Original Articles

Varying relationships between fish length and scale size under changing environmental conditions – Multidecadal perspective in Atlantic herring

Szymon Smoliński [a,b,*], Florian Berg [a]

[a] *Institute of Marine Research, P.O. Box 1870 Nordnes, N-5817 Bergen, Norway*
[b] *Department of Fisheries Resources, National Marine Fisheries Research Institute, Kołłątaja 1, 81-332 Gdynia, Poland*

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ABSTRACT

Calcified structures are valuable indicators being used in fisheries research for the estimation of fish ages or back-calculations of fish lengths. Such back-calculations typically assume constant proportional growth of fish and calcified structures independent of internal or environmental factors. We analyzed extensive data (1935–2020) of scale measurements from Norwegian spring-spawning herring. We applied linear quantile regressions to investigate the fish length – scale size relationship and environmental influences on individuals growing at different rates. We demonstrated that the fish length – scale size relationship varied over time and between cohorts, individuals of the same year-class. Parts of this variation can be attributed to changing environmental conditions. We identified a negative effect of stock total biomass and a positive effect of temperature on fish length when conditioned on scale size. The effect of stock total biomass varied considerably but the effect of temperature was similar between fish characterized by different growth rates. Our results are essential for long-term studies highlighting potential biases associated with environmental effects and different growth rates of individuals. These biases should be accounted for in growth history reconstructions and applications of the calcified structures as ecological indicators.

1. Introduction

Calcified structures, such as scales and otoliths are characterized by continuous incremental growth, which is usually closely related to the somatic growth of fish (Harvey et al., 2000). Therefore, distributions of the fish length at capture in the past can be reconstructed based on archival or archeological materials, e.g., deposited otoliths, by measuring the size of these calcified structures (Avigliano et al., 2020). When seasonality of the environmental conditions occurs, causing seasonal differences in growth rates of fish, calcified structures form annual increments visible as consecutive zones of the periods of slower and faster growth (Campana, 2001). These annual increments are used for the aging of fish, providing essential information in fisheries science (Panfili et al., 2002; Ricker, 1975). Moreover, with known fish length at capture, measurements of these increments allow back-calculating the individual growth throughout their life and estimation of fish length at ages prior to capture (Francis, 1990; Vigliola and Meekan, 2009). Such methods can be used for the reconstruction of fish growth histories and are known in fisheries science for more than a century (Lea, 1910; Spurgeon et al., 2020).

Estimations of unknown fish length at capture or back-calculations are based on the assumption of the proportional growth of fish and calcified structures, which does not vary systematically with growth rate, and further, that the regression parameters can be accurately estimated from random samples of the population (Campana, 1990). Inconsistencies in the relationships between fish length and size of calcified structures may seriously affect any estimations based on the simple assumptions of linear relations (Heidarsson et al., 2006). Currently, in historical reconstructions, these relationships are often assumed to be consistent through time. Lack of temporal consistency in the relationships was previously shown e.g., for Pacific sardine (Landa, 1953). These time-varying relationships may be caused by environmental effects (Reznick and Kindbeck, 1989). For example, the temperature had an immediate effect on the relationships between larval size and otolith size (Fey and Greszkiewicz, 2021). Also, when food supply is higher, at least some calcified structures of fish grow disproportionately faster (Casselman, 1990). Decoupling between the growth of calcified structure and somatic growth of fish can be also caused by life-history events, such as migrations in anadromous species (Morrison et al., 2019). The establishment of how intrinsic and extrinsic factors, in

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particular temperature, affect the relationship between somatic growth and calcified structure growth is essential for the reliability of the biochronological studies (Morrongiello et al., 2012; Neat et al., 2008).

The potential differences in the environmental impacts on fish length – scale size relationships between the groups of individuals of varying growth rates is a perspective less explored in the fisheries research. Fish that grow fast (or slow) may differently respond to the varying environmental conditions (Biro and Dingemanse, 2009). These differences can be mediated by the variability in the individual plasticity or differences in the behavior (Geffen, 2009; Mitchell and Biro, 2017) and may affect the long-term reconstructions of the fish growth, such as biochronologies that are currently been developing (Izzo et al., 2016; Moyano et al., 2020; Smoliński, 2019; Tanner et al., 2019). For example, non-random selection of the individuals characterized by more clear annual growth patterns (and possibly a certain range of growth rates) may introduce biases into the reconstructed time series (Peharda et al., 2021; Schirripa and Goodyear, 1997).

We selected one of the classical examples in fisheries science, Norwegian spring-spawning herring (NSSH), which has a long history of the research of scales (Hjort and Lea, 1914; Lea, 1938, 1910; Ottestad, 1938). We used a long-term (1935–2020) database of measurements of 117,166 herring scales. The aim of this study was to investigate the hypotheses that the relationship between fish length and scale size is not constant temporally (hypothesis 1) and may be affected by environmental conditions (hypothesis 2). Further. we hypothesized that environmental effects on the fish length – scale size relationships are different for the fish groups growing at different rates (hypothesis 3). To test the null hypotheses associated with the alternative hypotheses presented above, we modeled aspects of fish length – scale size relationships other than the central tendency with quantile regression techniques (Cade et al., 2005; Koenker and Bassett, 1978). These techniques allowed us to investigate environmental influences on the slow-, medium- and fast-growing individuals in parallel. Additionally, we evaluated potential errors that can be introduced in the predictions of fish length based on the scale size under the assumption of consistent fish length – scale size relationships across cohorts. Our results are essential for long-term studies and highlight potential biases associated with the assumption of the temporally constant fish length – scale size relationships in the growth history reconstructions and applications of the calcified structures as ecological indicators.

2. Materials and methods

2.1. Fish and scale data

We obtained the data from the long-term (1935–2020) database of the Institute of Marine Research in Bergen, Norway. Fish from NSSH stock were collected from commercial and scientific samples. The fish length was measured from the tip of the snout to the tip of the longer lobe of the caudal fin (total length). Scales of fish were extracted and processed using standard methodology developed in the 1920s (Mjanger et al., 2020; Runnstrøm, 1936). The scales were mounted on glass plates and the annual rings were identified visually and the age was estimated using a microscope (de Barros and Holst, 1995). With the information on the year of catch and estimated fish age-at-catch, individuals were assigned to the cohort – a group of fish hatched in a given year. Scale size was measured as total radius along the axis, from scale core to the edge, using an ocular micrometer in the microscope (de Barros and Holst, 1995). Hereafter, we use fish length and scale size when referring to the actual total length of a fish and the total radius of a scale, respectively.

In order to avoid potential effects caused by fishing gear selectivity (Berg et al., 2017a), we selected only fish caught with trawls and seine from the database. Moreover, to minimize seasonal effects we selected only fish captured in February and March. We used only well-represented length classes (1 cm interval) within the range of 25–40 cm. We selected only cohorts with at least 10 length classes and 200

individuals present. The selection of well-represented length classes and cohorts allowed us to reduce the effects of unbalanced data on the quantile regression parameters. In total, we selected 90,553 fish from 59 cohorts for the analysis.

2.2. Data analysis

We used a linear quantile mixed model (Geraci, 2014) to analyze fish length – scale size relationships. Quantile regression offers a more complete statistical analysis of the relationships among variables than mean regression because it allows to model in parallel central tendency and other quantiles of the response variable (Challier et al., 2006; Garrido et al., 2015). By the application of quantile regression, we were able to investigate environmental influences on the slow-, medium- and fast-growing individuals. We assumed that environmental effects on the fish length – scale size relationships can have different strengths in fish characterized by diverse growth rates, defined by varying fish lengths for a given scale size.

We fitted a model with fish length as a response variable and scale size as a predictor variable. Both variables were standardized to have a mean of 0 and a standard deviation of 1. We allowed for the random intercept and random scale size-slope for each cohort. We modeled every 5th quantile (τ) within the range from $\tau = 10$th to $\tau = 90$th in order to investigate the fish length – scale size relationships across the gradient of slow-, medium- and fast-growing individuals. We contrasted residuals from the standard linear mixed model (Bates et al., 2015) with the length anomaly. These residuals can be seen as an equivalent of the 'quantiles' in the quantile regression. Fish length anomaly was calculated as fish length scaled to the mean and divided by their respective standard deviations within each age group. This preliminary test supported our interpretation that for example, individuals of the lowest quantiles (having the smallest fish length for a given scale size) represent slow-growing individuals and that these differences are not confused with other sources of variation. The same fact occurs for medium- or fast-growing individuals (Fig. S1).

We obtained standard errors and confidence intervals for the parameter estimates of linear quantile mixed model with a bootstrap approach (100 iterations). Furthermore, we did the same for a standard linear mixed model for comparisons. Cohort-specific intercepts and slopes of fish length – scale size relationships were extracted from the linear quantile mixed model using Best Linear Unbiased Predictors (BLUPs; Henderson, 1975) and visualized. Long-term temporal trends in BLUPs were assessed with linear regression.

We used mean monthly Sea Surface Temperature (SST) from HadISST data (Rayner et al., 2003) within the main NSSH occupancy area ($60°N - 75°N, 10°W - 50°E$) (ICES, 2020; Olsen et al., 2010). We obtained NSSH stock dynamics data since 1988 from the reports of the Working Group on Widely Distributed Stocks (WGWIDE) of the International Council for the Exploration of the Sea (ICES, 2020). Historical stock data from 1935 to 1988 was provided by ICES (2018) using an XSAM like the currently used assessment model. Data on total biomass and spawning stock biomass were available for the analysis, but we included only total stock biomass due to the high correlation between variables (R = 0.93). Total biomass was assumed to be a better proxy for the density-dependent effects, as it also reflects processes during the immature phase of fish life.

We modeled potential environmental effects on the fish length – scale size relationships by the inclusion of the environmental variables in the baseline linear mixed model as fixed effects. Because environmental conditions can have effects on fish biology in different periods of life, we applied a statistical approach to rigorously identify the most critical period in which selected environmental variables (SST and total stock biomass) had the strongest effect on fish TL. We tested different ranges of years (from the year of the hatch to the 10th year of cohort life). We used the difference in Akaike Information Criterion (ΔAIC) for the selection of the model which best explained the variance in the fish

length, conditioned on the scale size effect. Best environmental signals identified using the linear mixed model were incorporated into the baseline linear quantile mixed model.

For linear quantile mixed models, we calculated the τ-specific version of AIC and averaged AIC difference (ΔAIC_τ) between baseline model and environmental model to perform inference on the significance of the tested environmental effects (Burnham and Anderson, 2004). We calculated and averaged AIC weights (AICw$_\tau$) across the studied quantiles comparing the baseline model and environmental model to assess the relative likelihood of a model given a data set and two tested models (Allen and Vaughn, 2010; Fornaroli et al., 2015).

We demonstrated potential error in the reconstructions of the historical fish lengths based on the sizes of scale using relationships obtained from the more recent data. Typically, in such historical reconstruction, it is assumed that the fish length – scale size relationships are constant over time. We predicted the fish lengths in cohorts hatched before 1950 based on the linear mixed model refitted on the same data from cohorts < 1950 (N = 10637, hereafter called model < 1950) and the model refitted on the data from cohorts hatched after 1980 (N = 51644, hereafter called model > 1980). We developed an additional model > 1980, but with the investigated environmental predictors included, in order to test if the incorporation of these predictors can improve the prediction accuracy. We compared the measured fish lengths with lengths predicted by these three models using pairwise t-tests with Bonferroni correction. Additionally, we evaluated the models' prediction accuracy with the biplots and by calculation of root mean squared error (RMSE).

Data analysis was conducted using *R* scientific language v. 4.0.2. (R Core Team, 2020) and quantile regression models were developed with *lqmm* (Geraci and Bottai, 2014) and *quantreg* (Koenker, 2013) packages and linear mixed models with *lme4* package (Bates et al., 2015).

3. Results

The mean scale size (total radius) in our data subset (N = 90553) was 5.80 mm (SD = 0.77 mm), while the mean fish length (total length) was 323.1 mm (SD = 27.04 mm). A linear relationship between fish length and scale size was visible (Fig. 1). Among the visualized quantiles (τ = 10th, 50th, and 90th), cohort-specific regression lines seem to have the highest spread for the 90th quantile. A gradual shift of the quantile

regression lines from the earliest cohorts (i.e., prior to 1950) to the latest cohorts (2000 onwards) was observed.

BLUPs extracted from linear quantile mixed model indicated a gradual increase in cohort-specific random intercepts (linear year effect = 5.1×10^{-3}, p = 0.001), but approximately from 2007, there was a sharp decrease in the random intercepts (Fig. 2a). Conversely, BLUPs showed no significant long-term changes in cohort-specific scale size-slopes (linear year effect=-4.3×10^{-4}, p = 0.541) (Fig. 2b). Despite the long-term directionality of these changes, there were some year-to-year deviations. BLUPs of the random scale size-slopes were characterized by higher interannual variability than BLUPs of the random intercepts.

The best time window identified for total stock biomass was from the 5th year to the 6th year of fish life (Fig. 3a). The inclusion of this variable significantly improved the model fit (ΔAIC = -30.74). For all investigated time windows total stock biomass effect on fish length was negative and ranged from -0.20 to -0.13 (Fig. 3b). The best time window selected for SST was from the 6th year to the 10th year of fish life (Fig. 3c). The inclusion of this variable significantly improved the model fit (ΔAIC = -11.96). Estimates of the effect of SST on fish length ranged from -0.03 to 0.08. Within the first 3–7 years of fish life, the SST effect was negative, while further (including the best time window selected), it was positive (Fig. 3d).

Estimates of parameters from the linear quantile mixed model, in line with expectations, showed increasing intercepts with increasing τ (Fig. 4a), and decreasing slope for scale size with increasing τ (Fig. 4b). The estimates for τ = 50th were almost identical to the results obtained with least-squares solution from a linear mixed model (Fig. 4a and Fig. 4b). The inclusion of selected environmental effects into the baseline linear quantile mixed model significantly improved the model fit (average ΔAIC_τ = -436.81). Across the studied quantiles average AICw$_\tau$ = 0.71, indicating a high relative likelihood of the environmental model.

Parameters of environmental effects on fish length estimated with linear quantile mixed model have changed along the τ gradient (Fig. 4c and Fig. 4d). There was a decrease in estimates for the total stock biomass effect from -0.14 (τ = 10th) to -0.30 (τ = 70th). Within the upper range of quantiles (τ from 75th to 90th), estimates were elevated up to -0.14, but are associated with a higher level of uncertainty and may be biased (Fig. S2). Parameter estimates for the SST effect along the τ gradient showed fewer differences, ranging between 0.07 and 0.14 (τ
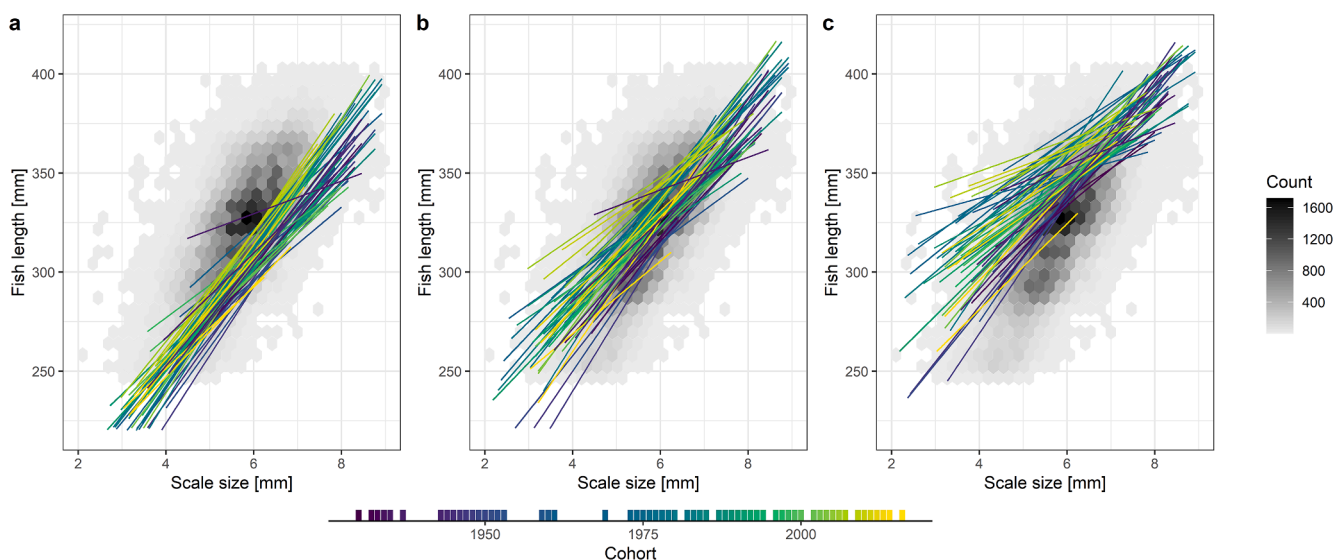

Fig. 1. Linear quantile regression of fish length and scale size (total radius) fitted for 10th (a), 50th (b), and 90th (c) quantile separately for each cohort. Cohorts are indicated with the color gradient. The density of the data points is indicated with the grey gradient. For simplicity density of data points is calculated for all cohorts, while quantile regression lines are fitted separately to each cohort. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)
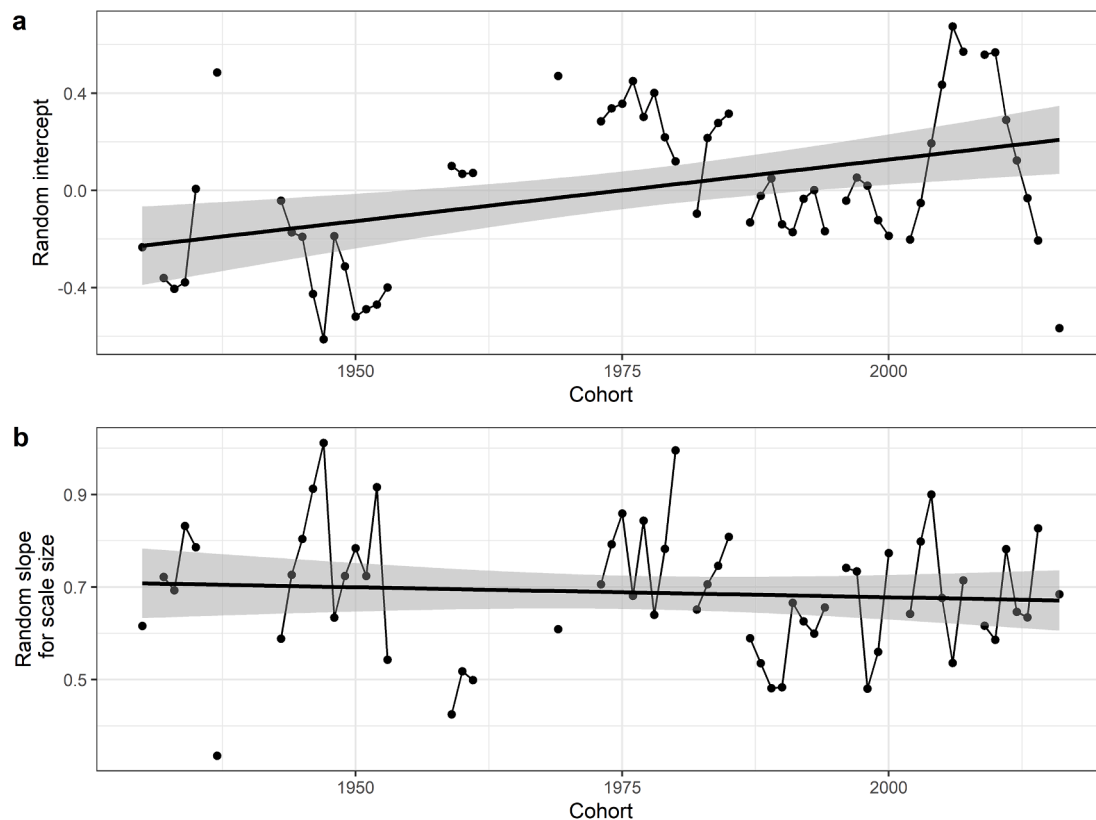
Fig. 2. Best Linear Unbiased Predictors (BLUPs) of random intercepts (a) and random scale size-slopes (b) for fish cohorts and $\tau = 50$th quantile. Prior to the analysis fish length (response variable) and scale size (predictor variable) were standardized to have a mean of 0 and a standard deviation of 1. The trend lines were fitted to the BLUPs with linear regression.

from 10th to 70th). Similar to total stock biomass estimates, there were values elevated up to 0.28 within the upper range of quantiles (τ from 75th to 90th), but again they are associated with a higher level of uncertainty and may be biased (Fig. S2). In both cases, we considered these results for the higher quantiles as an artifact and a product of model instability and discarded them from the interpretation.

The two linear mixed models of fish length – scale size relationship fitted separately to the data from selected cohorts < 1950 and cohorts > 1980 obtained the conditional coefficient of determination $R^2 = 0.64$ and $R^2 = 0.56$, respectively. Addition of environmental predictors to the model > 1980 improved the conditional coefficient of determination to $R^2 = 0.58$. In the example reconstruction, there were no significant differences ($p > 0.05$) between the mean measured length of fish from cohorts < 1950 and the length predicted by the model < 1950 (Fig. 5a). However, there were significant differences ($p < 0.001$) between the measured length of fish and the length predicted with the model > 1980. No significant differences ($p > 0.05$) were observed between the measured length of fish and the length predicted with the model > 1980, when the environmental predictors were included. The model > 1980 overestimated the length of fish based on the information on the scale size, on average by 8 mm, while model > 1980 with environmental predictors underestimated the length on average by 1 mm. The prediction of the model < 1950 had RMSE = 14.49, while prediction of the model > 1980 had RMSE = 18.36, increasing the RMSE by $\sim$ 27% when compared to model < 1950 (Fig. 5b). Further addition of environmental predictors to the model > 1980 reduced the prediction error to RMSE = 16.57 ($\sim$14% higher RMSE when compared to model < 1950).

4. Discussion

We used an extensive time series covering multiple decades to

investigate the relationship between fish length and scale size. The identified relationships varied over time and between cohorts, and this variation can be attributed to changing environmental conditions. Two selected environmental variables showed significant effects (negative for total biomass and positive for SST) on fish length when conditioned on the scale size. The extent of these effects varied for selected time frames of life, but the most critical time periods (strongest effects) coincide with the periods of life where fish are potentially most vulnerable to the changes in these environmental factors. Total biomass differently affected fish with different growth rates in relation to their scales (two times higher effect size on faster-growing individuals in comparison to the slowest-growing fish). The temperature had a similar effect on all fish.

In line with hypothesis 1, this study demonstrates varying fish length – scale size relationships for fish from different cohorts. It has been shown earlier that this relationship is not constant over time (e.g., Landa 1953) but this variation is rarely considered in biochronology studies (Morrongiello et al., 2012). A constant relationship is often assumed in the back-calculations based on calcified structures, but interannual variability in the parameter estimates identified in this study shows that this assumption can be wrong. Currently, considerable sources of errors are typically neglected, which can lead to inaccurate approximations and predictions of somatic growth. Especially, the long-term trends in the parameters of the fish length–scale size relationships call for caution, as they might cause spurious inference on the directional changes in the long-term studies and applications of these calcified structures as ecological indicators of somatic growth.

In accord with hypothesis 2, we showed that the temporal variation in fish length – scale size relationship can be associated with environmental conditions experienced by fish during their lifetime. The environmental impact on the fish length – scale size relationship varied
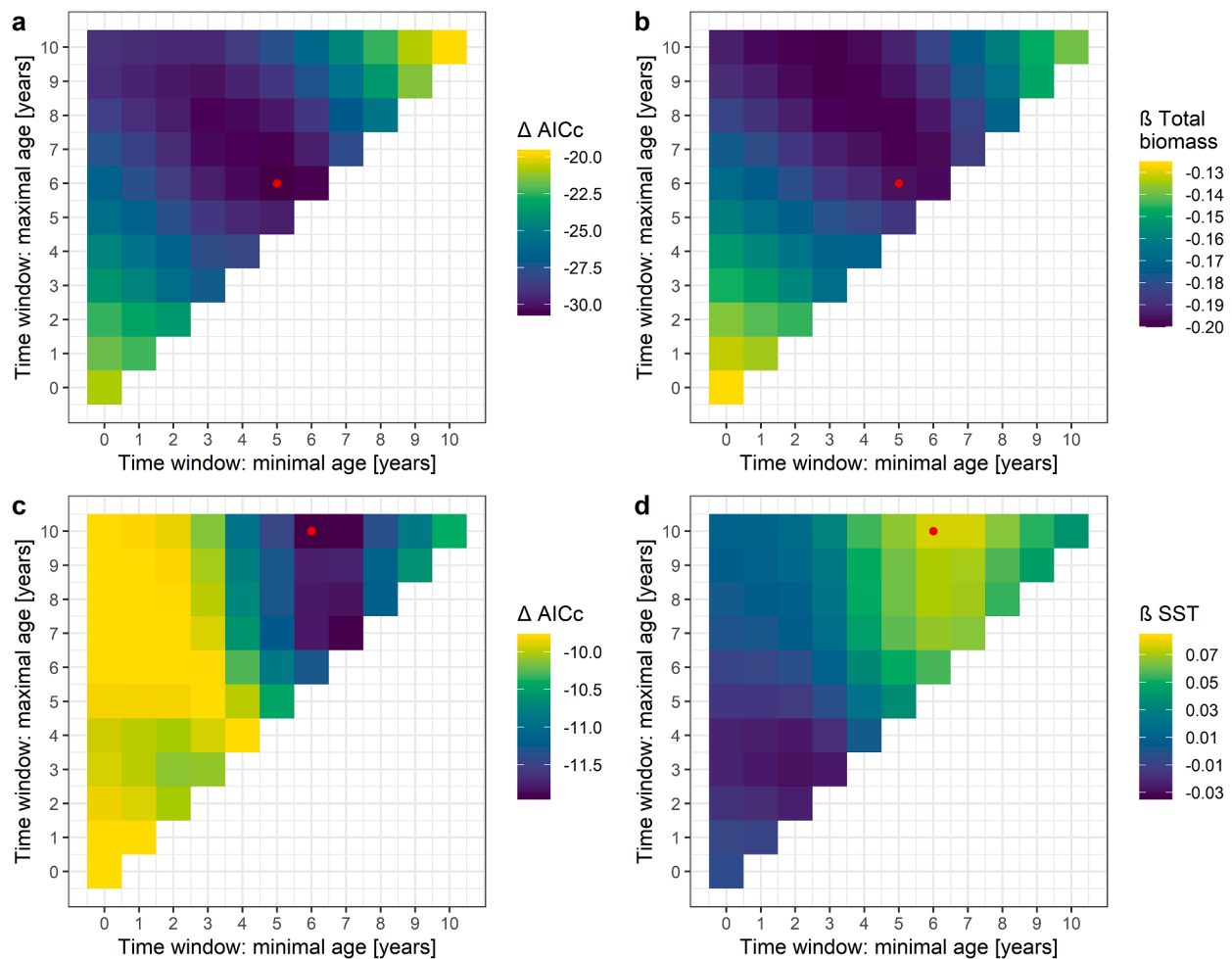
Fig. 3. Results of the sliding window analysis when integrating total biomass (a, b) and sea surface temperature (c, d) in the baseline linear mixed model. ΔAIC is the difference between the particular model and model without environmental variables. β is the estimated parameter of the slope of the environment variable. The optimal time window is indicated with the red dot. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

across the periods of the fish lifetime. The strongest effect on the relationship was observed when including the total biomass experienced at age 5–6 as a covariate. Fish of age 5–6 usually accomplish the highest total biomass of the NSSH stock (Fig. S4). Therefore, density-dependent effects play a crucial role at this age. Higher total biomass led to reduced prey availability and high competition, reducing growth and fish body sizes. We consider this basic ecological mechanism as the most likely explanation of the stock biomass effects on the fish length – scale size relationships. We showed also that the effect of temperature on the fish length – scale size relationship was strongest at age 6–10. At this age herring usually reach their asymptotic maximum length (Berg et al., 2017b), and the growth differences may become visible. Temperature, as one of the prominent environmental factors, directly affects fish metabolism and growth (Tanner et al., 2019). Temperature influences also ecosystem productivity and thus, indirectly affects fish growth processes, e.g., through food supply (Huntley and Lopez, 1992; Smoliński and Mirny, 2017). Therefore, the temperature may also modulate the relationships between fish length and the size of calcified structures. Interestingly, the temperature effect in our modeling was negative during the first years of cohort life, and positive at the older ages. These contrasting relationships are in line with previous findings and the general temperature–size rule, indicating that temperature can differently affect the growth of juvenile and adult fish (Huss et al., 2019; Smoliński et al., 2020a).

Environmental conditions certainly affect the growth of fish and may

in consequence cause decoupling of fish length and scale size (Casselman, 1990; Fey, 2006). Two internal biological effects identified in fisheries research can play a role and mediate these environmental influences: age effect and growth effect (Reznick and Kindbeck, 1989; Secor and Dean, 1989). The age effect occurs when the size of calcified structures increases in non-growing fish (Morita and Matsuishi, 2001). The growth effect occurs when calcified structures from slow-growing fish are larger than those from fast-growing fish of the same size (Reznick and Kindbeck, 1989; Sirois et al., 1998). When using length anomalies, within the same ages, as a proxy for slow- and fast-growing individuals, we found a higher ratio between scale size and fish length for slow-growing fish than for fast-growing fish (Fig. S3). These results indicated the growth effect (Ashworth et al., 2017; Mosegaard et al., 1988), which can be directly associated with the recognized environmental influences.

The novelty in this study is the investigation of hypothesis 3 assuming varying responses of individuals from different quantiles (representing slow- and fast-growing fish) to experienced environmental conditions. We observed a more negative stock biomass effect in the higher quantiles than in the lower quantiles. The effect of stock biomass, through density-dependence mechanisms, might be the most prominent in fish with higher growth rates and larger body sizes, since they demand more food and energy to maintain their growth level and suffer most under food-limited conditions (Ross et al., 2018). Since the estimated effect of temperature was the same among the quantiles, it seems that
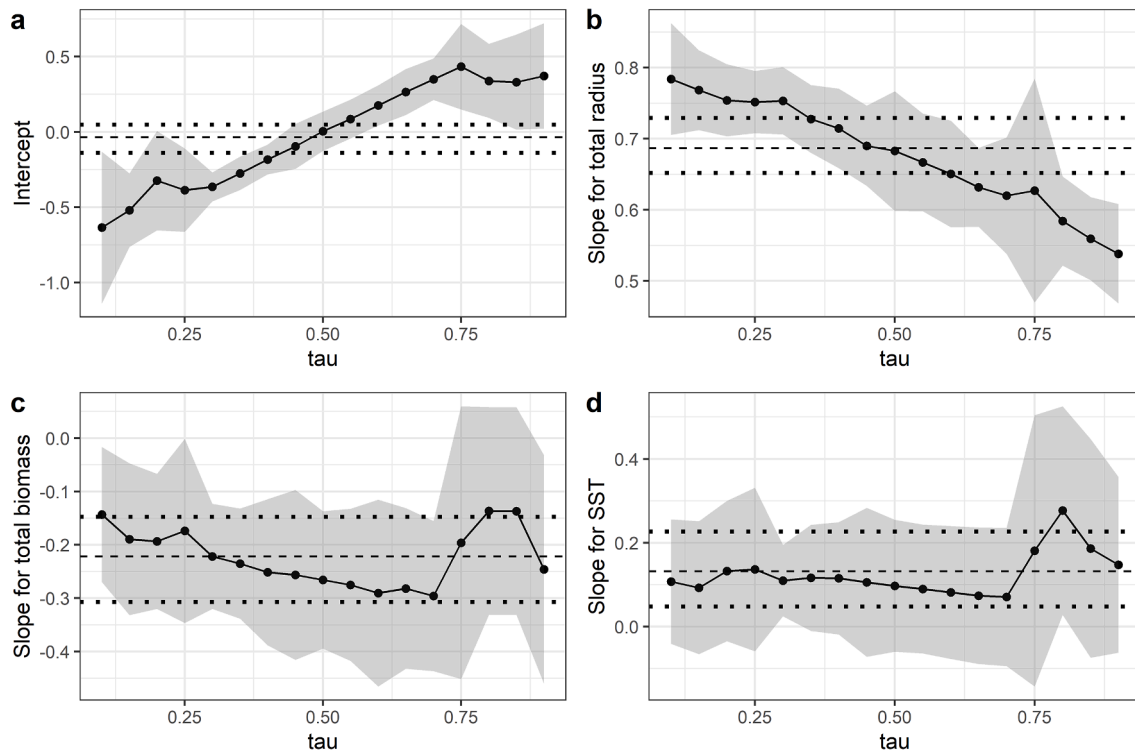
Fig. 4. Estimates of parameters from the linear quantile mixed model for a range of investigated quantiles (taus): intercept (a), total radius (b), total stock biomass (c) and sea surface temperature (d). The least-squares solution from a linear mixed model (dashed line) and the 95% confidence interval (dotted lines) are provided for comparison. The response and explanatory variables were standardized to have a mean of 0 and a standard deviation of 1 prior to the analysis.

temperature-driven decoupling of fish length – scale size relationships was independent of the actual growth rate.

The variability of responses to the changing environmental conditions is of crucial importance for the evolutionary fitness of a species (Melbinger and Vergassola, 2015). Following the assumption that individuals of the same cohort experience similar environmental conditions, it is interesting that individuals with different growth rates respond unequally (Xiao, 1996). This varying reaction norm can be explained by personality traits such as boldness, activity, and aggression which can lead to differences in growth rates (Biro and Post, 2008; Biro and Stamps, 2008; Dingemanse et al., 2009). However, these aspects can have also methodological consequences in biochronological studies focused on the indication of ecological processes. During the selection of the biological material, the calcified structures from fast-growing individuals can be preferred due to the wider and clearer annual increments, but in consequence, they might introduce biases into biochronologies (Peharda et al., 2021; Smoliński et al., 2020b).

We showed example reconstruction of the historical fish lengths based on the model of fish length – scale size relationships fitted to the more recent data. In our example reconstruction, fish length was overestimated when using the model from the more recent cohorts, and the accuracy of the predictions was considerably lowered. This inaccuracy was linked to the systematic temporal deviances from the linear fish length – scale size relationships described herein. As mentioned previously, such systematic errors can cause wrong interpretation of the long-term changes in the average growth of the population. However, part of these biases can be reduced when the environmental effects are considered. Therefore, it is highly recommended to account for differences in these relationships when reconstructing fish length based on calcified structures and appropriately correct for the environmental effects. Further simulation studies are recommended to investigate how time-varying relationships might affect reconstructions of growth dynamics and biochronologies which typically rely on constant relationships.

Atlantic herring is known for its plasticity and extensive annual migrations (Geffen, 2009). These circumstances are challenging when investigating relationships between fish of different ages, growth rates, or migration habits within their environment. The trade-off in our study is that we have used fixed temperature and stock biomass for all individuals within a given year. Even though selecting the optimal time ranges, temperature data still represent mean environmental conditions, and not necessarily experienced conditions. Especially herring experience a variety of environmental conditions during their annual migrations which are not considered. We recommend that further studies could also account for this spatial–temporal variability.

Using long time series always introduces some bias as methods might have changed over time. According to the protocol, scale measurements have been standardized (Mjanger et al., 2020), but there are still some potential limitations. The scale size is not constant within an individual, as their size varies with body region. This should be limited since scales are generally collected from the same body regions, but if no scales are available, they were collected from other regions (Mjanger et al., 2020). However, given the high sample size, this effect should be minor. There are also certain modeling issues that should be considered when interpreting the results. While the relationships between fish length and size of calcified structures can be asymptotic (Casselman, 1990; Souza et al., 2020), we assumed that this effect is negligible, and for simplicity, we applied a linear model. At first, we tested also generalized additive quantile regression, but the model fit was better with the currently used linear quantile regression. Also, the historical data for the total stock biomass might be relatively uncertain (ICES, 2018). Using assessment model outputs for the subsequent analyses leads to inevitable uncertainties which not always are possible to quantify (Brooks and Deroba, 2015).

In conclusion, our study provides novel knowledge about the temporal changes in the fish length – scale size relationship and associated parts of this variation with the influences of environmental conditions. These impacts might vary between fish with different growth rates and
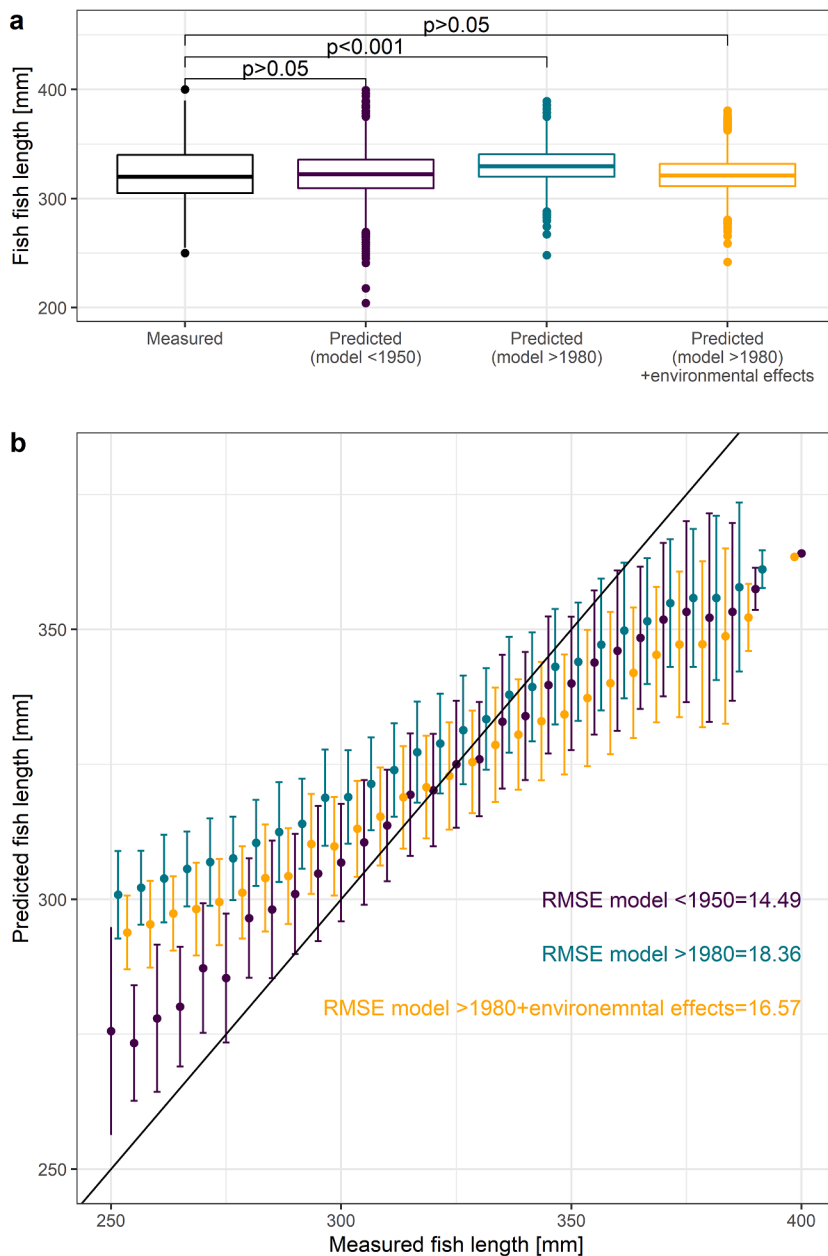
a

b

Fig. 5. Comparison of the length of fish measured from the selected cohorts hatched prior to 1950 and predicted by the three linear mixed models fitted on the data from cohorts < 1950 (indigo), cohorts > 1980 (turquoise), or cohorts > 1980 but with environmental predictors included (orange). In boxplots (a) lines, boxes, and whiskers are medians, interquartile range (IQR), and 1.5 × IQR, respectively. P-values of the pairwise *t*-test comparisons are provided. In the biplot of the measured and predicted fish length (b), data points for the model > 1980 were shifted horizontally by + 1.5 and model > 1980 with environmental predictors by −1.5 to avoid overlapping. The solid black line indicates perfect prediction. Root mean squared errors (RMSE) of models' predictions are provided. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

during different periods of life. Therefore, these time-varying relationships in fish length – scale size, which can be differently modulated by the environment at various growth rates, need to be taken into consideration in future research. Accounting for this variability will improve future reconstructions of organisms' growth and applications of biochronologies as ecological indicators.

CRediT authorship contribution statement

Szymon Smoliński: Conceptualization, Methodology, Formal analysis, Writing – original draft, Writing – review & editing. **Florian Berg:** Conceptualization, Methodology, Formal analysis, Writing – original draft, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2021.108494.

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