



Regional variation in the otolith chemistry of blue marlin (*Makaira nigricans*) and white marlin (*Tetrapturus albidus*) from the western North Atlantic Ocean

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ABSTRACT

Stable carbon ($\delta^{13}\text{C}$) and oxygen ($\delta^{18}\text{O}$) isotopes in the whole otoliths of blue marlin (*Makaira nigricans*) and white marlin (*Tetrapturus albidus*) were quantified, and regional variation in otolith composition was used to examine the population structure of both species in the western North Atlantic Ocean from collections taken over three decades (1981–2007). Otolith $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ of blue marlin and white marlin varied significantly among the regions investigated (Gulf of Mexico, Straits of Florida, Caribbean Sea, and U.S. Atlantic). Overall cross-validated classification success was 62% for blue marlin and 46% for white marlin (collected in three of four regions), with highest classification success for blue marlin in the Gulf of Mexico (85%) and for white marlin along the U.S. Atlantic (58%). Variability in otolith $\delta^{18}\text{O}$ of blue marlin and white marlin was higher in regions where individuals displayed a greater degree of movement based on previous tagging studies in the same regions. Reduced variability in otolith $\delta^{18}\text{O}$ of blue marlin in the Gulf of Mexico combined with high classification success of individuals from this region suggests that movement out of this basin may be more limited than in other regions investigated. Conversely, higher variability in otolith $\delta^{18}\text{O}$ and lower classification success for white marlin signifies that mixing among regions may be more common for this species. These results suggest that the concept of migratory contingents may have some application to istiophorids in the western North Atlantic Ocean (i.e. blue marlin), but continue to support the concept of single Atlantic wide stocks for both species.

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1. Introduction

Blue marlin (*Makaira nigricans*) and white marlin (*Tetrapturus albidus*) support economically important recreational fisheries throughout the Atlantic Ocean (Prince and Brown, 1991). However, the greatest source of fishing mortality is the incidental bycatch of the multi-national longline fisheries targeting tunas and swordfish (ICCAT, 2004). Stock assessments conducted under the auspices of the International Commission for the Conservation of Atlantic Tunas (ICCAT) have reported both marlins as overfished, with estimated biomass ratios well below the level needed to maintain maximum sustainable yield (ICCAT, 1998, 2000). Continued exploitation of blue marlin and white marlin by Atlantic longline fisheries has hindered rebuilding efforts (Serafy et al., 2004), and increased the need for an improved understanding of their spatial and temporal patterns of distribution (Horodysky et al., 2007; Goodyear et al., 2008).

Several studies have documented that blue marlin and white marlin are capable of long-distance migrations (e.g., >1000 km, Ortiz et al., 2003; Orbesen et al., 2008), consisting of both trans-Atlantic and trans-equatorial movements (Orbesen et al., 2010; Snodgrass et al., 2010). Due to the highly migratory nature of these species, mixing of individuals from different regions of the Atlantic is expected to be high. In fact, Graves and McDowell (2003) found no evidence of genetic heterogeneity within the Atlantic for both blue marlin and white marlin, which is consistent with the idea of regional mixing. Conventional tagging data also indicates that movement among regions in the Atlantic occurs regularly; however, seasonal tag returns within certain regions has been observed (Mather et al., 1972; Orbesen et al., 2008). As a result, it appears that some level of population structuring may be present even though genetic data and conventional tagging data are consistent with a single Atlantic-wide stock for both species.

Otolith chemistry is one approach used to examine divergent movement patterns or behaviors (i.e., migratory contingents) within a fish population (Secor, 1999). However, otolith chemistry data from Atlantic blue marlin and white marlin has yet to become available to the ICCAT billfish working group for its deliberations on stock structure. The approach is often used to investigate population-level processes because chemicals incorporated into

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the aragonite matrix of the otolith are related to the physico-chemical conditions of the surrounding water mass, thus serving as a natural tag (Campana and Neilson, 1985; Bath et al., 2000). Chemical signatures in the otolith core are often used to retrospectively determine an individual's natal origin (Thorrold et al., 2001; Rooker et al., 2008a,b) and migratory history (Goto and Arai, 2006), and therefore serve as useful markers for assessing population connectivity (Secor and Rooker, 2005). In addition, whole otolith signatures represent an integrated measure of an individual's entire life history and the bulk chemistry approach has been used to assess lifetime exposure to different environmental conditions (Campana et al., 2000; Stephenson et al., 2001).

Here, we quantified stable carbon ($\delta^{13}\text{C}$) and oxygen ($\delta^{18}\text{O}$) isotopes in the whole otoliths of adult blue marlin and white marlin to examine variation among distinct geographic locations. Previous work has shown that regional differences in $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ in seawater (Gruber et al., 1999; LeGrande and Schmidt, 2006) and otoliths of Atlantic bluefin tuna (*Thunnus thynnus*, Rooker et al., 2008a,b; Schloesser et al., 2010) exist in the western North Atlantic Ocean, supporting the use of these natural markers. For example, Rooker et al. (2008a) demonstrated mean otolith $\delta^{18}\text{O}$ for yearling Atlantic bluefin tuna was significantly enriched in the eastern nursery (Mediterranean Sea) relative to the western nursery (Gulf of Mexico). Our working hypothesis was that whole otolith $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ represented a lifetime signature of environmental exposure for both blue marlin and white marlin, and distinct spatial variation in otolith chemistry would be observed if migratory histories or residency periods of individuals differed among regions.

2. Materials and methods

2.1. Sample collections

Collections were obtained by the National Marine Fisheries Service (NMFS) (Southeast Fisheries Science Center), Texas Parks and Wildlife Department, and Texas A&M University at Galveston. Otolith samples were opportunistically obtained during fishing tournaments from 1981 to 2007 throughout the western North Atlantic Ocean. Otoliths of 65 blue marlin and 40 white marlin were obtained over the collection period. In addition, recent genetic studies have discovered a historical misidentification problem involving Atlantic white marlin and the anatomically similar roundscale spearfish (*Tetrapturus georgii*) (Shivji et al., 2006; Beerkircher et al., 2009), therefore it is possible that a small fraction of the white marlin sample was comprised of the congener. Collection areas were classified into regions similar to the ICCAT Billfish Management Areas and U.S. Domestic Sub-management Areas (Orbesen et al., 2008). Our regions included (1) Gulf of Mexico, (2) Straits of Florida (Florida Keys, Bahamas), (3) Caribbean Sea (Puerto Rico) and (4) U.S. Atlantic (North Carolina to New York, U.S.). No white marlin samples were obtained from the Caribbean Sea. Upon collection, the lower jaw fork length (LJFL) was estimated to the nearest cm and otoliths were removed, rinsed with freshwater, and stored in plastic vials.

2.2. Stable isotope analysis

Prior to analysis, sagittal otoliths were carefully cut in half with a knife along the sulcus to separate the rostrum and antirostrum and one half was used for stable isotope analysis while the other half was saved for future analysis. Sagittal otoliths were then cleaned with 18 M Ω doubly deionized water (DDIH₂O), moved to a 3% hydrogen peroxide solution for 5 min to remove biological residue, and then transferred to a new DDIH₂O bath for 5 min to remove surface residue. Paired samples of rostrum and antirostrum were

analyzed from a sub-sample of blue marlin ($n=9$) from the Straits of Florida and no difference was detected for either $\delta^{13}\text{C}$ (paired t -test, $p=0.886$) or $\delta^{18}\text{O}$ (paired t -test, $p=0.823$). Otolith halves were ground to a fine powder using a mortar and pestle, and samples were sent to the University of Arizona's Environmental Isotope Laboratory. Otolith $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ were quantified on an automated carbonate preparation device (KIEL-III) coupled to a gas-ratio mass spectrometer (Finnigan MAT 252). Powdered samples were reacted with dehydrated phosphoric acid under vacuum at 70 °C. The isotope ratio measurement was calibrated based on repeated measurements of National Bureau of Standards (NBS), NBS-19 and NBS-18, with six standards ran for every 40 samples and precision was $\pm 0.11\%$ (standard deviation, SD) for $\delta^{18}\text{O}$ and $\pm 0.08\%$ (SD) for $\delta^{13}\text{C}$.

2.3. Statistical analyses

Multivariate analysis of covariance (MANCOVA) was used to test for differences in otolith $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ among collection regions, with length as the covariate. Pillai's trace statistic was used to test for significance due to its robustness to violations of the homogeneity of covariance assumption (Wilkinson et al., 1996). Univariate tests for both $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ were then analyzed using analysis of covariance (ANCOVA). Due to unbalanced collections by year, temporal differences for each species were evaluated using linear regression analysis. Quadratic discriminant function analysis (QDFA) was used to classify blue marlin and white marlin among collection regions. Jackknife cross-validated classifications are given and, due to low and unequal sample sizes, reclassifications were evaluated using the randomization method outlined by White and Ruttenberg (2007). Briefly, this procedure is designed to estimate the probability that reclassification success is better than random for low and unequal sample sizes. Jackknife reclassification success was evaluated using MATLAB 7.5 (The MathWorks, Inc.), and all other statistical analyses were performed using SYSTAT 10.0 (SYSTAT Software Inc., Richmond, CA). Significance was determined at the alpha level of 0.05.

3. Results

Inter-annual variation in otolith $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ was detected for blue marlin, but no significant temporal effect for either marker was observed for white marlin (Fig. 1). A general pattern of depleted $\delta^{13}\text{C}$ and enriched $\delta^{18}\text{O}$ existed for blue marlin when combined across the four regions over the years investigated (1981–2007) (Fig. 1A). However, within each of the regions, temporal variation in otolith $\delta^{13}\text{C}$ or $\delta^{18}\text{O}$ was not significant ($p > 0.05$). Correction factors for blue marlin were calculated by measuring the rate of change in otolith $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ over time (slopes of linear regressions) and were $-0.028\% \cdot \text{y}^{-1}$ for $\delta^{13}\text{C}$ and $0.008\% \cdot \text{y}^{-1}$ for $\delta^{18}\text{O}$. Thus, adjusted otolith $\delta^{13}\text{C}$ of blue marlin was used to account for depletion in the heavier isotope (^{13}C) due to anthropogenic CO_2 into the ocean known as the Suess effect (Keeling, 1979).

Otolith $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ of blue marlin significantly differed among regions (MANCOVA, $p < 0.01$), with samples from the Gulf of Mexico, Caribbean Sea, and U.S. Atlantic differing most from one another. Specifically, otoliths of blue marlin from the Gulf of Mexico were significantly depleted in $\delta^{13}\text{C}$ and enriched in $\delta^{18}\text{O}$ relative to the Straits of Florida, Caribbean Sea, and U.S. Atlantic (ANCOVA, $p < 0.05$) (Fig. 2A, Table 1). Mean otolith $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values of Gulf of Mexico blue marlin were -5.37% (± 0.11 standard error, SE) and -0.37% (± 0.02), respectively. In contrast, samples from the Caribbean Sea were most enriched in otolith $\delta^{13}\text{C}$ (mean = $-4.46\% \pm 0.16$), while otolith $\delta^{18}\text{O}$ was depleted in samples from the U.S. Atlantic (mean = $-0.68\% \pm 0.07$).

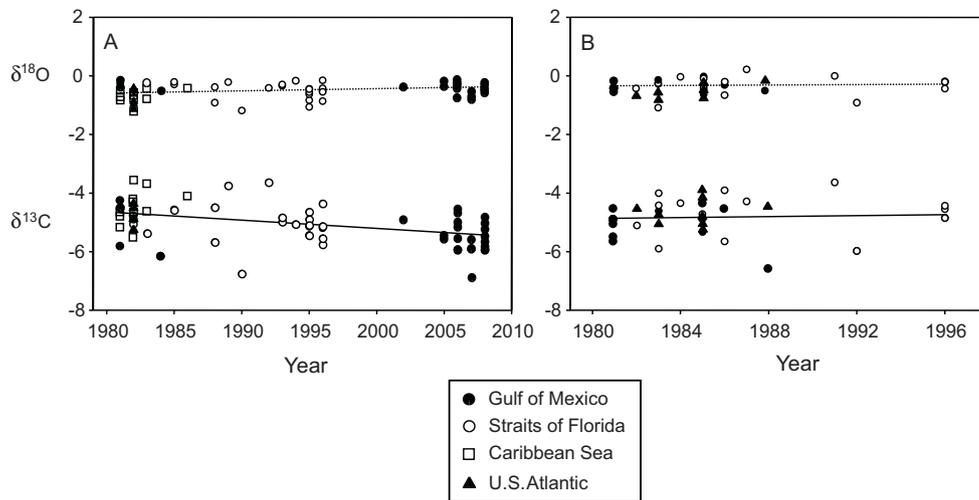


Fig. 1. Temporal patterns in otolith $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ of blue marlin (A) and white marlin (B) from different regions in the western North Atlantic Ocean. Linear regressions for blue marlin ($\delta^{13}\text{C} = -0.028\text{year} + 51.5$, $r^2 = 0.183$; $\delta^{18}\text{O} = 0.008\text{year} - 15.8$, $r^2 = 0.123$) and white marlin ($\delta^{13}\text{C} = 0.008\text{year} - 20.6$, $r^2 = 0.003$; $\delta^{18}\text{O} = 0.004\text{year} - 8.0$, $r^2 = 0.004$).

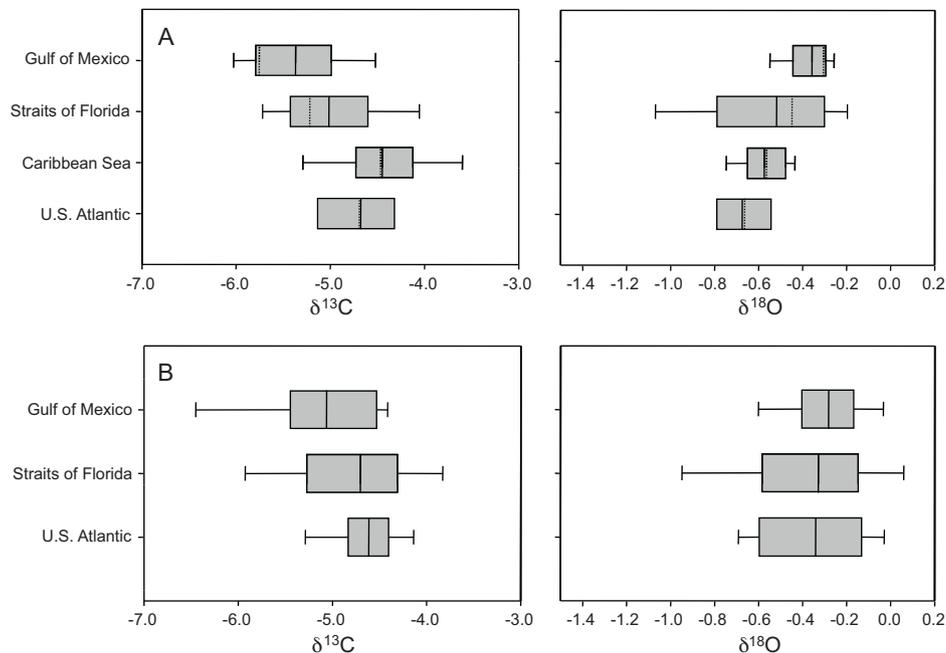


Fig. 2. Otolith $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ of blue marlin (A) and white marlin (B) collected from different regions throughout the western North Atlantic Ocean. Box boundaries represent 25th and 75th percentiles around the mean, error bars represent 5th and 95th percentiles, solid line represents the mean (uncorrected), and dotted line represents the mean using the time-adjusted correction factor (corrected) for blue marlin. No error bars present on blue marlin from U.S. Atlantic due to $n = 4$.

For white marlin, otolith chemistry varied significantly among regions (MANCOVA, $p < 0.01$); however, no regional differences were detected individually for otolith $\delta^{13}\text{C}$ or $\delta^{18}\text{O}$ (ANCOVA, $\delta^{13}\text{C}$: $p = 0.260$; $\delta^{18}\text{O}$: $p = 0.710$). Nevertheless, white marlin otoliths were depleted in $\delta^{13}\text{C}$ and enriched in $\delta^{18}\text{O}$ in the Gulf of Mexico with mean values of -5.06‰ (± 0.20) and -0.28‰ (± 0.05),

respectively. In contrast, enriched $\delta^{13}\text{C}$ (mean: $-4.68\text{‰} \pm 0.10$) and depleted $\delta^{18}\text{O}$ (mean: $-0.36\text{‰} \pm 0.07$) were observed in samples from the U.S. Atlantic, similar to trends for blue marlin (Fig. 2B, Table 1).

Estimated variability (± 1 SE) in otolith $\delta^{18}\text{O}$ of blue marlin and white marlin varied among the regions investigated, with SE being

Table 1
Summary statistics of blue marlin and white marlin collected for otolith stable isotope ratio analysis. Sample size (n), mean lower jaw fork length (LJFL) (± 1 standard error, SE), and mean $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values (± 1 SE) in otoliths of each species according to region (with and without correction factors for blue marlin).

Species	Region	n	LJFL (cm)	$\delta^{13}\text{C}$	$\delta^{18}\text{O}$	$\delta^{13}\text{C}$ (correction)	$\delta^{18}\text{O}$ (correction)
Blue marlin	Gulf of Mexico	26	271.1 (± 10.1)	-5.37 (± 0.11)	-0.37 (± 0.02)	-5.79 (± 0.12)	-0.31 (± 0.02)
Blue marlin	Straits of Florida	24	249.2 (± 10.7)	-5.01 (± 0.13)	-0.53 (± 0.06)	-5.22 (± 0.14)	-0.45 (± 0.06)
Blue marlin	Caribbean Sea	11	212.6 (± 8.8)	-4.46 (± 0.16)	-0.58 (± 0.03)	-4.48 (± 0.16)	-0.57 (± 0.03)
Blue marlin	U.S. Atlantic	4	225.9 (± 5.0)	-4.70 (± 0.22)	-0.68 (± 0.07)	-4.71 (± 0.22)	-0.67 (± 0.07)
White marlin	Gulf of Mexico	13	162.0 (± 6.7)	-5.06 (± 0.20)	-0.28 (± 0.05)	NA	NA
White marlin	Straits of Florida	15	162.7 (± 5.0)	-4.75 (± 0.17)	-0.34 (± 0.08)	NA	NA
White marlin	U.S. Atlantic	12	160.5 (± 4.7)	-4.68 (± 0.10)	-0.36 (± 0.07)	NA	NA

Table 2

Jack-knife classification success (%) from quadratic discriminant function analysis of blue marlin both with and without correction factors, and white marlin. No white marlin samples were obtained from the Caribbean Sea, thus not applicable (NA).

Species	Region				Total
	Gulf of Mexico	Straits of Florida	Caribbean Sea	U.S. Atlantic	
Blue marlin	92	29	27	75	57
Blue marlin (correction factor)	85	50	27	75	62
White marlin	38	44	NA	58	46

lower for individuals collected in the Gulf of Mexico and higher for those collected in the Straits of Florida and U.S. Atlantic (Fig. 2, Table 1). Standard error values of otolith $\delta^{18}\text{O}$ for blue marlin and white marlin in the Gulf of Mexico were ($\pm 0.02\%$) and ($\pm 0.05\%$), respectively; while otolith $\delta^{18}\text{O}$ SE in the Straits of Florida and U.S. Atlantic ranged from 0.06 to 0.07‰ for blue marlin and 0.07–0.08‰ for white marlin. Differences between 25th and 75th percentiles of otolith $\delta^{18}\text{O}$ were 0.16‰ for blue marlin and 0.24‰ for white marlin in the Gulf of Mexico, lower than other regions: Straits of Florida (0.49‰ blue marlin, 0.44‰ white marlin), Caribbean Sea (0.18‰ blue marlin), and U.S. Atlantic (0.25‰ blue marlin, 0.47‰ white marlin) (Fig. 2). Variability in otolith $\delta^{13}\text{C}$ was high for both species among all regions with standard error values ranging from $\pm 0.11\%$ (Gulf of Mexico) to $\pm 0.22\%$ (U.S. Atlantic) and $\pm 0.10\%$ (U.S. Atlantic) to $\pm 0.20\%$ (Gulf of Mexico) for blue marlin and white marlin, respectively.

Total cross-validated classification among the four regions examined was 57% and 46% for blue marlin and white marlin, respectively. It should be noted that only three regions were included in the model for white marlin, suggesting that the difference in classification success is even greater than the reported value of 11% between the two species. Moreover, total classification success of blue marlin improved to 62% when otolith $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ correction factors were applied to account for temporal variability; no temporal adjustment was required for white marlin data (Table 2). Using time-adjusted otolith $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values, blue marlin classification success by region was highest for samples collected from the Gulf of Mexico (85%) followed by U.S. Atlantic (75%), Straits of Florida (50%), and Caribbean Sea (27%). Regional classification success of white marlin was lowest for samples collected from the Gulf of Mexico (38%), improving for the Straits of Florida (44%), and highest for individuals collected in the U.S. Atlantic (58%).

4. Discussion

Over the 27-year period investigated, depletion of otolith $\delta^{13}\text{C}$ and enrichment of otolith $\delta^{18}\text{O}$ was observed for blue marlin in the western North Atlantic Ocean. Here, we used whole otoliths which represent a composite signature that integrates all of the water masses inhabited. In addition, samples were obtained within some regions (Caribbean Sea, U.S. Atlantic) during a limited time frame and sizes among regions differed for blue marlin which may bias overall rates of enrichment or depletion when averaging across space and time due to age differences. Nevertheless, the rate of depletion in otolith $\delta^{13}\text{C}$ of blue marlin (-0.028% y^{-1}) was remarkably similar to that of Atlantic bluefin tuna (-0.026% y^{-1} ; Schloesser et al., 2009), and may have resulted from an increase in ^{13}C -depleted CO_2 into the atmosphere. Oceanic uptake of atmospheric CO_2 derived from anthropogenic sources that are depleted in ^{13}C has resulted in depletion of $\delta^{13}\text{C}$ dissolved inorganic carbon (DIC) in ambient seawater over time (Quay et al., 1992) and has consequently resulted in depletion of otolith $\delta^{13}\text{C}$ (Schloesser et al., 2009). Anthropogenic DIC in the upper 1000 m of the North Atlantic Ocean increased over a 44-year period (1950–1993) at a rate of $1.21 \pm 0.07 \mu\text{mol kg}^{-1} \text{y}^{-1}$ resulting in depletion of seawater $\delta^{13}\text{C}$ of $-0.026 \pm 0.002\%$ y^{-1} (Kortzinger et al., 2003), similar to

temporal trends observed in this study. White marlin otolith $\delta^{13}\text{C}$ did not show an effect over the time range examined and this result may be a product of low sample size and only a small fraction (15%) of the sample comprised of individuals collected during the later half of the 15-year period investigated. Rates of enrichment in otolith $\delta^{18}\text{O}$ for both blue marlin (0.008% y^{-1}) and white marlin (0.004% y^{-1}) also paralleled those of Atlantic bluefin tuna (0.004% y^{-1} , Schloesser et al., 2009). The observed enrichment of otolith $\delta^{18}\text{O}$ is in accord with the salinity increase (ca. 0.1–0.4‰) observed in the upper 500 m for western basins of the Atlantic Ocean from the 1950s to 1990s (Curry et al., 2003).

Blue marlin and white marlin showed similar trends in otolith $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ among the three regions that both species were collected, with samples collected in the Gulf of Mexico most depleted in otolith $\delta^{13}\text{C}$ and most enriched in $\delta^{18}\text{O}$. In contrast, enriched otolith $\delta^{13}\text{C}$ and depleted $\delta^{18}\text{O}$ were observed in fish from the U.S. Atlantic. Differences in otolith $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ are similar to mean regional trends in seawater $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ (Gruber et al., 1999; LeGrande and Schmidt, 2006), where seawater $\delta^{13}\text{C}$ values were enriched by about 0.5‰ in the U.S. Atlantic region of this study compared to lower latitude regions due to temperature-dependent air-sea exchange resulting in cooler waters having enriched seawater $\delta^{13}\text{C}$ (Gruber et al., 1999). Moreover, depleted seawater $\delta^{18}\text{O}$ values in the U.S. Atlantic coincided with depleted otolith $\delta^{18}\text{O}$ for both species, which may have been a product of along-shelf and cross-shelf mixing processes that led to depleted seawater $\delta^{18}\text{O}$ ($< -1\%$) in the region (Chapman and Beardsley, 1989; Khim and Krantz, 1996). In contrast, enriched seawater $\delta^{18}\text{O}$ in higher evaporative regions such as the Gulf of Mexico, Straits of Florida, and Caribbean Sea (Curry et al., 2003) paralleled the enriched otolith $\delta^{18}\text{O}$ values for both species, in particular the Gulf of Mexico seawater, which has been reported to be enriched by 1‰ relative to the global sea surface average (Surge and Lohmann, 2002; LeGrande and Schmidt, 2006). Regional-scale differences in environmental conditions therefore appear sufficient to support the application of using otolith chemistry to examine population structure of these two species.

Otolith $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ were used in the present study as a measure of lifetime exposure, and observed regional variation of blue marlin and white marlin suggest that environmental and/or migratory histories may differ for certain regional components of both populations. Cross-validated classification success of blue marlin was high in the Gulf of Mexico (85%), and variability in otolith $\delta^{18}\text{O}$ for individuals collected in this region was reduced relative to other regions. Therefore, it is possible that many of these individuals were exposed to similar environmental conditions and may not have spent the majority of time in other regions examined. In contrast, variability in otolith $\delta^{18}\text{O}$ was highest and classification success was lower for blue marlin collected in the Straits of Florida, indicating that this group may have been comprised of individuals exposed to varying environmental conditions, which may signify that this region represents a mixing zone and is comprised of individuals with varying migratory histories. Conventional tagging data on blue marlin by Orbesen et al. (2008) reported higher recapture rates in the Gulf of Mexico (78% recapture success) relative to other areas investigated here (e.g. Straits of Florida = 32%), which is con-

sistent with the hypothesis of increased retention within the Gulf of Mexico. For white marlin, classification success among regions was substantially lower than blue marlin even though the model only included three regions (four for blue marlin). In particular, the classification success of Gulf of Mexico (38%) sampled white marlin was lower than the two other regions (ranging from 44% to 58%). Low discrimination success among regions is not surprising given that previous studies using molecular markers demonstrated that white marlin move significantly among the regions investigated in the current study (Graves and McDowell, 2003). Samples were only collected from the western Atlantic Ocean basin and the lack of individuals from the eastern Atlantic could potentially affect region-specific classification. Consequently, further research needs to be done using a suite of approaches (i.e., otolith chemistry, genetics, electronic and conventional tagging) throughout the Atlantic Ocean basin to further clarify population structure of these two species.

Movement data among the regions examined from previous electronic tagging studies combined with otolith chemistry data presented here suggests that variability in otolith $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ maybe linked to documented movement patterns of blue marlin and white marlin. This is based on the assumption that regions comprised of individuals that frequent multiple regions are likely to have more variable otolith $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ relative to regions comprised of individuals that are more residential to one region over others (low net displacement). Mean displacement distances (km day^{-1}) of both blue marlin and white marlin obtained from previous electronic tagging studies (Table 3) were compared to variability (1 SE) in otolith $\delta^{18}\text{O}$ for each region. Otolith $\delta^{18}\text{O}$ was assumed to be a better environmental proxy of water mass properties than $\delta^{13}\text{C}$ since kinetic and metabolic effects are less pronounced (Hoie et al., 2003). For both species, variability in otolith $\delta^{18}\text{O}$ was lower in the Gulf of Mexico and Caribbean Sea than in the U.S. Atlantic and Straits of Florida by an average 62% and 33% for blue marlin and white marlin, respectively. Net displacement distance of both species increased with increasing variability in $\delta^{18}\text{O}$ (Fig. 3) from an average low of 11.7 km day^{-1} (blue marlin) and 10.4 km day^{-1} (white marlin) in the Gulf of Mexico to an average high of 37.4 km day^{-1} (blue marlin) and 37.6 km day^{-1} (white marlin) in the U.S. Atlantic, lending support to the hypothesis that migratory histories or residency periods may be region-specific, although not absolute, within the western North Atlantic Ocean.

ICCAT currently manages both blue marlin and white marlin as single Atlantic-wide stocks based on mark-recapture and genetic studies (ICCAT, 2006). Our results using otolith $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ showed that discrimination of blue marlin from the western North Atlantic Ocean was relatively high in certain regions, while regional

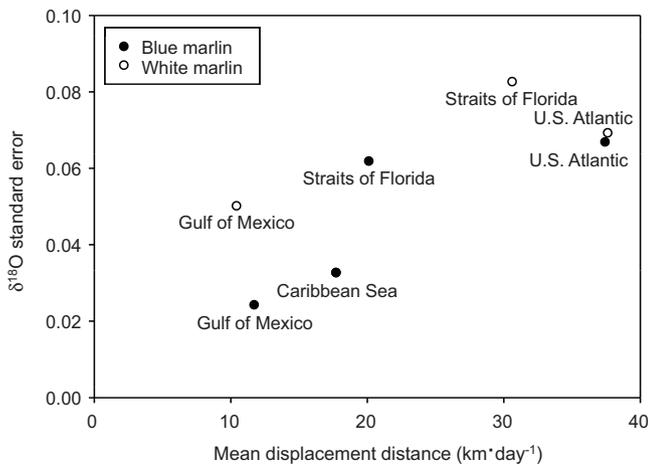


Fig. 3. Otolith $\delta^{18}\text{O}$ standard error of blue marlin and white marlin relative to mean displacement distance of individual fish (km day^{-1}) from previous tagging studies.

Table 3 Mean linear displacement distances of blue marlin and white marlin from electronic tagging studies throughout the western North Atlantic Ocean. Mean displacement distances are represented in km day^{-1} and were obtained by dividing the total displacement distance by the number of days at large.

Species	Region	Study location	Mean displacement distance (km day^{-1})	Number of fish (n)	Study years	Citation
Blue marlin	Gulf of Mexico	NW Gulf of Mexico	11.7	44	2003–2008	Kraus and Rooker (2007) Rooker (unpublished)
Blue marlin	Straits of Florida	Florida East Coast	37.4	4	2000	Kerstetter et al. (2003)
Blue marlin	Caribbean Sea	Florida East Coast & Bahamas	17.8	30	2002–2004	Goodyear et al. (2008)
Blue marlin	U.S. Atlantic	Dominican Republic	10.2	1	2003	Prince et al. (2005)
Blue marlin	U.S. Atlantic	Puerto Rico	18.5	9	2002–2004	Goodyear et al. (2008)
White marlin	Gulf of Mexico	North Carolina & Virginia	54.4	2	2001	Kerstetter et al. (2003)
White marlin	Gulf of Mexico	Bermuda	33.2	8	1999	Graves et al. (2002)
White marlin	Straits of Florida	NE Gulf of Mexico	10.4	2	2006	Edwards (2008)
White marlin	Caribbean Sea	Florida East Coast	30.6	3	2004	Kerstetter and Graves (2006)
White marlin	U.S. Atlantic	Dominican Republic	6.3	6	2003	Prince et al. (2005)
White marlin	U.S. Atlantic	Dominican Republic	14.4	4	2002	Horodysky and Graves (2005)
White marlin	U.S. Atlantic	Windward Passage	11.1	1	2004	Kerstetter and Graves (2006)
White marlin	U.S. Atlantic	New Jersey	17.6	7	2002–2003	Horodysky and Graves (2005)
White marlin	U.S. Atlantic	Mid-Atlantic Bight	50.6	12	2003–2004	Kerstetter and Graves (2006)
White marlin	U.S. Atlantic	North Carolina, Virginia, & New Jersey	36.9	19	2005–2006	Graves and Horodysky (2008)

discrimination of white marlin was lower, suggesting that white marlin likely mix more frequently than blue marlin among the regions investigated. Moreover, it appears that dispersive behaviors and environmental histories of marlin inhabiting certain regions, specifically blue marlin in the Gulf of Mexico, may be distinct from other regions. Previous studies have found divergent movement patterns or behaviors within fish populations across a wide range of fish taxa (referred to as “migratory contingents”, Secor, 1999) including highly migratory species such as Atlantic bluefin tuna (Fromentin and Powers, 2005).

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