NOAA Technical Memorandum NMFS

FEBRUARY 2022

A SUMMARY REPORT OF LIFE HISTORY INFORMATION ON THE CENTRAL SUBPOPULATION OF NORTHERN ANCHOVY (ENGRAULIS MORDAX) FOR THE 2021 STOCK ASSESSMENT

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NOAA-TM-NMFS-SWFSC-659

U.S. DEPARTMENT OF COMMERCE
National Oceanic and Atmospheric Administration
National Marine Fisheries Service
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A summary report of life history information on the central subpopulation of Northern Anchovy (*Engraulis mordax*) for the 2021 stock assessment

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Table of Contents

2

Abstract

The Northern Anchovy (*Engraulis mordax* Girard) is one of the most abundant forage fishes in the northeastern Pacific Ocean and an important part of the food web as prey for marine mammals, seabirds, and predatory fishes. Northern Anchovy is a monitored species under the Coastal Pelagic Species Fishery Management Plan, and recently the Pacific Fisheries Management Council recommended that the central subpopulation of Northern Anchovy (CSNA) be assessed in 2021. The overall goal of this report is to summarize the life history information collected, analyzed, and submitted for consideration in the 2021 benchmark stock assessment for CSNA. The specific objectives are to: (1) determine the birthdate to be used for age assignments; (2) compute the ageing error matrices for the stock assessment model; and (3) generate an updated estimate of length at maturity for female CSNA.

The data presented in this report were collected in spring 2017 and 2021 and in summer 2015-2019 during trawl surveys for coastal pelagic species conducted by the Southwest Fisheries Science Center and from fishery samples collected monthly from port landings by the California Department of Fish and Wildlife in 2014-2021. Whole otoliths were used to age individual fish, and marginal increment and edge analyses were used to determine an overall birthdate for the CSNA. Final age assignments were based on the capture date and the interpretation of the most distal pair of increments. Female CSNA gonads collected during the 2017 and 2021 spring trawl surveys were histologically processed and classified as mature or immature using standardized terminology. Logistic, non-linear regression was used to generate maturity ogives and estimate length at maturity.

Fish ages from the CSNA ranged from 0 to 6 years for both the trawl survey and fishery samples. Samples from both datasets were dominated by age 0-, 1-, and 2-year-old fish (88% and 90%, respectively) and a low proportion of age 4+ individuals (8% and 2%, respectively). The level of ageing precision varied between years and ages for both datasets, with the lowest ageing precision generally observed for age 4+ fish. Observed variations in ageing precision were influenced by the identification of the first annulus, presence of checks, and determination of edge type. Age-reading variability among readers and years is expected to decrease as the collective understanding of the patterns of opaque and translucent depositions increases through an increased focus on age validation research (e.g., OTC-marked otoliths) and rapid age estimation methods (e.g., Fourier transform near-infrared spectroscopy), which are priorities moving forward.

Initial model runs to estimate length at maturity for the CSNA indicated the possibility of a small year effect, which through further analyses was attributed to the inclusion of samples of females collected in colder waters north of the main spawning area (i.e., north of Point Conception) during the 2021 trawl survey. To best represent the main spawning area, the samples outside the Southern California Bight were excluded and revised estimates of length at maturity were nearly

identical between 2017 and 2021. Consequently, a pooled dataset composed only of fish sampled from the Southern California Bight was used to generate a single estimate of length at maturity (L_{50}) of 98.2 mm standard length. A von Bertalanffy growth function using all aged females from 2015 to 2021 produced an estimated age at maturity (A_{50}) of -0.085 years from the L_{50}, indicating that more than 50% of female CSNA are mature at age 0. Future research will focus on evaluating the accuracy and utility of using visual (macroscopic) methods to estimate length at maturity in CSNA by comparing results to those verified through histological examinations.

The data, methods, and results presented in this document represent that which was provided to the stock assessment team for consideration in the 2021 stock assessment of the central subpopulation of Northern Anchovy. However, the stock assessment team made the determination of the methods and data used in the final assessment model in consideration of recommendations provided by external reviewers during the Stock Assessment Review (STAR) Panel meeting held on December 7-10, 2021. Therefore, we refer the reader to the postscript section for changes made to the age and maturity data that were used in the final stock assessment. The completed stock assessment report that discusses the final stock assessment model will be submitted to the June 2022 Pacific Fisheries Management Council Briefing Book.

1. Introduction

The Northern Anchovy (*Engraulis mordax* Girard) is one of the most abundant forage fishes in the northeastern Pacific Ocean and an important part of the food web as prey for marine mammals, seabirds, salmon, sharks, tunas, and many other species (Koehn et al. 2017; Thompson et at. 2019; Harvey et al. 2020; Sydeman et al. 2020). The species ranges from northern British Columbia, Canada, to southern Baja California, Mexico, but it is most abundant in coastal waters from San Francisco, California (CA), USA, to Magdalena Bay, Baja California, Mexico (Baxter 1967; Miller and Lea 1972). Northern Anchovy are pelagic schooling fish that occupy the epipelagic zone from inshore to 200 miles or more offshore and from the surface to 300 m in depth where they filter feed on a wide variety of planktonic prey species, including euphausiids, copepods, fish eggs, diatoms, larval fishes, and gelatinous zooplankton (Scura and Jerde 1977; Hunter and Kimbrell 1980; Bakun 2014; Brodeur et al. 2019). Adults tend to remain farther offshore, whereas young-of-year are found mostly in shallower waters closer to shore, and juveniles inhabit both nearshore and offshore areas (PFMC 1978; Parrish et al. 1985).

The Northern Anchovy is typically divided into northern, central, and southern subpopulations based on electrophoretic, morphometric, and meristic characteristics (McHugh 1951; Vrooman et al. 1981), although there is no apparent genetic structure across its range (Lecomte et al. 2004). The northern subpopulation (NSNA) is estimated to range between British Columbia, Canada, to north of Monterey, CA, although Fiedler et al. (1986) showed the southern limit of NSNA to be near Cape Mendocino, CA. The central subpopulation (CSNA) ranges between San Francisco, CA, to the middle of the Baja peninsula, Mexico, and the southern subpopulation (SSNA)

extends from the middle to the end of the Baja peninsula and into the Gulf of California, Mexico (McHugh 1951; Vrooman et al. 1981). However, subpopulations of Northern Anchovy do exhibit seasonal and annual movements in relation to climate and ocean conditions that result in overlapping distributions, interchanges between major fishing grounds (e.g., between central CA, southern CA, and northern Baja California, Mexico), and range shifts (Haugen et al. 1969; Weber and McClatchie 2010; Sydeman et al. 2020).

Similar to other clupeoid fishes, Northern Anchovy are characterized by high interannual variability in recruitment success and population abundance (Lasker 1988; Alheit 1989; Litz et al. 2008; MacCall et al. 2016; Thayer et al. 2017). Comprehensive monitoring of CSNA began in the 1950s with the start of the California Cooperative Oceanic Fisheries Investigations (CalCOFI) time series of egg and larval abundances. The stock declined in the early 1950s but then rebounded during the 1960s (Ahlstrom 1965; Sydeman et al. 2020). Large recruitment events were periodically observed during the 1970s and 1980s, with abundances then fairly stable from that period to the early 2000s before declining to record lows from 2009 through 2015 (Methot 1989; MacCall et al. 2016; Thompson et al. 2019; Sydeman et al. 2020). Abundances of young-of-year CSNA increased drastically during the marine heatwaves in 2015 and 2016 (Zwolinski et al. 2017; Thompson et al. 2019), and fishery-independent surveys from 2018 to 2020 observed historic catches of anchovy (Stierhoff et al. 2019; Thompson et al. 2019; Stierhoff et al. 2020; Weber et al. 2021), leading to the assumption that the overall population size is currently at its highest level since the development of quantitative monitoring in the California Current Ecosystem (Thompson et al. 2019; Harvey et al. 2020).

Population dynamics of CSNA have been reported to be influenced by environmental conditions (e.g., temperature and current flow), climate (e.g., Pacific Decadal Oscillation), ocean stability (e.g., upwelling), food availability and feeding success, fishing, and density-dependent mechanisms (e.g., predation, competition, cannibalism) at local to regional scales that determine survival and mortality (Methot 1983; Lasker 1988; Schwartzlose et al. 1999; Rykaczewski and Checkley 2008; MacCall 2009; Lindegren et al. 2013; Checkley et al. 2017; Rykaczewski 2019; summarized in Sydeman et al. 2020). However, a recent review by Sydeman et al. (2020) found no physical or biological variables that related to CSNA biomass across a multi-decadal time series (1951 to 2015) and concluded external drivers of population dynamics in CSNA were non-stationary. Moreover, the historically high recruitment success and population abundance of CSNA that have occurred during the extraordinarily warm waters of the past 7 years further challenge our understanding of the processes that control their population dynamics (Thompson et al. 2019).

Northern Anchovy have historically been caught for human consumption, live and dead bait, food for hatcheries, and reduction to oil and fish meal, with reliable records dating back to 1916 (Messersmith 1969; PFMC 1978). The Northern Anchovy fishery in the U.S. emerged in the

early 1950s after the collapse of the Pacific Sardine (*Sardinops sagax* Girard) industry (PFMC 1978), with the majority of landings occurring in California but also occasional landings in Oregon and Washington (Sweetnam 2011). Annual landings for Northern Anchovy in California were negligible prior to 1952, peaked at 340 KMT in 1981, dropped to less than 5 KMT in the 1990s, and have remained mostly below 20 KMT for the past two decades (Jacobson et al. 1995; Sydeman et al. 2020). Northern Anchovy are an important part of the California recreational fishing industry as they are a large component of the live bait used, but a small, localized food-fish fishery occurs off Monterey when squid are not available (PFMC 2020; Sydeman et al. 2020).

The Fisheries Management Plan (FMP) for Northern Anchovy in U.S. waters was created in 1978 (PFMC 1978), and the last assessment for the CSNA occurred in 1995 (Jacobson et al. 1995), while the NSNA has never been formally assessed. In 1999, the Northern Anchovy FMP was modified to manage the entire CPS fishery (i.e., Pacific Sardine, Northern Anchovy, Pacific (Chub) Mackerel *Scomber japonicus*, Jack Mackerel *Trachurus symmetricus*, and Market Squid *Doryteuthis (Amerigo) opalescens*), with the name being changed to the Coastal Pelagic Species FMP (PFMC 2019). Currently, Northern Anchovy is a monitored species under the Coastal Pelagic Species FMP (PFMC 2020), and recently the Pacific Fisheries Management Council recommended that the CSNA be assessed in 2021. Since the 1995 assessment, the CSNA has been monitored continuously through fishery-dependent collections and fishery-independent surveys, resulting in a series of formal biomass estimates (e.g., Fissel et al. 2011; MacCall et al. 2016; Thayer et al. 2017; Dorval et al. 2018).

The overall goal of this report is to summarize the life history information collected, analyzed, and submitted for consideration to be used in the 2021 benchmark stock assessment for CSNA, including detailed descriptions of the methods, assumptions, results, and challenges underlying the production of age and reproductive maturity data. For age data, the specific objectives are to determine the birthdate to be used for age assignments and compute the ageing error matrices for the stock assessment model for data collected during CPS trawl surveys by NOAA Southwest Fisheries Science Center (SWFSC) and data collected by the California Department of Fish and Wildlife (CDFW) during port sampling of commercial fishery landings. For the reproductive maturity data, the objective is to generate an updated, length-based maturity ogive for female CSNA based on histologically-prepared gonad samples collected during the Spring 2017 Daily Egg Production Method (DEPM) and Spring 2021 trawl surveys. Additionally, we evaluated potential issues and priorities for future life history research on CSNA to inform stock assessments.

As noted in the Abstract, this report was completed prior to and may differ from the stock assessment report. Therefore, we refer the reader to the postscript section within this document and the final stock assessment report that will be published in the June 2022 Pacific Fisheries

Management Council Briefing Book for details on the methods and data related to age and maturity that were used in the final stock assessment model.

2. Description of Data Sources and Collection Methods

The data presented in this report were collected in spring 2017 and 2021 and in summer 2015-2019 during research trawl surveys for CPS conducted by SWFSC (Table 2.1; Figure 2.1). The spring 2017 survey was a full Daily Egg Production Method (DEPM) for CSNA conducted aboard the NOAA ship RV Reuben Lasker (21 March – 22 April 2017) that collected data and samples from San Diego, CA, (32.55°N) to north of San Francisco, CA (ending at 38.06°N, north of CalCOFI line 60). Ichthyoplankton and eggs were collected using Paired Vertical Egg Tow (Pairovet) nets, bongo nets, and the Continuous Underway Fish Egg Sampler (CUFES), and CPS were sampled using surface trawls. The design and data collection methods of the 2017 DEPM survey and 2015-2019 summer surveys are described in detail in Dorval et al. (2018) and Zwolinski et al. (2017), Zwolinski et al. (2019), Stierhoff et al. (2018), Stierhoff et al. (2019), Stierhoff et al. (2020), and Stierhoff et al. (2021a,b) respectively. Therefore, we only briefly described the 2015-2019 summer surveys and focused on providing more details for the 2021 spring survey (see sections 2.1 and 2.2 below).

Table 2.1. Summary of data available for the 2021 stock assessment of the central subpopulation of Northern Anchovy.

Cruise	Ship	Total hauls	Hauls with anchovies	LW (mm & g)	Sex & maturity	Gonads Saved	Otoliths Saved	# Ages
Summer 2015 (201507)	SH	56	31	722	240	25	498	490
Summer 2016 (201607)	RL	65	32	1193	1143	387	1051	732
Spring 2017 (201704)	RL	64	23	823	823	410	616	548
Summer 2017 (201707)	RL	30	7	257	107	34	132	129
Summer 2018 (201807)	RL	93	55	1811*	952	0	956	666
Summer 2019 (201907)	RL	86	63	3094*	1361	411	1559	1072

Cruise	Ship	Total hauls	Hauls with anchovies	LW (mm & g)	Sex & maturity	Gonads Saved	Otoliths Saved	# Ages
Spring 2021 (202103)	RL	50	41	2391	2315	396	910	879

* There were 350 individuals from 201807 and 10 from 201907 that only had fork length (FL) measurements and no measurements for standard length (SL). The following equation from Palance et al. (2019) was used to estimate SL from FL: SL = 0.965*FL - 5.736.

2.1 2015-2019 Summer Trawl Surveys

Although the SWFSC has been conducting annual CPS summer surveys since 2008 along the Pacific coasts of the U.S. and Canada, Northern Anchovy became a primary target species of these surveys in 2015 (Dorval et al., *In review*). Surveys for CPS have been conducted under several different names (e.g. SaKe, California Current Ecosystem Survey), but from 2015 to 2019, Northern Anchovy were collected using similar methods with the primary goal of producing length and age composition data for acoustic biomass estimates and stock assessment models. The 2015 summer (SaKe) survey was conducted from San Diego, CA (latitude 32.8°N), to British Columbia, Canada (50.8°N), from 15 June to 10 September 2015 aboard the NOAA RV Bell M. Shimada. However, during the 2016-2019 period, summer surveys began off British Columbia in June or July and ended off CA in August or September. This approach allowed better coverage and more efficient sampling of all CPS subpopulations, which typically migrate northward in summer. Since 2016, all summer surveys have been conducted aboard the NOAA RV Reuben Lasker. The total area covered by the RV Reuben Lasker varied with survey goals and the number of days allocated to each annual survey (Figure 2.1; also see Zwolinski et al. 2017; Dorval et al. 2018; Zwolinski et al. 2019; Stierhoff et al. 2018; Stierhoff et al. 2019; Stierhoff et al. 2020; Stierhoff et al. 2021a,b).

Nighttime trawl locations were identified with the help of daytime acoustics and CUFES. Trawl locations were selected, in descending priority, in areas with high CPS backscatter or CPS eggs in CUFES during the day and previous trawl locations and catches. If no CPS backscatter or eggs were observed during the day, trawl locations were placed at random sites with attempts made to place trawls alternatively inshore and offshore. Each night, two to four 45-min surface trawls were conducted using a Nordic 264 rope trawl with 3.0 m^2 foam core doors outfitted with a modified marine mammal excluder device (Dotson et al. 2010).

During the 2015 and 2016 summer surveys, a maximum of 50 Northern Anchovy were randomly selected from each haul and measured for biological characteristics, with all sagittal otoliths extracted for ageing. In 2017-2019, otolith samples were collected based on a two-stage sampling design. For the first stage, a maximum of 50 fish were collected from each haul, and

each was measured for SL to the nearest millimeter and weighed to the nearest 0.5g. For the second stage, 25 fish were selected for otolith extraction and ageing using a 20 mm length-bin scale (Dorval et al., *In review*). Sex and visual maturity stage were determined for all fish measured for length and weight following the criteria set by Lo et al. (2010), and up to 10 ovaries were extracted and preserved in 10% formalin for each haul for subsequent analyses (e.g., batch fecundity, microscopic staging of maturity phase).

2.2 2021 Spring Trawl Survey

The main objectives of the 2021 spring trawl survey were to: (1) collect biological data for developing length and age compositions to be combined with acoustic data to estimate fish biomass for CPS (i.e., ATM method; see Zwolinski et al. 2017); and (2) collect and process samples of female CSNA gonads (and other CPS) to generate an updated estimate of length at maturity. The trawl survey was conducted aboard the RV Reuben Lasker from 20 March to 7 April 2021. The RV Reuben Lasker covered the area off CA from San Diego (32.24°N, south of CalCOFI line 93) to just north of San Francisco (ending at 38.14°N north of CalCOFI line 60), with the survey beginning at the southernmost transect and then proceeding northward (Figure 2.1).
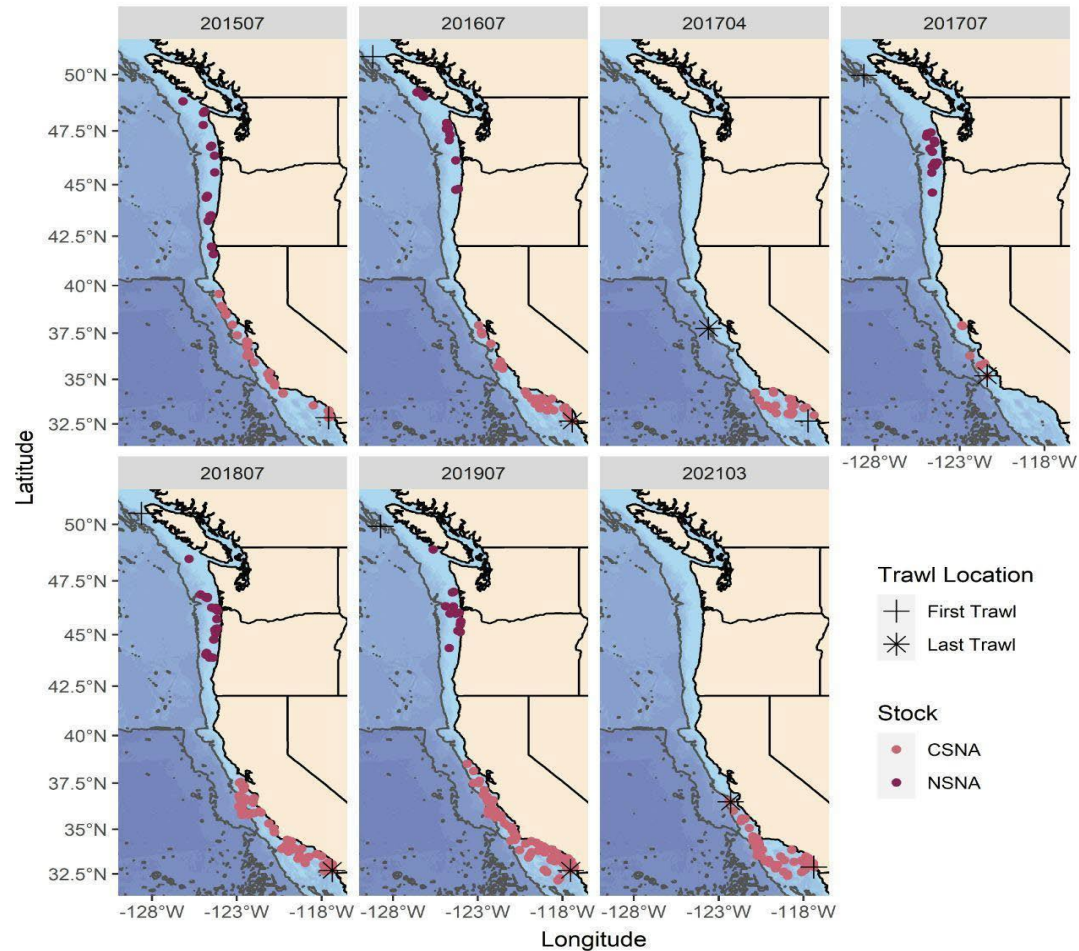
Figure 2.1. Map of the catch locations for both the northern subpopulation (NSNA) and central subpopulation (CSNA) of Northern Anchovy during the SWFSC spring and summer CPS trawl surveys from 2015-2021. Also included are the first and last trawl locations for each survey. The last trawl location for 201507 was located in mid British Columbia (-132.617°W, 52.8098°N) and was not included on the map as no anchovy were collected up there.

Sampling for life history data focused on collecting fish samples from night-time surface trawls, and thus no Pairovet or Bongo tows were taken during the survey, but eggs were collected continuously during the daytime using CUFES. Methods for collecting length, weight, reproductive information, gonad samples, and otoliths closely followed methods used during the summer trawl surveys from previous years. For Northern Anchovy, the sample size for length and weight measurements was increased to 75 fish such that all Northern Anchovy were processed if a trawl catch contained 75 or less fish. Otherwise, 75 fish were randomly sampled from each positive trawl (Table 2.1), and otoliths were extracted from 25 of these 75 fish for ageing. Contrary to the 2017-2019 surveys, a bin length scale was not used to select otolith samples for ageing. Feedback from previous cruise participants suggested that the binning method was inefficient and overly time-consuming. Therefore, a new method was tested with the intent of collecting a sufficient number of otoliths from all length (and age) classes in a more efficient manner.

For age and growth studies, it is important to sample and age a sufficient number of otoliths from all length (and age) classes of a species or population to accurately approximate the true variation in length at age and minimize bias due to sampling distribution (Bolser et al. 2018). To achieve this goal, samples of Northern Anchovy were chosen for otolith extraction using a combination of direct selection and randomization (i.e. "Selective-Random"). After the random subsample of 75 individual Northern Anchovy was taken from the entire catch, several of the smallest and largest individuals were selected for otolith sampling, and then additional fish (from the random 75 subsample) were then selected at random to reach a total of 25 samples of otoliths for the trawl. To examine if a large enough sample size was being obtained for each length class across the entire length range of fish sampled during the survey, a plot examining the length distribution of all individuals measured for length versus the length distribution of those whose otoliths were extracted was created and updated continuously throughout the survey (Figure 2.2). If a certain length class or range was undersampled, individuals from this range were targeted for otolith extraction each night until a minimum sample size of 50 individuals was achieved (if possible). This method provided a rapid way to select subsamples as a visual examination for size ranges can be done quickly and the plots can be created on the ship computer or by someone on land. Consequently, this method can be conducted rapidly to substantially reduce the amount of processing time per haul. Furthermore, an examination of the length distributions from the 2021 spring survey indicated that this method was effective in collecting a sufficient number of otolith samples across the entire length distribution relative to past years when no binning or binning were performed (Figure 2.2). Therefore, this method is suggested to be used in future surveys.
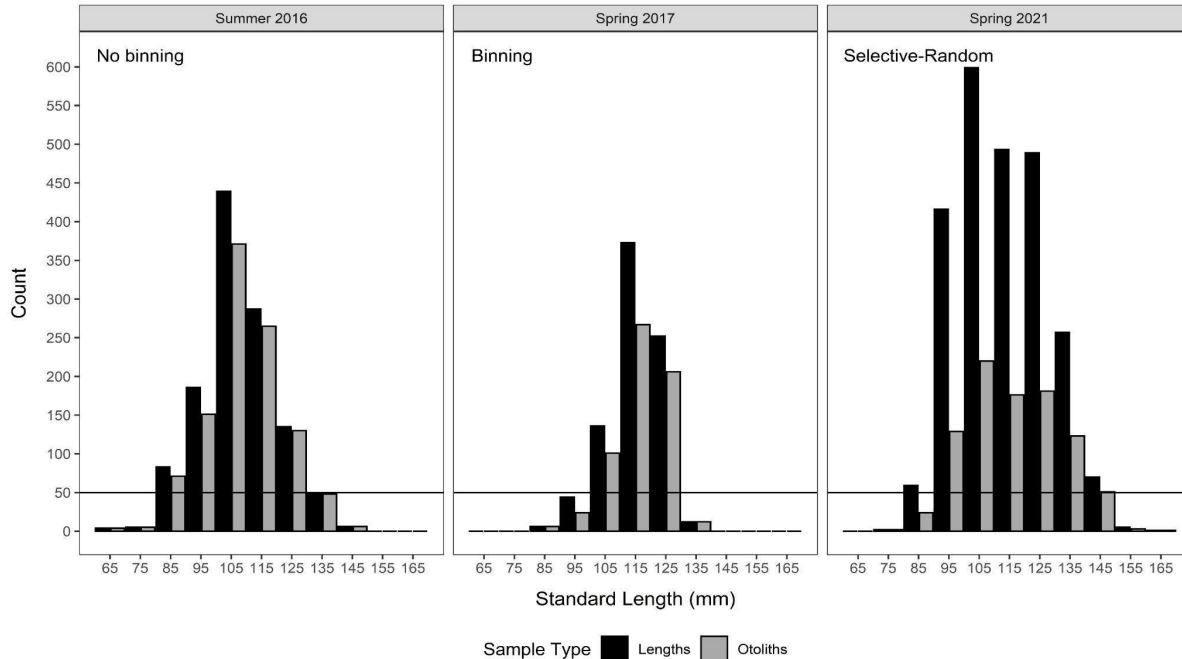
Figure 2.2. Histogram showing the number of CSNA in 10 mm length bins that were measured for standard length (mm) and that had otoliths extracted during three different trawl surveys (Summer 2016, Spring 2017, Spring 2021), where fish whose otoliths were extracted were chosen, respectively, randomly (i.e. binning was not used, "No binning"), using a 20 mm length bin scale ("Binning"), and by both selective and random methods ("Selective-Random"). The black line at 50 indicates the preferred minimum sample size per 10 mm length bin.

3. Age and Length Data

3.1 Background

Somatic growth in Northern Anchovy with respect to body length is rapid during the first year of life and then decreases substantially thereafter, with relatively small seasonal fluctuations in mean SL (Mallicoate and Parrish 1981). Conversely, more substantial seasonal fluctuations exist for growth in terms of body weight, with Northern Anchovy in CA gaining most of their annual net increase in weight from February to April (Mallicoate and Parrish 1981). After April, young fish generally maintain their weight until the following February, but by September, older fish will have lost more than half of their weight gain due to the investment of energy and fat reserves in reproduction (Hunter and Leong 1981; Mallicoate and Parrish 1981). The seasonal fluctuation in weight varies regionally, with an annual net increase in weight three to four months later for Northern Anchovy from central California compared to those from the Southern California Bight (SCB) (Mallicoate and Parrish 1981).

Age and growth of Northern Anchovy in the California Current Ecosystem became widely studied from the 1970s through the 1990s after the establishment of a technique for determining

the age of anchovies from otoliths by Collins and Spratt (1969). Northern Anchovy have been reported to live up to 8 years (Mallicoate and Parrish 1981), but older individuals (i.e., age 4+) are thought to be relatively scarce (Collins 1969; Spratt 1975; Mallicoate and Parrish 1981; Parrish et al. 1985). Large length ranges have been observed within each age class, with the largest length ranges usually found for age 1 fish (Collins 1969; Spratt 1975; Mallicoate and Parrish 1981; Parrish et al. 1985). For their studies on Northern Anchovy age and growth, Mallicoate and Parrish (1981) and Parrish et al. (1985) assumed a February birthdate to determine age composition due to February being the peak spawning month. Work on larval anchovy validated the deposition of daily rings, although the number of daily rings did not exactly track true age in days but was usually within 5 days (Brothers et al. 1976).

Regional differences in length and age structure have been observed in adult Northern Anchovy. A larger maximum length has been found for NSNA (250 mm SL; Litz et al. 2008) compared to CSNA (184 mm SL; Clark and Phillips 1952). Less work has been conducted on age and growth of SSNA, but both Parrish et al. (1985) and Mais (1974) observed the maximum length to be ~125 mm SL. A greater proportion of older fish have been found in central California compared to the SCB (Mallicoate and Parrish 1981), and older individuals were found for CSNA (range = 1-7 years old) compared to SSNA (range = 1-5 years old) (Parrish et al. 1985).

Additionally, regional and spatial differences in growth rates have been observed in both juvenile and adult Northern Anchovy. For adults, SSNA were found to have a slower growth rate than CSNA, and while CSNA exhibited a constant growth rate after 1.5 years, SSNA showed only minor growth after 1.5 years (Mais 1974; Parrish et al. 1985). For juveniles, growth was also higher for the CSNA compared to the SSNA, but within the CSNA, faster growth was observed for those fish in central California than those in the SCB (Parrish et al. 1985). Additionally, faster juvenile growth was observed in individuals caught in offshore areas compared to inshore areas, with the offshore area of the SCB exhibiting the fastest juvenile growth (Parrish et al. 1985).

Somatic growth rate is an important determinant of population growth and recruitment in Northern Anchovy (Lo et al. 1995), particularly as it relates to survival of early and late larval stages (Butler et al. 1993). Major influences of Northern Anchovy individual (somatic) growth include food quantity and quality, ocean temperature, upwelling intensity and timing, and early life history mortality rates. For juvenile NSNA, delayed upwelling was found to contribute to reduced growth rates due to low food availability (Takahashi et al. 2012). Growth rates of *Engraulis* spp. decreased in response to diet shifts towards smaller plankton (Canales et al. 2016), and nearshore, eutrophic waters where large zooplankton are abundant have been identified as areas with the highest potential for adult Northern Anchovy growth (Rykaczewski 2019). Food availability and varying metabolic rates from temperature changes also directly impact growth rates of larval and juvenile CSNA (Butler 1989). Optimal growth temperatures have been reported for *Engraulis* spp. (Takasuka et al. 2007), but Methot and Kramer (1979)

found no obvious relation between larval Northern Anchovy and temperature, although sampling occurred within a relatively narrow temperature range.

Northern Anchovy have shorter lifespans during unfavorable years, with the maximum age appearing to drop from 8 to 4 years (MacCall 2009). Prior to 1977, fisheries landings were composed of mostly 2- and 3-year-old fish along with substantial catches of older fish, but in the years that followed, older age groups have diminished and catches were heavily dominated by age 0 and 1 fish (Mais 1981). Additionally, after 1977, Northern Anchovy in the SCB exhibited smaller sizes and earlier maturation (MacCall 2009). These abrupt changes in the life history of Northern Anchovy have since been linked to a regime shift in the California Current that occurred in 1976, in which ocean temperatures drastically increased and mimicked conditions more typical of Baja California where SSNA occur (McGowan et al. 2003; MacCall 2009).

Ageing of fish has become widely important due to the increased use of age-structured stock assessment models, such as those used to assess CPS biomass along the U.S. Pacific west coast (i.e., Methot 1989; Hill et al. 2011; Crone et al. 2019l; Kuriyama et al. 2020). Ageing errors can influence the process of estimating demographic parameters for fish populations, the performance of assessment models, and ultimately management measures derived from these analyses (Reeves 2003; Punt et al. 2008). These errors may affect estimates of biological parameters, such as age-at-maturity, length-at-age, and weight-at-age, and fishery data such as catch-at-age and catch-per-unit effort indices (Reeves 2003). Further, in assessment models, these errors tend to smooth out estimates of recruitment and total allowable catch allocated to fisheries (Reeves 2003). Consequently, ageing errors can significantly mask important stock-recruit relationships and the effects of environmental factors on year-class strength (Fournier and Archibald 1982; Richards et al. 1992).

Since 2009, Stock Assessment Review (STAR) panels have recommended that systematic age-reading comparisons be conducted in each of the major CPS ageing laboratories. Accordingly, from 2011 to 2020, the Age-Reading Error Matrix Estimator (Agemat model) developed by Punt et al. (2008) has been used to compute ageing errors for Pacific Sardine and Pacific Mackerel by laboratory, fishery, and trawl surveys (see Hill et al. 2011; Dorval et al. 2013). As recommended by the 2009 STAR panel, the development of these ageing errors has involved research collaborations between the six major CPS ageing laboratories along the Pacific west coast, namely: CDFW, Washington Department of Fish and Wildlife (WDFW), Oregon Department of Fish and Wildlife (ODFW), Fisheries and Ocean Canada (DFO), Centro Interdisciplinario de Ciencias Marinas del Instituto Politécnico Nacional (CICIMAR-IPN), and SWFSC. A similar collaborative effort was initiated for developing ageing methodology for the CSNA via a virtual workshop hosted by the SWFSC in summer 2020. However, due to the COVID-19 pandemic, collaborative research to estimate ageing precision for the CSNA was restricted to CDFW and SWFSC laboratories. The 2021 CSNA stock assessment model will integrate data collected from fishery port sampling by CDFW and trawl surveys by SWFSC. Therefore, it was necessary to

develop similar ageing methodology among these two laboratories while also computing ageing errors for both the California fishery samples and CPS trawl survey datasets.

3.2 Ageing Methods

The sagittal otolith is the primary hard part used for ageing Northern Anchovy collected in U.S. waters (Figure 3.1). For both the CDFW and SWFSC ageing labs, otoliths were stored dried in individual capsules. Ageing methodology followed those previously established for determining age of Pacific Sardine and Pacific Mackerel using whole (i.e., un-sectioned) otoliths (Fitch 1951; Collins and Spratt 1969; Yaremko 1996). The method is straightforward and generally recommends that the age reader: (1) immerses the otolith in distilled water in a glass dish with a black background for no longer than three minutes; and (2) counts the number of annuli observed on the distal side of the otolith and determines edge type using a dissecting microscope with reflected light at a magnification of 25x. An annulus is defined as the interface between an inner translucent growth increment and the successive outer opaque growth increment (Fitch 1951; Collins and Spratt 1969; Yaremko 1996; Figure 3.1).
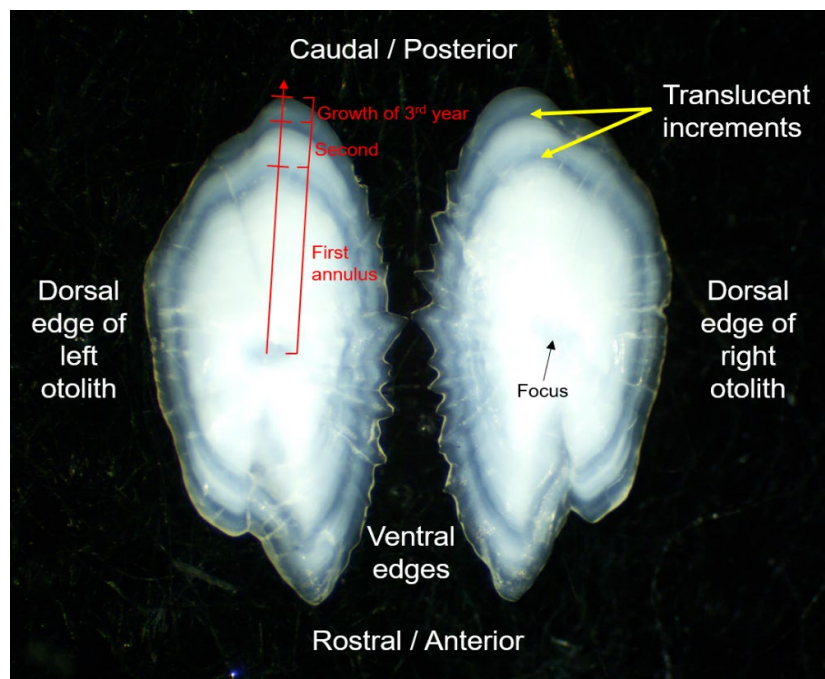

Figure 3.1. Image of a typical Northern Anchovy sagittal otolith pair illustrating the overall anatomy and growth features. An annulus is defined as the interface between an inner translucent growth increment (dark band) and the successive outer opaque growth increment (white band). This otolith pair has two fully formed annuli with a third annulus forming. The photo is looking at the distal side of the otolith, and the proximal side with the sulcus into the page.
Edge types were assigned as opaque (O), translucent (T), opaque going to translucent (O/T), or translucent going to opaque (T/O). For the trawl survey data, A digital image (photo) of each otolith pair was taken at the 25x magnification after age reading occurred using an AmScope™

camera and software package to create a digital library. Additionally, some images were marked with the annuli that were counted so that readers could review and discuss their age assignments. All age assignments were based on the in-person reading of the otolith and not from viewing an image.

In 2020, a digital library of a selected subset of otolith pairs was created by CDFW for Northern Anchovy samples collected from a newly re-emerged commercial fishery starting in 2014. The Northern Anchovy otolith pairs selected for imagery were based on the fishery samples assigned for all readers to age, referred to as "all-reads", which were used to monitor and optimize between reader precision. The images were taken at 25x magnification using a Levenhuk™ digital microscope camera and software packages after age reading by the designated reader whose ages were used for that all-read sample. The images were then used by the other readers for age assignments and discussions, including any differences among readers. All final age assignments were based on the in-person reading of the otolith structure by the designated reader. The process of all-reads is an established practice for the CDFW age lab. However, due to COVID-19 restrictions that prevented opportunities for all readers to age the otolith structure and then meet in-person to directly compare and discuss readings, digital images were reviewed and discussed remotely via virtual meetings with shared viewing of the otolith image.

3.2.1 Marginal Increment Analysis

The margin of an otolith can be translucent or opaque depending on the month of capture; translucent increments are generally laid down during periods of slow growth in winter, and opaque increments are laid down during periods of fast growth in summer (Campana 2001; Quist and Isermann 2017). Peak timing of translucent increment formation for CSNA is late spring, and by June 1st nearly all otoliths exhibit an opaque edge (i.e. a newly completed annulus; Collins and Spratt 1969). Timing of marginal increment formation, however, has been found to vary by ages in the European Anchovy (*E. encrasicolus*), with opaque increments forming earlier in younger fish (Uriarte et al. 2016). Preliminary analyses of our CSNA data also showed that opaque increments may form earlier in younger fish. Thus, it was important to further examine whether marginal increment formation of CSNA is consistent with the current assumption for annual deposition of increment type and across different seasons (time at capture).

Samples for marginal increment analysis were gathered from three different sources: the SWFSC CPS spring and summer trawl surveys, the CDFW fishery samples, and collections by the SWFSC of CSNA from the bait barge in Mission Bay (Everingham Bros., Bait Co.) in San Diego, CA. Samples from these different sources were combined so that measurements could be made from samples spanning all twelve months of the year. As three different sources were used, we assessed whether samples from different sources in the same month exhibited similar measurements. Measurements were similar among the three sources, thus all sample types were pooled within each month. Due to the variability in increment width between age classes and the

difficulty in edge determination in older fish, we only measured the width of the translucent band forming on the edge for fish with an annulus count of one. To keep measurements consistent between samples, measurements were only made by reader 15 for all sample types.

After the edge type was determined, a mark was made on the image where the translucent increment began (for those fish with a T edge), and then measurements to the nearest 0.001 mm were made on the posterior margin of the otolith using Image Pro v.10 software. For consistency, the left otolith was used for measurements unless the left otolith was vaterized, deformed, or the edge was broken. Overall, the width of the translucent increment on the posterior margin was largest in October and November, and gradually declined until September (Figure 3.2). However, it should be noted that sample sizes were low for the months of May and June.
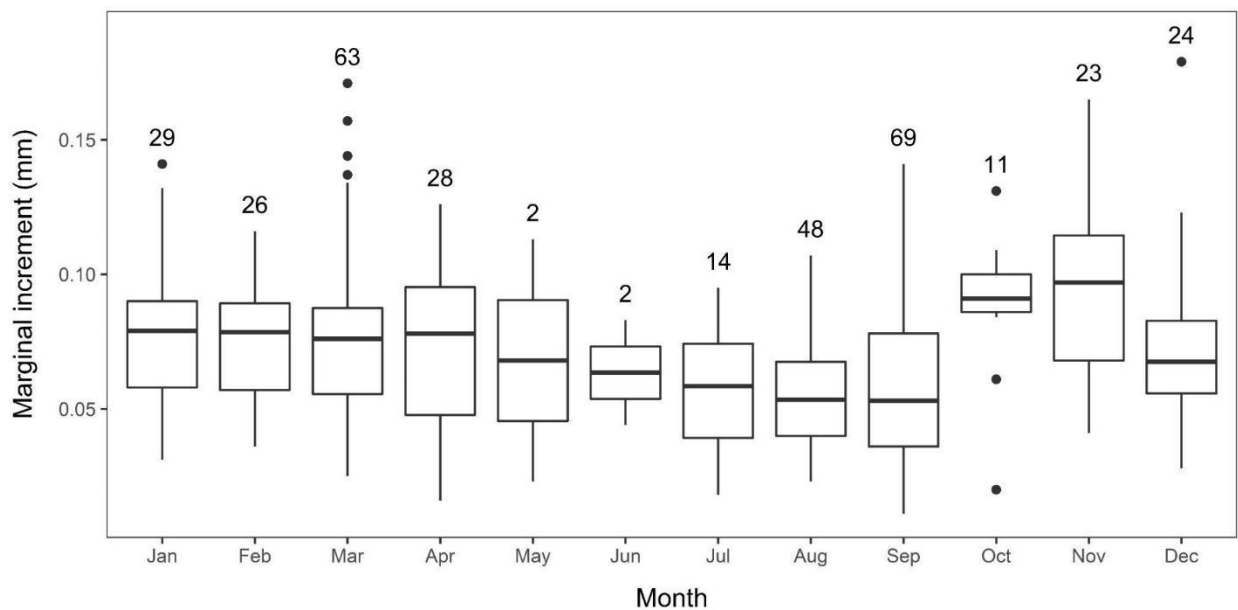

Figure 3.2. Boxplot of the measurement of the translucent increment on the margin of CSNA from otolith samples collected during the SWFSC spring and summer surveys, the CSNA fishery sampled by CDFW, and the bait barge in San Diego, CA. The horizontal line represents the median, the lower and upper hinges correspond to the 25th and 75th percentiles, the upper and lower whiskers goes to the largest value no further than 1.5 * interquartile range (IQR), and the dots represent outliers. The sample size for each month is listed above each box plot.

3.2.2 Edge Analysis

For edge analysis, we used samples from both the trawl survey and fishery port samples, and examined the number of fish exhibiting an opaque or translucent edge type for fish with an annulus count of one, similar to that done by Barnes and Foreman (1994) for young Pacific Sardine. We restricted the data set to those with an annulus count of one to allow for direct comparisons with the results of the marginal increment analysis. To include any new growth

occurring on the edge, all T/O edges were considered as those assigned an O edge, and O/T edge types were considered as those assigned a T edge. March was found to contain the most fish that exhibited a translucent edge, and by June and July, very few fish exhibited a T edge (Figure 3.3). The largest number of fish exhibiting an opaque edge were found in August and September. As very few fish exhibited a translucent edge in June and the number of fish with an opaque edge started to increase, this was determined to be the time of formation of a complete annulus (Figure 3.3).
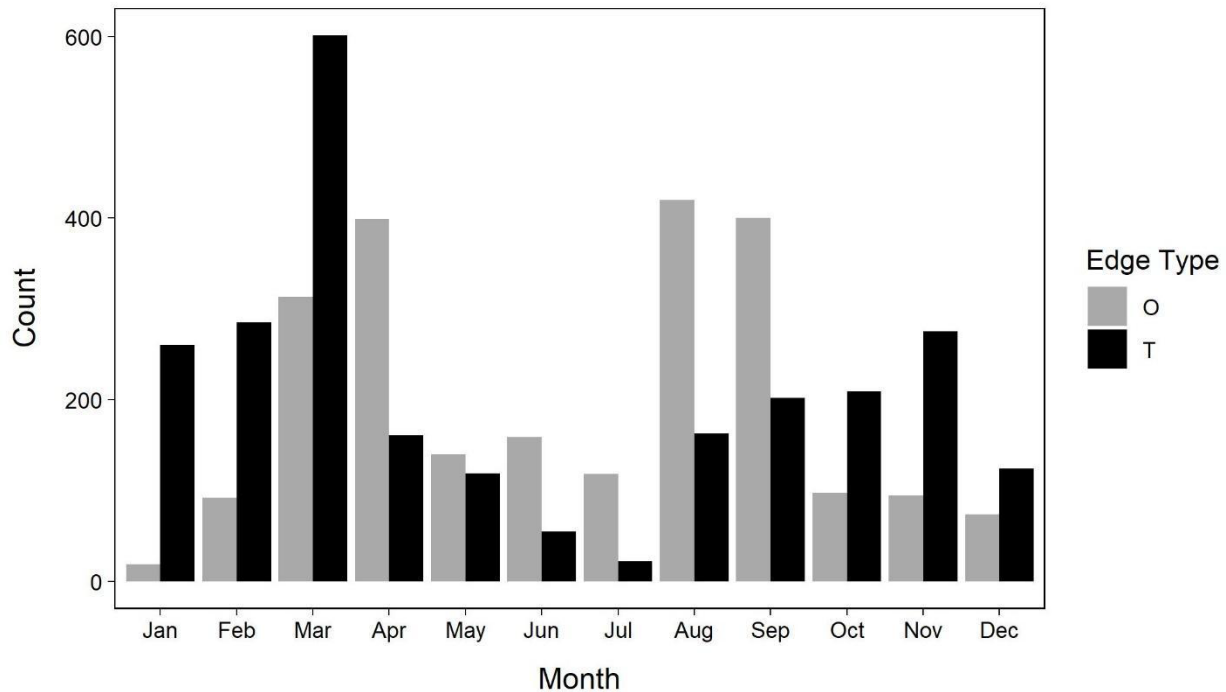

Figure 3.3. The frequency of opaque (O) and translucent (T) edge types from CSNA otoliths with an annulus count of one collected by both trawl surveys (2015-2021) and fishery port samples (2014-2021). The trawl data presented here only include those fish read by one reader for readers 14 and 15 only.

Based on the results of the edge and marginal increment analyses, we assumed a June 1 birthdate for all individual fish hatched off California within a calendar year. June 1st was also the birthdate assumed by Collins and Spratt (1969) from an examination of when newly completed rings were formed in otoliths. Northern Anchovy have a prolonged spawning season, with a peak in spawning from February through April, but most fish completed their first year of life in June 1 (Figure 3.3), justifying the assumption of a June 1 birthdate for CSNA. Final age assignment by readers was based on the capture date and the interpretation of the most distal pair of increments based on the following criteria:

(1)   Fish caught in the first 5 months of the calendar year (January-May) have not yet reached their June 1 birth date; therefore, their most distal pair of opaque and translucent increments should not be counted, even if exhibiting the early beginning of an opaque increment (see Yaremko 1996, Page 12).

(2)   Fish caught in June-December have completed a year since their last birthdate; therefore age is equal to the number of annuli counted in their otolith regardless of edge type.

3.3 Trawl Survey Ageing Data

As the 2021 stock assessment for Northern Anchovy is focused on biomass estimates of CSNA, age readings were only conducted on otolith samples collected from south of Cape Mendocino, CA, to San Diego, CA, during spring (2017, 2021) and summer (2015-2019) trawl surveys. All otoliths collected in summer 2015 and 2017 were aged, and at least 70% of samples were aged from all the other trawl surveys (Table 2.1). From each survey, otolith samples were randomly selected by haul and by length bin (20 mm), and approximately 50% of the selected samples were randomly allocated to each of the two SWFSC age readers, identified as readers 14 and 15. This selection scheme maintained the spatial and temporal integrity of the trawl sampling and the distribution of length at age in space and time.

In addition to age data produced by readers 14 and 15, 30-39% of otolith samples per year were double-read by these readers and reader 2 from CDFW. These double reads were performed without prior information on the age composition of the allocated sample sets and thus were used to estimate ageing error matrices for inclusion in stock assessment models. Additional double-readings were conducted and were used, in addition to the first set of double-readings, to evaluate potential bias in ageing readings and to identify age classes that were potentially misidentified by reader 14 or 15 in each year. During the course of the ageing process, several bias plots were generated until the level of bias among age readers was reduced. As readers had prior knowledge of age compositions produced by other readers, and all samples were not re-read, these additional double-readings were not used in computing ageing errors in order to avoid significant bias in these parameter estimates. However, age data produced by readers 14 and 15 for the assessment were corrected based on these bias plots. The final dataset submitted for the assessment combined single age readings from all three readers in 2015-2018 but only fish aged by readers 14 and 15 in 2019 and 2021 (n = 4516).

3.4 Ageing Data from Fishery Port Samples

Fishery samples were collected from 2014 to 2021 from port landings in southern and central CA (San Pedro to Santa Barbara; Monterey Bay region). Fish were collected following CDFW standard protocols (CDFW 2020), targeting a sampling unit of 25 fish per landing-boat and a total of 12 samples per month and port during the fishing season. All collected fish samples were randomly assigned to single age readers, here identified as readers 2, 21, and 22. However, every

third (2015) or fourth sample (2016-2021) was read by each age reader, deemed an "all-read" sample. Readings continued on each all-read sample until the percent of disagreement among all three readers was 25% or less. As only the first set of all-read-readings were performed without prior knowledge of age composition of the allocated sample sets, they were aggregated and used for computing ageing errors in this report. Further, we selected all-reads conducted in 2015-2021, because in 2014 only fishery samples aged by reader 2 were selected for developing the stock assessment model. Fishery sample datasets were built using only complete reported age-readings among the three readers (i.e., observations containing missing values were discarded). Although a total of three readers participated in ageing fishery samples, final age data provided for assessing the CSNA did not contain reader-specific information.

3.5 Ageing Error Estimation

Age-reading error matrices by reader were carried out following the approach described by Punt et al. (2008) and calculated using the nwfscAgeingError R package (Thorson et al. 2012). The Agemat model computed ageing error matrices based on otoliths that were aged by more than one reader, while assuming that: (1) ageing bias depends on reader and the true age of a fish; (2) the age-reading error standard deviation depends on reader and the true age; and (3) age-reading error is normally distributed around the expected age (see Punt et al. 2008). For the purpose of this report, we were mostly interested in estimating the *SD*s-at-age for age data from the trawl and fishery surveys. The Agemat model typically estimates ageing errors by reader, but age data input and precision cannot be included in Stock Synthesis by reader. As an alternative, we followed similar methods used in the past for Pacific Sardine and Pacific Mackerel assessments (Dorval et al. 2013; Crone et al. 2019; Kuriyama et al. 2020) and defined various model scenarios, comparing models that assumed equal or unequal *SD*s among agers for the trawl survey and fishery sample data sets. Dorval et al. (2013) used AICc (Akaike Information Criterion with a correction for finite sample sizes) to select the best model and determine whether there was enough evidence to support the assumption of equal *SD*s among agers for the age-reading data sets considered in a given model. As stated above, only the first set of readings were used in estimating ageing errors for both the trawl survey and fishery sample data sets.

Agemat models were developed for three specific time periods for both the trawl survey and fishery sample datasets due to variability among years in the percent agreement of age-readings. More specifically, the trawl survey dataset contained double readings performed on trawl samples collected in 2015-2016, 2017-2018, and 2019-2021, and the Agemat models for the fishery sample dataset were based on all-reads conducted in 2015-2016, 2017-2018, and 2019-2020 (Table 3.1). Although 50 ages from the fishery samples were submitted to the assessment for 2021, none of these were double read, so an Agemat model was not developed for 2021. The *CV*s and *SD*s computed for the 2015-2016 fishery samples should be applied to the 2014 age data as double readings were not performed in 2014. The maximum expected age for CSNA was set at 9 years for trawl survey models and 6 years for fishery sample models. For these datasets, we

selected the model that assumed all readers are unbiased and have a similar *SD* (model C in Dorval et al. 2013). The functional form of random ageing-error precisions was assumed to follow a curvilinear *SD* for 2015-2021 fishery readings and 2015-2018 survey readings, and a curvilinear *CV* for 2019 and 2021 readings based on a three-parameters, Hollings-form relationship of *SD* or *CV* with true age (see Punt et al. 2008; Thorson et al. 2012, Dorval et al. 2013). Further, the maximum *SD* allowed in model runs was 40.

Table 3.1. Coefficient of variation (*CV*) and standard deviation (*SD*) at age estimated for CSNA collected by trawl surveys (2015-2021) and fishery port samples (2015-2021). All estimates were calculated using the latest version of the nwfscAgeingError R package (Thorson et al. 2012) based on the assumptions that, within each ageing laboratory, there was no bias in ageing among readers, and readers had a similar *SD*.

Collection type	Collection year	Data set ID	Sample size	Number of readers	Age	Agemat model *CV*	Agemat model *SD*
Trawl Survey	2015-2016	1	397	3	0	0.56	0.56
					1	0.56	0.56
					2	0.70	1.41
					3	0.57	1.72
					4	0.46	1.83
					5	0.37	1.87
					6	0.31	1.89
	2017-2018	2	424	3	0	0.66	0.66
					1	0.66	0.66
					2	0.62	1.25
					3	0.49	1.46
					4	0.38	1.54
					5	0.31	1.57
					6	0.26	1.58
					7	0.23	1.58
					8	0.20	1.58
	2019-2021	3	450	2	0	0.65	0.65
					1	0.65	0.65
					2	0.65	1.30
					3	0.65	1.95
					4	0.65	2.60

					Age	CV	
					5	0.65	3.25
					6	0.65	3.90
					7	0.58	4.05
					8	0.51	4.10
					9	0.51	4.58
Fishery Sample	2015-2016	1	763	3	0	0.45	0.45
					1	0.45	0.45
					2	0.24	0.48
					3	0.22	0.66
					4	0.44	1.75
					5**	1.66	8.28
					6**	7.88	47.25
	2017-2018	2	552	3	0	0.38	0.38
					1	0.38	0.38
					2	0.19	0.38
					3	0.13	0.38
					4	0.13	0.50
					5**	0.77	3.86
					6**	16.7	100.0
	2019-2020	3	617	3	0	0.39	0.39
					1	0.39	0.39
					2	0.19	0.39
					3	0.13	0.39
					4	0.11	0.42
					5	1.53	7.64

**Ageing precision computed for Ages 5 and 6 were not reliable and should be replaced by age-4 *CV* or

3.6. Results and Discussion

3.6.1 Age and Length Compositions

Ages of the CSNA ranged from 0 to 6 years for those individuals collected during the trawl surveys from 2015 to 2021, with age 0 and 1 fish accounting for 65% of samples, and a steady decline in the frequency of older aged fish, with age 4+ fish only accounting for 8% of the samples (Figure 3.4). For individuals from the fishery survey, CSNA ages ranged from 0 to 6 years, with age 1 and 2 fish accounting for 68% of samples and a very low proportion of age 4+ individuals (2% of samples; Figure 3.4). In general, greater numbers of smaller and younger fish were caught in the trawl survey in 2015, 2016, and 2017, with a higher frequency of larger and older fish observed in 2018, 2019, and 2021 (Figure 3.5). Conversely, similar lengths and ages were consistently observed in the fishery samples from 2014-2021, although slightly larger fish, on average, were observed in 2017 (Figure 3.6).
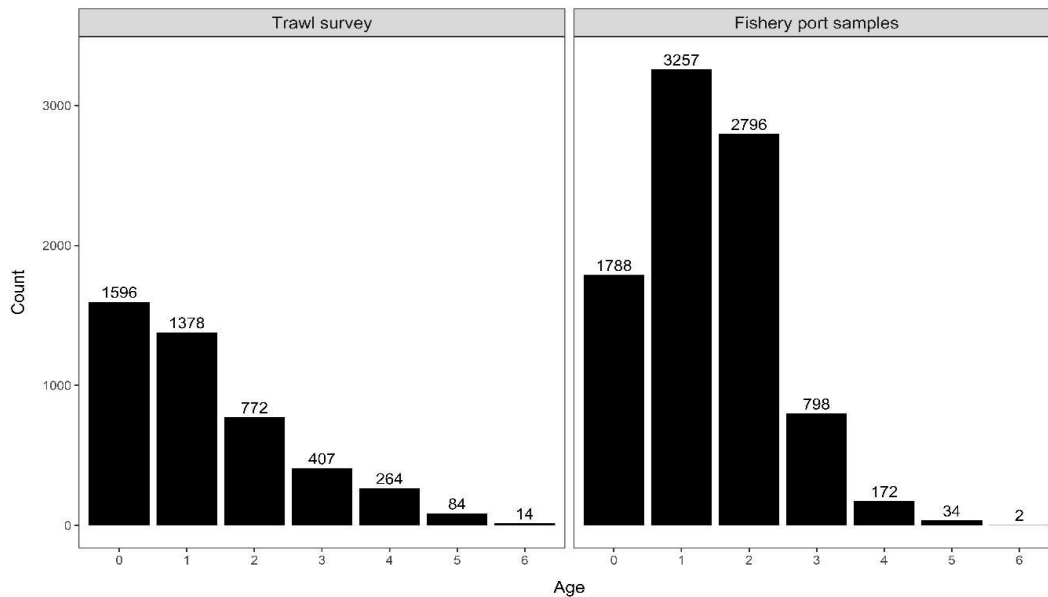

Figure 3.4. Age frequency distributions of CSNA collected by the SWFSC trawl surveys from 2015 to 2021 (left) and the CDFW fishery port samples from 2014 to 2021 (right) for all readers. The trawl data presented here only include those fish read by one reader for readers 14 and 15 only, and both surveys represent the corrected ages based on additional double readings. The number above each bar represents the sample sizes for that age class.
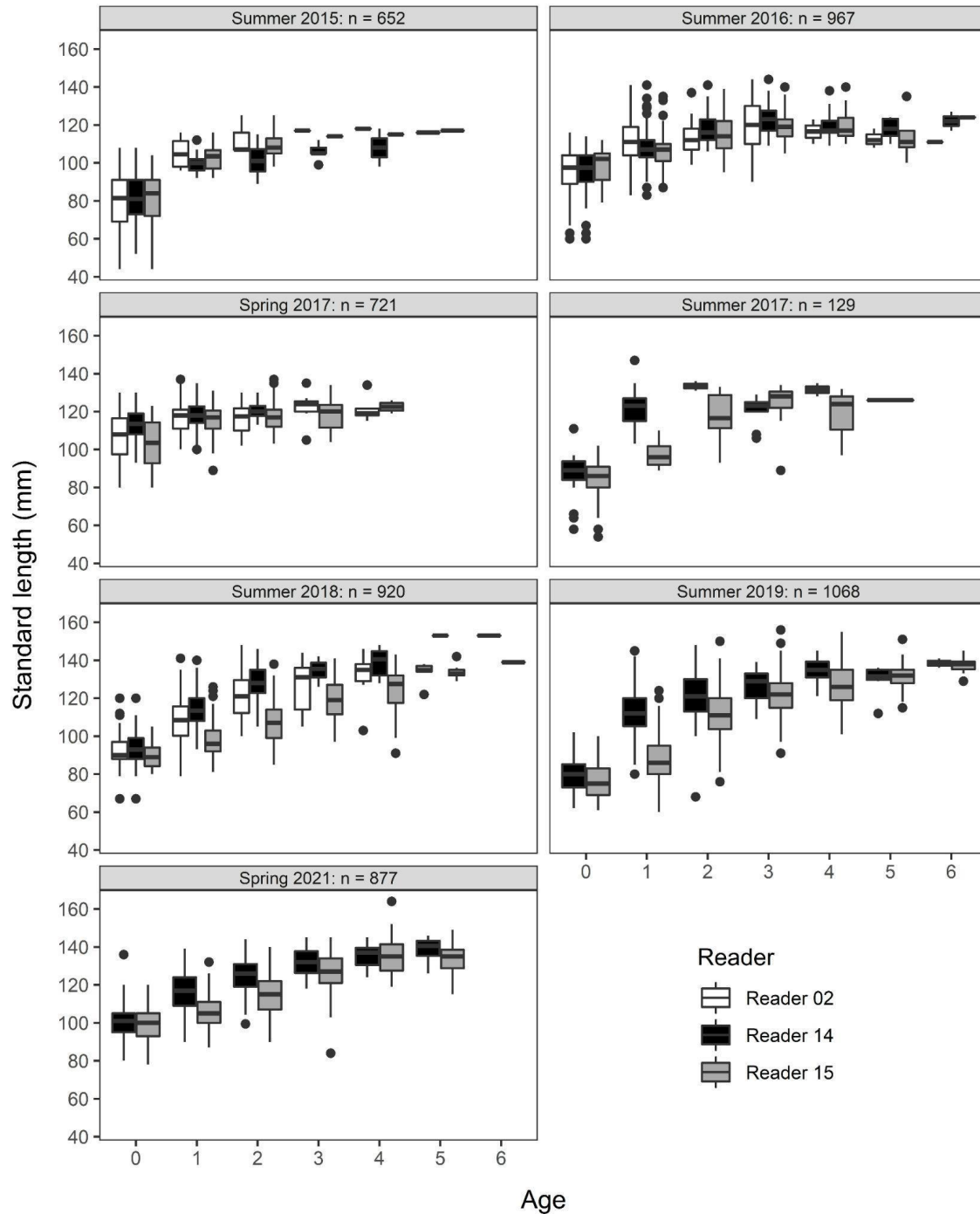
Figure 3.5. Boxplots of CSNA age versus standard length (mm) for each reader from the trawl surveys conducted in 2015-2021. The data presented here only include those fish read once by each reader and represent the corrected ages based on additional double readings by the same ager. The horizontal line represents the median, the lower and upper hinges correspond to the 25th and 75th percentiles, the upper and lower whiskers goes to the largest value no further than 1.5 * interquartile range (IQR), and the dots represent outliers.
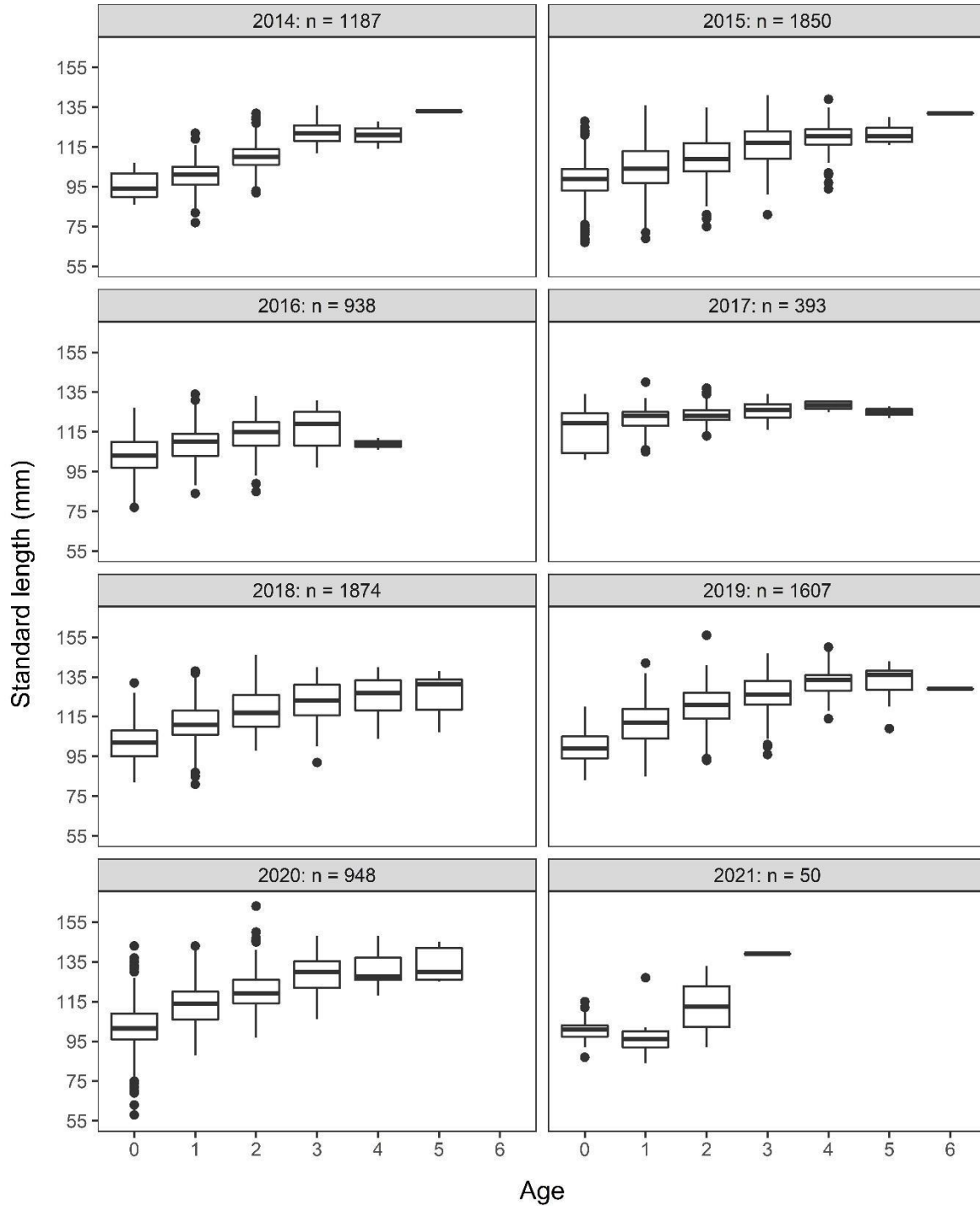
Figure 3.6. Boxplots of CSNA age versus standard length (mm) from the fishery port samples in 2014-2021. The horizontal line represents the median, the lower and upper hinges correspond to the 25th and 75th percentiles, the upper and lower whiskers goes to the largest value no further than 1.5 * interquartile range (IQR), and the dots represent outliers.

3.6.2 Age-Reading Errors

Ageing errors for the trawl survey data were estimated using 1271 otoliths collected from 2015 to 2021. Level of precision was moderate in 2015-2016 and 2017-2018 and much lower in 2019-2021 (Figure 3.7). In 2015-2016, the percent agreement between readers 2 and 14 was 66% for age 0 and 48% for age 1, whereas the agreement level between readers 2 and 15 was 95% for age 0 and 61% for age 1. However, in 2017-2018, agreement between readers 2 and 14 increased (87% and 61%, respectively for ages 0 and 1), while agreement between readers 2 and 15 decreased markedly (34% for age 0 and 55% for age 1). In 2019-2021, agreement between readers 14 and 15 was very low across the age range, with age readings showing a strong systematic bias (Figure 3.7).
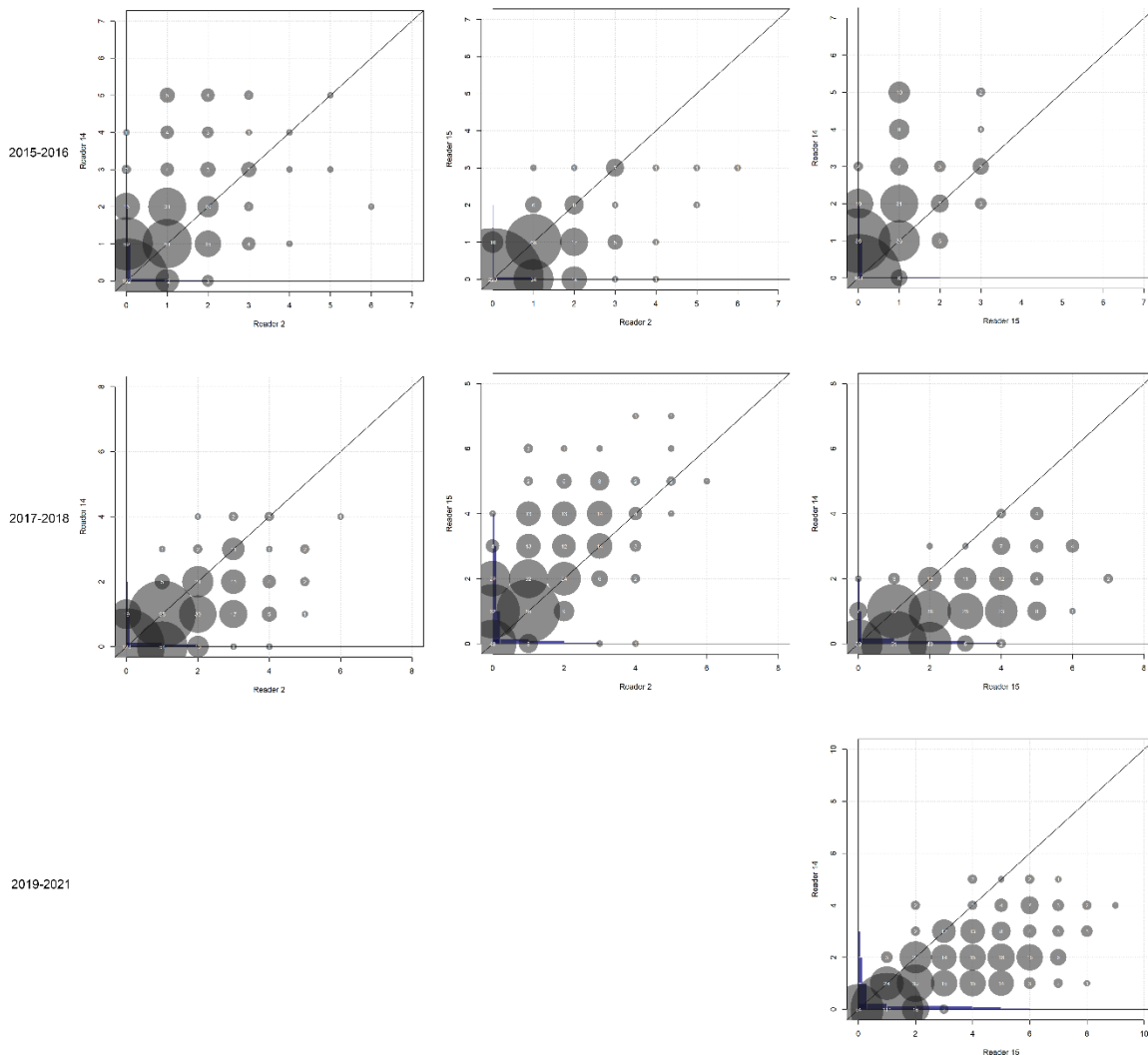

Figure 3.7. Age bias plots from the Agemat models for readers 2, 14, and 15 for CSNA collected from trawl surveys in 2015-2021.

Standard deviations were higher for older ages but varied among the three time periods (Figure 3.8). These levels of variability in age-reading precision among readers and periods likely reflected the ability of each reader to detect the first annulus and to identify the marginal increment in otoliths collected from each trawl survey. As the stock biomass of CSNA increased from 2015 to 2019, increment deposition patterns (as associated with growth rate) in CSNA otoliths might have also changed, making it more difficult for age readers to apply the ageing criteria consistently across years.
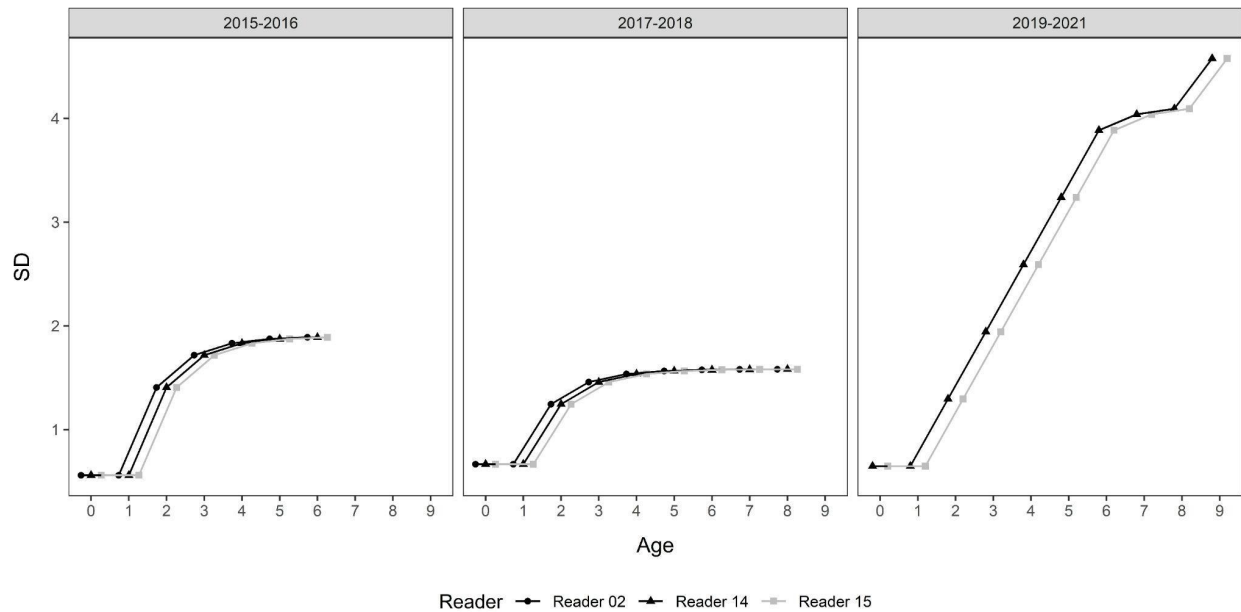

Figure 3.8. Standard deviations (SD)-at-age estimated for trawl surveys conducted in 2015-2016, 2017-2018, and 2019-2021, assuming that all readers in each time period were unbiased and have similar SDs.

Ageing errors were also computed for the fishery port sampling data by time periods (2015-2016, 2017-2018), as they also showed strong temporal patterns (Figure 3.9). In 2015-2016, readers 2 and 21 had 81% agreement in assigning age 0, but only 52-53% for ages 1 and 2. Readers 2 and 22 had agreement levels of 78% for age 0, 65% for age 1, and 71% for age 2. However, in 2017-18, levels of agreement were moderate to high among all readers. Specifically, agreement levels between readers 2 and 21 ranged from 72% for age 2 to 87% for age 0. In contrast, readers 2 and 22 agreed on 79% of otoliths for age 0, 69% for age 1, and 75% for age 2. In 2019-2020, levels of agreement between readers 2 and 21 for ages 0, 1, and 2 were 80%, 72%, and 59%, respectively; whereas agreement between readers 2 and 22 were 70%, 73%, and 65% respectively for ages 0, 1, and 2. Consequently, the ageing precision of fishery data did improve in both the 2017-2018 and the 2019-2020 periods compared to 2015-2016 (Figure 3.9). Fishery *SD*s-at-age trends were similar to those of the trawl survey in 2015-2016 but much lower in 2017-2018 and 2017-2020 (Figure 3.10; Table 2.1). Further, fishery age readings show no evidence of systematic bias among readers (Figure 3.10). Note that ages 5 and 6 were observed

in the fishery port sampling data, but sample sizes in all-read data sets were 1, 2, or 5 for age 5 and 0 for age 6. Thus, ageing precision computed for these ages are not reliable, and should be replaced by the age-4 *CV* or *SD* in assessment models.
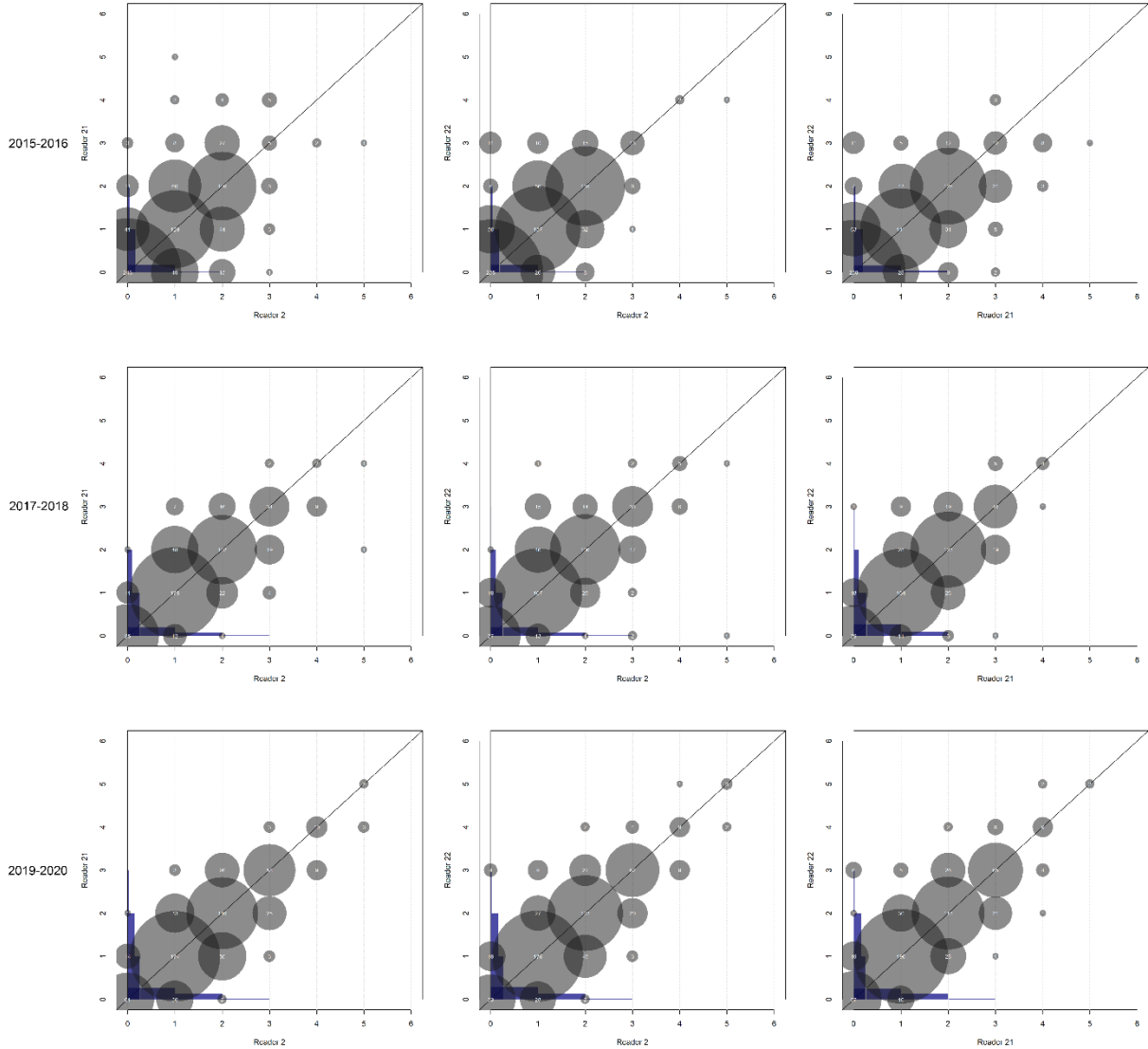

Figure 3.9. Age bias plots of readers 2, 21, and 22 for CSNA collected from fishery port samples in 2015-2020.
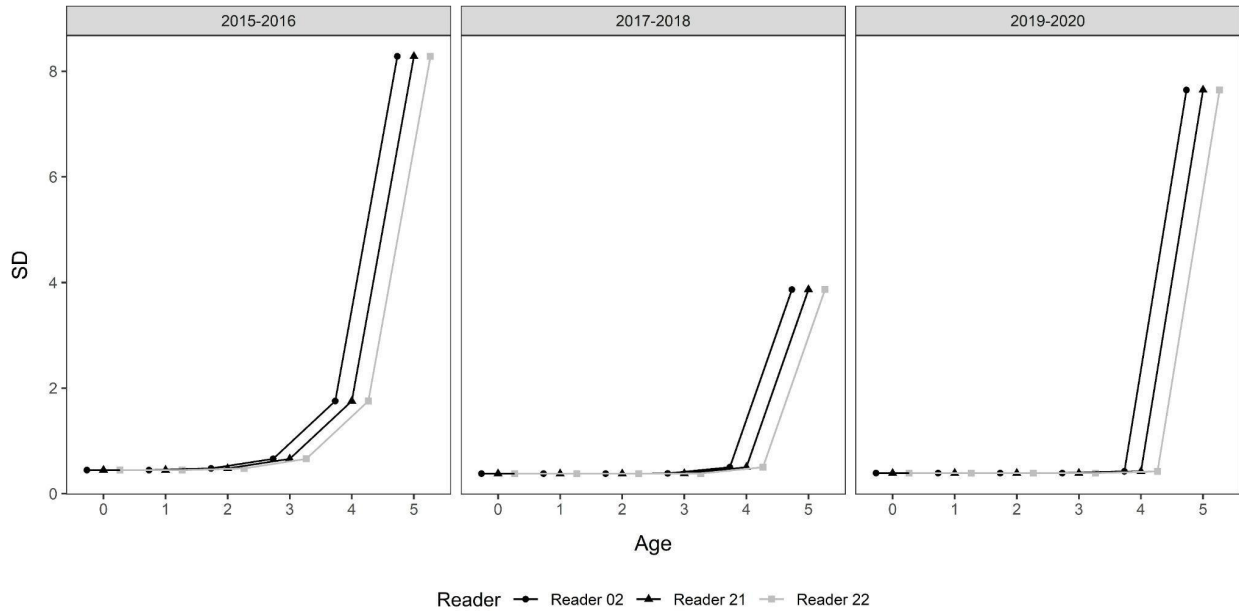
Figure 3.10. Standard deviations (SD)-at-age estimated for the fishery port samples from 2015-2016, 2017-2018, and 2019-2020 assuming that all readers in each time period were unbiased and have similar SDs. Age 6 fish were removed from this plot as the SD was 100 (see Table 3.1), and no age 6 fish were observed in all-read sets.

3.7 Age-Reading Issues

As Northern Anchovy have not been aged for more than two decades and no age validation studies have been completed for the species, several issues (described below) likely contributed to differences in age interpretation between readers, which need to be addressed further to increase the precision of and to reduce potential systematic bias in age assignment. Although to a lesser extent, it should be noted that significant variability among readers and among years have been also observed in ageing other CPS such as Pacific Sardine, Pacific Mackerel (Dorval et al. 2013, *In review*), and other anchovy species (ICES 2010), so the issues and challenges experienced for Northern Anchovy seem relatively consistent with those experienced elsewhere.

The first challenge that may contribute to age interpretation differences is the identification of the first translucent increment. Incorrectly identifying the first translucent increment will lead to age determinations that are consistently wrong by a constant amount (Campana 2001). Timing of the first translucent increment formation can be affected by both environmental (e.g. seasonal temperature changes, food availability) and endogenous (e.g. reproductive potential, growth rate) factors, in which growth rate may also be impacted by environmental factors and population size (Spratt 1975; Beckman and Wilson 1995; Aldanondo et al. 2016); therefore, formation, can vary among years with different environmental conditions and may contribute to interannual differences in ageing precision. During a virtual workshop in 2020 with the ageing labs from SWFSC, CDFW, and WDFW, it was decided that if the first translucent increment appeared

close to the core but is distinct, it should be counted as the first annulus (Figure 3.11). No quantification exists on what designates "close", so measurements will be taken by the SWFSC to create a range of measurements to the beginning of the first translucent increment. For Pacific Sardine, the first translucent increment is likely to be considered a check if it is narrow and near the focus for young fish, but this same mark could be interpreted as an annulus in older fish if it was located farther away from the focus (Yaremko 1996), which may provide inconsistent ageing. One way to address this issue is to examine other preparation methods. For example, McFarlane et al. (2010) found that polishing older Pacific Sardine otoliths aided in identifying the first translucent increment and increasing ageing precision.
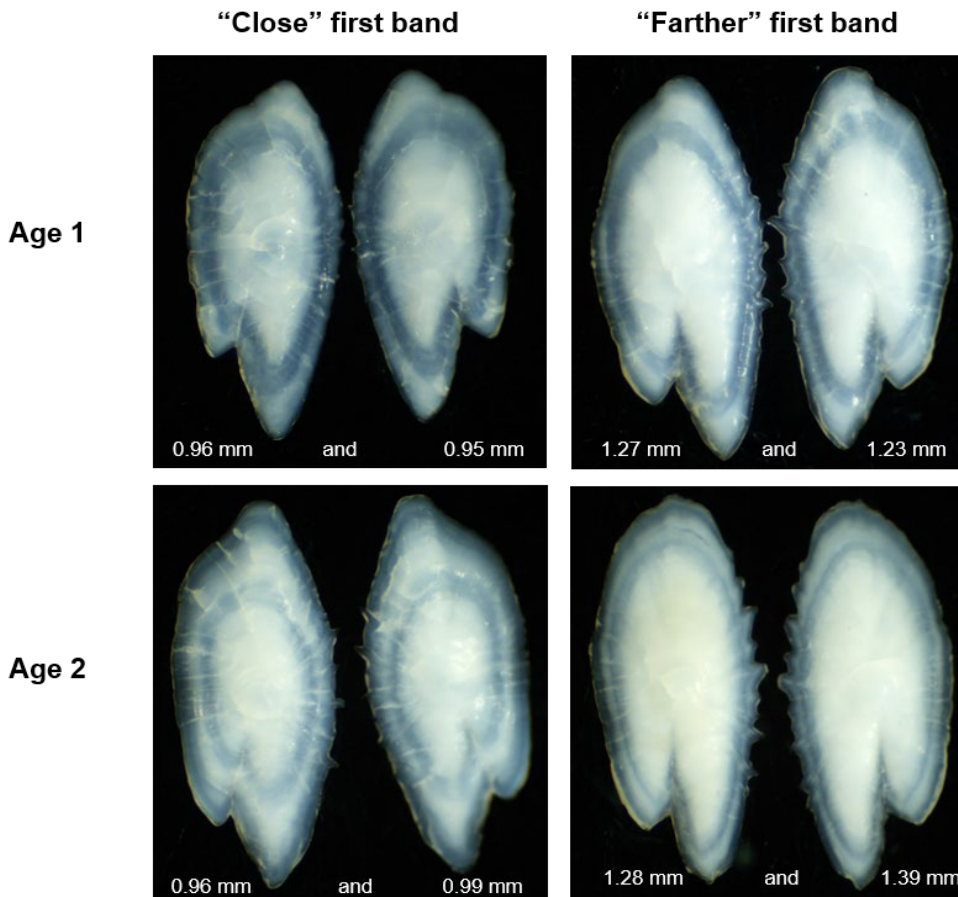

Figure 3.11. Images of otoliths from age 1 and age 2 Northern Anchovy that have a first translucent increment possibly considered "close" and "far" from the core. Measurements in millimeters from the focus to the start of the first translucent increment are provided.

The second challenge is discriminating false increments from true translucent increments. False increments can come in two forms: (1) checks, and (2) split translucent increments. Checks are translucent marks that generally form during perturbations or stress to the fish (e.g. extreme temperature changes, spawning periods) and may or may not form a complete ring around the otolith (Campana and Neilson 1985). Split translucent increments occur when a translucent

increment is interrupted by short periods of opaque growth, thus giving the appearance of two increments, which can occur in fast growing fish if food and temperatures are favorable (Uriarte et al. 2016). The presence of presumed checks and split increments has been found for some CSNA caught in trawl surveys, in which the age may differ by multiple years depending on how potential checks and splits bands are counted by each reader (Figure 3.12), which will ultimately impact the age structure and thus stock assessment model inputs. As checks can be associated with stressful events and split increments with favorable events, being able to identify each of these properly also suggests the potential to define the size and/or age at which life history transitions occur.
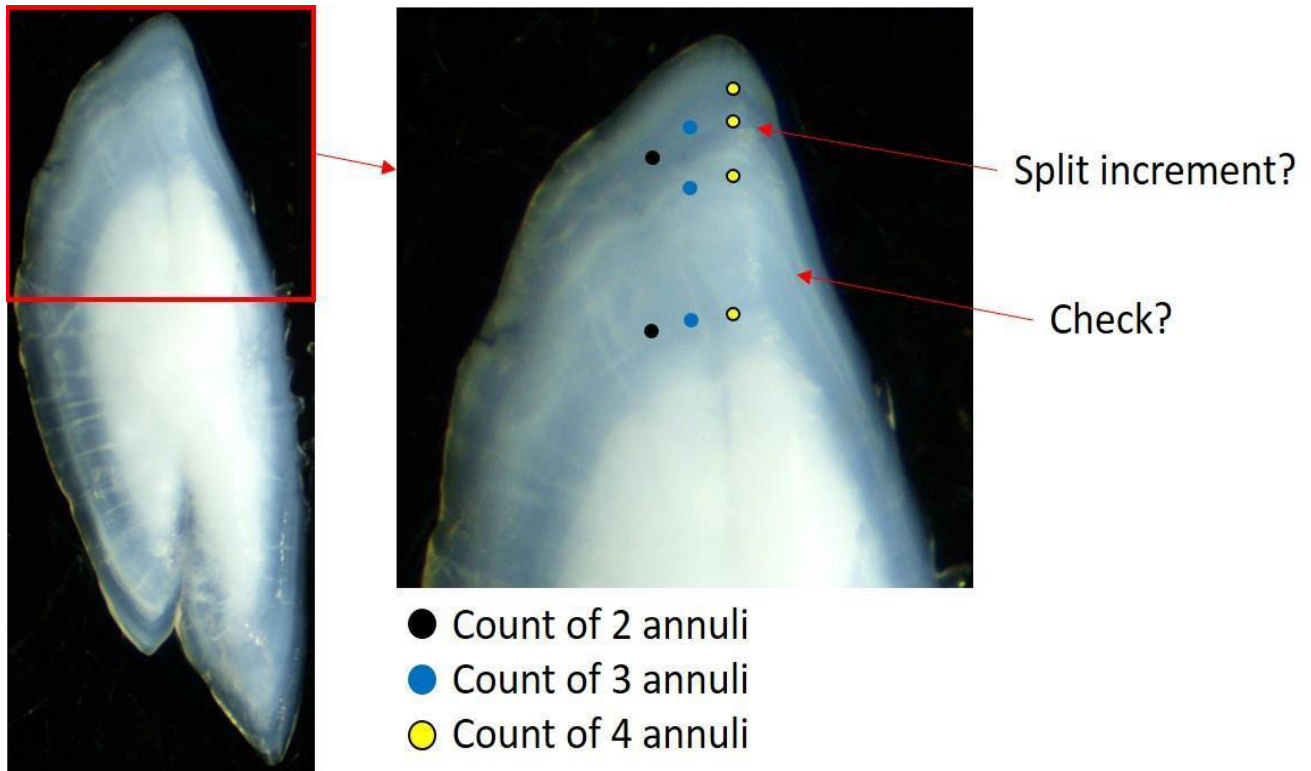

Figure 3.12. Image of a CSNA otolith that could be aged as a 2-, 3-, or 4-year-old depending on the determination of a check and split increment by the reader. The black dots represent how one could get a count of 2 annuli if the second faint band is believed to be a check and the following two bands are believed to be one split increment. The blue dots represent how one could get a count of 3 annuli if the second faint band is believed to be an increment and the following two bands are believed to be one split increment. The yellow dots represent how one could get a count of 4 annuli if the second faint band is believed to be an increment and the following two bands are actually two separate increments instead of a split increment.

31

Differences in determinations of edge type among readers is also an issue when ageing CSNA otoliths. Marginal increment formation varies with age in anchovies such that opaque increments form earlier in younger fish (Uriarte et al. 2016, Schwarzkopf et al. unpublished data), so this could be one reason edge types may not follow typical patterns. Additionally, edge type is very difficult to determine for older fish due to the decrease in widths for both opaque and translucent increments as age increases (Collins and Spratt 1969). The interpretation of edge type can have an effect on age assignment for fish collected during the first half of the year (January-May), with ages varying by one year if one reader interprets an edge as opaque and another reader as translucent. Compared to whole otolith surface ageing, polishing has been found to improve identification of translucent increments near the margin of age 5+ Pacific Sardine (McFarlane et al. 2010), and sectioning was found to enhance the ability to differentiate opaque and translucent edge types of flathead *Platycephalus speculator* (Hyndes et al. 1992), thus these two methods should be examined for Northern Anchovy.

One way to address the issues listed above is by understanding Northern Anchovy otolith growth patterns and deposition of both opaque and translucent increments throughout their lifetime. It is assumed that a typical growth pattern for anchovies would be a decrease in spacing between consecutive annuli, corresponding to a decrease in growth rate as a fish ages (ICES 2010; Uriarte et al. 2016). Timing and width of increments, in which increment width corresponds to growth rate, is influenced by age, temperature, food availability, and spawning potential and patterns (Beckman and Wilson 1995; Uriarte et al. 2016; Denechaud et al. 2021). Differences in growth patterns have been observed for CSNA, with some individuals exhibiting larger spacing between year 1 and year 2 (Figure 3.11, age 2 "close" first increment), compared to individuals with a less spacing (Figure 3.11, age 2 "farther" first increment). It is important to determine if this spacing corresponds to growth rate and is affected by the biotic and abiotic factors listed above as it will help aid in interpreting first translucent increments, checks, and marginal increments. For example, checks have been found to be easily recognizable in other CPS with established annual growth patterns in which checks are usually fainter and of less intensity than a true translucent increment and may not form a complete ring around the otolith (Yaremko 1996; Uriarte et al. 2016); typically checks form during the first (age 0 to 1) and second year (age 1 to 2) of growth.

Working conditions during the pandemic also likely contributed to the level of ageing errors estimated in this report. Normally, all age readers from SWFSC and CDFW would meet multiple times each year to examine a subset of otoliths in person, an activity referred to as "all-reads". These in-person discussions on age assignments and edge type interpretations allow for a detailed understanding of what each reader observes and what they consider an annulus for otoliths collected during any given sampling event and year. Unfortunately, due to work-related restrictions associated with the pandemic, in-person all-reads could not be completed. Instead, such meetings were conducted remotely (virtually) with discussions of age assignments and edge types relying on the shared viewing of otolith images. Although this scenario was deemed the

safest and most practical solution under the circumstances, otoliths can look slightly different in person than what is captured on a photo, and edge type is nearly impossible to determine using images. Once in-person meetings are allowed again, in-person all-reads and discussions will resume, which should help improve ageing precision among readers.

4. Length and Age at Maturity

4.1 Background on Reproductive Biology of CSNA

Although some spawning activity may occur during all months of the year, the peak spawning season for CSNA is from January through April (Brewer 1978; Hunter and Leong 1981; Richardson 1981; Reiss et al. 2008), which accounts for an estimated 50% of the annual production of larvae (Lasker and Smith 1977). During this period, the highest abundance and density of Northern Anchovy eggs are distributed in nearshore waters within the SCB (Fiedler et al. 1986; Hedgecock et al. 1994; Reiss et al. 2008; Dorval et al. 2018). Some spawning in CSNA also occurs off Monterey Bay but for a shorter season that ends by March (Hunter and Macewicz 1980, 1985b). Moreover, spawning for the NSNA off Oregon is reported to occur from June to August in association with the Columbia River plume that provide favorable conditions for survival of first feeding larvae (Richardson 1981).

The Northern Anchovy is a multiple batch spawner with indeterminate fecundity, asynchronous oocyte development, a protracted spawning season, and a relatively high spawning frequency (Hunter and Macewicz 1980; Hunter and Leong 1981; Alheit 1989). Hydration begins as early in the day as 0600 h, and spawning occurs from sunset to 0200 h with peak spawning occurring at 2200-2300 h (Hunter and Macewicz 1980). On average, individual females spawn every 6-10 days and up to 20 times per year (Hunter and Goldberg 1980; Hunter and Macewicz 1980; Parrish et al. 1986). Spawning fractions (i.e., daily percentage of collected females actively spawning) peak in January through February begin to decrease in March and April and then decline precipitously by June (Hunter and Goldberg 1980; Hunter and Macewicz 1980). The decrease in spawning fractions late in the spawning season indicates that spawning intervals (i.e., days between spawning events) increase, an increasing number of females cease spawning as the season progresses, or a combination of both events (Hunter and Macewicz 1985b). Batch fecundity, spawning frequency, and spawning season duration in Northern Anchovy increases with female size (both length and weight) and age such that larger, older females contribute disproportionately more to total annual egg production relative to first-time spawners (Hunter and Macewicz 1985b; Parrish et al. 1986). For example, young adult (1 yr old) females have a shorter spawning season and an earlier spawning peak than older females (Hunter and Macewicz 1985b; Parrish et al. 1986). Moreover, fourth year spawning females reproduce more times per year than first time females (23.4 vs. 5.3, respectively; Parrish et al. 1986), and batch fecundity is an exponential function of gonad-free female body mass (Hunter and Macewicz 1980).

An early study by Clark and Phillips (1952), which included samples collected from both southern and northern California, estimated that 50% of female Northern Anchovy reached sexual maturity (L_{50}) at 130 mm SL, with a few females maturing at 90-100 mm SL. Conversely, later studies by Brewer (1978) and Hunter and Goldberg (1980) from the SCB found large numbers of mature females at lengths less than 90 mm SL. Hunter and Macewicz (1980) collected samples of female CSNA from the SCB during the winter (January-February) and spring (March-April) of 1979 and estimated L_{50} to be 96 mm SL for both. In that study, females began to mature at 76-80 mm SL, and all females were mature by 130-160 mm SL. Dorval et al. (2018) estimated L_{50} at 96.9 mm SL for female CSNA sampled during the spring spawning season in 2017 in the SCB, with the smallest mature female measured at 89 mm SL and all females mature at lengths greater than 116 mm SL. Notably, the NSNA off Oregon and Washington have been reported to begin to mature at larger lengths (> 107 mm SL) and older ages (2 yrs) than the CSNA (Laroche and Richardson 1980).

Food availability, energy reserves, and associated feeding activity are viewed as a major determinant of the timing, frequency, and duration of spawning and the overall investment in egg production in CSNA (Leong and O'Connell 1969; Leong 1971; Brewer 1975; Hunter and Goldberg 1980). Eggs are produced primarily from fat reserves generated from feeding during the previous spring and summer zooplankton blooms, with remaining energy requirements met by active feeding during the current spawning season (Lasker and Smith 1977; Hunter and Leong 1981). Spawning activity and larval density tends to track zooplankton density, supporting the hypothesis that adult Northern Anchovy spawn under conditions and at levels that yield consistent survival probabilities for their offspring (Brewer 1978; Richardson 1981; Owen et al. 1989). Both Smith (1972) and Hunter and Leong (1981) observed that increases in the duration of the peak spawning period of Northern Anchovy coincided with the decline of Pacific Sardine and speculated that increased food availability (or reduced competition for food) as a causal factor.

Temperature also exerts a strong influence on reproduction in Northern Anchovy, with numerous studies reporting similar thermal ranges in spawning. Laboratory studies that maintained spawners year-round housed individuals at temperatures between 12 to 18°C (Leong 1971; Brewer 1975). Ahlstrom (1967) found most anchovy eggs were collected in water temperatures from 13 to 17.5°C, and larvae were most abundant in temperatures of 12 to 18°C. Several studies conducted in the 1980s reported that the northern range of spawning in the Northern Anchovy was correlated with the 14.5°C isotherm (Lasker et al. 1981; Picquelle and Hewitt 1983; Hewitt 1985). Satellite imagery and sampling for eggs and adults showed that Northern Anchovy avoided areas of cold (< 14°C), upwelled, entrained waters of the California Current during the peak spawning season (Lasker et al. 1981). Lluch-Belda et al. (1991) concluded that Northern Anchovy spawn from 11.5 to 16.5°C with a peak of 14°C and prefer cooler temperatures for spawning compared to Pacific Sardine. Finally, Dorval et al. (2018) reported spawning in CSNA

from 11 to 17°C (mean = 14.4°C), with high density areas of eggs located mostly between the 13-14°C isotherms.

Accurate estimation of the length, age, or weight at first maturity, as well as the age structure of the spawning population (i.e., adult females) will have a measurable impact on estimates of total annual egg production (Hunter and Leong 1981; Lowerre-Barbieri et al. 2011a). This is because batch fecundity, spawning frequency, spawning season duration, and other metrics associated with reproductive potential increase with increasing size and age of females in Northern Anchovy and many other broadcast-spawning marine fishes (Hunter and Macewicz 1985b; Cooper et al. 2013; Barneche et al. 2018). As a result, model applications show substantial sensitivity to such parameter estimates, which can affect biological reference points (e.g., spawning stock biomass, spawning potential ratio) used to set harvest rates (Murawski et al. 2001; Fitzhugh et al. 2012; Erisman et al. 2014; Marshall et al. 2021).

4.2 Materials and Methods

Northern Anchovy gonads inspected and dissected during the 2017 and 2021 spring trawl surveys were initially categorized following a visual classification system developed by Lo et al. (2010). Gonad samples were then collected from a subset of females, placed in tissue-tek cassettes, and preserved in 10% neutral buffered formalin. For histological processing and examination, pieces of gonad samples were embedded in paraffin, sectioned at 6 μm, mounted on slides, stained with Mayer's haemotoxylin-eosin, and observed under a compound microscope (Humason 1972). Tissue samples were sectioned transversely in larger gonads, but some smaller gonads were sectioned longitudinally in their entirety.

Gonad samples of female CSNA from 2017 were examined by B. Macewicz (see Dorval et al. 2018), and samples from 2021 were examined by B. Erisman. Both readers used the standardized terminology for describing reproductive development in marine fishes developed by Brown-Peterson et al. (2011) to classify each sampled female CSNA as either immature (never spawned) or mature (previously spawned or first spawning) (Figure 4.1). Females with ovaries containing no oocytes undergoing vitellogenesis but numerous oocytes in the cortical alveolar stage of development were classified as mature, because fish sampled during the middle of the spawning season at this phase of development usually spawn during the season (Murua and Saborido-Rey 2003; Wright 2007; Lowerre-Barbieri et al. 2011a,b). Conversely, female CSNA with ovaries containing no vitellogenic oocytes and only one or two oocytes in the early cortical alveolar stage of development were classified as immature (Figure 4.1). Additional histological features used to distinguish between immature and mature regenerating females included the thickness of the ovarian wall, presence of muscle bundles and/or atretic follicles, and the level of organization within the lamellar structure (Hunter and Macewicz 1985a; Morrison 1990; Shapiro et al. 1993; Lowerre-Barbieri et al. 2011b). We assumed that restricting our collections to the
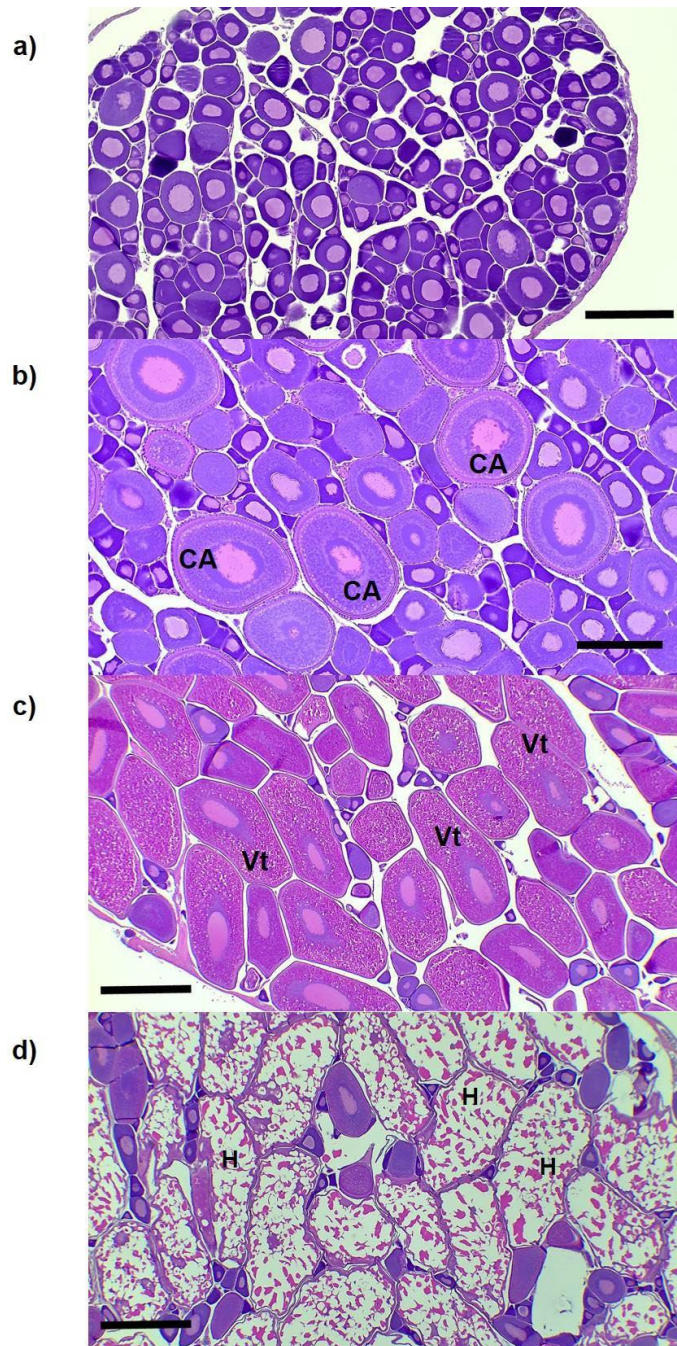
Figure 4.1. Histological sections of gonads of female CSNA collected during the spring 2021 trawl survey. (a) Immature female, 105 mm SL, 100x magnification, scale bar equal 0.2mm; (b) Mature, developing female with numerous oocytes in early cortical alveoli (CA) stage, 101 mm SL, 100x magnification, scale bar equals 0.2 mm; (c) Mature, spawning capable female with numerous vitellogenic (Vt) oocytes, 134 mm SL, 400x magnification, scale bar equals 0.5mm; (d) Mature, actively spawning female with hydrated (H) oocytes, 128 mm SL, 400x magnification, scale bar equals 0.5 mm.

middle of the spawning season for CSNA would minimize the mis-diagnosis of gonad maturity phases, because few regenerating mature females should be present during this time (Hunter and Macewicz 1985b, 2003; ICES 2008; Ferreri et al. 2009).

Following common practice for engraulids and other small pelagic fishes, the length at sexual maturity for CSNA were each estimated using an analytical method based on logistic, non-linear regression (Hunter et al. 1992; Macewicz et al. 1996; Roa et al. 1999; Lo et al. 2005; Basilone et al. 2006). Specifically, we followed the methods described by McBride (2016), which used a binomial model in R (R Core Team 2020) to the estimate the length at 25, 50, and 95% maturity and the uncertainty around the predicted relationship between length or age and percent maturity (Formula: Maturity ~ SL). Maturity ogives were first generated for 2017 and 2021 data separately to allow for direct comparisons between years, but maturity estimates using pooled datasets (all data and data from Southern California Bight only) were also produced (see below).

To determine whether length-based maturity ogives for female CSNA were different between years, four model scenarios were run on pooled 2017 and 2021 data with 'immature' or 'mature' as the binomial response variable: (1) SL only; (2) year only; (3) SL and year included as factors with an interaction term; and (4) SL and year included without an interaction term. It is important to note that since there was a different reader for 2021 compared to 2017, it was challenging to disentangle a year versus reader effect (but see results below). The models were compared using a corrected form of Akaike Information Criterion (AICc) to account for small sample sizes, Bayesian Information Criterion (BIC), and likelihood ratio tests (AICcmodavg package in R; Burnham and Anderson 2002). The likelihood ratio test results supported the AICc and BIC results in all tests and thus are not presented. Differences in AICc and BIC were calculated as $\Delta AICc = AICc_i - AICc_{min}$ and $\Delta BIC = BIC_i - BIC_{min}$, where $AICc_{min}/BIC_{min}$ denotes the minimum of the AICc/BIC values for the models being compared (Burnham et al. 2011). The lowest $\Delta AICc$ and ΔBIC values indicate the best model. Models with $\Delta AICc$ values <4 are well supported in that the models do not lose much information relative to another model, $\Delta AICc$ values of 4-7 are plausible and somewhat supported, and $\Delta AICc$ values >9 are not supported (Burnham and Anderson 2002; Burnham et al. 2011). A model with a ΔBIC value <2 has little evidence against this model, values of 2-6 contain some evidence against this model, values of 6-10 have strong evidence against this model, and values >10 have very strong evidence against this model (Kass and Raftery 1995).

Length-at-maturity ogives were generated and the same four model scenarios were performed a second time on a subset of the data in which individuals collected north of Point Conception (> 34.5° N) were excluded to assess whether differences in estimated length at maturity were influenced by the different geographic extents of the 2017 and 2021 datasets. As described below in the Results, while all samples in 2017 were collected in the main spawning area of the Southern California Bight (SCB), a portion of samples from 2021 were collected north of SCB in colder waters below the thermal spawning peak of approximately 14°C (Lasker et al 1981;

Hewitt 1985; Lluch-Belda et al. 1991; Dorval et al. 2018). We considered including temperature as a factor in the model scenarios, but temperature data were not recorded for all samples. Also, temperature data were collected at a coarse scale in which a single temperature value was assigned to all samples collected in the same haul based on a value recorded at the deployment of the trawl.

To examine age at sexual maturity for CSNA, identical methods were carried out as that done with length at sexual maturity. Three of four age-based maturity ogives for CSNA produced negative values for the estimated age at 50% maturity (see Results). Therefore, a length at age relationship was created by fitting a von Bertalanffy growth function (VBGF) to all female CSNA collected, measured, and aged from trawl surveys from 2015 to 2021. The 'FSA' v0.9.1 package in R was used to fit the VBGF (Ogle et al. 2021). For consistency, we first attempted to fit a VBGF to the same datasets used to generate age-based maturity ogives. However, the model did not converge or was best explained by a linear model, which was deemed as unrealistic from a biological perspective and likely due to incomplete sampling or a biased sample distribution (Bolser et al. 2018; Scherrer et al. 2021). Age at a specified length for female CSNA was determined following the method established by Ogle and Isermann (2017). Briefly, this method includes age at specified length as a parameter in the von Bertalanffy growth function, which allows this parameter to be directly estimated and a confidence interval can be constructed.

4.3 Results

A total of 408 and 389 gonad samples of female CSNA from 2017 and 2021, respectively, were examined histologically and classified as either immature (juvenile) or mature (adult). Of those females with gonads examined, ages were available for 354 individuals from 2017 and 377 individuals from 2021. All gonad samples from 2017 were from females collected inside the Southern California Bight (SCB; < 34.5° N; Figure 4.2). For 2021, 294 gonad samples were collected inside the SCB (< 34.5° N), and the remaining 95 samples were collected from Point Conception to Monterey, CA (> 34.5° N). Sea temperatures ranged from 11.5 to 16.7 °C for 2017 (mean = 14.6 °C ± 0.107 CI), 11.2 to 14.7 °C for 2021 from all areas (12.9 °C ± 0.103 CI), and 11.4 to 14.7 °C for 2021 within only the SCB (13.2 °C ± 0.12 CI; Figure 4.2). Notably, all samples collected outside the SCB in 2021 were associated with sea temperatures less than 13 °C.

The length distribution of female CSNA sampled for sexual maturity in 2021 (range = 79-164 mm SL) was larger than those from the 2017 trawl survey (range = 85-137 mm SL; Figure 4.3a). However, the mean length of sampled females was similar between years (2017: 116.9 mm SL ± 2.34 CI; 2021: 115.3 mm SL ± 2.76 CI). The smallest mature individual was 89 mm SL for 2017 and 91 mm SL for 2021. The largest immature individual was 116 mm SL for 2017 and 115 mm SL for 2021. Logistic regressions estimated L_{50} at 97.6 mm SL for 2017 and 102.0 mm SL for 2021 (Figure 4.4a,b).
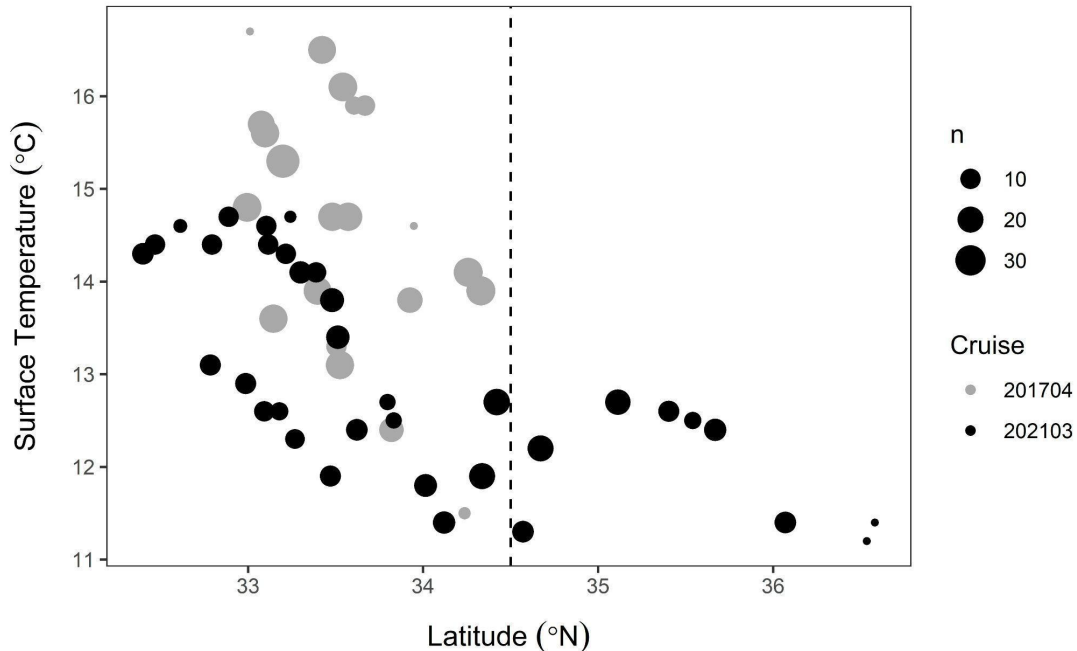
Figure 4.2. Latitude and temperature ranges for histological samples of CSNA collected in 2017 (gray circles) and 2021 (black circles). The size of the circle indicates the number of Northern Anchovy gonads analyzed. The vertical dashed line indicates the latitude cutoff for the Southern California Bight samples ($< 34.5°$ N).

The upper panel in Table 4.1 summarizes the results of the four model scenarios generated for all the pooled 2017 and 2021 data for female CSNA (see Appendix for detailed results on model outputs). Based on the ΔAICc values, model scenario (2) was not supported, and model scenario (1) was somewhat supported. Model scenario (4) had the lowest AICc that indicated a small difference in year-specific estimates of length at maturity for female CSNA. The interaction term for model scenario (3) was not significant ($p = 0.972$; see Appendix). Therefore, despite the low ΔAICc for model scenario (3), model scenario (4) was deemed more appropriate. Model scenario (4) produced the lowest ΔBIC value, but there was little evidence against model scenario (1), indicating that a year effect was not meaningful. The ΔBIC values indicated strong evidence against model scenario (3) and very strong evidence against model scenario (2).

Given the difference in the spatial distribution of gonad samples collected in 2017 versus 2021 (Figure 4.2), and assuming consistency in maturity assignments between years (readers), we speculated that the small difference in predicted length at maturity was driven by those samples ($n = 95$) collected north of Point Conception (i.e., outside the principle spawning area in colder waters) in 2021. After excluding these data and creating a new subset for 2021 that included only samples collected in the SCB (i.e., 2021 SCB), the logistic regressions estimated L_{50} at 98.4 mm SL for 2021 SCB, which overlapped completely with the estimate of 97.6 mm SL for 2017 (Figure 4.4c; Figure A1).
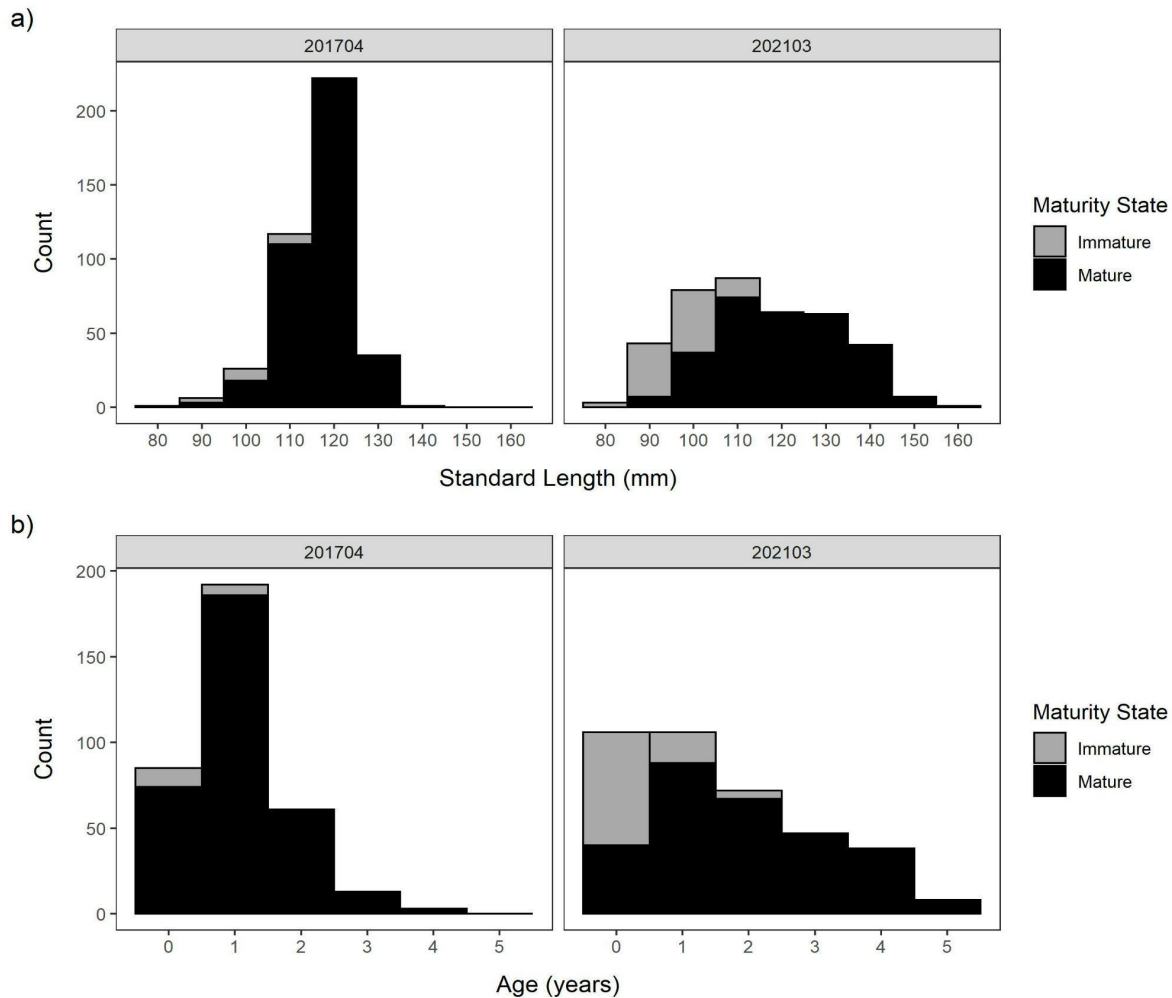
Figure 4.3. Histograms showing (a) length distributions and (b) age of immature vs. mature female CSNA in the 2017 and 2021 spring trawl surveys (201704 and 202103, respectively).

The lower panel in Table 4.1 summarizes the results of the four model scenarios that were generated using only samples collected inside the SCB in 2017 (all samples) and 2021 (subset). Based on ΔAICc values, model scenario (2) was not supported. The interaction term for model scenario (3) was not significant (p = 0.689), and model scenario (4) was also not significant (p = 0.432; see Appendix). Model scenarios (1), (3), and (4), were well supported (ΔAICc values <4), but model scenario (1) did not include year as a factor and therefore was the simplest model. ΔBIC values also identified model scenario (1) as the best model and there was evidence against each of the other models. Based on these results, the maturity ogive derived from samples collected in the SCB in spring 2017 and 2021 was selected as the most robust and reliable estimate of the relationship between length and sexual maturity for female CSNA. The logistic regression for this final dataset (2017 plus 2021 Bight; n = 702 gonad samples) estimated L_{50} at 98.2 mm SL (Figure 4.4d). However, a maturity ogive based on the pooled dataset of all gonad samples collected and analyzed in 2017 and 2021 was produced as a valid alternative (see

Appendix Figure A.2a; L_{50} = 101 mm SL), since it generated a very similar relationship between length and maturity. The very small difference (< 3 mm SL) between these estimates is unlikely to measurably affect estimates of age at maturity (see Appendix A.2b), total annual egg production, or spawning stock biomass.

Figure 4.4. Length-based maturity ogives of female CSNA based on trawl survey data collected in: (a) 2017; (b) 2021; (c) 2021 from Southern California Bight only; and (d) 2017 plus 2021 Southern California Bight only (pooled). Estimates of L_{25}, L_{50}, and L_{95} are in mm SL with 95% confidence intervals. Data are shown as jittered tick marks along the lower (immature fish) and upper (mature fish) axis. The solid line represents the predicted curve, and the dashed lines depict the 95% confidence intervals.

Table 4.1. Akaike Information Criterion corrected for small sample size (AICc) and Bayesian Information Criterion (BIC) results from the four model scenarios assessing the effects of standard length (SL) and year on estimated length at maturity from all female CSNA sampled during trawl surveys in 2017 and 2021 (upper panel; all data pooled) and from only females collected inside the Southern California Bight (SCB) in 2017 and 2021 (lower panel; 2017 + 2021 SCB only). Differences in AICc and BIC were calculated as $\Delta AICc = AICc_i - AICc_{min}$ and $\Delta BIC = BIC_i - BIC_{min}$, where $AICc_{min}/BIC_{min}$ denotes the minimum of the AICc/BIC values for the models being compared.

Data	Model (Scenario #) & Formula	AICc	Δ AICc	BIC	Δ BIC
2017 + 2021 (All)	(4) Maturity ~ SL + Year	323.60	0	337.6	0
	(3) Maturity ~ SL + Year + SL*Year	325.62	2.02	344.3	6.68
	(1) Maturity ~ SL	329.22	5.62	338.5	0.95
	(2) Maturity ~ Year	593.85	270.25	603.2	265.59
2017 + 2021 (SCB only)	(1) Maturity ~ SL	245.75	0	254.8	0
	(4) Maturity ~ SL + Year	247.15	1.40	260.8	5.94
	(3) Maturity ~ SL + Year + SL*Year	249.01	3.26	267.2	12.33
	(2) Maturity ~ Year	418.69	172.95	427.8	172.95

Based on the final age assignments for CSNA collected and aged from spring 2017, 87% of females were mature at age 0, 97% were mature at age 1, and all females were mature by age 2 (Figure 4.3b). For spring 2021, 37% were mature at age 0, 83% were mature at age 1, 93% were mature at age 2, 98% were mature at age 3, and all females were mature by age 4 (Figure 4.3b). A pooled dataset (spring 2017 + 2021) resulted in 60% of females mature at age 0, 92% at age 1, 96% by age 2, 98% by age 3, and all females were mature by age 4. When referring to the pooled 2017 and 2021 SCB data, the age-based maturity ogive estimated that 72.6% of female CSNA were mature at age 0, 93.1% were mature at age 1, and 98.5% were mature at age 2 (Figure 4.5d). Age-based maturity ogives resulted in negative A_{50} for three out of four ogives (Figure 4.5), indicating that more than 50% of CSNA mature before they are one year old, but these ogives were not useful to estimate A_{50} as negative age values are biologically unrealistic. Using the VBGF for female CSNA (Figure 4.6), an L_{50} of 98.2 mm SL equates to an A_{50} of -0.085 years (95% CI:-0.170, -0.017), further supporting that more than 50% of female CSNA are mature at age 0. Additionally, the smallest mature female CSNA of 89 mm SL equated to an estimated age of -0.644 years, and all females were estimated to be mature by 2.042 years of age (120 mm SL) based on the VBGF. For reference, a length- and age-based maturity ogive based on the pooled

dataset of all samples collected and analyzed in 2017 and 2021 (with assigned ages) is provided in the Appendix (see Figure A.2a,b).
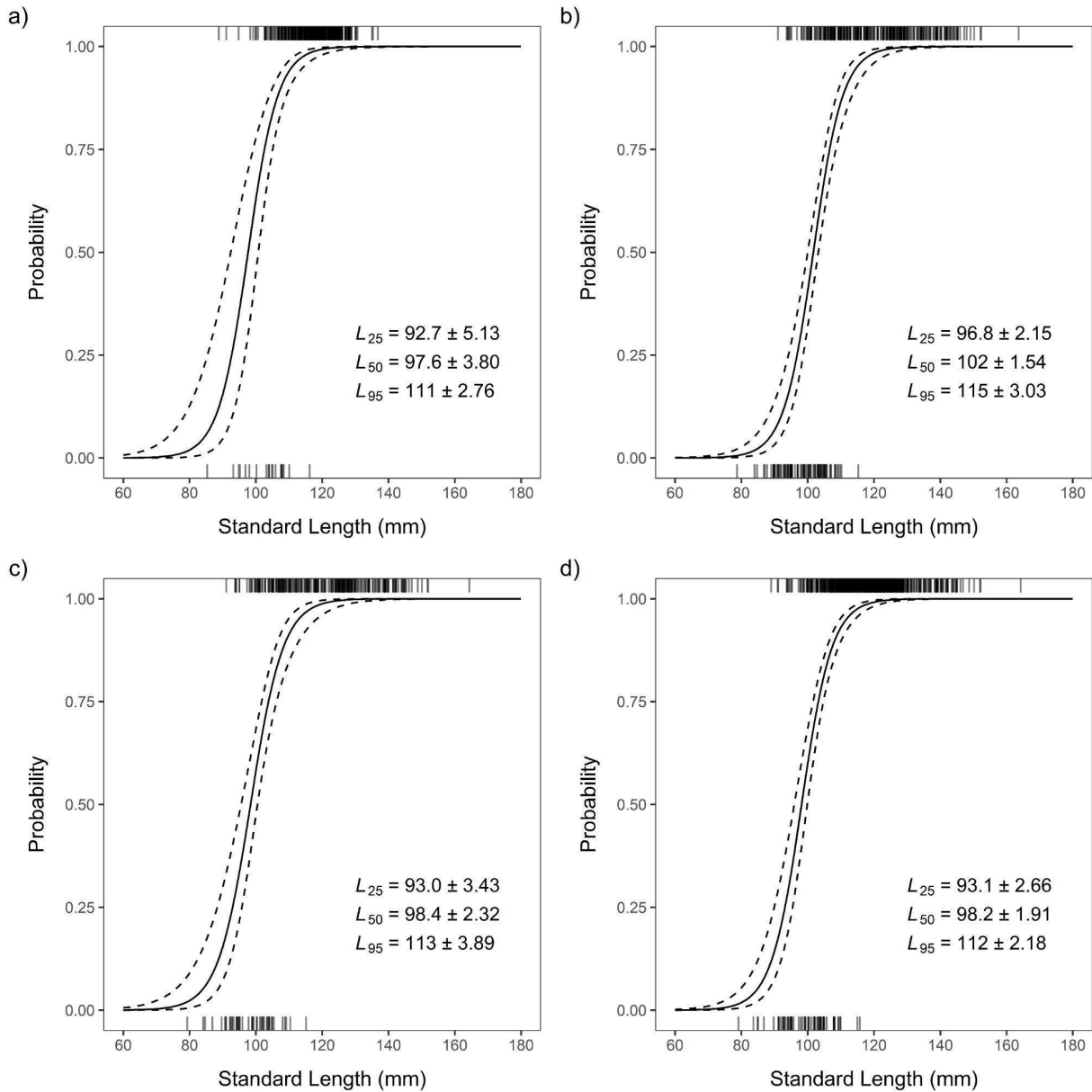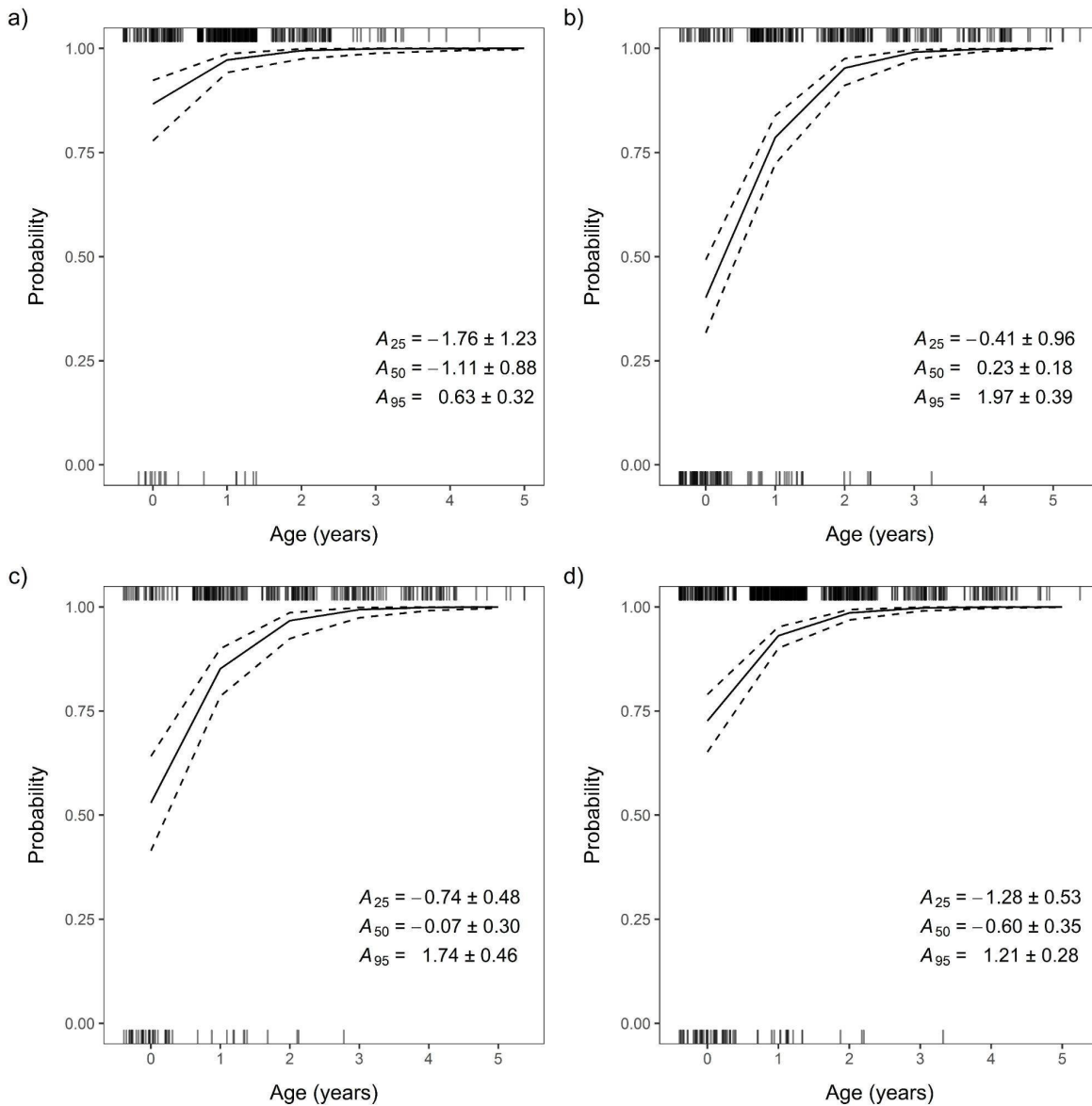

Figure 4.5. Age-based maturity ogives of female CSNA based on trawl survey data collected in: (a) 2017; (b) 2021; (c) 2021 from Southern California Bight only; and (d) 2017 plus 2021 Southern California Bight only (pooled). Estimates of A_{25}, A_{50}, and A_{95} are in age in years with 95% confidence intervals. Data are shown as jittered tick marks along the lower (immature fish) and upper (mature fish) axis. The solid line represents the predicted curve, and the dashed lines depict the 95% confidence intervals.
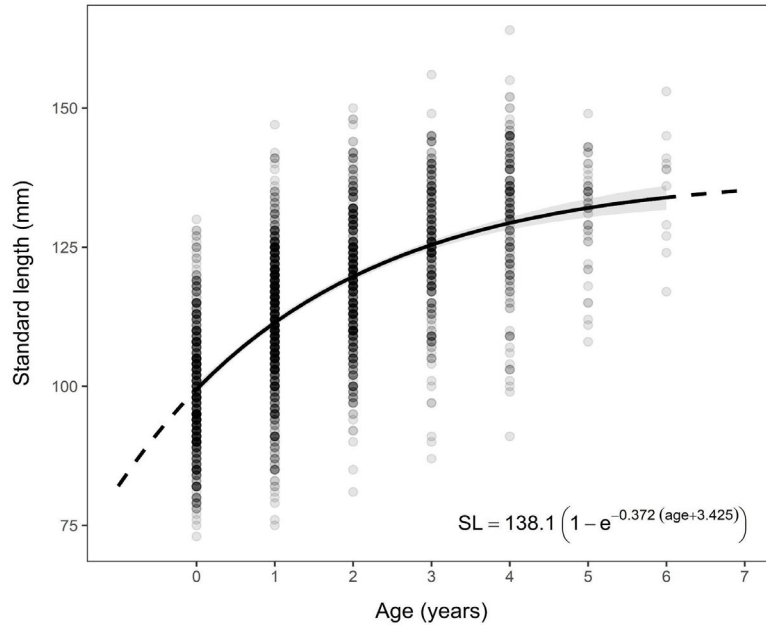
Figure 4.6. Standard length-at-age with fitted von Bertalanffy growth curve and equation for female CSNA collected during SWFSC trawl surveys from 2015 to 2021 (n = 2042). The grey shading depicts the 95% confidence intervals.

4.4 Potential Sources of Error

Analyses of histologically examined samples of female CSNA gonads collected during the peak spawning months in 2017 (April) and 2021 (March-April) produced very similar results with respect to estimated lengths at first maturity and average maturity. Both the smallest mature fish and the largest immature fish collected were nearly identical across years, and the estimated L_{50} values were also very similar, with a mean difference of only 4.4 mm SL. However, subsequent analyses using ΔAICc values suggested the possibility of a small difference in year-specific estimates of length at maturity for female CSNA.

Differences in sample distribution between years may have produced this small effect, as the length distribution of samples collected in spring 2017 was truncated with few small and large samples in comparison to the spring 2021 survey (Figure 4.3a). Next, since there was a different reader in 2017 than in 2021, it was plausible that the small year effect actually reflected differences between the readers in the methods used to assess maturity, since the methods used to categorize fish as mature or immature is known to affect the estimated length at maturity (Hunter and Macewicz 2003). However, both readers have several decades of experience studying the reproductive biology and development of marine fishes, and both also followed the exact same classification system and terminology described by Brown-Peterson et al. (2011), now widely considered as the gold standard. Notably, this standardized classification system specifies that the presence of oocytes in the cortical alveolar stage or later (e.g., vitellogenic, hydrated, ovulated) signifies that secondary gonad development is occurring and an individual female is

sexually mature. Using this type of straightforward protocol with well-defined criteria promotes a high-degree of consistency among readers and reduces opportunities for error in assessing maturity. Our results support this argument, as female gonads collected in the SCB in 2017 and 2021 showed nearly identical estimates for length at maturity. We therefore concluded that the small year effect was not related to a reader effect.

The small difference in estimated length at maturity observed between survey years may also be due to differences in the latitudinal distribution of sampling, which has been shown to influence the accuracy of the resulting estimate (Hunter and Macewicz 2003; Lowerre-Barbieri et al. 2011a). To minimize misclassification of sexual maturity in female marine fishes, it's best to sample in locations and during times when immature females are present but few regenerating females are present, which typically occurs at the principle spawning areas and during the spawning season (Hunter and Macewicz 1985a; Murua et al. 2003; ICES 2008). In accordance, all of the gonad samples of female CSNA from 2017 were collected in April at the main spawning grounds in the SCB (Dorval et al. 2018). Similarly, the majority of samples from 2021 were collected in the same manner. Therefore, it's not surprising that the estimates from 2017 and 2021 using only these data were indistinguishable from each other. For these reasons, it was concluded that the pooled data set using samples from SCB only represented the most robust and reliable estimate of length at maturity.

Further examination of the female CSNA gonad samples collected north of the SCB provided additional insights on the potential influence of sampling on maturity estimates. For this study, the estimated length at maturity that included all samples from 2021 was slightly higher than estimates for samples collected only in SCB (2017 data; 2017 plus 2021 SCB data). This result was consistent with previous studies showing that estimates of length and age at maturity from samples collected outside the main spawning grounds or outside the main spawning season tend to be higher than those based on data collected with consideration of principle spawning periods and locations (Hunter and Macewicz 2003; Lowerre-Barbieri et al. 2011a,b). Samples from 2021 collected north of SCB experienced colder sea temperatures (< 13°C) that were below the peak spawning temperature (14°C), and consequently, they had a higher proportion of gonads that were visually assessed as immature/inactive (F1 phase) or developing (F2 phase) (see Lo et al. 2010). The proportion of female CSNA that were larger than 100 mm SL and classified as immature were also higher among samples collected north of the SCB. Microscopically, these ovaries were composed almost entirely of previtellogenic oocytes packed within well-organized lamellae, but they also contained 1-2 oocytes at the very earliest cortical alveoli stage. Since CSNA are thought to spawn earlier off central California (i.e., spawning ends in March; Hunter and Macewicz 1980, 1985b), and these samples were collected in late March through early April, they were classified as immature females unlikely to continue development towards spawning that season. However, classifying this small number of females as mature would likely have

generated a slightly lower estimated length at maturity similar to estimates from SCB samples collected in 2017 and 2021.

5. Conclusions and Future Priorities

5.1 Age and Growth

As Northern Anchovy have not been assessed nor have their otoliths been aged in more than two decades, there is still much work to be done to address issues with ageing precision and accuracy and improve our collective understanding of growth patterns in this ecologically and economically important species. Northern Anchovy was a relatively new species for age readers, and thus readers have not yet gained sufficient years of experience compared to ageing other CPS. Consequently, it is likely that over time each reader will develop a better understanding of the patterns of opaque and translucent depositions in Northern Anchovy otoliths. As a result, we anticipate that age-reading variability among readers and years will decrease markedly in the future, and hence the need to develop time-specific error matrices for both the trawl and fishery data (as was done in this report) will be reduced as well. However, until age validation is complete, we can only realistically address ageing precision and cannot assess bias.

Validation and corroboration of annual ages has not been conducted for Northern Anchovy, and as a result, it is among the highest priorities for future research. Although marginal increment and edge analysis can be used as a first step for validation of ages for young, fast growing fish (Basilone et al. 2020), marginal increment analysis may have low resolving power if edge type determination is difficult, and validation may not be accurate for older ages if there are changes in seasonal timing of increment formation (Campana 2001; Vitale et al. 2019). Due to these difficulties, more robust age validation techniques are also needed. For validation of annual deposition of annuli, an experimental captive growth experiment with juvenile anchovies was carried out in 2014-2016. For the captive growth experiment, individuals were marked with oxytetracycline (OTC) and raised in tanks held at 3 different temperatures (13°C, 15°C, 17°C) for up to one year. The otoliths extracted from these fish are currently being analyzed to measure growth beyond the OTC mark for annual validation of annuli and to test for the effect of temperature on growth and increment deposition.

For validation of the first annulus deposition, two main research experiments are being explored. The first is a laboratory-based experiment with reared individuals, in which juvenile anchovy (3-6 months) would be reared up to a year to determine when the first translucent increment deposition occurred. Additionally, individuals would be reared across the temperature range of the central and northern subpopulations to examine whether temperature plays a role in annulus formation. Prior to this experiment, individual fish would be tagged and marked with OTC. The second is to use existing age-0 and just turned 1-year old otoliths that have been collected and measure the length from the focus to the beginning of what is deemed the first translucent increment (for the whole otolith). After this measurement is taken, the otolith would then be

polished, and daily rings would be counted. Aldanondo et al. (2016) found that the first translucent increment for the European Anchovy forms approximately three months after the birthdate (~100 days old). Therefore, a measurement would be taken to the ~100th ring, and this measurement would be compared to the measurement taken on the whole otolith to determine if they are similar. This measurement will also help ascertain if there is a threshold measurement to designate whether or not an increment is "too close" to the core and therefore should not be counted as the first annulus.

As the readability of otoliths may vary with fish age and annual ocean conditions, other ageing methods will be employed to explore whether they improve readability. For example, some otoliths have been found to be very thick, so there is a possibility that annuli are being missed and fish are being under aged. Methods that will be tested on 1+ year old fish to see if readability is improved include: 1) surface polishing; 2) sectioning and polishing; and 3) staining. As mentioned above, polishing may aid in identification of the first annulus, checks, translucent increments near the edge in older fish, and edge type.

Another research priority is to increase ageing precision and speed up the process of ageing in general. In line with this, the Life History Program is part of a NOAA multi-year strategic initiative with the goal of conducting research & development which will lead to operational readiness of Fourier transform near-infrared spectroscopy (FT-NIRS) technology in 5 years across all NOAA Fisheries ageing laboratories at all six NOAA Fisheries Science Centers. FT-NIRS quantitatively measures the absorption of near-infrared energy in organic molecules for use in rapid collection of fisheries biological data, and this technology has been adapted as a means of estimating fish age from the spectral analysis of otoliths (Wedding et al. 2014). Wedding et al. (2014) found that FT-NIRS predictive models had a high degree of accuracy in predicting the age of Saddleback Snapper (*Lutjanus malabaricus*) based on calibration curves developed in Australia. Following these promising results, the NOAA Alaska Fisheries Science Center began a study to assess the use of FT-NIRS in ageing Eastern Bering Sea Walleye Pollock (*Gadus chalcogrammus*), and found that the FT-NIRS method had as good or slightly better precision in ageing than the standard method (Helser et al. 2019). The Life History Program has started evaluating the feasibility of using FT-NIRS as a complementary method of ageing for Northern Anchovy, Pacific Sardine, other CPS, and several species of tunas. A FT-NIRS spectrometer has already been delivered to and installed at the SWFSC, and scanning has begun.

5.2 Length and Age at Maturity

Gonadal histology is the most accurate method to assess reproductive condition in marine fishes (Kjesbu et al. 2003; Murua et al. 2003; Tomkiewicz et al. 2003). However, visual (macroscopic) assignments of maturity is a much faster and cheaper method that allows for the rapid collection and analyses of data that has been demonstrated to produce comparable estimates of length at maturity for CPS (Ferreri et al. 2009; Basilone et al. 2021) when sampling is designed and

executed properly. The main limitations of the visual method are the inability to distinguish between resting, mature females and immature females that have never spawned (West 1990; Trippel and Morgan 1996; Afonso-Dias et al. 2008). However, during the main spawning season and within the principle spawning grounds, the proportion of resting females is minimal, and it is reasonable to assume that undeveloped ovaries reflect immaturity (Lowerre-Barbieri et al. 2011a,b). Difficulties in distinguishing between spawning capable, actively spawning, and post-spawning females also reduce accuracy and limit the quality and resolution of data generated by visual methods (Hunter and Macewicz 1985b; Klibansky and Scharf 2015). Fortunately, such distinctions are not critical and do not impact the results of maturity studies, because all these phases are classified as mature. Moreover, visual (macroscopic) assignments of maturity can effectively be validated through subsampling of gonads for histological analyses followed by implementing a correction factor to reduce the misclassification between immature and mature females (Lowerre-Barbieri et al. 2011b; Erisman et al. 2010, 2012). It is also important to examine gonads soon after capture and avoid freezing samples to minimize errors in visual maturity assignments (Lasker 1985). In summary, despite some misclassifications, macroscopic assignments produce similar estimates as histological examinations of length at maturity and spawning seasonality (García-Diaz et al. 1997; Klibansky and Scharf 2015; Ferreri et al. 2009).

Gonads are visually inspected and staged for sex and maturity for all CSNA whose otoliths are removed for ageing during both spring and summer CPS trawl surveys conducted by SWFSC, which has resulted in visual maturity data for several thousand samples of CSNA over the past decade. More specifically, visual methods are used to assign female CSNA gonads to one of four categories (immature, intermediate, active, hydrated; Lo et al. 2010). Historically, these data have not been used to generate maturity ogives for CSNA due to concerns over their accuracy, particularly samples from the summer months that are highly prone to error in visual maturity assignments since relatively few fish are spawning during that time. Consistency in visual maturity assignments is also perceived as an issue, since many different staff (both experienced and inexperienced) have participated in this activity over time. Similar to data collected by SWFSC, CDFW records visual maturity data from Northern Anchovy samples from their monthly port surveys of the commercial fishery, but due to concerns of inaccuracy and inconsistency, such data are only used to examine general maturity trends over time.

We plan to compare the existing maturity data generated using both visual and histological methods (e.g. spring and summer CPS trawl survey data and CDFW fishery port sampling data) to assess the accuracy and efficacy of maturity ogives generated through visual methods. More specifically, we will examine the percent agreement between the methods in relation to data source, year, month or season, reproductive phase, and assessor. For this study, histology will be assumed to produce an accurate estimate. However, we also plan to estimate error and bias by having multiple readers of the histologically-prepared gonads and conducting the same analyses as used for ageing analyses. Based on preliminary comparisons of the maturity data generated

from the spring 2021 CPS survey comparing visual and histological methods, data produced from previous summer CPS surveys, and the conclusions of previous studies on this topic (see references above), we speculate that the visual method will generate accurate estimates of length at maturity for CSNA if such data are restricted to being collected during the peak spawning season (i.e., February through April) and within the main spawning area of the SCB. Similarly, we expect that visual maturity data collected outside the peak spawning season or main spawning area will produce inaccurate and uninformative results. If our predictions are correct, it would suggest that: (1) visual methods (by an experienced reader) can be used during spring surveys in SCB to generate length at maturity estimates; (2) the number of gonad samples collected during spring surveys and processed for histology can be reduced to a subset used to validate visual maturity data; and (3) visual maturity data should no longer be collected for CSNA during summer CPS surveys.

6. Acknowledgements

7. References

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8. Postscript

The draft stock assessment model proposed by Kuriyama et al. (2021) to the Stock Assessment Review (STAR) panel included ages from all three readers from 2015-2016 for trawl surveys, but did not include ages from reader 15 for trawl surveys conducted from 2017-2021. However, as noticed by the STAR panel, the age reading error vectors calculated for this period did not reflect the removal of the ages from reader 15 (PFMC 2022). Accordingly, the panel requested that ageing error vectors be re-calculated for the trawl survey in 2017-2021 and that the assessment model be re-run to reflect the removal of these ages and associated assumptions regarding ageing bias and precision. Figure 8.1 shows the bias plot between the 2 readers (reader 2 and 14) whose ages were kept in the final assessment model; whereas Table 8.1 and Table 8.2 showed the ageing precisions for readers 2 and 14, and a biased corrected ageing vector for reader 14. For 2017-2018, two Agemat models were used: a) Model A assumed that reader 2 was unbiased and reader 14 was biased, but that both readers had different SDs-at-age; b) Model C assumed, as in Section 3.5, that both readers were unbiased and had similar SDs-at-age. As approved by the STAR panel, the final stock assessment model applied the common SDs-at-age from Model C to the 2017-2018 survey period; whereas for 2019-2021 the reader specific SDs-at-age and the ageing vector corrected for bias for reader 14 based on Model A were used. For the maturity data, the final model used the age maturity ogive for the 2017 plus 2021 SCB data (Figure 5d).
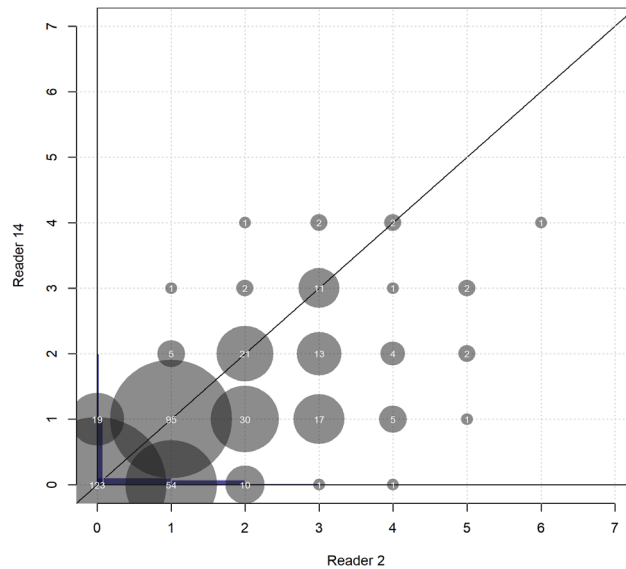

Figure 8.1. Age bias plots from the Agemat models for readers 2 and 14 for CSNA collected from trawl surveys in 2017-2018.

Table 8.1. Updated coefficient of variation (*CV*) and standard deviation (*SD*) at age estimated for CSNA collected by trawl surveys in 2017-2018 and 2019-2021 as requested by the STAR Panel. Age date from reader 15 were removed from 2017-2021. All estimates were calculated using the latest version of the nwfscAgeingError R package (Thorson et al. 2012). Model C assumes no bias in ageing between reader 2 and 14, and readers had a similar *SD*s. There are no ageing error values for the 2019-2021 period as Reader 2 did not complete any double reads for this time period.

Collection type	Collection year	Data set ID	Sample size	Number of readers	Age	*CV* (Reader 2, 14)	*SD* (Reader 2, 14)
						Agemat model C	
Trawl Survey (Recommended scenario)	2017-2018	4	424	2	0	0.43	0.43
					1	0.43	0.43
					2	0.54	1.07
					3	0.44	1.31
					4	0.35	1.40
					5	0.29	1.43
					6	0.24	1.44

Table 8.2. Updated coefficient of variation (*CV*) and standard deviation (*SD*) at age estimated for CSNA collected by trawl surveys in 2017-2018 and 2019-2021 as requested by the STAR Panel. Age date from reader 15 were removed from 2017-2021. All estimates were calculated using the latest version of the nwfscAgeingError R package (Thorson et al. 2012). Model A assumes that only reader 2 is unbiased and has a different *SD* than reader 14.

Collection type	Collection year	Data set ID	Sample size	Number of readers	Reader	Age	*CV*	*SD*	Expected age
							Agemat model A		
Trawl Survey (Recommended scenario)	2017-2018	4	424	2	Reader 2	0	0.37	0.37	
						1	0.37	0.37	
						2	0.29	0.59	
						3	0.27	0.81	
						4	0.26	1.05	
						5	0.26	1.30	
						6	0.26	0.26	
					Reader 14	0	0.32	0.32	0.53
						1	0.32	0.32	1.15

						Agemat model A		
					2	0.33	0.66	1.79
					3	0.30	0.90	2.45
					4	0.26	1.05	3.12
					5	0.23	1.16	3.80
					6	0.21	1.23	4.50
	2019-2021 (No double reads because Reader 15 was dropped)	4	424	2	Reader 14	0	0.32	0.32	0.53
						1	0.32	0.32	1.15
						2	0.33	0.66	1.79
						3	0.30	0.90	2.45
						4	0.26	1.05	3.12
						5	0.23	1.16	3.80
						6	0.21	1.23	4.50

Postscript references

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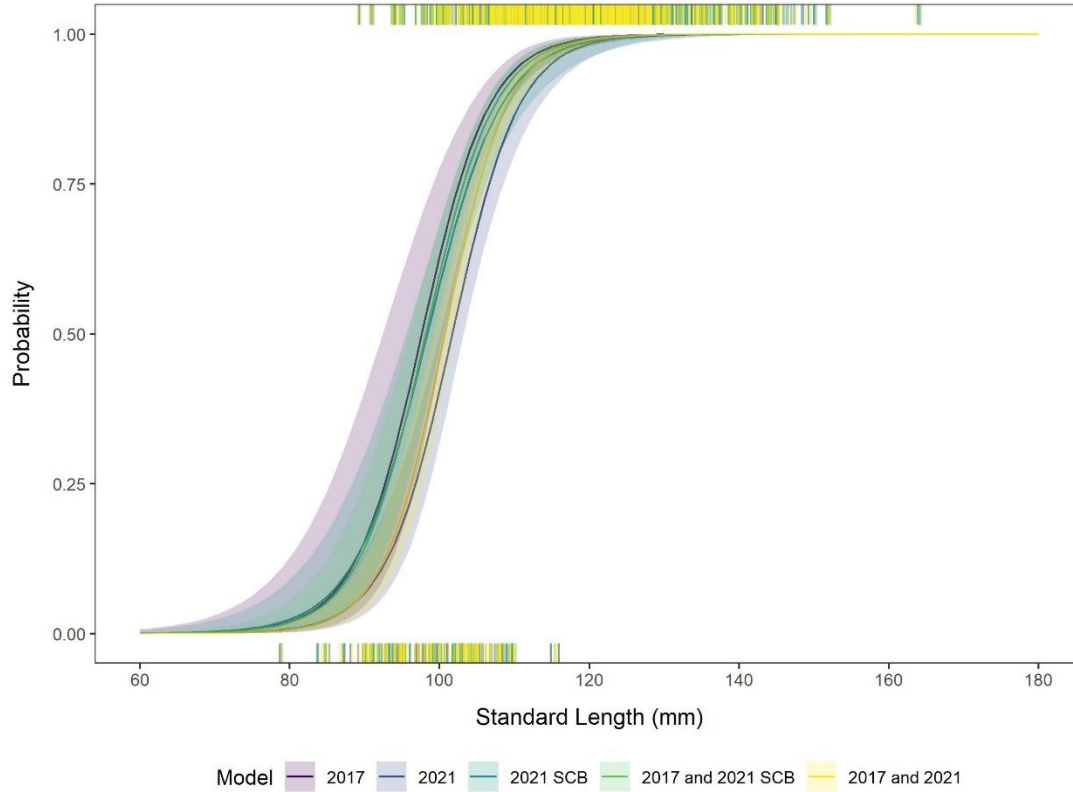
Figure A1. Length-based maturity ogive plot of female CSNA from trawl surveys combining all five data sets (2017 only [purple]; 2021 only [blue]; 2021 from southern California Bight (SCB) only [teal]; pooled fish from 2017 plus 2021 SCB [green]; and pooled fish from 2017 plus 2021 [yellow]). Data are shown as jittered tick marks along the lower (immature fish) and upper (mature fish) axis. The solid lines represent the predicted curve, and the shaded areas depict the 95% confidence intervals.
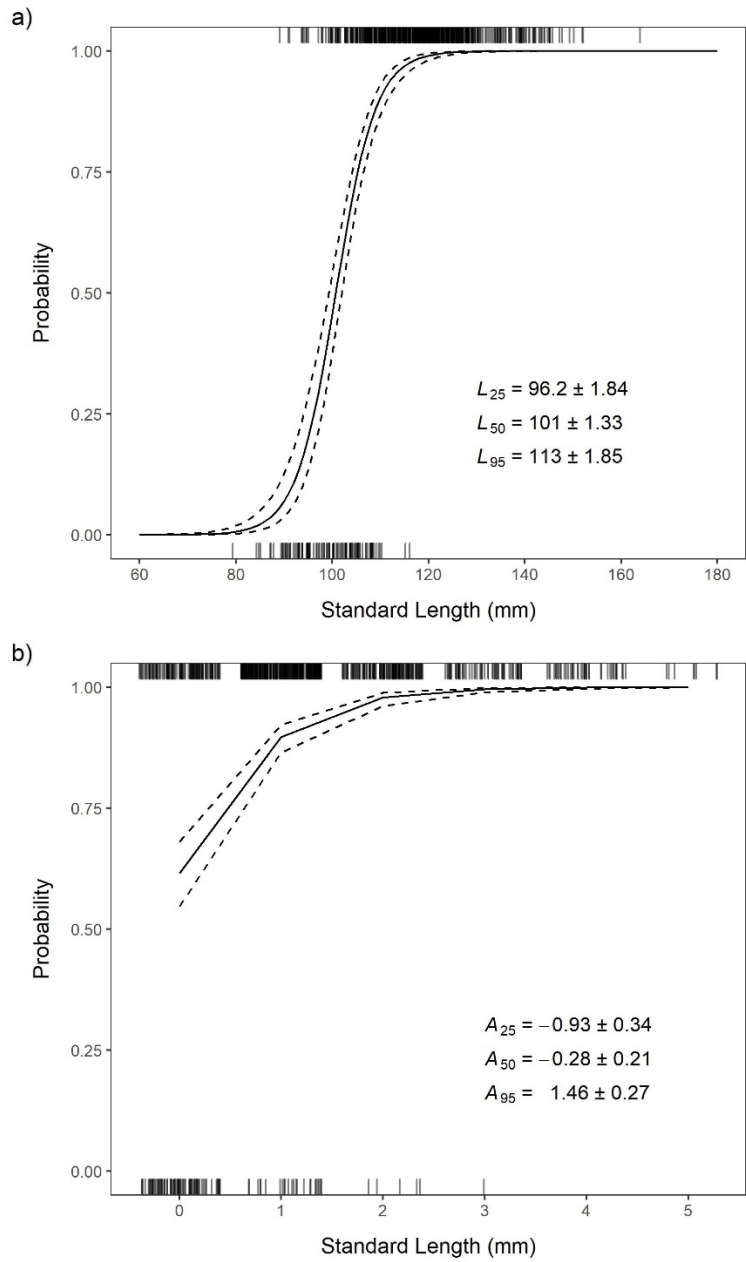
Figure A.2. a) Length-based maturity and b) age-based maturity ogives of female CSNA based on trawl survey data collected in 2017 and 2021 (pooled). Estimates of L_{25}, L_{50}, and L_{95} are in mm SL with 95% confidence intervals, and estimates of A_{25}, A_{50}, and A_{95} are in age in years with 95% confidence intervals. Data are shown as jittered tick marks along the lower (immature fish) and upper (mature fish) axis. The solid line represents the predicted curve, and the dashed lines depict the 95% confidence intervals.

R output of binomial models fit to histological maturity data.

All models are in the general form: glm(formula = y ~ x, family = binomial(logit)), where y is maturity (mature / immature).

<u>Model 1: 2017 histological data</u>

Explanatory variables: Standard Length (mm)

Deviance Residuals:

Min	1Q	Median	3Q	Max
-2.86516	0.08396	0.13088	0.22735	2.02932

Coefficients:

	Estimate	Std. Error	z value	Pr(>|z|)	
(Intercept)	-21.73510	3.93227	-5.527	3.25e-08	***
standardLength_mm	0.22261	0.03677	6.055	1.40e-09	***

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

(Dispersion parameter for binomial family taken to be 1)

Null deviance: 159.62 on 407 degrees of freedom
Residual deviance: 100.90 on 406 degrees of freedom
AIC: 104.9

Number of Fisher Scoring iterations: 7

<u>Model 2: 2021 histological data</u>

Explanatory variables: Standard Length (mm)

Deviance Residuals:

Min	1Q	Median	3Q	Max
-2.46219	0.00630	0.08288	0.39089	2.22980

Coefficients:

	Estimate	Std. Error	z value	Pr(>|z|)

(Intercept)   -22.80145   2.76472   -8.247   <2e-16 ***
standardLength_mm   0.22420   0.02667   8.407   <2e-16 ***

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

(Dispersion parameter for binomial family taken to be 1)

Null deviance: 430.21 on 388 degrees of freedom
Residual deviance: 216.67 on 387 degrees of freedom
AIC: 220.67

Number of Fisher Scoring iterations: 7

Model 3: Modified 2021 histological data excluding individuals North of Point Conception (Latitude < 34.5) (aka 2021 Bight)

Explanatory variables: Standard Length (mm)

Deviance Residuals:
    Min   1Q   Median   3Q   Max
-2.61176   0.02115   0.08537   0.41475   1.84501

Coefficients:
                        Estimate   Std. Error   z value   Pr(>|z|)
(Intercept)   -19.99589   3.22774   -6.195   5.83e-10 ***
standardLength_mm   0.20324   0.03157   6.437   1.22e-10 ***

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

(Dispersion parameter for binomial family taken to be 1)

   Null deviance: 255.05 on 293 degrees of freedom
Residual deviance: 140.05 on 292 degrees of freedom
AIC: 144.05

Number of Fisher Scoring iterations: 7

Model 4: Pooled 2017 & 2021 histological data

Explanatory variables: Standard Length (mm)

Deviance Residuals:

Min	1Q	Median	3Q	Max
-2.72690	0.04633	0.13724	0.31662	2.40483

Coefficients:

	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	-24.3525	2.21363	-11.00	<2e-16 ***
standardLength_mm	0.24178	0.02114	11.44	<2e-16 ***

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

(Dispersion parameter for binomial family taken to be 1)

Null deviance: 654.24 on 796 degrees of freedom
Residual deviance: 325.20 on 795 degrees of freedom
AIC: 329.2

Number of Fisher Scoring iterations: 7

Model 5: Pooled 2017 & 2021 histological data

Explanatory variables: Year

Deviance Residuals:

Min	1Q	Median	3Q	Max
-2.4558	0.3170	0.3170	0.7438	0.7438

Coefficients:

	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	2.9653	0.2293	12.933	< 2e-16 ***
Year(2021)	-1.8216	0.2581	-7.059	1.68e-12 ***

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

(Dispersion parameter for binomial family taken to be 1)

Null deviance: 654.24 on 796 degrees of freedom
Residual deviance: 589.83 on 795 degrees of freedom
AIC: 593.83

Number of Fisher Scoring iterations: 5

Model 6: Pooled 2017 & 2021 histological data

Explanatory variables: Standard Length (mm) and Year with an interaction term

Deviance Residuals:
```
    Min      1Q   Median      3Q     Max
-2.86516  0.04815  0.11715  0.28186  2.22980
```

Coefficients:

	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	-21.735102	3.932266	-5.527	3.25e-08 ***
standardLength_mm	0.222612	0.036765	6.055	1.40e-09 ***
Year(2021)	-1.066343	4.806910	-0.222	0.824
standardLength_mm x Year(2021)	0.001589	0.045420	0.035	0.972

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

(Dispersion parameter for binomial family taken to be 1)

Null deviance: 654.24 on 796 degrees of freedom
Residual deviance: 317.57 on 793 degrees of freedom
AIC: 325.57

Number of Fisher Scoring iterations: 7

Model 7: Pooled 2017 & 2021 histological data

Explanatory variables: Standard Length (mm) and Year with no interaction term

Deviance Residuals:

```
    Min      1Q   Median    3Q      Max
-2.86850  0.04762  0.11634  0.28226  2.22700
```

Coefficients:

	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	-21.84645	2.31851	-9.423	< 2e-16 ***
standardLength_mm	0.22366	0.02158	10.363	< 2e-16 ***
Year(2021)	-0.89856	0.33050	-2.719	0.00655 **

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

(Dispersion parameter for binomial family taken to be 1)

Null deviance: 654.24 on 796 degrees of freedom
Residual deviance: 317.57 on 794 degrees of freedom
AIC: 323.57

Number of Fisher Scoring iterations: 7

Model 8: Pooled 2017 and 2021 Bight (Latitude < 34.2) histological data

Explanatory variables: Standard Length (mm)

Deviance Residuals:
```
    Min      1Q   Median    3Q      Max
-2.79984  0.06043  0.12969  0.27671  2.06422
```

Coefficients:

	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	-21.46398	2.37612	-9.033	<2e-16 ***
standardLength_mm	0.21865	0.02281	9.585	<2e-16 ***

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

(Dispersion parameter for binomial family taken to be 1)

Null deviance: 437.68 on 701 degrees of freedom
Residual deviance: 241.73 on 700 degrees of freedom
AIC: 245.73

Number of Fisher Scoring iterations: 7

Model 9: Pooled 2017 and 2021 Bight (Latitude < 34.2) histological data

Explanatory variables: Year

Deviance Residuals:
```
   Min     1Q   Median     3Q     Max
-2.4558  0.3170  0.3170  0.5834  0.5834
```

Coefficients:

	Estimate	Std. Error	z value	Pr(>|z|)	
(Intercept)	2.9653	0.2293	12.933	< 2e-16	***
Year(2021)	-1.2805	0.2799	-4.575	4.77e-06	***

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

(Dispersion parameter for binomial family taken to be 1)

```
    Null deviance: 437.68  on 701  degrees of freedom
Residual deviance: 414.67  on 700  degrees of freedom
AIC: 418.67
```

Number of Fisher Scoring iterations: 5

Model 10: Pooled 2017 and 2021 Bight (Latitude < 34.2) histological data

Explanatory variables: Standard Length (mm) and Year with an interaction term

Deviance Residuals:
```
    Min      1Q    Median      3Q      Max
-2.86516  0.06297  0.11715  0.25371  2.02932
```

Coefficients:

	Estimate	Std. Error	z value	Pr(>|z|)	
(Intercept)	-21.73510	3.93227	-5.527	3.25e-08	***
standardLength_mm	0.22261	0.03677	6.055	1.40e-09	***

Year(2021)   1.73921   5.08734   0.342   0.732
standardLength_mm x Year(2021)   -0.01937   0.04846 -0.400   0.689

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

(Dispersion parameter for binomial family taken to be 1)

   Null deviance: 437.68 on 701 degrees of freedom
Residual deviance: 240.95 on 698 degrees of freedom
AIC: 248.95

Number of Fisher Scoring iterations: 7

Model 11: Pooled 2017 and 2021 Bight (Latitude < 34.2) histological data

Explanatory variables: Standard Length (mm) and Year with no interaction term

Deviance Residuals:
    Min   1Q   Median   3Q   Max
-2.83113   0.06229   0.12571   0.26214   1.94651

Coefficients:
                        Estimate   Std. Error   z value   Pr(>|z|)
(Intercept)   -20.58879   2.58772   -7.956   1.77e-15 ***
standardLength_mm   0.21188   0.02407   8.803   < 2e-16 ***
Year(2021)   -0.28769   0.36608   -0.786   0.432

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

(Dispersion parameter for binomial family taken to be 1)

   Null deviance: 437.68 on 701 degrees of freedom
Residual deviance: 241.11 on 699 degrees of freedom
AIC: 247.11

Number of Fisher Scoring iterations: 7