Original Article

Northwest Atlantic mackerel population structure evaluated using otolith $\delta^{18}O$ composition

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The Northwest Atlantic mackerel (*Scomber scombrus*) population is comprised of northern and southern contingents, each with distinct natal regions in the United States and Canada. We tested hypotheses on natal origin and contingent mixing by analysing natal otolith $\delta^{18}O$ values, evaluating the approach through an out-group comparison with the Northeast Atlantic population. Otolith $\delta^{18}O$ values varied according to expectations between the Northeast (higher) and the Northwest (lower) Atlantic basins, and between contingents within the Northwest Atlantic stock, although contingent differences varied between years. Most adults (age-3+ years) sampled from US waters (1999–2003) represented the northern contingent (Canadian spawning site). The confirmation of the seasonal mixing of older and larger fish between the two contingents provides support and justification for the development of bi-national (United States–Canada) assessment and management of Northwest Atlantic mackerel.

Keywords: Atlantic mackerel, otolith stable isotopes, population structure

Introduction

Atlantic mackerel (*Scomber scombrus* Linnaeus 1758), like many other marine and coastal fish, has a complex population structure that influences its ecological and economic roles. The species has two distinct populations, one in the Northwest Atlantic, centred off the United States and Canada, and another in the Northeast Atlantic (Jansen and Gislason, 2013). Both populations have independently experienced large shifts in abundance, landings, and distribution over time (Overholtz *et al.*, 2011; ICES, 2013; NEFSC, 2018; Olafsdottir *et al.*, 2019). In the last two decades, the Northeast Atlantic population has experienced irruptive changes in abundance and distribution and supports one of the world's largest fisheries by weight (Brunel *et al.*, 2018; Nikolioudakis *et al.*, 2019; Olafsdottir *et al.*, 2019). During this same period, the Northwest Atlantic population experienced depressed abundance and apparent age truncation causing lost revenue to coastal US and Canadian fishing interests (NEFSC, 2018).

Although both populations require careful inter-jurisdictional management, the Northwest Atlantic population has had a long history of study into the influence of sub-populations, or contingents, on landings in US and Canadian fisheries. Scientists and managers generally accept that there are two main centres of spawning for Northwest Atlantic mackerel, one in the southern Gulf of St. Lawrence in July, and another in southern New England during May (Figure 1) (Sette, 1950). In work that continues to guide the modern understanding of this population, Sette (1950) tracked seasonal length modes in US Atlantic mackerel fisheries, uncovering a consistent yearly pattern of a single small-length mode during summer, followed by the sudden

addition of a new large-length mode during fall, winter, and spring. Sette assigned the reoccurring large-length mode to members of a northern contingent that migrated south from Atlantic Canada shelf regions and then returned to spawn and forage in these shelf waters from June to November. More modern methods applied to track migration and natal origin, including genetic analysis, otolith morphometrics and microstructure, and tagging have failed to clearly differentiate between the northern and southern contingents (Moores *et al.*, 1975; Castonguay *et al.*, 1991; Simard *et al.*, 1992; Lambrey de Souza *et al.*, 2006). During periods of significant overlap, mixing between US and Canada origin contingents may curtail the establishment of genetically discrete populations (Moores *et al.*, 1975; Castonguay *et al.*, 1991; Lambrey de Souza *et al.*, 2006).

Uncertainty surrounding the population structure of Northwest Atlantic mackerel has contributed to past challenges for assessment and management of the population across US–Canada Exclusive Economic Zone (EEZ) boundaries (Deroba *et al.*, 2010; Overholtz *et al.*, 2011; Wiedenmann, 2015). Large spawning areas within each nation and migratory patterns that span the US and Canadian EEZs mean that loosely coordinated international efforts may not be sufficient to appropriately manage the population. This dilemma is demonstrated by the contrasting jurisdictional management assumptions of the two countries: the United States assesses a single unit stock incorporating both nation's landings in its management, while Canada has been assessing only the northern contingent (DFO, 2017; NEFSC, 2018). However, based on results from Redding (2017), the 2019 Canadian analytic assessment estimated, for the first time, catches of northern contingent mackerel in US winter fisheries (DFO, 2019). The US assessment concluded that Atlantic mackerel are overfished, overfishing is occuring, and there is an absence of older fish but an apparent recent increase in recruitment. Canadian data indicate a steep collapse in spawning stock biomass by the northern contingent after 2010 and have been

used to justify reductions in harvest and quotas (DFO, 2014, 2017, 2019). If the two contingents do substantially mix, uncoordinated management actions by the two nations could impact the entire resource.

This study utilizes otolith stable isotope values as a marker of natal origin, relevant to testing hypotheses on contingent structure, and changes in spatial distributions of Northwest Atlantic mackerel. Stable oxygen isotope composition in meteoric waters varies along a latitudinal gradient that reflects global patterns of precipitation that in turn cause fractionation and ultimately depletion of the heavier isotope, ^{18}O at colder temperatures. Temperature also independently influences the isotopic composition of otoliths through equilibrium fractionations during carbonate formation; increases in otolith $\delta^{18}O$ values are observed at lower temperatures, which can overwhelm the latitudinal gradient in certain areas (Nelson *et al.*, 1989; Edmonds and Fletcher, 1997; Thorrold *et al.*, 1997; Campana and Thorrold, 2001). As a result, although high northern latitude surface seawater is relatively depleted in $\delta^{18}O$ (due ultimately to precipitation depleted in ^{18}O at higher latitudes), isotopic fractionation during carbonate formation at colder temperatures will lead to a higher otolith $\delta^{18}O$ value. For example, Trueman *et al.* (2012) showed that temperature had a stronger impact than seawater $\delta^{18}O$ values on cod otolith $\delta^{18}O$ values; fish originating in and around the Gulf of St. Lawrence had an $\sim$2‰ higher otolith $\delta^{18}O$ value than those originating from US Mid-Atlantic Bight (MAB) waters.

In this study, we tested for differences in the stable oxygen isotope composition of natal otolith material from Atlantic mackerel originating from (i) the Northwest and Northeast Atlantic Ocean, (ii) Canada and the United States, and (iii) sub-regions within the United States. The initial comparison of oxygen isotopic composition of Northwest and Northeast Atlantic mackerel otoliths served to substantiate the approach using the Northeast Atlantic sample as an out-group (Cadrin, 2010), testing for higher (more positive) $\delta^{18}O$ values in accordance with expectations (Trueman *et al.*, 2012) prior to investigating more subtle differences between groups within the Northwest Atlantic. Our goal in this study was to discriminate between southern and northern contingent juveniles collected in US and Canadian waters and then seek to classify adult winter/spring aggregations sampled in US waters.

Due to latitudinal temperature gradients, otolith $\delta^{18}O$ values should be most positive in out-group samples from Iceland and Norway, less positive in the northern contingent, and lowest in the southern contingent. Within the southern contingent, we hypothesized that subtle to nil sub-regional differences would occur in otolith $\delta^{18}O$ values, due to high regional mixing of oceanic source waters and likely high dispersal by individuals between sub-regions. In classifying individuals to northern or southern contingents, inter-annual variation in temperature and oceanographic features could confound abilities to discriminate contingents (Thorrold *et al.*, 2001; Rooker and Secor, 2019). Therefore, we developed year-class-specific baselines (age-1) with which to compare unknown Atlantic mackerel (ages > 1) assigned to the same year-classes. Using these baselines, the relative performance of three different statistical classification procedures was compared.
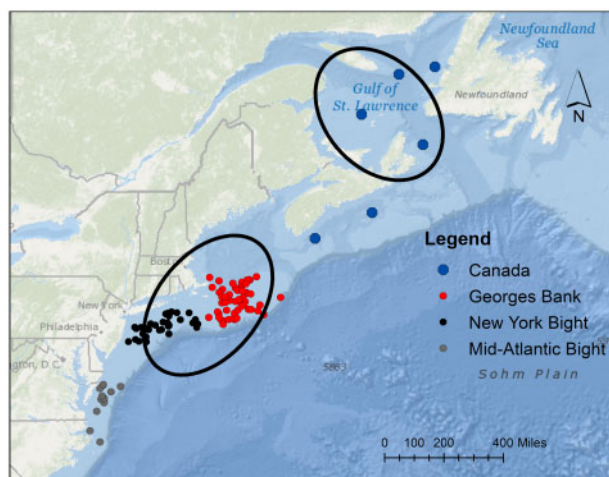

Figure 1. Map depicting spawning areas for the northern and southern contingents (black ovals) and sample locations for Atlantic mackerel otoliths from the Northwest Atlantic, including Canadian and US samples. For US samples, the points indicate the spring bottom trawl survey tows in which the fish was captured. For Canadian samples, the point indicates the approximate centre of the statistical areas from which commercial samples were collected.

Methods

Atlantic mackerel otoliths were selected from survey samples taken during the month of March [Northeast Fisheries Science

Center (NEFSC) trawl survey] and archived at the NEFSC Fisheries Biology Program in Woods Hole, MA, United States. Selected Canadian commercial fishery samples were collected during July–September and are archived at Fisheries and Oceans Canada (DFO), Maurice Lamontagne Institute, Mont-Joli, Québec, Canada.

Age-1 fish were used for classification baselines and to differentiate natal habitats because this age was commonly sampled across targeted regions and years. Age-0 fish in contrast were infrequently sampled in surveys and fisheries. Otolith material associated with the first year of life (material within the first annulus, Figure 2A, termed hereafter as natal $\delta^{18}O$) was extracted and used for baselines. This approach assumes that the age-1 capture locations reflected age-0 juvenile natal ranges, based on the limited evidence of exchange between the contingents before adulthood (Lambrey de Souza *et al.*, 2006). Baseline samples that included age-1 fish from 1999, 2000, and 2001 represented year-classes 1998, 1999, and 2000, respectively. These years were chosen based on the availability of matched US and Canadian samples (target $N > 10$) and represented a period of relatively high abundance (DFO, 2017; NEFSC, 2018). For the US baseline, sub-regions

were compared among Georges Bank (GB), New York Bight (NYB), and MAB (Figure 1). An unmatched set of US-collected samples representing the 2011 year-class was also analysed against US-collected test samples.

Test samples were classified according to baselines to evaluate the contribution of the northern contingent to fish collected in US waters at ages >1. To the extent of their availability, age-classes ≥ 2 were matched to baseline year-classes (Table 1).

An out-group test was conducted comparing Northeast Atlantic adult samples captured in 2015 (from ages 3 to 12) and obtained from the Institute of Marine Research in Norway and the Marine Research Institute in Iceland. Because these samples contained multiple year-classes, they were deemed suitable for an out-group comparison, although year-classes were not matched with the US–Canada baseline. Distribution of out-group samples is shown in Supplementary Figure S1.

Otolith preparation

Isolation of material from the age-0 (natal) portion of the otolith was carried out using a precision micromill (New Wave Research Micro-Mill). Care was taken to avoid including the mounting media in the otolith carbonate powder that was analysed. When possible, the right sagittal otolith was selected. The age-0 portion of the otolith was identified and the milling path configured to lie entirely within the first opaque zone (Figure 2). A series of 30-μm-deep milling passes sufficient to mill the entire thickness of the otolith (generally 9–14 passes) was conducted with a 500-μm carbide dental drill bit (Brasseler USA®) in order to obtain >200 μg material. Milled powder was carefully collected and stored in plastic vials. The drillbit, microspatula, and other tools were cleaned with 100% ethanol to prevent cross-contamination between samples.
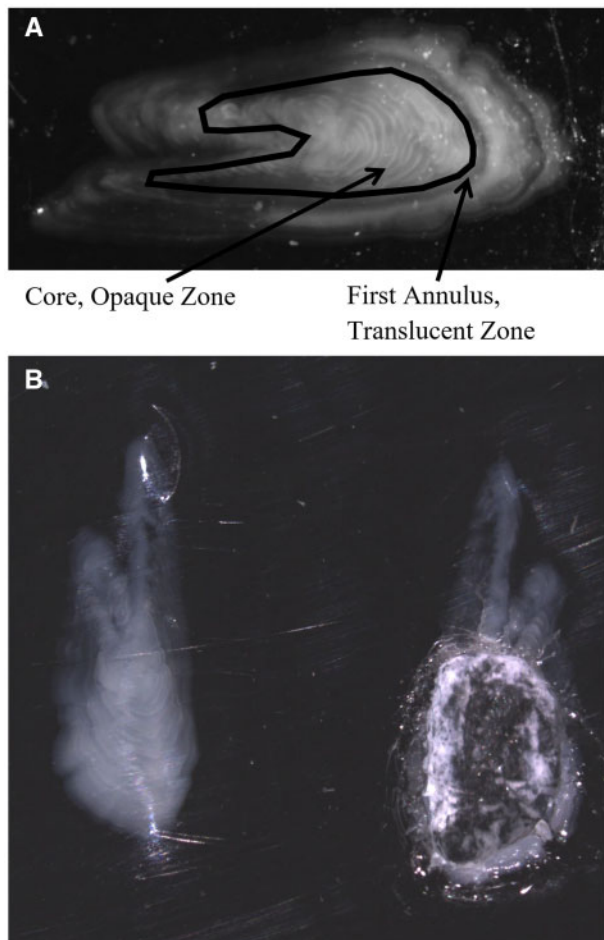

Core, Opaque Zone First Annulus, Translucent Zone

Figure 2. (a) Unmilled Atlantic mackerel otolith with the area corresponding to the first year of growth indicated by the black outline. Note translucent zone that delimits the natal region of the otolith and (b) a pair of otoliths in which the right one has been milled using a micromill.

Table 1. Samples of Northwest Atlantic mackerel otoliths obtained from US and Canadian sources.

Country	Age	N	$\delta^{18}O$ Mean	$\delta^{18}O$ SD
1998 year-class				
Canada	1	15	−1.40	0.84
Canada	2	13	−0.60	0.44
United States	1	32	−3.27	0.96
United States	2	21	−2.18	0.69
United States	3	19	−0.58	0.56
United States	5	2	−0.57	0.51
1999 year-class				
Canada	1	12	−1.18	0.33
Canada	2	15	−1.29	0.38
United States	1	27	−2.66	0.87
United States	2	30	−2.13	0.51
United States	4	23	−1.05	0.50
2000 year-class				
Canada	1	12	0.00	0.34
United States	1	39	−2.09	0.76
United States	3	15	−0.35	0.50
2011 year-class				
United States	1	20	−1.32	0.49
United States	2	20	−1.53	0.45
United States	3	20	−1.07	0.56
United States	4	20	−0.89	0.48

Mean and SD levels of natal $\delta^{18}O$ correspond to milled material deposited during the first year of life.

Stable isotope analysis

Otolith powder was placed in glass vials ($\sim$200 µg/individual) and heated in a 60°C drying oven for 10 min to remove any moisture. Vials were sealed, flushed with ultra-pure helium gas, and the carbonate powder was converted to CO_2 by dissolving it in water-free 100% phosphoric acid using a ThermoFisher Gasbench® peripheral at a temperature of 50°C. The $\delta^{18}O$ and $\delta^{13}C$ composition of the CO_2 was analysed using a ThermoFisher Delta Plus continuous flow stable isotope ratio mass spectrometer. The carbon stable isotope data are documented elsewhere in a thesis (Redding, 2017). Repeated measures of laboratory carbonate standards show that the *SD* for $\delta^{18}O$ isotope values was $\sim\pm0.1\permil$. An in-house otolith standard composed of homogenized white perch *Morone americana* (J. F. Gremlin, 1789) otoliths was used as a measure of instrumental precision for otoliths (as opposed to mineral carbonate standards mentioned above). Precision of this white perch otolith standard measurement was $\pm0.16\permil$ for $\delta^{18}O$ values ($n = 22$).

To assess the impact of otolith mounting media (see Redding, 2017 for description of these media), these materials were processed and analysed identically to carbonate powder as samples discussed above. None of these media produced a measurable amount of gas. We also assessed asymmetry in oxygen isotope composition between 24 paired left and right Atlantic mackerel otoliths. There was no significant difference between these paired otoliths (paired difference = $0.04 \pm 0.10\permil$, $p = 0.63$).

Statistical methods

Regional and sub-regional differences in otolith composition were tested using analysis of variance (ANOVA). Data were assessed for homogeneity of variance using Levene's test and residuals were tested for normality using the Shapiro–Wilks test. Unless otherwise stated, all statistical analysis was performed using R version 3.3.0 (R Core Team, 2016) with a significance alpha of 0.05.

Classification of age >1 samples collected in US waters was conducted using random forest discrimination to explore mixing between the contingents. The random forest discrimination was performed using the "randomForest" package in R (Liaw and Wiener, 2002). In this approach, a collection of 500 classification trees is created. Each tree is constructed by random sampling of the regional baselines with replacement, meaning the same sample could be used more than once in construction. This creates a binary classification tree. The final classification for a sample comes from the full set of 500 trees, where an individual "unknown" sample is evaluated using each tree. The most frequent assignment within the forest determines the final classification. To account for the smaller northern contingent baseline group, Canadian captured samples are weighted at a 2:1 ratio in the random sampling compared to those samples from US waters, to have more even selection. Error is estimated using the "out-of-bag" (OOB) samples in the random forest procedure, where the samples that were not used to construct an individual tree acted as a testing set to assess the accuracy of that tree. Because random forest classification relies on a random process, procedures were repeated five times to evaluate the repeatability of classifications and the OOB error rate.

Random forest classifications were compared with parametric discrimination procedures, quadratic discriminant analysis (QDA) and logistic regression. To estimate error in QDA

classification, the baseline data were separated into year-specific training and testing sets: 75% of the data were randomly assigned to the training set and the remaining 25% to the testing set. The training set was used as the baseline. The testing set provides an estimate of the accuracy of classifications. For logistic regression, a logistic function was fitted through regression to the baseline data with a threshold classification probability of 0.5.

Results

Isotopic differences across natal habitats

Northwest Atlantic mackerel otolith natal isotopic composition differed significantly from the composition of the Northeast Atlantic out-group (ANOVA, $p < 0.001$). *Post hoc* analysis revealed significantly higher natal $\delta^{18}O$ values in Northeast Atlantic samples from Iceland and Norway (Figure 3, Tukey Honest Significant Difference (HSD) $p_{\text{Norway–Iceland}} = 0.95$, $p_{\text{Norway/Iceland–Canada}} < 0.001$, $p_{\text{Norway/Iceland–United States}} < 0.001$). Additionally, within the Northwest Atlantic, Canadian Atlantic mackerel had significantly higher natal $\delta^{18}O$ values than their US counterparts for the combined 1998 through 2000 year-classes (Figure 4; Tukey HSD, Canada–United States: $p < 0.001$).

When examining individual year-classes, Canadian age-1 samples were found to have significantly higher natal $\delta^{18}O$ values than US samples for the three year-classes from 1998 through 2000 (Figure 4; ANOVA, $p < 0.001$). Tukey tests showed that year-classes of Canadian samples had consistently higher average $\delta^{18}O$ values than the corresponding US samples. Additionally, within each country, year-classes showed significant differences in natal $\delta^{18}O$ values (Figure 4; Canada—ANOVA, $p < 0.001$; United States—ANOVA, $p < 0.001$). Tukey tests showed that for Canadian origin samples, there were no significant differences in natal $\delta^{18}O$ values between the 1998 and 1999 year-classes (Tukey HSD, $p = 0.99$) and for US origin samples, there was no difference between the 1999 and 2000 year-classes (Tukey HSD, $p = 0.06$), but overall, there was an increase in natal $\delta^{18}O$ values in later year-classes. Statistically significant differences in natal $\delta^{18}O$ composition of US-captured fish were found across age for all year-classes including the 2011 US year-class (Figure 5; ANOVA, $p_{1998} < 0.001$, $p_{1999} < 0.001$, $p_{2000} < 0.001$, $p_{2011} = 0.0002$).
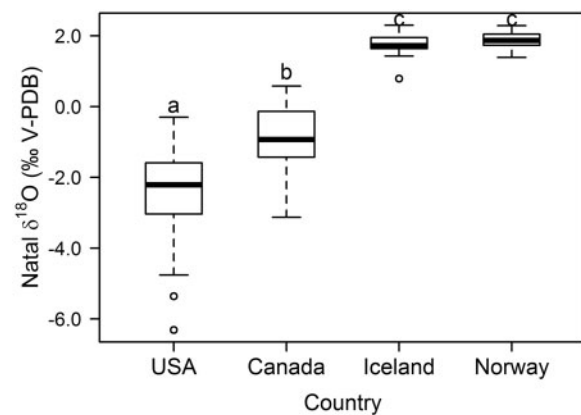

Figure 3. Boxplot of Atlantic mackerel natal otolith $\delta^{18}O$ values sorted by country of origin. For US and Canadian Atlantic mackerel samples, these values come from age-1 fish. For Iceland and Norway, samples are from older fish, ranging from age-3 to age-12 captured in 2015. Countries with different letters correspond to statistically differing groups (ANOVA; Tukey *post hoc* test).
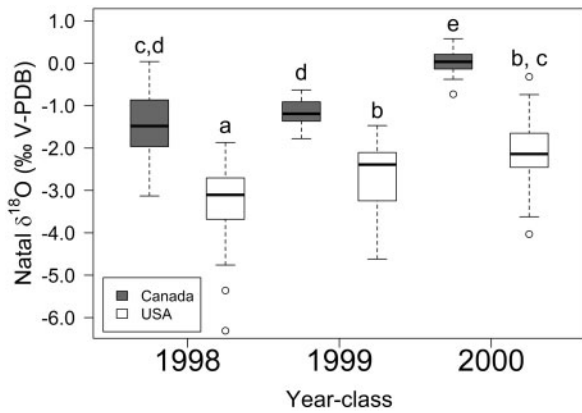
Figure 4. Boxplot of year-specific Atlantic mackerel natal otolith $\delta^{18}O$ values in the United States and Canada. The values correspond to the natal material of age-1 fish, representing the 1998 through 2000 year-classes. Groups with different letters correspond to statistically differing groups (ANOVA; Tukey *post hoc* test).

For US-captured Atlantic mackerel older fish tended to have more positive natal otolith $\delta^{18}O$ values.

Natal otolith material from age-1 fish available for GB and the NYB for 1998–2000 year-classes revealed no significant differences between sub-regions (Figure 6) (two-way ANOVA on cubic root transformed $\delta^{18}O$ values, $p_{sub-region} = 0.81$, $p_{year} < 0.001$). Across years, otolith $\delta^{18}O$ values rose significantly in a similar pattern to that observed in US and Canadian samples over time.

Classification of US adult Atlantic mackerel

Classifications of adult US samples showed a majority or equivalent contribution by the northern contingent, regardless of classification method (Table 2 and Figure 7). Random forest classification assigned the majority of samples to the Canadian baseline (northern contingent) for the 1998 and 2000 year-classes (66.7 and 86.7%, respectively), but suggested a more even composition in the 1999 year-class, with 47.2% assigned to the Canadian baseline. In age-classes >2, the majority of samples are assigned to the northern contingent for all three year-classes, indicating the ages tested here may impact the overall proportion of samples assigned to the Canadian baseline. The other two classification methods yielded similar results. For the random forest
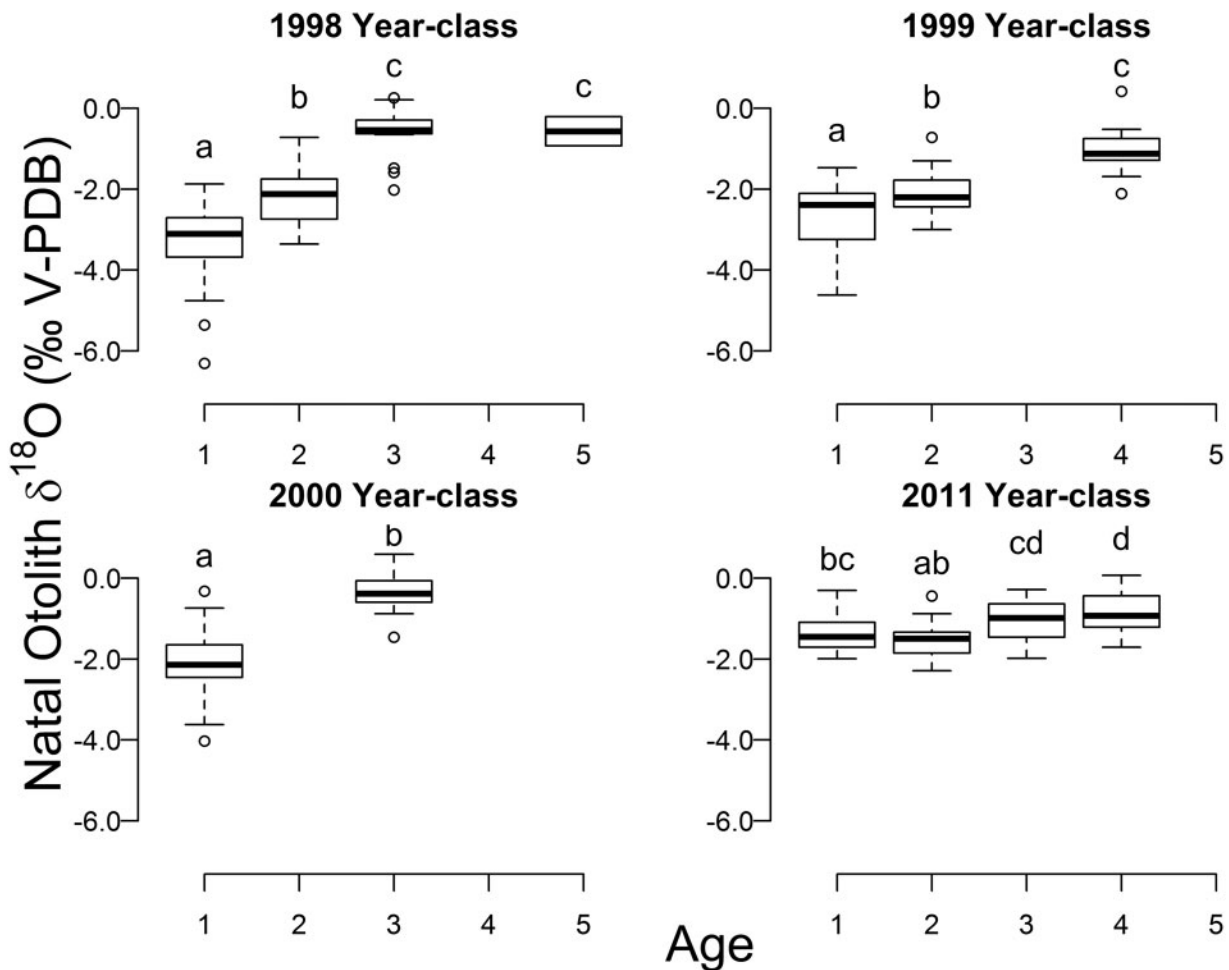

Figure 5. Boxplots of age-specific natal otolith $\delta^{18}O$ values by year-class for US-captured Atlantic mackerel. Ages with different letters correspond to statistically differing groups (ANOVA; Tukey *post hoc* test).
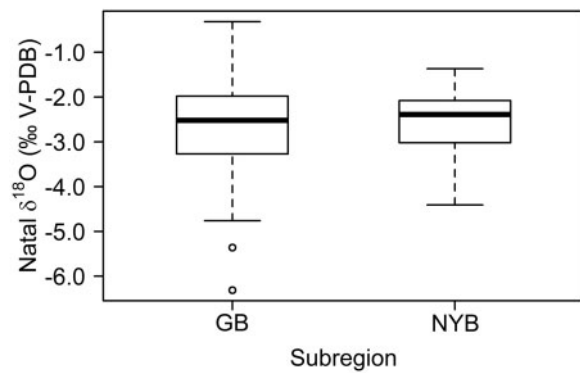
Figure 6. Boxplot of age-1 Atlantic mackerel natal otolith δ^{18}O values compared across sub-regions.
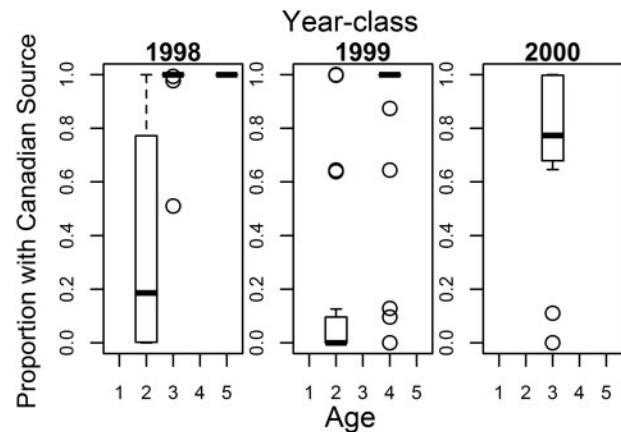

Figure 7. Random forest classification of age-classes for three year-classes of Atlantic mackerel sampled in the Spring NEFSC trawl survey (US waters). Box plots represent the distribution of all probabilities of classification to the northern contingent.

Table 2. Classification results for adult Atlantic mackerel samples captured in US waters.

Year-class	N	Method	Canadian baseline assignment	US baseline assignment	% Northern	% Southern	Error estimates (%)
1998	42	Random forest	28	14	66.7	33.3	25.53
		Logistic regression	29	13	69.0	31.0	–
		QDA	29	13	69.0	31.0	8.3–25.0
1999	53	Random forest	25	28	47.2	52.8	7.69
		Logistic regression	24	29	45.3	54.7	–
		QDA	24	29	45.3	54.7	0–10
2000	15	Random forest	13	2	86.7	13.3	7.84
		Logistic regression	10	5	66.7	33.3	–
		QDA	13	2	86.7	13.3	0–15

Mackerel were classified to US and Canadian regions, using year-class-specific age-1 δ^{18}O baselines. The number of adult samples classified, N, is reported, along with the numbers and percentages assigned to each region of origin. Random forest, logistic regression, and QDA were performed for each year-class. Error estimates for random forest are derived from the OOB error rate and separate training and testing sets were used to estimate classification success in QDA. The reported error estimate for QDA is (1 − classification success %).

procedure, estimated classification error ranged between 7.7 and 25.5%, which was similar to the error found in the QDA method for which error was calculatable (0.0–25.0% error). The proportion of samples assigned to the northern contingent (or probability of this assignment) increased with age (Figure 7). The unmatched 2011 year-class samples supported no differentiation between Northwest Atlantic mackerel contingents, and without distinct baselines, samples were not classifiable. Still, significantly higher levels of δ^{18}O in ages 3–4 than in ages 1–2 (Figure 5) are consistent with increased contribution of the northern contingent at older ages for US spring aggregations.

Discussion

Distinct differences in the natal δ^{18}O values of otoliths between US and Canadian spring-captured individuals support Sette's (1950) conclusion of separate, distinguishable natal habitats and migratory sub-groups of Northwest Atlantic mackerel that mix at older ages. Natal baselines were supported on a year-class-specific basis for age-1 mackerel sampled from Canada and the United States. Classification of US fish >2 years in age showed substantial mixing, with increased incidence of northern contingent origins at older ages for all years examined.

Significant differences in natal δ^{18}O values between US/Canadian samples and Icelandic/Norwegian out-group samples supported hypothesized differences due to greater heavy isotope fractionation associated with the colder seawater of the Northeast Atlantic. Observed differences within the Northwest Atlantic population between US and Canadian samples were not as strong as those between the Northwest and Northeast Atlantic populations, likely reflecting more modest differences in thermal regimes that influence isotopic fractionation. More resolved sub-regional differences within US waters were not present in age-1 fish, but we were unable to obtain a robust sample of MAB otoliths, and greater geographic separation may have yielded larger isotopic differences (Figure 6).

This study further advances the application of stable isotopes in otoliths for understanding fish population structure (Gao *et al.*, 2001; Hanson *et al.*, 2010; Newman *et al.*, 2010; Siskey *et al.*, 2016). In our case, distinguishing contingents was possible for a pelagic species with overlapping seasonal distributions (Sette, 1950; Maguire *et al.*, 1987), but with an ~1500 km separation between the two Northwest Atlantic natal habitats. Micromilling of Atlantic mackerel otoliths allowed precise targeting of natal otolith material deposited in late spring, summer,

and fall (Dery, 1988), when contingent distributions show the greatest geographic separation. Observed differences in δ^{18}O values between Atlantic mackerel from the northern and southern natal habitats, 1.7‰, are consistent with the range of predictions of Trueman et al. (2012). In the Northwest Atlantic, the observed mean δ^{18}O values for US age-1 fish from the 1998 through 2000 year-classes was somewhat below Trueman et al.'s predicted range of −2 to +2‰, with a mean of −2.63 ± 0.99‰. Canadian age-1 fish were within the predicted range with a mean at −0.9 ± 0.85‰. In the Northeast Atlantic, isotopic composition was within the predicted δ^{18}O range of +1 to 4‰ (Iceland mean = +1.75 ± 0.33‰, Norway mean = +1.89 ± 0.24‰). Trueman et al.'s (2012) estimates were derived from regional measurements of sea surface δ^{18}O values aggregated over a 30+ year time period and cannot reasonably be expected to document δ^{18}O value changes within a single year or season. Additionally, it should be noted that the δ^{18}O temperature fractionation relationship shown in Trueman et al. (2012) was not based on Atlantic mackerel otoliths. Because of this, there may be some unaccounted for biological effects specific to Atlantic mackerel, but relative differences should still hold.

Increases in otolith δ^{18}O values in both US and Canadian age-1 samples across the 1998 through 2000 year-classes (Figure 4) may originate from shifts in temperature and seawater δ^{18}O values caused by oceanographic processes including the North Atlantic Oscillation and the relative strength of the Gulf Stream, which both increased during the period from 1998 to 2000 (NEFSC, 2012). These processes drive changes in temperature, precipitation, and source water, directly shifting δ^{18}O composition of seawater and indirectly shifting the fractionation of oxygen isotopes during incorporation into otoliths. While it is difficult in this study to directly attribute the observed change in natal otolith δ^{18}O to these large-scale processes, they represent an important source of annual variation in variables that impact the isotopic composition of otolith carbonate. The consequence of this annual variation is that year-class-specific baselines are likely required for contingent classification. For this isotopic baseline development to be most effective, samples should be drawn from as wide a geographic range as possible to bracket the otolith δ^{18}O values in any given natal habitat.

Increased natal δ^{18}O values across age-classes (Figure 5) is consistent with the introduction and increasing prevalence of northern contingent Atlantic mackerel in US-sampled fish as year-classes progress in age, which has not been previously described for Northwest Atlantic mackerel. Results of classification showed the relative dominance of northern contingent individuals at older age-classes and the broad agreement in these assignments using all three classification methods. Alternatively, the shift in δ^{18}O values with age could be an artefact of milling whole otoliths. This introduces a potential source of contamination and error due to otolith growth overburden and drilling through thin layers of material deposited at ages >0, but we do not consider this a likely source of error. Targeting years with good availability of age-0 samples and milling a subset of samples using methods designed to entirely eliminate overburden would be valuable next steps to verify this assumption.

The dominance of northern contingent fish in the older age-classes of the NEFSC spring trawl survey catch raises the question of the southern contingent's fate. During the past decade, the NEFSC spring trawl survey has documented high abundances of 1 and 2 year olds but a severe decline in older fish (NEFSC, 2018).

Results reported here indicate a degree of fidelity by the southern contingent during the first and second year of life with some level of mixing apparent by age 2. At ages >2, contributions by the southern contingent to spring US aggregations are minor. As a result, following year-classes from juveniles to adults will be biased in the NEFSC survey. It is unknown whether the age-specific loss of the southern contingent is related to high mortality, a shift in distribution, and/or biases in sampling. Additionally, this study focused on US test samples only, under an untested presumption that contingent mixing is more likely to occur in US fisheries rather than in Canadian fisheries (Sette, 1950). Future studies should evaluate possible southern contingent mixing with Canadian fisheries.

Stock assessment models assume a closed population but this assumption is often violated in migratory species (Secor, 2015). Northwest Atlantic mackerel population structure is clearly complex and structured by contingents, which differentially recruit to regional (US and Canada) fisheries. Our findings support the spatial scale used in US stock assessments, which consider the entire Northwest Atlantic mackerel as a single mixed stock that depends upon two regions of egg production (e.g. NEFSC, 2018). Future studies are recommended that will allow assessments to more accurately model fishing mortality of northern contingent mackerel while in US waters (Van Beveren et al., 2019). A remaining question is whether the low representation of the southern contingent in US fisheries is the result of higher mortality rate, a shift in distribution, or lower recruitment, and whether this has always been the case.

Supplementary data

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

Acknowledgements

Funding

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Handling editor: Francis Juanes