

## EVALUATION OF THE INFLUENCE OF AGE AND LENGTH ON PACIFIC SARDINE (*SARDINOPS SAGAX*) MATURATION AND CHARACTERIZATION OF ITS TEMPORAL VARIABILITY

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### ABSTRACT

Pacific sardine collected during the spawning season off the coast of California (US) were used to investigate the process of female maturation. Pacific sardine maturation is better described as an age-based rather than a length-based process, and its temporal variation is better described by annual rather than cohort effects. Temporal variation in maturation is large with the age at 50% maturity annually varying by more than 1 year. This results supports that annual variability is substantial and may be driven by environmental rather than density dependent factors. Including time-varying age-based maturation into the assessment model improved model prediction of recruitment. It is recommended that future assessments consider inclusion of this temporal variability of an age-based process.

### INTRODUCTION

Understanding the life history of exploited populations plays a critical role in the assessment of their status and the determination of future prospects. Life history commonly takes the forms of the rates of growth and natural mortality, as well as various aspects of the reproductive biology. For assessment purposes, life history is usually quantified as a mathematical relationship or a series of empirical estimates that serves as biological processes governing the population dynamics (Maunder and Piner in press). Although the parameters governing these model processes can be estimated as part of the parameter optimization, reproductive life history such as fecundity relationships (e.g., eggs per gram of spawning female) or female maturation rates are usually specified as fixed values. It is important that life history studies conducted with the goal of informing stock assessments take into consideration how stock assessment models use these biological processes.

The importance of identifying the correct biological units (example: age or length) of a biological process has been shown to have significant effects on the reliability of assessment results (Lee et al., in press). Variability in the population age structure can affect the implications of age-based biological processes very differently

than length-based ones (Lee et al. 2017). Differentiating between the units of age and length is problematic because these attributes are highly correlated (von Bertalanffy 1938) and can operate concurrently (Schnute and Richards 1990). Despite these difficulties, life history studies aimed at informing stock assessments should attempt to characterize their results in the most appropriate units.

The rate at which females mature is one of the most important aspects of reproductive biology. Maturation rate has been characterized as both a length- as well as age-based process. Maturity ogives applied to the population age or length structure determine the segment of the population that contributes to spawning. For highly variable populations, spawning biomass characterized by age-based maturation rates can be substantially different from length-based ones (Piner et al. 2018). In integrated assessments, spawning biomass is linked to estimates of the underlying dynamics through the spawner-recruit process. The spawner-recruit process makes up an important component of the assessment model's production function, which in turn partially determines the population response to fishing (Sippel et al., in press). Accurate depiction of the production function will be crucial to reliably estimating population scale (Lee et al. 2014) and predicting a population's future prospects.

Beyond establishing the biological units for a process like maturity, understanding the most appropriate units of its temporal variability will also be important (Stawitz et al. 2015). Annual (year-specific) changes in life history rates have been linked to environmental forcing (Hagen and Quinn 1991; Black et al. 2008; Stawitz et al. 2015) which affects all age classes present, while cohort-level variability has been linked to density dependent effects (Rijnsdorp and van Leeuwen 1996; Helser and Almeida 1997; Whitten et al. 2013). Characterizing temporal variability (Silva et al. 2006) can be used to help understand the roles of density dependence and environmental influence on population regulation, which in turn has profound impacts on how exploited stocks should be managed (Chavez et al. 2003; Jacobson and MacCall 1995).

Accurate representation of biological processes including their temporal variation is perhaps nowhere more important than for Pacific sardines (*Sardinops sagax*). Pacific sardine are a small pelagic fish that is, at times, a major component of the forage base in California Current ecosystem (Parrish et al. 1989). The northern subpopulation of Pacific sardine is distributed from northern Baja California, Mexico, to British Columbia, Canada, and supports important commercial fisheries (Smith 2005) in addition to providing an important forage base in the ecosystem. Pacific sardine abundance has declined significantly, which has led to serious conservation concerns (Hill et al. 2017) and unwelcomed consequences for both human and nonhuman predators alike (Punt et al. 2016). Due to its relatively short life-span in a fluctuating environment (Chavez et al. 2003), Pacific sardine are thought to have highly plastic life history characteristics (Butler et al. 1996; Silva et al. 2006; Dorval et al. 2015; Brosset et al. 2016) making characterization of temporal variation in maturation potentially important for stock assessment.

The objectives of this study were to evaluate three basic questions on the process of female maturation in the northern subpopulation of Pacific sardine. The first question is whether maturation is better described by an age- or length-based process. It is possible that maturation can be related to both age and length (Schnute and Richards 1990), but for stock assessment purposes do fish mature because they are older or because they are larger? After deciding the biological units of maturation, the second objective is to assess if the temporal variability in maturation is better described by an annual or cohort effect. Finally, this work quantifies the magnitude of the temporal variability and evaluates if this additional process variability should be considered in future stock assessments.

## MATERIALS AND METHODS

### Study area and sample collection

Adult sardine were collected off of the West Coast of the United States during spring trawl surveys in 1994, 1997, and from 2004–15 (Macewicz et al. 1996; Lo et al. 2005; 2010; Dorval et al. 2015). Females were sampled from trawl gear and standard lengths were measured to the nearest millimeter (mm). Otoliths were removed, cleaned and stored dry. Gonads were removed from females and preserved in 10% neutral buffered formalin. For our analysis, those data were filtered to include only samples collected off of southern and central California between 30°–37°N latitude and 117°–126°W longitude ( $n = 3,818$ ) to ensure only samples from the northern subpopulation were included in the study.

### Age and maturation determination

Age determinations were done by counting annual increments on whole sagittae otoliths following the procedures of Yaremko (1996). Ageing error for sardine varies by reader but generally increases above age 4 (Dorval et al. 2013). A piece of the preserved ovary was removed and prepared as a histological slide with hematoxylin and eosin stain. Female maturation was determined through a combination of gross visual and histological examination (Macewicz et al. 1996).

### Age- or length-based process

Conditional analysis was used to separate the effects of age- from length-based maturation. The general theory of conditional analysis is an extension from the analytical treatment of paired age-length data developed to estimate growth (Piner et al. 2016) and subsequently to determine age- versus length-based movement (McDaniel et al. 2016). Paired age-length data with maturation information can be analyzed by conditioning the observed distribution of one measurement (age or length) on a discrete unit of the other correlated measurement. Because there is variability in the age-length relationship, each age contains a distribution of lengths, and similarly a distribution of ages for each length. In this example, a solely length-based process of maturation (higher proportion of fish maturing due to increasing length) would lead to identical age distributions of mature and immature fish at length (age conditioned on length). However, if maturation is age-based, the age of mature fish for individual lengths will be older. Conditioning on length rather than age is generally preferred because it is not influenced by size-based sampling, while conditioning length on age is heavily influenced by size selection (Piner et al. 2016).

After determination of the biological units of maturation, the probability of the difference in the observed mean age of mature versus immature fish at length was evaluated using randomization methods. Observations of maturation state were randomized ( $n = 1000$ ) within length to create new mean age of each maturation state. A distribution of possible test statistics (TS) was compared to the observed  $TS_{obs}$ . The test statistic is:

$$TS = \sum_l (\mu_{ml} - \mu_{iml})$$

where the test statistic (TS) is mean age at length of mature ( $\mu_m$ ) minus mean age at length immature  $\mu_{im}$  summed across all lengths ( $l$ ).

### Annual or cohort variability

After determination of the biological units of maturation, evaluation of the temporal variability as either an annual (year-specific) or cohort effect (year-class) was

done using multi-model inference. We fit the maturity data by individual year and by cohort using the logistic function in R with the general linear model procedure with formula of the form:

$$\log\left(\frac{P}{1-P}\right) = \alpha + \beta(X * I) + \varepsilon$$

where  $P$  is a probability of mature (being immature as 0 or being mature as 1),  $X$  is either length or age depending on the previous evaluation of biological units of maturation,  $I$  is year/cohort,  $\alpha$  is the inflection,  $\beta$  is the slope of the logistic relationship, and the error term  $\varepsilon$  follows a binomial distribution with mean zero and variance equal to  $P(1-P)$ . Akaike information criterion (AIC, Akaike 1974) weights ( $w_i$ ) were computed for each formula and used to quantify the strength of evidence (Burnham and Anderson 1998) for one hypothesis or the other.

$$AIC = -2\ln L + 2k$$

where  $L$  is likelihood function and  $-2\ln L$  is known as the deviance and  $k$  is number of parameters in the model.

After determination of the units of temporal variability, a separate logistic regression was fit to predict the length or age at 50% maturity ( $X_{50}$ ) for each year or cohort depending on the previous evaluation of the units of temporal variability. The logistic regression followed the form:

$$\log\left(\frac{P_{X_i}}{1-P_{X_i}}\right) = a + bX_i + e$$

where  $P_{X_i}$  is a probability of mature for a given length or age ( $X_i$ ),  $a$  is the inflection,  $b$  is the slope of the logistic relationship, and the error term  $e$  follows a binomial distribution with mean zero and variance equal to  $P_{X_i}(1 - P_{X_i})$ .

The length or age at which 50% of fish that have reached maturity was calculated by solving the above equation with  $P_{X_i} = 0.5$ .

$$X_{i,50\%} = -\frac{a}{b}$$

### Consistency with population dynamics

To evaluate if the final temporal estimates of maturity are important for our current understanding of the population dynamics, our time-varying maturation estimates (empirical and not model based) replaced the time-invariant (average) maturation estimates in the current stock assessment model (Hill et al. 2017). The estimates of maturity were compiled in the appropriate biological (age or length) and temporal (annual or cohort) units based on the preceding methods. Temporal units with missing maturity information used the long-term average maturity at the appropriate biological unit. This long-term average is the same as in the

current assessment. The current assessment model estimates dynamics from 2005 to 2017 based on a fishing year (July 1–June 30). The 2 parameters of the spawner-recruitment relationship ( $\ln R_0$ - unfished recruitment and  $h$ -curvature of the relationship) was estimated as part of the integrated assessment model assuming a Beverton and Holt functional form. The assessment model used an empirical weight-at-age approach with catch, observations of the age-structure of the catch, and an acoustic absolute estimates of abundance and its age compositions as likelihood components. The empirical weight-at-age assessment approach bypasses the need for modelling the length-at-age by specifying annual weight-at-age for each fleet and survey. This approach allows considerable flexibility in specifying empirical estimates of the temporal variability in biological processes. For a complete description of the model see Hill et al. (2017).

Model improvement from using the observed temporal variability in the maturity schedule was evaluated using the change in the magnitude of the recruitment residual relative to the model with time-invariant maturity. The recruitment residual is the difference between the estimated recruitment and the expectation based on the spawner-recruit process. Deviations from the spawner-recruit expectation includes not only real fluctuation in recruitment but also process error due to model misspecification. Because the catch-at-age and survey estimates of abundance are the same between models, the absolute recruitment estimates should be the same between models. Therefore any reduction in the recruitment residual would be due to reduction of the process error associated with incorrect specification of the maturity schedule. Thus reduction in the absolute value of the recruitment deviation can be construed as evidence for better consistency between the estimated spawner-recruit process and the data driven estimates of recruitment.

We quantified the change in the recruitment residuals from a model using annual versus time-invariant (table 1) maturity schedules using a measure of relative change ( $\Delta p$ ):

$$\Delta p = (abs(p) - abs(\hat{p})) / (abs(p))$$

Where  $p$  is the year-specific residual from the assessment model that included time-invariant maturity and  $\hat{p}$  is the year-specific residual from the assessment model that included time-varying maturity. Positive  $\Delta p$  is the proportional improvement in consistency of the prediction based on variable maturity and negative  $\Delta p$  would be proportional degradation. If the temporal estimates of the maturity schedule are more consistent with the model structure and the data, we expect mostly positive  $\Delta p$ . Mostly negative or random  $\Delta p$

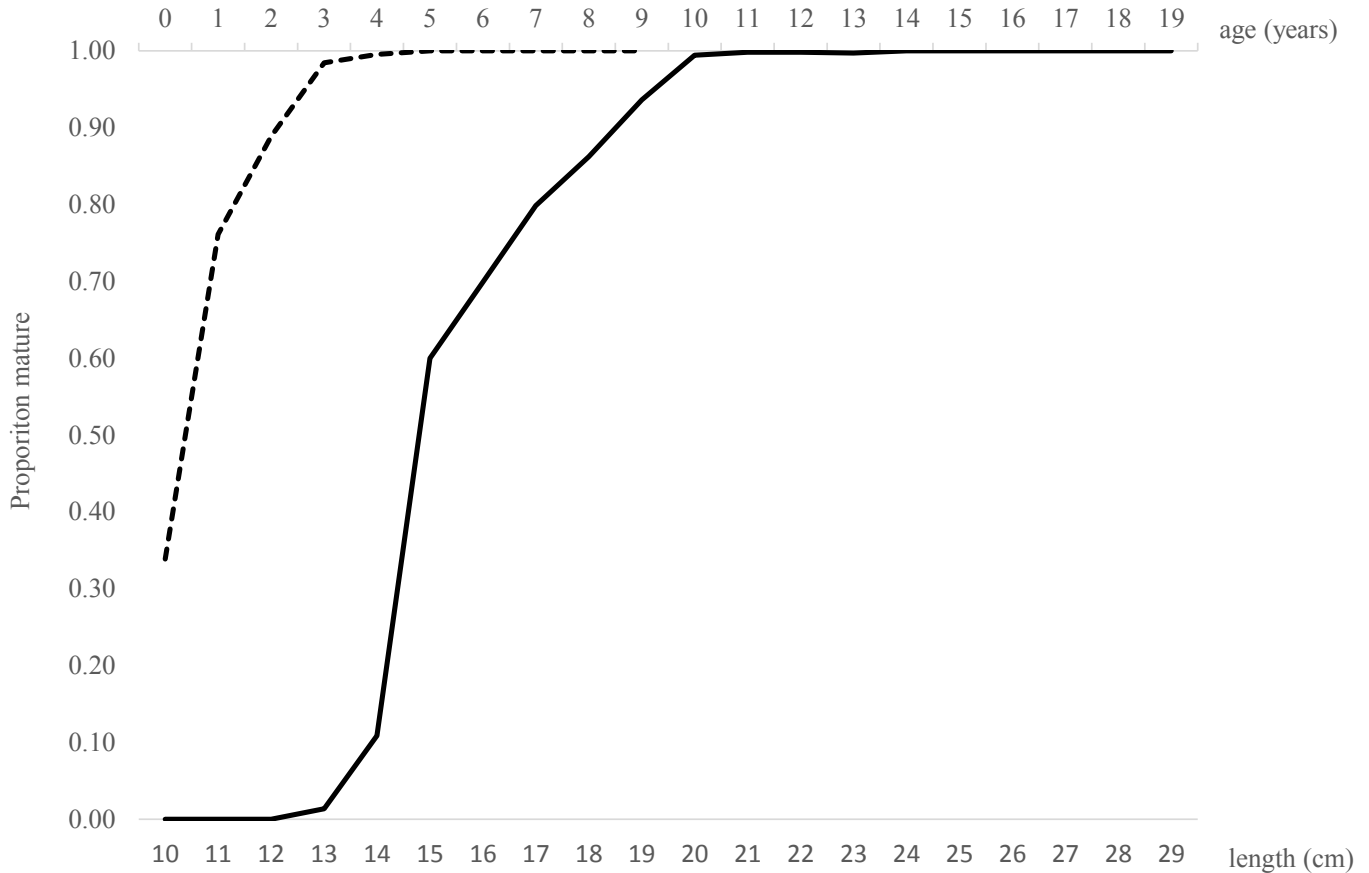


Figure 1. Empirical estimates of the proportion of female Pacific sardine mature by age (dashed line) and length (solid line). Age x-axis is given above the plot and length below. Data were aggregated across all years.

**TABLE 1**  
**Description of the data used in this study to**  
**determine female maturity schedules. Sample sizes (*n*)**  
**and proportion mature are given by age and length.**  
**Samples were aggregated across all years.**

age (yr)	<i>n</i>	prop	length (cm)	<i>n</i>	prop
0	251	0.34	10	1	0.00
1	703	0.76	11	2	0.00
2	808	0.89	12	30	0.00
3	840	0.98	13	73	0.01
4	663	1.00	14	92	0.11
5	374	1.00	15	85	0.60
6	135	1.00	16	216	0.70
7	36	1.00	17	362	0.80
8	7	1.00	18	399	0.86
9	1	1.00	19	330	0.94
			20	342	0.99
			21	504	1.00
			22	565	1.00
			23	349	1.00
			24	206	1.00
			25	160	1.00
			26	77	1.00
			27	19	1.00
			28	5	1.00
			29	1	1.00

would indicate those changes in maturation schedules were not consistent with improvement in our understanding of sardine dynamics.

## RESULTS

### Age- or length-based process

A total of 3,818 fish were used to determine maturation schedules (table 1), which display a pattern of an increasing proportion mature with both increasing age and length (fig. 1). For every length, the proportion mature increases with increasing age (fig. 2). A bimodality exists in the size distribution of age-0 fish that is also related to the state of maturity. The smaller age-0 length mode was primarily immature fish. By age-1 the modal size of immature and mature fish converges but a similar difference between the mean size of immature and mature fish exists for every age. These patterns are consistent with both age- and length-based processes of maturation.

When the mean age of mature and immature fish is conditioned on length, mature fish are roughly 0.25–0.75 years older than immature fish at every length

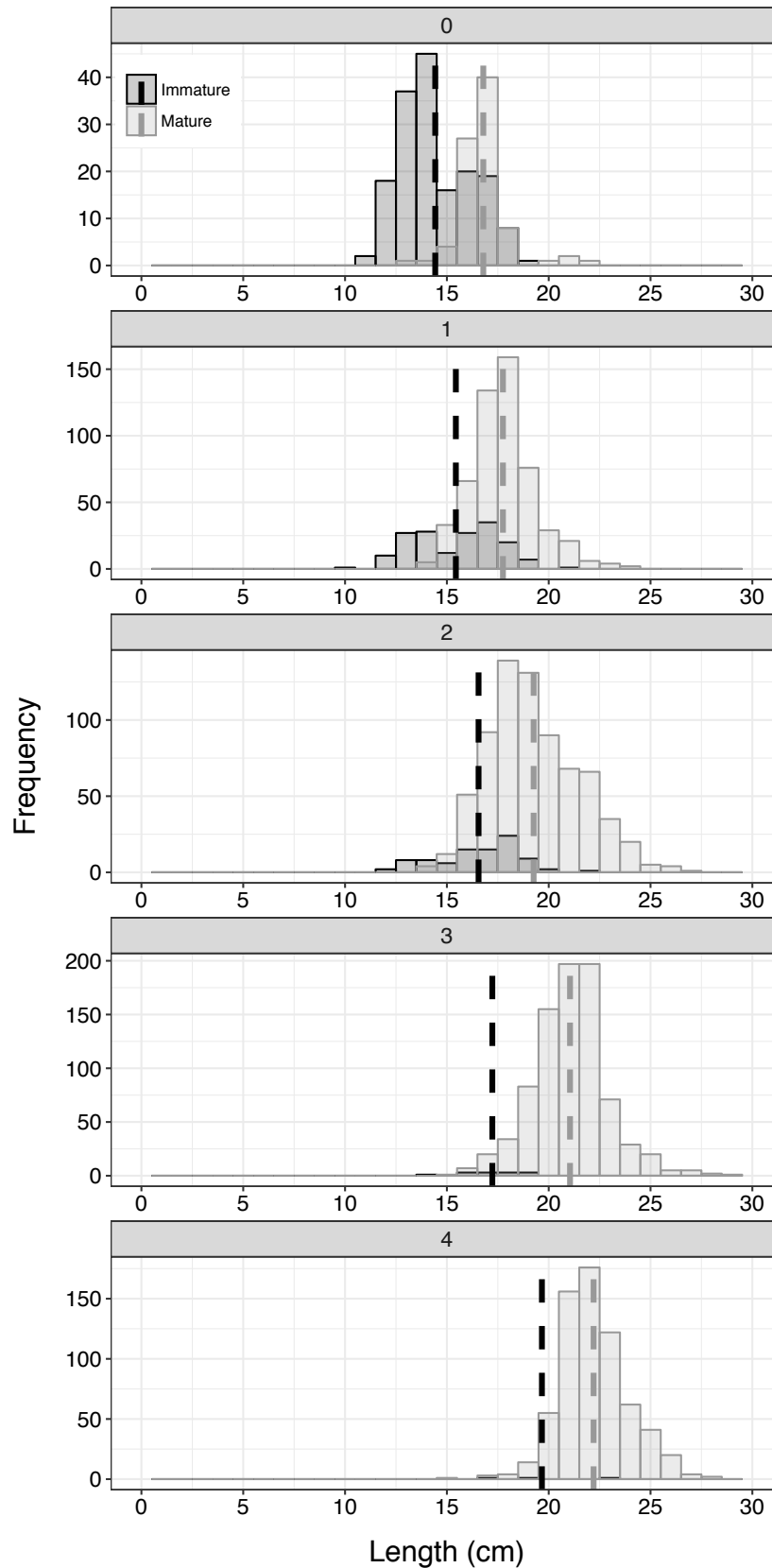


Figure 2. Length frequency of mature (light bars) and immature (dark bars) Pacific sardine by age (age-0 top to age-4 bottom panel). Dark dashed line is mean length of immature and light dashed line is mature fish. Data were aggregated from 1994–2015.

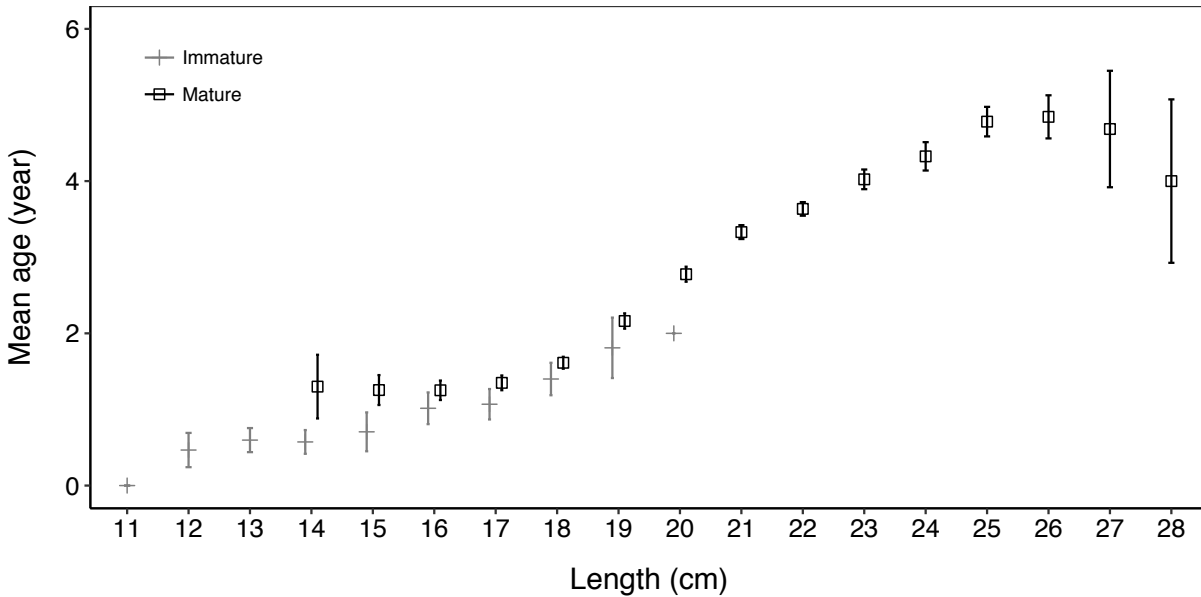


Figure 3. Mean age-at-length of Pacific sardine collected from 1994–2015. Mature fish are depicted by dark squares and immature fish by light crosses. The means of mature fish are plotted offset from lengths by 0.25 cm for presentation. Vertical lines are empirical 95% confidence intervals. Ages are integer ages. All fish greater than 20 cm are mature.

TABLE 2

**Number of estimated parameters, model deviances (and degrees of freedom), AIC values and weights ( $w_i$ ) for two competing age-based logistic models. One model treats temporal variability in female maturity rates as a function of year of collection the other as cohorts. Strength of evidence favoring one model or another can be interpreted from  $w_i$ , with values approaching 1 indicating all weight should be given to this model.**

Annual model	Estimate (df)
parameters	16
Null deviance	2728.6 (3817)
Residual deviance	1530.8 (3802)
AIC	1562.8
$w_i$	1.0
Cohort model	
parameters	28
Null deviance	2728.6 (3817)
Residual deviance	1578.0 (3790)
AIC	1634.0
$w_i$	0.0

(fig. 3). This pattern of older mature fish at every length is unlikely to be random for the given set of data ( $p < 0.001$ ) and is consistent with an age-based process of maturation. However, the randomization procedure does not consider correlations in the data, therefore care should be taken drawing inference to the real population.

### Annual or cohort temporal variability

Temporal variability in female maturity schedules was better explained by annual rather than cohort-specific variability. The strength of model evidence heavily

favored the alternative hypothesis of annual ( $w_i = 1.0$ ) rather than cohort ( $w_i = 0.0$ ) as the temporal units of the variability (table 2). The model used to estimate the age at 50% maturity generally fit the data well, although for some years the absence of younger age groups precluded estimation of that age (fig. 4). Annual variation in the estimated age at 50% maturity ranged by more than 1-year (table 3, fig. 5).

### Consistency with population dynamics

Recruitment estimated from the model assuming annual variability in maturity schedules was more consistent with the spawner-recruit process than those estimated assuming a time-invariant (average) maturation schedule. Values of  $\Delta p$  were positive for all years (fig. 6) with some improvement in consistency exceeding 50%. Improvement in estimated recruitment consistency was not due to changes in the population dynamics between models. Recruitment estimates between models was identical with the exception of the poorly informed (limited data informing) last year (fig. 7). Identical catch-at-age was an input into both models (removals) and thus the estimated population numbers at age were the same between models. The changes in spawning biomass (fig. 7) were due solely to the changes in age groups used to calculate spawning biomass from time varying maturation schedules. Changes in the calculation of spawning biomass between models resulted in a small change in the estimated population resilience ( $h = 0.36$  time-invariant,  $h = 0.35$  time-varying) based on spawner-recruit curvature (fig. 7).



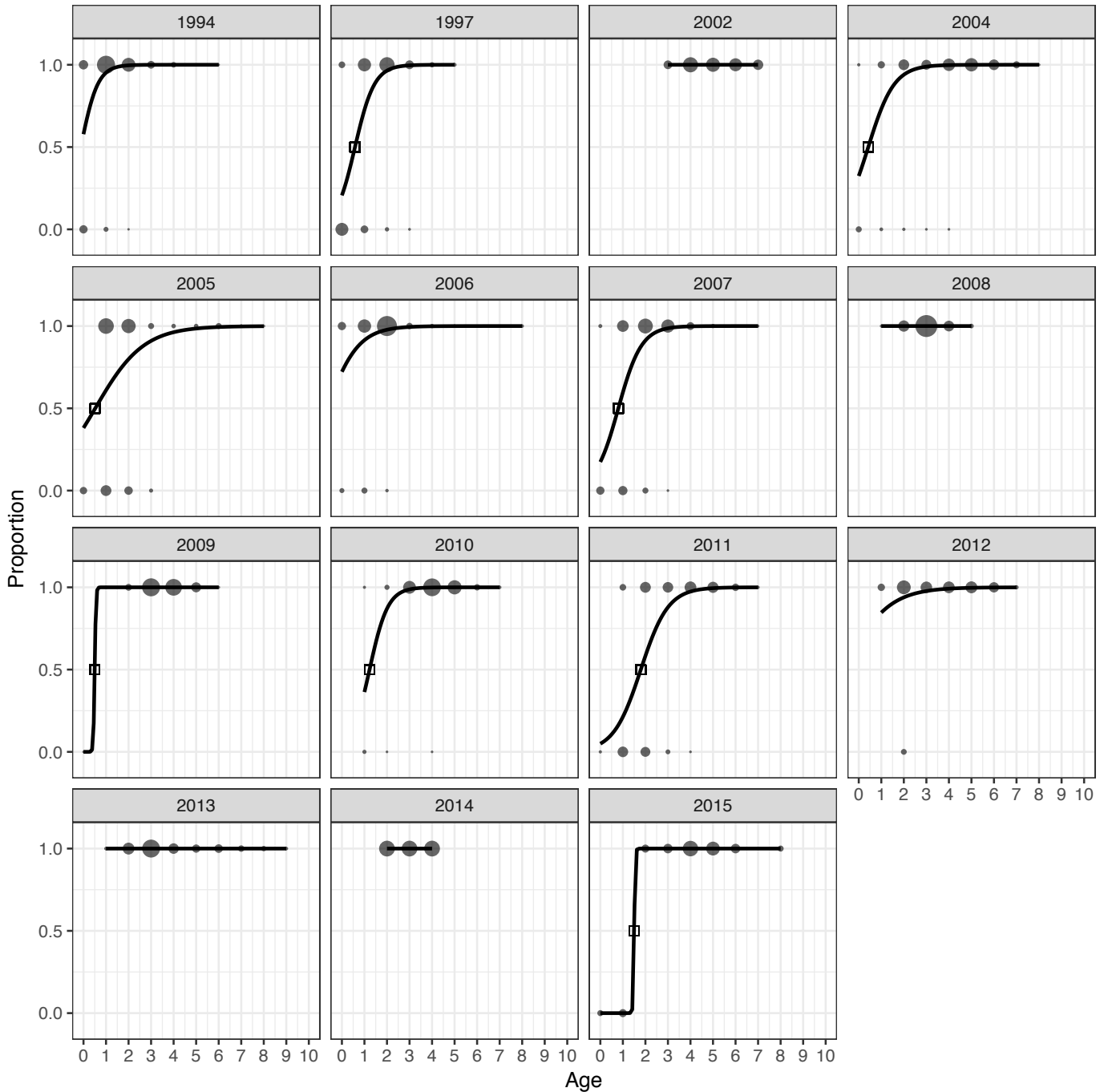


Figure 4. Model predictions of the proportion of Pacific sardine that were mature-at-age by year (solid line). Data are given as shaded circles, with the size of the circle representing the fraction of the total number of fish in that year that were either mature (given on the y-axis 1) or immature (y-axis 0) at a specific age. The open square represents the estimate of the age-at-50% maturity.

## DISCUSSION

The process of female maturation in Pacific sardine is better described by an age-based process rather than a length-based one. If maturation was controlled by the size of the body cavity, it would be expected that the ages of mature and immature fish at the same length would have been the same. However, it should not be ruled

out that size-based processes may also operate (Schnute and Richards 1990; Richards et al. 1990). The potential length effects are perhaps most strongly displayed in age-0 fish with its demonstrably smaller mode of immature fish. Three possible explanations for this include: a minimum body size influencing the start of maturation, the larger and mostly mature age-0 fish were born prior

TABLE 3  
 Year-specific estimates of parameters of the logistic model fit to annual female maturity-at-age data. Year, sample size (*n*), parameters (standard deviation), and the derived quantity of age at 50% maturity (standard deviation) are given. Standard deviations were generated by bootstrapping. NA denotes that A50 could not be derived from parameter estimates.

year	<i>n</i>	<i>a</i>	<i>b</i>	A50
1994	532	0.32 (0.21)	2.67 (0.37)	-0.12 (0.09)
1997	289	-1.35 (0.27)	2.32 (0.33)	0.58 (0.07)
2002	12	25.57 (0.00)	0.00 (0.00)	NA (NA)
2004	339	-0.73 (0.99)	1.74 (1.03)	0.42 (0.22)
2005	258	-0.49 (0.29)	0.93 (0.21)	0.52 (0.25)
2006	143	0.96 (0.57)	1.41 (1.09)	-0.68 (1.45)
2007	374	-1.56 (0.32)	1.95 (0.25)	0.80 (0.09)
2008	234	26.57 (0.00)	0.00 (0.00)	NA (NA)
2009	562	-18.39 (22.08)	36.93 (17.55)	0.50 (1.34E+11)
2010	398	-3.02 (11.08)	2.46 (8.05)	1.23 (4.81)
2011	358	-2.95 (0.4)	1.65 (0.18)	1.80 (0.1)
2012	156	0.68 (1.77)	1.03 (0.16)	-0.66 (8E+8)
2013	118	26.57 (0.00)	0.00 (0.00)	NA (NA)
2014	6	24.57 (0.00)	0.00 (NA)	NA (NA)
2015	28	-65.99 (22.45)	43.88 (12.01)	1.50 (2E+29)

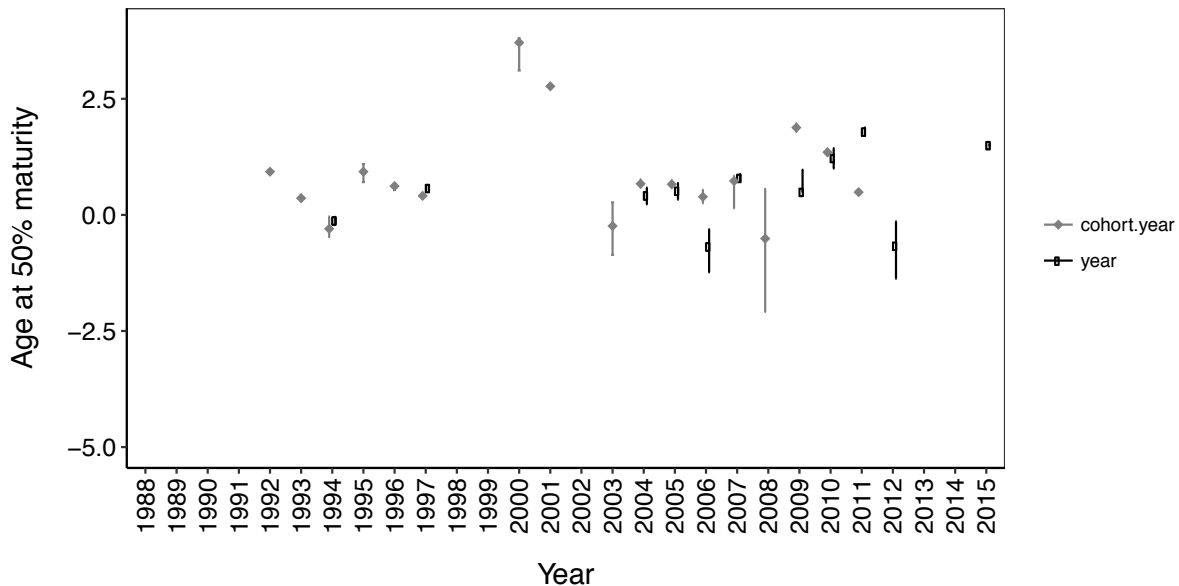


Figure 5. Model estimates of Pacific sardine age at 50% maturity. Model estimates using cohort year are given by lighter symbols and annual by darker symbols. Annual estimates are plotted offset from cohort estimates by 0.25 years for presentation. Ages were integer ages. Predicted values less than zero indicate for that time period age-0 fish were greater than 50% mature. The 80% Confidence Intervals were generated by bootstrapping the data (*n* = 1,000).

to immature fish and therefore potentially age related, or ageing error. Because hatch date may be contributing to the bimodality, future work calculating hatch date for these two groups is warranted. Whatever the cause, it does appear that immature fish at a given age are more likely to be smaller fish, but that for all lengths older fish are more likely to be mature. For assessment purposes where maturity is typically incorporated as either age- or length-based, our results support age as the better unit to describe the maturation process.

Assuming age-based maturation is the best descriptor of the process, our results support that the local environment is perhaps more important than cohort density

on the observed maturation process. Our results provide indirect support for environmental forcing of Pacific sardine population dynamics, which has already been postulated (Jacobson and MacCall 1995; Chavez et al. 2003) and forms a basis for control rules governing its management (Hill et al. 2017). The annual changes in maturation seems to be biologically significant as the age at 50% maturity ranged by more than the average difference in ages between immature and mature fish and by a significant fraction of the total lifespan of Pacific sardine. It may be worth considering that annual effects themselves are closely related to age-based processes, as year is directly related to age.



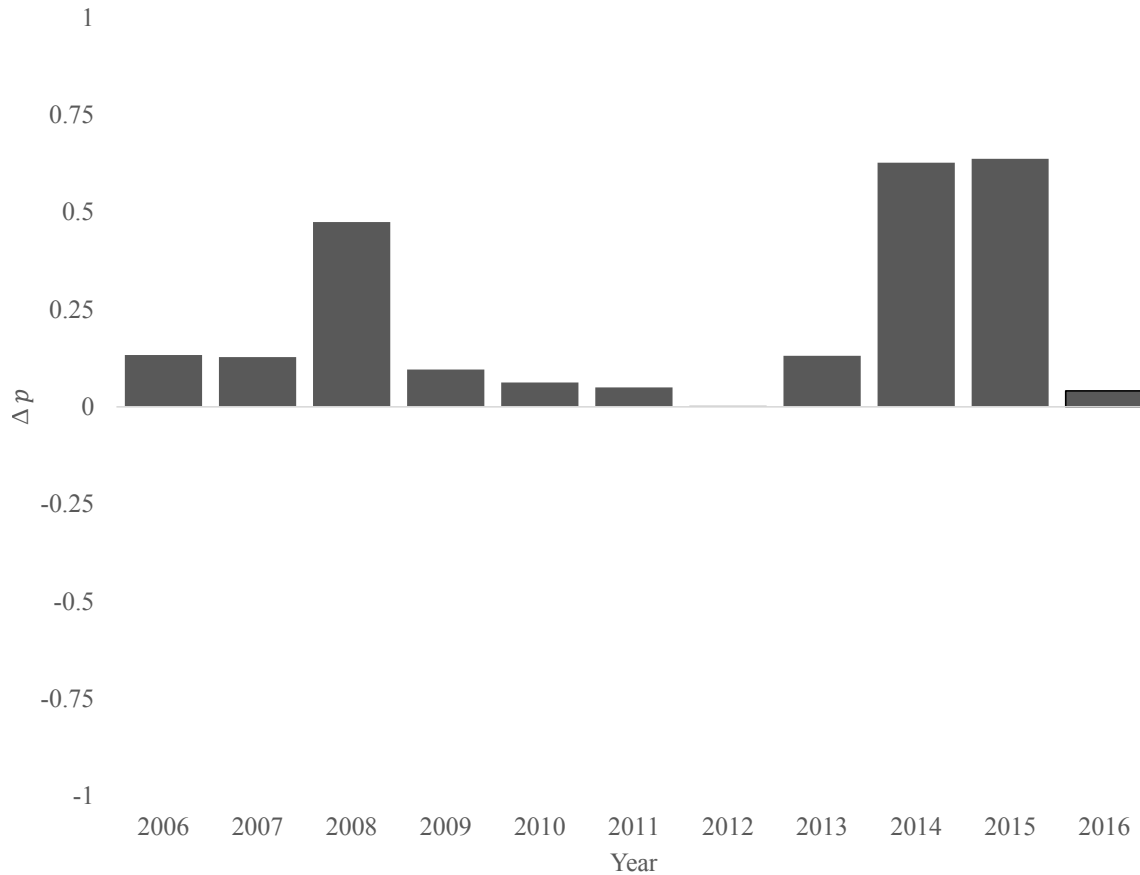


Figure 6. Proportional change in the recruitment residual ( $\Delta p$ ) from the expectation of the estimated spawner-recruit relationship. Positive  $\Delta p$  indicated reduced residual when annual variability in maturity schedules is used relative to time-invariant maturity schedule. Negative  $\Delta p$  would indicate a larger residual associated with annual empirical estimates of the maturity schedule. Terminal model year is omitted because estimated recruitment is the expected from the spawner-recruit relationship.

For stock assessments of populations with high natural mortality rates and high variability in recruitment, changes in maturity-at-age can have large effects on the effective spawning stock size. To more completely elucidate the role of maternal stock size, more consideration should be given to other aspects of spawning biology such as variability in the number of egg batches. Unless properly modelled in the stock assessment, temporal variability in reproductive processes could obscure any relationship between maternal stock size and recruitment. It should be noted that the current assessment covers a limited time period of declining recruitment and spawning biomass, and care in interpreting results from a period with a one-way trip in abundance is always warranted.

The comparison of the alternative hypothesis of age- or length-based maturation did not use a model based approach due to differences in data quality between age and length. Sardine mature across 6–8 discrete units of length but only 2–3 units of integer age, and the primary source of measurement error is likely to be ageing error, which affects only age-based models. The different degrees of data coarseness and measurement error pre-

cluded our attempting to use a model-based inference. Instead, we relied on the conditional methods of separating the correlated effects of age from length effects (McDaniel et al. 2016). Our final estimates of maturity schedule were ultimately empirical to avoid the functional form assumptions and to be consistent with how the current stock assessment treats the same data.

Two important criteria must be addressed when developing an analysis to evaluate the alternative hypotheses (Burnham and Anderson 1998). The first question regards if the set of candidate models are objective, reasonable, and defined before beginning the data analyses. This study easily meets the first criteria as the candidate models were relevant for population assessment and determined a priori. Equally important is the appropriateness of the laboratory procedures and sampling designs for the questions examined. The laboratory work followed accepted practices by experienced laboratory scientists. We note that the determination of fish age is the most difficult during the spring spawning season when our samples were taken. This difficulty arises because fish have not yet reached their presumed July

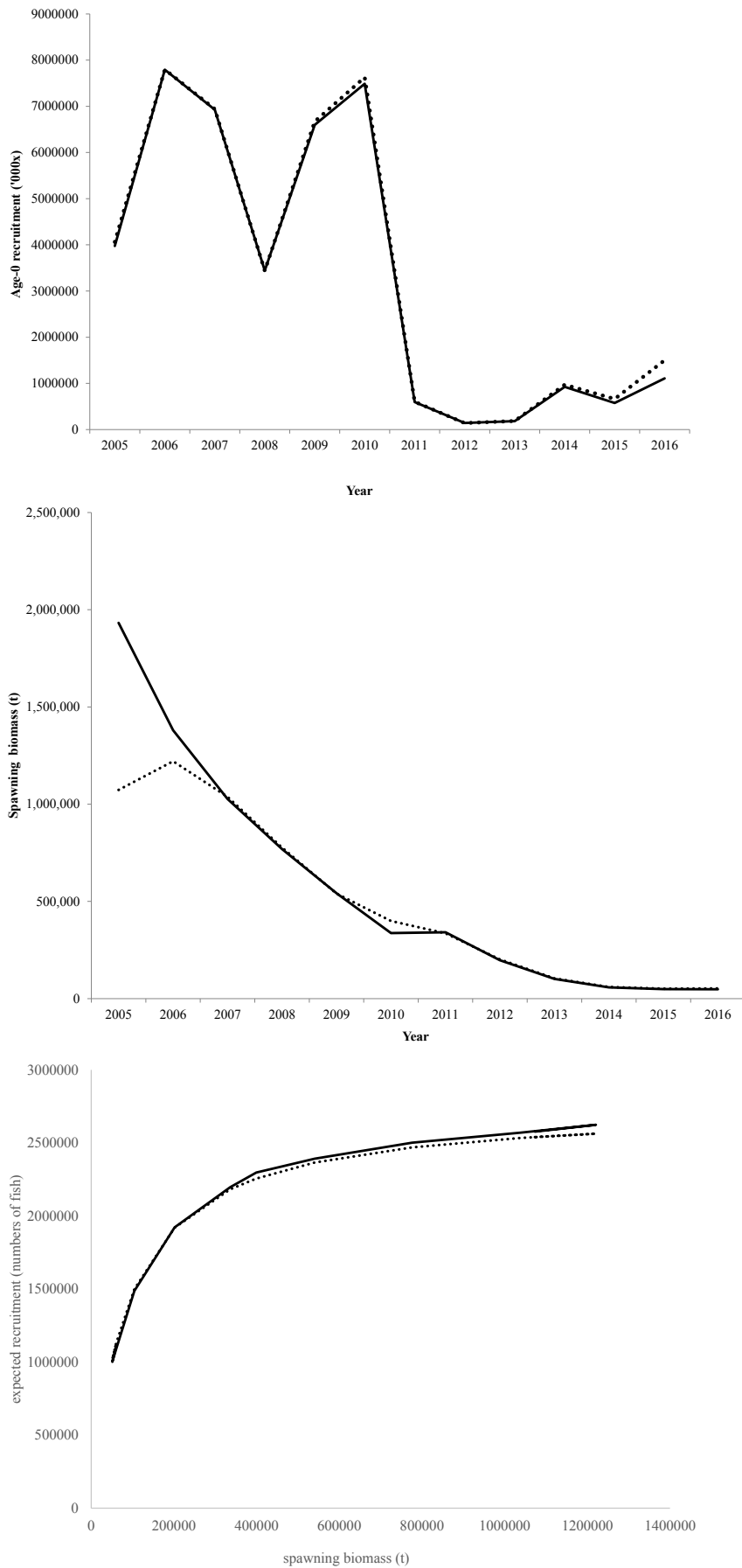


Figure 7. Recruitment (upper panel), spawning biomass (middle panel) and (bottom panel) spawner-recruit estimates from the current assessment (dotted) that uses a time-invariant maturity schedule and a model that includes a time-varying maturity schedule (solid). Terminal model year is omitted because estimated recruitment is the expected from the spawner-recruit relationship.

1st birthday and age assignment can require a subjective determination of the edge classification (annulus formed or is going to form). Ageing errors associated with an incorrect edge classification may be more likely to result in an underestimation of age.

Perhaps our largest caveat relates to the sampling design. Although the samples were taken from a fishery independent survey with established biological sampling protocols, we cannot be certain that sampling issues have not biased our results. Conditioning the maturity information on length removes the size-based sampling issues that are common in fisheries (Piner et al. 2016). Spatial patterns by age (McDaniel et al. 2016) are not as easily dismissed. Preliminary analysis (not shown) of inshore-offshore stratification produced similar conclusions about age-based maturation, but more consideration of the effects of spatial sampling may be needed.

Despite the caveats described above, these are currently the best available data on the process of Pacific sardine maturation and incorporating our results into future stock assessments are relatively straightforward. Maturity should be included as a function of age and not length. Additionally, given the magnitude of the annual variability in maturation some thought in future assessments should be given to including that variability. More specific estimates of spawning biomass could reduce the amount of the recruitment process variability and help clarify the maternal role in recruitment. Given the importance of recruitment strength in predicting safe catch levels for short-lived highly variable species, further work in this area is certainly warranted.

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