out annually in August, a period when water temperatures are typically highest and perch are widely distributed across the coastal zone (Mustamäki et al., 2014; Naddafi et al., 2022). The standardized structure of these surveys along the entire Swedish Baltic coast allows for regional and national assessments of fish communities (Säterberg & Olsson, 2026), and thus allowed me to follow different latitudes along the Swedish Baltic Sea in this study (Figure 1).

2.3 Length and Sex

All captured fish were individually measured for total length (tip of the snout to the end of the caudal fin). To ensure statistical strength and consistency across datasets, length measurements were pooled into full 1.0 cm groups. Approximately the first 10 to 20 perch individuals per centimeter class were sexed, aged, and weighed. The female proportion (sex ratio) was used as a key biological indicator in this study.

2.4 Environmental and biological factors

Catch-per-unit-effort (CPUE) of perch and roach were included as measures of local abundance to explore whether fish density and interspecific competition co-vary with the observed sex ratio patterns across sites and years. CPUE serves as an index for relative species abundance, indicating fish density. CPUE was calculated as the total number of fish caught divided by the total fishing effort (number of nets). CPUE data for the study species and for common roach *(Rutilus rutilus)*, a competitor for food, are summarized in Appendix Table A.1.
The water temperature was recorded in each area by an automated temperature logger. The temperature of the water surface was sampled every two hours, and daily averages were recorded by these loggers, giving a continuous thermal profile of the coastal habitat. Cumulative degree days were calculated for fish growth and activity as the "water degree temperature" to quantify the amount of thermal energy available. The metric was defined as the sum of the daily temperature values above 10°C. The 10°C threshold is biologically relevant for perch, and has been shown to be the lower boundary for substantial somatic growth and metabolism (Naddafi et al., 2022; Bergström et al., 2024). The dates of the temperature loggers and the total degree days that were reached are summarized in Appendix Table A.2.

2.5 Statistical analyses

All statistical analyses were done using R version 4.5.3 (R Core Team, 2026). Two generalized linear mixed models (GLMMs) were fitted to assess the spatial and temporal variation in the sex ratio of Eurasian perch, using the $glmer$ function in the $lme4$ package (Bates et al., 2015). For both models, sex ratio was analyzed as a binomial response variable, and the number of females and males in each length group for each location-year combination was entered as paired counts. Each observation is modeled as a proportion that is constrained between 0 and 1, for which the binomial family with a logit link function is appropriate.

2.5.1 Spatial analysis

Data from 14 locations (Figure 1) from 2020 to 2024 were used for the spatial model. Length group (centered) and latitude (LAT) (centered) were fixed effects, and the model was used to determine if there was systematic variation in sex ratio across the latitudinal gradient of the Swedish Baltic coast, while controlling for body size. A random slope for latitude was allowed to vary by year to accommodate the expectation that a year-to-year variation in the relationship of latitude to sex ratio may occur. To cover the possible year-to-year variation in size-structured variation in sex ratio, an added random effect is included for the interaction between year and length group. The spatial model is given as:

$cbind(NO.females, NO.males)\ Lengthgroup_c + LAT_c + (1 + LAT_c|Year_c) + (1|Year_c : Lengthgroup_c)$

2.5.2 Temporal analysis

For the temporal model, data from 11 locations (Figure 1) with data from 2007 to 2024 were used. Year (centered) and length group (centered) were fixed effects, with year treated as continuous to allow for any directional trends to be captured in sex ratio over time. To allow for any variations in sex ratios across the year, a random slope for year was included in the model, meaning that the slope for each area was allowed to vary from the overall average. An additional random effect for area * length group was also added to the model to account for the size-structured variation of sex ratio by location. The temporal model is specified as:

$cbind(NO.females, NO.males)\ Lengthgroup_c + Year_c + (1 + Year_c|Area) + (1|Area : Lengthgroup_c)$

2.5.3 Association of environmental and biological factors

A Principal Component Analysis (PCA) was performed using the PCA function in the $FactoMineR$ package (Lê et al., 2008), plot results in the $factoextra$ package (Kassambara & Mundt, 2020), with the following variables included: sex ratio for three length groups (small 7-14 cm, medium 15-22 cm, large 23-35 cm), CPUE of perch and roach, and degree temperature (sum of daily temperatures above 10°C over the year at each site). The year, latitude, and longitude were also included as secondary quantitative variables. The temporal dataset was used for the PCA because it contained more observations and allowed for a greater amount of variation to be captured.

Before performing the PCA, missing values were filled in with the $missMDA$ package (Josse & Husson, 2016). Variables with more than 80% of missing values were removed because imputing near-empty variables would introduce more noise than information. The number of imputation dimensions for the remaining variables was determined using k-fold cross-validation with the estim_ncpPCA function that estimates the dimensionality that minimizes the prediction error on the held-out observations (Podani et al., 2021). Following the retained variables from the last step, values were then estimated iteratively using $imputePCA$, which is based on the shared covariance structure among retained variables to fill data gaps. Entries that are missing are reported as "unknown" instead of zero, as in this dataset, missing entries occur due to practical constraints, such as gear selectivity or lack of temperature data, and not due to an actual zero value. All active variables were standardized to unit variance before analysis to account for differences in measurement scale.

3 Results

3.1 Spatial variation in sex ratios

The general linear mixed effects model revealed that the proportion of females in the catches was positively and significantly associated with the fish length, but that latitude did not have a significant effect (Table 2, Figure 2). The intercept was estimated at 0.855 (Table 2), corresponding to a perch caught in Forsmark (mid-Sweden latitude) and 21 cm body length (mid-range), at which the predicted female proportion was well above 50%. As shown in Figure 2, the smallest size classes of perch (7 cm) showed the predicted proportions of females around 30%, which increased with body length, approaching 95% in the largest size classes (30 cm). The random effects considered in the model accounted for variation across year-length group interactions, year, and latitude (Table 2), suggesting some temporal and spatial variation in sex ratios beyond what the fixed effects could explain alone. Despite not being significant, latitude showed a slight positive effect on the proportion of females with the proportion of females at the population level remaining consistently around 65–70% (Table 2, Figure 2). The exploratory plot of raw mean sex ratios by latitude shows considerable variation among areas, but no clear sount-north trend in mean sex ratio (Figure 2).

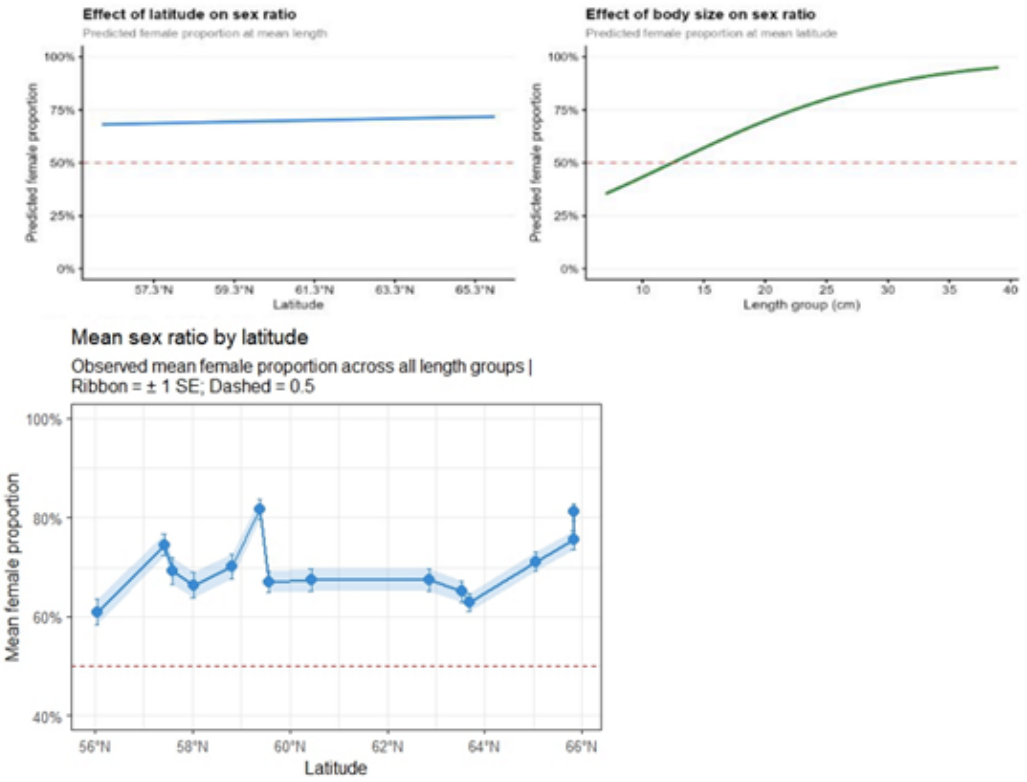

Figure 2: Predicted female proportion of Eurasian perch in the average size (21cm) across 14 monitoring locations (Upper left). Predicted sex ratio per length group across mean latitude (Forsmark) (Upper right). Mean sex ratio by latitude (Bottom left).

Table 2: Fixed and random effect estimates from the generalized linear mixed-effects model examining sex ratio variation across 14 sites from 2020 to 2024.

Random effects			
	σ^2	SD	
Year_c:Lengthgroup_c	0.051	0.226	
Year_c	0.0004	0.020	
Latitude_c	0.004	0.0197	
Fixed effects			
	b	SE	p value
(Intercept)	0.855	0.027	<0.001
Latitude_c	0.018	0.009	0.0648
Lengthgroup_c	0.111	0.004	<0.001

The three northernmost sites (Råneå, Seskaröfjärden, and Kinnbäcksfjärden) show consistent dimorphism, with females generally larger than males (Appendix Figure A.1), and the pattern is stable across years. The sex ratio increased sharply from roughly 0.3-0.4 at the smallest size classes (7-8 cm) to close to 1.0 at lengths above 30 cm (Figure 3). In contrast, Holmön, Norrbyn, and Gaviksfjärden, which are also all found in the north, showed more irregular patterns with the sex ratio being relatively similar across the entire length range, from 0.4 (0.5 in Gaviksfjärden) to 0.7, with wide confidence intervals and no meaningful increase at larger sizes (Figure 3).

Among the mid-coast sites, Forsmark, Lagnö and Asköfjärden, all maintained a consistent though moderate dimorphism over time (Appendix Figure A.1). The mid-coast location Askrikefjärden, however stands out in having an unusually large size difference between sexes (Appendix Figure A.1) and an increasing trends with a sex ratio starting at as low as 0.2 in the 8cm lengthgroup to 1.0 in larger fish, around 23 cm in 2020, but with notable variation between years, especially in smaller length classes (Figure 3).

Further south, Kvädöfjärden, Östra Gotlands m kustvatten, Simpevarp, and Torhamn showed a moderately increasing sex ratio with body length, but with considerable year-to-year variation across all length classes (Figure 3). In Figure A.1, it is obvious that these sites show moderate and consistent differences across the years, with a small male-female size variation over the years.

Licknevarpefjärden, the no-take zone (established in 1979; Bergström et al., 2022), stood out for having the largest fish across the study area (Appendix Figure A.1) and showed a gradual increase in the proportion of females with body length, reaching close to 1.0 at larger sizes. The pattern appeared consistent across the available years and was broadly comparable to what was observed in the northern sites.

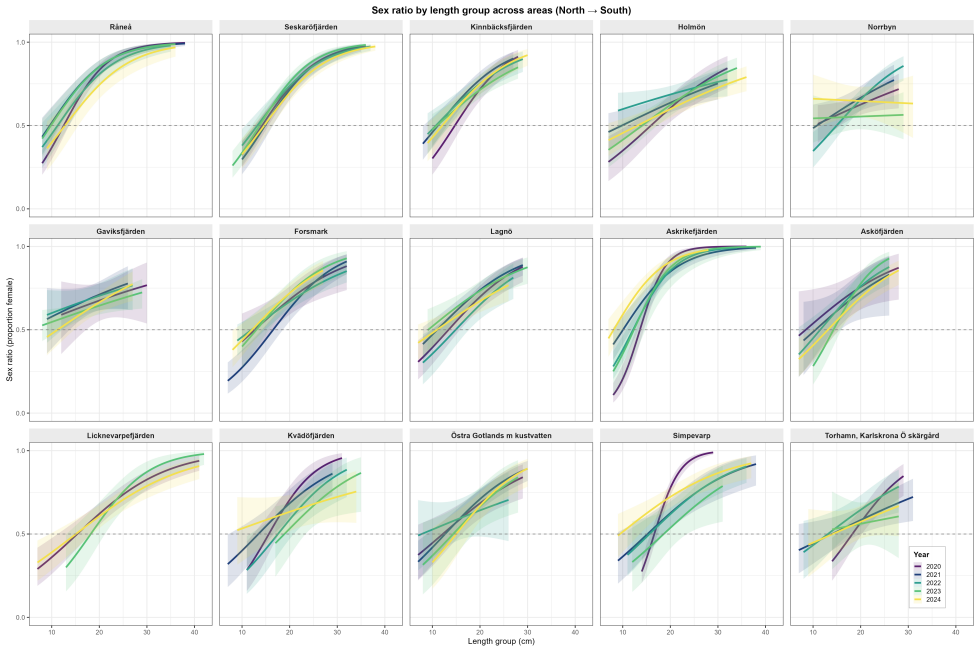

Figure 3: Exploratory plots of female proportion by fish length (cm) across the 14 spatial monitoring sites (north to south). Each line represents one sampling year (2020-2024).

3.2 Temporal variation in sex ratios

For temporal variation, the general linear mixed-effects model shows that fish length had a significant positive influence on the proportion of females in the catches, and that there was no significant influence of year on the proportion of females (Table 3, Figure 4). The baseline proportion of females was estimated at 0.887 (Table 3), which is still above 50%. The impact of the year was marginally negative and not statistically significant, and the model predictions bore this out, with the proportion of females being approximately 65% throughout the entire sampling period from 2007 to 2024 (Figure 4). The time series of the exploratory plot (Figure 4) of the mean sex ratio indicated a relatively stable trend around 65-70% throughout time, though with a slight indication that there may have been a slight decrease in sex ratios in more recent years.

The random effects in the model showed that the interaction between location and length group accounted for the highest unexplained variance, followed by location alone (Table 3), which indicates that there was a high variance in size-dependent sex ratio across sites.

There are neverthelesssex ratio variations over time in individual sites, as illustrated in Figure 5. Generally, the northernmost site (Råneå) presented the most consistent and stable size dimorphism pattern (Appendix Figure A.2) and in sex ratio curves (Figure 5) throughout the 17 years compared to the other northern sites (Holmön, Norrbyn, and Gaviksfjärden) with more irregular pattern between years (Figure 5).

For the mid-coast sites, Långvindsfjärden Forsmark, Finbo, and Lagnö had a moderate dimorphism with some temporal variation, but without any significant directional change (Appendix Figure A.2), while the sex ratio was moderately variable between years and generally followed the general pattern, similar to one in Råneå (Figure 5). The sex ratio curves are significantly flatter than in all other years during the last year (2024) in the southernmost areas known as Kvädöfjärden and Torhamn (Figure 5).

Despite the inter-annual differences in sex ratio curves, the sex ratio curves in most sites in most recent years, particularly 2023 and 2024, show decreasing female proportions across larger length classes than earlier years in the time series.

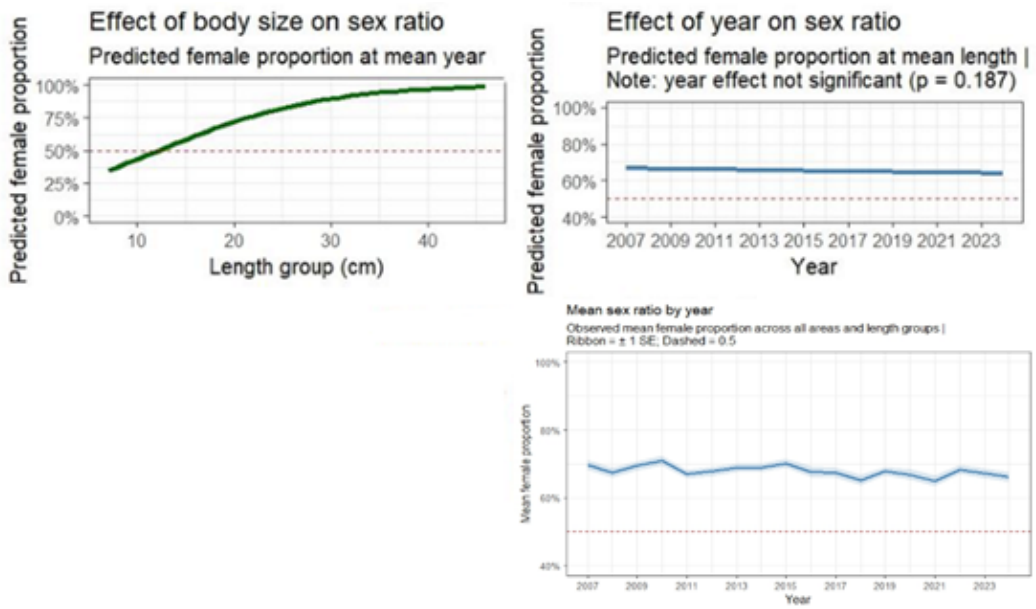

Figure 4: Predicted female proportion of Eurasian perch in averaged (21cm) across 17 years (Upper right). Predicted sex ratio per length group across mean year (2016) (Upper left). Mean sex ratio by year (bottom right).

Table 3: Fixed and random effect estimates from the temporal generalized linear mixed-effects model examining sex ratio trends in Eurasian perch across 11 locations from 2007-2024.

Random effects			
	σ^2	SD	
Area:Lengthgroup_c	0.144	0.380	
Area	0.085	0.292	
Year_c	0.0003	0.017	
Fixed effects			
	b	SE	p value
(Intercept)	0.887	0.092	<0.001
Year_c	-0.007	0.005	0.187
Lengthgroup_c	0.121	0.004	<0.001

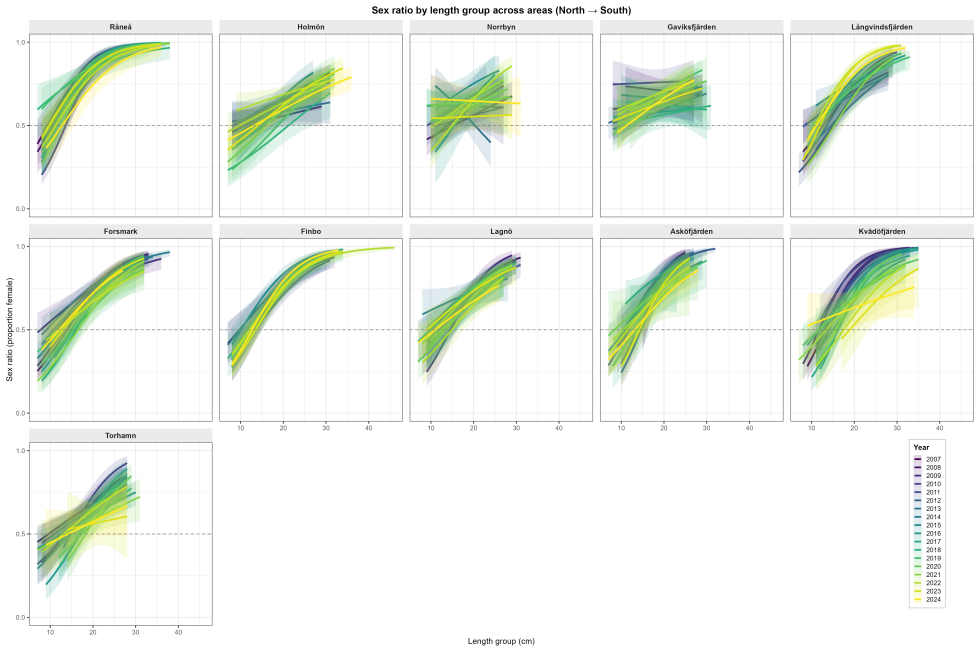

Figure 5: Exploratory plots of female proportion by fish length (cm) across the 11 temporal monitoring locations (north to south). Each line represents one sampling year (2007-2024).

3.3 Association of environmental and biological factors

The first four axes of the PCA together explained 84.4% of the total variation, with PC1 and PC2 accounting for 33.0% and 21.3%, respectively (Appendix Table A.3). PC1 broadly represented a co-occurences of locations characterised by higher water temperature (0.658), perch abundance (0.646), and female-biased sex ratios in larger size classes (0.806), all loading strongly and positive with PC1 (Appendix Table A.4, Figure 6). On the countrary, sex ratio in the smallest size class (7–14 cm) loaded negatively on PC1 (-0.478), suggesting that locations characterised by lower temperatures and less abundance of perch tended to have a more male-biased sex ratio among small perch.
PC2 showed the variation in sex ratio of smaller and medium-sized fish as both sr_medium (0.765) and sr_small (0.583) loaded positively and degree temperature loading negatively with the axis (-0.414). This implies that the female-biased sex ratios of the small and medium size classes were not associated with warmer conditions.
The 95% confidence ellipses for most locations did not differ in this PC1–PC2 biplot, indicating low separation between the sampling locations in this ordination space; however, some locations (e.g., Råneå and Gaviksfjärden) seemed to be separated in PC1, which may reflect differences in temperature regime and perch abundance (Appendix Table A.3 and A.4).

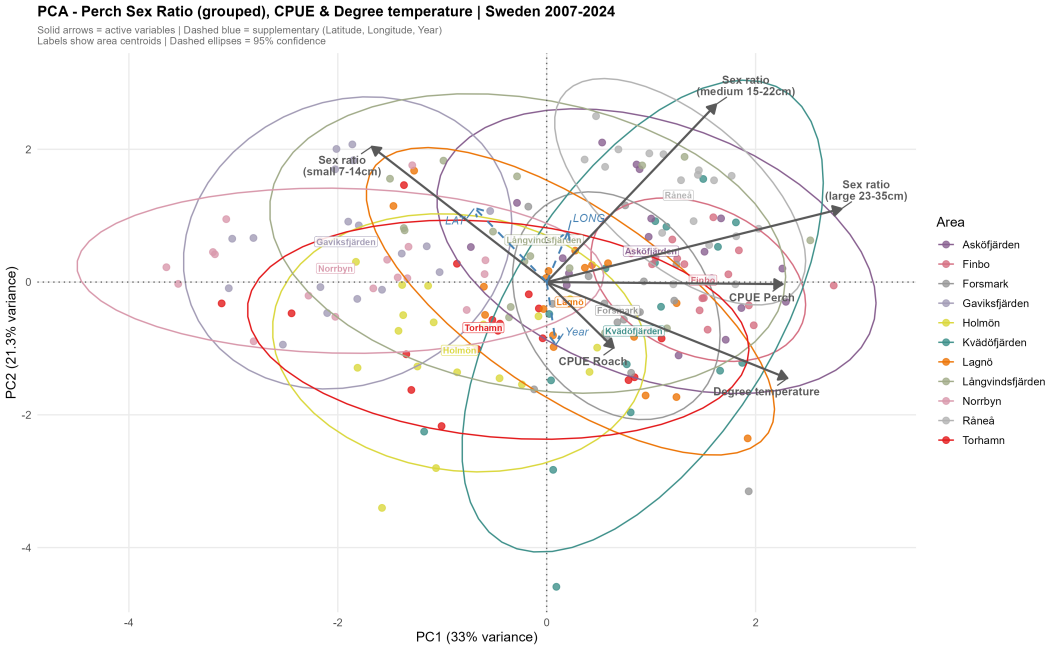

Figure 6: PCA biplot of the first two principal components (PC3 and PC4), based on sex ratio in three size classes, perch and roach CPUE, and degree temperature across 11 monitoring locations (2007–2024). Arrows represent active variable loadings; 95% confidence ellipses are drawn around site centroids. Latitude, longitude, and year are shown as supplementary variables.

In addition to PC1 and PC2, the patterns in PC3 and PC4 (Appendix Figure A.5) were also examined to capture more of the variance and avoid missing out on any patterns in the other two components. PC3 and PC4 are shown in a supplementary biplot (Appendix Table A.3) and explain an additional 17.8% and 12.4% of the total variance, respectively.
The abundance of roach was strongly associated with a positive load on PC3 (0.881), indicating that

the abundance of roach was largely independent of variation from the temperature and size-structured sex ratio patterns captured in PC1 and PC2.
PC4 showed negative loadings for CPUE Perch (-0.688) and positive loadings for degree temperature (0.439), which may represent years or sites where high temperature was not associated with high perch catch.
The supplementary variables latitude, longitude, and year contributed relatively little to all four PC axes and did not contribute to the overall variation in the data set (Appendix Table A.4). This finding is similar to the outcome of the mixed-effect model analysis, which revealed no strong directions of effects of these variables on sex ratio.

4 Discussion

This study examined the spatial and temporal variation in the sex ratio of Eurasian perch along the Swedish Baltic Sea coast, and possible environmental and biological influences on this variation. The results indicate that fish size was the best predictor of the female proportion in the monitoring catches in all areas and that there were no statistically significant effects of either latitude or year. Instead, it appears that water temperature and the abundance of perch in a location are influential for the sex ratio of perch, with a female-biased sex ratio in warmer locations that have high perch abundances.

The pattern of a high positive correlation of fish size and female proportion of catches was the most consistent result of this study and was observed over both space and time. The percentage of females in the monitoring catches in the smallest size class (7-8 cm) was approximately 30%, but in large sizes (25-30 cm), the percentage of females reached nearly 95%. This type of sex ratio development with size is well documented in percid fishes (Rennie et al., 2008; Prchalova et al., 2022) and is directly linked to female-biased sexual size dimorphism (SSD) (Prchalova et al., 2022), which is the tendency for females to be larger than males of the same age. At its core, the pattern causing SSD is the difference in energy allocation between males and females throughout their development. In perch, the males mature earlier and at a smaller size than females (Craig, 1974, cited in Ning et al., 2025). Once mature, male growth slows down considerably, since energy that could go into somatic growth is increasingly directed towards reproductive investment instead (Rennie et al., 2008). In females, on the other hand, there is a strong selection for increased growth as larger females produce more eggs and generally have higher reproductive success (Olin et al., 2012; Barneche et al., 2018). This results in males and females being increasingly different as they grow older (Prchalova et al., 2022) and thus is the reason why, more females than males are larger and older, in gillnet catches (Prchalová et al., 2008; Olin et al., 2016). Thus, males are not missing from the population, but merely lack the same abundance of the sizes represented in the catches when using gillnets.

The most straightforward explanation for a male domination of smaller size classes (in my study, 7-8 cm) is hence that females simply grow out of that size (Horppila et al., 2011; Estlander et al., 2015). An apparent excess of male fish at the small end of the size spectrum may be due, at least in part, to the fact that males are at a different stage of growth than females at a specific time. Moreover, because SSD in percids can only be recognized at or after maturity (van Dorst et al., 2023), there is little divergence between the sexes at very small sizes, and the male-biased pattern could at least partly be due to the pre-maturation window when size differences are still low. None of this suggests more males are born since the sex ratio at birth is expected to be close to 1:1 (Fisher, 1930).

I found no strong effect of latitude on sex ratio patterns in this study, despite the fact that the Swedish Baltic Sea coastline covers an almost 10-degree latitude span, with the range of conditions, from cold and almost freshwater-like in the north to warmer and more saline conditions in the south (HELCOM, 2023; Stockmayer & Lehmann, 2023). In general, perch tend to grow more slowly with increasing latitude and age at maturity, and lifespan tends to be higher at high latitudes (Heibo et al., 2005; Estlander et al., 2017). It has long been recognized that year-class strength and growth rates in perch are dependent on summer water temperatures in th Baltic (Neuman, 1976; Böhling et al., 1991), and a latitudinal gradient is hence expected. Fish in warmer and more southern regions grow faster and reach a larger size at a given age (Heibo et al., 2005), and since body size is the main factor that induces SSD, the more southern regions should exhibit more female-dominated size classes than the more northern regions (Heibo et al., 2005; Estlander et al., 2017). In this thesis, however, I found the opposite with a weak positive trend where the proportion of females increased slightly with latitude. The distribution of a location at the coast is nevertheless not a good predictor

of the sex ratio pattern in perch. This is probably because the fish size gradient (within-location) is so powerful that it outweighs any larger spatial scale gradient.

The time trend analysis of sex ratio variation (2007-2024) indicated a non-significant effect of year on the sex ratio of perch. But the model showed a slight negative trend over time, suggesting a tendency for a lower proportion of females at a given size during later years. The 17-year span considered in this study might hence not be long enough to detect potential demographic changes. Despite this, however, there was substantial inter-annual variation in sex ratios in the surveyed sites. In the last few years of the time series, 2023 and 2024, show decreasing female proportions across length classes along the Swedish Baltic coast. Looking at the raw data, this is not caused by fewer females at large sizes, but by males increasingly reaching length classes that were previously dominated almost entirely by females. Experimental work on this exact population found, explained above, that warming increases female growth while suppressing male growth above roughly 10 cm and age two, which would be expected to steepen the sex ratio pattern rather than flatten it (van Dorst et al., 2023). Relaxed competition due to lower fish density is also unlikely here, since CPUE perch has generally increased rather than decreased over the same period at most sites. Higher density would typically be expected to constrain growth further through competition, not release it (Persson & Greenberg, 1990).
A more plausible explanation is reduced mortality specifically among males, allowing more of them to survive to large, older size, rather than any change in individual growth rates. This would be consistent with a broader recovery of coastal perch populations in parts of the Baltic Sea following a period of decline linked to increased stickleback predation on perch larvae (Bergström et al., 2015). This, however, was not tested directly in the present study, since it would require separate analysis of male-specific length-at-age and survival data.

In addition to the two GLMMs presented above, a PCA was done to investigate the relationship between sex ratios variation across size, temperature, and abundance of fish (perch and roach) across sites and years. The PCA was not applied to test specific hypotheses, but to identify multivariate patterns that could not be identified by univariate models. The PCA accounted for a significant proportion of the overall variance and revealed a relationship between high abundance of the perch, warm waters, and the presence of female-dominated large size classes.

The associatios between warm-temperature and higher sex ratio skew towards females in larger size classes is consistent with what was previously described, where warming has different effects on males and females. At small sizes, both sexes grow faster in the warmer water, but as indicated above, after about 10 cm and 2 years of age, the growth trajectories split (van Dorst et al., 2023). This benefits and accelerates growth in all sizes for females but slows down growth in males (van Dorst et al., 2023). Metabolic costs of maintaining a large body in warm water seem to dominate feeding returns in males, but not in females, who continue to obtain additional reproductive returns with further growth (Craig, 1987; Rennie et al., 2008; Ohlberger et al., 2012). The result is that warm, productive sites show a greater sex size dimorphism, not only due to SSD in general, but also due to the increase in sex size dimorphism caused by warming. The impact of warming on perch growth is size-specific and cumulative across generations, suggesting that the effect is strongest at sites experiencing chronic warming (Huss et al., 2019).

It further makes sense that male fish are selectively more abundant in smaller size classes at warm sites than females in smaller size classes. While there are no fewer females produced in warmer conditions, females grow faster through small size classes, leaving smaller size classes more male-dominated (Rennie et al., 2008; Prchalová et al., 2022; van Dorst et al., 2023). Warming also brings

maturation at smaller body sizes and younger ages (Niu et al., 2023), which means that the transition from a male-biased to a female-biased sex ratio with body size also moves to an earlier stage in the life history. Lindmark et al. (2022) further showed that the optimum growth temperature for perch actually declines with body size- smaller fish have a higher thermal optimum than larger ones. This implies there may be true differences in processes driving the sex ratio of juvenile and mid-sized fish, as compared to large fish. From what data was available, or rather chosen to be considered in this study, it is hard to determine if sex-specific differences in juvenile survival, recruitment, or early growth causes the observed patterns, and the results should perhaps be regarded as a suggestion that the juvenile dynamics of sex ratio trajectories of smaller fish are not as straightforward as the simple SSD theory.

Another evident relationship that was suggested from the PCA was that of high perch abundance being associated with large size and female biased sex ratios. The SSD could be explained by the linear relationship between water temperature and perch abundance (Bergström et al., 2016), where the high proportion of female in the larger fish is merely a result of the warmer water temperature. Thus, the higher the temperature and level of abundance of perch at a locations, the higher the proportion of the largest size classes being female (van Dorst et al., 2023). There might hence not a direct causal relationship between abundance and sex ratio, but rather a link with the same underlying condition, namely thermal productivity.

Roach was added to the analysis as it is also a commonly occurring species in the Baltic coastal waters and it shares similar food items with perch, especially when they are juveniles, when both species compete for zooplankton and invertebrate prey (Persson & Greenberg, 1990). Interspecific competition with roach may hence play a role in structuring perch populations on a local scale, but I was unable to find any association with roach abundance and sex ratios over any size, suggesting that roach does not have a major structuring role for determining the sex ratio patterns observed in my data set.

In my study, I found that fish in Licknevarpefjärden, a long-term no-take zone for perch and pike in the Baltic Sea (Bergström et al., 2022), were consistently among the largest ones in the entire dataset, and the sex ratio patterns were notably stable across years, exhibiting far less interannual variation compared to other locations considered where fishing takes place. The SSD in Licknevarpefjärden was clearly expressed, with female proportion rising steeply with body length according to the expected pattern. What stood out, however, was that the point at which total female dominance appeared to be reached occurred at a larger body length than at most other sites, and near-complete female dominance was hence pushed further up the size spectrum. In the absence of fishing, males are also able to grow larger than they typically do in fished populations.

5 Conclusion and future perspective

Overall, the results presented in this thesis show that the variation in sex ratio in Eurasian perch along the Swedish Baltic Sea coastline is mainly related to the sexual size dimorphism resulting in male dominance of smaller fish size and female dominance in larger sizes. The reason for this is that females grow more quickly and benefit from freaching bigger body length.
No clear temporal or latitudional trends were observed, but the slight flattening of sex ratio patterns in recent years may reflect an early response to the continued environmental change. This further indicates that potential changes in size distributions with future warming and changes in ecosystem productivity may have indirect effects on sex ratios and reproductive potential, and that the location trends in sex ratio appear to be more important than the regional trend.
The results obtained in this study could be important to future management of perch as warming seems to have different effects on the growth of males and females. Meanwhile, there are several things to be aware of. Gillnet surveys are size selective, and estimates of sex ratios of the smallest and largest fish are less certain. Furthermore, age and maturation data were not considered in the study, and it is hence difficult to distinguish the effects of maturation from the effects of age on sex ratios. There is hence a potential to use aging and tagging data with the monitoring data to further understand and explain the patterns observed. Ongoing monitoring will also be useful to identify if the recent trend, as I have observed in this study, is indicative of long-term change or short-term fluctuations.

Acknowledgements

I would like to thank all staff involved in collecting the coastal fish monitoring data I have used in the thesis. I would like to thank my supervisors, Jens Olsson and Matilda Andersson, for their support, guidance, and valuable comments throughout the period.

6 Popular Science Summary

The European perch *(Perca fluviatilis)* is one of the most common fish species in the coastal waters of the Baltic Sea. It plays a central role in the coastal food web, both as predator and prey, and is important for recreational and small-scale fisheries along the Swedish coast. Because it is so widespread and has been monitored for decades, perch is also a convenient species for tracking how fish populations respond to a changing coastal environment.

One basic but often overlooked property of a fish population is its sex ratio, the proportion of females relative to the total population. This matters because it directly affects how many offspring a population can produce, and therefore how resilient it is over time. In theory, a stable environment should produce a roughly even 1:1 ratio of males to females. In practice, this balance is rarely seen in wild fish populations. Sex ratios can shift for several reasons: natural differences in how fast males and females grow, differences in survival between the sexes, or human pressures such as fishing, which tends to remove the largest individuals from a population, and in perch, the largest individuals are almost always female.

I wanted to find out whether the proportion of females in the population changes across the coastline or over time, and what biological or environmental factors could help explain any patterns found. To answer this, I used data from the Swedish National Coastal Fish Monitoring programme, covering up to 14 sites and up to 17 years of sampling. Alongside sex ratio, I also looked at water temperature and the abundance of perch and its food competitor, common roach, as possible drivers of the patterns observed.

The results showed that fish size, not location or year, was by far the strongest predictor of sex ratio. This size pattern was remarkably consistent across the entire coastline and through the whole seventeen-year period. Neither latitude nor year had a meaningful effect on its own, even though the Swedish coast spans large differences in temperature and salinity from north to south. When looking more closely at temperature and perch abundance together, sites with warmer water and more perch tended to have a stronger female bias among the larger fish, hinting that local growth conditions, rather than latitude itself, are what really shape these patterns.

One thing I did notice in the most recent years of the monitoring data was a slight flattening of this size-to-sex-ratio relationship at several sites, meaning that more males were showing up in size classes that used to be almost entirely female.

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8 Appendix

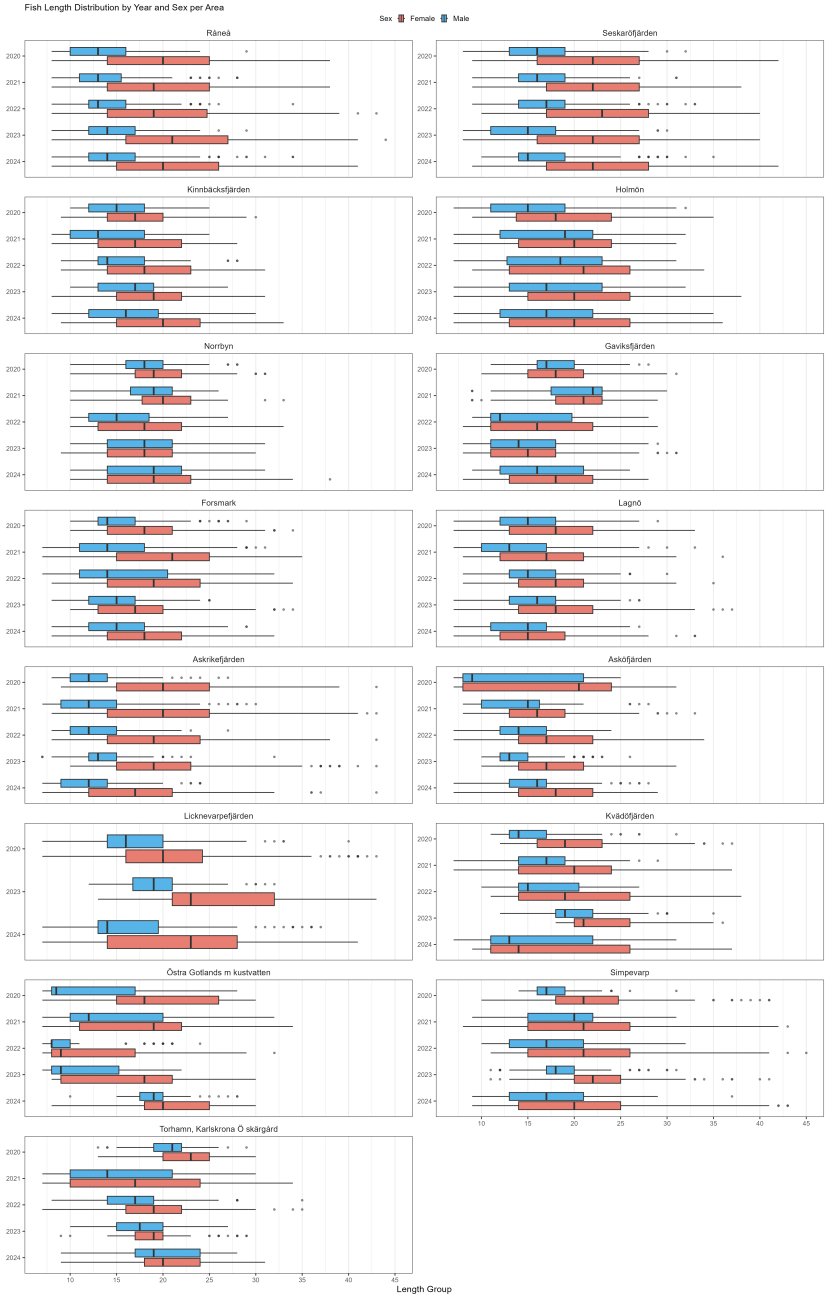

Figure A.1: Mean total length of male and female Eurasian perch at each of the 14 spatial monitoring locations, shown separately by sex. Bars represent mean length with standard error, illustrating the degree of sexual size dimorphism at each site.

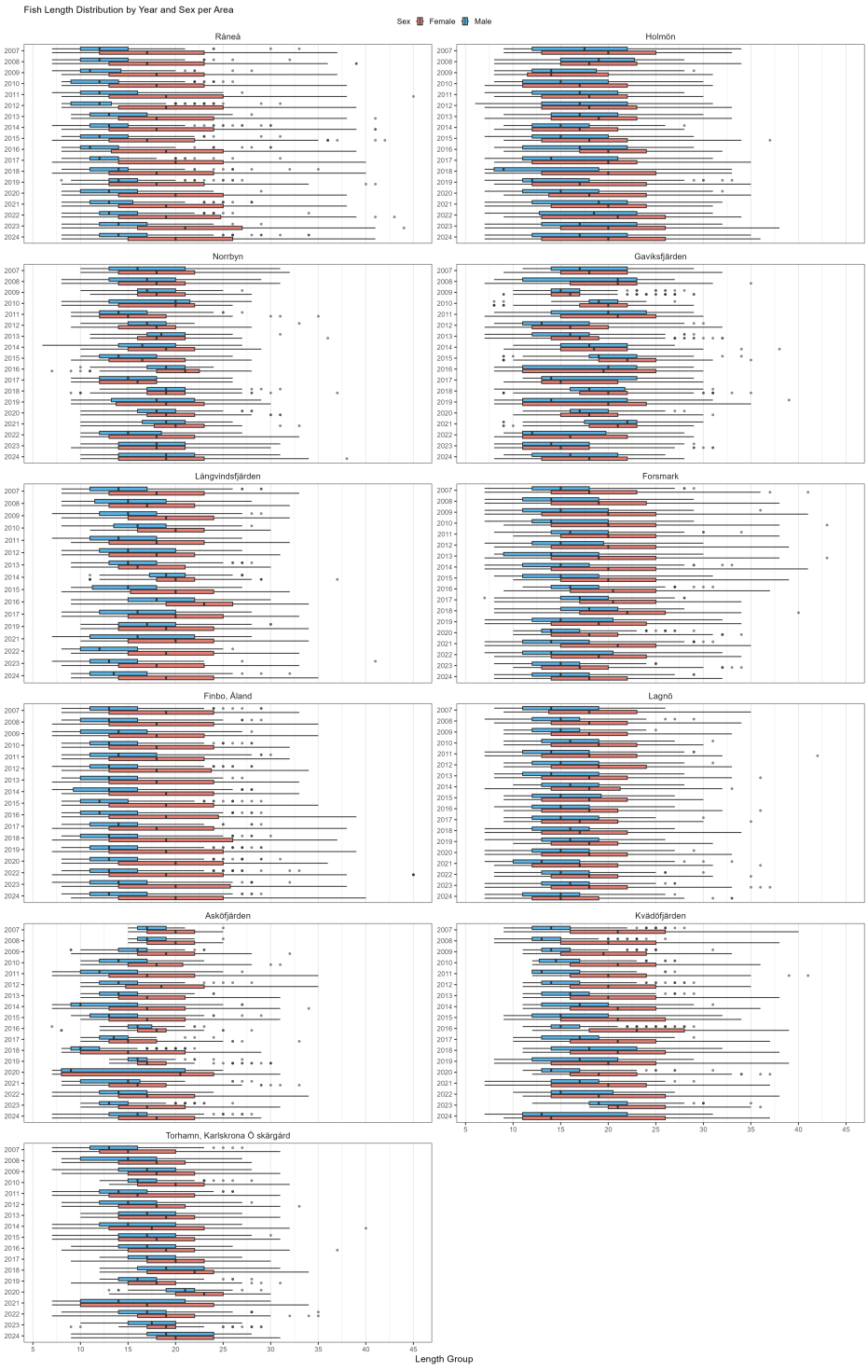

Figure A.2: Mean total length of male and female Eurasian perch at each of the 11 temporal monitoring locations across the 2007–2024 sampling period, shown separately by sex and year to illustrate temporal trends in sexual size dimorphism.

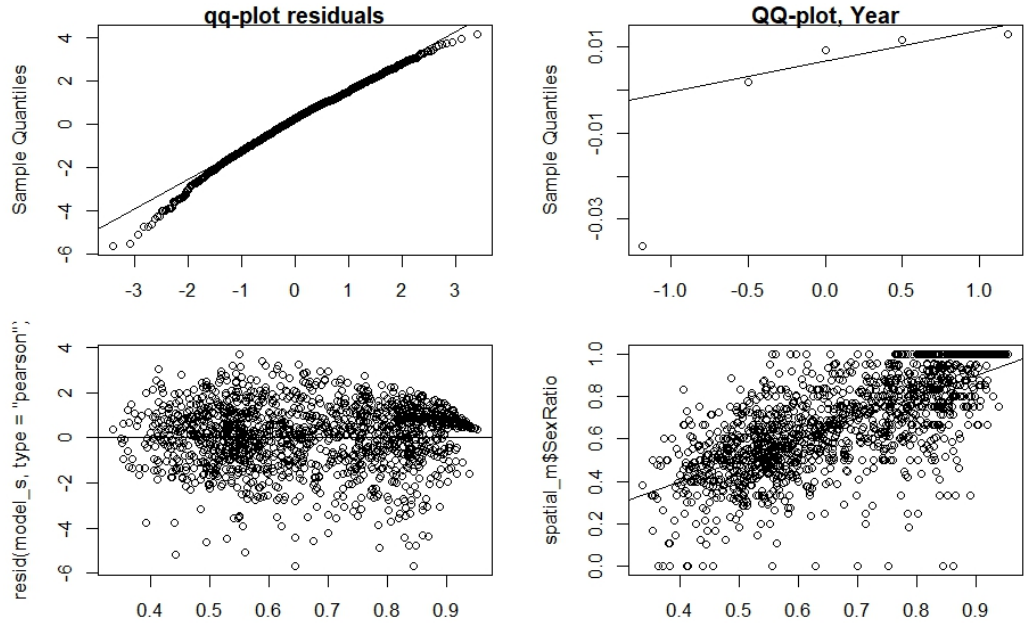

Figure A.3: Quantile-quantile (Q-Q) plot of the general linear mixed-effect model for spatial data set.

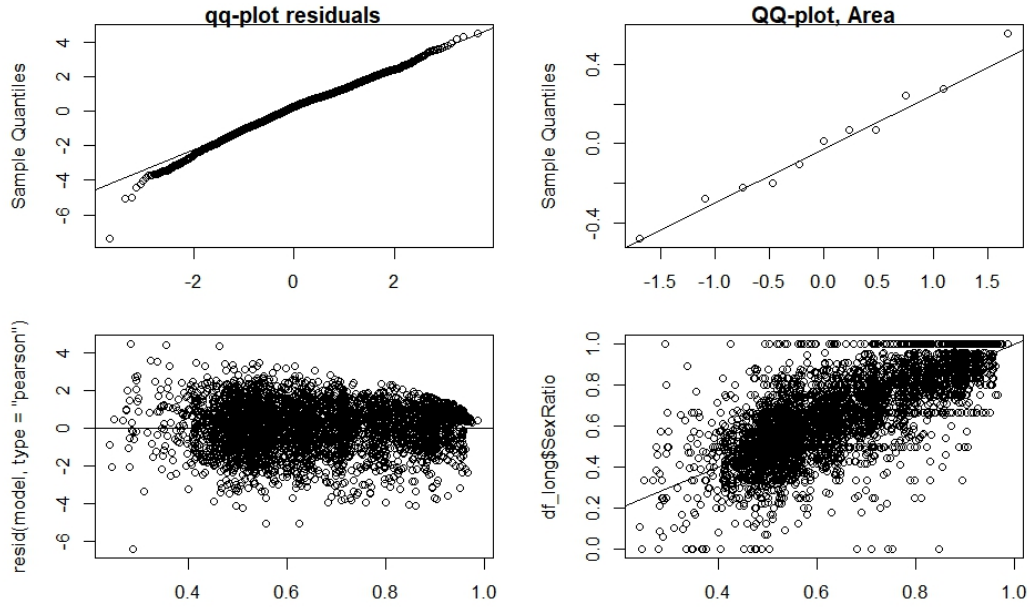

Figure A.4: Quantile-quantile (Q-Q) plot of the general linear mixed-effect model for temporal data set.

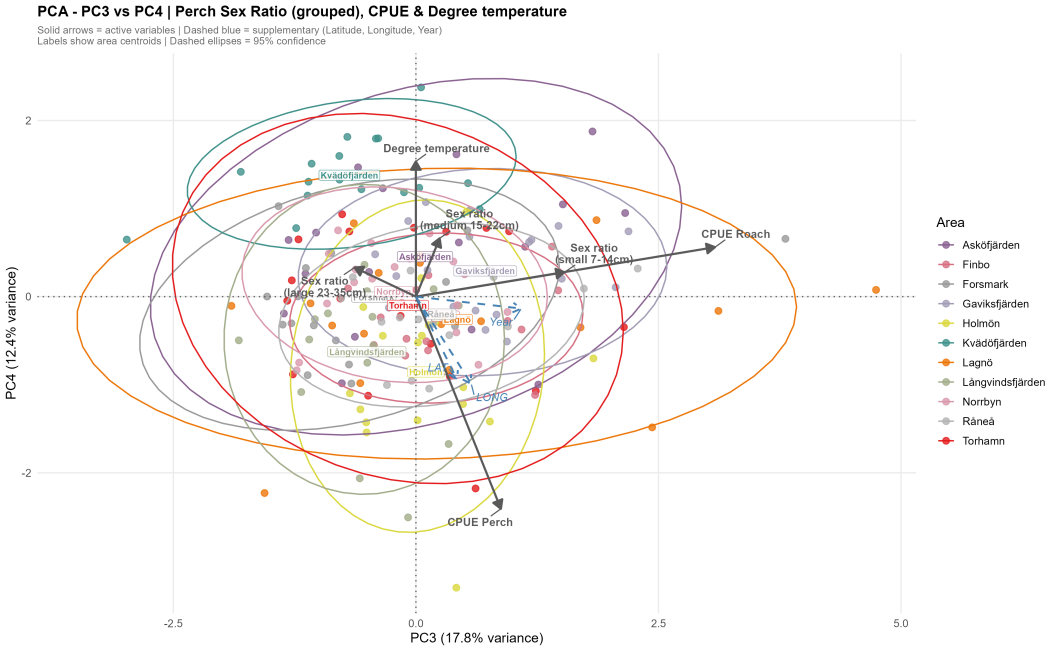

Figure A.5: PCA biplot of the 3rd and 4th principal components (PC1 and PC2), based on sex ratio in three size classes, perch and roach CPUE, and degree temperature across 11 monitoring locations (2007–2024). Arrows represent active variable loadings; 95% confidence ellipses are drawn around site centroids. Latitude, longitude, and year are shown as supplementary variables.

Table A.1: (CPUE summary). Catch-per-unit-effort for Eurasian perch and common roach at each monitoring location included in the PCA, summarised across the 2007–2024 sampling period.

Area	Year	CPUE perch	CPUE roach
Asköfjärden	2007	31.42	17.84
Asköfjärden	2008	21.13	34.55
Asköfjärden	2009	18.23	1.58
Asköfjärden	2010	14.80	1.67
Asköfjärden	2011	30.07	5.86
Asköfjärden	2012	22.70	4.81
Asköfjärden	2013	20.19	10.92
Asköfjärden	2014	30.48	1.74
Asköfjärden	2015	17.39	16.67
Asköfjärden	2016	5.85	9.68
Asköfjärden	2017	8.37	14.65
Asköfjärden	2018	3.83	12.08
Asköfjärden	2019	9.96	8.03
Asköfjärden	2020	2.72	27.19
Asköfjärden	2021	18.21	21.05
Asköfjärden	2022	18.53	30.97
Asköfjärden	2023	29.32	16.11
Asköfjärden	2024	35.97	21.22
Finbo	2007	28.27	14.56
Finbo	2008	30.42	7.93
Finbo	2009	25.56	12.58
Finbo	2010	28.29	10.79
Finbo	2011	22.18	7.67
Finbo	2012	26.84	11.56
Finbo	2013	30.36	11.65
Finbo	2014	29.36	10.16
Finbo	2015	23.80	23.07
Finbo	2016	25.69	13.37
Finbo	2017	20.09	13.93
Finbo	2018	23.24	12.77
Finbo	2019	28.13	18.40
Finbo	2020	30.00	22.89
Finbo	2021	28.97	16.74
Finbo	2022	25.97	22.95
Finbo	2023	32.00	16.11
Finbo	2024	43.12	20.79
Forsmark	2007	17.80	2.37
Forsmark	2008	28.05	5.53
Forsmark	2009	14.22	2.97
Forsmark	2010	15.71	4.97
Forsmark	2011	27.11	6.31
Forsmark	2012	30.91	5.12
Forsmark	2013	26.87	3.63
Forsmark	2014	29.13	1.11
Forsmark	2015	20.49	4.86

Table A.1: (CPUE summary). Catch-per-unit-effort for Eurasian perch and common roach at each monitoring location included in the PCA, summarised across the 2007–2024 sampling period.

Area	Year	CPUE perch	CPUE roach
Forsmark	2016	23.62	1.60
Forsmark	2017	20.67	7.69
Forsmark	2018	11.68	2.09
Forsmark	2019	26.18	15.71
Forsmark	2020	17.44	18.46
Forsmark	2021	26.44	52.89
Forsmark	2022	19.31	17.57
Forsmark	2023	19.34	6.54
Forsmark	2024	19.09	14.89
Gaviksfjärden	2007	7.98	16.15
Gaviksfjärden	2008	2.83	9.19
Gaviksfjärden	2009	10.51	12.48
Gaviksfjärden	2010	8.02	13.83
Gaviksfjärden	2011	9.89	20.08
Gaviksfjärden	2012	9.87	18.20
Gaviksfjärden	2013	13.33	8.15
Gaviksfjärden	2014	24.29	10.55
Gaviksfjärden	2015	10.49	22.33
Gaviksfjärden	2016	6.81	24.37
Gaviksfjärden	2017	7.02	22.89
Gaviksfjärden	2018	9.89	15.74
Gaviksfjärden	2019	7.40	12.03
Gaviksfjärden	2020	9.09	10.10
Gaviksfjärden	2021	4.89	8.36
Gaviksfjärden	2022	3.48	7.75
Gaviksfjärden	2023	6.58	16.28
Gaviksfjärden	2024	16.55	15.08
Holmön	2007	24.40	3.33
Holmön	2008	24.86	5.46
Holmön	2009	16.57	7.80
Holmön	2010	15.87	8.03
Holmön	2011	20.53	11.90
Holmön	2012	28.23	11.83
Holmön	2013	29.90	21.87
Holmön	2014	21.30	10.93
Holmön	2015	28.63	12.90
Holmön	2016	6.44	25.24
Holmön	2017	9.40	11.33
Holmön	2018	11.40	17.97
Holmön	2019	19.30	12.56
Holmön	2020	31.43	9.33
Holmön	2021	17.40	12.87
Holmön	2022	29.86	13.83
Holmön	2023	33.87	13.70
Holmön	2024	37.23	10.93

Table A.1: (CPUE summary). Catch-per-unit-effort for Eurasian perch and common roach at each monitoring location included in the PCA, summarised across the 2007–2024 sampling period.

Area	Year	CPUE perch	CPUE roach
Kvädöfjärden	2007	13.96	12.00
Kvädöfjärden	2008	11.33	12.39
Kvädöfjärden	2009	11.18	8.60
Kvädöfjärden	2010	8.18	10.94
Kvädöfjärden	2011	12.51	8.14
Kvädöfjärden	2012	16.29	5.20
Kvädöfjärden	2013	13.02	10.46
Kvädöfjärden	2014	10.42	10.26
Kvädöfjärden	2015	12.11	12.49
Kvädöfjärden	2016	9.56	9.00
Kvädöfjärden	2017	6.40	10.94
Kvädöfjärden	2018	11.75	14.44
Kvädöfjärden	2019	11.96	13.86
Kvädöfjärden	2020	13.76	14.17
Kvädöfjärden	2021	18.26	19.89
Kvädöfjärden	2022	7.18	11.76
Kvädöfjärden	2023	4.91	5.97
Kvädöfjärden	2024	8.29	17.51
Lagnö	2007	19.31	5.14
Lagnö	2008	20.64	2.57
Lagnö	2009	13.42	0.97
Lagnö	2010	20.07	2.97
Lagnö	2011	30.58	4.51
Lagnö	2012	20.93	8.26
Lagnö	2013	19.69	9.60
Lagnö	2014	14.70	6.00
Lagnö	2015	15.55	27.03
Lagnö	2016	9.07	13.66
Lagnö	2017	12.50	14.61
Lagnö	2018	38.05	10.89
Lagnö	2019	25.72	19.50
Lagnö	2020	30.33	19.26
Lagnö	2021	26.32	25.09
Lagnö	2022	44.21	33.00
Lagnö	2023	32.34	34.40
Lagnö	2024	32.80	50.83
Långvindsfjärden	2007	17.40	10.60
Långvindsfjärden	2008	18.78	12.54
Långvindsfjärden	2009	21.65	5.79
Långvindsfjärden	2010	12.57	4.50
Långvindsfjärden	2011	21.89	13.31
Långvindsfjärden	2012	14.81	2.49
Långvindsfjärden	2013	19.53	10.26
Långvindsfjärden	2014	12.00	2.18
Långvindsfjärden	2015	15.53	7.09

Table A.1: (CPUE summary). Catch-per-unit-effort for Eurasian perch and common roach at each monitoring location included in the PCA, summarised across the 2007–2024 sampling period.

Area	Year	CPUE perch	CPUE roach
Långvindsfjärden	2016	10.48	12.94
Långvindsfjärden	2017	14.18	16.56
Långvindsfjärden	2018	24.32	5.00
Långvindsfjärden	2019	11.86	0.79
Långvindsfjärden	2020	28.22	11.06
Långvindsfjärden	2021	37.14	9.21
Långvindsfjärden	2022	20.40	5.54
Långvindsfjärden	2023	42.65	14.12
Långvindsfjärden	2024	42.26	6.97
Norrbyn	2007	13.18	2.00
Norrbyn	2008	12.41	2.42
Norrbyn	2009	7.40	4.45
Norrbyn	2010	2.57	4.03
Norrbyn	2011	6.48	8.68
Norrbyn	2012	3.16	3.63
Norrbyn	2013	9.98	6.03
Norrbyn	2014	15.71	9.60
Norrbyn	2015	3.76	4.90
Norrbyn	2016	3.84	15.67
Norrbyn	2017	4.31	12.24
Norrbyn	2018	5.40	6.47
Norrbyn	2019	13.89	9.97
Norrbyn	2020	9.24	8.29
Norrbyn	2021	5.59	12.76
Norrbyn	2022	6.03	10.97
Norrbyn	2023	15.60	12.29
Norrbyn	2024	26.48	10.98
Råneå	2007	23.68	18.15
Råneå	2008	14.52	13.70
Råneå	2009	29.51	14.23
Råneå	2010	17.48	11.34
Råneå	2011	24.33	13.86
Råneå	2012	34.00	10.14
Råneå	2013	34.16	8.77
Råneå	2014	25.33	20.23
Råneå	2015	16.23	12.74
Råneå	2016	25.78	9.06
Råneå	2017	14.51	7.23
Råneå	2018	26.67	26.29
Råneå	2019	23.13	20.77
Råneå	2020	27.05	14.88
Råneå	2021	23.97	10.57
Råneå	2022	28.54	14.20
Råneå	2023	28.68	9.74
Råneå	2024	36.69	9.40

Table A.1: (CPUE summary). Catch-per-unit-effort for Eurasian perch and common roach at each monitoring location included in the PCA, summarised across the 2007–2024 sampling period.

Area	Year	CPUE perch	CPUE roach
Torhamn	2007	14.25	22.96
Torhamn	2008	8.62	10.74
Torhamn	2009	9.10	10.44
Torhamn	2010	14.26	10.10
Torhamn	2011	14.05	11.90
Torhamn	2012	23.40	10.10
Torhamn	2013	27.10	9.38
Torhamn	2014	21.25	4.72
Torhamn	2015	24.53	13.58
Torhamn	2016	21.75	9.78
Torhamn	2017	22.53	27.85
Torhamn	2018	12.20	6.83
Torhamn	2019	28.38	11.65
Torhamn	2020	18.70	24.88
Torhamn	2021	4.15	5.97
Torhamn	2022	13.40	14.51
Torhamn	2023	8.74	14.90
Torhamn	2024	4.42	16.53

Table A.2: Cumulative degree temperature (sum of degrees, that are above 10) at monitoring location included in the PCA, summarised across the 2007–2024 sampling period.

Area	Year	Months (Temperature)	Degree temperature (degrees)
Finbo	2007	April- November	875.84
Finbo	2008	April- November	880.63
Finbo	2009	April- November	880.10
Finbo	2010	April- November	875.69
Finbo	2011	April- December	1025.52
Finbo	2012	April- December	847.34
Finbo	2013	April- December	997.05
Finbo	2014	April- December	1039.81
Finbo	2015	March- November	884.41
Finbo	2016	April- November	966.90
Finbo	2017	April- November	831.22
Finbo	2018	April- December	1063.73
Forsmark	2007	January- December	891.26
Forsmark	2008	April- November	953.40
Forsmark	2009	April- December	808.19
Forsmark	2010	May- November	867.11
Forsmark	2011	April- December	896.71
Forsmark	2012	April- November	862.98
Forsmark	2013	May- Oktober	966.78
Forsmark	2014	March- November	909.36
Forsmark	2015	April- November	845.19
Forsmark	2016	April- December	890.42
Forsmark	2017	January- Oktober	864.94
Forsmark	2018	May- November	1175.89
Forsmark	2019	May- November	888.42
Forsmark	2020	May- November	1028.11
Forsmark	2021	May- November	1011.63
Forsmark	2022	April- December	1029.76
Forsmark	2023	May- November	875.62
Forsmark	2024	April- November	848.56
Gaviksfjärden	2008	May- December	595.33
Gaviksfjärden	2009	May- November	524.73
Gaviksfjärden	2010	May- November	563.57
Gaviksfjärden	2011	April- November	710.83
Gaviksfjärden	2012	April- November	478.65
Gaviksfjärden	2013	May- Oktober	632.10
Gaviksfjärden	2014	April- November	786.05
Gaviksfjärden	2015	April- November	485.92
Gaviksfjärden	2016	April- Oktober	549.50
Gaviksfjärden	2018	May- Oktober	542.42
Gaviksfjärden	2019	May- Oktober	541.56
Gaviksfjärden	2020	April- Oktober	598.63
Gaviksfjärden	2021	May- Oktober	537.82
Gaviksfjärden	2022	May- November	569.95
Gaviksfjärden	2024	May- Oktober	656.35

Table A.2: Cumulative degree temperature (sum of degrees, that are above 10) at monitoring location included in the PCA, summarised across the 2007–2024 sampling period.

Area	Year	Months (Temperature)	Degree temperature (degrees)
Holmön	2007	April- November	651.62
Holmön	2008	May- December	644.71
Holmön	2009	May- November	724.31
Holmön	2010	June- November	619.45
Holmön	2011	May- December	812.60
Holmön	2012	May- November	678.76
Holmön	2013	May- Oktober	837.19
Holmön	2014	April- December	855.52
Holmön	2016	May- December	732.81
Holmön	2017	May- December	631.20
Holmön	2018	January- November	914.09
Holmön	2019	May- Oktober	704.58
Holmön	2020	May- December	781.67
Holmön	2021	June- December	775.51
Holmön	2022	May- December	765.40
Holmön	2023	January- Oktober	879.30
Holmön	2024	July- November	275.04
Kinnbäcksfjärden	2007	May- Oktober	671.97
Kinnbäcksfjärden	2008	May- Oktober	543.04
Kinnbäcksfjärden	2009	May- November	674.69
Kinnbäcksfjärden	2010	May- November	586.23
Kinnbäcksfjärden	2011	May- December	783.00
Kinnbäcksfjärden	2012	May- November	582.71
Kinnbäcksfjärden	2013	May- November	777.22
Kinnbäcksfjärden	2014	May- November	856.91
Kinnbäcksfjärden	2015	May- November	676.44
Kinnbäcksfjärden	2016	May- November	634.80
Kinnbäcksfjärden	2017	May- November	531.16
Kinnbäcksfjärden	2018	June- November	730.91
Kinnbäcksfjärden	2019	May- November	689.80
Kinnbäcksfjärden	2020	May- November	775.17
Kinnbäcksfjärden	2021	May- Oktober	721.60
Kinnbäcksfjärden	2022	May- November	711.85
Kinnbäcksfjärden	2023	May- November	812.60
Kinnbäcksfjärden	2024	May- November	799.28
Kvädöfjärden	2007	March- December	980.57
Kvädöfjärden	2008	April- November	1059.36
Kvädöfjärden	2009	April- December	935.42
Kvädöfjärden	2010	April- November	1026.78
Kvädöfjärden	2011	April- December	1090.72
Kvädöfjärden	2012	March- December	893.24
Kvädöfjärden	2013	April- December	1121.56
Kvädöfjärden	2014	March- December	1181.58
Kvädöfjärden	2015	March- December	971.90
Kvädöfjärden	2016	March- December	1083.39

Table A.2: Cumulative degree temperature (sum of degrees, that are above 10) at monitoring location included in the PCA, summarised across the 2007–2024 sampling period.

Area	Year	Months (Temperature)	Degree temperature (degrees)
Kvädöfjärden	2017	March- December	938.93
Kvädöfjärden	2018	April- December	1322.44
Kvädöfjärden	2019	April- December	993.72
Kvädöfjärden	2020	March- December	1097.19
Kvädöfjärden	2021	March- December	1188.41
Kvädöfjärden	2022	March- December	1134.99
Kvädöfjärden	2023	March- November	1047.95
Kvädöfjärden	2024	March- December	1090.27
Lagnö	2008	September- December	63.31
Lagnö	2009	May- December	705.61
Lagnö	2010	May- November	803.54
Långvindsfjärden	2007	March- December	623.20
Långvindsfjärden	2008	May- December	760.46
Långvindsfjärden	2009	April- December	565.50
Långvindsfjärden	2010	April- November	578.65
Långvindsfjärden	2011	April- December	734.07
Långvindsfjärden	2012	March- November	559.03
Långvindsfjärden	2013	April- December	636.18
Långvindsfjärden	2014	April- November	701.53
Långvindsfjärden	2015	April- December	597.94
Långvindsfjärden	2016	April- November	465.10
Långvindsfjärden	2017	April- November	539.11
Långvindsfjärden	2018	April- November	661.71
Långvindsfjärden	2019	April- November	448.79
Långvindsfjärden	2020	April- December	709.04
Långvindsfjärden	2021	May- Oktober	693.52
Långvindsfjärden	2022	May- Oktober	651.72
Långvindsfjärden	2023	April- September	782.27
Långvindsfjärden	2024	April- November	487.09
Norrbyn	2007	April- December	556.64
Norrbyn	2008	May- December	540.89
Norrbyn	2009	April- December	583.58
Norrbyn	2010	May- November	532.48
Norrbyn	2011	April- December	710.93
Norrbyn	2012	April- December	497.34
Norrbyn	2013	May- December	675.80
Norrbyn	2014	April- December	749.42
Norrbyn	2015	March- December	556.87
Norrbyn	2016	January- December	548.84
Norrbyn	2017	April- November	497.77
Norrbyn	2018	May- December	670.27
Norrbyn	2019	April- November	551.04
Norrbyn	2020	May- December	625.62
Norrbyn	2021	May- November	516.64
Norrbyn	2022	May- December	642.25

Table A.2: Cumulative degree temperature (sum of degrees, that are above 10) at monitoring location included in the PCA, summarised across the 2007–2024 sampling period.

Area	Year	Months (Temperature)	Degree temperature (degrees)
Norrbyn	2023	May- November	782.50
Norrbyn	2024	May- November	758.66
Råneå	2007	May- November	603.25
Råneå	2008	May- Oktober	589.23
Råneå	2009	June- Oktober	747.77
Råneå	2010	May- Oktober	664.24
Råneå	2011	May- Oktober	805.86
Råneå	2014	May- Oktober	859.29
Råneå	2015	May- Oktober	671.73
Råneå	2016	May- Oktober	732.81
Råneå	2017	May- Oktober	551.07
Råneå	2018	May- Oktober	825.66
Råneå	2019	May- Oktober	711.53
Råneå	2020	May- Oktober	804.57
Råneå	2021	May- Oktober	721.60
Råneå	2022	May- Oktober	784.37
Råneå	2023	May- Oktober	836.69
Råneå	2024	May- Oktober	976.94
Simpevarp	2007	April- December	810.89
Simpevarp	2008	April- December	964.79
Simpevarp	2009	April- December	579.39
Simpevarp	2011	April- December	826.36
Simpevarp	2012	January- December	686.91
Simpevarp	2013	April- December	837.22
Simpevarp	2014	January- December	1027.27
Simpevarp	2015	February- December	805.09
Simpevarp	2016	January- December	908.97
Simpevarp	2017	January- December	840.79
Simpevarp	2018	January- December	1133.20
Simpevarp	2019	January- December	854.27
Simpevarp	2020	January- December	908.56
Simpevarp	2021	January- December	1063.77
Torhamn	2011	January- December	575.10
Torhamn	2012	January- December	581.81
Torhamn	2013	April- November	911.17
Torhamn	2014	March- December	1087.19
Torhamn	2015	June- December	747.84
Torhamn	2016	April- December	993.37
Torhamn	2017	May- December	692.60
Torhamn	2019	August- December	252.23
Torhamn	2020	January- August	432.92
Torhamn	2021	August- December	225.73
Torhamn	2022	January- December	933.68
Torhamn	2023	January- December	886.56
Torhamn	2024	January- August	686.22

Table A.3: Variance explained by each principal component and cumulative variance explained across the first six components.

	percentage of variance	cumulative percentage of variance
comp 1	32.96	32.96
comp 2	21.26	54.22
comp 3	17.80	72.02
comp 4	12.38	84.39
comp 5	9.29	93.69
comp 6	6.31	100.00

Table A.4: Variable loadings on the first four principal components from the PCA. Active variables include sex ratio in three size classes (small: 7–14 cm, medium: 15–22 cm, large: 23–35 cm), CPUE of perch and roach, and cumulative degree temperature. Latitude, longitude, and year were included as supplementary variables.

Active variables				
	Dim.1	Dim.2	Dim.3	Dim.4
sr_small	-0.478	0.583	0.438	0.079
sr_medium	0.463	0.765	0.070	0.189
sr_large	0.806	0.315	-0.181	0.094
CPUE Perch	0.646	-0.009	0.250	-0.688
CPUE Roach	0.183	-0.283	0.881	0.161
Degree temperature	0.658	-0.414	0.000	0.439
Supplementary variables				
	Dim.1	Dim.2	Dim.3	Dim.4
Latitude	-0.197	0.319	0.122	-0.269
Longtitude	0.059	0.219	0.163	-0.283
Year	0.025	-0.269	0.310	-0.039