Environ Biol Fish (2015) 98:1787–1801
DOI 10.1007/s10641-015-0398-0

Age estimation and lead-radium dating of golden tilefish, *Lopholatilus chamaeleonticeps*

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Received: 31 July 2014 / Accepted: 11 February 2015 / Published online: 28 February 2015
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Abstract There is a growing concern over the lack of life history information for many deepwater fisheries species, including golden tilefish, *Lopholatilus chamaeleonticeps*. Fundamental life history characteristics, like age and growth, are required for effective, age-structured stock assessments and management decisions. A previous effort to validate golden tilefish age estimates using bomb radiocarbon dating was inconclusive, which led to an application of lead-radium dating in the current study. Lead-radium dating uses the radioactive disequilibrium of lead-210 (^{210}Pb) and radium-226 (^{226}Ra) in otoliths as an independent estimate of age. Ages were also estimated using traditional age estimates by counting growth zones in thin otolith sections and lead-radium dating was used to test these estimates. Radiometric ages (corrected for time since capture) were similar to age estimates from growth zone counts for two of the female age groups and the two oldest age groups of unknown sex, which confirmed an annual growth zone deposition. However, radiometric ages did not agree with age estimates from growth zone counts for males. The difference may be attributed to geographical variations in radium levels, growth rates and growth zone formation by gender or gender transition. Male sagittal otoliths revealed inconsistent growth zone patterns in thin sections, which may have contributed to underageing. Golden tilefish longevity was confirmed to 26 years.

Keywords Age validation · Radiometric ageing · Lead-210 · Radium-226 · Malacanthidae · Great Northern tilefish

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Introduction

Golden tilefish (*Lopholatilus chamaeleonticeps*, Goode and Bean) is a commercially important demersal fish found along the deep continental margin of the northwestern Atlantic and Gulf of Mexico (Dooley 1978). Although the stock status of golden tilefish in the Gulf of Mexico was determined to be in good standing (SEDAR 2011a), this species has characteristics that make it highly susceptible to capture, such as a burrowing behavior and a unique habitat preference (Able et al. 1982; Grimes et al. 1986; Grimes and Turner 1999). In addition, golden tilefish are thought to be long-lived and slow growing with a complex breeding and reproductive strategy that is not

completely understood (Turner et al. 1983; Grimes et al. 1988; Harris et al. 2001; Palmer et al. 2004; Lombardi-Carlson 2012). Previous assessments for golden tilefish along the U.S. Atlantic Seaboard concluded stocks were both overfished and undergoing overfishing (SEDAR 2004; NEFSC 2005). Stricter management regulations led to the designation of these stocks as being in stages of rebuilding (NEFSC 2009; SEDAR 2011b), but no study to date has provided an age-validated basis for golden tilefish life history parameters that are used in stock assessments.

An age-structured stock assessment for golden tilefish would rely on accurate estimates of fish age to provide proper information for effective management decisions. Underestimated age and longevity have led to fishery problems in other long-lived fishes (Beamish and MacFarlane 1983; Andrews et al. 2009). Use of underestimates of age can lead to assessments that predict larger than sustainable harvest practices (Mace et al. 1990; Forrest et al. 2010). Previous age estimation research on golden tilefish used sagittal otoliths and anal fin rays to estimate age (Turner et al. 1983; Harris and Grossman 1985; Harris et al. 2001; Palmer et al. 2004). Otolith interpretation was difficult for each study and included problems with identification of the otolith core and the first annual growth zone, consistency of growth zone identification along the various growth axes, and grouping or splitting of narrow growth zones, resulting in low agreement between readers (Turner et al. 1983; Palmer et al. 2004). Despite the difficulties in otolith interpretation, longevity was estimated to 40 years. In addition, attempts to validate annual growth zone deposition using marginal increment analysis were inconclusive for both ageing structures (Turner et al. 1983; Harris and Grossman 1985).

Earlier efforts to validate the age of golden tilefish using bomb radiocarbon dating provided complicated results that were not fully explained (Harris 2005). This technique relies on the uptake of bomb-produced radiocarbon by the marine environment and is reported as delta carbon-14 ($\Delta^{14}C$) in reference to a pre-nuclear standard (Stuiver and Polach 1977). The distribution of $\Delta^{14}C$ levels measured from otolith cores of golden tilefish by Harris (2005) were lower than expected based on two selected $\Delta^{14}C$ chronologies. Harris (2005) attributed the attenuated and possibly phase-lagged $\Delta^{14}C$ values to an unknown combination of a deep-water carbon source (depleted in $\Delta^{14}C$) and a misinterpretation of annuli.

Because golden tilefish may live several decades, lead-radium dating can be applied to the otoliths as a method of validating estimates of age. This method of radiochemical dating uses the natural decay of radium-226 (^{226}Ra) into lead-210 (^{210}Pb) as a natural clock that provides an estimate of age that can be compared to traditional age estimations from growth zone counting. For fishes, lead-radium dating depends on the incorporation of radium-226 into the otolith from the environment where it subsequently decays to lead-210 at a known rate (Smith et al. 1991; Panfili et al. 2002). This validation method is unique because it is regulated by the passage of time and can serve as a form of validation for age estimation procedures, such as traditional growth zone counting (Kastelle et al. 1994; Andrews et al. 1999a, 2009). This approach has an advantage over bomb radiocarbon dating, because it is not dependent upon the uptake of an event-related signal.

Accurate age and growth assignment to golden tilefish would provide insight into the life history of this species. Validated life history parameters, such as age at maturity, longevity, and lifetime productivity would provide a defensible basis for age-structured stock assessments and fishery management decisions. Because age and growth studies have thus far have been incomplete for golden tilefish, the objectives of this study were to, 1) establish a traditional age estimation procedure using thin-sectioned, sagittal otoliths, and 2) test the validity of the annual growth zone interpretations of the age estimation procedure using lead-radium dating.

Material and methods

Sample collection

Golden tilefish used in this study were harvested in 2007 from the commercial long-line fishery along the east coast of Florida (Fig. 1). Federal port sampling agents targeted golden tilefish from a large distribution of lengths (range of 300 to 1000 mm, fork length=FL), specifically for this study. The smallest fish was a female (402 mm FL) and the largest fish was of unknown sex (900 mm FL). Port agents provided field measurements of fish length (fork length ±1 mm) and they extracted both sagittal otoliths and gonads used in this study. Sex was assigned using macroscopic description of whole gonads (female – oval in shape, pinkish to red in color,

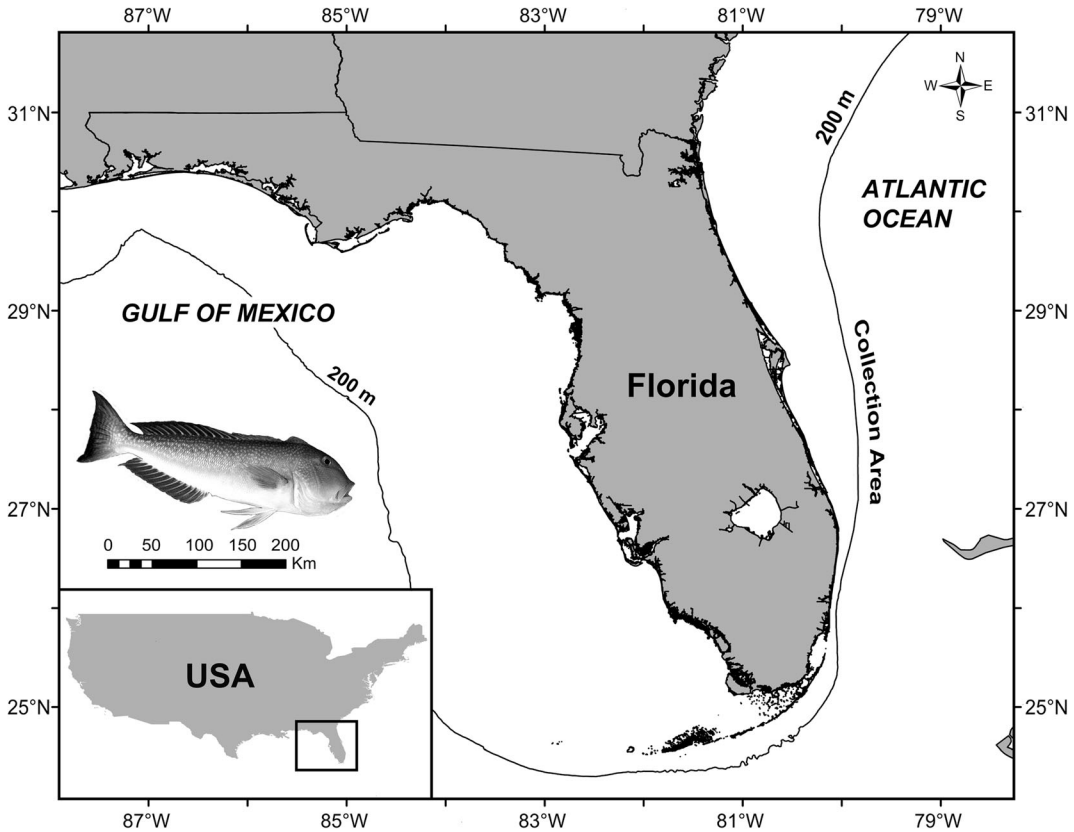

Fig. 1 Map of the continental shelf regions around Florida, USA with the 200 m depth contour delineated. Golden tilefish used in this study were intercepted from commercial long-line vessels that fished along the 200 m contour off the east coast of Florida. The Florida, collection area was primarily between 27–29°N latitude. A photograph of a large adult golden tilefish (*Lopholatilus chamaeleonticeps*) is provided out of interest

n=95; male – thin, taper to a point, normally white in color, *n*=101; no gonad collected, *n*=27).

Traditional age estimation

The basis of this age validation project relied on initial estimates of age from thin sectioned, sagittal otoliths. Counting pairs of opaque and translucent growth zones were interpreted from thin-sectioned, sagittal otoliths (traditional age estimation) (Fig. 2). One otolith from each pair was transversely sectioned (dorso-ventral plane) with a Hillquist[1] petrographic saw (Cowan et al. 1995). Sectioned otoliths were mounted to microscope slides and two readers aged the otolith sections using transmitted light with a stereomicroscope. This approach was similar to previous golden tilefish age estimation studies (Turner et al. 1983; Palmer et al. 2004).

[1] Reference to Trade Names does not imply endorsement by NMFS.

Each reader made initial estimates of age by examining the otolith sections with wide-ranging magnification to fully investigate a broad range of potential growth zone interpretations. The two readers conferred on initial readings to establish traditional age estimation criteria. The otolith sections were read several times by each reader using the established criteria. The final three reads were used to determine indices of precision (average percent error (APE), coefficient of variation (CV) and percent agreement ±1 and ±2 zones; Beamish and Fournier 1981) as a measure of age estimate consistency between readers. Both readers agreed on final age estimates for the otoliths used in lead-radium dating and an average sample age was calculated for each age group.

Otolith growth zone deposition

Growth zones in the otolith sections were described both qualitatively and quantitatively to determine dimorphic

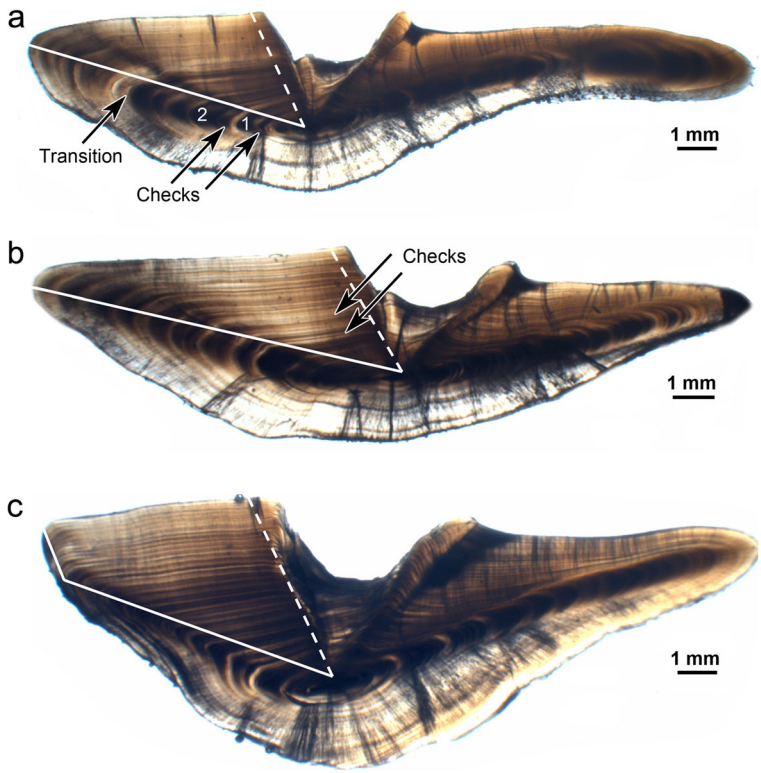

Fig. 2 Examples of thin-sectioned golden tilefish sagittal otoliths (**a**) male (age 11 yrs, 810 mm FL, GTL 10–13 M2) and (**b**) male (age 10 yrs, 758 mm FL, GTL 10–13 M2), and (**c**) female (age 26 yrs, 734 mm FL, GTL 20–27), viewed using a stereomicroscope with transmitted light (15×). Traditional age estimates were determined by interpreting opaque zones along the ventral growth axis (solid lines) and along the ventral sulcus (dashed lines), with consideration of the otolith morphology. Thinner, non-continuous opaque and translucent zones (checks) and possible area of transition are identified

patterns of growth that may be attributed to sex. The regions of quantifiable growth zones were characterized as either along the ventral side of the sulcus or along the ventral growth axis, and structural differences were examined (Fig. 2). Each thin-sectioned otolith was photographed with a digital camera (Hitachi, Model KP D50 color[2]) connected to a desktop computer. The distance between the core and the end of each completed growth zone (a pair of translucent and opaque zones) was measured along the ventral growth axis to quantitatively describe growth zone deposition, using Image Tool Software (Wilcox et al. 2002).

Lead-radium age groups

There are four major limitations of lead-radium dating that must be considered before forming age groups. These limitations are: 1) core size and potential age of juvenile otoliths; 2) individual and collective otolith sample mass availability for juvenile and cored adult otoliths; 3) potential radium-226 activity; and 4) total sample age (estimated age plus time since capture). Based on previous otolith studies, radium-226 activity in otolith material is typically between 0.03 to 0.05 dpm·g^{-1} and results in a calculated minimum of 0.5 g of core material for each lead-radium age group (see review in Andrews 2009). An optimal mass of more than 1.0 g for each age group was targeted to increase radiometric measurement precision.

Only one juvenile otolith was available as a reference for adult otolith coring because of its rarity in collections. Age-readers agreed the juvenile tilefish was less than 3 years of age and its dimensions were used as a template in otolith coring (Fig. 3). The target of core extractions was approximately 8 mm × 4 mm × 1 mm (length × width × thickness) and a weight of 0.05 g. Hence, the minimum number of otoliths required for an adequate sample size of 0.5 g was approximately 10, but more than 10 otoliths were selected to increase potential lead-radium activities.

After otoliths were chosen for each of the lead-radium age groups (based on traditional age estimation), each otolith was cored to the dimensions as described above by: 1) grinding on a lapidary wheel and 2) comparing the extracted core microscopically and

[2] Reference to Trade Names does not imply endorsement by NMFS.

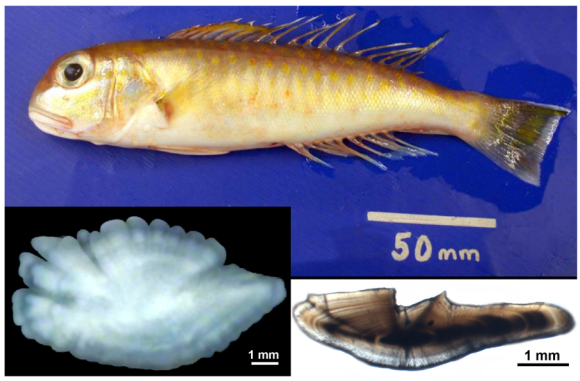

Fig. 3 Image of the only juvenile golden tilefish available with the whole otolith viewed with reflected light at 15× (left) and the thin-sectioned otolith viewed with transmitted light at 25× (right)

macroscopically to the reference juvenile otolith. Proximal and distal layers were removed by grinding these surfaces to expose the 1 mm thick medial plane of the otolith. Alternating pairs of opaque and translucent growth zones visible in the otolith were used to verify the concentric structure of each core (Fig. 3). Careful consideration was given to the shape of the juvenile reference otolith as the extraction took place. The core extraction was complete when dimensions were met and the otolith core weight was similar to the reference otolith. Finalized otolith cores were pooled into the respective age groups and were prepared for lead-radium dating analysis.

Lead-radium dating

Dried and weighed samples (otolith core age-groups) were dissolved and prepared for alpha-spectrometry in a series of steps described in detail elsewhere (Andrews et al. 1999b, 2009). In general, the alpha decay of polonium-210 was used as a daughter-proxy to determine lead-210 activity. A yield tracer (polonium-208) provided a basis for measuring the sample Po-210 activity, and consequently the activity of Pb-210. The remaining solution after polonium assays was dried and saved for radium-226 analyses, the details of which are described in detail elsewhere (Andrews et al. 1999b, 2009).

Radiometric age was calculated using the measured lead-210 and radium-226 activities in a standardized equation derived from Smith et al. (1991). This model compensates for the ingrowth gradient of lead-210 from radium-226 in the otolith core. A radiometric age range was calculated for each sample using error propagation through to the final age determinations (2 SE). Calculated and measured error included standard sources (i.e., pipetting, spike and calibration uncertainties, etc.), alpha-counting statistics, and the ICP-MS analysis routine.

Radiometric versus traditional age estimation

Traditional (otolith growth zones counts) and radiometric (lead-radium dating) age estimations were compared by direct comparison of age estimates and indirectly relative to the expected lead-210:radium-226 ingrowth curve. The 95 % confidence interval for radiometric age was used to interpret the validity of growth-zone counting and the limits of age confirmations. Age estimate agreement or disagreement was considered relative to the potential error (2 SE). Radiometric ages were plotted with observed lengths and annulus-derived ages from a larger dataset of golden tilefish collected along the east coast of Florida (SEDAR 2011b), along with the fit of this data to a von Bertalanffy growth model (non-linear minimization; R Core Team 2011).

Results

Traditional age estimation

Traditional age estimation criteria were established to increase the consistency of identifying growth zones. Thin-sectioned, sagittal otoliths of golden tilefish have a variety of growth zone patterns and a variety of shapes in otolith sections (stocky vs. elongate). Growth zones were more consistently viewed using the ventral side of the otolith section, and the more prominent, evenly spaced and continuous zones (viewed from the ventral sulcus to the ventral axis) were interpreted as complete growth zones. Growth zones varied in appearance from thin, equally spaced opaque and translucent zones, to wider opaque zones composed of several thinner, non-continuous opaque and translucent zones (accessory checks), or a combination of these patterns (Fig. 2). Otolith sections were viewed at no more than 20× magnification with the use of transmitted light on a stereomicroscope. Differences in otolith morphology appear to be related to sex (see below for more detail).

The first criterion of traditional age estimation is identification of the first annulus. The first annulus for golden tilefish typically consisted of a thin translucent

zone and a wider opaque zone and often included an accessory check (Fig. 2a). The next four growth zones have a much wider opaque zone when compared to the corresponding translucent zone; these growth zones may also contain accessory checks. In some golden tilefish, growth zones 6–10 appear as uniformly spaced, alternating opaque and translucent zones (Fig. 2c), but in other fish these zones appear similar to growth zones 1–5 (Fig. 2b). For older fish (> 10 yrs), growth zones appear as evenly spaced, opaque and translucent zones and there may be a shift in the deposition of zones along the proximal surface (Fig. 2c).

The resulting indices of precision were fairly good, taking into consideration the longevity and the various growth zone patterns. Reader agreement was 28 % overall and was 78 % within ±1 zone and 95 % within ±2 zones. Age-reading precision was calculated as an APE at 5.5 % and a CV of 7.7 %. Final age estimates for each fish, used collectively for analysis of age and growth parameters, were based on the agreed pattern of growth zone counting. The estimated age range (based on traditional age estimates) for fish used in this study was 5 to 28 years (Table 1). One fish was estimated to be 2+ years old and the dimensions of this otolith were used as the template to core the adult otoliths.

Otolith growth zone deposition

Golden tilefish otoliths show sexually dimorphic differences in the otolith morphology of thin-sections. Adult females tended to deposit growth zones in a manner that thickened the proximal side of the otolith (sulcal ridges), creating a more stocky growth structure (Fig. 2c). Males deposited growth zones in a direction aligned with the ventral growth axis, leading to a more elongate growth structure (Fig. 2a, b). The observed sexual dimorphism in structure was also reflected in growth zone deposition. Average growth zone distances were similar between genders until age 8; thereafter, males deposited growth zones at greater distances from the core as females began to shift growth to the proximal side (Fig. 4). Additionally, males tended to produce an irregular growth zone deposition within the first four growth zones. These growth zones were composed of what appeared to be subannual growth (thin bands) or accessory checks that were lumped together as a single year of growth. A more regular pattern was evident, on average, after 5 years of age, which may be related to the transition of gender (Fig. 2a).

Table 1 Summary of estimated age with fish and otolith characteristics for golden tilefish age groups from the east coast of Florida that were processed in this study

Age group & sample number	Age (yr) (range)	Age (yr) (mean)	FL (mm) (mean, 2 SE)	FL (mm) (range)	Otolith wt. (g) (mean, 2 SE)	Otolith wt. (g) (range)
GTL 5–7 M1	6–7	6.4	549 (39)	436–860	0.470 (0.034)	0.348–0.596
GTL 5–7 M2	5–7	6.3	520 (17)	465–620	0.453 (0.030)	0.330–0.663
GTL 5–7 F1	5–7	6.4	483 (28)	402–535	0.391 (0.046)	0.277–0.504
GTL 5–7 F2	5–7	6.2	467 (16)	412–508	0.366 (0.039)	0.270–0.488
GTL 10–13 M1	10–12	10.6	698 (26)	620–796	0.890 (0.080)	0.681–1.198
GTL 10–13 M2	10–13	10.8	729 (40)	570–810	0.964 (0.095)	0.630–1.261
GTL 10–13 F1	10–13	11.1	613 (22)	524–660	0.776 (0.071)	0.592–0.964
GTL 10–13 F2	10–13	11.4	620 (24)	570–725	0.757 (0.073)	0.589–1.063
GTL 15–19 A	15–19	16.8	699 (31)	620–780	1.024 (0.037)	0.899–1.124
GTL 15–19 B	15–19	16.4	750 (36)	643–842	1.345 (0.095)	1.139–1.628
GTL 20–27	20–27	22.5	731 (28)	680–824	1.287 (0.086)	1.073–1.521
GTL 22–28	22–28	25.2	763 (43)	700–900	1.710 (0.096)	1.541–2.002

Traditional age estimates, mean traditional age, fork length (FL), and otolith weights are given. The sex composition was signified by an 'M' or 'F' for samples GTL 5–7 and 10–13. Sexes were mixed or unavailable for the older age groups. Two 15–19 year groups were separated by otolith weight into a low (A) and high (B) weight classification

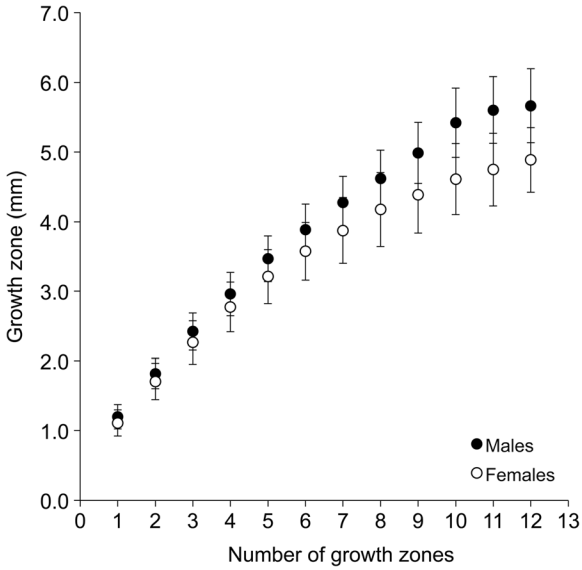

Fig. 4 Number of growth zones with the associated growth zone measurements (distance from the core to the end of the growth zone, specifically the end of the opaque zone) for males and females reported as the mean±standard deviation. Note the gradual departure in the distance of the growth zone between sexes with increasing age, exemplifying the differences observed in otolith shape

Lead-radium dating age groups

Twelve age groups were formed for the lead-radium dating analysis of golden tilefish otoliths (Table 1). Estimated age for the series of groups ranged from 5–7 years to 22–28 years, with sexes separated for the first two age groups. Within the separate-sex age groups, each was randomly split into sample replicates, resulting in two male and two female groups for both 5–7 year and 10–13 year age groups. Randomization led to age ranges that differed slightly (i.e., GTL 5–7 M1=6–7 years and GTL 10–13 M1=10–12 years); however, the average estimated age was relatively consistent at 6.2 to 6.4 years for the 5–7 yr groups, and 10.6 to 11.4 years for the 10–13 yr age groups. The older age groups could not be separated by sex, because reproductive tissue was not collected for many of the samples, and the number of otoliths available was low. In addition, it was observed that otolith weight, at a given estimated age, had a considerable range; hence, two 15–19 year groups were designated by otolith weight (low weight (A) and high weight (B)). A similar situation resulted for the oldest age groups and randomization led to slightly different age ranges; the low otolith weight age group ranged from 20 to 27 years and the high otolith weight group ranged from 22 to 28 years.

Fish length was lowest, on average, for the 5–7 yr female age groups and increased to more than 750 mm FL, on average, for the oldest age groups (Table 1). In general, the length of fish increased with estimated age, but some age groups included some relatively large individuals (e.g., GTL 5–7 M1, maximum length= 860 mm FL). Whole otolith weight was also lowest for the 5–7 yr female age groups at below 0.4 g, on average. Otoliths for adults were massive and exceeded 1.7 g, on average, for the 22–28 yr age group. For the younger randomized age groups, average otolith weight was lower for females relative to males in all cases. Hence, relative to estimated age, females were typically smaller, with lighter otoliths for the first two age groups (5–7 yr and 10–13 yr). For the two older age groups, the heaviest 15–19 yr group (GTL 15–19 B) was similar on average for both fish size and otolith weight to the 20–27 yr age group. The oldest age group (GTL 22–28) exceeded almost all groups in terms of otolith weight, both on average and in range; only GTL 15–19 B included otoliths that overlapped in otolith weight.

Lead-radium dating

Radiometric age determinations were made for all 12 age-group samples (Table 2). The number of otoliths that made up each age group ranged from 9 to 21, and total sample weights ranged from ~0.6 g to >1.5 g. Mean core weight was slightly greater than the target weight of 0.05 g and ranged from approximately 0.063 g to 0.081 g across the age groups. This was anticipated to an extent because the cleaning process usually removes ~5 % of the external material, but only 1–3 % was removed in this case. To make a better approximation on the representation of core age in radiometric modeling, 3 years was used for the core age, because the juvenile otolith used as a reference, had growth past the end of the second completed growth zone. Lead-210 activity increased as expected from the youngest to the oldest age groups by a factor of ~3 (0.00419± 13.8 % dpm·g^{-1} for GTL 5–7 F1 to 0.01359± 6.7 % dpm·g^{-1} for GTL 22–28) (Table 2). Radium-226 activity was lower than expected for the region and ranged from near 0.01413±22.6 % dpm·g^{-1} to 0.02573±16.1 % dpm·g^{-1}. Radium-226 recovery was low for a few samples and the runs were deemed unreliable (error greater than 30 % and close to background

Table 2 Coring and radiometric results for golden tilefish age groups from the east coast of Florida that were processed in this study

Age group & sample #	n	Sample weight (g)[a]	Mean core weight (g)[b]	^{210}Pb (dpm·g^{-1}) ±% error[c]	^{226}Ra (dpm·g^{-1}) ±% error[c]	^{210}Pb:^{226}Ra (2 SE)
GTL 5–7 M1	20	1.52521	0.07626	0.00491±7.8 %	0.01989±15.7 %[d]	0.2469 (0.0432)
GTL 5–7 M2	21	1.57928	0.07520	0.00589±6.1 %	0.01989±15.7 %[d]	0.2961 (0.0497)
GTL 5–7 F1	9	0.57104	0.06345	0.00419±13.8 %	0.02478±18.2 %[e]	0.1692 (0.0319)
GTL 5–7 F2	10	0.70606	0.07061	0.00564±9.9 %	0.02478±18.2 %[e]	0.2276 (0.0369)
GTL 10–13 M1	15	1.02671	0.06845	0.00783±6.6 %	0.01413±22.6 %[e]	0.5538 (0.0960)
GTL 10–13 M2	14	1.03334	0.07381	0.00737±6.8 %	0.01413±22.6 %[e]	0.5217 (0.0908)
GTL 10–13 F1	11	0.75149	0.06832	0.00593±8.9 %	0.02083±13.1 %[f]	0.2846 (0.0451)
GTL 10–13 F2	11	0.89425	0.08130	0.00766±7.0 %	0.01989±15.7 %[d]	0.3852 (0.0660)
GTL 15–19 A	12	0.79502	0.06625	0.00866±7.1 %	0.01758±23.2 %[f]	0.4926 (0.0440)
GTL 15–19 B	10	0.67835	0.06167	0.00862±8.2 %	0.01917±14.1 %[f]	0.4498 (0.0478)
GTL 20-27	10	0.67733	0.06773	0.00886±7.8 %	0.01788±20.1 %[f]	0.4955 (0.1067)
GTL 22-28	10	0.68193	0.06819	0.01359±6.7 %	0.02573±16.1 %[f]	0.5283 (0.0921)

The total number of otoliths (n), age group sample weight and the mean core weight are listed with the measured ^{210}Pb and ^{226}Ra activities for the samples (±2 SE). Calculated activity ratios and their corresponding margin of error were used to calculate sample age and uncertainty (Table 3)

[a] Cleaned and dried sample weight prior to processing

[b] Extracted otolith cores after cleaning

[c] Calculation based on propagation of 2 SE using the delta method (Knoll 1989) and the ICP-MS analysis routine (±2 SE)

[d] Poor radium recovery from original sample led to use of a mean radium activity from all sample specific measurements below 25 % error

[e] Mean radium-226 for within sample group replicates

[f] Sample specific radium-226

counts on the ICP-MS). The most massive samples may have overloaded the Sr column with barium, causing radium recovery to suffer (estimated less than 10 % recovery). To recover the opportunity to age the samples, an average of all measured values with less than 25 % error (13–23 %) was used in place of the unreliable values (n=3; 0.01989±15.7 % dpm·g^{-1}); this replacement occurred for GTL 5–7 M1, M2, and GTL 10–13 F2. For the other randomly split age groups, an average of the measured values for the pair was used as the radium-226 activity for the groups. For the older age groups that were not randomly split, sample specific radium-226 activities were used.

Radiometric versus traditional age estimation

Age comparisons revealed agreement and disagreement between the methods (Table 3). To directly compare traditional age with radiometric age, a correction for the time since capture was applied (1.2 to 1.5 yr reduction to radiometric age). Agreement can be gauged by plotting the total sample age with respect to the measured lead-radium ratio and the ingrowth curve. In general, agreement was good for some sample groups and markedly different from what was expected for other groups (Fig. 5). Sample measurements to the left of the ingrowth curve were underestimated for age using growth zone counting, which was most apparent with all 4 male groups, especially GTL 10–13 M1 and M2.

Thin-sectioned sagittal otoliths were aged using the same criteria for all sections; even so, some otolith sections were underaged. Radiometric and traditional age estimates were largely in agreement for two of the four female age groups and for the oldest mixed-sex age groups, but underestimated by at least 5 years for six of the age groups (male, female, and unknown) and underestimated by at least 14 years for the two 10–13 yr male age groups. Males age 10–15 were the most difficult to interpret, given the presence of multiple checks per growth zone (Fig. 2a, b).

The von Bertalanffy growth model predicted similar growth for the observed juvenile, female and unknown

Table 3 Comparison of mean traditional age estimates for each sample group and the resultant radiometric age for golden tilefish processed in this study

Age group & sample number	Time since capture (yr)	Traditional age Age (yr) (mean)	Radiometric age	
			Age (yr) (mean)	Corrected age (yr) (range)
GTL 5–7 M1	1.3	6.4	10.6	9.3 (7.6–11.2)
GTL 5–7 M2	1.3	6.3	12.8	11.5 (9.3–13.8)
GTL 5–7 F1	1.4	6.4	7.5	6.1 (4.9–7.4)
GTL 5–7 F2	1.2	6.2	9.8	8.6 (7.1–10.1)
GTL 10–13 M1	1.4	10.6	27.4	26.0 (19.8–33.8)
GTL 10–13 M2	1.4	10.8	25.2	23.8 (18.2–30.5)
GTL 10–13 F1	1.4	11.1	12.3	10.9 (8.9–13.0)
GTL 10–13 F2	1.4	11.4	17.1	15.7 (12.4–19.4)
GTL 15–19 A	1.5	16.8	23.3	21.8 (17.9–23.3)
GTL 15–19 B	1.5	16.4	20.7	19.2 (17.6–23.4)
GTL 20–27	1.5	22.5	23.5	22.0 (15.9–29.7)
GTL 22–28	1.4	25.2	25.6	24.2 (18.5–31.2)

Radiometric age was calculated from the measured ^{210}Pb:^{226}Ra activity ratios and the age range was based on error propagation of the analytical uncertainty (±2 SE). Radiometric age, corrected for time since capture, was calculated for direct comparison with the mean traditional age estimates for each sample group

radiometric age groups (Fig. 6). The resulting von Bertalanffy growth parameters were an asymptotic length of 779 (±28, standard error) mm FL, a growth coefficient of 0.19 (±0.45) year^{-1}, and a size at time zero of 0.15 (±0.01) mm FL. The predicted asymptotic length was similar to the average largest tilefish within the radiometric age groups (GTL 22–28, 763 mm FL). The radiometric ages for the male age groups were inconsistent with the predicted growth curve, but the respective range (SE) of the radiometric ages encompassed fish of similar observed length and age (by traditional age estimation).

Discussion

This study had two major objectives, 1) establish a traditional age estimation procedure using thin-sectioned, sagittal otoliths, and 2) test the validity of the annual growth zone interpretations of the traditional age estimation procedure using lead-radium dating. To properly address the first objective, acceptable and repeatable ageing estimation criteria were established. These traditional ageing methodologies were based on previous published methods for ageing golden tilefish sagittal otoliths (Turner et al. 1983; Palmer et al. 2004), along

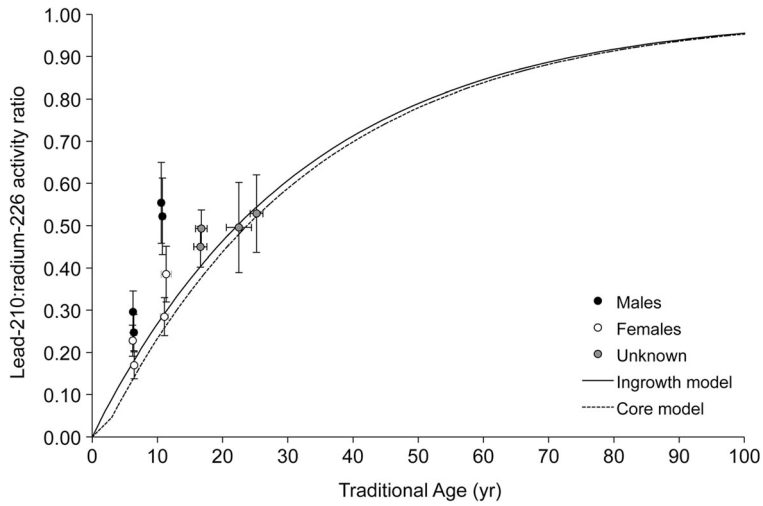

Fig. 5 Measured ^{210}Pb:^{226}Ra ratios from golden tilefish age groups plotted with the direct ^{210}Pb:^{226}Ra ingrowth curve (solid line) and a core model that compensates for a 3-year-ingrowth period (dashed line). Horizontal error bars represent ± 2 standard errors (SE) of the mean traditional age estimate and the vertical error bars represent the analytical uncertainty of the ^{210}Pb:^{226}Ra ratio (± 2 SE)

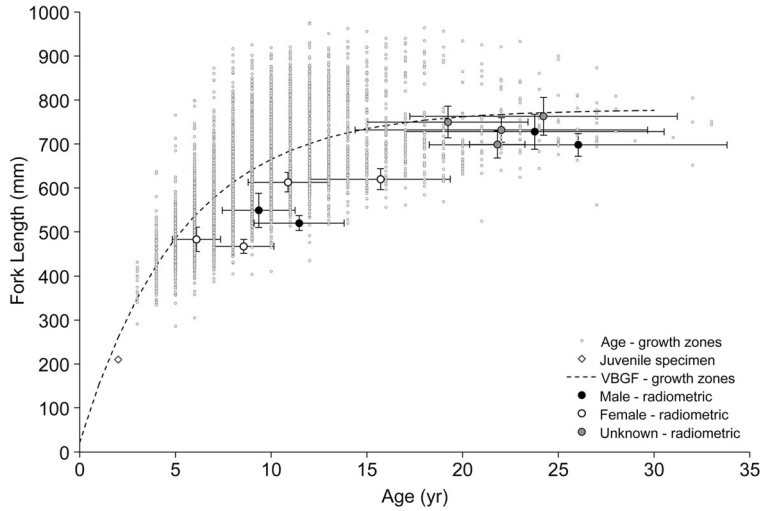

Fig. 6 von Bertalanffy growth curve determined by traditional age (growth zone counts) relative to fork length for golden tilefish from the east coast of Florida, plotted with radiometric ages (yr) at the mean fork length for each age group. Vertical bars represent ±standard errors (2 SE) for the mean fork length for age groups. Horizontal bars represent ±2 SE for the radiometric age estimates. Juvenile sample is identified separately, because it is unique

with the integration of methods used for interpreting yelloweye rockfish (*Sebastes ruberrimus;* Andrews et al. 2002). The ageing criteria described in this study were also supported by multiple expert readers from three ageing facilities (National Marine Fisheries Service, Beaufort, NC and Woods Hole, MA; South Carolina Department of Natural Resources; SEDAR 2011c).

The use of lead-radium dating to validate annual growth zone deposition relies on the precision of the traditional age estimation procedures and the incorporate of radium-226 into the otolith matrix from the environment. The maximum traditional age estimates for golden tilefish from off eastern Florida were supported by lead-radium dating, given the agreement of lead-radium dating and traditional age estimations for the oldest age group (lead-radium 26±6 yrs, traditional average age 25.2±3 yrs). These estimates of longevity (incorporating the range of ages) were very similar to those published for golden tilefish from other ageing studies (35 yr, Turner et al. 1983; 33 yr, Harris and Grossman 1985; 34 yr, Harris et al. 2001; 40 yr, Palmer et al. 2004). Not only has longevity been supported using the natural decay of radium-226 to lead-210, but a more consistent method to interpret growth zones in thin sectioned, sagittal otoliths has been described. Even though radiometric and traditional age estimation methods were in agreement in the oldest age groups and two female groups, these methods did not agree in the male age groups, with ages differing by 5–15 years. The differences in traditional age versus lead-radium dating in male tilefish may be due to: 1) the uptake of ^{226}Ra differed from the mean values used, 2) misinterpretation of growth zones, or 3) the pattern of growth zone deposition and subsequent growth rates by gender.

The application of lead-radium dating relies on several assumptions: 1) the otolith is a closed system with no loss or gain of ^{226}Ra, 2) the uptake of exogenous ^{226}Ra is negligible, and 3) the uptake of ^{226}Ra is in constant proportion to the otolith mass growth rate (Kimura and Kastelle 1995). This study addressed each of these assumptions by using an improved technique (Andrews et al. 1999b) that used otolith cores (the first years of growth) so that any difference in ^{226}Ra intake, given the changes in growth rate of the otoliths, was minimized.

Even though multiple precautions were taken, the radium-226 levels in the otolith cores were still lower than expected (typically 0.03 to 0.05 dpm·g^{-1}) and this was difficult to explain in the broader context of measured values from other lead-radium dating fish studies to date (Andrews 2009). The flux of radium-226 is typically greatest near continental margins and sea floors with low sedimentation rates (Broecker and Peng 1982), or from nearshore environments like the coastal waterways of Florida (Fanning et al. 1982). Even though seasonal fluctuations of radium isotopes exist along the southeastern U.S. continental shelf (Moore 2007), ^{226}Ra levels have been shown to increase by

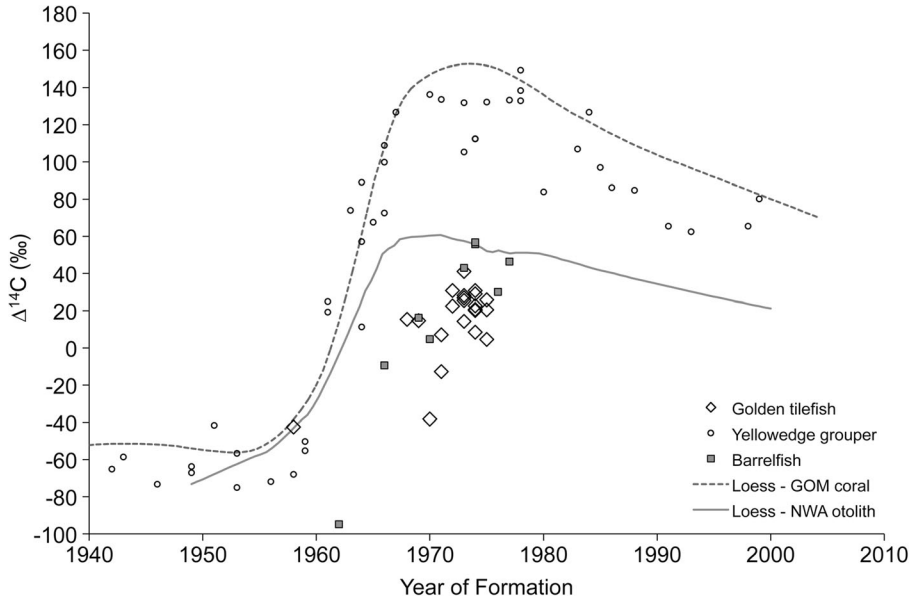

Fig. 7 Time series of bomb radiocarbon data plotted as $\Delta^{14}C$ to facilitate comparisons of golden tilefish measurements made previously (Harris 2005) with other $\Delta^{14}C$ from regional fishes and temporal references. $\Delta^{14}C$ measurements from yellowedge grouper (*Epinephelus flavolimbatus*, Cook et al. 2009) and barrelfish (*Hyperoglyphe perciformis*, Filer and Sedberry 2008) provided an offset context of $\Delta^{14}C$ values, relative to the regional time-specific $\Delta^{14}C$ references from the Northwestern Atlantic (Loess – NWA otolith, Campana et al. 2008) and the Gulf of Mexico (Loess – GOM coral, Andrews et al. 2013a), and a basis for exploring the possible reasons for the anomalous $\Delta^{14}C$ values measured for golden tilefish (Harris 2005). Loess curves are a smoothed function to provide a visual representation of the trends provided by the original data series

depth and by distance from shore (W. Moore pers. comm.[3]). Exact capture locations were not available, but most fish were reported as caught within the same general geographical location (approximate locations: latitude 27–29° N, longitude 79–80° W, depth range 183–270 m). There is very little information regarding the golden tilefish early life history (larval and juvenile stages) but of the few larval golden tilefish that have been identified, these were collected at depths >100 m (D. Drass pers. comm.[4]) with most adults residing at a minimum of 100 m (SEDAR 2011a). Therefore, it is assumed male and female juveniles, sub-adults, and adults settle in similar habitats (with limited movement, Grimes et al. 1983) and are exposed to similar levels of radium; therefore, the intake of radium should be the same regardless of sex.

A prior application of bomb radiocarbon dating to validate the age of golden tilefish was deemed inconclusive either due to misinterpretation of growth zones or lower environmental radiocarbon (^{14}C) levels (Harris 2005). To account for differences in growth zone interpretation, the validated age estimation criteria (as described above) were applied to the sectioned otoliths from the tilefish bomb ^{14}C study (Harris 2005) and the birth years were adjusted. Even though the adjusted birth years differed slightly (earliest birth year of 1958 was shifted to 1955 and the latest birth year of 1975 was shifted to 1973), the $\Delta^{14}C$ levels for the U.S. South Atlantic were considerably lower than the $\Delta^{14}C$ levels established for the Gulf of Mexico (GOM; Andrews et al. 2013a) and the deeper-dwelling yellowedge grouper (*Epinephelus flavolimbatus*, Cook et al. 2009), but similar to the Northwestern Atlantic otolith reference (NWA; Campana et al. 2008) late in the $\Delta^{14}C$ record (Fig. 7). Because golden tilefish spend a majority of their lives below depths of 200 m, it would be expected that $\Delta^{14}C$ levels in otolith material formed at these depths would be attenuated relative to the more timely GOM coral $\Delta^{14}C$ record. Yellowedge grouper and golden tilefish share similar adult habitat preferences (depths>200 m), with adult yellowedge grouper inhabiting golden tilefish

[3] W. Moore 2011 Pers. Comm. University of South Carolina, Department of Earth and Ocean Sciences, Columbia, SC 29208
[4] D. Drass 2010 Pers. Comm. NMFS, 3209 Frederic Street, Pascagoula, MS 39567–4112

burrows (Jones et al. 1989). Even though juvenile yellowedge grouper can recruit to shallower depths (25–125 m; Cook et al. 2009), reduced $\Delta^{14}C$ levels in otoliths of this species indicate it may typically recruit to greater depths with a prompt migration to even greater depths (Andrews et al. 2013a). In addition, golden tilefish $\Delta^{14}C$ levels were similar in timing, if traditional age estimates are correct, to those reported for barrelfish (*Hyperoglyphe perciformis*) collected from off South Carolina (Filer and Sedberry 2008; Fig. 7), which share similar adult habitats near depths greater than 200 m. Growth zone counting error for barrelfish could not explain the offset from a more timely $\Delta^{14}C$ rise and may be indicative of a deep-water signal, as seems to be the case for golden tilefish. Oceanographic circulation patterns, such as upwelling and strong stratification, can directly influence environmental ^{14}C levels (Haltuch et al. 2013; Helser et al. 2014) and may also provide some explanation for the observed $\Delta^{14}C$ pattern from tilefish otoliths (e.g., Andrews et al. 2013b); however, at present there is no reference chronology for $\Delta^{14}C$ from the deeper waters occupied by golden tilefish and any conclusions drawn from these data are speculative. Thus, the results of the bomb radiocarbon dating were confounded by the lack of a reference chronology for $\Delta^{14}C$ from the U.S. South Atlantic and potential ageing error due to the misinterpretation of growth zones.

It is also possible, that growth zones were misinterpreted for some golden tilefish and this was the cause for the differences in traditional age estimates versus lead-radium dating for some of the age sample groups. Growth zones in deep water species are known to be difficult to count accurately due to slow growth and finer growth zone structures [e.g., orange roughy (*Hoplostethus atlanticus*; Mace et al. 1990; Andrews 2009), sablefish (*Anoplopoma fimbria*; McFarlane and Beamish 1995) and Patagonian toothfish (*Dissostichus eleginoides*; Andrews et al. 2011)]. All golden tilefish growth zones were interpreted using the same criteria for all fish, as stated above, but it is obvious that these criteria may not be sufficient for all fish, specifically male tilefish age sample group 10–13 yrs. It is possible that certain growth zones represent more than 1 year of growth (as described for orange roughy, Mace et al. 1990) or growth zones need to be interpreted at a higher magnification and/or along another growth axis for male golden tilefish (e.g., Chilton and Beamish 1982; McFarlane and Beamish 1995).

Golden tilefish otoliths also have structural differences in otolith morphology that suggest variations in growth zone deposition and growth rates by gender. Male golden tilefish do grow faster and obtain much larger sizes than female golden tilefish (Lombardi-Carlson 2012). During the initial stages of this study, it was assumed golden tilefish exhibited a gonochoristic reproductive strategy (as reflected in current literature; Grimes et al. 1988; Harris et al. 2001) and gonads were only staged macroscopically when creating radiometric age groups. However, further examination of golden tilefish gonadal tissue revealed characteristics more similar to a protogynous hermaphrodite reproductive strategy (satisfying the criteria of Sadovy and Shapiro 1987) (Lombardi-Carlson 2012). Thus, the differences in growth rate, deposition of growth zones and morphology of sagittal otoliths between the genders is most likely due to some females transitioning into males. Although, lead-radium dating only used the core material composed of the first 3 years of otolith growth, which was deposited at similar distances from the core by both genders. There are proven differences in growth zone deposition, otolith morphology, and otolith structural composition for primary (some males deriving from a male immature phase) and secondary (males transitioning from females) males in other protogynous hermaphroditic species (Munday et al. 2004, 2009; Walker and McCormick 2009). Each of the male radiometric age groups included both primary and secondary males with at least 70 % of the male gonads in each age group having female gametes of varying degree of development; thus, an age group with various male types may have clouded the average traditional age and the lead-radium dating results. The social hierarchy of golden tilefish is mostly unknown (Grimes et al. 1988; Harris et al. 2001; Lombardi-Carlson 2012), but most protogynous hermaphrodites exhibit various behaviors ultimately affecting their daily and annual growth rates (Sadovy de Mitcheson and Liu 2008) and subsequent otolith accretion rates (Walker and McCormick 2009).

For some fishes, traditional age estimations are difficult even with successful validation studies [e.g., splitnose rockfish (*Sebastes diploproa*; Bennett et al. 1982) and Patogonian toothfish (*Dissostichus eleginoides*; Andrews et al. 2011)]. Determining sustainability in fish stocks relies on estimates of growth, age at maturity, longevity, natural mortality, and recruitment variability; all of which rely on accurate estimates of age and growth. In situations where age estimates are both imprecise and biased, an ageing error matrix can be incorporated into the modeling process to incorporate variation around the age estimates (Stewart and Piner 2007; Punt et al. 2008; Gertseva and Cope 2011; Candy et al. 2012). Therefore, it is

recommended that an ageing error matrix should be used in golden tilefish assessment models [as applied in Gulf of Mexico (SEDAR 2011a) and South Atlantic (SEDAR 2011b) assessments] to incorporate the uncertainty (given the lack of validation for all age groups) in traditional age estimates using lead-radium dating.

Acknowledgments We thank Heather Hawk at Moss Landing Marine Laboratories for assistance with sample processing and Craig Lundstrom at University of Illinois at Urbana-Champaign for ICP-MS processing of the purified radium samples. We appreciate Claudia Dennis (National Marine Fisheries Service, Miami, FL) for collection of biological samples at the docks and Laura Goetz Thorton (National Marine Fisheries Service, Panama City, FL) for sectioning the otoliths used in this study. We also thank Bryon White and Marcel Reichert at South Carolina Department of Natural Resources, Marine Resources Research Institute, Marine Resources Monitoring, Assessment and Predication Program in providing golden tilefish radiocarbon values and otolith sections. The primary author recognizes her doctoral committee (Micheal Allen, William E. Pine, III, Carl Walters, Debra Murie, Alan Bolten, and Clay Porch) at the University of Florida, School of Forest Resources and Conservation, Fisheries and Aquatic Sciences Program for their comments and suggestions on this research as it appears in her dissertation. Opinions expressed herein are of the authors and do not imply endorsement by National Marine Fisheries Service. Financial support was provided by the U.S. Department of Commerce, National Marine Fisheries Service, Marine Fisheries Initiative Program (07MFIH007).

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