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Discriminating among yellowfin tuna *Thunnus albacares* nursery areas in the Atlantic Ocean using otolith chemistry

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ABSTRACT: Otolith chemistry of young-of-year (YOY) yellowfin tuna *Thunnus albacares* was examined to determine whether chemical signatures are distinct across major spawning areas in the Atlantic Ocean. YOY yellowfin tuna otoliths were collected from 4 locations in the Atlantic Ocean (Gulf of Mexico, Caribbean Sea, Cape Verde, and Gulf of Guinea) from 2013–2015, and trace element (Li, Mg, Mn, Sr, Zn, and Ba) and stable isotope ($\delta^{13}C$ and $\delta^{18}O$) analyses were conducted to investigate regional variation in otolith chemical composition. Results indicated that significant regional differences in chemical signatures existed for each cohort of YOY yellowfin tuna investigated. Quadratic discriminant function analysis showed that nursery assignment accuracies based on otolith trace elements and stable isotopes were 64–85% for each cohort, justifying the use of these natural tracers as regional discriminators for yellowfin tuna. Significant interannual variability in regional signatures was also detected, highlighting the importance of age-class matching when using the baseline of nursery signatures to estimate the origin of sub-adult and adult yellowfin tuna. This study clearly demonstrates that baseline chemical signatures in the otoliths of YOY yellowfin tuna are distinct and can therefore serve as an effective tool for assigning older individuals to their nursery of origin, ultimately providing a way to improve our understanding of the population connectivity and mixing rates of this species in the Atlantic Ocean.

KEY WORDS: Yellowfin tuna · Atlantic Ocean · Otolith chemistry · Nursery discrimination · Trace elements · Stable isotopes

INTRODUCTION

Yellowfin tuna *Thunnus albacares* is a valuable international resource and an important predator in the open-ocean ecosystem, yet heavy fishing pressure over the last few decades has caused population declines in the Atlantic Ocean. The most recent stock assessment shows that yellowfin tuna in the Atlantic Ocean are very close to being overfished (ICCAT 2016). Not only are yellowfin tuna one of the main targets of pelagic longliners throughout the Atlantic Ocean, but the majority of landings are from purse-seine vessels in spawning and nursery areas in the eastern Atlantic Ocean (ICCAT 2011). While yellowfin tuna are currently managed as 1 panmictic (mixed) stock in the Atlantic Ocean (NMFS 2001), little is known regarding the migratory behavior and population connectivity of yellowfin tuna in the

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Atlantic Ocean, despite the fact that this information is critical to the development of effective management strategies.

Multiple spawning areas exist for yellowfin tuna in the Atlantic Ocean, but the primary spawning area is thought to be in the eastern Atlantic Ocean, with production centered in the Gulf of Guinea (ICCAT 2011). Commercial landing and tagging data suggest that age-1 and age-2 yellowfin tuna that spawn in this region migrate across the Atlantic Ocean into US waters, with some individuals entering the Gulf of Mexico (Hazin 1993, Fonteneau & Soubrier 1996). Migration back to the eastern Atlantic Ocean generally occurs once these fish reach maturity at about 3 yr of age (Diaha et al. 2016), although the degree of homing to natal sites is presently unknown (Fonteneau & Soubrier 1996, Arocha et al. 2001). It is presumed that east to west trans-Atlantic migrations are for feeding purposes and return migrations (west to east) are for spawning; however, spawning has also been documented in the western Atlantic Ocean (Lang et al. 1994, Arocha et al. 2001, Frank et al. 2015). In fact, it has been suggested that there are at least 3 other spawning areas in the Atlantic Ocean, including the eastern Caribbean Sea, Gulf of Mexico, and Cape Verde (Arocha et al. 2001, ICCAT 2011). The spawning season in the Eastern Atlantic lasts from December to April/May (Diaha et al. 2016), and spawning in the Gulf of Mexico occurs between April and August (Frank et al. 2015). While differences in size and spawning seasons may suggest that multiple spawning stocks exist, results of genetic studies have not indicated any evidence of significant heterogeneity of yellowfin tuna in the Atlantic Ocean (Scoles & Graves 1993, Ward et al. 1997, Talley-Farnham et al. 2004), indicating that at least some mixing occurs among spawning populations. Thus, additional research is necessary to determine the relative importance of different spawning areas, and to better understand the degree of population connectivity and mixing of yellowfin tuna in the Atlantic Ocean.

Several approaches have been developed to examine the migration ecology and population connectivity of pelagic fishes, including archival tags (Block et al. 2005, Hoolihan et al. 2014), surveys of molecular markers and population genetics models (Ward et al. 1997, Purcell & Edmands 2011), and natural markers in hard parts (Rooker et al. 2008b, 2014). Examining natural chemical markers in hard parts, especially in otoliths (ear stones), is a particularly effective and widely used technique in fisheries ecology (reviewed by Campana & Thorrold 2001 and Elsdon et al. 2008). Otoliths precipitate material as a fish grows and elements are incorporated into the calcium carbonate–protein matrix in relation to concentrations in the surrounding seawater (Campana 1999). Material is not resorbed once deposited, and therefore incorporated chemical markers are preserved (Campana & Neilson 1985). As a result, the chemical composition of otolith material deposited during the early juvenile stage serves as a natural marker of the individual's nursery region. Previous research has shown that trace elements and stable isotopes ($\delta^{13}C$ and $\delta^{18}O$) can serve as effective natural tags in fish otoliths (Thorrold et al. 2001, Forrester & Swearer 2002), and recent studies have demonstrated that these chemical markers can be used to reliably predict the origin of tropical and temperate tunas (Wells et al. 2012, Rooker et al. 2014, 2016).

The purpose of this study was to determine whether young-of-the-year (YOY) yellowfin tuna from different nursery areas in the Atlantic Ocean have distinct chemical signatures in their otoliths. If so, otolith chemistry could be used to retrace the origin of adult fish and determine the degree of stock mixing by yellowfin tuna from different production zones in the Atlantic Ocean, which may provide useful information for determining whether the population should be separated into distinct stocks. In this study, we created a comprehensive database of chemical signatures (trace elements and stable isotopes) for all putative nursery areas in the Atlantic Ocean (Gulf of Guinea, Cape Verde, Caribbean Sea, and Gulf of Mexico). Further, we evaluated the interannual variability in nursery-specific chemical signatures of YOY yellowfin tuna collected over a 3 yr period (2013–2015) to determine whether nursery signatures are stable across time. Ultimately, this information will help to determine nursery origin and trans-oceanic migration patterns, as well as population connectivity and mixing rates of yellowfin tuna in the Atlantic Ocean.

MATERIALS AND METHODS

Sample collections

YOY yellowfin tuna were collected from 4 geographically distinct nursery areas in the Atlantic Ocean: (1) Gulf of Mexico, (2) Eastern Caribbean Sea (Martinique and Saint Lucia, hereafter referred to as Caribbean Sea), (3) Gulf of Guinea, and (4) Cape Verde (Table 1, Fig. 1). YOY were collected over a 3 yr period (2013–2015), and all specimens were captured either by hook and line (Gulf of Mexico, Carib-

Table 1. Summary data for young-of-the-year (YOY) yellowfin tuna collected from 4 regions of the Atlantic Ocean. Mean (± SD) fork length (FL) is provided for each region and cohort

Region	Cohort	N	Mean FL (cm)
Cape Verde	2012	34	47.4 ± 5.3
	2013	15	46.0 ± 2.7
	2014	21	38.3 ± 3.1
Gulf of Guinea	2012	35	37.2 ± 3.4
	2013	22	46.6 ± 2.2
Gulf of Mexico	2012	20	35.9 ± 4.0
	2013	16	38.3 ± 3.3
	2014	6	34.2 ± 5.1
Caribbean Sea	2012	23	29.0 ± 2.3
	2013	26	28.9 ± 2.4
	2014	20	39.1 ± 5.2

bean Sea) or purse seine (Gulf of Guinea, Cape Verde). Samples were collected across multiple years in each region to investigate interannual variability in nursery signatures. Further, within each nursery area, samples were collected on multiple dates and/or from multiple locations each year to account for natural variability in region-specific chemical signatures. For all samples collected, fork length (FL), capture date, and capture location were recorded. An effort was made to collect only the smallest juveniles available (<45 cm FL) to minimize the possibility that any large-scale movement occurred prior to sampling, as it is currently thought that yellowfin tuna migrate from nursery areas in the Atlantic Ocean once they attain 60–80 cm FL (i.e. in their second year of life; Fonteneau & Soubrier 1996, ICCAT 2002). Thus, specimens were considered to have been collected in the same region as their place of origin. While specimens of this size were not always available, the majority of yellowfin tuna collected (80%) were approximately 5–9 mo of age, and all fish were less than 1 yr old (ca. <55 cm FL; based on growth curves developed by Shuford et al. 2007).

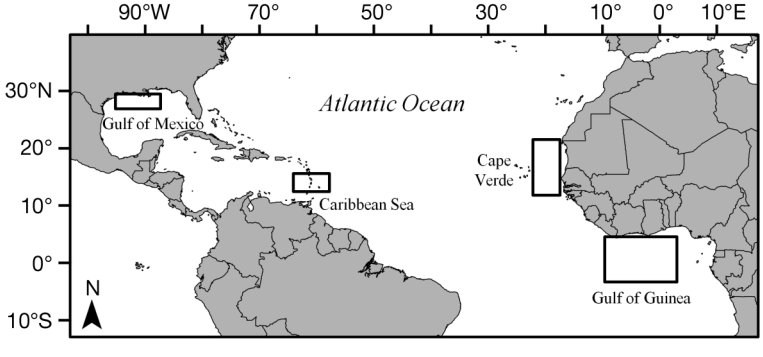

Fig. 1. The 4 nursery areas sampled for young-of-year (YOY) yellowfin tuna in the Atlantic Ocean: Gulf of Mexico, eastern Caribbean Sea, Cape Verde, and Gulf of Guinea. Approximate collection areas are denoted by black boxes

Otolith preparation

Sagittal otoliths from fresh or frozen yellowfin tuna were extracted from the cranial cavity, cleansed of adhering tissue, rinsed with deionized water, and stored dry in plastic vials. One otolith from each specimen was embedded in EpoFix resin (Struers) and sectioned using a low-speed ISOMET saw (Buehler) to obtain a 1.5 mm section of the core of the otolith, following protocols described by Rooker et al. (2008a). Thin sections were mounted onto a glass slide using Crystalbond thermoplastic glue (SPI Supplies/Structure Probe) and polished using 0.3 mm MicroPolish Alumina Powder and 600–1200 grit silicone-carbide paper (Buehler). All otoliths were polished until the antirostrum became transparent, which indicated that the core was exposed.

Trace element analysis

Trace element concentrations were measured using a laser ablation inductively coupled plasma mass spectrometer (LA-ICP-MS) at Texas A&M University (Galveston Campus). The system consists of an ultraviolet laser ablation unit (NWR 213, New Wave Research) connected to a XSeries II Thermo Scientific ICP-MS. Eight elements were measured in all otoliths: ^{7}Li, ^{24}Mg, ^{55}Mn, ^{59}Co, ^{65}Cu, ^{88}Sr, ^{137}Ba, and ^{66}Zn. The element ^{44}Ca was also measured and was used as an internal standard to correct for variations in ablation yield among samples (Rooker et al. 2001); this element was assumed to be evenly distributed in otoliths at a concentration of 38% (Yoshinaga et al. 2000). Ablation occurred inside a sealed chamber, and ablated material was carried by helium gas (800 ml min^{-1} flow rate) to the ICP-MS where it was mixed with argon gas. Prior to ablation, the chamber was purged for 10 min to remove any gas or particle contamination. The National Institute of Standards and Technology (NIST) 614 standard was used to create calibration curves for each sample and monitor instrument drift (measured every 2 samples). Mean counts of a background reading taken before each

ablation point were used as the blank and were subtracted from the raw ion counts for each element. The laser was operated with a repetition rate of 10 Hz with a scan speed of 5 µm s^{-1} for all analyses. In order to remove any surface contamination, the entire area of each sampling spot (50 µm diameter) was pre-ablated for approximately 10 s prior to analysis. Five replicate spots were ablated in the core region of the otolith, which contains material accreted within the first 3 mo of life (Fig. 2A). Ablation spots were 50 µm diameter circles, and each spot was ablated by the laser for approximately 12 s. The first ablation spot was always placed at the otolith core (narrowest part of the section), followed by 2 spots placed approximately 15 µm apart on each side of the core. Trace element data from the 5 replicate ablation sites were averaged to create a composite signature for each individual yellowfin tuna. Samples from multiple capture locations were analyzed in the same runs to prevent any bias resulting from instrument drift (Hamer et al. 2003). Detection limits (in µg g^{-1}) for each element were calculated as 3× the standard deviation (SD) of the blank signal and were: ^{7}Li: 0.48, ^{24}Mg: 2.08, ^{55}Mn: 0.33, ^{59}Co: 0.25, ^{65}Cu: 0.52, ^{88}Sr: 3.71, ^{137}Ba: 1.24, and ^{66}Zn: 0.94. Trace element concentrations (E, ppb) were converted to element:Ca ratios (µmol mol^{-1}) based on the molar mass of each element (M, g mol^{-1}) standardized to ^{44}Ca concentrations:

$$\text{element:Ca} = \frac{E}{1000}\left(M\,\frac{0.38}{44}\right)^{-1} \quad (1)$$

Stable isotope analysis

A high-resolution mill (New Wave MicroMill System) was used to isolate material from the otolith cores of YOY yellowfin tuna for δ^{13}C and δ^{18}O analysis. After trace element analysis, otoliths were polished lightly (removing ~30–50 µm) until all ablation pits completely disappeared and the antirostrum was no longer visible, allowing for all chemical analyses to be conducted on a single otolith. Similar to Wells et al. (2012), a drill path was developed from otolith measurements of the 5 smallest YOY yellowfin tuna in our set of samples (24–30 cm FL). This drill path covers the area of the otolith corresponding to the first 5–6 mo of life (Fig. 2B), with a larger area of the otolith sampled for stable isotopes than trace elements due to differences in sample material requirements. Otoliths were milled to a depth of ~770 µm (14 passes, 55 µm depth) using a 350 µm diameter carbide bit (Brasseler). Powdered core material was collected in weigh paper and sent to the Environmental Isotope Laboratory at the University of Arizona for stable isotope analysis, where otolith δ^{13}C and δ^{18}O were quantified using an isotope ratio mass spectrometer (Finnigan MAT 252, Thermo Fisher Scientific) equipped with an automated carbonate preparation device (KIEL-III, Thermo Fisher Scientific). Isotopic ratio measurements were calibrated based on repeated measurements of NBS-18 and NBS-19 (National Bureau of Standards). Otolith δ^{13}C and δ^{18}O values (‰) are expressed in standard delta (δ) notation as $^{13/12}$C and $^{18/16}$O ratios (R) relative to an in-house standard calibrated against Vienna Pee Dee Belemnite:

$$\delta_{sample} = \left(\frac{R_{sample} - R_{standard}}{R_{standard}}\right) \times 10^{3} \quad (2)$$

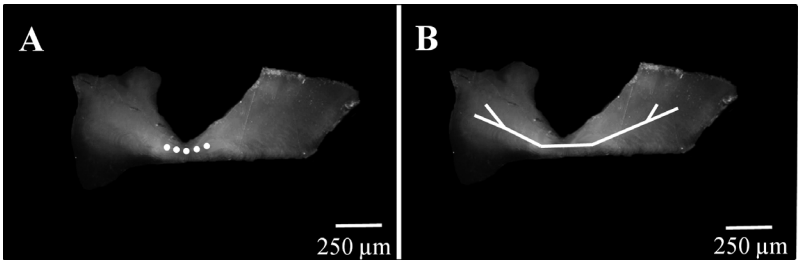

Fig. 2. Transverse section of a young-of-year (YOY) yellowfin tuna otolith displaying (A) the approximate location of laser ablation spots for trace element analysis and (B) the MicroMill drill path used for stable isotope analysis. All material within 175 µm on each side of the drill path was isolated due to the width of the drill bit

Data analysis

Individual ages were estimated based on a published age–length curve for yellowfin tuna in the Atlantic Ocean (Shuford et al. 2007), and spawning dates were back-calculated from the date of capture. Individuals were assigned to 1 of 3 cohorts based on their estimated spawning dates. Those spawned from mid (June) 2012 to early (May) 2013 were assigned to the 2012 cohort (hereafter '2012'). Similarly, individuals spawned from mid-2013 to early-2014 were assigned to the 2013 cohort ('2013') and those spawned from mid-2014 to early-2015 were assigned to the 2014 cohort ('2014'). These time periods

were chosen based on observed gaps in the spawning dates of samples used in this study (Fig. 3).

To determine whether the otolith chemistry of YOY yellowfin tuna varied spatially, multivariate analysis of variance (MANOVA) was used to test for differences in element:Ca ratios and $\delta^{13}C$ and $\delta^{18}O$ values among regions and cohorts. Statistical significance was determined based on Pillai's trace statistic, because it is the most robust to violations of homogeneity of variance (Wilkinson et al. 1996). Univariate tests for individual stable isotopes and trace elements were analyzed using analysis of variance (ANOVA), and *a posteriori* differences among means were detected with Tukey's honestly significant difference (HSD) test. Additionally, quadratic discriminant function analysis (QDFA) was performed to test the ability of trace element and stable isotope signatures to discriminate among the 4 nursery areas. QDFA is the preferred classification method because it does not require multivariate normality or assume homogeneity of the covariance matrices (McGarigal et al. 2000). Jackknifed cross-validation classification accuracies were calculated to estimate the success of classification to the regions in which the samples were collected. QDFAs were performed for each cohort as well as a combined dataset including all cohorts. Additional QDFAs were run for each cohort using pooled eastern and western Atlantic nurseries to determine whether this technique is effective in detecting trans-Atlantic migration. The constituents most important in distinguishing yellowfin tuna from different nursery areas were identified through stepwise discrimination procedures for each QDFA, and only significant variables were retained in the final model. Canonical variate coefficients were plotted to visualize the separation in chemical signatures among nursery areas. All statistical analyses were performed using MYSTAT (SYSTAT Software) and JMP 13 (SAS Institute), and significance was determined at an α level of 0.05.

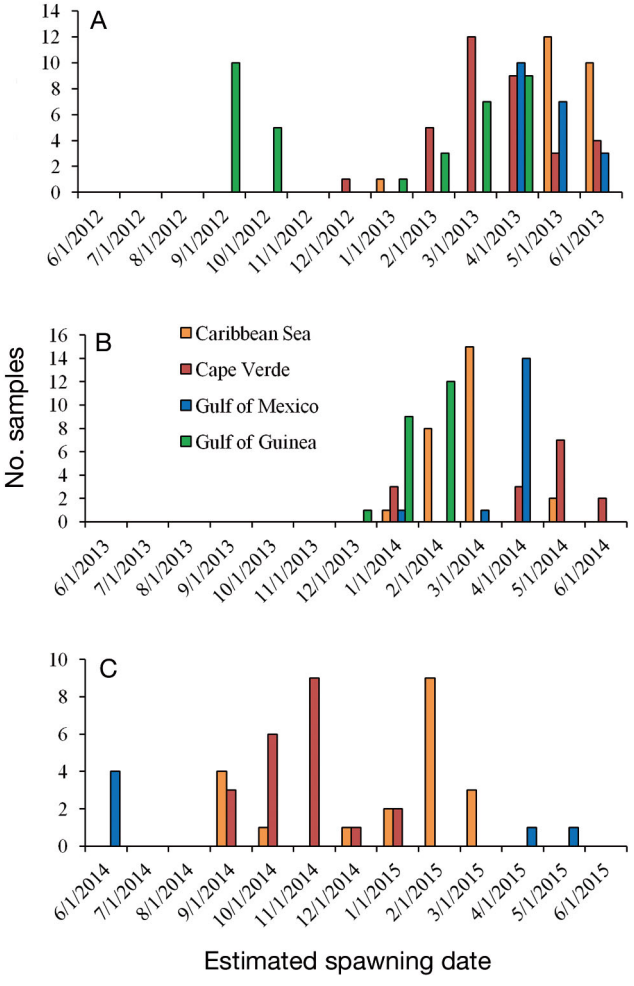

Fig. 3. Distribution of estimated spawning dates (mo/d/yr) for (A) 2012, (B) 2013, and (C) 2014 cohorts of young-of-the-year (YOY) yellowfin tuna collected from 4 nursery areas in the Atlantic Ocean

RESULTS

In total, otoliths from 238 YOY yellowfin tuna collected from 4 nursery regions were analyzed for trace elements and stable isotopes (Table 1). Otoliths were collected from all 4 nursery areas for each cohort except in 2014, for which no samples could be obtained from the Gulf of Guinea. Sizes were similar across regions and years, and the overall mean FL of YOY yellowfin tuna used in this study was 38.6 (±7.4 SD) cm. Spawning dates ranged widely for YOY from the Gulf of Guinea, Cape Verde, and Caribbean Sea, but the majority of YOY captured in the Gulf of Mexico were spawned during spring months (March–May, Fig. 3). Concentrations of 6 trace elements examined (Li, Mn, Mg, Zn, Sr, Ba) were consistently above detection limits for all samples, and these elements (in addition to $\delta^{13}C$ and $\delta^{18}O$) were used in all subsequent analyses.

Several geographic trends in otolith element:Ca ratios were observed; however, region-specific chemical signatures also varied significantly among years (MANOVA, $p < 0.001$). For instance, otolith Li:Ca values showed significant regional differences each year (ANOVA, $p < 0.05$), but trends were not consistent across time. Eastern Atlantic Ocean samples were enriched in lithium relative to western Atlantic Ocean samples in 2013, while an opposite

pattern was observed in 2014 (Fig. 4). Mg:Ca ratios were significantly different among nursery areas for 2 out of the 3 years in the baseline (ANOVA, $p < 0.01$), with the highest Mg:Ca values observed in Caribbean Sea samples in 2012 and 2014 (484 and 463 µmol mol^{-1}, respectively). Mn:Ca values of eastern Atlantic Ocean samples were nearly double those of other regions in 2013 and 2014, although no significant regional differences were detected in 2012. Zn:Ca values in Gulf of Guinea samples were more than an order of magnitude higher than all other regions in 2013 (Gulf of Guinea: 119 µmol mol^{-1}, other regions: 2.4–3.9 µmol mol^{-1}); however, in 2012, Gulf of Guinea samples were statistically similar to values in other areas. Sr:Ca ratios also showed significant regional differences, with Gulf of Mexico Sr:Ca values distinct from Caribbean Sea samples each year (Tukey's HSD, $p < 0.05$). Ba:Ca values varied regionally, although significant differences were only detected in 2012 and 2013 (ANOVA, $p < 0.01$); as with other elements, Ba:Ca patterns were not consistent across time. In general, all but 1 or 2 element:Ca ratios were distinct among nursery areas each year (ANOVA, $p < 0.05$), and each element showed significant regional differences in at least 1 year of the baseline.

Regional variability was also observed in $\delta^{13}C$ and $\delta^{18}O$ values of YOY yellowfin tuna otoliths (Fig. 5). Otolith $\delta^{13}C$ values were distinct among nursery areas for all 3 cohorts (ANOVA, $p < 0.05$). In 2013 and 2014, YOY otoliths from Cape Verde and the Gulf of Mexico were depleted in $\delta^{13}C$ by >0.34‰ relative to the Caribbean Sea and Gulf of Guinea, but this trend was not observed in 2012. A temporal effect was detected in $\delta^{13}C$ signatures, with all regions showing significant interannual variability (ANOVA, $p < 0.01$) except the Gulf of Mexico. Otolith $\delta^{13}C$ values of Cape Verde samples were depleted in 2013 (mean ± SD: −10.22 ± 0.42‰) relative to 2012 (−9.88 ± 0.33‰) and 2014 (−9.70 ± 0.40‰). In the Caribbean Sea, otolith $\delta^{13}C$ values became more enriched each year, with 2014 samples enriched by 0.64‰ compared to 2012. Geographic variability in $\delta^{18}O$ values were only observed in 2012, when Caribbean Sea samples were depleted by more than 0.25F‰ relative to other nursery areas. No significant differences in otolith $\delta^{18}O$ were detected in 2013 and 2014, with regional mean differences <0.08‰. Interannual variability in $\delta^{18}O$ was detected in samples from 2 regions: Caribbean Sea (ANOVA, $p < 0.001$) and Gulf of Guinea (ANOVA, $p < 0.01$). In 2012, $\delta^{18}O$ values were enriched in the Gulf of Guinea (−1.55 ± 0.27‰) relative to 2013 (1.75 ± 0.17‰), while $\delta^{18}O$ values were depleted in the Caribbean Sea (−1.97 ± 0.18‰) compared to 2013 (−1.66 ± 0.24‰) and 2014 (−1.69 ± 0.26‰). Despite the observed interannual variability, regional differences in $\delta^{13}C$ and $\delta^{18}O$ were maintained when 2012, 2013, and 2014 cohorts were

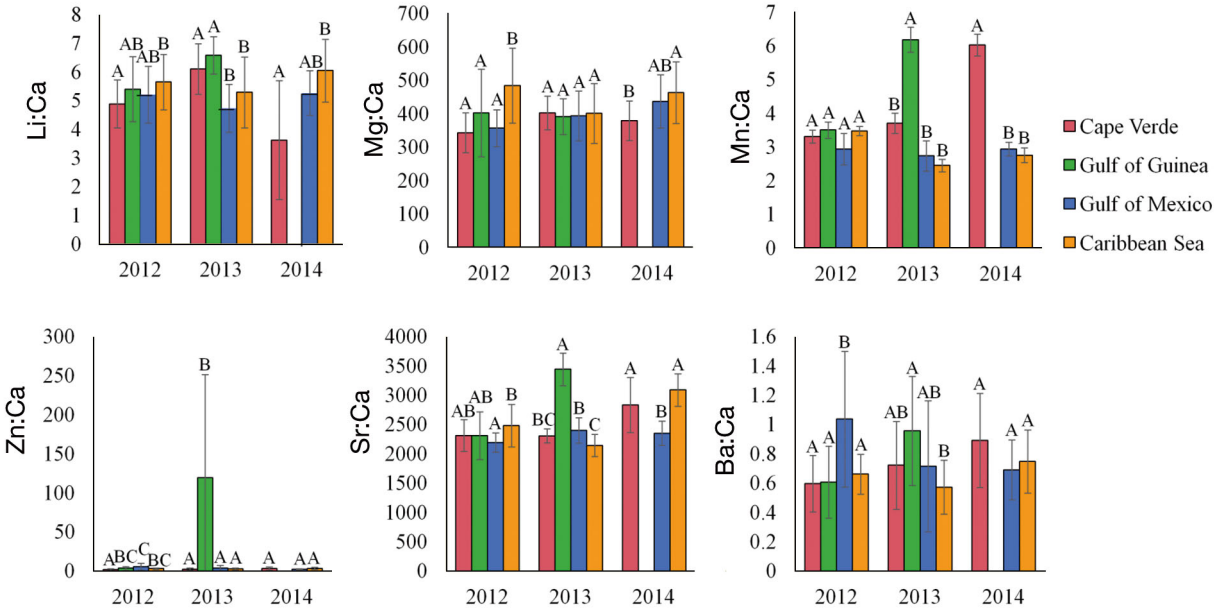

Fig. 4. Mean (± SD) element:Ca ratios (µmol mol^{-1}) in otolith cores of young-of-the-year (YOY) yellowfin tuna collected from 4 nursery areas in the Atlantic Ocean. Lettering above each bar indicates Tukey's HSD pairwise comparisons results; for each region, values with different letters are significantly different ($p < 0.05$)

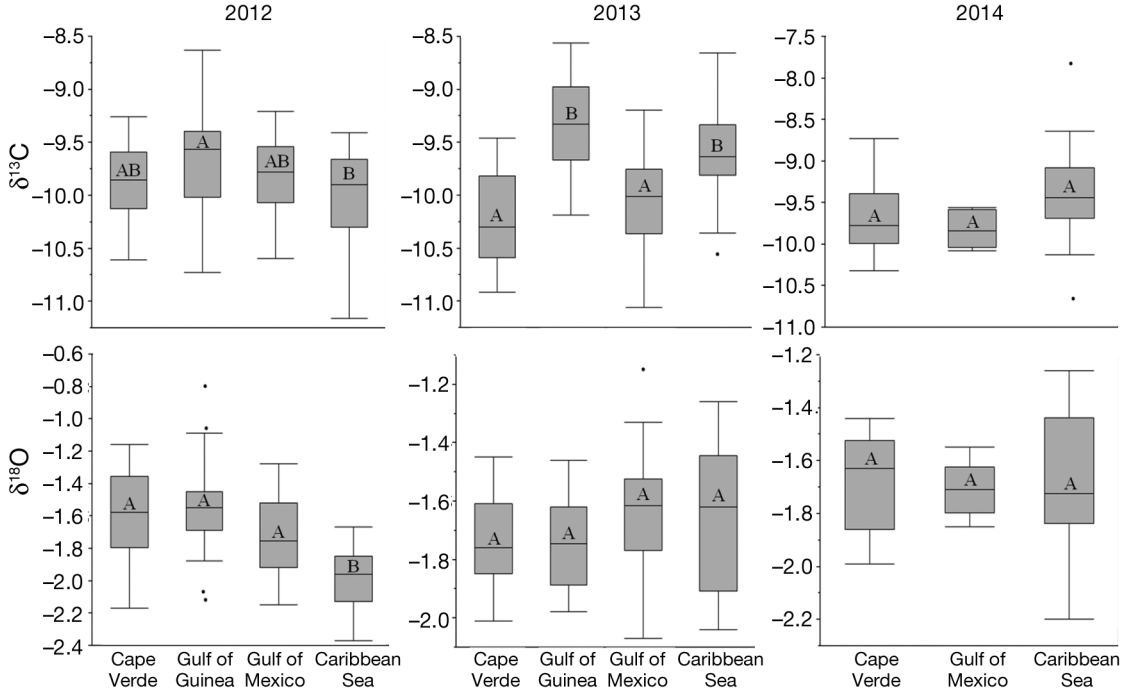

Fig. 5. Otolith $\delta^{13}C$ and $\delta^{18}O$ for young-of-the-year (YOY) yellowfin tuna from 4 nursery areas in the Atlantic Ocean. Box: interquartile range (25^{th} and 75^{th} percentiles); midline: median; error bars: range (excluding outliers, dots); lettering: significant regional differences (Tukey's HSD, $p < 0.05$)

pooled (ANOVA, $\delta^{13}C$: $p < 0.001$, $\delta^{18}O$: $p < 0.01$), with samples from the Gulf of Guinea and Caribbean Sea generally exhibiting more enriched $\delta^{13}C$ values relative to Cape Verde and the Gulf of Mexico (Tukey's HSD, $p < 0.05$), and with Caribbean Sea samples showing more depleted $\delta^{18}O$ signatures relative to nurseries in the eastern Atlantic Ocean (Tukey's HSD, $p < 0.05$).

The elemental composition of YOY yellowfin tuna otoliths differed significantly among nursery areas in each year of this study (2012–2014: MANOVA, $p < 0.001$). QDFAs parameterized with otolith element:Ca (Li, Mg, Mn, Zn, Sr, Ba) and stable isotope ($\delta^{13}C$, $\delta^{18}O$) values from 2012 YOY indicated an overall classification success (jackknifed) of 64% to the 4 nurseries (Table 2), with an expected classification success of 25% based on random assignment. High classification success (i.e. >70%) was observed for samples from the Caribbean Sea, Gulf of Mexico, and Cape Verde in 2012 (74–78%, Table 2). Some overlap was observed between Cape Verde and Gulf of Guinea signatures; thus, an additional QDFA was performed using otolith chemistry data from both of these areas combined. By using the combined dataset, classification success increased from 64 to 79%, with 87% of samples correctly assigned to the eastern Atlantic Ocean (Cape Verde + Gulf of Guinea). In 2013, the overall classification success to the 4 nursery areas was 78%, with 100% of samples correctly assigned to the Gulf of Guinea and 80% correctly assigned to

Table 2. Region-specific quadratic discriminant function analysis (QDFA, %) classification successes for 2012, 2013, and 2014 young-of-year (YOY) yellowfin tuna cohorts. Results are shown for QDFAs using data from (1) all 4 nurseries, (2) eastern Atlantic nurseries combined, and (3) eastern and western Atlantic nurseries combined. NA: data not available

Grouping	Region	2012	2013	2014	All cohorts
1	Cape Verde	74	80	86	81
	Gulf of Guinea	40	100	NA	44
	Gulf of Mexico	75	50	67	43
	Caribbean Sea	78	77	90	83
	Overall	64	78	85	66
2	Eastern Atlantic	87	86	86	
	Gulf of Mexico	60	50	67	
	Caribbean Sea	74	77	90	
	Overall	79	76	85	
3	Eastern Atlantic	84	73	86	
	Western Atlantic	67	93	92	
	Overall	78	84	89	

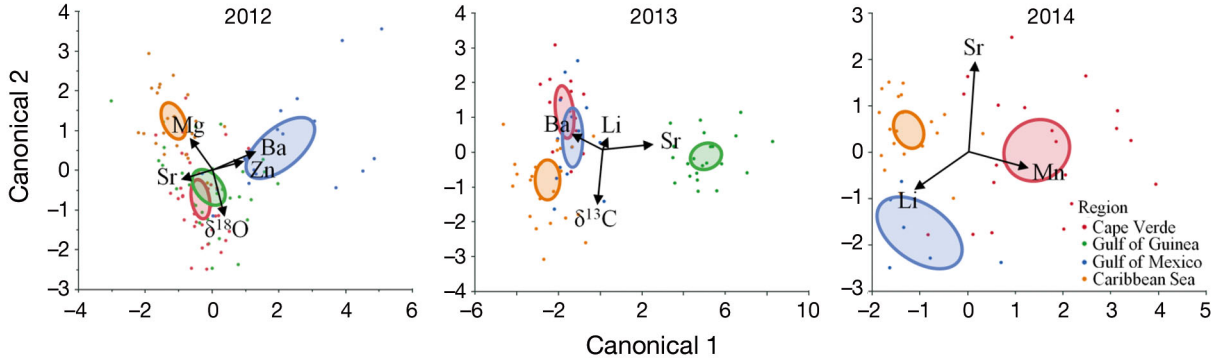

Fig. 6. Canonical scores based on trace elements (Li:Ca, Mg:Ca, Mn:Ca, Zn:Ca, Sr:Ca, and Ba:Ca ratios) and stable isotopes ($\delta^{13}C$, $\delta^{18}O$) in young-of-the-year (YOY) yellowfin tuna otoliths collected from 4 nursery areas in the Atlantic Ocean: Cape Verde, Gulf of Guinea (2012 + 2013 only), Gulf of Mexico, and Caribbean Sea. Ellipses represent 95% confidence limits around each multivariate mean, and biplot vectors show the relative influence of each element on regional discrimination

Cape Verde. Although samples were not available from 1 region (Gulf of Guinea) in 2014, the overall classification success was high that year (observed: 85%, expected based on random assignment: 33%). When data from 2012, 2013, and 2014 cohorts were pooled, regional differences in signatures were still observed (MANOVA: $p < 0.001$, QDFA classification success: 66%); however, region-specific classification success was relatively low for the Gulf of Guinea and the Gulf of Mexico. An additional QDFA was performed to determine whether chemical signatures in otoliths were different for yellowfin tuna from the eastern Atlantic Ocean (Cape Verde + Gulf of Guinea) and western Atlantic Ocean (Gulf of Mexico + Caribbean); overall jackknifed classification success based on eastern and western nursery areas was consistently high, with 78, 84, and 89% of samples successfully classified in 2012, 2013, and 2014, respectively.

In 2012, $\delta^{18}O$, Ba:Ca, and Mg:Ca ratios were the 3 most significant variables in the QDFA ($p < 0.001$), providing clear separation among Cape Verde/Gulf of Guinea, Gulf of Mexico, and Caribbean Sea samples, respectively (Fig. 6). Regional discrimination in 2013 was primarily influenced by Sr:Ca and Ba:Ca ratios, and $\delta^{13}C$. The QDFA plot indicates that Sr:Ca ratios played an important role in distinguishing Gulf of Guinea samples in 2013, which is expected given the high Sr:Ca values in the Gulf of Guinea (mean: 3442 µmol mol^{-1}) relative to other areas investigated that year (Cape Verde: 2306 µmol mol^{-1}, Gulf of Mexico: 2398 µmol mol^{-1}, Caribbean Sea: 2143 µmol mol^{-1}). In 2014, the strongest regional differences were observed in otolith Mn:Ca, Sr:Ca, and Li:Ca ratios ($p < 0.001$), and these 3 elements alone provided clear separation among nursery areas. Thus, the otolith Sr:Ca ratio was a significant variable in QDFAs for each cohort ($p < 0.001$) and was the only element to be included in all 3 models. Li:Ca and Ba:Ca ratios were significant in 2 out of the 3 models, and all other elements ($\delta^{13}C$, $\delta^{18}O$, Mg:Ca, Mn:Ca, Zn:Ca) were only retained in QDFAs for 1 cohort.

Additional QDFAs were performed to determine whether stable isotopes or trace elements alone would be effective in discriminating yellowfin tuna from nursery areas in the Atlantic Ocean. QDFAs based on stable isotopes ($\delta^{13}C$ and $\delta^{18}O$) yielded low overall classification success rates, ranging from 47% (2012) to 52% (2013). Stable isotopes were most successful in distinguishing Caribbean Sea samples, with classification success rates of 65% (2014) to 74% (2012); however, these isotopes were not useful for classifying Gulf of Mexico samples (2012: 0%, 2013: 25%, 2014: 0%). Trace elements provided higher classification success rates than stable isotopes alone (2012: 57%, 2013: 78%, 2014: 85%). In fact, overall classification success rates for trace elements alone were identical to QDFAs including the full dataset in 2013 and 2014. However, classification success improved with the addition of stable isotope data in 2012 (57 vs. 64%), and $\delta^{13}C$ was a significant factor in the 2013 QDFA, suggesting that combining both chemical markers is a more effective method for discriminating yellowfin tuna from different nursery areas in the Atlantic Ocean.

DISCUSSION

Regional differences in otolith chemistry were detected for YOY yellowfin tuna collected from 4 nursery areas in the Atlantic Ocean using multiple tracers. Element:Ca ratios provided the highest dis-

criminatory power among nursery areas and usually matched expected patterns based on local environmental conditions. In particular, the otolith Sr:Ca ratio showed significant variability among regions, and was an influential variable in QDFAs for each cohort of YOY yellowfin tuna. Several studies have shown that strontium concentrations in otoliths generally exhibit a positive relationship with ambient salinity (Limburg 1995, Secor & Rooker 2000, Zimmerman 2005). Mean sea surface salinities (calculated from cumulative sea surface salinity data from HYCOM+NCODA Global 1/12 Degree Analysis) were relatively homogenous across regions, with Cape Verde and the Gulf of Mexico exhibiting only slightly higher salinities (35.7 ± 0.3 and 35.5 ± 0.5 SD, respectively) than sampling locations in the Caribbean Sea (35.2 ± 0.2) and Gulf of Guinea (35.0 ± 0.3). Thus, variability in the otolith Sr:Ca ratio appears to have been influenced more by local climate events rather than large-scale regional differences. For example, countries bordering the Gulf of Guinea experienced much higher than average air temperatures during the spring and summer of 2014 (NOAA 2015); increased salinities were also observed in the Gulf of Guinea during this time period relative to previous years (2012, 2013), likely as a result of increased evaporation rates due to higher temperatures. This would have affected the 2013 cohort, as these individuals would have been <6 mo old at the time of capture, thus explaining the significantly higher Sr:Ca ratios observed in Gulf of Guinea samples that year.

The otolith Li:Ca ratio, which also tends to exhibit a positive relationship with salinity (Hicks et al. 2010, Sturrock et al. 2014), followed similar patterns as Sr:Ca ratios, with peak Li:Ca and Sr:Ca values both occurring in the same regions each year (2012: Caribbean Sea, 2013: Gulf of Guinea, 2014: Caribbean Sea). Barium exhibits a nutrient-type distribution in seawater and is typically found in higher concentrations in coastal regions or in areas of riverine input (Coffey et al. 1997, Elsdon & Gillanders 2005). In late 2012 and early 2013, discharge from the Mississippi River into the Gulf of Mexico was 20% higher than in other years examined (USACE 2016). Most of the YOY yellowfin tuna collected from this region were captured in the vicinity of the Mississippi River plume and would therefore have been impacted by variability in river runoff; thus, increased freshwater discharge during that time period may be responsible for the significantly enriched otolith Ba:Ca values observed in Gulf of Mexico samples in the 2012 cohort relative to other regions/years.

Significant regional differences were also detected in manganese, magnesium, and zinc concentrations in YOY yellowfin tuna otoliths. Atmospheric dust is a major source of manganese in seawater (Statham & Chester 1988, Guieu et al. 1994), and peak manganese concentrations in the Atlantic Ocean typically occur off the west coast of Africa near 5–20° N where dust deposition from the Sahara Desert is greatest (Chester 1990, Statham et al. 1998). As expected, the highest mean otolith Mn:Ca values were observed in samples from the Gulf of Guinea (2013: 6.2 µmol mol^{-1}) and Cape Verde (2014: 6.0 µmol mol^{-1}). Increased dust deposition in 2013 in the Gulf of Guinea would likely have increased primary productivity in these regions (due to increased nutrient input), which correlates well with the increased Ba:Ca values observed in these regions. While the relationship between otolith Mg:Ca and environmental conditions remains unclear, it is thought that magnesium uptake rates increase in warmer waters, potentially as a function of increased otolith precipitation and somatic growth (Martin & Thorrold 2005). In support of this, enriched otolith Mg:Ca values were observed in Caribbean Sea samples each year, which was the region with the warmest mean sea surface temperature (27.8 ± 0.2°C, based on sea surface temperature data from HYCOM+NCODA Global 1/12 Degree Analysis) relative to other regions examined (Cape Verde: 23.9 ± 1.6°C, Gulf of Guinea: 26.8 ± 0.9°C, Gulf of Mexico: 25.4 ± 0.8°C). Zinc, a physiologically active metal, is typically bound to protein, and otolith Zn:Ca values do not necessarily reflect zinc concentrations in the surrounding seawater (Campana 1999, Miller et al. 2006). Instead, dietary uptake is thought to be the primary route through which zinc accumulates in otoliths (Ranaldi & Gagnon 2008). Therefore, the highly enriched Zn:Ca values observed in Gulf of Guinea samples in 2013 are most likely due to a shift in the zinc concentrations of prey items rather than any change in seawater concentrations. Although zinc may not be a reliable indicator of water mass residency, it can nonetheless be a useful discriminator of populations that have unique dietary histories.

Otolith $\delta^{13}C$ values also differed significantly among nursery regions for all 3 cohorts. Previous research has shown that otolith $\delta^{13}C$ values can be influenced by $\delta^{13}C$ in dissolved inorganic carbon (DIC) in seawater (Thorrold et al. 1997, Solomon et al. 2006). In equatorial upwelling zones, DIC in surface waters tends to become enriched in $\delta^{13}C$ due to air–sea gas exchange (Lynch-Stieglitz et al. 1995). The Gulf of Guinea (in the equatorial Atlantic Ocean) is characterized by an extensive seasonal upwelling

system (Bakun 1978), and intense upwelling generally occurs from July to September (Roy 1995), which is when most YOY yellowfin tuna collected from this region were approximately 1–6 mo old. Therefore, regional upwelling is likely responsible for the significantly enriched otolith $\delta^{13}C$ values observed in Gulf of Guinea samples. Otolith $\delta^{13}C$ matched patterns of global seawater $\delta^{13}C_{DIC}$, with the Gulf of Guinea exhibiting the most enriched $\delta^{13}C$ values relative to other nursery areas in the Atlantic Ocean (McMahon et al. 2013). Equatorial upwelling also occurs in the Caribbean Sea along the northern coast of Venezuela, although this upwelling system is not as extensive as in the Gulf of Guinea (Muller-Karger et al. 2004). Thus, seasonal equatorial upwelling may also be the reason why otolith $\delta^{13}C$ values in Caribbean samples were enriched compared to northern nursery areas (Cape Verde and the Gulf of Mexico) in 2013 and 2014. Interannual variability in otolith $\delta^{13}C$ values was observed for most regions surveyed, potentially due to variability in the intensity and/or timing of seasonal upwelling. However, temporal differences in otolith $\delta^{13}C$ values could be due to changes in diet or metabolism, as these factors are also known to influence otolith $\delta^{13}C$ (Høie et al. 2003). Regardless, regional differences in otolith $\delta^{13}C$ were still detected when 2012, 2013, and 2014 cohorts were pooled, indicating that geographic variability was stronger than temporal variability in otolith $\delta^{13}C$ values.

Regional variation in otolith $\delta^{18}O$ was observed for YOY yellowfin tuna, although significant differences were only detected in 2012. $\delta^{18}O$ values of both seawater and carbonates are predictably linked to salinity and sea surface temperature, becoming more depleted as temperature increases (Thorrold et al. 1997, Høie et al. 2004) and as salinity decreases (Elsdon & Gillanders 2002, Kerr et al. 2007). The warmest sea surface temperatures and lowest salinities were observed in the Caribbean Sea sampling location, and as expected, otolith $\delta^{18}O$ values were significantly depleted in this region in 2012 relative to all other regions. However, temporal variability in otolith $\delta^{18}O$ was observed in the Caribbean Sea sample; sea surface temperatures decreased and salinities increased in 2013 (27.8°C, 35.5) and 2014 (27.7°C, 35.2) relative to 2012 (28.1°C, 35), which resulted in enriched otolith $\delta^{18}O$ values and less regional discrimination for these cohorts (2013, 2014: ANOVA, $p > 0.05$). Interannual variability was also observed in Gulf of Guinea otolith $\delta^{18}O$ values, with significantly depleted otolith $\delta^{18}O$ values observed in the Gulf of Guinea in 2013 relative to 2012. As previously discussed, this region experienced much higher than normal temperatures in the spring/summer of 2014 (affecting the signatures of the 2013 cohort), which likely explains the depleted otolith $\delta^{18}O$ values observed for that cohort. Despite this, regional differences were still observed when data from the 3 cohorts were pooled, indicating that interannual variability may not be strong enough to outweigh geographical differences in otolith $\delta^{18}O$. Similar to $\delta^{13}C$, otolith $\delta^{18}O$ values followed the same pattern observed in isoscapes developed from global seawater $\delta^{18}O$ values, with lowest $\delta^{18}O$ values occurring in the Caribbean Sea relative to other nursery areas in the Atlantic Ocean (Schmidt et al. 1999, McMahon et al. 2013).

Regional variability in otolith chemistry resulted in the successful classification of YOY yellowfin tuna to 4 nursery areas in the Atlantic Ocean, with classification accuracies ranging from 64–85% for 2012–2014 cohorts. Classification accuracies in this study were similar to those reported for yellowfin tuna in the Pacific Ocean (Wells et al. 2012, Rooker et al. 2016). Classification success was lowest in 2012 (64%) due to overlap between Gulf of Guinea and Cape Verde signatures, which resulted in a greater number of misclassified individuals; however, classification success improved significantly (79%) when Gulf of Guinea and Cape Verde signatures were combined, with strong separation observed among Gulf of Mexico, Caribbean Sea, and eastern Atlantic Ocean nurseries. Success rates remained high when both eastern Atlantic (Cape Verde and Gulf of Guinea) and western Atlantic (Gulf of Mexico and Caribbean Sea) regions were pooled, suggesting that these chemical signatures could be effective for detecting trans-Atlantic migrations of yellowfin tuna. Combining the 4 nursery signatures from all 3 years resulted in modest overall classification success (66%); however, region-specific classification success was less than 50% for certain regions (Gulf of Mexico and Gulf of Guinea), highlighting the need to age-class match adult yellowfin tuna to the appropriate baseline year when predicting nursery origin.

The majority of studies involving nursery discrimination of tunas and other pelagic fishes have primarily utilized stable isotope ($\delta^{13}C$ and $\delta^{18}O$) signatures in otoliths (Wells et al. 2010, 2012, Rooker et al. 2014) rather than trace elements combined with stable isotopes. To test the effectiveness of using stable isotopes alone in this study, QDFAs were run for each cohort using only $\delta^{13}C$ and $\delta^{18}O$ signatures. Results showed that classification success decreased significantly (by up to 34%) when only stable isotopes were

included in the model; this was particularly true for Gulf of Mexico samples, for which classification successes were no higher than predicted success based on chance alone. Conversely, QDFAs using only trace elements provided success rates similar to (but slightly lower than) models using both classes of tracers. A recent study tested the effectiveness of using otolith trace elements vs. stable isotopes to discriminate among nursery areas of yellowfin tuna in the Pacific Ocean, and contrary to findings in the present study, adding trace element data to the baseline of stable isotope signatures did not significantly improve classification success (Rooker et al. 2016). Thus, while stable isotopes alone may be sufficient for nursery discrimination of yellowfin tuna in the Pacific Ocean, trace elements proved to be significantly more effective for discriminating among nursery areas in the Atlantic Ocean. It is possible that differences in classification success between the 2 types of tracers could be due to the fact that a smaller area of the otolith was sampled for trace elements than stable isotopes. While the portion of the otolith analyzed for trace elements corresponds to ~3 mo, stable isotope signatures encompassed the first 5–6 mo of life. Thus, decreased resolution using stable isotopes alone could be due to increased movement of individuals after 3 mo of age. Stable isotopes alone (primarily $\delta^{18}O$) have proven to be effective in discriminating Atlantic bluefin tuna from different nursery areas (Rooker et al. 2008a). However, large temperature differences exist between the 2 major bluefin tuna spawning areas (Gulf of Mexico and Mediterranean Sea), likely driving regional differences in otolith $\delta^{18}O$ values. In contrast, yellowfin tuna spawn in warm tropical waters (>26°C, Shuford 2005), and temperature differences among nursery regions are relatively small. As a result, otolith $\delta^{18}O$ values alone provide less regional discrimination, so additional tracers are required to effectively discriminate nursery areas. Nonetheless, all tracers indicated separation among the 4 nursery regions for at least 1 cohort, and strongest discriminatory power was obtained by combining trace element and stable isotope data.

In summary, otolith chemistry can be used to discriminate YOY yellowfin tuna from the 4 major nursery areas in the Atlantic Ocean. Chemical signatures (otolith element:Ca, $\delta^{13}C$, $\delta^{18}O$) of YOY yellowfin tuna varied significantly among regions and classification success was high, indicating that these tracers can be used in future studies to determine the nursery of origin of sub-adult and adult yellowfin tuna in the Atlantic Ocean. However, interannual variability in otolith trace elements and stable isotopes was also detected, highlighting the importance of age-class matching when sourcing adults using the baseline of nursery signatures. Thus, additional sampling of nursery areas would be required to source adults that are not matched with the baseline signatures provided in this study. Ultimately, baseline signatures for YOY yellowfin tuna developed in this study can be used to elucidate trans-oceanic migration patterns and evaluate population connectivity and mixing rates of this species. As a result, fundamental questions regarding the stock structure of yellowfin tuna in the Atlantic Ocean may soon be resolved in future otolith-based studies.

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