4-19-2023

Age and Growth for Three Members of the Family Gempylidae: Escolar (Lepidocybium Flavobrunnuem), Oilfish (Ruvettus Pretiosus), and Snake Mackerel (Gempylus Serpens)

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Thesis of
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Submitted in Partial Fulfillment of the Requirements for the Degree of

Master of Science
Marine Science

Nova Southeastern University
Halmos College of Arts and Sciences

April 2023

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Age and growth for three members of the family Gempylidae: Escolar (*Lepidocybium flavobrunnuem*), Oilfish (*Ruvettus pretiosus*), and Snake Mackerel (*Gempylus serpens*).

By

Sydney Daniels

Submitted to the Faculty of Halmos College of Arts and Sciences in partial fulfillment of the requirements for the degree of Master of Science with a specialty in:

Marine Science

Nova Southeastern University

April 2023

Abstract

Escolar, *Lepidocybium flavobrunnuem* (Smith, 1849), Oilfish, *Ruvettus pretiosus* (Cocco, 1829), and Snake Mackerel, *Gempylus serpens* (Cuvier, 1829) belong to the family Gempylidae and are bycatch of the tuna-targeting pelagic longline fishery. There is limited know life-history information on these mesopelagic fishes, especially regarding growth rates. Age estimates were assigned by counting pairs of increment bands formed on the sagittal otoliths of Escolar (n = 133), Oilfish (n = 49), and Snake Mackerel (n = 46) collected between 2007 and 2022. Marginal increment analyses were used to validate age estimates and periodicity of increment formation, but no significant trends were observed and annual band deposition could not be confirmed. Length-frequency analyses were performed on NOAA pelagic observer catch data ranging from 1992-2020 and predicted theoretical maximum size (L_∞), growth coefficient (k), time of hatching (t_{anchor}), and age bins. Five growth functions were modeled using maximum likelihood (ML) and nonlinear least-squares (NLS) techniques. The Akaike's information criteria (AICc) indicated that the Logistic growth function was the best fit for fork length-at-age data for Escolar, the modified VBGF (ML) and 2-parameter VBGF (NLS) were the best fit for fork length-at-age data for Oilfish, and the 2-parameter VBGF was the best fit for fork length-at-age data for Snake Mackerel. Ultimately, sample size and gear selectivity limited this study, estimating parameters outside expected ranges and leading to issues in those predicted models. The data collected in this study is a starting point in understanding growth rates of these valuable non-target fishes.

Acknowledgments

Table of Contents

List of Tables

Introduction

Study Species

Escolar, Oilfish, and Snake Mackerel are fishes in the family Gempylidae, known to be large, swift mesopelagic predators, often with fang-like teeth and elongate semifusiform body shapes (Nakamura & Parin, 1993). These three fishes are all widely distributed in tropical and temperate oceans between 40°N and 40°S (Nishikawa, 1982; Nakamura & Parin, 1993; Riede, 2004). They spend the daylight hours at depths typically greater than 250 meters, over or near the continental slope, and migrate upwards in the water column to feed on squid, crustaceans, and a variety of fishes in waters as shallow as 60 meters at night (Nakamura & Parin, 1993; Pakhorukov & Boltachev, 2001; Kerstetter et al., 2008). Escolar, *Lepidocybium flavobrunnuem* (Smith, 1849) are typically black or dark brown in color, with large iridescent green-gold eyes that aid in low-light foraging (Merret, 1968; Nakamura & Parin, 1993). They have been recorded with maximum standard lengths between 150-200 centimeters and are believed to reach sexual maturity at 30-35cm (Maskimov, 1970; Nakamura & Parin 1993). Oilfish, *Ruvettus pretiosus* (Cocco, 1829), appear dark grey or brown in color and are covered in scales interspersed with spinous bony tubercles, making the skin very rough (Nakamura & Parin, 1993). Oilfish utilize their scales to their advantage in a unique hunting strategy, using their powerful caudal fin to dart at speeds of 5-7m/s and inflict severe blows to the prey items (Pakhorukov & Boltachev, 2001). Fresh squids with scraped skin were repeatedly found within the stomachs of Oilfish, reinforcing the success of this hunting pattern (Pakhorukov & Boltachev, 2001). Oilfish can range in maximum standard length from 150 cm to 3 m long, and no length-at-maturity data currently exist for Oilfish (Nakamura & Parin, 1993; Keller & Kerstetter, 2014). Snake Mackerel, *Gempylus serpens* (Cuvier, 1829) has a much more elongated and compressed body form than Escolar and Oilfish (Nakamura & Parin, 1993). Snake Mackerel typically grow to between 60-100 centimeters standard length, with males reaching sexual maturity around 43cm in length and females around 50cm (Nakamura & Parin, 1993; Keller & Kerstetter, 2014).

The family Gempylidae and the family Trichiuridae form the monophyletic superfamily Trichiuroidea, a sister to the family Scombridae (Brendtro, 2006). Historically, the suborder Scombroidei was accepted to include five families: Gempylidae, Trichiuridae (cutlassfishes), Scombridae (mackerels, tuna, and bonitos), Istiophoridae (billfishes, marlins, and sailfishes), and Xiphiidae (swordfishes) (Johnson, 1986). While gempylids and trichiurids are considered more

primitive scombroids, they exhibit a first dorsal pterygiophore inserting alone in the second interneural space, which is a derived trait unique to scombroids (Johnson, 1986). Molecular and genomic data from an updated classification study by Betancur-R and colleagues (2017) has grouped the family Gempylidae along with the families Scombridae and Trichiuridae, among others, into the order Scombriformes, with families Istiophoridae and Xiphiidae creating their own order Istiophoriformes.

Global importance of mesopelagic fishes

Mesopelagic fishes, especially those that perform synchronous or asynchronous vertical migration, provide important contributions to the global biological carbon pump. These fishes ingest carbon at the surface, migrate back to depth, and then lose that carbon in the form of excretory products, defecation, respiration, and mortality (Woodstock et al., 2022). Approximately 61% of carbon ingested by mesopelagic fishes in the Gulf of Mexico is exported and sequestered at depth, proving to be an integral part of the removal of carbon from surface waters (Woodstock et al., 2022).

Mesopelagic fishes also provide valuable resources to human populations, being used mostly for fishmeal and fish oil, rich in omega-3 fatty acids (Moore, 1999). Few deep-water fishes, such as those targeted in this study, have been harvested for human consumption. Despite being sold in restaurants and markets around the globe, the ingestion of Escolar and Oilfish can be problematic (Brendtro et al., 2008). Escolar and Oilfish are not able to metabolize wax esters naturally found in their diet, forcing them to deposit these compounds in their tissues and leaving their body weight approximately 20% indigestible oil (Nichols et al., 2001; Rochman et al., 2016; Aldsworth, 2017). These esters, commonly referred to as gempylotoxins, have purgative properties that lead to a variety of relatively short-lived gastrointestinal symptoms such as numbness of tongue, headache, dizziness, nausea and vomiting, and oily diarrhea called 'keriorrhea' (Shadbolt et al., 2002; Feldman et al., 2005). In addition to high levels of gempylotoxin in Escolar and Oilfish, these species exhibit high concentrations of histidine in their tissue, more commonly seen in the family Scombridae (Feldman et al., 2005; Aldsworth, 2017). If these fishes are not adequately refrigerated or left too long before cooking, bacteria multiply and convert histidine to histamine and other amines, collectively referred to as scombrotoxin, which has the potential to be more life-threatening than keriorrhea (Feldman et al., 2005; Ling et al., 2008). The United States

2

permits the sale of Escolar and Oilfish with the FDA advising against ingesting large quantities (Aldsworth, 2017). Australia, another country permitting the consumption of Escolar, catches up to 400 tons of the fish annually, while Japan, South Korea, and Italy have banned the sale of Escolar and Oilfish altogether (Shadboldt et al., 2002; Aldsworth, 2017).

Escolar, Oilfish, and Snake Mackerel are non-target species of pelagic longline fisheries and contribute approximately 1.1% to the bycatch of the tuna-targeting pelagic longline fishery (Lawson, 2001). Escolar was initially perceived as a species with little economic value and was a common bycatch of tuna and swordfish pelagic longlining (Levesque, 2010). Other gempylid fishes, such as Snake Mackerel, are still considered bycatch with no commercial value, but the incidental catch of Escolar and, to a lesser extent Oilfish has provided fisheries with another source of income due to its popularity in the sashimi market (Milessi & Defeo, 2002; Watson & Kerstetter, 2006). Despite not being a target for fisheries, the daily vertical migration habit of these fishes allows for them to be caught more easily due to the creation of aggregations in shallow waters at night (Moore, 1999).

Importance of understanding growth rates

Biological data such as age, growth, mortality, and reproduction are integral in the formation of accurate stock assessments, particularly deep-sea species which may exhibit slow replacement rates (Moore, 1999). Without accurate stock assessments, the efficiency and sustainability of that fishery is questionable, and may put populations of mesopelagic species at risk of collapse from overfishing (Drew et al., 2006; Green et al., 2009). Additionally, species that previously or currently have low economic value may become more important target species over time as current fisheries become overexploited.

Previous research on gempylid fishes has revealed valuable information of the size at sexual maturity and spawning periods throughout the year. That said, no information on spawning season exists for Escolar, but gonadosomatic index (GSI) information suggests Oilfish spawn in mid- to late summer and Snake Mackerel spawn year-round (Vasilakopoulous et al., 2011; Keller & Kerstetter, 2014). Combining size at sexual maturity, GSI data, and growth rates allows fisheries management to understand the relationship between size and age and predict at what age these fishes reach sexual maturity. Escolar, Oilfish, and Snake Mackerel have never been aged before, and given their relative abundance in pelagic longline bycatch, it is important to be able to

understand growth rates, age class distributions, and replacement rates for these mesopelagic fishes.

Introduction to age determination

Fishes can be aged by examining growth patterns in a variety of structures, such as scales, opercular bones, fin rays, vertebrae, and otoliths. These structures possess growth increments, typically in the form of visible rings, that are deposited at a particular rate unique to the environmental conditions that fish lives in. Increment formation can occur daily, annually, seasonally, or aperiodically (e.g., after a single meal), and are assumed be indicative of growth, or show significant periods of energy acquisition and usage (Green et al., 2009). Understanding this formation rate is necessary to accurately estimate age from increment counts. In this study, sagittal otoliths from the target species are examined. Otoliths, unlike scales and fin rays, begin deposition at the earliest developmental stage, continue to grow throughout the fish's lifetime, and do not show evidence of being resorbed under stressful conditions (Campana & Neilson, 1985).

Otoliths are sets of structures found within otic vesicles at the base of the skull of bony fish species (Campana & Neilson, 1985). There are three sets of otoliths, termed the lapilli, sagittae, and asterisci, each of which are located within their own sacs, or vestibules, termed the utriculus, sacculus, and lagenus, respectively (Secor et al., 1992). These otoliths function as part of the inner ear sensory organs, aiding in equilibrium and hearing (Campana & Neilson, 1985; Green et al., 2009). Of the three pair of otoliths, sagittal otoliths are typically the largest, earliest formed, and with the widest and most visible increments, making them used in approximately 60% of ageing studies (Campana & Neilson, 1985; Secor et al., 1992; Green et al., 2009). Lapilli and asterisci are typically much smaller but may still be used if sagittae are small or cannot be located (Campana & Neilson, 1985).

As such important features of the sensory experience, otoliths maintain precise configurations according to species. Otoliths form through continuous, but irregular, accretion of aragonite and otolin, creating pairs of light mineral-deficient zones and dense mineral-rich zones (Green et al., 2009). Even though the exact cause of increment development is still debated, the bands reflect environmental and developmental changes, such as photoperiod, seasonal water temperature changes, or changes in food and nutrient availability, with light bands reflecting

periods of fast growth and dark bands reflecting periods of slow growth (Ehrhardt, 1992; Green et al., 2009).

The process of ageing mesopelagic fishes has historically been more difficult than ageing fishes found in temperate epipelagic or coastal systems. The assumption that growth increments occur over the course of a year relies on environmental conditions to have seasonality and spawning to occur once or in one discrete period. Mesopelagic fishes that vertically migrate experience seasonality, or a change in temperature and food availability on the scale of hours instead of months, allowing for the potential formation of daily increment relating to diurnal feeding cycles (Gartner, 1991). In most cases, growth and age are non-linear, meaning that growth slows as the fish ages due to the energetically costly nature of increasing body mass (Choat et al., 2009). For otoliths to be useful in estimating age, they must have an incremental structure, these increments must be meaningful and determinable, and the otoliths must continue to grow as the fish does (Fowler, 2009).

Age Validation Techniques

Validation techniques confirm that bands on otoliths are indicators of age, what timespan each increment represents, and prove the efficacy of age estimation methods (Geffen, 1992; Iverson, 1996; Panfili et al., 2002). The temporal meaning of the increments may vary between different species based on habitat temperature and food availability and should thus be validated when ageing previously understudied populations (Geffen, 1992; El-Haweet et al., 2005).

Marginal increment analysis is a technique to validate the periodicity of otolith increment formation by measuring the growth of the otolith since the last completed band (Ihde & Chittenden, 2003). For marginal increment analysis to be successful, fish samples, and therefore otolith samples, must be distributed across a meaningful timeframe. If daily increments are observed, samples should span a 24-hour timeframe, while annual increment formation is best observed when samples are collected across each month of the year (Gartner, 1991; Smith, 2014). These calculations present ratios of the marginal increment over the typical distance between two bands, which should range from 0, indicating beginning of formation, to 1, indicating a complete increment (Campana, 2001). Each month's MIR values will be averaged and plotted against the month the sample was collected (Smith, 2014). If the bands form annually, this plot will show a sinusoidal curve, with the average MIR value approaching one as the increment completes

formation, and at zero when a new increment begins to form (Lessa et al., 2006). Despite the popularity of this validation technique, marginal increment analyses can provide misleading results. Marginal increments are easiest to track and more often accurately confirm annual increment formation in younger, fast-growing fishes, and can be difficult to measure in older fishes whose growth rate may be reaching a plateau (Campana, 2001). Additionally, when a fish does not have a defined reproductive period, it can be difficult to determine discrete annual age classes or annual increment formation (Lessa et al., 2006).

Length frequency analyses are non-lethal methods of estimating yearly age cohorts, which can corroborate other validation techniques. Length measurements are collected over a period of time, frequency of each length is plotted against the given time period, and modes of the distribution can be estimated to be different age cohorts (Iverson, 1996). Similar to the marginal increment analyses, length frequency analyses function optimally with fishes that spawn over a short period of time, and two or more modes can appear and indicate groups of different sized but same age individuals if this is not the case (Iverson, 1996). Additionally, for a length-frequency analysis to be accurate, it requires a large number of samples in a wide size range, typically with age at first capture known in order to define the first modal group (Iverson, 1996).

Methodology

Sample Collection

Samples used in this study were a combination of previously extracted otoliths and freshly caught specimens that were frozen before otolith extraction. These samples span from 2007, when the project was originally started by graduate student Kerri Bolow, through 2022. Samples were obtained by graduate students and Principal Investigator participating in a research program aboard a pelagic longline vessel operating in the western North Atlantic. For larger specimens, the heads were removed posterior to the operculum and retained while the rest of the body was kept by the crew. For smaller specimens, the whole body was retained. Each sample was labeled, and the species type, location, catch date, fork length in centimeters, and sample number were recorded. Sex was generally not recorded, and thus comparison of growth rate between sexes is not incorporated into this study. All specimens were kept frozen until time of otolith extraction. Sample information of archived otoliths had been recorded in a different format, with some

samples having a recorded total length (TL) instead of fork length (FL). For those samples, a length-length conversion equation developed by Keller and Kerstetter (2014) was used to convert total length to fork length.

Otolith Extraction and Sectioning

Specimens were allowed to thaw in a bucket of warm water to loosen the sacculi and provide ease in cutting through the flesh. Before otolith removal, all samples were reevaluated for correct species identification. Sagittal otoliths were removed by the guillotine method as described by Secor et al. (1992), in which a transverse cut was made from the top of the head through the preopercle to expose the posterior end of the sacculi (Figure 1). The exposed otoliths were then gently worked back and forth to remove them without breaking (Secor et al., 1992). After removal, the otoliths were manually cleaned with forceps to remove the sacculus membrane, rinsed, and allowed to air dry. All otoliths were stored dry in labeled vials until time of mounting and sectioning (Morales-Nin, 1992) (Figure 2).

Otoliths were embedded in a 5:1.1 mixture of epoxy (Araldite-Bisphenol A:Aradur 956-2), placed into a 12-cavity flat embedding mold and left to dry for at least 24 hours. After drying, all otoliths were affixed to cardstock and labelled with species and sample number. Otoliths were sectioned transversely through the otolith's nucleus to ensure that no portion of the increment sequence was missed (Morales-Nin, 1992). Sectioning was done using a Buehler low-speed Isomet saw (South Bay Technology Inc., San Clemente, CA, USA; model 650) fit with high concentration diamond wafering blades (Ted Pella, Inc. Prod #812-316) to create 0.3-0.5-mm sections. These sections were mounted onto individual labeled glass slides using Cytoseal 60 (Richard Allen Scientific, Kalamazoo, MI, USA). Sections were viewed and photographed using an Olympus CX31 microscope affixed with a Lumenera Infinity 1 camera. The Infinity 3 Analyze software was used to photograph the sections and preliminarily edit the photos with white balance and edge emphasis filters. Additional image enhancement occurred in Adobe Photoshop (Adobe Photoshop v.23.4.1) to adjust image brightness and contrast for better visualization of growth increments.

Figure 1. Transverse cut through Escolar to expose the posterior end of sagittal otoliths .
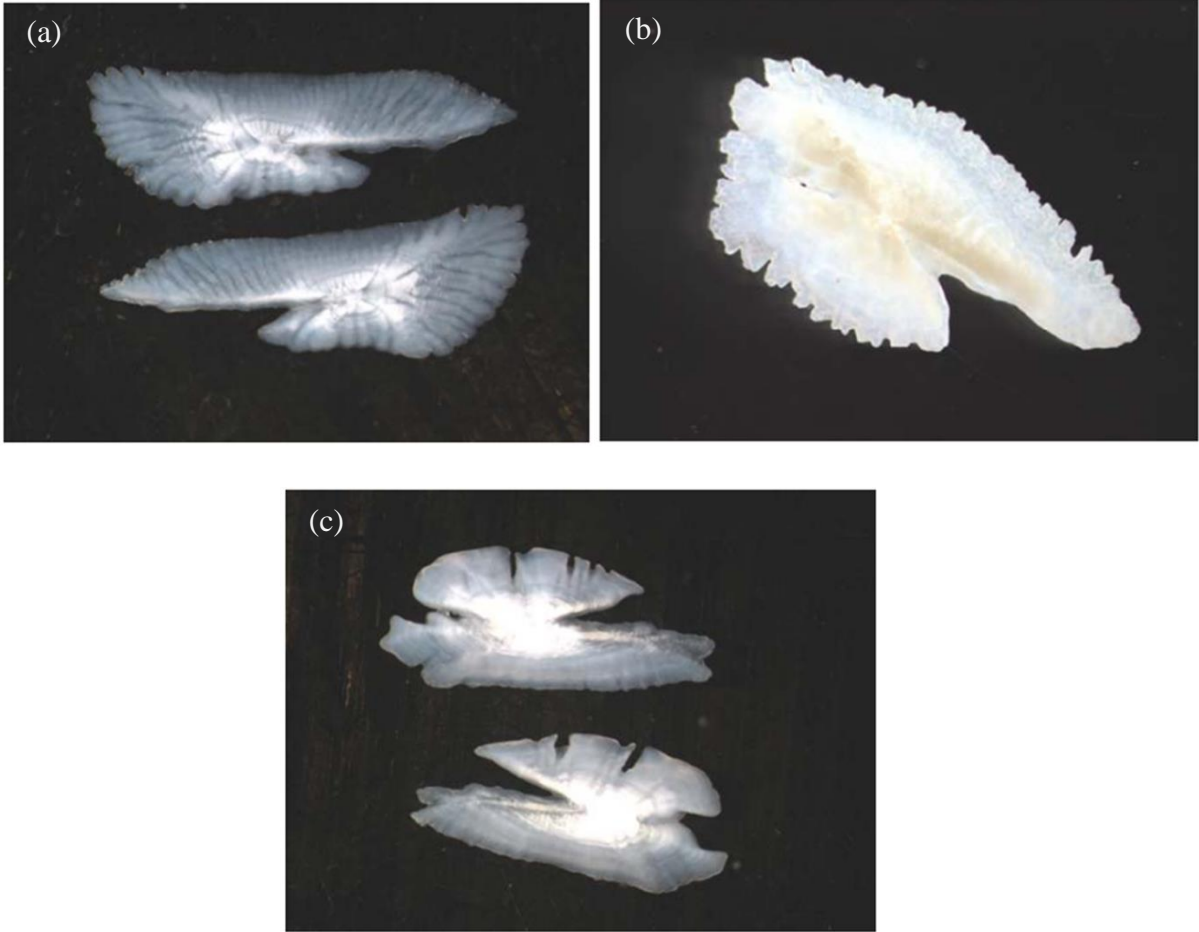
Figure 2. Whole sagittal otoliths extracted from (a) Escolar (*L. flavobrunneum*), (b) Oilfish (*R. pretiosus*), and (c) Snake Mackerel (*G. serpens)*. Courtesy of Kerri Bolow, 2009.
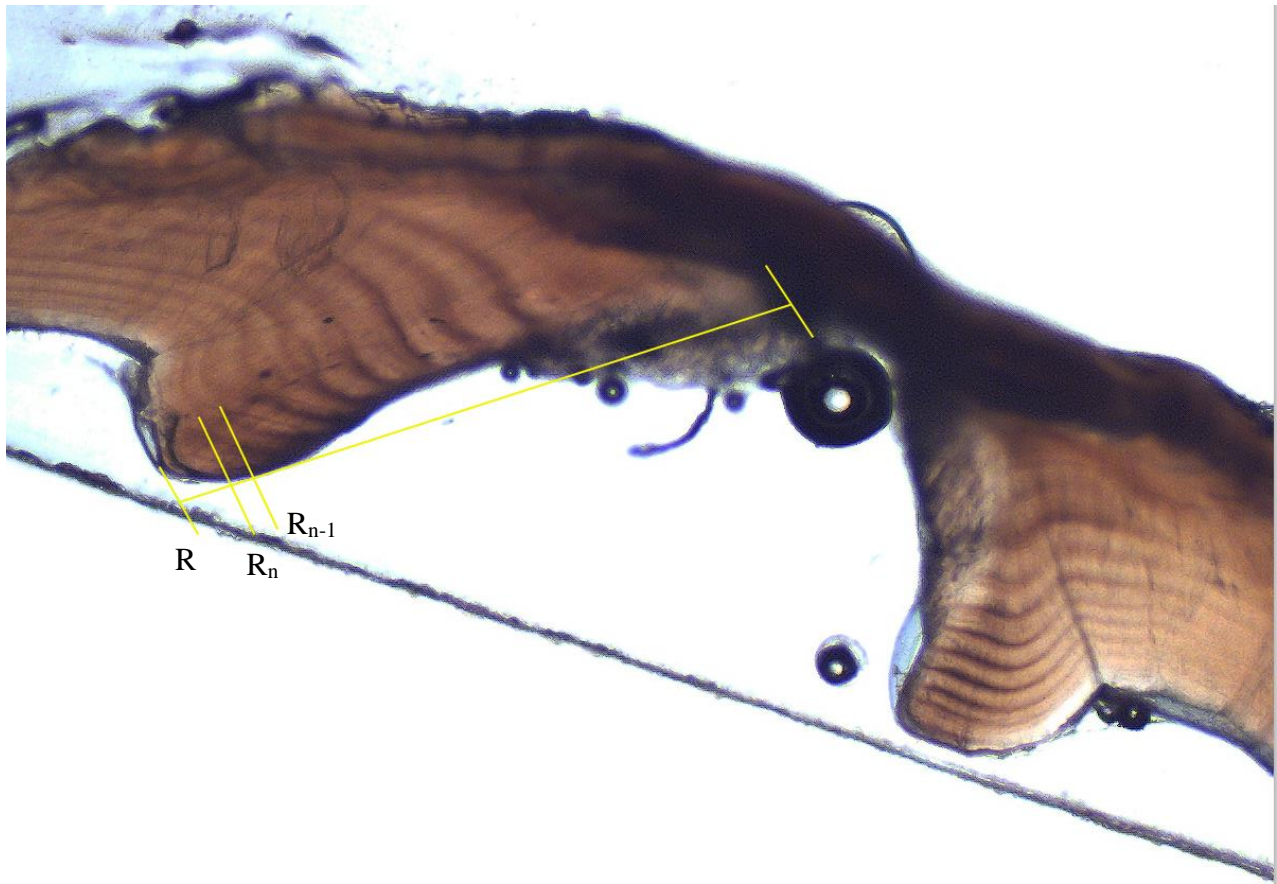
Figure 3. Transversely sectioned Escolar otolith with deposition bands. Yellow lines mark the measurements recorded in order to calculate marginal increment ratios. Photo captured using Olympus CX31 microscope affixed with a Lumenera Infinity 1 camera.

Age Determination & Validation

Two independent readers performed two blind counts of all otolith images with no knowledge of the sample's fork length. Prior to visual counts, readers discussed and confirmed the criteria for band pair estimations to limit inconsistencies. Edited images were sent from the first reader to the second reader, with each reader's band estimations marked on individual layers and hidden from the other reader until analyzed for consensus. Age estimations were only accepted if three of the four counts were in agreement, and all remaining samples were rejected.

The accuracy and precision of growth increment count estimations were determined using percent agreement (PA), average percent error (APE) and average coefficient of variation (ACV) both between and within readers. Percent agreement is defined as:

$$PA = \frac{No.\,agreed}{No.\,read} \times 100$$

Average percent error is defined as:

$$APE_j = 100\% \times \frac{1}{R} \sum_{i=1}^{R} \frac{|X_{ij} - X_j|}{X_j}$$

where X_{ij} is the ith band estimation for the jth fish, X_j is the mean band count estimate of the jth fish, and R is the number of times each fish is visually read for band counts (Campana, 2001). The average coefficient of variation is defined as:

$$CV_j = 100\% \times \frac{\sqrt{\sum_{i=1}^{R} \frac{(X_{ij} - X_j)^2}{R-1}}}{X_j}$$

Where CV_j is the band count estimate for the jth fish (Campana, 2001).

Periodicity of band deposition was validated using marginal increment analysis (MIA), which compares ratios of marginal increment distance to the month the sample was collected. The marginal increment ratio (MIR) was calculated by:

$$MIR = \frac{(R - R_n)}{(R_n - R_{n-1})}$$

where R is the distance between the focus and the edge of the otolith, R_n is the distance between the focus and the last annual band, and R_{n-1} is the distance between the focus and the penultimate, or second to last, annual band, as seen in Figure 3 (Coelho et al., 2010). The above equation creates a ratio of the marginal increment over the typical distance between two bands, which should range from 0, indicating beginning of formation, to 1, indicating a complete increment (Campana, 2001). Each month's MIR values were averaged and plotted against the month the sample was collected (Smith, 2014). If the bands form annually, this plot will show a sinusoidal curve, with the average MIR value approaching one as the increment completes formation, and at zero when a new increment begins to form (Lessa et al., 2006).

Length frequency analysis (LFA) was performed on all three species using catch data from 1992-2020 contributed by the National Oceanic and Atmospheric Administration (NOAA) pelagic observer program. Within each species, 10-cm length bins were created and the frequency of fish in each length bin was totaled and separated by time period. Data from 1992-2004 were provided with dates of catch and were thus organized by month of catch for the purpose of the LFA. Data from 2005-2020 were provided in catches by quarter, and thus remained organized by quarter. These length-frequency matrices were manipulated to create compiled data sets, adding up the catches in each time period across the 28-year data collection span. This provided more complete and readable plots. Plots were created using ELEFAN, or the electronic length frequency analysis method, within the TropFishR package in R (Mildenberger et al., 2017). ELEFAN utilizes the mid-lengths of defined classes, sampling dates, and frequency of catches within each class to derive growth parameters of the von Bertalanffy growth function (Mildenberger et al., 2017). A response surface analysis on the data sets compiled by quarter for each species predicted parameters that were then utilized as preliminary inputs for maximum likelihood and nonlinear least-squares estimations.

Growth Models

Various growth models were fit to fork length-at-age data following Cailliet et al. (2006) and Cotton et al. (2011). The von Bertalanffy growth function (VBGF) is equation that predicts the length of a fish as a function of its age. The function is as follows:

$$L(t) = L_\infty - (L_\infty - L_0)e^{-kt}$$

where L(t) represents the length at age t, L_∞ is the asymptotic or mean maximum length, k is the growth coefficient, and L_0 is length at age zero found as the y-axis intercept (Bertalanffy, 1938, cited by Pardo et al., 2013; Cailliet et al., 2006).

In addition to the original version of the VBGF, two variations of VBGF, Gompertz, and Logistic models were compared to determine which model best fit the length-at-age data. The first variation of the VBGF model is a modified form, henceforth mentioned as VBGFmod:

$$L(t) = L_\infty(1 - e^{-k(t-t0)})$$

where t_0 is the theoretical age when length is equal to zero (Cailliet et al., 2006). The second variation of the VBGF model is a two-parameter, henceforth called VBGF2par, uses the original VBGF model but fixing L_0 to size at birth. This fixed value is most easily assigned with the use of term embryos in elasmobranchs or measurements of newly hatched fry in hand-raised fish populations. In this study, L_0 was fixed using the average predicted value across the other growth models.

A form of the Gompertz model was defined as (Cotton et al., 2011):

$$L(t) = L_0 e[G(1 - e^{-kt})] \quad \text{where G} = \ln(L_\infty/L_0)$$

A form of a logistic function, was defined as (Ricker, 1979; Cotton et al., 2011):

$$L(t) = \frac{L_\infty}{1 + e^{-k(t-t0)}}$$

All growth models were fitted using maximum likelihood estimation (ML) and nonlinear least-squares (NLS) with R statistical software. The model with the best fit was determined using AICc values, a form of Akaike's information criterion (AIC) that corrects for biases that can occur with small sample sizes (Cotton et al., 2011). The AICc variant used for ML-fitted models is defined as:

$$AICc = \frac{-2\ln(\mathcal{L}(\theta)) + 2k + (2k(k+1))}{(n-k-1)}$$

where $\mathcal{L}(\theta)$ is the likelihood estimate, k is the number of model parameters, and n is the sample size (Cotton et al., 2011). The AICc variant used for NLS-fitted models is defined as:

$$AICc = n\left(1 + \ln\left(2\pi \times \frac{RSS}{n}\right)\right) + 2k + (2k(k+1))/(n-k-1)$$

where RSS is the residual sum of squares of the model (Cotton et al., 2011).

Results

Age Determination

A total of 133 Escolar, 49 Oilfish, and 46 Snake Mackerel otoliths were aged by two independent readers. Of the 133 Escolar otoliths aged, 76 counts agreed; of the 49 Oilfish otoliths aged, 32 counts agreed; of the 46 Snake Mackerel otoliths aged, 21 counts agreed. Campana (2001) defines high precision with an ACV value $\leq 7.6\%$ and an APE value $\leq 5.5\%$. The ageing of Escolar showed a high level of precision, with APE values both within readers and between readers $\leq$ 4.1%, and ACV value between readers at 5.88%. When ageing Oilfish, reader 1 had ACV and APE values above the aforementioned thresholds, while reader 2 remained below them and displaying higher precision. When ageing Snake Mackerel, both readers had ACV and APE values above the precision thresholds. Table 1 shows these ACV and APE values. Percent agreement (PA) was calculated within each reader, when both readings agreed, and then between readers when three out of four readings agreed. Between both readers, 57.14% of Escolar readings agreed, 65.31% of Oilfish readings agreed, and 45.65% of Snake Mackerel readings agreed. Percent agreement, as it relates to the size distribution of samples of each species, is shown in Figure 3 a, b, and c.

Table 1 Mean precision estimates of ACV, APE, and PA within both individual readers, and between both readers, for Escolar (n=133), Oilfish (n=49), and Snake Mackerel (n=46).

	Reader 1	Reader 2	Between both readers
Escolar			
ACV	5.90	8.98	5.88
APE	2.93	4.04	3.33
PA	59.40	56.39	57.14
Oilfish			
ACV	9.51	6.35	9.37
APE	6.04	3.30	5.37
PA	63.27	61.22	65.31
Snake Mackerel			
ACV	12.02	11.45	10.31
APE	7.47	6.32	6.41
PA	36.96	41.30	45.65
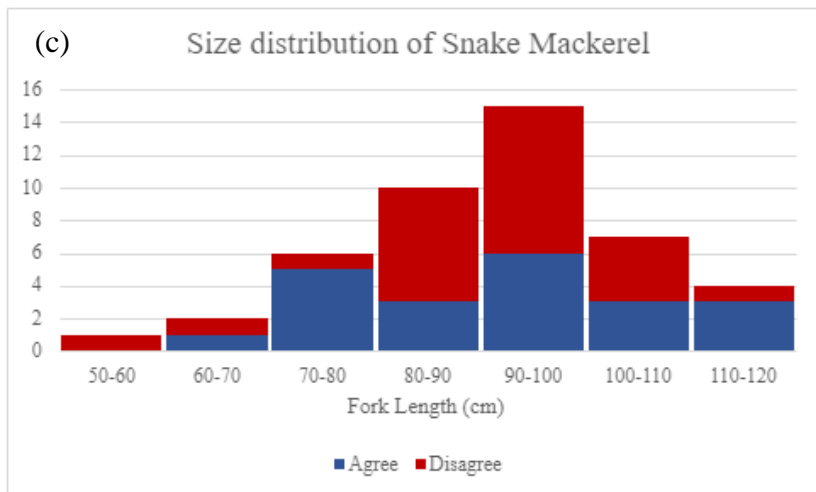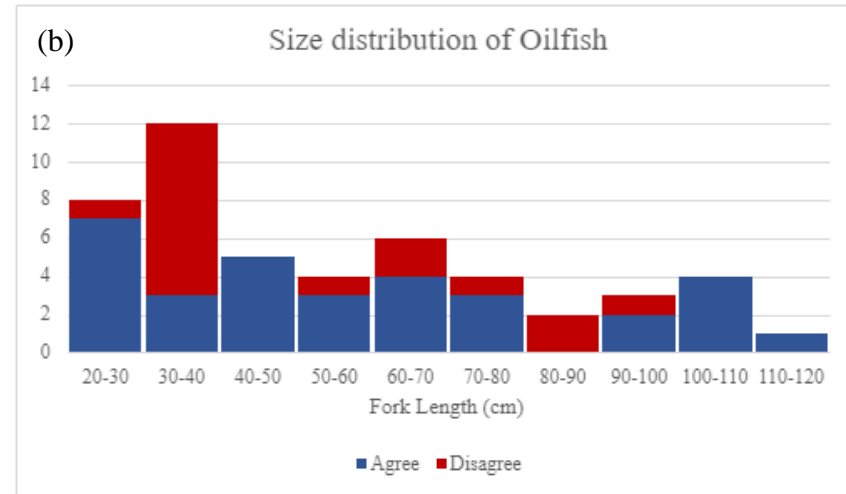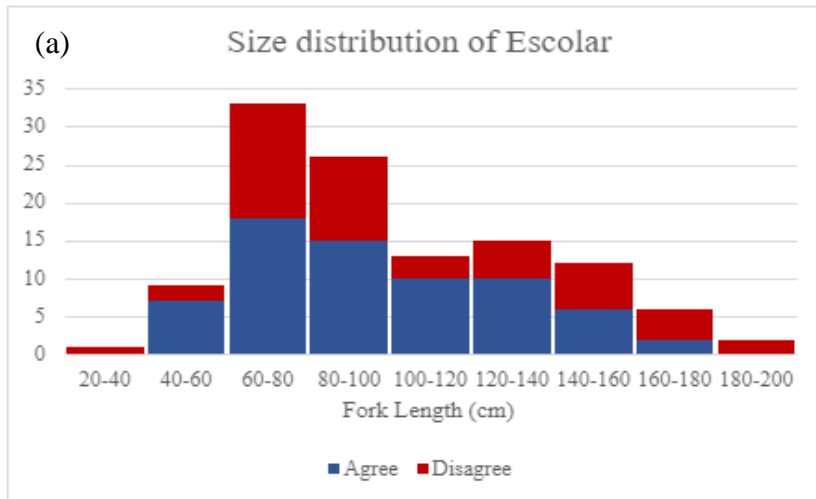
Figure 4. Size distribution histogram of samples whose age was agreed upon by 75% of readings, and those that were discarded due to lack of consensus. (a) shows size distribution for Escolar, (b) for Oilfish, and (c) for Snake Mackerel.

Marginal Increment Analysis

   Marginal increment analysis measurements showed no distinct trends in growth over the course of a year for Escolar (Kruskal-Wallis, P= 0.4373), Oilfish (Kruskal-Wallis, P=0.4335), or Snake Mackerel (Kruskal-Wallis, P=0.4373). Mean marginal increment ratios (MIRs) were calculated from 54 samples of Escolar otoliths, 26 samples of Oilfish otoliths, and 19 samples of Snake Mackerel otoliths. Within those samples of Escolar, the largest mean MIR occurred in January (1.894 ± 0.550, n=2) and the smallest occurred in June (0.597 ± 0.246, n=2) (Figure 5). Within samples of Oilfish, the largest mean MIR occurred in September (12.315, n=1) which could be considered an outlier due to the significantly higher value attributed by its unique banding pattern (Figure 6a, 6b). Disregarding this outlier, the largest MIR for Oilfish occurred in July (2.239 ± 3.01, n=6) and the smallest occurred in April (0.667 ± 0.057, n=3) (Figure 6c). Within the samples of Snake Mackerel, the largest MIR value occurred in June (2.195, n=1) and the smallest occurred in August (0.607, n=1) (Figure 7).
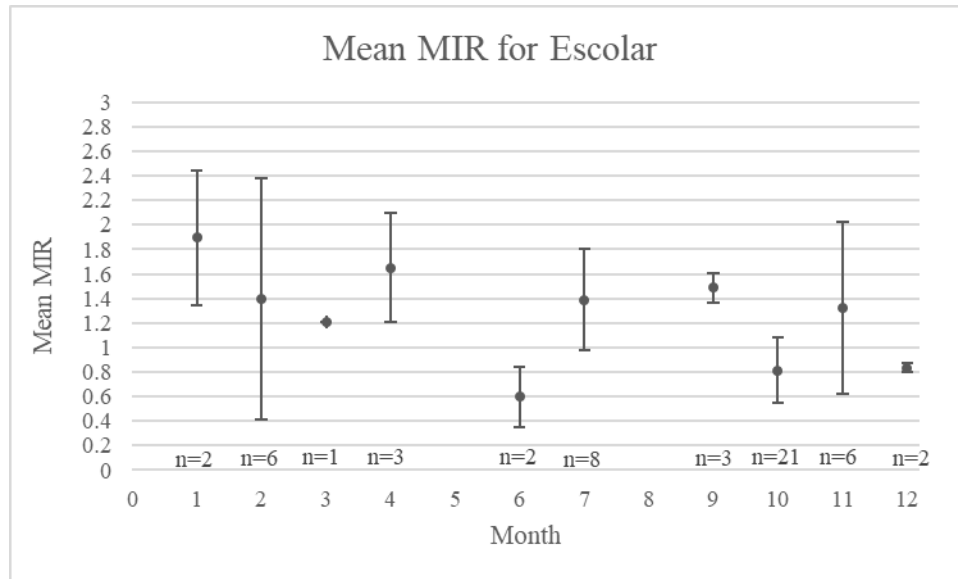
Figure 5. Marginal increment analysis for all size classes of Escolar (n=54).
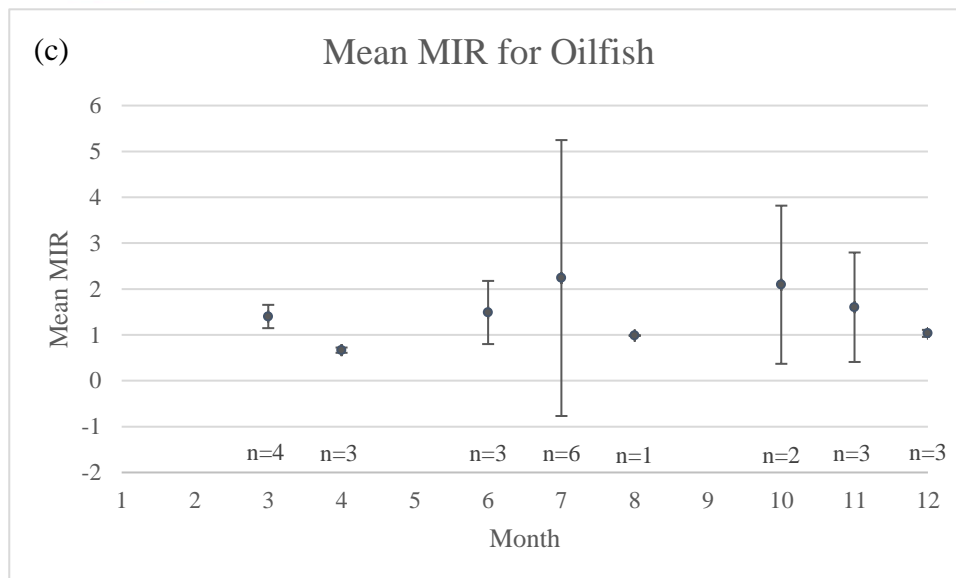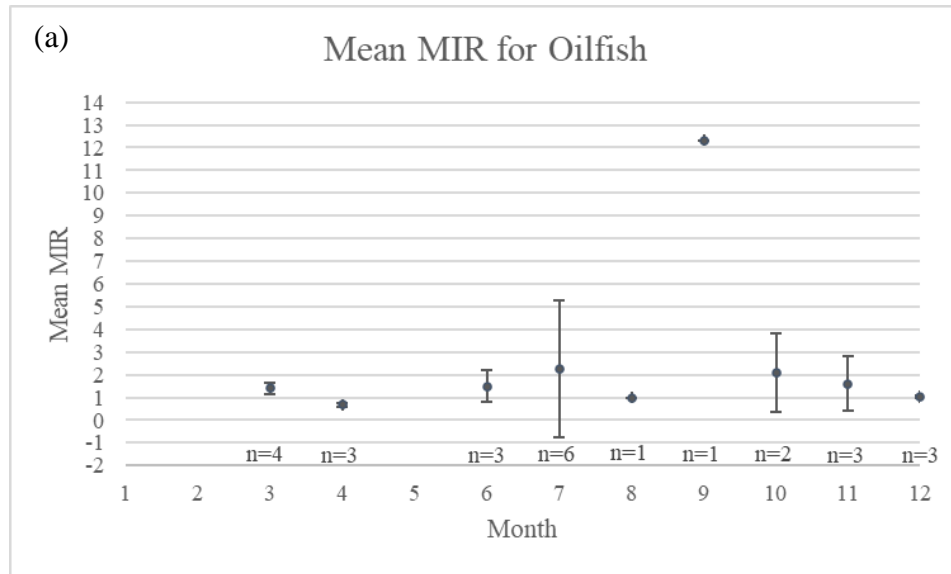
Figure 6. (a) Marginal increment analysis for all size classes of Oilfish (n=26).
(b) Unique banding pattern of sample OIL20 with MIR value 12.315.
(c) Marginal increment analysis for Oilfish disregarding outlier sample OIL20.
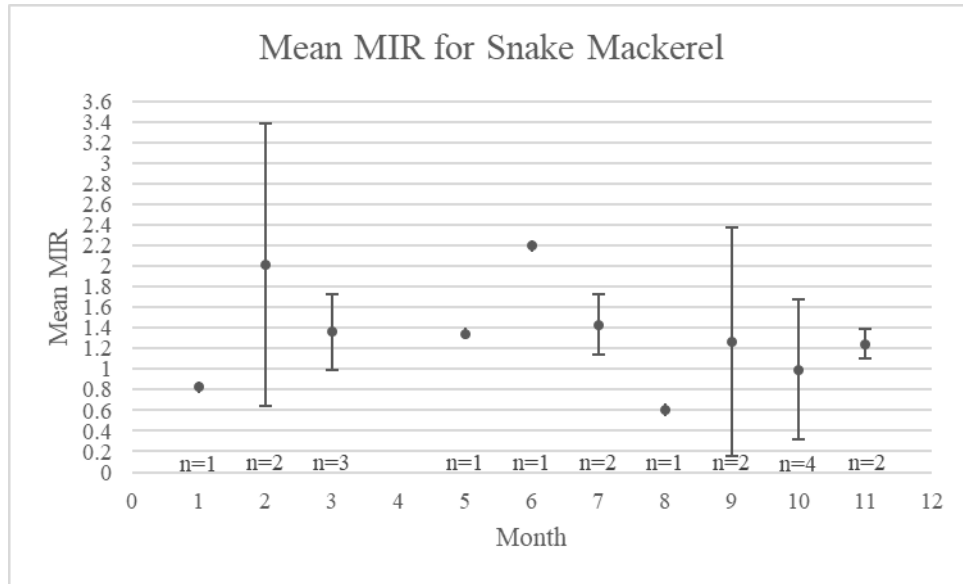
Figure 7. Marginal increment analysis for all size classes of Snake Mackerel (n=19).

Length-Frequency Analysis

Length-frequency plots were created using data compiled by month and by quarter and used to predict VBGF parameters. When compiled by month, the catch data for Escolar spanning 1992-2004 (n = 5,676) predicted L_∞= 144 cm and k = 0.67 year^{-1} (Figure 8a). When compiled by quarter, Escolar catch data spanning 1992-2020 (n = 19,071) predicted L_∞= 142 cm and k = 1.12 year^{-1} (Figure 8b). When compiled by month, the catch data for Oilfish spanning 1992-2004 (n = 967) predicted L_∞= 185 cm and k = 0.39 year^{-1} (Figure 9a). When compiled by quarter, Oilfish catch data spanning 1992-2020 (n = 3,181) predicted L_∞= 178 cm and k = 1.02 year^{-1} (Figure 9b). When compiled by month, the catch data for Snake Mackerel spanning 1992-2004 (n = 356) predicted L_∞= 151 cm and k = 0.37 year^{-1} (Figure 10a). When compiled by quarter, Snake Mackerel catch data spanning 1992-2020 (n = 905) predicted L_∞= 193 cm and k = 0.25 year^{-1} (Figure 10b). Response surface analysis fit the provided length data with extrapolated age bins and t_{anchor}, a term defined as the x-intercept of the extrapolated age bins (predicted time of hatching).
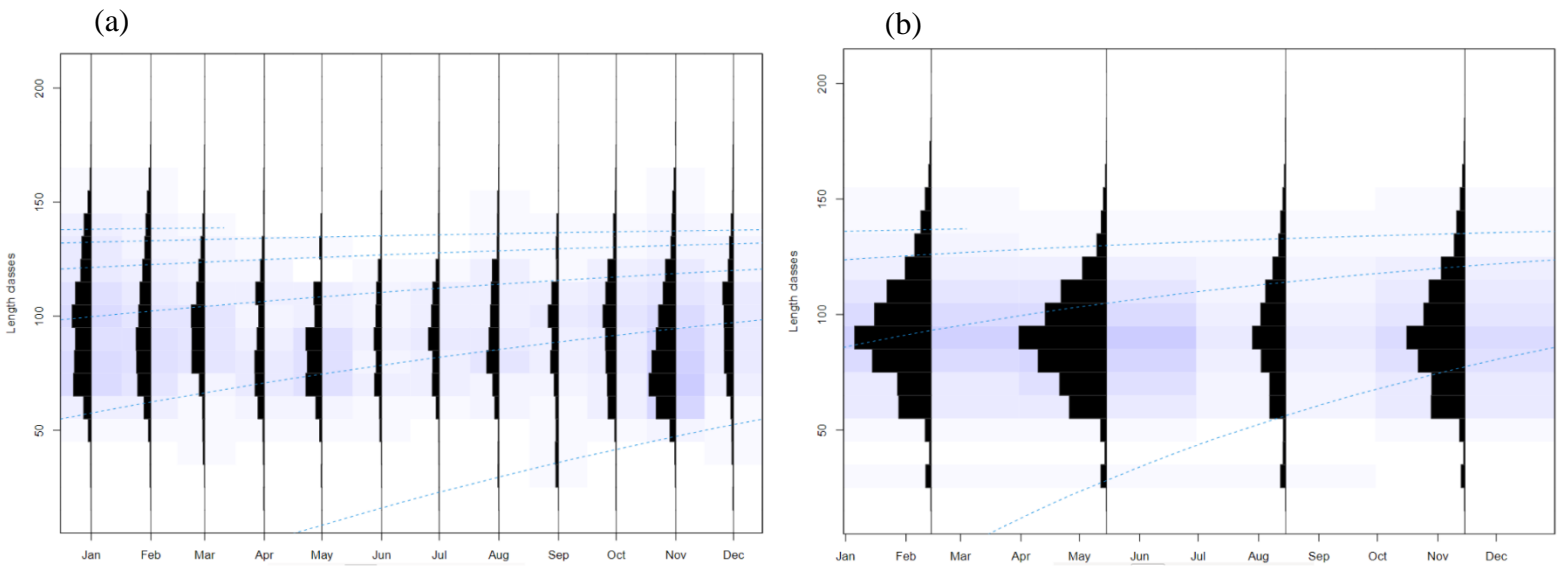
Figure 8. Length-frequency plots for Escolar compiled by (a) month (n = 5,676) showing five age bins and (b) quarter (n = 19,071) showing three age bins.
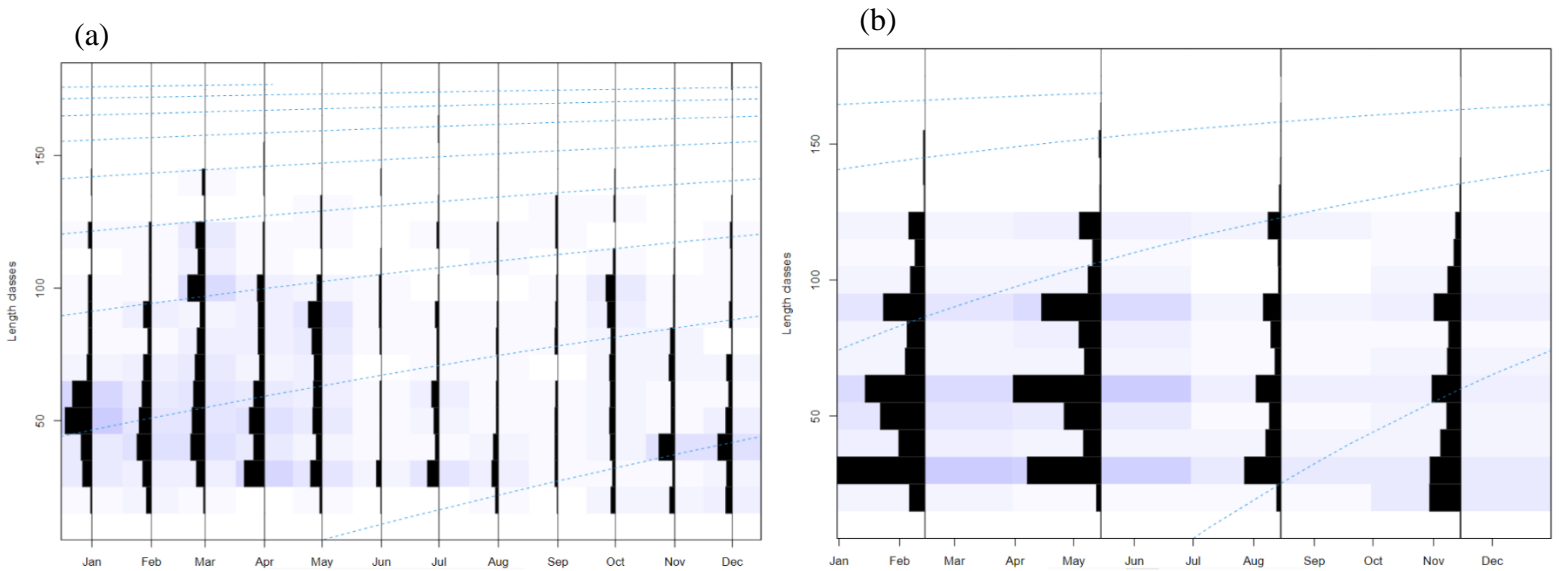
Figure 9. Length-frequency plots for Oilfish compiled by (a) month (n = 967) showing eight age bins and (b) quarter (n = 3,181) showing three age bins.
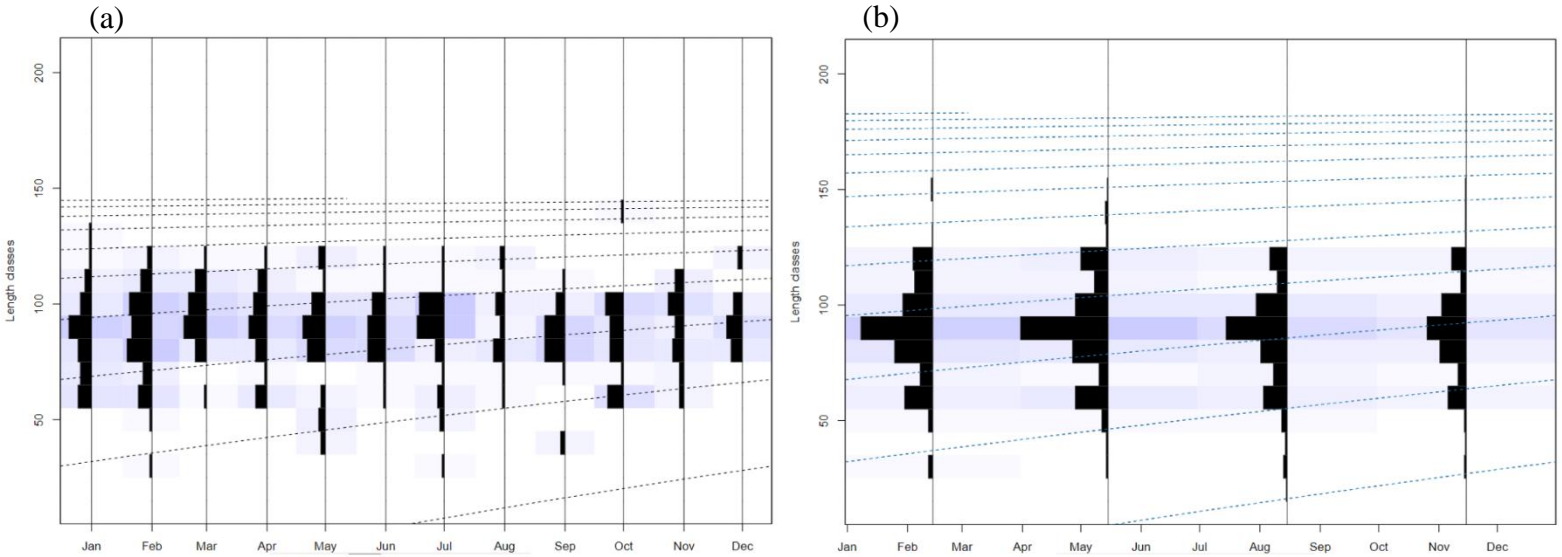
Figure 10. Length-frequency plots for Snake Mackerel compiled by (a) month (n = 356) showing nine age bins and (b) quarter (n = 905) showing 12 age bins.

Growth Models

FL-at-age data were fit to growth models for samples with agreed-upon ages for Escolar (n=69), Oilfish (n=32), and Snake Mackerel (n=20). NLS and ML list inputs for L_∞ parameters were determined by the largest sample recorded in the historical pelagic observer program data provided by NOAA. List inputs for *k* parameters were decided by the output from the monthly LFA, and L_0 was set to 0.4 cm based on known larval size of Atlantic bluefin tuna (*Thunnus thynnus*) due to the families Scombridae and Gempylidae being sister groups (Johnson, 1986; Le Francois et al., 2010; Betancur-R et al., 2017). The model with the best fit was determined by the lowest AICc value for each species.

For Escolar, the growth model with the lowest AICc was the logistic model, providing L_∞ parameters of 195.2 cm (ML) and 194.6 cm (NLS), *k* parameters of 0.212 year^{-1} (ML & NLS), and t_0 parameters of 4.43 years (ML) and 4.40 years (NLS) (Table 2). The modified VBGF model estimated the highest L_∞ values and lowest *k* values across all models, predicting an L_∞ of 247.0 cm (ML) and 435.0 cm (NLS) and a *k* value of 0.065 year^{-1} (ML) and 0.028 year^{-1} (NLS). The logistic model and Gompertz model predicted such similar parameters that the growth curves plotted from maximum likelihood estimations overlay each other (Figure 11).

Oilfish FL-at-age growth models show the VBGF$_{mod}$ model to be the best fit based on maximum likelihood estimations, and the VBGF$_{2par}$ model to be the best fit based on nonlinear least-squares estimations (Table 3). The VBGF$_{mod}$ model predicted an L$_\infty$ of 162.4 cm (ML) and 96.2 cm (NLS), while the VBGF$_{2par}$ model predicted an L$_\infty$ of 176.5 cm (ML) and 90.9 cm (NLS). The VBGF$_{mod}$ model predicted k values of 0.094 year^{-1} (ML) and 0.295 year^{-1} (NLS), while the VBGF$_{2par}$ model predicted k values of 0.130 year^{-1} (ML) and 0.391 year^{-1} (NLS). In both models, NLS predicted lower L$_\infty$ values and higher k values. For maximum likelihood estimations, the VBGF$_{2par}$ model had the largest **Δ**AICc, making it the least best fit for this method of model estimation, and resulting in a plotted growth curve that is distinct from the other models (Figure 12).

Growth function models for Snake Mackerel FL-at-age data also showed the VBGF$_{2par}$ model to be the best fit. L$_0$ was fixed to 0.4 cm and produced a L$_\infty$ parameter 92.8 cm and a k parameter of 1.579 year^{-1} for both ML and NLS modelling techniques (Table 4, Figure 13). This model produced the lowest values for L$_\infty$ and highest values for k.

Table 2 Model parameter estimations, standard deviation (σ, for ML-fitted models), residual sum of squares (RSS, for LS-fitted models), and model selection statistics (AICc and ΔAICc) for FL-at-age data for Escolar. L_0 set to 0.4 cm for VBGF 2 parameter model.

Model	L_∞	k	L_0	t_0	σ	RSS	AICc	ΔAICc
Maximum Likelihood								
VBGF	201.74	0.095	47.26		17.66		599.865	6.057665
VBGF modified	247.04	0.065		-3.5	17.11		597.561	4.078488
VBGF 2 parameter	136.90	0.358	*0.4*		23.182		635.964	42.480745
Gompertz	203.15	0.142	52.52		16.99		595.414	1.931071
Logistic	195.16	0.212		4.43	16.76		593.483	0
Nonlinear least-squares								
VBGF	435.01	0.028	53.17			20271.0	596.555	3.0722
VBGF modified	435.01	0.028		-4.61		20271.0	596.555	3.0722
VBGF 2 parameter	136.78	0.359	*0.4*			37078.1	635.963	42.481103
Gompertz	230.30	0.119	54.12			19819.4	594.999	1.5177
Logistic	194.59	0.212		4.40		19388.2	593.482	0

Table 3 Model parameter estimations, standard deviation (σ, for ML-fitted models), residual sum of squares (RSS, for LS-fitted models), and model selection statistics (AICc and ΔAICc) for FL-at-age data for Oilfish. L_0 set to 0.4 cm for VBGF 2 parameter model.

Model	L_∞	k	L_0	t_0	σ	RSS	AICc	ΔAICc
Maximum Likelihood								
VBGF	163.88	0.093	25.816		24.302		303.509	0.0141
VBGF modified	162.42	0.094		-1.85	23.625		303.495	0.0000
VBGF 2 parameter	176.54	0.130	*0.4*		25.722		305.53	2.0351
Gompertz	155.81	0.161	31.483		24.789		304.241	0.7464
Logistic	160.55	0.234		5.33	24.968		305.467	1.9724
Nonlinear least-squares								
VBGF	96.22	0.295	12.978			17471.1	301.976	2.1977
VBGF modified	96.22	0.295		-0.49		17471.1	301.976	2.1977
VBGF 2 parameter	90.87	0.391	*0.4*			17705.5	299.778	0.0000
Gompertz	93.44	0.454	18.306			16992.2	301.086	1.3084
Logistic	92.37	0.634		1.96		16541.5	300.226	0.4481

Table 4 Model parameter estimations, standard deviation (σ, for ML-fitted models), residual sum of squares (RSS, for LS-fitted models), and model selection statistics (AICc and ΔAICc) for FL-at-age data for Snake Mackerel. L_0 set to 0.4 cm for VBGF 2 parameter model.

Model	L_∞	*k*	L_0	t_0	σ	RSS	AICc	ΔAICc
Maximum Likelihood								
VBGF	144.104	0.035	82.226		12.577		168.805	2.8131
VBGF modified	142.42	0.039		-21.84	12.585		168.809	2.8174
VBGF 2 parameter	92.79	1.579	*0.4*		12.722		165.992	0
Gompertz	141.91	0.046	82.458		12.613		168.818	2.8256
Logistic	150.97	0.05		-3.912	12.62		168.835	2.8431
Nonlinear least-squares								
VBGF	96.23	0.463	68.271			3143.421	168.571	2.5789
VBGF modified	96.23	0.463		-2.669		3143.421	168.571	2.5789
VBGF 2 parameter	92.79	1.579	*0.4*			3237.17	165.992	0
Gompertz	95.84	0.522	68.47			3144.577	168.578	2.5863
Logistic	95.46	0.592		-1.568		3145.597	168.585	2.5928
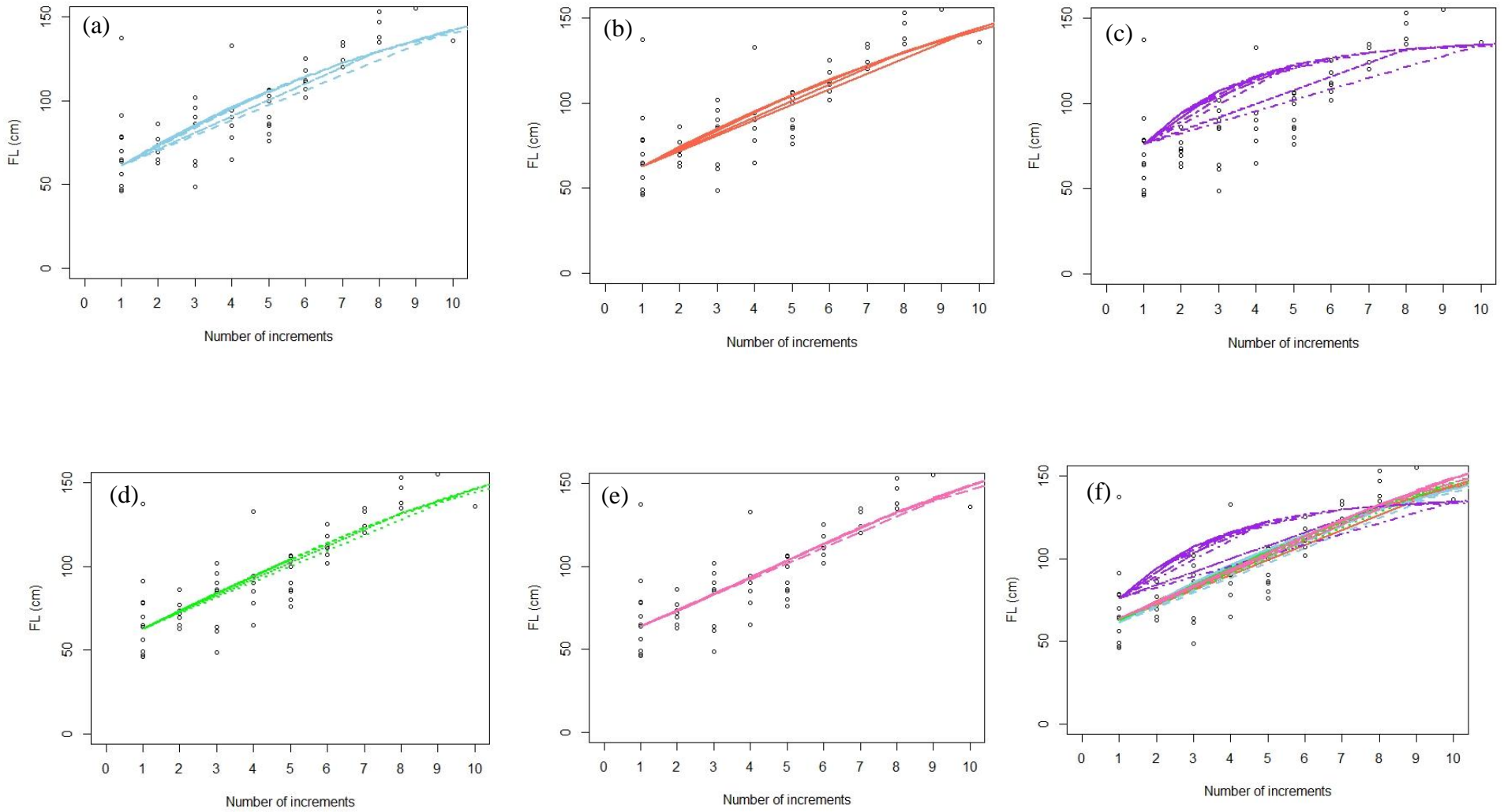
Figure 11. Growth models for FL-at-age data for Escolar: (a) original VBGF, (b) modified VBGF, (c) 2-parameter VBGF, (d) Gompertz, (e) Logistic, (f) all models combined.
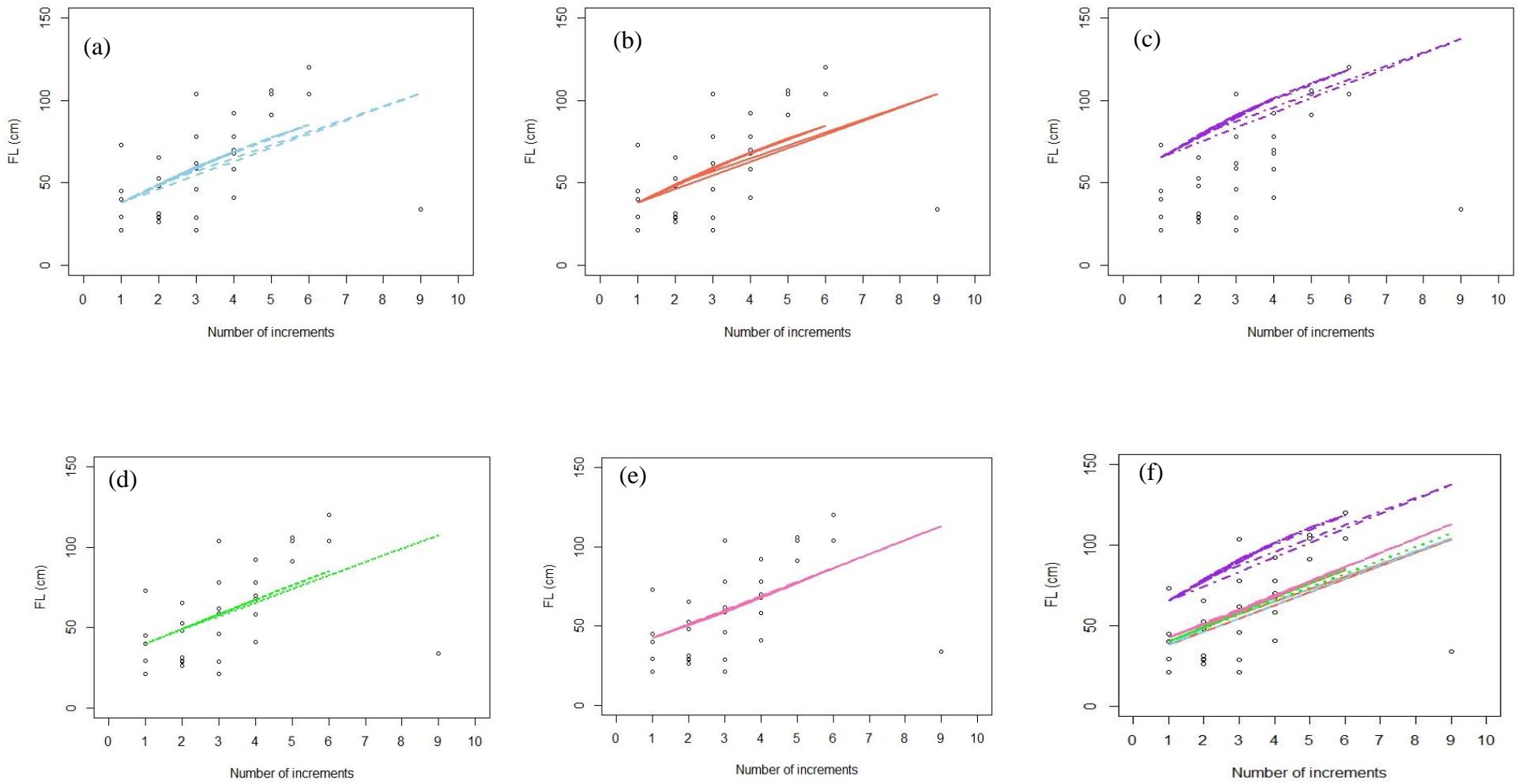
Figure 12. Growth models for FL-at-age data for Oilfish: (a) original VBGF, (b) modified VBGF, (c) 2-parameter VBGF, (d) Gompertz, (e) Logistic, (f) all models combined.
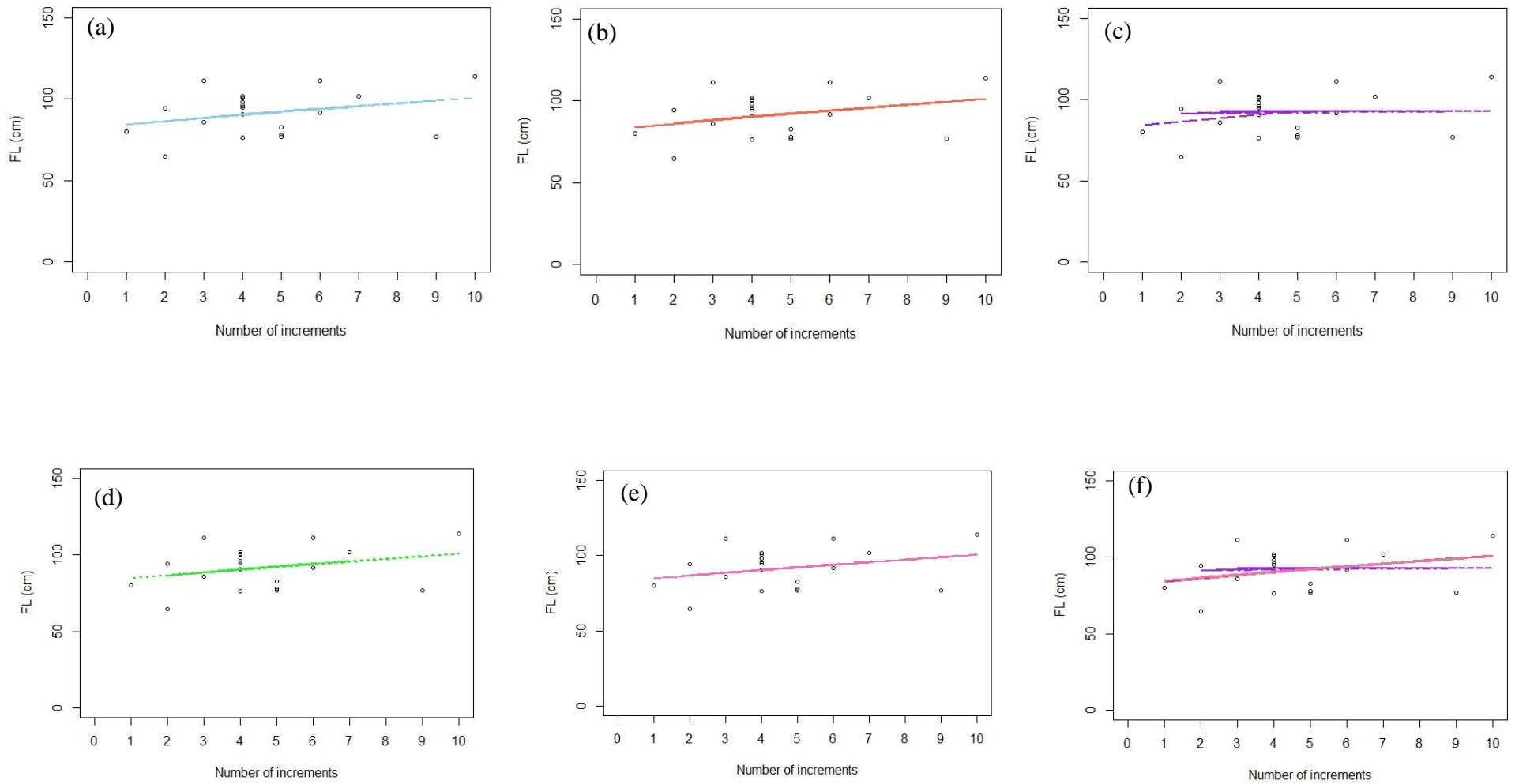
Figure 13. Growth models for FL-at-age data for Snake Mackerel: (a) original VBGF, (b) modified VBGF, (c) 2-parameter VBGF, (d) Gompertz, (e) Logistic, (f) all models combined.

Discussion

Age Determination

Age determination proved to be more difficult than expected, with less than 35% of all otoliths across the three species, both archived and extracted, having growth increment estimations that three out of four readings agreed upon. Out of 207 Escolar otoliths, 133 were aged, and 76 agreed. Out of 108 Oilfish otoliths, 49 were aged, and 32 agreed. And out of 63 Snake Mackerel otoliths, 46 were aged, and 21 agreed. Many of the archived otoliths from a previous project were missing biological data, or data sheets had been misplaced. Figure 3 shows the size distribution of samples where readings agreed and disagreed, broken down by species. For Escolar, disagreements outweighed agreements in the smallest size class and two largest size classes. The samples in the two largest size classes were samples with greater than 10 growth increments visible on the otolith sections. Within Oilfish, disagreements outweighed agreements in samples between 30-40 cm and 80-90 cm FL. These disagreements occurred in otolith samples with between one and five visible growth increments. In Snake Mackerel, disagreements outweighed agreements in the majority of samples, especially those in the 80-110 cm FL range. To increase percent agreement and sample sizes in the future, otoliths with disagreements may be re-aged and discrepancies between readers may be corrected while viewing problematic otoliths simultaneously and assigning a reconciled increment count (Kimura & Anderl, 2005).

Marginal Increment Analysis

Marginal increment analysis has been discussed to be increasingly unreliable for species without a defined reproductive period, or those that lack environmental seasonality such as tropical and mesopelagic species (Campana, 2001; Lessa et al., 2006). The periodicity of bands on otoliths is assumed to correspond with fast and slow growth due to energy constraints like food availability, temperature variations, or spawning (Green et al., 2009). Contrary to the assumption that mesopelagic fishes experience less seasonality than pelagic or coastal fishes, Sarmiento-Lezcano and colleagues (2018) note that daily vertical migrators, such as the three gempylids focused on, as well as a variety of fishes in the families Myctophidae and Gonostomatidae, experience a seasonal change in the thermocline through which they travel. In warmer months the water column is stratified with a strong thermocline, which then dissolves during colder months to create a more homogeneous water column (Sarmiento-Lezcano et al., 2018). This temperature gradient

difference may be why we still have successful validation of annual growth increments for mesopelagic fishes such as *Notoscopelus resplendens* (Sarmiento-Lezcano et al., 2018).

GSI information suggests that Oilfish spawn in mid- to late late summer, Snake Mackerel spawn year-round, with no information on spawning season for Escolar (Vasilakopoulous et al., 2011; Keller & Kerstetter, 2014). With knowledge of Oilfish spawning season, one could expect to see the highest MIR value before spawning and lowest MIR after these summer months, indicating the completion of the most recent growth increment corresponding to this slower growth period. However, no significant trend was observed, with the lowest value occurring in April and the highest occurring in July. The estimation of a summer spawning season for Oilfish can be corroborated with the LFA extrapolated age bins, which predict time of hatching in July. Under the assumption that Snake Mackerel spawn year-round with evidence from GSI studies, drawing conclusions from MIA for this species is especially difficult because it relies on discrete age classes in each season. With species that spawn all year, individuals, even from the same year class, are in different stages of an annual growth period and thus create essentially overlapping growth curves starting at different points of the year, making MIA impractical for Snake Mackerel. LFA response surface analysis places estimated time of hatching around June, which corresponds with the highest observed MIR value. However, due to the limited sample size, no significant correlational relationships can be drawn between LFA and MIA. No known GSI information currently exists for Escolar, and LFA predicted time of hatching around April. MIR values were the lowest in June, once again showing no correlation to spawning period predictions.

Despite expectations of MIR values to range from 0-1, with 0 indicating the beginning of a new increment and 1 indicating the completion of the previous increment, all three species showed MIR values above 1. These larger ratios that show more recent increments to be wider than previous increments indicate a change in growth rate throughout a fish's life. Ideally, samples of each species would have been separated by band counts, with mean MIR being plotted within each assigned age group, to take these growth rate changes into account. However, all three gempylid fishes are rare-event bycatch, and this separation could not be made due to limited sample sizes. Additionally, many months were missing samples, or some months had only one sample, furthering the point that no meaningful conclusions on band periodicity can be made until larger sample sizes can be analyzed.

Techniques similar to marginal increment analysis have shown to be successful in Patagonian toothfish *(Dissostichus eleginoides)*, which are found between 70 and 2000 m depth around subantarctic islands (Horn, 2002). Instead of measuring increment ratios, proportions of otoliths with opaque margins were presented monthly and showed at what points of the year translucent material is laid down versus when opaque material is laid down, confirming that one opaque and one translucent zone are laid down each year (Horn, 2002).

Length-Frequency Analysis

Length-frequency analysis has been a common way to predict growth parameters, age cohorts, and corroborate other validation techniques for fish species because of its non-lethal methods and ability to utilize large amounts of data over varying timespans (Iverson, 1996). This study utilized catch records from the pelagic longlining industry in the western North Atlantic between 1992-2020. Over this 28-year course, data were provided with specific dates, and then just by quarter. When plotting length-frequency data and estimating both age cohorts and growth parameters by monthly and quarterly data, both compilation methods created tradeoffs. By compiling data monthly from 1992-2004, more detail about growth over the year can be inferred but excludes the most recent 16 years of catch data. On the other hand, compiling data quarterly from 1992-2020 loses that detail but includes the entire scope of catch data. When comparing monthly and quarterly parameter predictions by species, Escolar and Oilfish showed the same trend. In these two species, monthly L_∞ parameters were higher than quarterly predictions, and monthly *k* parameters were lower than quarterly predictions. The opposite was the case for Snake Mackerel, with monthly L_∞ parameters lower than quarterly predictions and monthly *k* parameters higher than quarterly predictions. Parameters predicted by quarter were used as the preliminary inputs for maximum likelihood and nonlinear least-squares estimations to increase the scope of catch data used, at the expense of introducing bias in *k* value estimations. In relation to growth functions, a lower *k* value indicates a slower growth rate (Pardo et al., 2013). The increase in *k* value in Escolar and Oilfish accounts for the fewer predicted age cohorts provided by the response surface analysis for quarterly data.

Using ELEFAN to predict VBGF parameters for expectedly long-lived species can introduce a significant bias in *k* estimates (Wang et al., 2021). Estimating VBGF parameters using

this program has been more reliable in short- and medium-lived species, whereas fishing pressures on long-lived species can unevenly impact different age and length classes via gear selectivity (Wang et al., 2021). Due to hook size used in pelagic longlining, it is likely that the catch data used in this study failed to account for the youngest age-class.

In addition to bias introduced by gear selectivity and ELEFAN estimations, the VBGF parameters predicted for Snake Mackerel may not be accurate due to the identification and labeling system used in data collection. Species caught have three letter codes used for data collection to help ensure consistent notation across all longline vessels. The three-letter code for Snake Mackerel (TRX) has been known to include other species in the Gempylid family that have a similar morphology to Snake Mackerel, such as Black Gemfish and Roudi Escolar, but are not *Gempylus serpens*. Because the data used for LFA were historical catch data, confirmation of species identification, as done with the samples that otoliths were collected from, was not possible. Therefore, it is likely that the predicted age cohorts may be altered by the introduction of morphologically similar species with different growth parameters.

Growth Models

The von Bertalanffy growth function (VBGF), has been the most widely accepted model for growth across a wide range of taxa (Pardo et al., 2013). Using multiple growth functions, including logistic and Gompertz, allow for the estimation of parameters such as L_0 and L_∞, that may only be available by hand-raising a population. Growth model estimations for Escolar show a logistic model to be the best fit age and growth curve. Oilfish displayed mixed results, with maximum likelihood estimations predicting a modified von Bertalanffy growth model to fit best, while nonlinear least-squares estimations predicted a 2-parameter von Bertalanffy growth model to fit best. Finally, the 2-parameter VBGF model was estimated to be the best fit for fork length-at-age data for Snake Mackerel. All L_0 parameters were initially set to 0.4 cm, and the original VBGF and Gompertz models used this parameter as a starting point of the model, but ultimately predicted L_0 based on the data provided. However, the 2-parameter VBGF functions on a know size at birth or hatching, and fits the model with that known parameter, so setting L_0 to 0.4 cm created much different curves than those with model-estimated L_0 parameters. Pardo and colleagues (2013) compared estimated and observed L_0 parameters and discussed how fixing L_0 parameters in $VBGF_{2par}$ models increase bias in growth k estimations. By fixing L_0 with a value

larger than true size at birth, k is underestimated, and by fixing L_0 with a value smaller than true size at birth, k is overestimated (Pardo et al., 2013). This is what was observed with the parameters estimated for Snake Mackerel, where the 2-parameter VBGF was the best fit. While all the other models have a k between 0.03-0.59 year^{-1}, the 2-parameter VBGF predicted a k of 1.58 year^{-1}. The growth coefficient k is used to define the rate at which growth approaches L_∞, in that a k value larger than 1 indicates a fast growth rate, and a k value smaller than 1 indicates a slow growth rate (Pardo, 2013). This large discrepancy in model parameter predictions is the difference between estimating Snake Mackerel to be a fast- or slow-growing species. Because of these introduced biases in the VBGF$_{2par}$ model, future age and growth studies on these species are encouraged to utilize either of the three-parameter VBGF models.

Despite initially setting L_0 to 0.4 cm in the models, the original VBGF and Gompertz models used the provided data to predict L_0 parameters that are much larger than expected. For Escolar, the original VBGF predicted L_0 to be 47.3 cm (ML) and 53.2 cm (NLS), while Gompertz predicted L_0 parameters of 52.5 cm (ML) and 54.1 cm (NLS). The smallest Escolar sample collected was 37 cm fork length. In Oilfish, the original VBGF predicted L_0 to be 25.8 cm (ML) and 13.0 cm (NLS), while Gompertz predicted L_0 parameters of 31.5 cm (ML) and 18.3 cm (NLS). The smallest Oilfish sample collected was 18 cm fork length. Finally, for Snake Mackerel original VBGF predicted L_0 to be 82.2 cm (ML) and 68.3 cm (NLS), while Gompertz predicted L_0 parameters of 82.5 cm (ML) and 68.5 cm (NLS). The smallest Snake Mackerel sample collected was 57.5 cm fork length. Because these estimated sizes at birth were extrapolated using data sets subject to gear bias, it is likely that they were all overestimated due to lack of younger age classes being collected and have thus likely influenced the k parameter towards a slower growth rate in models besides the 2-parameter VBGF.

A similar age and growth study on the myctophid *Notoscopelus resplendens* found the Gompertz model to be the best fit growth curve with an average $k = 0.770$ year^{-1} and $L_\infty = 86.1$ mm (Sarmiento-Lezcano et al., 2018). These differences in best model fit, growth rate, and theoretical maximum size highlight the different life history strategies of larger, slower growing fishes and smaller, faster growing fishes. Caiger (2021) explained that, generally, species that vertically migrate daily have relatively slower growth than other non-migratory species due to the energy consumption of the daily migration. Non-migratory fishes can shift energy between growth and reproductive development, leading to more rapid linear indeterminate growth patterns,

whereas daily vertically migrating fishes will store more energy for travel and shift less towards growth, creating an asymptotic growth curve typically observed with the VBGF models (Caiger et al., 2021). However, this does not account for the life history differences between myctophids, which will generally live to be between 9 months and 4 years old and rarely exceed 165 mm standard length, and larger, potentially longer-lived gempylids, both of which vertically migrate (Karnella, 1987). Instead, we can look towards the evolutionary history of these groups. As an order, Myctophiformes is nearly 20 million years older than Scombriformes (Betancur-R et al., 2017). And while both myctophids and gempylids vertically migrate, they perform different roles in the food web, with myctophids being a major prey item for large scombrids, gempylids, and other commercially valuable pelagic fishes (Gjosæter & Kawaguchi, 1980).

While most myctophids are an order of magnitude smaller than the gempylids studied, the Patagonian toothfish (*Dissostichus eleginoides*) and Antarctic toothfish (*Dissostichus mawsoni*) show comparable size to Escolar, Oilfish, and Snake Mackerel. *Dissostichus eleginoides* was found to have an average $k = 0.102$ year^{-1} and $L_\infty = 146.5$ cm, and *D. mawsoni* an average $k = 0.098$ year^{-1} and $L_\infty = 177.4$ cm between males and females (Horn, 2002). The parameters predicted by length frequency analysis for all three study species display similar k and L_∞ values, despite not being reflected in the VBGF growth models: Escolar $k = 0.112$ year^{-1} and $L_\infty = 142$ cm, Oilfish $k = 0.102$ year^{-1} and $L_\infty = 178$ cm, and Snake Mackerel $k = 0.025$ year^{-1} and $L_\infty = 193$ cm. With this comparison, we can estimate that these gempylid fishes grow at similar or slower rates to other large mesopelagic fishes.

Conservation Context

Levesque (2010) stated that two of the greatest challenges of fisheries management are controlling bycatch and understanding emerging fisheries, and both cases apply to Escolar, Oilfish, and Snake Mackerel. As diel vertical migrators, these species are becoming more common bycatch in tuna longlines, to the point of being commercially sold. Using age and growth research, we can better understand various aspects of life history and population dynamics. Adams (1980) defines a k-selected fish species as one with 1) high age at maturity, 2) low k value in the VBGF, 3) large L_∞ in the VBGF, 4) low instantaneous mortality, and 5) high maximum age. Size at maturity has been estimated to be 30-35 cm for Escolar and 43-50 cm for Snake Mackerel (Keller & Kerstetter, 2014). Typically, the growth model with best fit can be used to calculate the age at maturity based

on size at maturity and allow for limits regarding kept catch sizes to be created. As previously discussed, the L_0 parameters had been overestimated and thus are greater than the size at maturity found by Keller and Kerstetter (2014). Calculating ages from these sizes would result in negative ages, further showing that more data is needed to provide more accurate growth models. Escolar and Oilfish displayed k values less than 1, confirming a low k value for the second criterion. As previously stated, growth model and length frequency analysis results showed comparable L_∞ estimates to other large mesopelagic fishes, confirming the third criterion. As large, potentially long lived fishes, fisheries of Escolar, Oilfish, and Snake Mackerel are more sensitive to overfishing, as they would likely have a lower maximum yield per recruit that occurs at a later age (Adams, 1980).

Growth parameters can be used in a variety of other research and conservation methods. Fish length and otolith size relationships can be used to understand the age and size classes of prey items in trophic studies based on the hard parts found in stomach content studies (Sarmiento-Lezcano et al., 2018). Establishing a relationship between size at maturity and age at maturity can allow for the introduction of exclusion devices in commercial fishing gear. Commercial trawl nets can be designed with larger mesh size to minimize undersized or immature bycatch, and longline hooks can transition from J-style to circle to increase chance of survival of bycatch species (Kerstetter & Graves, 2006; Pauly et al., 2021). Additionally, establishing known spawning periods can aid in the incorporation of ecosystem-based management, allowing for temporary spatial closures (Grantham et al., 2008).

Conclusion

Escolar, Oilfish, and Snake Mackerel are members of the family Gempylidae that reside in the mesopelagic during the day and travel to the surface to feed during the night. They are large fishes with Escolar and Oilfish reaching lengths of two meters in fork length and Snake Mackerel reaching a meter in fork length. Catch data spanning from 1992-2020 used in length-frequency analyses predicted theoretical maximum size (L_∞), growth coefficient (k), time of hatching (t_{anchor}), and age bins for each species. Marginal increment analyses showed no distinct trends in growth over the course of a calendar year for the three species in focus and could not corroborate spawning season estimates from previous gonadosomatic index studies or confirm annual

periodicity of growth increments on otolith sections. Growth model estimates produced large L_{∞} parameters and small k parameters, predicting these species to be k-selected fishes. All three species fork length-at-age data were best fit by a 2-parameter von Bertalanffy growth function when size at birth (L_0) was fixed to the mean value estimated by the other models. Understanding growth rates of these fishes, and combining growth functions with size at maturity information, is vital in maintaining a healthy fishery for these valuable non-target species (Lawson, 2001). The age and growth data collected in this study are only a starting point, as sample size and gear bias were significant limiting factors in drawing more meaningful conclusions.

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