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Age and Growth of Three Coastal-Pelagic Tunas (Actinopterygii: Perciformes: Scombridae) in the Florida Straits, USA: Blackfin Tuna, Thunnus atlanticus, Little Tunny, Euthynnus alletteratus, and Skipjack Tuna, Katsuwonus pelamis

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AGE AND GROWTH OF THREE COASTAL-PELAGIC TUNAS (ACTINOPTERYGII: PERCIFORMES: SCOMBRIDAE) IN THE FLORIDA STRAITS, USA: BLACKFIN TUNA, *THUNNUS ATLANTICUS*, LITTLE TUNNY, *EUTHYNNUS ALLETTERATUS*, AND SKIPJACK TUNA, *KATSUWONUS PELAMIS*

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Background. Understanding the life history of a species is essential for fully understanding its role within an ecosystem. However, many of the fish species of high ecological value have not been studied due to their less prominent roles in local recreational and commercial fisheries in comparison to other targeted species. These valuable fishes are also important trophic linkages between small neritic fishes and large, economically valuable apex predators. This study describes for the first time the yearly age and growth patterns of three small tuna species inhabiting South Florida (USA) waters: blackfin tuna, *Thunnus atlanticus* (Lesson, 1831); little tunny, *Euthynnus alletteratus* (Rafinesque, 1810); and skipjack tuna, *Katsuwonus pelamis* (Linnaeus, 1758).
Materials and methods. Tuna specimens were collected in two ways: via donations obtained from various fishing tournaments and charter captains in the areas of the Florida Straits as well as hook-and-line catches performed especially for this project. Age determination was based on sagittal otolith hyaline deposition patterns. Marginal increment analysis was used as an indirect validation method. Growth parameters were determined by comparison of the fish fork length and the hyaline band measurements.
Results. Two hyaline bands formed each year in all three species—one in winter and one in summer. The von Bertalanffy growth equation produced a growth rate for each species: blackfin tuna, $L_\infty = 95.34$ cm, $K = 0.28$, and $t_0 = -1.53$; little tunny, $L_\infty = 77.93$ cm, $K = 0.69$, and $t_0 = -0.69$; and skipjack tuna, $L_\infty = 112.76$ cm, $K = 0.24$, and $t_0 = -1.70$. Parameters of each resulting von Bertalanffy equation were compared among species showing that little tunny grew the fastest, but skipjack had the largest estimated size. Results were also compared with growth rates currently used in stock assessments by fisheries management organizations, such as the International Commission for the Conservation of Atlantic Tunas (ICCAT).
Conclusion. Sectioned otoliths indicate two bands a year for these three species in the Florida Straits. Results were comparable to other studies, with a similar finding of two bands per year in hard parts for these species. Further knowledge of these populations will aid in stock assessments for these species and the ongoing shift to ecosystem-based management plans.

Keywords: age and growth, Atlantic, otoliths

INTRODUCTION

An insightful start to understanding a species' role within an ecosystem is describing its life history. With overfishing and stock depletion in many of the world's fisheries, there have been suggestions of ecosystem-based management, but there are frequently many gaps in the knowledge of smaller, less targeted species in an ecosystem (Richardson et al. 2010). Ecosystem-based management has been suggested due to the apparent ineffectiveness of single-species management, despite the fact that there is much to learn about the marine ecosystem as a whole (Botsford et al. 1997, Pikitch et al. 2004).

Coastal-pelagic fishes are broadly defined as those inhabiting open ocean (pelagic) waters near the surface, but remaining relatively near coastal areas. Small tunas are typically defined as species that reach maximum size

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at 5 kg or less (Menard et al. 2000). Small tunas are seasonally important to artisanal and recreational fisheries in many areas around the Atlantic Ocean. Seasonal changes in abundance in coastal areas are attributed to the tunas' migratory tendencies (James et al. 1988). Small tunas such as blackfin tuna, little tunny, and skipjack tuna are important in Florida, either as target species themselves or as bait, in addition to being prey for larger, targeted species such as blue marlin, *Makaira nigricans* Lacepède, 1802, or sailfish, *Istiophorus platypterus* (Shaw, 1792). Some life history aspects have been described for a few of these small tuna species in the Atlantic and surrounding areas; however, these have generally been for populations and species in the Mediterranean Sea, while only limited studies have come from the western North Atlantic and Gulf of Mexico populations (Table 1).

For the small tunas within the US coastal–pelagic complex, what little domestic fisheries regulation that does exist simply groups these tunas together into a general small-tuna complex, with no differentiation between species. Currently there is no federal management for blackfin tuna or little tunny and no federal or state regulations for skipjack tuna, though some states have limited regulations. In this case, a comparison of these age-growth parameters may allow more defined harvest regulations on a species-specific basis. Differences in current measures of growth rates could require a re-evaluation of the current stock assessment for the species. Of the three study species, only the skipjack tuna is included in the Highly Migratory Species (HMS) management regime as implemented by the US National Marine Fisheries Service (NMFS) and ICCAT via recommendations extrapolated from stock assessments by NOAA*. The other two species are not currently regulated for the US Atlantic fisheries.

This project focused upon blackfin tuna, *Thunnus atlanticus* (Lesson, 1831), little tunny, *Euthynnus alletteratus* (Rafinesque, 1810), and skipjack tuna, *Katsuwonus pelamis* (Linnaeus, 1758). Though there have been a few age-growth studies done on them, these small tuna species do not have many recent data and almost no studies have been done in the western Atlantic populations (see Table 1). This study describes the age and growth rates of these tunas and compares their growth parameters. Because they co-occur within the study area, the study also compares the values between the three species of the von Bertalanffy equations-derived growth rates (K), the estimated age at L_∞ in the von Bertalanffy equation, and the timing of band formation on the otoliths, including whether the time of band formation differs between species. Patterns of band formation for each of the three species are also described for the area of the Florida Straits and compared to patterns observed in other areas through past studies.

MATERIALS AND METHODS

Sample collection. The study area was primarily the Florida Straits, which is located between Cuba on the south, the Bahamas on the east, and Florida on the west and north. This project sampled 207 blackfin tuna (in respective calendar quarters—Q1 = 44, Q2 = 102, Q3 = 9, Q4 = 52), 203 little tunny (Q1 = 3, Q2 = 71, Q3 = 110, Q4 = 19), and 76 skipjack tuna (Q1 = 6, Q2 = 7, Q3 = 43, Q4 = 20) (Figs. 1 and 2). Individual tunas were collected in the general Florida Straits area. The majority of samples were obtained as a pre-filleted or "loined head and

Table 1

Published records on ageing studies of small tuna (blackfin tuna, *Thunnus atlanticus*; little tunny, *Euthynnus alletteratus*; and skipjack tuna, *Katsuwonus pelamis*) in the Atlantic Ocean and surrounding waters

Species	N	Sample dates	Ageing method	Location	Paper
Thunnus atlanticus	76	Nov 1999–Jan 2001 (daily)	Otoliths	Martinique Island	Doray et al. 2004
Thunnus atlanticus	15		Otoliths, vertebrae, spines	West Indies	Neilson et al. 1994
Thunnus atlanticus		1979	Spines	Cuba	García Coll et al. 1984
Euthynnus alletteratus	413	Jan 2008–Dec 2009	Spines	Mediterranean	Hajjej et al. 2012
Euthynnus alletteratus	105	2003–2006	Spines	Mediterranean	Valeiras et al. 2008
Euthynnus alletteratus	1454 + 145	Apr 1994–May 1998	Spines	Mediterranean & Aegean Sea	Kahraman and Oray 2001
Euthynnus alletteratus	200 + 150	1987–1989 (daily)	Otoliths	Mississippi & Gulf of Mexico	Allman and Grimes 1998
Katsuwonus pelamis	613	1986–1988	Spines	SW Atlantic	Andrade and Kinas 2003
Katsuwonus pelamis	4084	1960–2002	Tagging	E Atlantic	Gaertner et al. 2008
Katsuwonus pelamis	558	1964–1965	Spines	North Carolina	Batts 1972

N = number of individuals aged for each study; Two N-values correspond respectively to the two locations listed in the study; Note that all of these prior studies focused on a single species.

* http://www.nmfs.noaa.gov/sfa/hms.

skeleton" (so-called "racks") with any remaining viscera attached. The head and the rest of the axial skeleton remained intact other than the removal of the dorsal musculature; total and fork lengths of "racks" and whole tunas were therefore assumed to be equal. Samples were obtained from local charter vessels and recreational anglers in Miami and Fort Lauderdale, as well as several local fishing tournaments from Monroe, Dade, and Broward counties in South Florida (USA) as donations. Individuals were also caught by rod-and-reel off a Nova Southeastern University (NSU) research vessel using local standard techniques and lures.

Laboratory processing. Standard-, fork-, and total length of each tuna were recorded in cm. When measurements were possible, pre-anal-, pre-dorsal-, pre-pelvic-, pre-pectoral length, body depth, head length, pre-orbital length, eye diameter, and upper jaw length were also recorded in cm. Measurements were taken from the snout to the beginning of the body part. Specifically, pre-anal length was measured from the snout down the midline of the body to insertion of the anal fin, head length was measured to the end of the operculum, and body depth was measured from the dorsal to the ventral of the fish in the widest place, typically near the center of the first dorsal (Anderson and Neumann 1996). These made it possible to estimate the fork length of individuals that were obtained as only heads. For the 18 individuals obtained as heads only, eye diameter, pre-orbital length, upper-jaw length, and head length, measurements were taken; when possible, pre-pectoral-, pre-dorsal-, and pre-pelvic lengths were also taken. Sex was determined via direct gonad observation.

Ageing. Yearly age was estimated based on sagittal otoliths. The sagittal otoliths were removed via a transverse section though the dorsal side of the brain cavity and pulled out through the utricle with forceps. Using a paintbrush, they were rinsed in tap water and removed of any excess tissue, then stored dry in separate vials for each individual fish. Otoliths were embedded in a 2-part epoxy resin consisting of Araldite 502 and Aradur 956-2 and cut with a low-speed Isomet-type saw (South Bay Technology, Inc., Model 650) transversally through the core, then the sections were glued to a microscope slide (Doray et al. 2004). Four blades were used in order to obtain three simultaneous sections with spacers in between, creating 0.3–0.4 µm sections. Sections were then rinsed in tap water, dried, and glued to a slide using Flo-texx (Thermoshandon) mounting medium. Readings were done on the section containing the core while using the other two sections for comparison. Alternating hyaline and opaque bands were present on the otoliths of all three species. Counts were done starting from the core and counting completed hyaline bands using an Olympus CX31 microscope and images were taken using an Infinity 1 Olympus U-TV0.6XC camera at 5× magnification. The images were then analyzed using the software Infinity Analyze (Version 5.0.3) to determine the marginal increment width. Hyaline bands were chosen due to them being the darker, thinner of the two bands. The darker color was most likely due to a higher density than the opaque bands and corresponding to a slower growth period (Campana 2001).

Marginal increment analysis (MIA) was done via measurements from the core to the edge of the otoliths and complete bands in the otoliths (Lessa and Duarte-Neto 2004, Zaboukas and Megalofonou 2007). Each otolith was read twice by the same reader, a month apart,

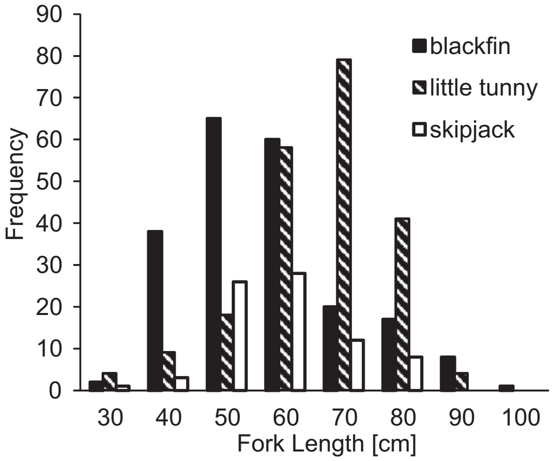

Fig. 1. Length frequencies of blackfin tuna (*Thunnus atlanticus*), little tunny (*Euthynnus alletteratus*), and skipjack tuna (*Katsuwonus pelamis*) that were aged in the presently reported study; Fork length is in groupings of 10 cm with the upper cap of the range representing the group (i.e., "30" represents individuals 20–30 cm FL)

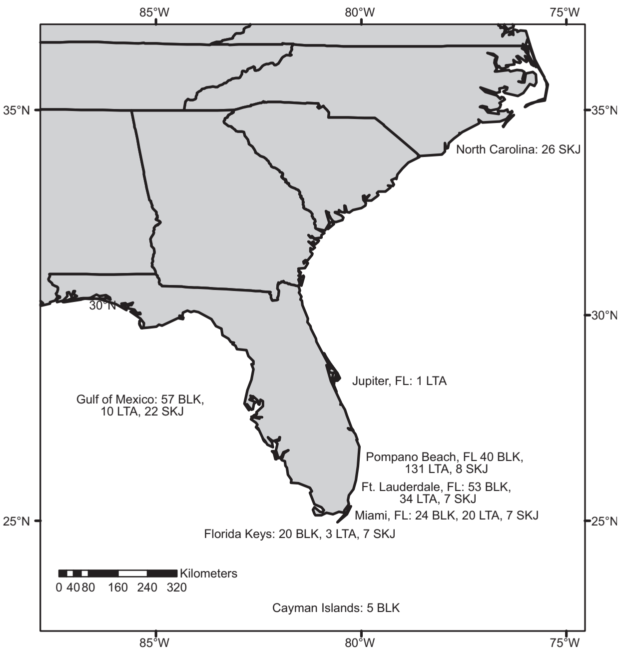

Fig. 2. Map of the southeastern United States where tuna samples were obtained; Numbers are indicated for each species where BLK is blackfin tuna (*Thunnus atlanticus*), LTA is little tunny (*Euthynnus alletteratus*), and SKJ is skipjack tuna (*Katsuwonus pelamis*)

without knowledge of the fish size, sex, catch date, or any previous readings (Gillanders et al. 1999). If the two initial readings did not agree, a third reading was done; if still no agreement, the individual was not included in the analysis. Growth parameters were determined by comparison of fish fork length to otolith band count measurements; resulting comparisons produced a growth rate for the species. An index of percent error was also calculated to compare the reproducibility of age determination between two readings:

$$\text{IPAE} = \frac{100}{N}\sum_{j=1}^{R}\left[\frac{1}{R}\sum_{i=1}^{R}\frac{|X_{ij}-X_j|}{X_j}\right]$$

where N is the sample size, R is the number of readings performed on an otolith, X_{ij} is the ith count done in the jth individual (Beamish and Fournier 1981).

Data analysis. Fork length (FL) was calculated from other measurements taken for individuals that were missing a fork length measurement. Linear regressions were calculated for each measurement type against FL for each species (Table 2). If the coefficient of determination (R^2) was > 0.80, the model was considered to explain a significant amount of the variation between the measurements. For individuals obtained as heads only, a mean of the values determined from the regression equations of the measurements taken with significant coefficients of determination were used at the calculated FLs. Regressions with coefficients less than 0.80 were only used if a measurement was not available corresponding to a regression with a higher coefficient of determination.

Analysis consisted of age validation via marginal increment analysis. Though an exact calendar-age for a fish cannot be determined, a comparison of the growth rates between species can be made. The marginal increment ratio (MIR) was calculated using the equation:

$$\text{MIR} = \frac{(\text{OD}-D_n)}{(D_n-D_{n-1})}$$

where OD is the distance to the edge of the otolith lengthwise, D_n is the distance to the last completed hyaline band, and D_{n-1} is the distance to the previous completed band (Lessa and Duarte-Neto 2004, Zaboukas and Megalofonou 2007). The MIR was plotted against calendar quarter as well as month to determine the time of band formation (Das 1994). The MIR was also plotted against South Florida seasons, where winter included December, January, and February; spring included March, April, and May; summer included June, July, and August; and autumn included September, October, and November. The seasons were grouped this way due to the general temperature trends of the local area as well as balancing out the distributions of the appearance of each species in the samples. This analysis was not used due to the end and beginning of band formation clearly being present in the same defined season, resulting in the overall P-values not being significant at the $P < 0.05$ level for all three species. ANOVA and Tukey's tests were performed to determine if there were differences between quarters and between which quarters those differences were significant.

Age and growth information was determined by applying the von Bertalanffy growth function to the otolith and length data (Doray et al. 2004):

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

This equation determines the maximum length (L_∞) and the growth rate (K). The t_0 term is an estimated age of which a fish length is equal to zero (Haddon 2001).

RESULTS

All three tuna species had otolith sections of similar shape, though the whole otoliths varied in appearance (Fig. 3).

Table 2

Regression equations for three species of small tunas (blackfin tuna, *Thunnus atlanticus*; little tunny, *Euthynnus alletteratus*; and skipjack tuna, *Katsuwonus pelamis*) in the western North Atlantic to determine fork length measurements from other length measurements, used for samples obtained as heads only

Measurement	*Thunnus atlanticus*		*Euthynnus alletteratus*		*Katsuwonus pelamis*	
	Regression	R^2	Regression	R^2	Regression	R^2
Total length	$y = 0.94x - 0.84$	0.99	$y = 0.96x - 1.03$	0.99	$y = 0.97x - 1.31$	0.99
Standard length	$y = 1.08x - 0.05$	0.99	$y = 1.04x + 1.63$	0.98	$y = 1.02x + 3.19$	0.96
Pre-anal length	$y = 1.54x + 1.64$	0.92	$y = 1.27x + 12.45$	0.79	$y = 1.10x + 13.15$	0.76
Pre-dorsal length	$y = 2.56x + 8.76$	0.62	$y = 3.03x + 9.56$	0.80	$y = 2.17x + 12.37$	0.82
Pre-pelvic length	$y = 3.02x + 3.30$	0.90	$y = 2.90x + 12.47$	0.78	$y = 1.67x + 23.51$	0.73
Pre-pectoral length	$y = 3.38x + 0.26$	0.94	$y = 3.41x + 5.76$	0.88	$y = 2.07x + 17.51$	0.79
Body depth	$y = 2.06x + 19.78$	0.79	$y = 2.12x + 25.07$	0.59	$y = 1.67x + 28.90$	0.74
Head length	$y = 3.48x + 1.81$	0.92	$y = 3.49x + 7.44$	0.86	$y = 2.50x + 13.76$	0.82
Pre-orbital length	$y = 10.23x + 5.53$	0.90	$y = 9.60x + 18.24$	0.79	$y = 9.58x + 7.78$	0.80
Eye diameter	$y = 23.05x - 8.78$	0.78	$y = 24.42x + 7.32$	0.45	$y = 25.50x - 3.46$	0.61
Upper jaw length	$y = 8.36x + 6.33$	0.78	$y = 8.69x + 11.31$	0.82	$y = 6.39x + 19.44$	0.78

In each equation, y is the resulting FL calculated from the corresponding length measurement x.

The ventral side was wider and more clearly marked than the dorsal side. The distal, dorsal side of the otoliths developed an additional bump near the core region towards the posterior of the otolith. A similar variation to the edge of an otolith was seen in all three species with increasing size. The edge, in particular the ventral edge, for all three species would develop curves or bumps along with linear or physical division of the otolith that occurred at the convex points of the bumps, looking similar to fingers lined up next to each other. In some cases, the first “finger” next to the sulcus would have a physical space between it and the subsequent fingers; up to six “fingers” were seen to develop on the ventral side and up to four on the dorsal. Banding patterns would often become confined to one of the outer or center fingers with increasing age.

Blackfin tuna, *Thunnus atlanticus*. A total of 212 specimens of blackfin tuna were collected, though useable otoliths were only extracted from 207 individuals (29.5 to 92 cm FL). Regressions with coefficients of determination found to significantly explain the variation with fork length were the measurements of total length (R = 0.99), standard length (R = 0.99), pre-anal length (R = 0.92), pre-pelvic length (R = 0.90), pre-pectoral length (R = 0.94), head length (R = 0.92), pre-dorsal length (R = 0.88), body depth (R = 0.80), and pre-orbital length (R = 0.89). Lengths of individuals with omitted fork length data were calculated from the mean of values obtained from the linear regression equations with significant coefficients of determination corresponding to measurements that were present in the data.

The first two to four bands on the otolith appeared either very wide or as multiple fine bands close together. These bands also had larger opaque zones in between them than future bands. The first and second as well as the third and fourth bands occurred closer to each other than the second and third bands. In some instances, a wider opaque band occurred between the first and second hyaline bands, with a smaller opaque zone between the second and third. Subsequent bands appeared more defined and evenly spaced, though they did not always continue across the entire otolith. The ventral edge of the otolith divided into two to six fingers with increasing otolith size. A gap between fingers was occasionally observed. Hyaline band formation often only continued up the outermost or one of the middle fingers with increasing size and rarely appeared on the innermost finger once distinct, regular bands began to form.

Of the otoliths sectioned, 99% resulted in an age determination in 1–3 readings, with 43% requiring a third reading. The index of percent error for the sample was 13.3%. The ANOVA found a significant effect of calendar quarter on the MIR at the $P < 0.05$ level for the conditions [F (3, 125) = 26.90, $P < 0.0001$]. Tukey’s test indicated that quarters one and three were significantly different from quarters two and four. The 95% confidence intervals produced by Tukey’s test between quarters one and two were 0.36 to 0.72, between quarters two and three were –0.05 to 0.96, between quarters three and four were 0.05 to 1.07, and between quarters four and one were 0.45 to 0.85. Minimum marginal increment values occur in quarters one and three, indicating hyaline band formation in both winter and summer. Though the months of January and July are missing from the graph, a more detailed trend of increment formation can be seen when MIR is graphed against month instead of quarter (Fig. 4). The ANOVA found a significant effect of calendar month on the MIR at the $P < 0.05$ level for the conditions [F (9, 119) = 21.78, $P < 0.0001$]. Tukey’s test indicated that the months of June and November were significantly different than the months adjacent to them. The 95% confidence intervals produced by Tukey’s test between May and June were 0.08 to 0.57, between June and August were 0.17 to 1.66, between October and November were 0.02 to 0.52, and between November and December were 0.52 to 1.99, indicating hyaline band completion in both June and November. The calculated von Bertalanffy parameters were $L_\infty = 95.34$ cm, $K = 0.28$, and $t_0 = -1.53$ (Fig. 5). When separated by sex the parameters for the male (N = 114)

Fig. 3. Sectioned otoliths for the three small tuna species in the presently reported study from the western North Atlantic: (**A**) otolith of blackfin tuna (*Thunnus atlanticus*), (**B**) otolith of little tunny (*Euthynnus alletteratus*), and (**C**) otolith of skipjack tuna (*Katsuwonus pelamis*)

curve were $L_\infty = 118.57$ cm, $K = 0.15$, and $t_0 = -2.25$, and the parameters for the female ($N = 51$) curve were $L_\infty = 88.62$ cm, $K = 0.30$, and $t_0 = -1.58$. The oldest blackfin tuna in this study was aged at 7.5 years and measured 80 cm FL.

Little tunny, *Euthynnus alletteratus*. A total of 213 little tunny were collected and otoliths were successfully extracted from 203 of the specimens (25 to 83.2 cm FL). Regressions with coefficients of determination found to significantly explain the variation with fork length were the measurements of total length ($R = 0.99$), standard length ($R = 0.98$), pre-pectoral length ($R = 0.92$), head length ($R = 0.91$), pre-anal length ($R = 0.81$), pre-dorsal length ($R = 0.84$), pre-pelvic length ($R = 0.83$), pre-orbital length ($R = 0.83$), and upper jaw length ($R = 0.87$). Regressions of fork length with body depth ($R = 0.65$) and eye diameter ($R = 0.49$) produced coefficients of variation less than 0.70. Lengths of individuals with omitted fork length data were calculated from the mean of values obtained from the linear regression equations with significant coefficients of determination corresponding to measurements that were present in the data.

The first two to three bands often occurred between blotchy check marks or in close proximity to false bands. Hyaline bands became more regular and distinct as the fish aged. The innermost finger on the ventral side of the otolith often grew separately from the rest and sometimes the dorsal side would do the same. Hyaline bands were often observed on the innermost ventral finger corresponding to older, regular bands, but only occasionally exhibited a mark corresponding to the first few bands.

Of the otoliths sectioned, 99% resulted in an age determination in 1–3 readings, with 37% requiring a third reading. The index of percent error was 6.7%. The ANOVA found a significant effect of calendar quarter on the MIR at the $P < 0.05$ level for the conditions [F (3, 169) = 238.51, $P < 0.0001$]. Tukey's test indicated that quarters one and three were significantly different from quarters two and four. The 95% confidence intervals produced by Tukey's test between quarters one and two were 0.44 to 1.02, between quarters two and three were 0.69 to 0.84, between quarters three and four were 0.66 to 0.99, and between quarters four and one were 0.46 to 1.11. Minimum marginal increment values occur in quarters one and three, indicating hyaline band formation in both winter and summer. Though the months of December, January, and February are missing from the graph, a more detailed trend of increment formation can be seen when MIR is graphed against month instead of quarter (Fig. 4). The ANOVA found a significant effect of calendar month on the MIR at the $P < 0.05$ level for the conditions [F (8, 164) = 225.00, $P < 0.0001$]. Tukey's test indicated that the months of March, June, and July were significantly different than the months adjacent to than. The month of October was also significantly different than the month prior. This indicates hyaline band completion in June, but the winter quarter cannot be accurately determined due to a lack of samples from December through February. The 95% confidence intervals produced by Tukey's test between November and March were 0.38 to 1.11, between March and April were 0.19 to 0.64, between May and June were 0.19 to 0.50, between June and July were 0.90 to 1.06, between July and August were 0.00 to 0.19, and between September and October were 0.44 to 0.84. The von Bertalanffy parameters were $L_\infty = 77.93$ cm, $K = 0.69$, and $t_0 = -0.69$ (Fig. 5). When separated by sex the parameters for the male ($N = 121$) curve were $L_\infty = 87.91$ cm, $K = 0.37$, and $t_0 = -1.65$ and the parameters for the female ($N = 63$) curve were $L_\infty = 77.49$ cm, $K = 0.64$, and $t_0 = -0.76$. The oldest little tunny in this study was aged at 5 years and measured 83.2 cm FL.

Skipjack tuna, *Katsuwonus pelamis*. A total of 78 skipjack tuna were collected and otoliths were pulled from 76 of the specimens (29 to 78 cm FL). Regressions with coefficients of determination found to significantly explain the variation with fork length were the measurements of total length ($R = 0.99$), standard length ($R = 0.95$), head length ($R = 0.90$), pre-orbital length ($R = 0.86$), and upper jaw length ($R = 0.81$). Regressions of fork length with pre-pelvic length ($R = 0.69$) and eye diameter ($R = 0.61$) produced coefficients of varia-

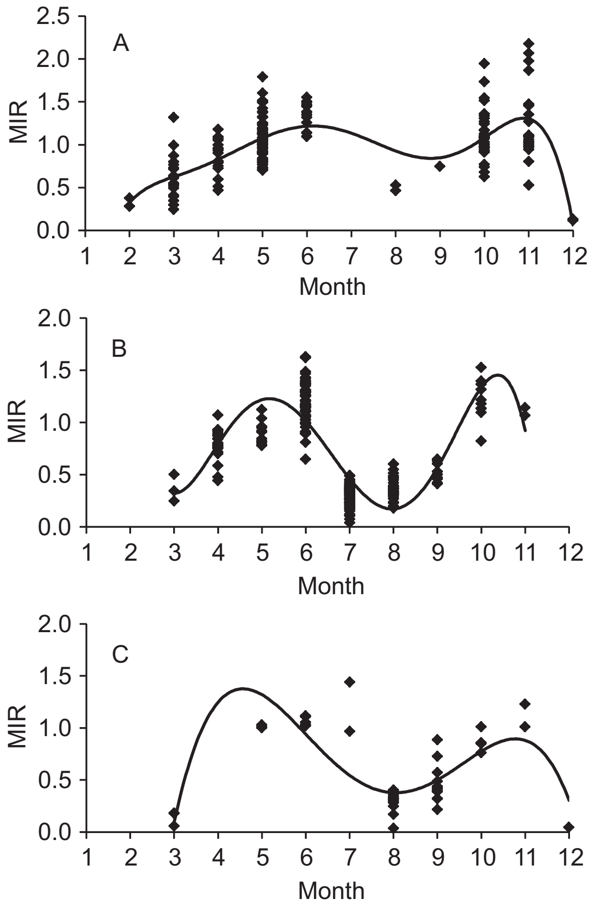

Fig. 4. Marginal Increment Ratios (MIR) vs. month for otoliths from three coastal-pelagic small tunas from the western North Atlantic: (**A**) blackfin tuna (*Thunnus atlanticus*), (**B**) little tunny (*Euthynnus alletteratus*), and (**C**) skipjack tuna (*Katsuwonus pelamis*) per month; Minimum values indicate the beginning of a new opaque zone

tion less than 0.70. Lengths of individuals with omitted fork length data were calculated from the mean of values obtained from the linear regression equations with significant coefficients of determination corresponding to measurements that were present in the data.

Skipjack tuna otoliths were much smaller than the other two species. Banding patterns tended to stay somewhat consistent over the years, unlike the other two tunas. At times, bands occurred alternating between check marks and in other individuals hyaline bands appeared clearly across the otolith with no additional dark marks. The ventral side of the otolith was occasionally divided into up to four fingers while the dorsal side remained as one or two. The innermost finger rarely started growing separately from the rest.

Of the otoliths sectioned, 99% resulted in an age determination in 1–3 readings, with 39% requiring a third reading. The index of percent error was 7.4%. The ANOVA found a significant effect of calendar quarter on the MIR at the $P < 0.05$ level for the conditions [F (3, 35) = 13.51, $P < 0.0001$]. Tukey's test indicated that quarters one and three were significantly different from quarters two and four. The 95% confidence intervals produced by Tukey's test between quarters one and two were 0.38 to 1.24, between quarters two and three were 0.32 to 0.99, between quarters three and four were 0.08 to 0.70, and between quarters four and one were 0.13 to 0.95. Minimum marginal increment values occurred in quarters one and three, indicating hyaline band formation in both winter and summer. Though the months of January, February, and April are missing from the graph, a more detailed trend of increment formation can be seen when MIR is graphed against month instead of quarter (Fig. 4). The ANOVA found a significant effect of calendar month on the MIR at the $P < 0.05$ level for the conditions [F (8, 30) = 62.13, $P < 0.0001$]. Tukey's test indicated that the months of March, July, October, and November were significantly different than the months adjacent to them. Due to the missing months, precise months of hyaline band formation cannot be determined. The 95% confidence intervals produced by Tukey's test between December and March were –0.14 to 0.56, between March and May were 0.50 to 1.03, between June and July were –0.02 to 0.71, between July and August were 0.79 to 1.45, between September and October were 0.21 to 0.63, and between October and November were 0.01 to 0.59. The von Bertalanffy parameters were $L_\infty = 112.76$ cm, $K = 0.24$, and $t_0 = –1.70$ (Fig. 5). Parameters for the curves of each sex were not calculated due to the small sample size of sexed individuals ($N_{male} = 33$; $N_{female} = 30$). The oldest skipjack tuna in this study was aged at 3.5 years and measured 77 cm FL.

DISCUSSION

In comparison to each other, skipjack tuna produced the highest asymptotic size estimation and little tunny produced the smallest. Values obtained from this study were plotted with values obtained from other studies for comparison (Fig. 6). The value calculated for blackfin tuna was slightly higher than other studies, little tunny was lower than other studies, and skipjack fell within the range of other studies. The skipjack value was within the range of values previously calculated for the Atlantic and Pacific oceans, but was much higher than those calculated for the Indian Ocean. Most of the little tunny values

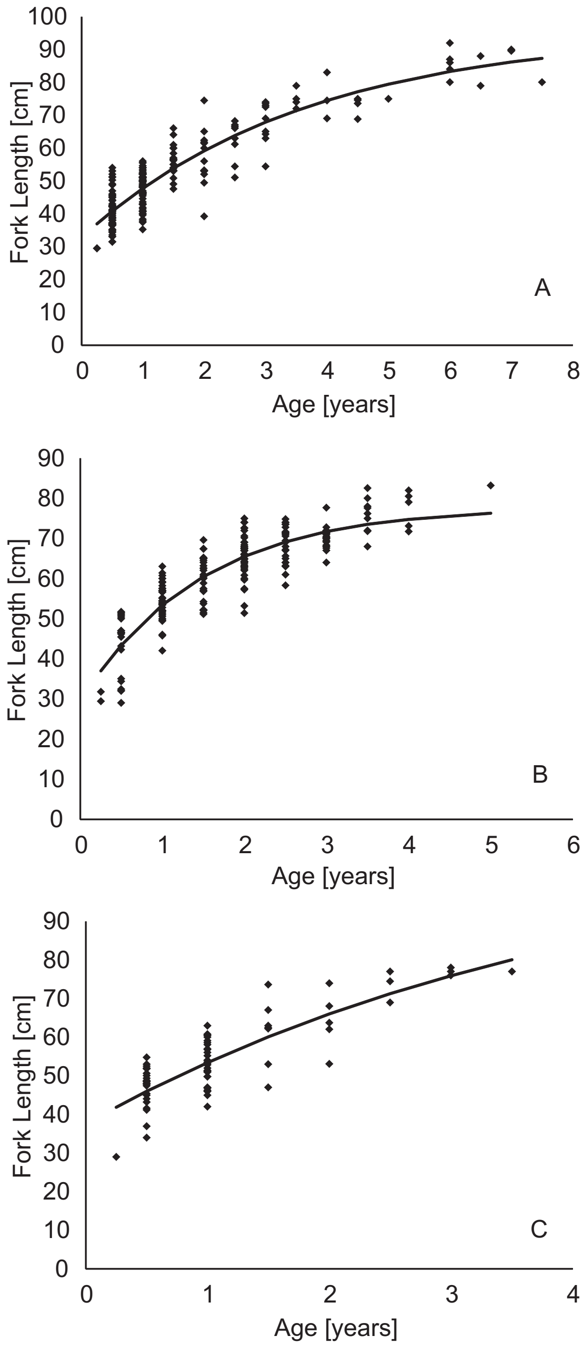

Fig. 5. von Bertalanffy growth curves for three coastal-pelagic small tunas from the western North Atlantic (with the calculated parameters): (**A**) blackfin tuna (*Thunnus atlanticus*) ($L_\infty = 95.34$ cm, $K = 0.28$, $t_0 = –1.53$; $N = 207$), (**B**) little tunny (*Euthynnus alletteratus*) ($L_\infty = 77.93$ cm, $K = 0.69$, $t_0 = –0.69$; $N = 203$), and (**C**) skipjack tuna (*Katsuwonus pelamis*) ($L_\infty = 112.76$ cm, $K = 0.24$, $t_0 = –1.70$; $N = 76$)

were from the Mediterranean Sea, but the few that were from the Atlantic Ocean were from the northeast Atlantic. Compared to the average value from other studies in the Atlantic, this study produced values 28% higher for blackfin, 42% lower for little tunny, and 24% higher for skipjack. Compared to other studies as a global whole, this study produced values 28% higher than the average for blackfin, 34% lower for little tunny, and 22% higher for skipjack.

The differences seen in the growth parameters of this study compared to previous studies may be due to differences between study periods and locations. Growth dynamics may change over time as a population evolves due to the stress of a changing environment and changes in fishing pressure (Hoffmann and Sgrò 2011). Static or dynamic parameters in different regions may also affect the growth rate and it has been found that skipjack tuna grow larger, but slower in more temperate waters than in more tropical waters (Gaertner et al. 2008). None of these three tuna species have been observed in a trans-Atlantic migration and are often considered to consist of multiple stocks (Bard et al. 1993). This stock separation could be another explanation for the differences seen in growth parameters. The wide range of asymptotic lengths calculated from 78.4 to 142.5 cm for skipjack alone in an example of the variety that can result from various areas (Batts 1972, Chi and Yang 1973, Appukuttan et al. 1977, Uchiyama and Struhsaker 1981, Chur and Zharov 1983, Mohan and Kunhikoya 1985, James et al. 1987, Tanabe et al. 2003, Gaertner et al. 2008). The sizes and ages represented in a sample can also have an effect on the resulting von Bertalanffy curve. The most accurate curve would be produced from a large sample size from juveniles to pre-senescent adults and all ages and sizes in between. A sample that is biased to a limited size range will also result in a biased curve that will more accurately fit the growth rate during that particular time period of a population's life, but not over the average lifespan of an individual in the population.

Validation by marginal increment analysis, though it is the most common age validation method used, has its challenges and is by no means an absolute validation method (Campana 2001). A tag-recapture method would be the most beneficial, but is more difficult with pelagic and highly migratory species such as tunas. To be done effectively, however, the mark-recapture method requires the capture and tagging or marking of juvenile fish known to be less than a year old and the recapturing of individuals years later. The main reasons that the mark-recapture method was not being used in this study are the time span required to do such a study as well as tunas being highly migratory species, which further reduces the percentage of recaptured individuals.

To conduct marginal increment analysis most accurately, each age class should be analyzed and plotted separately. Due to only having a few hundred (rather than thousands) in this study's sample size, all individuals with band counts of two or more were analyzed in the same analysis. A ratio was used instead of the direct measurement of the increment in order to compensate for the fact that each opaque band becomes narrower with age. The inclusion of all ages may also explain why some quarters had a wider range of marginal increment ratios. Quarters were chosen as the primary analysis grouping because of having multiple months with no samples for each species.

Marginal increment analysis is also best used for young, fast growing species as increment deposition may change with age (Campana 2001). For the most part, the individuals in the sample were fairly young, but there were a few handfuls of individuals on the older side of the spectrum. All three of the species were observed to form two bands per year, which has also been observed in small tunas by other studies (Chi and Yang 1973, Johnson 1983, Lessa and Duarte-Neto 2004).

All three species were found to form bands twice a year rather than once a year as is seen in the majority of other species, completing them in summer and in winter. Band completion for all three species occurred from January to March and August to September. Annular instead of double bands were seen on blackfin tuna vertebrae (Richards and Bullis 1978). The studies that have found two spawning peaks in blackfin found them in the spring and the summer, which roughly corresponds to

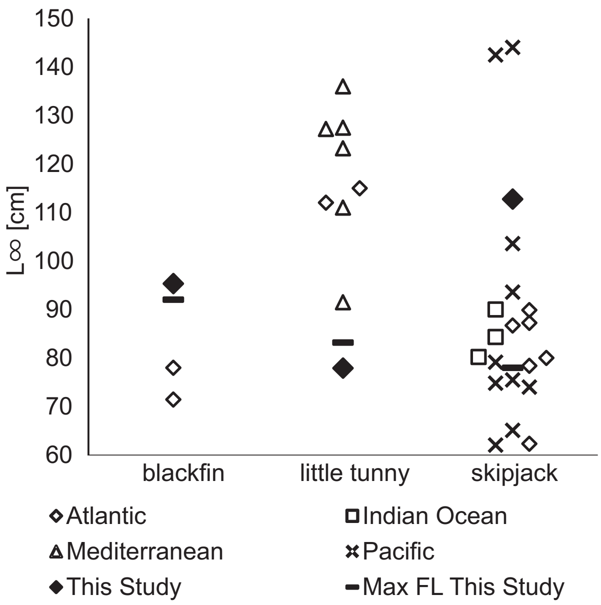

Fig. 6. Comparison of L_∞ values between this study and others for three species of coastal-pelagic small tunas: blackfin tuna (*Thunnus atlanticus*), little tunny (*Euthynnus alletteratus*), and skipjack tuna (*Katsuwonus pelamis*); Values are categorized by the corresponding body of water in which the study took place (see list of authors in Table 1); The value for blackfin tuna in this study is higher than other studies done in the Atlantic Ocean; the value for little tunny in this study is lower than those found in both the Atlantic Ocean and Mediterranean Sea; and the value for skipjack tuna in this study falls within the range of other studies, but is closest to a study (Gaertner et al. 2008) done in the eastern Atlantic

increment formation (Hare et al. 2001). Little tunny were found to grow the fastest of the three species with a *K*-value of 0.69, while skipjack tuna were found to grow the slowest with a *K*-value of 0.24. Two bands were seen in spines of another tuna species—the bluefin tuna, *Thunnus thynnus* (Linnaeus, 1758), though the winter and summer opaque bands did not appear even as in this study and therefore the second band was treated as a false band (Santamaria et al. 2009). Two bands per year were observed in other little tunny studies as well on dorsal spines and vertebrae (Johnson 1983) as well as skipjack studies on vertebrae (Chi and Yang 1973). Spawning intensity for all three species has been found to increase during the spring (Collette and Nauen 1983, Hare et al. 2001), which could explain the second band.

Though some environmental factors, such as water temperature, feeding opportunity, and spawning stress, have been attributed to periodic band formation, it is believed that an undefined physiological rhythm, possibly caused by factors such as pituitary secretions or genetics, is primarily responsible for the bands (Das 1994). Comparison aging studies between hard structures have found that otoliths are oftentimes simply the most reliable, accurate, and time efficient method for ageing fish (Prince et al. 1986, Lowerre-Barbieri et al. 1994, Ihde and Chittenden 2002, Sipe and Chittenden 2002, Isermann et al. 2003, 2010, Li et al. 2006).

An in-depth histological gonadal analysis of all three species in the Florida Straits area would provide a more detailed view of specific times of increased spawning activity. If these times were to synchronize with increment formation, spawning could more confidently be correlated with band formation. The change in seasons and water temperatures is most often attributed to annulus formation, but being tropical tunas, these species do not see such drastic environmental changes. These species also form two bands a year, which therefore cannot be labeled as "annuli." Continued studies on other biological aspects such as diet and migration patterns for this area are also needed in order to describe these populations to the extent that they have been separately described in the Mediterranean Sea and Pacific Ocean. Recreational fishing data could be utilized, in part, along with the commercial data presumably reported to ICCAT to determine the extent of fishing pressures exhibited on the populations of these three small tuna species.

CONCLUSIONS

Sectioned sagittal otoliths were shown to be a reliable method for determining the age of blackfin tuna, little tunny, and skipjack tuna. Results were comparable to other studies, therefore showing a consistency in the estimates while still providing information on local effects to growth rates. Direct validation via tag-recapture is still needed for these populations to confirm the results. With a planned shift to ecosystem-based assessment methods under the HMS management plan (Anonymous 2006), all of the various small scombrid fishes should be included in future biological studies, including these three small tuna species with economic value to both commercial and recreational fisheries.

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