Original Article

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

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Over the past 40 years, northwestern Atlantic bluefin tuna (*Thunnus thynnus*) have experienced high rates of exploitation, targeted fishing on the largest size classes of the population, and an unknown degree of Mediterranean-stock contribution. Lack of recovery despite targeted re-building efforts by management prompted an evaluation of the population for changes in age-structure, size-at-age, and stock mixing over three samples (1974–8, 1996–2002, and 2009–14) coinciding with a cycle of exploitation that initially targeted smaller fish, but then showed strong selectivity for the largest and oldest members of the population. Ages and mixing levels were estimated using port- and observer-sampled otoliths collected by the US National Marine Fisheries Service. A comparison of age structure between the 1970s sample and two later samples indicated strong age truncation had occurred, where both mean age (13, 4, and 7 years) and mean length (191, 166, and 159 cm curved fork length) declined among samples. In addition, minor changes in size-at-age were detected among the three samples. Otolith stable isotope analysis indicated fluctuating stock composition, with a substantially higher contribution of Mediterranean-origin fish in the 1990s (48% eastern stock contribution) than in the 1970s (0% contribution) and the most recent sample (4% contribution). Higher mixing and severe age truncation in the 1990s indicated that the northwestern Atlantic population was at a depressed state. Reduced mixing and a slightly expanded age structure in the most recent sample could suggest that recovery has begun. Still, to evaluate the hypothesized cycle of collapse and modest recovery more rigorously, an integrative assessment framework is needed to consider the dynamic nature of stock productivity, trans-oceanic migrations, and fishing selectivity.

Keywords: age structure, bluefin tuna, connectivity, growth, otolith chemistry, size-selective fishing, stock mixing.

Introduction

Steep declines in commercially important fish populations during the past 50 years are well documented (Hutchings, 2000; Myers and Worm, 2003), as are the effects of fishing on ecosystems and population production (Pikitch *et al.*, 2004; Worm *et al.*, 2009). With markets and gear that specifically target certain size (and age) categories, fisheries can lead to short-term demographic changes. Long-term exploitation and selection of larger individuals of a cohort has been associated with reductions of size, age, size-at-maturity, and reproductive capacity (Hutchings, 2000; Hixon *et al.*, 2014). Fishing has been associated with decreased size in rockfishes (*Sebastes* spp.; Harvey *et al.*, 2006) and decreased size and age in Chinook salmon (*Oncorhynchus tsha-wytscha*) (Ricker, 1981). Sustained fishing pressure on red porgy

(*Pagrus pagrus*) reduced mean size-at-age, growth rate, and size-at-maturity over a 20-year period (Harris and McGovern, 1997).

Recruitment variance is expected to be higher in populations that undergo age truncation, driven by a reduction in storage effect (Secor, 2007), which describes the degree to which age structure and overlapping generations allow populations to sample across years that vary in conditions which may or may not favor early larval and juvenile survival (Warner and Chesson, 1985; Anderson *et al.*, 2008; Rouyer *et al.*, 2012). Age truncation and a compromised storage effect are especially detrimental to periodic strategists, such as Atlantic bluefin tuna (*Thunnus thynnus*; ABFT), a large (maximum size = 330 cm; Cort *et al.*, 2013), iteroparous teleost with a moderate longevity (>30 years) and low early survival. These fish depend on a broad and diverse adult age structure to sample multiple reproductive seasons for favourable spawning and larval conditions in order to produce strong, successful year-classes (Secor, 2007).

Atlantic bluefin tuna consists of two spawning populations, or stocks: a Gulf of Mexico/US Atlantic-spawning (western) stock in the western North Atlantic, and a Mediterranean-spawning (eastern) stock in the eastern North Atlantic (Figure 1; Rooker *et al.*, 2007; Fromentin *et al.*, 2014; Richardson *et al.*, 2016). The two stocks of ABFT are assessed under the restrictive assumption that an equal number of individuals mix between stocks (i.e. no net mixing) (SCRS, 2014). However, ample evidence of migration across the international management boundary now exists via tagging, genetics, and otolith chemistry studies, allowing this assumption to be tested (Rooker *et al.*, 2008; Dickhut *et al.*, 2009; Wilson *et al.*, 2015).

Otolith stable isotope analysis of δ^{13}C and δ^{18}O values has greatly expanded our understanding of stock separation (natal homing) and mixing (trans-oceanic migration) (Rooker *et al.*, 2008; Secor *et al.*, 2015), and has revealed key elements of stock structure in ABFT, including (i) no mixing occurs in the two principal spawning areas; (ii) at times, a variable but considerable eastern stock subsidy contributes to North American (USA and Canadian) fisheries [0–57% for 1997–2000 and 2011–2013 samples]; (iii) in these same North American fisheries, juveniles size-classes [<180 cm curved fork length (CFL)] exhibit much higher levels of mixing than adults; and (iv) contribution of the western stock to eastern North Atlantic and Mediterranean fisheries is minimal [<7% for 2003–7, 2010–11 samples (Rooker *et al.*, 2008; Rooker *et al.*, 2014)]. Mixing levels likely vary through time, possibly influenced by stock-specific production and trans-oceanic migrations. However, the degree of these fluctuations is not well known (Secor *et al.*, 2015).

The development of selective fishing in the western ABFT fishery from growth overfishing (exploitation of younger age categories with the purse seine fisheries of the 1950s and 1960s) to recruitment overfishing (targeting larger individuals in the 1960s and 1970s) paired with chronic, long-term exploitation and subsequent low levels of abundance may have caused a substantial reduction in age structure and a shift to a lower production level (Secor *et al.*, 2015). Further, under scenarios of moderate stock mixing, perceived strong year-classes in the western North Atlantic could in fact result from eastern stock subsidy instead of pulses in western-stock production [National Research Council (NRC), 1994; Rooker *et al.*, 2008; Graves *et al.*, 2015]. Accordingly, we posited that long-term fishing on northwest ABFT has resulted in age truncation and increased mixing with northeast ABFT originating in the Mediterranean Sea (the eastern stock). Further, we hypothesized that as larger, faster-growing individuals were fished out of the population, size-at-age in more recent periods would reflect slower growth rates (Conover and Munch, 2002; Walsh *et al.*, 2006).

The objective of this study was to evaluate historical changes in stock mixing, age structure, and size-at-age of the western stock ABFT in response to long-term and fluctuating size-selective exploitation intensity. Therefore, we examined age-frequency, mixing levels, and size-at-age in three samples of port-sampled otoliths collected by the US National Marine Fisheries Service (NMFS) during 1974–1978, 1996–2002, and 2009–2014. These
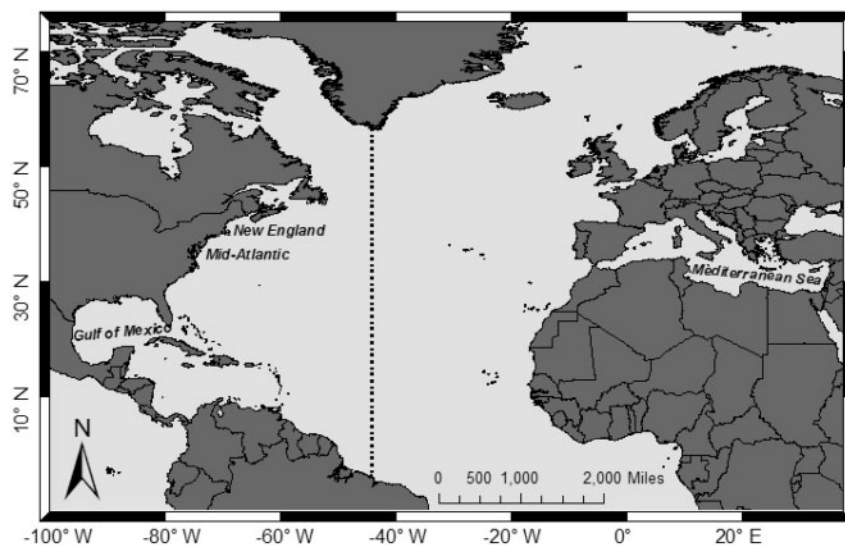
Figure 1. Map showing spawning grounds for western (Gulf of Mexico) and eastern (Mediterranean Sea) stock Atlantic bluefin tuna (*Thunnus thynnus*) and sampling regions (New England, Mid-Atlantic, Gulf of Mexico). Black dashed line denotes 45-degree Meridian used to delineate stock management boundaries.

time periods represented (i) increased intensity in exploitation (1970s), (ii) sustained intense exploitation (1990s), and (iii) a potential recovery. Ages were estimated directly from otoliths and adjusted for fishing selectivity over 43 years of assessment history (SCRS, 2014). Mixing levels (contribution of each stock to US fisheries) were evaluated using otolith stable isotope analysis. Pooled and stock-specific life-time growth rates (size-at-age) were also evaluated for any changes over time. Because estimates of stock-specific growth and age structure can be confounded in mixed stock samples, western stock growth curves and age structures were reconstructed using an individual stock assignment method, which selected individuals that had a high probability of western stock origin.

Methods

Archived sagittal otoliths were obtained from the US-NMFS archive at the National Oceanographic and Atmospheric Administration's (NOAA) Southeast Fisheries Science Center in Miami, FL, the Marine Forensics Archive at the NOAA Center for Coastal Environmental Health and Biomolecular Research in Charleston, SC, the NOAA Southeast Fisheries Science Center in Panama City, FL, and the Chesapeake Biological Laboratory in Solomons, MD. For most otolith samples, length, date of capture, gear, and port of landing were recorded. ABFT otoliths were initially collected through directed port (dockside) or observer campaigns from 1974 to 2014.

Individuals from each sample were selected based on size-class and region of capture to test hypotheses on age structure and mixing levels among (i) samples (as a proxy for decadal period), (ii) size-classes, and (iii) regions (Table 1). A few size-class × region strata were absent samples (e.g. Gulf of Mexico in the 1990s). Regions included New England (Maine, New Hampshire, Massachusetts, and Rhode Island), the Mid-Atlantic (New York, New Jersey, Delaware, Maryland, Virginia, and North Carolina), and the Gulf of Mexico (western Florida, Louisiana, and Texas) (Figure 1). Unfortunately, because the otoliths were port-sampled, information on location of capture (latitude/longitude) was unavailable. However, general capture location data was obtained from the ICCAT Catch & Effort database (https://www.iccat.int/en/accesingdb.HTM). This data showed that the majority of fishing occurred in US shelf waters well within the stock boundary (45-degree meridian) (Supplementary Figure S1).

The period of sampling included in our study brackets the period of fishery development for the sushi market (1970s: 1974–78), overfishing (1990s: 1996–2002), and the current period of sustained overfished status for the western stock of ABFT (2010s: 2009–2014). These salient phases of the population dynamics, which are presumably related to exploitation, were fortuitously captured in three intensive field campaigns by NMFS to obtain

biological tissues from ABFT and other large pelagics from principal commercial and recreational fisheries. Although samples were obtained through long-line fisheries (principally in the Gulf of Mexico) and purse seine and harpoon fisheries (principally in New England regions), the vast majority of landings represented by these sampling efforts came from commercial and recreational hook and line (Supplementary Table S1). During the three Large Pelagic Biological Surveys, government and contract samplers stationed themselves at harbors and fish houses to sample otoliths and other tissues as fish were filleted and processed. Because small vessels predominate in these hook and line fisheries, most fish were landed near ports where they were captured. Still, the adventitious nature of port sampling of hook and line fisheries biased the representativeness of otolith samples with regard to length distributions in the fishery, which led us to adjust our age distributions according to age-specific selectivities, as described later.

The seasonality of our samples corresponds well to the seasonality of the fisheries (Supplementary Figure S2); however, otolith samples were biased towards certain gear types. Rod-an-reel landings were overrepresented in the 1990s (99.6%) and 2010s (84. 6%) and longline landings underrepresented (Supplementary Figure S3). In the 1970s sample, the otolith sample was more distributed among gears: longline (28%), rod-and-reel (36%), purse seine (21%), other gear (14%), or unspecified (1%). In the fishery, the relative contribution of gear types contributing to the total USA and total western stock landings has changed somewhat over time, with the rod-and-reel fleet becoming dominant in the two more recent periods. In the 1970s, purse seine (52%) and rod-and-reel (34%) contributed the majority of landings to reported US landings. In the 1990s and 2010s, purse seine fisheries continued to diminish (rod-and-reel 1990s: 63%, 2010s: 64%; purse seine 1990s: 16%, 2010s: 2%; longline 1990s: 13%, 2010s: 28%.

Regardless, size frequency data from the otolith sample did represent all size classes present in landings data reported to the International Commission for the Conservation of Atlantic Tunas (ICCAT) (Supplementary Figures S4 and S5). In all periods, the largest size classes were present, although there was a bias towards large size classes in the 1970s otolith sample in comparison to landings data, particularly for rod-and-reel and longline gear categories (Supplementary Table S1). For the latter two periods, where rod-and-reel samples predominated, mean CFL of landed fish were within 20 cm of the mean sample CFL.

A single sagittal otolith was randomly selected from each individual and embedded in Struers epoxy resin (Struers A/S, Denmark). A 2.0-mm thick transverse section containing the core region was removed using a Buehler IsoMet saw (Buehler, Lake Bluff, Illinois). The otolith section was then attached to a glass slide in preparation for micromilling, a procedure that extracts

Table 1. Distribution of Atlantic bluefin tuna (*Thunnus thynnus*) otolith samples by size (cm; curved fork length), region, and sampling period.

Size (cm)	1974–1978 (N = 350)			1996–2002 (N = 234)		2009–2014 (N = 1359)		
	New England	Mid-Atlantic	Gulf of Mexico	New England	Mid-Atlantic	New England	Mid-Atlantic	Gulf of Mexico
50-100	38	54		28	26	5	147	
101-200	1	48	1	45	53	261	641	1
201-250	48		27	65		29	56	92
251-300	58		75	17		14	3	110

powdered carbonate from the core region of the otolith for stable isotope analysis. After milling, section thickness was reduced to ~1 mm for examination of annuli and age determination.

Investigations of stock mixing relied on stable isotope analysis of otolith core material circumscribed by the first opaque zone, material which corresponds to early life growth and residence on natal nursery grounds. Discrimination between reproductive stocks relies primarily on differences in $\delta^{18}O$ values between the Mediterranean Sea and western Atlantic shelf waters, south of the Gulf of Maine. Because the Mediterranean Sea is a more evaporative basin than western Atlantic shelf waters, cumulative evaporation leads to more positive $\delta^{18}O$ values in surface seawater, resulting in more positive $\delta^{18}O$ values in juvenile ABFT otoliths (Rooker *et al.*, 2008). In this work, otolith material extracted from individuals of unknown stock origin was compared to material previously extracted and analyzed from juveniles of known stock origin (baseline data). The methods used in milling and stable isotope analysis closely follow Schloesser *et al.* (2010). To extract otolith material, a New Wave Research MicroMill (Freemont, California) was used. Using a 500-µm diameter Brasseler round carbide bit (Brasseler USA, Savannah, Georgia), a series of 55-µm passes occurred along a predetermined otolith milling template patterned after the shape of a yearling ABFT otolith.

Otolith material was analyzed for $\delta^{13}C$ ($^{13}C/^{12}C$) and $\delta^{18}O$ ($^{18}O/^{16}O$) using an automated carbonate preparation device (Kiel-III; Thermo Fisher Scientific, Inc., Bremen, Germany) coupled to an isotope ratio mass spectrometer (Finnigan MAT 252; Thermo Fisher Scientific, Inc., Bremen, Germany) at the University of Arizona's Environmental Isotope Laboratory. Analytical precision of the mass spectrometer was determined to be ±0.1 for $\delta^{18}O$ and ±0.08 for $\delta^{13}C$ (1 SD) (Schloesser *et al.*, 2010). Otolith $\delta^{13}C$ became more depleted over the last several decades, likely due to $\delta^{13}C$-depleted fossil fuel emissions (termed the Suess effect; Verburg, 2007). Adjustment to $\delta^{13}C$ was made as follows,

$$\text{Suess Effect}_{13C} = \beta_{13C} \times (\text{Year of Baseline} - (\text{Year of Capture} - \text{Age}))$$

Where β_{13C} is the slope of $\delta^{13}C$ values over time and Year of Baseline (2006) was chosen as the modal year over which the baseline sample was collected (1998–2011). Here, $\beta_{13C} = -0.039$ ($N = 1953$; $R^2 = 0.62$). Otolith $\delta^{18}O$ showed a slight ($\beta_{18O} = 0.0015$) but significant ($R^2 = 0.005$; $p = 0.001$) long-term trend, but lack of a corresponding trend in northwestern Atlantic nursery areas rendered correction across time unnecessary (Siskey, 2015).

Isotope data for individual samples of unknown origin were compared with yearling baseline data composed of age-1 juveniles collected in the US Mid-Atlantic Ocean and Mediterranean Sea from 1998–2011 ($N = 265$; data publically available from Rooker *et al.*, 2014, http://www.int-res.com/articles/suppl/m504p265_supp.xls) and assigned to eastern or western nursery categories using a maximum likelihood approach with the FORTRAN program HISEA (Millar, 1990). Historical (1974–78; 1996–2002) and recent (2009–14) levels of stock mixing were estimated by region and size-class.

Age determinations employed standardized otolith ageing protocols (Secor *et al.*, 2014a), which include visual enhancement

and notation of otolith images using Adobe Photoshop CS6, a "Y" section type (Supplementary Figure S6; anti-rostrum present), interpretation criteria for the first annulus, and calibration of the reader to a reference collection. Two blind counts of annuli were conducted for each image. If counts differed by <2 annuli, the second count was accepted. If counts differed by ≥2 annuli, the image was read a third time, with the reader consulting the first two count estimates for a final age estimate. In some instances, only a 'V' section type (anti-rostrum absent) was available for ageing. In these instances, a single year was added to the direct age estimate based on the findings of Secor *et al.* (2014a) that a 0.77-year ageing bias exists between 'V' and 'Y' section types. In addition, with spawning time during April–June, we assumed that the completion of each annulus (opaque zone) occurred during the second half of the calendar year (Mather *et al.*, 1995). Therefore, if the fish was landed within the first 6 months of the year (January–June), 1 year was added to the estimated age.

To evaluate bias in the oversampling of larger individuals in the 1970s, as discussed above, length frequency of the otolith dataset and the ICCAT landings data were plotted across gear types. Smaller individuals landed via longline were underrepresented in the otolith dataset, while larger individuals landed by rod-and-reel were overrepresented. Due to this bias inherent in the sampling methodology, an analysis of age structure which only compared larger individuals (220–260 cm CFL) across decadal samples was performed to ensure inferences made on the entire otolith dataset were robust to the sampling bias.

Age frequency distributions of the whole otolith dataset and the subset of larger individuals (220–260 cm CFL) were also corrected for changing fisheries selectivity across time, where smaller, younger fish were targeted in the 1970s and larger, older fish were targeted in the 1990s and 2010s. To adjust for this bias, age-specific fishing mortality estimates were drawn from the 2014 ICCAT virtual population analysis (SCRS, 2014), and for each year, age-specific fishing mortality estimates were converted to selectivity by dividing the fishing mortality by the maximum age-specific mortality within that year ($S_{age} = \frac{F_{age}}{F_{max}}$). To account for the shift in fisheries selectivity that occurred in the late 1960s, decadal age-specific selectivity was calculated by averaging age-specific selectivities across years within each sample, and these sample-specific selectivities were then used to adjust age frequency in the three samples by dividing each age by the corresponding average age-specific selectivity. All inferences made on age structures henceforth utilized the age-specific selectivity-corrected age distribution.

To investigate changes in growth models over time, a von Bertalanffy growth model was fitted to size-at-age data from each of the three samples (1970s, 1990s, and 2010s) following the equation:

$$L_t = L_\infty [1 - e^{(-k(t-t_0))}]$$

where L_∞ is the asymptotic length, k is the rate at which the asymptotic length is approached, and t_0 is the hypothetical age at length 0. If CFL was not recorded, CFL was estimated from straight fork length or snout length, using conversions from Secor *et al.* (2014b). Differences in growth models (size-at-age) between pairs of samples (1970s vs. 1990s, 1990s vs. 2010s, and 1970s vs. 2010s) were investigated by comparing corrected

Akaike's Information Criterion (AIC$_C$; Burnham and Anderson, 2002):

$$AIC_C = -2log\left(\mathcal{L}\left(\hat{\theta}\right)\right) + 2K\left(\frac{n}{n-K-1}\right)$$

where $\mathcal{L}\left(\hat{\theta}\right)$ is the likelihood function, K is the number of model parameters, and n is the sample size. Here, AIC$_C$ values of full models, which estimated decade-specific parameters (e.g. separate L_∞ estimates for the 1970s and 1990s, etc.), were compared to AIC$_C$ values of reduced models, which only estimated one parameter for the pooled data (e.g. one L_∞ estimated for the combined 1970s and 1990s data). All three von Bertalanffy parameters (L_∞, k, and t_0) were allowed to differ between samples in the full models. It is important to note here that differences in von Bertalanffy parameters were tested jointly rather than one parameter at a time. The AIC$_C$ method used to compare models incorporated the traditional von Bertalanffy parameters and a set of deviation parameters. Depending on which sample the individual belonged to (e.g. 1970s or 1990s), a dummy variable was used to select whether $L_{\infty\ (1970s)}$ or $L_{\infty\ (1990s)}$ should be used in the calculation of predicted length.

A similar method was used in the AIC$_C$ method to compare growth between decadal samples of western stock-only fish. Growth models were further fitted to data, which was censored for likely western stock membership. Because the maximum likelihood approach used to assess the degree of mixing in a sample does not allow for individual assignment to a stock, we used δ^{18}O (the more influential discriminating tracer) to isolate those individuals most likely to be of western stock origin (lower δ^{18}O values) from the remainder of the sample. The 90th percentile δ^{18}O value of the western stock (δ^{18}O $= -0.925$) was chosen as the threshold.

Results

Age structure

Individuals from the 1970s sample (1974–78; $N = 350$) ranged from 50 to 306 cm CFL, while individuals from the more recent samples had similar, but smaller ranges: 53–274 cm and 63–296 cm for the 1990s and 2010s samples (Figure 2), respectively. Modes occurred at 70 and 250 cm for the 1970s; 80, 190, and 230 cm for the 1990s; and 110, 190, and ∼250 cm for the 2010s. The weighted mean length decreased considerably over time: 191 cm in the 1970s, 166 cm in the 1990s, and 159 cm in the 2010s. Using analysis of variance on the weighted means, mean size was found to differ significantly between samples ($p < 0.001$). Tukey's Honest Significant Differences (HSD) test showed significant differences between the 1970s and 1990s ($p < 0.001$) and the 1970s and 2010s ($p < 0.001$), but not between the 1990s and 2010s (p > 0.05).

Age-specific selectivities calculated from the age-specific mortalities given by ICCAT's VPA output showed a shift in age-classes targeted over time (Figure 3). In the 1970s age 2–5 fish were heavily selected. In the 1980s, age 2 and 3 fish were still heavily selected, but age 15 and 16+ fish were also strongly selected. In the 1990s, selection of the youngest ages fell and, in general, selectivity began to spread more evenly across adult age-classes ($\geq$ age–8). Over the past 30 years, adult age-classes represent the most highly selected component of the stock. Between 2000 and 2013, some years show strong selectivity for juvenile fish (ages 3–6). The observed diagonal pattern of full selectivity in this time period potentially indicates the selection of a strong year-class over sequential years.

Prior to correction of age frequency data for fishing selectivity, weighted mean age was found to differ significantly between samples (p < 0.001), where mean age was 13, 7, and 8 in the 1970s,
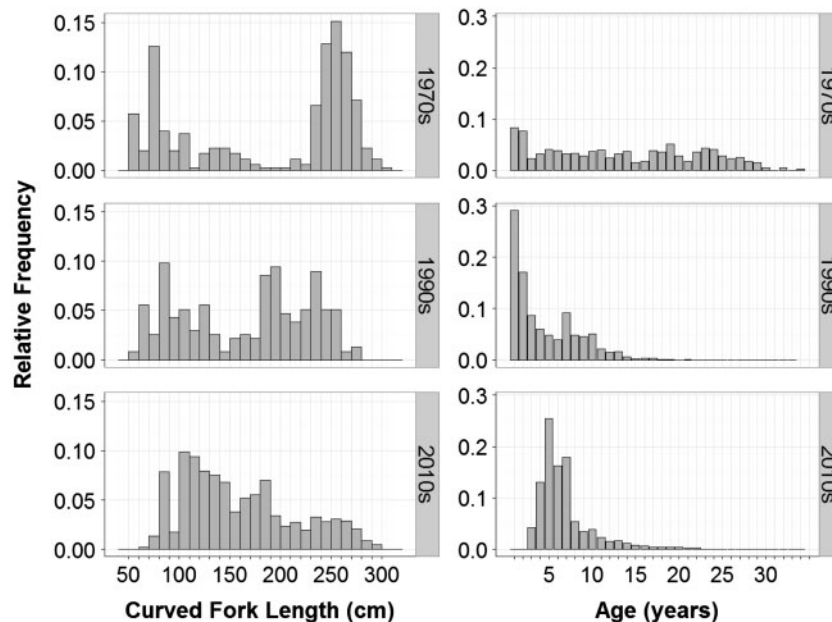

Figure 2. Relative size frequency distributions (cm, curved fork length) for Atlantic bluefin tuna (*Thunnus thynnus*) individuals landed in the 1970s ($N = 350$), 1990s ($N = 234$), and 2010s ($N = 1359$). Bin width $= 10$ cm (left panel). Relative age frequency of Atlantic bluefin tuna landed in the 1970s, 1990s, and 2010s adjusted for age-specific selectivities occurring during the time period of collection (SCRS, 2014) (right panel).

1990s, and 2010s, respectively. Similar to mean size, Tukey's HSD test detected significantly higher mean age in the 1970s in comparison to the two more recent samples. Differences in age were significant between the 1970s and 1990s ($p < 0.001$) and the 1970s and 2010s ($p < 0.001$), but not between the 1990s and 2010s ($p > 0.05$). Following decadal corrections for fishing selectivity, estimated age distributions retained a diminished age structure for the 1990s and 2010s samples (Figure 2). The mean age of the selectivity-adjusted 1990s sample (age 4) and 2010s (age 7) was considerably lower than that of the historical sample (age 13). The distribution shows a much more dispersed age structure in the 1970s in comparison to the 1990s and 2010s. Individuals from the 1970s sample ranged from 1 to 34 years in age, while individuals landed in the 1990s only ranged from 1 to 21 years. In particular, the 1990s sample exhibited the highest bias towards the youngest age-classes. The age structure of the 2010s sample

was similar to the 1990s sample, although ages more broadly ranged from 3 to 34 years, with a very small fraction of the sample ($< 1\%$) over age 21. Modes at ages 1 and 19 in the 1970s, ages 1 and 7 in the 1990s, and age 5 in the 2010s indicate potentially strong year-classes in each sample. The 2010s age structure is less skewed with higher abundances of intermediate age-classes (ages 4–7). Application of the $\delta^{18}O$ threshold to exclude most eastern stock individuals did not substantially alter age distributions.

The age structure analysis on a subset of larger individuals (220–260 cm CFL) generally showed that inferences made on age truncation using the entire otolith dataset were robust to the bias presented through the sampling methodology. Following correction for changing fisheries selectivity, larger individuals ranged from 9 to 34 years in age in the 1970s, 8–18 years in the 1990s, and 8–22 years in the 2010s (Figure 4). Mean age was 19, 11, and 13 years in the 1970s, 1990s, and 2010s, respectively. The age distribution of the 1970s sample was more uniformly distributed than the 1990s and 2010s samples, which were unimodal and skewed to the right.
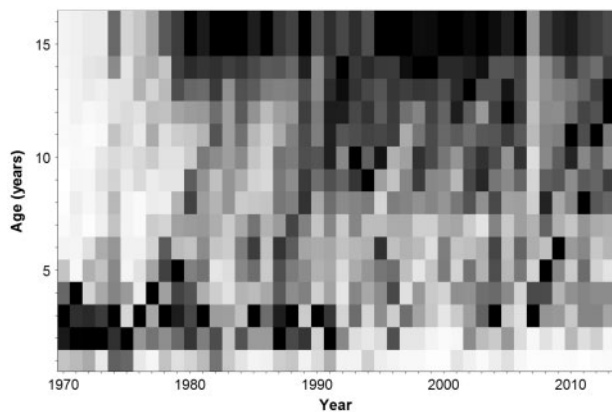
Stock mixing

Stock discrimination analyses using otolith stable isotope data showed little to no contribution of the eastern stock in the 1970s sample (0%), a large increase in eastern stock subsidy in the 1990s sample (48%), and a return to low-level eastern contribution in the 2010s sample (4%) (Table 2). The 1990s sample showed considerable eastern stock subsidy across regions: New England and Mid-Atlantic regions showed 41 and 63% contribution of eastern stock fish, respectively. In comparison to the 1990s sample, the contribution of eastern fish to the 2010s sample declined across regions, with New England, Mid-Atlantic, and Gulf of Mexico samples estimated to include 1, 10, and 0% eastern fish, respectively.

More mixing was detected in juvenile size classes (<200 cm CFL) than in adult size classes (Table 3). In the 1990s, the highest contribution of eastern stock fish was observed in the smallest size-class (73% eastern stock fish; 50–100 cm CFL category), after
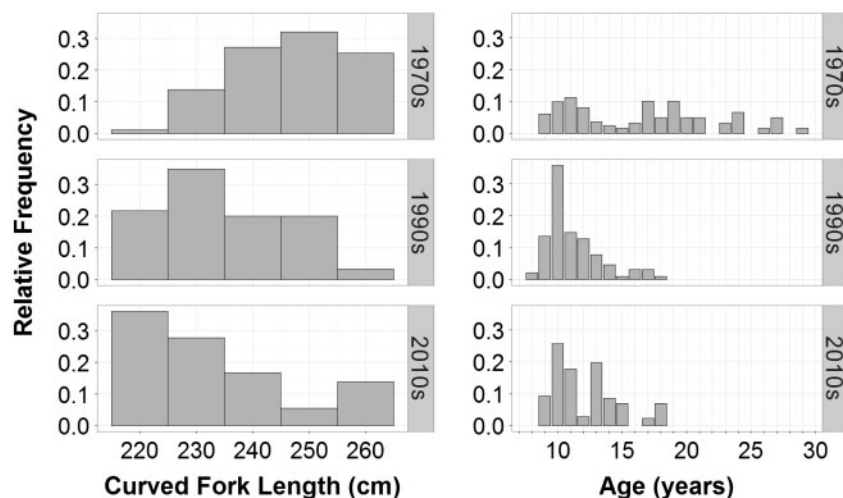

Figure 3. Age-specific selectivities for Atlantic bluefin tuna (*Thunnus thynnus*) from 1970–2013, calculated from age-specific fishing mortality rates estimated in the 2014 Atlantic bluefin tuna stock assessment's virtual population analysis performed by ICCAT (SCRS, 2014). White boxes correspond to selectivity of 0, while dark boxes correspond to full selectivity (selectivity = 1).

Figure 4. Relative size frequency distributions (cm, curved fork length) for Atlantic bluefin tuna (*Thunnus thynnus*) landed in the 1970s ($N = 165$), 1990s ($N = 59$), and 2010s ($N = 189$) in a 220–260 cm CFL size bin. Bin width = 10 cm (left panel). Relative age frequency of Atlantic bluefin tuna landed in the 1970s, 1990s, and 2010s in the 220–260 cm CFL size bin, adjusted for age-specific selectivities occurring during the time period of collection (SCRS, 2014) (right panel).

Table 2. Estimated population mixing levels in Atlantic bluefin tuna (*Thunnus thynnus*) samples from Gulf of Mexico, New England, and Mid-Atlantic fisheries in the 1970s, 1990s, and 2010s.

Year class	Years sampled	Location	N	Population	MLE%	MLE SD
1944–1974	1974-1978	New England, Mid-Atlantic, Gulf of Mexico	349	west	100	0.0
				east	0	
1947-1974	1975-1977	New England	145	west	100	0.2
				east	0	
1966-1974	1974-1977	Mid-Atlantic	102	west	100	0.0
				east	0	
1944-1967	1976 & 1978	Gulf of Mexico	102	west	100	1.2
				east	0	
1975-1997	1996-2002	New England, Mid-Atlantic	229	west	52	4.7
				east	48	
1975-1997	1996-2002	New England	153	west	59	5.6
				east	41	
1985-1997	1996-2000	Mid-Atlantic	76	west	37	7.7
				east	63	
1978-2011	2009-2014	New England, Mid-Atlantic, Gulf of Mexico	1375	west	96	1.2
				east	4	
1988-2009	2010-2014	New England	318	west	99	1.3
				east	1	
1993-2011	2010-2014	Mid-Atlantic	854	west	90	1.7
				east	10	
1978-2006	2009-2014	Gulf of Mexico	203	west	100	0.0
				east	0	

Table 3. Estimated population mixing levels in Atlantic bluefin tuna (*Thunnus thynnus*) samples from fisheries in the 1970s, 1990s, and 2010s by size class.

Decade	Size (cm)	n	Population	MLE%	MLE SD
1970s	50-100	92	west	99	1.7
			east	1	
	101-200	50	west	100	0.8
			east	0	
	201-250	74	west	100	0.1
			east	0	
	251-300	133	west	100	0.0
			east	0	
1990s	50-100	54	west	27	8.2
			east	73	
	101-200	93	west	49	7.4
			east	51	
	201-250	64	west	68	9.3
			east	32	
	251-300	14	west	100	1.5
			east	0	
2010s	50-100	152	west	93	4.4
			east	7	
	101-200	903	west	92	1.7
			east	8	
	201-250	177	west	100	0.8
			east	0	
	251-300	127	west	100	1.2
			east	0	

Growth

Length-at-age followed a similar, overlapping trajectory for all three samples (Figure 5). von Bertalanffy growth curves fit to the three samples overlapped considerably (Figure 5), with similar, yet different, values for L_∞, k, and t_0 in the 1970s and 1990s samples (Table 4). Differences between these two curves and the 2010s curve were largely reflected by t_0 and L_∞, estimates, which may have been biased due to lack of age 1, age 2, and age 21+ individuals in the 2010s sample. However, k also decreased over the three samples from the 1970s to the 2010s. Despite very modest differences in decadal growth curves, AIC_C model selection consistently chose curves that incorporated decade-specific model parameters (Table 5). Based on AIC_C differences, reduced models received little support. The decline in k, in addition to the decline in mean length over time, suggests the lower growth rates are occurring during the recent sampling periods.

Application of the $\delta^{18}O$ threshold to exclude most eastern stock individuals did not substantially alter growth curve parameter estimates; AIC_C again supported curves that incorporated sample-specific parameters for each decade (Table 5). Fitted growth curves were similar to the western stock growth curve accepted by ICCAT and used in management of this species (Figure 5; the Restrepo growth curve, described in Restrepo *et al.*, 2010). The 2010s curve more closely resembled the Restrepo growth curve, but differences in t_0 and lengths predicted for intermediate ages still existed between the two curves (Table 4). Observed differences between the 1970s/1990s and the 2010s/Restrepo pairs of curves are likely influenced by L_∞, which may have been inaccurately estimated in the 2010s sample due to very low sample sizes for ages > 21 years. Further, there was an overall decrease in k over the three samples from the 1970s to the 2010s,
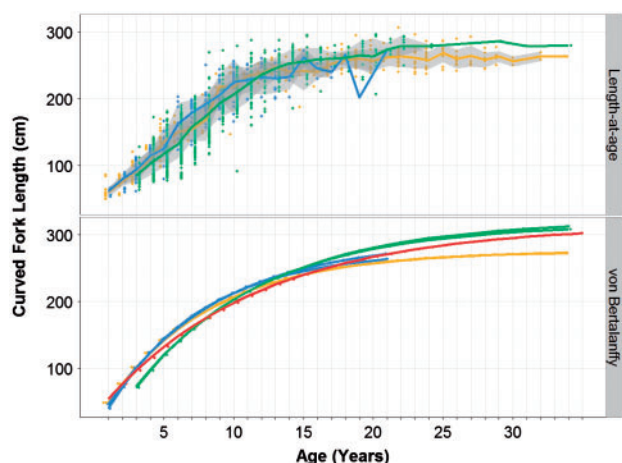
which contribution declined with increased size (51%, 101–200 cm; 32%, 201–250 cm; 0%, 251–300 cm). In the 2010s, mixing levels were low (≤ 8% eastern stock fish), but higher levels of eastern stock contribution were again observed in smaller-category fish (7%, 50–100 cm; 8%, 101–200 cm; 0%, 201–250 cm; 0%, 251–300 cm).

Figure 5. Length-at-age for Atlantic bluefin tuna (*Thunnus thynnus*) individuals landed in the 1970s (gold; $N = 350$), 1990s (blue; $N = 234$), and 2010s (green; $N = 1359$) (top panel). Lines connect mean length-at-age; clouds are ± 1 *SD*. Mixed-stock and western-stock von Bertalanffy growth curves (points indicate predicted mean size-at-age) for Atlantic bluefin tuna individuals landed in the 1970s (gold), 1990s (blue), and 2010s (green) in comparison to the accepted growth curve for the western stock (red; Restrepo *et al.*, 2010) (bottom panel). Mixed-stock and western-stock curves overlap. Please refer to the online version of this publication to view color images.

Table 4. von Bertalanffy parameters of growth curves [L_∞ (asymptotic length; cm CFL), k (rate at which asymptotic length is approached), and t_0 (length at age-0)] produced for mixed stock and assigned western stock Atlantic bluefin tuna (*Thunnus thynnus*) samples landed in the 1970s, 1990s, and 2010s.

	1970s		1990s		2010s		Restrepo	
	Value	SE	Value	SE	Value	SE	Value	SE
				Mixed stock				
L_∞	275.6	2.205	291.0	10.31	322.2	6.085	314.9	5.8
k	0.132	0.005	0.126	0.011	0.104	0.004	0.089	0.003
t_0	−0.47	0.101	−0.38	0.181	0.540	0.116	−1.13	0.035
				Western stock				
L_∞	275.9	2.274	276.8	10.34	321.3	6.219	314.9	5.8
k	0.132	0.005	0.145	0.016	0.107	0.005	0.089	0.003
t_0	−0.46	0.104	−0.08	0.242	0.619	0.122	−1.13	0.035

which may have contributed to AIC_C selecting curves that incorporated sample-specific parameters for each decade.

Discussion

We analysed age structure, size structure, growth, and stock mixing in a large historical sample, and found evidence for a truncated age structure after intensive fishing in the 1970s and 1990s, followed by a modest recovery in age structure in the most recent decade. This investigation also confirmed some of the key elements of stock structure and migratory behaviour in ABFT: (i) substantial levels of eastern stock subsidy have existed in the western North Atlantic (Table 2), (ii) little to no mixing occurs on spawning grounds (Gulf of Mexico; Table 2), (iii) the Mid-Atlantic region hosts the highest mixing levels (Table 2), and (iv) eastern stock contribution decreases with fish size (Table 3). The

Table 5. Comparisons of Corrected Akaike's Information Criteria (AIC_C) for mixed and assigned western stock Atlantic bluefin tuna (*Thunnus thynnus*) growth models (e.g., 1970s W), which included or excluded decadal effects. Full Model refers to models that incorporated separate decadal parameters. Reduced Model refers to models that used one set of parameters for both decades. Δ_i denotes the AIC_C difference between the full and reduced model.

	Mixed		
	1970s v. 1990s	*1970s v. 2010s*	*1990s v. 2010s*
Full Model	3931.6	12012.5	11326.8
Reduced Model	3941.7	12272.6	11469.6
Δ_i	10.1	260.1	142.8
	Western		
	1970s W v. 1990s W	*1970s W v. 2010s W*	*1990s W v. 2010s W*
Full Model	3045.2	10631.4	9399.8
Reduced Model	3052.2	10874.3	9469.4
Δ_i	7	242.9	69.6

observed fluctuation in stock mixing does not support the assumptions of constant stock composition (no net mixing) made in the ICCAT stock assessments (see also Rooker *et al.*, 2008; Secor, 2014; Secor *et al.*, 2015) and indicates that the assessment model should be revised to include these dynamics of stock mixing.

The samples used in this study were drawn from fisheries and represent the seasonality of catch and the size distribution of catch (Supplementary Figures S2, S4, and S5); however, they do over-represent larger (~older) fish in the population, particularly for the 1970s period (Supplementary Table S1). Related to the bias of fish lengths represented, the otolith dataset over represented the rod-and-reel landings of the 1990s and 2010s, and underrepresented both the contribution of the purse seine category in the 1970s and the contribution of the longline category in all time periods (Supplementary Table S2 and Figure S3). Further, changes in fishing selectivity may have biased comparisons of age structure. We evaluated whether our analysis of age structure was robust to the sampling bias by performing a separate analysis of age structure for only larger individuals (220–260 cm CFL), which yielded similar conclusions that age truncation was present in the 1990s and 2010s samples. We addressed the bias of fisheries selectivity by adjusting age frequencies by estimates of age-specific selectivity within decadal samples.

Under the dual influences of growth overfishing (overfishing juveniles) and recruitment overfishing (overfishing adults), we expected to see age truncation and reduced growth. Size and age distributions showed significant reductions in both mean size and age over time, providing evidence of diminished age structure in the 1990s and 2010s, which is consistent with diminished trends in abundance of the age 16+ age-class as reported in the most recent ICCAT stock assessment (SCRS, 2014). However, age structure has recovered slightly in the recent sample (2010s): the span of age and year-classes increased, but the adult population is still predominantly comprised of first- or second-time spawners, termed recruit spawners (young adult spawners, age < 12).

The loss of age structure during the past 40 years mirrors the decline of fishery yield (SCRS, 2014). Together, growth and recruitment overfishing had the potential to deplete abundance, cause age truncation, and decrease the potential to produce

strong year-classes as has been reported in other marine fishes (Berkeley et al., 2004). Fisheries for bluefin tuna in the western North Atlantic in the 1970s primarily targeted juveniles with purse seines. As indicated by age-specific selectivity, targeted age-classes principally included those < 5 years (Figure 3). In 1972, increased incentives from Japanese markets to catch large bluefin catalysed rapid growth of the New England purse seine fishery, in addition to harpoon, handline, and sport fisheries (Mather et al., 1995). Reduced catch in the purse seine fishery in the mid-1970s generated concern for declines in recruitment (Fromentin and Powers, 2005). Coincidently, heavy exploitation by the Japanese longline fleet on medium- to large-sized individuals in the western Atlantic Ocean continued to deplete this component of the stock, primarily targeting large individuals (> 185 cm CFL) spawning in the Gulf of Mexico and giants (> 205 cm CFL) foraging in Canadian waters (Mather et al., 1995). The increased selectivity for ages > 12 in the early 1980s (Figure 3) is consistent with expansion of the longline and sport fisheries targeting larger individuals from the mid-1970s forward. With recruitment dwindling and the focus of commercial fisheries shifting, the removal of old individuals would have had both direct and indirect effects on the population.

The decadal changes observed in northwestern ABFT stock mixing may have resulted from the combined influences of (i) changing migration behavior by the eastern stock, (ii) changing biomass (production) of the eastern stock, and (iiii) changing biomass (production) of the western stock. One view is that the increased mixing detected in the 1990s may be representative of an expansion of the eastern stock's range in response to depletion of the western stock. The relative recovery of forage abundance (Atlantic herring, Atlantic mackerel) from the mid- to late-1980s in the western North Atlantic may have facilitated this expansion of the eastern stock into western North Atlantic waters (Overholtz, 1989; Overholtz and Friedland, 2002). Range expansion for this highly migratory bluefin tuna may have been prompted by oceanographic changes, shifts in forage availability, and fishing, as previously suggested for the sudden emergence of bluefin tuna aggregations off Brazil (termed the "Brazilian Episode") and the collapse of the Norwegian and North Sea fisheries in the 1960s (Fromentin, 2009; Fromentin et al., 2014). Recently, ABFT have been reported following irruptions of Atlantic mackerel and herring into boreal waters off Iceland and Greenland (MacKenzie et al., 2014).

Alternatively, fluctuations in stock mixing could be attributed to changes in production. Nemerson et al. (2000) posited that due to large inherent differences in stock size, westward migration by eastern stock fish would have a relatively larger effect on observed dynamics in the western fishery. Because the eastern stock is substantially larger than the western stock (–5 to 10 times larger), a reduction in western stock abundance could amplify the level of the eastern stock's contribution. This would explain why substantially higher levels of eastern contribution were observed in the 1990s, a time when abundance of the western stock was extremely low. Currently, there is no definitive means to separate the relative influence of changing migration and abundance on changes in stock mixing levels. To understand the role of migration and production on fluctuations of stock mixing, simulation modeling and sensitivity analyses are needed (Taylor et al., 2011; Kerr et al., 2012).

Size-at-age growth models such as those presented here provide a coarse representation of individual growth rates and therefore may be relatively insensitive to decadal changes in growth (Mulligan and Leaman, 1992). Still, AIC_C model selection chose models with parameter values that were specific to samples (Table 5), suggesting a change in growth between samples despite similarities in the von Bertalanffy growth curves (predicted size-at-age) (Figure 5). A moderate change in growth over samples is further evidenced by the decrease in the k parameter over samples (1970s to 2010s) in both the mixed-stock and western-only AIC_C comparisons. This result agrees with the hypothesis that size at age may decline as the result of selective fishing on higher growth components of the stock. Alternatively, rejection of the pooled growth curve model could have been influenced by differences in sample-specific maximum length, absence of the oldest age-classes in the 1990s sample, low frequencies of the old age-classes in the 2010s, and absence of 1- and 2-year old fish in the 2010s. Still, it should be expected that ABFT growth is responsive to decadal changes in the western North Atlantic forage base (Overholtz, 1989; Overholtz and Friedland, 2002). Although bluefin tuna tagging studies present formidable challenges in obtaining reliable estimates of size increment during the period the fish is at large (Restrepo et al., 2010; Ailloud et al., 2014), they may offer an alternative approach for resolving decadal patterns in growth.

Recovery of age structure in ABFT should be an objective of management, but could face economic and technical constraints. Market price for ABFT is primarily related to quality metrics: freshness, fat content, color, and shape (Carroll et al., 2001). Quality metrics and a price plateau at weights 150–250 kg (CFL 198.2–233.2 cm; ages 10–14; Restrepo et al., 2010) suggest the price-size relationship of ABFT is parabolic (Mylonas et al., 2010), and indicate that shifting effort from the largest individuals could be economically viable (Mullon et al., 2012). A maximum size limit of 240 cm CFL would correspond to individuals age 15+, and could protect large, old spawning individuals that may not be particularly favored by the Japanese market (individuals ≥ 240 cm CFL comprised 15% of the 2010s sample in this study). Stokesbury et al. (2011) provided evidence that catch-and-release should, in fact, be an option for management and protection of larger individuals, reporting a low post-release mortality of 3.4% for individuals caught in southern Gulf of St. Lawrence.

Periodic-strategists such as bluefin tuna, cod, striped bass, and other large fecund species are particularly susceptible to age truncation due to their dependence on an intact age structure to buffer against unproductive years (Rouyer et al., 2012). Therefore, loss of adult age structure may contribute to higher recruitment variability, a decreased capacity to produce strong year-classes, and higher susceptibility to population collapse. Further, loss of age structure can diminish early survival through the loss of high-quality eggs and larvae, and certain types of spawning or migration behaviours, which are typically supplied to the population by older adults (Hixon et al., 2014; Secor, 2015). Loss of age structure can cause populations to cross nonlinear thresholds as they move from one abundance state to another (Dixon et al., 1999; Hsieh et al., 2005; Secor et al., 2015). On the other hand, recovered age structure can promote population resilience and stability, as observed for Atlantic striped bass (Morone saxatilis; Secor, 2000) and northwestern Atlantic cod (Gadus morhua; Rose and Rowe, 2015). Here, we argue that protection of the largest and oldest Atlantic bluefin tuna could promote resilience in a

population that has exhibited a multi-decadal period of depressed abundance.

Finally, owing to the extent of stock mixing that typically occurs in highly migratory species, stock assessments can often be biased and misleading under assumptions of closed populations (aka the unit stock). As observed in this study, stock mixing can fluctuate over time, suggesting that spatiotemporal variability in stock mixing should be quantified and incorporated into assessment. As technological advances in our ability to evaluate natal origins and migrations expand, integrative assessment frameworks will become increasingly necessary to effectively evaluate the dynamic nature of stock productivity, trans-oceanic migrations, and the effects of fisheries' exploitation and selectivity.

Supplementary data

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

Acknowledgements

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