

DO SHIFTS IN OTOLITH MORPHOLOGY OF YOUNG PACIFIC SARDINE (*SARDINOPS SAGAX*) REFLECT CHANGING RECRUITMENT CONTRIBUTIONS FROM NORTHERN AND SOUTHERN STOCKS?

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ABSTRACT

An investigation of otolith morphology of young Pacific sardine (*Sardinops sagax*) caught off San Diego and Monterey, California during 2006–12 revealed an increase in the lighter, more rugose phenotype that predominates in otoliths of sardine captured off Baja California, Mexico. This increase began in July 2008, correlated with decreasing spawning biomass of the northern (cold) stock, and coincided with the decline in growth rates of adult sardine interpreted from otolith weight–fish length relationships. Measurements of habitat temperatures inferred from oxygen stable isotope composition in juvenile otoliths showed morphology and temperature were independent variables, but inferred temperatures were about 2°C higher after July 2008. The shift in otolith morphology did not appear in the adult population in 2009–12. Environmental factors related to a cold phase of the Pacific Decadal Oscillation may have influenced these shifts in juvenile otolith shapes. The results are consistent with a declining contribution of northern stock recruits to the fishery off California.

INTRODUCTION

Pacific sardine (*Sardinops sagax*) is a major pelagic species in the California Current ecosystem. Currently, the range of the commercial sardine fishery extends from Vancouver Island (British Columbia, Canada) to Bahía Magdalena (Baja California Sur, Mexico) (fig. 1). A sardine fishery also occurs in the warm waters of the Gulf of California. Young sardine (age–0 to age–3, <200 mm length) form the basis of a lucrative coastal fishery in southern and central California.

The overall population can be divided into three major subpopulations that differ in preferred temperature, season of spawning, and major areas of spawning (reviewed by Smith 2005): 1) a cold or northern stock that extends from British Columbia to Ensenada (northern Baja California); 2) a temperate or southern stock that extends from southern California to the tip of Baja California; and 3) a warm or Gulf of California stock. Three areas of high spawning activity correspond to these stocks, respectively: one off central and south-

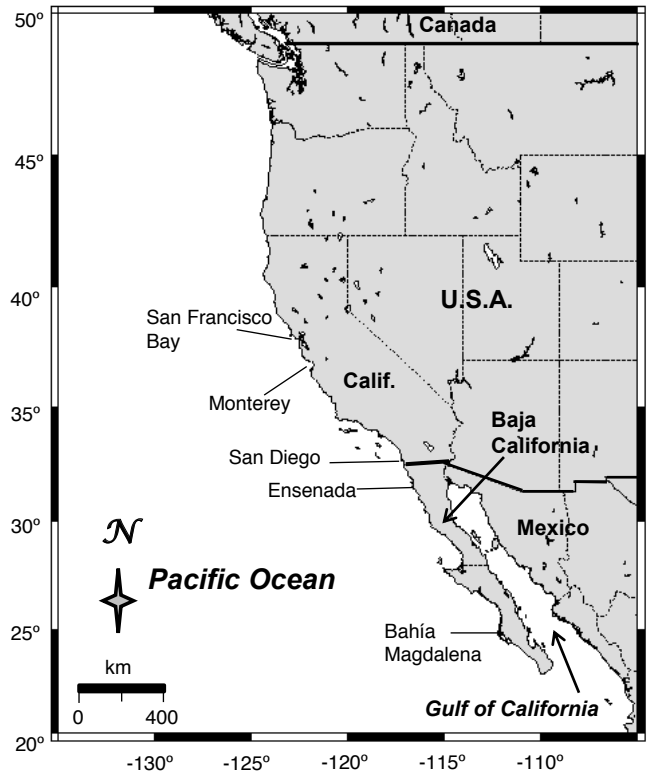


Figure 1. Map of the collection sites of *S. sagax*.

ern California; one off Bahía Magdalena; and a third in the Gulf of California. However, data from decades of California Cooperative Oceanic Fisheries Investigations (CalCOFI) surveys suggest that if conditions are favorable, sardine eggs may be found almost anywhere along the coast (Southwest Fisheries Science Center [SWFSC] data). All three stocks undertake annual seasonal migrations, and they likely have regions of overlap in distribution (Félix-Uraga et al. 2004, 2005; Smith 2005).

Following the historic collapse of the California sardine fishery in the 1940s and 1950s, and its recovery beginning in the 1980s, fisheries scientists and the CalCOFI program have conducted extensive research into sardine biology and modeling their associated oceanographic conditions in the California Current system (e.g., articles in every volume of CalCOFI Reports; Norton and Mason 2005; Reiss et al. 2008; Rykaczewski

and Checkley 2008; McClatchie et al. 2010; Zwolinski et al. 2011; Song et al. 2012; Lindegren and Checkley 2013). However, a number of key factors remain poorly understood, such as the sources of recruitment to the spawning stock; survival of eggs, larvae, and schooling young sardine; and the extent of drift and migratory behavior of young juveniles.

Older juvenile sardine that are targeted by commercial fisheries migrate seasonally within preferred temperature zones that shift north and south (Félix-Uraga et al. 2004, 2005; Zwolinski et al. 2011). The maximum sea surface temperature (SST) associated with potential habitat for the northern stock, 16.4°C, serves as an indicator to separate southern and northern stocks when temperature-at-catch is monitored (Juan Zwolinski, pers. comm., 29 March 2013). The average monthly SST values near Ensenada and San Pedro, CA (180 km north of San Diego) during 1982–2012 indicated winter temperatures (January–April) were consistently <16.4°C, and summer temperatures (July–November) were consistently >16.4°C at both locations.

Besides temperature at catch, other methods have been employed to identify unique characteristics of regional sardine stocks with variable degrees of success, including egg, larval, and adult surveys; fish morphometrics; vertebral counts; tags; parasites; and acoustic-trawl surveys (Smith 2005; Lo et al. 2005, 2010, 2011; Baldwin 2010; Demer et al. 2012). Genetic studies have not yielded regional markers so far (Hedgecock et al. 1989; Grant and Bowen 1998; Pereyra et al. 2004; García-Rodríguez et al. 2011). However, otolith studies show promise for evaluating regional and age characteristics (Félix-Uraga et al. 2004, 2005; Valle and Herzka 2008; Javor et al. 2011; Dorval et al. 2011; Javor and Dorval, submitted).

Spawning seasons of sardine have regional features. The warm (Gulf) stock spawns during the late fall and winter in the Gulf of California while the southern (temperate) stock spawns during the summer in Bahía Magdalena (Smith 2005). The northern stock spawns principally in southern and central California during the early spring (Lo et al. 2005), although migrating adults can spawn in the summer in the Pacific Northwest (Emmett et al. 2005; Lo et al. 2010). Prior to the mid-1990s, the northern stock also regularly spawned near shore in southern California during the summer (SWFSC and CalCOFI data; Andrew Thompson, pers. comm., 29 March 2013).

The spawning off California is probably the source of many of the juveniles commercially caught near San Diego (southern California) and Monterey (central California). It is generally believed sardine recruit to the offshore California stock upon reaching maturity. Although juveniles from both locales are considered members of

the same stock, otolith morphology (Javor et al. 2011) and oxygen stable isotope composition (Javor and Dorval, submitted) indicate they have distinct regional characteristics, at least until they reach maturity.

Since Campana and Casselman 1993 showed Atlantic cod (*Gadus morhua*) growth rates significantly correlated with otolith shape, morphometric analysis of otoliths has been widely used as a tool to detect stock structure and interannual variability in fish. Genetic, physiological, and environmental factors control otolith shape. Fast growth rates are associated with smaller otolith sizes relative to fish length in a number of species (Fletcher 1995; Strelcheck et al. 2003; Kristoffersen 2007). Feeding condition may affect both growth and otolith morphology (Gagliano and McCormick 2004; Hüsey 2008). Temperature influenced otolith size in tank-reared fish (Høie et al. 1999), and it likely regulates otolith growth in natural populations of *Merluccius* spp. and *Coelorhynchus* spp. (Lombarte and Leonart 1993; Bolles and Begg 2000).

A combination of otolith morphology and weight, termed perimeter-weight profiles or PWP, described regional phenotypes in Pacific sardine juveniles (Javor et al. 2011). Otoliths from southern stock captured off Baja California tended to be more rugose and lighter than otoliths of sardine from northern stock caught near Monterey that typically had smoother perimeters and heavier weights. Otoliths from juveniles captured near San Diego generally had an intermediate mixture of PWP features.

Another characteristic of otoliths that indicates regional environmental conditions is oxygen stable isotope content. It provides a proxy for seawater temperature because fish deposit ¹⁸O in their calcium carbonate otoliths in or near thermodynamic isotopic equilibrium with their environment (Kalish 1991; Iacumin et al. 1992; Thorrold et al. 1997; Campana 1999). Otolith stable isotope analyses have been used to distinguish stocks of Australian *S. sagax* (Edmonds and Fletcher 1997), and to identify habitat temperatures of fish at different life stages (Gao and Beamish 2003; Gao et al. 2004; Shephard et al. 2007) or seasons (Weidman and Millner 2000; Begg and Weidman 2001; Gao et al. 2001; Høie and Folkvord 2006).

Pacific sardine inhabit a broad temperature range of water, from <10°C in Oregon and Washington (Emmett et al. 2005) to >25°C in southern Baja California (Félix-Uraga et al. 2004, 2005). Dorval et al. 2011 experimentally derived a $\delta^{18}\text{O}$ -temperature calibration model for sardine otoliths in southern California. Javor and Dorval (submitted) applied those equations to a study of young and adult sardine off North America, from Canada to Mexico, that demonstrated: 1) $\delta^{18}\text{O}$ values reflected seawater H_2^{18}O content and temperature of the region of

juvenile capture; and 2) the results depended on the size of the otoliths because young sardine apparently spent progressively more time at depth (i.e., in colder water) as they grew to adulthood.

The overall goal of this survey conducted during 2006–12 was to test methods by which Pacific sardine otoliths could be used to enhance knowledge of the species and aid stock assessment and fishery management. Using otoliths of juveniles collected over 600 km apart off California (San Diego and Monterey), the study focused on significant long-term changes that commenced in mid-2008. The specific research aims were to compare morphological characteristics of otoliths of young and adult sardine using five approaches: 1) Time: seven-year study to evaluate temporal trends in juvenile otolith morphology 2) Temperature: stable oxygen isotope composition to determine the relationships between morphology, temperature, and date of capture 3) Relative abundance of rugose-light and smooth-heavy otoliths among young and mature sardine 4) Relationships to spawning condition, standard length, and growth rates 5) Correlation with an independently-derived population index, spawning stock biomass. Finally, these otoliths were compared with those of sardine landed off Mexico to demonstrate possible shifts in stock parentage of the juveniles caught off California.

MATERIALS AND METHODS

Sardine collections and measurements

Sardine were collected from a live bait receiver in Mission Bay, San Diego, CA (Everingham Brothers), from Monterey Bay, CA (California Department of Fish and Game port samples), and from annual SWFSC surveys during April along the central and southern California coast. During the course of this investigation, the SWFSC also conducted two summer surveys (2008 and 2012) between British Columbia, Canada, and the United States–Mexican border. Sample sizes were 25 fish per haul for the San Diego and Monterey samples, and 25–40 fish per haul for the SWFSC surveys. To compare whole fish attributes (length and condition factor), all fish captured in the survey cruises were evaluated. Otolith collectors, samples, and measurements were previously described for sardine caught off Mexico (Javor et al. 2011). Ages were determined using Yaremko's 1996 method. Condition factor (CF) was calculated by dividing fish weight (g) by the cube of the SL (cm), and multiplying the result by 100. CF, a measure of robustness of a fish, is generally known to be influenced by age, sex, maturation, season, and fat content.

The live bait supplier reported larger adults were sometimes found near shore in shallow water, but the seiners generally avoided catching them for the live bait

market. The seiners typically captured sardine within a few km of shore when the fish were easy to find, but they fished as far as 50 km from shore when necessary. The supplier reported extensive bait schools sometimes aggregated in San Diego; for example, 5 km long schools spanning from just outside the surf zone to about 15 m depth water. Such schools were transient, and the site, size, and hour of the aggregations changed. Everingham Brothers has been in business over 60 years, and they have developed fishing logistics predicated by when sardine form near-surface aggregations conducive for day or night seining (Buck Everingham, pers. comm., 13 August 2012).

During 2008–12, the sardine fishery in Monterey Bay was limited to summer months due to quotas. During 2012, sardine were not available for this study. Most of the fishing took place in the bay or close to it.

Fishery-independent SWFSC surveys do not target schools of sardine. Instead of seining, they trawl at night at specific stations using protocols to provide statistically representative catch data that can be incorporated into stock assessment calculations (Hill et al. 2010, 2011, 2012; Lo et al. 2011; www.calcofi.org, accessed 14 February 2013).

During 2004, 65% of the sardine captured in the SWFSC survey measured ≥ 240 mm, but in the 2005–12 surveys, only 1%–5% of the sardine measured ≥ 240 mm (Hill et al. 2012; SWFSC unpublished cruise data). Except for age-0 sardine captured in a few trawls, nearly all the sardine caught in spring surveys were in near-spawning or spawning condition (testes scored 2 or 3 on a maturation scale of 3, and ovaries scored 3 or 4 on a maturation scale of 4).

Otolith measurements

Otoliths were cleaned, aged, weighed, photographed, and processed through an image analysis protocol that resulted in a description termed perimeter-weight profile (Javor et al. 2011). Using >2200 *S. sagax* otoliths collected across their North American range, linear regression equations were derived for pairs of otolith measurements that compared perimeter vs. area, perimeter vs. length, and weight vs. length. The PWP calculation for a sample otolith compares the measured feature to that of the average otolith represented on the regression lines, resulting in positive or negative perimeter and weight residuals. The three PWP values are expressed as the percentage of positive residuals in the sample. A score of 50% is average for the population (half the residuals above the line and half below it).

Javor et al. 2011 found sardine otoliths from their southernmost range off Mexico and within the Gulf of California had generally greater perimeters than the population average because they were more rugose (multi-

lobed), and they were typically light in weight. Otoliths from Monterey Bay had generally smaller perimeters (relatively smooth outlines) and were typically heavier than the population average. Because the perimeter and weight features of the PWP together were descriptive of these regional subpopulations, this report also compares sets of otoliths simultaneously by both perimeter (based on length) and weight (based on length) residuals. Type-1 (rugose-light) is defined by positive perimeter and negative weight residuals. Type-2 (smooth-heavy) is defined by negative perimeter and positive weight residuals.

Stable oxygen isotope analysis

Protocols for cleaning otoliths and measurement of $\delta^{18}\text{O}$ followed Dorval et al. 2011 and Javor and Dorval (submitted). Briefly, otoliths were cleaned in 2% sodium dodecyl sulfate, washed with Milli-Q[®] water (MQ-water), treated for 3–5 min in 30% hydrogen peroxide, and washed with multiple rinses of MQ-water. Because $\delta^{18}\text{O}$ in juvenile sardine otoliths from a region changes with growth (Javor and Dorval, submitted), the range of weights within each sample set selected for comparison was narrow to mitigate size bias (maximum difference of 0.2 mg). Isotope analyses were conducted on a triple collector gas ratio mass spectrometer (VG Prism) at the University of Southern California. Ultiss reference standards, calibrated to the Vienna Pee Dee Belemnite standard (NBS-19), were run before, between sample blocks, and after each daily set. The average precision was $\pm 0.07\text{‰}$ (standard deviation, sd) estimated from the Ultiss reference measurements. The raw data were corrected and reported relative to the Pee Dee Belemnite reference standard. Temperature was calculated according to Dorval et al. 2011 based on the composition of seawater near San Diego:

$$\delta^{18}\text{O}_{\text{otolith}} (\text{‰}) - \delta^{18}\text{O}_{\text{water}} (\text{‰}) = (-0.132 \times \text{Temperature } ^\circ\text{C}) + 2.455.$$

Calculations and statistics

PWP values were determined from the equations of Javor et al. 2011. Data were compared by linear regressions, two-tailed Student's *t* tests with equal variance, two-way ANOVA, and correlation analysis.

RESULTS

Distributions of type-1 and type-2 otoliths in juveniles

Monthly collections of nearshore sardine captured for the live bait market in San Diego during 2006–12 consisted of immature specimens with a maximum standard length (SL) close to 180 mm (fig. 2). They were mostly age-0 to age-2, with occasional age-3 fish. In some years,

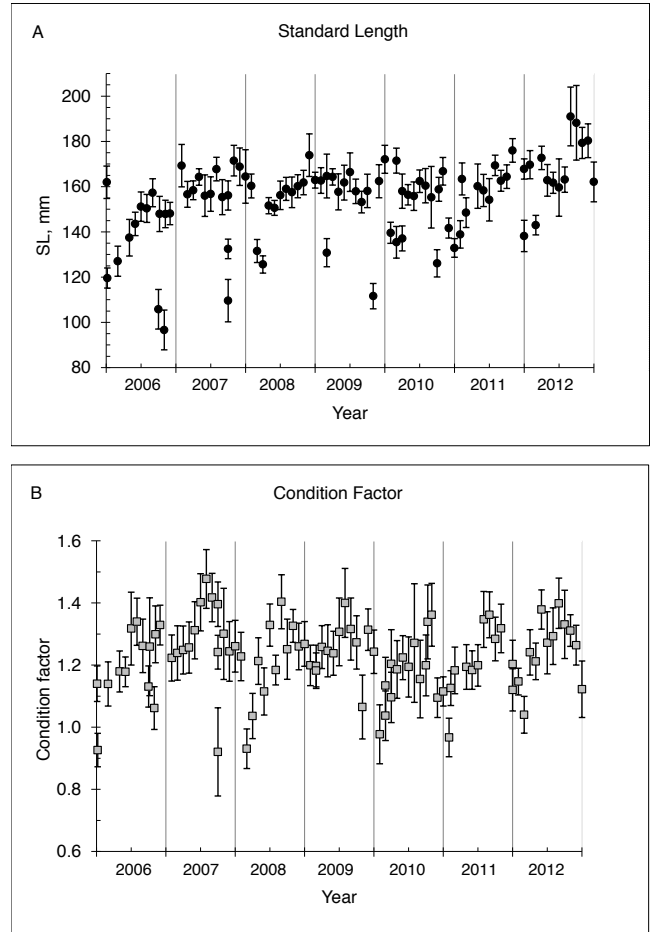


Figure 2. *S. sagax* collected near San Diego, CA, 2006–12. 2A: Standard length \pm sd. 2B: Condition factor \pm sd.

evidence of growth in the local population was apparent from the steady month-to-month increase in length. The CF of the juvenile sardine always increased during summer, but the gonads of these young fish were never observed to be close to spawning condition.

The average (\pm sd) SL and CF of sardine captured in Monterey during 2009–11 (170 ± 15 mm and 1.35 ± 0.11 , respectively; $n = 548$) were similar to those of live bait caught in San Diego during the same months of capture (160 ± 11 mm and 1.29 ± 0.13 , respectively; $n = 175$). For sardine captured in the 2008 summer SWFSC survey, the mean SL was 205 ± 23 mm, and the mean CF was 1.27 ± 0.14 ($n = 901$). This CF value overlapped that of the juveniles captured in the summer near San Diego and Monterey during the course of this study.

During 2006–12, monthly PWP values of otoliths from age-0 to age-2 sardine captured near San Diego showed a distinct change beginning July 2008 (fig. 3A). From 2006 through June 2008, on average there was a nearly equivalent distribution of type-1 (21% of the total) and type-2 (24% of the total) otoliths, with no significant prevalence of one type over the other (two-

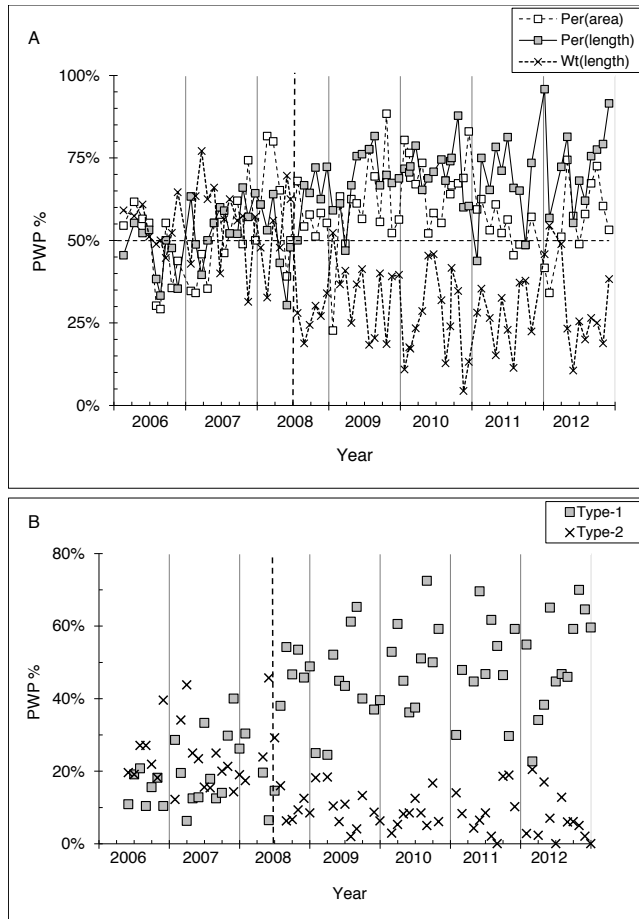


Figure 3. PWPs of *S. sagax* otoliths caught near San Diego. 3A: Monthly perimeter (based on area or length) and weight (based on length) profiles. 3B: Monthly profiles of two features together representing type-1 and type-2 otoliths (described in Materials and Methods).

tailed *t* test, $p = 0.0416$, $n = 23$). From July 2008 through 2012, type-1 otoliths (49% of the total) dominated over type-2 (9% of the total), a significant difference ($p < 0.0000$, $n = 44$) (fig. 3B). There was no significant difference between the two ways to assess the perimeter profile (vs. area or length) before July 2008 ($p = 0.8439$, $n = 27$), but after that date, the PWP values for the two ways to assess the perimeter were not similar ($p = 0.0001$, $n = 48$; data not shown). In other words, more than one geometric dimension of the otoliths changed. Seasonal migration patterns among fish with type-1 and type-2 otoliths were not apparent. A two-way ANOVA test of the ratio of type-1 to type-2 otoliths, sorted by time period (before and after July 2008) and season (January–April and July–November), showed no significant seasonal effects within each time period ($p = 0.4400$, $n = 60$; data not shown).

Comparisons of average annual PWP values of juveniles caught off Monterey showed similar temporal trends (data not shown). The most pronounced shift was the decline in PWP-weight which steadily decreased from

68% in 2007 down to 20% in 2011. During the same period, PWP-perimeter (based on length) increased from 20% to 46%. PWP values for 1996–97 were similar to those for 2006–07.

Relationships of otolith morphology to temperature in juveniles

If the shift in dominant otolith morphologies in immature sardine in 2008 resulted from the immigration of southern stock from Mexico, it might follow that this stock preferred warmer temperatures. The question of whether temperature covaries with otolith morphology in sardine, or whether it might be an indicator of immigrant stock, was tested with our San Diego and Monterey collections of juvenile otoliths by the measurement of oxygen stable isotopes.

The variations in temperatures calculated from $\delta^{18}\text{O}$ composition between sample sets of San Diego otoliths of similar weight were compared across survey dates and PWP type. There was no significant difference in temperatures between type-1 and type-2 otoliths for samples collected before July 2008 (fig. 4 and table 1A). Likewise, there was no significant difference between temperatures of the two morphotypes in samples collected after June 2008. However, there was a significant difference in average temperatures for both otolith types between the two time periods, $13.6^{\circ}\text{--}14.6^{\circ}\text{C}$ and $15.7^{\circ}\text{--}16.0^{\circ}\text{C}$, respectively, or about 2°C warmer after mid-2008.

The Monterey collection was tested to compare type-1 and type-2 otoliths in three periods: 1996–97, 2008, and 2009. The otolith weights were similar within each collection period, but different between the sampling years which prevented the interannual comparison of calculated temperatures between sardine of equivalent size. Within each collection period, there were no significant differences in temperatures between otolith types (table 1B). As expected, the small juvenile sardine (2008) recorded warmer temperatures ($16.2^{\circ}\text{--}17.4^{\circ}\text{C}$) than the older fish ($11.0^{\circ}\text{--}12.9^{\circ}\text{C}$). These results indicate there likely was no direct effect of temperature on otolith morphology in sardine.

Immature vs. mature sardine

If the post-2008 population of adults recruited predominantly from local juveniles, there should have been an increase in abundance of type-1 otoliths in the mature population if: 1) there was no bias in mortality; and 2) PWP morphology did not change with maturity. No evidence of a shift in type-1 or type-2 otoliths was detected when adult otoliths were compared in five different years between 2004 and 2012, i.e., all the trawls had similar mixes of the two morphological types of otoliths (fig. 5). For this figure, all three PWP criteria were assessed to define type-1 and type-2 oto-

liths to increase stringency of the evaluation (perimeter based on both area and length, and weight based on length). The *t*-test *p* values of type-1 vs. type-2 abundance ranged within years from 0.905 in 2004, to 0.082 in 2009, and overall for all five years was 0.980. Only

one trawl out of the 43 examined in the five years of sampling captured a group of sardine with an otolith PWP resembling a type-1 profile.

Spawning condition, SL, and growth rates

If type-1 and type-2 otoliths are genetically associated with southern and northern stock, respectively, the season of spawning might be different for the two types. To test this theory, otoliths from the 2012 spring survey (fig. 5) were sorted by fish sex and maturity, and identified as type-1 and type-2 by the three PWP criteria. Among the mature males, 20% and 23% had type-1 and type-2 otoliths, respectively (*n* = 156). Among the mature females, 24% and 28% had type-1 and type-2 otoliths, respectively (*n* = 114). The overall averages were similar for those spring trawls, regardless of sex and maturity: 21% type-1 otoliths, and 26% type-2.

Otoliths continue to accrete calcium carbonate when fish growth slows with maturity, and when environmental conditions inhibit growth. Comparison of the slopes of linear regressions of fish standard length (*x*) and otolith weight (*y*) provides a relative estimate of fish growth rate in the population, and the associated coefficients of determination (*R*²) describe the relative composition of slow-growing and fast-growing sardine. Juveniles col-

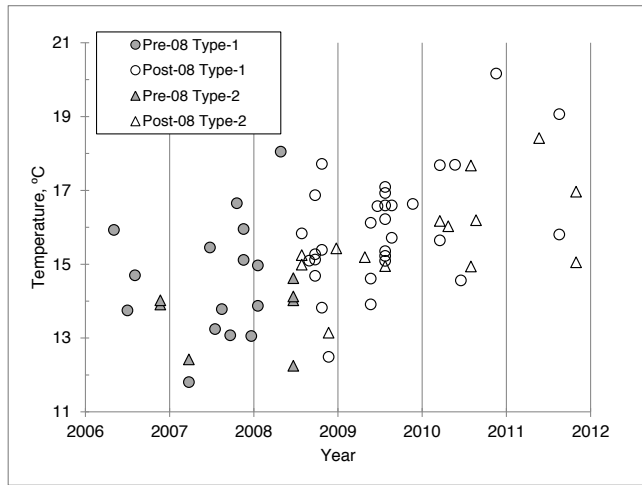


Figure 4. Calculated temperatures of otoliths from juvenile *S. sagax* captured near San Diego before July 2008 (Pre-08) and after June 2008 (Post-08). Otoliths were separated by type-1 and type-2 PWPs as described in the text. Supporting data are in table 1A.

TABLE 1

Comparisons of calculated temperatures and statistical significance of temperature–otolith morphology relationships over time in *S. sagax* captured near San Diego and Monterey. Otoliths were separated as type-1 or type-2 based on PWP parameters. Significance level was determined as *p* < 0.01. 1A: San Diego. Pre-July 2008 (Pre-08) and post-June 2008 (Post-08) data are also depicted in fig. 4. 1B: Monterey. Because of the differences in otolith weight between sample years, interannual comparisons were not calculated.

A. San Diego					
Otolith type and date	°C, avg	°C, ± sd	<i>n</i>	Wt, mg	Wt, ± sd
Type-1, Pre-08	14.6	1.6	15	1.078	0.062
Type-2, Pre-08	13.6	0.9	7	1.128	0.071
Type-1, Post-08	16.0	1.5	31	1.075	0.068
Type-2, Post-08	15.7	1.3	14	1.129	0.072
2-Tailed <i>t</i> -tests	<i>p</i>	Significance			
Pre-08, Type-1 vs. Type-2	0.147	–			
Post-08, Type-1 vs. Type-2	0.608	–			
Type-1, Pre-08 vs. Post-08	0.001	+			
Type-2, Pre-08 vs. Post-08	0.008	+			
B. Monterey					
Otolith type and date	°C, avg	°C, ± sd	<i>n</i>	Wt, mg	Wt, ± sd
Type-1 1996-97	12.9	1.0	7	1.565	0.075
Type-2 1996-97	12.2	1.6	8	1.570	0.065
Type-1 2008	16.2	1.2	8	0.538	0.043
Type-2 2008	17.4	1.3	10	0.507	0.042
Type-1 2009	11.0	1.1	8	1.423	0.034
Type-2 2009	12.0	1.2	7	1.362	0.090
2-Tailed <i>t</i> -tests	<i>p</i>	Significance			
1996–97, Type-1 vs. Type-2	0.334	–			
2008, Type-1 vs. Type-2	0.062	–			
2009, Type-1 vs. Type-2	0.122	–			

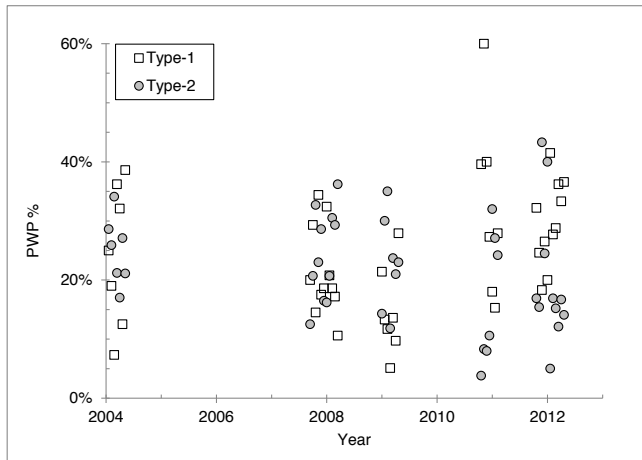


Figure 5. PWP% from annual SWFSC surveys of adult *S. sagax*. Each trawl is depicted with one type-1 and one type-2 point. The points are staggered within each year to facilitate visualization.

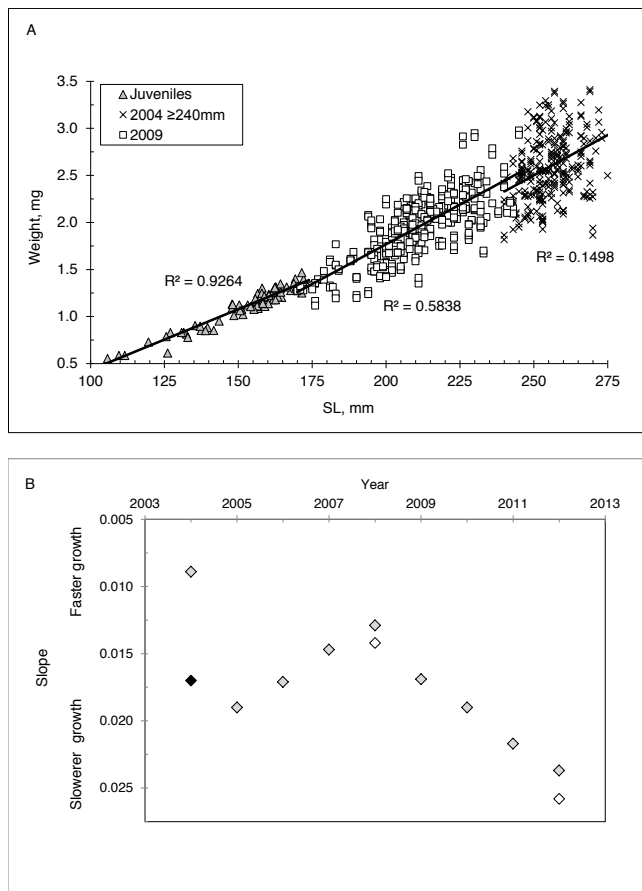


Figure 6. Standard length vs. otolith weight for *S. sagax*. 6A: Relationships for juveniles captured near San Diego in 2006–11, adults ≥ 240 mm captured in 2004, and sardine from the 2009 survey. R^2 values are noted on the figure. 6B: Relationships between year of capture and the slope of the linear regression of SL (x) vs. otolith weight (y). Shaded symbols are from spring surveys and open symbols are from summer surveys. The black symbol represents the slope from sardine ≥ 240 mm SL. The other slopes were derived from sardine measuring 190–230 mm. Supporting data are in table 2.

TABLE 2
 Slopes and R^2 values derived from the linear regression of SL (mm, x) and otolith weight (mg, y) for mature *S. sagax* (190–230 mm SL except where noted) captured in spring (2004–12) and in two summer SWFSC surveys where noted. The number of otoliths (n) is indicated. The slope data vs. year are depicted in fig. 6.

Year	Slope, m mg/mm	R^2	n	SL, avg	SL, sd	Notes
2004	0.0170	0.1488	263	255	8	>230 mm
2004	0.0089	0.1441	89	215	11	
2005	0.0190	0.8359	156	200	31	
2006	0.0171	0.6229	297	197	16	
2007	0.0147	0.5088	281	202	15	
2008	0.0129	0.6035	274	207	17	
2008	0.0142	0.6025	265	207	17	summer
2009	0.0169	0.5838	417	211	15	
2010	0.0190	0.5416	329	221	15	
2011	0.0217	0.8647	406	206	27	
2012	0.0237	0.6623	279	221	18	
2012	0.0258	0.6413	430	221	15	summer

lected near San Diego over 75 months (2006–11) and adults captured in the SWFSC surveys shared similar linear regressions with variable goodness of fit (fig. 6A and table 2). Growth of the juveniles was relatively homogeneous ($R^2 = 0.9264$) whereas the collection of sardine ≥ 240 mm in 2004 comprised such a diverse array of otolith weights ($R^2 = 0.1488$) that the actual slope of the relationship between otolith weight and SL was of questionable value as an indicator of growth.

To eliminate differences due to variations in fish size, only sardine measuring 190–230 mm SL were compared. When the slopes of the linear regressions for adult sardine were plotted for the 2004–12 surveys, a distinct change in trend occurred in 2008 (fig. 6B). The slope of the linear regression for the 2004 sardine with its correspondingly poor coefficient of determination did not conform to the pattern. From 2005 to 2008, the California population of mature sardine showed a general increase in growth rate that steadily reversed from 2008 to 2012. The linear regressions of the summer survey samples in 2008 and 2012 corresponded to the results of the spring surveys of those years. These results suggest subtle annual changes in growth attributes that have not been detected by other measurements.

Comparisons of juveniles to spawning stock biomass of mature sardine

Comparable trends in the mature parent stock would support the hypothesis of an overall 2008 shift in population composition. One theory is the dominance of type-1 otoliths among the juveniles after mid-2008 resulted from a decrease in the overall mature northern stock in California in conjunction with the immigration of immature sardine from southern stock where

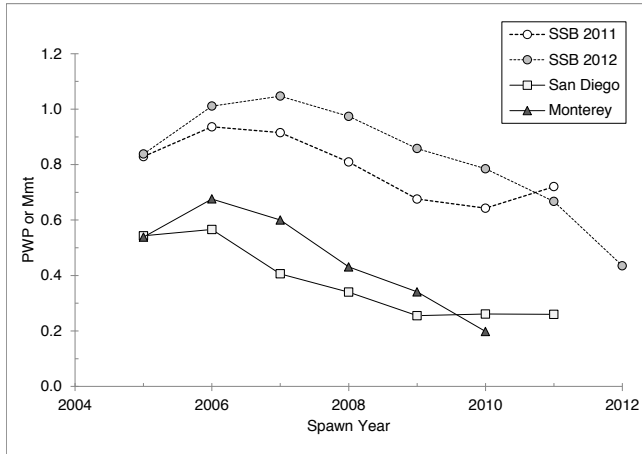


Figure 7. Spawning stock biomass (SSB in million metric tons; Hill et al. 2011, 2012) of *S. sagax* vs. annual average otolith PWP (weight based on length) for age-1 fish captured off San Diego and Monterey. PWP values are plotted for the year the sardine were spawned. Correlation values are in table 3.

TABLE 3

Correlation coefficients for *S. sagax* comparing spawning stock biomass (SSB; Hill et al. 2011) vs. annual average PWP values for otoliths of age-1 sardine captured near San Diego (spawned 2005–11) and Monterey (spawned 2005–10) according to spawn year (fig. 7). Correlation coefficients of the otolith PWP values for the two areas of capture are listed for spawn years 2005–10.

PWP factor	Correlation coefficient	
	San Diego vs. SSB	Monterey vs. SSB
Weight based on length	0.829	0.971
Perimeter based on area	-0.434	-0.384
Perimeter based on length	-0.646	-0.571

	San Diego vs. Monterey
Weight based on length	0.864
Perimeter based on area	0.686
Perimeter based on length	0.795

type-1 otoliths dominate. This theory was addressed by comparing the average annual PWP of age-1 sardine captured near San Diego and Monterey with the calculated annual spawning stock biomass of mature sardine in California (Hill et al. 2011, 2012). The trends in otolith morphology correlated with spawning stock biomass for the year the sardine near San Diego and Monterey were born (fig. 7 and table 3). During this survey period, both the biomass and the weight residuals of the otolith PWP measurements generally decreased. The 2011 stock assessment report provided values with excellent correlation coefficients between spawning stock biomass and PWP-weight for San Diego (0.829) and Monterey (0.971) otoliths. PWP perimeter profiles correlated negatively. The 2012 report updated those spawning stock biomass estimates, and correlation coefficients with San Diego (0.542) and Monterey (0.773) otolith PWP-weight were somewhat lower.

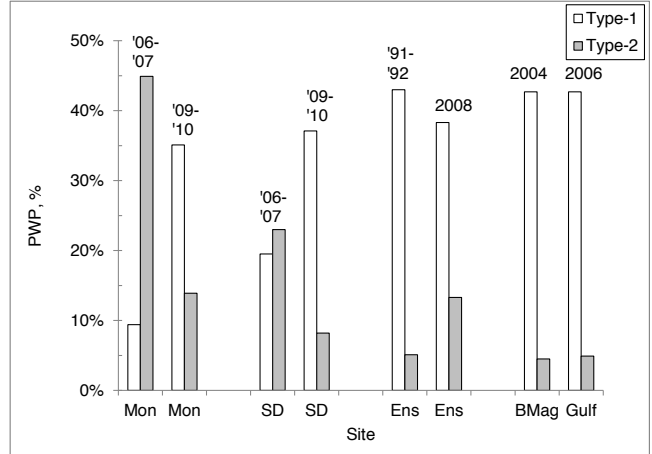


Figure 8. Comparisons of type-1 and type-2 otoliths of *S. sagax* to show the pre- and post-2008 differences in sardine captured near Monterey and San Diego. Number (*n*) of otoliths: Monterey (Mon), 2006–07 (822), 2009–10 (887); San Diego (SD), 2006–07 (847), 2009–10 (918); Ensenada (Ens), 1991–92 (158), 2008 (120); Bahía Magdalena (BMag), 2004 (89); and Gulf of California (Gulf), 2006 (328). Data for the Mexican otoliths and 2006–07 California otoliths are from Javor et al. 2011.

DISCUSSION

Distributions of type-1 and type-2 otoliths in juveniles

Customary methods of evaluating sardine stock from live bait and port samples (length, weight, condition factor, and age) between 2006 and 2012 revealed only typical annual fluctuations in young sardine captured near San Diego and Monterey. A more detailed assessment of otoliths incorporating weight and morphological measurements using PWP analysis demonstrated long-term shifts in the two California subpopulations, beginning in July 2008. The primary change was the increase and persistent residence of sardine with otolith PWP values similar to those caught in warmer waters off Baja California (fig. 8). At the time this study ended in 2012, the PWP values of San Diego sardine otoliths had not significantly changed since mid-2008, i.e., a large proportion of juveniles with type-1 otoliths remained in the region previously occupied by sardine represented by an approximately equal mixture of type-1 and type-2 otoliths (Javor et al. 2011). The change in ratios of type-1 and type-2 otoliths in juveniles caught near Monterey during the same period was similar to that of San Diego sardine.

Using PWP parameters, there was no evidence of reversing, seasonal north-south migrations of young sardine as previously reported for Baja California and southern California stocks during 1981–2002 that were based on SL, SST temperature at catch, and otolith length and width (Félix-Uraga et al. 2004, 2005; Smith 2005). The finding of the present study does not necessarily contradict the conclusions of the previous inves-

tigations, but it does imply the methods of our study may detect different phenomena. The timing of the shift in otolith morphologies between June and July 2008 is consistent with the migration model those authors proposed.

Relationship of otolith morphology to temperature in juveniles

There was no correlation between temperature and otolith morphology in immature sardine as Javor et al. 2011 proposed. In juveniles caught near San Diego after mid-2008, both type-1 and type-2 otoliths recorded $\delta^{18}\text{O}$ values that corresponded to water temperatures about 2°C warmer than in 2006 to early 2008. The most likely explanation for the change in temperatures is the juveniles controlled their thermal environment by the amount of time they spent at depth (Javor and Dorval, submitted). Sardine typically remain at about 15–35 m depth during daylight hours, and at the surface at night to follow and feed on plankton (van der Lingen et al. 2006; Cutter and Demer 2008). In 1995–2003, cohorts of age-1, southern California sardine recorded similar temperatures to those found in the present study, with mean temperature values varying up to 2°C from year to year (Dorval et al. 2011). They averaged between seawater temperatures at 0 m and 30 m depth in the Southern California Bight.

In the present study, a 2°C increase was consistent with an increase in the population of juveniles with type-1 otoliths if they came from southern stock migrants. Because sardine school, it is possible the majority of the juveniles with type-1 otoliths preferred warmer waters, and minority northern stock sardine (with a relatively higher proportion of type-2 otoliths) remained schooled with them. The present study also confirmed the correlation between increasing otolith size and cooler temperatures recorded in immature sardine as determined in the juveniles caught near Monterey (Javor and Dorval, submitted).

Immature vs. mature otolith PWP, SL, and growth rates

The lack of a shift in otolith phenotypes among the adult population off California and the Pacific Northwest in 2009–12 poses a problem: Where did the juvenile sardine with type-1 otoliths go after mid-2008? Did they join the offshore spawning stock and reach sexual maturity during the spring? Did their otoliths change morphology?

A comparison of the adult sexual maturity index with otolith PWP values showed no bias against sardine with type-1 otoliths, i.e., nearly all the adults were sexually mature or nearly mature. One theory to explain the

lack of increase of sardine with type-1 otoliths among the spawning stock during 2009–12 is greater mortality in cooler northern waters. If they had emigrated from warmer southern waters, this conclusion would be consistent with separation into regional races based on temperature.

Another hypothesis is the otoliths changed morphology with growth. In tank-reared sardine originally collected as juveniles in 2005, otoliths in the fish that survived a year at 13°C or 21°C both had relatively smoother and heavier profiles (type-2 morphology) at the end of the experiment (Dorval et al. 2011). Area-based perimeter values decreased from 63% at collection ($n = 49$) to 12%–21% ($n = 57$ –109); length-based perimeter values changed from 49% to 14%–44%; and length-based weight values increased from 51% to 73%–91% (the author's unpublished data). Otoliths of the fish that died during the experiment were not monitored to determine whether sardine with type-1 otoliths had higher mortality. Dorval et al. 2011 concluded the changes in morphology were likely to be artifacts of culture conditions. In light of the apparent disappearance of type-1 otoliths from juvenile to mature stages of sardine off California after mid-2008, the changes observed in tank-reared sardine may not have been artifacts. The shift in PWP profiles with maturity may have occurred in nature as well.

The relationship between otolith weight and standard length of mature sardine surveyed off California that shifted in 2008 represents the increasing presence of slower-growing sardine among the adults. The timing of the change was consistent with PWP shifts in regional juveniles.

To our knowledge, otolith weight–SL relationships in long-term population studies of adult fish have not been tracked as proxies for average annual growth rates. Kristofferson 2007 conducted a similar investigation with adult Müller's pearlside, *Maurollicus muelleri*, comparing relative growth rates of fish from different fjords and the Norwegian Sea, but only within single year collections. A study of Australian pilchards (*Sardinops sagax neopilchardus*) comparing monthly samples over a period of five years focused on assessing otolith weight–age relationships, not relative growth rates (Fletcher 1995). A re-examination of those data for otolith weight–SL relationships would provide corroborating evidence for Pacific sardine (*S. sagax caerulea*), a different subspecies from the West Coast of North America.

Age vs. fish length indices for Pacific sardine have been described, including one for the 2003–04 North American population (Lo et al. 2011). The data have statistical significance because of the large sample size ($n = 4349$ fish), but the regression curve is not very practical as a guide to ageing sardine. The curve

becomes asymptotic at three to five years of age, so a 220 mm fish might be three years old or it might be fifteen. Age-1 fish range from less than 100 mm in length to nearly 230 mm, while age-2 fish may reach 240 mm. In addition, aging has a high degree of subjectivity between otolith readers (Hill et al. 2011; Dorval et al. submitted).

By contrast, linear regressions of otolith weight vs. fish length are precise indices that can provide year-to-year assessments of relative growth. Although not evaluated in the present study, otolith weights could be compared to ages as a corroborating factor to describe annual stock characteristics.

Comparisons of juveniles to spawning stock biomass of mature sardine

Did shifts in otolith morphology of immature Pacific sardine captured off California reflect changing parentage from northern and southern stocks? The parallel decrease in PWP-weight of juvenile otoliths and the spawning stock biomass off California during 2006–12 may have been fortuitous. However, the high correlation coefficients support the hypothesis that young sardine with predominantly lighter-weight, type-1 otoliths from southern or temperate stock became proportionately more abundant as the northern population, with a higher proportion of heavier, type-2 otoliths, diminished. In the same period, there was a general decrease in daily egg production and sardine larvae measured during the spring cruises (Lo et al. 2011; SWFSC CalCOFI data). The estimate of the spawning stock biomass incorporates these and other factors into the assessment model which in turn may be updated from year to year (Hill et al. 2010, 2011, 2012). For this reason, the PWP-weight profile correlated with the multiyear spawning stock biomass values presented in the 2011 report better than the estimates presented in the 2012 report. However, no matter which year's assessment model is compared for this period, the overall trend of decreasing northern stock remains.

Why did the juvenile population shift?

Based on maximum landings and SST, Félix-Uraga et al. 2005 presented a model in which the northern stock migrates as far south as northern Baja California in the cooler months where their range overlaps with the southern, temperate stock that largely resides on the Pacific Coast of Baja California. Temperate-stock sardine migrate northward to southern California in the summer months, and as far south as Bahía Magdalena in the cooler months where they overlap with the range of the warm, Gulf stock. Further evidence from environmental modeling (Zwolinski et al. 2011) and acoustic-trawl surveys (Demer et al. 2012) supports this model. The data of the present study suggest the fidelity of the stocks may

not be that strict. Instead, northern and southern stocks may intermix off southern and central California with evidence of parentage recorded in juvenile otoliths.

The distance young sardine migrate is not known with certainty. It is linked to fish size and the bioenergetic costs of long-distance swimming (Nøttestad et al. 1999; Lo et al. 2011). Sardine with type-1 otoliths that first appeared in San Diego in July 2008 were relatively mature juveniles (160 mm average SL, and a mixture of age-1 and age-2 fish). If they were spawned in Mexico, how far did they swim and over what period of time? Mature adults in the summer migrations to the Pacific Northwest from southern and central California are greater than 200 mm SL (Lo et al. 2011).

Temperature changes in the California Current could have triggered the juvenile population shift in mid-2008. A warm, El Niño event occurred in 2009–10, between cooler La Niña conditions in 2007–08 and 2010–11 (ggweather.com/enso.oni.htm; accessed 29 May 2013). Therefore an incursion of warm, El Niño seawater did not accompany an initial 2008 northward migration and residence of temperate, southern juvenile stock in California.

Alternatively, the shift in the juvenile population may be coupled with the presently cold oceanographic regime of the Pacific Decadal Oscillation (PDO) cycle in the California Current (Zwolinski and Demer 2012). Since 2008, the PDO index has been negative following warm years from the mid-1970s to mid-1998, a cool phase during 1998–02, and a warm phase during 2002–05 (<http://www.nwafc.noaa.gov/research/divisions/fe/estuarine/oeip/ca-pdo.cfm>; accessed 29 May 2013). Coinciding with the shift in the PDO cycle, since 2008 there has been very limited spawning success of sardine off the Pacific Northwest (unpublished proceedings of the Trinational Sardine Forum <http://swfsc.noaa.gov/textblock.aspx?Division=FRD&id=18002>; accessed 29 May 2013). The success of each annual spawn is dependent on food availability for larval and juvenile sardine. The timing, abundance, and composition of spring phytoplankton blooms in the western North Pacific Ocean during 2001–09 correlated with the springtime PDO index (Chiba et al. 2012) and are probably similarly linked in the California Current ecosystem. Limited or negligible recruitment of northern stock offspring from off northern California and the Pacific Northwest is a likely factor in the diminished representation of juvenile sardine with type-2 otoliths since mid-2008.

The previous decrease in northern stock and collapse of the West Coast sardine fishery in the late 1940s and early 1950s coincided with the latter years of the last major cold PDO cycle (Zwolinski and Demer 2012). Lluch-Belda et al. 1991 theorized that fluctuations of

abundance of *S. sagax* along the Pacific Coast follow contraction–expansion patterns: during a cold regime the population contracts toward the south, and during warm periods it expands to the north. The population shifts detected during the 2006–12 study reported here may be a forerunner to further decreases in northern stock if the PDO continues its negative cycle. Commercial exploitation at present levels may also contribute to the decrease in northern stock (Zwolinski and Demer 2012), further opening a niche for immature sardine emigrating from the south.

Alternatively, the shifts in the juvenile population may have occurred in the past independently of PDO cycles (McClatchie 2012) and in the absence of methods such as otolith measurements to recognize the changes. The incursion of southern stock juveniles into California habitat underutilized by diminishing numbers of northern stock juveniles might occur even if the immigrating adults were not fit to reproduce successfully in cooler, northern waters. Data from Mexican surveys would help answer the question of the source of type-1 juvenile otoliths in California sardine, and retrospective analysis of otoliths from previous decades would demonstrate whether the trends noted in this study have a cyclic nature.

SUMMARY

1. During a 2006–12 survey of otoliths from juvenile Pacific sardine caught off California, a long-term shift towards the prevalence of the type-1 phenotype, similar to the phenotype associated with the southern stock off Baja California, began in mid-2008. This finding supports the conclusion that young sardine from Mexico took up residence in a region previously mixed with or dominated by northern stock. A similar geographic shift in otolith phenotypes was not detected in mature adults off California and the Pacific Northwest in 2009–12.
2. Significant differences in temperatures recorded in juvenile otoliths were detected between pre- and post-2008 dates of capture, but not between otolith phenotypes within each time period. After mid-2008, San Diego sardine otoliths of similar size recorded average temperatures about 2°C warmer than those caught before July 2008.
3. Otolith weight–standard length relationships gave a time-course picture of sardine growth rates of mature stock, with a notable shift to slower growth after 2008.
4. The temporal trend of increasing prevalence of type-1 otolith features in immature cohorts in California correlated with generally decreasing annual spawning biomass estimates of the northern stock during 2006–12.

5. Otolith weight and morphological measurements are statistically significant, quantitative means of assessing juvenile and adult sardine population characteristics including relationships to age, standard length, growth rates, stock biomass, and temporal trends in regional perimeter-weight profiles. Measurements of otoliths from immature sardine offer a potentially useful set of variables for forecasting population factors before recruitment to the mature, reproducing population.

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