Marine Biology (2024) 171:105
https://doi.org/10.1007/s00227-024-04425-2

ORIGINAL PAPER

Validation of periodicity of growth band formation in Pacific Sardine (*Sardinops sagax*) from a captive growth experiment

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Received: 12 July 2023 / Accepted: 13 March 2024

Abstract
Pacific Sardine (*Sardinops sagax*) in the Northeast Pacific Ocean are aged for stock assessments assuming the formation of two otolith growth bands (one opaque and one translucent) a year, but the periodicity of band formation has not been fully validated. To validate our ageing method, we investigated the periodicity of band deposition and somatic and otolith growth rate across a range of temperatures. Live Pacific Sardine (mostly age 0) were collected, marked with oxytetracycline (OTC), and raised in captivity at different temperatures (13 °C, 15 °C, 17 °C, and 21 °C) for up to one year. There was no clear pattern between temperature and somatic growth rate. Otolith growth rate was slower for Pacific Sardine in captivity at 13 °C than at 17 °C. All individuals that were in captivity for one year ($n=21$) deposited 2–3 growth bands distal to the OTC mark. Therefore, Pacific Sardine deposited bands in their otoliths at the rate expected for the formation of annuli across ecologically relevant temperatures (13–21 °C) in captivity. Vateritic otoliths were rare but did display an OTC mark at approximately the same distance from the otolith edge as the aragonitic otolith in the pair. The results of this study build upon previous validation research for Pacific Sardine and support the ageing methodology used for this species by all ageing laboratories in the US, Canada, and Mexico.

Keywords Oxytetracycline · Temperature · Otolith growth rate · Somatic growth rate

Introduction

Small pelagic fishes have highly variable growth that is strongly influenced by environmental conditions (Blaxter and Hunter 1982; Armstrong and Shelton 1990; Tanaka et al. 2023). Variable growth directly affects recruitment and population size of these species, which are important variables to track for fisheries management (Blaxter and Hunter 1982; Cole and McGlade 1998). Temperature is a well-documented environmental condition that affects growth rate (Pauly 1980; Fey 2006). In general, somatic and otolith growth rates are expected to be higher at higher temperatures (Neilson and Geen 1982; Campana and Neilson 1985; Mosegaard et al. 1988; Fey 2006). In contrast, the periodicity of band deposition in otoliths is not faster at higher temperatures (Taubert and Coble 1977). Experimental research has shown that it is difficult to disrupt the endogenous biological rhythm of two bands (one opaque and one translucent) a year (Johnson and Belk 2004; Neat et al. 2008; Buckmeier et al. 2017). Gaining more insight into how temperature affects growth rate and periodicity of band deposition would improve understanding of the cycles in abundance of small pelagic fishes.

The Pacific Sardine (*Sardinops sagax*) is an economically important forage fish in the Northeastern Pacific Ocean with high individual variability in growth (Dorval et al. 2015; unpubl data). Its range extends from southeastern Alaska to Baja California and into the Gulf of California, Mexico (Kramer and Smith 1971; Parrish et al. 1989). Pacific Sardine in this region are divided into three stocks for fisheries management: a warm (22–27 °C), a temperate (17–22 °C), and a cold (13–17 °C) stock that seasonally migrate along the West Coast of North America (Félix-Uraga et al. 2004). The Coastal Pelagic Species Fishery Management Plan of

Responsible Editor: W. Figueira.

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Published online: 28 March 2024

the Pacific Fishery Management Council (PFMC) manages the cold or 'northern' stock (Kuriyama et al. 2020). The northern stock is speculated to extend as far south as Ensenada, Mexico in the winter and as far north as British Columbia, Canada in the summer (Félix-Uraga et al. 2004; Ware 1999; Zwolinski et al. 2011).

Pacific Sardine ages are determined from counts of growth bands in sagittal otoliths assuming the annual deposition of annuli (Yaremko 1996). An annulus is composed of one opaque band and one translucent band, a complete annulus is counted at the interface between an inner translucent band and a distal opaque band (Collins and Spratt 1969; Yaremko 1996). For Pacific Sardine, translucent bands form in the late fall and winter and the opaque band begins during increased growth in the late spring and continues through early fall (Barnes and Foreman 1994; Yaremko 1996). This periodicity of growth band formation is consistent across many species of temperate marine fishes (Beckman and Wilson 1995; Wright et al. 2002; Begg et al. 2005; Hüssy et al. 2021a). A tri-national Pacific Sardine ageing workshop that included state (California Department of Fish and Wildlife (CDFW) & Washington Department of Fish and Wildlife (WDFW)), federal (Southwest Fisheries Science Center (SWFSC) of the National Oceanic and Atmospheric Administration), Canadian (Department of Fisheries and Oceans (DFO)), and Mexican (Centro Interdisciplinario de Ciencias Marinas (CICIMAR)) agencies was held in 2004 and confirmed that ageing methodology is consistent across agencies (Dorval et al. 2013). This collaboration is important as stock assessments of the northern stock of Pacific Sardine have incorporated age data generated by SWFSC, CDFW, WDFW, DFO, and CICIMAR.

Despite consistent ageing across agencies, the periodicity of growth bands in Pacific Sardine otoliths has only been validated up to age 2 with marginal increment analysis (Walford and Mosher 1943) and counting daily growth bands (Barnes and Foreman 1994). During Barnes and Foreman's (1994) validation work they found that Pacific Sardine that hatched in late fall did not deposit a translucent band that winter and subsequently had not formed an annulus by the following fall when they were one year old. Fall is not the peak spawning season for Pacific Sardine in California (Ahlstrom 1965; Blaxter and Hunter 1982; Watson 1992); therefore, the number of Pacific Sardine that skip depositing the first translucent band is likely low. Nevertheless, the skipping of the translucent band is an important phenomenon to consider. The mechanism behind seasonal deposition of opaque and translucent bands is not well understood, but has been assumed to be related to seasonality in somatic growth and environmental factors (Beckman and Wilson 1995; Wright et al. 2002; Neat et al. 2008).

Chemical marking of fish otoliths provides a known starting date for otolith growth to examine the periodicity of the deposition of growth bands. This paired with captive growth facilitates a controlled environment to observe otolith growth. Captive somatic growth is known to differ from wild somatic growth, but deposition of growth bands in otoliths in captivity has been demonstrated to continue irrespective of somatic growth (Mosegaard et al. 1988; Wright et al. 1990), and a controlled captive environment is ideal to examine somatic and otolith growth and the periodicity of the deposition of otolith growth bands.

The goal of this work was to investigate the periodicity of growth band deposition in Pacific Sardine otoliths using chemical marking paired with captive growth across ecologically relevant temperatures. The specific objectives were to: 1) assess the effect of different constant temperature conditions on somatic (length and weight) and otolith growth; and 2) assess the periodicity of otolith growth bands at a range of experimental temperatures. It is important to understand how temperature influences Pacific Sardine growth and confirm the ageing methodology used to manage this species.

Methods

Experimental design

Live, small Pacific Sardine were collected from the bait barge (Everingham Bros.) in San Diego, California and reared at the SWFSC Aquarium. The experiment was conducted in 2014 and repeated in 2015. Pacific Sardine for 2014 were collected from December 20th 2013 through January 2nd 2014. Pacific Sardine for 2015 were collected on November 4th and December 4th 2014. Individuals were acclimated to ambient temperature tanks at SWFSC for 3–8 weeks. Flow-through seawater was obtained from the Scripps Institution of Oceanography Pier, and thus ambient temperatures reflected daily oceanic conditions around the Pier during the acclimation period. After acclimation, Pacific Sardines were injected intraperitonially with 100 mg oxytetracycline (OTC, Liquamycin La-200®,[1] 200 mg ml^{-1}) per kg fish weight. Individuals were measured for standard length (SL), and total length (TL) in mm, weighed (W) to the nearest gram, and injected with a fluorescent 1.0 × 2.5-mm VI Alpha™ tag (Northwestern Marine Technology™) for individual identification. In 2014, individuals were tagged on the 15th, 21st, and 22nd of January. In 2015, individuals were tagged on the 2nd through 5th of February.

After tagging, individuals were randomly assigned to one of three temperatures: 13 °C, 17 °C, or 21 °C in 2014, and 13 °C, 15 °C, or 17 °C in 2015. Temperatures were

[1] Use of Trade Names does not imply endorsement from the National Oceanic and Atmospheric Administration.

Table 1 Number of Pacific Sardine at each scheduled sampling event (5, 8, & 12 months) for both experiment years (2014 & 2015). The experiment in 2014 was terminated at 8 months

		Scheduled Sampling Events		
Tag Date	Temperature	5 months	8 months	12 months
		Jun. 2014	Sep. 2014	
Jan. 2014	13 °C	0	5	
Jan. 2014	17 °C	10	13	
Jan. 2014	21 °C	9	3	
		Jul. 2015	Oct. 2015	Feb. 2015
Feb. 2015	13 °C	13	10	8
Feb. 2015	15 °C	15	9	10
Feb. 2015	17 °C	15	6	3

maintained within 0.5 °C of the target temperature. Temperatures were different among years to accommodate concurrent growth experiments on Pacific Mackerel (*Scomber japonicus*) in 2014 and Northern Anchovy (*Engraulis mordax*) in 2015, while also accounting for the range of temperature tolerance of each species.

Pacific Sardine were reared under a 12 h light, 12 h dark cycle in 2.8 m^3 oval tanks (one tank per temperature) located in an enclosed section of the SWFSC Aquarium. Individuals were fed a commercial pellet diet, Bio-diet brood formulation (Bio-Oregon®) throughout the day by hand, providing a daily ration equivalent to 1.5% of their body mass. Each tank had an initial density of 80 individuals, and Pacific Sardine were sampled at approximately 5, 8, and 12 months (Table 1), while incidental mortality occurred throughout the experiment. At each time step total biomass was measured in each tank, and accordingly the total daily ration was adjusted to average 1.5% of fish body mass. Individuals that died between each of these three-time steps were also collected and processed. At each scheduled sampling event, Pacific Sardine were euthanized with an overdose of 50 ppm tricaine methanesulfonate (MS222). Depending on their total weight, individuals were treated for 2–5 min in the MS222 solution bath.

Sample processing

Individuals were identified from the Alpha™ tag, length and weight measurements were taken, and the individual was frozen for removal of otoliths at a later date. Total length was recorded most frequently and was used for analyses; SL was converted to TL where necessary using the conversion TL = 1.157*SL + 0.724 from Palance et al. (2019). Individuals that died between scheduled sampling events were processed the same way. If the Alpha™ tag was lost, individual data were recorded as a new individual and the individual was saved for otolith extraction.

Pacific Sardine were thawed for otolith extraction. Both sagittal otoliths were extracted, cleaned with water, assigned an individual barcode, placed in black 0.6 mL microcentrifuge tubes, allowed to dry overnight in a dark place, and stored. Otoliths were submerged in water in a small dish with a black background and viewed under reflected white light and UV light (360/40 nm Excitation Filter) using a Leica™ MZ10 F fluorescence stereomicroscope with an integrated FLUOIII filter system. Otoliths were aged using white light without knowledge of duration in captivity or temperature following Yaremko (1996). Photographs were taken in white and UV light without moving the otoliths using an AmScope™ Microscope Digital Camera (MU1803). Images were superimposed in Adobe Photoshop™ Version 24.1.0.

Growth analyses

The TL and W of the starting populations were compared among years using Mann Whitney tests and among temperatures using Kruskal Wallis tests in R (R Core Team 2023) since TL and W were not normally distributed (Shapiro–Wilk normality test, TL: $W = 0.970$, $p = 0.021$; W: $W = 0.916$, $p < 0.001$) and did not have equal variances (F-test, TL $F(39,61) = 3.619$, $p < 0.001$; W: $F(39,57) = 3.793$, $p < 0.001$).

Somatic growth rate for individual fish was estimated based on both TL and W. Length-based somatic growth rate was calculated as TL at sampling minus TL at tagging divided by the number of days alive. Weight-based somatic growth rate was calculated as W at sampling minus W at tagging divided by the number of days alive. Somatic growth rate based on length and weight were normally distributed with equal variances for most temperatures and years (Table S1). The 13 °C treatment in 2014 was unable to be tested for homogeneity of variances because it was represented by only one sampling event (Table 1). The 21 °C treatment in 2014 had unequal variances for weight-based somatic growth rate (Table S1).

Using superimposed images, right and left sagittal otoliths were measured for otolith radius and OTC radius. The otolith radius was measured from the otolith focus to the farthest posterior edge of the otolith and the OTC radius was measured from the otolith focus to the inner edge of the OTC mark towards the posterior edge of the otolith. Both radii were measured on the same axis (Fig. 1). Right and left otolith radius measurements were compared to each other to assess consistency of measurements. Otolith radius was compared to TL and W at sampling to confirm that there was a positive relationship between otolith size and body size.

Right and left otolith radius measurements were not different (see Results). Therefore, right otoliths were used ($n = 115$) unless not available, then left otolith measurements were substituted in ($n = 14$). Otolith growth rate was

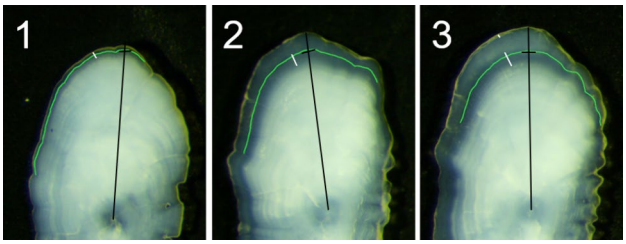

Fig. 1 Examples of otolith radius and oxytetracycline (OTC) radius measurements, and examples of '1', '2', and '3' bands past the OTC mark. Green line is the OTC mark and is in the translucent band in all three photographs. White lines indicate the width of the translucent bands. Black lines denote the otolith radius measurement from focus to posterior edge and the OTC radius is the black line from the focus to the black hatch at the inner edge of the OTC mark (green line). For '1' the OTC mark is in the ultimate band (a translucent). For '2' the OTC mark is in the penultimate band (a translucent) and there is growth of the opposite band (opaque) at the edge of the otolith. For '3' the OTC mark is in the antepenultimate band (a translucent) and there is a complete band (an opaque) and a partial band (a translucent) forming on the edge of the otolith

calculated as otolith radius minus OTC radius divided by the number of days alive. Otolith growth rate was normally distributed with equal variances for each temperature and year except 13 °C in 2014 which was unable to be tested because it was represented by only one sampling event (Table S1).

Growth rate comparisons

Based on the experimental design described above, and considering that all four temperature treatments could not be assigned at once in each year (i.e. only three tanks were available), somatic and otolith growth rates were compared using a split-plot with incomplete block design. In this setting we treated years as blocks ($n=2$), tanks as main plots ($n=3$), and sampling events within each tank (5, 8, and 12 months) as the sub-plots. Thus, we used a mixed-effect model to test whether there was significant difference among sampling events within each tank and then among temperature treatments for both somatic and otolith growth rates. Further, to account for the nature of the design (incomplete replication of temperatures across the 2 blocks) the mixed effect model used "Type III Mean Square Errors" to test for significant effects among temperature treatments, using the blocks and their interaction with sampling events as random effects. This assumption is consistent with the experimental design as fish reared in both years did not come from the same starting population. Note that covariances estimated for these random factors and the residuals were nearly 0 (5×10^{-8} to 1×10^{-2}) in all model runs. Hence, our primary focus was to test the significance of the following fixed factors: temperature, sampling event, and their interaction. In addition, as only the 13 °C and 17 °C treatments had adequate replication in both years, we planned to conduct only a single contrast to test for significant difference between their means in somatic or otolith growth rate. These analyses assumed that all data-groupings were normally distributed and had equal variances (see Table S1) and were conducted using the mixed procedure in the Statistical Analysis Software (SAS, version 9.4, see also Kuehl 1994).

Otolith growth band periodicity

Otolith growth bands (opaque and translucent) were identified during ageing and marked on the white light photo. The band (opaque or translucent) that contained the OTC mark was identified and termed '1'. Bands distal to the band that contained the OTC mark were also identified and counted. An otolith was a '1' when the OTC mark was present in the band on the edge of the otolith (Fig. 1). An otolith was a '2' when the OTC mark was in the penultimate band (Fig. 1). An otolith was a '3' when the OTC mark was in the antepenultimate band (third from last) (Fig. 1). The number of bands were compared over time (5, 8, and 12 months) by temperature and year.

Results

Experimental data

Across 2014 and 2015, otoliths extracted from 280 Pacific Sardine tagged with OTC had OTC marks that fluoresced. Across both years, 151 Pacific Sardine were excluded, because they had no sampling date, no biological data, the otoliths were partially or fully composed of vaterite, or the mortality was incidental. Pacific Sardine that experienced incidental mortality were excluded from growth analyses, because their growth may have been affected by stressors prior to mortality. The experiment in 2014 was terminated at 8 months. The final dataset included 129 samples from scheduled sampling events at 5 and 8 months in 2014 (temperatures: 13 °C, 17 °C, and 21 °C) and from 5, 8, and 12 months in 2015 (temperatures: 13 °C, 15 °C, and 17 °C; Table 1; Fig. 2). At collection most individuals were 0 years old ($n=125$), the remaining four were 1 year old.

Growth analyses

Total length ranged from 136 – 196 mm for the starting populations across both years. In, 2014, Pacific Sardine were shorter (169.6 mm ± 13.53, $n=40$) than in 2015 (175.9 mm ± 7.11, $n=62$; Mann Whitney U test, $U=864.5$, $N1=40$, $N2=62$, $p=0.010$; Figure S1). In both years, the starting TL was not significantly different across

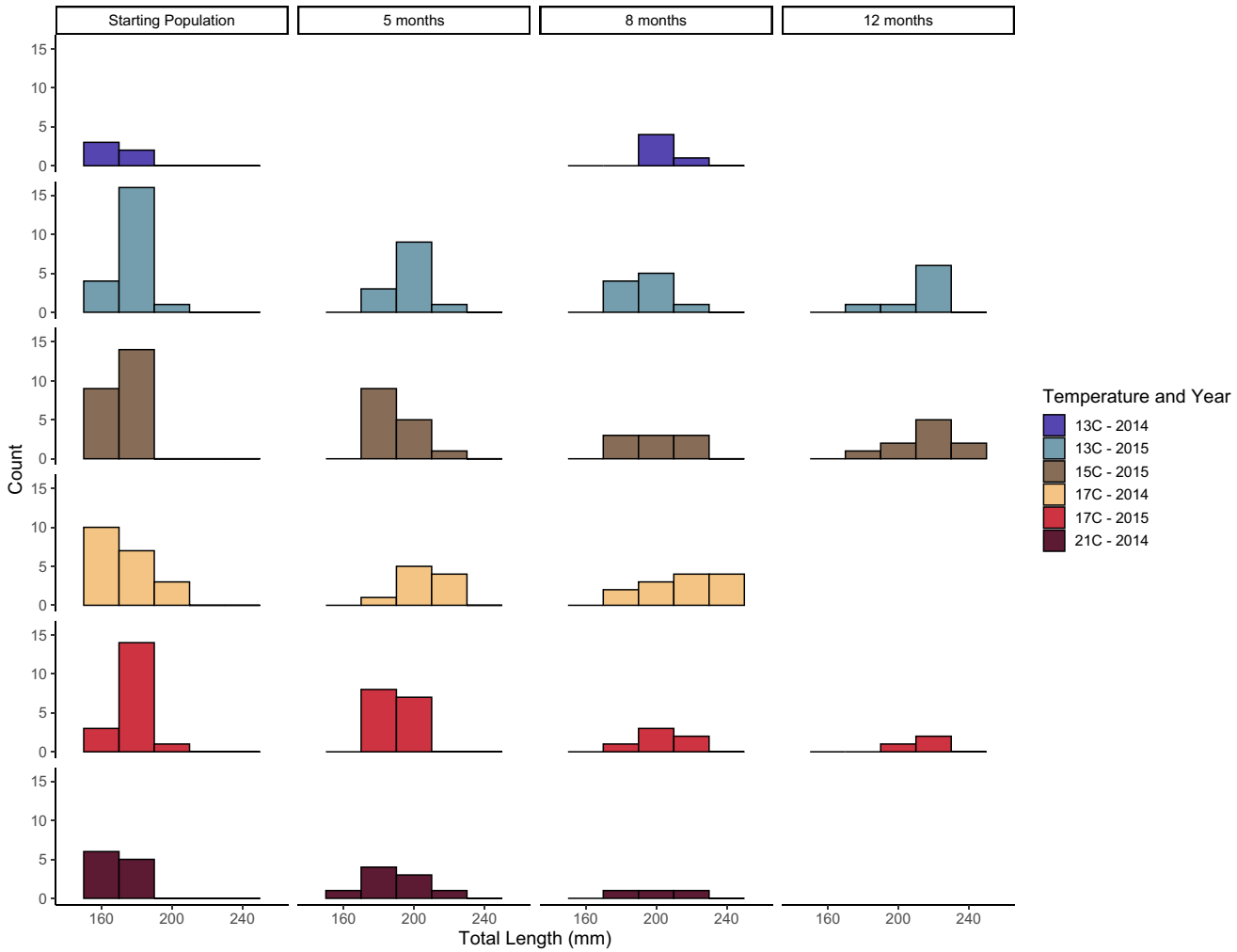

Fig. 2 Length frequency of Pacific Sardine at the start of the experiments and at each scheduled sampling event at approximately 5, 8, and 12 months across temperatures. Length bins are 20 mm

the three temperatures (Kruskal Wallis tests, 2014 TL: H2 = 0.015, $p = 0.992$; 2015 TL: H2 = 2.930, $p = 0.231$).

Weight ranged from 21.3 – 75.4 g for the starting populations across both years. The starting populations were not different in W between 2014 (43.71 g ± 14.18, $n = 40$) and 2015 (38.21 g ± 7.28, $n = 58$; Mann Whitney U test, U = 1359.0, N1 = 40, N2 = 58, $p = 0.151$). In both years, the starting W was not significantly different across the three temperatures (Kruskal Wallis tests, 2014 W: H2 = 1.210, $p = 0.547$; 2015 W: H2 = 5.947, $p = 0.051$).

Left and right otolith radii were similar to a 1:1 relationship ($\text{Radius}_{\text{Left}} = 0.951 * \text{Radius}_{\text{Right}} + 0.068$; slope S.E. = 0.029; Fig. S2) so either otolith could be used in analyses. The right otolith was used ($n = 115$), unless not available, then the left otolith was used ($n = 14$). Otolith radii had a positive relationship with both TL and W at sampling (Fig. S3).

Growth rate comparisons

Using the mixed effect model, we first tested the effects of three fixed factors, temperature, sampling event, and their interaction on somatic growth rate (Table 2A, B). For length-based somatic growth rate, there was no significant interaction between temperature and sampling event ($p = 0.644$), indicating the effect of temperature on growth rate in length did not change across sampling events. Additionally, there was no significant effect of sampling events on the length-based somatic growth rate ($p = 0.598$). There was a significant effect of temperature on length-based somatic growth rate ($p = 0.004$), but we found no significant difference between length-based somatic growth rate measured at 13 °C and 17 °C ($p = 0.819$; Fig. 3a). Similarly, for weight-based somatic growth rate, there was no interaction between temperature and sampling event ($p = 0.599$),

Table 2 Summary of the mixed-effect model comparing the fixed effect of sampling event, temperature, and their interaction on otolith and somatic growth rates of captive juvenile Pacific Sardine in 2014 and 2015. The contrast with sufficient replication was tested

Response variable	Effect	Type III Test of Fixed Effects			
		Numerator *df*	Denominator *df*	*F*	*P* > *F*
A) TL: Somatic growth rate ($n=102$)	Sampling_Event	2	1	0.90	0.598
	Temperature	3	89	4.78	**0.004**
	Temperature* Sampling_Event	5	89	0.67	0.644
	Contrast (13 °C vs. 17 °C)	1	89	0.05	0.819
B) W: Somatic growth rate ($n=98$)	Sampling_Event	2	1	0.74	0.636
	Temperature	3	85	3.12	**0.030**
	Temperature*Sampling_Event	5	85	0.74	0.599
	Contrast (13 °C vs. 17 °C)	1	85	0.23	0.634
C) Otolith growth rate ($n=129$)	Sampling_Event	2	1	0.25	0.818
	Temperature	3	116	5.75	**0.001**
	Temperature* Sampling_Event	5	116	0.54	0.742
	Contrast (13 °C vs. 17 °C)	1	116	11.38	**0.001**

and no significant effect of sampling events on this variable ($p=0.636$). There was a significant effect of temperature on weight-based somatic growth rate ($p=0.030$), but there was no significant difference between weight-based somatic growth rate at 13 °C and 17 °C ($p=0.634$; Fig. 3b).

The mixed effect model was also used to determine whether temperature, sampling event, and their interaction affected otolith growth rate (Table 2C). The interaction between temperature and sampling event was not significant ($p=0.742$), nor was sampling event ($p=0.818$). However, otolith growth rate among temperature treatments was significant ($p=0.001$), and the otolith growth rate measured at 13 °C and 17 °C was significantly different ($p=0.001$; Fig. 3c).

Otolith growth band periodicity

The number of bands distal to the OTC mark ranged from 1 to 3 (Fig. 1). The OTC mark was present in the opaque band in 50.4% of the samples ($n=65$) and was present in the translucent band for the remaining samples ($n=64$). The OTC mark was present in the opaque increment more frequently in 2015 (65.2%; $n=58$) than in 2014 (17.5%; $n=7$).

The proportion of individuals with 2 or 3 bands past the OTC mark increased as days in captivity increased (Fig. 4). In 2014, all but one individual at 5 and 8 months had 2 and 3 increments past the OTC mark. In 2015, the majority of individuals had 2 or 3 bands past the OTC mark by 8 months. Warmer temperatures had a higher proportion of 2 or 3 band at 5 and 8 months. The proportion of otoliths that had 2 or 3 increments at 8 months was higher in 2014 than 2015 regardless of temperature. Though not included in analyses, all fish that were held in captivity fewer than 122 days had '1' band meaning that the OTC mark was deposited in the band present at the edge of the otolith.

All of the individuals that were captive for 12 months ($n=21$; 2015 only) exhibited 2 or 3 bands past the OTC mark (Fig. 4). These individuals were age 0 at the beginning of the experiment and the OTC was present in the opaque band in 28.6% of the samples ($n=6$). For these individuals, the band pattern of translucent, opaque, translucent was the most common ($n=9$), followed by the pattern of translucent, opaque ($n=6$), opaque, translucent ($n=5$), and opaque, translucent, opaque ($n=1$; Fig. 5). The first band listed was the one with the OTC mark, and the other bands represent subsequent growth.

Discussion

Pacific Sardine held in captivity deposited bands in their otoliths at the rate expected across ecologically relevant temperatures (13–21 °C). Even though there were four band deposition patterns observed in otoliths after 12 months of captivity, each pattern supports the current ageing methods used in the US, Canada, and Mexico. This is a critical result, since ages generated by SWFSC, CDFW, WDFW, DFO, and CICIMAR have been directly incorporated into the Pacific Sardine stock

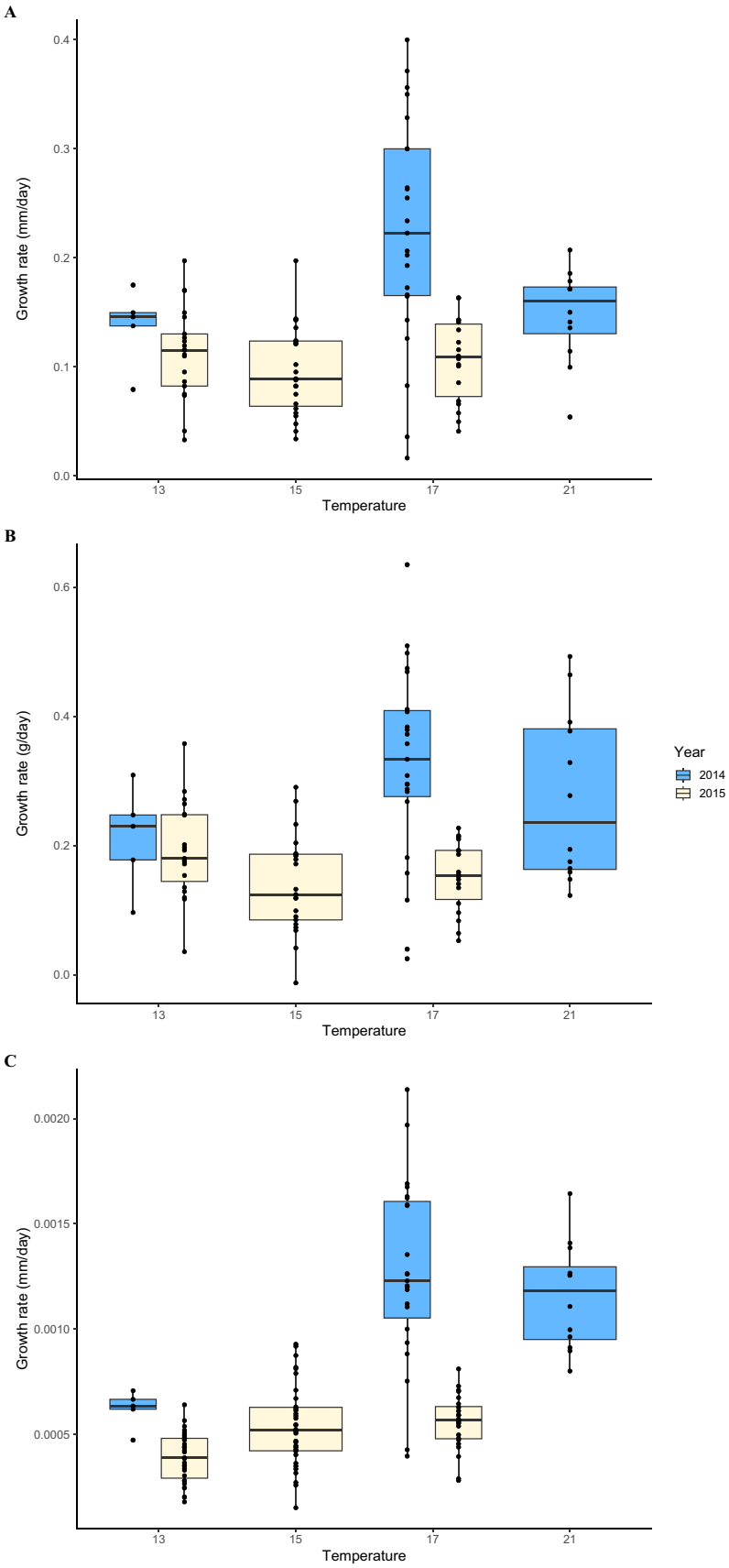

Fig. 3 Boxplot of somatic growth rate in (**a**) Total Length (TL; mm/day), (**b**) Weight (W; g/day), and (**c**) otolith growth rate (mm/day) by temperature (℃) and year pooled across sampling events. Horizontal line within each box is the median, the box represents the interquartile range, and the whiskers represent 1.5 times the interquartile range. Black points are each individual growth rate

assessment model that estimates age 1 + biomass upon which fisheries management parameters such as the overfishing limit are determined annually. Previous work done on growth in Pacific Sardine by Barnes and Foreman (1994) counted daily increments in juveniles to confirm annual periodicity of annuli. Marginal increment analysis has also been used to confirm annual periodicity of growth increment deposition for Pacific Sardine in the Northeastern Pacific (Walford and Mosher 1943; Barnes and Foreman 1994), off Chile (Aguayo et al. 1987), off South Africa (Thomas 1983; Kerstan 1997), and for closely related species (Tsikliras et al. 2005). The results generated by this study are the first chemical marking of captive Pacific Sardine that confirms the periodicity of band formation in otoliths.

This study explored Pacific Sardine growth across four ecologically relevant temperatures. Higher temperatures generally result in higher somatic and otolith growth rates (Neilson and Geen 1982; Campana and Neilson 1985; Mosegaard et al. 1988; Fey 2006). There was a temperature effect on somatic and otolith growth rates, however with the incomplete block design we were only able to conclude that otolith growth rate was different between 13 °C and 17 °C and somatic growth rate was not. No pattern in somatic growth rate may be expected within the core temperature range of the northern stock of Pacific Sardine (13–17 °C; Félix-Uraga et al. 2004; Ware 1999; Zwolinski et al. 2011), like the temperatures used here. Pribyl et al. (2016) showed that fish acclimated to the maximum temperature (i.e. 17 °C) in the core thermal range of the northern stock had a physiological ideal temperature range of 11–21 °C, therefore temperatures used here may not elicit different somatic growth. The otolith growth rate was lower for 13 °C than 17 °C, which is consistent with previous research (Mosegaard et al. 1988; Fey 2006; Neat et al. 2008). For all growth rates, there was high individual variability within each temperature. In general, growth differences within this temperature range may be too small to reliably detect and other factors (e.g., food availability, body condition, density-dependence) may have a stronger effect on somatic growth than otolith growth. Dorval et al. (2015) concluded that shifts in the size and age distribution of Pacific Sardine collected from 1994 to 2010 were a result of density-dependent growth and unrelated to temperature. Japanese Sardine (*Sardinops melanostictus*) in the western North Pacific exhibit density-dependent somatic growth that is influenced by temperature and prey density (Takahashi et al. 2008). Feltrim and Ernst (2010) suggested environmental factors (e.g. temperature), food quality, and food availability can influence somatic growth rate variability in Common Sardine (*Strangomera bentincki*) off Chile. An experiment with a wider temperature range may better elucidate somatic or otolith growth patterns with respect to temperature.

Water temperature was held constant for each treatment, which does reflect temperatures experienced in the wild over the course of a year, but the constant temperatures did not disrupt the annual cycle of deposition of opaque and translucent bands within the otoliths. Temperature is only one factor that contributes to the seasonal switching of opaque and translucent bands in otoliths. Other environmental factors that play a role include photoperiod and feeding frequency (Campana and Neilson 1985; Schramm 1989). Physiological processes (e.g., somatic growth and reproduction; Beckman and Wilson 1995; Johnson and Belk 2004; Neat et al. 2008) and an endogenous biological rhythm (Johnson and Belk 2004; Neat et al. 2008; Grønkjær 2016) also affect seasonal band deposition. The mechanisms that drive seasonal band deposition (opaque vs translucent) are still not well understood, but the periodicity has been repeatedly shown to be approximately annual for temperate marine fishes (Beckman and Wilson 1995; Wright et al. 2002; Begg et al. 2005; Hüssy et al. 2021a).

Pacific Sardine are expected to deposit translucent bands in the winter and opaque bands in the summer (Barnes and Foreman 1994; Yaremko 1996). This general pattern is shared across the otoliths of many species of temperate marine fishes, but there is substantial variability in the timing of band deposition across individuals, populations, and species (Beckman and Wilson 1995; Wright et al. 2002; Grønkjær 2016; Whitledge 2017). In this study, both opaque and translucent bands were present on the edge of Pacific Sardine otoliths at each scheduled sampling event, which included February, June, July, September, and October. Both band types were also present at the time of tagging (January and February) as evidenced by the location of the OTC mark. Variability in the pattern of seasonal band deposition can stem from a variety of sources including rapid temperature changes, development, and spawning date (Schramm 1989; Wright et al. 2002; Johnson and Belk 2004; Pilling et al. 2007; Hüssy et al. 2021b).

Rapidly changing temperatures have been shown to induce a change in band type on both daily (Campana and Neilson 1985) and seasonal (Schramm 1989; Pilling et al. 2007) scales. Neat et al. (2008) subjected Atlantic Cod (*Gadus morhua*) to high temperatures and the formation of a narrow translucent band was induced within an opaque band. The formation of a translucent band was thought to be a response to temperature stress (Neat et al. 2008). If these translucent bands are narrow and discrete, they are generally considered checks rather than bands and are not counted during ageing (Yaremko 1996). Pacific Sardine were collected at winter ambient temperatures (12–17.5 °C; Carter et al. 2022) and after acclimation allocated to temperatures of 13 °C, 15 °C, 17 °C or 21 °C. Approximately half of the Pacific Sardine were depositing translucent bands during OTC injection. The rest that were depositing opaque bands did not exhibit a narrow translucent increment within the opaque band. After the initial placement in tanks of different

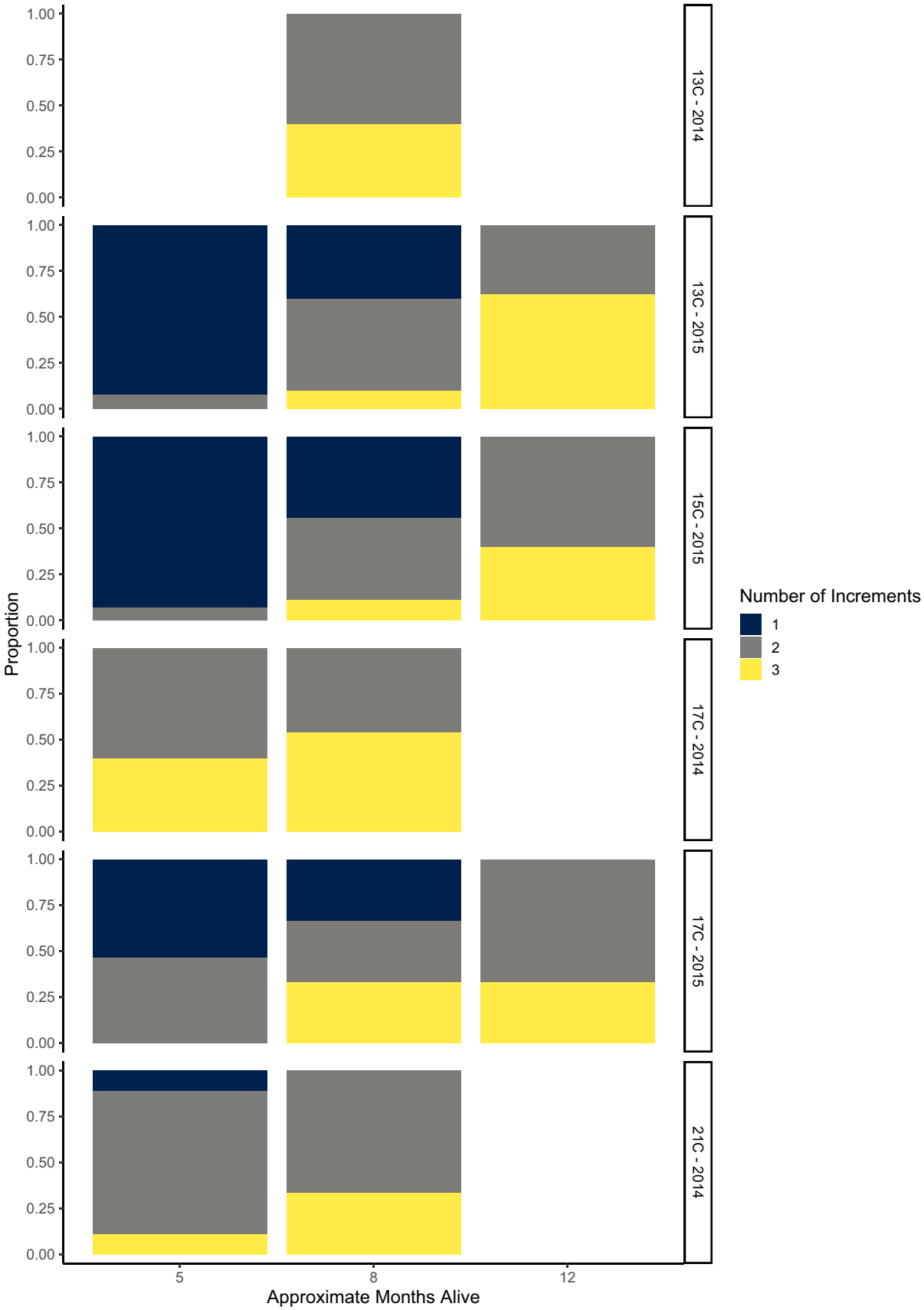

Fig. 4 Proportion of individuals exhibiting 1, 2, and 3 bands past the oxytetracycline mark at 5, 8, and 12 months by temperature and year

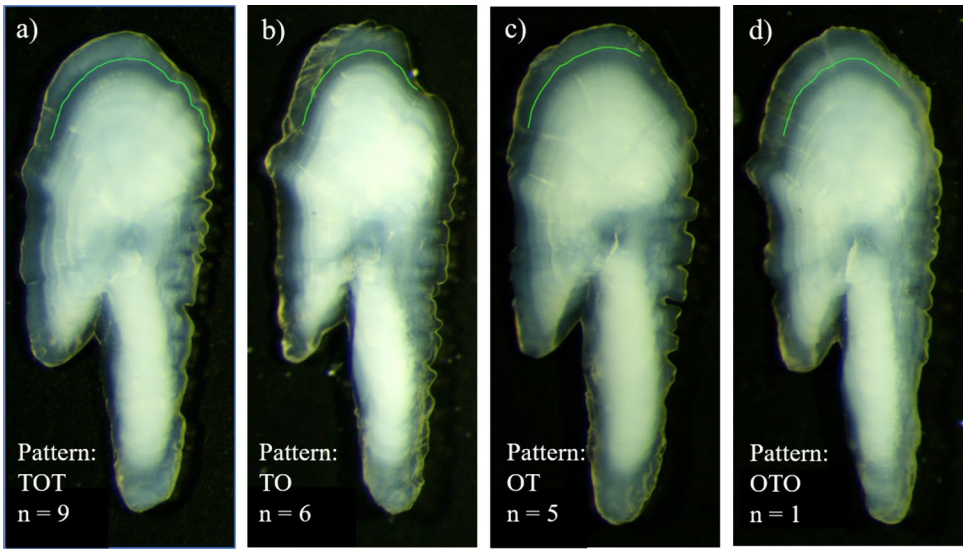

Fig. 5 Examples of otoliths in captivity for 12 months that represent all band type combinations. For each panel the oxytetracycline mark is in the first listed band type. (**a**) translucent, opaque, translucent (TOT), (**b**) translucent, opaque (TO), (**c**) opaque, translucent (OT), and (**d**) opaque, translucent, opaque (OTO)

temperatures, each tank stayed within 0.5 °C of the specified temperature for the remainder of the experiment. Therefore, rapidly changing temperatures do not explain the presence of both opaque and translucent bands throughout the experiment.

Development may affect the timing of formation of opaque and translucent bands (Wright et al. 2002). Yaremko (1996) noted that Pacific Sardine in the first two years tend to deposit opaque bands earlier in the year than older individuals. For South African Sardine, Kerstan (1997) found the completion of annuli to vary up to 6 weeks among year classes within age one and older ages had completed annuli later in the year. The same phenomenon has been documented in the Northern Anchovy (Schwartzkopf et al. 2022), which co-occurs with Pacific Sardine and in the European Anchovy (*Engraulis encrasicolus*; Uriarte et al. 2016). The earlier formation of opaque bands in young individuals means that the large percentage of individuals that were depositing opaque bands when tagged in February 2015 was not unusual.

Spawning date may affect the timing of formation of opaque and translucent bands (Barnes and Foreman 1994). Barnes and Foreman (1994) documented that Pacific Sardine hatched at the end of September through November did not deposit a translucent band that winter; hypothetically a two-year-old Pacific Sardine could only have one annulus. Besides this extreme example, there are examples of fishes from different areas depositing bands at different times related to their spawning peaks. European Anchovy from the Bay of Biscay completed the translucent band in April (Aldanondo et al. 2016), while European Anchovy from the Strait of Sicily completed the translucent band from May through July (Basilone et al. 2020). Spawning peaks are different for European Anchovy in each location and completion of the translucent band occurred approximately one month before the spawning peak in each location (Basilone et al. 2020). While peak spawning for Pacific Sardine off California occurs in the Spring (Ahlstrom 1965), seasonal peaks in spawning in this region vary considerably at annual to decadal scales (Ahlstrom 1959; Moser et al. 1993), and Pacific Sardine along the Pacific coast can spawn throughout the year (Blaxter and Hunter 1982; Watson 1992). Therefore, individual variation in the timing of deposition of opaque and translucent bands in Pacific Sardine is expected, particularly if an individual is hatched outside of the peak spawning season. For example, Pacific Sardine that hatch at the beginning of the spawning season may deposit the translucent band earlier in the season, and subsequently, the next opaque band is deposited earlier as well.

There is a limit to how closely captive growth can resemble wild growth. Yet, the appeal of captive experiments lies in their ability to control for environmental variables. This study used ecologically relevant temperatures but held the temperatures constant to investigate the effect of temperature on somatic and otolith growth without the influence of a seasonal effect. The photoperiod was held constant, and feeding was a constant percent of body weight in each tank. Since this study was not designed to accurately reflect growth in the wild, somatic and otolith growth rates in this captive experiment may differ from wild growth rates. Instead the somatic and otolith growth rates presented here represent possible ranges of growth rate over several ecologically relevant temperatures. The timing of deposition of opaque and translucent bands is not expected to differ from the timing of wild Pacific Sardine, because the timing is affected by environmental factors (Campana and Neilson 1985; Schramm 1989), physiological processes (Beckman and Wilson 1995; Johnson and Belk 2004; Neat et al. 2008), and the endogenous biological rhythm (Johnson and Belk 2004; Neat et al. 2008;

Grønkjær 2016). Therefore, we are confident that the pattern of band deposition seen here applies to wild Pacific Sardine as well.

Counting annuli present on fish otoliths to estimate fish age comes with many assumptions. This study addresses the assumption that annuli are deposited annually. However, there are other assumptions about fish somatic and otolith growth that are made beyond the periodicity of band deposition, and these should be addressed whenever possible. The first assumption is that otolith size increases with fish size. It is straightforward to demonstrate a positive relationship exists between otolith growth and fish growth, but the shape of the relationship varies by species, ontogeny, and other factors (Brothers 1995; Casselman 1995; Ashworth et al. 2017; Buckmeier et al. 2017). For Pacific Sardine in this study, otolith growth had a positive relationship with both TL and W. We were not interested in defining the relationship between otolith growth and somatic growth, but a positive relationship does confirm the assumption that the otoliths grow as the body grows and therefore otoliths are an appropriate ageing structure. Another assumption is that there is no difference between left and right otoliths in both growth and deposition of bands. We had the opportunity to measure both otoliths a majority of the time and found a linear relationship with a slope close to 1. Otoliths composed of mostly vaterite (i.e. as opposed to composed of aragonite), where opaque and translucent bands cannot be distinguished, are an exception in that their appearance is different. Vateritic otoliths were excluded from analyses, but the shape of the otoliths was generally not different between otolith pairs where one was composed of vaterite and the other composed of aragonite. In a vateritic otolith, the OTC mark was clearly visible, measurable, and in approximately the same place as the aragonitic otolith in the pair. Thoroughly addressing background assumptions is an important and sometimes overlooked step.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00227-024-04425-2.

Acknowledgements We thank Patrick Appel for overseeing the collection of live Pacific Sardine and maintaining their culture at the SWFSC Aquarium. We also thank Julianne Taylor, Helena Aryafar, and Jenny McDaniel for their assistance with fish collection and sample processing. We thank Brittany Schwartzkopf for constructive conversations on revisions. We thank the reviewers for their contributions. This study was supported by the National Oceanic and Atmospheric Administration Internal Research Program: Habitat Information Use in Stock Assessment.

Author contributions Emmanis Dorval led the study conception, design, and execution. Data collection was performed by Emmanis Dorval and Kelsey C. James. Data analyses were performed by Kelsey C. James and Emmanis Dorval. All authors contributed to the scope of this manuscript. The first draft of the manuscript was written by Kelsey C. James and all authors reviewed and edited previous versions of the manuscript. All authors read and approved the final manuscript.

Funding This research was funded by the National Oceanic and Atmospheric Administration Internal Research Program: Habitat Information Use in Stock Assessment (Internal Proposal FY2014).

Data availability The datasets generated and analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Conflict of interest The authors have no relevant financial or non-financial interests to disclose.

Ethical approval This study was conducted at the SWFSC Aquarium under Fish and Invertebrate Protocol #SW1301 in compliance with state and national guidelines for sampling, care, and experimental use of fish. This protocol is available upon request.

This study was supported by the National Oceanic and Atmospheric Administration Internal Research Program: Habitat Information Use in Stock Assessment. The authors declare no conflict of interest. This study was conducted at the SWFSC Aquarium under Fish and Invertebrate Protocol #SW1301 in compliance with state and national guidelines for sampling, care, and experimental use of fish.

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