Addressing Critical Life History Gaps for U.S. Caribbean Yellowtail Snapper: Bomb radiocarbon of age estimation method and a summary of the regional demographic patterns for size, age, and growth

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SEDAR84-DW-07

22 January 2024

Updated: 15 February 2024

Please cite this document as:

Shervette, Virginia, Jesus Rivera Hernandez, Sarah Zajovits. 2024. Addressing Critical Life History Gaps for U.S. Caribbean Yellowtail Snapper: Bomb radiocarbon of age estimation method and a summary of the regional demographic patterns for size, age, and growth. SEDAR84-WP-07. SEDAR, North Charleston, SC. 22 pp.

Addressing Critical Life History Gaps for U.S. Caribbean Yellowtail Snapper: Bomb radiocarbon validation of age estimation methods and literature review

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Working Document SEDAR 84

Much of the text included in this report is based on a manuscript in preparation for submission to Environmental Biology of Fishes and from the 2021 thesis document of S. Zajovits. To ensure proper citation of this work, authors' permission is required.

ACKNOWLEDGEMENTS

Thank you to Nancie Cummings, formerly of NOAA Caribbean Branch, for guidance and assistance during the past decade. Thank you to Wilson Santiago Soler and Kayley Kirkland who assisted extensively in collection and processing of samples. The overall investigation on yellowtail smapper life history would not have been possible without the collaboration and support of U.S. Caribbean fishers. The St. Thomas Fisherman's Association was instrumental in sampling efforts – Julian Magras, the Leedee Brothers, Ruth Gomez, Bobby Vicente, and Tony Blanchard. In Puerto Rico, Marcos Hanke, Carlos Velasquez, Gerardo Ramirez, Pedro Silva, Benigno Rodrıguez, Felix Diaz and many more fishers assisted with sample collections. We thank the following STX fishers: Gerson "Nicky" Martinez, G. "Nick Jr." Martinez, Bobby Thomas, Omar Hughes, and Tom Daley. We also thank the following students and scientists for their assistance in the field and for logistic support: David Jones, Delaney Drake, Graham Wagner, Sara Thomas, Karlen Correa Vélez, Emmanuel Irizarry, Noemi Peña Alvarado, Wilfredo Torres, Luis A. Rivera, Aida Rosario, Veronica Seda, Marcos Hanke, and Rick Nemeth. The Nature Conservancy of St. Croix graciously allowed us space for processing samples when working in St. Croix.

INTRODUCTION

The sustainable management of fisheries species requires a detailed understanding of their life history strategies (Chale-Matsau et al. 2001, King and McFarlane 2003). Snapper species (family Lutjanidae) inhabit tropical and subtropical regions of all oceans and are economically valuable to fisheries around the world. Yellowtail snapper *Ocyurus chrysurus* (Fig. 1) is a popular recreational and commercial snapper species throughout much of its geographical range. Yellowtail snapper occurs in the western Atlantic as far north as Massachusetts to southeastern Brazil; however, it is most abundant in subtropical and tropical waters of Florida and throughout the Caribbean (Manooch and Drennon 1987, Lindholm et al. 2005). In the U.S. Caribbean, yellowtail snapper is one of the top three commercially landed reef-associated fish species and is highly sought after due to its exceptional quality as a food fish and common occurrence (CFMC 2018).

Figure 1. Examples of yellowtail snapper from the U.S. Caribbean.

U.S. Caribbean yellowtail snapper was previously assessed through the SEDAR process in 2005 (SEDAR 8) and again as part of the 2016 U.S. Caribbean data-limited species assessment (SEDAR 46). The SEDAR 8 assessment concluded that yellowtail snapper data were "insufficient to provide a signal to underpin management advice" and "of the many research

suggestions made, highest priority was assigned to the carrying out of fishery-independent surveys, the collection of more catch data, including specifically recreational fishery, and the collection of age and length data from commercial and recreational catches and from fishery-independent surveys." For SEDAR 46, the stock assessments of six U.S. Caribbean data-limited species were "addressed" using data-limited techniques and the final stock assessment reports document was provided to the CFMC SSC which was then tasked "with recommending whether the assessments represented Best Available Science" and whether the results were "useful for providing management advice and developing fishing level recommendations for the Council." The PR yellowtail snapper stock was one of the six species addressed. No management recommendations resulted for any of the SEDAR 46 species; however, the assessment identified specific life history research needs for all of the species examined: (1) Representative sampling across size/age spectra; (2) Updated studies of life history that focus on sampling under-represented size classes, particularly large (old) fishes to provide more accurate estimates of asymptotic length; (3) Additional sampling for improving stock-specific maturity schedules.

Habitat Use and Feeding Ecology

Yellowtail snapper utilizes a range of habitats as individuals develop and mature (Manooch and Drennon 1987, Watson et al. 2002, Allman 2007). Juvenile yellowtail snapper aggregate in seagrass beds, such as turtle grass *Thallasia testudinum*, and mangrove wetlands (Kimmel 1985). This species undergoes a 2-phase recruitment process, whereby early juvenile fish subject to high post-settlement mortality are relatively sedentary in juvenile habitats for several weeks, before moving to more rugose habitat as older juveniles (Watson et al. 2002). Adults inhabit shelf waters mostly associate with hard substrates including coral reefs; they commonly form large pelagic aggregations and exhibit high site fidelity (Grimes 1977, Lindholm et al. 2005). Unlike many snapper species, adult yellowtail snapper are a more pelagic, (sometimes referred to as "semi-pelagic") often occurring above the substrate (McClellan and Cummings 1998, Lindholm et al. 2005). Yellowtail snapper occurs at depths up to 120 m (McClellan and Cummings 1998) with adults commonly found between 20 – 40 m (GMFMC, 2013; Thompson and Munro, 1974).

Saillant et al. (2012) investigated the population genetic structure of yellowtail snapper among the Florida Keys, Puerto Rico (east and west coasts), St. Thomas/St. John, and St. Croix. The study used nuclear-encoded genetic markers (microsatellites) and a mitochondrial (mt)DNA coding gene to specifically determine if genetically defined stocks of yellowtail snapper occurred among the study localities sampled. The study reported that "results of the analysis of spatial genetic variation provided evidence of significant although weak genetic differences" among the study localities and concluded "that the range of genetic divergence among the localities is fairly low and that results of various analyses were at best mixed." Saillant et al. (2012) also noted that a major issue with the study design was that fish were only collected from one sample event for each locality examined. From this, it is unclear whether genetically distinct stocks occur within the Greater Caribbean. However, a study from Brazil examined population genetic structure for yellowtail snapper from eight localities spanning 21° latitude along the Brazilian coast (da Silva et al. 2015). The study used three intragenic nuclear markers (ANT-1, GH-5, IGF-2) and two mitochondrial markers (Cytochrome b and the control region) to assess the genetic connectivity among yellowtail snapper samples collected from eight sites distributed along more than 3000 km of the coast of the western South Atlantic and concluded that the population represented one single genetic stock along the entire coast of Brazil. Based on the lack of population genetic

structure for yellowtail snapper spanning a distance of 3000+ km across 21° latitude from the Brazil study, it is likely that yellowtail snapper from the U.S. Caribbean (which spans less than 500 km in max distance and less than 2° latitude) also lacks population genetic structure among the three island management platforms.

Yellowtail snapper is a generalist carnivore, consuming a wide array of smaller fishes and invertebrates from pelagic and benthic habitat (Piedra 1969, Barbieri and Colvocoresses 2003). This species feeds during the day and at night; U.S. Caribbean fishers often target feeding aggregations of large yellowtail snapper at night (G Martinez, St. Croix fisher, and J Magras, St. Thomas fisher, personal communications). Seasonal variability in feeding has been observed in yellowtail snapper; a study conducted in Cuba noted that the frequency of individuals with full stomachs increased outside of spawning season (Carrillo de Albornoz and Ramiro 1988). Similar observations were reported of yellowtail snapper off south Florida by Collins and Finucane (1989). Interestingly, according to STFA (2013), commercial fishing of yellowtail snapper in the U.S. Caribbean often occurs at night, probably because fishers understand the nocturnal feeding behavior of this species.

Reproductive Biology and Population Demographic Patterns

Yellowtail snapper may form spawning aggregations of 25 to 30 individuals, although these aggregations are not well defined spatially or temporally (Claro et al. 2009, Trejo-Martínez et al. 2011). Studies from Florida documented yellowtail snapper spawning occurred mainly in the spring and summer, with a peak from May – July; year-round spawning has been reported in the southern Florida Keys (Collins and Finucane 1989, Muller et al. 2003). Yellowtail snapper populations occurring at lower latitudes such as in the Caribbean and southern Gulf of Mexico (GOM) appear to have more protracted spawning seasons. A study from Jamaican waters observed that yellowtail snapper spawn year-round with a peak in March – April, and a secondary minor peak in September (Munro et al. 1973). A study on yellowtail snapper reproduction in waters of Campeche Bank, off the Yucatan Peninsula, observed that female yellowtail snapper in spawning condition occurred in all months of the year (Trejo-Martínez et al. 2011). Energetic investment of year-round spawning exhibited by low latitude populations may be a contributor to observed differences in regional growth rates of yellowtail snapper.

A few studies have reported on yellowtail snapper age and growth, but this information is limited spatially and temporally. Johnson (1983) collected 807 fish from southeastern Florida waters from 1979-1980 and reported a maximum estimated age of 14 years. Garcia et al. (2003) sampled 1528 fish from southeastern Florida, during the years of 1994-1999 and documented a maximum age of 13 y. Allman et al. (2005) collected 6679 yellowtail snapper samples from waters of the east coast of Florida from 1980-2002 and reported a maximum age of 17 y. The mean maximum length (von Bertalanffy growth model parameter L_∞) of fish from these three Florida studies ranged from 410-484 mm FL, the Brody growth coefficient (K) ranged from 0.17-0.30, and the age at which size would equal zero (t_0) ranged from -2.03 to -0.36 (Table 1). A study from U.S. Caribbean waters collected 468 yellowtail snapper in 1983-1984 and reported a maximum age of 17, L_∞= 503 mm FL, K = 0.14, and t_0 = -0.96 (Manooch and Drennon 1987). The U.S. Caribbean study noted that yellowtail snapper increments were relatively difficult to discern (Manooch and Drennon 1987). Prior to the current study, more recent information (post-1984) did not exist on age and growth for yellowtail snapper from waters of the U.S. Caribbean.

Table 1. Summary of yellowtail snapper studies focused on estimating growth parameters. *indicates that a fixed t_0 value of -0.96 was used so that other growth parameter results from the current study could be compared to results from Manooch and Drennon (1987). **indicates that a fixed t_0 value of -1.93 was used so that other growth parameter results from the current study could be compared to results from Florida (SEDAR 2020).

Study Area Study Citation	Time period (n) sample source	Size range (mean) mm	Age range (mean) y	$L_\infty/K/t_0$ Opaque zone formation	Comments
U.S. Caribbean Current study	2013-2023 (1554) FI + FD	FL: 28-572 (291)	0-26 (5)	FL: 508/0.12/-2.73 424/0.23/-0.96* 467/0.16/-1.93** Mar-Jun	Age validation via radiocarbon
U.S. Caribbean Manooch and Drennon 1987	1983-1984 (468) FD	FL: 140-590	1-17	FL: 503/0.14/-0.96 Mar-May	Used back-calculated size-at-age
Cuba Claro 1983	1972-1974 (3593) FD	FL: 160-460	0-6	FL: 681/0.16/-0.85 Mar-Jun	No validation of age estimates; otoliths read whole
FL east coast Allman et al. 2005	1980-2002 (6679) FI + FD	FL: 115-605 (312)	1-17 (4)	FL: 410/0.27/-2.03 Feb-May	
Southeast FL Garcia et al. 2003	1994-1999 (1528) FD	FL: 220-561	1-13	FL: 484/0.17/-1.87 Mar-May	
Southeast FL Johnson 1983	1979-1980 (807) FD	FL: 134-567	1-14	FL: 451/0.28/-0.36	
Florida SEDAR 2020	1980-2017 (42,985) FD (<1% FI)	FL: 100-600*	0-28	FL: 426/0.20/-1.93 Mar-Jun	Growth model accounted for truncated size-at-age

Age, a parameter essential to understanding population dynamics, is estimated via enumeration of growth increments (alternating translucent and opaque zones) from thin sagittal otolith sections of bony fishes like yellowtail snapper. However, the quantification of increments as means of ageing is simply an estimate. Therefore, validation of the otolith increments as annuli is essential for studying age and growth; especially for species that reside in tropical regions that lack distinct cold and warm seasons (Manooch and Drennon 1987). Analysis of bomb radiocarbon temporal trends is a useful tool that has been utilized in the validation of fish ageing estimation for Caribbean species (Shervette et al. 2020, Shervette et al. 2021, Shervette and Rivera Hernández 2022, Overly and Shervette 2023). Radiocarbon (^{14}C) was introduced into the atmosphere through nuclear bomb testing in the 1950s through the 1960s (Broecker et al. 1995). As a result, ^{14}C dissolved into oceanic CO_2 and was incorporated into the aragonite (biogenic $CaCO_3$) skeletons of hermatypic corals (Knutson et al. 1972, Druffel and Linick 1978, Nozaki et al. 1978), carbonate-based shells of mollusks (Turekian et al. 1982, Weidman and Jones 1993), and aragonite and carbon-rich structures of fishes such as otoliths (Kalish 1993, Andrews et al. 2013, Shervette et al. 2021) and eye lenses (Shervette et al. 2020, Shervette and Rivera Hernández 2022, Overly and Shervette 2023). The incorporation of bomb-produced radiocarbon is reported as $\Delta^{14}C$ in reference to a pre-nuclear proliferation standard (Stuiver and Polach 1977). The temporal marine record of radiocarbon increase and decline has been documented for multiple oceanic regions through the analysis of $\Delta^{14}C$ in annual accretions of

biogenic $CaCO_3$ in hermatypic corals (Knutson et al. 1972, Druffel and Linick 1978, Nozaki et al. 1978) and aragonite structures of fishes (Kastelle et al. 2008, Andrews et al. 2013, Shervette et al. 2021). The time-specific $\Delta^{14}C$ aragonite records provide regional reference chronologies that can be used to evaluate fish age estimates through comparison of $\Delta^{14}C$ measured in fish eye lens core material that formed during the first year of life (Shervette et al. 2020, Shervette and Rivera Hernández 2022, Overly and Shervette 2023). Direct validation of the age estimation method used for yellowtail snapper, enumeration of growth increments from thin sections of sagittal otoliths, is needed to ensure that age estimates are accurate.

Documenting the population size/age structure and growth characteristics of data-deficient/data-poor Caribbean fisheries species is critical for assessing the current stock status of a species. The overall goal of this study was to provide essential life history information in support of more effective fishery management for an important reef fish fisheries species in the U.S. Caribbean, yellowtail snapper. Utilization of region-specific and current information on life history information is key for assessing the local stock of yellowtail snapper. Age and growth estimates are fundamental to reliably estimating biological reference points and are required to facilitate the transition to age-based stock assessments. The specific objectives of this study were: 1) to validate the age estimation method for yellowtail snapper using bomb radiocarbon; and 2) to provide a detailed review of yellowtail snapper life history and management information pertinent to the U.S. Caribbean.

METHODS

Study Area and Management

The U.S. Caribbean (Fig. 2) is located in the northeast Caribbean Sea and consists of two territorial jurisdictions: Puerto Rico (PR) and the U.S. Virgin Islands (USVI). The Caribbean Fisheries Management Council (CFMC) oversees the management of marine fisheries resources within this region. Waters of PR contain the main island of PR and several smaller islands including Mona and Desecheo, off the west coast, and Vieques and Culebra in the east. The USVI consists of the major islands of St. Thomas (STT), St. John (STJ), and St. Croix (STX), and roughly 50 surrounding minor cays. Coral reefs cover approximately 3,370 km^2 within 3-nm of PR and 298 km^2 in the USVI (Catanzaro et al. 2002, Causey et al. 2002).

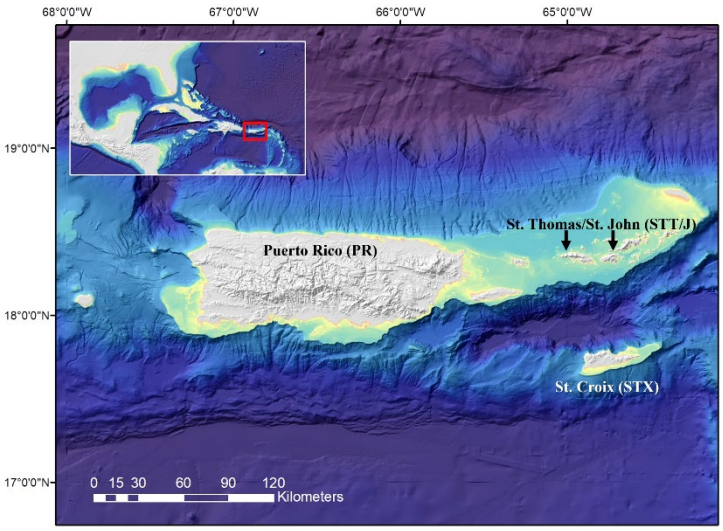

Figure 2. North Caribbean sampling region. Map indicates the general north Caribbean region including the major islands of the U.S. Caribbean.

Commercial fishers in the U.S. Caribbean mainly target yellowtail snapper with hook and line gear, although a small proportion of landings come from trap fishing. CFMC and territorial resource managers utilize a few regulatory tools that limit the commercial harvest of yellowtail snapper including individual ACLs for each of the three management platforms (PR, STT/J, and

STX), a minimum harvest length of 305 mm TL (260 mm FL), and area closures that prohibit fishing with specific gears, area closures that do not allow fishing at all within the boundaries year-round, and area closures that do not allow fishing within a closed season for the area[1].

Fish Collection and Processing

Fish samples for this study were obtained through two main sources: 1) fisheries-independent (FI) collections via hook-and-line; and 2) fisheries-dependent (FD) collections that consisted of purchasing fish directly from local fishers. For each sample, general area of capture, date of capture, and gear typed used were recorded. All fish samples were measured for standard length (SL), fork length (FL), and total length (TL) to the nearest mm and weighed to the nearest g. Sagittal otoliths were extracted, rinsed of adhering tissue, dried, and placed in labeled coin envelopes for later processing. Starting in 2018, fish eyes were dissected from carcasses once otoliths were removed and placed in foil, labeled as right or left, and frozen in labeled plastic bags. Gonads were removed, weighed (to the nearest 0.01 g) and preserved for further processing. In the lab, gonad samples were processed using standard histological procedures for gonochoristic species (Kelly-Stormer et al. 2017, Rivera Hernández et al. 2019) to obtain the sex of each sample.

Age, Bomb Radiocarbon Age Validation, and Growth

Yellowtail snapper otoliths were processed for age estimation utilizing the methods previously described for snapper species in Shervette et al. (2021). Briefly, an otolith was embedded in epoxy resin, sectioned transversely through the core (section thickness of ~ 0.4 mm), and then sections were affixed to microscope slides using a clear mounting medium. Age estimates for all otoliths were determined based on the number of increments (alternating translucent and opaque zones) counted within an otolith section viewed using a stereomicroscope with transmitted light at a magnification range of 15-40x (see Appendix for annotated examples of U.S. Caribbean yellowtail snapper otolith sections).

The accuracy of the yellowtail snapper age estimation method used in the current study was evaluated using the bomb radiocarbon validation analysis for north Caribbean species (Shervette et al. 2020, Shervette et al. 2021, Shervette and Rivera Hernández 2022, Overly and Shervette 2023). Samples for age estimation validation were selected from yellowtail snapper samples collected during 2018-2020 efforts and the selection process incorporated information on fish size and estimated age. A subset of 16 yellowtail snapper samples was used to obtain birth year bomb radiocarbon signatures by measuring the $\Delta^{14}C$ an individual fish experienced during its first year of life as recorded in the eye lens cores (Shervette and Rivera Hernández 2022, Overly and Shervette 2023). Forceps and glassware used in the process of obtaining lens cores for $\Delta^{14}C$ analysis were pretreated to remove any potential carbon contamination by baking in a muffle furnace for a minimum of 6 hours at a temperature of 500^{o}C. Frozen eye samples were thawed at room temperature and the whole lens was extracted from each eye then lenses were placed in pretreated glass petri dishes and allowed to fully dry. As a lens dries, its concentric outer layers begin to peel back and reveal inner layers. Once a lens was fully dry, the concentric layers were peeled off until the lens core was reached. Each core was weighed (to the nearest 0.1 mg) and placed in a pretreated glass vial for shipment.

[1] https://www.fisheries.noaa.gov/southeast/rules-and-regulations/seasonal-and-area-fishing-closures-us-caribbean accessed 10 June 2021

Lens cores were analyzed for $\Delta^{14}C$ with the accelerator mass spectrometry (AMS) at the NOSAMS facility at Woods Hole Oceanographic Institute in Falmouth, Massachusetts. The isotope ^{13}C was reported as the delta value $\delta^{13}C$ (‰), which is calculated as the ratio of $^{13}C/^{12}C$ relative to a standard (Pee Dee Belemnite). Radiocarbon (^{14}C) was reported as a delta value ($\Delta^{14}C$) that represents the activity of a sample relative to a standard (Stuiver and Polach 1977) 1977) and corrected for age and $\delta^{13}C$.

The $\Delta^{14}C$ value from the eye lens core and corresponding estimated birth year for each of the 16 yellowtail snapper age validation samples were overlaid on the north Caribbean radiocarbon reference time series (Shervette et al. 2021). The estimated birth year of a sample equals the year of collection minus the increment count obtained from the otolith section. The accuracy of the age estimation method was evaluated through examining potential ageing bias by purposely shifting the estimated ages by +/- 1 to 3 years and superimposing $\Delta^{14}C$ lens core values on the north Caribbean $\Delta^{14}C$ reference time series (Kastelle et al. 2008, Shervette et al. 2021, Shervette and Rivera Hernández 2022, Overly and Shervette 2023). The original age estimate represented an age bias of 0 (null model), age biases of +1, +2, +3 shifted age estimates older, and age biases of -1, -2, -3 shifted age estimates younger. Next, we computed the sum of squared residuals (SSR) from predicted versus observed birth years for the validation samples and repeated this for each of the purposely biased age estimate models. The model with the lowest SSR is considered the most parsimonious prediction of birth years; if the null model for a species produces the lowest SSR, then the age estimation method is considered accurate (Kastelle et al. 2008).

RESULTS

Bomb Radiocarbon Age Validation

Age estimates ranged from 0-17 y for Caribbean yellowtail samples (n = 16) that were analyzed for $\Delta^{14}C$ (Table 2). Estimated birth year (year of collection minus age) corresponded well with the $\Delta^{14}C$ north Caribbean reference series (Fig 3). Results from the ageing bias analysis of yellowtail snapper eye lens core $\Delta^{14}C$ values relative to the regression fit of the north Caribbean $\Delta^{14}C$ reference time series indicated that yellowtail snapper birth year estimates derived from sagittal otolith thin section opaque zone counts are accurate, given that the original age estimates had the lowest SSR (193), while the purposefully biased age estimates resulted in SSR values ranging from 260 for +1 y to 1008 for -3 y (Table 3).

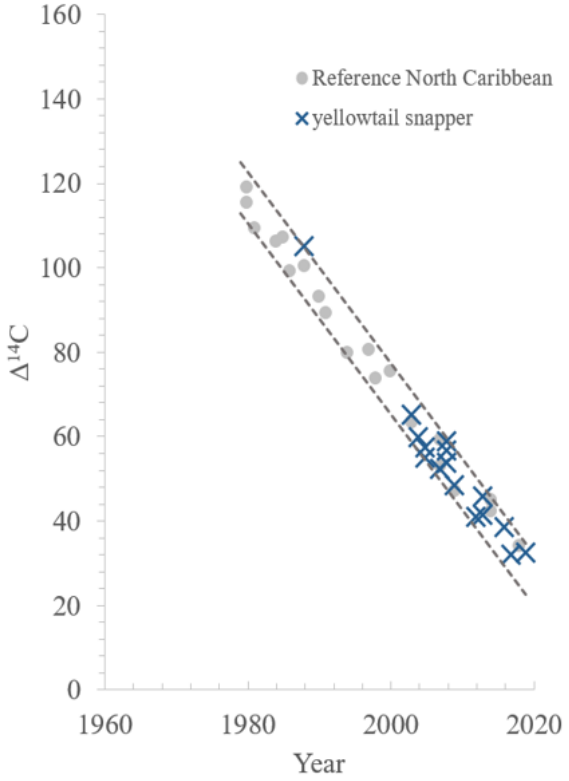

Figure 2. Results of $\Delta^{14}C$ analysis via AMS. $\Delta^{14}C$ values (‰) versus year of formation for U.S. Caribbean yellowtail snapper age validation samples (n = 16). Dashed lines represent the upper and lower Prediction Intervals from the Reference North Caribbean time series.

Table 2. U.S. Caribbean samples analyzed for $\Delta^{14}C$ with AMS.

Sample number	Sample date	FL mm	Age	Year of Formation	$\Delta^{14}C$	+/- SE
YT-STT-1	27 Aug 2019	84	1	2018	32.47	2.3
YT-STT-2	8 May 2019	151	3	2016	38.49	3.2
YT-STT-3	9 May 2019	305	6	2019	41.57	2.2
YT-STX-1	26 Oct 2018	279	7	2011	40.95	2.0
YT-STX-2	27 Oct 2018	285	11	2007	59	2.1
YT-STX-3	13 Apr 2019	347	16	2003	60	2.2
YT-STX-4	15 Apr 2019	303	11	2008	48.53	2.2
YT-PR-1	9 Jun 1988	44	0	1988	105.24	3.4
YT-PR-2	19 Jul 2019	406	13	2006	52.31	2.6
YT-PR-3	10 Oct 19	345	15	2004	55.05	2.8
YT-PR-4	10 Oct 19	316	12	2007	53.77	2.5
YT-PR-5	14 Oct 19	282	15	2004	57.54	2.6
YT-PR-6	4 Oct 19	261	7	2012	45.88	2.3
YT-PR-7	4 Oct 19	195	3	2016	32.06	2.4
YT-PR-8	14 Mar 19	337	17	2002	65.29	2.1
YT-PR-9	14 May 19	328	12	2007	56.62	2.2

Table 3. Results from ageing bias analysis

Age Model	Bias applied years	Yellowtail Snapper SSR
Null	0	193
-1	-1	295
-2	-2	567
-3	-3	1008
+3	+3	901
+2	+2	496
+1	+1	260

CONCLUSIONS

Results from the current study showed that sagittal otolith section opaque zone counts provide accurate age estimates for Caribbean yellowtail snapper. Therefore, while the oldest age directly validated using the $\Delta^{14}C$ chronometer was 17 y, the validated age estimation method used in this study documented a maximum age of 26 y for yellowtail snapper from U.S. Caribbean waters. Application of $\Delta^{14}C$ reference time series to validate age estimation for shallow water snapper species is well established and has been used to validate age estimates for gray snapper *Lutjanus griseus* (Fischer et al. 2005, Andrews et al. 2020), red snapper *L. campechanus* (Baker and Wilson 2001, Andrews et al. 2019), and mutton snapper *L. analis* (Shervette et al. 2021).

The current study is the first to validate directly opaque zone counts on sectioned sagittal otoliths as representing the true age of yellowtail snapper samples. Fish ageing accuracy is assessed through validation and verification (Campana 2001). An extensive review of accuracy in fish age determination and age validation emphasized the distinction between methods that validate ageing accuracy and those that only verify the periodicity of opaque zone formation for a narrow range of age estimates of a species (Campana 2001). The concept of age validation has been inaccurately used in past yellowtail snapper ageing studies that only verified the periodicity of growth increment formation (Johnson 1983, Manooch and Drennon 1987, Garcia et al. 2003). Moreover, Campana (2001) noted that more than 50% of studies utilizing marginal increment analysis to verify annual periodicity of growth increments did not examine periodicity for the most problematic groups, the oldest and/or youngest age groups. True ageing validation must use a method that determines the true age of a set of fish samples, and application of the $\Delta^{14}C$ reference time series is considered one of the best approaches to do this (Kalish 1993, Campana and Jones 1998, Choat et al. 2009). The main limitation of correctly applying this method to ageing validation of Caribbean reef fishes was the lack of a region-specific $\Delta^{14}C$ reference time series that covered the actual time period for potential birth years of species under evaluation, however this is no longer an issue for the north Caribbean. A recent investigation established the $\Delta^{14}C$ temporal relationship for north Caribbean waters utilizing known-age otolith material from reef fish collected from the same areas that yellowtail snapper samples occurred in the current study (Shervette et al. 2021). Therefore, the results of yellowtail snapper age estimation validation in the current study provide the most comprehensive evidence to-date that the ageing method used in this study resulted in accurate age estimates.

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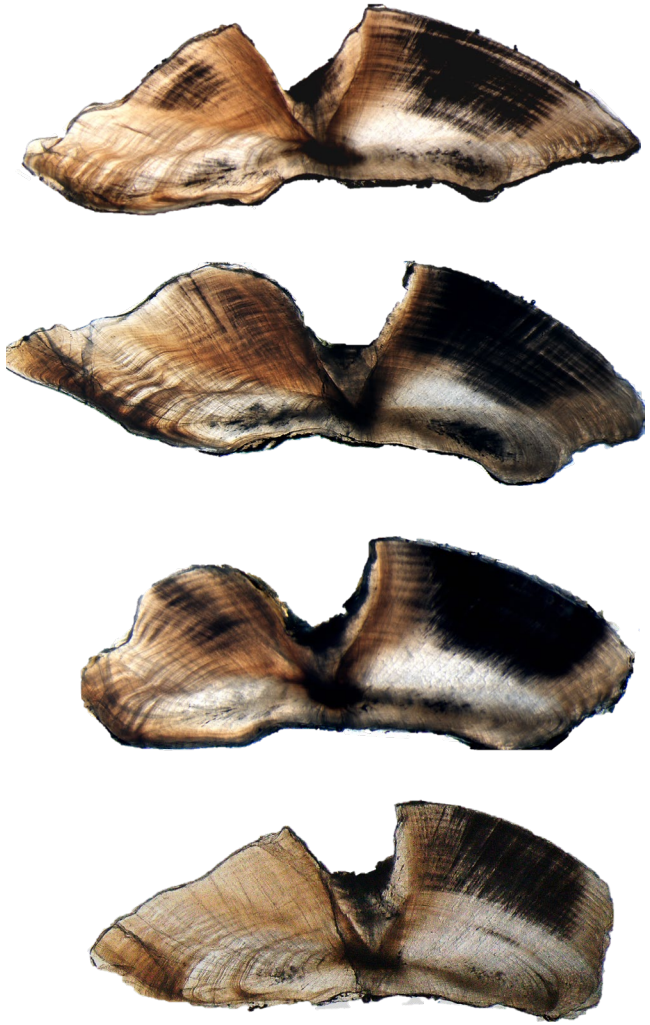
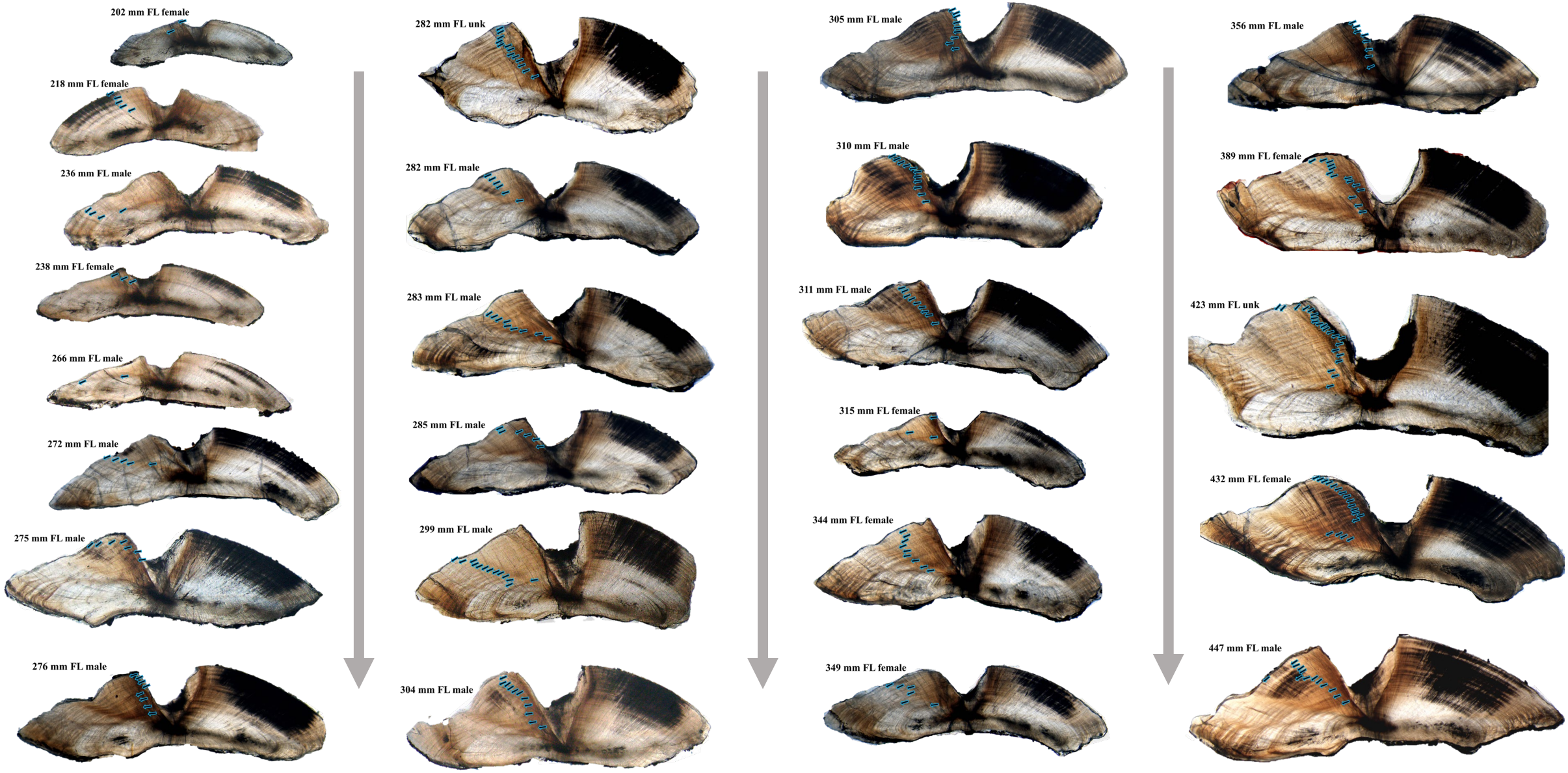
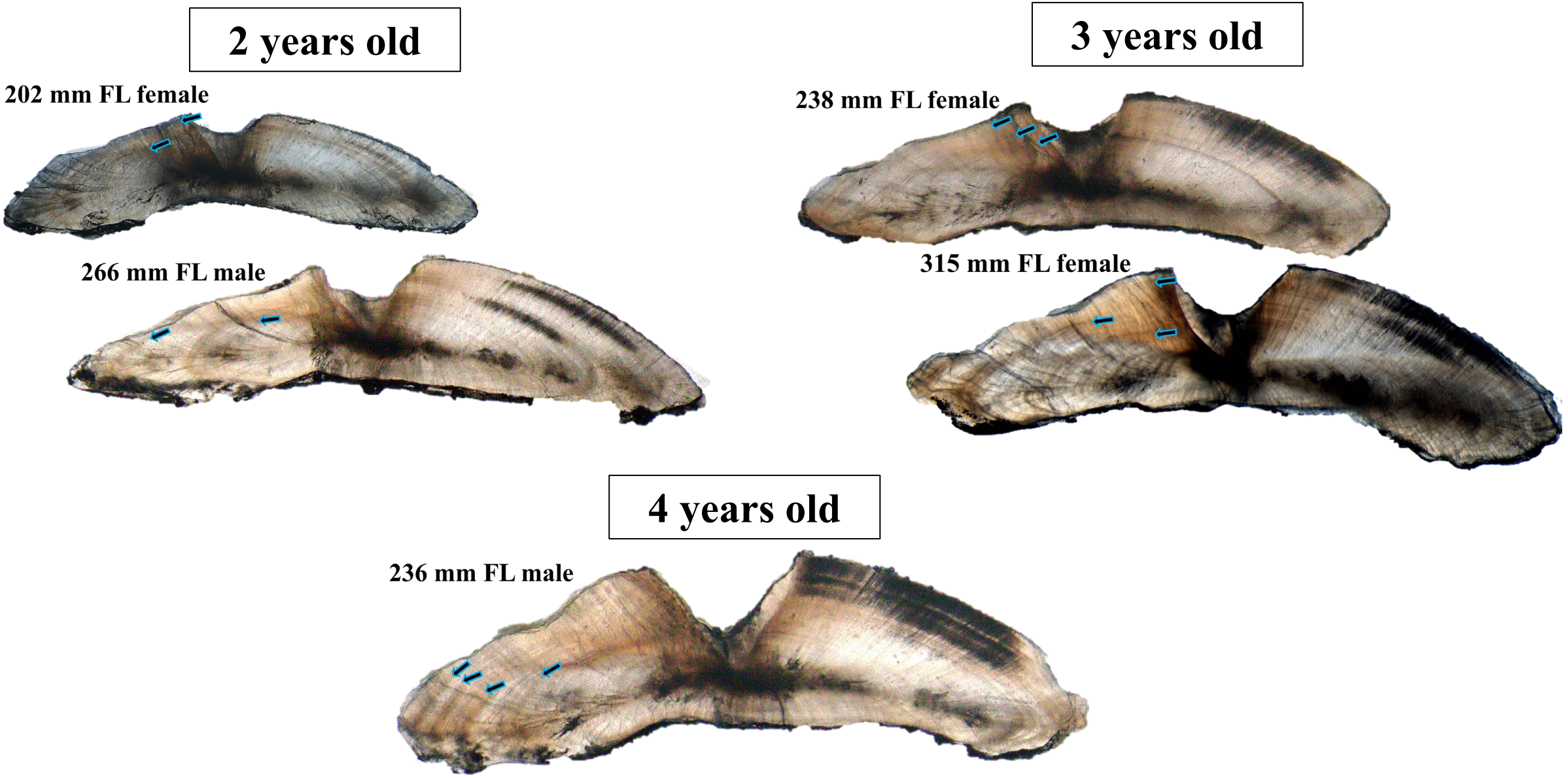
Appendix

Photographic examples of U.S. Caribbean yellowtail otolith sections

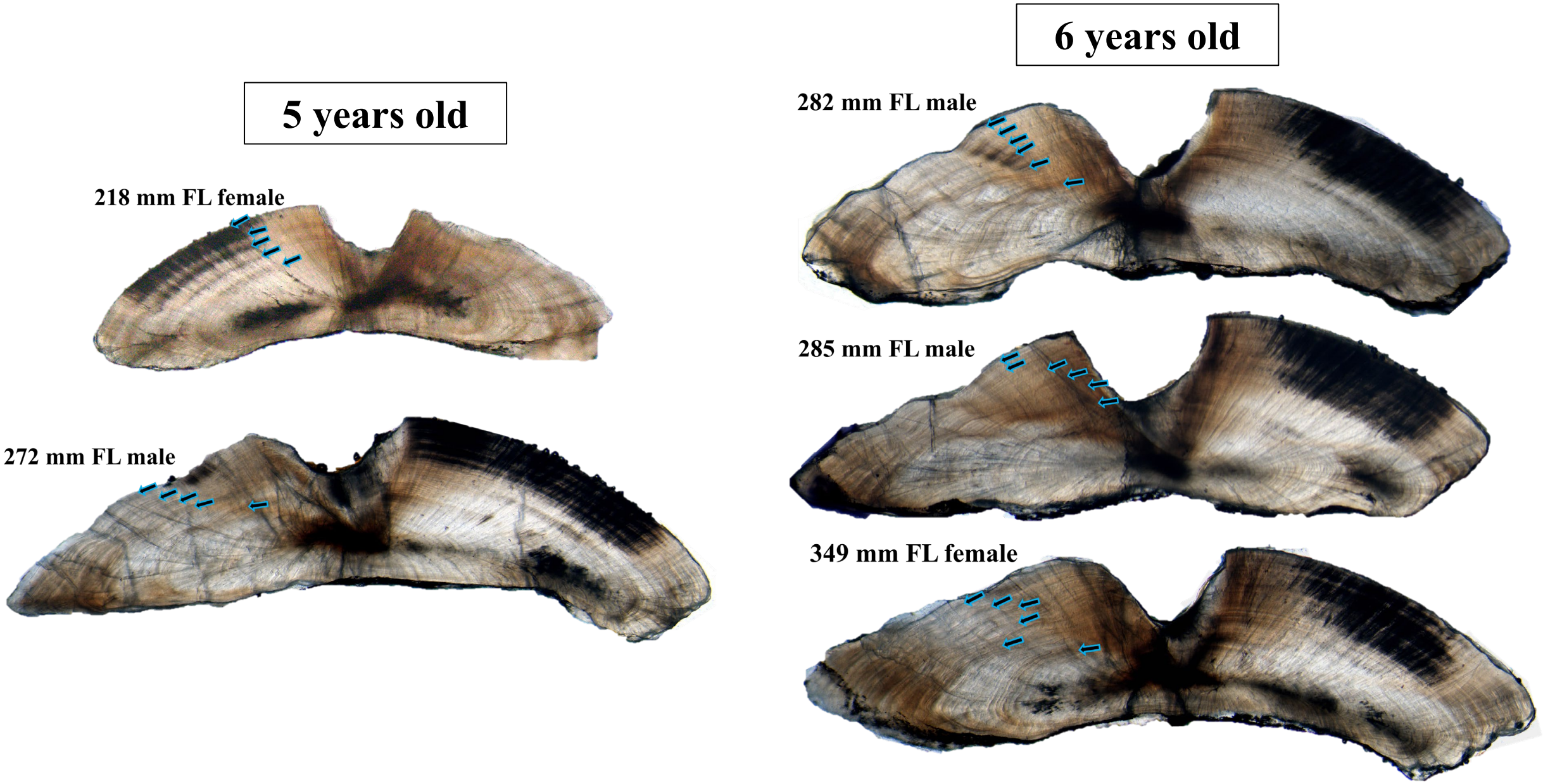




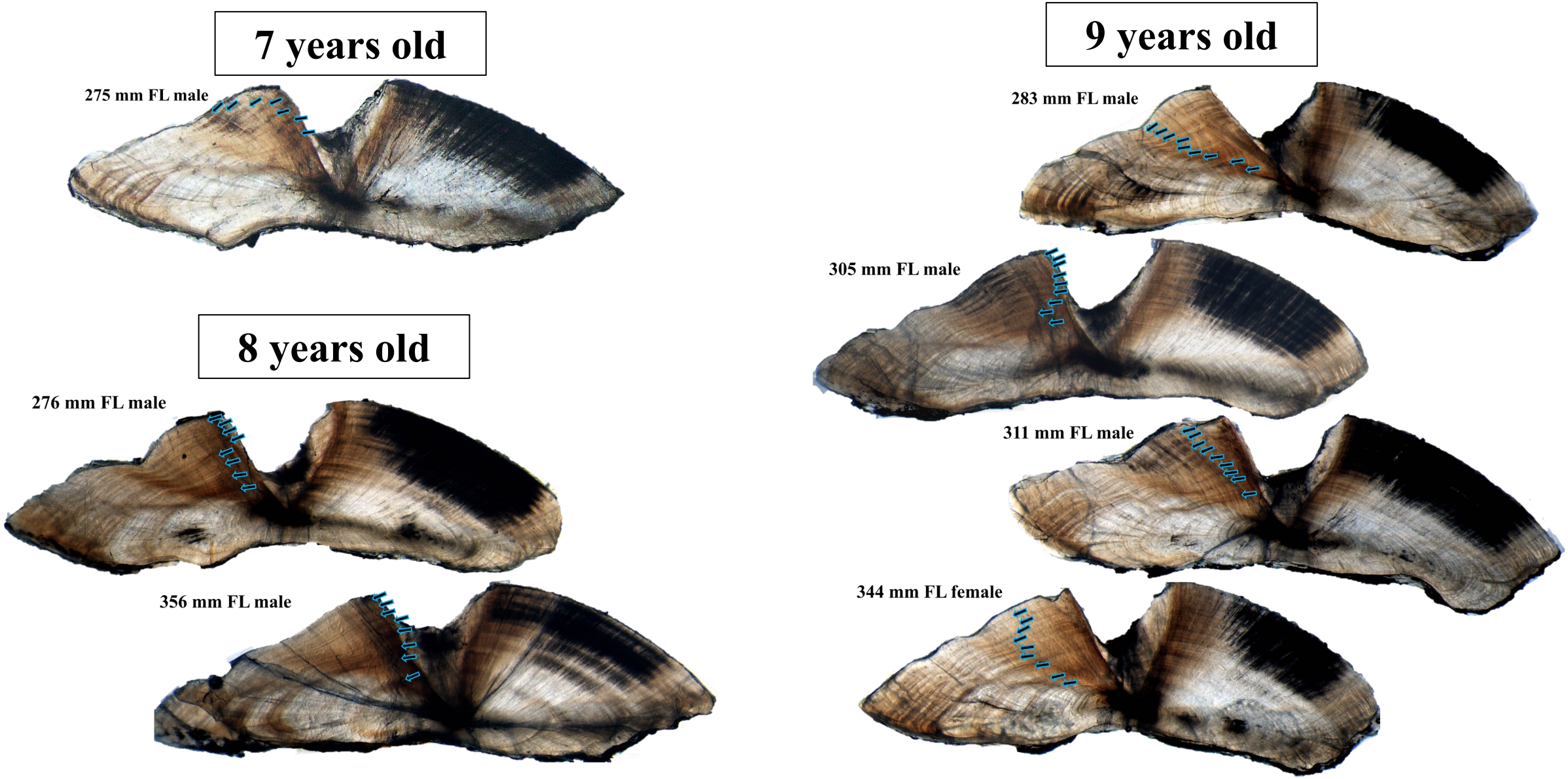
Appendix Figure 1. Annotated U.S. Caribbean yellowtail snapper otolith sections to illustrate the extreme variability of age with size. Images are organized in four columns with smallest example in the top left; fish length increases from top to bottom and left to right.



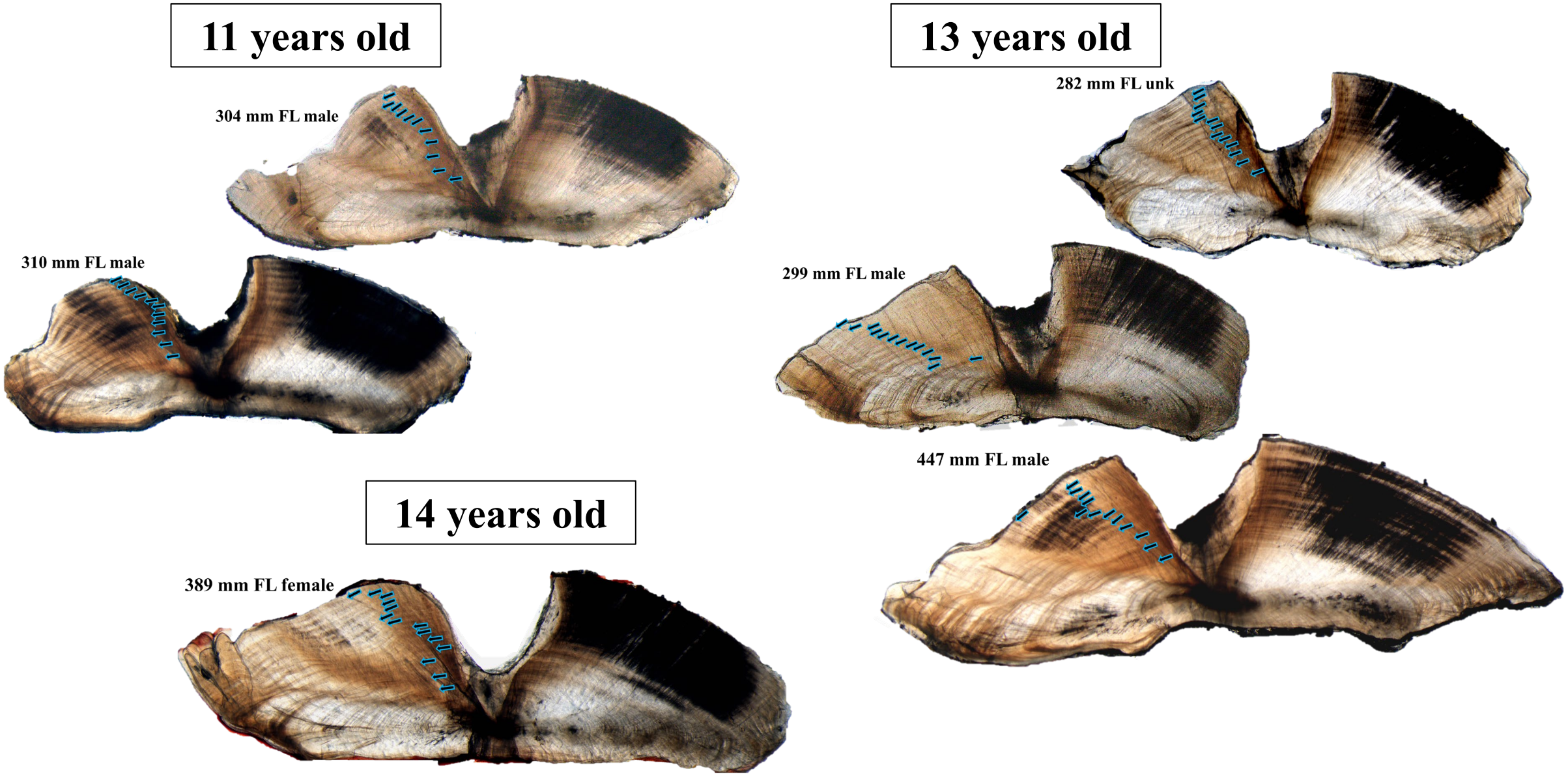
Appendix Figure 2. Annotated U.S. Caribbean yellowtail snapper otolith sections to illustrate the variability of fish length within ages 2 – 4 y.



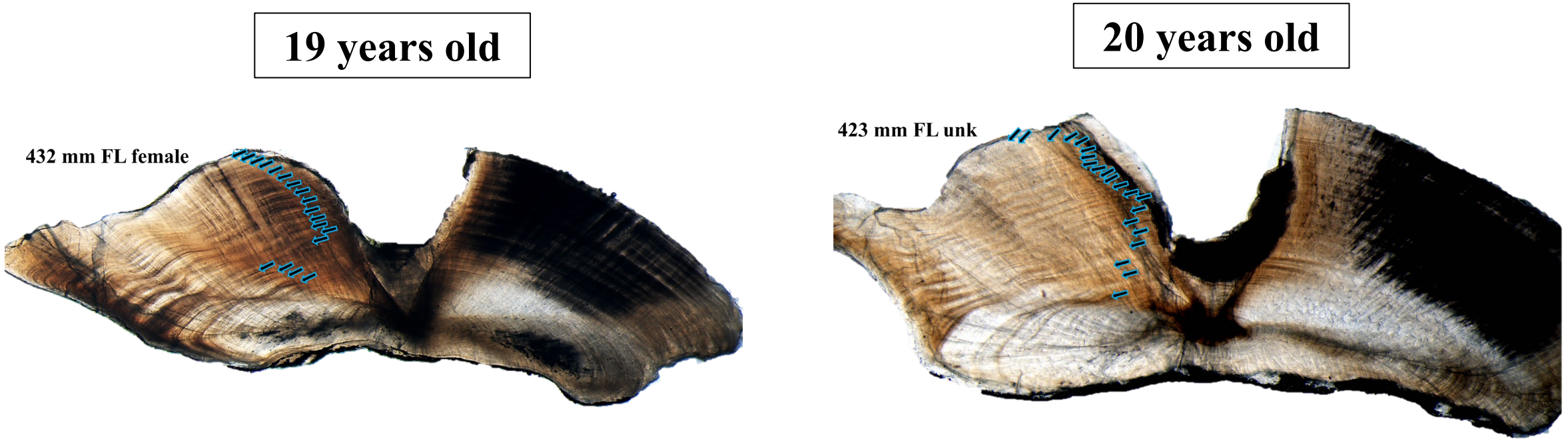
Appendix Figure 3. Annotated U.S. Caribbean yellowtail snapper otolith sections to illustrate the variability of fish length within ages 5 – 6 y.



Appendix Figure 4. Annotated U.S. Caribbean yellowtail snapper otolith sections to illustrate the variability of fish length within ages 7 – 9 y.



Appendix Figure 5. Annotated U.S. Caribbean yellowtail snapper otolith sections to illustrate the variability of fish length within ages 11 – 14 y.



Appendix Figure 6. Annotated U.S. Caribbean yellowtail snapper otolith sections to illustrate the variability of fish length within ages 19 – 20 y.