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Norwegian spring-spawning herring as the test case of piecewise linear regression method for detecting maturation from growth patterns

L. Baulier*†‡ and M. Heino†*§

**Institute of Marine Research, P. O. Box 1870 Nordnes, N-5817 Bergen, Norway, †Department of Biology, University of Bergen, P. O. Box 7800, N-5020 Bergen, Norway and §Evolution and Ecology Programme, International Institute for Applied Systems Analysis, A-2361 Laxenburg, Austria*

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Data from Norwegian spring-spawning herring *Clupea harengus*, were used empirically to assess the performance of a regression method aimed at detecting the time of the onset of maturation from growth trajectories. At the level of the whole dataset, the piecewise linear-regression method was accurate and showed only a minor bias (−0·17 years) relative to age at maturation visually read from scales. The method, however, was relatively imprecise and provided an estimate of age at maturation equal to the one read from the scale in less than half of the cases (47·6%). Moreover, bias was strongly dependent on age at maturation: the age at maturation of early maturing fish was often overestimated, whereas the opposite was true for late-maturing fish. Accuracy and precision of the regression method relative to visual readings also depended on the growth type (determined by the nursery area of young *C. harengus*) and cohort but not on sex. Modifying the original regression method enabled marginally improving the precision of the approach but a strong maturation age-dependent bias persisted. The results with *C. harengus* suggested that age-at-maturation estimates from the piecewise linear regression method should be treated with caution.

Key words: age at maturation; growth-reproduction trade-off; growth trajectory; piecewise linear regression.

INTRODUCTION

Assessing age at first reproduction and the consequences of reproduction on growth is of major interest, not only in fisheries stock assessment but also in studies of fish ecology and life histories in general. The energetic cost of reproductive investment is manifest as a slowing down of growth, starting from some time before the first reproductive event (Roff, 1983, 1984; Jennings & Philipp, 1992; Lester *et al.*, 2004). Hence, in growth models with mechanistic

‡Author to whom correspondence should be addressed. Tel.: +47 55584244; fax: +47 55584450; email: loic.baulier@imr.no

underpinning in energy allocation, maturation is marked by individual growth trajectories bending downward (Roff, 1983; Lester *et al.*, 2004). This led Rijnsdorp & Storbeck (1995) to suggest that the onset of maturation could be detected from individual growth curves that were available for female North Sea plaice *Pleuronectes platessa* L. through otolith back-calculations. To test this idea, they devised a statistical method based on fitting a piecewise linear regression model to growth data. The main advantage of this method, in comparison to other methods such as artificial neural networks and discriminant analysis (Engelhard *et al.*, 2003), is that it does not require training or calibration data, *i.e.* data from individuals with known age at maturation. Unfortunately, Rijnsdorp & Storbeck (1995) could not empirically validate their method with individual-level data because the true age at maturation was not known in their study material. Instead, they used individual-level data generated by a simple growth model to assess the performance of their method. Rijnsdorp & Storbeck (1995) concluded that their method could be applied to identify the onset of maturation for female *P. platessa* as long as maturation is not too early.

In this study, the performance of Rijnsdorp & Storbeck's (1995) regression method (the RS method), together with some variants of it, were evaluated using data where individual-level estimates of age at maturation were available through visual observation of growth patterns. In Norwegian spring-spawning herring (NSSH), currently the largest population of Atlantic herring *Clupea harengus* L. (ICES, 2007), age at maturation can be inferred from spawning marks in scales (Runnström, 1936). Similar spawning marks are visible in otoliths in some populations of Atlantic halibut *Hippoglossus hippoglossus* (L.) (Devold, 1938) and Atlantic cod *Gadus morhua* L. (Rollefsen, 1933). These visual estimates of age at maturation are subject to errors, and therefore, the data do not allow absolute validation of the RS method. The data, however, allow a validation of the method relative to an established and independent method. Because reproductive investment in *C. harengus* is high (Slotte, 1999; Óskarsson *et al.*, 2002), channelling surplus energy to gonads was expected to be readily visible in individual growth patterns of fish. Indeed, the same data as used here have already been used successfully to infer age at maturation with discriminant analysis and neural networks (Engelhard *et al.*, 2003). NSSH is thus a good candidate for testing the piecewise linear regression method devised by Rijnsdorp & Storbeck (1995).

MATERIALS AND METHODS

NORWEGIAN SPRING-SPAWNING HERRING

NSHH is a population that is characterized by a long and energetically costly spawning migration and extensive feeding migrations (Slotte, 1999). The spawning takes place in winter but can extend to early spring (Runnström, 1936), and energy allocation to gonads takes place during the previous summer (Slotte, 1999). Since age in *C. harengus* is conventionally expressed in full years, with birth date arbitrary set to 1 January, the age at the onset of maturation is 1 year less than the age at first spawning. For simplicity, the former is age refered to as age at maturation.

FISH DATA

The Norwegian Institute of Marine Research has carried out research and monitoring of NSSH since the early 1900s. For fish sampled between 1935 and 1973, age at capture and age at first spawning were routinely read from scales. From the same scales up to the first nine growth annuli as well as the total radius were also measured. Other data on individual fish include total body length, sex, and, based on the biological intercept method (Campana, 1990), estimated body length at age corresponding to the measured growth annuli. Furthermore, scales have been classified into distinct 'northern' and 'southern' growth types. The northern type scales can be distinguished from the southern ones by a sharper definition of the coastal winter rings (Lea, 1929; Runnström, 1936). These peculiar growth patterns tally with particular life histories: when drifting northward from spawning grounds to nursery areas, some larvae are retained in the fjords of western Norway, whilst the main part continues its drift towards the Barents Sea. Those larvae retained along the Norwegian western coast are in an environment allowing considerably faster growth (southern growth type) than those ending up further north (northern growth type).

An important assumption underlying the use of scale (or otolith) measurements to infer maturation is that growth of scales is correlated with body growth. In *C. harengus*, the relationship between scale length and body length is approximately linear within the age range where maturation occurs (Lea, 1910).

A priori, the RS method cannot be expected to work unless the observed growth trajectory covers both pre-maturation growth and post-maturation growth. Therefore, only fish having spawned at least once before the formation of the last measured summer growth ring were considered. Furthermore, in order to have sufficient number of data points per individual, only individuals caught at an age $\geq$8 years were selected. As the length of fish at hatching is unknown and no more than the nine first annuli were measured, seven or eight annual growth increments are available for each fish. These filtering steps resulted in the selection of a set of 27 905 individual growth trajectories, well balanced between males (13 672 individuals) and females (14 233 individuals).

PIECEWISE LINEAR REGRESSION METHOD

The piecewise linear regression method by Rijnsdorp & Storbeck (1995) is based on regressing age-specific mass increments against mass at age. It is assumed that mass increments increase until the onset of maturation and decrease thereafter. Rijnsdorp & Storbeck (1995) suggested that maturation in such data can be detected from a break point in a piecewise linear regression (Fig. 1).

Since the energetic content of a fish is more closely correlated with mass than with length, Rijnsdorp & Storbeck (1995) transformed length estimates into mass assuming a cubic relationship between length and body mass, $M = aL^3$, where a is a parameter. Annual mass increments between age t and $t + 1$ are then calculated as:

$$\Delta M_t = a(L_{t+1}^3 - L_t^3) \tag{1}$$

Using age-specific body masses as independent variables and mass increments between age t and $t + 1$ as dependent variables, Rijnsdorp & Storbeck (1995) then fitted the following regression model consisting of two linear segments: $\Delta M_t = p + s_1\,(M_t - M_B)$ for $t \leq B$ and $\Delta M_t = p + s_2\,(M_t - M_B)$ for $t > B$. This model has four free parameters: age at the break point, B (in whole years), value on the y-axis at the break point, p (corresponding to the model-estimated mass increment at the break point) and slopes of the first and second segment, s_1 and s_2. The break point in the best-fitting model is expected to correspond with a peak in a plot of mass increments as a function of individual mass. With the convention of assigning mass increment between age t and $t + 1$ to age t (Equation 1), this

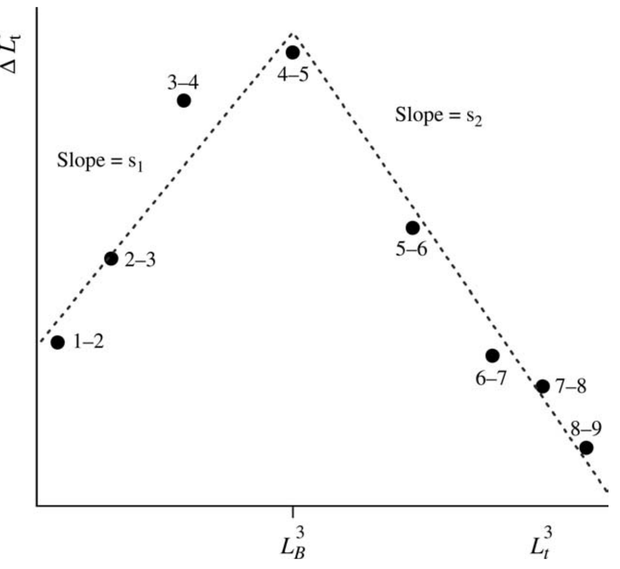

FIG. 1. Schematic illusration of Rijnsdorp & Storbeck's (1995) piecewise regression method. Here size at age (L_t^3) is plotted against size increments (ΔL_t^3) between age t and $t + 1$. In this example, backcalculated length at age is available for ages 1–9 years. The best-fitting regression model consisting of two linear segments has a break point at size L_B^3. Age at the onset of maturation is thus estimated at 5 years ($B = 4$).

break point should occur 1 year before the age at maturation and 2 years before first spawning.

Here, a more general formulation of the model was adopted. First, because the actual value of parameter a in the length–mass relationship has no bearing for the estimation, the model was simplified by choosing $a = 1$. Second, other transformations of length than the cubic one (corresponding to mass) were also considered. The piecewise linearity of mass increments as a function of body mass regression is a specific assumption, rather than a well-established prediction in energy allocation theory. Thus, while the RS method is driven by energy allocation principles, it can be interpreted as a pattern detection method. Power transformations of length other than the cubic one might improve model performance if they enable more linear relationships; this power transformation might also be used to account for allometric scale or otolith growth. The transformed length is denoted as L^b, with power $b = 3$ corresponding to the original model. For simplicity, the transformed length L^b is then referred to as 'size'. The generalized model is now: $\Delta L_t^b = p + s_1(L_t^b - L_B^b)$ for $t \leq B$ and $\Delta L_t^b = p + s_2(L_t^b - L_B^b)$ for $t > B$.

A piecewise linear regression model using an alternative, more flexible model formulation was also fitted. While original RS model constrains the breakpoint to occur at a size coinciding with an observation, it is conceivable that a less constrained model would give better estimates of the breakpoint. Another parametric representation of the model was adopted: $\Delta L_t^3 = p_1 + s_1(L_t^3 - L_B^3)$ for $L_t^3 \leq L_B^3$ and $\Delta L_t^3 = p_2 + s_2(L_t^3 - L_B^3)$ for $L_t^3 > L_B^3$, where p_1 and p_2 are the intercepts for the first and second regression lines and L_B^3 is the size of the fish at the break point. Notice that L_B^3 is not a free model parameter. Instead, it is defined by the intersection of the two regression lines, calculated as $L_B^3 = (p_1 - p_2)(s_2 - s_1)^{-1}$.

Estimated L_B^3 does generally not correspond to size at an integer age. To obtain an integer-valued age at maturation, L_B^3 was rounded to a size at an integer age; age at maturation was then that age +1 year. Alternative ways of rounding were tested: (1) rounding L_B^3 to the closest observed size at age ('normal rounding'), and (2) rounding

L_B^3 to the observed value of size immediately inferior or (3) superior to it. Finally, normal rounding after transforming L_B^3 back to body length was tested as the fourth alternative. Normal rounding on length was *a priori* expected to lead to more frequent rounding towards a higher age, and thus, to higher average age at maturation, than rounding on cubic-transformed length.

Two quantities were used to summarize the performance of the method: (1) the percentage of matching between read and estimated ages at maturation and (2) the average difference between read and estimated ages at maturation, *i.e.* the bias of the piecewise regression model relative to visual estimations.

PARAMETER ESTIMATION

Piecewise linear regression was fitted to each individual growth pattern using the least-squares method. The fits were obtained with simulated annealing. The method was chosen because a low number of data points resulted in frequent lack of convergence when simpler methods were applied. The implementation of simulated annealing in function 'optim' of the software R was used (R Development Core Team, 2008).

Both model formulations have four free parameters. Parameter estimation is easier in the original formulation by Rijnsdorp & Storbeck (1995), because one parameter (age at break point) is constrained to integer values. In the alternative formulation, all parameters are real numbers. In this case, parameter estimation was robust only when the algorithm was provided with reasonable starting values. To reduce the risk of suboptimal model fits, particularly in cases of growth patterns displaying several peaks of growth increments or no clearly identified peak, two sets of starting values were systematically generated.

Initialization values associated with the first segment of the piecewise linear regression (parameters p_1 and s_1) were estimated as the intercept, and slope of a linear regression model fitted beforehand to (1) the first three observed values and (2) between the first observed point and the one corresponding to the highest growth increment reported. For the second segment, only one set of initial values was used. The starting value for the parameter p_2 was fixed to the average value observed in initial trials, $125\,000^{0\cdot33b}$ $\text{cm}^{0\cdot33b}$ year^{-1}, while the starting value for slope s_2 was set at $-0\cdot3^{0\cdot33b} \times$ the initialization value used for s_1, based on preliminary examination of the data. The piecewise-regression model was then fitted using both sets of initial values, and the one yielding lower residual sum of squares was selected. Because the starting values for the second segment of the piecewise linear regression were rougher than those for the first one, the control argument 'parscale' of the optim function (R Development Core Team, 2008) was adjusted to give more latitude to the fitting algorithm when searching for the best estimates of the parameters of the second segment.

In a small percentage of cases (*c*. 1·3%, 358 individuals), the algorithm with the non-constrained break point failed to converge for at least one set of initialization values. These individuals were excluded from the subsequent analyses.

RESULTS

RIJNSDORP & STORBECK'S (1995) ORIGINAL MODEL

In the whole data set, there was only a small bias (−0·17 years) towards estimated ages being lower than read ages at maturation (Table I). In less than half of the cases (47·6%), however, read and estimated ages at maturation were in full agreement (Table I and Fig. 2). Agreement between read and estimated age at maturation was the most frequent case only for individuals with read age at maturation at 5 years or earlier. For *C. harengus* maturing later, underestimation by 1–2 years was the most frequent result.

TABLE I. Comparison of the performance of variants of the piecewise linear-regression method relative to the age at maturation read from scales of Norwegian spring-spawning *Clupea harengus*. The table shows the distribution (%) of the magnitude of the difference as well as mean bias. Generalized Rijnsdorp & Storbeck's (1995) model with $b = 3$ corresponds to the original model (highlighted with boldface)

Method	Estimated-read age at maturation					Average difference (years)
	<–1 year	–1 year	0 year	+1 year	>+1 year	
Generalized Rijnsdorp & Storbeck's (1995) model						
Parameter b in transformation L^b						
1·0	13·1	25·0	40·1	16·6	5·3	–0·29
2·0	8·8	25·9	45·5	15·9	4·0	–0·22
3·0	**7·1**	**25·0**	**47·6**	**16·4**	**3·8**	**–0·17**
4·0	5·9	22·1	48·7	19·1	4·3	–0·07
5·0	5·1	18·1	47·4	23·7	5·7	+0·06
6·0	4·4	15·3	44·6	28·4	7·4	+0·19
7·0	3·8	12·8	41·9	32·2	9·3	+0·32
Alternative model formulation with non-constrained break point						
Rounding on mass						
Normal rounding*	7·1	26·8	46·9	15·5	3·8	–0·19
Rounding down	14·0	38·1	38·5	7·6	1·7	–0·59
Rounding up	3·7	10·5	38·0	38·4	9·3	+0·40
Rounding on length						
Normal rounding*	6·6	25·0	47·3	17·0	4·1	–0·14

*Rounding to the nearest observation.

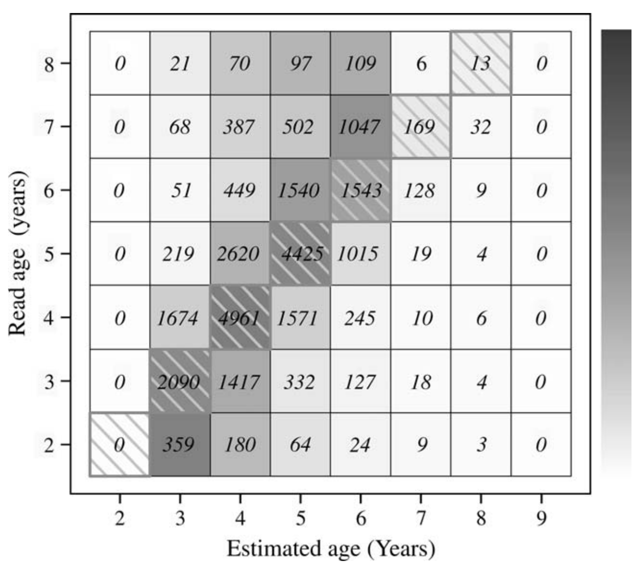

FIG. 2. Matrix of correspondence between age at maturation of Norwegian spring-spawning *Clupea harengus* read from scales by expert readers and age at maturation estimated with Rijnsdorp & Storbeck's (1995) original method. Colour intensity of cells reflects the relative distribution of estimations for each read age at maturation (rows). The diagonal where the estimates are in agreement with the read values is highlighted.

As the scope for underestimation of the age at maturation of early maturing *C. harengus* was restricted, the method could not yield maturation at age 1 year (the expected break point being then outside the range of observations). In addition, fixing no constraint on the parameter values (*e.g.* allowing both slopes to be negative) favoured a two-segment regression at the expense of a one-segment regression because goodness of fit was the only criterion used to select a model. A corollary is that when L_B^3 is made to coincide with an observation, a one-segment regression will never be selected, preventing estimations of maturation at age 2 (639 fish in the data) or 9 years (never observed). Excluding patterns for which the estimate of the first slope was negative led to a slight increase in the frequency of agreement between the two ages at maturation (48·3%).

ALTERNATIVE MODEL FORMULATIONS

Two generalizations of the original RS method were assessed. First, the exponent b was varied in length transformation L^b in the original RS method (Table I); power $b = 3$ corresponds to the original mass-based method, and power $b = 1$ amounts to purely length-based method. As power b was increased from one to four, the frequency of matching between the read and estimated ages increased, while the absolute value of the bias gradually decreased until $b = 5$ (Table I). For higher powers ($b = 6$ and $b = 7$), the overall performance started to decline again. Thus, a suitable power transformation would allow reducing the average bias to zero, or alternatively, the power transformation could be tuned to maximize the frequency of matching estimates. Power transformations, however, did not change the age-dependent bias (Fig. 3).

Second, a model formulation that does not constrain the break point to occur at an integer age was considered. Age at maturation, however, still needs to be expressed in full years, and rounding is needed after fitting the model. Several alternatives for rounding were explored: rounding size at break point on cubic-transformed length to the nearest observation ('normal rounding'), rounding up, rounding down and finally, normal rounding on length. These explorations were restricted to the cubic length transformation ($b = 3$).

Normal rounding in the model with unconstrained break point resulted in marginally weaker performance compared to the original RS model (Table I). This is most noticeable for late-maturing individuals, particularly at age 5 years. The bias was similar for the two methods. When rounding down, the frequency of agreement between the two estimates dropped substantially (Table I) and the mean bias tripled relative to normal rounding. This happened, not surprisingly, because underestimation by 1 year increased in frequency and became predominant for individuals maturing from age 5 years onwards (with the exception of age 8 years, at which few fish matured). Rounding up led to a similar decrease of the percentage of matching (Table I), with overestimation by 1 year becoming the most frequent outcome. The mean bias was more than twice the one yielded with normal rounding but of opposite sign (Table I). The best model performance was obtained with normal rounding on length, with slight improvements in the frequency of matching (47·3%) and the bias (−0·14 years) when compared to normal rounding on mass.

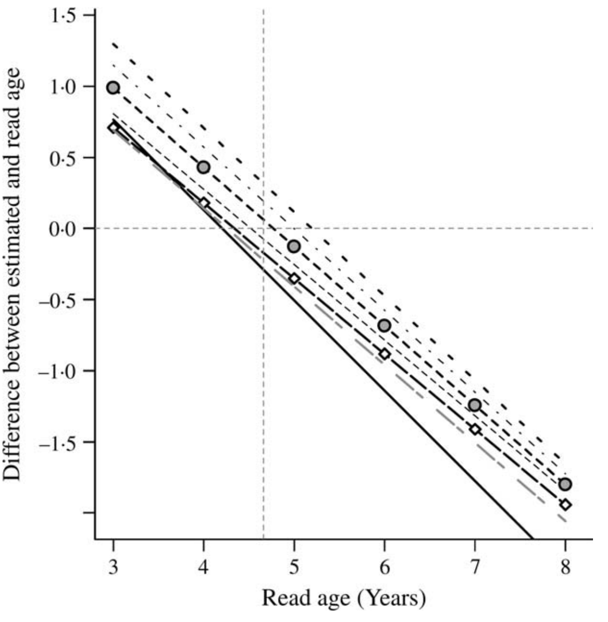

FIG. 3. Age-dependent bias of the break point regression method for different values of b in the power transformation L^b. Age dependence of bias is illustrated here by linear regressions fitted to data on read and estimated age at maturation of Norwegian spring-spawning *Clupea harengus*. ——, $b = 1$; — -, $b = 2$; –◇–, $b = 3$, ······· $b = 4$; –●–, $b = 5$; - - -, $b = 6$ and ▪ ▪ ▪ ▪, $b = 7$. The bias obtained for the whole data set is read at the intersection of a regression line and the dashed vertical representing mean read age at maturation.

INFLUENCE OF INDIVIDUAL CHARACTERISTICS

How performance of the RS method depended on characteristics of individual *C. harengus* was assessed. The read age at maturation had, as already stated above, a large influence on how well the read and estimated ages at maturation agreed. With the notable exception of individuals maturing at age 2 years, the chances of deducing the age at maturation from using RS method were higher for individuals maturing relatively young (Fig. 2), the maximum matching frequency being obtained with fish having matured as 4 years old (58·6% agreement with the read age). Bias was also age-dependent and reached highest absolute values for *C. harengus* maturing late (Fig. 3).

Sex had practically no influence on the distribution of estimates of the age at maturation (Fig. 4), and mean bias was similar for both sexes. The performance of the method, however, depended on the growth type of *C. harengus* (Fig. 5): read and estimated ages at maturation were in agreement for 48·3% of the 'northern' growth type *C. harengus*, while the same figure for the 'southern' type was 45·7%. In terms of bias, the method worked better with the southern type *C. harengus* (+0·25 years) than with the northern type (−0·32 years). Notice, however, that the biases had opposite signs.

The number of observations available to fit the piecewise regression model had only a moderate influence on the estimation of the age at maturation (Fig. 6). The 'loss' of the last observation in the growth pattern led to a slight

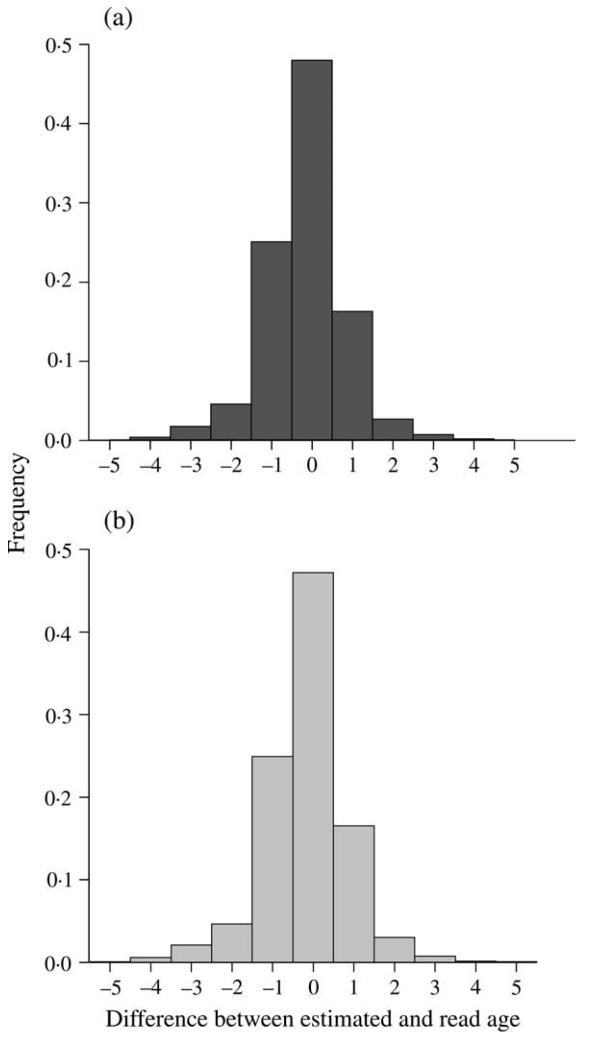

FIG. 4. Sex-specific distributions of differences between read and estimated age at the onset of maturation for (a) male (n = 13 503 cases) and female (b) (n = 14 044 cases) Norwegian spring-spawning *Clupea harengus*.

increase in the percentage of matching from 47·3 (individuals with eight increments) to 48·4% (individuals with seven increments) while the absolute bias decreased from −0·20 to −0·10 years.

When examining how the matching frequency between the read and estimated age at maturation changed over time, only cohorts from which >50 individuals had been sampled were considered. For every cohort except for 1934, matching read and estimated age at maturation was the most frequent category (Fig. 7). The bias, however, changed over time. The frequency of underestimation was higher for cohorts 1922–1939, whilst the frequency of overestimation rose for later cohorts (with the exception of cohort 1950). This generated higher values of bias in the more recent cohorts. This trend was concomitant

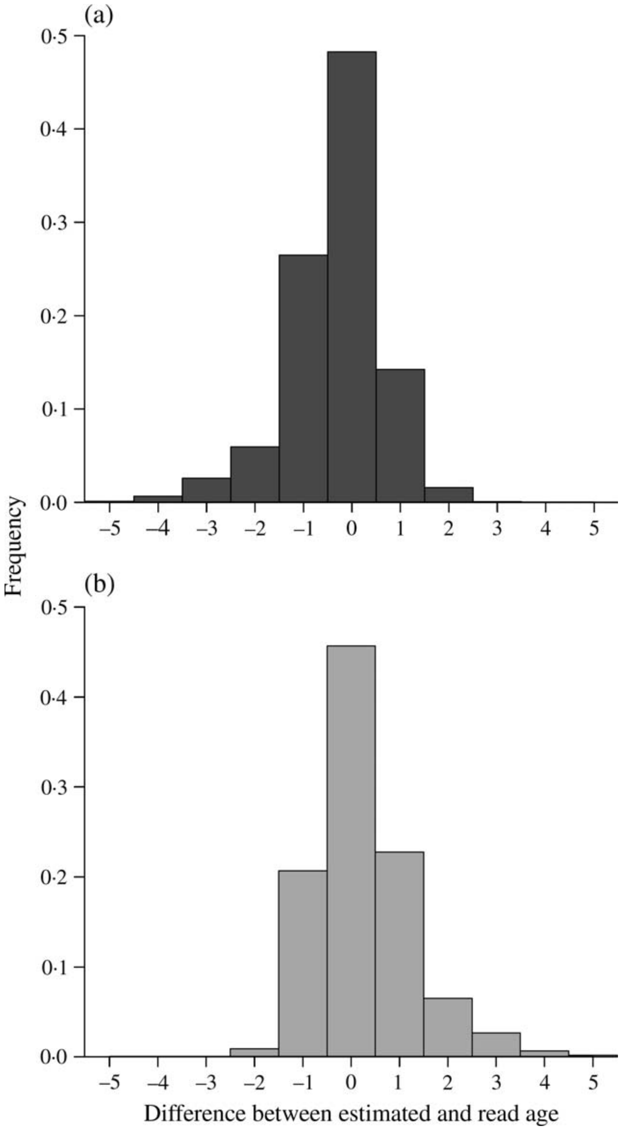

FIG. 5. Distribution of differences between read and estimated age at the onset of maturation as a function of growth type (a) the northern type (n = 20 476 cases) and (b) the southern type (n = 7062 cases) Norwegian spring-spawning *Clupea harengus*.

with the decrease of the average age at maturation observed in the samples corresponding to the last cohorts.

DISCUSSION

The application of the piecewise linear regression method (Rijnsdorp & Storbeck, 1995) to estimate age at maturation in NSSH showed that at the level of the entire data set the method is, relative to age at maturation read

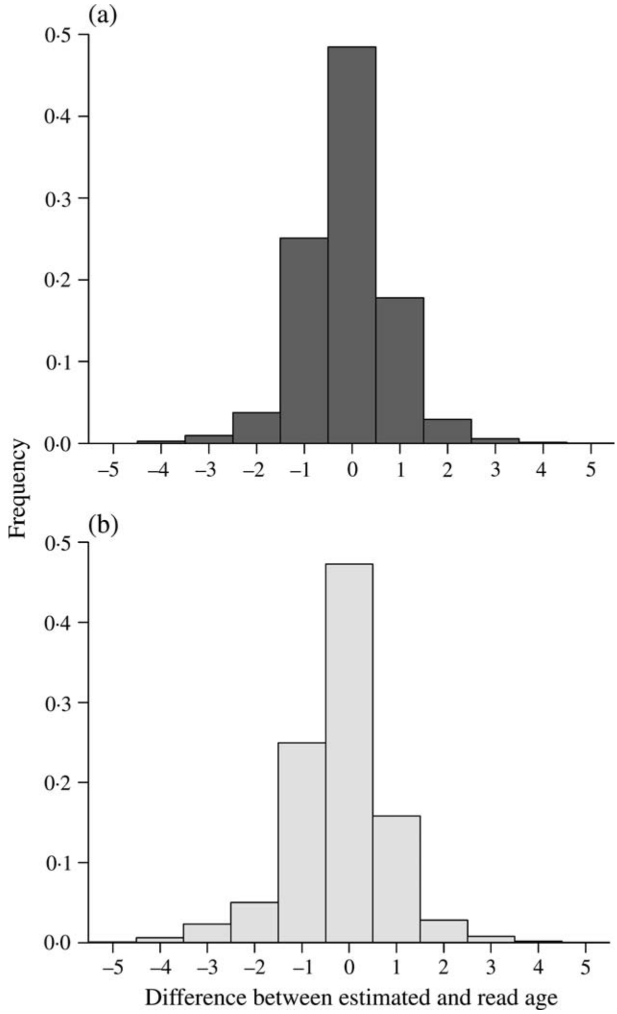

FIG. 6. Distribution of differences between read and estimated age of Norwegian spring-spawning *Clupea harengus* at the onset of maturation as a function of the number of observations for (a) seven growth increments ($n = 8209$ cases) and (b) eight growth increments ($n = 19\ 338$ cases).

from scales, accurate (mean bias –0·17 years) but imprecise (proportion of matching estimates: 47·6%). At individual level, the method is found to be inaccurate as the bias is strongly dependent on maturation age. The modifications of the model tested here allowed for marginal improvements in the performance of the method in terms of its overall accuracy but did not help with maturation age-dependent bias.

The main advantage of the RS method is that it can be used even without any training data. If, however, training data are available, a user would have better control over the performance of the method. Methods taking full advantage of training data, however, may offer better performance. For example, Engelhard *et al.* (2003) applied discriminant analysis and artificial neural

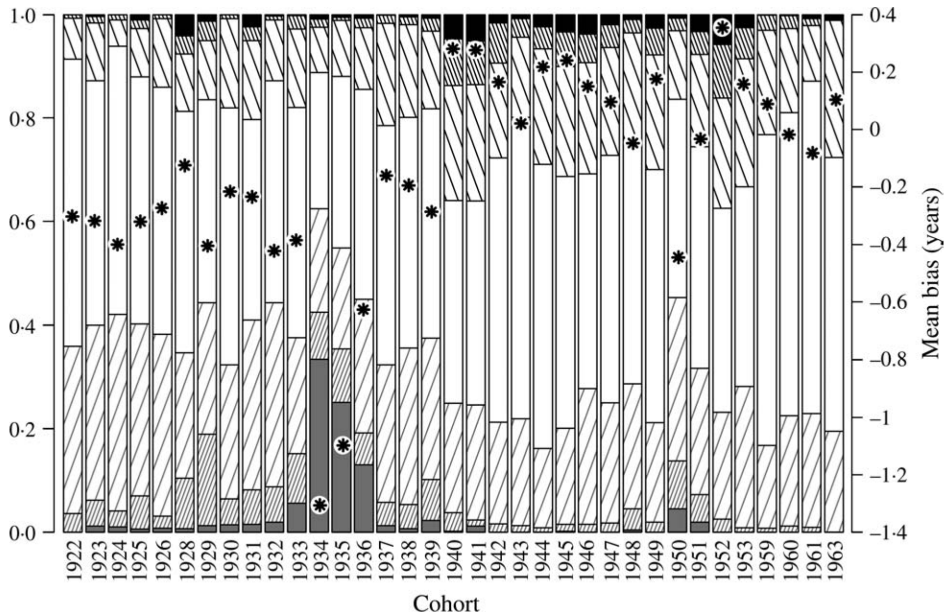

FIG. 7. Relative distribution of discrepancies between read and estimated age of Norwegian spring-spawning *Clupea harengus* at maturation and mean bias (✱) as a function of cohort. Only cohorts with >50 sampled individuals were included: ■, overestimation by >2 years; ▧, overestimation by 2 years; ◺, overestimation by 1 year; □, match between the two estimates of the onset of maturation; ▱, underestimation by 1 year; ▨, underestimation by 2 years; ■, underestimation by >2 years. ⊛, the average bias by cohort.

networks to data extracted from the same database but with less restrictive selection criteria and achieved matching of 68·0 and 66·6%, respectively. The better performance of these methods compared to the RS method is expected as the former make fuller use of the quantitative information in the scale measurements, without constraining assumptions. These methods, however, also displayed age-dependent bias, despite their greater flexibility (Engelhard *et al.*, 2003).

The piecewise regression method was most successful in repeating the visual estimates of age at maturation for *C. harengus* maturing at early to intermediate ages (3–5 years), with the notable exception of fish maturing very early, at the age of 2 years. In this respect, the results differ from those Rijnsdorp & Storbeck (1995), who used an energy allocation model to generate data that suggested that the cost of reproduction was least perceptible in growth of individuals maturing early.

The main limitation of the *C. harengus* data analysed here is that, because visual estimations of age at maturation have not been independently validated, the data only allow a relative validation of the piecewise linear regression method. The error frequency and the bias in the visual estimations are unknown, but it is believed that estimations are of reasonably good quality. Scale readers had more visual information available than only the measured ring widths, and the growth patterns in scales have been linked with the ecology of NSSH (Lea, 1929; Runnström, 1936; de Barros & Holst, 1995).

Nevertheless, it remains a possibility that the estimates from the piecewise linear regression method could be more 'correct' than the visually read ages at maturation.

The major factor affecting the correspondence between the read and regression-based estimates was age at maturation. This is a severe drawback because the bias depends on the same variable that is being estimated. This problem, however, might to some extent be specific to NSSH because similar age dependence has also been observed with other methods (Engelhard *et al.*, 2003). The age-dependent bias might be caused by problems in the visual estimates of maturation or reflect characteristics of *C. harengus* life cycle and bioenergetics.

Poor performance with late maturing *C. harengus* might stem from a linkage between growth of fish and their age at maturation. In the present data, late maturing *C. harengus* had a lower early juvenile growth (negative slope in the linear regression between backcalculated body mass at age 2 years and age at maturation; $F_{1,27\ 545}$, $P < 0{\cdot}001$) and higher annual growth rates later in their lives (positive slope in the linear regression between the last mass increments and age at maturation; $F_{1,19\ 336}$ for the eight increment, $F_{1,27\ 545}$ for the fifth to seventh increment, $P < 0{\cdot}001$). In other words, growth of late maturing *C. harengus* appeared to be less influenced by maturation than growth of early maturing fish.

Allometries of energy acquisition and metabolism suggest another factor explaining the poor performance of the method for late-maturing individuals. Bioenergetic growth models usually take the form $dMdt^{-1} = aM^{\alpha} - bM^{\beta}$, where aM^{α} and bM^{β} represent the rates of energy acquisition and energy losses linked to metabolism, respectively (West *et al.*, 2001). It is commonly assumed that energetic investment in metabolism increases faster with respect to mass than energy intake (*i.e.* $\beta > \alpha$). Consequently, mass increments will start to decline above a certain size, even in absence of maturation. The examination of individual mass increment plots in the *C. harengus* data set tends to corroborate this explanation, as many individuals display a dome-shaped mass-increment profile even during their juvenile phase. These particular patterns would then 'mislead' the fitting algorithms to underestimate age at maturation.

In addition to age at maturation, growth type of NSSH influenced the correspondence between the two estimates. The main difference was a higher frequency of overestimation, and larger bias for fish classified in the southern growth type as compared to the northern one. The differences in results between growth types probably are partly linked to differences in age at maturation. The southern growth type *C. harengus* from the nursery areas along the Norwegian west coast grow faster and mature earlier than the northern growth type fish from the nursery areas along the Norwegian north coast and in the Barents Sea (Lea, 1929; Runnström, 1936; de Barros & Holst, 1995). Since the age at maturation and the bias were negatively correlated, a larger bias for the southern than the northern growth type fish was expected. The observed discrepancies between the two growth types, however, cannot be ascribed to different maturation ages alone: when considering only individuals maturing during their fourth year, the RS method yielded a matching of the two estimates in 68·2% of the northern growth type *C. harengus v.* 40·3% for individuals of the southern growth type.

A variation of the relative frequencies of *C. harengus* of the two growth types in samples is also a plausible explanation contributing to the observed trend in bias over the time series (Fig. 7). The proportion of sampled individuals displaying a northern-type growth dropped from 87·6% before cohort 1940 to 68·8% in the cohorts from the later part of the series. At the same time, declining trend in age at 50% maturity (Engelhard & Heino, 2004) is expected to have changed the bias towards the positive direction. The change in bias, however, could simply be artefactual if scale reading, and measurements had changed over time.

Sex had hardly any influence on the results. This was not unexpected because sample distributions of read ages at maturation for males and females are similar, and therefore, age-dependent differences in the performance of the method were not sufficient alone to cause sex-specific differences of performance. Moreover, the energetic investment into the development of reproductive organs is similar in both sexes in *C. harengus*: the gonado-somatic index of males and females are very similar during the period immediately preceding reproduction and at the end of the spawning season (Slotte, 1999; Slotte *et al.*, 2000). Hence, maturation is expected to similarly influence the growth in both sexes.

A practical challenge in fitting the piecewise linear-regression method to NSSH is the absence of clear peaks in growth increments for some individual trajectories. When a single and easily identifiable peak appeared, the difference between the estimated and the read age at maturation seldom seemed to exceed 1 year. Larger discrepancies arose either when two or sometimes more peaks were identified, or when no clear maximum was distinguishable. This reveals the variability in growth that, combined with the low number of observations available per individual, hampers the RS method and any method relying on information in growth increments. This variability reflects not only environmental fluctuations but also diversity of life histories in NSSH. The classification of juvenile growth patterns into two main categories is simplistic: juvenile growth displays a latitudinal gradient (Husebø *et al.*, 2007), and even within the same area, juvenile herring growing by the entrance and at the edge of the fjords will also follow distinct growth trajectrines (Runnström, 1936). In addition, timing of the migration from nursery areas to the feeding areas in the open ocean varies between individuals and so does the time spent in the open ocean before the first spawning migration (Lea, 1911, 1929; Runnström, 1936).

In conclusion, the piecewise linear-regression method designed by Rijnsdorp & Storbeck (1995) had a low overall bias but only a modest precision when applied to the NSSH. The bias at individual level, however, was linked to age at maturation, suggesting that sample bias might vary from one sample to another. This characteristic impedes the general applicability of the method. With small modifications to the original model, the overall bias could be reduced, but the precision did not improve significantly and the dependence of bias on maturation age remained. Furthermore, these modifications have no mechanistic basis, and without additional information it is impossible to select the best one. Current results thus suggest that outcomes obtained using the piecewise linear regression method should be treated with caution, unless the performance of the method can be verified with additional data. On the positive side, the *C. harengus* data demonstrated that maturation is leaving a detectable, albeit noisy mark in growth patterns. This indicates that, as already suggested by Rijnsdorp & Storbeck (1995), methods that are more tightly linked to the principles of energy allocation might allow better predictions of age at maturation than the piecewise linear-regression method.

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