




Original Article

Long-term temporal stability of Northeast Arctic cod (*Gadus morhua*) otolith morphology

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Otolith shape analysis provides a robust tool for the discrimination of many fish stocks in the context of fisheries management. However, there has been little research to examine within-stock temporal stability of otolith morphology in relation to changes in the environment and stock conditions. This study investigated the variability of Northeast Arctic (NEA) cod (*Gadus morhua*) otolith shape between 1933 and 2015, using elliptical Fourier descriptors extracted from archived material of 2968 mature fish. Series of hierarchical multivariate models were developed to relate shape to the identified optimal windows of some environmental drivers. Differences between years accounted for <3% of the observed variation and no significant differences were found between the average cohort shapes. The models not only confirmed that fish growth was the strongest driver of shape differences, but also highlighted effects of temperature and biomass-related variables at different life stages. Extrinsic factors described only a small fraction of the observed variance, which indicates that environmental changes over time likely account for less than the natural inter-individual variability in otolith shape. These results suggest that overall shape remains relatively stable through time within NEA cod, which further contributes towards a consensus on the biological interpretation of shape differences.

Keywords: elliptical Fourier analysis, environmental factors, multivariate models, otolith shape, sliding window

Introduction

Otoliths are widely used in fisheries science (Campana, 2005). They form annual and daily growth structures, are metabolically inert, and hold permanent records of life-history events, making them reliable indicators of individual fish age and population age structure (Campana, 1999, 2001). Otolith shape is also specific to species and often populations within species, and shape analysis can support the identification and discrimination of fish stocks. This analysis provides a basis for understanding population dynamics, which is of primary importance for the conservation and successful management of marine fish resources (Hammer and Zimmermann, 2005). Analysis of otolith shape has been successfully applied to stock discrimination in multiple instances (Campana and Casselman, 1993; Stransky and MacLellan, 2005; Petursdottir *et al.*, 2006; Stransky *et al.*, 2008).

While otolith traits such as annuli spacing are well understood and biologically interpretable, the determinants of otolith shape remain less clear. Inter-population variations in otolith shape

have been linked to both genetic and environmental influences (Campana and Casselman, 1993; Lombarte and Leonart, 1993; Cardinale *et al.*, 2004; Stransky and MacLellan, 2005; Vignon and Morat, 2010), but these studies also highlighted a strong variability related to individual-specific factors such as year-class, sex or age, as well as to growth and the local environment. While overall shape is genetically constrained and species- or stock-specific (Lombarte and Leonart, 1993), a non-negligible proportion of the observed variations seems to be of environmental origin but few analyses quantify or distinguish the relative influence of each factor (Campana and Casselman, 1993; Cardinale *et al.*, 2004; Vignon and Morat, 2010).

Local intra-population variability in otolith shape has been little studied in comparison with larger-scale variations (Vignon, 2015). While the latter is expected to be associated with significant shape differences, local environment has also been identified to be an important contributor to shape variability (Vignon, 2017). Yet, studies aiming at discriminating stocks based on

otolith shape often neglect potential sources of within-stock variability in favour of the variations found among different stocks. Castonguay *et al.* (1991) emphasized the need to separate stocks with caution when relying on otolith morphology because year-class effects between samples could be mistaken for stock difference, and most stock discrimination studies successfully apply these recommendations. It was, therefore, suggested that the characteristics of otolith shape used in stock discrimination should be recalculated each year (Begg and Brown, 2000). However, the underlying assumption that otolith shape can vary between years has seldom been tested. Jónsdóttir *et al.* (2006) reported greater differences between locations than among years within a location for Icelandic cod, and Vignon (2015) reported similar findings for eight species of tropical fish from Pacific ocean islands. However, both studies used only otoliths from two or three consecutive years and to date, there has not been a comprehensive attempt at evaluating its stability through longer periods of time. The present study quantifies otolith shape variability within a single stock unit and discusses its variability in relation to environmental changes.

This study investigated the temporal stability of otolith shape in Northeast arctic (NEA) cod, the stock designation for the large migratory Atlantic cod (*Gadus morhua*) population inhabiting the Barents Sea. NEA cod otoliths have been collected during fisheries surveys for nearly a century, and this archival collection is ideal for assessing the within-stock temporal variability of sagittal otolith shape, to test the hypothesis that otolith morphology has changed throughout the last century in response to changing environmental conditions. Otoliths from a single stock were collected from archived material and their outline described using elliptical Fourier descriptors. Series of hierarchical multivariate models were then developed to compare these descriptors between years and to relate them with different environmental variables. Conditions during a fish's early life stages could be the most influential on otolith shape, and to verify this hypothesis a sliding window analysis was conducted to identify the optimal time windows of the predictors driving shape differences. Quantifying the stability of otolith shape over the last century could bring new insights about its resilience to changing environmental conditions, which can be of importance to understanding and identifying the factors driving shape variability.

Material and methods

Sample collection

At the Institute of Marine Research in Bergen (Norway), otoliths have been routinely used for age determination purposes since 1932, and, for most of these, information on catch location, date, and biological parameters (age, length, weight, and sex) are available. Sagittal otoliths of mature NEA cod from the period 1933 to 2015 were randomly selected and retrieved from the extensive archive available at the institute. The otoliths had all been previously broken for age estimation, and so only one whole otolith from each pair could be collected intact. Consequently, the samples studied here consisted of a mixture of left and right otoliths from different fish, without the possibility to include both from the same pair. Norwegian coastal cod (NCC) is the stock designation used to refer to a collection of genetically distinct local coastal populations that exhibit different life-history traits and environmental exposures from the migratory NEA cod population (Salvanes *et al.*, 2004). Both stocks have been successfully

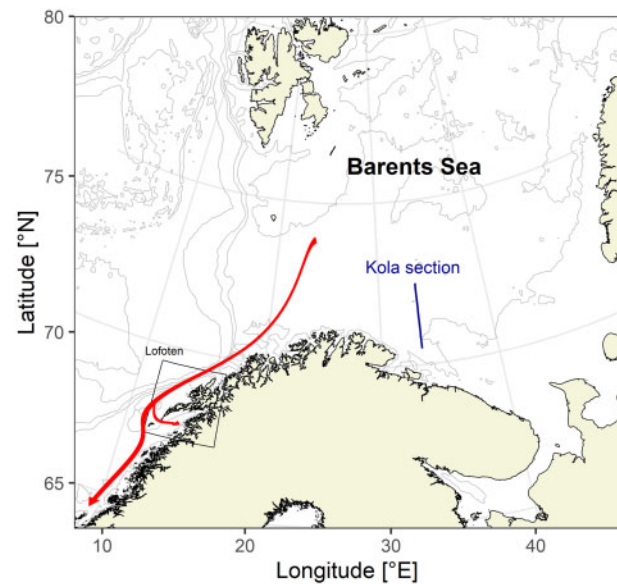


Figure 1. Map of the Northeast Atlantic region, including the northern coast of Norway and the Barents Sea with added depth contour. Framed area represents the Lofoten spawning grounds. Blue line represents the Kola transect of *in situ* temperature measurements. Red arrows represent the general direction of NEA cod spawning migration.

separated using inner zone morphology, otolith outer shape and genetic methods (Rollefsen, 1934; Berg *et al.*, 2005; Stransky *et al.*, 2008; Dahle *et al.*, 2018; Johansen *et al.*, 2018). To prevent the inclusion of otoliths from NCC in the present study, only fish classified “certain NEA cod” by experienced age readers based on inner otolith morphology (Stransky *et al.*, 2008) were selected. The mean annual proportion of uncertain NEA cod otolith in the archives was only 5.24%. Proportions of otoliths assigned to the different cod stock in the Barents Sea ecoregion are presented in detail in [Supplementary material 1](#).

All the samples used in this analysis were fished in the Lofoten spawning grounds (Figure 1), which encompasses a large area along the north-western Norwegian coast, comprising both the Lofoten archipelago and the Vesterålen region. Because there was no single source going back as far as 1933, this selection comprised a mixture of survey-caught fish as well as samples collected from commercial landings. Preliminary analysis showed a potential selectivity bias of gillnets towards bigger, faster-growing fish, and samples caught that way were thus excluded from the selection, limiting it to either bottom trawls, longlines, or seine.

The initial sampling comprised >4000 individuals of age 7–21 of which 3913 otoliths were intact. For the purposes of this study, only fish of age 8 were retained to limit the influence of age on the shape analysis and focus on between-cohort (year-class) differences. This yielded a total of 2968 otoliths and at least 10 otoliths per year, representing 1467 females, 1388 males, and 113 fish of unspecified sex, divided between 1456 left-hand and 1512 right-hand orientations (see [Supplementary material 1](#) for detailed information about the repartition of samples per year).

Otolith shape analysis

Each otolith was first manually cleaned to remove residual tissue and then weighed on a high-resolution scale. Individual images of

the whole otolith were taken under reflected light using a Nikon SMZ25 stereomicroscope mounted with a Nikon Digital Sight DS-Fi2 camera and a Nikon SHR Plan Apo 0.5× WD:71 lens. The otoliths were all positioned with the proximal surface and *sulcus acusticus* facing up, and the dorsal side at the top of the image. Acquisition parameters such as shutter speed, aperture, white balance and sensitivity (ISO) were kept uniform between all samples.

Images were processed for outline extraction directly in R (R Core Team, 2016) with the packages *imager* (Barthelemy, 2019) and *Momocs* (Bonhomme et al., 2014). Each image was first converted to greyscale, then colour-inverted and binarized to generate a dark shape on a white background. Because the otoliths comprised both orientations, right otoliths were mirrored horizontally during this processing step. The outlines were then detected and extracted by intensity thresholding, based on the transition from black to white pixel values. Because of fibre leftovers or black mould spots caused by humidity, the outside image boundary of some of the older otoliths was often deteriorated. The first batch of outlines generated was consequently superimposed on their associated original pictures and each of them was visually inspected for failures or artefacts in the detected outline. Whenever the superimposed outline deviated from the otolith shape, the original image was imported into Adobe Photoshop 2019, corrected, and reprocessed.

To analyse the variations in shape, an elliptical Fourier analysis (EFA) was performed on the delineated otolith contours (Lestrel, 1997). While cod otoliths often display finer scale crenulations and lobes that require high numbers of harmonics to be recreated with precision, too many will often come at the cost of computational speed. For each otolith, the first 99 harmonics (H) were thus arbitrarily extracted and normalized by the first to provide elliptical Fourier descriptors (EFDs) invariant to size, rotation, or starting point (Kuhl and Giardina, 1982). In addition, the extraction path was made homologous for all otoliths by selection of a starting point located to the left of the centroid. This was done to further prevent mirroring effects wherein unguided outline extraction can sometimes produce inverted shapes (Bonhomme et al., 2014). To determine the number of harmonics needed to optimally reconstruct the otolith contour, the cumulated Fourier power (P_F ; Lestrel, 1997) was calculated on a subset of 100 otoliths randomly selected across the whole dataset. The number of harmonics used in the analysis (n_{\max}) was then chosen such that $P_F(n_{\max})$ explained 99.99% of the variance in contour coordinates, i.e. 99.99% of the otolith shape obtained at 99 harmonics was recreated at n_{\max} .

Statistical analyses

To investigate the relation between shape and environment, a shape matrix **S** was built with individual fish in rows and corresponding EFDs in columns. A total of three explanatory matrices were evaluated in relation to the shape matrix **S**:

- (1) A year matrix **Y**, to investigate potential variations of shape over time. Since every fish was of the same age, the years were used as proxies for cohorts (or year class) and likely reflected inter-annual differences.
- (2) An individual matrix **I**, grouping biological variables related to each sample. This matrix was included as conditional factor to remove the effects of individual variables on otolith

shape. It was composed of fish length (L) to account for shape variation related to growth rates differences between individuals, sex (S_x) as a factor potentially affecting fish metabolism and otolith mineralization, and otolith orientation (Or) to account for potential confounding effects of directional asymmetry (Mahé et al., 2019).

- (3) An environmental matrix **E**, grouping external variables related to the environment and population dynamics, composed of four main variables. The monthly and yearly Barents Sea temperatures (T°) of the 0–200 m depth layer between 1921 and 2015 were extracted from the Kola section *in situ* records provided by the Russian Polar Research Institute of Marine Fisheries and Oceanography (Bochkov, 1982; Tereshchenko, 1996). This proxy offers a good representation of climatological conditions within the area occupied by the NEA cod both during its juvenile and adult stages (Dippner and Ottersen, 2001). The total stock biomass (TS), spawning stock biomass (SSB), and recruitment (R) were obtained from the Arctic Fisheries Working Group at the International Council for the Exploration of the Sea for the period 1946–2015 (ICES, 2018), and from the extended virtual population analysis carried out by Hysten (2002) for the period 1920–1945.

Hierarchical redundancy analyses (RDA) were then conducted to model the matrix **S** in relation to the different explanatory matrices with a statistical protocol similar to Mille et al. (2016). RDA is an extension of principal component analysis, wherein the variation in a set of response variables is related to a set of explanatory variables through the extension of multiple linear regressions to multivariate data (Legendre and Legendre, 2012). For each model, the exploratory matrix of interest was first tested in relation to **S** through a normal RDA. Then, a similar partial RDA (pRDA) was built using the matrix **I** as a conditional factor, which removed the variance in shape associated with fish-specific variables before constraining with the tested explanatory matrix. This step was done to ensure that potential significant differences through time or environmental effects found in the initial RDA were not caused by any measured confounding factors, in case of a strong joint effect. To test the significance of each model or explanatory matrix, ANOVA permutation tests (999 iterations, marginal effects, Type II) were performed (Legendre and Legendre, 2012). In addition, the potential collinearity between explanatory variables was investigated by calculating their variance inflation factors (VIF) with a more conservative threshold defined at $VIF < 2$ (Borcard et al., 2018). No evidence for multicollinearity was found in any of the analyses. Finally, variation partitioning was performed to quantify the respective contributions of **Y**, **E**, and **I** to otolith shape differences within each model.

The environmental descriptors associated with each cohort usually describe only a snapshot of an older individual's exposure because they lack fine temporal resolution, especially for pre-instrument records. Such environmental proxies are not representative of the diversity of environmental conditions experienced throughout the life of an organism, nor will they reveal the contrasted effects similar changes can have at different times of the year (Cook et al., 2012; Kruuk et al., 2015; Roberts et al., 2015). This is especially true for mobile organisms like NEA cod, which starts migrating thousands of kilometres southward to the

spawning grounds once it reaches sexual maturity, and thus experiences diverse conditions throughout its life cycle (Robichaud and Rose, 2004). A preliminary analysis sequentially compared models built using values of environmental variables at the year of catch to those at the year of hatch and found significant differences between their respective contribution to shape differences (see Supplementary material 2). To account for this problem, optimal time windows of the four environmental variables were explored with a sliding window analysis, which allowed for the statistical identification of the best predictors and their associated critical time windows (van de Pol et al., 2016). Different time windows were investigated sequentially within an 11-year period (counted backwards from the year of capture), covering both the life of the fish and the conditions up to 2 years prior to its hatch in case of eventual lagged effects. Collinearity of identified environmental predictors was tested with Pearson's correlation tests. Because the high number of time windows analysed could potentially lead to the misidentification of an environmental signal (or false positive), Monte Carlo randomization tests were then conducted to assess the probability of obtaining similar strong statistical support of the model by chance (van de Pol et al., 2016; Smoliński, 2019). Detailed statistical methodology is available in Supplementary material 3. The illustrated workflow is presented in Figure 2.

This first analysis utilized a large number of individual shapes, but because the environmental values associated with each fish were consistently repeated within the same cohort, the identification of an environmental signal was potentially masked by inter-individual variability. In a second analysis, the sliding window analysis and environmental models were thus recreated using a shape matrix S_{year} composed of EFDs averaged per year, wherein each cohort ($N=78$) was represented by a single average shape. Similarly, the individual matrix I was also replaced by I_{year} , where the mean fish length for each year was computed as the mean cohort body length at age 8. This cohort-based analysis achieved three aims: to reduce variability associated with between-individual shape differences, to determine if average shape changed during the period investigated, and to directly relate it to environmental factors.

All analyses were conducted using the R scientific computing language (R Core Team, 2016) and following packages: *vegan* (Oksanen et al., 2019), *PerformanceAnalytics* (Peterson et al., 2019), and *tidyverse* (Wickham, 2017).

Results

Analysis of individual shapes

Based on the Fourier power calculated at 99 harmonics, the first 54 harmonics explained at least 99.99% of the variation in otolith contour (Figure 3) and were thus selected for further analysis. Year-to-year variations in shape were significant but only accounted for a minor portion of the observed variability. In models 1.a and 1.b (respectively, Y only and Y with conditional removal of I), matrix Y explained 2.67% and 2.41% of the variability in otolith shape (Table 1). Variation partitioning (Figure 4) indicated that the matrix I used as a set of conditional factors explained around 2.2% of the variability in shape, with a joint contribution of both matrices equal to 0.3%.

The first iteration of the sliding window analysis for environmental variables identified total stock from the second to seventh year of fish life as the optimal environmental signal (Figure 5).

Similarly, the next iteration identified mean SSB from the third to seventh year of fish life as the second-best predictor for shape variation between the different variables. Both predictors showed a wide critical window covering late juvenile stages to average age of sexual maturity. During the third and final iteration, mean temperature from September to December of the year prior to hatch was identified as the third best predictor. Contrary to the first two iterations, this step revealed a narrower period strongly supported by models, although the overall window was generally situated from hatch to recruitment age. Monte Carlo tests conducted with 1000 iterations (Figure 5) indicated that the likelihood of obtaining similar strong signals by chance was minimal for total stock and SSB ($p < 0.001$). The probability obtained for the temperature signal was higher but still significantly different to chance ($p = 0.045$). Correlation tests conducted on the identified optimal predictors revealed that total stock and SSB had a moderate positive correlation ($R = 0.47$, $p < 0.001$). The temperature had a low positive correlation with SSB ($R = 0.29$, $p < 0.001$) but no correlation with total stock. Because recruitment was not identified as an optimal predictor during the sliding window analysis and had no significant effect in any of the preliminary models, the variable was removed from matrix E .

Using the identified optimal environmental windows, models 2.a and 2.b explained 1.15% and 1.11% of shape variability (Table 1). Total stock and SSB were the most significant variables ($p < 0.001$) and explained the highest percentage of variation (respectively, 0.80%/0.42% in model a and 0.89%/0.32% in model b). The temperature was slightly less significant in model 2.b ($p = 0.003$) and explained only 0.14% of shape variation in both models. When matrix I was included as an exploratory matrix, model 3 explained 3.54% of the total variation in otolith shape. Both body length and otolith orientation had the most significant effect on shape ($p < 0.001$) and explained, respectively, 1.33% and 0.94% of the variability. Fish sex was less significant ($p = 0.010$) and only accounted for 0.15%. Matrix E had a similar contribution as in model 2.b. The variation partitioning (Figure 4) revealed no joint contribution of matrices E_{opt} and I .

Analysis of average cohort shapes

Visual exploration of the morphospace occupation prior to analysis showed no significant clustering between individuals from different cohorts (Figure 6). When visualized, average cohort shapes reconstructed with the inverse Fourier transformation showed a consistent overlap (Figure 6), further demonstrating the low contribution of year-to-year variations previously found and the overall temporal stability of otolith shape.

The previous statistical analysis was then repeated using these average cohort shapes. During the second sliding window analysis, total stock was again identified as the first optimal best predictor in the first iteration, with a critical window from third to sixth year of fish life. On the second iteration, the identified second-best predictor was SSB from the third to seventh year of fish life, which was identical to the second-best predictor identified in during the sliding window analysis for individual shapes. The final iteration identified mean temperature during the end of second year of fish life as the third optimal predictor (Supplementary material 1, Figure S4). Correlation tests carried out on the identified predictors revealed moderate correlation between total stock and SSB ($R = 0.49$, $p < 0.001$). However, correlation between temperature and both total stock and SSB was

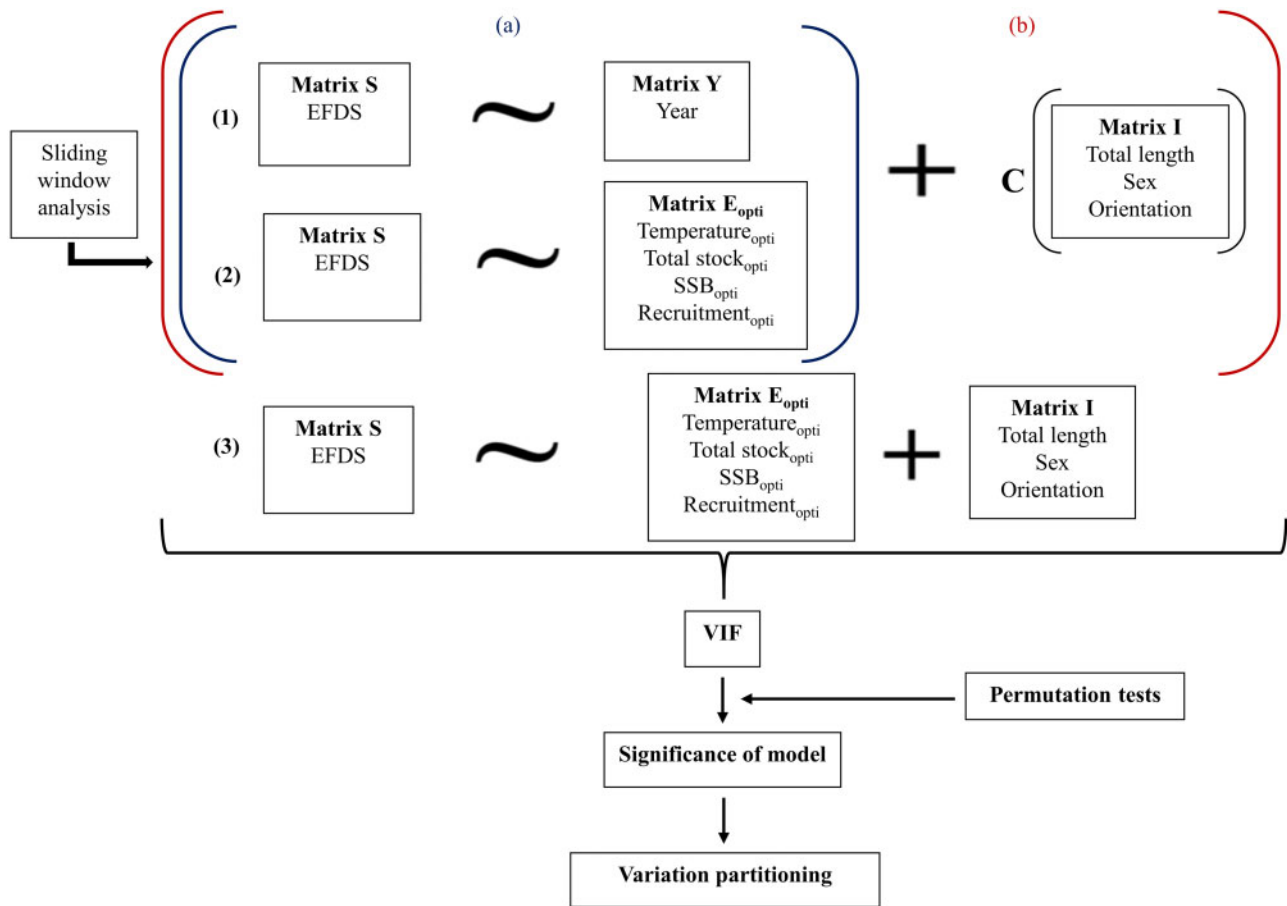


Figure 2. Schematic representation of the hierarchical RDA analyses performed in the EFA: (1) the global relationship between shape and cohort (year-class), (2) the influence of environmental conditions at the identified optimal windows, and (3) the global influence of both environmental and biological variables. Steps (a) and (b), respectively, refer to the RDA and associated partial RDA (where the variance attributed to matrix I was removed).

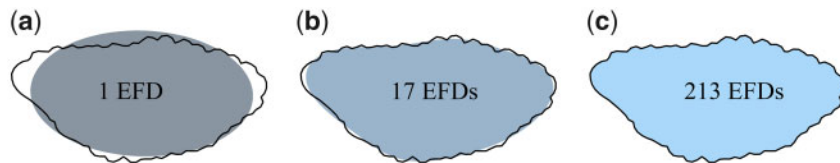


Figure 3. Fourier reconstruction of an NEA cod otolith at 1 (a), 5 (b), and 54 (c) harmonics. Corresponding number of elliptical Fourier descriptors after normalization of the first harmonic is indicated.

moderate but higher than in the first sliding window analysis ($R=0.27$, $p=0.01$ and $R=0.38$, $p<0.001$). Monte Carlo tests conducted at 1000 iterations found again a minimal probability of finding these optimal windows for total stock and SSB by chance ($p=0.002$ and $p=0.005$), confirming the strength of the signal. However, the probability of the identified critical windows for temperature to be a product of chance was significantly higher ($p=1.505$) and above the generally accepted threshold ($p=0.05$). The predictor was still retained and included in the following redundancy analysis to see if they contributed significantly to the models.

Using the identified optimal environmental windows, models 2.a and 2.b explained 20.03% and 17.00% of shape variability,

respectively (Table 2). The total stock was the main significant variable in both models ($p<0.001$) and explained, respectively, 13.99% and 15.63% of shape variability. The contribution of SSB was also significant but lower (8.59%, $p=0.001$ and 5.75%, $p=0.001$). While the identified optimal window for temperature showed a higher probability to be a product of chance, the variable still contributed significantly to the models (respectively, 2.61% and 2.73%) but was less significant ($p=0.037$ and $p=0.031$). When matrix I was included as an exploratory matrix, model 3 explained 26.77% of the total variation in otolith shape. Average cohort body length had a significant effect on shape ($p<0.001$) and explained 7.36% of its variability. Matrix E_{opti} had a similar contribution as in model 2.b. The variation partitioning (Figure 4) revealed a significant joint

Table 1. Results of the hierarchical RDA models for individual shapes detailed in Figure 2.

| | | Variables | | | | | | Model | | | |
|-----------------|-----|-----------|-------|-------|-------|-------|-------------|-------|----|-------|---------|
| | | Year | T° | TS | SSB | L | Sx | Or | df | % | p-Value |
| Model 1 | (a) | | | | | | | | 73 | 2.67 | 0.001 |
| Year | | 5.06% | | | | | | | | | |
| | (b) | 0.001 | | | | | Conditional | | 73 | 2.41 | 0.001 |
| | | 4.86% | | | | | | | | | |
| | | 0.001 | | | | | | | | | |
| Model 2 | (a) | | | | | | | | 3 | 1.15% | 0.001 |
| Optimal windows | | | 0.14% | 0.80% | 0.42% | | | | | | |
| | | | 0.001 | 0.001 | 0.001 | | | | | | |
| | (b) | | | | | | Conditional | | 3 | 1.11 | 0.001 |
| | | | 0.14% | 0.89% | 0.32% | | | | | | |
| | | | 0.003 | 0.001 | 0.001 | | | | | | |
| Model 3 | | | | | | | | | 7 | 3.54 | 0.001 |
| Global | | | 0.14% | 0.87% | 0.31% | 1.33% | 0.15% | 0.94% | | | |
| | | | 0.001 | 0.001 | 0.001 | 0.001 | 0.010 | 0.001 | | | |

Adjusted R^2 for partial RDA is calculated using Ezekiel's formula as the fraction of variance explained by that model after removing the fraction associated with the eventual covariables. "Variables" gives the percentage of explained variance and p -values for each significant variable within a model ($p < 0.05$). "Model" gives the df and the adjusted percentage of variation (based on adjusted R^2) explained by each model with associated p -value. df , degrees of freedom.

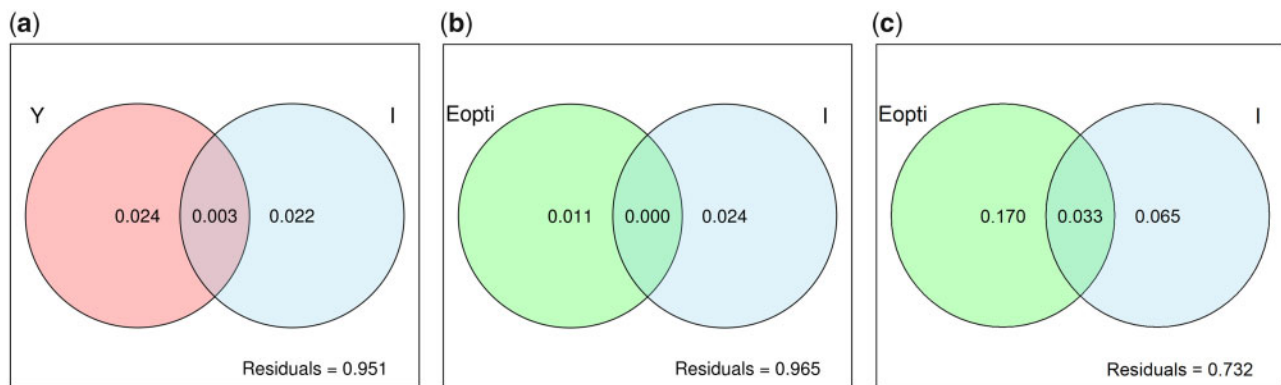


Figure 4. Venn diagrams of variation partitioning between the matrices (year Y, individual I, and environmental E_{opti}) tested in the analysis of individual shapes (a, b) and the analysis of average cohort shapes (c). Values in the non-overlapping parts of each circle represent the strict contribution of the corresponding matrix to the model. The value in the overlapping section represents the joint contribution of both matrices.

contribution of E_{opti} and I (3.3%), indicating that some of the environmental effects on otolith shape take place indirectly through changes in fish growth.

Discussion

Stability of NEA cod otolith morphology

Earlier studies have acknowledged the risks of mixing individuals from different year-classes and ages when using otolith shape as a stock discrimination tool. Begg and Brown (2000) warned that a discriminant analysis of shape variables could incorrectly separate a population based on significant differences, which were related in fact to inter-individual variability. Although they suggested that the baselines for stock separation be reconsidered each year, otolith morphology studies have often assumed that the variations of shape within a particular stock were minimal through time.

The present study found that the year-class effect, although significant, accounted for <3% of the overall variation in NEA cod

otolith shape over an 80-year period. Because all individuals included in the analysis were of the same age-class (8 years old), this study also minimized differences related to age or maturity status effects, previously identified as strong sources of variability (Cardinale et al., 2004; Hüsey, 2008; Capoccioni et al., 2011). The weak effect found thus corroborates the common assumption that shape remains largely consistent through time within a single population. Within-stock shape stability should now be studied for a broader range of species to determine whether temporal stability can always be assumed within a stock, or if stability itself is species-specific. Studying the temporal changes of shape within different stocks from the same species, where genetic variations are limited, would also provide essential insight on how much fish somatic and otolith growth is influenced by environmental parameters and under what conditions.

Some discrimination studies based on otolith shape have used individuals from multiple age- and/or year-classes (Campana and

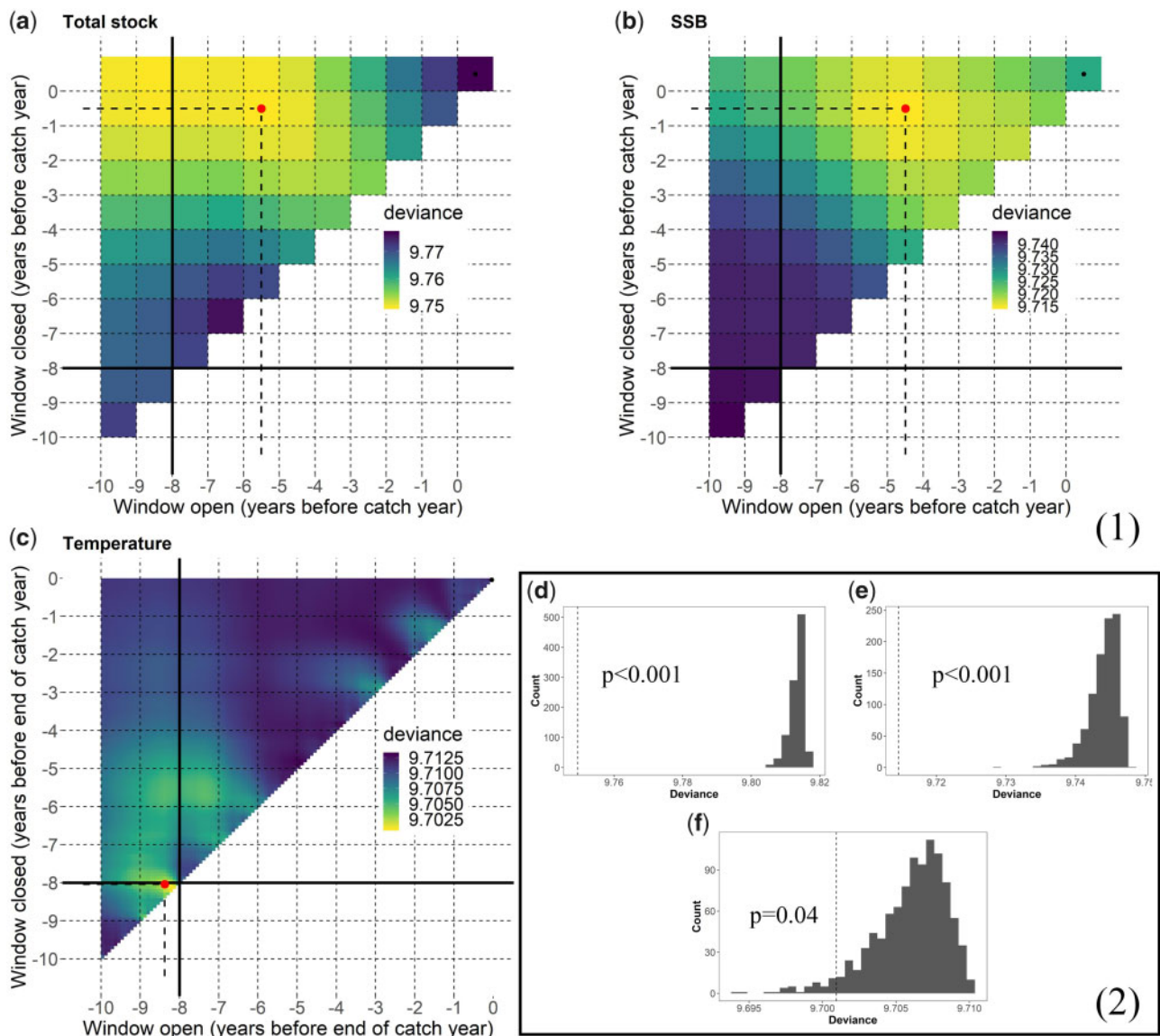


Figure 5. Results of the sliding window analysis on individual shapes for: (a) total stock (first best predictor), (b) SSB (second-best predictor), and (c) temperature (third best predictor). Squares represent time windows with corresponding years (a, b) and months (c) of fish life at which it was opened or closed. Axes are graduated with years for readability. Intersecting bold lines correspond to theoretical hatch of an individual. Colour gradient shows the deviance of model generated for each window where lowest deviances indicate best model fit. The green circle and dotted lines indicate the identified optimal window. Corresponding histograms of randomized deviance distributions (1000 iterations) are shown in (2) for: (d) total stock, (e) SSB, and (f) temperature. Dashed lines indicate the deviance of the optimal window and p -values the probability of obtaining the same signal by chance.

Casselman, 1993; Friedland and Reddin, 1994; Jónsdóttir *et al.*, 2006; Tracey *et al.*, 2006; Mahe *et al.*, 2016) and found no significant differences between years of sampling. While this study focused on evaluating the temporal stability of otolith shape within a single stock, it is also essential to quantify whether its accuracy as a stock discriminant between genetically distinct populations can fluctuate as a response to extrinsic drivers. Further work should now investigate if the accuracy of the discrimination of known stocks also remains stable over time. Such study would provide interesting conclusions on the reliability over time of stock discrimination using otolith shape, and consequently on how different local stocks might respond to changes in the environment or in their population structure.

However, even if these results are promising, some limitations must be considered. Because this study focused on within-stock stability of otolith shape, it comprised fish from a single stock unit and only individuals whose origin was previously determined with certainty based on inner otolith morphological features. While the separation criteria used by age readers have shown high agreement with independent genetic analyses (Berg *et al.*, 2005), it is possible that excluding the individuals of uncertain origin in our analysis consequently removed some of the variability occurring within the NEA cod stock. However, mean annual percentage of uncertain NEA cod in the archives was low at only 5.24% (see Supplementary material 1). During the 1980s, the proportion of cod labelled as uncertain NEA was higher, primarily due to the

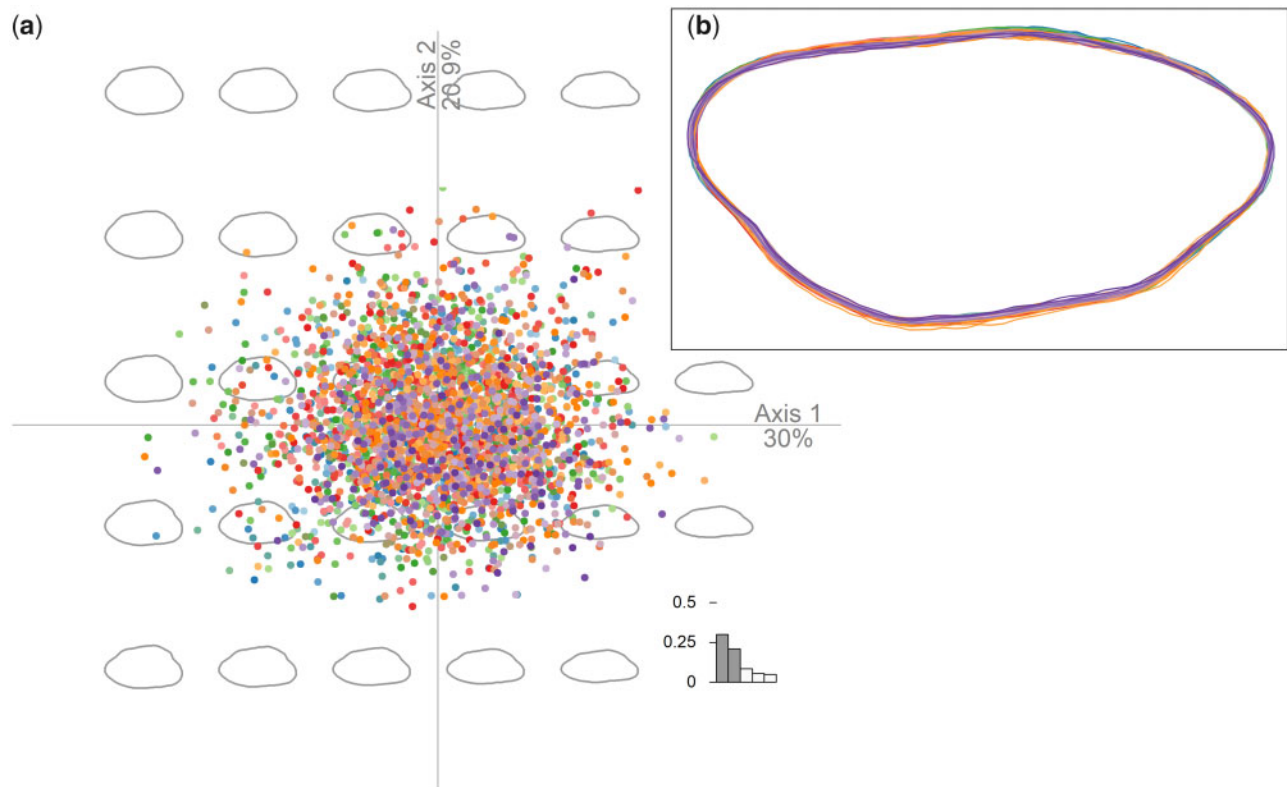


Figure 6. Morphospace occupation of individual (a) and average cohort (b) otolith contours. Each cohort is associated with a colour.

Table 2. Results of the hierarchical RDA models for average cohort shapes.

| | | Variables | | | | Model | | |
|-----------------|-----|-------------|--------|-------|-------------|-------|-------|---------|
| | | T° | TS | SSB | L | df | % | p-value |
| Model 2 | (a) | 2.61% | 13.99% | 8.59% | | 3 | 20.03 | 0.001 |
| Optimal windows | | 0.037 | 0.001 | 0.001 | | | | |
| | (b) | 2.73% | 15.63% | 5.75% | Conditional | 3 | 17.00 | 0.001 |
| Model 3Global | | 0.031 | 0.001 | 0.001 | | | | |
| | | 2.53% | 14.48% | 5.33% | 7.36% | 4 | 26.77 | 0.001 |
| | | 0.033 | 0.001 | 0.002 | 0.001 | | | |

Adjusted R^2 for partial RDA is calculated using Ezekiel's formula as the fraction of variance explained by that model after removing the fraction associated with the eventual covariables. "Variables" gives the percentage of explained variance and p -values for each significant variable within a model ($p < 0.05$, dash indicates non-significance). "Model" gives the df and the adjusted percentage of variation (based on adjusted R^2) explained by each model with associated p -values. df , degrees of freedom.

changes in the readers' organization. Besides, the discrimination criterion discussed here relies on the use of inner ring morphology, which is not directly comparable with the outer contour used in our analysis. Therefore, we presume that the potential effect of our sample selection is rather negligible when quantifying within-stock NEA cod otolith shape variability.

Moreover, otoliths are physical structures whose features are defined in three dimensions, but the elliptical Fourier decomposition used here considers only the 2-dimensional projection of the otolith contour and in turn ignores potential differences in the three-dimensional shape. This method has been shown to downweigh the importance of higher-order harmonics, having most of the shape variance expressed in the first harmonics (Harbitz and Albert, 2015). This essentially means that many studies are biased against higher-order variations, which could

mask subtle shape differences and factors of biological importance. In addition, elliptical Fourier descriptors are not completely independent from one another since each subsequent harmonic is built on the previous one, meaning that inherent biases could confound the statistical evaluation of shape differences (Haines and Crampton, 2000). While it remains one of the most widespread and accessible tools for shape analysis, EFA is ultimately one technique among many. For example, both geometric morphometrics and wavelet analysis show promising results and solve some of the Fourier decomposition shortcomings (Monteiro *et al.*, 2005; Tuset *et al.*, 2006; Vignon and Morat, 2010; Sadighzadeh *et al.*, 2014). Results presented herein are thus constrained to the EFA approach applied on the selected stock and might not be applicable on a more general scale without further research.

Sources of shape variation

In accordance with previous studies, individual-specific variables contributed most to the observed variability in individual otolith shape (Campana and Casselman, 1993; Hüsey, 2008; Capoccioni *et al.*, 2011). Body length, in particular, had a significant effect on shape and improved the models substantially, which is why most of the variation of otolith shape is usually attributed to allometry (Simoneau *et al.*, 2000; Monteiro *et al.*, 2005). By using fish of a single age-class throughout the analysis, differences in body length served as a proxy for different growth rates. These findings thus confirm that, while the ontogenetic trajectory of otolith shape is consistent between conspecific adults, changes in rate or timing of fish growth can lead to significant inter-individual differences in otolith morphology. Otolith orientation had also a significant effect on otolith shape. If bilateral asymmetry is prevalent, results of shape analyses can be affected by using different combinations of left, right, or both orientations (Mahé *et al.*, 2019). Our findings could thus support the use of only left or right otoliths in further analyses. However, due to the age estimation routines, only one whole otolith from each fish was available and used in our analysis. The proportion of variability explained by otolith orientation was consequently inflated, since it also reflected inter-individual differences in shape that were not explained by the other predictors included in our models.

In contrast, most extrinsic variables had a significant albeit much weaker effect on shape, which could indicate that changes in the environment or population dynamics over time account for less than the inter-individual variability occurring within a population. Although the reconstructed average cohort shapes were closely similar, their analysis revealed more clearly the effect of the different environmental variables. Interestingly, it also highlighted a large joint contribution of environmental variables and average cohort fish length, which suggests that environmental factors could exert an indirect influence on otolith shape through changes in fish growth rates.

The influence of temperature on fish growth has been well documented (Brander, 2000; Björnsson *et al.*, 2001) and has been linked to variations in otolith shape (Lombarte and Leonart, 1993; Cardinale *et al.*, 2004). However, because somatic growth is also consumption-dependent, feeding has been proposed as another important source of variability in otolith shape (for cod in Cardinale *et al.*, 2004; Hüsey, 2008; for various flatfishes and roundfishes in Mille *et al.*, 2016). Food availability depends in part on environmental conditions regulating the abundance of prey populations, as well as on competition for the access to food resources. Consequently, the relatively higher effect of total and spawning cod biomass on otolith shape, as well as the large joint contribution of extrinsic and intrinsic factors observed on average cohort shapes could, in fact, be representative of changes in growth rate driven by density-dependent effects on prey availability. However, the influence of such effects has long been debated for *Gadus morhua* due to the numerous other factors influencing food availability, which were not tested for here (Jørgensen, 1992; Brander, 2007). Further research should focus on the extent to which density-dependence can affect cod growth and in turn otolith growth.

Ultimately, these extrinsic factors only explained a minor portion of the observed variability and the otolith shape of NEA cod appeared mostly stable within the stock. However, it should be stressed that this study focused on long-term, between-cohort

changes in otolith shape in relation to the environment. A recent study has challenged the common paradigm that only long-term environmental differences drive changes in otolith shape by showing how acute, short-term episodes of environmental disturbances during early life can have similar results (Vignon, 2018). As such, significant otolith shape differences could likely occur within cohorts of the same stock following extreme climatic episodes. Further work is thus needed to fully understand the mechanisms behind changes in otolith shape in contrasted environmental conditions and at different scales, both temporally and spatially.

Exploration of optimal environmental signals

Identifying the critical window of action for an environmental factor is essential to interpreting biological responses of interest, where simplistic or wrongly identified signals can often depart from biological realities (van de Pol *et al.*, 2016). In that context, the sliding window analysis provides a promising tool to investigate and identify optimal signals with a systematic and statistically sound approach. However, it is essential to interpret the results with caution considering the exploratory nature of technique.

Constrained ordination methods like redundancy analysis do not provide a likelihood statistic and it is not possible to calculate an associated Akaike information criterion (AIC) or deviance. As explained by Oksanen *et al.* (2019), the “deviance” parameter generated for multivariate analysis used in this study is, in fact, akin to the residual sum of squares. According to both Borcard *et al.* (2018) and Oksanen *et al.* (2019), this criterion is not completely trustworthy and its interpretation can be quite liberal. The authors consequently stressed that it should be used carefully, and other criteria should be considered when available. It is nonetheless worth noting that this “deviance” parameter is also often used for the stepwise reduction of variables commonly seen in multivariate models, where similar caveats apply. In the absence of a likelihood statistic suitable for model comparison within this sliding window approach (Bailey and van de Pol, 2016; van de Pol *et al.*, 2016), this artificial deviance criterion still provided a convenient tool for identifying optimal models. Besides, the sliding window analysis carried out in this study investigated factors that ultimately explained very low variability in the otolith shape decomposed into Fourier descriptors. Therefore, the models generated during the sliding window analysis identified optimum signals based on a limited proportion of the overall variance, which is statistically challenging. In this context, biological interpretations can be difficult and conclusions should be drawn carefully.

Prior to analysis, it was hypothesized that environmental variables associated with the stock dynamics would have the most prominent effects during the early life of fish, since it is then most sensitive to cannibalism and lasting effects of early competition on its ontogeny (Folkvord and Otterå, 1993; Yaragina *et al.*, 2009). However, total stock and spawning biomass critical windows were both identified for a period beginning at the transition from juvenile stage to adult and ending around the age cod reaches sexual maturity (Jørgensen, 1990). Because total stock and spawning biomass estimations do not comprise the youngest fish that have not been recruited yet, both variables could be more significant at later stages because they constitute proxies of the magnitude of the competition observed further during the fish life cycle. The density-dependent effects in the early life of

fish are, therefore, not captured properly and identification of these relationships may be impossible. However, multiple studies have shown a strong ontogenetic development of Atlantic cod diet, in terms of both size and age. Link and Garrison (2002) observed ontogenetic shifts in Northeast Atlantic cod diet, wherein juveniles fed on small pelagic invertebrates, medium cod on a mix of benthic invertebrates and fish, and bigger cod on a larger amount of fish. Similarly, Jaworski and Ragnarsson (2006) described comparable shifts in the diet of Atlantic cod around Iceland. The present results could indicate that the density-dependent effects on fish growth (and consequently on otolith growth and shape) may be more significant during early adult life up to sexual maturity, when growth will then slow down. Moreover, randomization tests for both predictors confirmed that the identified optimal signal was strongly supported, which further justifies its biological relevance.

In contrast, the optimal window identified for temperature revealed a narrower, earlier period of influence beginning prior to hatching and covering the juvenile stage of an individual's life. Temperature is known as one of the major drivers of biological changes in fish such as growth rate and maturity (Brander, 2000), and its influence on otolith growth can be both indirect through changes of fish growth or through its direct effects on material deposition (Campana and Casselman, 1993; Campana, 1999). Indeed, otolith growth is an acellular process under different regulations than somatic growth (Simkiss, 1974), where biomineralization depends in part on the local chemistry (Borelli et al., 2003). Because these processes are directly affected by temperature (Casselman, 1990; Lombarte and Leonart, 1993) changes in environmental conditions during early life, when both fish and otolith growth are maximal, could have a more significant influence on the final morphology of adult fish otoliths.

Alternatively, early life temperature exposure could also have an indirect influence on fish and otolith growth through its effects on prey availability. Because Atlantic cod diet at the youngest life stages mostly consists of zooplankton for the larvae and small invertebrates for the juveniles (Link and Garrison, 2002; Jaworski and Ragnarsson, 2006), changes in temperature during these periods could lead to a mismatch with prey abundance and result in higher competition and poorer growth (Cushing, 1990; Rogers et al., 2011). Indeed, Hüsey (2008) showed that feeding level directly influenced otolith shape of young-of-year cod by affecting the number and dimensions of growth centres and lobes forming the crenulated edges of cod otolith. Differences in growth rate and otolith formation linked to temperature and feeding during early life could, therefore, have long-lasting effects on the shape of otoliths (Irgens et al., 2017) between individuals of the same stock. Interestingly, similar results were experimentally found by Cardinale et al. (2004). While this temperature signal was significant it should, however, be more carefully interpreted, because randomization tests showed a higher probability of getting a model supported by chance than for the previously identified optimal windows.

Likewise, the average cohort shape analysis showed a high probability of the temperature signal to be a product of chance. However, this window was closely similar to the one previously identified in the analysis of individual shapes, and the signal for both total stock and SSB remained strongly supported by randomization tests. Furthermore, the reconstructed average cohort shapes were shown to be almost identical, so it can be hypothesized that the differences in explained variance between different

tested time windows were, in fact, simply too low to be accurately separated. Because they closely resembled the windows identified in the analysis of individual shapes, including the temperature window in the models can still be justified since it significantly improved them. The identification of optimal windows using average cohort shapes should, however, be carefully considered, as it may have a limited statistical power in comparison with the individual analysis due to their low inter-variability.

Despite its exploratory nature, the sliding window analysis offers compelling evidence that models accounting for environmental factors should be contrasted to best represent biological realities. The present study shows the potential of this approach not only to investigate environmental predictors selected *a priori* based on formulated hypotheses, but also to uncover potentially unknown signals of biological relevance. These results encourage future research to delve deeper into newer techniques that challenge common assumptions, especially when investigating the biological responses to environmental changes.

Conclusions

The present study generated a valuable continuous database of otolith shape extending over 82 years (1933–2015), the longest to date for this specific stock of Atlantic cod. This first long-term analysis of NEA cod otolith shape stability revealed that the general within-stock morphology remains largely unchanged through time and changing conditions. Similar work should now be conducted to identify shape stability within other species or stocks where shape analysis is a critical asset to fisheries management. In addition, the hierarchical modelling approach helped disentangle and partition the effects of different suspected sources of variation, further quantifying the resilience of otolith shape to changing environmental conditions. The sliding window approach and the effects of identified optimal signals on shape give new insights into the mechanisms behind otolith shape variability, which further contributes towards a consensus on the biological interpretation of shape differences.

Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

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Author contributions

C.D., A.J.G., and S.S. conceived and designed this study. C.D. collected and processed the samples. C.D. and S.S. conducted data analysis and interpretation. C.D. wrote the manuscript. A.J.G., S.S., and J.A.G. edited and revised the manuscript.

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