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Caribbean Yellowtail Snapper *Ocyurus Chrysurus*: Filling In Critical Gaps in Research for Life History and Novel Ageing Validation Utilizing $\Delta^{14}\text{C}$

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CARIBBEAN YELLOWTAIL SNAPPER *OCYURUS CHRYSURUS*: FILLING IN
CRITICAL GAPS IN RESEARCH FOR LIFE HISTORY AND NOVEL AGEING
VALIDATION UTILIZING $\Delta^{14}\text{C}$

by

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ABSTRACT

Yellowtail snapper *Ocyurus chrysurus* is an important fisheries species in the US Caribbean; in waters of Puerto Rico, it ranks second for reef fishes in terms of annual total commercial landings. However, a paucity of information exists concerning basic life history information for Caribbean yellowtail snapper populations. This study provides the first comprehensive documentation of age, growth, and reproductive biology of yellowtail snapper from the Caribbean and is the first to directly validate age estimation in this species. Sampling of 1731 yellowtail snapper occurred in Puerto Rico and the U.S. Virgin Islands during 2013-2021 from fisheries-dependent and –independent efforts. Fish ranged in size from 68-690 mm (total length) and in age from 0-26 years. Regression equations were calculated to determine length-length and length-weight relationships using total length (TL), fork length (FL), standard length (SL), and weight. Total length and age data fit to a von Bertalanffy growth curve for all samples combined from across the U.S. Caribbean, but not including the cast net age-0 samples, yielded the following relationship: $TL_t = 537[1 - e^{-0.11(t + 3.32)}]$. Yellowtail snapper in the U.S. Caribbean demonstrated a male to female sex ratio of 1:1.14 and exhibited year-round spawning with a peak spawning period in April. Age validation was conducted comparing bomb radiocarbon $\Delta^{14}\text{C}$ measured in snapper eye lenses formed during the first year of life. Information from this study can be used by fisheries resource managers when evaluating the health of the yellowtail snapper fishery in the region.

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CHAPTER 1

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 commercially valuable to fisheries around the world (Cummings, 2007; Uehara et al., 2020). Yellowtail snapper (*Ocyurus chrysurus*) is a highly sought-after snapper species that has a distribution in the western Atlantic as far north as Massachusetts to southeastern Brazil; however, it is most abundant off southern Florida and in the Caribbean (Lindholm et al., 2005; Manooch and Drennon, 1987). In the U.S. Caribbean, yellowtail snapper is one of the top three commercially landed reef fish species and is highly sought after due to its great taste, absence of parasites, and common occurrence (Manooch and Drennon, 1987; Watson et al., 2002; Collins, 1984). Despite its popularity, yellowtail snapper is considered a data-deficient species, lacking information on key life history parameters such as age, growth, and reproduction, which are necessary to conduct rigorous stock assessments for fisheries species to determine the current stock status in relation to current exploitation rates (Branch et al., 2011).

Yellowtail snapper, characterized by its streamlined body and deeply forked tail (Figure 1.1), is moderately long-lived and utilizes a range of habitats as individuals develop and mature (Manooch and Drennon, 1987; Allman et al., 2005; Watson et al., 2002). Juvenile yellowtail snapper aggregate in seagrass beds, such as turtle grass

Thalassia testudinum, and mangrove wetlands (Kimmel, 1985). Yellowtail snapper 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 are most associated with coral reefs and hard substrates in shallow waters; they commonly form large schools and exhibit high site fidelity (Grimes 1976; Lindholm et al., 2005). Unlike most snappers, yellowtail is a more pelagic species, often occurring above the substrate in transient aggregations (Hoese and Moore, 1998; Lindholm et al., 2005). Yellowtail snapper occurs in association with structured habitats at a depth range of 10 – 70 m with adults most commonly found between 20 – 40 m near the shelf edge (GMFMC, 2013; Thompson and Munro, 1974).

Yellowtail snapper is a generalist carnivore, consuming an array of smaller fishes and invertebrates (Piedra, 1969; Barbieri and Colvocoresses, 2003). Unlike other Lutjanidae, yellowtail snapper is not restricted to nocturnal feeding, but rather forages opportunistically throughout the day (Longley and Hildebrand, 1941; reported in Thompson and Munro, 1974). Yellowtail snapper appear to exhibit seasonal variability in feeding; a study conducted in Cuba observed that the frequency of individuals with full stomachs increased outside of spawning season (de Albornoz and Ramiro, 1988). Similar observations were reported of yellowtail off south Florida by Collins and Finucane (1989).

Yellowtail snapper may form spawning aggregations of 25 to 30 individuals, although these aggregations are not well defined spatially or temporally (Trejo-Martinez et al., 2011; Claro et al., 2009). 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 (Muller et al., 2003; Collins and Finucane, 1989). 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-Martinez 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 age and growth of yellowtail snapper, 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) also 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 size (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. A study from U.S. Caribbean waters collected 468 yellowtail snapper in 1983-1984 and reported a maximum age of 17, L_{∞} = 0.14, K = 0.30, and t_0 = -0.96 (Manooch and Drennon). The

U.S. Caribbean study noted that yellowtail snapper increments were relatively difficult to discern (Manooch & Drennon, 1987). More recent information does not exist on age and growth for yellowtail snapper from waters of the north Caribbean.

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 & Drennon, 1987). The bomb radiocarbon chronometer is a useful tool that has been utilized in the validation of fish ageing estimation for Caribbean species (Shervette et al. 2021a). Radiocarbon (^{14}C) was introduced into the atmosphere through nuclear bomb testing from the 1950's to the 1970's (Broecker and Peng, 1982). 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 the aragonite and carbon-rich structures of fishes such as otoliths (Kalish, 1993) and eye lenses (Shervette et al. 2020, Patterson et al. 2021). The incorporation of bomb-produced radiocarbon is reported as $\Delta^{14}\text{C}$ 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 $\Delta^{14}\text{C}$ in annual accretions of biogenic CaCO_3 in hermatypic corals (Knutson et al., 1972; Nozaki et al., 1978) and aragonite structures of

fishes (Kastelle et al., 2008; Andrews et al., 2013; Barnett et al., 2018, Shervette et al. 2021a). The time-specific $\Delta^{14}\text{C}$ aragonite records provide regional reference chronologies that can be used to evaluate fish age estimates through comparison of $\Delta^{14}\text{C}$ measured in fish eye lens core material that formed during the first year of life (Shervette et al. 2020, Patterson et al. 2021).

Documenting the age, growth, and reproduction of data-deficient/data-poor Caribbean fisheries species is critical for assessing the current stock status of a species (SEDAR 2011, 2016). The overall goal of this study was to provide essential life history information in support of more effective fishery management and conservation for an important reef fish fisheries species in the U.S. Caribbean, yellowtail snapper. Improving on the quantity and quality of the available life history information is key for creating more accurate fishing management metrics including Annual Catch Limits (ACLs) and Maximum Sustainable Yields (MSY). Age and growth estimates are fundamental to reliably estimating biological reference points and are required to facilitate the transition to age-based stock assessments in the future. The specific objectives of this study were: 1) to investigate age and growth of yellowtail snapper across the U.S. Caribbean, 2) report spawning seasonality of yellowtail snapper, and 3) to use bomb radiocarbon to validate the ageing method for this species.



Figure 1.1 Caribbean yellowtail snapper

CHAPTER 2

METHODS

Study Area and Management

The U.S. Caribbean (Figure 2.1) 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 km² within 3-nm of PR and 298 km² in the USVI (Causey et al. 2002; Catanzaro et al., 2020).

Commercial fishers in the U.S. Caribbean mainly target yellowtail snapper with hook and line gear (SEDAR 2016). 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 size of 305 mm TL (260 mm FL), and area closures that prohibit fishing with specific gears, do not allow fishing at all within the boundaries year-round, or do not allow fishing within a closed season for the area¹.

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

Fish Collection and Processing

Fish samples for this study were obtained through two main sources: 1) fisheries-independent (F-I) collections via hook-and-line; and 2) fisheries-dependent (F-D) collections that consisted of purchasing fish directly from local fishers. For each sample, GPS coordinates of capture location, date of capture, and gear type used were recorded. All fish samples were measured for standard length (SL), fork length (FL), and total length (TL) to the nearest 1.0 mm and weighed to the nearest 1.0 g. Gonads were removed, weighed (to the nearest 0.01 g) and preserved for further processing. Sagittal otoliths were extracted, rinsed of adhering tissue, dried, and placed in labeled coin envelopes for later processing. 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.

Long-term, consistent, and widespread fish length data are limited for Caribbean reef fish species like yellowtail snapper. Conversions of length serve as a helpful tool to bridge gaps in scientific sampling and measuring between studies (Jones et al. 2021). Due to logistical or physical reasons, different studies may utilize differing measurement methods; for example, one study may report SL, while another primarily utilizes FL. The creation of accurate conversions of length improves upon the amount of available data for Caribbean fisheries species and promotes the sharing of data across different researchers and managers who had previously used differing measurement methodologies. Regression equations based on a large sample size of yellowtail snapper were calculated to create length-length and length-weight conversions. The length-weight regressions were in the form of $W = a L^b$; where W = weight (g), L = length (mm), and a and b are the intercept and slope parameters, respectively.

A two factor ANOVA was used to test for significant differences in mean fish size between males and females and between the two sample sources, F-I and F-D. Separate Kolmogorov-Smirnov (K-S) tests were used to determine if significant differences occurred in size frequency distributions between males and females, and between F-D vs. F-I samples.

Age and Growth

Yellowtail snapper otoliths were processed for ageing estimation utilizing the methods previously described for reef fish species in Shervette et al. (2021a). 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 20-40x (Figure 2.2). Two independent readers assessed increment counts for each yellowtail snapper otolith without knowledge of fish size or date of collection. In cases of between-reader increment count disagreements, the two readers concurrently evaluated the otolith section together and reached a consensus age estimate. For each otolith, readers evaluated if the last opaque zone occurred on the otolith edge (Jones et al. 2021). The monthly proportion of otoliths with opaque zones on the edge was calculated using age-4 to age-12 fish and then all monthly proportions were plotted to evaluate the time of year that the opaque zone forms on the otolith margin (Smylie et al. 2016, Kelly-Stormer et al. 2017, Jones et al. 2021).

Average percent error (APE) between ages assigned by readers was calculated using the following equation (Beamish and Fournier, 1981):

$$\text{APE} = \frac{1}{n} \sum_{j=1}^n \left[\frac{1}{R} \sum_{i=1}^R \frac{X_{ij} - \bar{X}_j}{\bar{X}_j} \right];$$

where n = number of samples aged, R = number of readers, X_{ij} is the i^{th} age determination of the j^{th} fish, and \bar{X}_j is the average age calculated for the j^{th} fish.

Separate pairwise K-S tests were used to compare the age frequency distributions between sexes and sample sources. A two-factor ANOVA was used to determine if mean age differed significantly between sexes and between sample sources. For all yellowtail snapper size-at-age data, F-D size-at-age data, and F-I size-at-age data, separate von Bertalanffy growth functions were fit to estimated ages with the least squares method using the solver function in Microsoft Excel (Haddon, 2010). The von Bertalanffy growth function is:

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

where L_t represents the estimated average fork length at age t , L_{∞} represents the mean asymptotic fork length, K is the von Bertalanffy growth coefficient, and t_0 represents the age at which fish have a theoretical FL of 0 (von Bertalanffy 1938, Jones et al. 2021). To provide a more biologically representative estimate of growth, age-0 yellowtail snapper caught with a cast net in PR were included in the growth model (Kelly-Stormer et al. 2017). A two-factor ANOVA was used to test the effect of sample source on estimated size at age for ages 4-9, the most prevalent age classes present in the data. The dependent variable for this was FL. The independent variables were age class and sample source.

A subset of 16 yellowtail snapper samples was used to validate the accuracy of yellowtail snapper ageing estimation via application of the bomb ^{14}C chronometer by

measuring the $\Delta^{14}\text{C}$ an individual fish experienced during its first year of life as recorded in the eye lens cores (Shervette et al., 2020; Patterson et al., 2021). Forceps and glassware used in the process of obtaining lens cores for $\Delta^{14}\text{C}$ 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°C. Frozen eye samples were thawed at room temperature and the whole lens was extracted from each eye by making a slit through the cornea and applying slight pressure to the side of the eye. 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. Cores were analyzed for $\Delta^{14}\text{C}$ with the accelerator mass spectrometry (AMS) at the NOSAMS facility at Woods Hole Oceanographic Institute in Falmouth, Massachusetts (additional information on exact methods used can be found online: www.whoi.edu/nosams/radiocarbon-data-calculations).

The isotope ^{13}C was reported as the delta value $\delta^{13}\text{C}$ (‰), which is calculated as the ratio of $^{13}\text{C}/^{12}\text{C}$ relative to a standard (Pee Dee Belemnite). Radiocarbon (^{14}C) was reported as a delta value ($\Delta^{14}\text{C}$) that represents the activity of a sample relative to a standard (Stuiver and Polach, 1977) and corrected for age and $\delta^{13}\text{C}$.

The $\Delta^{14}\text{C}$ value from the eye lens core and corresponding estimated birth year for each of the 16 yellowtail snapper ageing validation samples were overlaid on the north Caribbean reference chronometer (Shervette et al. 2021a). The estimated birth year of a sample equals the year of collection minus the opaque zone count from the otolith

section. Potential ageing bias was examined by purposely shifting the estimated ages by +/- 1-3 years and superimposing $\Delta^{14}\text{C}$ eye lens core values on the north Caribbean reference $\Delta^{14}\text{C}$ time series (Shervette et al. 2021a). The original age estimates represented an age bias of 0 (null model), while age biases of +1, +2, +3 shifted age estimates to the left (older), and age biases of -1, -2, -3 shifted age estimates to the right (younger). The sum of squared residuals (SSR) was then computed from predicted versus observed birth years for the eye lens core samples and repeated for the purposely biased age estimate models (Kastelle et al., 2008, Shervette et al. 2020, Shervette et al. 2021a).

Reproduction

Gonads removed from each sample were fixed in 10% buffered formalin or PAGA fixative (Zanini et al., 2012) for up to two weeks, then transferred to 70% isopropanol. Gonad samples were processed using standard histological procedures for gonochoristic species (Kelly-Stormer et al., 2017; Rivera Hernandez et al., 2019). The tissue samples were vacuum-infiltrated and blocked in paraffin wax. At least three transverse sections (~7 μm thick) were cut from each gonad using a rotary microtome, sections were mounted on glass slides, stained with double-strength Gill hematoxylin, and counter-stained with eosin-y. Stained gonad section slides were cover-slipped with a clear mounting medium.

Gonad slides were viewed using a compound microscope to determine sex and reproductive phase according to histological criteria for gonochoristic species (Rivera Hernández et al., 2019). Two readers independently assigned sex and maturity without knowledge of date of capture, specimen length, or specimen age. When differences in the assignment of reproductive phases occurred, readers examined the slide

simultaneously to obtain a consensus assignment. If no consensus was reached, then that specimen was eliminated from the analyses. The sex ratio was calculated for all yellowtail snapper samples with histologically confirmed sex. The monthly proportion of females in the spawning capable phase relative to all mature females was calculated to determine the peak spawning period. The monthly proportion of males in the spawning capable phase relative to all mature males was also calculated.

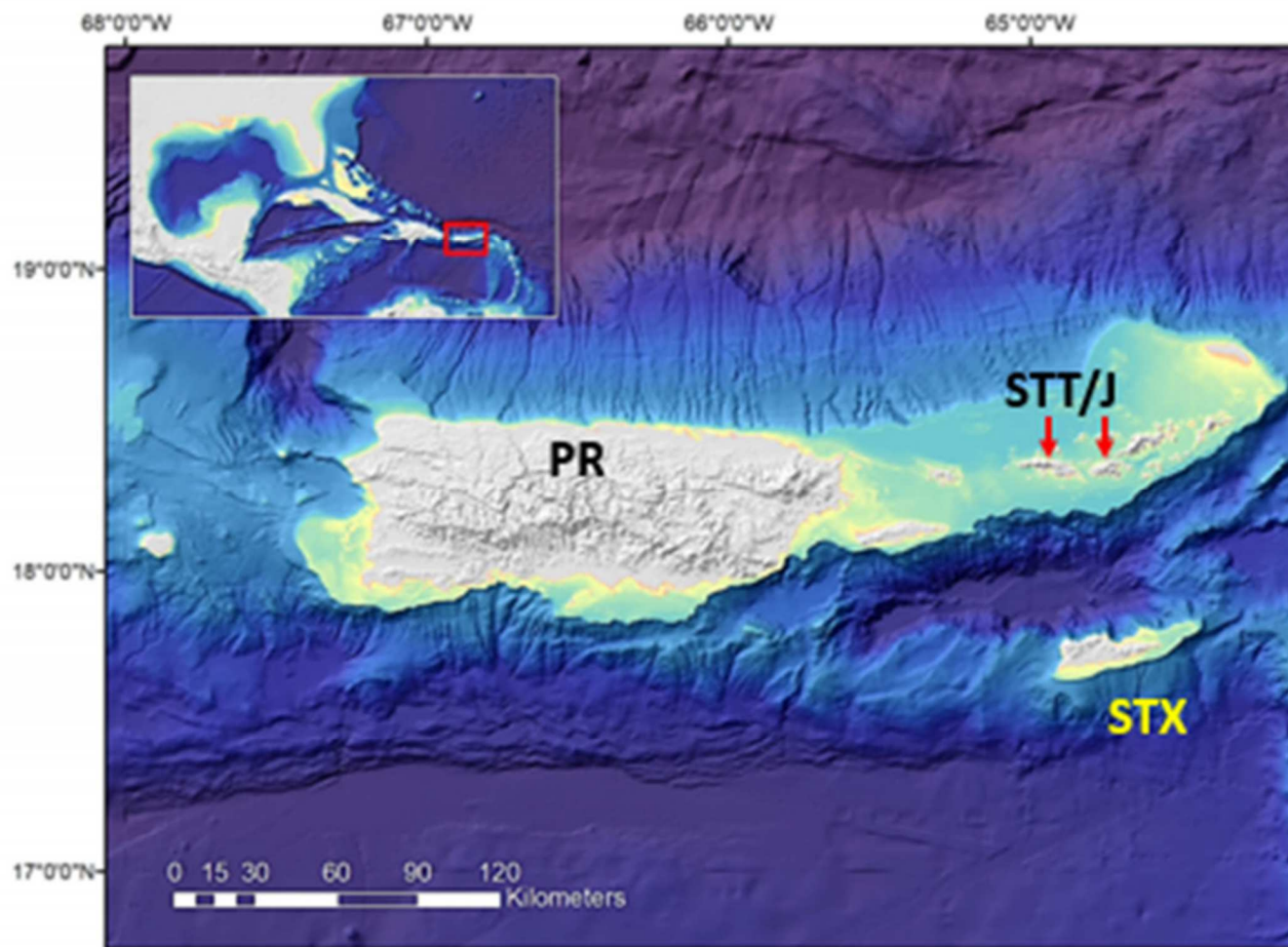


Figure 2.1 Sampling region in the north Caribbean. Sampling regions include both the east and west side of Puerto Rico, and the shelf waters of the U.S. Virgin Islands of St. Thomas (STT) and St. Croix (STX).

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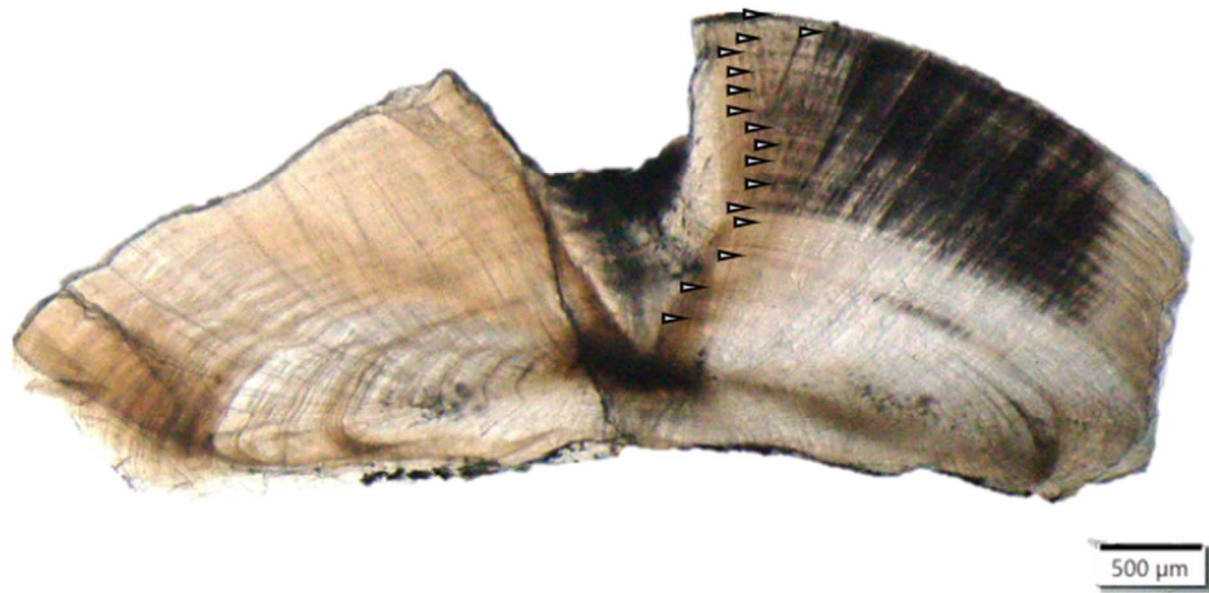


Figure 2.2 Sectioned sagittal otolith of yellowtail snapper. Alternating opaque and translucent zones indicate an age of 16 years.

CHAPTER 3

RESULTS

Fish Collection

A total of 1,731 yellowtail snapper were collected and processed for this study between the years of 2013 – 2021: 1353 (78%) from PR, and 378 (22%) from the USVI (Table 3.1). In PR samples ranged from 64 – 541 mm FL (mean \pm SD; 247 \pm 56 mm). Samples collected from the USVI ranged from 84 – 538 mm FL (mean \pm SD; 322 \pm 53 mm). Sex was determined via gonad histology for 1018 samples: 651 from PR and 376 from USVI. All linear regression analyses of length-length relationships for standard length (SL), fork length (FL), and total length (TL) were significant (Table 3.2). Length-weight regressions were conducted for all three length measurements, and TL had the highest R^2 value of 0.98 (Table 3.2). Mean size did not significantly differ between males and females but did differ significantly between F-D and F-I samples (Table 3.3), with the mean size of F-D fish (315 mm FL) significantly larger than F-I fish (243 mm FL; Table 3.3). Size frequency distributions did not differ significantly between female and male yellowtail snapper (Table 3.4). Size frequency distributions did differ significantly between F-D versus F-I samples; F-D samples had a higher proportion of larger fish compared to F-I samples (Table 3.4; Figure 3.1).

Age, Growth, and Ageing Validation

Age estimates ranged from 0-17 y for Caribbean yellowtail samples (n = 16) that were analyzed for $\Delta^{14}\text{C}$ (Table 3.5). Estimated birth year (year of collection minus age)

corresponded well with the known-age otolith $\Delta^{14}\text{C}$ north Caribbean reference series (Figure 3.2). Results from the ageing bias analysis of yellowtail snapper eye lens core $\Delta^{14}\text{C}$ values relative to the regression fit of the known-age north Caribbean $\Delta^{14}\text{C}$ reference decline 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 3.6).

Ages were estimated for 1051 yellowtail snapper: 675 from PR (64%) and 376 from the USVI (36%). Of these 1051 fish, 480 were from F-D sources (45.7%) and 571 from F-I sources (54.3%). Results from the marginal increment analysis indicated that opaque zones formed in the otoliths from March – June with a peak in April (Figure 3.3). The ages of PR samples ranged from 0 – 26 y with a mean age of 5.3 y; USVI samples ranged in age from 1 – 20 y with a mean of 8.4 (Table 3.1). APE between readers was 6%. Age frequency distributions did not differ significantly between females versus males; but did differ between F-D versus F-I samples (Table 3.4). Samples from F-D collections had a higher proportion of older fish compared to F-I samples (Figure 3.1; Table 3.3). Mean age did not significantly differ between males and females but did differ significantly between F-D and F-I samples (Table 3.3), with the mean age of F-D fish (8.0 y) significantly older than F-I fish (5.1 y).

Total length and age data fit to a von Bertalanffy growth curve for all samples combined from across the U.S. Caribbean, but not including the cast net age-0 samples, yielded the following relationship: $TL_t = 537[1 - e^{-0.11(t + 3.32)}]$ (Table 3.7; Figure 3.4). When age-0 fish were included, the growth equation was $TL_t = 481[1 - e^{-0.17(t + 1.79)}]$

(Table 3.7). Fork length data fit to the growth curve (juveniles included) resulted in the following equation: $FL_t = 390[1 - e^{-0.17(t + 1.99)}]$ (Table 3.7). The two factor ANOVA indicated that mean size varied significantly among the age groups (4-9) and between F-D and F-I samples (Table 3.8; Figure 3.5).

Reproduction

Sex and reproductive phase of yellowtail snappers were assessed histologically for 1018 fish (Table 3.1). The sex ratio of males to females in this study was 1:1.14. A subsample of 233 female yellowtail snapper were assigned a reproductive phase from the gonad histology slides (Table 3.9). The number of females per month with reproductive phase information ranged from 8 for the month of August, to 64 for the month of July. Females with indicators of spawning activity were collected in all months of the year, except October. Peak spawning was observed in March-April (Table 3.9). A subsample of 233 male yellowtail snapper had information on reproductive phase from the gonad histology slides (Table 3.10). The total number of males per month with reproductive phase information ranged from 8 for August, to 50 for October. Males with indicators of spawning were observed in all months of the year.

Table 3.1 Sampling summary of Caribbean yellowtail.

	PR			USVI			Combined		
Variable	ALL	FD	FI	ALL	FD	FI	ALL	FD	FI
Number measured	1353	129	1224	378	367	11	1731	496	1235
Number aged	675	115	560	376	365	11	1051	480	571
Number gonad histo	651	78	573	367	365	2	1018	443	575
Female									
TL range (mean)	118-650 (306) n=599	295-561 (358) n=63	118-650 (300) n=536	318-690 (403) n=198	318-690 (403) n=191	374-443 (416) n=7	118-690 (330) n=797	295-690 (392) n=254	118-650 (301) n=543
FL range (mean)	105-530 (250) n=599	242-455 (289) n=63	105-530 (246) n=536	253-538 (326) n=198	253-538 (325) n=191	307-360 (338) n=7	105-538 (269) n=797	242-538 (316) n=254	105-530 (247) n=543
Age range (mean)	1-18(5.2) n=323	3-11(5.8) n=53	1-18(5.0) n=270	4-20(8.6) n=197	4-20(8.5) n=190	7-12(9.9) n=7	1-19(6.4) n=520	3-19(7.9) n=243	1-18(5.2) n=277
Male									
TL range (mean)	99-648 (301) n=530	300-648 (365) n=41	99-525 (296) n=489	94-661 (392) n=178	284-661 (395) n=174	94-466 (289) n=4	94-661 (324) n=708	284-661 (389) n=215	94-525 (296) n=493
FL range (mean)	90-502 (246) n=530	242-502 (295) n=41	90-430 (242) n=489	84-527 (318) n=178	249-527 (319) n=174	84-374 (236) n=4	84-527 (264) n=708	242-527 (315) n=215	84-430 (242) n=493
Age range (mean)	1-17(4.8) n=267	4-14(6.6) n=37	1-17(4.6) n=230	1-20(8.2) n=177	4-20(8.2) n=173	1-14(6.5) n=4	1-20(6.2) n=444	4-20(7.9) n=210	1-17(4.6) n=234
Unknown									
TL range (mean)	68-678 (296) n=224	303-455 (344) n=25	68-678 (290) n=199	377-396 (387) n=2	377-396 (387) n=2	NA	68-678 (297) n=226	303-455 (348) n=27	68-678 (290) n=199
FL range (mean)	64-541 (242) n=224	242-359 (278) n=25	64-541 (238) n=199	288-318 (303) n=2	288-318 (303) n=2	NA	64-541 (243) n=226	242-359 (280) n=27	64-541 (238) n=199
Age range (mean)	0-26(6.8) n=85	3-14(7.0) n=25	0-26(6.7) n=60	5-6(5.5) n=2	5-6(5.5) n=2	NA	0-26(6.8) n=87	3-14(6.9) n=27	0-26(6.7) n=60
Overall									
TL range (mean)	68-678 (302) n=1353	295-648 (357) n=129	68-678 (297) n=1224	94-690 (398) n=378	284-690 (399) n=367	94-466 (370) n=11	68-690 (323) n=1731	284-690 (388) n=496	68-678 (297) n=1235

	PR				USVI				Combined		
Variable	ALL	FD	FI		ALL	FD	FI		ALL	FD	FI
FL range (mean)	64-541 (247) n=1353	242-502 (289) n=129	64-541 (243) n=1224		84-538 (322) n=378	249-538 (322) n=367	84-374 (301) n=11		64-541 (264) n=1731	242-538 (314) n=496	64-541 (243) n=1235
Age range (mean)	0-26 (5.2) n=675	3-14 (6.3) n=115	0-26 (5.0) n=560		1-20 (8.4) n=376	4-20 (8.4) n=365	1-14 (8.6) n=11		0-26 (6.4) n=1051	3-20 (7.9) n=480	0-26 (5.1) n=571

Table 3.2 Regression equations. (Wt weight in grams, TL total length, FL fork length, SL standard length (mm); $p < 0.001$ for all regressions.)

Size Conversion Relationship	Equation	R-squared
SL-FL	$y = 1.1149x + 6.2144$	$R^2 = 0.9929$
SL-TL	$y = 1.4175x - 0.7735$	$R^2 = 0.9826$
SL-Wt	$y = 0.0001x^{2.736}$	$R^2 = 0.9747$
FL-SL	$y = 0.8906x - 3.4242$	$R^2 = 0.9929$
FL-TL	$y = 1.2767x - 13.201$	$R^2 = 0.9893$
FL-Wt	$y = 4E-05x^{2.8582}$	$R^2 = 0.9778$
TL-SL	$y = 0.6932x + 4.8405$	$R^2 = 0.9826$
TL-FL	$y = 0.7749x + 13.127$	$R^2 = 0.9893$
TL-Wt	$y = 5E-05x^{2.7048}$	$R^2 = 0.9797$

Table 3.3 ANOVA testing for significant differences in mean size and mean age.

Source	df	Sum of Squares	Mean Square	<i>F</i>	<i>P</i>
Length (FL mm)					
Sex	1	3627	3627	1.4	0.237
Source	1	1629966	1629966	628.1	<0.001
Sex x Source	1	943	943	0.4	0.547
Error	1495	3879697	2595		
Age					
Sex	1	18	18	2.0	0.156
Source	1	2219	2219	253.5	<0.001
Sex x Source	1	23	23	2.6	0.107
Error	960	8376	9		

Table 3.4 Kolmogorov-Smirnov test.

Comparison	N	Z-statistic	<i>P</i>
Length (FL mm)			
Female versus male	797 + 708	1.16	0.134
F-D versus F-I	496 + 1229	10.75	< 0.001
Age (y)			
Female versus male	520 + 444	0.80	0.538
F-D versus F-I	480 + 571	7.84	< 0.001

Table 3.5 Eye lens core samples analyzed for $\Delta^{14}\text{C}$ with AMS.

Sample number	Sample date	FL mm	Age	Year of Formation	$\delta^{13}\text{C}$ ‰	$\Delta^{14}\text{C}$	+/- SE
YT-STT-1	27 Aug 2019	84	1	2018	-17.63	32.47	2.3
YT-STT-2	8 May 2019	151	3	2016	-18.45	38.49	3.2
YT-STT-3	9 May 2019	305	6	2019	-16.94	41.57	2.2
YT-STX-1	26 Oct 2018	279	7	2011	-14.75	40.95	2.0
YT-STX-2	27 Oct 2018	285	11	2007	-15.32	59	2.1
YT-STX-3	13 Apr 2019	347	16	2003	-14.63	60	2.2
YT-STX-4	15 Apr 2019	303	11	2008	-14.73	48.53	2.2
YT-PR-1	9 Jun 1988	44	0	1988	-1.39	105.24	3.4
YT-PR-2	19 Jul 2019	406	13	2006	-15.85	52.31	2.6
YT-PR-3	10 Oct 19	345	15	2004	-10.78	55.05	2.8
YT-PR-4	10 Oct 19	316	12	2007	-17.21	53.77	2.5
YT-PR-5	14 Oct 19	282	15	2004	-15.78	57.54	2.6
YT-PR-6	4 Oct 19	261	7	2012	-14.04	45.88	2.3
YT-PR-7	4 Oct 19	195	3	2016	-14.04	32.06	2.4
YT-PR-8	14 Mar 19	337	17	2002	-12.98	65.29	2.1
YT-PR-9	14 May 19	328	12	2007	-14.1	56.62	2.2

Table 3.6 Squared residual 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

Table 3.7 von Bertalanffy growth parameters for Caribbean yellowtail.

Model	n	L_{∞}	K	t_0	R^2	P-value
All Samples Combined						
TL without juveniles	1051	537	0.11	-3.32	0.63	<0.001
TL with juveniles	1061	481	0.17	-1.79	0.66	<0.001
FL with juveniles	1061	390	0.17	-1.99	0.67	<0.001
Fisheries-Dependent FL (with juveniles)	490	393	0.20	-0.88	0.65	<0.001
Fisheries-Independent FL (with juveniles)	581	325	0.29	-0.98	0.66	<0.001
Females (with juveniles)	530	367	0.21	-1.32	0.66	<0.001
Males (with juveniles)	545	371	0.21	-1.26	0.73	<0.001

Table 3.8 ANOVA testing for significant differences in mean size at age.

Source	df	Sum of Squares	Mean Square	<i>F</i>	<i>P</i>
Length (FL mm)					
Age (4-9 y)	5	291803	53361	76.9	<0.001
Source	1	96636	96636	127.4	<0.001
Age x Source	5	7703	1541	2.0	0.079
Error	633	480775	633		

Table 3.9 Subsample examination of female gonad histology (n=233).

Month	Developing	Spawning	Regressing Regenerating	Total Females
January	2	11	12	25
February	12	11	2	25
March	6	22	15	43
April	0	18	0	18
May	9	6	5	20
June	17	1	13	31
July	43	10	11	64
August	1	6	1	8
September	7	7	6	20
October	11	0	26	37
November	10	1	23	34
December	1	6	13	20

Table 3.10 Subsample examination of male gonad histology (n=233).

Month	Developing	Spawning	Regressing Regenerating	Males Total
January	18	4	0	22
February	12	16	0	28
March	2	13	16	31
April	2	7	0	9
May	2	10	7	19
June	11	5	8	24
July	2	34	4	40
August	1	5	2	8
September	12	11	0	23
October	34	9	7	50
November	19	8	4	31
December	0	27	3	30

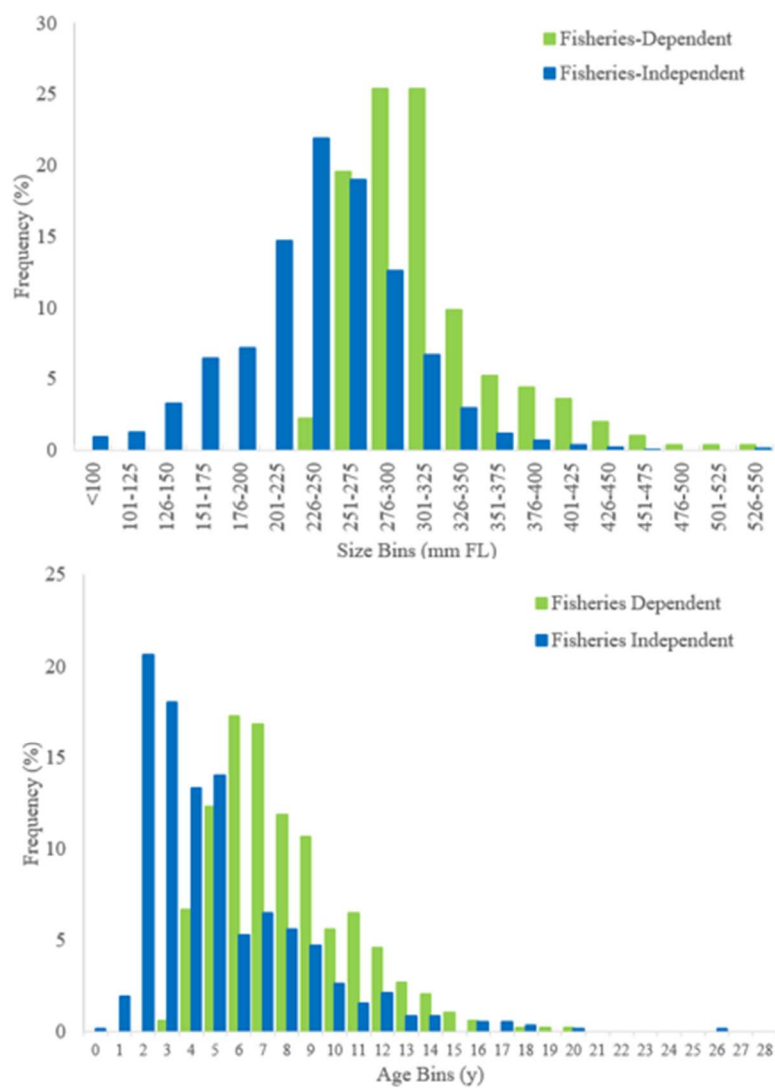


Figure 3.1 Size and Age Frequencies. Proportion of size (top) and age (bottom) frequencies between fishery-dependent and -independent sources.

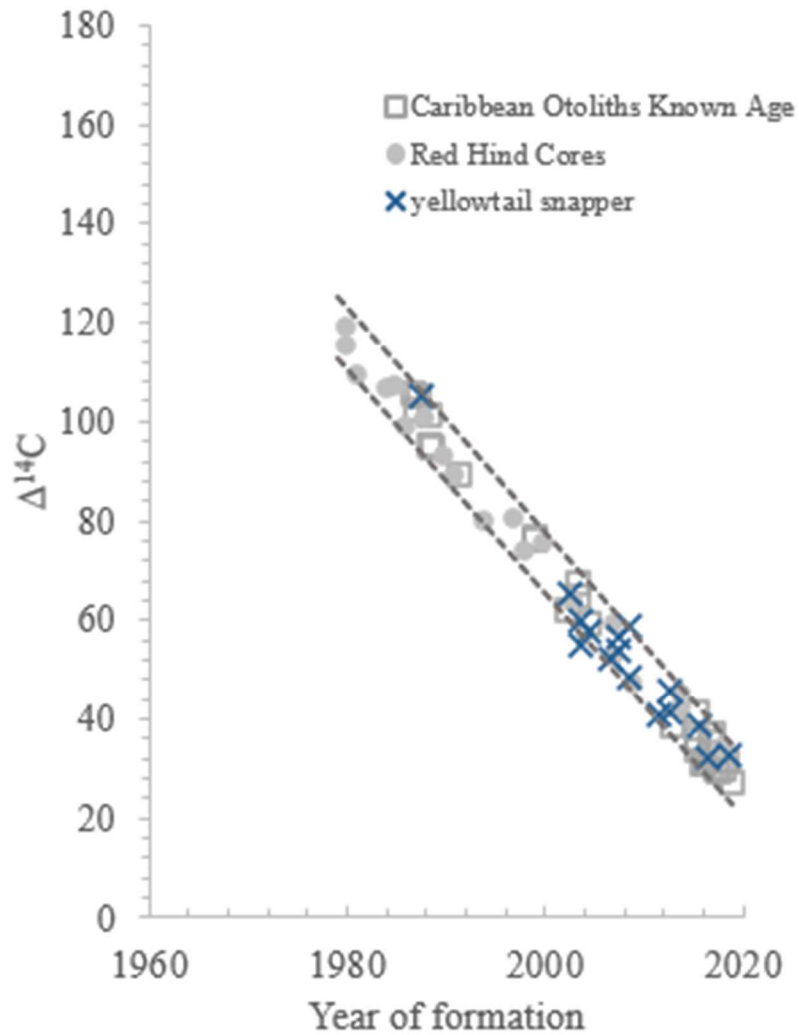


Figure 3.2. North Caribbean reference $\Delta^{14}\text{C}$ chronometer. Lens core estimated birth years, based on sagittal otolith increment counts and corresponding $\Delta^{14}\text{C}$ results for yellowtail snapper samples from U.S. Caribbean were overlaid on the reference chronometer. (dashed lines = 95% prediction intervals).

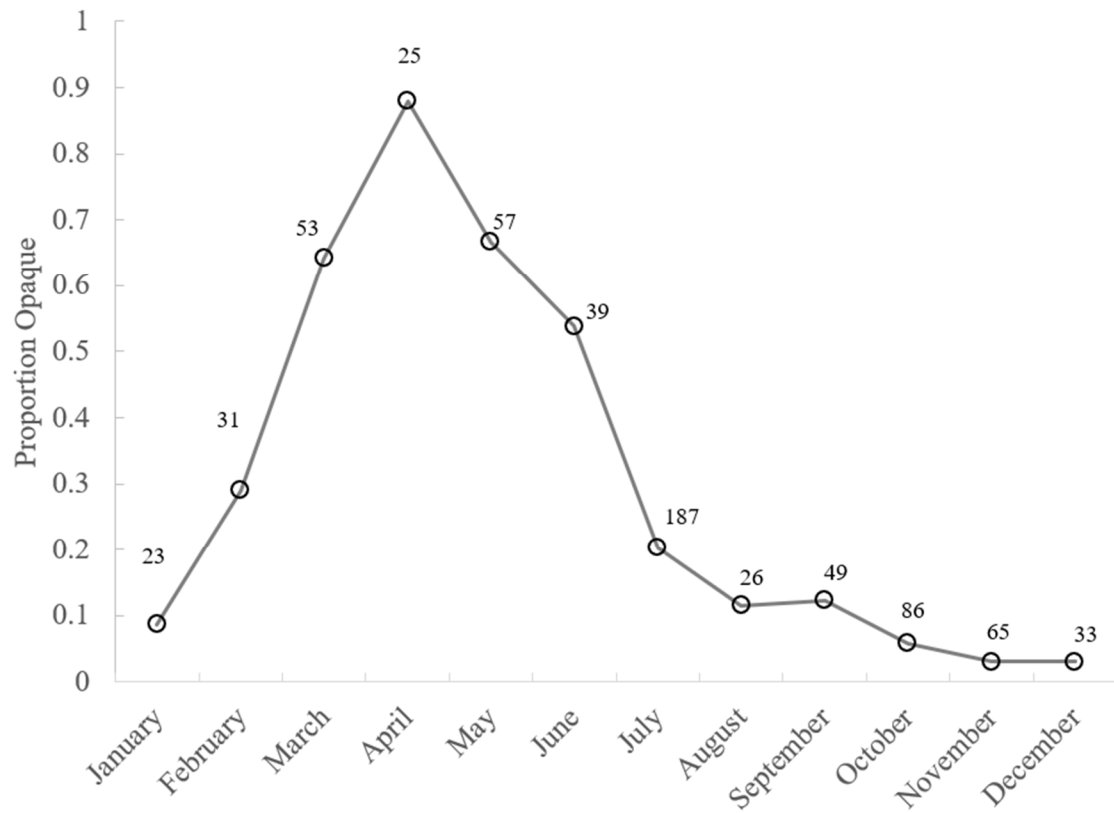


Figure 3.3 Marginal increment analysis. Proportion of otoliths demonstrating opaque zone on the margin. Numbers above each circle indicate total number of otoliths for that month with otolith margin type noted for 3-8 y individuals.

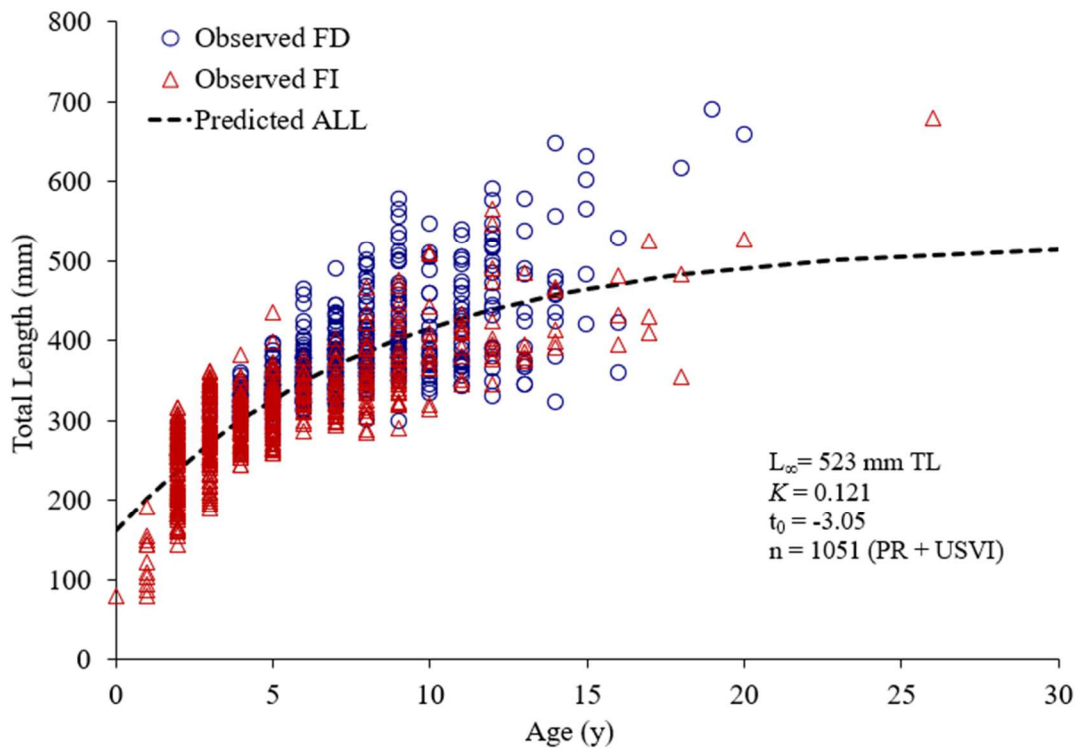


Figure 3.4 von Bertalanffy growth curve of Caribbean yellowtail snapper. 1051 fishery-dependent (FD) and fishery-independent (FI) samples collected from Puerto Rico and USVI were combined into a single growth function. VBGF parameters L_{∞} and k were found to be 523 mm TL and 0.121, respectively.

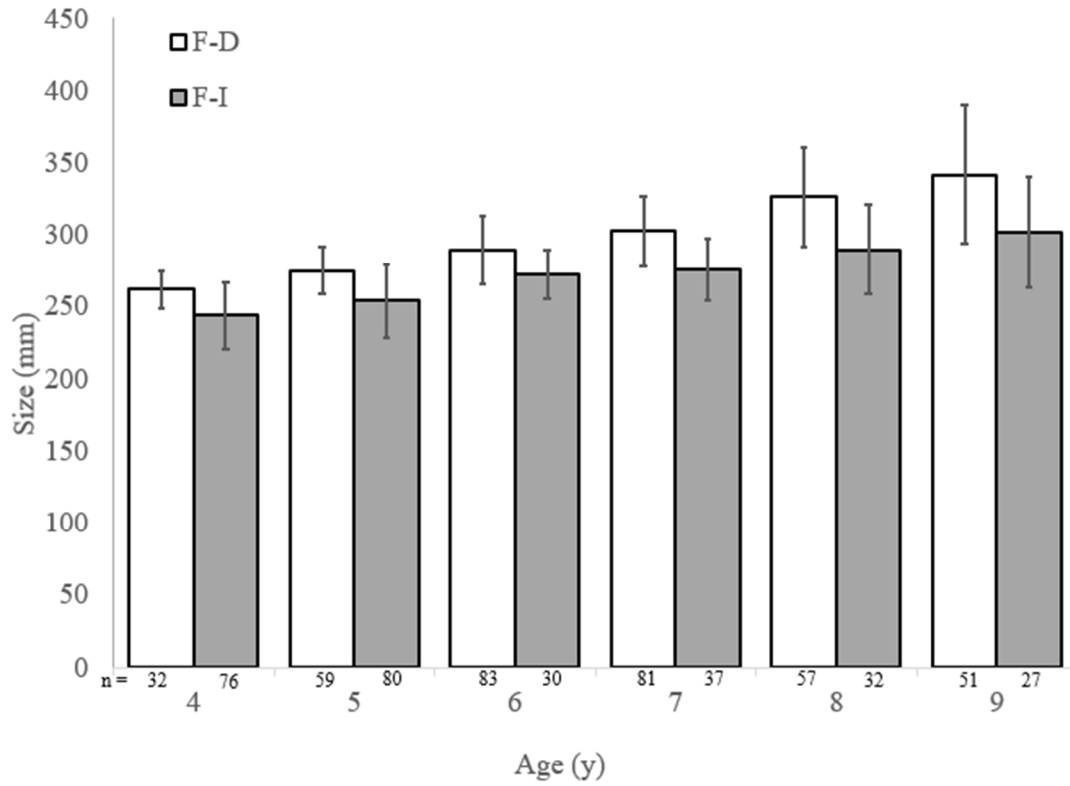


Figure 3.5. Size at age frequencies from ages 4-9. Frequencies of size in yellowtail snapper samples by age class (4-9).

CHAPTER 4

DISCUSSION

This is the first study to comprehensively report on Caribbean yellowtail snapper age, growth, and reproductive biology utilizing F-D and F-I samples. It is also the first study to directly validate the accuracy of ageing estimation for this species. Yellowtail snapper in the U.S. Caribbean is a moderately long-lived species, with a maximum age of 26, and exhibits year-round spawning.

Ageing Validation

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 $\Delta^{14}\text{C}$ chronometer was 17 y, the validated ageing method used in this study documented a maximum age of 26 y for yellowtail snapper from U.S. Caribbean waters. Application of the $\Delta^{14}\text{C}$ chronometer to validate ageing 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; Barnett et al., 2018; Andrews et al., 2019), and mutton snapper *L. analis* (Shervette et al., 2021). However, previous radiocarbon ageing validation efforts of reef fishes have relied on the use of technologically advanced, computerized micromilling systems to extract otolith core material in obtaining the $\Delta^{14}\text{C}$ signal experienced by a fish sample during its birth year

(Andrews et al., 2013; Sanchez et al., 2019; Barnett et al., 2020; Shervette et al., 2021a). The micromilling equipment is essential for coring otoliths because it enables the precise extraction of just the desired targeted material for AMS analysis, but a computerized micromill set-up is cost prohibitive and not easily attainable for most small and medium-sized labs conducting fish life history research on tropical species. A recent study used several GOM reef fish species to demonstrate eye lens cores provide similar $\Delta^{14}\text{C}$ birth year signals compared to otolith cores (Patterson et al., 2021) and eye lens cores provide a low-cost, accessible and accurate alternative for ageing validation efforts with Caribbean reef fish species with small, fragile otoliths (Shervette et al., 2020). The equipment requirements for obtaining the eye lens core of a snapper species are minimal. For the current study, standard forceps and glassware common for fish biology research labs were used. The only additional equipment necessary was access to a muffle furnace so that forceps and glassware could be pre-baked to ensure any rouge carbon sources present were burned off to prevent contamination. The use of eye lens cores to validate ageing estimation of yellowtail snapper in the current study further demonstrates the usefulness of this novel alternative to milled otolith core material.

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 ageing 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 $\Delta^{14}\text{C}$ chronometer 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 $\Delta^{14}\text{C}$ chronometer 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 $\Delta^{14}\text{C}$ 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., 2021a). Therefore, the results of yellowtail snapper ageing validation in the current study provides the most comprehensive evidence to-date that the ageing method used in this study resulted in accurate age estimates.

As previously mentioned, several papers that have examined age and growth in yellowtail snapper have reported on periodicity of growth and increment formation in sagittal otoliths (Johnson, 1983; Garcia et al., 20003; Allman et al., 2005). One study from the Caribbean reported that opaque zones formed from March – May (Manooch and Drennon, 1987). Another study from Florida reported increment formation from May – July (Johnson, 1983). Garcia et al. (2003) found that opaque zone formation occurred

once annually in the spring with a peak in April which is consistent with our observations (Figure 3.3). Caribbean yellowtail snapper peak opaque zone formation coincided with peak spawning. Previous studies on white grunt *Haemulon plumieri* (Potts and Manooch, 2001), and gray triggerfish *Balistes capriscus* (Kelly-Stormer et al., 2017) also have noted a similar relationship between the timing of opaque zone formation and peak spawning period.

Yellowtail Snapper Population Demographics

The male to female sex ratio documented in the current study was slightly skewed toward more females than males, but was within range of sex ratios reported from other studies on yellowtail snapper (Figuerola et al., 1998; Trejo-Martínez et al. 2011). Minor deviations from 1:1 sex ratios are common for gonochoristic fish species and was observed in other yellowtail snapper populations. Male to female sex ratios from previous studies range from 1:0.8 – 1:1.35 (Table 4.1). A study from the southern Gulf of Mexico on yellowtail snapper reproductive biology documented a 1:1.0 male to female ratio (Trejo-Martínez et al., 2011). A study from the Caribbean that utilized gonad histology of yellowtail snapper documented a male to female sex ratio of 1:1.35 (Figuerola et al., 1998).

In the current study, no significant difference in mean size between male and female yellowtail snapper was observed. Previous studies on yellowtail snapper from the GOM, Southeast Florida, and Cuba have also reported that mean size did not differ between male and female yellowtail snapper (Trejo-Martínez et al., 2011; Allman et al., 2005; Figuerola et al., 1998; Claro, 1983). Similar size structure between males and

females has been observed in red snapper *Lutjanus campechanus* from the GOM (Patterson et al., 2001).

The current study documented differences in mean size and size frequency distributions between F-D and F-I samples. This difference is mainly explained by the minimum size limit for commercially caught yellowtail snapper. Previous studies utilizing F-I and F-D samples have also noted differences in mean length between F-D and F-I samples (Allman et al., 2005; Potts and Manooch, 2002). Additionally, gear selectivity can impact size trends among fish samples caught utilizing different collection methods. Sampling programs that utilize randomized sampling designs to obtain F-I samples of reef fishes require the use of a standard series of hook sizes while commercial fishers utilize larger hook sizes to target larger fish. Allman et al. (2018) noted that in their study on age and growth of gray triggerfish, sample source (F-I versus F-D) impacted size trends; the larger hook size used by the commercial fishers resulted in significantly larger F-D samples.

Maximum size of yellowtail snapper from the current study was 538 mm FL/690 mm TL which is well below the maximum reported size attained by this species (682 mm FL/ 863 mm TL; Cervigón, 1993). The maximum reported sizes from Florida studies were 605 mm FL (Allman et al. 2005), 567 mm FL (Johnson 1983), and 561 mm FL (Garcia et al. 2003; Table 4.1). A study from the north Caribbean reported a maximum size for yellowtail of 590 mm FL (Manooch and Drennon 1987). One study on yellowtail snapper from the Yucatan Peninsula had a smaller maximum size (455 mm FL; Trejo-Martinez et al., 2011) than the current study. One possible reason for the smaller maximum size of Caribbean yellowtail snapper in the current study may relate to the

relatively low number of F-D samples; out of over 1700 fish measured, only 481 were F-D and most of those were from commercial boats that mainly target yellowtail snapper with hand-line gear (SEDAR 2016). Florida commercial and recreational gear used to catch yellowtail snapper may employ other hook-and-line gear that fish deeper and utilize larger hook sizes (SEDAR 2020). This is another example of the potential impacts of gear selectivity when comparing life history parameters for a species across investigations utilizing different sample collection methods. Additionally, yellowtail snapper over 700 mm FL have been measured during dockside intercept statistical surveys of commercial catches in the U.S. Caribbean (Stevens et al. 2019). Applying the FL-TL conversion equation derived from the current study (Table 3.2) to a FL = 700 mm yielded an estimated maximum size of > 880 mm TL for the region, which exceeds the maximum reported size for the species. Additional sampling efforts from F-D sources may be needed to ensure that the full upper range of sizes are included for a more comprehensive understanding of life history parameters for U.S. Caribbean yellowtail snapper.

The average maximum size of U.S. Caribbean yellowtail snapper ($L_{\infty} = 390$ mm FL) and the growth coefficient ($K = 0.17$) fell within the lower portion of the ranges for L_{∞} and K reported from other yellowtail snapper growth studies (Table 4.1). Most studies reporting on yellowtail snapper growth have mainly utilized F-D samples (Manooch and Drennon, 1987; Johnson, 1983; Garcia et al., 2003). A study from the north Caribbean examined yellowtail snapper growth for F-D samples collected from 1983-1984 and reported an average maximum size of 503 mm FL and a growth coefficient of 0.14 (Manooch and Drennon, 1987). A Florida study that examined growth of yellowtail

snapper from F-D collections for the years of 1994-1999 reported an average maximum size of 484 mm FL and a growth coefficient of 0.17 (Garcia et al., 2003). Another study from Florida that focused on age and growth of yellowtail snapper from F-D sources collected in 1979-1980 reported an average maximum size of 451 mm FL and a growth coefficient of 0.28. Allman et al. (2005) utilized a combination of F-D and F-I samples to estimate growth for east Florida yellowtail snapper collected from 1980-2001 and reported a more moderate average maximum size of 410 mm FL and a growth coefficient of 0.27. Direct comparisons of growth parameters for a species among studies may be inappropriate due to potential differences in sampling gears, sampling designs, sampling efforts, and even differences in the calculation of the growth model (Shervette et al. 2021b). For yellowtail snapper, several studies reporting on growth only utilized F-D samples (Garcia et al. 2003, Johnson 1983, Manooch and Drennon 1987). A few of the yellowtail snapper growth studies utilized back-calculated size-at-age estimates for estimating growth parameters (Johnson 1983, Manooch and Drennon 1987), while other studies, including the current one, used observed size-at-age data for growth model calculations (Allman et al., 2005).

Regional differences in growth of a species may relate to a combination of factors including inherent differences in growth rates among genetically distinct populations, differences in habitat quality and quantity, differences in fishing pressure, and differences in reproductive output (Shervette et al. 2021b). A more biologically direct approach to compare differences in growth among studies is by examining the size trends at age between or among studies/regions (Zivkov et al. 1999). A comparison of the size ranges reported from two Florida studies for each age class with yellowtail snapper size ranges

from the current study (Figure 4.1) shows that the F-D fish from Florida overlapped in size with yellowtail snapper from the U.S. Caribbean in most age classes (Garcia et al. 2003; Johnson 1983). The main age class where size did not overlap between the two regions was age-1. Florida has a recreational and commercial minimum size limit for yellowtail snapper of 12 in TL (~305 mm TL) so the F-D samples are truncated, lacking fish in the smaller size classes (Figure 4.1). This means that any age-1 fish that did occur in the samples were relatively large as seen in the comparison (Figure 4.1). Additionally, yellowtail snapper populations in the Caribbean are genetically distinct from the Florida population (Sailant et al. 2012) so genetic differences in growth could be a factor.

Another contributing factor to potential differences in growth rates between Caribbean and Florida yellowtail snapper could be the observed differences in spawning seasons; our study documented year-round spawning for yellowtail snapper, while Florida yellowtail snapper spawning occurs over a shorter period (SEDAR 2020). Caribbean yellowtail snapper are potentially investing more energy in spawning and less in somatic growth due to their year-round spawning season compared to Florida yellowtail snapper that spawn for fewer months.

Reproduction

In this study, spawning capable female yellowtail snapper were observed in every month of the year with the exception of October, and actively spawning males were observed in all months. An older study on the reproductive biology of yellowtail snapper from PR waters noted that female spawning capable fish occurred from February-October (Figuerola et al. 1998). The combined results of the two studies support the general findings that yellowtail snapper exhibit year-round spawning in Caribbean waters. Other

studies reporting on yellowtail snapper spawning seasonality have also observed year-round spawning (Munro et al., 1973; Trejo-Martinez et al., 2011). Caribbean yellowtail snapper in the current study had a peak in spawning from March – April which is consistent with peak spawning period for the species documented in waters of the Yucatan Peninsula (Trejo-Martinez et al., 2011), Cuba (Claro, 1983), and Jamaica (Munro et al., 1973). As previously noted, yellowtail snapper populations from regions at higher latitudes experience a less protracted spawning season compared to populations at lower latitudes. Spawning season in Florida is shorter than that observed in the Caribbean and extends from spring to summer with a peak from May – July (Muller et al., 2003). The signal which yellowtail utilize to initiate spawning aggregations within peak months is not fully known. Trejo-Martinez et al. (2011) speculated that the new moon phase may play a role in igniting aggregations, but further study is necessary to determine if the monthly spawning pattern of yellowtail snapper correlates with moon phase.

Table 4.1 A comparison of yellowtail snapper studies. NA = not applicable; NR = not reported; *indicates that lengths were estimated from a figure

Study Area	Time period (n) sample source	Size range (mean) mm	Age range (mean)	Sex ratio M:F	Spawning season (peak)	$L_{\infty}/K/t_0$ Opaque zone formation	Reference; comments
U.S. Caribbean	2013-2020 (1685) F-I + F-D	TL: 94-690 (323) FL: 84-538	All: 0-26 (6.4) F-D: 3-20 (8.0) F-I: 0-26 (5.1)	1:1.14	All moths except October (Mar-Apr)	TL: 537/0.11/-3.32 FL: 390/0.17/-1.99 Mar-Jun	Current study; utilized gonad histology; validation via radiocarbon
USVI	2016-2020 (365) F-D	FL: 249-538 (322)	4-20 (8.4)	NA	NA	FL: 426/0.14/-1.99	Current study; growth modelled for just USVI F-D samples
Puerto Rico	1996-1997 (322) F-D	FL: 111-475 (253)	NR	1:1.35	Feb-Oct (Apr- Jul)	NR	Figuerola et al. 1998; utilized gonad histology
USVI; <10% from PR	1983-1984 (468) F-D	FL: 140-590	1-17	NR	NR	FL: 503/0.14/-0.96 Mar-May	Manooch and Drennon 1987; used back-calculated size-at-age
Jamaica	1969-1971 (575) F-D	NR	NR	1:0.8	Year-round (Feb-Apr; Sep)	NR	Munro et al. 1973
Campeche Bank, Mexico	2008-2009 (1657) F-D	FL: 119-455	NR	1:1.0	Year-round (Apr-May)	NR	Trejo-Martinez et al. 2011

Study Area	Time period (n) sample source	Size range (mean) mm	Age range (mean)	Sex ratio M:F	Spawning season (peak)	$L_{\infty}/K/t_0$ Opaque zone formation	Reference; comments
FL east coast	1980-2002 (6679) F-I + F-D	FL: 115-605 (312) nFL: 148-540 sFL: 152-528	All: 1-17 (4.0) nFL: 1-12 (2.6) sFL: 1-17 (4.7)	NR	NR	FL: 410/0.27/-2.03 $t_0=0$: 365/0.65 Feb-May	Allman et al. 2005
Southeast FL	1994-1999 (1528) F-D	FL: 220-561	1-13	NR	(May-Jun)	FL: 484/0.17/-1.87 Mar-May	Garcia et al. 2003
Southeast FL	1979-1980 807 F-D	FL: 134-567	1-14	NR	NR	FL:451/0.28/-0.36	Johnson 1983
Florida	1980-2017 42,985 F-D (<1% F-I)	FL: 100-600*	0-28	NR	NR	FL: 426/0.20/-1.93 Mar-Jun	SEDAR 2020; Growth model accounted for truncated size-at-age
Cuba	1972 – 1974 3,593 F-D	FL: 160-460	0-6	NR	(April)	FL: 681/0.159/-0.85 Mar – Jun	Claro 1983

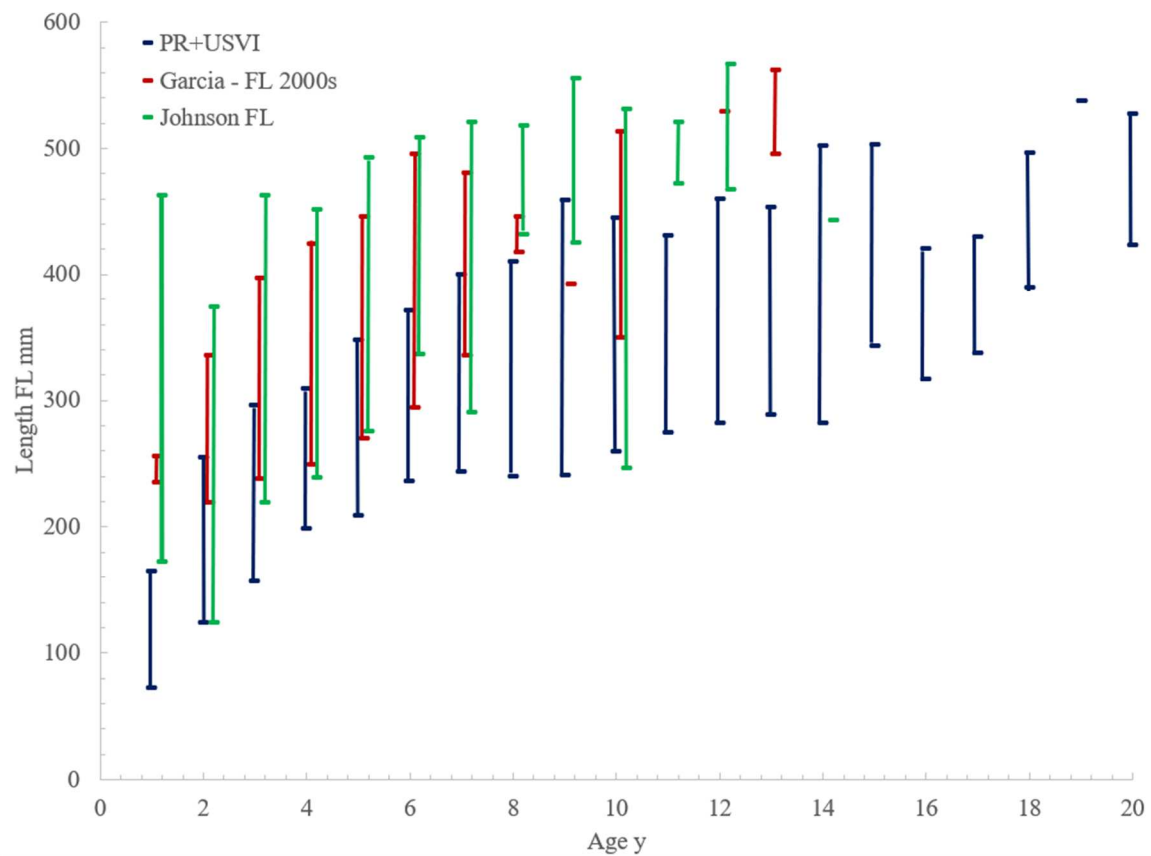


Figure 4.1 Comparison of observed size range at age between studies. The current study is compared to size range at age of two Florida studies (Garcia et al., 2003; Johnson, 1983).

CHAPTER 5

CONCLUSIONS

The current study provided critical life history information on population demographics, growth, and spawning seasonality previously unknown for U.S. Caribbean waters. These data are critical for the fisheries management stock assessment process that evaluates the impacts of exploitation rates of fisheries species, determines if stocks are overfished or experiencing overfishing, and results in recommendations for scientific-based management strategies to ensure the long-term sustainability of fisheries resources. The current study also provided direct validation of ageing estimates of this species, an important step in assessing the accuracy of ageing methods for a fisheries species. The current study showed that Caribbean yellowtail snapper can reach a maximum age of at least 26, have a relatively slow growth rate, and exhibit year-round spawning.

REFERENCES

- Allman, R. J., W. F. Patterson III, C. L. Fioramonti, and A. E. Pacicco. 2018. Factors affecting estimates of size at age and growth in grey triggerfish *Balistes capriscus* from the northern Gulf of Mexico. *Journal of fish biology* **92**(2):386-398.
- Allman, R. J. 2007. Small-scale spatial variation in the population structure of vermilion snapper (*Rhomboplites aurorubens*) from the northeast Gulf of Mexico. *Fisheries Research* **88**(1-3):88-99.
- Allman, R. J., L. R. Barbieri, and C. T. Bartels. 2005. Regional and fishery-specific patterns of age and growth of yellowtail snapper, *Ocyurus chrysurus*. *Gulf of Mexico Science* **23**(2):8.
- Andrews, A. H., B. K. Barnett, R. J. Allman, R. P. Moyer, and H. D. Trowbridge. 2013. Great longevity of speckled hind (*Epinephelus drummondhayi*), a deep-water grouper, with novel use of postbomb radiocarbon dating in the Gulf of Mexico. *Canadian Journal of Fisheries and Aquatic Sciences* **70**:1131-1140.
- Andrews, A. H., B. K. Barnett, J. P. Chanton, L. A. Thornton, and R. J. Allman. 2020. Influences of upper Floridian aquifer on radiocarbon in the otoliths of gray snapper (*Lutjanus griseus*) in the Gulf of Mexico. *Radiocarbon*:1-20.
- Andrews, A. H., C. Yeman, C. Welte, B. Hattendorf, L. Wacker, and M. Christl. 2019. Laser ablation–accelerator mass spectrometry reveals complete bomb ¹⁴C signal in an otolith with confirmation of 60-year longevity for red snapper (*Lutjanus campechanus*). *Marine and Freshwater Research*.

- Baker, S. J. M., and C. A. Wilson. 2001. Use of bomb radiocarbon to validate otolith section ages of red snapper *Lutjanus campechanus* from the northern Gulf of Mexico. *Limnology and Oceanography* **46**:1819-1824.
- Barbieri, L.R. and J. A. Colvocoresss. 2003. Southeast Florida reef fish abundance and biology. Five-year performance report to the U.S.
- Barnett, B. K., J. P. Chanton, R. Ahrens, L. Thornton, and W. F. Patterson III. 2020. Life history of northern Gulf of Mexico Warsaw grouper *Hyporthodus nigrilus* inferred from otolith radiocarbon analysis. *PloS one* **15**:e0228254.
- Barnett, B. K., L. Thornton, R. Allman, J. P. Chanton, W. F. Patterson III, and H. e. E. Anderson. 2018. Linear decline in red snapper (*Lutjanus campechanus*) otolith $\Delta^{14}\text{C}$ extends the utility of the bomb radiocarbon chronometer for fish age validation in the Northern Gulf of Mexico. *ICES Journal of Marine Science* **75**:1664-1671.
- Beamish, R. J., & D. A. Fournier. 1981. A method for comparing the precision of a set of age determinations. *Canadian Journal of Fisheries and Aquatic Sciences* **38(8)**:982-983.
- Branch, T. A., O. P. Jensen, D. Ricard, Y. Ye, and R. A. Y. Hilborn. 2011. Contrasting global trends in marine fishery status obtained from catches and from stock assessments. *Conservation biology* **25(4)**:777-786.
- Broecker, W. S., and T.-H. Peng. 1982. *Tracers in the Sea*, Lamont–Doherty Geological Observatory, Columbia University, Palisades, N.Y.

- Campana, S. E. 2001. Accuracy, precision, and quality control in age determination, including a review of the use and abuse of age validation methods. *J. Fish Biol.* **59**:197–242.
- Campana, S. E., and C. M. Jones. 1998. Radiocarbon from nuclear testing applied to age validation of black drum, *Pogonias cromis*. *Fishery Bulletin* **96**.
- Carroll, J., K. Rynerson, and B. Barbara, (2019). SEDAR64-DW-07.
- Catanzaro, D., C. Rogers, Z. Hillis-Starr, R. Nemeth, and M. Taylor (n.d.). Status of Coral Reefs in the U.S. Virgin Islands. Retrieved August 05, 2020, from https://www.coris.noaa.gov/portals/pdfs/status_coralreef_usvi.pdf
- Causey, B., J. Delaney, E. Diaz, R. E. Dodge, J. R. Garcia, J. Higgins, ... and D. D. Turgeon. 2002. Status of coral reefs in the US Caribbean and Gulf of Mexico: Florida, Texas, Puerto Rico, US Virgin Islands and Navassa.
- Cervigón, F. 1993. Los peces marinos de Venezuela. Volume 2. Cientifica Roques, Caracas, Venezuela. 497 pp.
- CFMC. 1985. Fisheries management plan, final environmental impact statement, and draft regulatory impact review for the shallow-water reefish fishery of Puerto Rico and the U.S. Virgin Islands. Caribbean Fisheries Management Council and NOAA NMFS.
- Chale-Matsau J. R., A. Govender, L. E. Beckley. 2001. Age, growth and retrospective stock assessment of an economically extinct sparid fish, *Polysteganus undulosus*, from South Africa. *Fish Res* **51**(1):87–92. [https://doi.org/10.1016/S0165-7836\(00\)00235-6](https://doi.org/10.1016/S0165-7836(00)00235-6)

- Choat, J., J. Kritzer, and J. Ackerman. 2009. Ageing in coral reef fishes: do we need to validate the periodicity of increment formation for every species of fish for which we collect age-based demographic data? Pages 23-54 Tropical fish otoliths: Information for assessment, management and ecology. Springer.
- Choat, J. H., Robertson, D. R., Ackerman, J., & Posada, J. M. (2003). An age-based demographic analysis of the Caribbean stoplight parrotfish *Sparisoma viride*. Marine Ecology Progress Series, 246, 265–277.
- Claro, R., Y. Sadovy de Mitcheson, K. C. Lindeman, and A. R. García-Cagide. 2009. Historical analysis of Cuban commercial fishing effort and the effects of management interventions on important reef fishes from 1960–2005. Fisheries Research **99**:7–16.
- Claro, R., K.C. Lindeman, and L.R. Parenti. 2001. Ecology of the marine fishes of Cuba. Smithsonian Institution Press, Washington and London. 253p
- Claro, R. 1983c. Ecology and life cycle of the knight *Lutjanus griseus* (Linnaeus), on the Cuban platform. Identity, distribution and habitat, feeding and reproduction. Rep. Invest. Oceanol. Acad. Science Cuba **7**:1-30.
- Claro, R. 1983. Ecología y ciclo de vida de la rabirrubia, *Ocyurus chrysurus* (Bloch), en la plataforma Cubana II. Edad y crecimiento, estructura de poblaciones, y pesquerías. Academia de Ciencias de Cuba, Reporte de Investigación del Instituto de Oceanología **19**:33 p.
- Collins, M. R. 1984. *Hatshekia oblonga* (Copepoda, Caligoida) from yellowtail snapper (*Ocyurus chrysurus*) in the Florida Keys. Journal of Wildlife Diseases **20**(1):63-64.

- Collins, L.A. and J. Finucane. 1989. Reproductive biology of yellowtail snapper, *Ocyurus chrysurus*, from the Florida Keys. US Department of Commerce, NOAA, NMFS, SEFSC, Panama City Laboratory, PCL Contrib. No. 89-11, 23p.
- Cummings, N. J. 2007. The Commercial Yellowtail Snapper fishery off Puerto Rico, 1983-2003.
- Cummings N.J. 2004. The Commercial Reef Fish Fishery in Puerto Rico with Emphasis on Yellowtail Snapper, *Ocyurus chrysurus*: Landings, Nominal Effort, and Catch Per Unit of Effort from 1983 through 2003. Sustainable Fisheries Division Contribution (SFD) No. 2004-045 and SEDAR-8 Data Workshop Report (DW) Doc-8. Charleston, SC, USA: Southeast Data Assessment and Review (SEDAR), 81 pp
- Cummings, N. 2004. The biology of yellowtail snapper, *Ocyurus chrysurus*, with emphasis on populations in the Caribbean. Sustainable Fisheries Division Contribution SFD. No. 2004- 045 [SEDAR8-DW-4. SEDAR, North Charleston, SC. 28 pp.]
- de Albornoz, C. and M.E. Ramiro. 1988. Estudio biológico de la rabirrubia (*Ocyurus chrysurus*) en el W de la plataforma SE de Cuba. I. Edad y crecimiento. Rev. Invest. Mar. **9**(1):9–24 (in Spanish).
- Druffel, E. M., and T. W. Linick. 1978. Radiocarbon in annual coral rings of Florida. Geophysical Research Letters **5**(11):913-916.
- Figuerola, M., D. Matos-Caraballo and W. Torres. 1998. Maturation and reproductive seasonality of four reef fish species in Puerto Rico. Proc. Gulf Carib. Fish. Inst. **50**:938–968.

- Fischer, A. J., M. S. Baker Jr, C. A. Wilson, and D. L. Nieland. 2005. Age, growth, mortality, and radiometric age validation of gray snapper (*Lutjanus griseus*) from Louisiana. *Fishery Bulletin* **103**:307-319.
- Garcia, E. R., J. C. Potts, R. A. Rulifson, and C. S. Manooch. 2003. Age and growth of yellowtail snapper, *Ocyurus chrysurus*, from the southeastern United States. *Bulletin of Marine Science* **72**:909-921.
- Grimes, C. B. 1976. Certain aspects of the life history of the vermilion snapper *Rhomboplites aurorubens* (Cuvier) from North and South Carolina waters. Ph.D. Diss., Univ. North Carolina, Chapel Hill, North Carolina. 240 p.
- GMFMC. 2013. Framework Action to Set the Annual Catch Limit and Bag Limit for Vermilion Snapper, Set Annual Catch Limit for Yellowtail Snapper, and Modify the Venting Tool Requirement. 171 pp.
- Harris, P. J., D. M. Wyanski, D. B. White, P. P. Mikell, and P. B. Eyo. 2007. Age, growth, and reproduction of greater amberjack off the southeastern US Atlantic coast. *Transactions of the American Fisheries Society* **136**(6):1534-1545.
- Hoese, H.D. and R.H. Moore. 1998. *Fishes of the Gulf of Mexico: Texas, Louisiana, and adjacent waters*, 2nd Edition. Texas A&M University Press, College Station, Texas
- Johnson, A. G. 1983. Age and growth of yellowtail snapper from South Florida. *Transactions of the American Fisheries Society* **112**:173-177.
- Jones, D. D., J. M. R. Hernández, and V. R. Shervette. 2021. Princess parrotfish *Scarus taeniopterus* age, growth, maturity, and transition. *Environmental Biology of Fishes* **104**(5):581-595.

- Kadison, E., M. Brandt, R. Nemeth, J. Martens, J. Blondeau, T. Smith. 2017. Abundance of commercially important reef fish indicates different levels of over-exploitation across shelves of the U.S. Virgin Islands. Plos One **12**(7): e0180063.
<https://doi.org/10.1371/journal.pone.0180063>
- Kalish, J. M. (1989). Otolith microchemistry: validation of the effects of physiology, age and environment on otolith composition. Journal of Experimental Marine Biology and Ecology **132**(3):151-178.
- Kalish, J. M. 1993. Pre-and post-bomb radiocarbon in fish otoliths. Earth and Planetary Science Letters **114**:549-554.
- Kastelle, C. R., D. K. Kimura, and B. J. Goetz. 2008. Bomb radiocarbon age validation of Pacific Ocean perch (*Sebastes alutus*) using new statistical methods. Canadian Journal of Fisheries and Aquatic Sciences **65**(6):1101-1112.
- Kelly-Stormer, A., V. Shervette, K. Kolmos, D. Wyanski, T. Smart, C. McDonough, and M. J. Reichert. 2017. Gray triggerfish reproductive biology, age, and growth off the Atlantic Coast of the Southeastern USA. Transactions of the American Fisheries Society **146**:523-538.
- Kimmel, J. J. 1985. A new species-time method for visual assessment of fishes and its comparison with established methods. Environmental Biology of Fishes **12**(1):23-32.
- King, J. R., and G. A. McFarlane. 2003. Marine fish life history strategies: applications to fishery management. Fisheries Management and Ecology, **10**(4):249-264.
- Knutson, D. W., R. W. Buddemeier, and S. V. Smith. 1972. Coral chronometers: seasonal growth bands in reef corals. Science **177**(4045):270-272.

- Kojis, B. L., and N. J. Quinn. 2006. A census of US Virgin Islands commercial fishers at the start of the 21st century. In Proceedings of the 10th International Coral Reef Symposium **1326**(1334):417-423
- Kojis, B.L., N.J. Quinn, J.J. Agar. 2017. Census of licensed fishers of the US Virgin Islands (2016)
- Lek, E., D. Fairclough, N. Hall, S. Hesp, and I. Potter. 2012. Do the maximum sizes, ages and patterns of growth of three reef-dwelling labrid species at two latitudes differ in a manner conforming to the metabolic theory of ecology? Journal of Fish Biology **81**:1936–1962.
- Lindholm, J., L. Kaufman, S. Miller, A. Wagschal, and M. New- ville. 2005. Movement of yellowtail snapper (*Ocyurus chrysurus* Block 1790) and black grouper (*Mycteroperca bonaci* Poey 1860) in the northern Florida Keys National Marine Sanctuary as determined by acoustic telemetry. Marine Sanctuaries Conservation Series MSD-05-4. Silver Spring, MD: U.S. Department of Commerce, National Oceanic and Atmospheric Administration, Marine Sanctuaries Division, 17 pp.
- Manooch, C., and C. Drennon. 1987. Age and growth of yellowtail snapper and queen triggerfish collected from the U.S. Virgin Islands and Puerto Rico. Fisheries Research **6**:53-68.
- Meekan, M., J. Ackerman, and G. Wellington. 2001. Demography and age structures of coral reef damselfishes in the tropical eastern Pacific Ocean. Marine Ecology Progress Series, **212**:223–232.
- Muller, R. G., M. D. Murphy, J. deSilva, L. R. Barbieri. 2003. A stock assessment report of yellowtail snapper, *Ocyurus chrysurus*, in the southeast United States. SEDAR

- 3 Assessment Report 1. South Atlantic Fishery Management Council. Charleston, SC. 330p.
- (http://www.sefsc.noaa.gov/sedar/download/SEDAR3_SAR1_Final.pdf?id=DOCUMENT)
- Munro, J. L., V. C. Gaut, R. Thompson, and P. H. Reeson. 1973. The spawning seasons of Caribbean reef fishes. *Journal of Fish Biology* **5**(1):69-84.
- National Oceanic and Atmospheric Administration, (2009, June 29). CoRIS - Regional Portal - Puerto Rico. Retrieved August 05, 2020, from <https://www.coris.noaa.gov/portals/puertorico.html>
- Nozaki, Y., D. M. Rye, K. K. Turekian, and R. E. Dodge. 1978. A 200-year record of carbon-13 and carbon-14 variations in a Bermuda coral. *Geophysical Research Letters* **5**(10):825-828.
- Patterson, W. F., B. K. Barnett, T. C. TinHan, and S. K. Lowerre-Barbieri. 2021. Eye lens $D^{14}C$ validates otolith-derived age estimates of Gulf of Mexico reef fishes. *Canadian Journal of Fisheries and Aquatic Sciences*. doi: 10.1139/cjfas-2020-0237.
- Patterson III, W. F., J. H. Cowan Jr, C. A. Wilson, and R. L. Shipp. 2001. Age and growth of red snapper, *Lutjanus campechanus*, from an artificial reef area off Alabama in the northern Gulf of Mexico. *Fishery Bulletin*, **99**(4):617-628
- Pauly, D. 1978. A preliminary compilation of fish length growth parameters.
- Piedra, G. (1969). Materials on the biology of the yellowtail snapper (*Ocyurus chrysurus* Bloch). Soviet-Cuban fishery research. Translated from Russian: Israel Program for Scientific Translations, Jerusalem, Israel 251-269.

- Potts, J. C., and C. S. Manooch III. 2002. Estimated ages of red porgy (*Pagrus pagrus*) from fishery-dependent and fishery-independent data and a comparison of growth parameters. *Fishery Bulletin*, **100**(1):81-89.
- Potts, J. C., and C. S. Manooch. 2001. Differences in the age and growth of white grunt (*Haemulon plumieri*) from North Carolina and South Carolina compared with southeast Florida. *Bulletin of Marine Science* **68**(1):1-12.
- Rivera Hernández, J. M., N. Peña Alvarado, K. Correa Vélez, R. Nemeth, R. Appeldoorn, and V. Shervette. 2019. Queen Triggerfish Reproductive Biology in US Caribbean Waters. *Transactions of the American Fisheries Society* **148**(1):134-147.
- Sanchez, P. J., J. P. Pinsky, and J. R. Rooker. 2019. Bomb Radiocarbon Age Validation of Warsaw Grouper and Snowy Grouper. *Fisheries* **44**:524-533.
- SEDAR (2016). SEDAR 41 – South Atlantic Red Snapper Assessment Report. North Charleston, SC: Southeast Data, Assessment, and Review.
- SEDAR (2016). SEDAR 46 Stock Assessment Report – U.S. Caribbean Data-Limited Species. North Charleston, SC: Southeast Data, Assessment, and Review.
- SEDAR 2020. SEDAR 64 Stock Assessment Report - Southeastern US Yellowtail Snapper. North Charleston, SC: Southeast Data, Assessment, and Review.
- Shepard, K. E., W. F. Patterson, D. A. DeVries, and M. Ortiz. 2010. Contemporary versus historical estimates of king mackerel (*Scomberomorus cavalla*) age and growth in the US Atlantic Ocean and Gulf of Mexico. *Bulletin of Marine Science* **86**:515-532.

- Shervette, V., J. M. Rivera Hernández, D. Drake, N. Peña-Alvarado, W. Santiago Soler, and J. Magras. 2020. NOAA COOPERATIVE RESEARCH PROGRAM FINAL REPORT: Caribbean Hogfish: documenting critical life history information for a data-poor species in collaboration with U.S. Caribbean fishers.
- Shervette, V. R., K. E. Overly, and J. M. Rivera Hernández. 2021a. Radiocarbon in otoliths of tropical marine fishes: Reference $\Delta^{14}\text{C}$ chronology for north Caribbean waters. *PloS one* **16**:e0251442
- Shervette, V. R., Rivera Hernández, J. M., & Nunoo, F. K. E. 2021b. Age and growth of grey triggerfish *Balistes capriscus* from trans-Atlantic populations. *Journal of Fish Biology*, 98(4), 1120-1136.
- Stuiver, M., and H. A. Polach. 1977. Discussion reporting of ^{14}C data. *Radiocarbon* **19**(3):355-363.
- Smylie M, V. Shervette, C. McDonough. 2016. Age, growth, and reproduction in two coastal populations of longnose gars. *Trans Am Fish Soc* **145**(1):120–135.
- Stuiver, M., and H. A. Polach. 1977. Discussion reporting of ^{14}C data. *Radiocarbon* **19**(3):355-363.
- Thompson, R., and J. L. Munro. 1974. The biology, ecology and bioeconomics of the snappers, Lutjanidae. In Munro, J.L. (ed.) Caribbean coral reef fisheries resources. Manila: ICLARM. Studies Review 7, pp. 94–109.
- Trejo-Martínez, J., T. Brulé, A. Mena-Loría, T. Colás-Marrufo, and M. Sánchez-Crespo. 2011. Reproductive aspects of the yellowtail snapper *Ocyurus chrysurus* from the southern Gulf of Mexico. *Journal of Fish Biology* **79**:915-936.
- Turekian, K. K., J. K. Cochran, Y. Nozaki, I. Thompson, and D. S. Jones. 1982. Determination of shell deposition rates of *Arctica islandica* from the New York

- Bight using natural ^{228}Ra and ^{228}Th and bomb-produced ^{14}C . *Limnology and Oceanography* **27**(4):737-741.
- Uehara, M., A. Ebisawa, and I. Ohta. 2020. Comparative age-specific demography of four commercially important deep-water snappers: implication for fishery management of a long-lived lutjanid. *Journal of Fish Biology* **97**(1):121-136.
- Vaughan, D., A. Schueller, J. Smith, and S. VanderKooy. 2011. SEDAR 27: Gulf Menhaden stock assessment report. Southeast Data, Assessment, and Review, North Charleston, SC.
- Watson, M. J., J. L. Munro, and F. R. Gell. 2002. Settlement, movement, and early juvenile mortality of the yellowtail snapper, *Ocyurus chrysurus*. *Marine Ecology Progress Series* **237**:247–256.
- Weidman, C. R., and G. A. Jones. 1993. A shell-derived time history of bomb ^{14}C on Georges Bank and its Labrador Sea implications. *Journal of Geophysical Research: Oceans* **98**(C8):14577-14588.
- Zanini, C., E. Gerbaudo, E. Ercole, A. Vendramin, and M. Forni. 2012. Evaluation of two commercial and three home-made fixatives for the substitution of formalin: a formaldehyde – free laboratory is possible. *Environmental Health* **11**(1):59.
- Živkov, M. T., T. A. Trichkova, and G.N. Raikova-Petrova. 1999. Biological reasons for the unsuitability of growth parameters and indices for comparing fish growth. *Environmental Biology of Fishes* **54**(1):67-76.