The Future of Bluefin Tunas

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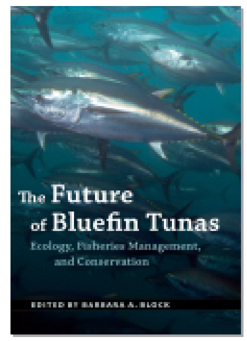

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CHAPTER 2

Otolith Microchemistry

Migration and Ecology of Atlantic Bluefin Tuna

Jay R. Rooker and David H. Secor

Introduction

Atlantic bluefin tuna (*Thunnus thynnus*) exhibit strong population structure, with two dominant spawning areas in the Mediterranean Sea and the Gulf of Mexico, producing recruits that occupy areas within these marginal seas or adjacent waters in the North Atlantic Ocean. This view that there are two dominant stocks in the Atlantic Ocean was initially supported by the distribution of fisheries, conventional tagging data, and ichthyoplankton surveys (e.g., Mather et al. 1995). Although early conventional tagging data indicated a small degree of mixing between the two populations, particularly at young ages (Rooker et al. 2007), the International Commission for the Conservation of Atlantic Tunas (ICCAT) codified population structure with separate assessments for eastern and western stocks (NRC 1994), which have continued for more than 30 years. The premise of two stocks with limited connectivity or mixing has been challenged (e.g., Block et al. 2005, Fromentin and Powers 2005), and it is now widely accepted that significant mixing between eastern and western stocks is important, with individuals commonly migrating across the 45°W management boundary (Galuardi et al. 2010, Rooker et al. 2014, Graves et al. 2015). Given that the population dynamics of Atlantic bluefin tuna appear highly sensitive to the migration and mixing of individuals (Taylor et al. 2011, Kerr et al. 2012), findings of increased connectivity underscore the need to better characterize the annual migratory patterns and stock mixing of Atlantic bluefin tuna throughout their range.

A variety of approaches have been used to investigate the movements, migrations, population structure, and mixing of Atlantic bluefin tuna and other tuna populations, including conventional tags, electronic tags, genetics, pollutant tracers, and chemical markers in calcified structures or hard parts (Gunn and Block 2001, Rooker et al. 2007, Teo and Boustany 2015). Of these, natural chemical markers in otoliths (ear stones) appear to show the greatest potential for determining natal origin, stock integrity, and the collective movements of Atlantic bluefin tuna (Magnuson et al. 2001, Rooker et al. 2008a,b). This is because otoliths precipitate material (primarily $CaCO_3$) as the tuna grows, and the chemical composition of newly accreted otolith material is reflective of the physicochemical conditions of the seawater inhabited by the individual (Rooker et al. 2001a, Elsdon and Gillanders 2003). As a result, the chemical composition of otolith material deposited within the first annulus (i.e., during the first year of life) is often linked to the seawater chemistry at the individual's place of origin. Additionally, the movement ecology of individual tunas can be inferred by changes in chemical composition of otoliths during the early life period (Baumann et al. 2015), although this approach has not yet been applied to Atlantic bluefin tuna. To date, two classes of chemical markers—trace elements and stable isotopes—have been widely used to investigate the origin and stock mixing of both tropical (Wells et al. 2012, Rooker et al. 2016) and temperate tunas, including recent research on Atlantic bluefin tuna (Rooker et al. 2014, Secor et al. 2015, Siskey et al. 2016).

This chapter is a synthesis on stock composition and migration studies on Atlantic bluefin tuna using otolith chemistry. These studies have spanned nearly 20 years and have culminated with the operational use of otolith-based population assignments in stock-assessment models (Taylor et al. 2011, Kerr et al. 2017). Both the development of the approach and the application of these novel tracers are reviewed, and a synopsis of the stock composition (i.e., mixing levels) of Atlantic bluefin tuna is presented for different regions of the North Atlantic Ocean. Three primary questions related to the migration ecology of Atlantic bluefin tuna are addressed: (1) What is the degree of transatlantic movement, and which geographic regions and fisheries represent hot spots for stock mixing? (2) Following transatlantic movement, is homing to natal sites in the east (the Mediterranean Sea) and west (the Gulf of Mexico) prevalent? (3) Can natural chemical markers be used to document age-specific egress/ingress from nursery areas? We end the chapter by discussing the potential impacts of different migration and mixing scenarios on the current assessment frameworks used to manage Atlantic bluefin tuna. In this retrospective, we recognize that mixing represents an emergent property influenced by transatlantic movements and the relative productivity of populations. Further, additional spawning areas and population structure (subpopulations and contingents) likely exist (Fromentin et al. 2014, Richardson et al. 2016) and have yet to be evaluated with otolith chemistry.

History of the Approach

The earliest attempt to use chemical markers in hard parts to discriminate Atlantic bluefin tuna stocks was performed by Calaprice (1985). This study demonstrated that trace elements and stable isotopes in the vertebrae of Atlantic bluefin tuna showed potential for identifying individuals of eastern and western origin. Still, uncertainties in predictions of geographic origin and stock mixing from this research were relatively high, and the National Research Council (1994) recommended that new analytical approaches were necessary to further advance this line of research. In 1997 a workshop of international experts identified rigorous analytical methods and standardization as chief technological constraints for applying this approach to Atlantic bluefin tuna (Secor and Chesney 1998). Initial research followed related work on its congener in the Pacific Ocean (*T. orientalis;* Rooker et al. 2001b), and it focused on trace element comparisons between otoliths from eastern and western nurseries and evaluation of decontamination, accuracy, and standardization protocols (Rooker et al. 2001a, 2002; Secor et al. 2002). Using a suite of influential elements (Li, Mg, Mg, Sr, Ba) in the whole otoliths of juvenile (age 0, age 1) Atlantic bluefin tuna, Rooker et al. (2003) demonstrated that classification of individuals to eastern and western nurseries was possible. However, classification success was relatively modest (60%–85%), indicating that the discriminatory power of the approach needed to improve prior to full-scale investigations of stock mixing.

Concurrent with these investigations, a second class of chemical markers in otoliths, stable oxygen and carbon isotope ratios ($\delta^{18}O$, $\delta^{13}C$), was being used in conjunction with trace elements to improve the classification of marine fish populations to natal sites (e.g., Thorrold et al. 2001). In response, Rooker and Secor (2004) assessed the utility of $\delta^{18}O$ and $\delta^{13}C$ for discriminating yearling Atlantic bluefin tuna of eastern and western origin and showed that classification success was nearly 100% with these chemical markers alone. This research also demonstrated that the successful discrimination of eastern and western yearlings was almost entirely due to differences in one marker: otolith $\delta^{18}O$. The observed differences in otolith

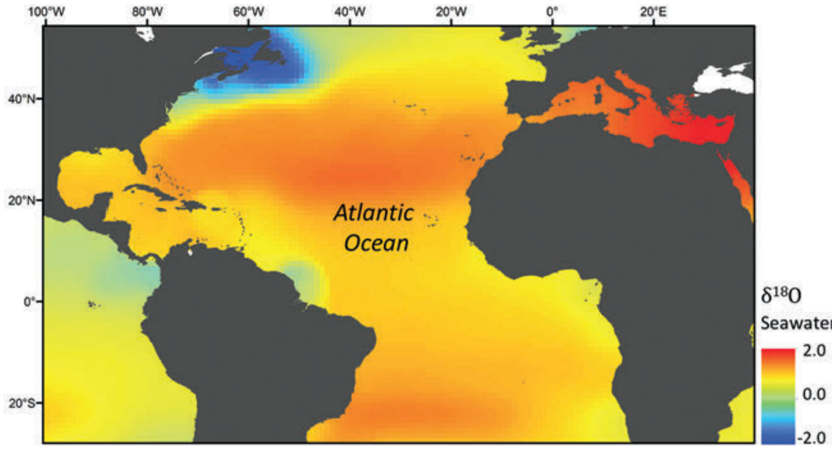

Figure 2.1. Gridded global seawater $\delta^{18}O$ data (1° resolution) downloaded from the National Aeronautics and Space Administration Goddard Institute for Space Studies (http://data.giss.nasa.gov/o18data/) and displayed in ArcGIS 10.2 (Esri Inc.) to visualize spatial differences in seawater $\delta^{18}O$ across the Atlantic Ocean. Originally described by LeGrande and Schmidt 2006, this data set uses relationships between regional seawater $\delta^{18}O$ and salinity, as well as PO_4, to delineate water mass margins and interpolate seawater $\delta^{18}O$ values.

$\delta^{18}O$ were not entirely unexpected, given the observed geographic variation in seawater $\delta^{18}O$ across the Atlantic Ocean, with significantly higher values observed in the Mediterranean Sea relative to the Gulf of Mexico spawning areas (LeGrande and Schmidt 2006; Figure 2.1). The promise of otolith $\delta^{18}O$ as a birth certificate led some scientists to speculate that this chemical marker represented the "Rosetta Stone" for explaining longstanding questions about stock mixing and migration. However, the impact of interannual variability in otolith $\delta^{18}O$ and $\delta^{13}C$, which is known to influence the utility of these natural markers, was not fully assessed in Rooker and Secor (2004) because only two year classes of yearling Atlantic bluefin tuna were included.

Since the initial discovery of otolith $\delta^{18}O$ as a discriminator of nursery origin for Atlantic bluefin tuna, subsequent papers have confirmed the promise of this marker for retrospective determination of stock origin. In fact, yearlings from many year classes have been pooled to support more robust classification procedures that could apply to all year classes, but this has resulted in greater overlap in stable isotopes between principal nurseries. Still, classification success remained sufficiently high (87%) to support stock composition analysis (Rooker et al. 2008a,b). This juvenile baseline was later updated with improved and consistent methods for milling otolith material and was comprised of yearlings sampled in the Mediterranean Sea and US natal regions over a longer period (1998–2011) (Rooker et al. 2014; Figure 2.2). For the years represented by this baseline, western yearlings showed much greater variability in otolith $\delta^{18}O$ than eastern yearlings (Figure 2.2). We speculate that overlap in the distribution of otolith

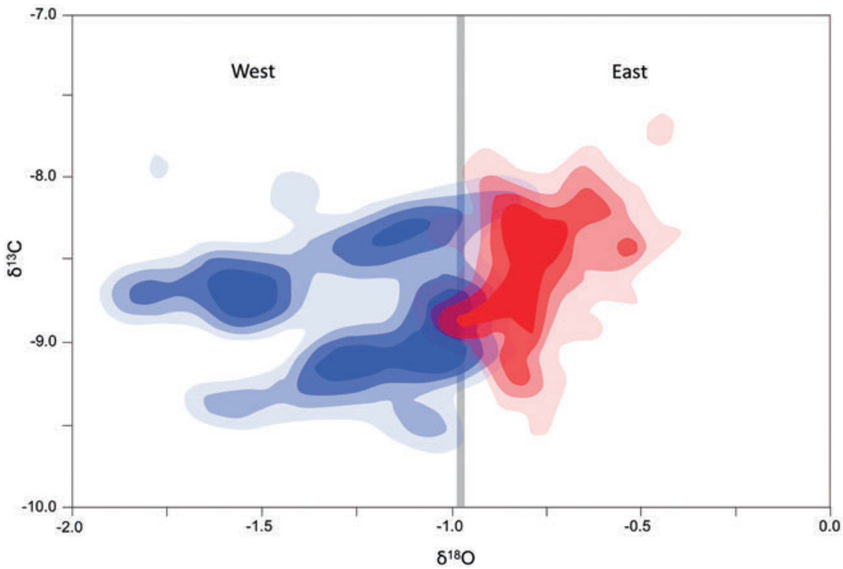

Figure 2.2. Otolith $\delta^{18}O$ and $\delta^{13}C$ values expressed as contour plots for yearling (12+ months) Atlantic bluefin tuna from eastern (*red*) and western (*blue*) nurseries. Contour plots shown at four levels (from dark to light fill colors, 20%, 40%, 60%, and 80%). Data for plot derived from Rooker et al. 2014. Otolith $\delta^{18}O$ threshold value of approximately −0.9 (*denoted by line*) represents the tentative boundary between eastern and western occurrence.

$\delta^{18}O$ values between eastern and western yearlings may be due in part to transatlantic migrations during the yearling period, particularly from the Mediterranean Sea population, which has been documented through past conventional tagging studies (Rooker et al. 2007). Further, modalities in otolith $\delta^{18}O$ for the western sample are evident and possibly indicative of additional spawning areas in the western Atlantic Ocean (Richardson et al. 2016) or of the presence of contingents with distinct migration pathways or egress patterns (e.g., different residency periods in the Gulf of Mexico nursery).

Transatlantic Movement and Stock Mixing

Otolith $\delta^{13}C$ and $\delta^{18}O$ values from milled cores (corresponds to yearling period) of Atlantic bluefin tuna collected from several regions of the North Atlantic Ocean (western, central, and eastern) were used to assess stock mixing and transatlantic migrations. An overview of observed stock composition and mixing within each of the three major regions follows.

Northwestern Atlantic Ocean

Atlantic bluefin tuna collected in the 1990s and the early 2000s from US fisheries exhibited high levels of mixing, particularly for school (~< 60 kg, < 148 cm straight fork length [SFL], < 152 cm curved fork length [CFL]) and medium (~60–140 kg, 148–198 SFL cm, 152–204 cm CFL) category

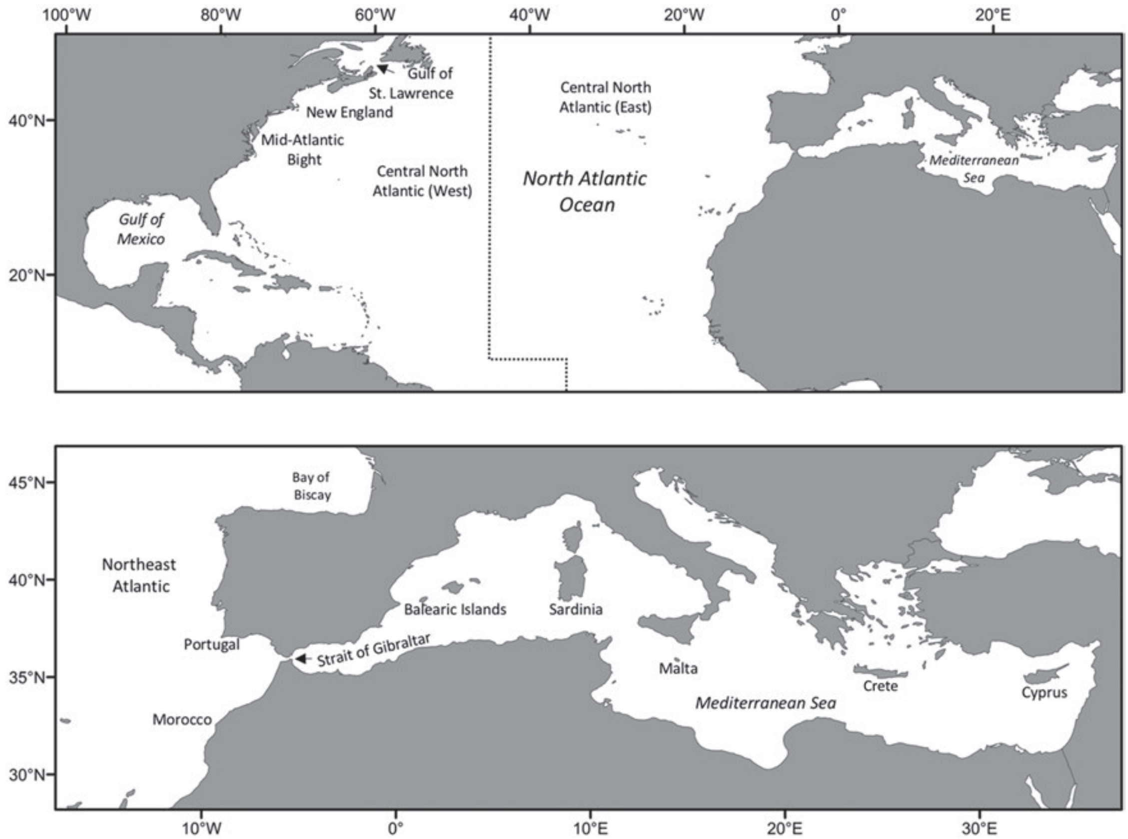

Figure 2.3. Map of primary collection areas for Atlantic bluefin tuna. Management boundary (45°W longitude) denoted with dashed line.

fish. Initial estimates of stock mixing in the US Atlantic Ocean (Figure 2.3) were published by Rooker et al. (2008a) using a six-year baseline sample of otolith $\delta^{13}C$ and $\delta^{18}O$ values for yearling Atlantic bluefin tuna. Findings from this study indicated that a large fraction of the Atlantic bluefin tuna from US fisheries in the mid-Atlantic were of eastern (Mediterranean) origin, with eastern migrants accounting for 57% and 44% of the school and medium category fish sampled, respectively (Table 2.1). The presence of eastern migrants in samples of giant category Atlantic bluefin tuna (~> 140 kg; > 198 cm SFL; > 204 cm CFL) from both the mid-Atlantic (35%) and the Gulf of Maine (5%) was lower, suggesting that transatlantic movement and stock mixing may be more prevalent for younger or smaller individuals. Using the new baseline produced by Rooker et al. (2014), Siskey et al. (2016) evaluated a new sample of Atlantic bluefin tuna from the mid-Atlantic and New England during this same period (1996–2002)

Table 2.1. Summary of stock composition for Atlantic bluefin tuna collected from several regions within both the eastern and western management areas

Region	Year(s) sampled	N	Size class	% West	% East	1SD (%)	Reference
West							
Gulf of Mexico	1976–1978	102	G	100.0	0.0	0.0	Siskey et al. 2016
Gulf of Mexico	2004–2007	42	G	99.3	0.7	1.7	Rooker et al. 2008a
Gulf of Mexico	1999–2011	183	G	100.0	0.0	0.5	Secor et al. 2014
Gulf of Mexico	2009–2014	203	G	100.0	0.0	0.0	Siskey et al. 2016
US Atlantic (mid-Atlantic)	1974–1977	102	S,M,G	100.0	0.0	0.0	Siskey et al. 2016
US Atlantic (mid-Atlantic)	1996–2002	154	S, M,G	54.3	45.7	7.2	Rooker et al. 2008b
US Atlantic (mid-Atlantic)	1996–2000	76	S,M,G	37.0	63.0	7.7	Siskey et al. 2016
US Atlantic (mid-Atlantic)	2010–2014	854	S,M,G	90.0	10.0	1.7	Siskey et al. 2016
US Atlantic (New England)	1996–2002	153	S,M,G	59.0	41.0	5.6	Siskey et al. 2016
US Atlantic (New England)	1996–1998	72	S,M,G	94.8	5.2	5.3	Rooker et al. 2008b
US Atlantic (New England)	2010–2014	318	M,G	99.0	1.0	1.2	Siskey et al. 2016
US Atlantic (mid-Atlantic, New England)	2015	175	S,M,G	28.4	71.6	5.0	Barnett et al. 2016
CA Atlantic (Gulf of St. Lawrence)	1975–2007	224	G	100.0	0.0	0.1	Schloesser et al. 2010
CA Atlantic (Gulf of St. Lawrence)	2011–2012	191	G	100.0	0.0	0.2	Busawon et al. 2014
CA Atlantic (Maritime)	2011–2012	151	M,G	85.0	15.0	5.4	Busawon et al. 2014
Central North Atlantic							
West of 45° management boundary	2010–2011	25	M,G	56.0	44.0	16.8	Rooker et al. 2014
East of 45° management boundary	2010–2011	177	M,G	15.1	84.9	4.9	Rooker et al. 2014
East							
Mediterranean Sea (Malta, Spain)	2003–2007	132	M,G	4.2	95.8	3.1	Rooker et al. 2008a,b
Mediterranean Sea (Spain)	2011	13	M,G	0.0	100.0	0.0	Rooker et al. 2014
Mediterranean Sea (Sardinia)	2011	20	M,G	0.0	100.0	0.0	Rooker et al. 2014

(continued)

Table 2.1. ***continued***

Region	Year(s) sampled	N	Size class	% West	% East	1SD (%)	Reference
Mediterranean Sea (Malta)	2011	82	M,G	0.0	100.0	0.0	Rooker et al. 2014
Mediterranean Sea (Cyprus)	2011	48	M,G	0.9	99.1	2.9	Rooker et al. 2014
Northeast Atlantic (Bay of Biscay)	2009–2011	217	S,M	0.7	99.3	0.6	Fraile et al. 2015
Northeast Atlantic (Portugal, Strait of Gibraltar)	2010–2011	109	M,G	0.0	100.0	0.0	Rooker et al. 2014
Northeast Atlantic (Morocco)	2011–2012	81	M,G	6.1	93.9	4.7	Rooker et al. 2014

Notes: Percent composition is based on maximum likelihood estimates (MLE). Standard deviation (SD) of MLE-based proportions is also given for each study. Sampling years, sample sizes (N), and size/weight categories of fish are shown for each study. Size classes (approximate weights and curved fork lengths [CFL]) of individuals included in each study: School (S, < 60 kg; xx CFL cm), Medium/Large (M, 60–140 kg; xx CFL cm), Giant (G, > 140 kg; xx CFL cm).

and also observed high levels of eastern stock contributions for smaller size-class fish: 73%, 51%, 32%, and 0% eastern fish for sizes 50–100 cm, 101–200 cm, 201–250 cm, and 251–300 cm CFL, respectively.

More recently, Siskey et al. (2016) investigated stock mixing of Atlantic bluefin tuna under varying periods of fishing and recruitment levels for the western stock over a 40-year period. In contrast to the higher levels of eastern stock contributions for collections in the 1990s and early 2000s, mixing was undetected for samples collected in the 1970s, regardless of size. This period preceded a major increase in fisheries targeting giants for the sushi market and was characterized by several strong year classes of western fish (Mather et al. 1995) Thus, any eastern-origin fish migrating into the western management area would likely have been rare relative to the more abundant western fish from these strong year classes. For more recent sampling (2009–2014), Siskey et al. (2016) observed a return to minimal stock mixing (<5% across all size classes), potentially an indication of recovery for the western stock (Table 2.1; Figure 2.4). Nevertheless, other recent samples of US fisheries reported higher levels of stock mixing. Secor et al. (2015) reported 24% mixing by Mediterranean individuals in the North Carolina–Virginia winter fishery sampled in 2011–13, and Barnett et al. (2016) observed large numbers of eastern migrants (>70%) in a 2015 sample of US summer-caught Atlantic bluefin tuna, which was dominated by smaller school and medium category fish (Table 2.1).

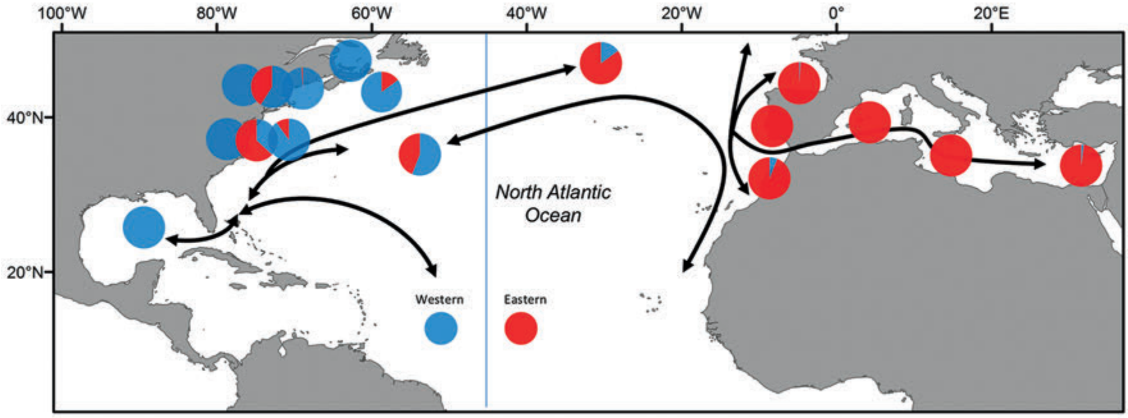

Figure 2.4. Most recent estimates of stock composition available for Atlantic bluefin tuna in key spawning, foraging, and fishing areas based on otolith $\delta^{18}O$ and $\delta^{13}C$. Estimates derived from several studies: Gulf of Mexico, mid-Atlantic, and New England (Siskey et al. 2016), Gulf of St. Lawrence and Canadian Maritime (Busawon et al. 2014), Central North Atlantic, Northeastern Atlantic Ocean (Morocco, Portugal), Mediterranean Sea (Rooker et al. 2014), and Bay of Biscay (Fraile et al. 2015). Generalized migration routes (*arrows*) are from Fromentin et al. 2014. See Table 2.1 for details about samples and mixing estimates derived for each study. Overlapping bubbles in the mid-Atlantic and New England denote retrospective estimates from three time periods (~1970s, 1990s, 2010s, *left to right*).

Stock mixing of Atlantic bluefin tuna in Canadian waters has been investigated in the Gulf of St. Lawrence, because this region represents an important foraging area for giant (adult) category fish (Mather et al. 1995). The origin of Atlantic bluefin tuna in the Gulf of St. Lawrence was first investigated by Rooker et al. (2008a), and this study indicated that ~100% of the giant category fish collected in this region were of western origin (Table 2.1). The importance of the Gulf of St. Lawrence for western fish was confirmed by Schloesser et al. (2010), with their study reporting that giants collected over multiple decades (1970s, 1980s, and 2000s) were almost exclusively (99%–100%) of western origin. However, there is recent evidence of eastern migrants in Canadian waters, with moderate mixing of eastern-origin fish (15%) observed in areas off Nova Scotia outside the Gulf of St. Lawrence (Busawon et al. 2014). The presence of eastern fish in the Gulf of St. Lawrence was also recently reported from electronic tag deployments, and fishery data from the same time period show an increased presence of small fish in this region (Busawon et al. 2014, Wilson et al. 2015).

Overall, the Northwestern Atlantic Ocean (NWAO) is a mixing hot spot for Atlantic bluefin tuna, with otolith chemistry research clearly showing that the US fisheries are dependent to some degree on production from the Mediterranean Sea (Figure 2.4). The extent of transatlantic movement and stock mixing in these waters appears to be highly variable across size/age classes, years, and decades. These results are supported in part by other approaches. Conventional tagging studies first indicated very low rates of mixing in the 1970s, whereas more recent electronic tagging studies showed transatlantic migration rates—mostly eastern-origin fish returning to the Mediterranean Sea to spawn—exceeding 15% (Kurota et al. 2009). Electronic tagging also suggested that a significant number of individuals in the North Carolina winter fishery migrated from the Mediterranean Sea as juveniles and returned as adults (Block et al. 2005). Higher mixing of juvenile (school category) Atlantic bluefin tuna (~ages 1–4) in the NWAO was also reported by scientists using organochlorine tracers (e.g., chlorodane:PCB ratios), with eastern-origin fish accounting for a significant fraction of the US recreational fishery in the mid-Atlantic from 2000 to 2008 (33%–88%; Dickhut et al. 2009) and from 2011 to 2012 (18%–33%; Graves et al. 2015).

Northeastern Atlantic Ocean

The origin of Atlantic bluefin tuna in several regions of the Northeastern Atlantic Ocean (NEAO) has generally shown low rates of mixing from the Gulf of Mexico population, with the exception of a few areas outside the Mediterranean Sea. The stock composition of medium and giant category fish from trap fisheries in two regions of the NEAO (Morocco and Portugal) was determined recently by Rooker et al. (2014), and a difference was observed regarding the presence of western migrants in the two fisheries. No western migrants were detected in the sample from the Portuguese traps located west of the Strait of Gibraltar (Table 2.1; Figure 2.4). Conversely, a small fraction of western migrants (6%) were detected in the trap fishery from the northwest coast of Africa off Morocco, suggesting that western-origin fish also display transatlantic movement and inhabit waters adjacent to the Mediterranean Sea spawning area. Fraile et al. (2015) examined Atlantic bluefin tuna present in the regional bait boat fleet operating north of these trap fisheries in the Bay of Biscay and also detected western migrants in this fishery, although they accounted for only 1% and 3% of the entire sample of juveniles and adults examined. Similar to stock-mixing estimates reported above for the NWAO and NEAO, contribution rates varied among years examined, with the presence of western migrants detected in the 2009 sample (2%–5%) only from the Bay of Biscay, whereas 2010 and 2011 samples were comprised entirely of fish produced from the Mediterranean Sea.

Central North Atlantic Ocean: East and West of 45°W

The first attempt to assess the origin of Atlantic bluefin tuna targeted by high seas fishing fleets (e.g., Japanese longline vessels) operating on each side of the 45°W management boundary was performed by Rooker et al. (2014). Significant stock mixing of Atlantic bluefin tuna was reported in this study, with both stocks commonly crossing the management boundary. The estimated contribution of western-origin fish in the Central North Atlantic Ocean (CNAO) fishery was 21% for specimens collected from 2010 to 2011, with the majority of Atlantic bluefin tuna (79%) in this region classified as eastern-origin fish (Table 2.1). Migrants from both spawning areas were detected on each side of the management boundary; 44% of the Atlantic bluefin tuna collected west of 45°W were classified as eastern-origin fish, whereas 15% of the Atlantic bluefin tuna collected east of 45°W were classified as western-origin fish. This finding confirms that the CNAO is an important mixing zone for Atlantic bluefin tuna, with both eastern and western stocks readily "crossing the line" and entering the other management zone (Figure 2.4).

Natal Homing to Gulf of Mexico and Mediterranean Sea

Natal homing—defined here as the return of adults to their place of origin—has been addressed by examining the otolith core $\delta^{18}O$ and $\delta^{13}C$ values of adult Atlantic bluefin tuna collected in each spawning area. Because chemical markers in otolith cores are nursery-specific tags that remain unchanged during the life of an individual, they are particularly suitable for investigations of natal homing. Central questions of philopatry (multigenerational return to the same spawning region) or spawning fidelity (multiple returns by an adult to the same spawning region, regardless of natal origin) are better addressed by genetic markers and electronic tagging approaches (Block et al. 2005, Secor 2015), although otolith chemistry is applicable in these types of studies.

Findings from several studies using stable isotopes indicate that despite the presence of transatlantic movement and stock mixing, homing to the Gulf of Mexico and Mediterranean Sea spawning areas exceeds 95%. Initial estimates of nursery origin of adults (giants) from both spawning areas were reported by Rooker et al. (2008a), and nearly all of the adults captured in the Gulf of Mexico (99%) and the Mediterranean Sea (96%) were from the same region in which they were collected, supporting the premise of natal homing. Investigations of giant Atlantic bluefin tuna collected in the Gulf of Mexico over longer periods (1974–2014, year classes 1944–2006; Siskey et al. 2016) found similar results, with all adults (100%) classified to the western stock. In the east, the origin of medium and giant category Atlantic bluefin tuna collected at both the entrance to (Strait of Gibraltar) and multiple locations within the Mediterranean Sea spawning area (Balearic Islands, Malta, Sardinia, and Cyprus) showed that fish in these locations were almost exclusively of eastern origin (99%–100%; Rooker et al. 2014). The presence of nearly homogenous populations of western-origin adults in the Gulf of Mexico and eastern-origin adults in the Mediterranean Sea clearly demonstrates that Atlantic bluefin tuna exhibit strong natal homing and that straying by either stock into the opposite spawning area appears to be uncommon (Figure 2.4). These results are consistent with genetic studies that show strong separation between larvae and young-of-the-year Atlantic bluefin tuna captured in the two spawning areas (Carlsson et al. 2007, Boustany et al. 2008).

Age-Specific Migration

Life history transects of otolith $\delta^{18}O$ from the core (nursery habitat) to the margin (recent habitat) serve as an emerging and promising tool for determining age-specific movements and natal homing patterns of adult Atlantic bluefin tuna. Using an otolith $\delta^{18}O$ threshold value of approximately −0.9 as the boundary between eastern (>−1.0) and western (<−0.9) habitation (Figure 2.2), Schloesser et al. (2010) provided preliminary evidence that the approach could be used to document resident and migratory patterns of Atlantic bluefin tuna. Here, we show the application of otolith $\delta^{18}O$ life history transects to identify different migration patterns displayed by Atlantic bluefin tuna using data from a pilot study. Three unique migratory contingents have been identified: NEAO/Mediterranean residents, NWAO/Gulf of Mexico residents, and transatlantic migrants.

Otolith $\delta^{18}O$ values of Atlantic bluefin tuna that fall within the expected range of only one region (east or west) during the life of an individual were classified as residents of this region. Examples of NEAO/Mediterranean res-

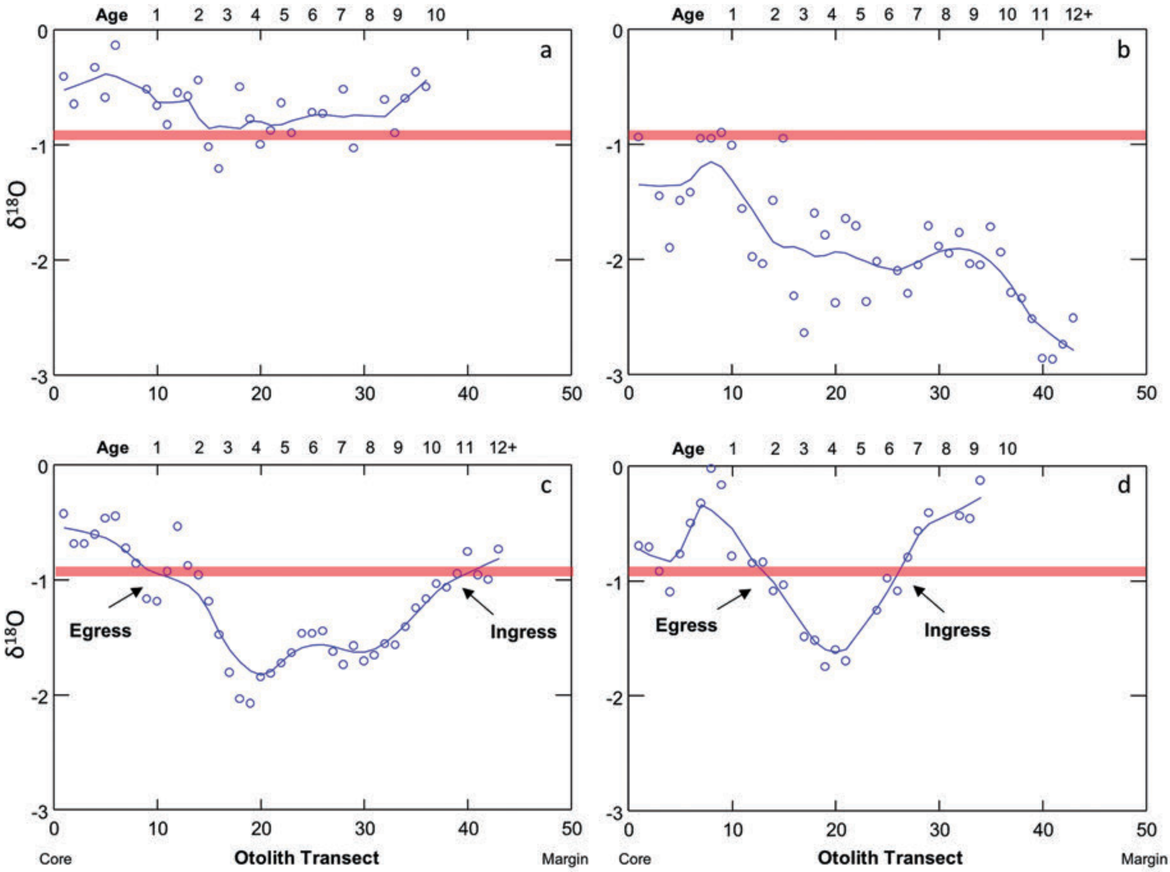

Figure 2.5. Otolith $\delta^{18}O$ life history transects for four adult Atlantic bluefin tuna. Otolith $\delta^{18}O$ threshold value –0.9 denotes the general boundary between eastern and western habitation. Three unique migration behaviors are shown: (*a*) Northeastern Atlantic Ocean / Mediterranean resident collected in Mediterranean Sea, (*b*) Northwestern Atlantic Ocean / Gulf of Mexico resident collected in the Gulf of Mexico, and (*c, d*) transatlantic migrants captured in the Mediterranean Sea. Putative timing of Mediterranean Sea egress and ingress denoted for the two specimens displaying transocean migrations. Otolith microstructure analysis was used to determine the age and distance of each annulus from the otolith core. Estimated age is provided at the top of each plot.

ident and NWAO / Gulf of Mexico resident (Figure 2.5a and b, respectively) do not appear to undergo transatlantic movement, because otolith $\delta^{18}O$ values remain within the expected range of eastern and western yearling values during the entire life of the individual. Intriguingly, the individual classified as a western resident (Figure 2.5b) shows a conspicuous decline in otolith $\delta^{18}O$ over time after age 1, which likely corresponds to an ontogenetic shift by this individual, which is possibly spending more time in the NWAO (i.e., Canadian waters) with increasing age because the lowest seawater $\delta^{18}O$ values in their presumed range occur here (see Figure 2.1). In contrast, the two other adult Atlantic bluefin tuna show otolith $\delta^{18}O$ profiles that are indicative of movement away from the Mediterranean Sea, followed by a return to this region later in life (Figure 2.5, c and d). Otolith $\delta^{18}O$ life history transects of both show potential egress from the Mediterranean Sea/NEAO around age 1 or age 2 into more depleted $\delta^{18}O$ waters in the NWAO, as indicated by reduced otolith $\delta^{18}O$ values <-1.0 after age 2. At approximately age 10 (Figure 2.5c) and age 7 (Figure 2.5d), otolith $\delta^{18}O$ values are again >-0.9, suggestive of movement back into the NEAO followed by homing to the Mediterranean Sea, which was the point of capture (otolith margin) for the specimens shown. Observed patterns of age-specific egress from the Mediterranean Sea followed by a return to this region several years later are in accord with otolith chemistry observations on both transatlantic movement and natal homing.

Application of Otolith Chemistry to Assessment and Management

A broad international community of fisheries scientists is now working to integrate otolith chemistry results into assessments and modeling frameworks that explicitly include stock mixing (SCRS 2016). This database, compiled by ICCAT's Atlantic-wide research program for bluefin tuna (GBYP) now contains more than 5,500 records of individual population assignments supplied by European Union, Japanese, Canadian, and US scientists. Age-based assessments, including virtual population analysis (VPA) and statistical catch-at-age models are now being applied by assessment scientists in a manner that explicitly includes stock-of-origin information emanating from thousands of analyzed otoliths collected from fisheries throughout the North Atlantic Ocean (Table 2.1). The obvious benefit here is that the same individual (otolith) analyzed for origin can be assigned an age (Siskey et al. 2016), so that fleets, fishing selectivity, and catch-per-unit-effort (CPUE) series are explicitly attributed to age class, year class, maturity, and stock of origin. Clearly, this application depends on representative sampling of principal fisheries and population components (e.g., spawners in the Gulf of Mexico and the Mediterranean Sea). Still, the approach is feasible, and ICCAT has invested heavily in developing the capacity to analyze thousands of otoliths and develop assessment frameworks that can incorporate such information (Pallarés et al. 2013, Carruthers 2015). This does not discount the contribution of other central sources of information such as electronic tags and other types of natural tags (e.g., genetic, contaminant), which can resolve patterns in seasonal and regional selectivity through fitting movement matrices (Taylor et al. 2011). Indeed, assessment scientists have efficiently utilized information from diverse applications in developing assessment parameters through the application of likelihood frameworks (e.g., Kurota et al. 2009)

Addressing Key Assessment Uncertainties

Assessment and management of Atlantic bluefin tuna is hampered by three uncertainties:

1. What stock boundaries best serve assessment and management aims, and can we scientifically support fixed boundaries for highly migratory Atlantic bluefin tuna?
2. Is stock productivity, particularly for the western stock, underlain by a single stock-recruitment function or multiple stock-recruitment functions?
3. How does stock mixing bias the western and eastern stock assessments?

Although these questions remain unresolved, otolith chemistry has provided important insights into each.

Analysis of chemical markers in otoliths has been particularly important in confirming that the 45°W management boundary in the Central Atlantic Ocean partially divides the two populations of Atlantic bluefin tuna: adults seasonally home to spawning areas on either side of that boundary (Rooker et al. 2008a, 2014; Siskey et al. 2016). However, the high level of mixing in US Atlantic fisheries supports the view that many Atlantic bluefin tuna cross the line, particularly juveniles emanating from natal sites in the Mediterranean Sea. Further, Atlantic bluefin tuna aggregations in the CNAO, targeted in high sea longline fleets, historically occurred as discrete fisheries on either side of the management boundary; however, over the past 20 years, this aggregation has been centered around the 45°W management boundary (SCRS 2014). To counter the artificial construct of a single boundary, assessment scientists have proposed more resolved stock boundaries that relate to specific population segments and seasonal migration behaviors for which otolith chemistry can provide support (Taylor et al. 2011, Kerr et al. 2017).

Assessments on each stock have shown independent abundance dynamics during the past three decades, but a dominant trend is the sustained depressed abundance and recruitment of the western stock at about one-third of its abundance in the 1970s (SCRS 2014). This has led to controversy on whether to reference the historical or the more recent abundance level in implementing harvest policy. In fact, two alternative stock-recruitment curves and their management implications are presented to ICCAT in each assessment cycle (e.g., SCRS 2014). Arguments center on (1) whether sustained high exploitation limits recovery to historical levels, (2) whether a regime change had occurred limiting juvenile production, and (3) whether the population has been altered in a manner (e.g., age truncation) that curtails recovery (Secor et al. 2015). In the late 2000s, a pulse of juvenile fish appeared in US fisheries, which was ascribed to a strong 2003 year class. If this year class was of western origin, then it goes against the latter two hypotheses related to a fundamental shift in western stock productivity. Through focused sampling of the size mode associated with this year class, Secor et al. (2015) used otolith chemistry to confirm that this year class was predominately comprised of western-origin juveniles. This result was confirmed further by Siskey et al. (2016), who showed overall lower mixing levels in juveniles and adults collected in US fisheries from 2009 to 2014, which is suggestive of higher recruitment emanating from the western stock. Still, a recent analysis indicates that a dominant year class produced in 2011 may now be moving through US fisheries, and initial evidence indicates that it is dominated by eastern-origin juveniles (Barnett et al. 2016).

With sufficient sampling of otoliths for population assignment across seasons, regions, fleets, and size classes, traditional assessment approaches such as VPA can be modified to evaluate the influence of regional fishing and stock mixing on spawner biomass across stocks (Butterworth and Punt 1994, Porch et al. 2000, Goethel et al. 2011). Indeed, it is probable that otolith chemistry data available in the GBYP database will enable scientists to parameterize VPAs according to stock of origin in future assessments (SCRS 2016). Beyond VPA approaches, more flexible statistical catch-at-age models can integrate information from electronic and conventional tagging, landings, CPUE series, and otolith chemistry into a single assessment that estimates yield and fishing mortality across fleets, regions, and seasons (Taylor et al. 2011). In an initial application of this modeling framework, otolith chemistry informed estimates of movement and yield pertinent to US fisheries, which in turn were used to evaluate the effect of fishery closures on Atlantic bluefin tuna recovery (Taylor et al. 2011).

Although it is feasible to refine statistical models such as those described above to include stock assignments in fitted catch, size, age, and CPUE data, these models are data intensive, often requiring parameters for which stock composition estimates are not available. In such instances, simulation approaches, known as operating models, can provide key insights by exploring the impact of alternate premises on population structure and of mixing on assessment outputs and management goals (Kerr and Goethel 2014). Scenarios in operating models can be guided by scientific consensus, new discoveries, or major controversies. Operating models should focus on important uncertainties, but in comparison to stock-assessment models, they do not require intensive data inputs and the narrow parameter constraints required for statistical convergence. Kerr et al. (2015) developed an operating model designed to evaluate how uncertainty in seasonal movements and stock productivity influenced stock mixing and fishery yields in NWAO fisheries. Tagging data informed movement matrices, which were used to model seasonal yields across fishing areas, and otolith chemistry was used to compare scenario results of eastern stock versus western stock yields across areas against observed mixing levels (Kerr et al. 2015). An ongoing emphasis within ICCAT is the development of management strategy evaluations, which develop operating models but then subject scenarios of mixing and other sources of uncertainty to monitoring, assessment, and harvest-control rules to evaluate the effectiveness of current management practices to principal sources of uncertainty (Carruthers 2015).

Future refinements and developments in otolith chemistry, including the numerical approaches for estimating stock composition (e.g., Hanke et al. 2016), will continue to aid in understanding the migration ecology of Atlantic bluefin tuna and provide information critical to their assessment and management. The use of this type of natural tracer is limited by the type of sampling required (lethal), cost constraints, and the type of information that can be generated—here, information related to seasonal exposures to ocean subbasins that differ in chemistry and temperature. As a result, other approaches such as population genomics will continue to be developed for Atlantic bluefin tuna, but they remain not yet operational in terms of the level of discrimination they can currently provide. This is likely to change in the near future, and molecular marker applications are highly relevant to assessing mixing, uncovering new population structures (subpopulations and contingents), and understanding migration behaviors. Further, molecular markers can directly assess stock abundance through close-kin genetics, and population genomics will likely be an important operational tool used in the near future to address Atlantic bluefin tuna migration ecology (Carruthers et al. 2016). The combination of this new, emerging technology with otolith chemistry and, potentially, information on other natural tracers will lead to more spatially explicit information on the origin, movement, and stock mixing of Atlantic bluefin tuna.

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