

ARTICLE

Corroborating otolith age using oxygen isotopes and comparing outcomes to scale age: Consequences for estimation of growth and reference points in northern pike (*Esox lucius*)

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Abstract

Accurate age estimates are crucial for assessing the life-histories of fish and providing management advice, but validation studies are rare for many species. We corroborated age estimates with annual cycles of oxygen isotopes ($\delta^{18}\text{O}$) in otoliths of 86 northern pike (*Esox lucius*) from the southern Baltic Sea, compared results with visual age estimates from scales and otoliths, and assessed bias introduced by different age-estimation structures on von Bertalanffy growth models and age-structured population models. Age estimates from otoliths were accurate, while age estimates from scales significantly underestimated the age of pike older than 6 years compared to the corroborated reference age. Asymptotic length (L_{∞}) was larger, and the growth coefficient k was lower for scale ages than for corroborated age and otolith age estimates. Consequentially, scale-informed population models overestimated maximum sustainable yield (MSY), biomass at MSY (B_{MSY}), relative frequency of trophy fish (≥ 100 cm), and optimal minimum length limit but underestimated fishing mortality at MSY (F_{MSY}). Using scale-based ages to inform management regulations for pike may therefore result in conservative management and lost yield. The overestimated asymptotic length may instill unrealistic expectations of trophy potential in recreational anglers targeting large pike, while the overestimation in MSY would cause unrealistic expectations of yield potential in commercial fishers.

KEYWORDS

age estimation, secondary ion mass spectrometry, stable oxygen isotopes, yield, $\delta^{18}\text{O}$

1 | INTRODUCTION

Most life-history traits of fish have a time dimension, such as age-at-maturity, growth rate, mortality, or longevity (Ahrens et al., 2020; Beverton & Holt, 1957; Denechaud et al., 2020). Counting periodic growth increments that form on calcified hard structures is the

most common fish age estimation approach (Campana et al., 1995; Denechaud et al., 2020). Errors in age estimation can lead to ill-informed reference points and mismanagement (e.g., incorrect harvest regulations), which may have serious consequences for fish populations and associated fisheries (Reeves, 2003; Tyszko & Pritt, 2017; Yule et al., 2008). Information on the accuracy and

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precision of age-estimation structures and methods, along with the range of ages on which they are applicable, are prerequisites for an accurate understanding of the life history and population dynamics of a managed fish species. Such information is particularly rare in inland and small-scale coastal fisheries that lack resources for annual monitoring (Beard Jr. et al., 2011; Brownscombe et al., 2019; Midway et al., 2016; Post et al., 2002), such as coastal fisheries in the southern Baltic Sea targeting northern pike (*Esox lucius*) in brackish environments (van Gemert et al., 2022).

Coastal pike stocks in the Baltic Sea have traditionally been exploited by commercial fisheries, but a strong recreational fishery has recently developed (Arlinghaus et al., 2023b; Bergström et al., 2022) that often has different objectives than commercial fisheries, such as favoring the catch of trophy fish or catch rate over biomass yield (Ahrens et al., 2020; Arlinghaus et al., 2019). Over the last decade, pike stocks have declined in many areas of the Baltic (Bergström et al., 2022; Fitzgerald et al., 2023; Lehtonen et al., 2009; Olsson et al., 2023). To align fishing mortality rates with shifts in fish abundance, assessment of contemporary growth rates and derivation of fisheries reference points that suit commercial and recreational fisheries are important (Ahrens et al., 2020). This, in turn, demands an assessment of possible sources of bias in age-estimation procedures and testing the effects of age-estimation errors on growth modeling and the estimation of management reference points (Tyszko & Pritt, 2017).

Age-estimation errors derive from process errors and interpretation errors (Beamish & McFarlane, 1995; Campana, 2001; Maceina et al., 2007). Process errors result from age-estimation structures that do not form true annual marks or annual marks that are not visually discernible, thereby preventing a reliable estimate of age. Process errors are thus errors of accuracy and are usually biased toward systematic under- or overestimation of age. Interpretation errors result from poor reproducibility of age estimates due to individual subjectivity and can be either biased or random (Beamish & McFarlane, 1995; Campana, 2001; Maceina et al., 2007). Both error types can have multiple explanations, such as environmental conditions affecting the readability of hard structures, ontogenetic transitions (e.g., change in prey type), disease, and slow growth rates that form sub-annual checks that are misinterpreted as annual marks (annuli) (Weyl & Booth, 1999), or blurred true annuli (Casselman, 1990; Weyl & Booth, 1999; Whiteman et al., 2004). Biased age estimates can lead to biased estimates of the growth and productivity of a fish stock that affect models estimating harvest resilience and reference points for fisheries management (Beamish, 1987; Bertignac & De Pontual, 2007; Campana, 1990). To reduce such errors, age validation or age corroboration is needed, although it is rare (Beamish & McFarlane, 1995; Maceina et al., 2007; Spurgeon et al., 2015).

Validation of fish age aims to confirm the temporal scale at which visual growth marks are deposited in a calcified structure (Beamish & McFarlane, 1983; Campana, 2001). Validating the true age of individuals can be done through mark recapture of known-age fish (Bruch et al., 2009; Crane et al., 2020; Hamel et al., 2014) or by using bomb-radiocarbon dating (Bruch et al., 2009; Casselman et al., 2019;

Hamel et al., 2008). Periodicity of growth mark deposition can also be used to validate age, such as through the release and recapture of chemically (e.g., tetracycline) marked wild-caught fish (Brown & Gruber, 1988; Laine et al., 1991). In contrast, corroborating age estimates of a sample of unmarked fish of unknown age do not validate true age (Kimura et al., 2006; Maceina et al., 2007). Age corroboration is used when no validated ages or known-age fish are available, and the species in question is not particularly long-lived (Heimbrand et al., 2020; Hüsey et al., 2020; Kimura et al., 2006), such as coastal pike, for which, to our knowledge, age-estimation methods have not been validated.

Age can be corroborated by quantifying the periodicity of seasonal variation in elemental cycles deposited in fish otoliths (Heimbrand et al., 2020; Hüsey et al., 2020; Kestelle et al., 2017; Weidman & Millner, 2000). For example, the relative abundance of oxygen isotopes ^{18}O to ^{16}O , notated as $\delta^{18}\text{O}$, varies as a function of isotopic composition and the temperature of ambient water and has been demonstrated to be a reliable thermal marker in fish (Hoie & Folkvord, 2006; Kestelle et al., 2017; Weidman & Millner, 2000). For example, $\delta^{18}\text{O}$ values followed a strong seasonal cycle in pike in Lake Annecy, France (Gerdeaux & Dufour, 2012). Methodological advancements over recent years have allowed the determination of $\delta^{18}\text{O}$ values with high precision and spatial resolution using secondary ion mass spectrometry (SIMS) transects on otoliths (Matta et al., 2013; Morissette et al., 2020). This method also allows measuring isotopic abundance on a standardized transect from core to margin without prior interpretation of annual structures.

The age of fish has been estimated from a multitude of calcified structures, including otoliths (Lai & Gunderson, 1987; Oele et al., 2015) and scales (Anwand, 1969; Harris, 2020; Van Oosten, 1929). While otoliths provide accurate and precise age estimates for several species (Blackwell et al., 2016; Hoie & Folkvord, 2006; Tyszko & Pritt, 2017), scales are debatable as a non-lethal structure for accurately estimating age. For example, scale ages of pike were accurate up to an age of 10 years (Anwand, 1969; Laine et al., 1991; Pagel et al., 2015), but were also inaccurate and imprecise for age estimation elsewhere (e.g., Blackwell et al., 2016; Mann & Beaumont, 1990; Oele et al., 2015). However, scales continue to be used to estimate the age of pike (Monk et al., 2021). Especially in the Baltic Sea, where age estimation from scales has been common (Berggren et al., 2022; Dorow, 2004; Droll, 2022; Hegemann, 1958; Juncker, 1988), and habitat-induced variability in readability of calcified tissues is likely (e.g., Baltic cod, *Gadus morhua*, Hüsey et al., 2016), further age validation is needed.

The objective of our study was to determine if age could be estimated accurately and precisely from otoliths and scales of pike collected from brackish lagoons of the southern Baltic Sea in Germany. First, we compared the age estimates derived from $\delta^{18}\text{O}$ chronologies on otoliths to visual age estimates from scales and otoliths. Next, we compared parameters of Von Bertalanffy (1938) growth curves estimated from structure-specific size-at-age estimates between age-estimation structures. Next, we used an age-structured population model to determine how growth parameter estimates

affected estimates of fisheries reference points, including maximum sustainable yield (MSY), fishing mortality at maximum sustainable yield (F_{MSY}), and biomass at maximum sustainable yield (B_{MSY}). Last, we estimated the optimal minimum-length limit from each growth model for multiple management objectives (Ahrens et al., 2020). We hypothesized that: (1) structures used to estimate pike age would differ in accuracy and precision from corroborated reference age, with scale-derived age estimates underestimating age of old pike; (2) age estimates from different structures would significantly affect population-level von Bertalanffy growth parameters, with scale-based age estimates overestimating asymptotic length (L_{∞}) and underestimating instantaneous growth (k); and (3) different estimates of growth parameters would affect model-based estimates of fisheries reference points and optimal harvest regulations, with scale-based growth parameters overestimating maximum sustainable yield and frequency of large fish in the population.

2 | METHODS

2.1 | Sampling

Pike were sampled between fall 2019 and spring 2021 in three major lagoon chains (called Bodden chains) in the southern Baltic Sea around the Island of Rügen, Germany (Figure 1): The Northern Rügen Bodden Chain (NRB), the Western Rügen Bodden Chain (WRB), and the Greifswalder Bodden (GB). The average salinity of lagoons ranged between 7.2 and 9.2 PSU (Figure 1), with extremes up to 14.2 PSU and down to 3.0 PSU. Mean annual temperature ranged from 2.0 to 20.5°C, with extremes from -0.5°C to 25.1°C. Additional fish were sampled from freshwater tributaries Barthe and Peene, Sehrowbach, Ziese, Neuendorfer Hechtsgraben (NHG), and Badendycksgraben (BKG). Fish were sampled with fyke nets, gill nets, rod and line, and electrofishing. The total length of each fish was measured (mm). We attempted to sample fish from all lagoons in a 1:1 ratio of males to females across the entire length-range, and supplemented lagoon samples with pike from tributaries to represent different environments and sexes. To assess the variability of water $\delta^{18}\text{O}$ ($\delta^{18}\text{O}_{\text{Water}}$) and test whether cyclic variations in otolith $\delta^{18}\text{O}$ ($\delta^{18}\text{O}_{\text{Otolith}}$) values were driven by seasonal temperature fluctuations, water samples were collected from a transect of the whole study system in June 2019, March 2020, and July 2020, and biweekly measurements at fixed locations from March 2020 until March 2021 (Figure 1) (Aichner et al., 2022).

2.2 | Scale processing

Scales were sampled from above the lateral line just anterior to the dorsal fin, cleaned and dried in paper envelopes to improve readability, and placed between two object slides that were taped together. A minimum of three scales per fish were mounted. Slides were viewed under a Leica MZ8 stereo microscope using a plan apochromat M objective, and images were taken from three scales

with a Leica MC190 HD microscope camera. Images were contrast-enhanced in the Fiji distribution of ImageJ (Schindelin et al., 2012).

2.3 | Otolith processing

Sagittal otoliths were extracted and cleaned in an ultrasonic water bath, placed into acid-washed Eppendorf tubes, and dried in a desiccator for 48 h. Otoliths were glued to an object slide with Crystalbond, and a section of 100 μm was removed from the center with an Isomet low-speed saw (BUEHLER Ltd 11-1180). Thin sections were polished with 3000 and 5000 grit sandpaper, labeled, and sent to the secondary ion microprobe facility at the German Research Center for Geosciences Potsdam (GFZ). Sections were embedded into SIMS sample mounts with Epofix epoxy resin, along with UWC3 and IAEA603 calcite reference materials (International Atomic Energy Agency, 2016; Kozdon et al., 2009). Mounts were polished to a surface quality of <10 μm , assessed by using white-light profilometry. Transects on otolith sections were marked digitally in a straight line from the core to the distal edge along the longest available axis crossing all visible annuli. Transect lines were chosen to overshoot the otolith core to ensure a complete transect from core to edge. Sample mounts were sputter-coated with a 35-nm thick, high-purity gold film, and placed in a specially designed high-vacuum storage chamber of the Cameca 1280-HR secondary-ion mass spectrometer. Point profiles were analyzed with a step size of ~35 μm along transects, with reference materials analyzed after each 10th otolith measurement. All $\delta^{18}\text{O}$ results were corrected for instrumental mass fractionation and reported in ‰ relative to Vienna Standard Mean Ocean Water (VSMOW). Otolith $\delta^{18}\text{O}$ values were converted to ‰ relative to the common Vienna Pee Dee Belemnite (VPDB) reference scale (Kim et al., 2015). After analysis, sample mounts were cleaned, and mosaic images of individual otoliths were taken under darkfield setting at 10 X magnification with a Nikon Eclipse motorized optical microscope.

2.4 | Seasonal $\delta^{18}\text{O}$ values in otoliths

The central assumption of age corroboration studies using $\delta^{18}\text{O}$ is that observed patterns of $\delta^{18}\text{O}_{\text{Otolith}}$ are primarily driven by seasonal temperature fluctuations. We used existing measurements of water $\delta^{18}\text{O}$ values and time series of water temperature within each lagoon to predict theoretical $\delta^{18}\text{O}$ values in pike otoliths during 2008–2022 (age range of our sample). Monthly variation in water $\delta^{18}\text{O}$ values was determined from biweekly samples taken between March 2020 and March 2021 (Aichner et al., 2022). We assumed the amplitude of seasonal variation was common across individual lagoons and used water $\delta^{18}\text{O}$ samples from three transects (Aichner et al., 2022) to estimate seasonal variation in $\delta^{18}\text{O}$ for each lagoon region. Two fractionation equations for biogenic carbonates were used to predict $\delta^{18}\text{O}_{\text{Otolith}}$: Equation 1 was proposed as a general equation for freshwater fish (Patterson et al., 1993); Equation 2 was proposed for a marine species, plaice, *Pleuronectes platessa* Linnaeus 1758

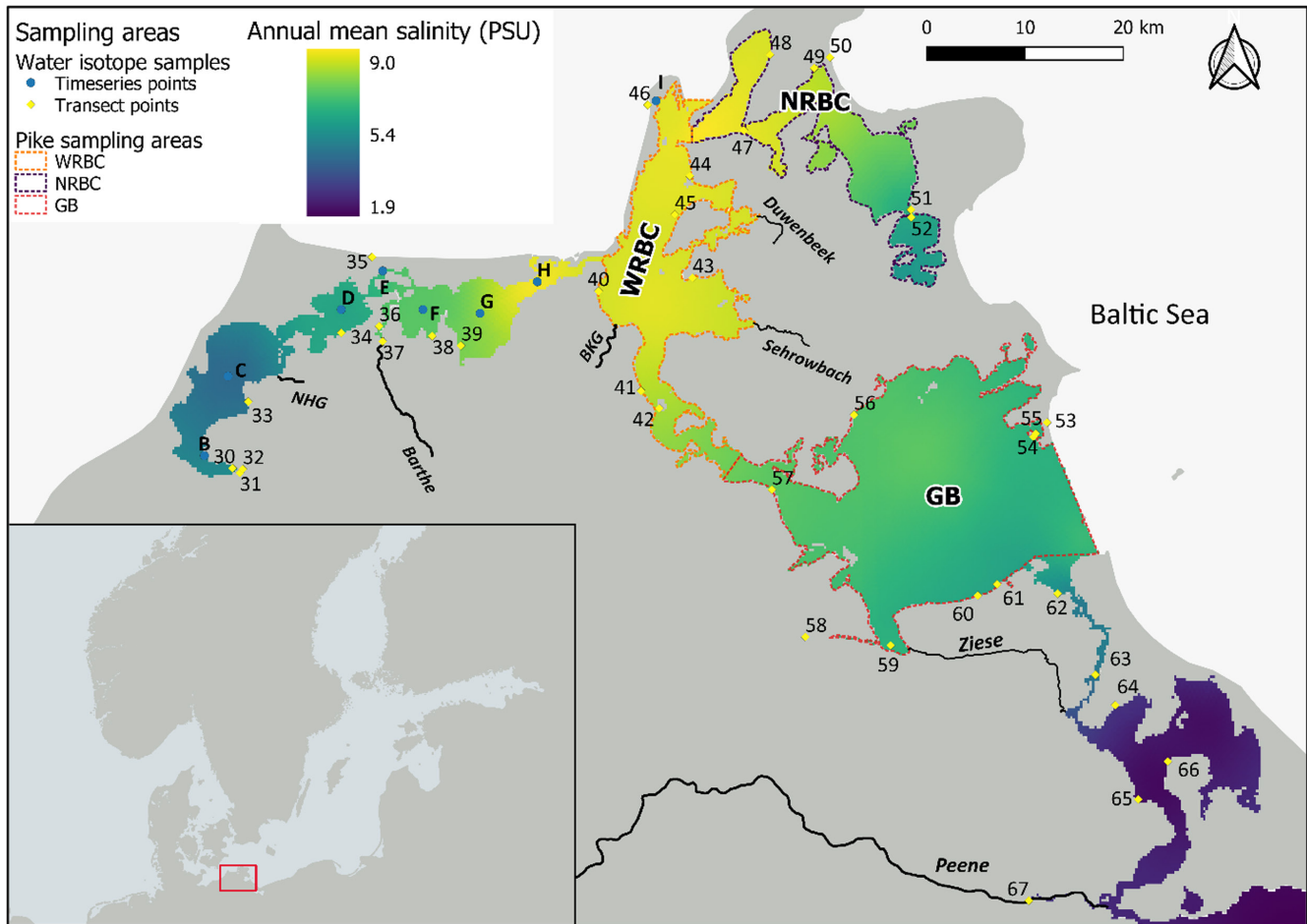


FIGURE 1 Study area around the island of Rügen, Germany, in the southern Baltic Sea, depicting three lagoon chains from which pike were sampled between June 2019 and November 2020. Lagoons are indicated by NRBC (Northern Rügen Bodden Chain), WRBC, (Western Rügen Bodden Chain), and GB (Greifswalder Bodden). Tributary abbreviations are NHG (Neuendorfer Hechtsgraben) and BKG (Badendycksgraben). Numbered yellow points mark sampling points of three $\delta^{18}\text{O}_{\text{Water}}$ measurement transects in June 2019, March 2020, and July 2020 (Aichner et al., 2022), blue points noted with letters B – I mark sampling points of biweekly $\delta^{18}\text{O}_{\text{Water}}$ measurements from March 2020 until March 2021. The average monthly salinity between 1 January 2008 and 1 January 2023 is shown as a color gradient.

(Geffen, 2012). The two equations were used because no species-specific fractionation equation exists for pike, and Baltic coastal lagoons cannot be easily classified as fully marine or fully freshwater. The two equations were of the forms:

$$1000\ln\alpha = 18.56(1000T(K)^{-1}) - 33.49 \quad (1)$$

$$\text{where } \alpha = \frac{1000 + \delta^{18}\text{O}_{\text{Oto}} \text{VSMOW}}{1000 + \delta^{18}\text{O}_{\text{Water}} \text{VSMOW}}$$

and

$$1000\ln\alpha = 15.99(1000T(K)^{-1}) - 24.25 \quad (2)$$

$$\text{where } \alpha = \frac{1000 + \delta^{18}\text{O}_{\text{Oto}} \text{VSMOW}}{1000 + \delta^{18}\text{O}_{\text{Water}} \text{VSMOW}},$$

where T is temperature in Kelvin (K), α is the fractionation factor between $\delta^{18}\text{O}_{\text{Water}}$ and $\delta^{18}\text{O}_{\text{Otolith}}$. A linear interpolation of $\delta^{18}\text{O}_{\text{Otolith}}$

values measured in pike otoliths was used to interpolate values to a period of 12 months within identified annuli to facilitate comparison to predicted values. Predicted and observed $\delta^{18}\text{O}_{\text{Otolith}}$ values were compared using a Spearman rank correlation coefficient. Some error of the correlation was expected from matching sample locations within otoliths to months and interpolation errors.

2.5 | Age estimation

Age was estimated on high-resolution images using the OtoJ macro (Norbert Vischer, Côme Denechaud, and Anders Thorsen) of the plugin ObjectJ in imageJ. Image names and order were randomized to avoid reader bias induced by knowledge about the capture location or length of individual fish. Age was estimated by three different readers (readers 1, 2, and 3). First, age was estimated from otoliths and scales by readers 1 and 2, where reader 1 was experienced (>2000 structures over more than 2 years) and reader 2 was

not experienced (no structures read). Scale-age estimates from three scales per fish were averaged to reduce the bias of individual scales. Each otolith was interpreted once by each reader. Second, to corroborate age estimates, $\delta^{18}\text{O}_{\text{Otolith}}$ profiles were matched one-to-one with otolith pictures (Figure 2) and age was estimated from the resulting isotope-corroborated images by readers 1 and 3, both with expertise in age estimation of otoliths and interpreting $\delta^{18}\text{O}_{\text{Otolith}}$ profiles on fish otoliths. Last, an automated peak-finding algorithm was defined for profiles using the ggpmisc package (Aphalo, 2022). The algorithm was set to detect peaks differing from the mean by at least 50% of the observed isotopic range of an individual and larger than at least four neighboring values. To decide upon a corroborated reference age, age estimates derived from otolith images overlaid with $\delta^{18}\text{O}$ profiles were compared between readers 1 and 3, using the age estimate by reader 1 as a reference, and both reader estimates were compared to the age estimate from the peak finding algorithm, using the age estimate of the algorithm as a reference. The age estimated by the peak-finding algorithm was assumed to be the least biased for subsequent comparisons because it was not influenced by the visual properties of otoliths and was used as corroborated age for further comparisons. For simplicity, we refer to the resulting age estimates as “scale age,” “otolith age,” and “isotope-based age” in the following.

2.6 | Age-estimation accuracy and precision of otoliths and scales

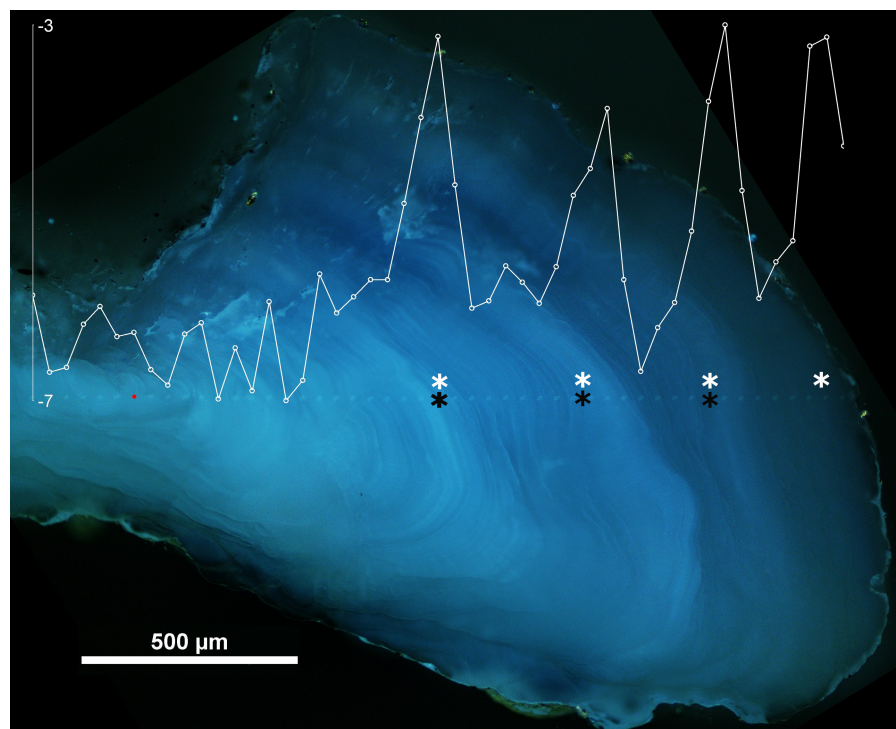
Accuracy and precision of age estimates were compared between readers and structures using percent absolute agreement, average coefficient of variation ACV (variation of ages across all fish in

percent with mean age as divisor), average absolute deviation AAD (deviation within individual fish in years, averaged across all fish), and average percent error APE (average percent error of ages within individual fish, using mean age as divisor), compared to the reference age. The ageBias function of the FSA package (Ogle et al., 2022) was used to test for significant differences between mean isotope-based age and mean structure age with one-sample *t*-tests adjusted for multiple comparisons. Wilcoxon's signed rank test, with a continuity correction (paired by structure), was used to compare the mean coefficient of variation (CV) for all age estimates by each reader from each structure for the isotope-based age. Age-bias plots were compared between readers and structures with the isotope-based age to assess systematic bias. To test each reader and structure for directional bias, the symmetry test of McNemar was used to test for whether the absolute number of individuals below the agreement line in the age contingency table was equal to the number above, and Evans-Hoenig's pooled test was used to compare the number of individuals under and above the agreement line grouped by distance from the agreement line.

2.7 | Population-level growth from size-at-age

To assess how age estimates with different levels of bias affected estimates of population-level growth parameters, von Bertalanffy growth models (Von Bertalanffy, 1938) were fitted to estimate length L_a at age a as a function of mean asymptotic length L_∞ (cm), the instantaneous growth coefficient k and age at length 0 t_0 : $L_a = L_\infty (1 - e^{-k(a-t_0)})$. Model parameters were estimated for each structure and reader using the rstan package, version 2.21.2 (Stan

FIGURE 2 Oxygen isotope values in a northern pike otolith sampled in May 2020 in the Western Rügen Bodden Chain (WRBC). The oxygen isotope profile is plotted over the image of the otolith (dark field image) with a precision of $<10\mu\text{m}$, $\delta^{18}\text{O}_{\text{Otolith}}$ (‰ VPDB) shown on the y-axis. Black asterisks mark ages estimated by visual estimation without isotope profile, white asterisks mark the age estimate from a combination of visual estimation and isotope profile.



development team 2020), a Bayesian approach implemented in Stan (version 2.21.0). To select priors and determine the sensitivity of the model to different levels of prior precision, the model was fitted multiple times for corroborated age data with different inputs for prior distributions of L_∞ and t_0 parameters, as suggested by Smart and Grammer (2021). Model performance was compared using the Leave One Out Information Criterion (LOOIC). The best-performing model was used for subsequent growth models (Appendix S1, section B). Final models were fit using a normally distributed prior determined by the reported maximum length of pike (150 cm, Froese & Pauly, 2022) for L_∞ and a normally distributed prior for t_0 , determined as the mean of all credible parameter estimates in Fishbase (Froese & Pauly, 2022). Similar to Smart and Grammer (2021), k was set to a uniform distribution bounded from 0 to a maximum probable value of 1, to produce an uninformative prior. Growth models for comparing structures were fitted to length-at-age for structure ages by readers 1 and 2. Data were pooled across sexes because few male pike were sampled and we sought to determine the most reliable parameter estimates based on model performance for subsequent comparisons, rather than estimate the most realistic growth model. Otolith age estimates of both readers were averaged after verifying no directional reader bias and no significant difference in mean age between readers existed. For scale-age estimates, separate models were estimated for readers 1 and 2, because the direction of bias and mean age estimates differed between readers. Four different growth models resulted, including an isotope-based growth model from isotope-based age estimates (i.e., automated age), a model based on otolith-age estimates, where age was averaged over readers, and two models based on scale age estimates, one for each reader.

2.8 | Assessing fisheries management reference points and optimal size limits

For assessing the impact of age-estimation bias on reference points and optimal harvest regulations, a variant of an age-structured population model was used (Appendix S1, F; Ahrens et al., 2020). The model included size-dependent maturity, fecundity, and natural mortality, as well as density-dependent recruitment (Table S2). We assumed size selectivity of the fishery in capture and retention and a constant instantaneous fishing mortality (F) over time, which implied a fixed fishing pressure for each scenario. Unlike Ahrens et al. (2020), we omitted the density-dependence of growth to examine how using growth parameters from different age estimation methods affected equilibrium predictions of fisheries metrics. Parameters informing the model were calibrated to the same stock for which age was estimated (Table S3).

Monte Carlo simulation (random parameter sampling) was used to account for parameter uncertainty in the growth coefficient k , asymptotic length L_∞ and reference natural mortality M_{ref} . Specifically, k was randomly sampled 100 times from a normal distribution within a 90% credibility interval estimated from growth models for each of the four sets of age estimates (Table S3, 4×100

parameter samples). L_∞ was then derived for each sampled k using $L_\infty = C k^{-0.33}$ (Jensen, 1997), where parameter C was specific for each set. To account for basic life history relationships and natural mortality, the reference natural mortality M_{ref} (natural mortality at length = 70 cm) of the Lorenzen size-dependent mortality function based on sampled growth parameters was calculated as $M_{\text{ref}} = 4.118 k^{0.73} L_\infty^{-0.33}$ (Then et al., 2015). This regression approach implied that natural mortality increased directly with k and inversely with L_∞ (Appendix S1, F).

To estimate fisheries reference points for each growth parameter sample, model scenarios were simulated with different values of F in steps of 0.001 year^{-1} between 0.0 and 0.6 year^{-1} among scenarios, while keeping the current minimum length limit of 50 cm, to estimate the fishing mortality that maximized yield (biomass harvested), F_{MSY} . The yield and biomass at F_{MSY} were defined as MSY (maximum sustainable yield) and B_{MSY} (biomass at which a fish population is capable of producing MSY). The model also provided: the number of pike harvested; the number of individuals vulnerable to capture; the number of trophy pike longer in total length than 100 cm, L_{trophy} ; and the relative frequency of trophy pike in the population (Table S3, Equations 20–24). The last three metrics are more important to recreational fisheries because they are proportional to the (trophy) catch rate, contributing to angler welfare (Koemle et al., 2022), while metrics describing yield and total number harvested are more relevant to commercial fisheries because harvest determines revenue for fishers (Ahrens et al., 2020).

To simulate the impacts of different growth models on fisheries policies, the minimum-length limit was varied as a common harvest regulation between 50 and 100 cm in steps of 1 cm among model scenarios with F fixed at 0.2 year^{-1} , to represent current fishing pressure estimated from stock assessment (van Gemert et al., 2022), using the same growth parameter samples as before. Output metrics expressed as yield or numbers were converted to relative values in a log-utility function (Table S3, Equation 25) to find suitable compromises in a mixed fishery with multiple management objectives (Ahrens et al., 2020). The minimum-length limit that maximized the log-utility function was defined as the optimal minimum length limit. A similar analysis was used to find the optimal maximum-length limit for harvest slots as an alternative harvest regulation by varying the maximum-length limit among scenarios with a fixed minimum-length limit (50 cm) and F (0.2 year^{-1}). Each model simulation was for 1000 years, and model outputs were averaged across the last 200 years to ensure the modeled population reached equilibrium. Ranges of values and medians for fisheries reference points and the optimal minimum- and maximum-length limits for each age estimation method were compared among the four age estimation methods to assess the impact of age-estimation bias.

3 | RESULTS

A final sample size of 86 pike was collected, including 53 females and 32 males. Sampling limitations did not allow for an equal sex ratio.

Therefore, 24 pike (13 females, 11 males) were captured in WRB, 22 (17 females, 5 males) in NRB, 18 (12 females, 6 males) in GB, and 22 (12 females, 10 males) from freshwater streams.

3.1 | Seasonality of $\delta^{18}\text{O}_{\text{Otolith}}$ values

Based on the seasonal temperature amplitude in the study area ($\sim 20^\circ\text{C}$, Figure 3a), $\delta^{18}\text{O}_{\text{Otolith}}$ was expected to fluctuate $\sim 5.6\text{‰}$. However, $\delta^{18}\text{O}_{\text{Water}}$ measured by Aichner et al. (2022) also fluctuated seasonally, consistent with evaporation effects, with lower values in winter (-7.1‰) and higher values in summer (-4.2‰ , Figure 3b), which could influence $\delta^{18}\text{O}_{\text{Otolith}}$ in the opposite direction as temperature and thereby buffer the seasonal fluctuation of $\delta^{18}\text{O}_{\text{Otolith}}$. Modeled otolith $\delta^{18}\text{O}$ fluctuated $\sim 4\text{‰}$ on average, with lowest values in August (Equation 1 = -6.0‰ , Equation 2 = -6.4‰) and highest values in January and February (Equation 1 = -2.0‰ , Equation 2 = -2.2‰ , Figure 3b). Modeled otolith $\delta^{18}\text{O}$ for fish from tributaries was $\sim 1\text{‰}$ lower than from lagoons (Figure 3b), with a similar seasonal fluctuation, which confirmed that the average seasonal temperature amplitude was the primary driver of modeled $\delta^{18}\text{O}_{\text{Otolith}}$ and seasonal fluctuations of $\delta^{18}\text{O}_{\text{Water}}$ did not outweigh the seasonal temperature effect. Observed mean $\delta^{18}\text{O}_{\text{Otolith}}$ for different areas was similar to predicted values, with a slight temporal offset of ~ 4 weeks (Figure 3c). Observed minimum and maximum $\delta^{18}\text{O}_{\text{Otolith}}$ were lower than predicted minima and maxima, which was largely caused by lower values in the first 2 years of individual pike. The Spearman rank correlation between predicted and observed $\delta^{18}\text{O}_{\text{Otolith}}$ for 86 pike was $r(86) = 0.45$ (Figure S1).

3.2 | Corroborated age estimate

Age estimates by readers 1 and 3 from otolith images, combined with $\delta^{18}\text{O}_{\text{Otolith}}$ profiles, agreed for only 29.7% of pike sampled, with an average coefficient of variation (ACV) of 17.3%. Between-reader bias was not directional (McNemar $\chi^2 = 0.00$, $df = 1$, $p = 1.00$; Evans-Hoenig $\chi^2 = 4.33$, $df = 4$, $p = 0.36$). Using age estimates by reader 1 as the reference, we found no significant differences between mean age estimates between reader 1 and reader 3 (t -tests $t = 0.00$, $df = 8$, $p = 0.93$). Age estimates from the automated count agreed with those by reader 1 for 40.7% of pike (ACV = 11.8%) and with those by reader 3 for 28.6% of pike (ACV = 18.7%). Estimated ages by reader 3 were not significantly different from automated age estimates (McNemar $\chi^2 = 0.02$, $df = 1$, $p = 0.90$; Evans-Hoenig $\chi^2 = 2.77$, $df = 4$, $p = 0.60$). Age estimates by reader 1 were also not biased in relation to automated age estimates (McNemar $\chi^2 = 0.30$, $df = 1$, $p = 0.59$; Evans-Hoenig $\chi^2 = 3.64$, $df = 4$, $p = 0.46$). The mean age estimates of both readers did not differ significantly from automated age estimates for all age classes (t -tests for reader 1: $t = 0.07$, $df = 85$, $p = 0.94$; t -tests for reader 3: $t = 0.07$, $df = 176.25$, $p = 0.94$).

3.3 | Age-estimation accuracy and bias of otoliths and scales

The agreement between ages estimated from otoliths and scales with corroborated ages was lower for scale age estimates (27.5% for reader 1 and 23.1% for reader 2, Table 1) than for otolith age estimates (36.3% for reader 1 and 35.2% for reader 2, Table 1). Scale-age estimates were more biased than otoliths, with higher coefficients of variation (CVs) (Wilcoxon's signed rank test, reader 1: $W = 3394.5$, $df = 170$, $p < 0.05$; reader 2: $W = 3285.5$, $df = 170$, $p < 0.05$), higher absolute and percent deviation, and higher percentages of fish outside of ± 1 and ± 2 years of deviation (Table 1). Reader 1 underestimated ages starting at age 6 (Figure 3), with mean reader age differing significantly from corroborated ages 7 and 11 (one-sample t tests, age 7: $t = -4.40$, $df = 85$, $p < 0.05$; age 11: $t = -9.80$, $df = 85$, $p < 0.05$). Reader 2 overestimated younger ages (Figure 4), with mean reader age differing significantly from corroborated age at age 3 ($t = 3.92$, $df = 85$, $p < 0.05$). Bias decreased for ages older than 3 and reversed for the oldest aged fish (age 11), with mean reader age significantly lower than corroborated age ($t = -8.66$, $df = 85$, $p < 0.05$). Reader 1 generally underestimated the age of older pike (McNemar $\chi^2 = 10.20$, $df = 1$, $p < 0.01$; Evans-Hoenig $\chi^2 = 15.6$, $df = 5$, $p < 0.01$), while Reader 2 overestimated age of young age classes and underaged older age classes (McNemar $\chi^2 = 8.20$, $df = 1$, $p < 0.01$; Evans-Hoenig $\chi^2 = 13.70$, $df = 6$, $p < 0.05$). Otolith age estimates were not significantly biased (reader 1 McNemar $\chi^2 = 0.16$, $df = 1$, $p = 0.69$; Evans-Hoenig $\chi^2 = 3.09$, $df = 5$, $p = 0.69$; reader 2 McNemar $\chi^2 = 1.10$, $df = 1$, $p = 0.29$; Evans-Hoenig $\chi^2 = 2.91$, $df = 4$, $p = 0.57$), and mean age estimates from otoliths did not differ significantly between readers across all age classes ($t = 0.15$, $df = 85$, $p = 0.88$).

3.4 | Population-level growth of pike using age data from different age estimation structures

Growth curves did not differ significantly between isotope-based ages and otolith ages, as indicated by overlapping outer 90% and inner 80% credible intervals (Figure 5a,b). Growth curves based on scale ages by reader 1 and on isotope-based ages diverged starting at age 6, as indicated by non-overlapping outer 90% credible intervals at ages 6 and 7, which predicted larger size-at-ages for pike older than 6 (Figure 5c). The growth curve based on scale-age estimates by reader 2 predicted significantly smaller sizes at age for pike younger than 8 years, as indicated by non-overlapping outer 90% credible intervals, with a steeper slope than the growth curve based on isotope-based ages that crossed the corroborated curve at age 10, and predicting a larger size-at-age thereafter that resulted in a larger asymptotic length (Figure 5d). Both scale-based growth models estimated a larger asymptotic length and lower k , the effect being stronger for age estimates by reader 2.

Growth parameters based on otolith ages were similar to parameters based on corroborated ages (Table 2). Scale-age estimates of L_∞ were higher than for corroborated age estimates, whereas

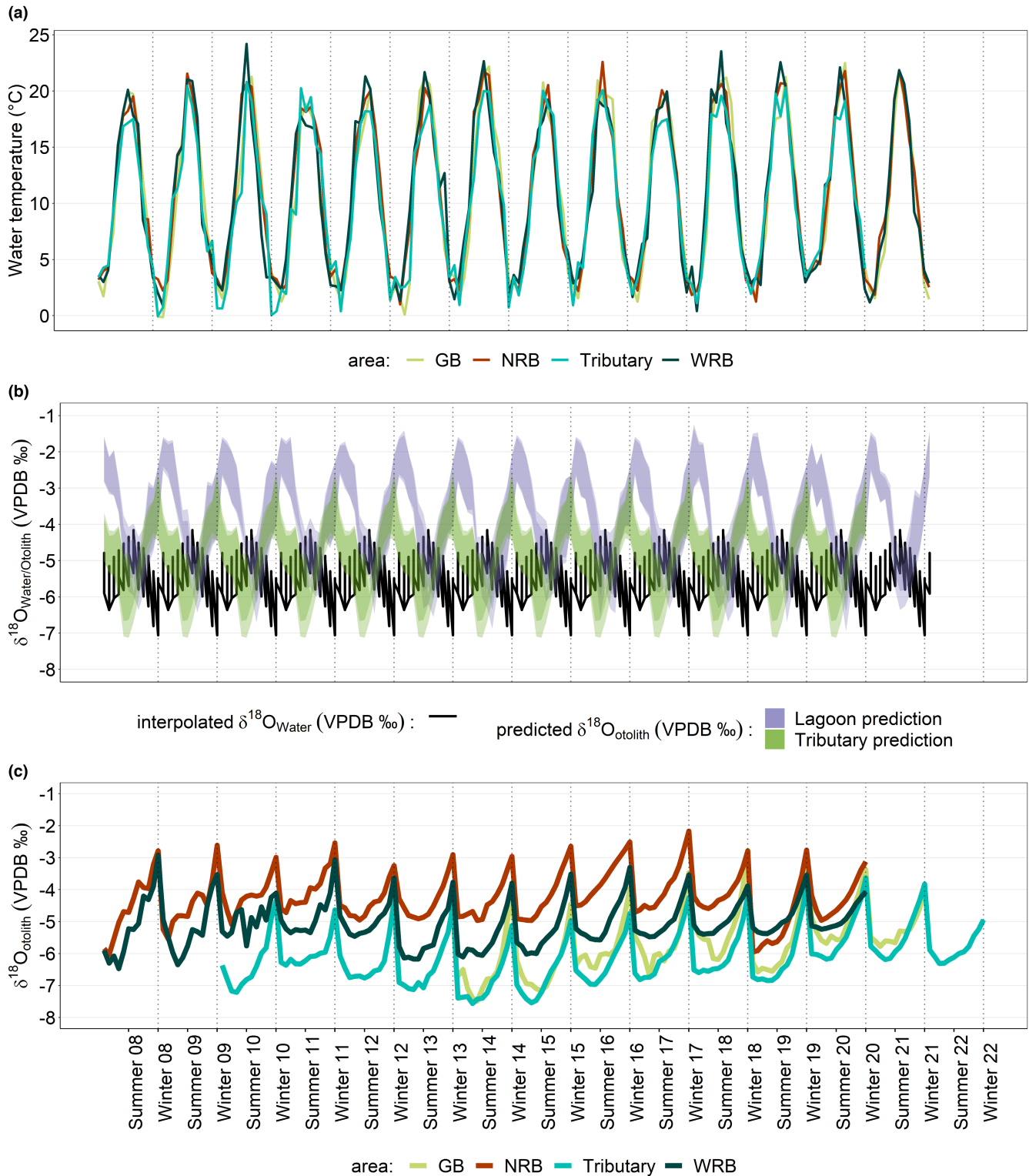


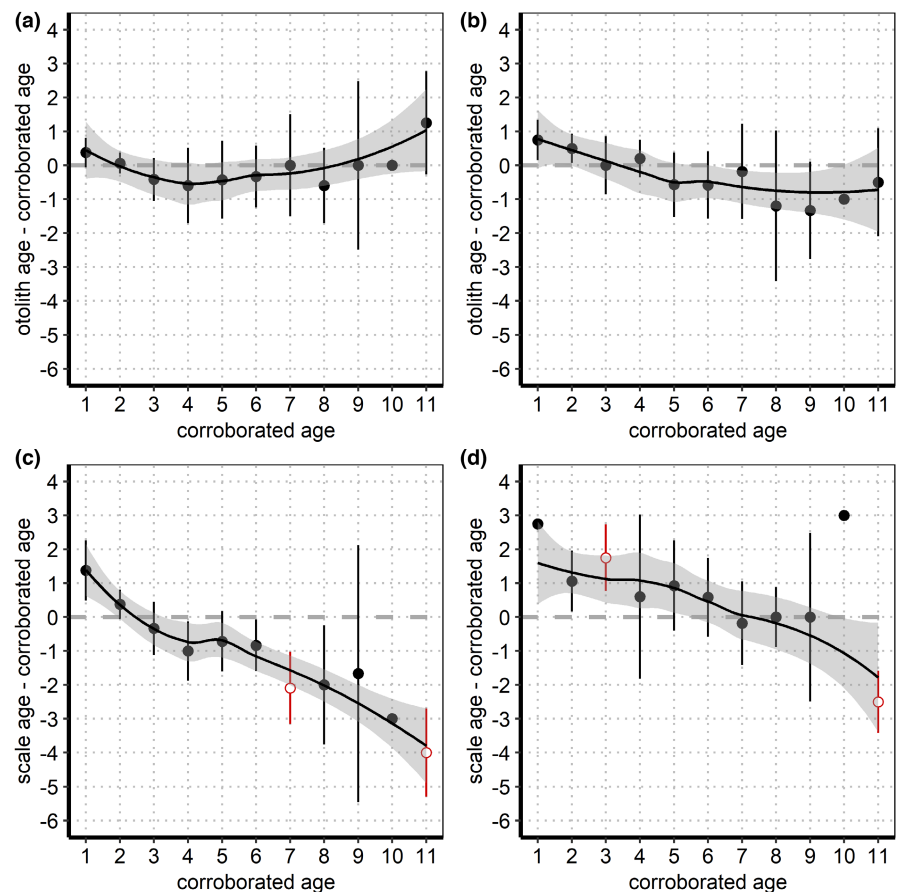
FIGURE 3 (a) Water temperature between January 2008 and December 2022 from the lagoon chains Greifswalder Bodden (GB), Northern Rügen Bodden Chain (NRBC), Western Rügen Bodden Chain (WRBC) and several tributaries, averaged across all tributaries (data source: LUNG MV). (b) $\delta^{18}\text{O}_{\text{Water}}$ values interpolated from time series (March 2020 to March 2021) and transect measurements (in June 2019, March 2020 and July 2020) from Aichner et al. (2022), along with theoretical $\delta^{18}\text{O}_{\text{Otolith}}$ values modeled with fractionation equations from $\delta^{18}\text{O}_{\text{Water}}$ and water temperature (Geffen, 2012; Patterson et al., 1993). (c) Mean observed $\delta^{18}\text{O}_{\text{Otolith}}$ in otoliths collected from pike in the aforementioned study areas. Vertical dotted lines mark the 1st of December of each year as the mid-winter season.

TABLE 1 Summary of age estimation precision and accuracy metrics for visual age estimates on scales and otoliths on 86 pike caught in three coastal lagoon chains and several tributaries around Rügen island in Germany between June 2019 and November 2020.

Structure	N	% agreement	± 1 year	± 2 years	Average coefficient of variation [%]	Average absolute deviation	Average percent error [%]
Reader 1 scale age	91	27.5	61.5%	83.5%	24.5	0.7	17.3
Reader 2 scale age	91	23.1	47.3%	73.6%	30.0	0.8	21.2
Reader 1 otolith age	91	39.6	78%	94.5%	16.1	0.5	11.4
Reader 2 otolith age	91	35.2	74.7%	91.2%	18.2	0.5	12.9

Note: Ages were estimated by readers 1 and 2, and precision and accuracy metrics were calculated relative to the isotope-based age.

FIGURE 4 Age bias plots showing the difference between the structure age estimate and the isotope-based age estimate on the abscissa and the isotope-based age on the ordinate. Age estimates were derived from the scales and otoliths of 86 northern pike collected between June 2019 and November 2020 from three coastal lagoon chains and several tributaries around Rügen Island in Germany. Negative values indicate underage estimation, and positive values indicate overage estimation by the respective structure. Vertical bars indicate the standard deviation of age estimates for a given age class by the reader. Red points indicate a significant result of the one-sample t-test for differences between mean structure age and corroborated isotope-based age. (a) Reader 1 otolith age estimate; (b) Reader 2 otolith age estimate; (c) Reader 1 scale age estimate; (d) Reader 2 scale age estimate.



estimates of k were lower (Table 2). Estimates of t_0 were similar among structures (Table 2). The uncertainty of L_∞ and k parameter estimates based on scale ages were higher than those based on corroborated ages and otolith ages. Posterior distributions differed between parameter estimates based on scale ages and corroborated ages (Figure 4; Figures S4–S7).

3.5 | Fisheries management reference points and optimal minimum-length limit

Fishing mortality at maximum sustainable yield (F_{MSY}) was substantially lower for model simulations parameterized with growth estimates

based on scale ages by readers 1 and 2 than when parameterized with otolith or corroborated ages (Figure 6a). Maximum sustainable yield (MSY), biomass at MSY (B_{MSY}), and relative frequency of trophy pike (≥ 100 cm) of the unfished stock ($freq_{trophy}$) were higher for scale-age models than otolith- and isotope-based-age models (Figure 6b–d). For scale-age models, the model based on age estimates by reader 1 was higher for all output metrics than the model based on age estimates by reader 2, with the most pronounced difference between models for MSY (Figure 6a–d). Models based on otolith ages and corroborated ages were similar for all four output metrics but tended to be slightly higher for otolith ages, especially MSY (Figure 6a–d). When using the output from the corroborated age model as a benchmark, the median values of scale model 1 underestimated F_{MSY} by 24% and B_{MSY} by 89%

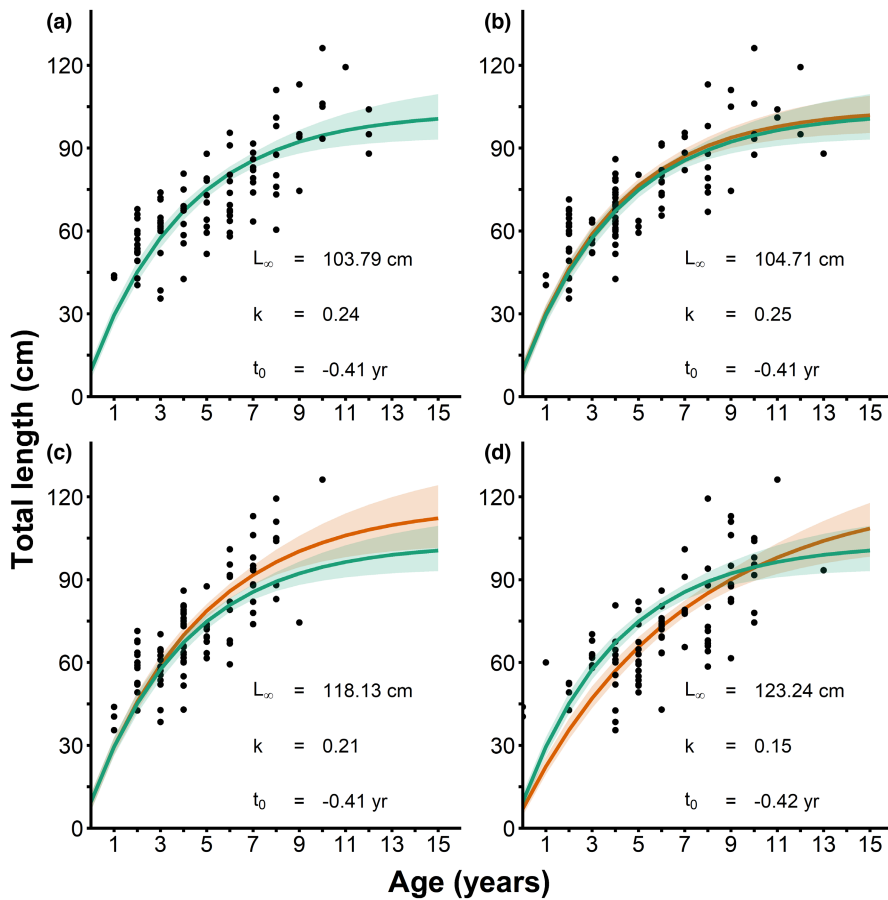


FIGURE 5 Von Bertalanffy growth curves for isotope-based age, otolith age, and scale age estimates of two age readers (reader 1 and reader 2) on 86 northern pike sampled from three coastal lagoon chains and several tributaries around Rügen island in Germany between June 2019 and November 2020. The growth curve for isotope-based ages shown in A is plotted in green color alongside the curves for different structures in orange color. (a) Growth curve for corroborated age estimates; (b) Growth curve for otolith age estimates; (c) Growth curve for scale age estimates of reader 1; (d) Growth curve for scale age estimates of reader 2.

Sample	N	L_{∞} [cm]	Brody growth coefficient k	Age at size 0 [yr]
Isotope-based age	86	103.8 ± 11	0.24 ± 0.06	-0.4 ± 0.15
Otolith age	86	104.7 ± 8.7	0.25 ± 0.05	-0.4 ± 0.15
Scale age reader 1	86	118.1 ± 16.4	0.21 ± 0.055	-0.4 ± 0.15
Scale age reader 2	86	123.2 ± 21.4	0.15 ± 0.045	-0.4 ± 0.15

TABLE 2 Summary of VBGF parameters from different age estimation methods based on size-at-age data of 86 pike sampled from three coastal lagoon chains and several tributaries around Rügen island in Germany between June 2019 and November 2020.

and overestimated MSY by 68% and $\text{freq}_{\text{trophy}}$ by 299%. The model based on scale ages by reader 1 underestimated F_{MSY} (-32%) more than the model based on scale ages by reader 2, but overestimated other metrics (MSY=26%, B_{MSY} =55%, $\text{freq}_{\text{trophy}}$ =179%). Overestimation was generally low for the model based on otolith ages (F_{MSY} : 2%, MSY: 11%, B_{MSY} : 8%, and $\text{freq}_{\text{trophy}}$: 17%), similar to the output of the model based on isotope-based ages, and supported by the overlap of interquartile ranges of model outputs, except for MSY (Figure 6a-d). In contrast, interquartile ranges of output metrics of models based on scale ages did not overlap with those based on otolith or isotope-based ages (Figure 6a-d).

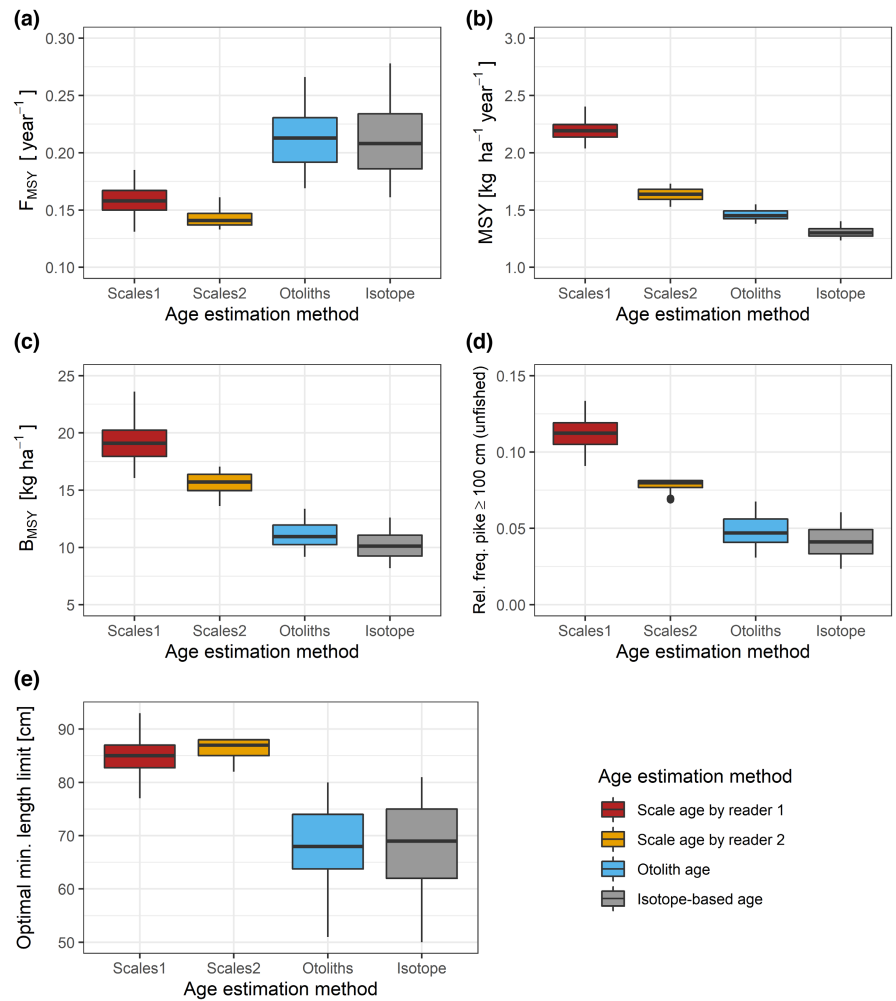
Models based on growth parameters estimated from different age-estimation methods differed in their effects on the optimal length limit (Figure 6e). The median optimal minimum-length limit that maximized benefits to both recreational and commercial fisheries was 69 cm for the model based on isotope-based ages, 19 cm higher than the current minimum-length limit of the fishery. Compared to an optimal 69-cm minimum length limit, which was

similar to the model based on otolith ages (68 cm), the model based on scale ages estimated by reader 1 overestimated the optimal minimum-length limit by 23% (85 cm) and the model based on scale ages by reader 2 by 26% (87 cm). Harvest slot limits that added a maximum size limit to the current minimum size limit did not differ significantly among models based on scale, otolith, or isotope-based ages (Figures S8 and S9).

4 | DISCUSSION

We used high-resolution SIMS data to corroborate ages estimated from 86 pike otoliths, which was among the largest samples employing $\delta^{18}\text{O}$ chronologies to date, given the high costs of such studies and the limited sample sizes of past studies (range=8–40 individuals for a single species; Hoie & Folkvord, 2006; Kastle et al., 2017; Kimura et al., 2006; Terwilliger et al., 2023; Weidman & Millner, 2000). In response to our first hypothesis, we found

FIGURE 6 Model outputs on fisheries reference points calculated from growth data derived from different age estimation methods of 86 northern pike sampled from three coastal lagoon chains and several tributaries around Rügen island in northern Germany between June 2019 and November 2020. (a) F_{MSY} , (b) MSY, and (c) B_{MSY} , (d) the relative frequency of trophy pike with a length ≥ 100 cm in the unfished stock, and (e) the optimal minimum-length limit, using growth parametrization informed by four different age estimation methods. Monte Carlo simulation was used to account for parameter uncertainty for the models informed by different growth parameters (Table 2) and natural mortality (mean of sampled M_{ref} : 0.28, 0.21, 0.32, and 0.31 year⁻¹ for scale model 1, scale model 2, otolith model, and corroborated model, respectively).



otoliths produced accurate and largely unbiased age estimates for Baltic pike by two readers, whereas scales were a less reliable age estimation structure that systematically overestimated the age of young pike by one reader and markedly underestimated the ages of pike older than age 6 by two readers. In response to our second hypothesis, von Bertalanffy growth curves derived from otolith age estimates were similar to those produced from isotope-corroborated age estimates, scale-age estimates strongly biased growth parameter estimates, overestimated asymptotic length L_{∞} and underestimated instantaneous growth coefficient k , despite differences in direction and range of age estimation bias between two readers. In response to our third hypothesis, we found that parameters of growth models using scale-age estimates caused biased estimates of fisheries reference points and optimal minimum-length limits, including overestimates of MSY, B_{MSY} , optimal minimum-length limit, and numbers of trophy fish in a population, and an underestimate of F_{MSY} .

4.1 | Age corroboration and the value of scales

We conclude that observed cyclic variations in $\delta^{18}\text{O}_{\text{Otolith}}$ were primarily driven by seasonal temperature variation and therefore can be used

as an age-validation tool. The close match of observed and predicted values showed the seasonal amplitude was robust against variations of $\delta^{18}\text{O}_{\text{Water}}$, which agreed with previous work on pike (Gerdeaux & Dufour, 2012). Lower minimum and maximum $\delta^{18}\text{O}_{\text{Otolith}}$ than predicted were likely because temperature was measured in pelagic zones of the lagoons, whereas pike in the Baltic often seek warmer, sheltered habitats in shallow areas (Pursiainen et al., 2021). Further, some pike in the Baltic Sea increase their body temperature during winter months by sunbathing (Nordahl et al., 2019), which might offset $\delta^{18}\text{O}_{\text{Otolith}}$ to lower values than would be expected from ambient water temperature. We found no indication of movement across salinity gradients in $\delta^{18}\text{O}_{\text{Otolith}}$ patterns, although this might be due to the relatively low difference of $\sim 1\text{‰}$ between lagoon and tributary being outweighed by a strong seasonal difference. Further, pike in our system were relatively stationary (mean size of extended home range: $6.58\text{km} \pm 5.77\text{km}$; Dhellemmes et al., 2023). Movement between freshwater and tributaries was relatively rare (6%; Möller et al., 2019) and usually only for short periods of less than 14 days (Arlinghaus et al., 2023a), which was likely too short to cause a shift in $\delta^{18}\text{O}_{\text{Otolith}}$ values.

Age estimates based on $\delta^{18}\text{O}$ profiles of otoliths were ambiguous between readers, as was also found by Kastle et al. (2017), who suggested an automated age estimation method for $\delta^{18}\text{O}$ transects instead of human readers. With only two readers for the

comparison of scales and otoliths, our study allows only limited conclusions about reader effects on scales. However, significant disagreement between readers was only found in scales, and reader effects have been reported before in pike (Oele et al., 2015). The first age of significant underestimation in scales (6 years) agreed with previous findings (Blackwell et al., 2016; Oele et al., 2015). Our findings confirmed that scales were difficult and inaccurate for age estimation, particularly for older pike, similar to previous studies of pike (Blackwell et al., 2016; Frost & Kipling, 1959; Mann & Beaumont, 1990; Oele et al., 2015) and other species (e.g., largemouth bass *Micropterus salmoides*, Tyszko & Pritt, 2017; Pacific salmon, Harris, 2020; muskellunge, *Esox masquinongy*, Fitzgerald et al., 1997; lake herring, *Leucichthys artedii*, Van Oosten, 1929; and whitefish, Van Oosten, 1923), but unlike others who found good accuracy of pike scales up to an age of 10 years (Laine et al., 1991; Pagel et al., 2015).

An explanation for the apparent discrepancy in readability of scales could be related to differences in growth rate in different populations but also to environmental effects induced by the brackish habitat, similar to findings in Baltic cod (Hüssy et al., 2016). Given the strong correlation of scale length to body length in fish, scales become difficult to read in older fish as the outer annuli are compressed, become indistinguishable, and may be resorbed during starvation periods (Casselman, 1990; Frost & Kipling, 1959; Harris, 2020; Van Oosten, 1923). The critical age after which scale readings become problematic seems to vary among readers and ecosystems because of variation in the growth of the local populations (Frost & Kipling, 1959; Mann & Beaumont, 1990). In contrast to scales, otoliths continue to grow when fish starve (Campana, 1990), which may explain the improved readability of otoliths at old ages among species. However, this also complicates the back-calculation of body size from otolith increments (Essington et al., 2022). Scales have the obvious advantage that they can be sampled non-lethally and are better suited for back-calculation of body size, especially at young ages (Pagel et al., 2015). Thus, the ultimate choice of the age estimation structures strongly depends on the research objective.

4.2 | Consequences of age estimation bias for growth and fisheries reference points

Overestimation of L_{∞} and underestimation of the metabolic parameter k by scale-age growth models was caused by underestimation of older fish, which led to overestimation of size-at-age for older age classes, as in other studies (Harris, 2020; Lai & Gunderson, 1987). Estimation of growth parameters from biased age estimates has consequences when populations are compared among systems (Quist et al., 2003) and for meta-analysis approaches, where estimates of growth parameters are extracted from multiple studies (e.g., Rypel, 2012; Smart & Grammer, 2021). The use of different structures that induce different levels of bias in age estimates therefore renders comparisons among systems and studies unreliable

(Campana, 2001; Tyszko & Pritt, 2017). Consequently, attention should be paid to which age estimation structures were used in the respective studies. Ideally, age corroboration or validation studies should be available for the species of interest (Campana, 2001; Tyszko & Pritt, 2017).

The population model based on scale-age growth parameters underestimated F_{MSY} and overestimated MSY and B_{MSY} when compared to otolith-based models. Underestimation of F_{MSY} by the scale-age model was caused by a lower estimated growth coefficient k and natural mortality (Horbowy & Hommik, 2022). Higher k and natural mortality causes higher F_{MSY} and lower B_{MSY} because stocks that grow fast at young ages and suffer high natural mortality must be harvested at high exploitation rates when fish reach harvestable size to reach MSY and reduce lost yield potential by natural mortality (Haddon, 2011). Overestimation of MSY and B_{MSY} by the scale-age model (relative to the corroborated age model) was mainly linked to lower natural mortality (Legault & Palmer, 2016) and a larger asymptotic length. In contrast to our findings, when the correlation between growth parameters and natural mortality was not considered, yield was similar in yield-per-recruit models parametrized with growth data based on scales and otoliths of largemouth bass (Tyszko & Pritt, 2017). However, like our findings, the frequency of large fish was overestimated by a scale-based model (Tyszko & Pritt, 2017).

Low F_{MSY} and high B_{MSY} predicted by our scale-age models could lead fisheries managers to apply conservative regulations to limit fishing mortality when the stock could be managed using an MSY objective, which would result in lost yield potential at the benefit of reducing the potential for growth overfishing (Hilborn, 2010). Although MSY was overestimated when using scale-age estimates, quota regulations informed by scale-age models would be conservative if quota estimates were based on fixed exploitation rates derived from F_{MSY} or B_{MSY} , rather than MSY (Walters & Martell, 2004). However, if management directly targets MSY , a scale-age model would suggest greater productivity than real. Similarly, for a trophy fishery oriented toward recreational fisheries (Ahrens et al., 2020), overestimation of maximum adult size by use of scale ages could lead to overly optimistic expectations about trophy fish production. In areas with co-exploitation of stocks by commercial and recreational fisheries, objectives for biomass and catch rate of trophy-sized fish are jointly relevant, so competing objectives must be compromised (Ahrens et al., 2020). Using an integrated multi-objective utility function, we found that scale-age models favored a higher optimal minimum-length limit than otolith-age models, which results in a more conservative management.

4.3 | Limitations

Our findings were limited by the decreasing temporal resolution of $\delta^{18}O_{\text{Otolith}}$ measurements with increasing fish age due to narrower increments, although resolution in the outermost visible annuli



exceeded 4 SIMS-points for the oldest individuals, which was sufficient for detecting the seasonal temperature signal (Kastelle et al., 2017; Weidman & Millner, 2000). In addition, we did not include density-dependent growth in our age-structured population model, which may have caused positive feedback from a harvest-induced reduction of biomass on pike growth due to decreased competition and social stress (Edeline et al., 2010). Such feedback would affect reference points and optimal size limits for different growth models but would not likely qualitatively change our results (Ahrens et al., 2020).

4.4 | Management recommendations

Our study of age estimation bias in pike calcified structures used high-resolution otolith $\delta^{18}\text{O}$ chronologies to corroborate annual growth checks in Baltic pike otoliths, but confirmed that scale-age estimates were of poor accuracy and precision. We also found that estimates of population-level growth and productivity based on scale ages were strongly biased, thereby justifying caution about the influence of age estimation structures on the growth and productivity assessment of fish. We found the age-estimation bias introduced in a growth model propagated to productivity and yield estimates, which could lead to suboptimal management strategies. First, we recommend that growth rate comparisons over time in a given area be based on the same age-estimation structure and age range for which the specific structure has been validated. Second, if the aim is to arrive at an unbiased population-level growth assessment or estimates of maximum age, we recommend the use of alternative structures other than scales, such as otoliths for estimating age in pike. Finally, growth estimates from scales can lead to conservative management strategies when based on MSY-related reference points or optimal size-selectivity and overly optimistic predictions of yield and trophy potential of the fishery, so we recommend using otolith-aged growth models and focusing on F_{MSY} and B_{MSY} as reference points for mixed commercial-recreational fisheries. The implications of our findings further underline the importance of quality control and validation studies for fish age estimation used for ecological inference or to meet fisheries objectives, and to carefully consider which age estimation structure to use depending on study objectives. For pike in the Baltic, we recommend further validation and corroboration studies with other nonlethally sampled age estimation structures, such as fin rays.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Code and data used are available at the repository <https://github.com/Traveller-2909/Pike-age-validation>.

ETHICS STATEMENT

This research was completed following German legislation for animal experimentation, approved by Landesamt für Landwirtschaft, Lebensmittelsicherheit und Fischerei Mecklenburg-Vorpommern – Veterinärdienste und Landwirtschaft – grant number 7221.3-1-052/19.

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[Correction added on 25 August 2023, after first online publication: the 'References' section has been updated in this version.]

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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