

Predicting juvenile Baltic cod (*Gadus morhua*) age from body and otolith size measurements

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Fey, D. P., and Linkowski, T. B. 2006. Predicting juvenile Baltic cod (*Gadus morhua*) age from body and otolith size measurements. — ICES Journal of Marine Science, 63: 1045–1052.

Six age-prediction models based on otolith size (weight, length, and width) and fish size (standard length, SL, and weight) were developed for juvenile Baltic cod *Gadus morhua* (SL, 40–153 mm; age, 90–230 d). Models were built based on stepwise selection and compared using the Akaike information criterion (AIC). Reference age was estimated by counting the growth increments in the transverse sections of sagittal otoliths ($n = 310$). Final comparison of the utility of the six models was based on the AIC. The best model included SL, fish weight, and sampling month as independent variables. Sampling month was added to account for differences in fish growth, after it was shown that otolith size at age was related to differences in somatic growth. The predicted age of all juveniles collected between 1991 and 1995 was used to estimate their hatch dates and growth rates. The average growth rate was 0.78 mm d^{-1} when estimated from predicted ages (1990–1995; $n = 2036$) and 0.73 mm d^{-1} when age based on direct increment enumeration was used (1990–1993; $n = 310$).

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Keywords: age prediction, cod, daily increments, *Gadus morhua*, juveniles, otolith.

Received 13 May 2005; accepted 30 March 2006.

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Introduction

Baltic cod (*Gadus morhua*) spawning-stock biomass has declined dramatically since the early 1980s (ICES, 2001). Therefore, it is important to explore the possible factors influencing the recruitment level of the species (ICES, 1996). One of the most important steps in studying the factors influencing recruitment success is to determine the age of larvae and juveniles; this is basic information that underpins, for instance growth-rate variation and hatch date frequency distribution of survivors. The daily otolith increment technique, developed in the early 1970s by Pannella (1971), has become a widely accepted tool routinely applied to age determination of many fish species. For cod larvae and juveniles, the daily character of increments in the sagittae and lapilli has been confirmed by Radtke and Waiwood (1980), Gjøsæter and Tilseth (1981), Bergstad (1984), Campana and Hurley (1989), Radtke (1989), and Hüssy *et al.* (2003a, b).

Despite the numerous advantages of employing the daily increment method, certain technical requirements limit its application. Although examination of otoliths of larvae is often possible without any sophisticated preparation process,

the otoliths of juvenile fish must be processed to allow enumeration of daily increments (see Secor *et al.*, 1992). This procedure is labour-intensive, time-consuming, and expensive. This is especially true if transverse sectioning is required (Secor *et al.*, 1992), as it is for the sagittal otoliths of juvenile cod. Therefore, it would be advantageous to develop an alternative method of age determination. One possibility is to develop an age-prediction model based on the relationships between body and/or otolith morphometrics and age (for a review, see Francis and Campana, 2004).

The primary goal of the current work was to evaluate age-prediction models on the basis of Baltic cod juvenile and otolith morphometrics. Growth rates and hatch dates of a larger sample of juvenile cod were then analysed based on the predicted age.

Material and methods

Data collection

Juvenile cod ($n = 2346$; 40–153 mm standard length, SL; Table 1) were collected during Polish young fish surveys carried out at seven stations in Gdańsk Bay (southern Baltic Sea) between 1991 and 1995. A bottom trawl fitted

Table 1. Sampling dates, number, and size range of Baltic cod juveniles.

Year class	Sampling period	<i>n</i>	SL range (mm)	Number of fish aged successfully
1990	January 1991	129	50–135	55
	March 1991	64	78–148	33
	April 1991	52	77–150	24
1991	December 1991	268	47–148	114
	January 1992	125	41–151	37
1992	January 1993	32	40–88	—
	February 1993	170	46–118	47
1993	December 1993	388	35–135	—
	January 1994	579	55–119	—
	March 1994	371	57–135	—
1994	February 1995	168	61–152	—
Total		2346		310

with a codend of 11-mm mesh was used to catch the fish. SL was measured to the nearest mm and wet weight to the nearest g.

Otolith preparation and analysis

Sagittal otoliths from 2346 juvenile cod collected between January 1991 and February 1995 were removed, cleaned with commercial bleach (5.25% sodium hypochlorite), washed, and air-dried. Weight was determined to the nearest 0.001 g using a CAHN 31 microbalance. The size of each otolith (length and maximum width) was measured to the nearest 0.01 mm with a compound microscope connected to an image analysis system (OPTIMAS 6.1, BioScan, USA). Age was estimated for 644 otoliths from juveniles collected between January 1991 and February 1993 by counting the daily increments (Table 1). For estimation of age, otoliths were prepared according to the procedure described by Secor *et al.* (1992). Samples were examined under light microscope at a magnification of 600 \times independently by two readers, who were unaware of fish size at the time of reading. The reading was accepted when the difference in results of the two readers did not exceed 5% of the number of growth increments, and the mean from the two readings was used as the age of the fish. When discrepancies were greater, the otoliths were discussed and recounted, or excluded. In all, 310 out of 644 juvenile cod readings were used for further analysis.

Data analysis

The age data obtained from direct increment enumeration (310 readings) were used to describe variations in juvenile

cod growth (size at age) in relation to sampling month and year. Five age-prediction model types were built using generalized linear models (GLMs; McCullagh and Nelder, 1986). The error distribution of age was assumed to have a Poisson distribution, as implied by the relation between variance and the mean. Unity was chosen as a link function. The following independent variables were used: (i) fish size (SL and weight), (ii) otolith weight, (iii) otolith length and width, (iv) all these variables, and (v) all these variables plus sampling month. Transformed independent variables (X^2) were used in all models as additional input variables to account for non-linearity if required. The significance of input variables, both transformed and untransformed, was evaluated for each of the five model types. The overall best model was chosen from the final models of each type using the Akaike information criterion (AIC; Akaike, 1974). The AIC not only examines the goodness-of-fit of a given model, but also accounts for model complexity (number of prediction variables). The AIC results were also used to compare the utility of models obtained for different sets of independent variables. The suitability of each model, i.e. whether the predicted age was not systematically over- or underestimated at any range, was confirmed by analysis of the relationships between predicted and observed values, as well as by the ANCOVA test for slopes different from 1, and intercepts different from 0 for that regression. The 95% prediction interval was calculated for each model as $1.96 \times$ the standard error estimated as $\sqrt{\text{RSS}/\text{d.f.}}$, where RSS is the residual sum of squares and d.f. the degrees of freedom.

Finally, the best overall model was used to predict the age of additional samples of juveniles collected between December 1993 and February 1995 ($n = 2036$) and those collected from 1991 to 1993 for which age was not successfully estimated from otolith microstructure. The predicted ages were then used to back-calculate the hatch dates and growth rates of all juvenile cod collected. All analyses were performed with Statistica 6.0 (StatSoft).

Results

Although there were evident differences in the size structure of juveniles collected on different dates between January 1991 and February 1995, as indicated by the length frequency distribution, the length distribution of the fish subsampled for otolith analysis was taken to be representative of the distribution of all juveniles collected during a given period (Figure 1).

Fish growth and condition

The length-at-age data pooled for all juveniles aged by counting increments (age, 90–230 d; $n = 310$) indicated a growth of 0.73 mm d^{-1} (Figure 2). Residuals for the SL-on-age regression were considered as growth-rate indicators of individual fish. However, to ensure

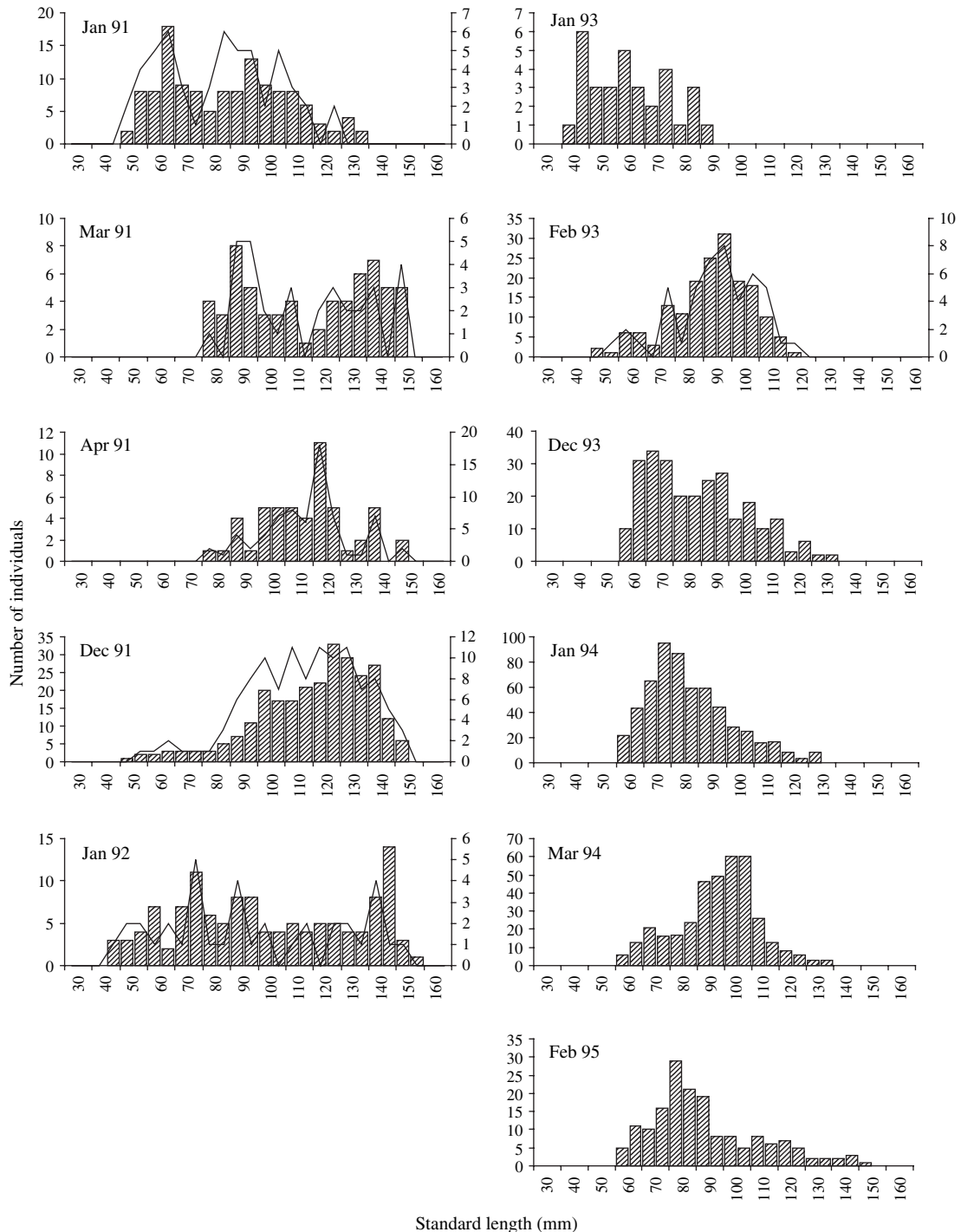


Figure 1. Length frequency distribution for juvenile cod collected in Gdańsk Bay (Baltic Sea) between December and April (1991–1995). The length frequencies for juveniles, the age of which was estimated from otolith microstructures, are indicated with a solid line.

homoscedastic variance of the residuals, the dependent variable (SL) was transformed ($1/x$), and second order polynomial regression was fitted to the transformed SL and age data ($y = 0.0466 - 0.0003x + 0.000001x^2$; $r^2 = 0.843$).

There were statistically significant differences in the residuals of size at age (Figure 3) among the sampling months related to differences between samples from April and those from all other months (Kruskal–Wallis test, $p < 0.001$;

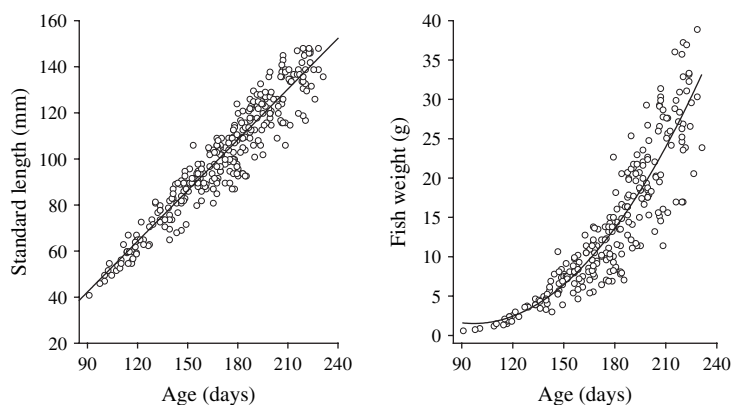


Figure 2. Length-at-age, $y = 0.734x - 23.732$, $r^2 = 0.908$ (left) and weight-at-age, $y = 0.342x + 0.002x^2 - 18.1$ (right) of juvenile Baltic cod ($n = 310$) collected in Gdańsk Bay (Baltic Sea) between December and April (1991–1995). Age was estimated by direct enumeration of daily increments.

Figure 3). Between-year differences in size at age were not observed (Kruskal–Wallis test, $p > 0.05$; Figure 3). The sampling location (seven stations located within a small sampling area) did not provide information on fish growth differences either (Kruskal–Wallis test, $p > 0.05$).

Age prediction

Age of cod juveniles was strongly correlated with their otolith size ($r^2 = 0.886$, 0.886 , and 0.904 ; respectively for otolith width, length, and weight). However, the

somatic-growth-related variation of age at a given otolith size was evident (Figure 4). For all models (Table 2), the slopes of predicted vs. observed age regressions were not different from 1 and intercepts were not different from 0 (ANCOVA, $p > 0.05$) confirming, together with the even residual distribution, the consistency and reliability of the models. The 95% confidence interval of predictions ranged between ± 16.3 and ± 20.4 d (Table 2). The model with otolith weight had a smaller AIC (i.e. higher strength) than the model with linear otolith size (length + width), but higher than the model with fish size (SL + fish weight). When all five variables were included in the analysis, SL, fish weight, and otolith weight were significant, and together provided a better model than models based on fish size, and on otolith size analysed separately. Finally, the best model was provided when sampling month was included in the analysis as additional variable (the final equation was based on SL, fish weight, and sampling month; Table 2). Note that sampling month was used as a continuous variable.

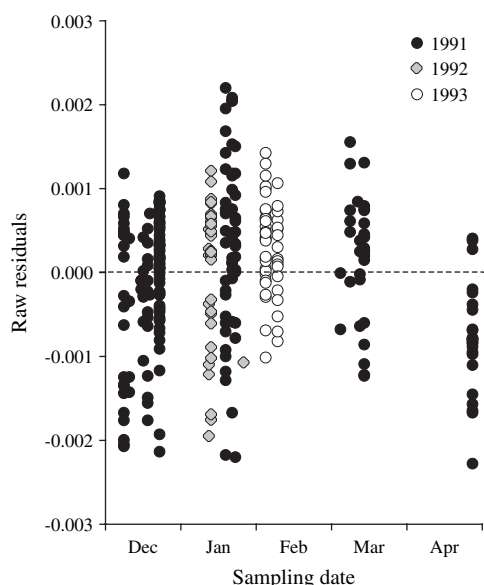


Figure 3. Distribution of SL-on-age raw residuals for juvenile Baltic cod collected in different months and years ($n = 310$). The SL data were transformed ($1/x$) to avoid homoscedastic variance of residuals.

Hatch date and growth rate back-calculation

Although the prediction model for age included fish SL, fish weight, and collection month, fish weight data were not available for all samples. The same applied to otolith weight. As otolith length and width data were available for all fish, the model based on those variables was used to back-calculate the age of all fish collected for this analysis during the years 1991–1995 ($n = 2036$) for which age was not estimated directly from increment counts. The back-calculated hatch dates for each individual showed similar distribution among years, with the exception of 1991 (Figure 5). The fish hatched mostly in August and September in 1990, 1992, 1993, and 1994, but in June and July in 1991. The average growth rate of juvenile cod hatched between 1990 and 1994 was 0.78 mm d^{-1} .

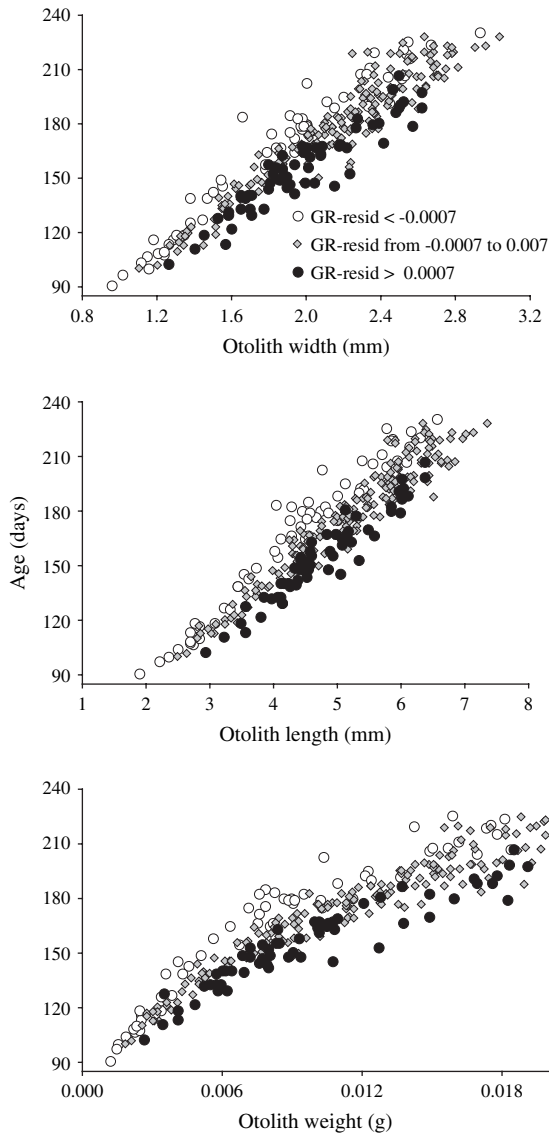


Figure 4. Relationship between age and otolith size of juvenile Baltic cod collected in Gdańsk Bay (Baltic Sea) between December and April (1991–1993). The somatic-growth-related variation was determined by splitting the data set into three groups on the basis of the raw residuals of the regression of transformed $SL(1/x)$ -on-age, indicating average, above average, and below average growth rates.

($n = 2036$, $r^2 = 0.966$), as estimated from the slope of the regression of SL -on-age.

Discussion

Although daily increment analysis may be a good source of information on age, growth, etc., there are some limitations with the method. In this study, age determination of

juvenile cod from sagittal otoliths required the preparation of transverse sections, which is a very laborious and time-consuming technique (Secor *et al.*, 1992). Moreover, damage to the core or adjacent increments during core area section preparation reduced the otolith material by approximately 50%. Steffensen (1980), in his work on daily growth increments in the otoliths of juvenile east Baltic cod, also found it difficult to estimate accurate age and hatch date because of problems with the proper preparation and interpretation of the nucleus of the otolith section. This was primarily due to the fact that the innermost increments in cod sagittal otoliths are narrow and densely packed (Bolz and Lough, 1988; Campana and Hurley, 1989; Radtke, 1989).

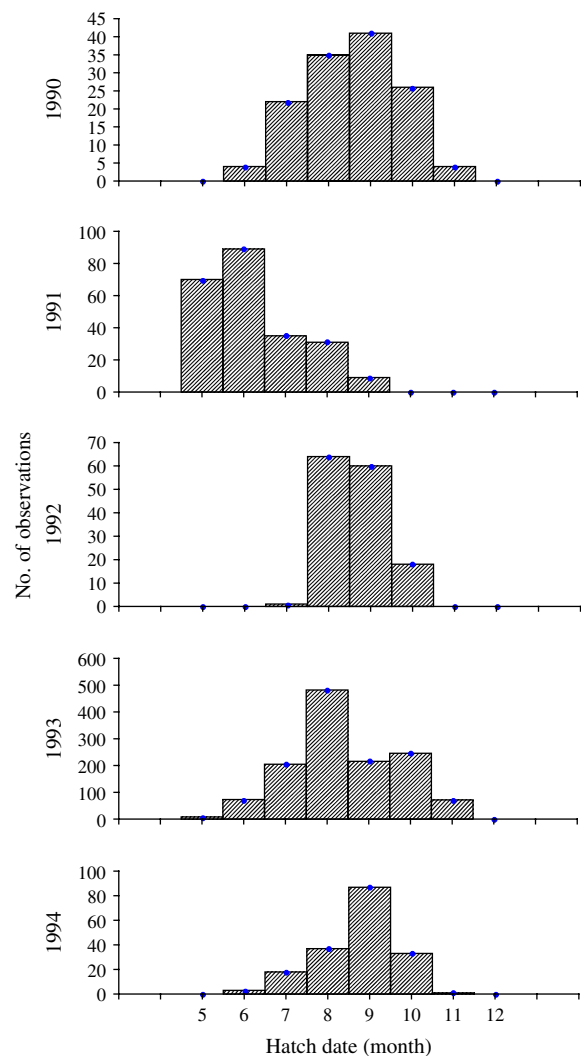


Figure 5. Hatching dates of all juvenile cod collected in Gdańsk Bay (Baltic Sea) between December and April (1991–1995; $n = 2346$). Age was estimated from the prediction model (otolith length + otolith width) for all fish except those aged by direct increment enumeration ($n = 310$).

Table 2. Age-prediction models estimated for juvenile Baltic cod (SL range 40–153 mm) with forward stepwise multiple regression analysis (error distribution: Poisson, link function: unity). Both transformed (X^2) and untransformed data were used as independent variables. Lower value of AIC corresponds to higher strength of the model. The prediction intervals represent average values for a model.

Predictors	AIC	95% Prediction interval (days)	Age-prediction equation	Adjusted r^2
SL	2 300	±19.8	Age = 45.9304 + 1.2292 (SL)	0.884
SL, fish weight	1 876	±19.2	Age = 27.71075 + 1.54747 (SL) – 1.00550 (fish weight)	0.891
Otolith weight	2 290	±19.4	Age = 90 + 9 874 (otolith weight) – 188 506.9 (otolith weight) ²	0.888
Otolith length, otolith width	2 325	±20.4	Age = 29.26836 + 14.39338 (otolith length) + 34.11927 (otolith width)	0.879
SL, fish weight, otolith weight	1 826	±18.0	Age = 37.52 + 1.17 (SL) – 3.56 (fish weight) + 0.05 (fish weight) ² + 6 146.63 (otolith weight) – 123 531.10 (otolith weight) ²	0.903
SL, fish weight, month	1 710	±16.3	Age = 65.3627 + 1.2755 (SL) – 0.4636 (fish weight) – 18.4576 (month) + 3.5857 (month) ²	0.922

This emphasizes the need for age estimation techniques other than increment counts to be applied to juvenile cod.

The idea of predicting age from other variables, i.e. fish length and/or otolith size, has quite a long history that began with the research of [Boehlert \(1985\)](#). He used multiple regression analysis to show for adult rockfish (*Sebastes diploproa*) that age prediction can be obtained with different otolith size parameters (primarily weight). Since then, possibilities for age prediction using otolith weight ([Pawson, 1990](#)) have been confirmed for different species, e.g. *Pomacentrus moluccensis* and *P. wardi* ([Worthington et al., 1994](#)), *Gadus morhua* and *Pleuronectes platessa* ([Cardinale et al., 2000](#)), *Trachurus symmetricus* ([Araya et al., 2001](#)), *Lethrinus mahsena* ([Pilling et al., 2003](#)), and *Melanogrammus aeglefinus* ([Cardinale and Arrhenius, 2004](#)). However, all these papers refer to adult fish, in which increases in otolith length and width decline with age much more than does gain in otolith weight ([Radtko et al., 1985](#)). As shown in the current study, juvenile otolith growth is not that weight-restricted, and linear parameters (width and length) are also good otolith size descriptors, although still worse than otolith weight. Not only otolith size, but also fish size can be a good predictor by itself. Again, in adults, the variation of age is usually lower with otolith size than with fish size ([Fletcher, 1991](#); [Cardinale et al., 2000](#)). In the present research on juvenile cod, including fish weight together with SL gave better predictions than a model based on otolith weight alone. As an alternative to predicting the age of fish, [Francis and Campana \(2004\)](#) suggested recently a new “mixture analysis” method that allows estimating proportions at age for a given population. Although it is important to mention their approach when discussing the subject of age prediction, the method does not provide an alternative as far as juvenile fish are concerned.

Despite the strong relationship between age and otolith size, there will always be variations in otolith size at age

related to age-independent otolith growth. The basic assumption is that the main factor responsible for growth of the otolith is somatic growth ([Campana and Neilson, 1985](#)). As sampling was restricted to one area (Gdańsk Bay), sampling location could not be used as a growth indicator. Sampling time (month), however, allowed the precision of age predictions to be improved considerably, and provided the best model.

Otolith growth rate can also be affected by temperature independently of somatic growth, in particular when temperature rises above the optimum range for somatic growth ([Mosegaard et al., 1988](#); [Folkvord et al., 2004](#); [Fey, 2005](#), in press). Although temperature differences within the optimum range do not seem to be that important ([Fey, in press](#)), poor feeding conditions may increase the risk of uncoupling the relationship between otolith growth rate and fish growth rate ([Otterlei et al., 2003](#)). For cod, the second possibility seems to be more realistic than encountering temperatures above the optimum for growth. On the other hand, the strong link between somatic and otolith growth described here reveals that the geographical and seasonal variation in somatic growth should be better described for a population if age-prediction models are to be improved.

In the present study, the growth rate estimated from the predicted ages of Baltic cod collected between December and April (1991–1995) averaged 0.78 mm d⁻¹. This is slower than juvenile Atlantic cod from the Georges Bank (1.70 mm d⁻¹ for fish of 107 mm; [Bolz and Lough, 1988](#)), but faster (comparison of length-at-age) than that of Atlantic cod sampled off of Nova Scotia by [Campana and Hurley \(1989\)](#) and [Suthers et al. \(1989\)](#). A growth rate similar to that obtained in this study was reported for newly settled Atlantic cod by [Tupper and Boutilier \(1995](#); 0.71 mm d⁻¹). The hatch-date peaks predicted in the current research were shifted towards the second part of the year by 1.5 months (except in 1991) compared with the

hatching indicated for the corresponding years from results of cod egg abundance (Wieland *et al.*, 2000). A possible explanation of this discrepancy is that juvenile cod collected in Gdańsk Bay are not a representative subsample of the population from which they originate, despite multi-year sampling. On the other hand, the hatch-date distribution of the fish analysed, which by definition represent survivals, might have resulted from the greater mortality of fish that hatched in the first half of the hatching period. The reasons for potential differences in survivorship between the first and second half of the year may be related to the uncoupling of larval production and prey availability, or the high mortality of cod eggs through predation by sprat and herring (Köster and Schnack, 1994; Mackenzie *et al.*, 1996; Jarre-Teichmann *et al.*, 2000; Hinrichsen *et al.*, 2005). Although the possibility of age underestimation in this work cannot be excluded either, the growth-rate results seem to support the accuracy of age estimates from increment counts. The uncertainty regarding the accuracy of age estimates from increment counts indicates, however, a need for research conducted under mesocosm conditions that provide a natural environment while simultaneously permitting work to be done on fish of known age.

In conclusion, although single predictors, e.g. otolith weight or fish length, provided relatively precise predictions, the inclusion of more predictors allowed a considerable increase in the precision of estimates. The best model was obtained when SL, fish weight, and sampling month were used as predictors.

Acknowledgements

We thank J. Netzel, who made the material from the Polish young fish surveys available to us, H. Wróblewska, P. Komorowski, and S. Block, for technical assistance, and K. Radtke and M. Wyszynski, who collected the additional material in December 1993. We are also grateful to two anonymous reviewers as well as the editor, V. Trenkel, for valued comments and suggestions.

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