

## ABSTRACT

Title of Document: NORTHWEST ATLANTIC MACKEREL (*SCOMBER SCOMBRUS*) POPULATION STRUCTURE EVALUATED USING OTOLITH STABLE ISOTOPES

Stephen Gray Redding, Master of Science Degree, 2017

Directed By: Professor David H. Secor  
Marine, Estuarine, and Environmental Science

Stock assessments for Northwest Atlantic mackerel (*Scomber scombrus*) assume a single stock, comprised of northern and southern contingents, each with distinct natal regions in the US and Canada. I hypothesized that otolith  $\delta^{18}\text{O}$  and  $\delta^{13}\text{C}$  values would provide discrimination between these regions based upon hydrographic differences, and such information could illuminate seasonal migrations and contingent structure. Otoliths from regions throughout the North Atlantic Ocean were carefully milled to extract carbonates corresponding to the first year of life. Significant differences occurred in otolith isotope composition across the Atlantic basin, and within the Northwest Atlantic stock, despite annual variability. In the Northwest Atlantic, two separate natal habitats and associated contingents were supported for juvenile mackerel, but incursions by the northern contingent into US waters occurred in older fish (age>2). These findings indicate that stock structure assumptions should be revisited in the assessment and management of Northwest Atlantic mackerel.

NORTHWEST ATLANTIC MACKEREL (*SCOMBER SCOMBRUS*) POPULATION  
STRUCTURE EVALUATED USING OTOLITH STABLE ISOTOPES.

by

Stephen Gray Redding

Thesis submitted to the Faculty of the Graduate School of the  
University of Maryland, College Park in partial fulfillment  
of the requirements for the degree of  
Master of Science  
2017

Advisory Committee  
Professor David H. Secor, Chair  
Professor Lee W. Cooper  
Professor Michael Wilberg  
Dr. Richard S. McBride

© Copyright by  
S. Gray Redding  
2017

## Acknowledgements

I first would like to thank my advisor, Dr. David Secor. You were a great mentor who helped me grow as an academic and person. Thank you very much for allowing me to be a part of your lab and for the great experiences on the White Salmon River and in the beautiful city of Riga, Latvia. Thank you also to Drs. Lee Cooper, Rich McBride, and Michael Wilberg for providing insight and feedback throughout my thesis.

The members of the Secor Lab also deserve my gratitude. Thanks to Brian Gallagher for being a great friend and indulging in hobbies with me. Thank you to Matt Siskey for helping teach me the micromill and the trouble it can bring. Thank you also to Mike O'Brien and Alex Atkinson for assistance and mentorship in the lab.

Many members of the CBL community were also important to my work and time as a graduate student, but thanks goes especially to Drs. Cedric Magen and Dana Biasatti for helping with isotopic analysis. Dr. Dong Liang was a great help in understanding the isotope classification methods used in the work. I also must thank Dr. Jay Rooker for use of his laboratory equipment. I owe tremendous gratitude to Drs. Martin Castonguay, Guðmundur Óskarsson, Aril Slotte and their associates for providing me with otolith samples from around the Atlantic.

I would like to thank my dear girlfriend, Sara Coleman, for the endless support and reason's to see new parts of the country and world. My family, Ivey, Sallie, and Tom, deserve some of the greatest thanks for helping to shape the person I am today and giving me the encouragement and motivation I needed to get this far.

## Table of Contents

Acknowledgements .....	ii
Table of Contents .....	iii
List of Tables .....	iv
List of Figures .....	v
<i>Introduction</i> .....	1
<i>Goals and Objectives</i> .....	10
<i>Methods</i> .....	12
<i>Results</i> .....	22
<i>Discussion</i> .....	27
<i>Conclusion</i> .....	43
<i>Table</i> .....	45
<i>Figures</i> .....	53
<i>References</i> .....	73

## List of Tables

**Table 1** Sample years for age-1 US and Canadian Atlantic mackerel baselines and unknown US adult samples of otoliths.

**Table 2** Inventory of archived Atlantic mackerel otoliths received from the Northeast Fisheries Science Center, Fisheries and Oceans Canada, Iceland's Marine Research Institute and Institute of Marine Research in Norway. In some instances degrees of latitude and longitude associated with each sub-region are presented within parentheses.

**Table 3** Atlantic mackerel core otolith  $\delta^{18}\text{O}$  values (mean  $\pm$  standard deviation) across years, sub-regions or regions, and ages. GB=Georges Bank, NYB = New York Bight.

**Table 4** Atlantic mackerel core otolith  $\delta^{13}\text{C}$  values (mean  $\pm$  standard deviation) across years, sub-regions or regions, and ages. GB=Georges Bank, NYB = New York Bight.

**Table 5** Atlantic mackerel core otolith  $\delta^{18}\text{O}$  values (mean  $\pm$  standard deviation) for age-0 fish, across years and sub-regions. GB=Georges Bank, NYB = New York Bight, MAB = Mid-Atlantic Bight.

**Table 6** Atlantic mackerel core otolith  $\delta^{13}\text{C}$  values (mean  $\pm$  standard deviation for age-0 fish, across years and sub-regions. GB=Georges Bank, NYB = New York Bight, MAB = Mid-Atlantic Bight.

**Table 7** Classification results for adult Atlantic mackerel samples captured in US waters. Mackerel were classified to US and Canadian regions, using year-class specific age-1  $\delta^{18}\text{O}$  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 quadratic discrimination analysis (QDA) were performed for each year-class. Error estimates for random forest are derived from the "out-of-bag" (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 %).

**Table 8** Classification results for adult Atlantic mackerel samples captured in US waters. Mackerel were classified to US and Canadian regions, using year-class specific age-1  $\delta^{18}\text{O}$  and  $\delta^{13}\text{C}$  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 quadratic discrimination analysis (QDA) were performed for each year-class. Error estimates for random forest are derived from the "out-of-bag" (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 %).

## List of Figures

**Figure 1** US annual landings, in thousands of metric tons, of Atlantic mackerel from 1960 to 2013. Catch data comes from Wiedenmann (2015) and NOAA Office of Science And Technology (n.d.).

**Figure 2** Conceptual diagram showing how a spatial shift in a mackerel population (green circle) across a management boundary (top panel) could impact actual (middle) and perceived (lower panel) stock size. Green and blue segments in top panel indicate stock boundaries. The second panel shows the trend of the single population. The bottom panel indicates how the population would appear across two stock boundary regions.

**Figure 3** Map depicting 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 center of the statistical areas from which samples were collected.

**Figure 4** Map depicting sample locations for Atlantic mackerel otoliths from the Northeast Atlantic, including Norwegian and Icelandic samples. All of these points indicate the station at which fish were captured during their respective surveys.

**Figure 5 (A, B)** A) Unmilled Atlantic mackerel otolith with the area corresponding to the first year of growth indicated in red. Note translucent zone, which delimits the natal region of the otolith; B) A pair of otoliths in which the right one has been milled using a micromill.

**Figure 6 (A, B)** Boxplots of paired left and right Atlantic mackerel otolith A)  $\delta^{18}\text{O}$  values and B)  $\delta^{13}\text{C}$  values, assessing asymmetry between the two sides within the same individual. Box covers data from the 25th – 75th percentiles, the horizontal bar marks the median, and the whiskers extend to 1.5 \* inter-quartile range or the maximum/minimum value, whichever occurs first. Values outside of 1.5 \* the inter quartile range are displayed with an additional point on the graph.

**Figure 7** Biplot of otolith  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  values for age-1 Atlantic mackerel (from the 1998 through 2000 year-classes), plotted by US sub-regions. Solid and dashed ellipses indicate 90% and 60% percentile distributions of data respectively. Each point represents the isotopic value of an individual otolith and the analytical error bar represents the precision of each isotope measurement ( $\pm 0.1\text{‰}$ ).

**Figure 8 (A,B)** Boxplot of age-1 Atlantic mackerel otolith A)  $\delta^{18}\text{O}$  values and B)  $\delta^{13}\text{C}$  values compared across years and sub-regions. Box covers data from the 25th – 75th percentiles, the horizontal bar marks the median, and the whiskers extend to 1.5 \* inter-quartile range or the maximum/minimum value, whichever occurs first. Values outside of 1.5 \* the inter quartile range are displayed with an additional point on the graph. Letters above the boxes in (A) indicate significant differences between years observed in post hoc testing using Tukey HSD.

**Figure 9 (A, B)** Boxplot of age-0 Atlantic mackerel otolith A)  $\delta^{18}\text{O}$  values and B)  $\delta^{13}\text{C}$  values from 2003 across US sub-regions, GB=Georges Bank, NYB = New York Bight, MAB = Mid-Atlantic Bight. Box covers data from the 25th – 75th percentiles, the horizontal bar marks the median, and the whiskers extend to 1.5 \* inter-quartile range or the maximum/minimum value, whichever occurs first. Values outside of 1.5 \* the inter quartile range are displayed with an additional point on the graph.

**Figure 10 (A, B)** Boxplot of age-0 Atlantic mackerel otolith A)  $\delta^{18}\text{O}$  values and B)  $\delta^{13}\text{C}$  values the years 1996 and 2003 for the GB and NYB . Box covers data from the 25th – 75th percentiles, the horizontal bar marks the median, and the whiskers extend to 1.5 \* inter-quartile range or the maximum/minimum value, whichever occurs first. Values outside of 1.5 \* the inter quartile range are displayed with an additional point on the graph. Letters above the boxes indicate significant differences observed in post hoc testing using Tukey HSD.

**Figure 11** Biplot of age-1 otolith  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  values according to country and year-class. Solid and dashed ellipses indicate 90% and 60% percentiles respectively for each region and year-class combination. Each point represents the isotopic composition of an individual otolith and the analytical error bar represents the precision of each isotope measurement ( $\pm 0.1\text{‰}$ ).

**Figure 12 (A, B)** Boxplot of year specific Atlantic mackerel otolith A)  $\delta^{18}\text{O}$  values and B)  $\delta^{13}\text{C}$  values in the US and Canada. The values correspond to the natal material of age-1 fish, representing the 1998 through 2000 year-classes. Box covers data from the 25th – 75th percentiles, the horizontal bar marks the median, and the whiskers extend to 1.5 \* inter-quartile range or the maximum/minimum value, whichever occurs first. Values outside of 1.5 \* the inter quartile range are displayed with an additional point on the graph. Letters above the boxes indicate significant differences observed in post hoc testing using Tukey HSD.

**Figure 13** Biplot of otolith  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  values according to country. For US and Canadian Atlantic mackerel samples, these values come from age-1 fish (1998-2000 year-classes). For Iceland and Norway, samples are from older fish, ranging from age-3 to 12 captured in 2015. Solid and dashed ellipses indicate 90% and 60% percentiles respectively. Each point represents the isotopic composition of an individual otolith and the analytical error bar represents the precision of each isotope measurement ( $\pm 0.1\text{‰}$ ).

**Figure 14 (A, B)** Boxplot of Atlantic mackerel otolith A)  $\delta^{18}\text{O}$  values and B)  $\delta^{13}\text{C}$  values according to country. For US and Canadian Atlantic mackerel samples, these values come from age-1 fish (1998-2000 year-classes). For Iceland and Norway, samples are from older fish, ranging from age-3 to 12 captured in 2015. Box covers data from the 25th – 75th percentiles, the horizontal bar marks the median, and the whiskers extend to 1.5 \* inter-quartile range or the maximum/minimum value, whichever occurs first. Values outside of 1.5 \* the inter quartile range are displayed with an additional point on the graph. Letters above the boxes indicate significant differences observed in post hoc testing using Tukey HSD.



**Figure 15 (A, B)** Biplot of otolith  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  values measured in Atlantic mackerel from feeding grounds in the Norwegian Sea and spawning grounds west of Ireland. The fish were captured in 2015 (age range 3 to 12). Solid and dashed ellipses indicate 90% and 60% percentiles respectively. Each point represents the isotopic composition of an individual otolith and the analytical error bar represents the precision of each isotopic measurement ( $\pm 0.1\text{‰}$ ).

**Figure 16 (A, B)** Boxplot of Atlantic mackerel otolith A)  $\delta^{18}\text{O}$  and B)  $\delta^{13}\text{C}$  from the 1998 year-class (age-1 fish from 1999 and age-2 fish from 2000) from Canada and the US. Box covers data from the 25th – 75th percentiles, the horizontal bar marks the median, and the whiskers extend to 1.5 \* inter-quartile range or the maximum/minimum value, whichever occurs first. Values outside of 1.5 \* the inter quartile range are displayed with an additional point on the graph.

**Figure 17 (A, B, C)** Boxplot of Atlantic mackerel otolith A)  $\delta^{18}\text{O}$  and B)  $\delta^{13}\text{C}$  from the 1999 year-class (age-1 fish from 2000 and age-2 fish from 2001) from Canada and the US. Box covers data from the 25th – 75th percentiles, the horizontal bar marks the median, and the whiskers extend to 1.5 \* inter-quartile range or the maximum/minimum value, whichever occurs first. Values outside of 1.5 \* the inter quartile range are displayed with an additional point on the graph.

**Figure 18** Discrimination functions used to classify adult (age-3 and 4) Atlantic mackerel based on the 1998 (A), 1999 (B) and 2000 (C) US and Canadian otolith  $\delta^{18}\text{O}$  baseline data. Each panel shows the function for both logistic regression and random forest classification, along with the  $\delta^{18}\text{O}$  value for both the US and Canadian baselines. The  $\delta^{18}\text{O}$  value of the unknown samples is shown as the black points.

**Figure 19** Time series of regional sea surface temperature anomaly and Gulf Stream index in the US Northwest Atlantic from 1977 to 2008 and 1966 to 2008 respectively. The lines are the 5-year moving average value. (Graphic extracted from Ecosystem Assessment Program NEFSC, 2009).

**Figure 20** Time series of the Labrador Current volume transport and the percentage of Labrador subarctic slope water (LSSW) from 1977 to 2008. (Graphic extracted from Ecosystem Assessment Program NEFSC, 2009).

## Introduction

Atlantic mackerel (*Scomber scombrus* (L.)) is a schooling pelagic migratory species, which plays an important economic and ecological role in the North Atlantic. They are a forage fish shuttling energy up the food chain from zooplankton to higher trophic level predators (Tyrrell *et al.*, 2008) and at the same time supporting important commercial fisheries. The species has two distinct populations, one in the Northwest Atlantic, centered off the United States and Canada, and another in the Northeast Atlantic off northern Europe (Jansen and Gislason, 2013). Northwest Atlantic mackerel fisheries have fluctuated greatly, with US landings ranging from over 400,000 metrics tons (mt) per year in the 1970's to just 5000 mt in 2015, and intermediate but fluctuating landings in the interim (Figure 1, data from Wiedenmann, 2015, NOAA Office of Science And Technology, n.d.). The Northeast Atlantic fishery has also shown high variability, from a near collapse of the North Sea component in the 1970's following heavy exploitation (Jansen, 2014) to very high landings ( $> 800,000 \text{ mt yr}^{-1}$ ) and abundance in recent years (ICES, 2013). Thus, while the Northeast Atlantic population supports now one of the largest fisheries in the world (rank=9<sup>th</sup> in 2014 (Food and Agriculture Organization, 2016)), the Northwest Atlantic population seems to have collapsed with landings at  $<2\%$  of their historical peak (Figure 1).

No clear cause of the apparent Northwest Atlantic mackerel population collapse is known, but mackerel and other small pelagics such as sardines, anchovy, and herring are characterized by variability in abundance and recruitment as a result of environmental changes (Baumgartner *et al.*, 1992; Schwartzlose *et al.*, 1999; Fréon *et al.*, 2005). Large amplitude cycles in abundance occurred historically in Pacific sardines, northern anchovy and Pacific hake well before they were fished at an industrial scale (Baumgartner *et al.*,

1992; McClatchie *et al.*, 2017) suggesting that climactic and oceanographic forcing influence their dynamics. The high densities of these schooling fish in recent times have supported some of the world's largest fisheries, representing ~50% of the global commercial catch (Fréon *et al.*, 2005), yet they also play a vital role as forage for larger fish, marine mammals and seabirds (Moustahfid *et al.*, 2009). In some ecosystems, these middle trophic level forage fish can exert strong influence on the populations of both their predators and prey. In such “wasp-waisted” (Cury *et al.*, 2000) systems, the dynamics of the diverse plankton and piscivore communities are dominated by the boom and bust cycle of a single or very few mid level forage fish (Bakun, 2006) as opposed to top-down or bottom-up control food chains, which have been attributed to other aquatic ecosystems (Menge, 2000; Williams *et al.*, 2002; Hunt and McKinnell, 2006).

Changes in abundance for schooling pelagic fish often occur simultaneously with shifts in spatial distributions, where a stock of pelagic fish will either rapidly expand or contract their range in synchrony with their changing population size (Petitgas, 1998). For the Northeast Atlantic mackerel population, increasing abundance during the recent decade has been accompanied by a range expansion from Northeast Atlantic waters bordering Norway, UK, and France into distant waters off Iceland, Greenland, and Northern Scandinavia (Berge *et al.*, 2015; Nøttestad *et al.*, 2016). Scientists hypothesize that this population is “breaking-out” to utilize favorable thermal habitat arising from ocean warming (Jansen, 2014; Berge *et al.*, 2015), or migrating from high density areas where food limitation may occur (Nøttestad *et al.*, 2016; Pacariz *et al.*, 2016). As a result of this expansion, many new parties have entered the industrial mackerel fishery, complicating international management and allocation of the resource (Jensen *et al.*,

2015). The massive irruption into previously unoccupied habitats and subsequent “collapse” of Japanese sardine (*Sardinops melanostictus* (Jenyns)) during the 1970’s and 80’s is a highly referenced example of the irruptive dynamics of pelagic schooling species (Hiramoto, 1991; Bakun, 2001; Secor, 2015). MacCall (1990) conceives density-dependent range dynamics in his “basin model.” When a species reaches the carrying capacity of its local habitat, segments of the population spill over into less suitable habitats causing range expansion. As potentially seen in the Northeast Atlantic mackerel, this search for new habitat can lead to abrupt changes in distribution and nonlinear dynamics in abundance (Nøttestad *et al.*, 2016).

Whether the current depressed state of the Northwest Atlantic mackerel population is due to climate forcing, food web interactions, or fishing is unknown. Working hypotheses of the apparent collapse include an increase in natural mortality owing to predation (Moustahfid *et al.*, 2009), unsustainable rates of fishing, historical changes in the fleet affecting catch rates, or a spatial shift in the population away from the currently monitored area. As an important component of diet for larger fish, marine mammals and seabirds (Tyrrell *et al.*, 2008), Atlantic mackerel may have experienced enhanced predation during recent decades based on the regional abundance of predatory fish and marine mammals (Moustahfid *et al.*, 2009; Waring *et al.*, 2015). Additionally, unsustainable landings averaging 350,000 metric tons per year during the first half of the 1970’s likely caused depletion of the stock in subsequent years (NEFSC, 1996), and the effects of this historical overfishing may have carried over to recent population trends (Hsieh *et al.*, 2006; Secor *et al.*, 2015). During the 1970’s and 1980’s, heavily industrialized foreign vessels dominated the US fishery, but landings fell sharply after the

establishment of the Exclusive Economic Zone and the expulsion of these fleets (Fairfield *et al.*, 1993). The time series of landings may be disconnected from mackerel population abundance; instead reflecting changes in effort and fleet capacity.

A shift in the range or distribution of the Northwest Atlantic mackerel population could also appear as a decline in abundance, especially if a significant portion of the population no longer occupies the assessed or fished area (Figure 2, adapted from Link *et al.*, 2011). If undetected, this spatial shift could lend false support to more traditional explanations of collapse, even though the true abundance remains unchanged. Variation in migration and distribution is not unprecedented for Atlantic mackerel (Astthorsson *et al.*, 2012; Jansen, 2014), as their migration is somewhat sensitive to temperature both in terms of seasonal timing (Sette, 1950; D'Amours and Castonguay, 1992) and geographic extent (Overholtz *et al.*, 2011; Radlinski *et al.*, 2013; Jansen *et al.*, 2016). From 1968 to 2008, the geographic center of Northwest Atlantic mackerel catch in the Northeast Fisheries Science Center (NEFSC) spring trawl survey shifted almost 250 km to the northeast, and moved inshore to shallower continental shelf habitats (Overholtz *et al.*, 2011). In the face of both natural and anthropogenic climate change, distributional shifts have been observed in a variety of species in the Northwest Atlantic and these spatial changes are expected to continue (Nye *et al.*, 2009).

Northwest Atlantic mackerel occupy continental shelf waters ranging from Newfoundland to North Carolina. During spring and summer the fish move inshore to shallower waters, and migrate northward along the coast to spawning and feeding grounds as temperatures warm (Sette, 1950; Fisheries and Oceans Canada, 2014), with major spawning grounds occurring in both Canada and the US. From March to April,

fish spawn along the US coast from Virginia to Rhode Island, and later in the year, around June and July, spawning occurs centered around the southern Gulf of St. Lawrence. As temperatures begin to fall, the fish swim south along the coast and eventually return to deeper waters on the continental shelf (Moore *et al.*, 1975; Fisheries and Oceans Canada, 2014). Mackerel begin maturing around 2 years of age and are almost all mature by age-3 (O'Brien *et al.*, 1993; Fisheries and Oceans Canada, 2014).

Marine and coastal fish populations contain complex population structures, which influence their seasonal spatial distributions. The spatial structure of Atlantic mackerel has been traditionally broken into contingents, or sub-groups with different migratory behaviors (Sette, 1950). Note here that the term contingent does not entail or exclude the possibility that these migratory behaviors are associated with self-contained populations. Rather it is a practical term that recognizes non-homogeneity in the manner with which individuals move within populations or metapopulations (Secor, 1999). In the Northwest Atlantic, it is believed that there are northern and southern contingents of mackerel, which exhibit distinct migration patterns but whose distributions overlap seasonally. Further, it is hypothesized that straying occurs between US and Canada spawners at a sufficient rate to curtail the establishment of discrete populations (Sette, 1950; Lambrey de Souza *et al.*, 2006).

Varying abundance and migrations between contingents or sub-populations can have important impacts on the overall dynamics of a population. Changes in a segment of the population can appear as shifts in abundance, or total collapse of the population in one region, even if true abundance remains the same (Figure 2; Link *et al.* 2011). Such misconceptions likely are frequent when the entire extent of a population's range is

incompletely fished or assessed for abundance (Reiss *et al.*, 2009; Link *et al.*, 2011; Secor, 2014). The application of simulations to understand the consequences of incorrect assumptions regarding population structure, stands as a powerful tool when the data is available for a species (Link *et al.*, 2011; Secor, 2015). Yet such methods require improved information on likely population structure under conditions of varied abundance.

Uncertainty surrounding the population structure of Atlantic mackerel has contributed to problems with assessment and management for the species (Deroba *et al.*, 2010; Overholtz *et al.*, 2011; Wiedenmann, 2015). Broad spawning areas and migrations that extend thousands of kilometers complicate definitions of the fished stocks that traverse the border between the US and Canada. The two nations treat the stocks differently, with the US assessing a single unit stock incorporating both US and Canadian landings, and Canada assessing the northern contingent separately (TRAC (Transboundary Resource Assessment Committee), 2010). In 2009, a binational effort between the US and Canada, the TRAC, was tasked with resolving conflicting trends in mackerel data sources, including a recent increase in overall juvenile abundance as indexed by the NMFS (National Marine Fisheries Service) spring trawl survey, which contrasted with lower landings and the relative absence of older age classes of fish in surveys and landings. The assessment team failed to reach consensus on the current status of Northwest Atlantic mackerel, and in the US, the stock is managed as a data-poor species requiring an *ad hoc* management reference point based on historical catch levels (Mid-Atlantic Fisheries Management Council (MAFMC), 2015). More recently, Canadian government scientists have noted a large collapse in egg production by the

northern contingent and have recommended large reductions in quota (Fisheries and Oceans Canada, 2014). That the two nations treat the stocks differently in assessment and management could be problematic should there be no basis for population structure, or if the two contingents substantially mix, because actions by one nation could directly impact the entire resource. Under these scenarios, Northwest Atlantic mackerel should be jointly assessed and managed by these two nations. For effective management, it is therefore vital to understand how the Northwest Atlantic mackerel population is spatially structured and how much mixing occurs. Further, the historically broad spawning area of the southern contingent could contain multiple distinct natal habitats, meaning a more complex population structure than previously believed. Within this thesis project, I used the chemistry of archived otoliths to classify natal habitat of mackerel, and thereby infer the movement and mixing of the two potential contingents.

Here, I develop otolith stable isotopes as a marker of natality, relevant to testing hypotheses on contingent structure and changes in spatial distributions of Northwest Atlantic mackerel. The current two contingent hypothesis for Northwest Atlantic mackerel is based on 60 year-old work which sought to understand the fluctuating catch at the time (Sette, 1950). By tracking the length frequency of US commercial catch through multiple years, Sette was able to detect seasonal changes in the size composition. In late spring, lengths showed a bimodal frequency distribution, but this bimodal pattern would disappear temporarily, only to reappear in late fall. Because this pattern held throughout multiple years, Sette interpreted this as evidence of two distinct groups, which co-occurred during spring and fall, but separated during the summer when the northern contingent was in Canadian waters. More modern methods including genetic analysis,



otolith morphometrics and tagging have been used to track migration and natal origin, but none have demonstrated strong differentiation between the northern and southern contingents (Moore *et al.*, 1975; Castonguay *et al.*, 1991; Lambrey de Souza *et al.*, 2006). These methods failed to find support for separation of the contingents likely because of mixing between the groups during periods of significant spatial overlap, which could prevent genetic differentiation and morphometric differences (Moore *et al.*, 1975; Castonguay *et al.*, 1991; Lambrey de Souza *et al.*, 2006). Otolith stable isotopes have been demonstrated as a useful means to discriminate spatial origins of migratory species in the North Atlantic (Rooker *et al.*, 2008; Secor *et al.*, 2013) and other systems (Gao *et al.*, 2001; Elsdon *et al.*, 2008; Newman *et al.*, 2010). In carbonates, oxygen stable isotopes vary along a latitudinal gradient due to differences in temperature and meteoric conditions (evaporation/precipitation rates). Higher  $\delta^{18}\text{O}_{\text{Seawater}}$  values are observed in the evaporative lower latitudes and lower  $\delta^{18}\text{O}_{\text{Seawater}}$  values seen at more polar latitudes (Fairbanks, 1982; LeGrande and Schmidt, 2006; McMahon *et al.*, 2013). Carbon isotopic composition in otoliths is a second commonly used tracer, which has been associated with diet, metabolism and environment (Edmonds and Fletcher, 1997; Trueman *et al.*, 2012; McMahon *et al.*, 2013).

Within the range of Northwest Atlantic mackerel, large scale oceanographic features amplify the latitudinal trend in oxygen stable isotopes (McMahon *et al.*, 2013). The Gulf Stream advects warm, relatively high  $\delta^{18}\text{O}$  waters into US Mid-Atlantic and Southern New England waters, while Canadian waters and the Gulf of Maine receive cool, fresh, and relatively low  $\delta^{18}\text{O}$  waters from the north through the Labrador Current and Gulf of St. Lawrence freshwater flow (Epstein and Mayeda, 1953; Fairbanks, 1982;

Chapman and Beardsley, 1989). These currents produce gradients in seawater  $\delta^{18}\text{O}$  values. Seawater  $\delta^{18}\text{O}$  is incorporated into fish otoliths (earstones) in near equilibrium throughout their lifetime, with larger fractionations (departures from source water) occurring at lower temperatures (Nelson *et al.*, 1989; Edmonds and Fletchere, 1997; Thorrold *et al.*, 1997; Campana and Thorrold, 2001). Isotopes of the same element have slight thermodynamic differences from one another. Changes in the molecular vibration frequencies and crystalline lattice allow heavier isotopes to be more readily accommodated into otolith carbonate crystals at cooler temperatures (Urey, 1947; O'Neil *et al.*, 1969; Kalish, 1991). Latitudinal patterns in seawater  $\delta^{18}\text{O}$  are in opposition to those for temperature. The seawater  $\delta^{18}\text{O}$  composition of more polar waters is relatively low, but the colder temperatures of this water would lead to a greater positive  $\delta^{18}\text{O}$  fractionation when incorporated into the otolith. Trueman et al. (2012) assessed the relative influence of these factors, by creating global and North Atlantic maps of modeled otolith  $\delta^{18}\text{O}$  values. In the range of Northwest Atlantic mackerel, the natal habitat for the northern contingent was predicted to have higher otolith  $\delta^{18}\text{O}$ , suggesting that fractionation due to differences in temperature outweighs the geographic gradients in seawater  $\delta^{18}\text{O}$ . The latitude driven patterns in  $\delta^{18}\text{O}$  are consistent over a mackerel's life, but significant year-to-year variation may exist in the temperature and relative influence of different water masses. Therefore, when comparing the stable isotope composition of otoliths, it will be important that samples originate from the same year-class, defined as the cohort of fish born in a given year. Many of the processes that influence otolith stable isotope composition including temperature, meteoric conditions and oceanographic

conditions are variable from year to year. Comparing within a given year-class allows us to eliminate this temporal variation and focus on the spatial differences in composition.

### Goals and Objectives

This project seeks to use otolith stable isotopes to track the origin of Northwest Atlantic mackerel to investigate contingent structure and changes in spatial distribution along a latitudinal, temperature and oceanographic gradient. Goals include:

1) Assess the influence of year-class and region (or sub-region) of origin on the  $\delta^{18}\text{O}$  and  $\delta^{13}\text{C}$  composition of natal otolith material in Atlantic mackerel. Isotopic differences in fish from these areas will establish the potential for distinct natal regions and associated contingent structure. I predict that year-classes will significantly influence  $\delta^{18}\text{O}$  otolith composition at both the regional and sub-regional scale, reflecting interannual effects of climate and oceanography. Objectives within this goal include:

1.1. Test for sub-regional differences between the Georges Bank (GB) and New York Bight (NYB) to understand natal origins within the presumed southern contingent.

1.2. Test for regional differences between the US and Canada for three year-classes.

1.3. Test for ocean basin scale differences between Northwest Atlantic (US and Canadian samples) and Northeast Atlantic (Norway and Iceland).

2) Using US and Canadian baselines and multiple classification procedures, assess site fidelity and repeated migration to natal regions in older Atlantic mackerel (age-2+).

2.1) Compare the stable isotope composition of US and Canadian Atlantic mackerel otoliths from the same year-class and region, but captured at older ages in subsequent years. This will test whether age-2 and older fish return to natal habitats or adopt another migratory route, and offer evidence of repeated migration across ages.

2.2) Classify “unknown” adult US Atlantic mackerel (age-3 and 4) samples to regions of likely origin based on year-class and region specific baselines using multiple classification methods. Based on a similar published comparison (Mercier *et al.*, 2015), I expect the random forest method to exhibit the lower classification error than quadratic discriminant function analysis and logistic classification procedures..

## Methods

### *Samples*

Archived Atlantic mackerel otolith samples were identified to address key objectives including: (1) Compare regional and sub-regional differences in Atlantic mackerel otolith composition within the North Atlantic basin based on natal habitat and year-class, primarily focused on the Northwest Atlantic; and (2) extend analysis of Atlantic mackerel natal otolith composition to older ages, to look for evidence of repeated migration to natal habitats using either direct comparison of age-1 and 2 fish within a year-class or year-class specific classification. Otoliths were requested and received from archived sample collections from the Fisheries Biology Program at the NEFSC in Woods Hole, Massachusetts, United States; Fisheries and Oceans, Mont Joli, Quebec, Canada (Maurice Lamontagne Institute); Institute of Marine Research in Norway; and the Marine Research Institute in Iceland.

US Northwest Atlantic otolith samples (Figure 3) came from the NEFSC spring (age $\geq$ 1) and fall (age-0) bottom trawl surveys. In both seasons, the US Atlantic coast is surveyed, from Cape Hatteras to the Gulf of Maine, using a stratified random sampling design based on geographic region and depth. All samples were collected using a #36 Yankee bottom trawl with 3/8" mesh cod end and a sweep of 24-25 meters towed at approximately 3.5 knots for 30 minute hauls (NEFSC, 2002; Brown *et al.*, 2008). Captured Atlantic mackerel were enumerated, weighed, measured, and otoliths were collected for age analysis by NEFSC staff. Sagittal otoliths were archived in 50 well plastic trays within Permout™ mounting media (Fisher Scientific) to aid with visual interpretation of ageing structures and for storage.

Canadian Northwest Atlantic mackerel otoliths (Figure 3) came from fishery-dependent sampling of mackerel principally captured in the Gulf of St. Lawrence and on the Scotian Shelf. Otoliths were extracted and mounted in 50 well plastic plates using dichloroethane or Cytoseal <sup>TM</sup> 60 cps (Richard-Allan Scientific) diluted in 80% toluene. Otoliths were then aged through visual interpretations of their annuli by DFO staff and archived. Prior to milling and mass spectrometric analysis, these otoliths were removed from their well using a scalpel and then shipped in small paper envelopes.

Atlantic mackerel from Iceland (Figure 4) were sampled from commercial landings in 2015, with otolith ages ranging from 3 to 11. Icelandic samples were extracted from the fish, cleaned, aged and stored whole. Additional northeast Atlantic mackerel representing fish between 3 and 12 years of age were captured in Norwegian cruises. Half of these samples (n=14) were captured on spring spawning grounds west of Ireland, and the other 15 were captured on autumn feeding grounds in the Norwegian Sea (Figure 4). Spawning ground samples ranged from age-3 to 9, while feeding ground samples were between age 4 and 8. These otoliths were embedded in 25 well plastic trays, using Entellan® (EMD Millipore Corp.) resin.

Age-1 fish were used to differentiate natal habitats because this age is commonly sampled across targeted regions and years. Younger fish (age-0) by contrast are infrequently sampled in surveys and fisheries. Two assumptions were made in using these samples. First, the chemical composition of the age-1 Atlantic mackerel otolith reflects the natal region of that fish. For an age-0 Atlantic mackerel, the initial otolith growth zone from hatching until early autumn is visually opaque under reflected light. A visual ring (annulus) then forms during winter and spring as a translucent zone and marks

the end of the first growth season, operationally defined as the juvenile's natal period (Dery, 1998) (Figure 5). In late fall, age-0 fish migrate offshore (Sette, 1950), meaning the material within the first annulus (translucent ring) should reflect inshore juvenile natal habitat. A second assumption is that once formed, otolith material is not chemically altered, which is well supported in the literature (Campana, 1999). A limited sample of age-0 fish was available from the NEFSC archive (1996, 2000, 2003) to evaluate sub-regional differences. No such samples occurred to support other regional comparisons.

Otoliths from age-1 and age-2 US and Canadian fish (Figure 3) were obtained for the years 1999, 2000 and 2001. These years represent a period of relatively strong juvenile Atlantic mackerel abundance and wide regional availability, allowing for spatial stratification across the GB, NYB, and MAB sub-regions. This sampling design allows a natal (year-class) compositional signal to be tracked through a number of ages. For instance, the 1998 year-class (natal signal) is present in age-1 fish in 1999 and then tracked into age-2 fish of the same year-class in 2000. Adult mackerel (age-3 or older) were also obtained from the years 2001 and 2003, at ages that corresponded to the targeted year-classes (age-3 from 2001, age-3 and 4 from 2003, Table 1).

For US juvenile fish, 20-30 otoliths were sought from each combination of age, year and sub-region. Target samples sizes were met for all but one combination of year- and age-class within NYB and GB sub-regions (Table 2). Mid Atlantic Bight samples were relatively scarce for the years requested, and this small sample size restricted the ability to compare all sub-regions. For strata where more than 30 samples were obtained, 30 otoliths were randomly selected. Subsamples of 20 to 30 otoliths were also sought for

each year and age combination from Canadian fish, but due to time and analytical constraints only 10 to 15 otoliths were analyzed for some strata.

### *Otolith Preparation*

Collection of material from the core of otoliths (Figure 5) was carried out using precision micro-milling equipment consisting of a 500  $\mu\text{m}$  bit mill and an automated stage connected to an imaging system (New Wave Research Micro-Mill; ESI, Inc). Otoliths obtained from the NEFSC, captured in the US, had been previously embedded in Permout™ media in 50 well black plastic trays. Prior to milling, the trays of otoliths were cut into smaller sections to facilitate mounting on the micromill stage and micrographs of each otolith were obtained for measurement and archiving purposes. The Entellan® media around Norwegian otoliths liquefied during milling due to the heat, so it needed to be removed. Trays were first placed in a 60°C drying oven to slightly soften the resin. Otoliths were then cut away from the majority of the resin using a scalpel and any remaining Entellan® was dissolved using 99% acetone. Whole (unembedded) otoliths from Iceland, Canada and Norway were mounted on glass microscope slides using Crystalbond 509™ (SPI Supplies) thermoplastic adhesive. Because of the way otoliths were shipped or extracted from their archival trays, some were broken into two or more pieces. Mounting in Crystalbond 509™ allowed these otoliths to be pieced back together and milled normally. Stable isotope analysis of foreign materials associated with the otoliths sampled, including Permout™, Crystalbond 509™, Entellan®, acetone, and mixtures of these materials with acetone indicated that none of these potential contaminants produced measureable levels of  $\delta^{13}\text{C}$  or  $\delta^{18}\text{O}$  when reacted with phosphoric acid, which is the analytical method used for analyzing the otoliths. While this shows



these mounting media and other chemicals do not affect the stable isotope composition of samples, care was still taken to avoid including these extraneous materials in the otolith carbonate powder that was analyzed, particularly Permout™, which was the most likely material to be introduced. When necessary, this included carefully scraping away excess media prior to milling to expose the otolith.

For each fish, the otolith removed from the right side of the fish's head was selected for milling to avoid any possible asymmetry in the composition, that has been observed in flatfishes (Kajajian *et al.*, 2014). We tested for this asymmetry in a set of 24 paired left and right otoliths captured in the US by milling both and comparing composition in a paired t-test. For these samples, there was no significant difference between paired otoliths from the same fish for either  $\delta^{18}\text{O}$  ( $0.04 \pm 0.10\text{‰}$ ,  $p = 0.63$ ) (Figure 6A) or  $\delta^{13}\text{C}$  ( $0.15 \pm 0.13\text{‰}$ ,  $p = 0.18$ ) (Figure 6B). The central core of the otolith represents the first year of life and is identified under reflected light as the otolith region occurring within the first translucent annulus (Figure 5). The milling path was configured to lie entirely within the opaque zone. A series of 30  $\mu\text{m}$  deep milling passes were conducted using a 500- $\mu\text{m}$  diameter carbide dental drill bit (Brassler USA). Milled powder was collected using both a microspatula and by tapping the underside of the mounted sample to dislodge the powder onto weighing paper, which was carefully folded and stored in plastic vials. The drillbit, microspatula and other tools used to mill and collect the otolith powder were cleaned with 100% ethanol to prevent cross contamination between samples. Because multiple samples are on the same slide or tray, milled samples were lightly doused with ethanol and briefly sprayed with compressed air

to remove any residual powder prior to the next milling. The entire milling procedure required approximately 20 minutes per specimen.

### *Stable Isotope Analysis*

The values of carbon and oxygen stable isotopes are reported in delta ( $\delta$ ) notation, relative to the Vienna-Pee Dee Belemnite standard (V-PDB). In this notation, the ratio of each stable isotope to its base configuration,  $^{13}\text{C}$  to  $^{12}\text{C}$ , or  $^{18}\text{O}$  to  $^{16}\text{O}$ , is compared to this ratio in the V-PDB international standard, and the per mil (‰) difference is quantified by the following equation:

$$\text{Equation 1: } \delta_{\text{sample}} = \left( \frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) \times 1000.$$

$R_{\text{sample}}$  refers to the ratio of heavy isotopes ( $\text{O}^{18}$  or  $\text{C}^{13}$ ) to light isotopes ( $\text{O}^{16}$  or  $\text{C}^{12}$ ) in our sample. This value is divided by  $R_{\text{standard}}$ , or the ratio of heavy to light isotopes in a globally accepted standard. For stable isotope analysis, approximately 200  $\mu\text{g}$  of otolith powder was weighed and placed into glass Exetainer® (Labco Ltd.) vials. The vials containing otolith powder were heated in a drying oven at 60°C for 10 minutes to evacuate any moisture and then sealed. Sealed vials were flushed (>atmospheric pressure) with ultrapure helium for 10 minutes to remove atmospheric gases. After flushing, 3 drops of phosphoric acid, which had been heated and evacuated to remove all traces of water, were injected into each vial without introducing new atmospheric gases. Vials were placed in a heating block at approximately 50°C, and left to react for 3 to 6 hours, by which time all the carbonate material had been converted to  $\text{CO}_2$  gas. Internal carbonate laboratory standards of known isotopic composition were treated and analyzed

in series with the samples to assess the accuracy and precision of the measurements. Additionally, blank vials with no material were also used to assess whether there were significant background levels of carbon dioxide that were contributing to the gas analyzed. Blanks were flushed with ultrapure helium like sample vials, but were not acidified. Standards and blanks were placed at the start and end of each sample batch, and interspersed throughout. The stable isotope composition of the extracted CO<sub>2</sub> was measured following introduction into a ThermoFisher Delta Plus continuous flow stable isotope ratio mass spectrometer (IRMS) using a Gasbench® peripheral for reacting and purifying the carbon dioxide at the Chesapeake Biological Laboratory. Repeated measure of the laboratory carbonate standards show a standard deviation for both  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  isotope values of approximately 0.1‰. Due to limited material availability, the isotopic composition of each otolith was generally analyzed only once, but this analysis consisted of 6-10 individual isotopic measurements. The standard deviation of those 6 to 10 measurements generally ranged from 0.05 to 0.10‰ for both isotopes and samples with standard deviations higher than 0.10‰ were deemed unreliable and removed from analysis. Throughout the project I measured a new in house standard composed of homogenized Hudson River, NY, white perch *Morone americana* (J. F. Gremlin) otoliths. Repeated measures of this otolith standard resulted in a SD of 0.16‰ for  $\delta^{18}\text{O}$  and 0.13‰ for  $\delta^{13}\text{C}$ .

### *Statistical Methods*

Differences in the stable isotope composition of juvenile and adult otoliths based on their region or sub-region of origin (Goal 1) were assessed using analysis of variance (ANOVA) and multivariate analysis of variance (MANOVA). A two-way MANOVA,

with sub-regional and regional comparisons alongside sample year was be used to assess differences in age-1 and age-0 Atlantic mackerel across regions or US sub-regions and years (Objectives 1.1, 1.2). MANOVA's were followed by subsequent two-way ANOVA's for each isotope where a difference was present. The general form for these equations is:

$$\text{Equation 2: } \delta^{13}\text{C or } \delta^{18}\text{O} = \mu + \text{Year}_{(1999, 2000, 2001)} + \\ \text{Region}_{(\text{US, Can})}(\text{or Sub-region}) + \text{error}.$$

Regional comparisons across the US, Canada, Iceland and Norway (Objective 1.3) was conducted using separate one-way ANOVA's for each isotope

$$\text{Equation 3: } \delta^{13}\text{C or } \delta^{18}\text{O} = \mu + \text{Region}_{(\text{US, Can, Ice, Nor})} + \text{error}.$$

Comparison of age-1 and 2 Atlantic mackerel from the same year-class (Objective 2.1) was assessed using a separate nested ANOVA for each year-class and isotope, with the general equation being:

$$\text{Equation 4: } \delta^{18}\text{O or } \delta^{13}\text{C} = \mu + \text{Region}_{(\text{US, Canada})} + \\ \text{Age}_{\text{Nested in region}(\text{Age-1, Age-2})} + \text{error}.$$

This comparison evaluated whether multiple age-classes returned to the same natal region. For this portion of the study, the core stable isotope composition of age-2 through age-4 fish was compared to the composition of age-1 fish, with all samples originating from the same year-class.

Data were assessed for normality using the Shapiro Wilks test and homogeneity of variance using Levene's Test. When data were found to violate either of these assumptions, they were cubic-root transformed, and data which required transformation are identified. Equal covariance in the MANOVA tests was tested using the Box's M-test (Box, 1949), which generally uses an alpha of 0.001 because of the test's high

sensitivity (Tabachnick and Fidell, 2001). 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*

In order to classify “unknown-origin” adult samples collected in US waters (Objective 2.2), three separate statistical methods were tested, including quadratic discriminate analysis (QDA), logistic regression, and random forest discrimination. All three of these methods were applied twice using the year-class and region specific baseline isotope values for age-1 Atlantic mackerel to create the classification relationships. In the first application  $\delta^{18}\text{O}$  values were used as the only predictor because variation in oxygen isotopic composition was expected to be the main driver of regional differences, and second application used both  $\delta^{18}\text{O}$  and  $\delta^{13}\text{C}$  values. Classifications were made on year-class specific basis.

QDA and the related linear discriminate analysis (LDA) focus on maximizing the separability of data within categories by defining new axes that are combinations of the original explanatory variables. LDA assumes that the data are normally distributed and homoscedastic, but QDA relaxes the assumption of identical variances. 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 then used to define the QDA and classify both the adult data relevant to that year-class and the testing set. Because the region of origin (US or Canada) is known for a sample in the testing set, this analysis provides an estimate of the accuracy of classifications.

Logistic regression fits a logistic curve to baseline data, defining the probability of falling into either the US and Canadian group with a threshold probability of 0.5 defining classification.

The random forest discrimination was performed using the randomForest package in R (Liaw and Wiener, 2002). Here, a collection of 500 classification trees is created. Each tree is constructed by randomly sampling the regional baseline data sets with replacement, also known as bootstrapping. This creates a simple, in this case binary, classification tree, and the unknown adult Atlantic mackerel samples are classified using each tree. The final classification for a sample comes from the combined forest, where the individual trees are polled for their assignment of a given sample. The most frequent assignment within the forest determines the final classification. For the random forest procedure, baseline data were weighted with a 2:1 ratio (Canadian vs US) to account for unequal numeric representation of these groups in the data. Error is estimated using the “out-of-bag” (OOB) samples in the random forest procedure. For this, baseline samples that were left out of the bootstrapped sample used to construct an individual tree were classified using that tree. This classification was compared to the known origin of these samples, giving an estimate of the rate of misclassification. Because random forest classification relies on a random process, procedures were repeated 5 times to evaluate the repeatability of classification results and the OOB error rate.

## Results

### *Isotopic differences across natal habitats (Objectives 1.1-1.3)*

Across years 1999-2001, otolith cubic-root transformed  $\delta^{18}\text{O}$  and untransformed  $\delta^{13}\text{C}$  values for age-1 mackerel broadly overlapped between the GB and NYB sub-regions (MANOVA,  $p = 0.004$ ; Figure 7, Table 3 and 4). Year of collection, but not sub-region significantly influenced  $\delta^{18}\text{O}$  values (two-way ANOVA,  $p_{\text{Sub-region}} = 0.80$ ,  $p_{\text{Year}} < 0.001$ ) (Figure 8A). For this analysis,  $\delta^{18}\text{O}$  values needed be cubic root transformed. A significant difference was found in the variance of untransformed  $\delta^{18}\text{O}$  between the two sub-regions (F-test,  $p=0.015$ ), with higher variance observed for the GB sub-region. No significant differences were found for otolith  $\delta^{13}\text{C}$  values among years or sub-region (Two-way ANOVA,  $p_{\text{Sub-region}} = 0.62$ ,  $p_{\text{Year}} = 0.79$ ) (Figure 8B).

Sample availability allowed for full sub-regional comparisons of Age-0 otolith isotope composition across GB, NYB and MAB for 2003 samples only. This analysis showed no significant difference between sub-regions of for either  $\delta^{18}\text{O}$  (ANOVA,  $p = 0.73$ ) (Figure 9A, Table 5) or  $\delta^{13}\text{C}$  (ANOVA,  $p = 0.11$ ) (Figure 9B, Table 6). There were sufficient samples available to compare the isotopic composition of Atlantic mackerel from the 1996 and 2003 year-classes in GB and NYB sub-regions. This analysis showed no significant difference in  $\delta^{18}\text{O}$  between years but there was significant difference between the two sub-regions (two- way ANOVA,  $p_{\text{Year}} = 0.43$ ,  $p_{\text{Sub-region}} = 0.03$ ) (Figure 10A). Analysis of  $\delta^{13}\text{C}$  was similar, with no significant difference across years, but difference between sub-regions (two- way ANOVA,  $p_{\text{Year}} = 0.31$ ,  $p_{\text{Sub-region}} = 0.03$ ) (Figure 10B).

Significant regional difference (US vs. Canada; Objective 1.2) were detected in otolith isotopic composition across sample years (multivariate response of  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$ ) (Two-way MANOVA,  $p_{\text{Year}} < 0.001$ ,  $p_{\text{Region}} < 0.001$ ; Figure 11, Table 3 and 4). Subsequent testing showed significantly lower  $\delta^{18}\text{O}$  values for US as compared to Canada origin samples (ANOVA,  $p < 0.001$ ), and significantly higher  $\delta^{13}\text{C}$  in the US compared to Canada (ANOVA,  $p = 0.005$ ). Canadian origin samples showed a similar temporal pattern to that previously described for age-1 US samples (ANOVA,  $p < 0.001$ ) (Figure 12A). Tukey tests showed that the year-specific Canadian samples had consistently higher  $\delta^{18}\text{O}$  values than the corresponding US samples from the same years. No significant difference was found between the 2000 and 2001 US origin samples (Tukey HSD,  $p = 0.06$ ). When just US data were examined previously (Figure 8A), 2000 and 2001 had significantly different  $\delta^{18}\text{O}$  values. The different outcomes are likely a result of more stringent p-value correction with the higher number of comparisons in the two-country test. There were no year specific differences in  $\delta^{13}\text{C}$  values (Tukey HSD) (Figure 12B).

Otolith isotopic composition differed significantly between ocean basin regions (Objective 1.3; Figure 13, Table 3 and 4). US and Canada samples within the Northwest Atlantic showed some overlap but in combination significantly differed in  $\delta^{18}\text{O}$  values to Northeast Atlantic samples. Northeast Atlantic samples showed strong overlap between Norway and Iceland origin otoliths, but showed very distinct  $\delta^{18}\text{O}$  values in comparison to Northwest Atlantic samples. The covariance assumption was not met for the use of a MANOVA, so each isotope was assessed using an individual ANOVA. There were highly significant differences in  $\delta^{18}\text{O}$  values among countries of origin ( $p < 0.001$ ; Figure



14A). Post hoc analysis revealed significantly higher  $\delta^{18}\text{O}$  values in Iceland and Norway from the Northeast Atlantic and significant differences within the Northwest, with Canadian Atlantic mackerel having higher  $\delta^{18}\text{O}$  than their US counterparts. Analysis of  $\delta^{13}\text{C}$  values revealed a significant regional difference in  $\delta^{13}\text{C}$  values (ANOVA  $p = 0.001$ ) with post-hoc testing showing significantly higher  $\delta^{13}\text{C}$  values in US origin samples compared to those from Icelandic waters ( $p = 0.001$ ); all other groups showed similar  $\delta^{13}\text{C}$  values (Figure 14B). Norwegian and Icelandic origin samples showed strong overlap in stable isotope values (MANOVA,  $p = 0.09$ ) (Figure 13, 14A-B). Within the Norwegian samples, there were no significant differences between the samples captured in feeding and spawning sub-regions for either  $\delta^{18}\text{O}$  or  $\delta^{13}\text{C}$  values (MANOVA,  $p = 0.69$ ; Figure 15). There was, however, a significant difference in the  $\delta^{18}\text{O}$  value variance between sub-regions, with much greater variance observed for the spawning samples (F-test,  $p = 0.02$ ).

#### *Evidence for repeat migration (Objective 2.1)*

For 1998 and 1999 year-classes,  $\delta^{18}\text{O}$  in age-1 and age-2 fish indicated some repeat migrations to natal regions. Both age-1 and age-2 US samples had lower levels of  $\delta^{18}\text{O}$  in otolith core regions than Canadian samples of the same ages. In 1998 year-class comparisons of  $\delta^{18}\text{O}$  values, significant differences were observed between countries and between ages, nested within each country (Nested Anova,  $p_{\text{Country}} < 0.001$ ,  $p_{\text{Country:Age}} < 0.001$ ; Figure 16 A-B, Table 3). Posthoc analysis showed that ages differed in  $\delta^{18}\text{O}$  value composition within the US samples (Tukey HSD,  $p_{\text{US.2} - \text{US.1}} < 0.001$ ) and the difference was marginally significant for Canadian samples (Tukey HSD,  $p_{\text{Can.2} - \text{Can.1}} = 0.05$ ). For the 1999 year-class, a significant difference in cube-root transformed  $\delta^{18}\text{O}$  values was

found for both country of origin and age nested within country (Nested ANOVA,  $p_{\text{Country}} < 0.001$ ,  $p_{\text{Country:Age}} = 0.03$ ; Figure 17 A-B, Table 3). Subsequent posthoc analysis showed that  $\delta^{18}\text{O}$  values of US age-2 samples were significantly higher than their age-1 counterparts (Tukey HSD,  $p_{\text{US.2-US.1}} = 0.04$ ), which is similar to the 1998 year-class results, but Canadian origin samples were not significantly different by age (Tukey HSD,  $p_{\text{Can.2-Can.1}} = 0.95$ ; Figure 17 A). In both 1998 and 1999 year-classes, US samples had lower  $\delta^{18}\text{O}$  values on average than Canadian ones for both age-1 (identical to findings related to Objective 1.2) and age-2 fish.

#### *Classification of US adult Atlantic mackerel (Objective 2.2)*

For the test classification of age-3 and 4 samples, dating back to 1998-2000 year-classes, the three classification methods tested were in broad agreement (Table 7; Figure 18A-C). All three approaches assigned the majority (53-100%) of US captured adult samples to the Canadian baseline (northern contingent). When looking across the years sampled, the 1999 and 2000 year-classes had higher proportions assigned to US origin. Comparing the methods, there was a tendency for QDA to classify a higher fraction of samples to the southern contingent. For the random forest procedure, estimated classification error ranged between 7.4 and 23.9%, which was lower than for QDA (14.3 – 27.3%). Logistic and random forest procedures performed similarly (Figures 18 A-C). Between repeated applications of the random forest procedure, the 1998 year-class had the only variable “OOB” error estimate ranging from 21.7 – 23.9%, and 6.5 – 15.2% (Table 7)

When both  $\delta^{18}\text{O}$  and  $\delta^{13}\text{C}$  data were included in the classification procedures, results differed slightly (Table 8). When estimable, misclassification rates were lower

with the use of both isotopes, and slightly fewer fish were classified as Canadian origin (47-100%). Here again the random forest approach yielded lower classification error rates than the QDA (Table 8). Overall, for both single isotope and double isotope applications, the three classification methods largely agree within each year-class, especially the 1998 year-class. Both the 1999 and 2000 year-classes showed a more even mixture between US and Canadian origin fish than 1998. Similarly here, the 1998 year-class was the only sample to have variable “OOB” error estimate, ranging from 6.5 – 15.2% (Table 8).

## Discussion

Distinct differences in the  $\delta^{18}\text{O}$  values of otoliths between US and Canadian spring-captured individuals supported Sette's (1950) premise of unique natal habitats and potential migratory sub-groups of Northwest Atlantic mackerel (Figure 13). Discrete ranges of Northwest and Northeast Atlantic mackerel were also indicated by marked differences in otolith  $\delta^{18}\text{O}$  between US/Canadian samples and Icelandic/Norwegian samples. More resolved sub-regional differences within US waters were less apparent but a North-South latitudinal gradient in otolith  $\delta^{18}\text{O}$  values may be present in age-0 mackerel (Figure 10 A, Table 5). Evidence of site fidelity to the US and Canadian spring habitats was minimal, indicated by mostly dissimilar natal  $\delta^{18}\text{O}$  values for fish of the same year-class but sampled in sequential years as age-1 and age-2 individuals. For age-3 and 4 fish sampled from US waters, substantial mixing by the northern contingent was detected in both years examined (2001 and 2003). These findings offer limited support for Sette's explanation of mackerel seasonal migration and mixing patterns, but agree more than past evidence, which relied on conventional tagging, otolith morphometrics, and genetics (Moores *et al.*, 1975; Castonguay *et al.*, 1991; Lambrey de Souza *et al.*, 2006).

### *Isotopes as tool to understand population structure*

Otolith stable isotopes, and  $\delta^{18}\text{O}$  specifically, have been used to study population structure of marine fishes across species and diverse oceanographic settings (Gao *et al.*, 2001; Elsdon *et al.*, 2008; Rooker *et al.*, 2008; Newman *et al.*, 2010). Some particularly successful studies have taken advantage of clear, significant water isotope composition differences between ocean basins such as the Mediterranean Sea and the Northwest

Atlantic Ocean (Rooker *et al.*, 2008; Siskey *et al.*, 2016), the Southeast Pacific and Southwest Atlantic (Niklitschek *et al.*, 2014) and the full marine-freshwater salinity gradient encountered by diadromous fishes (Kerr *et al.*, 2007; Hanson *et al.*, 2010). Sufficient temperature differences within the range of a stock can also allow  $\delta^{18}\text{O}$  value separation (Newman *et al.*, 2009, 2010). For instance, Newman *et al.* (2009, 2010) used whole otolith  $\delta^{18}\text{O}$  composition in two separate studies to determine the spatial distribution structure for both *Scomberomorus commerson* (Lacépède) and *Scomberomorus semifasciatus* (Macleay), two species of Spanish mackerel. Each species population was associated with 4 separate stocks along the Australian Coast. Generally, the stocks of *Scomberomorus semifasciatus* were physically separated by large coastal embayments (Newman *et al.* 2010). In *Scomberomorus commerson* a latitudinal gradient was found in otolith  $\delta^{18}\text{O}$  values with higher latitudes corresponding to more elevated  $\delta^{18}\text{O}$  values (Newman *et al.* 2009). These findings are similar to the latitudinal  $\delta^{18}\text{O}$  patterns in the Northern Hemisphere for Atlantic mackerel.

Classifying population structure in Atlantic mackerel may be more complex than the previously described examples because of the degree of proximity and apparent mixing between the two northwest Atlantic contingents. These two contingents of Atlantic mackerel overlap on a seasonal basis (Sette, 1950) and the distance between the northern and southern natal habitats is only about 1500 km. While their spawning habitats are different, the two contingents are believed to have very similar overwintering areas on the continental shelf (Maguire *et al.*, 1987) and brief periods of overlap during spring and fall migrations (Sette, 1950). Carbonate that is isotopically distinct to the natal habitat should be deposited from late spring, summer and fall (Dery, 1998), when

contingent distributions show greatest separation. Within the Northwest Atlantic range of Atlantic mackerel, Trueman et al. (2012) predicted a latitudinal gradient in otolith  $\delta^{18}\text{O}$  values ranging from -2 ‰ (South) to 2 ‰ (North), which is significantly larger than the analytical measurement precision (0.1‰).

Atlantic ocean basin and shelf gradients in surface seawater  $\delta^{18}\text{O}$  (McMahon *et al.*, 2013) and predicted otolith  $\delta^{18}\text{O}$  values (Trueman *et al.*, 2012) conformed well with expectations for the Northwest Atlantic Ocean and between the Northwest and Northeast Atlantic Oceans. Trueman et al.'s (2012) predictions are based upon the negative linear relationship of water temperature ( $T$ ) to the difference between  $\delta^{18}\text{O}_{\text{seawater}}$  (Schmidt *et al.*, 1999) and  $\delta^{18}\text{O}_{\text{otolith}}$ :

$$\text{Equation 5: } (\delta^{18}\text{O}_{\text{oto}} - \delta^{18}\text{O}_{\text{w}}) = \beta - \gamma * T$$

with species specific parameters,  $\gamma = 0.2$  and  $\beta = 3.90$ , based on laboratory reared cod (*Gadus morhua* (L.)) (Høie *et al.*, 2004). Temperature affects the fractionation, or isotopic offset, which occurs when  $\delta^{18}\text{O}$  in seawater is incorporated into the otolith carbonate. In this relationship, a lower temperature results in more positive  $\delta^{18}\text{O}_{\text{otolith}}$  values in comparison to  $\delta^{18}\text{O}_{\text{seawater}}$ . Assuming the  $\delta^{18}\text{O}$  ranges reported in Trueman et al. (2012) are appropriate for Atlantic mackerel,  $\delta^{18}\text{O}$  values for the northeast Atlantic populations can be expected to fall between 1 and 4 ‰. These elevated values are likely an effect of colder temperatures in the area, and the lingering effects of the high  $\delta^{18}\text{O}$  values of offshore Gulf Stream waters (McMahon et al. 2013). The Northwest population as a whole was predicted to range somewhat lower, between -2 and 2 ‰, with more southerly-origin fish in the lower portion of that isotopic range (Trueman et al. 2012).

Within the southern contingent's range, Trueman et al. (2012) predicts decreasing  $\delta^{18}\text{O}$  values as one moves offshore and north, encompassing the entire -2 to 2 ‰ range. Even if these cod-derived parameter estimates are not accurate for mackerel, a variety of fish show the same basic linear relationship (Kalish, 1991; Thorrold *et al.*, 1997; Storm-Suke *et al.*, 2007; Kitagawa *et al.*, 2013), supporting the relative otolith  $\delta^{18}\text{O}$  values and ordering of regions reported in this thesis.

The relative relationships of my measured  $\delta^{18}\text{O}$  otolith values are consistent with, although in the lower range of Trueman et al.'s (2012) predictions. In the Northeast Atlantic, values were within the predicted  $\delta^{18}\text{O}$  range of 1 and 4 ‰ (Iceland mean =  $1.75 \pm 0.33\text{‰}$ , Norway mean =  $1.89 \pm 0.24\text{‰}$ ). In the Northwest Atlantic, the observed mean  $\delta^{18}\text{O}$  values for US age-1 fish is slightly below the expected range of -2 to 2‰, with a mean of  $-2.63 \pm 0.99\text{‰}$ , and Canadian age-1 fish were within the range with a mean at  $-0.9 \pm 0.85\text{‰}$ . This observed difference in the mean  $\delta^{18}\text{O}$  value of 1.7‰ is within the range predicted in Trueman et al. Within US waters, the sub-regional gradient observed in age-0 fish is opposite to Trueman et al.'s predictions, but agrees with the basin scale trend in  $\delta^{18}\text{O}$  value with latitude, as GB fish were observed to have the highest  $\delta^{18}\text{O}$  values (Figure 10 A). High modern temperatures in the Northwest Atlantic, relative to those observed during the 30 year  $\delta^{18}\text{O}$  data set, could explain the lower observed values of  $\delta^{18}\text{O}$  in otoliths (Nye *et al.*, 2009; Trueman *et al.*, 2012). Trueman et al.'s (2012) estimates were derived from regional measurements of sea surface  $\delta^{18}\text{O}$  aggregated over a 30+ year time period, which cannot capture  $\delta^{18}\text{O}$  changes within a single year or season. Further, the  $\delta^{18}\text{O}$  temperature fractionation relationship has not been parameterized for Atlantic mackerel otoliths, but relative differences should still hold.

As samples were drawn from more proximate regions, greater overlap in otolith  $\delta^{18}\text{O}$  was observed. At the largest scale, across the Atlantic basin, distributions of otolith  $\delta^{18}\text{O}$  values between Northwest and Northeast populations of Atlantic mackerel were completely distinct. At intermediate levels of proximity, within the individual Atlantic mackerel populations, distributions overlapped. Norwegian and Icelandic samples showed a high degree of overlap and no significant difference, potentially due to the many combined year-classes in this analysis. Even with the numerous year-classes (age-3 to 12),  $\delta^{18}\text{O}$  values showed low variability, as opposed to the Northwest Atlantic samples, which focused on a narrower range from age-0 to age-2, ( $\text{CV}_{\text{NW Atl}} = 57.5\%$  vs  $\text{CV}_{\text{NE Atl}} = 15.4\%$ ). These northeast samples were collected in just 4 tows (Figure 4), but the wide range of ages present means the samples are likely not from a single, homogenous school, because Atlantic mackerel tend to school with similar sized individuals (Sette, 1950). The lower than expected variation in  $\delta^{18}\text{O}$  values in Northeast Atlantic mackerel, may show that the natal habitats of this population have fairly stable thermal and hydrographic conditions. Significant differences were found between US and Canadian otolith  $\delta^{18}\text{O}$  samples, with substantial overlap in their distributions (Figure 11 and 13). Incomplete separation may be evidence of mixing between the groups, or true variances associated with nursery conditions experienced by each contingent.

For the US sub-regions, there were no significant differences found in the natal signal of age-1 fish. Despite this, an examination of age-0 fish captured in the fall survey indicated a modest North to South gradient in  $\delta^{18}\text{O}$  (Figure 10 A). However, this finding is difficult to compare to age-1 results because age-0 fish were not drawn from the same years. Given typical regional and sub-regional otolith  $\delta^{18}\text{O}$  variances, it may be difficult



to detect differences that are less than 1 ‰  $\delta^{18}\text{O}$  with reasonably achievable sample sizes. Thus, even with an analytical precision of  $\pm 0.1$  ‰, isotopic values associated with sub-regional differences were insufficient to support classification using isotopic approaches.

I used  $\delta^{18}\text{O}$  values from otolith carbonate milled from the first year of life as a “birth certificate” of regional origin. This approach assumes that the natal signal is stable across ages and years. By milling otoliths whole, I introduce a potential source of contamination and error due to otolith overburden and drilling through thin layers of material deposited at ages  $>0$ . Milling through this material could result in contamination of “natal” otolith  $\delta^{18}\text{O}$  levels, and represent one potential explanation of the significant differences between ages. Consistent with this,  $\delta^{18}\text{O}$  values for age-2 fish were greater than for age-1 for 1998 and 1999 year-classes sampled in the US and for the 1998 year-class in Canada. An alternate, more ecologically relevant explanation for this increase would be the intrusion of northern contingent fish into US waters at age-2. Comparison of just Canadian captured fish across ages showed increases in natal otolith  $\delta^{18}\text{O}$  levels with age for the 1998 year-class, but not in the 1999 year-class, offering some support for differences in the migration of Atlantic mackerel between the two regions. Since the age-based differences were not as prevalent in Canadian origin fish, some combination of the three following possibilities could be explanatory: (1) the influence of otolith overburden may be less important than mixing on the natal  $\delta^{18}\text{O}$  signal, (2) some immigration by northern contingent fish into US waters may occur as early as age-2, and (3) immigration of southern contingent fish into Canadian waters may not be prevalent. It is harder to explain the observed rise in age-2  $\delta^{18}\text{O}$  values for fish from the 1998 Canadian year-class. Because these fish are from the same year-class, year to year variation in the environment

is not the cause. No regional differences within the Canadian samples were detected (data not presented), but because sample size was low sampling error (biased sampling) between age-1 and age-2 fish cannot be ruled out.

The natal signal clearly varied between years for both the southern and northern contingents, perhaps the result of changing temperature and oceanographic conditions (see next section). To further develop the “birth certificate” approach for Atlantic mackerel, it will be necessary to establish a baseline for each year-class examined for classification. In each year’s baseline, samples should be drawn from as wide a range as possible to account for potential sub-regional differences.

#### *Isotopes and oceanography*

Both US and Canadian age-1 samples exhibited a similar increasing trend in core otolith  $\delta^{18}\text{O}$  values through the short time period of this study, which suggests an underlying oceanographic influence. Seawater temperature and  $\delta^{18}\text{O}$  value are the main determinants of otolith  $\delta^{18}\text{O}$ , and these factors vary across years. Regional temperatures have been rising in the Northwest Atlantic (Nye *et al.*, 2009), and the  $\delta^{18}\text{O}$  composition of seawater in the region is influenced by precipitation patterns and the strength of the region’s major currents, the Labrador and Gulf Stream. The relative strength of both of these currents is related to the North Atlantic Oscillation (NAO), an index of the atmospheric pressure gradient between Iceland and the Azores, which also affects temperature patterns and precipitation in the Northwest Atlantic (Ecosystem Assessment Program NEFSC, 2009). There was a small phase shift in NAO during the study period, shifting from negative to positive phase. Individual oceanographic drivers also shifted in line with this NAO change. For example, the influence of the Gulf Stream on the region

was increasing through a northward shift during which the regional influence of Labrador Current diminished (Figure 19 and 20). The combined impact of these changing currents would be the relative dominance of tropical water on the system, which would result in higher  $\delta^{18}\text{O}_{\text{seawater}}$  values, a pattern consistent with the observed trend in otolith  $\delta^{18}\text{O}$ . Regional sea surface temperature in the US Northwest Atlantic generally rose during and around the study period, which should result in lower  $\delta^{18}\text{O}_{\text{otolith}}$  values (Trueman *et al.*, 2012). However, the observed rise in otolith  $\delta^{18}\text{O}$  could indicate that changes to the isotopic composition of seawater outweighed changes that would have been due to rising temperatures. Canadian water temperatures were not assessed in this study, but they are expected to decline during a positive NAO phase (Ecosystem Assessment Program NEFSC, 2009), which would strengthen the  $\delta^{18}\text{O}$  gradient expected between the northern and southern natal habitats (Thorrold *et al.*, 1997; Trueman *et al.*, 2012). Causation or even correlation cannot be assessed with just a 3-year annual time series, but the pattern suggests that additional study over a longer time period might be useful for identifying important trends in oceanographic features and their impact on Atlantic mackerel.

Isotopic composition of the water also varies spatially, and a consistent shift in the distribution of Atlantic mackerel across the years of this study could influence otolith  $\delta^{18}\text{O}$  values. Open ocean seawater  $\delta^{18}\text{O}$  value is positively correlated with salinity (Frew *et al.*, 2000), indicating the influence of freshwater input, precipitation and evaporation. During the relevant natal years (1998 through 2000), there was no appreciable change in regional precipitation (National Environmental Satellite Data and Information Service, n.d.), but a shift in distribution from inshore to offshore in the 1998 through 2000 year-classes could result in a rising otolith  $\delta^{18}\text{O}$  for Atlantic mackerel. Similarly, there is

variation in  $\delta^{18}\text{O}$  with water depth (Frew *et al.*, 2000), so a shift in depth occupied could result in changing otolith  $\delta^{18}\text{O}$  over time. There is evidence of plasticity for Atlantic mackerel in both of these aspects of distribution (Overholtz *et al.*, 2011) which could offer another explanation for the  $\delta^{18}\text{O}$  variation over time.

In addition to changes in the amplitude of otolith  $\delta^{18}\text{O}$ , variance in oxygen isotope composition may also provide insights to regional oceanography. For instance, even though the Northeast Atlantic mackerel were drawn from a region (Iceland – Norway) of much greater areal extent than Northwest Atlantic mackerel, variance in otolith  $\delta^{18}\text{O}$  was much less, indicating more homogenous thermal and salinity conditions there. Within the Northwest Atlantic southern contingent, there was significantly higher variance in natal  $\delta^{18}\text{O}$  levels of age-1 mackerel sampled in GB than in the NYB (Figure 7) ( $\text{CV}_{\text{GB}} = 42.3\%$  vs  $\text{CV}_{\text{NY}} = 27.7\%$ ). This higher variance could relate to GB's proximity to Canada origin samples and the increased likelihood of mixing by northern contingent fish, which are believed to remain mostly east of the 70° W meridian (Gregoire *et al.*, 2010).

Interestingly, the isotopic variance of Norwegian mackerel otoliths sampled from spawning grounds was much higher than that of fish sampled from feeding grounds. The sample size for this comparison is low, but this pattern could imply that spawners were drawn from a more diverse set of habitats and oceanographic histories than foraging mackerel. Alternatively, the feeding ground mackerel represent fewer year-classes than those in the spawning ground sample, which could contribute to the lower variability.

#### *Implications of this study on the concept of mackerel population structure*

Owing to less structured habitats, schooling behaviors, and the capacity for migration, pelagic stocks are usually thought to be more open to straying and mixing and

therefore are less structured by processes such as spawning site fidelity (multiple return of adults to the same spawning habitat), natal homing (return of adults to birthplace for spawning purposes), and philopatry (multiple returns of adults to spawning habitat, eventually producing reproductive isolation) (Ciannelli *et al.*, 2013; Secor, 2015).

Atlantic mackerel are composed of two distinct populations displaced from each other across the North Atlantic Ocean. The Northeast Atlantic population has been separated traditionally into distinct southern, western and North Sea spawning contingents (International Council for the Exploration of the Sea, 1977, 2011), but directed research has failed to show clear separation among the groups despite a variety of approaches used (Eltink *et al.*, 1986; Hopkins, 1986; Jansen *et al.*, 2013). Instead the relative abundance and spawning intensity across the range is described as a cline, with high levels of straying and regional abundance determined by environmental conditions and mackerel behavior (Jansen and Gislason, 2013). In the Northwest Atlantic, the historical hypothesis of reproductively isolated migratory contingents (Sette, 1950) has lost favor, as more recent studies have failed to show separation or directly demonstrated mixing (Moores *et al.*, 1975; Castonguay *et al.*, 1991; Lambrey de Souza *et al.*, 2006). It is however widely acknowledged that these southern and northern contingents do have persistent migratory behavior that may have management and ecological implications.

The isotopic approach used here uncovered limited evidence of repeated seasonal migrations to the same region by age-1 and age-2 Atlantic mackerel in one year-class of Canadian origin fish, providing some support for the traditional contingent premise originally developed by Sette (1950). If these patterns of repeated migration are prevalent, they could contribute to contingent structure over time, and philopatry which

could lead to isolated populations. However, older adults showed very little evidence of natal homing because isotopically northern contingent fish were found to dominate in US waters at ages-3 and 4. Classifications of individuals suggested limited mixing between the contingents due to the absence of US adults in the 1998 and 1999 year-class samples. The lack of co-occurrence of the migratory groups points to a spatially structured population, but the details of this structure remain unknown. This study has limitations since it represents a short period of contingent structure analysis over a decade ago. Contingent mixing is expected to be dynamic across years and decades. In a recent study, Siskey *et al.* (2016) found substantial changes over a 40-year period in stock mixing between Mediterranean Sea and Northwest Atlantic populations of Atlantic bluefin tuna intercepted in US fisheries. Higher mixing was observed during periods of depressed abundance by the Northwest Atlantic population. Similarly, relative abundance between the two Northwestern Atlantic mackerel contingents has likely shifted over time, with expectations that the more abundant stock may spillover and subsidize the smaller stock, resulting in higher stock mixing levels. Further, the distribution of Atlantic mackerel is sensitive to environmental forcing, particularly changes in sea surface temperature (Overholtz *et al.*, 2011; Astthorsson *et al.*, 2012; Jansen *et al.*, 2016). Warming and other large-scale oceanographic changes would be expected to alter the degree of spatial overlap between the contingents. Additionally, age or size specific schooling in Atlantic mackerel (Sette, 1950) could affect mixing levels. During periods of mixing, large schools for one contingent may entrain individuals from the other in a density-dependent manner as has been described for Atlantic herring (McQuinn, 1997; Huse *et al.*, 2002).

An important finding of this study is the near complete absence of southern contingent fish in US waters at older ages (age-3 and 4). 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 (Deroba *et al.*, 2010). Landings from Canadian Atlantic mackerel fisheries have older fish and more robust age structures, but this age structure is still weaker than historical averages (Fisheries and Oceans Canada, 2014). Additionally, egg production, estimated from egg surveys in the Gulf of St. Lawrence, has collapsed during the recent decade and was at historically low levels in 2013 (Fisheries and Oceans Canada, 2014). My results suggest that in the early 2000's adults found in US waters were predominantly from the northern contingent. Should these individuals be spawning in US waters, a single population of interbreeding individuals would be supported. Alternatively, the timing of the spring bottom trawl survey (late March through early May) precedes the peak spawning period of the northern contingent which ranges from June to late July (Sette, 1950; Moores *et al.*, 1975). The survey could be capturing these northern contingent fish in their northerly migration towards spawning grounds in the Gulf of St. Lawrence and the Scotian Shelf. This possibility is supported by numerous “resting” and “developing” maturity classifications recorded during the NEFSC spring trawl survey (S. Sunderland, pers. comm., NEFSC, Woods Hole, Massachusetts; see also Burnett *et al.*, 1989). The presence of multiple spawning units within the collections of the spring trawl survey would be possible if northern contingent adults were still in transit to spawning grounds. Regardless, if measures of adult abundance in the survey are representative of the northern contingent while juvenile abundance is relevant to the southern contingent, the survey would be unable to track cohorts from juveniles to adults.

Its applicability in age specific stock assessments would therefore be very limited (Deroba *et al.*, 2010). A remaining question is the fate of adult southern contingent mackerel, which were scarce in adult samples captured in the spring trawl survey. Possible reasons for their apparent disappearance include high and selective mortality on adults owing to fisheries or predation, or a shift by older southern contingent fish to regions not well surveyed by the NEFSC spring survey. A shift in the distribution of this US contingent with age would likely not be discovered with a fixed-season, static survey (Link *et al.*, 2011).

The value of the NEFSC spring bottom trawl survey for assessing widely distributed pelagic stocks like Atlantic mackerel has often been questioned (Gregoire *et al.*, 2010; Radlinski *et al.*, 2013). The gear likely performs poorly in consistently capturing pelagic species such as Atlantic mackerel across tows and years, although mackerel is one of the most frequently encountered fish in the trawl (NMFS-NEFSC, 2001, 2016). Further, coverage is sparse or absent in large parts of the species range particularly in outer shelf and slope waters. Inconsistent catchability and availability to the survey gear add variability in the trawl survey index, which has fluctuated greatly since the late 1990's (Wiedenmann, 2015), and may no longer be reflecting trends in the mackerel stock (MAFMC, 2015). Because the majority of archived otoliths used in this study came from this survey, biases arising from incomplete spatial sampling could carry over to regional and sub-regional comparisons. Because patterns observed in age-1, and to a lesser extent, age-2 Atlantic mackerel conform to expectations of migration patterns (Sette, 1950) and regional ordering of  $\delta^{18}\text{O}$  values (Trueman *et al.*, 2012), the relative abundances of these juvenile age-classes can provide information on recruitment trends



to assessments. Late fall, winter and early spring are thought to be periods of contingent mixing (Sette, 1950) and more complete sampling across seasons would allow for improved understanding of annual cycles of migration and mixing. For US waters, opportunities exist for obtaining otolith samples from winter commercial fisheries and the fall NEFSC trawl survey, which would help understand what bias, if any, may be present in the US assessments, which rely heavily upon the spring trawl survey.

#### *Implications on mackerel management and assessment*

A major uncertainty in Atlantic mackerel management is stock structure (MAFMC 2015). This study shows separation of young fish (age-1) specific to the two natal habitats, but also found the extensive presence of, older, putative northern contingent fish in US waters, at a time when spawning could be occurring. The distinction between younger fish in US and Canadian waters provides the opportunity for divergence in growth and reproductive rates (Sette, 1950; D'Amours *et al.*, 1990) as well as differential exposure to fishing, predation, and other sources of mortality (Moustahfid *et al.*, 2009) in early life which could have population level impacts. The nature of this separation becomes less clear at age-3 and older when Canadian origin fish are found in US waters. Because of this apparent mixing, it seems advisable to assess and manage the two contingents as a single stock, as is now done by NMFS (US), taking into account Canadian landings, even though DFO (Canada) currently assesses and manages the northern contingent stock in isolation. To confirm the timeliness and relevance of the findings, these methods should be applied to more modern samples to determine if 1998 to 2000 year-class patterns of contingent structure and mixing have persisted. This is particularly relevant given the depleted status of both contingents (MAFMC, 2015).

This study has demonstrated capabilities to classify unknown samples to their likely region of origin, given year-class specific baselines. In this study, I compared mixing levels and precision of classifications among random forest, quadratic discrimination analysis and logistic regression methods. Within an individual year, the three methods largely agreed (Tables 7 and 8). Slightly more US classifications were made when using both  $\delta^{18}\text{O}$  and  $\delta^{13}\text{C}$  values rather than just  $\delta^{18}\text{O}$  values, which indicates that  $\delta^{13}\text{C}$  values could aid discrimination. Because the  $\delta^{13}\text{C}$  value is derived from both dissolved inorganic carbon and diet sources (Solomon *et al.*, 2006), there could be a difference in one of these two factors between the northern and southern natal regions. Potential differences include the relative amount of terrestrial origin carbon contributing to the inorganic carbon signal or the metabolic activity of the two contingents (Thorrold *et al.*, 1997). The existing NEFSC archive of Atlantic mackerel otoliths offers the opportunity to look at a number of contingent classifications across ages, years, and sub-regions. My analysis suggests that random forest classification may be the most accurate method, because it generally had lower error rates than QDA (Tables 7 and 8). However, based on the saw-toothed classification relationship, random forest may be overfitting the data (Figure 18 A-C). The results of the logistic regression classification appear to roughly match those of random forest, without the potential for overfitting. With these baseline sample sizes, logistic regression appears to be performing the best. The broad agreement in regional assignment of the three methods and relative ease of implementation means that an ensemble of approaches can be used to support inferences on stock mixing. Prior to adopting and operationalizing these classification procedures, it

would be prudent to compare these and other classification methods across a greater number of years.

## Conclusion

Previous studies that looked at the spatial structure of Northwest Atlantic mackerel have not shown a strong separation between putative northern and southern contingents. My study largely reinforces Sette's (1950) early conclusions that Atlantic mackerel contingent structure is underlain by two distinct natal habitats and some degree of repeated migration to regions of origin. Additionally, my study documented significant excursions of the northern contingent of Canadian origin into US waters at older ages. The fate of southern contingent Atlantic mackerel at these older ages remains unknown.

Atlantic mackerel is a dynamic stock, and a better understanding of mixing and underlying population structure will require broader sampling in time and space and the continued application of these methods to other years and decades. The timing of sample collection, primarily through the spring trawl survey, impacts the representation of Atlantic mackerel age, spatial structure, and mixing that I observed. Spring is a time of migration and change in the distribution of the species, so a static survey may not show the full dynamics of migrations. Related to this, based on the relative absence of US adults, there is either a large, unaccounted for source of mortality, or the spatial extent of the survey is more limited than the range of Atlantic mackerel. Future work could supplement this study by sampling from other seasons and areas and add to the limited number of years for which data currently exists. Fall trawl survey and winter fisheries are two potential sources to expand the timing and spatial extent of sampling.

Additional studies should also address environmental influences that cause year-to-year variation in observed otolith  $\delta^{18}\text{O}$  and the short-term pattern observed here for

1999-2001 of increased  $\delta^{18}\text{O}$  values with age for the same year-class. Otolith stable isotope composition offer one method to understand the dynamics of Atlantic mackerel, but the potential for shifts in distribution, abundance, and spatial structure in pelagic stocks means that unit stock assumptions must be regularly updated and reassessed with complementary methods and simulation exercises focused on population structure.

Tables

Table 1: Sample years for age-1 US and Canadian Atlantic mackerel baselines and unknown US adult samples of otoliths.

<b>Year-class</b>	<b>Age-1 Baseline Sample Year</b>	<b>Adult Sample Year</b>	<b>Adult Age</b>
1998	1999	2001	3
1999	2000	2003	4
2000	2001	2003	3

Table 2: Inventory of archived Atlantic mackerel otoliths received from the Northeast Fisheries Science Center, Fisheries and Oceans Canada, Iceland's Marine Research Institute and Institute of Marine Research in Norway. In some instances degrees of latitude and longitude associated with each sub-region are presented within parentheses.

Collection Year	Age- Class	Region	Sub- sample	Number Analyzed
<b>Juvenile Samples Received</b>				
1996	0	Mid Atlantic Bight (S of 38°N)	0	-
	0	New York Bight (39.5-41.0°N, 70-74°W)	16	10
	0	West Georges Bank (40-42°N, 66-70°W)	23	10
1999	1	Mid Atlantic Bight (S of 38°N)	1	1
	2	Mid Atlantic Bight (S of 38°N)	3	3
	1	New York Bight (39.5-41.0°N, 70-74°W)	29	25
	2	New York Bight (39.5-41.0°N, 70-74°W)	33	-
	1	West Georges Bank (40-42°N, 66-70°W)	49	30
	2	West Georges Bank (40-42°N, 66-70°W)	26	-
	1	Canada (Nova Scotia to Gulf of St Lawrence)	30	27
	2	Canada (Nova Scotia to Gulf of St Lawrence)	30	-
2000	1	Mid Atlantic Bight (S of 38°N)	7	3
	2	Mid Atlantic Bight (S of 38°N)	8	4
	1	New York Bight (39.5-41.0°N, 70-74°W)	24	8
	2	New York Bight (39.5-41.0°N, 70-74°W)	30	11
	1	West Georges Bank (40-42°N, 66-70°W)	81	19
	2	West Georges Bank (40-42°N, 66-70°W)	27	10
	1	Canada (Nova Scotia to Gulf of St Lawrence)	30	15
	2	Canada (Nova Scotia to Gulf of St Lawrence)	30	13
2001	0	Mid Atlantic Bight (S of 38°N)	8	6
	1	Mid Atlantic Bight (S of 38°N)	0	-
	2	Mid Atlantic Bight (S of 38°N)	6	6
	0	New York Bight (39.5-41.0°N, 70-74°W)	0	-
	1	New York Bight (39.5-41.0°N, 70-74°W)	16	15
	2	New York Bight (39.5-41.0°N, 70-74°W)	30	16
	0	West Georges Bank (40-42°N, 66-70°W)	11	10

	1	West Georges Bank (40-42°N, 66-70°W)	62	24
	2	West Georges Bank (40-42°N, 66-70°W)	80	14
	1	Canada (Nova Scotia to Gulf of St Lawrence)	31	15
	2	Canada (Nova Scotia to Gulf of St Lawrence)	29	15
2003	0	Mid Atlantic Bight (S of 38°N)	5	5
	0	New York Bight (39.5-41.0°N, 70-74°W)	15	9
	0	West Georges Bank (40-42°N, 66-70°W)	29	9

#### **Adult Samples**

2001	3	Mid Atlantic, New York Bight and Georges Bank Pooled	19	19
2003	3 to 4	Mid Atlantic, New York Bight and Georges Bank Pooled	60	41
2015	3 to 11	Iceland (64.3°N, 12.4°W and 64.4°N, 24.5°W)	30	18
2015	3 to 10	Norwegian Sea (Norwegian feeding area) (52.8°N, 11.9°W)	25	15
2015	3 to 12	West Coast of Ireland (Norwegian spawning area) (63.5°N, 0°E)	25	14



Table 3: Atlantic mackerel core otolith  $\delta^{18}\text{O}$  values (mean  $\pm$  standard deviation) across years, sub-regions or regions, and ages. GB=Georges Bank, NYB = New York Bight.

Year-class	Region or Subregion	N	Age	$\delta^{18}\text{O} \pm \text{SD}$	Year-class	Region	N	$\delta^{18}\text{O} \pm \text{SD}$
1998	US - GB	17	1	$-3.46 \pm 1.16$	Pooled ages	Iceland	18	$1.75 \pm 0.33$
		-	2	-		Norway	29	$1.89 \pm 0.24$
	US - NYB	14	1	$-3.10 \pm 0.63$				
		-	2	-				
	Canada	15	1	$-1.40 \pm 0.84$				
		-	2	-				
	US Pooled	31	1	$-3.30 \pm 0.96$				
		-	2	-				
		21	3	$-0.58 \pm 0.55$				
1999	US - GB	19	1	$-2.89 \pm 0.92$				
		10	2	$-2.19 \pm 0.65$				
	US - NYB	8	1	$-2.11 \pm 0.38$				
		11	2	$-2.17 \pm 0.75$				
	Canada	11	1	$-1.20 \pm 0.33$				
		13	2	$-0.60 \pm 0.44$				
	US Pooled	27	1	$-2.66 \pm 0.87$				
		21	2	$-2.18 \pm 0.69$				
		23	4	$-1.05 \pm 0.50$				
2000	US - GB	24	1	$-1.99 \pm 0.86$				
		14	2	$-2.15 \pm 0.42$				
	US - NYB	15	1	$-2.25 \pm 0.56$				
		16	2	$-2.12 \pm 0.59$				
	Canada	12	1	$0.00 \pm 0.34$				
		15	2	$-1.29 \pm 0.38$				
	US Pooled	39	1	$-2.09 \pm 0.76$				
		30	2	$-2.13 \pm 0.51$				
		15	3	$-0.35 \pm 0.50$				
Pooled Years	US	97	1	$-2.63 \pm 0.99$				
		51	2	$-2.15 \pm 0.58$				
	Canada	38	1	$-0.90 \pm 0.85$				
		28	2	$-0.97 \pm 0.53$				

Table 4: Atlantic mackerel core otolith  $\delta^{13}\text{C}$  values (mean  $\pm$  standard deviation) across years, sub-regions or regions, and ages. GB=Georges Bank, NYB = New York Bight.

Year-class	Region or Sub-region	N	Age	$\delta^{13}\text{C} \pm \text{SD}$	Year-class	Region	N	$\delta^{13}\text{C} \pm \text{SD}$
1998	US - GB	17	1	$-5.60 \pm 0.49$	Pooled ages	Iceland	18	$-6.27 \pm 0.57$
		-	2	-		Norway	29	$-5.93 \pm 0.56$
	US - NYB	14	1	$-5.50 \pm 0.54$				
		-	2	-				
	Canada	15	1	$-5.95 \pm 0.71$				
		-	2	-				
1999	US Pooled	21	3	$-5.54 \pm 0.48$				
	US - GB	19	1	$-5.87 \pm 0.62$				
		10	2	$-5.09 \pm 0.52$				
	US - NYB	8	1	$-5.45 \pm 0.87$				
		11	2	$-5.18 \pm 0.51$				
	Canada	11	1	$-6.14 \pm 0.46$				
2000		13	2	$-5.50 \pm 0.44$				
	US Pooled	23	4	$-5.50 \pm 0.48$				
	US - GB	24	1	$-5.51 \pm 0.53$				
		14	2	$-5.57 \pm 0.46$				
	US - NYB	15	1	$-5.75 \pm 0.43$				
		16	2	$-5.73 \pm 0.48$				
	Canada	12	1	$-5.77 \pm 0.67$				
		15	2	$-5.89 \pm 0.53$				
	US Pooled	15	3	$-5.33 \pm 0.46$				

Table 5: Atlantic mackerel core otolith  $\delta^{18}\text{O}$  values (mean  $\pm$  standard deviation) for age-0 fish, across years and sub-regions. GB=Georges Bank, NYB = New York Bight, MAB = Mid-Atlantic Bight.

<b>Year-class</b>	<b>Region or Sub-region</b>	<b>N</b>	<b>Age</b>	<b><math>\delta^{18}\text{O} \pm \text{SD}</math></b>
1996	US - GB	10	0	-0.61 $\pm$ 0.37
	US - NYB	10	0	-0.98 $\pm$ 0.29
2003	US - GB	9	0	-0.81 $\pm$ 0.44
	US - NYB	9	0	-0.94 $\pm$ 0.22
	US - MAB	5	0	-0.88 $\pm$ 0.31

Table 6: Atlantic mackerel core otolith  $\delta^{13}\text{C}$  values (mean  $\pm$  standard deviation for age-0 fish, across years and sub-regions. GB=Georges Bank, NYB = New York Bight, MAB = Mid-Atlantic Bight.

<b>Year-class</b>	<b>Region or Sub-region</b>	<b>N</b>	<b>Age</b>	<b><math>\delta^{13}\text{C} \pm \text{SD}</math></b>
1996	US - GB	10	0	-6.16 $\pm$ 0.51
	US - NYB	10	0	-6.46 $\pm$ 0.54
2003	US - GB	9	0	-6.29 $\pm$ 0.60
	US - NYB	9	0	-6.81 $\pm$ 0.53
	US - MAB	5	0	-6.23 $\pm$ 0.62

Table 7: Classification results for adult Atlantic mackerel samples captured in US waters. Mackerel were classified to US and Canadian regions, using year-class specific age-1  $\delta^{18}\text{O}$  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 quadratic discrimination analysis (QDA) were performed for each year-class. Error estimates for random forest are derived from the “out-of-bag” (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 %).

Year-class	N	Method	Canadian Baseline Assignment	US Baseline Assignment	% Northern	% Southern	Error Est.
1998	21	Random Forest	21	0	100 %	0%	21.7 – 23.9%
		Logistic Regression	21	0	100 %	0%	-
		QDA	20	1	95.2 %	4.8%	25%
1999	23	Random Forest	20	3	87.0 %	13.0%	14.3%
		Logistic Regression	21	2	91.3 %	8.7%	-
		QDA	22	1	95.7 %	4.3%	27.3%
2000	15	Random Forest	13	2	86.7 %	13.3%	7.41%
		Logistic Regression	10	5	66.7 %	33.3%	-
		QDA	8	7	53.3 %	46.7%	14.3%

Table 8: Classification results for adult Atlantic mackerel samples captured in US waters. Mackerel were classified to US and Canadian regions, using year-class specific age-1  $\delta^{18}\text{O}$  and  $\delta^{13}\text{C}$  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 quadratic discrimination analysis (QDA) were performed for each year-class. Error estimates for random forest are derived from the “out-of-bag” (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 %).

<b>Year-class</b>	<b>N</b>	<b>Method</b>	<b>Canadian Baseline Assignment</b>	<b>US Baseline Assignment</b>	<b>% Northern</b>	<b>% Southern</b>	<b>Error Est.</b>
1998	21	Random Forest	20	1	100%	0%	6.5 – 15.2%
		Logistic Regression	21	0	100%	0%	-
		QDA	21	0	100.0%	0.0%	7.3%
1999	23	Random Forest	18	5	78.3%	21.7%	11.9%
		Logistic Regression	17	6	73.9%	26.1%	-
		QDA	20	3	87.0%	13.0%	27.3%
		Random Forest	9	6	60.0%	40.0%	3.7%
2000	15	Logistic Regression	7	8	46.7%	53.3%	-
		QDA	7	8	46.7%	53.3%	7.1%

Figures

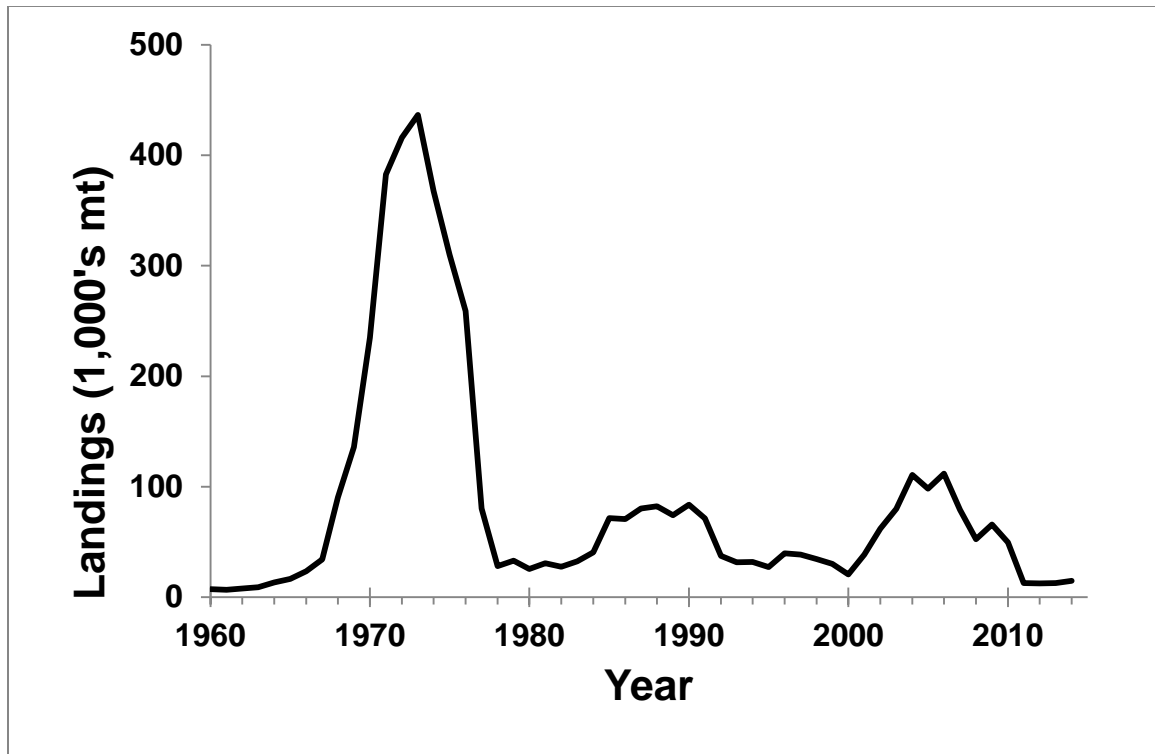


Figure 1: US annual landings, in thousands of metric tons, of Atlantic mackerel from 1960 to 2013. Catch data comes from Wiedenmann (2015) and NOAA Office of Science And Technology (n.d.).

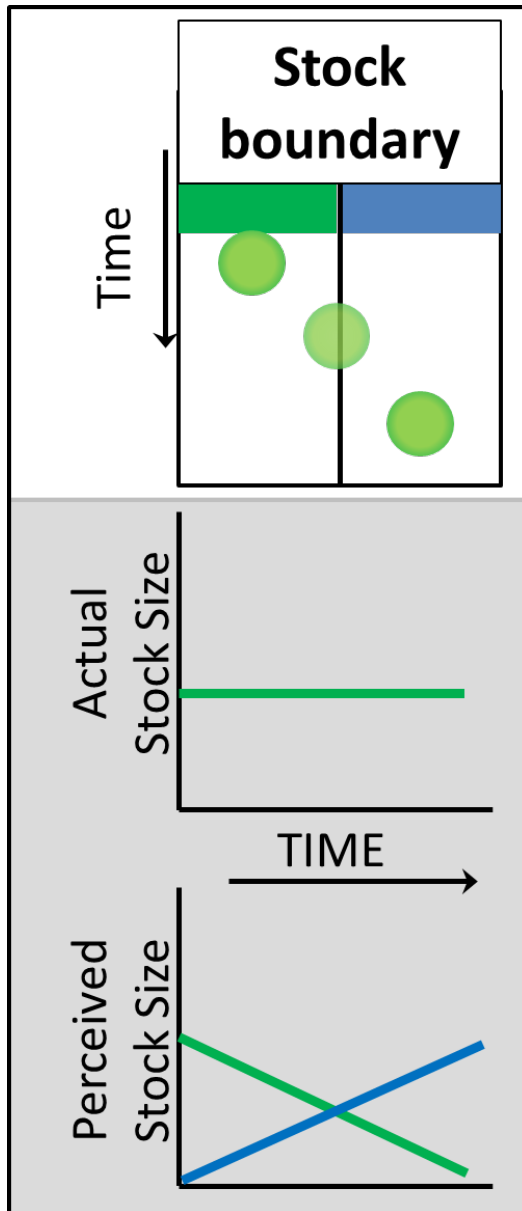


Figure 2: Conceptual diagram showing how a spatial shift in a mackerel population (green circle) across a management boundary (top panel) could impact actual (middle) and perceived (lower panel) stock size. Green and blue segments in top panel indicate stock boundaries. The second panel shows the trend of the single population. The bottom panel indicates how the population would appear across two stock boundary regions.

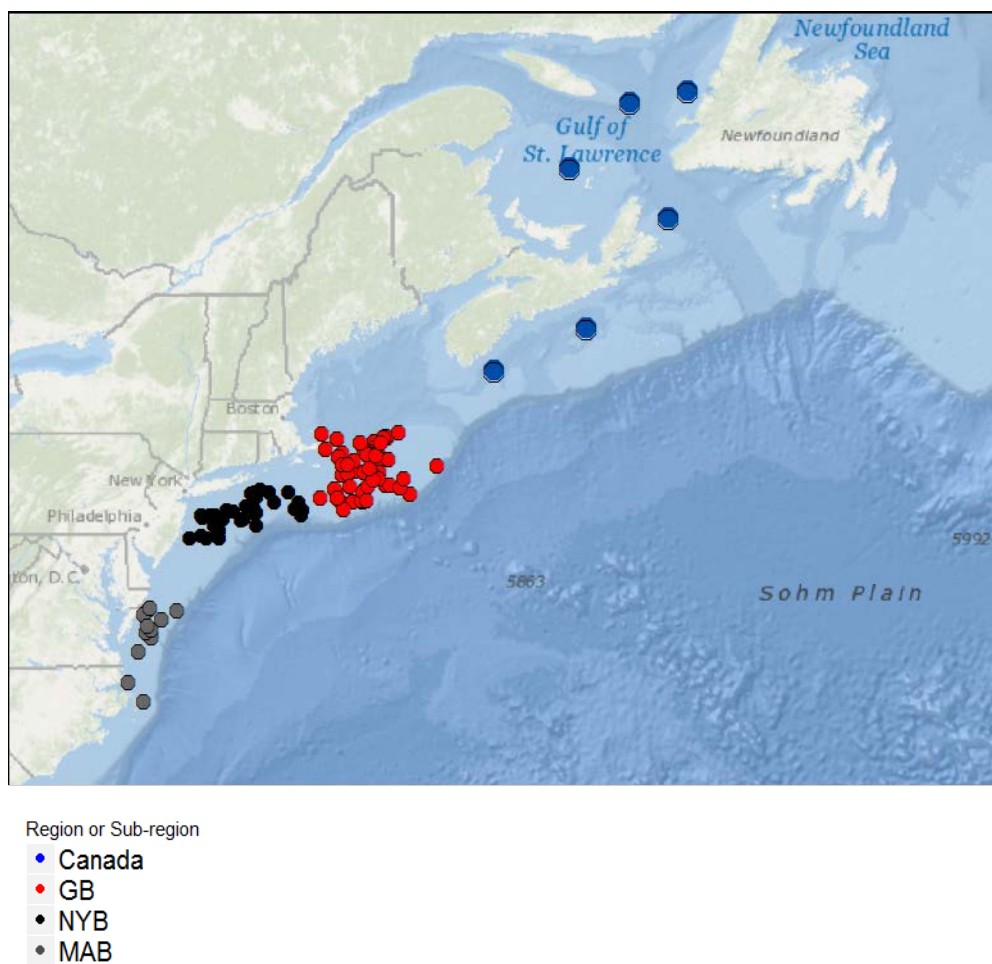


Figure 3: Map depicting sample locations for Atlantic mackerel otoliths from the Northwest Atlantic, including Canadian and US samples. For US samples, the points indicate the spring bottom trawl survey tows in which the fish was captured. For Canadian samples, the point indicates the approximate center of the statistical areas from which samples were collected.



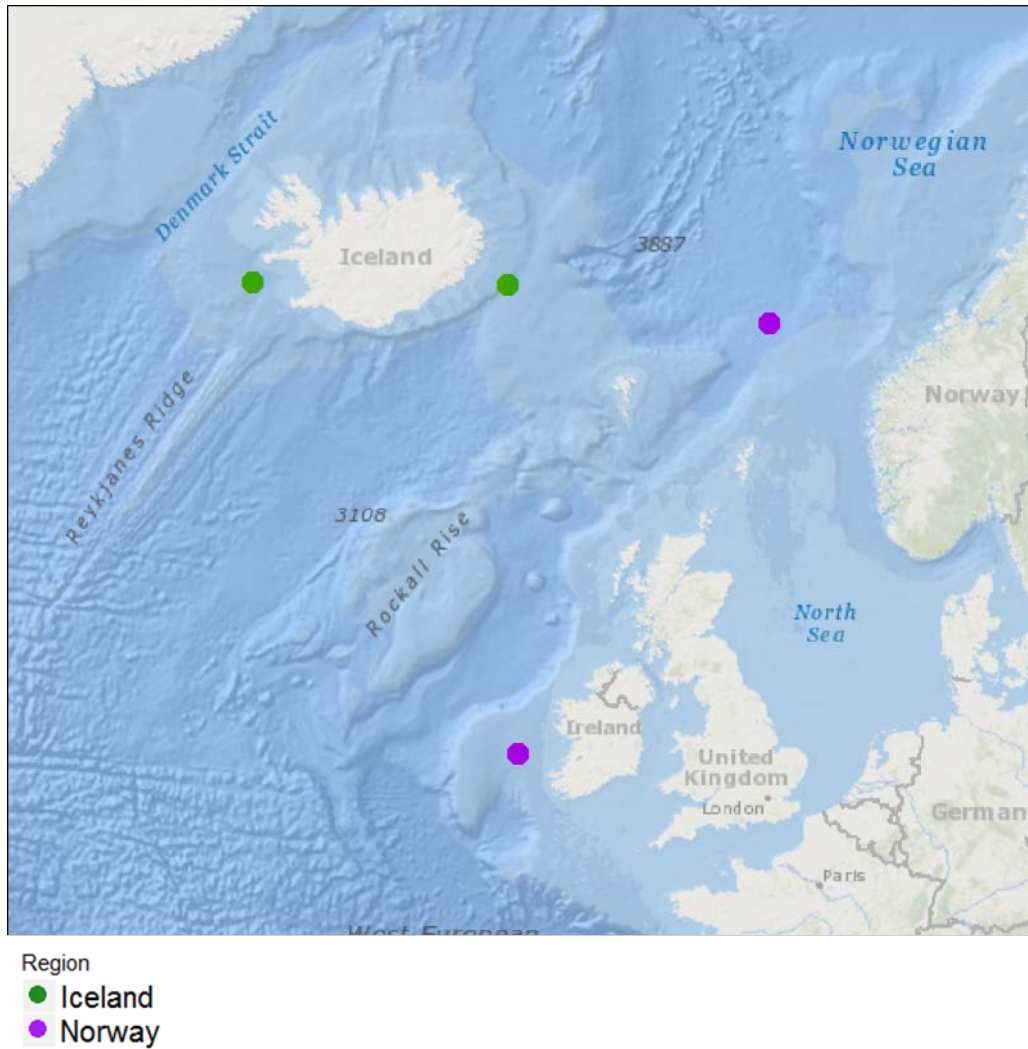


Figure 4: Map depicting sample locations for Atlantic mackerel otoliths from the Northeast Atlantic, including Norwegian and Icelandic samples. All of these points indicate the station at which fish were captured during their respective surveys.

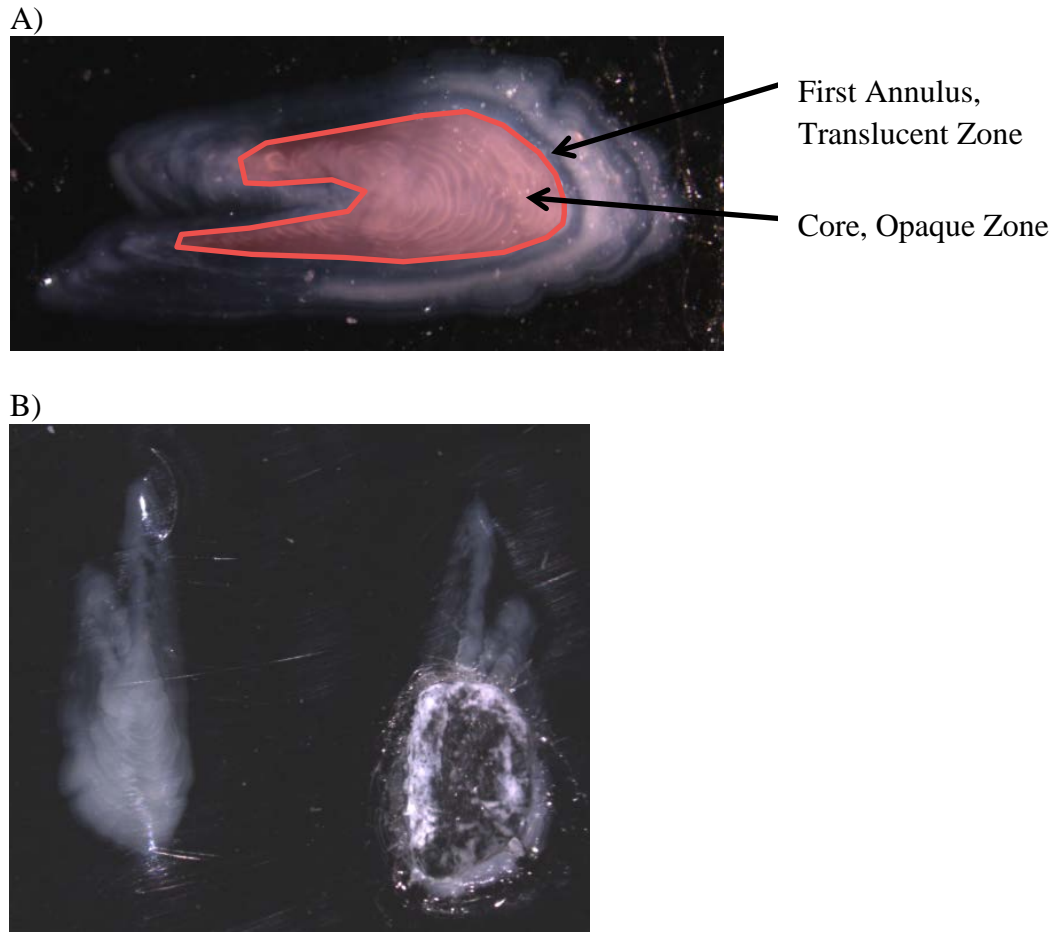


Figure 5 (A, B): A) Unmilled Atlantic mackerel otolith with the area corresponding to the first year of growth indicated in red. Note translucent zone, which delimits the natal region of the otolith; B) A pair of otoliths in which the right one has been milled using a micromill.

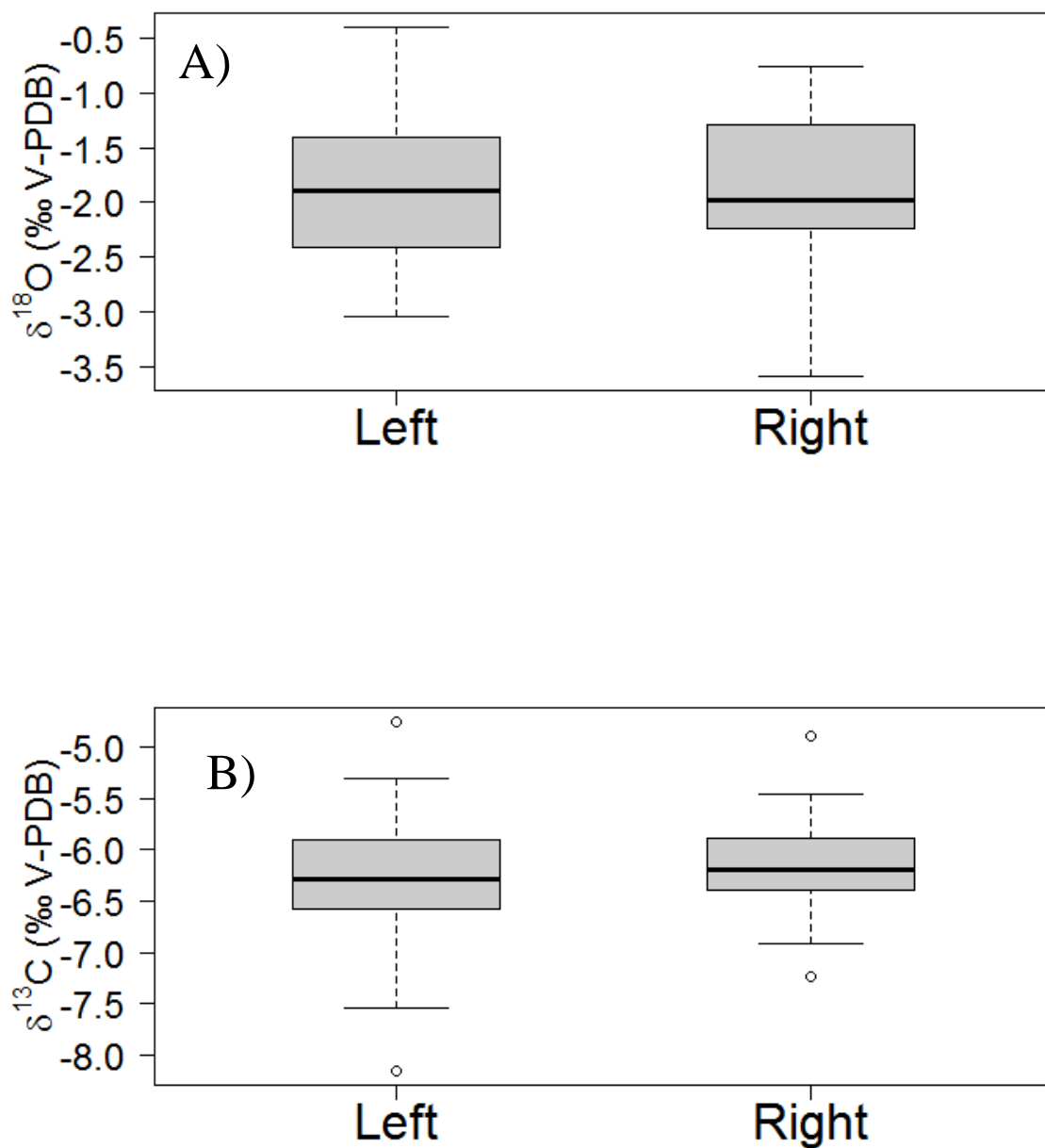


Figure 6 (A, B): Boxplots of paired left and right Atlantic mackerel otolith A)  $\delta^{18}\text{O}$  values and B)  $\delta^{13}\text{C}$  values, assessing asymmetry between the two sides within the same individual. Box covers data from the 25th – 75th percentiles, the horizontal bar marks the median, and the whiskers extend to 1.5 \* inter-quartile range or the maximum/minimum value, whichever occurs first. Values outside of 1.5 \* the inter quartile range are displayed with an additional point on the graph.

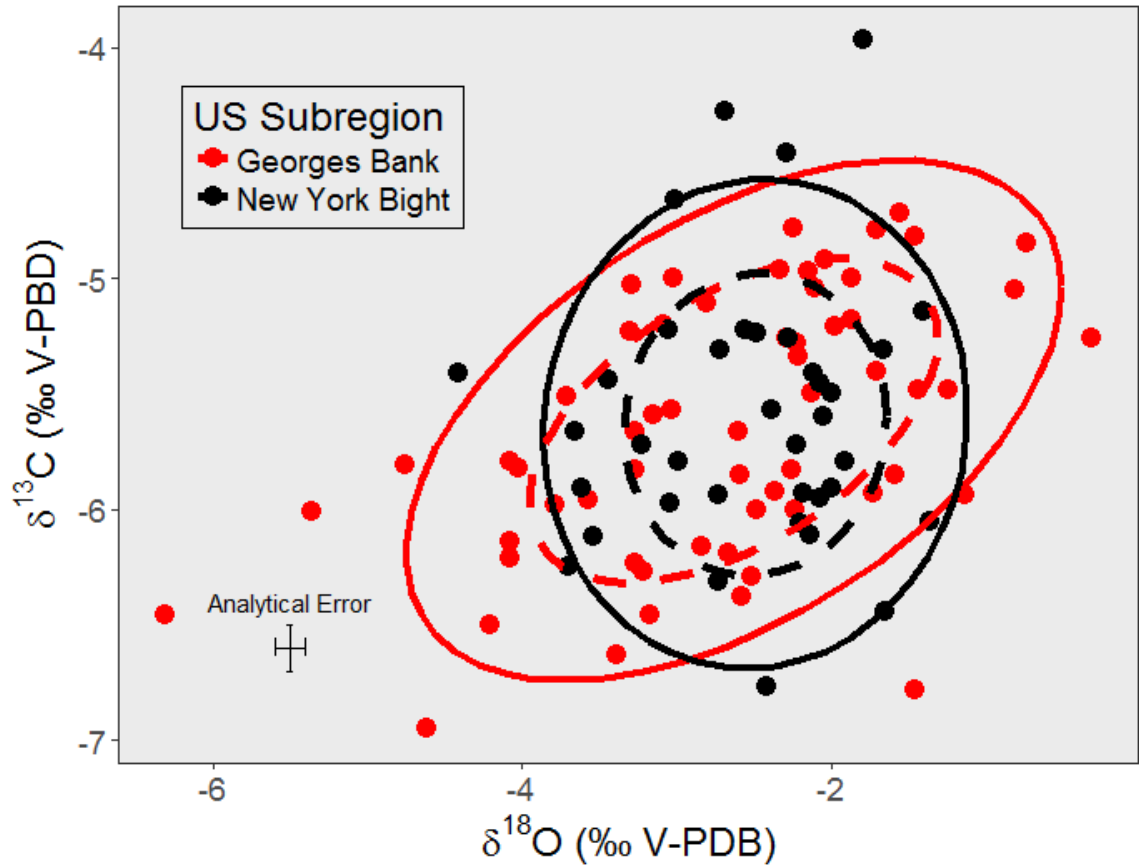


Figure 7: Biplot of otolith  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  values for age-1 Atlantic mackerel (from the 1998 through 2000 year-classes), plotted by US sub-regions. Solid and dashed ellipses indicate 90% and 60% percentile distributions of data respectively. Each point represents the isotopic value of an individual otolith and the analytical error bar represents the precision of each isotope measurement ( $\pm 0.1$  ‰).

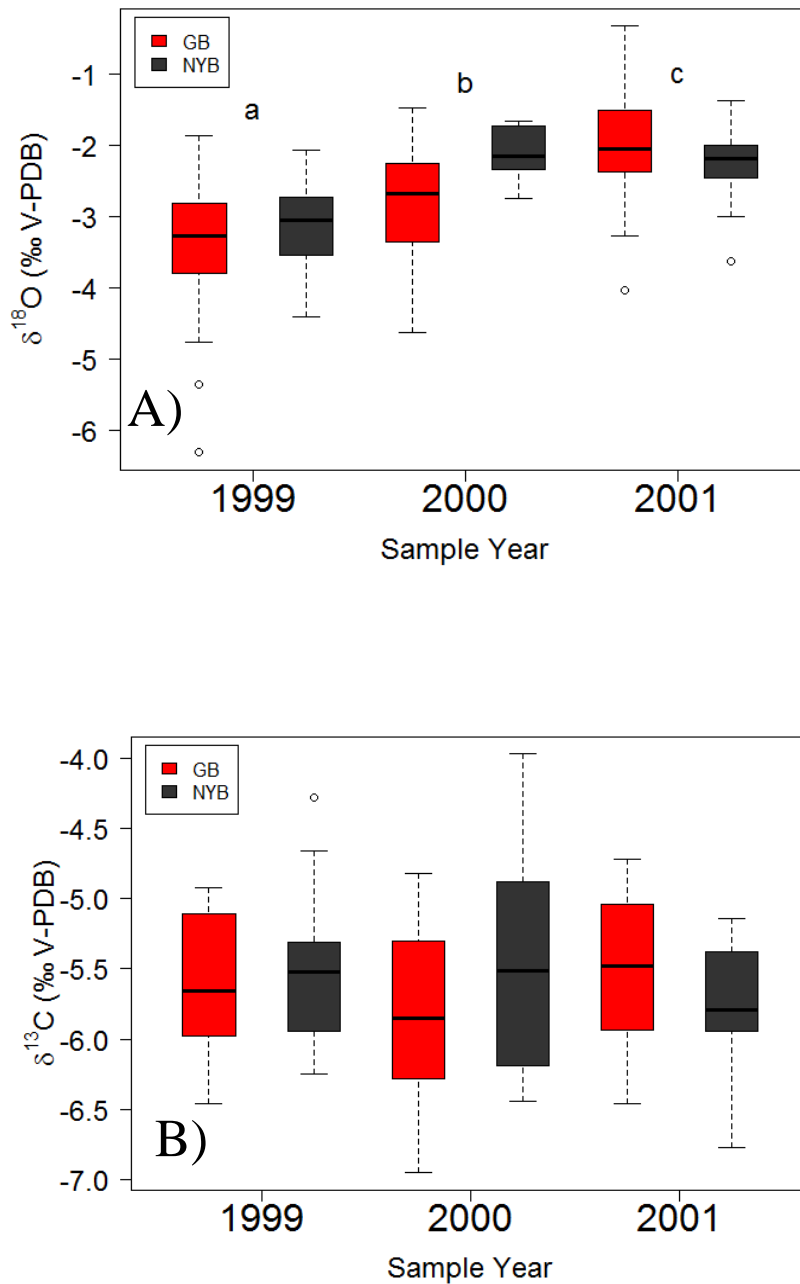


Figure 8 (A, B): Boxplot of age-1 Atlantic mackerel otolith A)  $\delta^{18}\text{O}$  values and B)  $\delta^{13}\text{C}$  values compared across years and sub-regions. Box covers data from the 25th – 75th percentiles, the horizontal bar marks the median, and the whiskers extend to 1.5 \* inter-quartile range or the maximum/minimum value, whichever occurs first. Values outside of 1.5 \* the inter quartile range are displayed with an additional point on the graph. Letters above the boxes in (A) indicate significant differences between years observed in post hoc testing using Tukey HSD.

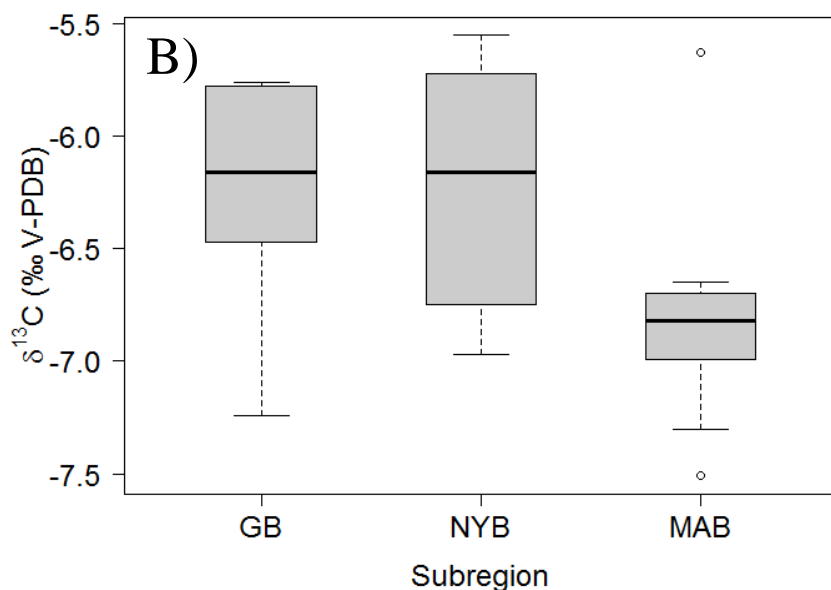
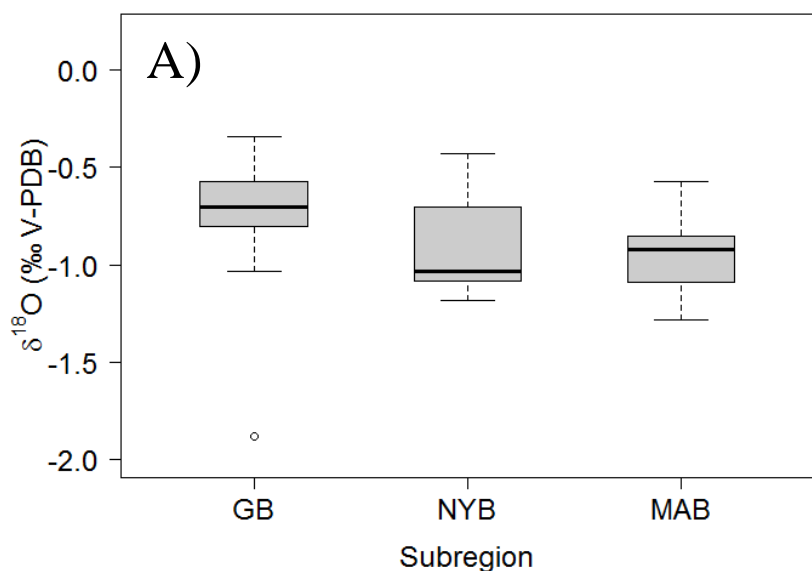


Figure 9 (A, B): Boxplot of age-0 Atlantic mackerel otolith A)  $\delta^{18}\text{O}$  values and B)  $\delta^{13}\text{C}$  values from 2003 across US sub-regions, GB=Georges Bank, NYB = New York Bight, MAB = Mid-Atlantic Bight. Box covers data from the 25th – 75th percentiles, the horizontal bar marks the median, and the whiskers extend to 1.5 \* inter-quartile range or the maximum/minimum value, whichever occurs first. Values outside of 1.5 \* the inter quartile range are displayed with an additional point on the graph.

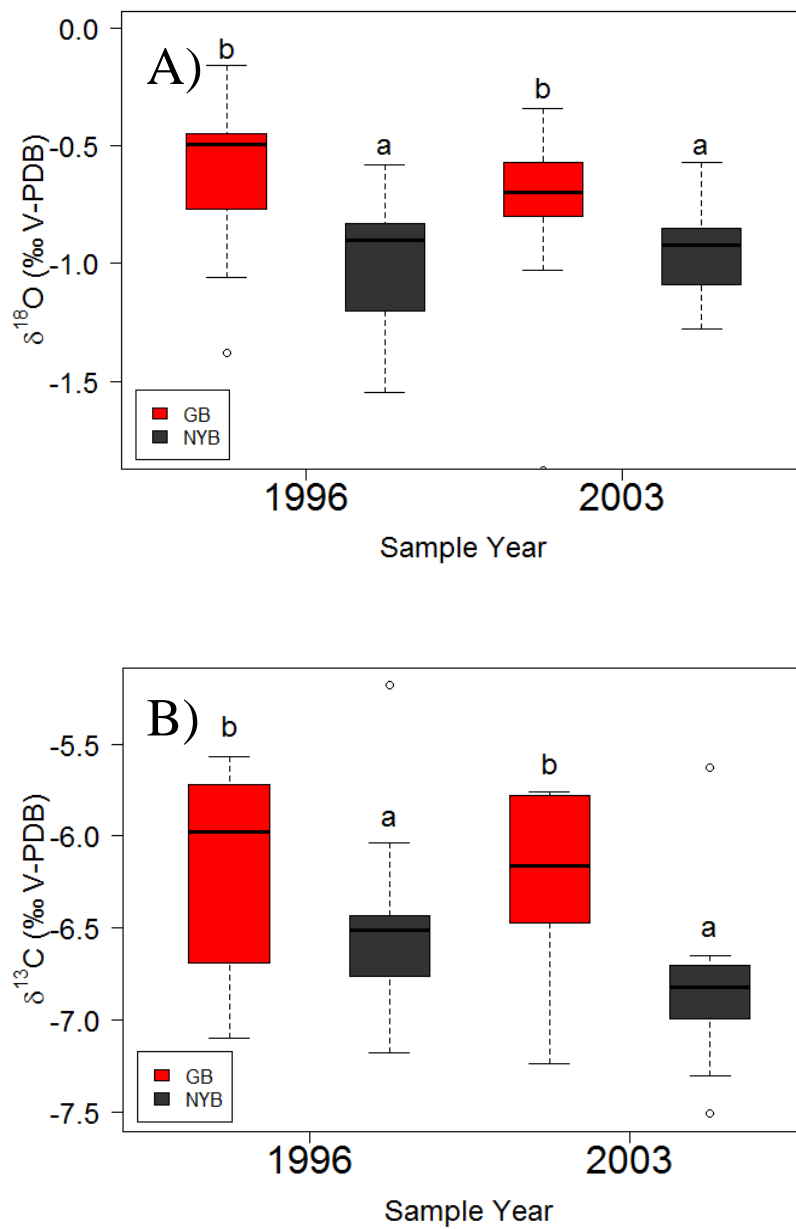


Figure 10 (A, B): Boxplot of age-0 Atlantic mackerel otolith A)  $\delta^{18}\text{O}$  values and B)  $\delta^{13}\text{C}$  values the years 1996 and 2003 for the GB and NYB . Box covers data from the 25th – 75th percentiles, the horizontal bar marks the median, and the whiskers extend to 1.5 \* inter-quartile range or the maximum/minimum value, whichever occurs first. Values outside of 1.5 \* the inter quartile range are displayed with an additional point on the graph. Letters above the boxes indicate significant differences observed in post hoc testing using Tukey HSD.

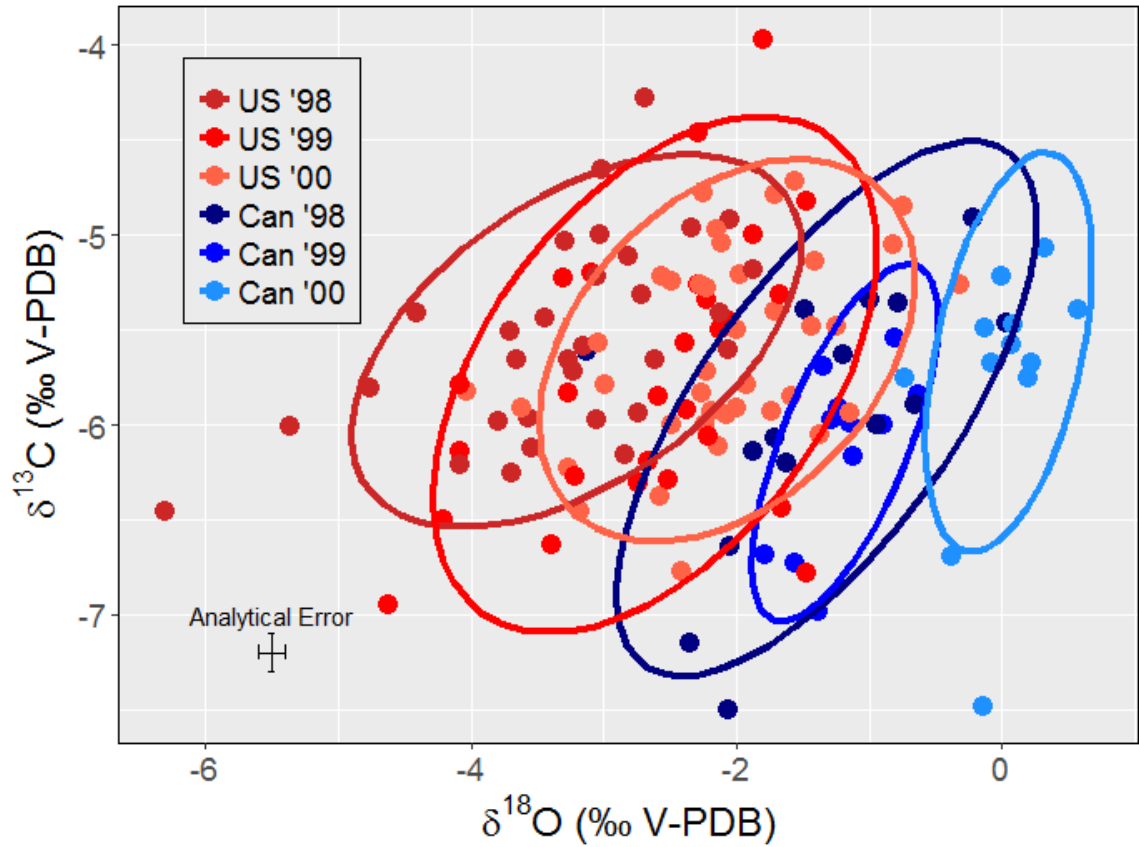


Figure 11: Biplot of age-1 otolith  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  values according to country and year-class. Solid and dashed ellipses indicate 90% and 60% percentiles respectively for each region and year-class combination. Each point represents the isotopic composition of an individual otolith and the analytical error bar represents the precision of each isotope measurement ( $\pm 0.1$  ‰).



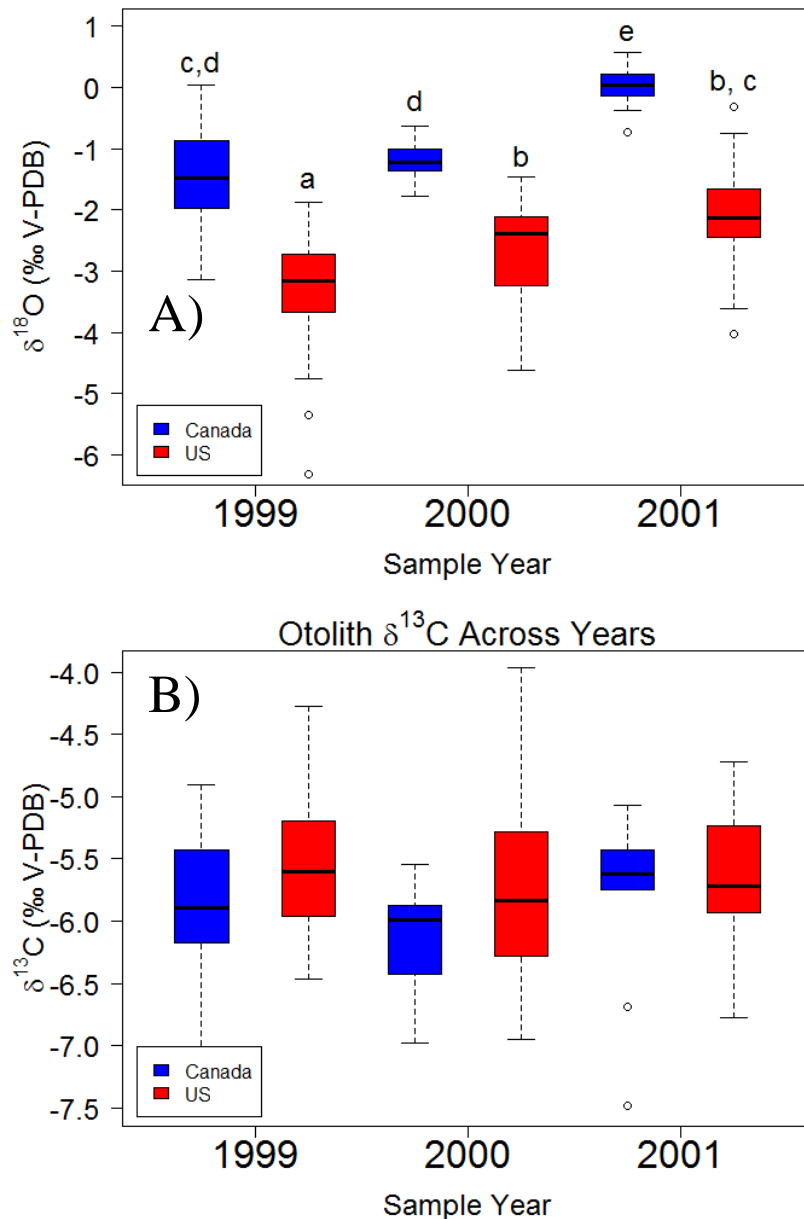


Figure 12 (A, B): Boxplot of year specific Atlantic mackerel otolith A)  $\delta^{18}\text{O}$  values and B)  $\delta^{13}\text{C}$  values in the US and Canada. The values correspond to the natal material of age-1 fish, representing the 1998 through 2000 year-classes. Box covers data from the 25th – 75th percentiles, the horizontal bar marks the median, and the whiskers extend to 1.5 \* inter-quartile range or the maximum/minimum value, whichever occurs first. Values outside of 1.5 \* the inter quartile range are displayed with an additional point on the graph. Letters above the boxes indicate significant differences observed in post hoc testing using Tukey HSD.

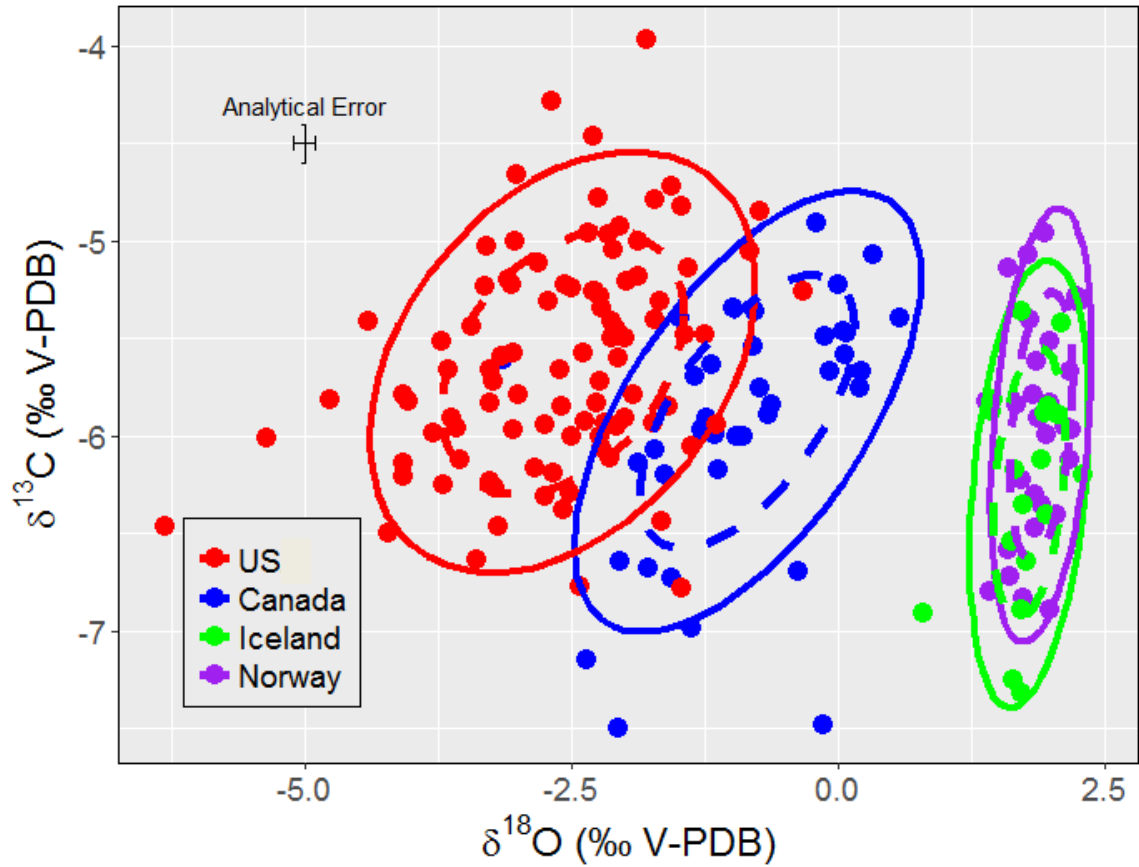


Figure 13: Biplot of otolith  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  values according to country. For US and Canadian Atlantic mackerel samples, these values come from age-1 fish (1998-2000 year-classes). For Iceland and Norway, samples are from older fish, ranging from age-3 to 12 captured in 2015. Solid and dashed ellipses indicate 90% and 60% percentiles respectively. Each point represents the isotopic composition of an individual otolith and the analytical error bar represents the precision of each isotope measurement ( $\pm 0.1$  ‰).

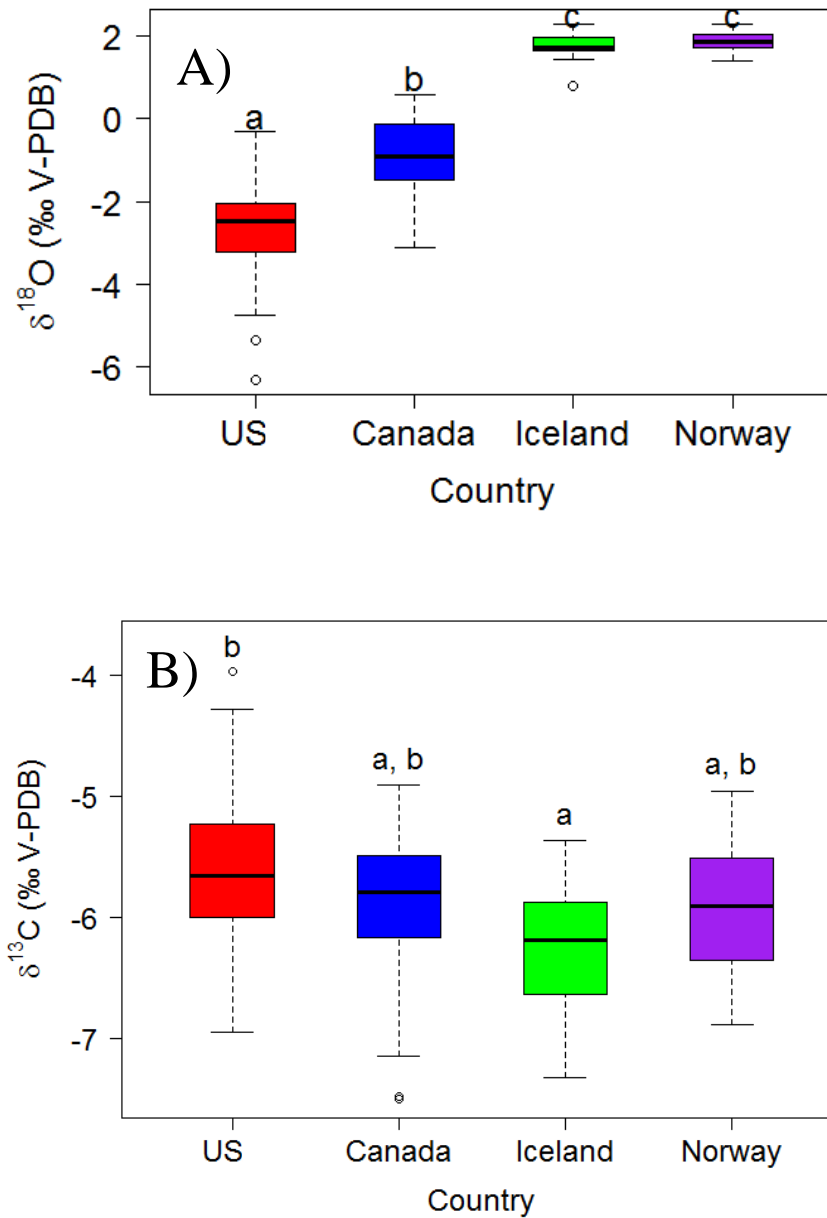


Figure 14 (A, B): Boxplot of Atlantic mackerel otolith A)  $\delta^{18}\text{O}$  values and B)  $\delta^{13}\text{C}$  values according to country. For US and Canadian Atlantic mackerel samples, these values come from age-1 fish (1998-2000 year-classes). For Iceland and Norway, samples are from older fish, ranging from age-3 to 12 captured in 2015. Box covers data from the 25th – 75th percentiles, the horizontal bar marks the median, and the whiskers extend to  $1.5 \times$  inter-quartile range or the maximum/minimum value, whichever occurs first. Values outside of  $1.5 \times$  the inter quartile range are displayed with an additional point on the graph. Letters above the boxes indicate significant differences observed in post hoc testing using Tukey HSD.

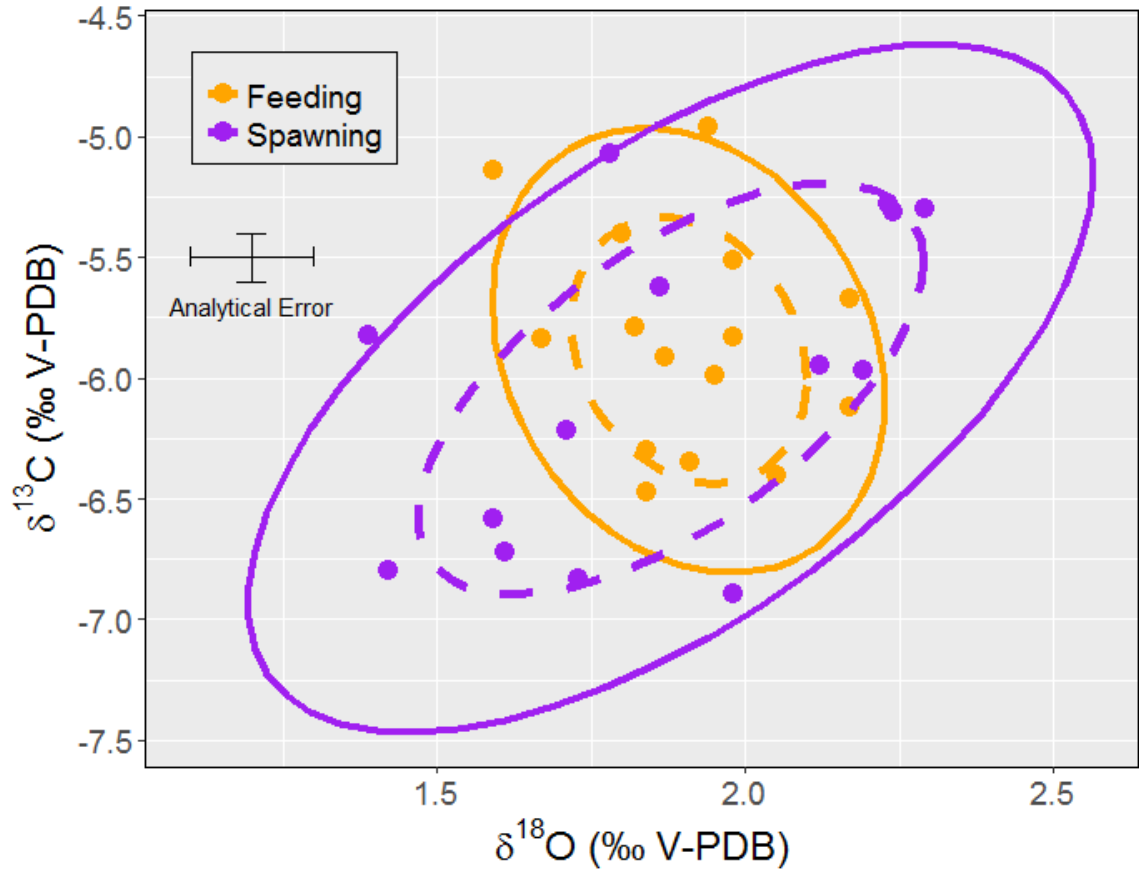


Figure 15: Biplot of otolith  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  values measured in Atlantic mackerel from feeding grounds in the Norwegian Sea and spawning grounds west of Ireland. The fish were captured in 2015 (age range 3 to 12). Solid and dashed ellipses indicate 90% and 60% percentiles respectively. Each point represents the isotopic composition of an individual otolith and the analytical error bar represents the precision of each isotopic measurement ( $\pm 0.1$  ‰).

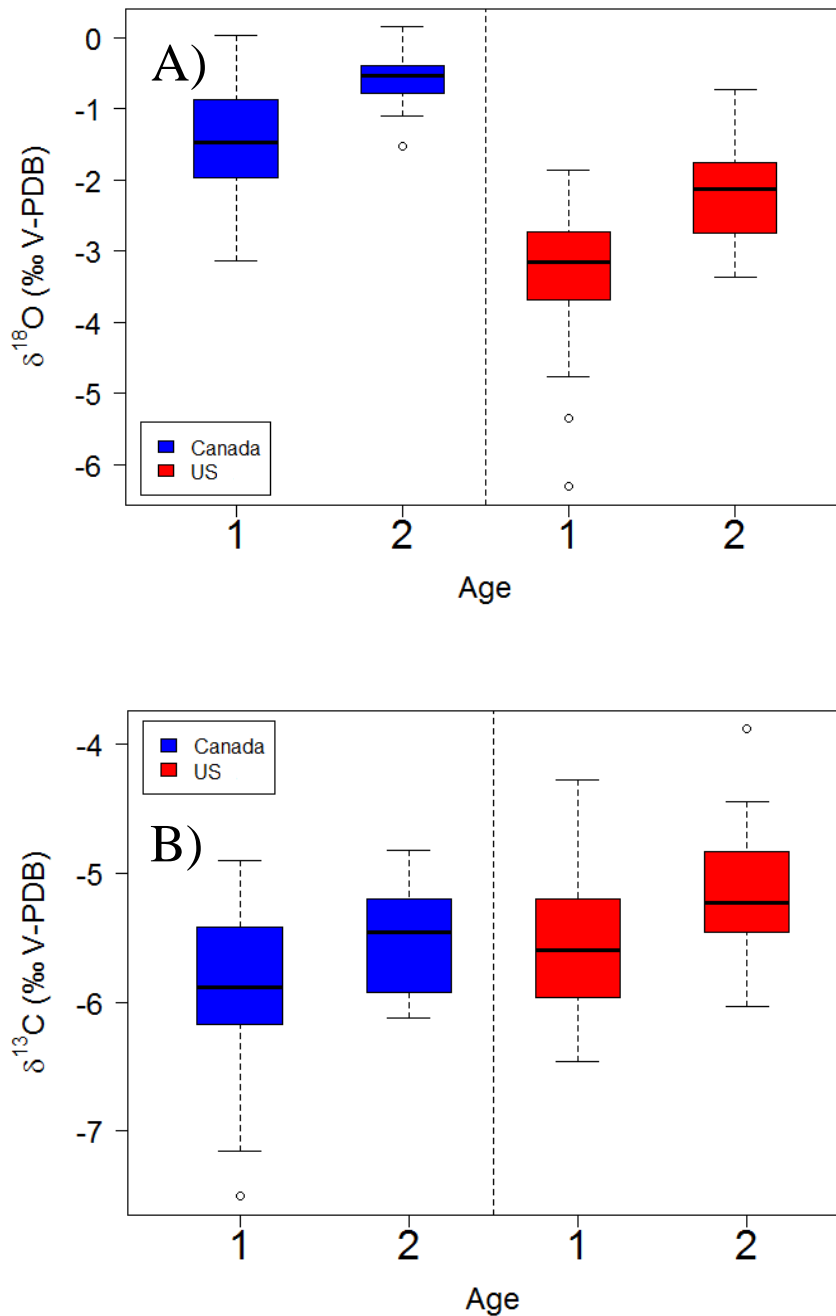


Figure 16 (A, B): Boxplot of Atlantic mackerel otolith A)  $\delta^{18}\text{O}$  and B)  $\delta^{13}\text{C}$  from the 1998 year-class (age-1 fish from 1999 and age-2 fish from 2000) from Canada and the US. Box covers data from the 25th – 75th percentiles, the horizontal bar marks the median, and the whiskers extend to 1.5 \* inter-quartile range or the maximum/minimum value, whichever occurs first. Values outside of 1.5 \* the inter quartile range are displayed with an additional point on the graph.

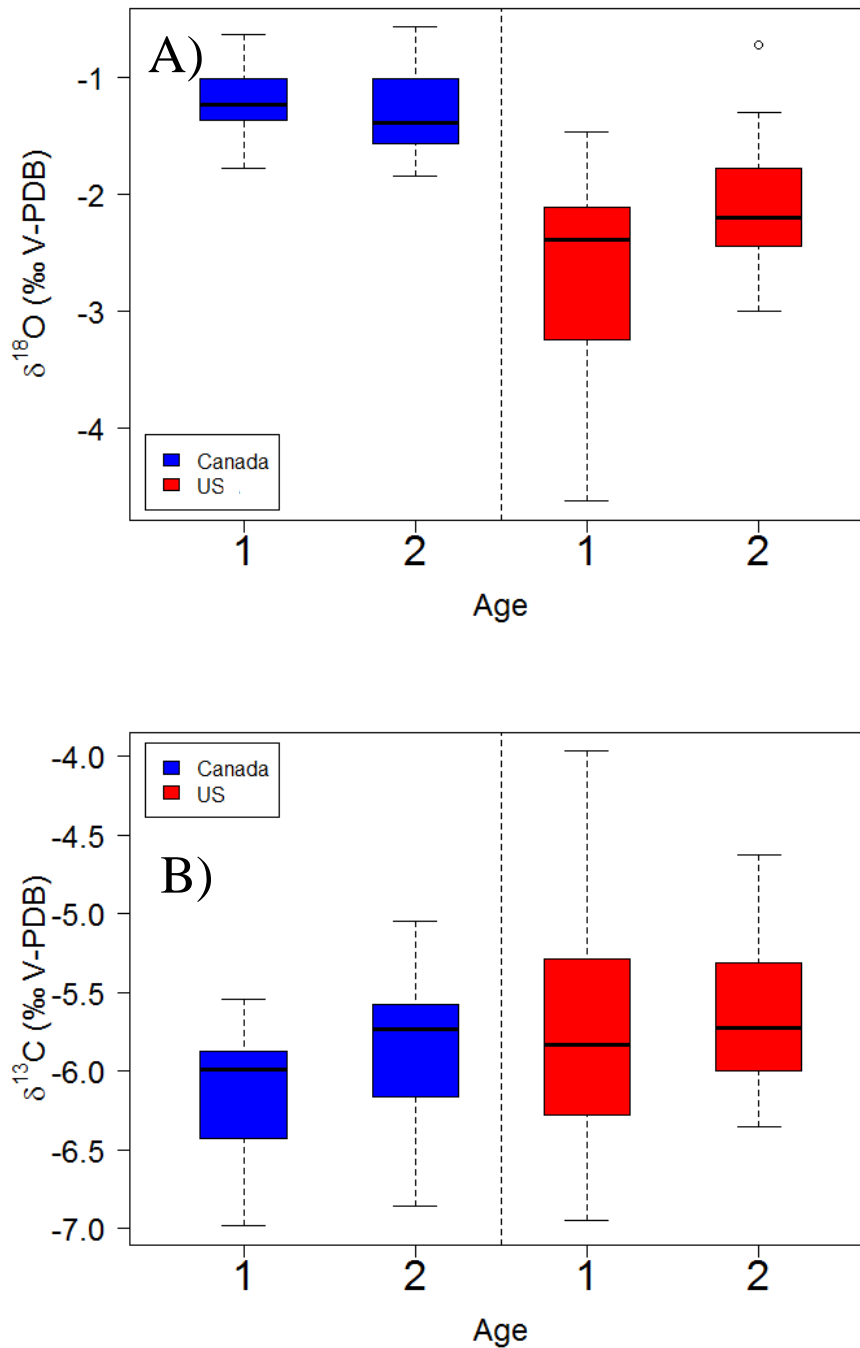


Figure 17 (A, B): Boxplot of Atlantic mackerel otolith A)  $\delta^{18}\text{O}$  and B)  $\delta^{13}\text{C}$  from the 1999 year-class (age-1 fish from 2000 and age-2 fish from 2001) from Canada and the US. Box covers data from the 25th – 75th percentiles, the horizontal bar marks the median, and the whiskers extend to 1.5 \* inter-quartile range or the maximum/minimum value, whichever occurs first. Values outside of 1.5 \* the inter quartile range are displayed with an additional point on the graph.

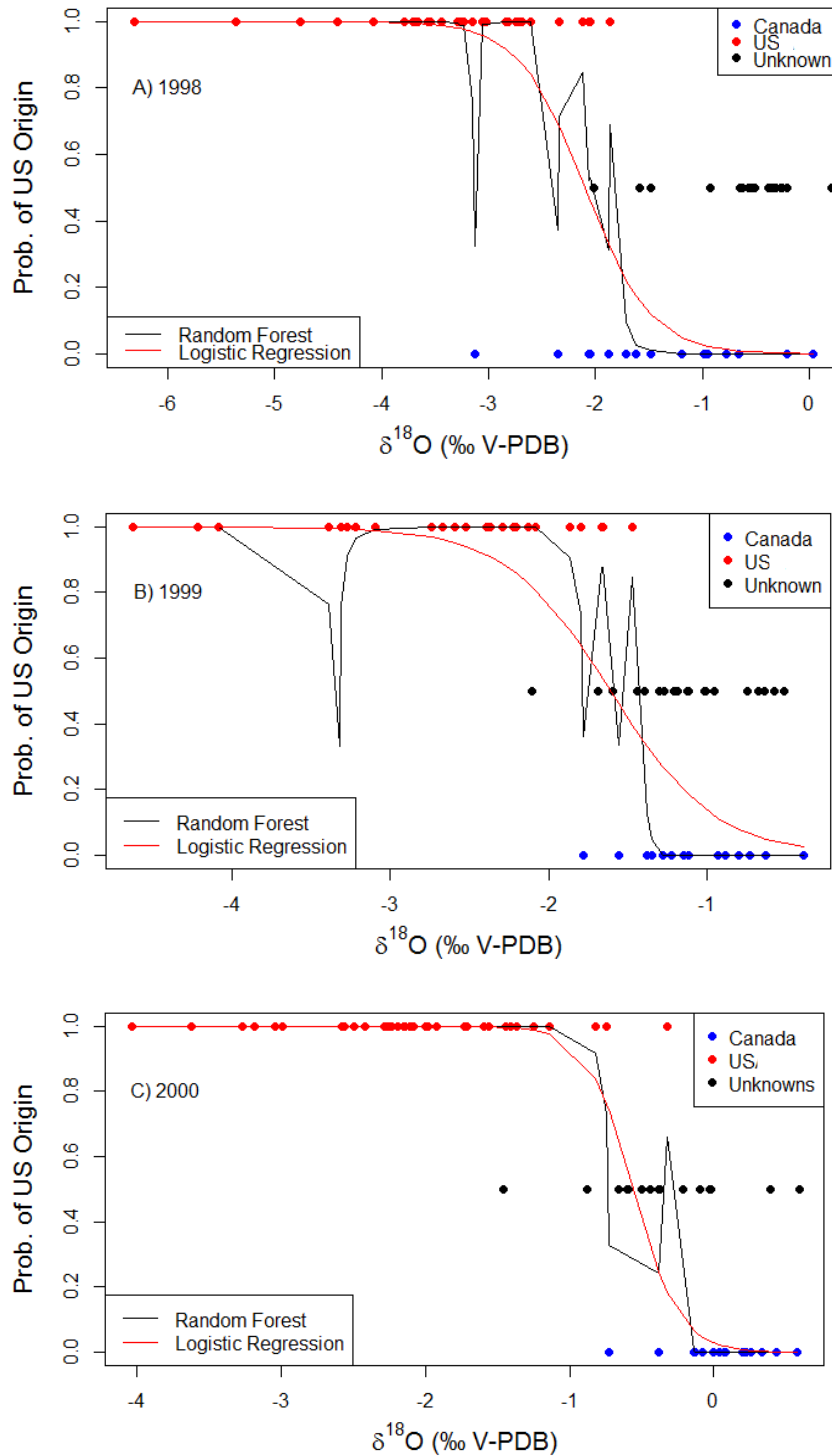


Figure 18 (A, B, C): Discrimination functions used to classify adult (age-3 and 4) Atlantic mackerel based on the 1998 (A), 1999 (B) and 2000 (C) US and Canadian otolith  $\delta^{18}\text{O}$  baseline data. Each panel shows the function for both logistic regression and random forest classification, along with the  $\delta^{18}\text{O}$  value for both the US and Canadian baselines. The  $\delta^{18}\text{O}$  value of the unknown samples is shown as the black points.

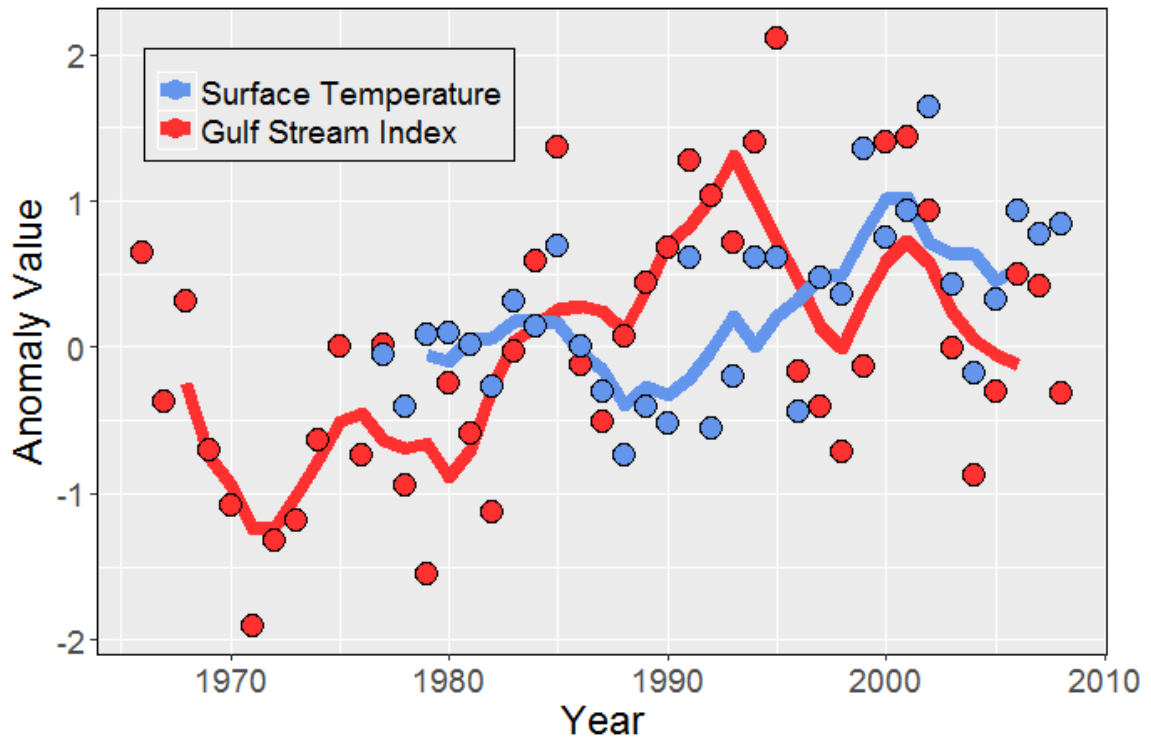


Figure 19: Time series of regional sea surface temperature anomaly and Gulf Stream index in the US Northwest Atlantic from 1977 to 2008 and 1966 to 2008 respectively. The lines are the 5-year moving average value. (Graphic extracted from Ecosystem Assessment Program NEFSC, 2009).



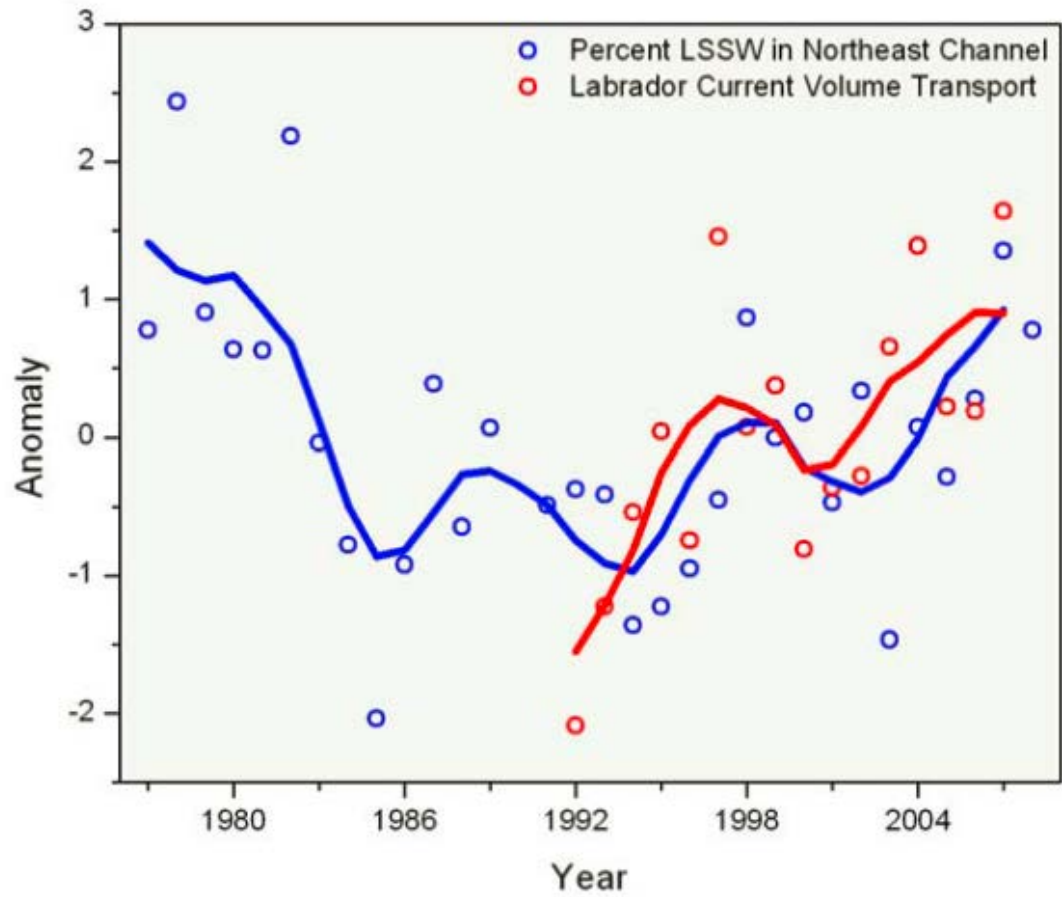


Figure 20: Time series of the Labrador Current volume transport and the percentage of Labrador subarctic slope water (LSSW) from 1977 to 2008. (Graphic extracted from Ecosystem Assessment Program NEFSC, 2009).

## References

- Asthorsson, O. S., Valdimarsson, H., Gudmundsdottir, A., and Oskarsson, G. J. 2012. Climate-related variations in the occurrence and distribution of mackerel (*Scomber scombrus*) in Icelandic waters. *ICES Journal of Marine Science*, 69: 1289–1297.
- Bakun, A. 2001. ‘School-mix feedback’: A different way to think about low frequency variability in large mobile fish populations. *Progress in Oceanography*, 49: 485–511.
- Bakun, A. 2006. Wasp-waist populations and marine ecosystem dynamics: Navigating the ‘predator pit’ topographies. *Progress in Oceanography*, 68: 271–288.
- Baumgartner, T. R., Soutar, A., and Ferreira-Bartrina, V. 1992. Reconstruction of the history of Pacific sardine and northern anchovy populations over the past two millennia from sediments of the Santa Barbara Basin, California. *California Cooperative Oceanic Fisheries Investigations*, 33: 24–40.
- Berge, J., Heggland, K., Lønne, O. J., Cottier, F., Hop, H., Gabrielsen, G. W., Nøttestad, L., and Misund, O. A. 2015. First records of Atlantic mackerel (*Scomber scombrus*) from the Svalbard Archipelago, Norway, with possible explanations for the extension of its distribution. *Arctic*, 68: 54–61.
- Box, G. E. P. 1949. A general distribution theory for a class of likelihood criteria. *Biometrika*, 36: 317–346.
- Brown, R. W., Fogarty, M., Legault, C., Miller, T., Nordahl, V., Politis, P., and Rago, P. 2008. Survey transition and calibration of bottom trawl surveys along the Northeastern continental shelf of the United States. *ICES CM Doc*: 1–25.
- Burnett, J., O’Brien, L., Mayo, R. K., Darde, J. A., and Bohan, M. 1989. Finfish maturity sampling and classification schemes used during Northeast Fisheries Center bottom trawl surveys, 1963–89. *NOAA Technical Memorandum*: 16.
- Campana, S. E. 1999. Chemistry and composition of fish otoliths: pathways, mechanisms and applications. *Marine Ecology Progress Series*, 188: 263–297.
- Campana, S. E., and Thorrold, S. R. 2001. Otoliths, increments, and elements: keys to a comprehensive understanding of fish populations? *Canadian Journal of Fisheries and Aquatic Sciences*, 58: 30–38.
- Castonguay, M., Simard, P., and Gagnon, P. 1991. Usefulness of fourier analysis of otolith shape for Atlantic mackerel (*Scomber scombrus*) stock discrimination. *Canadian Journal of Fisheries and Aquatic Sciences*, 48: 296–302.
- Chapman, D. C., and Beardsley, R. C. 1989. On the origin of shelf water in the Middle Atlantic Bight. *Journal of Physical Oceanography*, 19: 384–391.
- Ciannelli, L., Fisher, J. A. D., Skern-Mauritzen, M., Hunsicker, M. E., Hidalgo, M., Frank, K. T., and Bailey, K. M. 2013. Theory, consequences and evidence of eroding population spatial structure in harvested marine fishes: A review. *Marine*

- Ecology Progress Series, 480: 227–243.
- Cury, P., Bakun, A., Crawford, R., Jarre, A., Quiñones, R., Shannon, L., and Verheye, H. 2000. Small pelagics in upwelling systems: patterns of interaction and structural changes in ‘wasp-waist’ ecosystems. *ICES Journal of Marine Science*, 57: 603–618.
- D’Amours, D., and Castonguay, M. 1992. Spring migration of Atlantic mackerel, *Scomber scombrus*, in relation to water temperature through Cabot Strait (Gulf of St. Lawrence). *Environmental Biology of Fishes*, 34: 393–399.
- D’Amours, D. D., Landry, J., and Lambert, T. C. 1990. Growth of juvenile (0-Group) Atlantic mackerel (*Scomber scombrus*) in the Gulf of St. Lawrence. *Canadian Journal of Fisheries and Aquatic Sciences*, 47.
- Deroba, J. J., Shepherd, G., Grégoire, F., Nieland, J., and Link, J. 2010. Stock assessment of Atlantic mackerel in the Northwest Atlantic – 2009. [http://publications.gc.ca/collections/collection\\_2014/mpo-dfo/Fs3-5-2010-01-eng.pdf](http://publications.gc.ca/collections/collection_2014/mpo-dfo/Fs3-5-2010-01-eng.pdf).
- Dery, L. M. 1998. Atlantic mackerel *Scomber scombrus*. In NOAA Technical Report NMFS 72; Age Determination Methods for Northwest Atlantic Species, p. 77–84 <http://www.nefsc.noaa.gov/fbp/age-man/mack/m>. Ed. by J. Pentilla and L. M. Dery.
- Ecosystem Assessment Program NEFSC. 2009. Ecosystem status report for the Northeast U.S. continental shelf large marine ecosystem. <http://www.nefsc.noaa.gov/nefsc/publications/>.
- Edmonds, J. S., and Fletchere, W. J. 1997. Stock discrimination of pilchards *Sardinops sagax* by stable isotope ratio analysis of otolith carbonate. *Marine Ecology Progress Series*, 152: 241–247.
- Elsdon, T. S., Wells, B. K., Campana, S. E., Gillanders, B. M., Jones, C. M., Limburg, K. E., Secor, D. H., Thorrold, S. R., and Walther, B. D. 2008. Otolith chemistry to describe movements and life-history parameters of fishes: hypotheses, assumptions, limitations and inferences. *Oceanography and Marine Biology: An Annual Review*, 46: 297–330.
- Eltink, A., Warmerdam, M., and Heinen, A. 1986. Origin, migration and spawning of Southern North Sea mackerel with respect of the overspill of Western mackerel to the North Sea stock. *ICES CM Doc*: 17 p.
- Epstein, S., and Mayeda, T. 1953. Variation of  $O^{18}$  content of waters from natural sources. *Geochimica et Cosmochimica Acta*, 4: 213–224.
- Fairbanks, R. 1982. The origin of continental shelf and slope water in the New York Bight and Gulf of Maine: Evidence from  $H_2^{18}O/H_2^{16}O$  ratio measurements. *Journal of Geophysical Research*, 87: 5796–5808.
- Fairfield, C. P., Waring, G. T., and Sano, M. H. 1993. Pilot whales incidentally taken during the distant water fleet Atlantic mackerel fishery in the Mid-Atlantic Bight,

- 1984-88. Report of the International Whaling Commission Special Issue 14, 76: 107–116.
- Fisheries and Oceans Canada. 2014. Assessment of the Atlantic mackerel stock for the Northwest Atlantic (subareas 3 and 4) in 2013. [http://www.dfo-mpo.gc.ca/csas-sccs/publications/sar-as/2014/2014\\_030-eng.pdf](http://www.dfo-mpo.gc.ca/csas-sccs/publications/sar-as/2014/2014_030-eng.pdf).
- Food and Agriculture Organization. 2016. The State of World Fisheries and Aquaculture 2016. Contributing to food security and nutrition for all. Rome. 200 pp.
- Fréon, P., Cury, P., Shannon, L., and Roy, C. 2005. Sustainable exploitation of small pelagic fish stocks challenged by environmental and ecosystems changes: A review. *Bulletin of Marine Science*, 76: 385–462.
- Frew, R. D., Dennis, P. F., Heywood, K. J., Meredith, M. P., and Boswell, S. M. 2000. The oxygen isotope composition of water masses in the northern North Atlantic. *Deep Sea Research Part I: Oceanographic Research Papers*, 47: 2265–2286.
- Gao, Y. W., Joner, S. H., and Bargmann, G. G. 2001. Stable isotopic composition of otoliths in identification of spawning stocks of Pacific herring (*Clupea pallasii*) in Puget Sound. *Canadian Journal of Fisheries and Aquatic Sciences*, 58: 2113–2120.
- Gregoire, F., Castonguay, M., and Maguire, J. 2010. Is the index from the NEFSC spring research bottom trawl surveys representative of the abundance of the so-called northern contingent of Atlantic mackerel (*Scomber scombrus* L.)?
- Hanson, N. N., Wurster, C. M., and Todd, C. D. 2010. Comparison of secondary ion mass spectrometry and micromilling/continuous flow isotope ratio mass spectrometry techniques used to acquire intra-otolith  $\delta^{18}\text{O}$  values of wild Atlantic salmon (*Salmo salar*). *Rapid Communications in Mass Spectrometry*, 24: 2491–2498.
- Hiramoto, K. 1991. The sardine fishery and ecology in the Joban and Boso waters of central Japan. *In* Long-term variability of pelagic fish populations and their environment: Proceedings of the International Symposium, Sendai, Japan, 14-18 November, pp. 117--128. Ed. by T. Kawasaki. Pergamon Press.
- Høie, H., Otterlei, E., and Folkvord, A. 2004. Temperature-dependent fractionation of stable oxygen isotopes in otoliths of juvenile cod (*Gadus morhua* L.). *ICES Journal of Marine Science*, 61: 243–251.
- Hopkins, P. J. 1986. Mackerel stock discrimination using otolith morphometrics. [http://www.ices.dk/sites/pub/CM Documents/1986/H/1986\\_H7.pdf](http://www.ices.dk/sites/pub/CM Documents/1986/H/1986_H7.pdf).
- Hsieh, C., Reiss, C. S., Hunter, J. R., Beddington, J. R., May, R. M., and Sugihara, G. 2006. Fishing elevates variability in the abundance of exploited species. *Nature*, 443: 859–862.
- Hunt, G. L., and McKinnell, S. 2006. Interplay between top-down, bottom-up, and wasp-waist control in marine ecosystems. *Progress in Oceanography*, 68: 115–124.

- Huse, G., Railsback, S., and Fernö, A. 2002. Modelling changes in migration pattern of herring: collective behaviour and numerical domination. *Journal of Fish Biology*, 60: 571–582.
- ICES. 2013. Mackerel in the Northeast Atlantic (combined Southern, Western, and North Sea spawning components). [https://www.ices.dk/sites/pub/Publication Reports/Advice/2013/2013/mac-nea.pdf](https://www.ices.dk/sites/pub/Publication%20Reports/Advice/2013/2013/mac-nea.pdf).
- International Council for the Exploration of the Sea. 1977. Report of the Mackerel Working Group. Charlottenlund. <https://brage.bibsys.no/xmlui/handle/11250/102021>.
- International Council for the Exploration of the Sea. 2011. Report of the Working Group on Widely Distributed Stocks (WGWIDE). ICES CM: 642 p.
- Jansen, T. 2014. Pseudocollapse and rebuilding of North Sea mackerel (*Scomber scombrus*). *ICES Journal of Marine Science*, 71: 299–307.
- Jansen, T., Campbell, A., Brunel, T., and Worsøe Clausen, L. 2013. Spatial segregation within the spawning migration of North Eastern Atlantic mackerel (*Scomber scombrus*) as indicated by juvenile growth patterns. *PLOS ONE*, 8: e58114.
- Jansen, T., and Gislason, H. 2013. Population structure of Atlantic mackerel (*Scomber scombrus*). *PLOS ONE*, 8: e64744.
- Jansen, T., Post, S., Kristiansen, T., Óskarsson, G. J., Boje, J., MacKenzie, B. R., Broberg, M., and Siegstad, H. 2016. Ocean warming expands habitat of a rich natural resource and benefits a national economy. *Ecological Applications*.
- Jensen, F., Frost, H., Thøgersen, T., Andersen, P., and Andersen, J. L. 2015. Game theory and fish wars: The case of the Northeast Atlantic mackerel fishery. *Fisheries Research*, 172: 7–16.
- Kajanian, A., Schaffler, J. J., and Jones, C. M. 2014. Lack of equivalence in the elemental and stable isotope chemistry within the sagittal otolith of the summer flounder, *Paralichthys dentatus*. *ICES Journal of Marine Science*, 71: 356–364.
- Kalish, J. M. 1991.  $^{13}\text{C}$  and  $^{18}\text{O}$  isotopic disequilibria in fish otoliths: metabolic and kinetic effects. *Marine Ecology Progress Series*, 75: 191–203.
- Kerr, L. A., Secor, D. H., and Kraus, R. T. 2007. Stable isotope ( $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$ ) and Sr/Ca composition of otoliths as proxies for environmental salinity experienced by an estuarine fish. *Marine Ecology Progress Series*, 349: 245–253.
- Kitagawa, T., Ishimura, T., Uozato, R., Shirai, K., Amano, Y., Shinoda, A., Otake, T., Tsunogai, U., and Kimura, S. 2013. Otolith  $\delta^{18}\text{O}$  of Pacific bluefin tuna *Thunnus orientalis* as an indicator of ambient water temperature. *Marine Ecology Progress Series*, 481: 199–209.
- Lambrey de Souza, J., Sévigny, J., Chanut, J., Barry, W. F., and Grégoire, F. 2006. High

- genetic variability in the mtDNA control region of a Northwestern Atlantic teleost, *Scomber scombrus* L. Canadian Technical Report of Fisheries and Aquatic Sciences: 33 p.
- LeGrande, A. N., and Schmidt, G. A. 2006. Global gridded data set of the oxygen isotopic composition in seawater. *Geophysical Research Letters*, 33: 1–5.
- Liaw, A., and Wiener, M. 2002. Classification and regression by randomForest. *R News*, 2: 18–22.
- Link, J. S., Nye, J. A., and Hare, J. A. 2011. Guidelines for incorporating fish distribution shifts into a fisheries management context. *Fish and Fisheries*, 12: 461–469.
- MacCall, A. D. 1990. *Dynamic Geography of Marine Fish Populations*. University of Washington Press, Seattle. 153 pp.
- MAFMC. 2015. Memorandum, Report of the May 2015 meeting on squids, butterfish and Atlantic mackerel.  
<https://static1.squarespace.com/static/511cdc7fe4b00307a2628ac6/t/555e328de4b0e15bc3f35256/1432236685060/May+2015+SSC+Report.pdf>.
- Maguire, J. J., Chagnon, Y. C., Castonguay, M., and Mercille, B. 1987. A review of mackerel management areas in the Northwest Atlantic. *CAFSAC Res. Doc*, 71: 31.
- McClatchie, S., Hendy, I. L., Thompson, A. R., and Watson, W. 2017. Collapse and recovery of forage fish populations prior to commercial exploitation. *Geophysical Research Letters*, 44: 1877–1885.
- McMahon, K. W., Ling Hamady, L., and Thorrold, S. R. 2013. A review of ecogeochemistry approaches to estimating movements of marine animals. *Limnology and Oceanography*, 58: 697–714.
- McQuinn, I. H. 1997. Metapopulations and the Atlantic herring. *Reviews in Fish Biology and Fisheries*, 7: 297–329.
- Menge, B. A. 2000. Top-down and bottom-up community regulation in marine rocky intertidal habitats. *Journal of Experimental Marine Biology and Ecology*, 250: 257–289.
- Mercier, L., Darnaude, A. M., Bruguier, O., Vasconcelos, R. P., Henrique, N., Costa, M. J., Lara, M., Jones, D. L., Mouillot, D., Vasconcelos, P., Costa, J., Montpellier, U., Bataillon, P. E., Cedex, M., Montpellier, U., Bataillon, P. E., and Cedex, M. 2015. Selecting statistical models and variable combinations for optimal classification using otolith microchemistry. *Ecological Applications*, 21: 1352–1364.
- Moores, J. a., Winters, G. H., and Parsons, L. S. 1975. Migrations and biological characteristics of Atlantic mackerel (*Scomber scombrus*) occurring in Newfoundland waters. *Journal of the Fisheries Research Board of Canada*, 32: 1347–1357. NRC Research Press Ottawa, Canada.

- Moustahfid, H., Link, J. S., Overholtz, W. J., and Tyrrell, M. C. 2009. The advantage of explicitly incorporating predation mortality into age-structured stock assessment models : an application for Atlantic mackerel. *ICES Journal of Marine Science*, 66: 445–454.
- National Environmental Satellite Data and Information Service. (n.d.). NOAA Climatic Data Center. <https://www7.ncdc.noaa.gov/CDO/CDODivisionalSelect.jsp> (Accessed 25 March 2017).
- NEFSC (Northeast Fisheries Science Center). 1996. Report of the 20th Northeast Regional Stock Assessment Workshop (20th SAW). Northeast Fisheries Science Center Reference Document 95-19: 52 p.
- NEFSC (Northeast Fisheries Science Center). 2002. Report of the workshop on trawl warp effects on fishing gear performance, Marine Biological Laboratory, Woods Hole, Massachusetts, October 2-3, 2002. Northeast Fisheries Science Center Reference Document, 2: 80 p.
- Nelson, C. S., Northcote, T. G., and Hendy, C. H. 1989. Potential use of oxygen and carbon isotopic composition of otoliths to identify migratory and non-migratory stocks of the New Zealand common smelt: a pilot study. *New Zealand Journal of Marine & Freshwater Research*, 23: 337–344.
- Newman, S. J., Buckworth, R. C., Mackie, M. C., Lewis, P. D., Wright, I. W., Williamson, P. C., Bastow, T. P., and Ovenden, J. R. 2009. Spatial subdivision among assemblages of Spanish mackerel, *Scomberomorus commerson* (Pisces: Scombridae) across northern Australia: implications for fisheries management. *Global Ecology and Biogeography*, 18: 711–723.
- Newman, S. J., Wright, I. W., Rome, B. M., Mackie, M. C., Lewis, P. D., Buckworth, R. C., Ballagh, A. C., Garrett, R. N., Stapley, J., Broderick, D., Ovenden, J. R., and Welch, D. J. 2010. Stock structure of grey mackerel, *Scomberomorus semifasciatus* (Pisces: Scombridae) across northern Australia, based on otolith stable isotope chemistry. *Environmental Biology of Fishes*, 89: 357–367.
- Niklitschek, E. J., Secor, D. H., Toledo, P., Valenzuela, X., Cubillos, L. A., and Zuleta, A. 2014. Nursery systems for Patagonian grenadier off Western Patagonia: large inner sea or narrow continental shelf? *ICES Journal of Marine Science*, 71: 374–390.
- NMFS-NEFSC. 2001. Fishermen's report bottom trawl survey. [http://www.nefsc.noaa.gov/esb/mainpage/rsr/sbts/sbts\\_2001/large\\_file.pdf](http://www.nefsc.noaa.gov/esb/mainpage/rsr/sbts/sbts_2001/large_file.pdf).
- NMFS-NEFSC. 2016. Resource survey report bottom trawl survey. [http://www.nefsc.noaa.gov/esb/mainpage/rsr/sbts/sbts\\_2016/large\\_file.pdf](http://www.nefsc.noaa.gov/esb/mainpage/rsr/sbts/sbts_2016/large_file.pdf).
- NOAA Office of Science And Technology. (n.d.). Commercial Fisheries Statistics: Annual Commercial Landing Statistics. [https://www.st.nmfs.noaa.gov/st1/commercial/landings/annual\\_landings.html](https://www.st.nmfs.noaa.gov/st1/commercial/landings/annual_landings.html).

- Nøttestad, L., Utne, K. R., Guðmundur, J. O., Tangen, Ø., Anthonypillai, V., Aanes, S., Vølstad, J. H., Bernasconi, M., Holst, J. C., Jansen, T., Slotte, A., Debes, H., Smith, L., Sveinbjornsson, S., Holst, J. C., Jansen, T., and Slotte, A. 2016. Quantifying changes in abundance, biomass, and spatial distribution of Northeast Atlantic mackerel (*Scomber scombrus*) in the Nordic seas from 2007 to 2014. *ICES Journal of Marine Science*, 73: 359–373.
- Nye, J., Link, J., Hare, J., and Overholtz, W. 2009. Changing spatial distribution of fish stocks in relation to climate and population size on the Northeast United States continental shelf. *Marine Ecology Progress Series*, 393: 111–129.
- O'Brien, L., Burnett, J., and Mayo, R. K. 1993. Maturation of nineteen species of finfish off the Northeast coast of the United States, 1985-1990. NOAA Technical Report NMFS 113: 72 pp.
- O'Neil, J. R., Clayton, R. N., and Mayeda, T. K. 1969. Oxygen isotope fractionation in divalent metal carbonates. *The Journal of Chemical Physics*, 51: 5547–5558.
- Overholtz, W. J., Hare, J. A., and Keith, C. M. 2011. Impacts of interannual environmental forcing and climate change on the distribution of Atlantic mackerel on the U.S. Northeast continental shelf. *Marine and Coastal Fisheries*, 3: 219–232.
- Pacariz, S. V., Hátún, H., Jacobsen, J. A., Johnson, C., Eliassen, S., and Rey, F. 2016. Nutrient-driven poleward expansion of the Northeast Atlantic mackerel (*Scomber scombrus*) stock: A new hypothesis. *Elementa: Science of the Anthropocene*, 4:105: 13 p.
- Petitgas, P. 1998. Biomass-dependent dynamics of fish spatial distributions characterized by geostatistical aggregation curves. *ICES Journal of Marine Science*, 55: 443–453.
- R Core Team. 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Radlinski, M. K., Sundermeyer, M. A., Bisagni, J. J., and Cadrin, S. X. 2013. Spatial and temporal distribution of Atlantic mackerel (*Scomber scombrus*) along the northeast coast of the United States, 1985-1999. *ICES Journal of Marine Science*, 70: 1151–1161.
- Reiss, H., Hoarau, G., Dickey-Collas, M., and Wolff, W. J. 2009. Genetic population structure of marine fish: mismatch between biological and fisheries management units. *Fish and Fisheries*, 10: 361–395.
- Rooker, J. R., Secor, D. H., DeMetrio, G., Kaufman, A. J., Belmonte-Ríos, A., and Ticina, V. 2008. Evidence of trans-Atlantic movement and natal homing of bluefin tuna from stable isotopes in otoliths. *Marine Ecology Progress Series*, 368: 231–239.
- Schmidt, G. A., Bigg, G. R., and Rohling, E. J. 1999. Global Seawater Oxygen-18 Database– v1.21. <http://data.giss.nasa.gov/o18data/>.
- Schwartzlose, R. A., Alheit, J., Bakun, A., Baumgartner, T. R., Cloete, R., Crawford, R. J.



- M., Fletcher, W. J., Green-Ruiz, Y., Hagen, E., Kawasaki, T., Lluch-Belda, D., Lluch-Cota, S. E., MacCall, A. D., Matsuura, Y., Nevárez-Martínez, M. O., Parrish, R. H., Roy, C., Serra, R., Shust, K. V., Ward, M. N., and Zuzunaga, J. Z. 1999. Worldwide large-scale fluctuations of sardine and anchovy populations. *South African Journal of Marine Science*, 21: 289–347.
- Secor, D. H. 1999. Specifying divergent migrations in the concept of stock: the contingent hypothesis. *Fisheries Research*, 43: 13–34.
- Secor, D. H. 2014. The Unit Stock Concept: Bounded Fish and Fisheries. *In Stock Identification Methods: Applications in Fishery Science*, 2nd edn, p. 566. Ed. by S. X. Cadrin, L. A. Kerr, and S. Mariani. Academic Press, New York.
- Secor, D. H. 2015. *Migration Ecology of Marine Fishes*. Johns Hopkins University Press, Baltimore. 304 pp.
- Secor, D. H., Gahagan, B., and Rooker, J. R. 2013. Atlantic bluefin tuna stock mixing within the U.S. North Carolina recreational fishery, 2011-2012. *Collective Volume of Scientific Papers ICCAT*, 69: 947–954.
- Secor, D. H., Rooker, J. R., Gahagan, B. I., Siskey, M. R., and Wingate, R. W. 2015. Depressed resilience of bluefin tuna in the western atlantic and age truncation. *Conservation Biology*, 29: 400–408.
- Sette, O. E. 1950. Biology of the Atlantic mackerel (*Scomber scombrus*) of North America: Part II - Migration and habits. *Fisheries Bulletin of the Fish and Wildlife Service*, 51: 110 p.
- Siskey, M. R., Wilberg, M. J., Allman, R. J., Barnett, B. K., and Secor, D. H. 2016. Forty years of fishing: changes in age structure and stock mixing in northwestern Atlantic bluefin tuna (*Thunnus thynnus*) associated with size-selective and long-term exploitation. *ICES Journal of Marine Science: Journal du Conseil*: fsw115.
- Solomon, C. T., Weber, P. K., Cech, Jr., J. J., Ingram, B. L., Conrad, M. E., Machavaram, M. V., Pogodina, A. R., and Franklin, R. L. 2006. Experimental determination of the sources of otolith carbon and associated isotopic fractionation. *Canadian Journal of Fisheries and Aquatic Sciences*, 63: 79–89.
- Storm-Suke, A., Dempson, J. B., Reist, J. D., and Power, M. 2007. A field-derived oxygen isotope fractionation equation for *Salvelinus* species. *Rapid Communications in Mass Spectrometry*, 21: 4109–4116.
- Tabachnick, B. G., and Fidell, L. S. 2001. *Using Multivariate Statistics*. Pearson, New York. 963 pp.
- Thorrold, S. R., Campana, S. E., Jones, C. M., and Swart, P. K. 1997. Factors determining  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  fractionation in aragonitic otoliths of marine fish. *Geochimica et Cosmochimica Acta*, 61: 2909–2919.
- TRAC (Transboundary Resource Assessment Committee). 2010. Atlantic Mackerel in

- the Northwest Atlantic. TRAC Status Report: 12 p.
- Trueman, C. N., Mackenzie, K. M., and Palmer, M. R. 2012. Identifying migrations in marine fishes through stable-isotope analysis. *Journal of Fish Biology*, 81: 826–847.
- Tyrrell, M. C., Link, J. S., Moustahfid, H., and Overholtz, W. J. 2008. Evaluating the effect of predation mortality on forage species population dynamics in the Northeast US continental shelf ecosystem using multispecies virtual population analysis. *ICES Journal of Marine Science*, 65: 1689–1700.
- Urey, H. C. 1947. The thermodynamic properties of isotopic substances. *Journal of the Chemical Society*: 562–581.
- Waring, G. T., Josepkson, E., Maze-Foley, K., and Rosel, P. E. 2015. US Atlantic and Gulf of Mexico marine mammal stock assessments -- 2014. NOAA Tech Memo NMFS NE 231: 361.
- Wiedenmann, J. 2015. Application of data-poor harvest control rules to Atlantic mackerel. [http://sedarweb.org/docs/wsupp/S46\\_RD\\_09\\_Mackerel\\_ABC\\_reportOpt.pdf](http://sedarweb.org/docs/wsupp/S46_RD_09_Mackerel_ABC_reportOpt.pdf).
- Williams, A. E., Moss, B., and Easton, J. 2002. Fish induced macrophyte loss in shallow lakes : top down and bottom up processes in mesocosm experiments. *Freshwater Biology*, 47: 2216–2232.