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SYSTEMATIC REVIEW OF SOMATIC GROWTH PATTERNS IN RELATION TO POPULATION STRUCTURE FOR PACIFIC SARDINE (*Sardinops sagax*) ALONG THE PACIFIC COAST OF NORTH AMERICA

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Systematic review of somatic growth patterns in relation to population structure for Pacific Sardine (*Sardinops sagax*) along the Pacific Coast of North America

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Abstract

Management of the Pacific Sardine (*Sardinops sagax*) in the U.S. recognizes two biological subpopulations along the Pacific coast of North America based on the hypothesis formalized by Marr (1960), with presumed heritable differences in somatic growth patterns used as supporting evidence. Consistent with this hypothesis, length-at-age data and growth information are used as corroborative evidence for a habitat model that apportions Pacific Sardine sampled from scientific surveys and commercial catches to each subpopulation for use in annual stock assessments. We completed a systematic review of published scientific studies that examined somatic growth in Pacific Sardine along the Pacific coast, with an emphasis on those focused on population structure. We summarized the methods, results, and conclusions of each study and the prevailing hypothesis linking growth to population structure. We then evaluated the evidence in support of heritable growth patterns versus alternative explanations based on the quality of each study in light of best practices. Our review revealed that few studies have examined growth in Pacific Sardine in the study region and even fewer were properly designed to examine spatiotemporal patterns in growth; thus, knowledge on the topic is limited. Among those studies, only 8 investigated growth in Sardine in relation to population structure, and none presented valid evidence of regional differences in growth patterns to support the hypothesized existence of two subpopulations. Historical studies provided almost no statistical support for their reported differences in length-at-age or growth, and individual and annual variations in length-at-age within regions overlapped with and were larger than variations among regions. We also identified persistent sampling, analytical, and other methodological problems among studies that diminished the quality of the data and results and led to unsupported conclusions. The most parsimonious explanation, which is grounded in theoretical and empirical support and acknowledged by most historical and modern studies, is that somatic growth in Pacific Sardine is phenotypically plastic at the level of individual fish and varies spatially and temporally in response to environmental conditions and other factors. Reported regional patterns in length-at-age reflect a combination of the migratory behavior of Pacific Sardine, ontogenetic shifts in habitat, variable birth dates associated with protracted spawning seasons and regional variations in spawning, and biased length and age data from commercial catches and fishery-independent surveys. Therefore, length-at-age data and growth information should not be used to help delineate subpopulations or apportion biomass or catch for use in stock assessments of Pacific Sardine.

Introduction

Life history traits such as length-at-age and growth rate are among the most common data available to characterize populations of marine fishes, but their use as evidence of population structure has its limitations (Ihssen et al. 1981; Begg 2005; Swain et al. 2005). Regional differences in growth patterns may represent genetically heritable traits of populations that persist and have evolved in distinct environments (Begg and Waldman 1999; Wright and Trippel 2009; Lorenzen 2016). However, they may also reflect phenotypic plasticity, which is the expression of different phenotypes by a single genotype that allows individuals to tolerate a wide range of environmental conditions (Beverton and Holt 1957; Lorenzen 2016). Phenotypic plasticity is a fundamental property of fish growth, in which growth at the individual level is influenced by a range of abiotic and biotic factors that vary both spatially and temporally as the individual develops, matures, and shifts its habitat (Brander 1995; Sinclair et al. 2002). Phenotypic plasticity in growth commonly occurs in response to variable environmental conditions (e.g., temperature), ontogenetic or seasonal shifts in habitat, conspecific abundance (density dependence), prey availability (food supply), regional differences in the duration of seasonal growth periods, and other factors that are not indicative of underlying genetically-based variation and thus uninformative of population structure (Conover 1990; Begg et al. 1999; Higgins et al. 2015).

It is important to study phenotypic responses to environmental conditions (a.k.a. reaction norms) as a means to disentangle the degree to which growth is influenced by phenotypic plasticity versus evolutionary change at the population level (Enberg et al. 2012). Obtaining representative samples of a fish population to accurately estimate growth patterns and identify their drivers is challenging, since all sampling methods contain some level of size-selectivity, and length-at-age data are highly susceptible to sampling and analytical bias that can produce misleading results (Swain et al. 2005; Brophy 2014; McBride 2014; Bolser et al. 2018). Also, while growth and body size are correlated, many processes other than growth (e.g., maturation; timing of birth within a protracted spawning season) can influence observed temporal or spatial variations in length-at-age (Enberg et al. 2012). Therefore, growth data alone are insufficient for characterizing population structure and are best suited as supporting evidence once genetic differences are established (Begg et al. 1999; Gonzalez and Zardoya 2007; McBride 2014) and the association between growth, length-at-age, biotic and abiotic drivers, and other life history traits are examined (Enberg et al. 2012; Lorenzen 2016).

Applying growth information to methods used to delineate and assess fish stocks (i.e., management units) for management purposes is even more challenging. Growth is an important process in fish population dynamics that impacts biomass production, natural and fishing mortality, fecundity and reproductive output (Beverton and Holt 1957; Hilborn and Walters 1992). Hence, growth information is integral to most age and size-based fisheries assessment methods, the most obvious of which is to convert numbers-at-age to stock and catch biomass (Francis 2016; Lorenzen 2016). However, stock assessments typically provide scientific advice for management on time scales that are shorter (e.g., annual) than even the highest rates of environmentally or fisheries-induced evolution in growth (Enberg et al. 2012; Lorenzen 2016). Consequently, while empirical growth models (e.g., age-length keys) estimated on an annual basis for assessments have the potential to implicitly track growth changes to improve the accuracy of biomass estimates (Kuriyama et al. 2016), they may also reduce accuracy if based upon an insufficient sample size or a biased sample distribution (Bolser et al. 2018). Moreover, to use growth or other life history traits to discriminate subpopulations of fishes, the signal from among-group variation must exceed the noise of within-group variation (Waldman 1999).

The Pacific Sardine (*Sardinops sagax*; hereafter Sardine) is a coastal pelagic fish species that is distributed in the northeast Pacific Ocean from southeastern Alaska, U.S., to the southern Gulf of California, Mexico (Robertson and Allen 2024). Along the Pacific coast, it is common from British Columbia, Canada, and the Pacific Northwest (Washington and Oregon) to Southern Baja California, Mexico (Figure 1). In the U.S., the Sardine supports the California Current Large Marine Ecosystem (CCLME) as an important prey species for fishes, marine mammals, and seabirds (Kaplan et al. 2019; Thompson et al. 2019). Like other clupeoid fishes, Sardine naturally undergo large fluctuations in spatial distribution and abundance over annual to multidecadal time scales (Parrish et al. 1989; MacCall 1990; Baumgartner et al. 1992; Schwartzlose et al. 1999; McClatchie et al. 2017) in relation to food availability, productivity, environmental conditions, climate, and other factors (Lluch-Belda et al. 2003; Lindegren et al. 2013; Koenigstein et al. 2022). In response to this variability and similar to other small pelagic fishes classified as opportunistic strategists (King and McFarlane 2003), Sardine are characterized by rapid somatic growth with large variations in length-at-age and growth patterns reported at individual to population, seasonal to annual, and local to regional scales (Felin 1954; Marr 1960; Dorval et al. 2015).

Sardine have supported important commercial fisheries in the U.S., Mexico, and Canada for nearly a century (Radovich 1982; Wolf 1992; Cisneros-Mata et al. 1995). Sardine are managed in the U.S. under the Coastal Pelagic Species Fishery Management Plan of the Pacific Fishery Management Council (CPS FMP of the PFMC). Under this plan, two subpopulations of Sardine (northern and southern) along the Pacific coast (excluding a hypothesized third subpopulation within the Gulf of California) of Baja California, Mexico, the U.S., and Canada are recognized (PFMC 1998, Amendment 8, Appendix A, A-9). The northern subpopulation is hypothesized to range from Alaska to Northern Baja California, Mexico, whereas the southern subpopulation ranges from Southern California to the southern tip of the Baja California peninsula (Figure 2). Thus, both subpopulations are thought to inhabit U.S. waters in Southern California (Parrish et al. 1989; Félix-Uraga et al. 2004; Demer et al. 2014) but at different times of the year. However, only the northern subpopulation is managed by the U.S. (PFMC 1998, 2024).

A subpopulation, as defined specifically for Sardine by Marr (1957a,b), is a fraction of a population that is itself genetically self-sustaining with heritable differences. In contrast, he defined a stock as a portion of a population characterized by similarities that are not heritable but rather induced by the environment (Marr 1957a). Operationally, the definition of a subpopulation as it pertains to Sardine (discussed by Parrish et al. 1989) is equivalent to the modern, standard definition of a biological population (Pope et al. 2010; Kerr et al. 2017; Cadrin et al. 2023). It is important to clarify the origin and exact definitions of the terms subpopulation and stock as applied to Sardine population structure and management, which consistently emphasized genetics and heritable versus non-heritable traits (Felin 1954; Marr 1957a,b; Marr 1960; Murphy 1966), because this clear and important distinction that drove Sardine research for decades has been lost or obscured in recent studies (e.g., Smith 2005; Zwolinski and Demer 2023) that have cited these same historical references in support of evidence of subpopulations.

Figure 1. A map of North America showing the countries, regions, cities, and other landmarks mentioned in this review. BC = British Columbia; BCA = Baja California; CM = Cape Mendocino; CCA = Central California; CF = Cape Flattery; EN = Ensenada; MGB = Magdalena Bay; MTB = Monterey Bay; NCA = Northern California; OR = Oregon; PA = Punta Abreojos; PC = Point Conception; PE = Punta Eugenia; PNW = U.S. Pacific Northwest; SBCA = Southern Baja California; SCA = Southern California; SD = San Diego; SF = San Francisco; SP = San Pedro; SVB = Sebastián Vizcaíno Bay; WA = Washington.

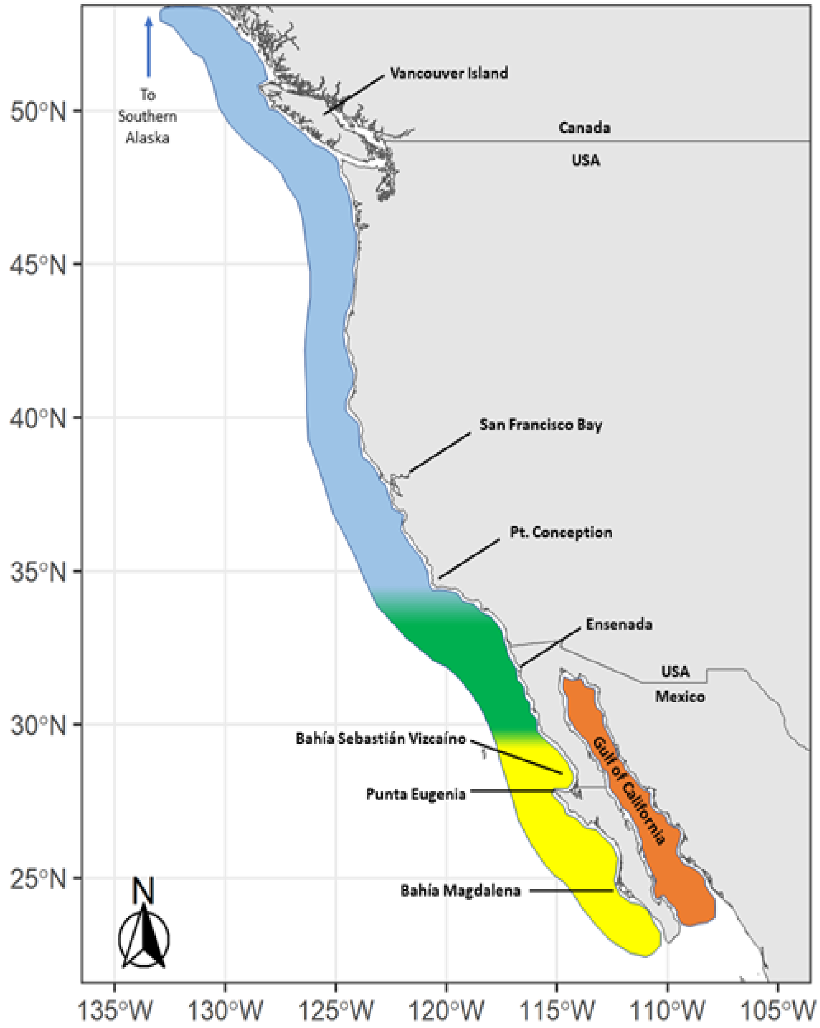

Figure 2. Generalized distributions of the hypothesized Northern Subpopulation (blue), Southern Subpopulation (yellow), and Gulf of California subpopulation (orange) of Pacific sardine (*Sardinops sagax*). Although the two subpopulations are not thought to fully occupy the same region at the same time, their range of overlap is shown in green.

The hypothesis of subpopulation divisions in Sardine was formally proposed in a comprehensive review of the fishery by Marr (1960), who considered the preliminary results of serological antigen responses (Sprague and Vrooman 1962), a primitive method thought at the time to represent genetic differences, purported as "unambiguous evidence" (Murphy 1966) of genetically distinct spawning groups of Sardine in the U.S. and Mexico. This hypothesis was restated in Vrooman (1964) following the completion of the serological antigen studies. Separation of these subpopulations (i.e., barriers to gene flow) was thought to be maintained by spatial separation of spawning areas and synchronous but non-overlapping seasonal migrations of adults along the coast, two phenomena that are often mentioned (e.g., Marr 1960; PFMC 1998; Smith 2005; Demer and Zwolinski 2014) but have never been adequately tested or validated and lack empirical support (Erisman et al. 2024; Craig et al. 2025). Moreover, later studies that employed a range of genetic approaches (e.g., Hedgecock et al. 1989; García-Rodriguez et al. 2011; Adams and Craig 2024) produced no evidence of population structure, including recent work using low coverage whole genome sequencing (Craig and Longo 2024; G. Longo and M. Craig, unpublished data).

Growth and other traits were used as supporting evidence of genetically distinct subpopulations of Sardine along the Pacific coast in several studies. Felin (1954) investigated growth characteristics and other traits in Sardine sampled from commercial fishing ports from California to British Columbia and reported regional differences in growth patterns, which she concluded was evidence of more than one population along the Pacific coast. Marr (1960) combined the data from Felin (1954) with additional data collected in subsequent years to reach a similar conclusion. Despite the fact that a formal evaluation of studies reporting differences in growth patterns in support of separate subpopulations was never completed, and the author considered that her observed patterns may reflect phenotypic plasticity in response to varying hydrographic conditions, Felin (1954) is commonly cited in more recent literature as having shown evidence of two subpopulations (e.g., "...two radically different growth patterns were detected"; Smith 2005).

While the CPS FMP acknowledges uncertainty in the subpopulation hypothesis for Sardine (PFMC 1998), in practice, it represents the archetype for management (Yau 2023). That is, the annual fishery-independent survey used to estimate the biomass and distribution of Sardine, which then informs the annual stock assessment that guides the management for the upcoming fishing year, are designed based on assumed differences in seasonal distributions, spawning patterns, growth patterns, and other traits in accordance with the subpopulation hypothesis (Renfree et al. 2022; Yau 2023; Kuriyama et al. 2024). Since 2014, the process has involved separating out only biomass and landings attributed to the northern subpopulation from U.S. biomass estimates for stock assessments using a habitat model (Hill et al. 2014; Zwolinski and Demer 2014; Kuriyama et al. 2024). More recently, reported differences in length-at-age among Sardine sampled from fishery-independent surveys in 2021 were used to corroborate the development of an updated habitat model and its use to classify and estimate the biomass of the northern subpopulation (Zwolinski and Demer 2023). Following a review by Council bodies, this recent approach was then used as part of the methods to generate age and length compositions from fishery-dependent and fishery-independent surveys and to apportion biomass and catches in the 2024 benchmark stock assessment for Sardine (Kuriyama et al. 2024).

Due to the importance of length-at-age data and growth information to surveys and stock assessments that guide the management of Sardine in the U.S., we completed a systematic review of the existing scientific literature that investigated patterns of somatic growth in Sardine in relation to population structure. Our specific aims were to comprehensively summarize the findings of each study, critically evaluate the quality of the data, methods, and findings presented, and assess the degree to which their results supported the hypothesis of multiple subpopulations with heritable differences in growth patterns. Based on our evaluation, we generated a conclusion on whether the use of length-at-age and growth data by the habitat model to delineate subpopulations and apportion biomass and catches for stock assessments is a valid approach.

Methods

A systematic review is one that collects all possible studies related to a given topic and design, and reviews and analyzes their results to assess the quality of the results and conclusions generated by individual studies (Moher et al. 2009; Crowther et al. 2010). Its purpose is to minimize the bias that results from cherry-picking studies in a non-systematic way. Following this approach, we conducted a comprehensive literature search to identify published scientific research that examined aspects of somatic growth in Sardine from the Pacific coast of North America. Our initial search involved the NOAA Central Library (NCL), the Web of Science Core Collection (WOS), and Google Scholar. For NCL, we used the search terms "Pacific Sardine growth - including *Sardinops sagax*" and "Pacific Sardine age - including *Sardinops sagax*". To ensure that survey and stock assessment reports were considered, we used the search term "Pacific Sardine" in the Institutional Repository within NCL and then reviewed citations and studies produced using the subject filters "Fish Stock Assessment", "Fish Surveys", and "*Sardinops sagax*" both separately and in various combinations. For WOS and Google Scholar, we used the terms "Pacific Sardine AND growth" and "Pacific Sardine AND age", both with the keyword "*Sardinops sagax*" added as one that must be included. For Google Scholar, we limited our review to the first 500 hits. All literature searches were completed by and updated on 1 June 2024.

Each study (i.e., a peer-reviewed manuscript or published technical report) was initially screened for relevance to our review. Following best practices (Côte et al. 2013), the following criteria were used to eliminate studies from the final list included in the systematic review: (1) studies not focused on *Sardinops sagax*; (2) studies focused on *Sardinops sagax* outside the northeast Pacific Ocean; (3) studies focused on the Gulf of California, Mexico; (4) studies not directly related to somatic or individual growth; (5) studies focused on embryological, larval, or juvenile growth (e.g., Butler 1987); and (6) modeling studies that generated results on somatic growth based on empirical data generated from other studies (e.g., Butler et al. 1993). The main text and literature cited sections of each study that remained was then reviewed to identify additional publications and reports relevant to the review. The final list of references included numerous annual reports that summarized age and length data of Sardine sampled from the commercial fishery (e.g., Wolf 1961). We did not scrutinize every one of those reports but do provide a general summary and several representative references in the Results.

This review was organized into four parts. Parts I and II contained detailed summaries of the papers reviewed. Part I summarized what we consider "historical" studies, or those published prior to and including Marr's (1960) synthesis. Part II summarized "modern" studies published after the U.S. fishery reemerged in the 1980s. For each study examined, we summarized the methods, results, and main conclusions while articulating details of the sampling design, data analyses and statistical methods employed, and data quality. In Part III, we evaluated the quality of the methods and results of each study, highlighted important considerations when examining compiled data, and discussed conceptual discordance between the subpopulation hypothesis and population theory. This included examining the results of these studies en toto and evaluating the quality and consistency of the data used to support the subpopulation hypothesis. We also assessed various sources of sampling bias and methodological issues present among the various studies and their effects on the quality of the results and the certainty of the conclusions. In some cases, this required the compilation and reanalysis of original data from more than one source, and this is noted and described where relevant. Lastly, we synthesized results from studies that were consistent with phenotypic plasticity and the life history, biology, and behavior of Sardine. We compared such results to the strength of the evidence supporting the hypothesis of regional differences in growth patterns as representations of subpopulations. These comparisons were used to draw a final conclusion on the use of length-at-age data and growth information by the habitat model (Zwolinski and Demer 2023) to delineate subpopulations and apportion biomass and catches for stock assessments. We summarized the main results and conclusions of our review in Part IV.

Results and Discussion

Part I: Historical investigations on somatic growth patterns in Sardine along the Pacific coast

The earliest studies on growth in Sardine (e.g., Scofield 1926; Thompson 1926; Clark 1931, 1936, 1939) were based on following the dominant length group (class/bin) through a fishery in successive years to estimate growth rates and indirectly assign age. Walford and Mosher (1943a,b) provided a more direct method to age Sardine when they demonstrated that rings in scales formed annually and thus could be used for age determination. Working under the assumption that fish growth and scale growth are directly proportional, Walford and Mosher also showed that fish length could be "back-calculated" to earlier ages by measuring body length and scale length at the time of capture and the length of the scale from its center to a particular ring (i.e., scale increment width). This approach was formalized in Walford (1946) as the 'direct proportion method', refined by Landa (1953), and used in subsequent studies that investigated growth patterns in relation to population structure in Sardine based on age determination from scales (e.g., Felin 1954; Marr 1960).

In 1948, a pair of papers were published together that provided detailed information on growth in Sardine from commercial landings off the Pacific coast of the United States and Canada during the 1940s. Felin and Phillips (1948) presented a detailed method of age determination for Sardine using scales. Phillips (1948) applied those methods to examine annual and regional variations in Sardine growth patterns among fishing ports in the Pacific Northwest (British Columbia, Washington, and Oregon), Central California (San Francisco, Monterey) and Southern California (San Pedro) based on calculated average length-at-age from a total of 46,045 aged fish. Phillips (1948) found that the average length of age-2 fish caught in Southern California was larger than for those caught in Central California and in the Pacific Northwest. Conversely, at age 4 and older, a clinal pattern was observed in which the mean length-at-age was progressively larger from Southern California to Central California to the Pacific Northwest (Figure 1 in Phillips 1948). Phillips (1948) also reported seasonal, annual, and sex-related differences in mean length-at-age within and among regions. As was the norm at the time, no formal statistical tests were performed to assess potential differences in length-at-age, growth patterns among regions, or to assess the influence of individual or annual variations in length-at-age as a means to justify the use of pooled age data. Rather, the conclusions were qualitative, based on perceived visual differences among regional growth curves, using only mean values (across all individuals and years) of length-at-age across all age classes from each region.

Based on those results, Phillips (1948) concluded there to be variations in growth patterns among fish sampled in the three regions. However, he emphasized that *"*when the effects of migrations are considered it is apparent that there are a number of complexities involved in attempting to calculate a growth curve that represents the populations of Sardines as a whole*"*. Specifically, he presented several possible explanations grounded in existing information on the biology of Pacific Sardine at the time. He noted previous work by Godsil (1931) showing that older adult fish off San Diego, California, occurred more offshore, whereas smaller immature and young adult fish were more common inshore. The commercial fishery actively avoided harvesting these smaller, inshore Sardine (Godsil 1931). Conversely, in the Pacific Northwest, age-2 fish were quite rare in general, because spawning and local recruitment was very infrequent in this region, and tagging studies (e.g., Clark and Janssen 1945) indicated that measurable proportions of adults had migrated there from the south. In combination, these factors explained differences in the relative number of larger age-2 fish in samples from the Southern California fishery versus those sampled from fishing ports in the Pacific Northwest (Figure 4 in Phillips 1948). Phillips (1948) also cited regional differences in the seasonal timing of spawning based on work by Tibby (1937) as another simple explanation for larger size-at-age of young fish from the Southern California fishery compared to northern regions. Essentially, fish born earlier in the year would be afforded a longer period of growth during their first year of life (i.e., before their first annulus was deposited). He then speculated that older aged fish captured off the Pacific Northwest could "overcome the handicap of a reduced growing period in the first year by the apparent more favorable conditions for growth in the more northerly latitudes" (Phillips 1948).

Phillips (1948) postulated that the "flatter growth pattern" of fish from Southern California after age 3 to 4 may result from the presence of "residual, slow-growing fish that failed to undertake a northward migration, or at most a limited one, perhaps accompanied by slower-growing fish that had shifted from Lower [i.e., Baja] California." This last observation is consistent with the concept of partial migration, a ubiquitous feature in marine fishes and other animals, defined as the simultaneous occurrence of resident and migratory members within the same population (Secor 2015). To support this assertion, Phillips (1948) cited the results of tagging studies (Clark and Janssen 1945) that showed that larger fish at age migrated much further distances than their smaller conspecifics. He also noted that due to their ephemeral (seasonal) presence in Southern California and their lower proportional abundance relative to younger fish (see also Hart 1943), only a small proportion of the larger, older adults that returned in spring to Southern California would be expected to be harvested by the fishery.

In summary, Phillips (1948) collectively considered the combined effects of mixing among fish born in different regions, partial migration based on condition (i.e., combination of size and age), and differences in the timing of birth on the length of fish when the first annulus was deposited. His results (summary tables in Phillips 1948) also demonstrated variations in individual growth within regions both within and among years, among seasons, and between sexes (both within and among seasons, years, and regions). Consequently, Phillips (1948) applied Walford's method to generate the first single growth curve for the entire population of Sardine from Southern California to British Columbia that considered the combined effects of individual variation, spatiotemporal variation, ontogeny, and migratory behavior (Figure 5 in Phillips 1948). He also observed an "apparent increased growth" in more recent year classes, which was more evident in the Pacific Northwest and Central California than in Southern

California, which he speculated to be a consequence of a “reduced stock living under more optimum conditions” (i.e., density-dependence).

The most commonly cited study on spatiotemporal patterns in growth in Sardine was completed by Felin (1954), who investigated whether the fished stocks from Southern California to Canada represented a single (homogeneous) population or a complex of different populations. To do so, she used evidence generated from analyses of length data, age data as recorded on scales, and other “vital statistics” from catches at five main fishing regions along the Pacific coast (British Columbia, Pacific Northwest, San Francisco, Monterey, San Pedro) from 9 fishing seasons (1941-42 through 1949-50). For each region, she calculated the mean observed lengths for each age class of all year classes sampled in the commercial catch for each of the seasons (his Table 1). From these values, Felin (1954) then calculated an unweighted mean length (i.e., mean of means) for each age class in each region across all years, which were then plotted to represent a generalized growth curve for each region. Using the direct-proportion approach (Walford 1946), she transformed the data and plotted the mean of mean lengths at age across all age classes and years in the five regions versus their predicted length-at-age in the successive year.

Felin (1954) provided a transparent explanation of the limitations of the direct-proportion method in the beginning of her report. She reminded her readers that several factors rendered the calculated growth during the first year (i.e., estimated distance from otolith core to its first annulus) as “only an approximation” (her p. 202). In congruence with Phillips (1948), she explained that spawning shifted northward as the spawning season progressed and also that the spawning season was protracted at any given location. These characteristics would produce unequal durations of the first year of growth among individual fish (i.e., from the time spawned until the formation of the first annulus the following winter). Consequently, calculated growth rates for the first year were not directly comparable to those of other years. Moreover, Felin (1954) reported that the appearance of the first annulus was much less clear than subsequent annuli, such that estimates of mean growth rate during the first year were less reliable than the years that followed. Despite challenges associated with the direct-proportion method itself and the absence of any statistical treatment of the data and the qualitative derivation of a linear relationship, Felin (1954) concluded that the “transformations show marked deviations from the linearity characteristic of this plot for more homogeneous groups of fish (or of other animals). They are illustrative, however, of growth characteristics of different areas.”

For her second analysis, Felin (1954) examined growth patterns of Sardine from the 1939 year-class that were harvested in British Columbia and San Pedro. She generated back-calculated lengths-at-age for all years of each fish from each region using the direct-proportion method. She then compared the growth curves derived from mean calculated lengths to those derived from mean observed lengths for each year class (Figure 3 in Felin 1954). She perceived that it was “not readily apparent” that the two growth curves were the same and therefore “transformed” (her words, details unclear) the data (Figure 4 in Felin 1954). Felin (1954) concluded that the slope of the regressions (*k*) for each region was linear but different between the two regions although no statistical analysis was reported to justify this conclusion.

For a third analysis, Felin (1954) constructed growth curves for the year classes of 1937 through 1942 for British Columbia and San Pedro using the same methods described above (i.e., combined both observed and calculated mean lengths at previous ages of the same fish) to compare growth parameters between these regions representing the northern- and southernmost regions. She posited that it was "probable that if significant difference were found in the growth characteristic *k* in certain individuals or segments of the population it would indicate genotypic difference." However, from analysis of covariance, Felin (1954) found no differences in mean *k* values among year classes or between the two regions, meaning that estimated mean growth rate was consistent among years for each port and similar between ports (Table 3 in Felin 1954).

Felin (1954) reported a significant difference "at the 1-percent level" in the predicted y-intercept from the transformations of mean calculated and observed maximum length between fish landed at the two ports that was maintained across each year class. Based on the relationship between the y-intercept and the maximum predicted length (L_∞), she concluded that L_∞ was different between these two regions (Table 3 in Felin 1954). Based on her previous research, Felin (1954) asserted that L_∞ may be useful in separating homogeneous populations in the absence of genetic evidence. Yet, Felin (1954) also stated that differences in estimated L_∞ "may represent phenotypic response of a plastic genotype to varying hydrographic environments" rather than heritable, "genetic differences". That is, she acknowledged that spatial and temporal variations in observed or predicted growth parameters could be influenced by environmental factors:

> *"It seems probable from existing evidence on growth characteristics of the fish in different geographical regions that there may be season-to-season fluctuations in the size and the location of optimum living areas associated with fluctuations in marine climate". (p. 210)*

Felin (1954) conceded that estimated ages predicted from back-calculated lengths were heavily biased, imprecise, and obscured individual variation in length-at-age (discussed in Part III below). Nevertheless, based on her evaluation on the smaller deviations from the transformations of mean calculated lengths (and the mean of annual mean lengths) of 4-6 ring Sardine of each year class, she concluded that the populations were more homogeneous within a single fishing season. Based on the series of analyses and comparisons of growth parameters (*k* and L_∞) generated from back-calculated and transformed data of mean lengths and mean of mean lengths, Felin (1954) concluded that "complete intermixture and homogeneity in populations of adult fish as sampled by the fishery were not evident." Her interpretation considered the results of tagging studies (e.g., Clark and Janssen 1945) that showed that larger individuals of each year class migrated the farthest. However, she argued that the:

> *"...greater size of fish in northern waters is not entirely explained by northern migration of the larger individuals of each year group. These northern pilchard may represent a separate stock grown to larger sizes rather than only a sorting out of larger fish from a whole coastal population". (p. 210)*

To support this hypothesis, Felin (1954) highlighted an apparent cline in growth characteristics based on the estimated L_∞ among regions, which increased with increasing latitude. She speculated this to be "indicative of intraspecific populations in which there is limited intermingling", and suggested "rather than a general coastwise migration pattern, a series of overlapping coastal migrations of more than one stock appears more consonant with observed data on growth". She cited the tendency for smaller sizes to remain in the southern part of the range (i.e., Central and Southern California) and the observed southward migration of some fish tagged off of Central California, which was reported by Clark and Janssen (1945), as a possible mechanism that maintained separation between fish of southern vs. northern origin. Based on the documentation of a major spawning area off Central Baja California (i.e., area surrounding Sebastián Vizcaíno Bay and Point Eugenia), Mexico, which had only recently been observed and that she assumed to be discrete from the other known spawning area at the time off Southern California, Felin (1954) reasoned that this area gave rise to catches off San Pedro and to a lesser extent to those in Central California. She hypothesized that larger fish originated off Southern California and occasionally to the north.

Felin's central thesis was presented on p. 212, where she stated:

> *"[F]ish in the northern part of the range of the fishery are perhaps distinguishable as large, long-ranging individuals, while southern stocks may be characterized by smaller size and more limited migration routes. These stocks appear to overlap in their distribution on fishing grounds as evidenced from the length-frequency data accumulated over a long period of years. Over the period of study of age composition of the catch for which length composition by age is also available, it is evident that the smaller sizes of each year class are rarely caught north of Central California".*

This hypothesis was used to explain why the fishery off San Pedro did not decline as severely as those in the Pacific Northwest. It was thought that while spawning and recruitment declined off California and to the north, new fish from the southern spawning area off Central Baja California must have supplied new recruits to San Pedro to maintain catches in that area in the 1949-1950 season. Thus, Felin (1954) reported that "differences in individual scale and growth patterns indicates some independence in the fished stock of the Pacific Northwest and Southern California."

While Felin (1954) assumed that her observed results on regional growth patterns were reflective of genetic differences among distinct subpopulations of Sardine that originated from different, discrete spawning areas and exhibited differences in migratory behavior and longevity, she repeatedly acknowledged that such results could also indicate phenotypic plasticity:

> *"The study of intraspecific clines in fishes is, of course, complicated by what Mayr (1944, p. 135) terms the "strong and only rather recently appreciated phenotypical plasticity of many species." (p. 210)*
>
> *"Whether the populations sampled by northern and southern fisheries have genetically distinct components has not been demonstrated. The significantly different levels of their mean growth transformations may indicate only phenotypic differences in growth ascribable to differing environmental conditions at time and place of spawning or in later life or both." (p. 211)*
>
> *"Whether the significant difference in attained ultimate size, L_∞, of southern as opposed to northern growth types arises by reason of primary difference either in location of spawning centers or in location of nursery grounds, or both, and whether in turn difference in origin of stocks also represents genetic difference await further data from spawning studies and determination of how discrete are the areas of spawning and of spawning stocks." (p. 212)*
>
> *"Whether heterogeneity in growth characteristics is the expression of genotypic difference or a phenotypic response of a species to its environment is not yet determined." (p. 223)*

The next study that evaluated growth patterns in relation to population structure in Sardine was by Clark and Marr (1955). In their report, they presented length-at-age data from fish landed in the Pacific Northwest (British Columbia, Washington, Oregon) and San Pedro, California. They discussed different “growth types" among fishery regions from California to British Columbia and postulated that these might reflect population divisions. No methods or analyses were presented in the paper. However, they generated an illustrative figure (Figure 14 in Clark and Marr 1955) showing different growth curves. These appear to be conceptual diagrams rather than based on empirical data. We suspect that the figure was derived from Felin (1954), as all other mentions of growth in the report referred to that study, and the authors produced a data table (Table 9 in Clark and Marr 1955) that appeared to reproduce data from Felin (1954).

Felin, Phillips, and colleagues published short annual reports on age and length compositions of Sardine off the Pacific coast of the U.S. and Mexico from the late 1940s through the late 1950s (e.g., Mosher et al. 1949; Felin et al. 1953; Felin et al. 1955; Felin et al. 1958). None discussed their results in relation to population heterogeneity or subpopulations, but their figures, tables, and summaries consistently reported high levels of individual and regional variations in length-at-age. For any given survey year, there were large overlaps in length distributions among age classes within regions that were equal to or greater than differences in length-at-age among regions. For example, a 204 mm fish from San Pedro during the 1955-56 season ranged from 1 to 5 years in age, and a 218 mm fish ranged from 2 to 7 years (Felin et al. 1958). In fact, the variation in observed length-at-age during a single year of sampling at a single location was reportedly larger than the calculated mean differences in length-at-age among regions as plotted in Felin (1954). Wolf et al. (1958) and Wolf (1961) presented similar results showing large variations in individual length-at-age and large overlaps in length distributions among age classes landed by the Southern California fishery. Age and length distribution and composition data from 1932 to 1960 for landings from Mexico to British Columbia (locations varied by year) consistently showed a similar pattern of within and among year variation (Wolf 1961). Annual summary reports of age and length composition of Sardine published in later years were not scrutinized in detail for this review but showed these same patterns (e.g., Wolf and Daugherty 1963; Daugherty and Wolf 1964; Blunt and Kimura 1966).

Building on the work of Clark and Marr (1955), the topic of fish subpopulations became formalized in a review paper by Marr (1957). The report included a short evaluation of previous studies by Phillips (1948), Landa (1953), and Felin (1954) and considered differences in growth rates to be the result of phenotypic plasticity rather than being heritable traits of separate subpopulation as the most plausible explanation for observed spatiotemporal variations in growth:

> *“These studies have shown that there are between-season, between-port and between-year-class differences in “size on age” curves. Similarly, there are within-season, within-port and within-year-class differences. Some of the differences appear to be associated with latitude. Insofar as the characteristics examined are concerned, the Sardine population, as sampled by the fishery is not homogeneous. The nature of the observed differences is not definitely known, but they are probably phenotypic.” (p. 113)*

Marr (1960) compiled available length and age data from previous studies (e.g., Felin and Phillips 1948; Clark and Marr 1955) for Sardine sampled at major fishing ports from San Diego to British Columbia from the 1916-1917 season through the 1958-1959 season. These data combined both direct estimates of age-at-length at time of capture and back-calculated estimates of length at previous ages for the same individual fish using the direct proportion method. Using this approach, Marr (1960) found the mean of the mean length of age-1 fish to be highest in San Pedro and lowest in British Columbia (Table 9 in Marr 1960). He also reported that the mean length of age-1 fish varied from year to year within individual ports. In several years, the mean length of age-1 fish from British Columbia was actually similar or higher than age-1 fish from San Pedro. Marr (1960) speculated this to be due to a density-dependent relationship between fish growth and competition for resources among young fish that are restricted in their movements compared to migratory adults.

Marr (1960) generated simple growth curves (Figure 22 in Marr 1960) for each port showing the mean of the mean length-at-age that produced results similar in some ways and dissimilar in others to those previously reported by Phillips (1948) and Felin (1954). Briefly, the mean of mean length-at-age was similar among ports from ages 0 to 2 but was largest in British Columbia by age 3. From age 3 to age 7, mean of mean length-at-age showed a clinal relationship that was highest in British Columbia and lowest off San Pedro. However, as was the case in previous studies, individual variation in length-at-age within and among ports was obscured by using the mean of annual means within ports, and no formal statistics were applied to evaluate potential differences in length-at-age at any level. Furthermore, the sample sizes were highly inconsistent among ports for many sample years, making it difficult to assess possible year effects.

Despite utilizing nearly all the same data as were available in his 1957 report and presenting similar results, Marr (1960) formulated a different explanation. He proposed there to be at least two groups of fish with different "growth histories", such that one group was characterized by the pattern observed in British Columbia and the other by the pattern observed in San Pedro; ports in between (Monterey and San Francisco) were thought to represent a mixture of the two groups. Marr (1960) acknowledged the results from tagging studies (e.g., Clark and Janssen 1945) supporting the conclusion that the south to north increase in average length-at-age could be accounted for by differential migration, whereby the largest individuals of a particular age tended to migrate further than smaller individuals that did not migrate or only migrated short distances. However, he concluded that such behavior could not fully account for the observed patterns in length-at age among the four regions (his p. 717). He postulated that fish represented by the early portion of the San Pedro growth curve were either short-lived, or they became unavailable to the fishery at older ages.

As a second analysis, Marr (1960) analyzed "relative growth measures" by averaging scale increments from several fishing seasons based on age-1 to age-5 fish, which produced what he referred to as "remarkably similar" growth curves among the four areas. He reasoned that this result indicated that the conditions influencing growth were similar over wide areas or that fish tended to all be in the same area during the period of growth.

In light of his formal proposal that hypothesized the existence of two subpopulations along the Pacific Coast of North America, Marr (1960) concluded that the southern subpopulation of fish may be expected to have a "more accelerated existence" that is characterized by rapid growth during early years and a reduced lifespan. Conversely, he hypothesized that northern Sardine may grow more slowly but attain a greater maximum age and length. Marr (1960) speculated that differences in food availability rather than differences in timing of spawning between the main spawning areas of the two subpopulations drove differences in growth rate during the first year (his p. 66). However, he included a statement in support of previous studies that demonstrated mixing among fish from Southern California to British Columbia via migration: “In general it appears that the differences observed between ports correspond to what one would expect from appropriate, according to the model, mixture of fish of these two growth histories.” By extending the time series of age data used in his study, he found no relationship between growth rate and population size (density-dependence) as reported previously by Phillips (1948).

Part II: Modern investigations on somatic growth patterns in Pacific Sardine along the Pacific coast

Following Marr’s (1960) review there were no publications examining growth in Sardine, presumably due to the absence of a dedicated fishery that resulted from historical low biomass. The next study on regional growth patterns was published by Butler et al. (1996) after Sardine abundance increased and the directed fishery had been reestablished. Notably, this study used otoliths rather than scales for age determination and followed the methods described by Yaremko (1996) that have since become the standard method for ageing Sardine in the U.S. The study examined 1,079 samples of Sardine collected from San Ignacio Lagoon in Central Baja California, Mexico, to Monterey, California, as part of a joint U.S.-Mexico survey in April to May of 1994 to estimate Sardine biomass using the daily egg production method (DEPM; see Macewicz et al. 1996 for details). Samples were collected by night-time surface trawls and commercial purse seine catches and pooled into 3 regions: Monterey (north of 34°N), Southern California (from 31°N to 34°N; i.e., Point Conception to Ensenada) and Baja California (south of 31°N; i.e., south of Ensenada to Punta Eugenia). The mean age among five readers was used for final age estimates, as the mean agreement among readers ranged from 31% (5 readers) to 62% (2 readers) (Butler et al. 1996). Length and age data were pooled across regions, and growth was estimated by fitting the data to a von Bertalanffy growth function (Figure 6 in Butler et al. 1996). Notably, the length distributions overlapped completely for all 5 age classes, and predicted growth rate asymptoted after age-2. The lack of small (<120 mm SL) and young (age 0) fish required the theoretical age at which fish would have zero length (t_o) to be set at zero. According to the authors, the theoretical maximum length at which growth rate is zero (L_∞) was greatly underestimated, which was likely due to a lack of samples older than age 5 (Butler et al. 1996).

Although unclear from viewing the figure presented in their study (their Figure 7), Butler et al. (1996) reported that the age composition varied among the three regions such that more young fish were collected from Baja California than in Southern California or Monterey. Despite issues related to age and ageing error estimation and sample distribution bias (see Bolser et al. 2018), they plotted and compared the mean sizes-at-age of 1-3 year old fish. No formal statistical tests were performed, but they reported that length-at-age differed between the 3 regions and followed a latitudinal cline (Figure 8 in Butler et al. 1996). Specifically, fish were “smaller at age off Baja California and larger off Monterey”. Length-at-age in Southern California fell in between the other two regions for ages 1 and 3 but was larger than Monterey for age 2.

Butler et al. (1996) pointed out some limitations in ascribing causality to their interpreted growth differences. Specifically, the authors highlighted two sources of error that likely influenced their results and conclusions: (1) variable periodicity for major growth increments, and (2) indistinct or ambiguous appearance of major growth increments that were complicated by false annuli or spawning checks in the otolith. They acknowledged that the variable timing of spawning peaks among years and regions was another potential source of error. Lastly, they emphasized that interpretations of annual growth patterns were somewhat ambiguous due to the low rate of agreement among readers that resulted in low ageing precision. Based on these concerns, Butler et al. (1996) concluded that it was uncertain whether observed regional differences in length-at-age were due to difference in growth patterns, small sample sizes, differences in spawning seasonality, or inaccurate age determination.

Smith (2005) presented a brief review of Felin's (1954) growth results. He interpreted the findings of the original study as evidence that "two radically different growth patterns were detected" and referred to differences in average body size and average length at 3 years of age between fish sampled in the south versus the north to support his argument. While much of his review focused on providing evidence in support of the existence and management of distinct subpopulations as a precautionary approach, Smith (2005) quoted the main conclusions presented by Felin (1954), including the statement that observed heterogeneity in growth patterns could represent either phenotypic plasticity or genetic differences (Smith 2005, p. 76).

Dorval et al. (2015) conducted the first statistically robust examination of growth patterns in Sardine. Their goal was to investigate potential changes in growth rate of Sardine collected off California in 1994 and 2004 - 2010. Age data were determined from the otoliths of fish collected during spring surveys (March to May) from San Diego to San Francisco. While the study was not designed to investigate regional patterns in growth, the intentional use of samples collected only during spring in a hypothesized "core spawning area" off California was meant to follow the subpopulation hypothesis and assumed that all such fish collected in that region and during that time would be from the putative northern subpopulation. The sample distribution (n = 4440) lacked small individuals (<107 mm SL), and the length distribution of aged fish varied by year (Figure 3 in Dorval et al. 2015). The data were aggregated into three cohorts to compare modeled growth patterns in fish born between 1986-1993, 1996-2003, and 2004-2010. Growth was modeled separately using a three-parameter von Bertalanffy growth function and a non-linear mixed-effects model (Figure 5 in Dorval et al. 2015). For the latter, three different models were used to determine which parameters should be modeled as fixed and random effects, and Akaike Information Criteria was used to select the best model to describe growth. For the first time, the influence of ageing error (i.e., differences in age estimates among readers) was accounted for as part of the model selection process. Dorval et al. (2015) compared the variability of length-at-age for each aggregated cohort and estimated the relative growth rate from age 0 to 5 years by dividing mean length-at-age for each cohort by L_∞ .

Statistical contrasts among the cohorts showed that the 1996-2003 cohort had a lower growth rate than the other two cohorts (Dorval et al. 2015). Moreover, they found a compensatory relationship between growth rate and estimated population size, which they attributed to feeding conditions and density-dependent factors (e.g., intraspecific competition for resources). Dorval et al. (2015) plotted the relationship between standard length and estimated age of all fish sampled (their Fig. 5), which showed highly overlapping length distributions among all age classes that reflected individual variation in length-at-age of sampled fish (Figure 5 in Dorval et al. 2015). For example, individuals measured at 16 cm SL ranged in age from 0 to 4 years, and those measured at 22 cm SL ranged in age from 0 to 7 years in age.

Dorval et al. (2015) concluded that temporal variations in the size and age distributions of Sardine among the three different time (i.e., aggregated cohort) periods were a consequence of the recovery dynamics of the population. For example, the prevalence of smaller fish in the 2004-2010 period was thought to be due to increased recruitment success during favorable environmental conditions. They also noted that differences in the inshore/offshore distribution of Sardine of different ages and sizes compared to the sampling locations likely generated biased length and age distributions in some years. These differences occurred because the surveys were not designed to investigate spatiotemporal patterns in growth but rather to estimate daily egg production by sampling fish from the spring core spawning area, including regions of high and low densities of eggs. Specifically, length distributions were potentially biased towards larger fish when sampling occurred in the main spawning grounds offshore, which likely missed the smaller, younger fish that occupied inshore areas. Conversely, a sampling bias towards smaller fish was observed during years when most trawls were taken inshore. They attributed the lack of larger fish collected after 2005 to be indicative of either: (1) larger adults (> 250 mm) having migrated to the Pacific Northwest and not returning south in subsequent years; or (2) the removal of large adults by the developing fishery in the Pacific Northwest and British Columbia, Canada (Dorval et al. 2015; see also Lo et al. 2011).

Age-0 fish from the 2003 cohort were observed to be larger than those collected in 1993 and from 2004 to 2008, but they were not observed again the following spring. Dorval et al. (2015) speculated these fast-growing fish belonged to the southern subpopulation and migrated south to spawn off Central or Southern Baja California. They then cited a previous study by Demer and Zwolinski (2014) to suggest that considerable mixing may occur between the two subpopulations (referred to as stocks), which could affect growth rate estimates (their p. 305).

Enciso-Enciso et al. (2022) evaluated somatic growth patterns of Sardine from the temperate stock (i.e., southern subpopulation) from commercial landings from Ensenada (Northern Baja California) to Magdalena Bay (Southern Baja California) from 2005 to 2014 using otoliths for age determination. The sample distribution (n = 3,509) lacked both small (<114 mm SL) and large (>226 mm SL) individuals, and the length distribution of sampled fish differed among years. To address this, sensitivity analyses were run to quantify the effects of sample distribution bias on the growth model outputs, and multiple growth models were fitted to data bolstered with simulated values. Similar to many previous studies, the length distributions among age classes overlapped such that individual fish of a given length could be represented by 1 to 6 age classes (Figure 7 in Enciso-Enciso et al. 2022). Additionally, they also observed interannual variability in growth parameters, which they found to be correlated with environmental indices. Approximately 82% of the fish sampled were 1 to 3 years in age, and the oldest fish sampled were 6 years old. The authors attributed this result to the warmer environmental (i.e., water temperatures) conditions off Baja California compared to northern latitudes. Consistent with the subpopulation hypothesis as it relates to somatic growth (e.g., Felin 1954), the authors speculated that colder waters would be expected to allow Sardine of the cold stock (northern subpopulation) to reach larger ages and sizes than the temperate stock (southern subpopulation) (Enciso-Enciso et al. 2022). Enciso-Enciso et al. (2022) reported a relationship between growth performance and several environmental indices (Pacific Decadal Oscillation, Upwelling Index, Oceanic El Niño Index), but effect sizes were low (r^2 ranged from 0.06 to 0.31), and no relationships were significant (p ranged from 0.09 to 0.51).

In a recent study evaluating a habitat model used to partition Sardine into subpopulations, Zwolinski and Demer (2023) presented data and results on length-at-age and growth patterns. Part of that study compiled age and length data from fish collected from the acoustic-trawl (A-T) survey led by the NOAA Southwest Fisheries Science Center during the summer of 2021 and investigated the "demographic structure of both groups…for signs of different growth patterns" (Zwolinski and Demer 2023). The age and length data came from four different sampling platforms: FSV Reuben Lasker (the primary sampling platform), FV Lisa Marie and FV Long Beach Carnage (supplemental nearshore sampling), and RV Dr. Jorge Carranza Fraser (supplemental sampling by Mexico). While some important sampling details were not reported by Zwolinski and Demer (2023), we provide them here for context. Sardine were infrequently encountered and collected from night-time surface trawls by the FSV Reuben Lasker. The vessel surveyed the offshore waters from Cape Flattery, Washington to the region just north of El Rosario in Northern Baja California, Mexico. Trawls were performed in areas where echoes from putative schools of focal species (i.e., Sardine, Northern anchovy, mackerel spp.) were observed in echograms earlier that day (Renfree et al. 2022). Up to 75 Sardine were randomly subsampled from each trawl to be measured and weighed, and up to 50 of these Sardine had their otoliths extracted for ageing. More details on the biosampling methodology associated with A-T surveys are described in Dorval et al. (2002) and Renfree et al. (2022). These fish were assigned to either the northern or southern stock by applying the northern stock potential habitat model developed by Demer and Zwolinski (2014). Notably, Zwolinski and Demer (2023) defined the term "stock" as equivalent to the term "subpopulation" (their p. 1). Only 39 of 127 trawls (31%) conducted contained any sardine, and from these, a total of 711 otolith pairs were collected. Of these, only fish assigned to the northern stock were aged (n = 395).

During post-survey data analysis, a portion of the age data from Sardine originally assigned to the northern stock (n = 162; 8 trawls) were re-assigned to the southern stock because of their small length-at-age (J. Zwolinski email and personal communication w/ authors; see also Figure 1 in Kuriyama et al. 2022). After this adjustment, age data for the northern stock was available for fish collected from only 11 of the 39 trawls (from the FSV Reuben Lasker) that contained Sardine, with five trawls accounting for 94% (223 of 233) of the final northern stock tally. The re-assigned fish represented the only southern stock Sardine aged from the FSV Reuben Lasker component of the A-T survey, all of which were collected off California. Three trawls accounted for 86% (140 of 162) of the Sardine aged and attributed to the southern stock. The majority of individuals collected during that portion of the survey and assigned to the southern stock, including all fish collected in Mexico, were not aged and thus not included in their analysis (n = 316). Additional age-at-length data were acquired from samples collected with purse seines from the nearshore component of the surveys by the FV Lisa Marie (Cape Flattery to San Francisco; n = 50 from 2 purse seine sets) and the FV Long Beach Carnage (Stewarts Point to San Diego; n = 749 from 19 purse seine sets). Thus, all length-at-age data for Sardine assigned to the southern stock used by Zwolinski and Demer (2023) were from California and mainly from nearshore waters (0-5 nmi; Steirhoff et al. 2023) despite the collection of length and weight data and otolith samples for many Sardine sampled off Mexico (their Fig. 8) by the FSV Reuben Lasker (U.S.-Mexico border to El Rosario) and the RV Dr. Jorge Carranza Fraser (El Rosario to Punta Abreojos). These details of the sample design are important to describe, because the study reported that "coast-wide ages for Sardine were available" for use in their study. This implies that growth data were collected across the entire survey area from Central

Baja California to British Columbia, which is not an accurate representation of the data used. More details on the 2021 A-T survey are described in Renfree et al. (2022).

Once all samples were assigned to their respective stocks, Wilcoxon rank tests were used to compare mean length-at-age of three age classes (ages 1-3) between fish assigned to each stock. Despite a large reported disparity in the samples analyzed for the northern (n = 283) and southern (n = 935 reported in Zwolinski and Demer 2023, but actual n = 911) stocks and the lack of any detailed reporting of statistical results, they reported that the lengths-at-age of northern stock Sardine were significantly larger for age classes 1, 2, and 3 (Figure 3). Sampled Sardine of ages 0 and 4-8 years were not tested for differences due to a lack of samples from one or both stocks. Samples assigned to the northern stock ranged in estimated age from 0 to 11 years, whereas those assigned to the southern stock ranged only from 0 to 4 years. Notably, the data set contained only one age-0 fish and five age-1 fish assigned to the northern stock and only 1 age-4 fish assigned to the southern stock (Figure 9 in Zwolinski and Demer 2023). While no growth models were generated for either stock and no methods were provided explaining how such a conclusion was reached, Zwolinski and Demer (2023) reported that "the northern stock appears to have a significantly larger asymptotic length".

Based on their results, Zwolinski and Demer (2023) concluded that their reported differences in growth patterns supported their separation of Sardine into two separate stocks and were in agreement with the "long-standing hypothesis of two stocks off the Pacific coast of the U.S. and Mexico" (their p. 10). They describe the northern stock as Sardine that spawn predominantly off southern and Central California, migrate to feed as far north as Canada in summer, and then return south and likely offshore in the late fall and winter. In contrast, the southern stock consists of Sardine that reside mostly off of Baja California, migrate seasonally, synchronously, and separately from the northern stock, and enter Southern California (and sometimes Central California) waters during the summer. As it relates to growth and consistent with Felin (1954) and Marr (1960), they described southern stock fish as being "smaller for their age or stubbier than northern stock Sardine" (Zwolinski and Demer 2023, p. 11). They contended that their results reflected "characteristics indicative of biological isolation", which implies they were genetically different, but provided no evidence to support this claim. In conflict with this reasoning, Zwolinski and Demer (2023) later described growth patterns as "phenotypical traits", stated that mixing of adults and/or recruits (i.e., mechanisms for gene flow) between stocks may occur off Southern California and that heterogeneity in life history traits indicative of stock separation may be genotypic or phenotypic in origin (their p. 11).

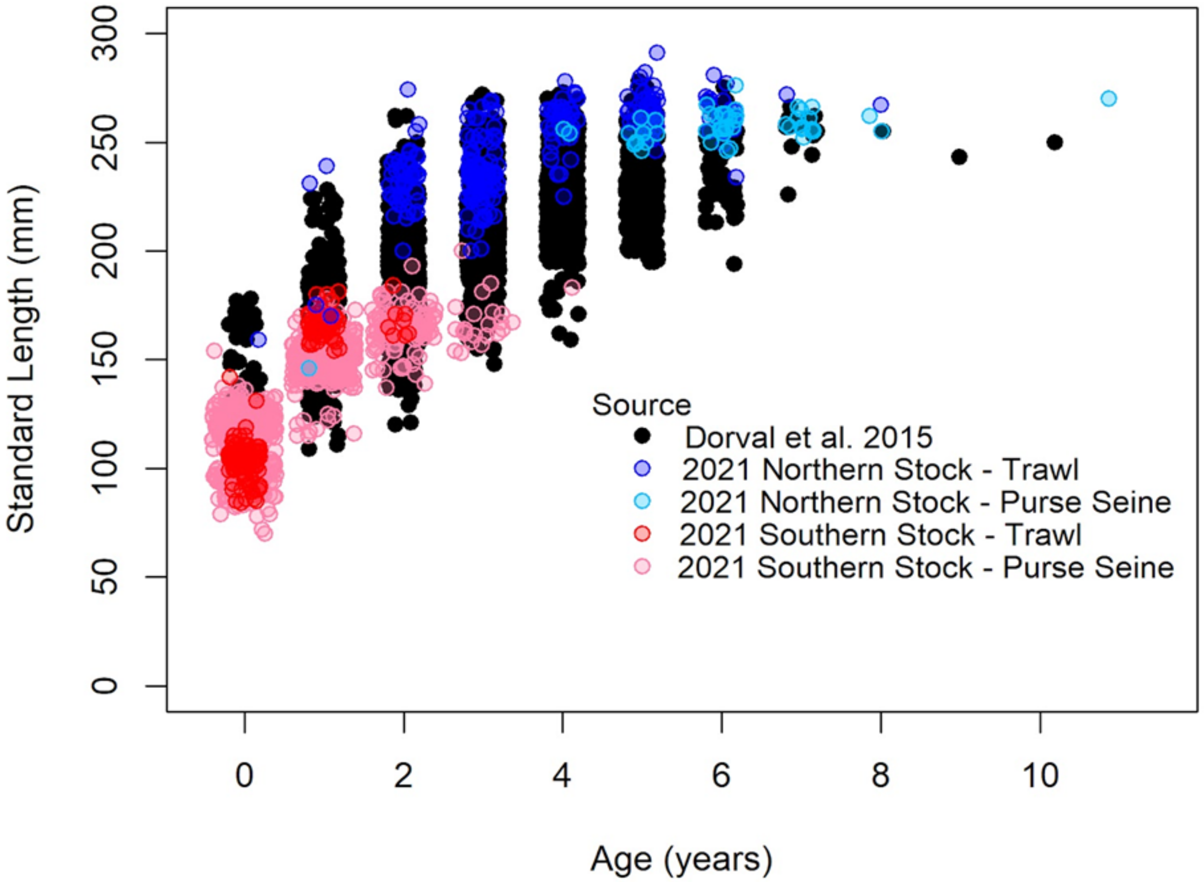

Figure 3. Length-at-age data of Pacific sardine (*Sardinops sagax*) sampled off California in Spring 1994, and 2004-2010 by Dorval et al. (2015) and off California in Summer 2021 by Zwolinksi and Demer (2023). Data from 2021 are color coded by assigned stock and gear type. Data points are jittered for visual clarity.

Part III: Evaluation of studies that investigated growth patterns in relation to population structure of Pacific Sardine along the Pacific Coast

Our evaluation of the literature produced 8 studies that investigated growth in Sardine in relation to population structure along the Pacific coast to some degree. Upon reviewing the prevailing hypothesis that regionally distinct and heritable growth patterns exist, we found that the collective supporting data were scant, uncertain, inconsistent, and lacked statistical support and validation. A deeper examination of the design and methods employed revealed serious issues related to sampling design, sample distribution, data analysis, and other methodological aspects that diminished the quality and certainty of results (i.e., type I error) and led to spurious conclusions. Table 1 summarizes the methods, results, and conclusions of each of these studies as well as the issues identified by our evaluation. A clear conclusion emerged from this evaluation. As acknowledged by all studies that investigated somatic growth patterns in relation to population structure of Sardine, phenotypic plasticity and the complex life history of Sardine represent the most parsimonious and plausible explanations for all observed and reported patterns in growth and length-at-age for Sardine along the Pacific coast.

The prevailing hypothesis of heritable differences in growth lacks genetic evidence

The prevailing hypothesis contends that regional differences in growth patterns exist and represent genetically heritable traits indicative of distinct subpopulations of Sardine. Support for this hypothesis stems from the results reported in studies by Felin (1954; summarized by Clark and Marr 1955), Marr (1960), and Zwolinski and Demer (2023) and editorial review paper by Smith (2005). We excluded the study by Phillips (1948) from the list, because despite reporting regional differences in length-at-age, he did not argue that his results were indicative of subpopulations. Rather, Phillips (1948) concluded that a single growth function was the most appropriate to model growth patterns along that range while considering the combined effects of individual variation, spatiotemporal variation, ontogeny, and migratory behavior in relation to length, age, and growth. We also excluded the results of Butler et al. (1996), since the authors concluded that it was uncertain whether their results were due to actual differences in growth patterns or an artifact of small sample sizes, variations in the duration of the first growing season, or inaccurate age assignments.

Table 1. Summary of methods, results, and limitations of 8 studies that examined somatic growth in Pacific sardine in relation to population structure along the Pacific coast of North America. BC (MX) = Baja California (Mexico); CA = California; OR= Oregon, WA =Washington; BC (CAN) = British Columbia (Canada).

Study	Sampling coverage	Growth data source(s)	Sampling groups	Working hypothesis and assumptions	Growth comparison methods	Estimated growth parameters	Results and conclusions	Limitations and issues
Phillips (1948)	Regions: CA, OR, WA, and BC (CAN) Fishing seasons: 1941-42 through 1946-47	Port sampling of commercial catch Measured length (n > 240,929) Age (0-10) estimated from scale readings (n = 46,045) Data taken from Phillips and Felin (1948)	Age Sex Year-class Season Region Period	Northern population from Alaska to central BC (MX) Evidence that Sardine from southern BC (MX) and Gulf of California constitute a separate population	Walford's plot derived from the direct-proportion method Visual comparison of growth curves from plots of mean length-at-age by year-class, season, sex, region	Mean length-at-age per year-class, season, sex, region, and period	Differential growth patterns between sexes, among year-classes, within and among regions, within and among periods Possible partial migration-at-age and at-size Population best represented by a single growth curve that considers migration, timing of birth, ontogeny	Graphical regression Non-independent length-at-age data Biased data (fishery-dependent) No formal growth model generated; no growth parameters estimated No variance estimates (e.g., within-group or among-group) No formal statistical tests Individual variation in length-at-age within regions much higher than variation among regions

Felin (1954)	Regions: CA, OR, WA, and BC (CAN) Ports: BC (CAN), Pacific Northwest (OR, WA), San Francisco CA, Monterey CA, San Pedro CA Fishing seasons: 1941-42 through 1949-50	Port sampling of commercial catch Fish samples (n > 33,244) Measured length and Back-calculated length data Age (0-8+) estimated from scale readings and length transformation based on the Walford (1946) method.	Age Year-class Season Port Region	Sardine from CA to BC (CAN) composed of more than one population, each with genetically distinct attributes including growth rate, habits, migration patterns, distribution, spawning areas, anatomy, physiology, birth and death rates	Walford's plot derived from the direct-proportion method; applied to both mean observed and mean calculated length data Modal analysis (Length frequency) ANCOVA to compare slopes of regressions for k and $L\infty$ Visual comparison of growth curves from plots of mean observed lengths-at-age by port	Mean length-at-age per year-class, season, port, region Grand mean length per age and region across seasons k (growth coefficient) per year-class, port $L\infty$ (maximum predicted length) per year class, port y (intercept) per year class, port	No significant difference in mean slopes k derived from transformed data for six year-classes in BC (CAN) and San Pedro CA Differences in y-intercepts among year classes Differences in $L\infty$ between BC (CAN) and San Pedro CA Data on mean calculated lengths indicates heterogeneity in adult populations among fishery regions Clinal pattern in $L\infty$ indicative of intraspecific populations Spawning from southern BC (MX) give rise to fish caught off Southern CA; larger fish originate off Southern CA Quantitative and qualitative differences in scale and growth patterns indicate some independence in the fished stock off Southern CA and BC (CA) Bimodal length frequency distributions indicate population heterogeneity Heterogeneity could be a genetic or phenotypic response to environment	Same as in Phillips (1948) Growth parameters derived from combination of various transformations Low precision in measurements from scale increments Length-at-age curves for all regions fall within the range of the northern stock

Clark & Marr (1955)	Regions: CA, OR, WA, and BC (CAN) Areas: Pacific Northwest (OR, WA), San Francisco CA, Monterey CA, San Pedro CA Fishing seasons: 1941-42 through 1945-46	Data likely from Felin (1954)	Age Season Year-class Area/Region	Sardine stocks from central BC (MX) to BC (CAN) may be heterogeneous based on several aspects, including differences in growth types, spawning areas, size and age composition, scale types, meristics, migration patterns	Conceptual growth models/ curves from mean age-at-length data by area Visual comparison of growth curves	Grand mean length-at-age for 7 age classes by area	The northern growth type grows slowly in first year and then rapidly thereafter; the southern type grows rapidly in first year and then slower thereafter Growth differences may be inherited (genetic) or environmentally produced (phenotypic)	Same as in Phillips (1948) and Felin (1954)

Marr (1960)	Regions: CA, OR, WA, and BC (CAN) Areas: BC (CAN), San Francisco CA, Monterey CA, San Pedro CA Fishing seasons: 1916-17 through 1958-59	Combined data from Felin and Phillips (1948), Eckles (1954), Clark and Marr (1955), Wolf (unpublished data), and others Measured length and Back-calculated length data Age (0-12) estimated from scale readings and length transformation based on the Walford (1946) method	Age Year-class Season Area/Region	Sardine population is not homogeneous based on migration, spawning, and growth patterns; the nature is unknown but likely phenotypic; multiple hypotheses equally plausible (Marr 1957) Sardine divided into subpopulations based on “genetics” (blood groups) and differences in spawning, migration, and growth patterns (this paper)	Conceptual growth models/curves from mean length-at-age data by area Visual comparison of growth curves Regression of average age-at-length Plots of relative growth by area, year-class, season based on scale increments	Grand mean length per age and area Mean size of scale increments by age, fishing, area, and season Linear relationship between average age and average length by area	Grand mean length of age-1 fish smallest in BC (CAN) and largest in San Pedro CA; annual variability Grand mean length of age-0 to age-2 fish similar among areas; largest in BC (CAN) by age-3; clinal pattern from age-3 to age-7 Two subpopulations with different growth histories: A southern subpopulation with rapid early growth and short lifespan; A northern subpopulation with slower early growth, faster growth later, and a greater maximum length and age.	Same as in Phillips (1948) and Felin (1954) Sample distribution bias: Inconsistent sample size within and between areas/regions Sample sizes highly variable among seasons

Butler et al. (1996)	Regions: BC (MX), Monterey CA, Southern CA Season: April to May 1994	DEPM survey (trawl and purse seine) Measured length (n = 1,079) Age (1-7) estimated from otolith readings by 2 to 5 readers (n = 1,079)	Age Year-class Region	Sardine may exhibit regional differences in growth patterns from central BC (MX) to Monterey CA	Parameters estimated by fitting a von Bertalanffy growth model (VBM) to age-at-length data with t_0 fixed to 0	Mean age among 2 to 5 readers Mean length-at-age per year-class and region Average percent error (APE) Index of precision Mean and range of percent agreement from combinations of 2 to 5 readers *k* (for whole data and per year class) *L*∞ (for whole data)	Mean length-at-age of age-1, 2, and 3 fish differed among regions Fish smallest at-age off BC (MX) and largest off Monterey CA, except age 2 Uncertain whether observed regional differences in length-at-age were due to difference in growth patterns, small sample sizes, differences in spawning seasonality, or inaccurate age determination	Low ageing agreement (mean = 31-62%) among readers; agreement inversely correlated with estimated age Low ageing precision; age estimated as mean of readers No age-0 samples (fixed t0) Inadequate model parameterization and poor model fitting to the data Sample distribution bias: few age classes represented; survey focused on adults VBM generated and inferences made on a single season of data collection

Dorval et. al (2015)	Region: CA Season: Spring (April-May) Period: 1994, 2004 through 2010	DEPM survey (trawl and purse seine) Measured lengths (n = 4,440) Age (0-10) estimated from randomly assigned otoliths to 3 readers (n = 4,440)	Age Aggregated cohort (1986-1993, 1996-2003, 2004-2008) Age reader (n=3)	Three stocks of Sardine in northeast Pacific adapted to different ocean temperature ranges Ocean temperature and population size may influence growth Biomass density may influence growth of aggregated-cohorts collected in the core spawning area of Sardine off CA Adult fish sampled off CA in Spring represent northern subpopulation Southern subpopulation larger at age 0	Standard and mixed-effect models (MEM) VBM based on the likelihood method. Model selection based on AIC and ΔAIC	k, $L\infty$ $t0$ a (intercept of a MEM) $\gamma 1$ (contrast between 1986-1993 and 1996-2003 cohorts) $\gamma 2$ (contrast between 1986-1993 and 2004 - 2008 cohorts)	Growth rate in 1996-2003 cohort lower than other cohorts Compensatory relationship between growth and population size Overlapping length distributions among age classes Age-0 fish from the 2003 cohort larger than other years; attributed to fast growing southern subpopulation	Sample distribution bias: low sample size of age-0 fish; survey targeted spawning adults Assignment of age-0 fish to southern subpopulation speculative and inconsistent with prevailing hypothesis

Encisco-Encisco et al. (2022)	Regions: Ensenada, BC (MX) to Magdalena Bay, BC (MX) Period: 2005 through 2014	Port sampling of commercial catch (purse seine fleet) Measured lengths (n = 3,509) Age (0.5 - 6.0) estimated from otolith readings (n = 3,509) for temperate stock	Age Year	Three Sardine subpopulations (stocks) in the northeast Pacific influenced by ocean temperature variability Ecosystem dynamics may influence individual growth Samples were representative of the temperate stock (southern subpopulation)	Growth parameters were estimated from four models: VBM (two and three parameter); Gompertz (GM); Logistic (LM), and Schnute (SM) Model selection based on AIC and WAICi Sensitivity analysis to assess the effect of sampling bias on growth parameters	*k* L_∞ *t0* *t0* (inflection point at an age *t* and size *Lt* for the GM and LM models) π (time constant relative growth rate from the SM) φ (interannual growth performance) Precision estimated from average percent error (APE) and coefficient of variation (CV)	Sardine growth best described by VBM Growth parameters varied annually Relationship between growth performance anomaly and environmental indices reported but non-significant (no effect) Overlapping length distributions across age classes Colder temperatures may allow northern subpopulation to reach larger sizes and older ages	Lack of small and large fish (sample distribution bias) Sample distribution bias: unbalanced age-at-length data (82% of fish were age 1 to 3)

Zwolinski and Demer (2023)	Regions: BC (MX), CA, OR, WA Environmental data: 1998 through 2019 Age data from CA, OR, WA: Summer 2021	SWFSC Acoustic-Trawl Survey (n = 395) Nearshore Acoustic Purse Seine Survey (n = 799) Age (0-11) from otolith readings collected between WA and CA (n = 1194) No age data from BC (MX) Age data for 283 fish assigned to northern subpopulation (233 trawl; 50 purse seine) Age data for 911 fish assigned to southern subpopulation (162 trawl, reassigned; 749 purse seine)	Age Stock/Sub population	Same definition for a stock and a subpopulation Three stocks in the northeast Pacific Northern stock spawns, primarily off CA in spring, migrates north as far as BC (CAN) in summer, returns south in fall/winter; occupy habitats with sea surface temperatures < ~16.7°C Southern stock resides of BC (MX) and migrates synchronously and separately from the northern stock; migrates as far north as southern to central CA in summer; occupy habitats with sea surface temperatures > ~16.7°C	Scatter Plot of length-at-age for fish assigned to northern and southern subpopulation Wilcoxon rank sum test to compare lengths-at-age between stocks for signs of different growth patterns	None	Age range of southern stock: 0-4 years Age range of northern stock: 0-11 years Lengths-at-age for age-1 to age-3 fish of southern stock smaller than northern stock Northern stock appears to have a larger asymptotic length Observed growth patterns support the existence of two non-mixing stocks from BC (MX) to BC (CAN) Southern stock Sardine are smaller at age or stubbier than northern stock fish Heterogeneity in life history traits indicative of stock separation may be phenotypic or genotypic in origin	Sampling bias: no age data from BC (MX) to represent southern subpopulation Sample distribution bias: inadequate and unbalanced sample size of stocks and age classes No formal growth model generated; no growth parameters estimated Biased (tautological) selection and/or removal of length and age data from stocks Statistical inferences made on a single year of data Results on length-at-age inconsistent with prevailing hypothesis Length-at-age distributions for both stocks fall within the range of the northern stock

Under this hypothesis, the northern subpopulation consists of fish that are spawned primarily off their primary spawning grounds off Southern and Central California, grow slowly at first but increase their growth rate as adults after undergoing northward migrations from their nursery grounds off California into favorable feeding grounds in the Pacific Northwest and Canada. They have relatively long lifespans and reach large body sizes. Conversely, the southern subpopulation is composed of fish with primary spawning grounds off Central and Southern Baja California, grow rapidly early in life but slow their growth rate as adults, possibly related to shorter or southerly migrations. They have relatively short lifespans and do not reach large body sizes. Differences in growth patterns between the two subpopulations are presumed to be heritable, and genetic isolation is maintained by fish originating from discrete spawning areas with different spawning habitat requirements (e.g., temperature) that undergo separate but synchronous migration patterns (Felin 1954; Marr 1960; Vrooman 1964; Zwolinski and Demer 2023).

Genetically heritable differences in growth rate can emerge in isolated groups of marine fishes that persist and evolve under different environmental conditions (i.e., populations; Begg and Waldman 1999; Begg 2005; Wright and Trippel 2009; McBride 2014). However, growth patterns and other life history traits are not well-suited to use as stand-alone evidence for diagnosing fish subpopulations or populations. This is because growth is phenotypically plastic in many fishes, and variation in growth can be driven by a variety of biotic and abiotic factors (Brander 1995; Begg 2005). Growth patterns are difficult to measure and estimate directly from field data, which makes it inherently challenging to quantify evolutionary changes in growth (Enberg et al. 2012; Lorenzen 2016). Phenotypic plasticity in growth is the dominant signal over short time scales, which can mask underlying evolutionary changes that occur over longer time scales (Enberg et al. 2012). Therefore, information on growth patterns should be used in conjunction with other life history traits to support direct evidence of mixing or isolation from genetic analyses (Begg et al. 1999; McBride et al. 2014).

Historical studies (Felin 1954; Marr 1960) that proposed the existence of Sardine subpopulations recognized the importance of genetic evidence to confirm that growth differences were heritable and not representative of phenotypic plasticity. Unfortunately, the original biochemical studies purported to show genetic evidence for population structure (Sprague and Vrooman 1962; Vrooman 1964) used flawed and outdated methods (Craig et al. 2023; Craig et al. 2025). Subsequent studies using more modern genetic techniques have shown results consistent with panmixia (Hedgecock et al. 1989; Bowen and Grant 1997; Lecomte et al. 2004; Gutiérrez Flores 2007; García-Rodriguez et al. 2011; Adams and Craig 2024), including whole genome sequencing that can detect genetic changes on generational scales (Craig et al. 2025; G. Longo and M. Craig, unpublished data). Therefore, results from genetic studies do not support a conclusion of heritable differences in growth patterns of Sardine.

The proposed mechanisms that promote and maintain subpopulations also lack empirical support. Contrary to perspectives by Marr (1960) and others, Sardine along the Pacific coast do not have isolated spawning areas, regionally distinct spawning seasons, or latitudinal differences in the environmental conditions associated with spawning (Erisman et al. 2024; Craig et al. 2025). Rather, the geographic range of spawning is broad and varies both seasonally and annually, with spawning occurring continuously throughout its range when conditions are favorable (Ahlstrom 1954, 1959; Hernandez-Vasquez et al. 1994). Sardine have a protracted spawning season with nearly year-round spawning at their primary spawning grounds off Central

Baja and measurable spawning during most months elsewhere along their range (e.g., California), with females capable of spawning daily to weekly (Macewicz et al. 1996; Lluch-Belda et al. 2003). The thermal range of spawning is consistent and broad along the entire Pacific coast, they are broadcast spawners with an extended pelagic larval duration and large dispersal potential, and juveniles remain in nursery areas for one or more years before engaging in seasonal migrations as adults (Godsil 1931; Ahlstrom 1959; Phillips 1952; Clark and Janssen 1945; Butler et al. 1993). Their reproductive dynamics, along with the large-scale seasonal migrations of adults, serve as mechanisms for frequent mixing and gene flow across a wide geographic range that explain the lack of any evidence of population structure from genetics (Parrish et al. 1989; Erisman et al. 2024). Moreover, while regional differences in water temperature, increased food availability, timing of spawning and birth, or reduced competition for resources as drivers of larger body sizes are cited as potential explanations for reported growth patterns (e.g., Felin 1954; Marr 1960; Enciso-Enciso et al. 2022), no effort has been applied to determine or explain the adaptive significance of this duality in growth.

Reports of regional growth differences are tenuous and inconsistent

Even if the lack of direct evidence from genetics and indirect (supporting) evidence from other aspects of their biology (e.g., spawning and migration patterns) of Sardine subpopulations are ignored, the collective results presented in support of distinct, heritable growth patterns are sparse and inconsistent. Support for differential growth in support of subpopulations was the focus of Felin (1954) and relied upon two results related to growth: (1) visual differences in the shapes of generalized growth curves among regions using unweighted means of mean lengths at age that combined observed and back-calculated data for the same individuals; and (2) differences in predicted maximum length (L_∞) between fish sampled in British Columbia versus San Pedro using the same data. Clark and Marr (1955) then plotted the same data, which graphically indicated that fish sampled in San Pedro were largest at age 1, and fish sampled among all ports were similar in length at age 2. From ages 3 to 7 years, there was a clinal pattern in which length-at-age was highest at the northernmost regions. Similar to Felin (1954) and using additional data, Marr (1960) reported that length-at-age was similar from ages 0 to 2 years across regions but with San Pedro showing the largest fish at age 1. The same clinal pattern was reported from ages 3 to 7 years. In contrast to historical studies, the results from recent studies did not indicate that fish from the southern subpopulation grew faster earlier in life. Butler et al. (1996) reported that length-at-age increased with increasing latitude for ages 1 to 3. Similarly, Zwolinski and Demer (2023) reported higher lengths at ages for northern subpopulation for ages 1, 2, and 3. Thus, the claim by Zwolinski and Demer (2023) that their results were consistent with the prevailing hypothesis (which predicted that age-1 and possibly age-2 fish from the southern subpopulation should be relatively larger or similar in size) was inaccurate. Similarly, Dorval et al. (2015) attributed age-0 fish from the 2003 cohort to the southern subpopulation due to their larger size-at-age than age-0 fish collected in other years, which also conflicted with the prevailing hypothesis.

Age distribution data were also inconsistent among studies and didn’t always fit the hypothesis regarding the longer lifespan predicted for the northern subpopulation. In Zwolinski and Demer (2023), fish assigned to the southern subpopulation ranged in age from 0 to 4 years, whereas fish from the northern subpopulation ranged from 0 to 11 years (but with few age-0 and age-1 samples), which is consistent with the predicted difference in lifespans between subpopulations. However, the sampled age distributions among historical studies reporting different lifespans (e.g., Felin 1954; Clark and Marr 1955; Marr 1960) ranged from 1 to 8 years or older for fish representing the growth patterns of both the northern and southern subpopulations. For example, Marr (1960) estimated the average number of year classes present in the catch across all fishing ports from 1932 to 1958 ranged from 8.01 (San Pedro) to 9.82 (see his Table 4).

Support for regional differences in growth patterns is further weakened by the fact that several studies, including those commonly cited, produced results showing no differences at all or claimed differences without evidence. For example, Marr's (1960) analysis of scale increments produced what he remarked as "remarkably similar" growth curves among fishing regions. Similarly, Felin (1954) found no statistical difference in the mean value of the growth coefficient (k) between San Pedro and British Columbia but nonetheless concluded that the two areas had different growth types. Recent studies also suffered from this problem, as Zwolinski and Demer (2023) concluded differences in asymptotic length (i.e., L_∞) without any statistical treatment of the data or growth models to generate or compare growth parameters.

Another limitation among studies proposing different growth patterns is that they all based their results on observed patterns in length-at-age rather than direct evidence of growth. Growth and body size are certainly correlated, but size is a state, whereas growth is the process that leads to that state. Although growth may depend on current environmental conditions, size-at-age is an indicator of lifetime growth history rather than current conditions (Lorenzen 2016). Thus, while this close linkage means that selection on growth may lead to indirect selection on size, many processes other than growth can influence observed variations in length-at-age (Enberg et al. 2012). For example, the timing of birth or maturation is known to influence size at a given age, and regional variations in both aspects have been reported in Sardine (Ahlstrom 1959; Macewicz et al. 1996) and acknowledged as an explanation for observed patterns in length-at-age in several studies (e.g., Phillips 1948; Felin 1954; Butler et al. 1996). Otolith biochronologies (e.g., Black et al. 2008; Erisman et al. 2021) and cohort-specific growth curves (Whitten et al. 2013) are useful methods to overcome limitations associated with size-at-age data to: (1) generate robust, quantitative, and empirically driven relationships between growth and other factors; (2) account for plasticity, environmental effects, and variations in other life history traits; (3) and help identify persistent regional differences in growth that may be heritable (McBride 2014; Lorenzen 2016).

Reported growth differences lack statistical support

Perhaps the most consistent result among fishery reports (e.g., Mosher et al., 1949; Felin et al., 1953; Wolf 1961) and studies reviewed (e.g., Phillips 1948; Felin 1954; Marr 1960; Dorval et al. 2015) was the reporting of large variations in individual length-at-age at all spatial and temporal scales. Their results showed large overlaps in the length distributions of individuals for each age class, both within and among years, within and among ports, and within and among regions. As one important example, the variation in observed length-at-age during a single year of sampling at a single location (Felin et al. 1958) was reportedly larger than the calculated mean differences in length-at-age among regions as plotted in Felin (1954). These results suggest there are no regional differences in length-at-age or growth and place the burden of proof on studies to demonstrate otherwise using appropriate methods and analyses.

In order to justify the use of life history traits to discriminate subpopulations of fishes, the signal from among-group variation must exceed the noise of within-group variation (Waldman 1999). In this case, the question is whether individual variation in length-at-age among fishing regions or subpopulations is greater and does not overlap with the individual variation. Variation in length-at-age both within (i.e., within region variation over time) and among (i.e., annual variation among regions over time) years is also an important consideration, and one that necessitates sampling over multiple years to draw informed conclusions. Unfortunately, historical studies by Felin (1954), Marr (1960), and others that reported differences in growth characteristics (e.g., mean length-at-age) lacked support from any formal statistical analysis. For these studies, representative growth curves contained no measures of variability but rather were composed of simple line charts that were visually assessed for differences. While these practices were sufficient at the time, they are inadequate by modern standards (Campana and Jones 1992; Chambers and Miller 1995; Isely and Grabowski 2007; Brophy 2014). In using simple (visual) comparisons of curves drawn from means of mean lengths at age among regions, important sources of variation within and among regions and years were obscured or not estimated, thus making any conclusions based on such metrics nugatory.

As a simple exercise to understand variation in growth within and among regions, we compared the regional growth curves of Felin (1954) generated from the mean of annual mean values (raw data not available) to the raw length-at-age data from Dorval et al. (2015). When this exercise was performed, the growth curves from Felin (1954) believed to represent different subpopulations all fell well within the center of the observed distribution of the raw length-at-ages from Dorval et al. (2015) presumed to represent only the northern subpopulation (Figure 4). Even without any measures of variability around mean values, the complete overlap of growth curves within the natural variability observed among fish sampled in California indicated there were no regional differences in growth patterns at all.

A comparison between the length-at-age data from a single summer survey by Zwolinski and Demer (2023) with data from Dorval et al. (2015) collected over 8 spring surveys produced the same result. Specifically, the entire distribution of data points across sampled fish assigned to both stocks fell within the ranges observed in the larger data set (Figure 3), which indicated that the proposed differences among subpopulations were less than the natural annual variation within fish assumed to be part of the northern subpopulation estimated from a more robust data set. It also serves as a reminder of the importance of a proper study design, which includes a sufficient number of samples per age class and sampling over multiple years, to effectively determine whether regional differences in growth patterns exist (Enberg et al. 2012; McBride 2014; Lorenzen 2016; Miranda and Colvin 2017).

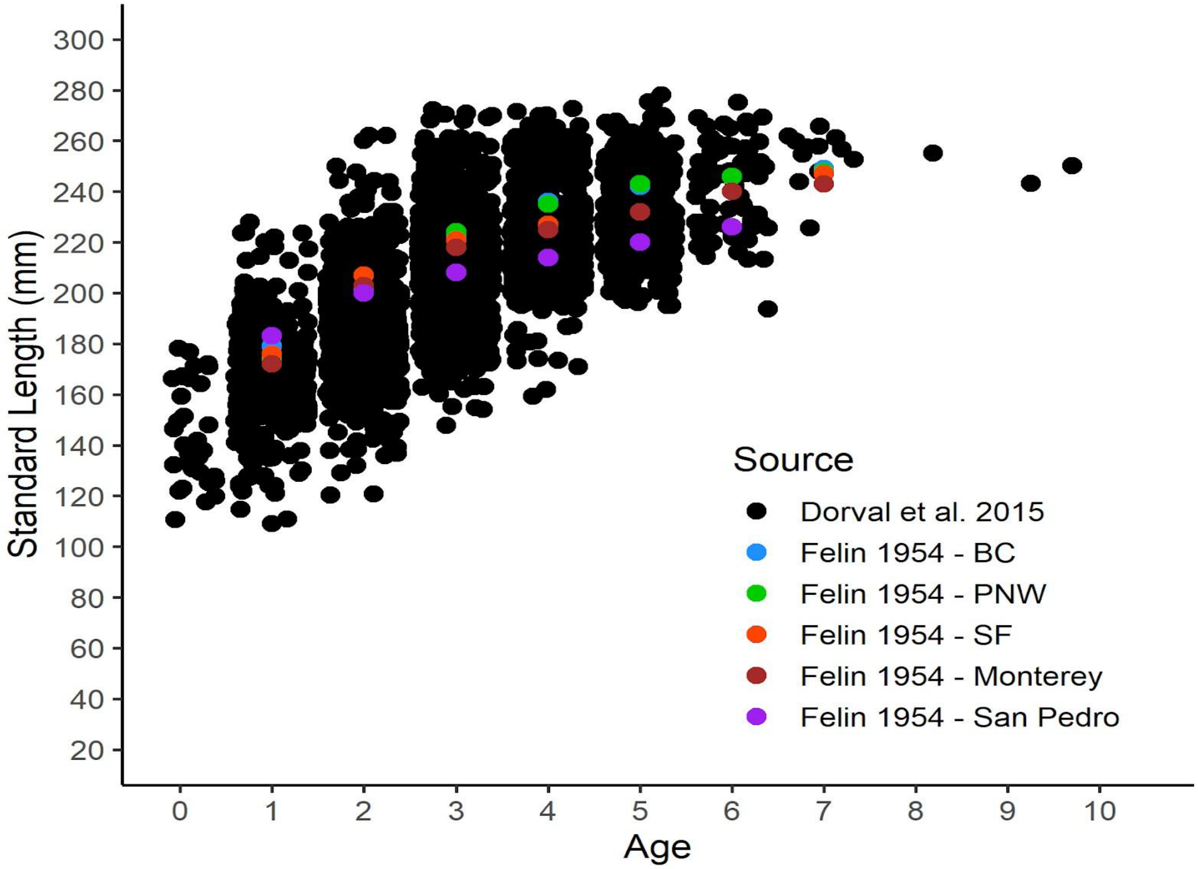

Figure 4. Length-at-age data of Pacific sardine (*Sardinops sagax*) sampled off California in 1994, and 2004-2010 by Dorval et al. (2015) and regional, mean length-at-age values from Felin (1954). BC = British Columbia; PNW = U.S. Pacific Northwest; SF = San Francisco. Data points from Dorval et al. (2015) are jittered for visual clarity.

Since the raw data were available for both studies, we then compared the average length-at-age of the northern and southern stock from Zwolinski and Demer (2023) to that of the northern stock data from Dorval et al. (2015) for age classes 1, 2, and 3. Given the tautological reasoning used to assign sampled fish to stocks by Zwolinski and Demer (2023; see section II above), we assumed clear differences in length-at-age would be found. The data for each age class did not conform to the assumptions of parametric testing (i.e., normality and homoscedasticity). Therefore, non-parametric tests were run to compare the average length-at-age for each age class. The median length of each age class was different among the three groups (Kruskal-Wallis test: Age 1: $\chi^2 = 218.97$, $df = 2$, $p = 2.2\text{e-}16$; Age 2: $\chi^2 = 244.58$, $df = 2$, $p = 2.2\text{e-}16$; Age 3: $\chi^2 = 187.02$, $df = 2$, p = 2.2e-16). For age-1, the southern stock of Zwolinski and Demer (2023), which only had 5 samples, was smaller than both the northern stock of Zwolinski and Demer (2023) and Dorval et al. (2015); the latter two groups were not different from each other (Dunn's test; Table 2; Figure 5). For age-2 and age-3 fish, all groups were different. The sample sizes for each age class from Dorval et al. (2015) were much larger than Zwolinski and Demer (2023) and spanned multiple years. Therefore, statistical differences were not necessarily meaningful from a biological perspective. The smaller age-1 fish from the southern stock may be due to the small sample size, but regardless, such a finding is inconsistent with the findings of historical studies (e.g., Phillips 1948; Felin 1954).

We then compared length and age data from Dorval et al. (2015) to the data from Zwolinski and Demer (2023) by year. The median length of each age class was different among years and stocks (Kruskal-Wallis test: Age 1: $\chi^2 = 278.89$, *df* = 9, *p* = 2.2e-16; Age 2: $\chi^2 = 491.08$, df = 9, *p* = 2.2e-16; Age 3: $\chi^2 = 560.78$, *df* = 9, *p* = 2.2e-16). Pairwise comparisons

Table 2. Pairwise comparisons from Dunn's tests of Dorval et al. (2015) and Zwolinski and Demer (2023) for age classes 1, 2, and 3. Asterisk indicates a significant difference. "Dorval" represents northern stock Sardine from 1994, 2004-2010 from Dorval et al. (2015). 'Zwolinski - N' represents northern stock Sardine from 2021 (Zwolinski and Demer 2023). 'Zwolinski - S' represents southern stock Sardine from 2021 (Zwolinski and Demer 2023).

Age	Group1	Group 2	n1	n2	Z	p	Adj. p	
1	Dorval	Zwolinski -N	441	5	0.83	4.08E-01	4.08E-01	
	Dorval	Zwolinski - S	441	369	-14.70	8.97E-49	2.69E-48	*
	Zwolinski -N	Zwolinski - S	5	369	-3.13	1.77E-03	3.54E-03	*
2	Dorval	Zwolinski -N	828	44	9.44	3.87E-21	3.87E-21	*
	Dorval	Zwolinski - S	828	118	-11.70	1.54E-31	3.09E-31	*
	Zwolinski -N	Zwolinski - S	44	118	-14.80	2.19E-49	6.56E-49	*
3	Dorval	Zwolinski -N	1221	88	11.30	1.01E-29	2.02E-29	*
	Dorval	Zwolinski - S	1221	22	-7.27	3.51E-13	3.51E-13	*
	Zwolinski -N	Zwolinski - S	88	22	-11.80	3.59E-32	1.08E-31	*

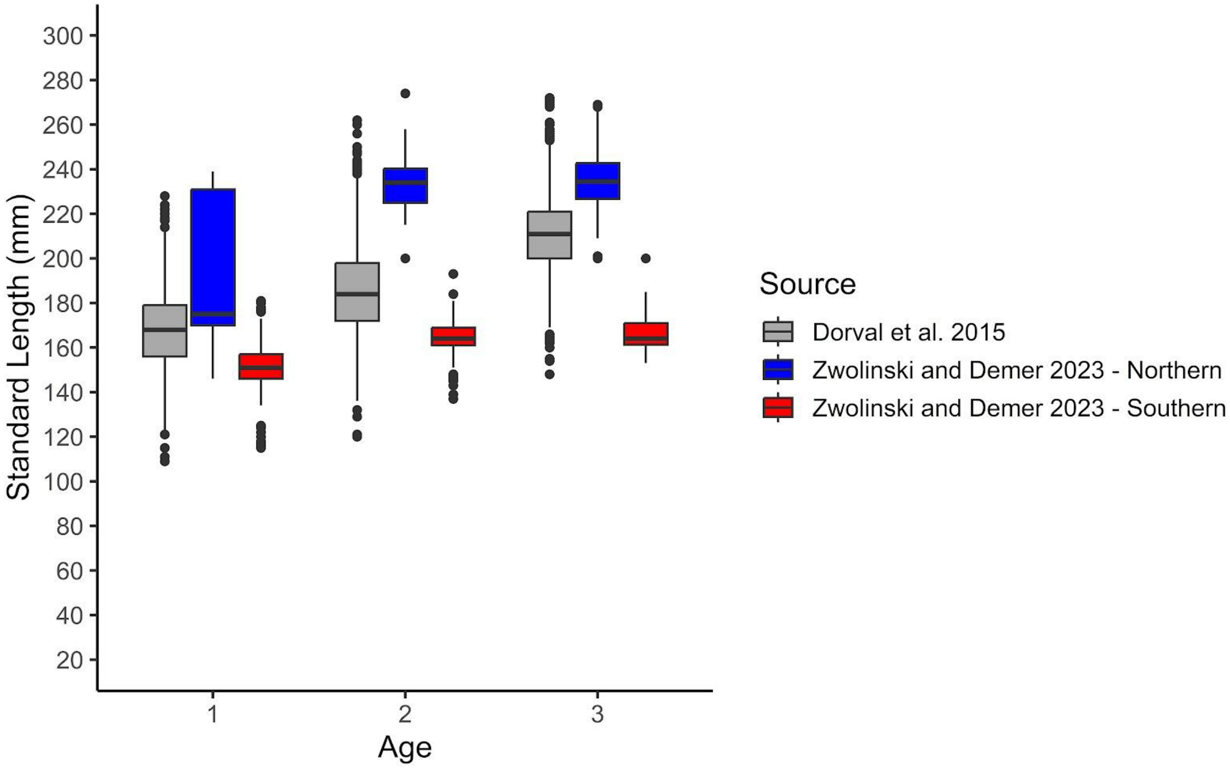

Figure 5. Boxplots of mean length-at-age for age classes 1, 2, and 3 of Pacific sardine (*Sardinops sagax*) sampled off California in Spring 1994, and 2004-2010 from Dorval et al. (2015) and off California in Summer 2021 by Zwolinski and Demer (2023).

indicated that the median length of each age class of the northern stock from Zwolinski and Demer (2023) in 2021 was different from Dorval et al. (2015) in some years but not different from all years across all three age classes (Table 3; Figure 6). These results further highlighted the high degree of variability in length-at-age observed at the individual and annual levels among fish assumed to be part of the northern stock, which overlapped with and were not different from fish assumed to be part of a separate stock.

From these analyses comparing the data from Zwolinski and Demer (2023) to Dorval et al. (2015), we concluded there was no evidence of persistent differences in length-at-age among assigned groups (stocks) that would indicate heritable differences in growth patterns (McBride 2015). More specifically, the length-at-age patterns observed for age-1 to age-3 Sardine sampled in 2021 were not different from previous years, and such patterns can be explained by the natural annual variation of length-at-age in Sardine reported by numerous reports and studies dating back to the 1940s (see section below on phenotypic plasticity).

Table 3. Pairwise comparisons from Dunn's tests of Dorval et al. (2015) and Zwolinski and Demer (2023) for age classes 1, 2, and 3 by year and stock. Only comparisons of years with 2021 northern and southern stock are included. Asterisk indicates a significant difference. '2021 - N' represents northern stock Sardine from 2021 (Zwolinski and Demer 2023). '2021 - S' represents southern stock Sardine from 2021 (Zwolinski and Demer 2023). All other years are northern stock from Dorval et al. (2015).

Age	Group 1	Group 2	n1	n2	Z statistic	p-value	Adj. p-value	
1	1994	2021 - N	76	5	-0.3168	7.51E-01	1.00E+00	
	2004	2021 - N	17	5	1.15137	2.50E-01	1.00E+00	
	2005	2021 - N	211	5	-1.4804	1.39E-01	1.00E+00	
	2006	2021 - N	48	5	0.52436	6.00E-01	1.00E+00	
	2007	2021 - N	66	5	-0.953	3.41E-01	1.00E+00	
	2008	2021 - N	3	5	0.3002	7.64E-01	1.00E+00	
	2009	2021 - N	6	5	0.32639	7.44E-01	1.00E+00	
	2010	2021 - N	14	5	-0.8383	4.02E-01	1.00E+00	
	1994	2021 - S	76	369	10.0137	1.33E-23	5.84E-22	*
	2004	2021 - S	17	369	8.03612	9.27E-16	3.89E-14	*
	2005	2021 - S	211	369	8.54866	1.25E-17	5.35E-16	*
	2006	2021 - S	48	369	10.7802	4.27E-27	1.92E-25	*
	2007	2021 - S	66	369	7.22514	5.01E-13	2.05E-11	*
	2008	2021 - S	3	369	2.80652	5.01E-03	1.55E-01	
	2009	2021 - S	6	369	3.90063	9.59E-05	3.55E-03	*

	2010	2021 - S	14	369	3.56589	3.63E-04	1.23E-02	*
	2021 - N	2021 - S	5	369	3.12655	1.77E-03	5.84E-02	*
2	1994	2021 - N	152	44	-8.4153	3.92E-17	1.33E-15	*
	2004	2021 - N	59	44	-0.8088	4.19E-01	1.00E+00	
	2005	2021 - N	158	44	-13.518	1.23E-41	5.15E-40	*
	2006	2021 - N	165	44	-7.2043	5.84E-13	1.63E-11	*
	2007	2021 - N	163	44	-9.796	1.17E-22	4.45E-21	*
	2008	2021 - N	59	44	-5.1437	2.69E-07	5.93E-06	*
	2009	2021 - N	54	44	-5.7408	9.43E-09	2.36E-07	*
	2010	2021 - N	18	44	-3.9389	8.19E-05	1.39E-03	*
	1994	2021 - S	152	118	9.52691	1.62E-21	5.83E-20	*
	2004	2021 - S	59	118	15.3556	3.25E-53	1.46E-51	*
	2005	2021 - S	158	118	2.50886	1.21E-02	1.57E-01	
	2006	2021 - S	165	118	11.5058	1.23E-30	5.06E-29	*
	2007	2021 - S	163	118	7.82068	5.25E-15	1.63E-13	*
	2008	2021 - S	59	118	9.94011	2.79E-23	1.11E-21	*
	2009	2021 - S	54	118	8.7867	1.54E-18	5.39E-17	*
	2010	2021 - S	18	118	5.95733	2.56E-09	6.67E-08	*

	2021 - N	2021 - S	44	118	14.773	2.19E-49	9.62E-48	*
3	1994	2021 - N	66	88	-11	3.81E-28	1.37E-26	*
	2004	2021 - N	90	88	0.4834	6.29E-01	1.00E+00	
	2005	2021 - N	23	88	-10.175	2.56E-24	8.72E-23	*
	2006	2021 - N	66	88	-13.994	1.69E-44	7.42E-43	*
	2007	2021 - N	153	88	-13.328	1.60E-40	6.70E-39	*
	2008	2021 - N	242	88	-7.8884	3.06E-15	8.27E-14	*
	2009	2021 - N	430	88	-11.529	9.41E-31	3.58E-29	*
	2010	2021 - N	151	88	-5.857	4.71E-09	8.49E-08	*
	1994	2021 - S	66	22	4.1561	3.24E-05	3.88E-04	*
	2004	2021 - S	90	22	12.138	6.64E-34	2.66E-32	*
	2005	2021 - S	23	22	1.44715	1.48E-01	5.91E-01	
	2006	2021 - S	66	22	2.17562	2.96E-02	1.78E-01	
	2007	2021 - S	153	22	4.52278	6.10E-06	7.93E-05	*
	2008	2021 - S	242	22	8.22887	1.89E-16	5.29E-15	*
	2009	2021 - S	430	22	6.70422	2.02E-11	4.45E-10	*
	2010	2021 - S	151	22	8.89065	6.08E-19	1.88E-17	*
	2021 - N	2021 - S	88	22	11.807	3.59E-32	1.40E-30	*

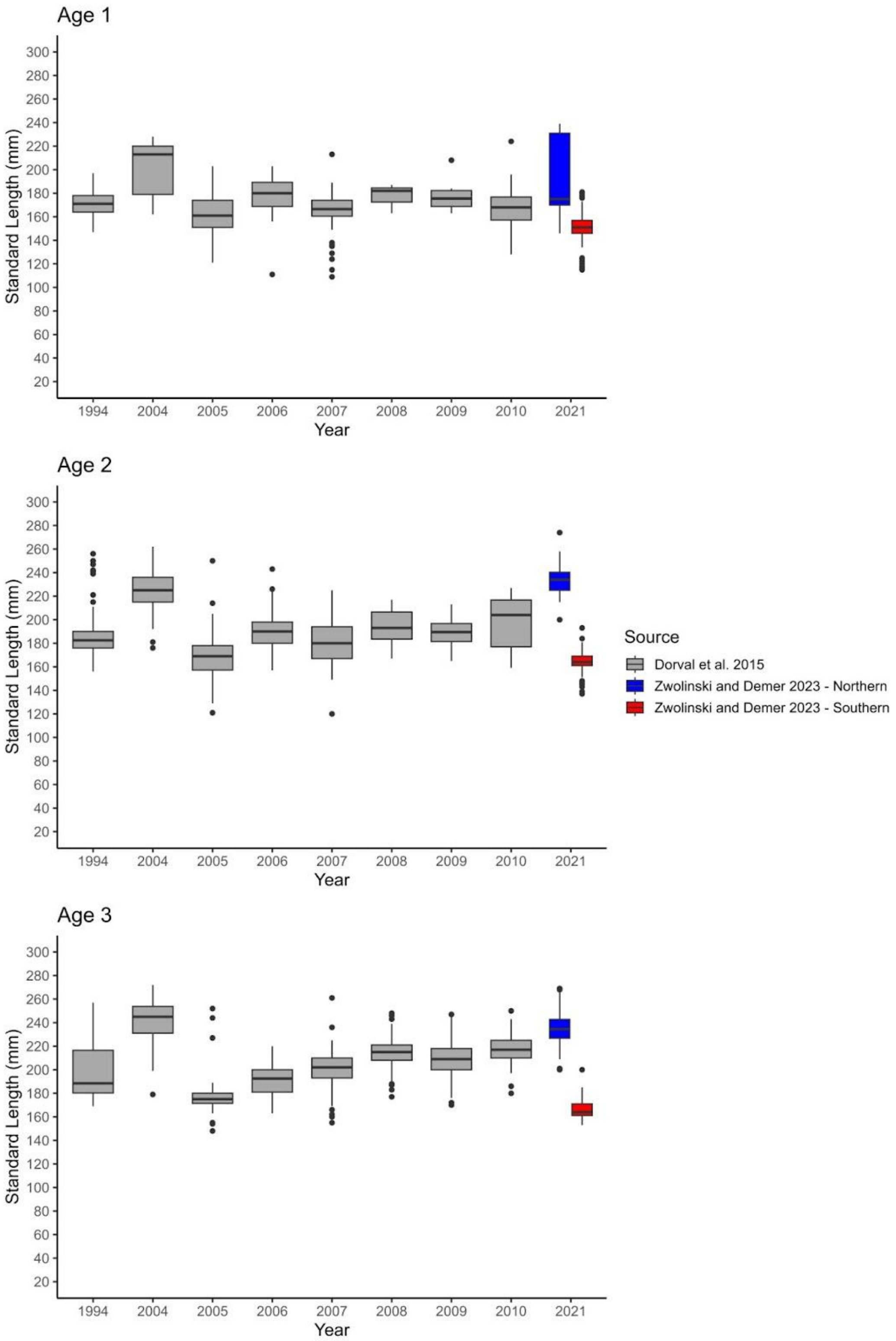

Figure 6. Boxplots of mean length-at-age by year for age classes 1, 2, and 3 of Pacific sardine (*Sardinops sagax*) sampled off California in Spring 1994, and 2004-2010 from Dorval et al. (2015) and off California in Summer 2021 by Zwolinski and Demer (2023).

Back-calculated estimates of length-at-age are problematic

When calculating means of mean length-at-age for each fishery region, early studies by Phillips (1948), Felin (1954), and Marr (1960) combined estimated age-at-length with back-calculated lengths at previous ages for the same individual fish. Modern studies on growth patterns in relation to stock identification rarely use back-calculated lengths as this approach comes with shortcomings that reduce the certainty with which results can be interpreted (Campana 1990; Brophy 2014). The first issue relates to the precision and accuracy of the length estimates produced by this method. As acknowledged by Felin (1954), it is difficult to determine the exact center of the scale when measuring scale increment widths to estimate lengths at previous ages. Both Felin (1954) and Butler et al. (1996) cited issues in the appearance of annuli, and particularly the first annulus, that affected the reliability of their age estimates and measurements. Moreover, the protracted spawning season and spatial variations in the seasonal timing of spawning mean that individual fish born in the same year will vary in their birth date, which will produce unequal durations in the first period of growth prior to production of their first annulus (Phillips 1948; Felin 1948; Butler et al. 1996). As a result, the estimated lengths at each previous age (particularly for youngest ages) will be imprecise and inaccurate. Felin's (1954) comparison of observed versus back calculated lengths highlights this problem; she found that they produced different results.

A more serious issue is the combined use of both observed lengths at age with back-calculated lengths at age from the same individual with the same analyzed data set (e.g., Felin 1954; Marr 1960). Multiple growth measurements taken from a single fish are not independent from each other because growth in adults often covaries with growth early in life (e.g., Erisman et al. 2021), particularly for short-lived, fast-growing fishes like Sardine where most of the lifetime growth occurs during the first two years of life (Dorval et al. 2015; Brophy 2014). Failure to account for non-independence of the sample distribution can obscure important information on individual variability in growth and result in erroneous statistical inference by inflating the degrees of freedom (Brophy 2014).

Felin (1954) recognized the bias and imprecision associated with the use of back-calculated lengths when she remarked that there were "greater deviations in mean observed lengths than in mean calculated lengths of a year class from its rectilinear transformation." She also commented that the variance of mean observed lengths at age was 10 times higher than the variance of calculated lengths in the growth curves for the 1942 class in San Pedro. That is, Felin (1954) understood that combining predicted ages (from back-calculated lengths) with observed ages to generate annual means and means of annual mean lengths for each age class within each port, both within and across years, would artificially reduce estimated variations in length-at-age among individual fish from a single port.

Growth studies in other clupeoid fishes have identified similar issues with the use of increment widths to infer growth rates. Takasuka et al. (2008) found that larvae of Japanese Sardine (*S. melanosticta*) and Japanese Anchovy (*Engraulis japonicus*) that grew slowly had larger otoliths than faster growing conspecifics of the same body size, which could lead to biases in the back-calculation and size estimation processes. Decoupled relationships between otolith and somatic growth rates have been reported for many species of marine fishes in response to food levels, temperature, and other factors (e.g., García et al. 1998; Fey 2006). Thus, while the correlation between otolith and somatic sizes remains a useful and practical tool for estimating earlier sizes and growth rates through back-calculations, such techniques should be scrutinized before applying them to draw inferences about the relationship between growth and population structure (Campana 1990, 2001).

Bias is pervasive in fishery-dependent (catch) data

All of the studies from Phillips (1948) through Marr (1960), as well as several more recent studies (e.g., Enciso-Enciso et al. 2022), used fish sampled from the commercial fishery landings at each particular region. The fishery-dependent data in these studies contained sampling bias associated with seasonal timing of fishing effort in relation to timing of spawning, the presence or absence of migrating adults, selectivity by vessels from particular regions for large or small fish depending on their markets (e.g., live bait vs. reduction fisheries; California fishery versus Pacific Northwest fishery; see Murphy 1966), and other factors that influenced the length distributions, age distributions, and length-at-age patterns generated. For example, the result by Phillips (1948) that younger Sardine were larger at age in Southern California than those from the Pacific Northwest was at least partially due to the fact that commercial fishing vessels targeted larger offshore fish and avoided smaller inshore fish, which would select against slower growing, smaller, immature fish that resided in known inshore nursery areas (Godsil 1931; Scofield 1934).

Upon a superficial examination of length and age distributions of Sardine sampled from the commercial fishing ports along the Pacific coast (e.g., Felin 1954; Wolf 1961), one could reach the conclusion that individuals off Southern California have shorter lifespans than those sampled farther north off the Pacific Northwest and Canada. Regional differences in age or length distributions, which can influence growth model parameters and interpretations of size-at-age patterns, can be influenced by size or age-dependent mortality due to either natural causes or fishing (Beverton and Holt 1957; Hilborn and Walters 1992). For example, it is possible that environmental conditions, resource availability or other characteristics of the more southern range of Sardine could result in higher mortality rates at larger body sizes or higher ages. Regional differences in size-selective fishing mortality (e.g., targeted removal of larger, older adults) or overall fishing intensity can also impact length and age distributions and even cause genetic changes to growth patterns (i.e., fishing-induced evolution; Conover and Munch 2002).

A more plausible explanation is that the length and age distributions of fish by the commercial fishery are biased and reflect the known biology of Sardine (e.g., seasonal migration patterns, regional differences in annual recruitment) and fishery behavior (e.g., size selectivity, seasonal fishing patterns) (Phillips 1948; Marr 1957; Marr 1960). Hart (1943) demonstrated that the largest size sardines were as abundant, or even more abundant, on the California fishing grounds as they were on the northern fishing grounds; however, they were “overshadowed” in the California catches by the disproportionately large numbers of small fish. Marr (1960) provided a detailed explanation of how the age distribution and average age of Sardine per port was influenced by the influx of a dominant year class recruiting into the fishery such that areas or years with successful spawning would artificially reduce the average age (e.g., southern region) and the lack of spawning (e.g., northern regions) would increase the average age. Clark (1952) reported that ‘winter fish’ off California ports prior to the early 1940s were larger than ‘fall fish’, which could impact the length and age composition of the catch depending on when the fishery was operating or when samples were collected from the fishery. While not emphasized, the age distributions of fish sampled from Southern California and assigned to the southern growth type by Felin (1954), Clark and Marr (1955), and Marr (1960) ranged from 1 to 8-12 years (e.g., Table 10 and Figure 22 in Marr 1960), which is the same as fish assigned to the northern growth type and contradicts the argument of a southern subpopulation with a shorter lifespan. In those studies, a shorter lifespan was concluded based on the low proportion of fish sampled from Southern California that were age 5 and older (e.g., Table 10 and Figure 14 in Clark and Marr 1955).

Locations of sampling relative to the hypothesized geographic ranges of the subpopulations can also lead to bias. The fishery regions sampled by Phillips (1948), Felin (1954), and Marr (1960) were not congruent with the hypothesized range of the two subpopulations. Sample locations often fell within the range of only the putative northern subpopulation, which is thought to occur from Northern Baja California to British Columbia (e.g., Marr 1960; Smith 2005; Demer and Zwolinski 2014; Kuriyama et al. 2024). For example, the analyses in Felin (1954) and Marr (1960) reporting differences focused on comparisons between San Pedro and British Columbia. It is known that individual adult Sardines migrate seasonally between these two regions (Clark and Janssen 1945). Also, fish from both subpopulations are thought to spawn off Southern California at different times of the year, and juveniles then occupy inshore areas for a year or more before maturing and migrating as adults (Godsil 1931; Marr 1960; Weber et al. 2015; McDaniel et al. 2016). These factors were not considered by Felin (1954), as all fish sampled from the San Pedro fishery were included in her analyses, which means they likely included some mixture of fish from both putative subpopulations. As recognized by Phillips (1948), if individual fish are born in one fishery region (e.g., Southern or Central California) and then are sampled as adults in another region (e.g., Pacific Northwest), then generating separate regional growth curves is not appropriate due to issues associated with non-independence. If growth patterns are to be compared between two groups, there should be some reasonable amount of certainty that sampled fish are accurately assigned to the correct group (or that these groups exist).

Results from the recent study by Enciso-Enciso et al. (2022) were also based on samples collected from commercial catches landed from Ensenada in Northern Baja California to Magdalena Bay in Southern Baja California. While the narrow range of ages and the rarity of fish older than 3 years is consistent with a short-lived southern stock, an equally plausible and simpler explanation is that such results are due to the biased sample distribution generated from a regional fishery with size and age selectivity. Specifically, the lack of large fish in the commercial catches could be due to the targeting of nearshore areas typically occupied by smaller, younger fish (e.g., to be processed as fish meal or as food for the local tuna mariculture industry) or a result of the high exploitation rate and fishing mortality of the Sardine fishery in this region that currently represents the most important commercial fishery in Mexico as measured by catch volume (Ojeda-Ruiz et al. 2022).

Bias present in fishery-independent (survey) data

Studies whose data and otolith samples were collected during fishery-independent surveys of Sardine also contained varying levels of bias, as the surveys themselves were not designed to study growth patterns. For example, data from both Butler et al. (1996) and Dorval et al. (2015) were collected primarily during spring surveys that targeted sampling of Sardine adults and eggs within the main offshore spawning areas off Central and Southern California. Consequently, small and younger fish (e.g., small age-0) that reside in inshore waters and that are not sexually mature were underrepresented in the data set, which then impacted the parameter estimates of the growth model. Recent A-T surveys have routinely captured individuals 100 mm SL and smaller in shallow waters (Zwolinski et al. 2016; Stierhoff et al 2019; Stierhoff et al. 2023).

Age and length data from Zwolinski and Demer (2023) were from the 2021 summer A-T survey. Biosampling methods employed for annual A-T surveys are not designed to assess spatial patterns in the length or age distribution of Sardine along the coast. For example, the survey does not actively search for schools of Sardine and then sample those schools to characterize length, age, or other traits over the entire survey range (Renfree et al. 2022). Moreover in 2021, very few trawls from the FSV *Reuben Lasker* had positive collections of Sardine (Zwolinski and Demer 2023, Fig. 8), such that the length and age data of putative northern stock sardine were from 5 trawls and 2 nearshore purse seine sets. For the southern stock, only one third of sardine collected from the FSV *Reuben Lasker,* and none from the RV Jorge Carranza Fraser were aged. Zwolinski and Demer (2023) supplemented the southern stock ages from the FSV *Reuben Lasker* with age data collected from 19 nearshore purse seine sets. Thus, the age at length data for the southern stock was based on a biased subset of fish primarily from nearshore Southern California (northern extent of their range), and a lack of any fish sampled in the center of their hypothesized range off Baja California. This is a clear example of cluster sampling (Nelson 2014), which creates issues of non-independence among sampled fish, can deviate from the basic assumptions of random sampling, and can greatly reduce the accuracy (increase bias) of results when data from these few clusters are used to estimate attributes of the entire population. Here, fish from the same haul (trawl or seine set) are likely from the same school or a nearby school and are clustered non randomly according to similarities in size or age (i.e., assortative schooling). The reliance upon nearshore samples from Southern California to represent length-at-age patterns of the southern stock also explains why their sample distribution was comprised mostly of small (< 180 mm SL) and young (0-2 years) fish, since these areas serve as nursery habitat for young Sardines (Godsil 1931; Weber et al. 2015). Thus, the regional distribution of samples in Zwolinski and Demer (2023) was not large enough to draw informed conclusions about growth patterns between putative stocks.

Sample distribution bias present in most studies

When modeling somatic growth in fishes, it is important to sample fish from each age and length class in sufficient quantities regardless of their relative abundance in order to generate robust growth models (Coggins et al. 2013; Miranda and Colvin 2017; Bolser et al. 2018). This sampling approach allows the model to achieve accuracy and produce results that mirror the biological reality of the population or species and the environmental conditions under which they've evolved. This is because length and age data used to model somatic growth in marine fishes are highly susceptible to sample distribution bias, particularly for short-lived, fast-growing species (Bolser et al. 2018; Enciso-Enciso et al. 2022). Specifically, estimates for predicted maximum length (L_∞) are highly sensitive to the number of samples of larger and older fish from the population. Failure to obtain a sufficient number of older aged fish in the population (e.g., due to rarity from overfishing or improper sampling design) results in an underestimate of L_∞ and overestimate of k (Miranda and Colvin 2017; Bolser et al. 2018). Conversely, L_∞ can be overestimated and k can be underestimated if seasonality is ignored in growth models of clupeoids and other marine fishes that display seasonal growth oscillations (Schwartzkopf et al. 2023). This often leads to spurious interpretations of differences in growth patterns among groups. Similarly, accurate estimates of t_0 require sufficient sampling of small age-0 fish, and undersampling may lead to overestimation. We mention this issue, because as described above in several places, sample distributions with respect to length and age classes were inconsistent among regions and years in nearly all of the studies that attempted to compare growth patterns among regions.

As one important example of the effects of sample distribution bias on growth models for Sardine, it is almost certain that the difference in L_∞ reported by Felin (1954) between Sardine collected off San Pedro versus British Columbia was due to the lack of larger, older adults included in samples from San Pedro. Older and larger fish do occur off San Pedro but are proportionally less abundant in the fishery catches than smaller, younger fish (Hart 1943; Marr 1960; Murphy 1966). As mentioned above, the sampled age distributions in historical studies (e.g., Felin 1954; Marr 1960) ranged from 1 to 8 years or older across all fishery regions. The same argument would apply to the collection of small, young fish from the Pacific Northwest despite their scarcity due to infrequent spawning and recruitment in that region. Studies by Butler et al. (1996) and Enciso-Enciso et al. (2022) also suffered from sample distribution bias that reduced the quality and increased the uncertainty of their results. When generating the growth models for each region, Butler et al. (1996) had to fix the theoretical age at which the fish would have zero length (t_o), because there were no ages for small or young fish that could anchor the growth curve. Similarly, the absence of larger fish older than age 6 resulted in an underestimation of the theoretical maximum (asymptotic) length at which growth rate is expected to be zero (L_∞). These issues, coupled with low accuracy and precision in age estimates led Butler et al. (1996) to conclude that it was uncertain whether their reported growth differences were due to actual patterns or bias and error. Enciso-Enciso et al. (2022) attempted to address sample distribution bias by bolstering the data set with simulated values, because their data set lacked any small, young or large, old fish such that 82% of the fish were 1 to 3 years of age.

The infrequent collection of Sardine and clustered sampling design generated inadequate sample sizes and sample distributions that weakened the conclusions of Zwolinski and Demer (2023) regarding evidence of different growth patterns among putative subpopulations. First, they reported a difference between length-at-age of 1 year old fish assigned to the northern and southern stock despite having only five samples from the northern stock (versus 369 for southern stock). They also reported a higher L_∞ for the northern stock despite the southern stock not having any samples larger than ~ 200 mm SL and older than 4 years of age and without any statistics. Notably, the maximum length and age of fish assigned to the southern stock by Zwolinski and Demer (2023) were smaller than the maximum length and age values reported for the same stock by Enciso-Enciso et al. (2022) (226 mm SL and 6 years) and fish following the southern growth type described by Felin (1954) (>250 mm SL and 8+ years). The limited sample size and biased sample distribution make it unreasonable to draw conclusions regarding growth patterns at the population level.

Reported growth patterns indicate phenotypic plasticity within a widely distributed population that experiences variable environmental conditions

Phenotypic plasticity in somatic growth is widespread among marine fishes, both at the individual (genotype) and population (sample of genotypes) levels, thus representing the default explanation when there is a lack of evidence of heritable differences (Sinclair et al. 2002; McBride 2015; Lorenzen 2016). Growth plasticity is the adaptive ability of organisms to exhibit different growth patterns in response to variable environmental conditions and is often visible in temporal, spatial, and ontogenetic patterns of growth in exploited fish populations (Beverton and Holt 1957; Brander 1995; Lorenzen and Enberg 2002). The signature of growth plasticity is readily evident when observed variations in spatial or temporal growth patterns are too high in magnitude and duration to reflect just noise and occur too rapidly to be a product of evolution (Lorenzen 2016). Furthermore, phenotypic plasticity in somatic growth at the individual and population level is predicted for species with large geographic ranges that span across large environmental gradients and are characterized by individuals that experience a diverse range of environmental conditions during their lifetime (Enbody et al. 2021).

Observed patterns in length-at-age and growth in Sardine match those associated with phenotypic plasticity and oppose those associated with distinct, regional adaptations. Large variations in individual length-at-age at all spatiotemporal scales is clearly the strongest signal in growth, as it has been consistently reported among studies from the 1940s to those published very recently (e.g., Phillips 1948; Felin 1954; Felin et al. 1955; Felin et al. 1958; Wolf et al. 1958; Marr 1960; Butler et al. 1996; Dorval et al. 2015; Enciso-Enciso et al. 2022). Most, if not all, of these studies showed large overlaps in the length distributions of individuals for each age class, both within and among years, within and among ports, and within and among regions. In fact, individual variation in length-at-age and growth is so large an individual collected from a single region and measured at a given length may occupy any of up to seven age classes (e.g., Felin 1954; Felin et al. 1958; Wolf et al. 1958; Marr 1960; Dorval et al. 2015). Related to this, Wolf et al. (1958) reported no difference in mean length among eight year-classes of Sardine collected from the Southern California fishery. Similar results showing large overlaps in length distributions among ages classes within regions, both within and among years, that were equal to or greater than any variations among regions are evident in the tables and graphs of Felin (1954) and the results reported by Phillips (1948), Mosher et al. (1949), Felin et al. (1958) and many other studies mentioned in this review.

Phenotypic plasticity in growth and other life history traits is predicted for Sardine, whose range in North America extends beyond the entire CCLME and spans three coastal zoogeographic provinces, three oceanic water masses, and a whole coastal upwelling zone (Moser et al. 1993). Environmental conditions in the CCLME vary on daily, interannual, and decadal scales (McClatchie 2014), which can create patchiness at fine to coarse scales in the distribution of both favorable and unfavorable habitat. Additionally, highly fluctuating environmental conditions can also lead to variability in assemblage, size structure, and abundance of zooplankton and phytoplankton that Sardine feed upon in the CCLME

(Rykaczewski 2019). Clupeoids in the CCLME and elsewhere are known to capitalize during periods of favorable environmental conditions through increases in feeding, survivorship, and growth, which directly translate into rapid increases in abundance and recruitment (Blaxter and Hunter 1982; Sydeman et al. 2020). From an eco-evolutionary perspective, this pattern is referred to as an opportunistic life history strategy (Armstrong and Shelton 1990; Winemiller and Rose 1992; King and McFarlane 2003), and it is characterized by early maturation, small body sizes, high fecundity, fast growth, short lifespans and other traits associated with Sardine.

Phenotypic plasticity has been reported to explain observed spatiotemporal variations in growth for Sardine, other clupeoids in the CCLME, and other sardine species. For Sardine, studies by Phillips (1948), Felin (1954), Marr (1957, 1960), Smith (2005), and others all acknowledged, in some cases repeatedly, that observed regional patterns in length-at-age could be explained by phenotypic plasticity, and none provided evidence to eliminate it as a plausible, alternative hypothesis to the subpopulation hypothesis. More broadly, phenotypic plasticity in growth matches the high levels of individual variation observed for spawning and other life history traits that collectively support the concept of a single, dynamic population of Sardine along the Pacific coast (Erisman et al. 2024; Craig et al. 2025). Under this scenario, connectivity is maintained by protracted spawning seasons with large annual and decadal variations in the spatiotemporal scale of reproduction, broadcast spawning and lengthy pelagic larval duration, and large-scale seasonal migrations of adults in response to environmental conditions (Parrish et al. 1989; Lluch-Belda et al. 2003). For other clupeoids in the CCLME, Schwarzkopf et al. (2023) provided evidence of phenotypic plasticity to explain growth patterns of the northern anchovy (*Engraulis mordax*), which follows the same opportunistic life history strategy and occupy the same ecological niche. Lastly, phenotypic plasticity in growth rate has also been demonstrated for the European sardine (*S. pilchardus*) in association with food quantity and availability (Boëns et al. 2023) and the onset of sexual maturation in response to environmental conditions, food availability, and abundance trends that influence body condition (Véron et al. 2020).

In summary, phenotypic plasticity is the defining characteristic in the growth of Sardine that likely evolved in response to variable environmental conditions, ontogenetic and seasonal shifts in habitat, conspecific abundance, prey food supply, regional differences in the duration of seasonal growth periods, and other factors. Consequently, the signal from within-group variation in length-at-age and growth greatly exceeds that from among-group variation, which means that growth is not useful for discriminating subpopulations of Sardine along the Pacific coast (Begg et al. 1999; Waldman 1999; Higgins et al. 2015).

Reported patterns in length-at-age reflect the complex life history of Sardine

Regional patterns in length-at-age in Sardine are readily explained by individual and regional variations in the seasonal migration patterns of adults that are correlated with body size and age, ontogenetic shifts in the preferred habitat and distributions of adults versus juveniles, a protracted spawning season that varies spatially and temporally at fine scales that determines the duration of the first year of growth, and regional differences in the frequency and intensity of spawning and recruitment (Phillips 1948; Felin 1954; Marr 1957b; Marr 1960; Parrish et al. 1989; Butler et al. 1996; McDaniel et al. 2016). When these aspects are combined with overwhelming evidence of phenotypic plasticity, sample distribution bias, and no direct evidence of regional differences in growth among the studies reviewed, the argument for subpopulations with distinct, heritable growth patterns evaporates.

Phillips (1948) was the first to thoroughly examine patterns in length-at-age from Sardine sampled among fishing regions from Southern California to the Pacific Northwest. He considered the combined effects of partial migration based on condition, mixing among fish born in different regions, and differences in the timing of birth on the length of fish when the first annulus was deposited to generate a single growth curve representing a single population along the Pacific coast. Phillips (1948) concluded that the known seasonal migrations of older adults farther north demonstrated from tagging studies (Clark and Janssen 1945) sufficiently explained the proportionally high abundance of much older age classes in the catches of Sardine from the northern region (Figure 12A; represents Figure 4 from Phillips 1948). Moreover, the much higher frequency and intensity of spawning in the south compared to the north (Scofield 1934; Clark 1935; Marr 1960) explained why younger age classes in Southern California were much more abundant and tended to be larger-at-age than those rarer, young fish harvested in the north. Phillips (1948) reasoned that older age classes of Sardine harvested from the northern regions were present due to better feeding conditions and less competition for food, which would also explain why adults migrated northward seasonally during the non-spawning season. In addition, the scarcity of larger fish at age from older age classes sampled in the catches in the south was attributed to their seasonal occurrence that did not coincide with the timing or locations of the regional fishing effort (Hart 1943).

Subsequent studies by Felin (1954), Clark and Marr (1955), Marr (1957, 1960), Butler et al. (1996), Smith (2005) and others provided various combinations of the same alternative explanations as Phillips (1948) that were grounded in empirical studies documenting the complex life history of Sardine. For example, Felin (1954) repeatedly acknowledged that regional variations in length-at-age she reported may reflect the spatial and temporal variations in environmental conditions associated with the timing of spawning, the juvenile nursery period (1-2 years), and ontogenetic and seasonal migrations of larger, older (adult) individuals. Similarly, Butler et al. (1996) concluded that their observed latitudinal cline in length-at-age for 1 to 3 year old fish could be attributed to variable timing of spawning (i.e., birth date) resulting in differences in the duration of the first growth season. Numerous studies have shown that, while seasonal peaks occur in some areas during some years, measurable spawning occurs during most or all months of the year throughout its range (e,g., Ahlstrom 1965; Hernandez-Vasquez 1994; Lluch-Belda et al. 2003). In fact, since the birth (hatch) date of individuals is unknown, when ages are assigned to sampled fish for use in stock assessments, it is assumed that all fish hatched during a calendar year are born on July 1st (Yaremko 1996).

Phillips' (1948) insights on partial migration in Sardine were remarkable for that time period. He posited that smaller adults-at-age may be those of lesser condition that do not migrate (or migrate lesser distances) and remain as residents in the south. The body of literature that has since emerged suggests this to be typical among migratory marine fishes (Chapman et al. 2011; Secor 2015). Migration within a population can be conditionally dependent on size, age, growth rate, maturity, physiological condition and change throughout the life cycle of the individual (Chapter 6 in Secor 2015). While the migratory behavior of Sardine hasn't been studied directly since the 1940s, it has been linked to age- and size-based ontogenetic changes associated with maturation (McDaniel et al. 2016). The rationale applied by Phillips (1948) has been used in more recent studies of sardine species as a reminder that failure to account for variations in migratory behavior can lead to misinterpretations of growth patterns. For example, Silva et al. (2008) attributed geographical variation in reported growth patterns to age-related migration in European sardine (*Sardina pilchardus*) that influenced the age and age length distributions of sampled fish.

As discussed in the preceding section on sampling bias and related to the ontogeny and life history of Sardine, it is important to consider seasonal, habitat, and regional differences in the distribution and relative abundance of different life stages (juveniles vs. adults), lengths, and ages of Sardine when interpreting survey data to characterize and model somatic growth patterns at a population scale. These patterns are reflected by regional differences in the age compositions and year-class strength of Sardine reported in historical studies (e.g., Figure 4 in Phillips 1948; Figures 16 and 30 in Marr 1960). Briefly, we should expect adults to be more common offshore compared to inshore and more abundant off the Pacific Northwest in the summer and fall months compared to Southern California. Conversely, juveniles and small adults (up to 2 years of age or older) are known to occupy and remain in nearshore habitats year-round and do not migrate. Moreover, we would expect to sample few small, young Sardine off the Pacific Northwest and Canada, since spawning and larval recruitment is less frequent, less expansive, and lower in magnitude in the Pacific Northwest and Canada compared to California and Baja (Parrish et al. 1989; Hernandez-Vazquez 1994; Lluch-Belda et al. 2003; Emmett et al. 2005; McFarlane et al. 2005). We would expect to sample larger numbers of young, small Sardine from nearshore areas off Southern and Central California that are known centers of spawning and recruitment (Godsil 1931; Phillips 1952; Parrish et al. 1989; Hernandez-Vazquez 1994). These same principles seem to apply to sardines in other regions of the world. For example, Rogers and Ward (2007) found large differences in the age distributions of inshore samples from commercial catches and offshore samples from fishery-independent surveys, and they concluded that using samples from both areas was necessary to ensure growth models were representative of the entire population.

Length-at-age data and growth information should not be used to corroborate the habitat model

The subpopulation hypothesis for Sardine represents the archetype for management of Sardine in the U.S. (PFMC 1998; Yau 2023), and as a result, it shapes the design of the annual fishery-independent survey used to estimate the biomass and distribution of Sardine that informs the annual stock assessment (Renfree et al. 2022; Kuriyama et al. 2024). Since 2014, a habitat model has been used to separate out northern subpopulation biomass and landings (Hill et al. 2014; Zwolinski and Demer 2014; Kuriyama et al. 2024). As part of an update of the habitat model, length-at-age data and growth information produced from the fishery-independent survey in 2021 were used to corroborate the apportionment to the northern subpopulation and estimate its distribution and biomass (Zwolinski and Demer 2023).

We disagree with the methods used by Zwolinski and Demer (2023) to separate length-at-age data into two stocks (Figure 8; their Figure 9) and to report differences in lengths between the stocks for ages 1-3. The study modeled the potential habitat of the northern stock with "data on sardine-egg presence and absence and concomitant satellite-sensed SST and chlorophyll-a concentration" from spring surveys in 1998-2019. Based on these data and previous studies suggesting there are distinct Sardine stocks with adults (Félix-Uraga et al. 2004) or spawning adults (Zwolinski et al. 2011) adapted to different temperature intervals, Sardine sampled during the summer 2021 A-T survey in waters with sea-surface temperatures less than ~16-17 °C (habitat model also considers chlorophyll-a concentrations) were assigned to the northern stock. By default, fish collected in waters above the threshold were assigned to the southern stock. However, Sardine spawning occurs during most months of the year from California to southern Baja (Ahlstrom 1965; Hernandez-Vazquez 1994), and there is no biological evidence of separate groups or subpopulations of Sardine adapted to different thermal ranges during spawning or non-spawning periods (Erisman et al. 2024; Craig et al. 2025). For example, Sardine exhibit a consistent, broad, unimodal distribution in spawning temperatures of approximately 9 to 28 °C along the Pacific coast, with the highest occurrences of eggs from approximately 13 to 18 °C (Tibby 1937; Ahlstrom 1954, 1959; Lluch-Belda et al. 1991). Moreover, the conclusion by Félix-Uraga et al. (2004) of groups of Sardine adapted to different temperature ranges lacks empirical, statistical, and theoretical support (reviewed by Craig et al. 2025). Therefore, the partitioning of length-at-age data from adult Sardine into separate stocks (their Figure 9) based on a temperature threshold was invalid.

A more serious issue is that the habitat model assigned nearly all small, young fish ($\lesssim$ 150 mm SL and 2 years of age) sampled from nearshore areas in the summer to the southern stock using the same temperature thresholds (their Figure 8 and 9). This is problematic, because the model was built using predicted habitat of spawning adults from offshore surveys, and thus it was not informed by any information on the thermal range or other habitat characteristics of juvenile Sardine known to inhabit inshore nursery areas off California and northern Baja year-round (i.e., a much wider thermal range). Since the model cannot resolve suitable habitats for juveniles, and most of these fish were collected in shallow, warm water areas above the temperature threshold (because they don't migrate; Clark and Marr 1955; McDaniel et al. 2016) and considered unsuitable habitat for the northern stock, they were mistakenly assigned to the southern stock.

Recognizing that the methods used to separate length-at-age data into two stocks was invalid for both adults and juveniles, if one simply removes the color (stock) assignments of the data plotted in their Figure 9, a single growth curve emerges. As predicted for the Sardine population, the data forming this single curve is comprised of small, young Sardine collected almost entirely from their known nursery habitat in nearshore waters (Godsil 1931; Scofield 1934; Weber et al. 2015), and the larger and older adult Sardine collected mostly from their known summer habitat off the Pacific Northwest (Clark and Janssen 1954). This explanation is consistent with the known life history of Sardine and matches the explanation given by the first growth curve published for Sardine by Phillips (1948). The same rationale can be applied to the disjoint length distributions of Sardine assigned to the northern and southern stocks by Zwolinski and Demer (2023) in 5 of the 7 summer surveys after 2014 (their Figures 8 and S4). During a period of historically low Sardine abundance along the Pacific coast of the U.S., a very patchy distribution of adults located mostly off the PNW (blue circles) and juveniles occupying nearshore nursery habitats (red circles) is expected for a survey conducted in the summer and fall months. These two groups don't represent distinct subpopulations with different growth patterns; they reflect length, age, and maturity-based, regional distributions that are well-documented in the literature (Figure 13) and representative of a single, panmictic population of Sardine along the Pacific coast.

Part IV: Summary of Main Conclusions

1. An exhaustive review of the available literature produced a total of 8 studies that examined spatiotemporal patterns in length-at-age and somatic growth of Sardine along the Pacific coast of North America (Phillips 1948; Felin 1954; Clark and Marr 1955; Marr 1960; Butler et al. 1996; Dorval et al. 2015; Enciso-Enciso et al. 2022; Zwolinski and Demer 2023). Surprisingly, only two of these studies (Dorval et al. 2015; Enciso-Enciso et al. 2022) were properly designed to examine patterns in somatic growth, and even these contained biases that impacted the quality and certainty of the results generated. Therefore, our understanding of spatiotemporal patterns in somatic growth of Sardine and the relative influence of various biotic and abiotic drivers is limited and warrants further investigation.
2. Among the studies reviewed, we found no evidence of regional differences in growth patterns to support the hypothesized existence of two subpopulations of Sardine along the Pacific coast. Reports of regional growth differences were sparse, inconsistent, and provided inadequate statistical support. Moreover, nearly all studies contained persistent sampling, methodological, and analytical practices that mis-specified sources of error, precision, and bias that weakened the quality and certainty of results (i.e., type I error) and led to unsupported conclusions. More broadly, there is no genetic evidence of subpopulations to support the idea of heritable differences in growth among Sardine from different regions, and proposed mechanisms to promote and maintain subpopulations (e.g., isolated spawning areas and separate migration patterns) also lack any empirical support.
3. As acknowledged in most studies examined and as first proposed by Phillips (1948), the most parsimonious explanation grounded in empirical support and offered in numerous historical studies is that perceived regional patterns in length-at-age are indicative of phenotypic plasticity in the growth patterns of individual Sardine in response to variations in environmental conditions and other factors. The signature of growth plasticity is evident from very large variations in length-at-age at all spatiotemporal scales, which represents the strongest signal in growth consistently reported in the literature. Phenotypic plasticity is predicted for opportunistic strategists like Sardine that have broad geographic ranges spanning across large environmental gradients and are characterized by individuals that experience a wide range of environmental conditions during their lifespan.
4. Reported patterns and distributions in length-at-age reflect the complex life history of Sardine. They are readily explained by individual and regional variations in the seasonal migration patterns of adults that are correlated with body size and age, ontogenetic shifts in the preferred habitat and distributions of adults versus juveniles, a protracted spawning season that varies spatially and temporally at fine scales that determines the duration of the first year of growth, and regional differences in the frequency and intensity of spawning and recruitment. Consequently, and as first summarized by Phillips (1948), somatic growth in Sardine is best described by a single growth model that integrates the complex ontogenetic behavior, complex life history, and broad geographic range of a single population along the Pacific coast.

5. Based on the lack of evidence of differences in growth, pervasive methodological issues among studies that reported differences, and the existence of more parsimonious explanations to explain the observed regional patterns in length-at-age data from fishery-dependent and fishery-independent sources, such information should not be used as corroborative evidence to assign Sardine sampled from fishery-independent surveys to specific stocks for use in biomass estimates and stock assessments. We caution against the sampling and analytical methods used by Zwolinski and Demer (2023), which deviate widely from best practices in sampling and experimental designs and growth studies in fishes, to evaluate growth differences and apply them to evaluations of population structure in Sardine.
6. Our conclusions on somatic growth are consistent with our reviews of other traits (e.g., genetics, spawning, demographics, migrations, vertebral counts, parasites, otolith morphology) showing no valid evidence to support the existence of multiple subpopulations of sardine along the Pacific coast (Craig et al. 2023; Erisman et al. 2024; Craig and Longo 2024; Craig et al. 2025.; G. Longo and M. Craig, unpublished data). The results of this and other reviews on population structure illuminate the need to re-evaluate the biological criteria used to design research surveys, shape our biomass estimates and stock assessments, and define management units (i.e., stocks) of Pacific Sardine in the U.S.

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