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Assessment and management of the temperate stock of Pacific sardine (*Sardinops sagax*) in the south of California Current System



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ABSTRACT

Knowing the population dynamics and the variations in the abundance of the Pacific sardine is essential for suitable fishing management. Due to the possibility that the different stocks of Sardinops sagax that can inhabit the south of California Current System (CCS) were present in the catches, the caught of the temperate stock were discriminated from the total landed and, subsequently was assessed the dynamics of temperate stock of Pacific sardine (TSPS) for the period from 1989 to 2021. For the above, we use a statistical analysis of catch-at-age (ACE), which is an integrated analysis model that includes three indices of relative abundance (catch rate, acoustic surveys and evaluations of eggs and larvae). Acoustic indices and capture rate (CPUE) denoted changes in population abundance better than the index of eggs and larvae. The total biomass has shown great interannual variability oscillating between 853,476 and 1,592,519 t; a similar trend was shown by the spawning biomass, oscillating between 404,189 t and 770,484 t. With the modified Ricker Stock-Recruitment model, the minimum biomass Bmin = 50,000 t and the exploitation rate in Emrsy = 0.251 year⁻¹ were estimated. Considering behavior of proportion between the recorded catch and the estimated biologically acceptable catch to each year (Cobs/BAC), we can infer that the TSPS has been sustainably exploited throughout analyzed period, except for 2014 and 2017 fishing seasons, when the BAC was exceeded by around 20%. Harvest control rule, by depending on a biomass fraction, estimated with an integrated model ACE, is considered a management suitable strategy to TSPS.

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1. Introduction

The Pacific sardine *S. sagax* is a resource that has supported one of the most important fisheries in the California Current system (CCS) (Wolf, 1992; Deriso et al., 1996). It has often been the dominant species among small pelagic fish throughout the CCS (Parrish et al., 1989; Emmett et al., 2005). It is distributed

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https://doi.org/10.1016/j.rsma.2023.102972 2352-4855/© 2023 Elsevier B.V. All rights reserved. throughout the CCS, from Alaska to the Gulf of California and, in cold years, it can extend to southern Sinaloa (Lluch-Belda et al., 1995).

Three stocks of this species have been identified (Hedgecock et al., 1989; Radovich, 1982; Félix-Uraga et al., 2004, 2005; Smith, 2005; Demer and Zwolinski, 2014; Dorval et al., 2015): a cold stock, a temperate one, and a warm one, dynamically overlapping in space and exhibiting temporal asynchrony influenced by sea surface temperature (SST) variability within the CCS. The cold or northern stock inhabits waters between 13 and 17 °C, the temperate or southern stock is adapted to temperatures between 17 and 22 °C, and the warm stock adapted to temperatures

between 22 and 27 °C (Félix-Uraga et al., 2004, 2005; Smith, 2005; Demer and Zwolinski, 2014; Dorval et al., 2015).

A distinctive feature of the species is the high variability in abundance. Different hypotheses have been presented trying to explain that the oscillations respond to a great extent to the climatic variability of diverse scales, beginning with the high frequency or interannual events (Hammann et al., 1995; Lenarz et al., 1995; Smith, 1995) up to those of low frequency or interdecadal (Kawasaki, 1983; Lluch-Belda et al., 1989). Oscillations in the abundances of small pelagic in the CCS have been shown to coincide with variations in environmental conditions (Jacobson et al., 2001; Fréon et al., 2005; Galindo-Cortes et al., 2010; Alheit and Bakun, 2010; Zwolinski and Demer, 2012; Lindegren and Checkley Jr., 2013; Zwolinski and Demer, 2014). Similarly, it is suggested that such fluctuations may also be due to the variability of population parameters (Dorval et al., 2015; De Anda-Montañez et al., 1999; Félix-Uraga et al., 2005; Checkley Jr. et al., 2017).

Recent estimates of cold stock abundance of S. sagax have shown a marked decrease in estimated exploitable biomass from 1.8 million t in the 2005-2006 season to 28,276 t in 2021-2022. This has forced the United States and Canadian governments to declare a moratorium on Pacific sardine fishing (Kuriyama et al., 2020, 2021). For the warm stock of S. sagax in the Gulf of California, Nevárez-Martínez et al. (2021), in their population analysis for the period 1971/1972 to 2019/2020, used the structured age model (Age Structured Assessment Program, ASAP), which, although it reflected a large interannual variability with bi-decadal oscillations, in recent years, the reproductive biomass or spawning biomass (Brep) ranged between 620 and 924 thousand tons (Nevárez-Martínez et al., 2021). Galindo-Cortes (2011) using a dynamic bioeconomic model, for Pacific sardine landed between Bahia Magdalena, Mexico, and British Columbia, Canada, during the period 1981 to 2008, found that the levels of total biomass (Btotal) remained around an average value of 290,000 t, with a reduction linear between 1997 and 2003 from 326,000 t to 231,000 t; for 2009 an abundance of 250 thousand t was estimated (Galindo-Cortes, 2011).

The regulatory framework for the small pelagic fishery suggests, among other measures, that permissible catch volumes of target species be established through a Catch Control Rule, which is defined based on a Biologically Acceptable Catch (BAC), which must be dynamic and will depend on the available biomass (active management, DOF, 2012).

Based on the above and recognizing the high variability in the abundance of the Pacific sardine, the management of the fishery requires continuous updates on the status of the different stocks (Lluch-Belda et al., 1989). With a comprehensive evaluation approach, in the present study a statistical analysis of catch at age (ACE) was applied, which integrates biological and fishing information together with some indices both dependent and independent of the fishery; thereby improving the evaluation of the temperate stock of Pacific sardine (TSPS), increasing the realism of the population dynamics. This, to provide suitable advice for management, is necessary for the sustainable use of this fishing resource so important for the region.

2. Materials and methods

The study area includes the distribution zone of the TSPS throughout of California Current System southern, which is where the commercial purse-seine fishing fleets operate off San Pedro, California in the USA, Ensenada, Baja California and Bahía Magdalena, Baja California Sur in Mexico (Fig. 1).

The information and data come from the small pelagic monitoring programs of the National Institute of Fisheries and Aquaculture (INAPESCA) and the Interdisciplinary Center for Marine



Fig. 1. Study area of the temperate stock of *S. sagax* on the western coast of the Baja California peninsula, grouped by landing port: San Pedro (SP), Ensenada (EN), Isla de Cedros (IC) and Bahía Magdalena (BM).

Sciences (CICIMAR). Catch data from San Pedro (1989–2014) were provided by Southwest Fisheries Science Center (Kevin Hill, pers. comm.). A database of catch and fishing efforts was integrated from 1989 to 2021 and included biometric information.

In order to divide the biological and fishery compositions attributed to each of the three stocks that inhabit the western coast of the Baja California peninsula, we used the discrimination criterion of catch by the temperature of the stocks present in landings (Félix-Uraga et al., 2004). Catch data for the period analyzed (1989-2021) were grouped monthly by collection area to define each stock component. This could be applied because each catch landed has the record of the area where the catch was made. The warm stock (WS) inhabits temperatures higher than 22 °C, the temperate stock (TS) inhabits temperatures from 17 °C to 22 °C, and the cold stock (CS) inhabits temperatures below 17 °C. To obtain sea surface temperature (SST), we used the Geospatial Interactive Online Visualization and Analysis Infrastructure (Giovanni) system developed and maintained by the National Aeronautics and Space Administration (NASA), Goddard Earth Sciences (GES) Data and Information Services Center (DISC) (https://giovanni.gsfc.nasa.gov, accessed on 11 November 2022). Monthly averages of sea surface temperature (SST) were obtained by quadrants of $2^{\circ} N \times 2^{\circ} W$ (Fig. 1); were 23 to $25^{\circ} N \times 112$ by 114° W for Bahía Magdalena, 27 to 29° $N \times 115$ to 117° W for Isla de Cedros, 30 to $32^{\circ} N \times 117$ to 119° W for Ensenada, and 32 to 34° $N \times 118$ to 120° W for San Pedro (Félix-Uraga et al., 2004).

The calculation of M was made considering the average obtained with the methods of Hewitt and Hoenig (2005) and Pauly (1980). The method based on the maximum age of the species (Hewitt and Hoenig, 2005) is:

$$LnM = 1.44 - 0.982 * Ln(Tmax)$$
(1)

Where: *Tmax* is the maximum age of the temperate stock of *S. sagax*, which is 8 years (Alvarez-Trasviña, 2012).

The empirical formula of Pauly (1980):

$$LnM = -0.0152 - 0.279LnL\infty + 0.65LnK + 0.463LnT$$
(2)

Where: *M* is the natural mortality rate, $L\infty$ and *K* are the parameters of the von Bertalanffy model and *T* is the average temperature of the habitat range for the TSPS, which is 19.5 °C (Félix-Uraga et al., 2004, 2005).

Conversions between standard length (LP) and weight (WT) were made using the constants estimated by Enciso-Enciso et al. (2022), for the length-weight relationship:

$$WT = 7.34 \times 10^{-6} LP^{3.155} \tag{3}$$

Catch at age was estimated considering the size structure of each year, grouped in 5-mm LP intervals, and later converted to age by using size-age keys obtained by Enciso-Enciso et al. (2022).

The stock assessment of the TSPS was implemented with an annual period of time, for age classes between 0 and 6 years, the analysis of capture by age (ACE) was applied (Haddon, 2011) and using a Microsoft Excel 2016 spreadsheet; A data series of 33 years (1989–2021) of catch at age was used, the initial values of recruitment were estimated with the function of Pope (1972). Also, both fishery-dependent (CPUE) and fishery-independent information were used, the acoustic biomass index (biomass estimated by fishery acoustics) and the egg abundance index (Egg production method); these indices were used to stabilize the model and reduce the uncertainty of the estimated parameters.

The basic population dynamics equation was used to estimate the number of organisms at age a + 1 at time t + 1 (Hilborn and Walters, 1992).

$$N_{a+1\,t+1} = N_{a\,t} * e^{-(M+F_{a,t})} \tag{4}$$

Where: $N_{a,t}$ is the number of sardines at age a at time t, the expression $e^{-(M+Fa,t)}$ is survival per cohort, where M is natural mortality and is considered constant for all cohorts over time, and $F_{a,t}$ is fishing mortality at age a during year t.

Fishing mortality was estimated considering the specific effect of selectivity at age (Haddon, 2011):

$$F_{a,t} = \hat{F}_t * S_a \tag{5}$$

Where \hat{F}_t is the instantaneous rate of fishing mortality for the time *t* estimated in the model, and S_a is the selectivity at age *a* that was estimated with the logistic model (Haddon, 2011):

$$S_a = \frac{1}{1 + (e^{-\ln(19)\frac{(a-a_{50})}{(a_{50}-a_{95})}})}$$
(6)

Where a_{50} and a_{95} are estimated parameters in the selectivity model at 50% and 95% respectively.

Once the number of organisms per age group was estimated, it was possible to generate the catch at the estimated age $\hat{C}_{a,t}$ (Baranov, 1918):

$$\hat{C}a, t = \frac{F_{a,t}}{M + F_{a,t}} N_{a,t} \left(1 - e^{-(M + F_{a,t})} \right)$$
(7)

The annual proportion of observed fishing mortality (*Fo*) at time t was also estimated; the *Fo* was standardized by the product of proportionality or catchability (q) by the effort, in number of fishing trips per time (f_t):

$$Fo_t = q * f_t \tag{8}$$

Since the estimated Fo_t values are an annual proportion or harvest rate (*E*) and not an instantaneous rate of fishing mortality they were recalculated (Haddon, 2011):

$$F_t = -LN(1 - Fo_t) \tag{9}$$

Recruitment for the second and subsequent years was estimated by the modified Ricker stock-recruitment (S-R) function (Chen et al., 2002):

$$R_{r,t+r} = \propto (S_{t-1} - \lambda)e^{-\beta(S_{t-1} - \lambda)}e^{\varepsilon}$$
(10)

Where: *r* is the age of recruitment, *t*+*r* is the year plus the length of time before recruits enter the fishery, S_t is the size of the spawning stock at time *t*, λ is the estimated minimum number of spawners which guarantees recruits next year. Parameters α , β and λ were obtained by fitting the modified Ricker S-R function.

Additionally, the CPUE index (catch/fishing trip) of the fleet during the fishing years 2000–2021 was incorporated into the model. This, as auxiliary information to stabilize the model and increase the precision in the estimation of the parameters (Deriso et al., 1985; Methot, 1989; Hilborn and Walters, 1992; Hilborn et al., 1994). Assuming observed CPUE is proportional to population abundance:

$$\overline{Y} = B_t * q \tag{11}$$

Where: B_t is the biomass at time t and q is the catchability for each CPUE, estimated as:

$$q = e^{\left[\frac{\sum_{t} ln\left(\frac{Y_{t}^{ODS}}{B_{t}}\right)}{n}\right]}$$
(12)

Where: *n* is the number of data available for the CPUE series and Y_t^{obs} represents the CPUE observed in the fleet at time *t*.

Likewise, information independent of the fishery, obtained from research cruises, was incorporated into the general ACE model: Egg abundance index (Egg production method) and Biomass index by acoustics. The estimation of the census of eggs and/or larvae was calculated with the abundance index, referring to the average number of eggs and/or larvae per 10 m² of seawater surface, extrapolating to the total area of each of the regions, this index is called the Larval Index of Smith and Richardson (1979), which is defined as:

$$IA = \frac{\sum N}{N+} * \left(\frac{N+}{Nt}\right) * C \tag{13}$$

Where: Al is the index of abundance of eggs or larvae (estimation of eggs and/or larvae in the region), $\sum N$ is the total sum of eggs or larvae standardized to 10 m² of sea surface, *N*+is the number of positive stations, *Nt* is the total number of stations where sampling was carried out and *C* is the number of area units of 10 m².

When an abundance indicator (CPUE or other) is used, it is necessary to transform it into a standardized estimated biomass (Eq. (11)), considering for this the catchability (Eq. (12)).

Finally, from acoustic survey cruises on the western coast of the Baja California peninsula during 2012, 2016 and 2018, an annual average biomass index was obtained. In this case, since the independent information is in units of biomass in all years, it was not necessary to estimate a proportionality coefficient.

Optimal parameter values were obtained by maximizing the log-likelihoods of each partial function (Haddon, 2011):

For the observed and predicted catches in number for each age *a* in each year *t*.

$$LL^{C} = \left(-\frac{n}{2}\right) * \left(\ln(2\pi) + 2 * \ln(\sigma_{C}) + 1\right)$$
(14)

For observed and forecast fishing mortalities in each year.

$$LL^{F} = \left(-\frac{n}{2}\right) * \left(\ln\left(2\pi\right) + 2 * \ln\left(\sigma_{F}\right) + 1\right)$$
(15)

For observed and forecast recruitment in each year.

$$LL^{R} = \left(-\frac{n}{2}\right) * \left(\ln(2\pi) + 2 * \ln(\sigma_{R}) + 1\right)$$
(16)

For the observed CPUE and the estimated exploitable biomass in each year.

$$LL^{CPUE} = \left(-\frac{n}{2}\right) * \left(\ln\left(2\pi\right) + 2 * \ln\left(\sigma_{CPUE}\right) + 1\right)$$
(17)

For the observed IA and the estimated total biomass in each year.

$$LL^{IA} = \left(-\frac{n}{2}\right) * \left(\ln\left(2\pi\right) + 2 * \ln\left(\sigma_{IA}\right) + 1\right)$$
(18)

For the acoustic index (Acust) and the estimated total biomass in each year.

$$LL^{Acust} = \left(-\frac{n}{2}\right) * \left(\ln(2\pi) + 2 * \ln(\sigma_{Acust}) + 1\right)$$
(19)

Where: *LL* is the log-likelihood, *n* is the number of observations, and σ is the standard deviation for the given function. The analytical solution of the standard deviation (σ) was:

For the captures:

$$\sigma_{C} = \sqrt{\frac{1}{n} \sum_{t=1}^{n} \left(lnC_{o,t} - ln\hat{C}_{o,t} \right)^{2}}$$
(20)

For the effort

$$\sigma_F = \sqrt{\frac{1}{n} \sum_{t=1}^{n} \left(lnF_o - lnF_E \right)^2}$$
(21)

For recruitment.

$$\sigma_R = \sqrt{\frac{1}{n} \sum_{t=1}^{n} (lnR_o - lnR_E)^2}$$
(22)

For the CPUE index.

$$\sigma_{CPUE} = \sqrt{\frac{1}{n} \sum_{t=1}^{n} (lnB_o - ln (q * CPUE))^2}$$
(23)

For the AI index.

$$\sigma_{Larvas} = \sqrt{\frac{1}{n} \sum_{t=1}^{n} \left(lnB_o - \ln(q * lA) \right)^2}$$
(24)

For the acoustic biomass index (Acust).

$$\sigma_{Acust} = \sqrt{\frac{1}{n} \sum_{t=1}^{n} (lnB_o - lnB_E)^2}$$
(25)

Where: Co, Fo, Ro and Bo are observed values and $\hat{C}_{e,t}$, \hat{F}_E , \hat{R}_E and \hat{B}_E are estimated values.

A final fit was made to the model maximizing the total loglikelihood objective function, the total objective cell is the sum of the partial functions: Catch at age, Effort, Recruitment, CPUE and Independent information (Megrey, 1989; Haddon, 2011):

$$LL^{total} = LL^{C} + LL^{F} + LL^{R} + LL^{CPUE} + LL^{AI} + LL^{Acust}$$
(26)

Once the model was adjusted, the annual biomass of the stock was estimated:

$$Bt = \sum N_{a,t} * WT_{a,t} \tag{27}$$

Where: $N_{a,t}$ is the number of organisms at age a, at time t and $WT_{a,t}$ is the average weight at age a at time t that was estimated with the average size at age of the growth models and the parameters of the length–weight relationship (Enciso-Enciso et al., 2022).

On the other hand, the uncertainty of the estimated management amounts was carried out through a sensitivity analysis on those parameters with the greatest uncertainty in the model (as the main sources of error): natural mortality (M), catchability (q) and the parameters α , β and λ of the modified Ricker S-R

function. Crystal Ball version 11.1.2.4 software (Oracle[®] Crystal Ball) was used, 10,000 iterations were performed for biomass and management amounts. The results were expressed in terms of correlation coefficients and percentage of explained variance between the input parameters, and their confidence intervals ($\alpha = 0.05$) were also obtained from the model outputs.

To validate the ACE model, the distribution of the catch data simulated by the model was compared with the catches reported during the analyzed period (1989–2021), through the non-parametric Kolmogorov–Smirnov test.

To show the evolution and current status of the level of exploitation of the fishery, the estimate of the biologically acceptable catch was made:

$$BAC = (SSB - SSB_{min}) * FRACTION$$
⁽²⁸⁾

$$FRACTION = (1 - e^{(-F_{MSY})})$$
(29)

Where BAC is the biologically acceptable catch (target reference point), SSB is the estimated spawning biomass, *SSB_{min}* is the minimum spawning biomass needed to avoid depletion, and FRACTION is the proportion of biomass above *SSB_{min}* that can be caught (exploitation rate).

3. Results

The values obtained from the catch at age, for the period from 1989 to 2021, are presented in Fig. 2. It is estimated that around 80% of the catch corresponds to the ages of 1 and 2 years. However, in recent years an increase has been observed in the proportion of the 0 and 1 year age groups and a decrease in the longest living organisms (3, 4, 5 and 6 years).

The fit of the ACE model to the Acoustics, Eggs-Larvae and CPUE indices are presented in Fig. 3. The indices showed different time scales, the longest time series and with the best fit was the CPUE index with twenty-one seasons analyzed (Fig. 3C), followed by the biomass index estimated by acoustics with a moderate adjustment, although with only three years analyzed (Fig. 3A); while the Eggs-Larvae index showed a poor fit to the data regarding total abundance, inferring that the proportion of Eggs-Larvae data is not very informative with the total abundance of the STSP (Fig. 3B).

The total abundance of TSPS (TTB) in the southern California Current has shown great interannual variability (Fig. 4A), ranging between 853,476 and 1,592,519 t, with an average of 1,206,435 t. For the last season (2021), TTB = 980.496 t was estimated with 95% confidence intervals between 901,006 t and 1,071,465 t. A similar trend is observed in the spawning biomass of the TSPS (SSB), which presents great interannual variability, without important fluctuations between 404,189 and 770,484 t, and an average of 587,004 t. For the 2021 season, $SSB_{2021} = 496.348$ t was estimated with 95% confidence intervals between 431,915 t and 569,418 t. The results of Pacific sardine abundance (in individuals number) estimated from ACE indicated two scales of variability, the first showed the short term changes, mainly interannual; while the second suggested long terms changes expressed as decadal variability. Both were identified for total abundance (Nt, dotted line), recruits abundance (R, bold line) and the abundance of the spawning stock (SS) (Fig. 4B). The interannual variability was more noticeable at the beginning and at the end of the time series of Nt and R, periods in which they reached the highest values, in particular the recruitment reached values between 10,850 and 12,350 million individuals. Both Nt and R showed a downward trend between 1999 and 2012, and then changed to an upward trend (Fig. 4B).

The annual rate of fishing mortality ranged between 0.071 year⁻¹ and 0.347 year⁻¹ (Fig. 5A), in most years they remained below the upper limit of the confidence interval of the target



Fig. 2. Catch by age of the TSPS for the period from 1989 to 2021: (A) Catch in weight (t) and (B) Catch in number of individuals.

reference point (Fmsy = 0.289 year⁻¹, Cl 0.253–0.325 year⁻¹), except for the fishing seasons of 1998, 2014, 2019 and 2021. A similar trend is shown by the annual exploitation rate ($E = 1-e^{(-F)}$), fluctuating between 0.069 year⁻¹ and 0.293 year⁻¹. While the harvest rate (E =Ctotal/Bexp) which ranged between 0.045 year⁻¹ and 0.266 year⁻¹, did not exceed the upper limit of the confidence interval of the target reference point (Emsy = 0.251 year⁻¹, Cl 0.223–0.278 year⁻¹), indicating a good state of the TSPS (Fig. 5B).

Fig. 6 shows the fit of the stock-recruitment relationship of the modified Ricker model. The relationship shows that spawning stock values ranged from 5.312 to 8.367 million individuals, while recruits ranged from 6.467 to 12.297 million individuals. The parameters estimated by the model were: the slope at the origin (density-independent mortality) $\alpha = 3.493$, the effect of compensatory mortality (density-dependent mortality) $\beta = 1.513 \times^{-10}$ and the value of the minimum spawning stock (minimum biomass, Bmin), $\lambda = 479$ million individuals, which is equivalent to ~50,000 t, considered here as the limit reference point in the management of this fishery (Fig. 6).

The validation of the ACE model through the comparison between the observed catch with the estimated one was successful (Fig. 7A, 7B), that is, the Pearson correlation statistical test did not show significant differences between the two ($r^2 = 0.975$, t = 34,676, $p < 2.2 \times 10^{-16}$, Fig. 7B). The output of the ACE model presented a pattern consistent with observed reality (Fig. 7A).

In Table 1, we show the sensitivity analysis in terms of correlation and in terms of percentage of estimated variance, in the estimation of the BAC (using Catch Control Rule) as output of the model. It was found that the value of *M* and the parameters α and λ of the modified Ricker's S-R model are the most sensitive parameters. The values of *M* and λ showed a negative correlation, negatively impacting the level of the BAC; while α presented a positive correlation and the rest of the parameters (β and

Table 1

Sensitivity analysis of the parameters of the ACE model in terms of
correlation and in terms of percentage of variance explained, for the
estimation of BAC (using the capture control rule) of the TSPS.

Parameter	Correlation	Variance explained (%)
Μ	-0.62	69.5
q	-0.01	1.0
α	0.36	23.8
β	0.01	1.0
λ	-0.16	4.8

q) showed little or no sensitivity in the model. The parameter *M* contributed the greatest contribution to the total variance obtained with 70.9%, followed by α with 24.2% and finally λ with only 4.8%; in this way, the variability in the values of the Control Rule is basically due to the uncertainty in the value of the parameter *M*, α and λ mainly. This result was taken into consideration for the incorporation of uncertainty in the ACE model.

Considering the estimated results of the Cobs/BAC ratio, it is inferred that the STSP population has generally been exploited below the BAC, except for the 2014 and 2017 fishing season, where the ratio was 1.24 and 1.19, respectively, which indicates that the BAC was exceeded by 24% and 19%, respectively, in both seasons (Fig. 8).

4. Discussion

A critical and fundamental step for the development of management strategies for any fishery resource is to determine the reference points since these are parameters that both scientists and managers use to compare the current status of a population or a fishery with the desirable status (or undesirable), allowing the ability to evaluate the fulfillment of the goals or the success of



Fig. 3. Fit to the (A) Acoustic Index, (B) Egg-Larvae Index and (C) CPUE Index of the ACE Model for the TSPS in the south of California Current System.

the management strategy. Managers should choose scientifically based reference points, which can be used as a guide to develop a useful and efficient control rule that provides an acceptable guarantee of fishery sustainability (Hilborn and Walters, 1992; FAO, 1995).

In the present work for the STSP, the estimated natural mortality was incorporated into the ACE model as a constant value in the stock assessment. However, when incorporating variation in the different input parameters for stock assessment, the results indicated that natural mortality is the parameter with the greatest sensitivity in estimating BAC (estimated with the Control Rule), which is the measure management recommended for the sardine resource in accordance with current regulations. Therefore, for future analyzes of the Pacific sardine, it is advisable to consider its variation to have greater certainty in its assessment and, above all, in fishing management.

In the 33 seasons analyzed in the present study (1989–2021), the high fluctuations in the abundance of the Pacific sardine are a challenge and two hypotheses have been considered for their explanation: environmental stochasticity that affects abundance (Jacobson et al., 2001; Nevárez-Martínez et al., 2001; Fréon et al., 2005; Galindo-Cortes et al., 2010; Alheit and Bakun, 2010; Zwolinski and Demer, 2012; Lindegren and Checkley Jr., 2013; Zwolinski and Demer, 2014) or the effects dependent on density, where an overcompensation mechanism in the Pacific sardine could be operating, for example, variability of population parameters, in cannibalism, among others (De Anda-Montañez et al., 1999; Félix-Uraga et al., 2005; Dorval et al., 2015; Checkley Jr. et al., 2017).

This study is the first to analyze changes in the abundance of the temperate Pacific sardine stock based on an integrated stock assessment model, in which different data sources were included, particularly some indices of relative abundance. The main assumption is that each relative abundance index is proportional to population abundance (Hilborn and Walters, 1992). However, statistical methods for fitting catch-at-age analysis that use indices of relative abundance are particularly sensitive to observational error; consequently, when multiple indices of relative abundance are used, all available indices are prone to this type of statistical



Fig. 4. (A) Total biomass (TTB) and spawning biomass (SSB) and their respective 95% confidence intervals (gray shade); (B) total abundance (Nt), recruits abundance (R) and abundance of spawning stock (SS), of the TSPS in the south of California Current in the period 1989–2021.



Fig. 5. (A) Fishing mortality (F), (B) Exploitation rate $(E = 1 - e^{(-F)})$ and harvest rate (E = Ctotal/Bexp) of the TSPS in the south of California Current, estimated annually for the period 1989 to 2021.

error (Shepherd, 1999; Linton and Bence, 2008). Therefore, it is assumed that the relative abundance indices analyzed through the ACE have multiplicative errors, and by transforming the data to a normal distribution, the variances can be stabilized and,

therefore, the indices make a better contribution to the stock assessment (Quinn II and Deriso, 1999; Dichmont et al., 2016). Due to the above, the expectation is that the indices can be informative about the abundance of the stock to be studied. Of the three indices analyzed in the present study (Acoustics-survey, Egg-larvae index, and CPUE catch rate index), the catch rate index was the most informative index on changes in the abundance of the temperate stock of Pacific sardine, probably because it has a wide spatial and temporal coverage; It was followed by the acoustic-survey index (independent of the fishery), which although it has a wide spatial coverage, did not have great temporal coverage, since data were only available for the end of the study period, it showed a good performance with the changes in stock abundance; On the other hand, the Egg-larvae index, with data for the middle part of the analyzed period, with variable spatialtemporal coverage from year to year, showed a contradictory trend to what was indicated by the CPUE and Acoustic-survey indices, so there is a possibility that the Egg-larvae index reflects only changes in the spatial distribution of Pacific sardines during the study period rather than changes in stock abundance.

The use of different indices of relative abundance to estimate abundance has been a recurring theme in stock assessments of the Pacific sardine fishery (Barnes et al., 1992; Deriso et al., 1996; Simmonds, 2003). Depending on the stock analyzed, the indices have shown different results in estimating changes in biomass. For the cold stock of the Pacific sardine, several indices of relative abundance have historically been included and/or discarded (breeding areas, number of marine stations with the presence of eggs or larvae, aerial observations, among others), their inclusion is conditioned to the spatial coverage that reflects the distribution of the stock, the availability of the time series and its precision associated with random and systematic errors (Jacobson and McCall, 1995; Lo et al., 1996; Richards and Schnute,



Fig. 6. Modified Ricker stock-recruitment model fit to the STSP in the south of California Current System.



Fig. 7. Comparison between the observed catch (Cobs) and the simulated catch (Csim) by the ACE model for the TSPS in the period from 1989 to 2021.

1998). In this study, the acoustic and CPUE indices were the ones that best denoted changes in the abundance of the temperate sardine stock.

The knowledge of the dynamics of generations is a key factor to understand the changes in abundance of an exploited population. Therefore, understanding how these changes occur helps to avoid overfishing, which can be defined in two ways: (1) growth overfishing defined as excess fishing mortality exerted on young organisms in a population; and (2) recruitment overfishing defined as excess fishing pressure on the adult fraction of the population to levels that reduce the intake of enough recruits to replenish mortality loss (Haddon, 2011). The main challenge of this type of analysis is not to explain how generational dynamics occur, but how to determine the mechanisms that govern it (Quinn II and Deriso, 1999). Within the context of population dynamics analysis and stock assessment, it is of great importance to periodically quantify abundance either in number of organisms or in terms of biomass. These quantifications will allow knowing several essential aspects of the populations, such as: The state of health "status", the level of exploitation, understanding the response to fishing pressure, predicting recruitment, predicting changes in the level of biomass. All the above, to make



Fig. 8. Projection of the level of exploitation considering the Cobs/BAC ratio as an indicator of sustainability for the TSPS on the western coast of Baja California during the period from 1989 to 2021.

management suggestions to achieve optimal use of the fishing stock.

The high value of the coefficient of determination $(r^2 =$ 0.975) between the observed and simulated catches with the ACE model is an indicator that the model was adequately adjusted to the observed data. The high interannual variability in abundance appears to be a response to successful recruitment (Félix-Uraga, 2006). The ACE model showed the importance of groups 0, 1 and 2, historically these were the most important age groups in the TSPS fishery. However, in recent seasons an increase in groups 0 and 1 (recruits) has been observed, their contribution to abundance has a consequence on the variability of the total abundance of the stock. Hence, the importance of recruitment in the fishery is widely recognized and can affect sudden drops in stock productivity (Jacobson and McCall, 1995; Morales-Bojórquez and Nevárez-Martínez, 2005; Hill et al., 2019). The contribution to the abundance of the age groups 3, 4, 5 and 6 years had little abundance; therefore, it is inferred that the fisherv for the temperate stock of Pacific sardine depends mainly on the abundance of recruits.

The interannual variability of biomass in the Pacific sardine may be associated with fluctuations in the environmental conditions of the CCS (Jacobson et al., 2001; Fréon et al., 2005; Galindo-Cortes et al., 2010; Alheit and Bakun, 2010; Zwolinski and Demer, 2012; Lindegren and Checkley Jr., 2013; Zwolinski and Demer, 2014). The abundance of the cold stock of Pacific sardine off the coast of California showed a period of population recovery starting from 1991 to 2010 (Wolf, 1992; Dorval et al., 2015; Hill et al., 2019). In the temperate stock, fluctuations in abundance have not been as marked as in the warm and cold stock, and it is inferred that they may be a consequence of habitat characteristics and dynamics (McFarlane and Beamish, 1999). Regime changes in the ocean environment are now recognized as important factors affecting the abundance of a wide diversity of species (Lluch-Belda et al., 1989; McFarlane and Beamish, 1999; Rodríguez-Sánchez et al., 2001). Although the intensity of fishing could also play an important role in the variability of the biomass of the Pacific sardine stocks. However, these are to a lesser extent than environmental changes.

The estimation of λ allowed obtaining values of critical biomass (Bmin) that represents the minimum size of the spawning stock, necessary for its recovery in case of population decline, with the modified Ricker model. This limit reference point that identifies and predicts the depletion of the sardine population, estimated

comprehensively by the ACE model, could be reached at a spawning biomass of 479 million individuals. Although this reference point can be useful to avoid recruitment failures, however, it does not define the spawning biomass that can positively influence successful recruitments (Frank and Brickman, 2000).

Regarding exploitable biomass, the ACE model suggests the existence of sufficient sardine biomass to be harvested. However, catch reports were lower compared to what was estimated by the model. According to Nevárez-Martínez et al. (1999), fishing mortality reduces the spawning biomass, causing a dense dependence, thereby affecting recruitment. This could occur with an annual fishing mortality greater than 0.325 (upper limit of the confidence interval of the target reference point); however, this study estimated that only the 1998, 2014, 2019, and 2021 fishing seasons exceeded that benchmark. Consequently, the variability in annual fishing mortality does not fully explain the changes in biomass. An explanation of the above could be associated with the availability of sardines for the fishing fleet; environmental stochasticity plays an important role in the spatial distribution of the stock, affecting its abundance, survival, growth and spawning success (Huato-Soberanis and Lluch-Belda, 1987; Nevárez-Martínez et al., 2001; Dorval et al., 2015).

While this issue of the relationship between the environment and the sardine population is particularly relevant, it is beyond the scope of this study, which relies primarily on an integrated catch-at-age analysis to model temporal changes in abundance, biomass, and recruitment. New analyzes are necessary to jointly understand the effects of the environment on the population dynamics of the Pacific sardine and thus deal with uncertainty in future conditions related to abundance levels and the environment.

The current management order for the small pelagic fishery indicates that the annual catch should be less than or equal to a BAC, estimated with the catch control rule. Under this consideration, with the results of this study, it is inferred that the temperate stock of *S. sagax* has been adequately exploited. In other words, catches in most seasons have not exceeded the BAC as a control rule, except for the 2014 and 2017 seasons when in both seasons the target reference point was exceeded by around 20%.

The management strategy based on a dynamic control rule, which depends on a biomass fraction, is considered a robust strategy to face the inherent uncertainty, which is generated by the climatic effect on fish populations (Walter and Martell, 2004). Which has also been recommended for populations whose level of abundance presents an inverse relationship with catchability (Martínez-Aguilar et al., 2009). However, it is suggested that such management strategy be complemented with the fishing effort control measure to avoid the occurrence of fishing overcapacity and, therefore, a negative impact on the economic income of users (Anderson and Seijo, 2010; Galindo-Cortes, 2011).

CRediT authorship contribution statement

Concepción Enciso-Enciso: Conceptualization, Data curation, Methodology, Formal analysis, Investigation, Writing – original draft, Software, Writing – review & editing. **Manuel O. Nevárez-Martínez:** Conceptualization, Data curation, Methodology, Formal analysis, Investigation, Writing – original draft, Software, Writing – review & editing, Supervision, Validation. **Rebeca Sánchez-Cárdenas:** Conceptualization, Data curation, Methodology, Formal analysis, Investigation, Writing – original draft, Software, Writing – review & editing, Supervision, Validation. **Luis A. Salcido-Guevara:** Supervision, Writing – review & editing, Validation. **Carolina Minte-Vera:** Supervision, Writing – review & editing, Validation. **Emigdio Marín-Enríquez:** Supervision, Writing – review & editing, Validation. **Martín E. Hernández-Rivas:** Supervision, Writing – review & editing, Validation.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The authors do not have permission to share data.

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References

- Alheit, J., Bakun, A., 2010. Population synchronies within and between ocean basins: apparent teleconnections and implications as to physical-biological linkage mechanisms. J. Mar. Syst. 79, 267–285.
- Alvarez-Trasviña, E., 2012. Variabilidad en el crecimiento individual de la sardina del pacífico Sardinops sagax (Jenyns, 1842) y su relación con el ambiente en Bahía Magdalena. (B.C.S. Tesis de Maestría). CICIMAR, p. 45.
- Anderson, L.G., Seijo, J.C., 2010. Bioeconomics of Fisheries Management, 1ra. Edition Wiley-Blackwell, New Jersey, p. 305.
- Baranov, F.I., 1918. On the question of the biological basis of fisheries. In: Nauchnge Issledovaniya Ikhtiologicheskii Instituta Izvestiya. Vol. 1, pp. 81–128.
- Barnes, J.T., Jacobson, L.D., MacCall, A.D., Wolf, P., 1992. Recent population trends and abundance estimates for sardine (Sardinops sagax). CalCOFI Reports, Vol. 33, pp. 60–75.

- Checkley Jr., D.M., Asch, R.G., Rykaczewski, R.R., 2017. Climate, anchovy and sardine. Annu. Rev. Mar. Sci. 9, 469–493.
- Chen, D.G., Irvine, J.R., Cass, A.J., 2002. Incorporating Allee effects in fish stock recruitment models and applications for determining reference points. Rev. Can. J. Fish. Aquat. Sci. 59, 242–249.
- De Anda-Montañez, A., Arrequín-Sánchez, F., Martínez-Aguilar, S., 1999. Length based growth estimates for pacific sardine (*Sardinops sagax*) in the Gulf of California, Mexico. CalCOFI Reports, Vol. 40, pp. 179–183.
- Demer, D.A., Zwolinski, J.P., 2014. Corroboration and refinement of a method for differentiating landings from two stocks of Pacific Sardine (Sardinops sagax) in the California Current. ICES J. Mar. Sci. 71, 328–335.
- Deriso, R., Barnes, J.T., Jacobson, L.D., Arenas, P.R., 1996. Catch-at-age analysis for Pacific sardine (*Sardinops sagax*), 1983–1995. CalCOFI Reports, Vol. 37, pp. 175–187.
- Deriso, R.B., Quinn II, T.J., Neil, P.R., 1985. Catch-age analysis with auxiliary information. Can. J. Fish. Aquat. Sci. 42, 815–824.
- Dichmont, C.M., Deng, R.A., Punt, A.E., Brodziak, J., Chang, Y.J., Cope, J.M., Ianelli, J.N., Legault, C.M., Methot Jr., R.D., Porch, C.E., Prager, M.H., Shertzer, K.W., 2016. A review of stock assessment packages in the United States. Fish. Res. 183, 447–460.
- DOF, 2012. ACUERDO Por el Que Se da a Conocer el Plan de Manejo Pesquero Para la Pesquería de Pelágicos Menores (Sardinas, Anchovetas, Macarela y Afines) del Noroeste de México. 8 de Noviembre de 2012. México.
- Dorval, E., McDaniel, J.D., Macewicz, B.J., Porzio, D.L., 2015. Changes in growth and maturation parameters of Pacific sardine Sardinops sagax collected off California during a period of stock recovery from 1994 to 2010. J. Fish Biol. 87 (2), 286–310.
- Emmett, R.L., Brodeur, R.D., Miller, T.W., Pool, S.S., Bentley, P.J., Krutzikowsky, G.K., McCrae, J., 2005. Pacific Sardine (Sardinops sagax) Abundance, Distribution, and Ecological Relationships in the Pacific Northwest. CalCOFI Reports, Vol. 46, pp. 122–143.
- Enciso-Enciso, C., Nevarez-Martínez, M.O., Sánchez-Cárdenas, R., Marín-Enriquez, E., Salcido-Guevara, L.A., Minte-Vera, C., 2022. Allometry and individual growth of the temperate Pacific sardine (*Sardinops sagax*) stock in the southern California Current System. Fishes 7 (226).
- FAO, 1995. Code of Conduct for Responsible Fisheries. FAO, Rome, p. 41.
- Félix-Uraga, R., 2006. Dinámica poblacional de la sardina del Pacífico Sardinops sagax (Jenyns 1842) (Cupleiformes: Clupeidae), en la costa oeste de la península de Baja California y el sur de California. (Tesis de Doctorado). CICIMAR. La Paz, B.C.S. México, p. 86.
- Félix-Uraga, R., Gómez-Muñoz, V.M., Quiñónez-Velázquez, C., Melo-Barrera, F.N., García-Franco, W., 2004. On the existence of Pacific sardine groups off the West Coast of baja california and southern california. CalCOFI Reports, Vol. 45, pp. 146–151.
- Félix-Uraga, R., Gómez-Muñoz, V.M., Quiñónez-Velázquez, C., Melo-Barrera, F.N., Hill, K., García-Franco, W., 2005. Pacific Sardine (Sardinops sagax) stock discrimination off the West Coast of baja california and southern california using otolith morphometry. CalCOFI Reports, 46, pp. 113–121.
- Frank, K.T., Brickman, D., 2000. Allee effects and compensatory population dynamics within a stock complex. Can. J. Fish. Aquat. Sci. 57, 513–517.
- Fréon, P., Cury, P., Shannon, L., Roy, C., 2005. Sustainable exploitation of small pelagic fish stocks challenged by environmental and ecosystem changes: a review. Bull. Mar. Sci. 76, 385–462.
- Galindo-Cortes, G., 2011. Enfoque precautorio aplicado a recursos pesqueros fluctuantes: Un análisis bioeconómico para la sardina del Pacífico. (Tesis de Doctorado). CIBNOR, La Paz, México, p. 111.
- Galindo-Cortes, G., De Anda-Montanez, J.A., Arreguin-Sanchez, F., Salas, S., Balart, E.F., 2010. How do environmental factors affect the stock-recruitment relationship? The case of the Pacific sardine (*Sardinops sagax*) of the northeastern Pacific ocean. Fish. Res. 102, 173–183.
- Haddon, M., 2011. Modeling and Quantitative Methods in Fisheries. Edit. Chapman-Hall, London, England, p. 433.
- Hammann, M.G., Palleiro-Nayar, J.S., Sosa, O., 1995. The effects of the 1992 El Niño on the fisheries of Baja California, México. CalCOFI Reports, Vol. 36, pp. 127–133.
- Hedgecock, D., Hutchinson, E.S., Li, G., Sly, F.L., Nelson, K., 1989. Genetic and morphometric variation in the Pacific sardine, Sardinops sagax caerulea: Comparisons and contrasts with historical data and with variability in the northern anchovy, Engraulis mordax. Fish. Bull. 87 (3), 653–671.
- Hewitt, D.A., Hoenig, J.M., 2005. Comparison of two approaches for estimating natural mortality based on longevity. Fish. Bull. 103, 433–437.
- Hilborn, R., Pikitch, E.K., McAllister, M.A., 1994. A Bayesian estimation and decision analysis for an age-structured model using biomass survey data. Fish Res. 19, 17–30.
- Hilborn, R., Walters, C.J., 1992. Quantitative Fisheries Stock Assessment: Choice, Dynamics and Uncertainty. Chapman and Hall, New York, EE.UU, p. 560.
- Hill, K.T., Crone, P.R., Zwolinski, J.P., 2019. Assessment of the Pacific Sardine Resource in 2019 for U.S. Management in 2019-20. US Department of Commerce. NOAA Tech. Memo. NMFS-SWFSC-615.

- Huato-Soberanis, L., Lluch-Belda, D., 1987. Masoscale cycles in the series of environmental indices related to the sardine fishery in the Gulf of California. CalCOFI Reports, Vol. 28, pp. 128–134.
- Jacobson, L.D., De Oliveira, J.A.A., Barange, M., Cisneros-Mata, M.A., Félix-Uraga, R., Hunter, J.R., Yeong, K.J., Matsuura, Y., Ñiquen, M., Porteiro, C., Rotschild, B., Sánchez, R.P., Serra, R., Uriarte, A., Wada, T., 2001. Surplus production, variability, and climate change in the great sardine and anchovy fisheries. Can. J. Fish. Aquat. Sci. 58, 1891–1903.
- Jacobson, L.D., McCall, A.D., 1995. Stock-recruitment models for Pacific sardine Sardinops sagax. Can. J. Fish. Aquat. Sci. 52, 566–577.
- Kawasaki, T., 1983. Why do some pelagic fishes have wide fluctuations in their numbers? Biological basis in fluctuation from the viewpoint of evolutionary ecology. In: Actas Para la Consulta de Expertos Para Examinar Los Cambios en la Abundancia y Composición Por Especies de Recursos de Peces Neríticos San José, Costa Rica, 18-29 de Abril de 1983. vol. 3, (291), FAO, Informe de Pesca, pp. 1065–1080.
- Kuriyama, P.T., Hill, K.T., Zwolinski, J.P., 2021. Assessment of the Pacific Sardine Resource in 2021 for U.S. Management in 2021-2022. U.S. Department of Commerce.
- Kuriyama, P.T., Zwolinski, J.P., Hill, K.T., Crone, P.R., 2020. Assessment of the Pacific Sardine Resource in 2020 for U.S. Management in 2020-2021. Pacific Fishery Management Council, Portland, OR. EE.UU, p. 189.
- Lenarz, W.H., Ventresca, D.A., Graham, W.M., Schwing, F.B., Chavez, F., 1995. Exploration of El Niño events and associated biological population dinamics off Central California. CalCOFI Reports, Vol. 36, pp. 106–119.
- Lindegren, M., Checkley Jr., D.M., 2013. Temperature dependence of Pacific sardine (*Sardinops sagax*) recruitment in the California Current Ecosystem revisited and revised. Can. J. Fish. Aquat. Sci. 70, 245–252.
- Linton, B.C., Bence, J.R., 2008. Evaluating methods for estimating process and observation error variances in statistical catch-at-age analysis. Fish. Res. 94, 26–35.
- Lluch-Belda, D., Arvizu, M.J., Hernández-Vázquez, S., Lluch-Cota, D.A., Salinas, C.Z., Baugartener, T., Hammann, G., Cota, V.A., Cotero, C.E., García, F.W., Pedrín, O., Lizárraga, S.M., Martínez, M.A., Morales, R., Nevárez, M.O., Santos, J.P., Ochoa, R., Rodríguez, S.R., Torres, J.R., Páez, F., 1995. Atlas Pesquero de México. Pesquerías Relevantes. Secretaría de Pesca/Instituto Nacional de la Pesca/Universidad de Colima. Centro Nacional Editor de Discos Compactos, p. 310.
- Lluch-Belda, D., Crawford, R.J.M., Kawasaki, T., MacCall, A.D., Parrish, R.H., Schwartzlose, R.A., Smith, P.E., 1989. Worldwide fluctuations of sardine and anchovy stocks: the regimen problem. S. Afr. J. Mar. Sci. 8, 195–205.
- Lo, N.C.H., Green Ruiz, Y.A., Cervantes, M.J., Moser, H.G., Lynn, R.J., 1996. Egg production and spawning biomass of Pacific sardine (*Sardinops sagax*) in 1994, determined by the daily egg production method. CalCOFI Reports, Vol. 37, pp. 160–174.
- Martínez-Aguilar, S., De Anda-Montañez, J.A., Arreguín-Sánchez, F., Cisneros-Mata, M.A., 2009. Constant harvest rate for the Pacific sardine (*Sardinops caeruleus*) fishery in the Gulf of California based on catchability-at-length estimations. Fish. Res. 99, 74–82.
- McFarlane, G.A., Beamish, R.J., 1999. Sardines return to British Columbia waters. In: Freeland, H., Peterson, W.P., Tyler, A. (Eds.), Proceedings of the 1998 Science Board Symposium on the Impacts of the 1997/98 El Niño Event on the North Pacific Ocean and Its Marginal Seas. PICES Scientific Report, vol. 10, N. Pac. Mar. Sci. Org, Sidney, Canada, pp. 77–82.
- Megrey, B.A., 1989. Review and comparison of age-structured stock assessment models from theoretical and applied points of view. In: Edwards, B.A. (Ed.), Mathematical Analysis of Fish Stock Dynamics. In: Am. Fish. Soc. Symp., Bethesda, pp. 8–48.
- Methot, R.D., 1989. Synthetic estimates of historical abundance and mortality for northern anchovy. Am. Fish. Soc. Symp. 6, 66–82.

- Morales-Bojórquez, E., Nevárez-Martínez, M.O., 2005. Spawner-recruit patterns and investigation of allee effect in pacific sardine (*Sardinops sagax*) in the *Gulf of California, Mexico*. CalCOFI Reports, Vol. 46, pp. 161–174.
- Nevárez-Martínez, M.O., Chávez, E.A., Cisneros-Mata, M.A., Lluch-Belda, D., 1999. Modeling of the Pacific sardine *Sardinops caeruleus* fishery of the Gulf of California, México. Fish. Res. 41, 273–283.
- Nevárez-Martínez, M.O., Lluch-Belda, D., Cisneros-Mata, M.A., Santos-Molina, J.P., Martínez-Zavala, M.A., Lluch-Cota, S.E., 2001. Distribution and abundance of the Pacific sardine (*Sardinops sagax*) in the Gulf of California and their relation with the environment. Prog. Oceanogr. 49, 565–580.
- Nevárez-Martínez, M.O., Martínez-Zavala, M.A., Jacob-Cervantes, M.L., Enciso-Enciso, C., Cotero-Altamirano, C.E., Lopez-Lagunas, A.E., Valdez-Pelayo, A., Santos-Molina, J.P., Gonzalez-Maynez, V.E., Arizmendi-Rodriguez, D.I., 2021. Peces Pelágicos Menores Sardinops sagax, Opisthonema Spp. Scomber japonicus, Engraulis mordax, Cetengraulis mysticetus, Etrumeus teres, Trachurus symmetricus, Oligoplites Spp. en Prensa: Sustentabilidad y Pesca Responsable en México: Evaluación y Manejo. SADER-INAPESCA, México.
- Parrish, R.H., Serra, R., Grant, W.S., 1989. The monotypic sardines, Sardine and Sardinops: Their taxonomy, distribution, stock structure, and zoogeography. Can. J. Fish. Aquat. Sci. 46, 2019–2036.
- Pauly, D., 1980. On the interrelationships between natural mortality, growth parameters and mean environmental temperature in 175 fish stocks. J. Cons. Int. Explor. Mer. 39 (2), 175–192.
- Pope, J.G., 1972. An investigation of the accuracy of virtual population analysis using cohort analysis. ICNAF Res. Bull. 9, 65–74.
- Quinn II, T., Deriso, R., 1999. Quantitative Fish Dynamics. Oxford University Press, New York. Primera Edición, p. 542.
- Radovich, J., 1982. The collapse of the California sardine fishery, What have we learned?. CalCOFI Reports, Vol. 23, pp. 56–77.
- Richards, L.J., Schnute, J.T., 1998. Model complexity and catch-age analysis. Can. J. Fish. Aquat. Sci. 55, 949–957.
- Rodríguez-Sánchez, R., Lluch-Belda, D., Villalobos-Ortiz, H., Ortega-García, S., 2001. Large-scale long-term variability of small pelagic fish in the California current system. In: Kruse, G.H., Bez, N., Booth, A., Dorn, M.W., Hills, S., Lipcius, R.N., Pelletier, D., Roy, C., Smith, S.J., Witherell, D. (Eds.), Spatial Processes and Management of Marine Populations. Univ. Alaska, Fairbanks, AK, pp. 447–462.
- Shepherd, J.G., 1999. Extended survivors analysis: an improved method for the analysis of catch-at-age data and abundance indices. ICES J. Mar. Sci. 56, 584–591.
- Simmonds, E.J., 2003. Weighting of acoustic- and trawl-survey indices for the assessment of North Sea herring, ICES J. Mar. Sci. 60, 463–471.
- Smith, P.E., 1995. A warm decade in the Southern California Bight. CalCOFI Reports, Vol. 36, pp. 120–126.
- Smith, P.E., 2005. A history of proposals for subpopulation structure in the Pacific Sardine (*Sardinops sagax*) Population off Western North America. CalCOFI Reports, Vol. 46, pp. 75–82.
- Smith, P.E., Richardson, S.L., 1979. Técnicas Modelo para Prospecciones de Huevos y Larvas de Peces Pelágicos. FAO Documentos Técnicos de Pesca 175, 107.
- Walter, C.J., Martell, S.J.D., 2004. Fisheries Ecology and Management. Princeton Univ. Press, Princeton, p. 399.
- Wolf, P., 1992. Recovery of the Pacific sardine and the California sardine fishery. CalCOFI Reports, Vol. 33, pp. 76–86.
- Zwolinski, J.P., Demer, D.A., 2012. A cold oceanographic regime with high exploitation rates in the northeast Pacific forecasts a collapse of the sardine stock. Proc. Natl. Acad. Sci. USA 109, 4175–4180.
- Zwolinski, J.P., Demer, D.A., 2014. Environmental and parental control of Pacific sardine (*Sardinops sagax*) recruitment. ICES J. Mar. Sci. 71 (8), 2198–2207.