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Title: Warmer water increases early body growth of northern pike (*Esox lucius*) but mortality has larger impact on decreasing body sizes

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Abstract

Large fish species often display truncated size distributions related to harvest. In addition, temperature, food availability and density-dependence affect body growth, and together with natural mortality influence population size structure. Here we study changes in body growth, size distributions and mortality in both harvested and non-harvested populations of northern pike over 50 years along the Baltic Sea coast and in Lake Mälaren, Sweden. For coastal pike, body growth has increased coincidentally with increasing water temperatures, yet in the last two decades there has been a decrease of larger individuals. In Lake Mälaren, in contrast, size distributions and body growth were stationary despite similar increases in water temperature. A dominance of slow-growing individuals in older age-classes was evident in all studied populations, also in the no-take zone, suggesting other factors than fishing contribute to the mortality pattern. We propose that increasing temperatures have favoured body growth in coastal areas, but this has been counteracted by increased mortality, causing pike sizes to decline. To regain larger coastal pike, managers need to consider multiple measures that reduce mortality.

Key words: back-calculated length, climate change, *Esox lucius,* fishing, marine protected area, Rosa-Lee's phenomenon, wing bone

Introduction

Understanding how natural and anthropogenic drivers act together to shape size distributions of fish populations is the key to develop efficient management schemes (Heino et al. 2015; Audzijonyte et al. 2016; Wilson et al. 2019). High fishing pressure, especially if size selective, can result in fisheries-induced evolutionary changes towards early maturation and slower growth, whereas predation, including cannibalism, may select for faster growing individuals (Carlson et al. 2007; Edeline et al. 2007; Heino et al 2015; Monk et al. 2021; Bouffet-Halle et al. 2021). A common pattern in exploited fish stocks is that size distributions are truncated as few individuals survive to become large (Biachi et al. 2000; Ginter et al. 2015; Tu et al. 2018). This pattern may be further accentuated in (size-selective) exploited stocks by a higher mortality rate of fast-growing individuals, as they become recruited to fisheries at a younger age, i.e. Rosa Lee's phenomenon (Lee 1920, Pierce et al. 2003).

Plastic responses to fishing and temperature variation can also lead to changes in somatic growth rates (Campana et al. 2020). Intense fishing may increase somatic growth of remaining fish through reduced density dependence (Lester et al. 2014; Ginter et al. 2015; Wilson et al 2019). As fish are ectotherms, an increase in temperature increases metabolism, respiration and energy- and oxygen consumption such that body growth may decrease with increased water temperature (Baudron et al. 2014; Waples and Audzijonyte 2016; Audzijonyte et al. 2019, 2020; Ikpewe et al. 2021). However, higher water temperatures can also increase food intake and digestion, and increase ecosystem productivity, improving body growth of ectotherms (Ohlberger 2013; Lindmark et al. 2018; Wilson et al. 2019; Audzijonyte et al. 2020; Campana et al. 2020). The effects of warming likely differ depending on the size of the fish. As respiration increases proportionally more than intake rates and oxygen supply with body size, the optimum temperature for body growth tends to decrease with increasing temperature, such that body growth increases among smaller fish but decreases among larger fish (Ohlberger 2013; Pauly and Cheung 2017; Lindmark et al. 2018; Huss et al. 2019).

Large piscivorous fish have a key ecosystem function in regulating lower trophic levels in aquatic food-webs (Eriksson et al 2009; Eklöf et al. 2020) and for management it is therefore important to understand how both temperature and fishing affect body growth and size distributions of fish. Here we study size-specific body growth, size distributions and mortality of the northern pike*, Esox lucius*, (hereafter pike) over five decades at three coastal sites and one large lake in Sweden (Suppl. Fig. S1). One of the coastal sites is a no-take zone (*NTZ*), where fishing has been prohibited since 1980. Fishing at the other sites was exclusively conducted by fishing-right owners until 1985, when all Swedish coastal waters and the five largest lakes (including Lake Mälaren) were made publicly available to recreational fishing with handheld gear, causing an overall increase in pike fishing. There were no specific regulations of pike fisheries until 2011, when a bag limit of three pike per person and day and a harvest slot (40-75 cm) was introduced on the coast. Thus, we have differences in fishing pressure both between and within the study populations over time.

We hypothesize that size distributions of pike have changed over time and between sites and predict that: 1) Increasing water temperature has increased body growth rates for smaller pike, but 2) decreased growth rates for larger pike in all sites, 3) there are faster growing and larger pike in the no-take zone due to low mortality, and there will be 4) higher total and stronger size-selective mortality in the other coastal sites and Lake Mälaren after 1985 due to an increase in size-selective recreational fisheries.

Materials and Methods

Study populations and sampling

We used pike that had been sampled in Lake Mälaren 59.5° N (17° E) and in three sites in the Baltic Sea (ICES subdivision 27; Suppl. Fig. S1): Aspöja 58.4° N (16.9° E), Marsö 57.5° N (16.7° E) and Licknevarp/Kvädöfjärden 58.1° N (16.8° E). Licknevarp is a sheltered bay closed to fishing since 1980. Samples at Licknevarp prior to 1980 are from the adjacent area Kvädöfjärden and we assume that pike at Kvädöfjärden had similar body growth patterns as in Licknevarp at that time. Study sites were categorised into three different *Habitat* categories, based on anticipated differences in mortality and growth rates, *i*) Exploited coastal populations, Aspöja and Marsö (Coast), *ii*) coastal no-take zone, Licknevarp (NTZ), and *iii*) exploited Lake population (Lake Mälaren).

Pike were sampled during spawning migration between years 1960-2018. Samples from Aspöja and Marsö after 1980, and Lake Mälaren 2015 were from commercial fisheries, whereas prior to 1980 and in Licknevarp/Kvädöfjärden samples were from environmental monitoring. Different gears have been used to sample the pike; 6433 pike came from pound-nets (57%), 4503 from fyke-nets (40%), 67 from gill-nets (<1%), 86 by angling (<1%, Licknevarp only) and 134 of unknown gear (1%). To account for differences in size selectivity between gears we divided *Gear* into 'Pound-nets' and 'Other' gears. Pound-nets should have low size selectivity as they have large openings (> 1 m high) and capture everything but small fish, but all sampled pike were mature (> 30 cm) and should not introduce bias. We also included the angled pike in this group as there is little upper size-selectivity in pike angling. Fyke-nets that are smaller (< 1 m) and gillnets with mesh sizes 45-50 mm might be size selective towards medium sized fish. We therefore grouped these gears including pike from unknown gears as "Other" (but mainly fyke-nets). There was only one period (B) and habitat (coast) we had samples from both groups of gears to compare pike from different gear. We therefore also did complementary analyses using only samples from pound-nets.

Water temperature

To calculate a measure of average summer water *Temperature* for the three coastal sites we used site-specific modelled water temperature data 1997-2017 from the Swedish Meteorological and Hydrological Institute (SMHI) Waterweb (2020). In addition we had weakly *in situ* measurements June-September at 1 m depth from Kvädöfjärden (close to Licknevarp) 1963-2017 (Suppl. Fig. S2), Aspöja (1994-2008), Marsö (1994-2001) (SLU 2018). The summer average *in situ* data at Kvädöfjärden June-September were positively correlated with the summer average modelled data (June-September) at Kvädöfjärden 1997-2017 (r =0.88). Monthly average *in situ* data from Kvädöfjärden, Aspöja and Marsö were also positively correlated to each other (*r* ranging 0.56-0.80, with lower correlation in June and highest in September). As time-series of water temperatures were generally positively correlated among sites we only used the longest available time-series as a proxy for average summer (June-September) water temperatures for all three coastal areas, hence, the weekly *in situ* data from Kvädöfjärden.

For average summer *Temperature* at Lake Mälaren we used monthly *in situ* water temperature from three different sites in May, July-September at 0.5-1 m depth 1964-2017 (Miljödata-MVM 2019), but data was missing for some sites some years. Therefore we used the yearly least-square means of summer temperatures May-September using the 'emmeans' package in R. On average, summer temperatures at both Kvädöfjärden and Lake Mälaren increased 2°C from 1964 to 2017 (Suppl. Fig. S2).

Study periods

To investigate the importance of fishing regulations we divided the study period into four *Periods*, *A-D*, based on differences in fisheries regulations, but also ageing methodology

(Table 1). Period A; before 1985 pike fishing access in Sweden was permitted by private fishing-right owners (including commercial fishers). Coastal pike from this period were age determined and length back-calculated using the operculum. In Period B (1985-1997) and C (1998-2010) anyone could fish with handheld gear in both coastal waters and Lake Mälaren without any catch restrictions (Swedish Government 2001). These periods are characterised by an increase in recreational and decrease in commercial pike fishing. There is no independent data, but during Period C catch-and release fisheries of pike have become more popular, lowering the direct recreational fishing mortality, although total effort in pike fisheries likely increased during Period C. In 2011, at the start of Period D, a bag limit of three pike per person and day and a harvest slot (40-75 cm) was introduced at the coast, but not in Lake Mälaren. Thus, we have differences in fishing pressure both between populations and within populations over time. In addition to changes in pike fisheries there have been substantial increases in pike predators, primarily the great cormorant (*Phalacrocorax carbo sinesis*) and grey seal (*Halichoerus grypus*), in the Baltic Sea since 1990 (Hansson et al. 2018). We do not have area-specific abundance estimates of predators, but overall cormorants and seals along the central Baltic coast reached numbers that can have significant effects on coastal fish populations in Period C-D (see Hansson et al. 2018). Data are unbalanced with missing data from Lake Mälaren in Period B and C and from NTZ in Period D, note that the fishing during Period A was before the no-take zone was enforced.

Age determination and back-calculated growth of wing bones

Pike grow considerably slower during the winter (Diana 1979), which results in annual differences in growth increments in calcified bone and scale structures that can be used for individual age determination (Le Cren 1947; Secor et al. 1995). For pike, age determination is preferably done by analysis of the wing-bone (metapterygoid: Thoresson, 1996; Sharma and Borgstrøm 2007; Suppl. Fig. S3). The annual zones were read with a stereo microscope (Leica MZ6, magnification: 0.78 × 10), with lightning against dark background and translucent light as a complement. The annual zone was measured in mm with a digital ruler attached to the microscope (Mitutyo Absolute Digimatic). The distance between annual rings has a specific relationship to the fish growth that year (Suppl. Fig. S3), which allows an estimate of age specific size by means of a back-calculation of distances between annual rings. Based on Thoresson (1996) body length (L) at age (i) was calculated as

$$L_i = L_s \times (r_i / R_w)^{b_w} \qquad \text{(eq.1)},$$

where L_s is total length at catch, r_i is measured distance in mm to the ring at age i, and R_w total size of the wing bone at catch. The scaling factor $b_w = 0.824$ has been derived for pike in the Baltic Sea by Thoresson (1996).

The model and scaling factor for back-calculated growth of pike have not been validated on the pike populations considered here, and there is a risk that growth rate itself affects the relationship between wing-bone size and body size (Campana 1990). An alternative could be to use r_i directly as a measure of size (Hare and Cowen 1995). However, for most coastal pike we only had access to modelled data. Moreover, r_i only provides a relative estimate of body size and we would lose the connection to the actual size of the pike, which is important for management. A gross validation on pike with available measurements (Suppl. Fig S4) shows that although the relationship between wing-bone size and body size at catch differs between sampling sites, there is no evident non-linearity between wing-bone and body size within populations. As eq. 1 scales back-calculated growth with wing-bone size (R_w), differences in the relationship between wing-bones and body size will be controlled for. Thus, with the available data we have no possibility to validate the back-calculated growth model, but there are no evident non-linear relationships that would invalidate the use of eq.1 for back-calculation of body length.

Pike sampled 2007-2008 and 2015-2018, were aged and back-calculated by the same person (TB), while individuals sampled 1980-2006 were aged by staff at the Swedish Board of Fisheries' age-reading laboratory in Öregrund.

Age determination and back-calculated growth of operculum bones

For pike sampled 1960-1972 operculum bones had been stored instead of wing bones, which is not ideal for back-calculations (Frost and Kipling 1959). We therefore derived a relationship for back-calculating pike size from the operculum bone by comparing annual ring distances between wing bone (r_i) and operculum ($r_{o,i}$) from 100 pike sampled 1980-1986 in Forsmark on the Swedish east coast. Inter-annual distances of the operculum were scaled to the wing bone derived length at age, L_i (eq. 1) according to the linear model:

$\log_e(L_i/L_s) = b_o \times \log_e(r_{o,i}/R_o)$ (eq. 2),

where R_O is total radius of operculum at catch and b_o is the scaling coefficient for the operculum bone. Hence, eq. 2 describes the linear scaling between L_i and L_s based on the wing-bone and between $r_{o,i}$ and R_o of the operculum. Linear regression of eq. 2 of these 100 pike gave $b_o = 1.15$, and b_o inserted in eq. 1 gives the formula for the operculum bone:

$L_i = L_s \times (r_{o,i}/R_o)^{1.15}$ (eq. 3).

Correlation between L_i from the wing bone and the operculum showed no structural deviation ($r^2 = 0.84$, $RMSE = 4.5$ cm; Suppl. Fig. S5). In the operculum, distances between yearly rings become shorter and difficult to identify in older pike. To avoid this problem we only used pike below age eight in the analysis of back-calculated growth.

In order to estimate measurement errors of back-calculated length at age between staff we (TB) back-calculated length at age from 100 previously measured wing bones. The coefficients of determination, r^2, between back-calculated lengths from original length estimates and recalculated lengths were $r^2 > 0.97$ for all 100 individuals. Thus, estimated measurement errors of back-calculated length are maximum 3% of total variation, but this does not include any structural errors arising from the used algorithms.

Analyses

We used R version 3.4.3 and Rstudio version 1.1.456 (R Core team 2017) for all statistical analyses, and all analyses were done separately for females and males due to differences in growth between sexes. To analyse changes in size and age distribution we applied a linear mixed model (LMM), using the *lmer*-function in the lme4 package (Bates et al. 2015), with study site and year as random factors. Length or age of individual pike at catch (L_s and A_s, respectively) were used as the dependent variables with *Period*, *Habitat* and *Gear* as fixed factors:

$L_s/A_s = Period + Habitat + Gear + (1|\mathrm{Site}) + (1|\mathrm{Year})$ (eq. 4).

To specifically test the influence of the no-take zone (NTZ) on size and age distributions we compared coastal sites and the NTZ during Period B and C (Period A was open for fishing and Period D had no data). To visualise changes in size and age distributions we used the 10th, 50th, and 90th percentiles (length *L* and age *A*, respectively), where *L10/A10* indicates changes among the smallest/youngest pike and *L90/A90* changes among the largest/oldest pike.

To analyse changes in back-calculated growth we used LMM following the framework proposed by Morrongiello and Thresher (2015). They analysed age-specific somatic growth rates, but here we analyse size-specific somatic growth as:

$L_{n,i+1} - b_g \times L_{n,i}$ (eq. 5),

where $L_{n,i}$ is length of pike *n* at age *i*, and $L_{n,i+1}$ is the length of the same pike at age $i+1$. b_g is the slope of the linear regression model $L_{n,i+1} = a + b_g * L_{n,i}$ for all pike divided by sex (Suppl. Fig. S6). Thus, b_g is the size-specific scaling coefficient of somatic growth.

To analyse factors contributing to body growth we first selected the random factors from models with only intrinsic factors (all pike assumed to be from a single population with no environmental variation, see Morrongiello and Thresher 2015): *Age-at-catch* (*AC*) as a fixed factor and individual (*ID*), *Cohort* (*C*; year of birth) and *Year* (*Y*) as random intercept factors:

$L_{n,i+1} - b_g * L_{n,i} = AC + (1|ID) + (1|C) + (1|Y)$ (eq. 6)

ID accounts for correlation in growth between years due to the repeated sampling on the same individual, *Cohort* accounts for correlation in growth between individuals spawned in the same year, and *Year* accounts for other factors that vary between years but are not considered in the model (Morrongiello and Thresher 2015). We also compared models with random slope of body size (*L*), i.e. allowing slopes of body growth to differ between *Cohorts*, *Year*, and *ID*:

$L_{n,i+1} - b_g * L_{n,i} = AC + (L|ID) + (L|C) + (L|Y)$ (eq. 7)

To evaluate the support for models with different random factors we used the function ‘aictab’ in the ‘AICcmodavg’-function in R (Mazerolle 2020) to compare Akaike’s information criterion corrected for small sample size (AICc) between models. We calculated marginal (fixed factors only) and conditional R^2-values (fixed and random factors) according to Morrongiello and Thresher (2015).

After we had identified which random factors gave the best fit for eq. 6 and 7 for each sex we used these random factors in a LMM adding also extrinsic factors in five different models (Table 2): *i*) *Habitat* (*H*). *ii*) *Period* (*P*), *iii*) *Temperature*, *iv) Habitat* and *Period*, and *v*) *Habitat* and *Temperature* (*T*). We did not include *P* and *T* in the same model as there was an average increase in water temperature over time (Suppl. Fig. S2). In all models also *Gear* (*G*) and *AC* were included as fixed factors. *Gear* tests differences between gears, *AC* assesses differences in size-specific growth between individuals that remain in the population or are removed early (Morrongiello and Thresher 2015). *Habitat* tests for spatial variation, *Period* for temporal variation, and *Temperature* if size specific body growth is related to water temperature. We also included the interaction terms between *H:L*, *P:L*, *T:L*, *H:AC*, *P:AC*, *T:AC* in the respective model. For example, the full models including extrinsic factors (*EF, i-v above*) with random factors from eq. 7 would be:

$L_{n,i+1} - b_g * L_{n,i} = G + AC + EF + EF{:}L + EF{:}L + (L|ID) + (L|C) + (L|Y)$ (eq. 8)

Interaction terms were removed if not contributing to the model fit (suboptimal models including or excluding interaction terms are not shown). The interaction terms test if size-specific growth differs between habitats or periods/temperature (*H:L*, *P:L*, *T:L*) and if Rosa Lee's phenomenon differs between habitats or periods/temperature (*H:AC*, *P:AC*, *T:AC*). We did not include any interactions between habitat and period due to lack of data in some habitats and periods (see Fig 1). To test the influence of the no-take zone (*NTZ*) on body growth we did a specific LMM using pike from the coastal sites and NTZ during period B and C.

To estimate total mortality in a population (*Z*) we used Chapman and Robson (1960) estimator of *Z* from the age distribution at catch for each *Period* and *Habitat* using the *FSA*-package for *R* (Ogle et al. 2020). For females we calculated Z between ages 4-13 as age 4 was the most common age for females and after age 13 observations were scattered. Corresponding ages were 3-12 for male pike.

To study size-selective mortality in the pike populations we compared, using a general linear model, if age-specific differences in mean length of cohorts (population mean) from one year to the next (mean length of the survivors, denoted *S'*) differed, between *Gear*, *Age*, *Period* and *Habitat*. A negative *S'* indicates that survivors from one year to the next is *S* mm shorter than the population mean, hence, a negative size selection on survival (Sinclair et al. 2002; Swain et al. 2007).

Results

Sample size, length at catch and age

From 1960 to 2019 a total of 9228 pike (54% female, 46% male) were analysed from the two exploited coastal sites Aspöja and Marsö, 469 pike (37% female, 63% male) from the *NTZ*, and 1526 pike (48% female, 52% male) from Lake Mälaren. An overview of hypotheses and results is presented in Table 2.

Pike varied both spatially and temporally in their length and age at catch (Suppl. Fig S7). Length at catch differed between periods and habitats for female pike (*Period*: $F_{3,38.8} = 31$, $P < 0.001$; *Habitat*: $F_{2,2} = 44$, $P < 0.001$) but for males only between periods ($F_{3,38} = 36$, $P < 0.001$) and not habitats ($F_{2,2} = 12$, $P = 0.08$). Pike were on average larger in pound-nets than in other gear types (Females: average difference 3.0 cm ± 0.6 SE, $F_{1,1337} = 16$, $P < 0.001$; Males: average difference 1.8 cm ± 0.4 SE, $F_{1,2581} = 18$, $P < 0.001$; Suppl. Fig. S7). Age distributions also differed between periods (Females: $F_{3,44.5} = 6.9$, $P < 0.001$; Males: $F_{3,62.5} = 11$, $P < 0.001$) but not between habitats (Females: $F_{2,2} = 4.0$, $P = 0.2$; Males: $F_{2,2} = 1.4$, $P = 0.4$) or gears (Females: $F_{1,3881} = 1.6$, $P = 0.2$; Males: $F_{1,4083} = 2.7$, $P = 0.1$).

Both female and male pike were smallest (Females: 44.5 cm ± 8.5 SD; Males: 41.2 cm ± 8.9 SD) and youngest at catch (3.8 y ± 1.3 SD; Males: 3.7 cm ± 1.5 SD) in Period A, and largest (Females > 70 cm, Males > 52 cm) in Period B-C in the NTZ (Period D not available) and in Period D at Lake Mälaren (Period B-C not available) (Fig. 1). Female pike in the NTZ were on average 11 cm larger than the coastal sites during Period B ($F_{1,23} = 11$, $p = 0.003$). An almost significant difference (of average 6 cm) was seen also for males ($F_{1,2.2} = 14$, $p = 0.055$) (Suppl. Fig. S7). In the NTZ there was a marked decline in median size (Female: 11 cm, Male: 5 cm) and age (Female 2 y, Male: 0.7 y) between Period B and C, which was not evident at the coastal sites (Fig. 1).

Back-calculated body growth

Length-specific body growth (eq. 5) differed between habitats and periods from around 12 and 14 cm per year for female and male pike in the coastal habitat during Period A to around 20 cm per year for both females and males in Lake Mälaren and coastal habitats in Period C (Suppl. Fig. S8i,j). The best growth model included all random factors *ID*, *Cohort* and *Year* and random slopes of body size (Table 3; Suppl. Fig. S8a-h). For both sexes, models including *Temperature* instead of *Period* as fixed factor had better fit and explained more variation (Table 2) and the best models also included *Habitat*, *Age at catch*, and *Gear*, in total explaining 29% of the variation in growth for females and 20% for males (Table 3), with a high amount of unexplained individual variation. Somatic growth rates of both female and male pike were positively associated with water temperature (Fig. 2a,b). There was an interaction term between *Habitat* and *Temperature* (Table 3) as there was a weaker association between growth and water temperature in Lake Mälaren (Fig. 2a,b). There was no significant difference in body growth between the NTZ and the coastal sites during Periods B-C (Females: $F_{1,1705} = 0.9$, $p = 0.3$; Males: $F_{1,1627} = 1.8$, $p = 0.2$). There was also an interaction between *Temperature* and body size for both sexes (Table 3), with a stronger positive effect on growth of smaller pike (Fig. 2c,d).

Removing *Gear* from the best extrinsic models (Table 3) increased AICc with dAICc = 299 for females and dAICc = 187 for males. The improvement in model fit related to gear type was because pike sampled from pound-nets had grown faster (Suppl. Fig S6c). However, a model selection of body growth of only pike sampled in pound-nets showed qualitatively identical models (Suppl. Table S1), indicating the results were not dependent on different gears used to sample pike.

There was a negative relationship between size-specific growth and *Age-at-catch*

(AC) (Fig. 2e,f). Hence, pike that became older had on average grown slower (up to 3 cm per year in coastal habitats) than population averages at younger ages, indicating fast growing individuals were removed from the population earlier than slower growing individuals, known as Rosa Lee's phenomenon. For both sexes the final model included interactions between *AC* and *Habitat,* and between *AC* and *Temperature* or *Period*. The slope of the relationship between body growth and *AC* was steeper in the coastal populations and became steeper towards the end of the study period (Fig. 2e,f), at higher temperatures.

Mortality

Estimated total mortality rates decreased over time. Mortality was highest ($Z > 0.6$) at the coast in Period A and has since decreased to $Z \approx 0.4$ for females and $Z \approx 0.5$ for males in Period C-D (Fig. 3). Mortality was consistently lower in the NTZ than at the coast, even in Period A before the no-take zone had been established (Fig. 3). Although estimated in different periods, total mortality in Lake Mälaren appears comparable to the NTZ (Fig. 3). There was no significant difference in estimated mortality between gears in Period B at the coast when both gears were used simultaneously (Females: $t_{1,18} = 1.0$, P =0.3; Males: $t_{1,18} = 0.7$, P =0.5), indicating no major gear effect on mortality estimates. Total mortality of pike sampled from pound-nets only were similar to the estimates using pike from all gears (Suppl. Fig. S9), again indicating no major influence of different gears.

There was a significant size-selective mortality, *S'*. The estimated back-calculated length of survivors in a cohort to the next year were on average 1.0 cm ± 0.1 S.E. shorter than the average length in the same cohort the previous year, *S'* (Females: $t_{1,291} = -13$, $P < 0.001$; Males: $t_{1,216} = -9.1$, $P < 0.001$; Fig. 4). Size-selective mortality was estimated to be stronger in pound nets, at least at the coast (Table 4; Fig. 4). For female pike, *S*' did not change consistently between ages, populations or periods (Table 4, Fig. 4), whereas male pike showed weaker size-selective mortality (increasing *S'*) with age and was lowest in the Lake Mälaren (Table 4, Fig. 4). When only using pike sampled from pound nets, *S'* differed between habitats for females (strongest at the coast) and periods (strongest in Period B-C) for males (Table 4).

Discussion

We have shown that body growth of smaller pike in the Baltic Sea was positively correlated with increasing water temperature from the 1960s, as predicted, but in contrast to our hypothesis we did not detect any decline in body growth with temperature among larger pike. In Lake Mälaren there was no correlation between body growth and water temperature (although there is a lack of data for the intermediate periods) suggesting that eventual temperature effects are site specific. Pike in a no-take zone in the Baltic Sea were significantly larger and older than in the exploited populations, but this seemed mainly to be due to lower mortality rather than differences in body growth. As expected, there were clear indications of positive size-selective mortality and fast-growing individuals were removed from the populations at earlier ages, i.e. Rosa-Lee's phenomenon, which was also evident in the no-take zone. Mortality and Rosa-Lee's phenomenon was lower in the no-take zone and Lake Mälaren, which is reflect in a higher proportion of large pike than at the exploited coastal populations.

In the Baltic Sea, length at catch and somatic growth were lowest in Period A (1960-1980). Lehtonen et al. (2009) also observed low mean weight of pike in the Gulf of Finland during this period. A commercial pike fishery dominated during this period and mortality rates appear to have been high ($Z > 0.6$). Hence, high reproduction rate (Lehtonen et al 2009) and high adult mortality (this study) in combination with colder and less productive coastal waters (Gustafsson et al 2017), may have contributed to the observed pattern of small and slow-growing pike.

During the 1970-1980's coastal waters became more nutrient rich (Gustafsson et al. 2017) and warmer, and total mortality seems to have decreased, contributing to faster body growth and larger pike in the Baltic Sea. The marginal variation explained by water temperature was only 3%, but was stronger for smaller pike, and we did not find any evidence that warmer waters reduced body growth for larger individuals. Although this was opposite to what we expected, Audzijonyte et al. (2020) found that for 45% of the studied species around Australia body growth increased with warmer temperature, and more often for fish species with large maximum body size. The increased metabolism and oxygen depletion of warmer waters may be offset by a higher food intake (higher prey availability/productivity) even for larger pike (cf. Campana et al. 2020). In Lake Mälaren, however, there was no positive relationship between body growth and temperature, despite a similar increase in water temperature, but we lack samples from 1980-2015, which introduces uncertainty in the comparison.

One reason as to why larger pike at the coast and pike in Lake Mälaren seem to respond less to water temperature may be variation in optimal temperature, *Topt*. We have not estimated *Topt* for pike here but other studies have estimated it to be around 18-22°C (Diana et al. 1983; Casselman 1996; Rypel 2012). For smaller pike in the Baltic Sea the increase in temperature may have brought temperatures closer to their optima (Peat et al. 2016). These Temperatures of 18-22°C are typically achieved in the Baltic Sea only for a short period during summer. We have only used surface temperature here and it may be that mainly smaller pike occupy shallower shore habitat that is more prone to warming, whereas larger pike may escape and seek refuge in cooler deeper waters if subject to temperatures over their optimum (Headrick and Carline 1993; Margenau et al. 1998; Peat et al. 2016). It has also been suggested that more sedentary fish species, like pike, will be less influenced by warming than more active species (van Rijn et al. 2017). During cooler years pike in Lake Mälaren grew substantially faster than at corresponding water temperatures at the coast (Fig 3a, b). We can only speculate why. Perhaps a relatively higher abundance of pelagic food sources like smelt (*Osmerus eperlanus*) and vendace (*Coregonus alba*) in Lake Mälaren provide more stable food conditions. In Lake Mälaren shallow areas with warm waters are abundant, perhaps enabling pike to find suitably warm habitat even before the climate-driven warming of waters observed in later periods.

We cannot exclude that the difference between smaller and larger pike is an artefact of the back-calculation growth model (Campana 1990; Hare and Cowen 1995). Little is known about growth in wing-bones over ontogeny in fish, however, it is well known that otolith growth changes over ontogeny (Campana 1990; Hare and Cowen 1995). Thus, it is possible that the growth model (eq. 1) fits poorly to larger pike. Unfortunately we do not have access to raw data and cannot validate eq. 1 in any other way. Our simple validation of wing-bone size and body size (Suppl. Fig S4) shows a consistent difference between study areas, i.e. wing bones were larger relative body-size than at another area, but does not show any alarming non-linearity in wing-bone growth relative to body size within study areas.

While increased somatic growth rates partly explain the increasing size of pike during the first part of the study period (A-B*,* 1960-1998), this cannot explain the stagnation and decrease of larger pike during the latter part (Period C-D, 1998-2018). Instead, adaptations, plastic or evolutionary (Wilson et al. 2019), related to mortality could have contributed to the decline of larger pike. All studied pike populations showed indications of slow-growing individuals remaining in the population to an older age, also known as Rosa Lee's phenomenon (Lee 1920), which was strongest in the exploited coastal populations. During the last study period (D, 2011-2018) there are steeper slopes between average size-specific growth of pike and age-at-catch at the coast for both sexes, indicating a stronger selection against fast-growing individuals. Importantly though, we also found Rosa Lee's phenomenon in the NTZ, with no fishing mortality (Period B-C, 1985-2010). This suggests natural causes contribute to the observed Rosa Lee's phenomenon. For example, fast-growing individuals, which generally exhibit a more active and risk-taking behaviour, may be more susceptible to cannibalism (Pierce et al. 2003), or at the coast also predation from top predators like great cormorant (*Phalacrocorax carbo sinensis*) and grey seal (*Halichoerus grypus*) that have increased manifold at the coast during the study period (Hansson et al. 2018).

Cohort-specific analysis also indicated positive size-selective mortality as pike surviving another year were, on average, 1 cm shorter than the age-specific mean of that cohort (*S'*). A gross estimate of the effect of size-selective mortality on body length, assuming additive effects over ages, is a 10 cm reduction in the average length at the maximum ages observed here. However, there were no clear differences in *S'* between periods or habitats that can explain the variation in size structure. Few observations of *S'* were available from the no-take zone, but do not stand out, again indicating that other mortality factors like cannibalism and predation (Pierce et al. 2003) may also contribute to this size-selective mortality pattern.

Total mortality rates are estimated to have decreased during the study period and differed between habitats. As expected, mortality was lowest in the no-take zone, but unexpectedly, mortality was also relatively low in Lake Mälaren despite a likely increase in recreational fisheries over time, possibly due to a catch-and-release fishery. The lower total pike mortality in Lake Mälaren despite a similar sized recreational fishery as at the coast could indicate that natural (predation) mortality is higher at the coast than in Lake Mälaren.

Interestingly, mortality of coastal pike was highest in *Period A*. This suggests that the decline of pike landings in commercial fisheries has not been offset by an increase in recreational fisheries. At the same time there has been an increased propensity for catch-and-release pike fisheries that may have lowered total mortality. The fishing regulations implemented in 2011 do not appear to have had any major effect on total mortality. Either fishing regulations have not affected mortality rates, or a lowered fishing mortality has been offset by a simultaneous increase in natural mortality. However, mortality estimations are from pike sampled in different gears and from only two exploited sites so the data is not suitable for a more general evaluation of these fishing regulations.

Pike in the *NTZ* population were larger and older than pike in the exploited coastal populations (Aspöja and Marsö), but there were no significant differences in body growth compared to exploited areas. This differs from the observations in Lake Windermere, where natural selection favours fast growing pike (Carlson et al. 2007; Edeline et al. 2007). Either fishing has induced little impact on pike growth rates, or increased density-dependence and cannibalism (Lorenzen and Enberg 2002; Pierce et al. 2003) in the *NTZ* have had counteractive effects. In 2005 pike abundance was more than twice as high inside the *NTZ* compared to two adjacent fished coastal areas (Edgren 2005), likely a consequence of the lower mortality. This may have resulted in increased resource competition (Jenkins et al. 1999; Lorenzen and Enberg 2002; Rose et al. 2001), cannibalism avoidance (Pierce et al. 2003; Craig 2008; Tiainen, 2017) and stress from intraspecific interactions (Edeline et al 2010) lowering food intake rates. We also note that there are relatively more large and old pike, especially females, in Lake Mälaren without any major differences in average growth, but substantially lower total and size-selective mortality. Thus, we conclude that variation in mortality is more important than variation in body growth for size distributions among the studied populations.

Northern pike is a keystone predator in aquatic ecosystems, exerting top-down predatory regulation on fish communities, where loss of large pike can result in trophic cascades with significant impacts on ecosystem functioning (Donadi et al. 2017; Eklöf et al. 2020). At the same time, pike has a major socioeconomic value due to its central role for recreational fishing. Therefore, to maintain vital coastal ecosystem functions and opportunities for a rewarding recreational fishery, regaining viable pike populations with large individuals should be a primary concern for management (Arlinghaus et al. 2010, Pierce 2010, Carlson 2016). Current management of pike in the coastal areas of Sweden focuses on a harvestable slot size (40-75 cm) and a bag limit of three pike per fisher and day in the recreational fisheries, in combination with closures for local spawning. The effect of these regulations remains unclear, but mortality rates must be proportionate to growth rates in order to recruit individuals exceeding the maximum length limit of fishing (Arlinghaus et al. 2010; Tiainen et al. 2017). Based on our data, only around 10% of pike will grow through the current catch window. This might be too low for fast growing pike to have an advantage in the current conditions. We conclude that warming so far seems to have had a positive influence on body growth of coastal pike, but to regain larger pike at the coast will require management actions towards reducing mortality, including from natural predation.

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Table 1. Periods used in the analyses, with important differences in methods used for age determination and in fishing regulations indicated. Handheld (fishing) gear includes all types of rod-based fishing techniques, e.g. spinning-, jig-, angle-, and ice-fishing.

Period	Years	Tissue	Recreational fishery
A	1960-1984	Opercula/Wing bone*	No*
B	1985-1997	Wing bone	Yes, handheld gear
C	1998-2010	Wing bone	Yes, handheld gear
D	2011-2018	Wing bone	Yes, bag limit (3/day, 40-75 cm)*

*In Lake Mälaren wing bone has been used consistently and there is no bag limit nor size regulation.

Table 2: Summary of main hypotheses, model analyses used, and qualitative results. Arrows indicate the sign of the relationship (↑ positive, → no relationship, ↓ negative). Agreement shows if results were according to the hypothesis. LMM is linear mixed models and ANCOVA is analysis of covariance, see Methods for explanations of Chapman-Robson and *S'*.

Hypothesis	Model analysis	Result	Agreement	Comment
1) Increased body growth with increasing water temperature for smaller pike	LMM of back-calculated growth (eq. 8)	↑	Yes	Not in Lake Mälaren
2) Decreased growth rates with increasing water temperature for larger pike	LMM of back-calculated growth (eq. 8)	→	No	
3a) Larger pike in the no-take zone	LMM of length at catch (eq. 4)	↑	Yes	
3b) Faster growing pike in the no-take zone	LMM of back-calculated growth (eq. 8)	↓	No	
3c) Lower mortality of pike in the no-take zone	Chapman-Robson Z estimation	↓	Yes	
4) Higher mortality of fast-growing pike	LMM of back-calculated growth (eq. 8)	↑	Yes	Also in the no-take zone (NTZ)
4b) Higher total mortality after 1985 (not NTZ) due to an increase in recreational fisheries	Chapman-Robson Z estimation	↓	No	
4c) Stronger size-selective mortality after 1985 (not NTZ) due to an increase in recreational fisheries	ANCOVA of *S'*	→	No	Evident size-selective mortality in all periods

Table 3: Selection of models for size-specific body growth by sex. The selection process is divided for models with *i*) only intrinsic (within area) factors (age at catch, cohort and year), and *ii*) intrinsic and extrinsic factors (Gear, Temperature, Period and Habitat). AC is Age at catch, L is body length, ID is fish individual, C is Cohort, Y is Year, H is Habitat, P is Period and T is water temperature. RF are the random factors from the best model with intrinsic factors. K is the number of parameters estimated in the models, AICc is Akaike's Information Criterion corrected for sample size and dAIC is the difference in AICc between a model and the best model. Marginal and conditional R^2 show the proportion of the variance explained by fixed factors only and the whole model, respectively.

Model	K	AICc	dAICc	Marginal R^2	Conditional R^2
Females intrinsic model					
AC+(L|ID)+(L|C)+(L|Y)	12	222922	0	0.15	0.50
AC+(L|ID)+(L|C)	9	223397	475	0.14	0.49
AC+(L|ID)+(L|Y)	9	223647	725	0.17	0.53
AC+(L|ID)	6	225489	2567	0.19	0.51
AC+(1|ID)+(1|C)+(1|Y)	6	225796	2874	0.13	0.47
AC+(1|ID)+(1|Y)	5	226109	3187	0.13	0.46
AC+(1|ID)+(1|C)	5	226207	3284	0.10	0.44
AC+(1|ID)	4	227452	4530	0.15	0.45
Females extrinsic model					
G+AC+H+T+H:L+AC:T+H:AC+T:L+(RF)	23	221915	0	0.29	0.60
G+AC+T+ AC:T+T:L+(RF)	16	222171	256	0.22	0.53
G+AC+H+P+H:L+AC:P+H:AC+P:L+(RF)	29	222364	449	0.24	0.56
G+AC+H+ H:P+H:L+(RF)	20	222431	516	0.26	0.60
G+AC+ P+ AC:P +P:L+(RF)	23	222630	715	0.22	0.50
Males intrinsic model					
AC+(L|ID)+(L|C)+(L|Y)	12	167802	0	0.20	0.56
AC+(L|ID)+(L|C)	9	168176	373	0.14	0.52
AC+(L|ID)+(L|Y)	9	168583	781	0.20	0.58
AC+(L|ID)	6	170087	2284	0.26	0.57
AC+(1|ID)+(1|C)+(1|Y)	6	170233	2431	0.15	0.56
AC+(1|ID)+(1|Y)	5	170532	2730	0.15	0.51
AC+(1|ID)+(1|C)	5	170537	2734	0.10	0.46
AC+(1|ID)	4	171766	3964	0.20	0.48
Males extrinsic model					

G+AC+H+T+H:L+AC:T+H:AC+T:L+(RF)	23	88448	0	0.20	0.50
G+AC+H+P+H:L+AC:P+H:AC+P:L+(RF)	29	88487	39	0.22	0.50
G+AC+T+ AC:T+T:L+(RF)	16	88510	62	0.31	0.51
G+AC+H+ AC:H+H:L+(RF)	20	88545	97	0.17	0.51
G+AC+ P+ AC:P +P:L+(RF)	23	88546	98	0.31	0.52

Table 4. F-values of size-selective mortality (*S'*) as a dependent variable in linear models.

Parameter	Females		Males	
	Both gear types	*Pound-net only*	*Both gear types*	*Pound-net only*
Gear	$F_{1,303}=8.3$**		$F_{1,219}=4.7$*	
Age	$F_{1,303}=1.3$	$F_{1,170}=3.0$	$F_{1,219}=16$***	$F_{1,116}=7.8$**
Habitat	$F_{2,303}=2.2$	$F_{1,170}=4.0$*	$F_{2,219}=3.8$*	$F_{1,116}=2.9$
Period	$F_{3,303}=1.0$	$F_{2,170}=1.4$	$F_{1,219}=1.6$	$F_{2,116}=4.2$*

*$P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

Figure 1. Median, lower and upper 10th percentile of length (A) and age (B) distributions of pike catches during different periods divided by *Habitat* (Coast represents the exploited Baltic Sea populations at Aspöja and Marsö, NTZ is the coastal no-take zone, and Lake is Lake Mälaren). '×'indicates the lower 10th percentile, '+' median value and '○' upper 90th percentile. Lines are only for illustrative purpose. Sample size for each sex is indicated by Nf (females) and Nm (males) below the figures.

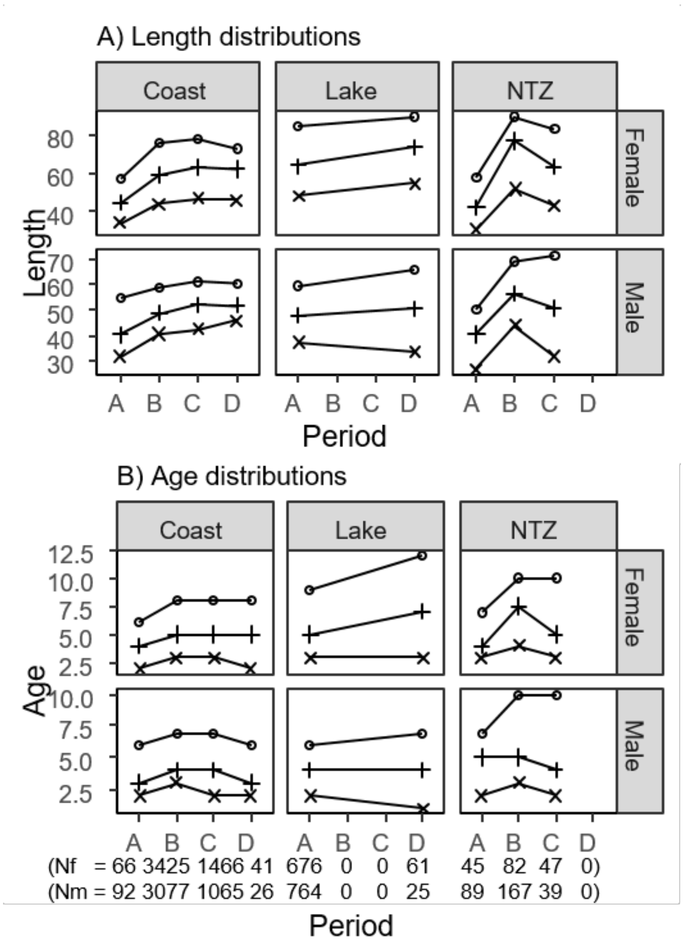


Figure 2. Length-specific somatic growth rates of female (A, C, E) and male (B, D, F) pike from different populations (Coast are the exploited Baltic Sea populations at Aspöja and Marsö, NTZ is the coastal no-take zone, and Lake is Lake Mälaren). A) and B) show size-corrected growth in relation to *Temperature*, indicating faster growth in warmer waters at the coast and NTZ but not in Lake Mälaren. C) and D) show that the positive relationship between *Temperature* and size-specific growth was stronger for smaller pike. Here large pike corresponds to female > 75 cm and male > 65 cm, medium to female 40-75 cm and male 35-65 cm, and small to female < 40 cm and male < 35 cm. E) and F) show pike surviving to older ages grow slower than the population average among younger pike. Brighter dots/lines indicate earlier periods and darker dots/line later periods.

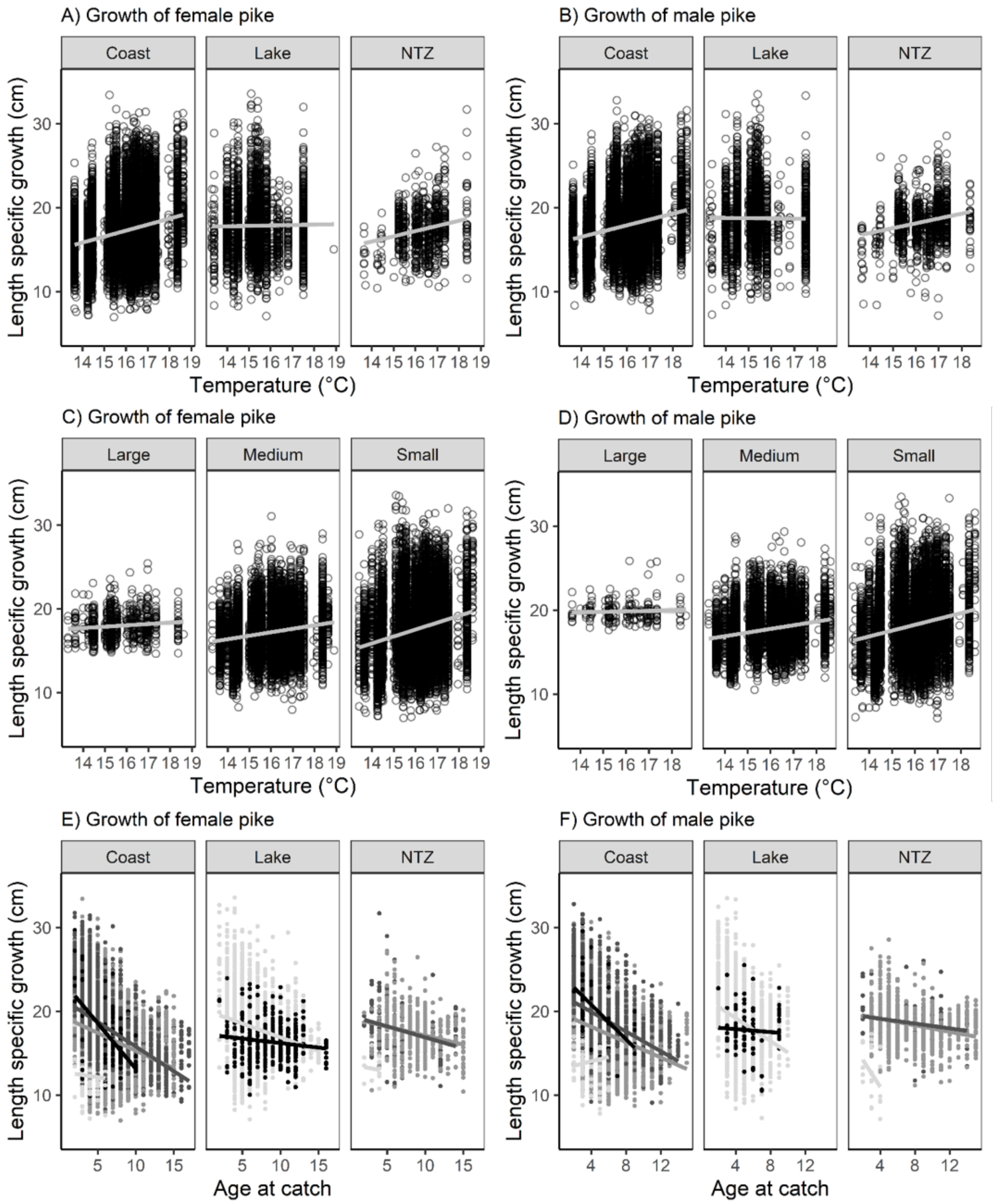

A) Growth of female pike
B) Growth of male pike
C) Growth of female pike
D) Growth of male pike
E) Growth of female pike
F) Growth of male pike
Coast
Lake
NTZ
Large
Medium
Small
Length specific growth (cm)
10
20
30
14 15 16 17 18 19
14 15 16 17 18
Temperature (°C)
5 10 15
4 8 12
Age at catch

Figure 3. Estimated total mortality of A) female and B) male pike for different habitats and periods. Total mortality is estimated from the catch-curve using the Chapman-Robson method. Error bars are standard error of the means.

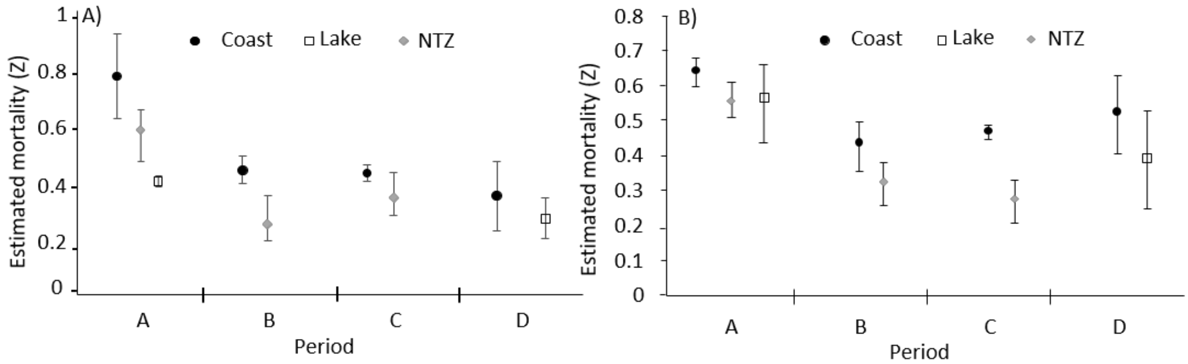
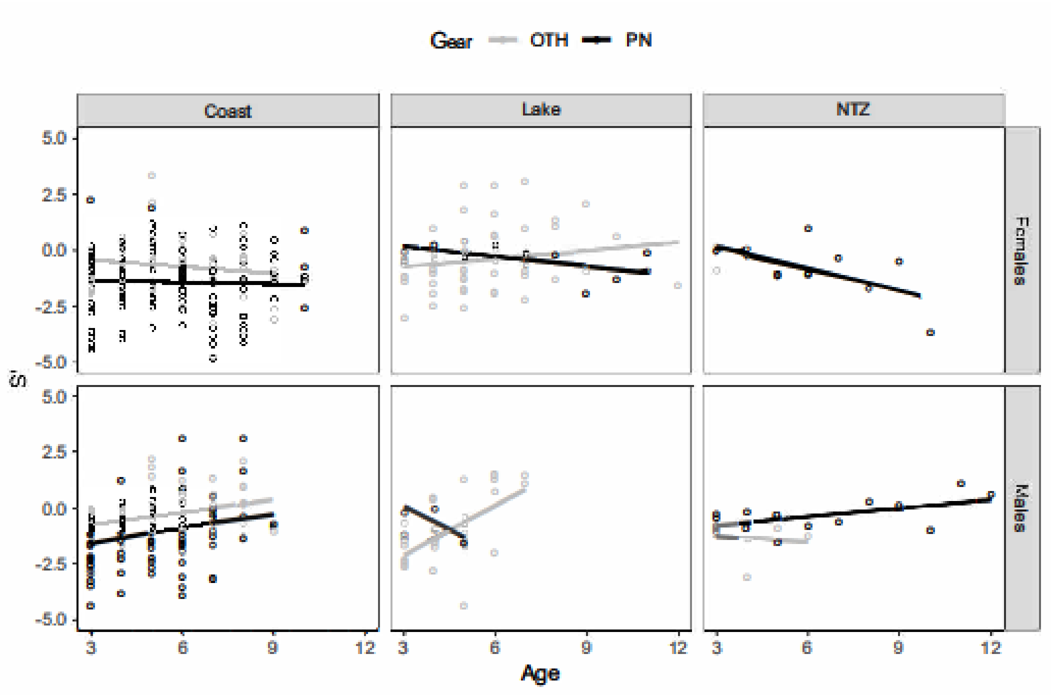


Figure 4: *S'*, the average difference (in mm) between the back-calculated length of pike surviving to the next year and cohort average, by age, area, sex and gear (PN – Pound-net, OTH – Others). Coast are the exploited Baltic Sea populations at Aspöja and Marsö, NTZ is the coastal no-take zone, and Lake is from Lake Mälaren.



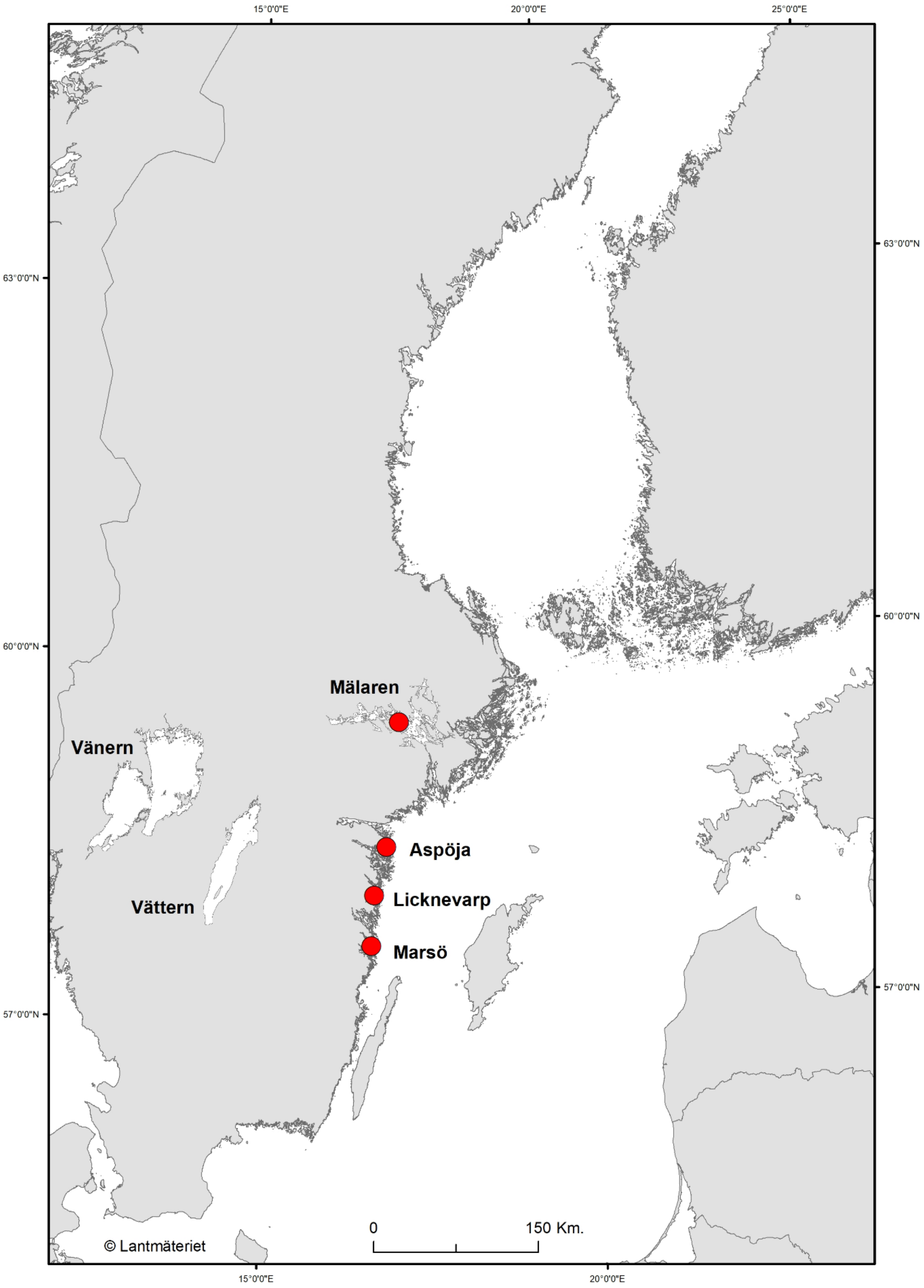
Supplementary Material

Supplementary Table S1: Selection of models for size-specific body growth of pike sampled in pound-nets only. The selection process is divided for models with *i*) only intrinsic (within area) factors (age at catch, cohort and year), and *ii*) intrinsic and extrinsic factors (Temperature, Period and Habitat). AC is Age at catch, L is body length, ID is fish individual, C is Cohort, Y is Year, H is Habitat, P is Period and T is Water temperature. In the extrinsic models RF is the random factors from the best model with intrinsic factors. K is number of parameters estimated in the models, AICc is Akaike's Information Criterion corrected for sample size and dAIC is the difference in AICc between a model and the best model. Marginal and Conditional R2 indicate the proportion of the variance explained by fixed factors only and the whole model, respectively.

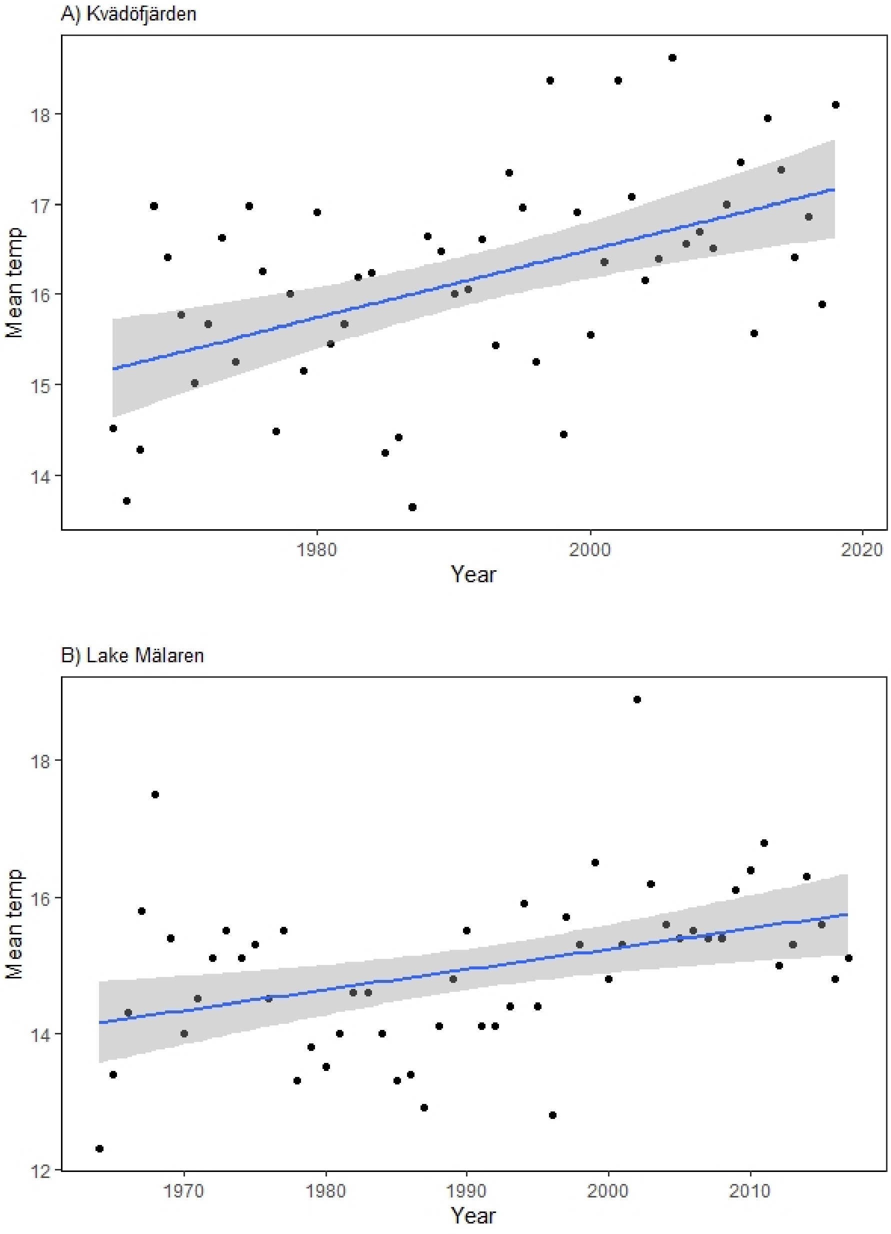
Model	K	AICc	dAICc	Marginal R^2	Conditional R^2
Females intrinsic model					
AC+(L|ID)+(L|C)+(L|Y)	12	132224	0	0.19	0.54
AC+(L|ID)+(L|C)	9	132545	320	0.19	0.57
AC+(L|ID)+(L|Y)	9	132616	392	0.20	0.55
AC+(L|ID)	6	133722	1498	0.26	0.49
AC+(1|ID)+(1|C)+(1|Y)	6	134127	1902	0.12	0.62
AC+(1|ID)+(1|Y)	5	134286	2062	0.11	0.62
AC+(1|ID)+(1|C)	5	134398	2173	0.12	0.57
AC+(1|ID)	4	135146	2921	0.20	0.43
Females extrinsic model					
AC+H+T+H:L+AC:T+H:AC+T:L+(RF)		131918	0	0.21	0.55
AC+T+ AC:T+T:L+(RF)		131981	63	0.22	0.54
AC+H+P+H:L+AC:P+H:AC+P:L+(RF)		132111	194	0.28	0.48
AC+P+ AC:P+P:L+(RF)		132150	232	0.27	0.48
AC+ P+ AC:P +P:L+(RF)		132168	250	0.19	0.55
Males intrinsic model					
AC+(L|ID)+(L|C)+(L|Y)	12	88578	0	0.19	0.52
AC+(L|ID)+(L|C)	9	88770	192	0.21	0.58
AC+(L|ID)+(L|Y)	9	88916	338	0.20	0.58
AC+(L|ID)	6	89840	1262	0.30	0.58
AC+(1|ID)+(1|C)+(1|Y)	6	89953	1374	0.15	0.69
AC+(1|ID)+(1|Y)	5	90087	1509	0.12	0.62

AC+(1|ID)+(1|C)	5	90161	1583	0.10	0.60
AC+(1|ID)	4	90978	2399	0.23	0.46
<u>Males extrinsic model</u>					
AC+H+T+H:L+AC:T+H:AC+T:L+(RF)	22	167370	0	0.20	0.50
AC+T+ AC:T+T:L+(RF)	15	167564	194	0.22	0.50
AC+H+P+H:L+AC:P+H:AC+P:L+(RF)	28	167578	208	0.31	0.51
AC+H+ AC:H+H:L+(RF)	19	167612	242	0.17	0.51
AC+ P+ AC:P +P:L+(RF)	22	167799	429	0.31	0.52

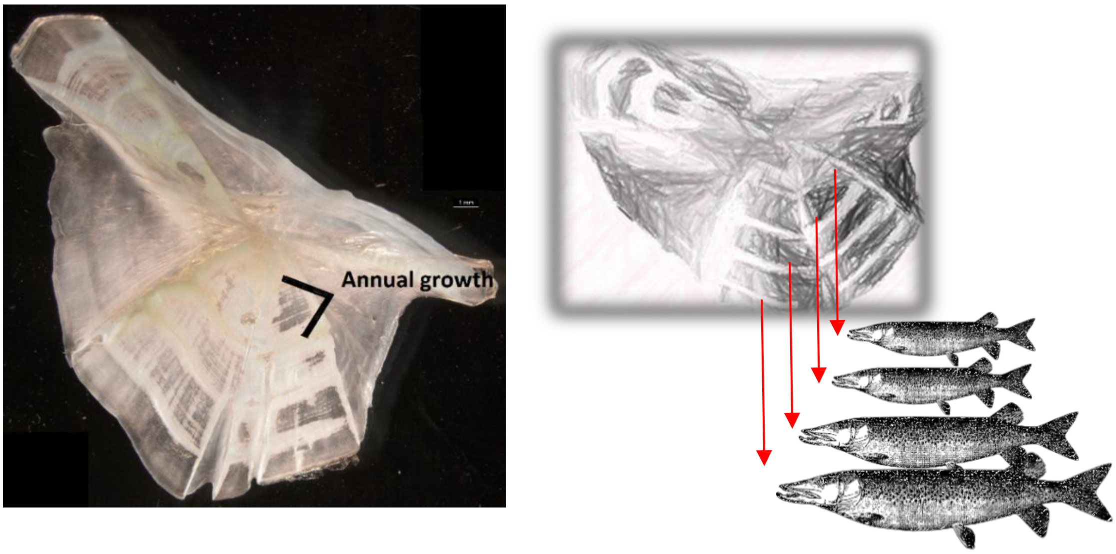
Supplementary Figure S1: The three study areas along the Swedish coast in the Baltic Sea and Lake Mälaren (Lake habitat). Licknevarp is the no-take zone (NTZ) and Marsö and Aspöja the coastal sites.



Supplementary Figure S2: A) Mean water temperature June-September in Kvädöfjärden 1964-2017, $r^2=0.21$ ($p<0.001$***), and B) Mean water temperature May-September (excluding June since June measurements ceased in 1995) from three sites in Lake Mälaren 1964-2017. Confidence interval in grey.

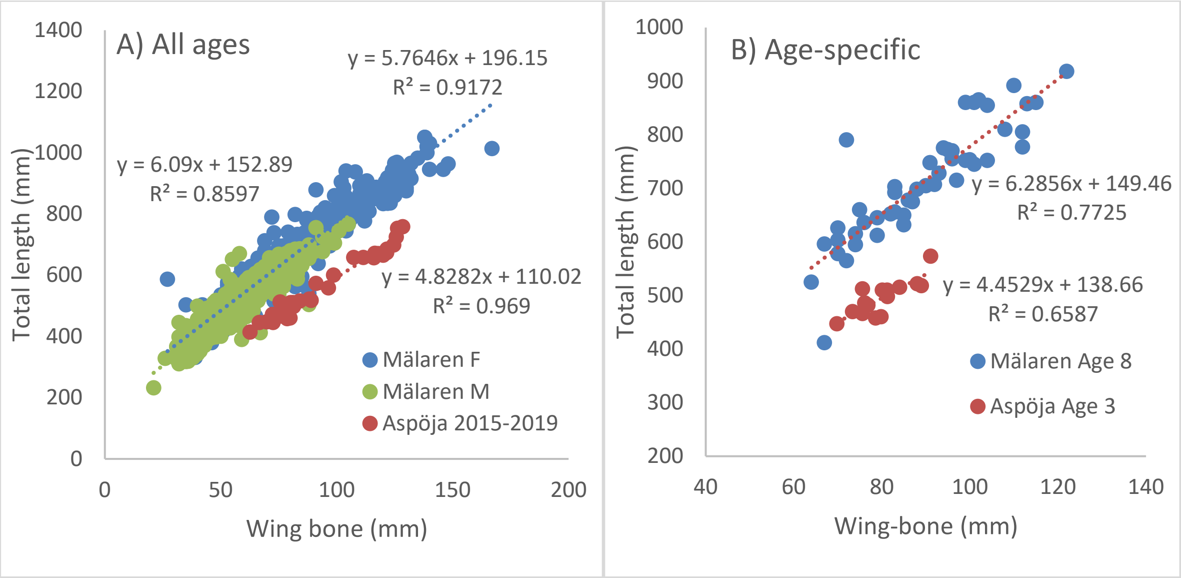


Supplementary Figure S3: A) Wing bone (metapterygoid) of pike displaying growth zones (dark translucent surface) and winter zones (white stripes) which together yield annual growth. Photo: Rickard Yngwe. B) Back-calculation of fish length using wing bone. Illustration from Thoresson (1996).

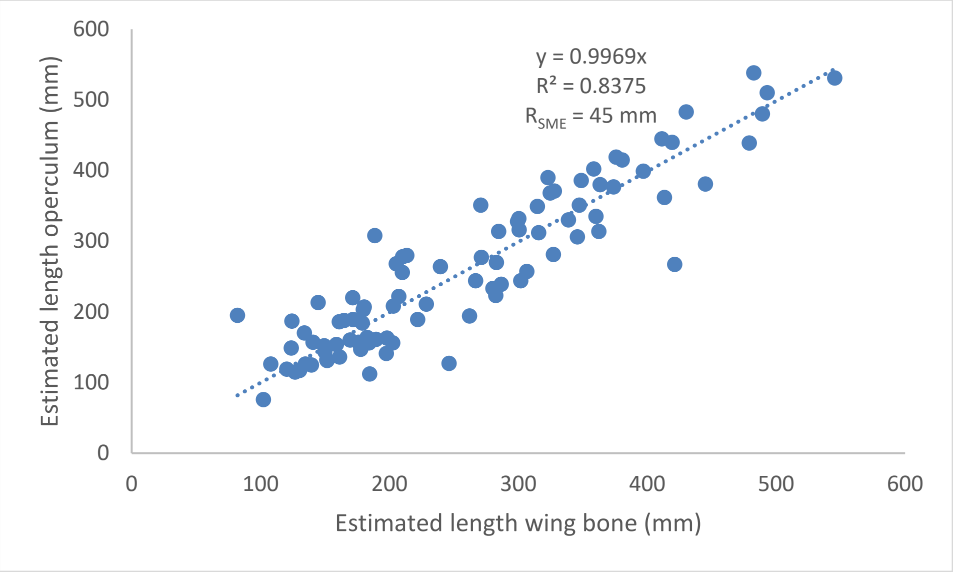


A) B)

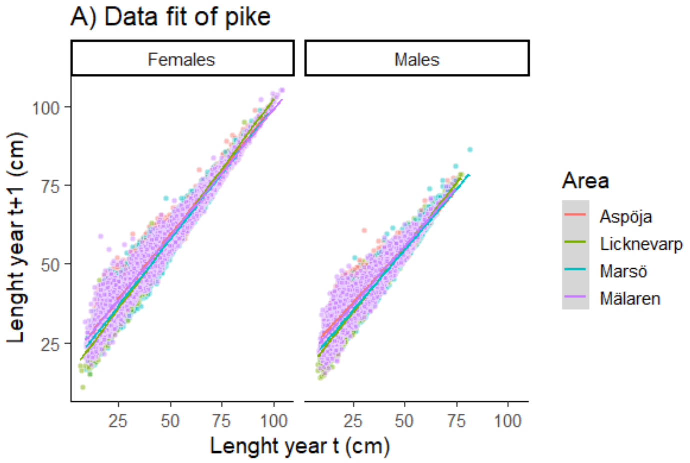
Supplementary Figure S4: A validation of the relationship between wing-bone size and length at catch for pike from Lake Mälaren (1969-2915) and Aspöja 2015-2019. A) Relationship across all ages for female (F) and male (M) pike at Lake Mälaren and both sexes at Aspöja. The relationship between wing bone size and body size is strong ($R^2 > 0.85$). Pike from Aspöja have larger wing bones relative to body size than both female and male pike from Lake Mälaren, but there is no evident structural deviance (i.e. non-linearity) among pike from the same area. B) Age-specific relationship between wing-bone size and body size (both sexes combined). Although explanatory power is lower (R^2 0.65-0.77), there is no structural deviance that would indicate that pike growing at different rates have different relationships between wing-bone size and body size. For back-calculated growth, body size is always scaled to wing-bone size (see eq. 1) so the difference in intercept between areas will be controlled for in the analyses.

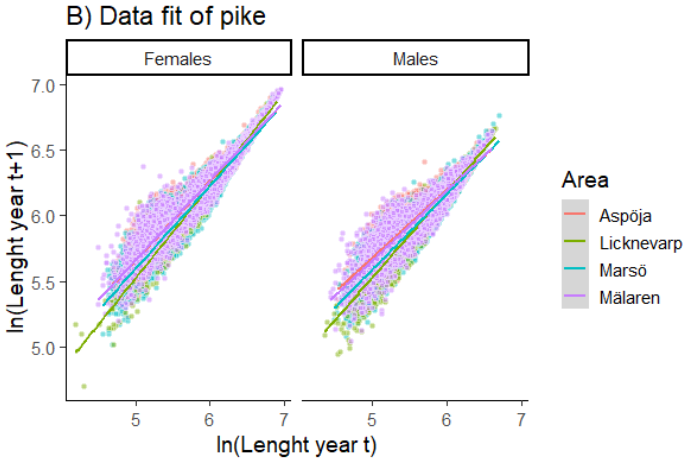


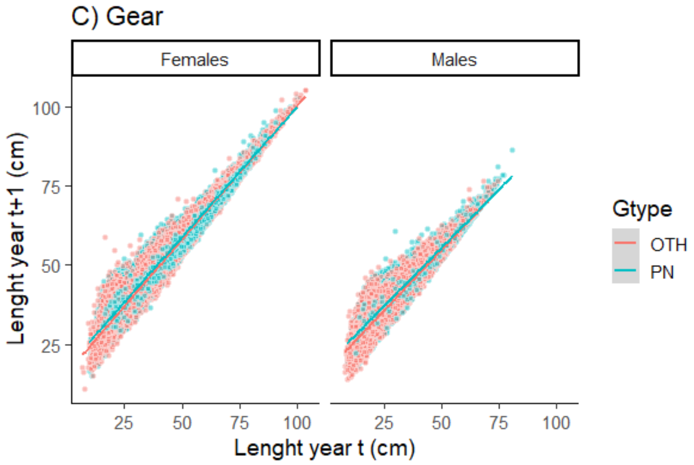
Supplementary Figure S5: The relationship between estimated back-calculated length from the wing bone (eq. 1) and the operculum bone (eq. 3) of 100 pike from the coastal area of Forsmark.



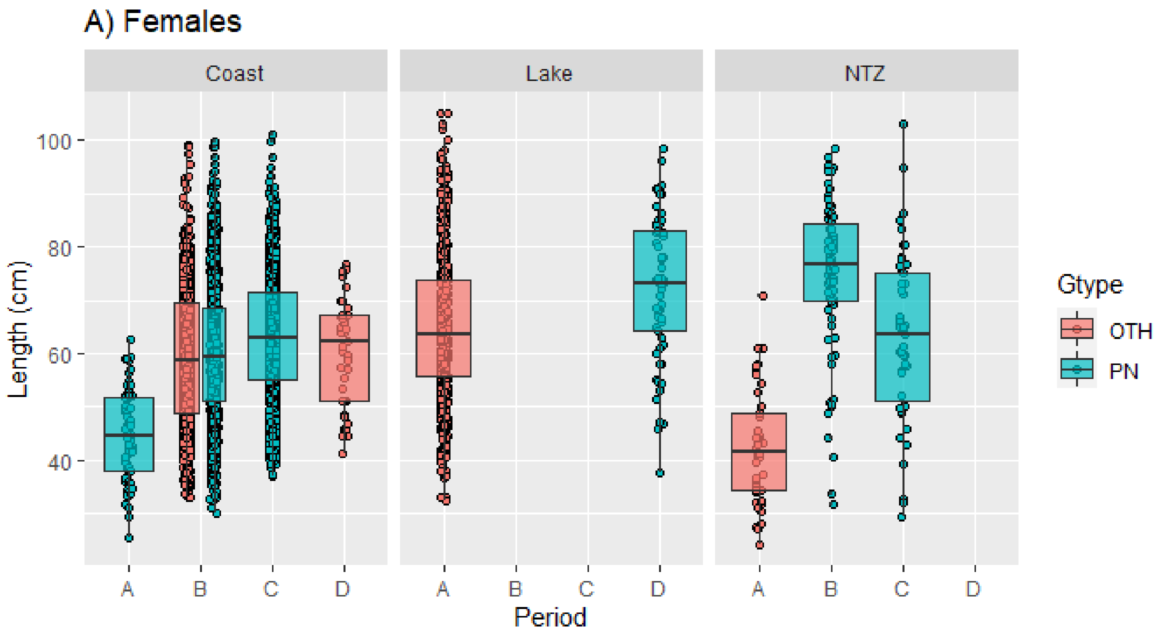
Supplementary Figure S6: Back-calculated length at year *t* and year *t*+1 of all pike (female and male) per sampling area using A) raw data, B) $\log_e$-transformed lengths ($\log_e(L_{i+1}) = 2.68 + 0.59*\log_e(L_i)$), and C) by gear type (Gtype) (PN is pound-net and OTH are other gears).

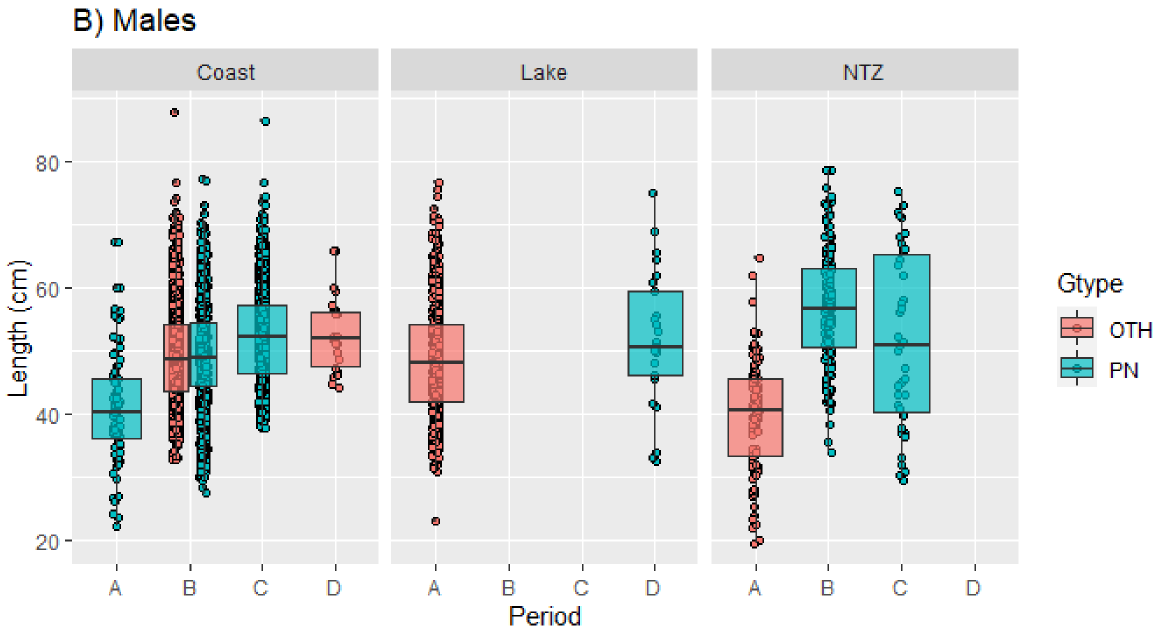




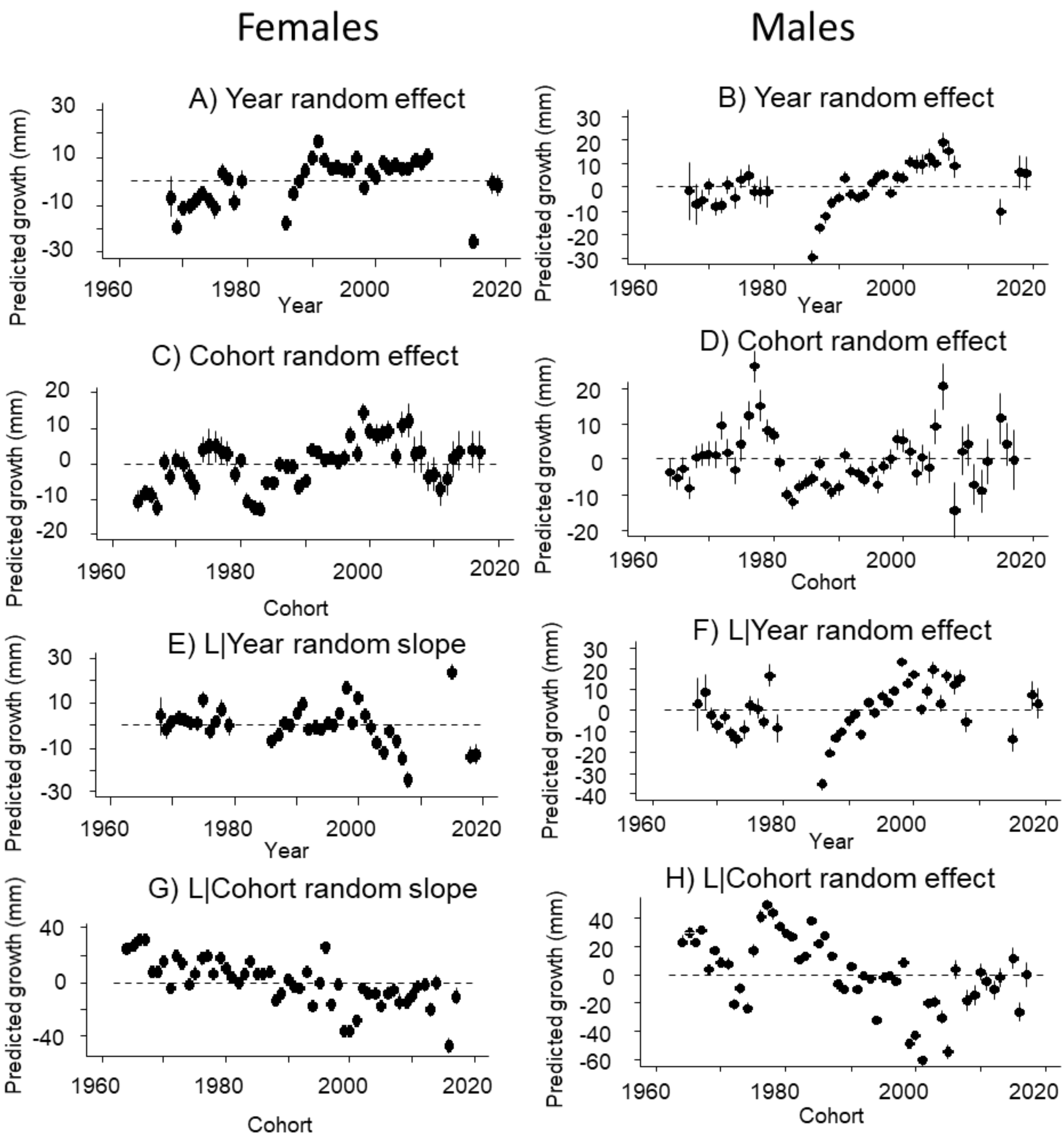


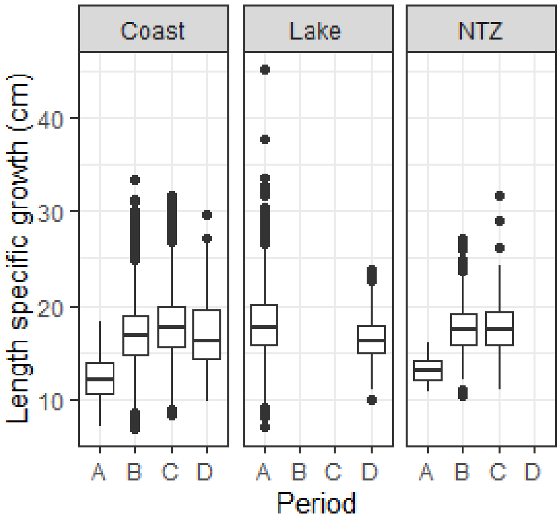
Supplementary Figure S7: Length distributions at catch shown for Habitat, Period and Gear type for A) female and B) male pike. Gear types (Gtyp) are PN – pound-net and OTH – others (fyke and gill nets and unknown).



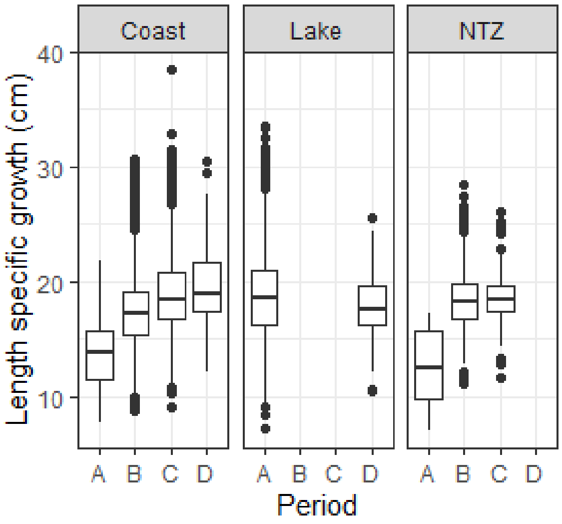


Supplementary Figure S8. A-H show plots of the random effects for the growth function female (A, C, E, G) and male (B, D, F, H) pike. A-B) show random intercept of sampling year, and C-D) cohort (*year of birth*). E-F) show random slope of growth of sampling year, and G-H) of cohort. I) and J) show length-specific somatic growth rates (cm year^{-1}, eq. 4) of I) female and J) male pike during the different time periods for the different habitats (Coast denotes the exploited Baltic Sea populations at Aspöja and Marsö, NTZ denotes the coastal no-take zone, and Lake is Lake Mälaren)





I) Growth of female pike



J) Growth of male pike

Supplementary Figure S9: Estimated total mortality of A) female and B) male pike sampled in pound nets in different *Habitat* and *Periods*. Total mortality is estimated from the catch-curve using the Chapman-Robson method. Lines are only for illustrative purposes to see changes in mortality between periods.