Utilities of larval densities of Pacific mackerel (*Scomber japonicus*) off California, USA and west coast of Mexico from 1951 to 2008, as spawning biomass indices

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Fish larval densities are frequently used as an index of spawning biomass. Three time series of larval densities of Pacific mackerel (*Scomber japonicus*) per 10 m^2 were estimated from 1951 to 2008 based on data collected by California Cooperative Oceanic Fisheries Investigations (CalCOFI) survey during peak spawning season off California: April to July, and by the Investigaciones Mexicanas de la Corriente de California (IMECOCAL) survey off Mexico: June-September. *1)* Daily larval production at hatching; *2)* bias-corrected larval densities; and *3)* simple mean larval densities. All three time series were constructed for California in 1951-2008. The third was constructed for the Mexican waters in 1951-1984, 1996 and 1998-2000. Weighted mean larval densities were obtained for the combined area of California and Mexico. Daily larval production index showed a major peak in 1987 (46.39·10 m^2·d^{-1}) and two minor peaks, in 1981 and 1986. All three time series indicated that larval densities have been decreasing since 1997 and were particularly low in 2003-2008. Larval densities off Mexico, higher than those off California in recent years, were high in the mid-1960's, and low in the early 1980's. The cost-effective fishery-independent time series off California and Mexico is informative for assessing the population fluctuation and beneficial to the Pacific mackerel stock assessment. Due to the different peak spawning periods off California and Mexico, periodic extensive coast-wide surveys to cover the whole time period are recommended, as they would contribute to a better understanding of the dynamics of the population along the Pacific coast.

Key words: Coastal pelagic species, Pacific mackerel, larval production, time series, spawning biomass index, west coast of American continent.

Utilidades de las densidades larvales como índices de la biomasa desovante de la macarela del Pacífico (*Scomber japonicus*) de California y costa occidental de México de 1951 a 2008

La densidad de las larvas de peces es usada frecuentemente como índice de la biomasa desovante. Tres series de tiempo de densidades larvales por 10 m^2 de la macarela del Pacífico (*Scomber japonicus*) fueron estimadas para el periodo 1951-2008, basadas en datos recolectados por California Cooperative Oceanic Fisheries Investigations (CalCOFI) durante el pico de reproducción en California: abril-julio, y por Investigaciones Mexicanas de la Corriente de California (IMECOCAL) en México: junio-septiembre. *1)* Producción diaria de larvas recién eclosionadas; *2)* densidad larval corregida por sesgo y *3)* densidades larvales promedio. Las tres series fueron construidas con los datos de California de 1951-2008 y la tercera con los de México de 1951-1984, 1996 y 1998-2000. Se obtuvieron los promedios ponderados de las densidades larvales para ambas áreas. El índice de producción diaria de larvas mostró un máximo en 1987 (46.39·10 m^2 ·d^{-1}), con incrementos menores en 1981 y 1986. Las tres series indicaron que la densidad larvaria ha disminuido desde 1997 y que fueron particularmente bajas las de 2003-2008. Las densidades registradas en México, mayores que las de California en años recientes, fueron altas a mediados de los años sesenta y bajas a principios de los ochenta. Los valores netos de las series de tiempo independientes de la pesquería de California y México son informativos para evaluar la fluctuación poblacional y útiles para evaluar el *stock* de la macarela. Debido a las diferencias en el desove de California y México, se recomienda una investigación periódica y muestreos extensivos a lo largo de la costa y para cubrir todo el periodo, ya que contribuirían a una mejor comprensión de la dinámica poblacional de la macarela en la costa del Pacífico.

Palabras clave: Especies pelágico costeras, macarela del Pacífico, producción larval, series de tiempo, índice de biomasa desovante, costa oeste del continente americano.

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Introduction

Relative indices of fish population abundance derived from independent surveys are essential to calibrate fisheries-dependent and biological data inputs in stock assessment models. There exist well established methods and survey designs to infer stock biomass for small pelagic species, *i.e.,* daily egg production methods (DEPM) for Pacific sardine (Lo *et al*., 1996, 2005; Stratoudakis *et al*., 2006), for northern anchovy off California and in the gulf of California (Lasker, 1985; Cotero-Altamirano & Green-Ruiz, 1997; Green-Ruiz & Cotero-Altamirano, 2009), and acoustic methods for South African anchovy *Engraulis capensis* Gilchrist, 1913 (Hampton, 1996). However, the effectiveness of such methods depends highly on the life history, biology and dynamics of a species. DEPM is an ideal method for species whose spawning behavior allows the aggregation of most eggs and larvae in one area. Hence, the application of this method has been difficult for species such as the Pacific mackerel *Scomber japonicus* Houttuyn, 1782 that spawn in small and patchy areas, leading to low density of larvae on a large scale. Further, DEPM requires accurate identification and staging of eggs and in some cases of larvae, which can be difficult to perform for some species such as the Pacific mackerel (Ahlstrom & Counts, 1955; Kramer, 1960; Funes-Rodríguez *et al*., 2004). Acoustic surveys are expensive and difficult to apply to species such as Pacific mackerel whose spawning behaviors are not well predicted and whose dynamics may span thousands of kilometers. Pacific mackerel in the northeastern Pacific range from southeastern Alaska to Banderas Bay (Puerto Vallarta, Mexico), including the gulf of California (Hart, 1973). They are common from Monterey Bay (California, US) to Cabo San Lucas (Baja California Sur, Mexico), but are most abundant south of Point Conception, California. Pacific mackerel usually occur within 30 km from shore but have been captured as far as 400 km offshore (Fitch, 1969; Frey, 1971; MBC, 1987; Allen *et al*., 1990). Furthermore, both DEPM and acoustic surveys require timely and well-coordinated surveys to be effective. Thus, it is difficult to apply these methods to transboundary species that tend to shift their core spawning area based on environmental conditions and that are managed by different nations. Indeed, there are possibly three Pacific mackerel spawning stocks along the Pacific coasts of the US and Mexico: one in the gulf of California, one in the vicinity of Cabo San Lucas, and one extending along the Pacific coast north of Punta Abreojos, Baja California (Collette & Nauen, 1983; MBC, 1987; Allen *et al*., 1990; Gluyas-Millán & Quiñonez-Velázquez, 1996). In some years the northeastern Pacific population tends to have peak spawning in the southern California Bight, whereas in other years spawning aggregations occur mostly in coastal waters off Baja California (Mexico) (Dorval *et al*., 2007). Further, Pacific mackerel is managed by the US and Mexico separately. Since 2000 NOAA-Fisheries has conducted an annual assessment for Pacific mackerel with biological and catch data from Mexico, but without Mexican ichthyoplankton survey data. IMECOCAL data are used to assess stock off Mexico.

The main objective of this paper was to develop a spawning biomass index based on Pacific mackerel larval data. The daily larval production procedures have been successfully developed for various species (Smith, 1972; Lo, 1986; Lo *et al*., 1989; Ralston *et al*., 2002; Lo, 2007). A similar index was used in the 2008 Pacific mackerel assessment as a proxy for the spawning stock biomass (SSB), but did not include Mexican survey data (Dorval *et al*., 2007). In this paper we analyze both California Cooperative Oceanic Fisheries Investigations (CalCOFI) and Investigaciones Mexicanas de la Corriente de California (IMECOCAL) surveys to derive three time series of Pacific mackerel larval densities as the indices for the spawning biomass of Pacific mackerel in the southern California current off California and Mexico, and we explored whether an index derived from one region was adequate or whether indices from both regions were required.

Materials and methods

CalCOFI survey data

Pacific mackerel larval data from CalCOFI surveys are readily available from 1951, and comprehensive correction algorithms can be applied

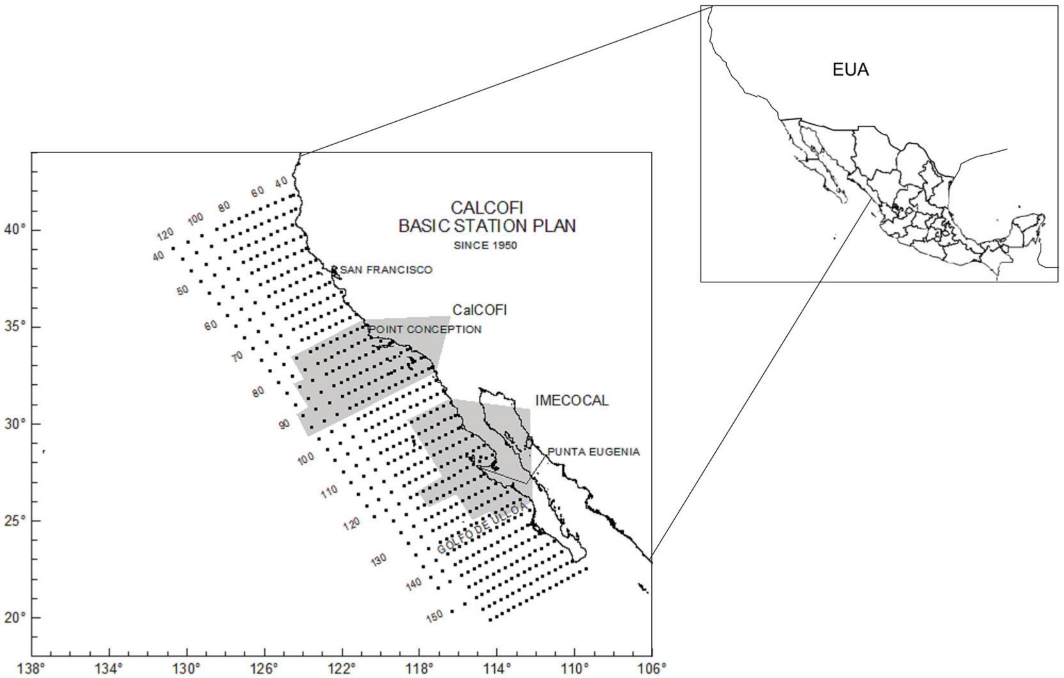

Fig. 1. IMECOCAL survey (lower shaded area) and the current CalCOFI area from San Diego to north of Point Conception (upper shaded area) within the historical CALCOFI survey area with line and station numbers.

to reduce possible biases in measurement, such as extrusion through the net mesh, and avoidance of the net. The CalCOFI survey was conducted annually from 1949 to 1966, then every three years through 1984, covering the area from Baja California to the north of San Francisco (Moser *et al.*, 1993). The time series of Pacific mackerel larval densities and distribution by month from 1951 to 1956 from San Francisco to Cabo San Lucas, Baja California Sur was reported by Kramer (1960) and from 1951 to 1984 by Moser *et al*. (1993) (Fig. 1). Starting in 1985, the survey area was reduced to primarily cover the Southern California Bight from San Diego to Avila Beach, just north of Point Conception (core area): CalCOFI line 93.3 – line 76.7 (Fig. 1, Moser *et al*., 2001).

Larvae were collected by oblique tows down to 140 m depth with a 1-m ring net from 1951 to 1968 (Kramer *et al*., 1972; Lo, 1983; Ohman & Smith, 1995). Sampling depth was increased to 210 m in 1969, whereas a Bongo net replaced the ring net in 1978. A standard haul factor (SHF) used to compute number of larvae ·10 m^{-2} was developed to account for variability in the volume of water filtered per unit of depth (Ahlstrom, 1948; Smith & Richardson, 1975).

Sample biases caused by net selectivity for small larvae and gear avoidance for larger larvae were adjusted by following the method of Lo (1985). Retention rates for extrusion can be expressed as a function of larval length and mesh size (Lenarz, 1972; Zweifel & Smith, 1981; Lo, 1983) and those for avoidance can be expressed as a function of larval length and the diurnal time of capture (Hewitt & Methot, 1982; Lo, 2007). Note that both extrusion and avoidance are length-specific. Larvae were measured in 0.5 mm size classes. All larval density data were adjusted to bias-corrected densities per 10 m^2 that conform to the following standard conditions: no extrusion, no day-night difference in avoidance, and a constant water volume filtered per unit depth. For the daily larval production ·10 m^{-2} (P_t) computation, we divided the corrected total number of larvae in each length group by the duration (*i.e*., the number of days larvae remain within each length group). A set of laboratory data on larval growth (Hunter & Kimbrell, 1980) was analyzed to model temperature-dependent larval growth curves, which were used to convert length to age from hatching. For analyses of the combined data from California and Mexico from 1998-2000, only the original counts per 10 m^2

were used as the data of total numbers for each tow from Mexico in recent years were only available (see below).

IMECOCAL *survey data*

IMECOCAL surveys have been conducted quarterly since October 1997, similar to the current CalCOFI survey schedule (Fig. 1). IMECOCAL survey data from October 1997-January 2001 were provided by Centro Interdisciplinario de Ciencias Marinas (CICIMAR-México). The survey covers an area of 193 000 km^2 from near the United States-Mexico border to south of Punta Eugenia (31-25° N). The sampling grid is the California Cooperative Fisheries Investigations (CalCOFI) station plan: lines 100-137 seaward to CalCOFI station 80. The lines are perpendicular to the coast extending seaward ~60 nm Survey lines are spaced 40 nm, with a distance between stations of 20 nm. Plankton was collected in bongo nets (0.6 m mouth diameter, 505-μm mesh) towed obliquely through the water between the surface and maximum depth of 200 m, when depth permitted. A flow meter in the mouth of each net was used to calculate the volume of filtered water. Plankton samples were preserved with 4% sodium borate-buffered formalin. A set of data off Mexico during August 1996 was also available from an extended CalCOFI survey.

Correction factors for larval counts from CalCOFI *survey*

Extrusion. There are no existing data on the length-specific extrusion rate for Pacific mackerel. Therefore, the retention coefficient of jack mackerel *Trachurus symmetricus* (Ayres, 1855) larvae due to extrusion was used as a proxy for Pacific mackerel. Jack mackerel larvae and Pacific mackerel larvae are approximately the same length at hatching and are morphologically similar: jack mackerel hatch at about 2-2.5 mm and Pacific mackerel at about 2-3 mm; morphology of both species is similar during the yolk sac stage. On average, Pacific mackerel tend to be slightly longer and more robust than jack mackerel (William Watson *pers. comm.*[1]). Hewitt *et al.* (1985) reported that only the smallest classes of jack mackerel larvae (3.0 mm) are extruded to a significant degree through the 0.505 mm CalCOFI nets, with 28% of the catch in that size class retained in the net. The extrusion correction factor is equal to 1/0.28 (i.e., 3.571). Although a 0.55 mm mesh net was used prior to 1968, the difference in extrusion of mackerel larvae is likely to be insignificant, as in the case of anchovy larvae (Lo, 1983).

Avoidance/evasion. The correction factor for avoidance/evasion was estimated using the algorithm developed for anchovy and Pacific hake *Merluccius productus* (Ayres, 1855) (Lo *et al.*, 1989; Lo, 2007). Because larvae are able to avoid or evade the net under sufficient light condition, and larger larvae are better able to avoid the sampler, we used the model developed by Lo *et al.* (1989) for the retention (or capture) coefficient of Pacific mackerel larvae for a specific larval length (L) and time of the day (in hour): $R_{L,h}$:

$$R_{L,h} = \left(\frac{1+D_L}{2}\right) + \left(\frac{1-D_L}{2}\right) * \cos\left(\frac{2\pi * h}{24}\right) \qquad \text{Eq. 1}$$

where D_L is the noon/night catch ratio for length *L*. Only data from 1951 to 1978 in the historical large area were used to model the catch ratio because including data from other years did not improve the modeling of the nonlinear regression of the day/night ratio against larval length:

$$D_L = \frac{\bar{y}_{L,noon}}{\bar{y}_{L,night}}$$

The numerator is the mean catch at noon (11:00 - 13:00) of larvae length *L* and the denominator is the mean catch in the night (21:00 - 3:00) of larval length *L*. We then used an exponential curve to model the relationship between D_L and larval length *L*.

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Shrinkage. The shrinkage factor was based on Bailey (1982) study, which estimated shrinkage (in standard length) of first-feeding Pacific hake larvae due to preservatives and time of handling. Shrinkage was estimated to be 8.9% for 3% formalin-preserved larvae (L). Because formalin is the standard CalCOFI preservative, a correction factor is needed to convert formalin-preserved length (L) to live length (L_L) in order to apply the larval Pacific mackerel growth curves derived from laboratory data (Hunter & Kimbrell, 1980). The multiplier applied to larvae from 2.5-11.5 mm from CalCOFI surveys is 1/(1-0.089) = 1.098 to convert formalin preserved-length to live length, *i.e.* $L_L = L \cdot 1.098$.

Growth of Pacific mackerel larvae

Growth curves. Hunter & Kimbrell (1980) reported growth data for seven groups of Pacific mackerel reared at different temperatures from 16.8 to 22.1 °C. We estimated larval length from Hunter & Kimbrell (1980) by using a temperature-dependent logistic growth curve, where the coefficient of the age is a polynomial function of temperature (Bartsch, 2005):

$$L_L = \frac{28.2616}{1+\exp(-\beta_{temp}\, t + 2.3476)} \quad \text{For } t < 25 \text{ d} \qquad \text{Eq. 2}$$

where
$\beta_{temp} = 0.2828 - 0.0229 * temp + 0.0007 temp^2$, t (days) is age (d) from hatch and L_L, live length, is greater than 2.45 mm and *temp* is temperature in °C where 2.45 mm (2.23 mm preserved length) was the livelength of the newly hatched larvae at t = 0.

To convert preserved length to age from hatching, we inverted equation (2) and obtained:

$$t = \frac{2.3476 - \ln(28.2616/(L*1.098) - 1)}{\beta_{temp}}$$

$$\text{for } 2.23 \text{ mm} <= L < 20 \text{ mm} \qquad \text{Eq. 3}$$

where *t* is age (days) after hatching and *L* is formalin-preserved length.

The larvae collected in each tow were grouped into length categories as 2.5 (2.0 mm - 3.0 mm), 3.75 (3.5 - 4.0 mm), 4.75 (4.5 - 5.0 mm). To determine the age-at-capture of an individual larva, the length-at-capture of a larva in each length group from each tow was generated by random selection from a uniform distribution between the minimum and maximum lengths within each length category. For example, for larvae of 2.5 mm, the length of each of *n* larvae would be randomly selected from a uniform distribution of 2-3 mm. For the larvae in the length category 2.5 mm, age 0 was assigned for Formalin-preserved length <2.23 mm (converted from 2.45 mm live length).

Size class duration and daily larval production

The duration for each length group was estimated by the difference of mid-ages, where mid-ages are the ages corresponding to mid-lengths (*i.e.*, the midpoint between two size groups: 3.75 mm and 4.75 mm is 4.25 mm). The daily larval production in each age group was the bias-corrected larval density in each age group divided by its duration.

Time series of larval densities

Three time series of Pacific mackerel larval densities from 1951 were constructed depending on data availability: Daily larval production at hatching (P_h), bias-corrected larval density ($\cdot 10 m^{-2}$) and simple mean density ($\cdot 10\ m^{-2}$). The data requirement decreased from P_h to the simple mean density. Thus, all three time series were constructed for southern California from 1951-2008 but only the time series of the simple mean density was constructed for Mexican waters. A time series of weighted simple mean was obtained for the combined Mexican and Southern California areas for years when data were available for both regions.

Daily larval production at hatching (P_h) off southern California in 1951-2008. The daily larval production at hatching (P_h) was estimated for each year from a larval mortality curve in the form of an exponential function, unlike that of northern anchovy (*Engraulis mordax*) (Lo, 1985, 1986) and Pacific hake (Hollowed, 1992;

Lo, 2007) whose daily mortality rates decreased with age. Larvae >11.75 mm length group largely avoided the net and were excluded. A weighted nonlinear regression was used to estimate the coefficients of the mortality curve for years with sufficient catch-length data:

$$P_t = P_h \exp(\alpha t) \qquad \text{Eq. 4}$$

where P_t is the daily larval production per 10 m^2 at age *t* (days) from hatching, and α is the daily instantaneous mortality rate.

For most years, we fitted equation (4) to the data using a weighted nonlinear regression to estimate the P_h and α, where the weight was 1/standard deviation for each four-day interval: 0-4, 5-8,…, 17-20 d. As few larvae older than 20 days occurred each year, the mortality curve was constructed based on larvae of age ≤ 20 days, to avoid bias. However, due to the patchiness of larvae (Matsuura & Hewitt, 1995) and their ability to avoid the net, the unweighted nonlinear regression was used for some years because the large variances in the young age categories down-weighted the corresponding daily larval production too much to produce reasonable estimates of P_h and mortality rate. Estimates of P_h from both weighted and unweighted regression are unbiased, but variance is higher from the unweighted regression than from the weighted regression (Draper & Smith, 1981). There were also some years when only one or two length groups were present, mostly small larvae, e.g. larvae <4 mm. In those years P_h was estimated by inverting the mortality curve (equation 4) as follows:

$$\hat{P}_h = \overline{P}_L \exp(-\hat{\alpha} t_L) \qquad \text{Eq. 5}$$

and the variance of $\hat{P}_h$ was estimated by:

$$\begin{aligned}
&\text{var}(\hat{P}_h) = \\
&\text{var}(\overline{P}_L)(\exp(-\hat{\alpha} t_L))^2 + \\
&(\overline{P}_L \exp(-\hat{\alpha} t_L)(-t_L))^2 \,\text{var}(\hat{\alpha}) - \\
&\text{var}(\overline{P}_L)(\exp(-\hat{\alpha} t_L)(-t_L))^2 \,\text{var}(\hat{\alpha})
\end{aligned}$$

where $\overline{P}_L$ is the mean daily larval production at length L = 2.5 mm, t_L is the associated age of 2.5 mm, and the overall mean mortality rate for 1951-2006 was used for $\hat{\alpha}$. The variance of $\hat{P}_h$ was based on the variance of the product of two random variables (Goodman, 1960).

The difference between estimates of P_h from equations 4 and 5 was primarily due to two factors: *1)* the estimates of $P_{2.5\,mm}$: one from the regression curve and the other one the direct mean values; and *2)* the estimates of the mortality rate: one from the nonlinear regression of each year and the other based on the overall estimate from 1951-2006 excluding 2007 and 2008 when zero larvae were caught. We computed the correlation coefficient of these two estimates of P_h for years when the nonlinear regression estimates were available to determine the suitability of using equation 5 for P_h.

Bias-corrected larval densities off southern California in 1951-2008. The length-specific bias-corrected larval densities were the product of the raw counts of larvae (x) and the standard haul factor (SHF) divided by length-specific avoidance rate (y) and length-specific extrusion rate Z: $\frac{x \cdot SHF}{y \cdot z}$. The final bias-corrected larval density for each tow was the sum of length-specific bias-corrected larval densities for length <11.75 mm because few larvae were greater than 12 millimeters.

Weighted larval densities off Southern California and Mexico in 1951-1984, 1996 and 1998-2000. A time series of weighted simple mean larval densities from 1951-2000 (1951-1984, 1996, 1998-2000) was constructed for the current CalCOFI and IMECOCAL survey areas during the peak spawning periods. Based on historical data, larval densities peaked in May off California and August off Mexico. To extend the months to increase sample size for this analysis, we chose months prior to and after the peak month: thus larval data from IMECOCAL in June-September and the current CalCOFI region in April-July were used to construct a new time series for the large survey area. Because the Mexican data did not include number by length group, it was impossible to compute the daily larval production (P_h) which requires larval counts by length. Therefore we computed a simple weighted mean larval density for each year during the peak larval months: The simple mean larval density 10 m^{-2} in the current CalCOFI area, 1951-2008 and in IMECOCAL area 1951-1984, 1996 and 1998-2000 during each peak spawning period. The final density estimates were weighted mean larval densities from these two regions with weights being the survey area size: 198 000 km^2 and 193 000 km^2 for CalCOFI and IMECOCAL, respectively, for 1951-1984, 1996 and 1998-2000 when both areas were covered (weighted mean$\cdot$10 m^{-2}).

The correlation coefficient of P_h off California and the weighted mean off California and Mexico for 1951-1984 (see later section) was computed to determine whether the time series of the daily larval production (P_h) in the CalCOFI area during April-July was representative for the whole area of California and Mexico.

Results

Avoidance

The relationship between the mean noon/night catch ratio (D_L) and larval length (L) based on data of 1951-1978 is:

$$D_L = 2.7\exp(-0.39L) \qquad \text{Eq. 6}$$

where the standard errors of the two coefficients were 0.47 and 0.05, respectively (Fig. 2). The day/night ratio decreases as the length of larvae increases as expected.

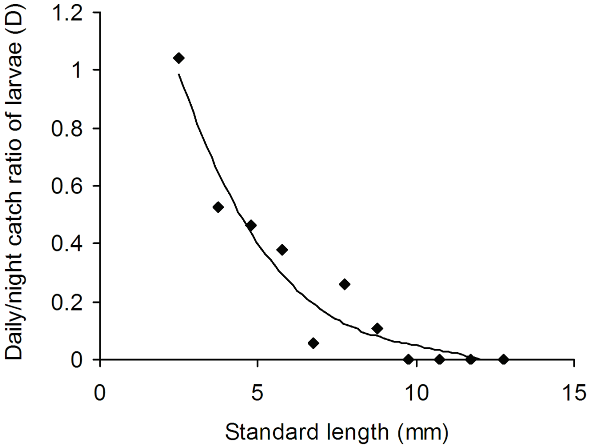

Fig. 2. Noon/night catch rates of Pacific mackerel larvae (D) and larval length (mm) based on data of 1951-1978.

The estimated capture rates of larvae by length and time of day (equation 1) are shown in *figure 3*. Fraction of larvae captured decreased with the length with lowest time at noon.

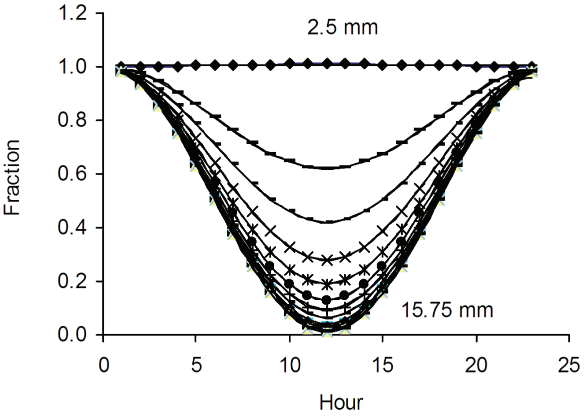

Fig. 3. Fraction of Pacific mackerel larvae captured as a function of time of day within the range of 2.5 mm -15.75 mm standard length.

The daily larval production at hatching (P_h) off Southern California in 1951-2008

The intercept of the mortality curves (equations 4 and 5) provides an estimate of the daily larval production at hatching when data are sufficient to estimate this parameter (Table 1). For those years, the estimates of the daily larval production$\cdot$10 m^{-2} were the intercepts of the mortality curves based on weighted nonlinear regression (equation 4) (index 1 or 2 in *table 1*). An unweigthed nonlinear regression was used for 1985, 1986, 1988 and 1992 survey data. For years with insufficient data, *i.e*. 1953, 1962, 1969, 1972, 1993, 1994, 2003 and 2006, an overall mortality rate was computed from equation (5). No larvae were observed in 2007 and 2008. The mortality curve and daily larval production at age for 1987 are given for illustration (Fig. 4).

Daily larval production ($P_h \cdot$10 m^{-2}) from 1951-2008 off the California coast, from San Diego to Avila Beach, near Point Conception, fluctuated, with the highest peak of 46.38 larvae$\cdot$day$^{-1}\cdot$10 m^{-2} in 1987 and minor peaks in 1981 and 1986 (Table 1 and Fig. 5). Daily larval production has been declining with moderate fluctuations since 1997 in this survey area.

Table 1

Time series of estimates of larval densities of Pacific mackerel from 1951-2008 based on CalCOFI and IMECOCAL surveys: Pacific mackerel larval production at hatch (P_h), the daily instantaneous mortality coefficient (α) ,their coefficients of variation (CV), total number of tows (n) , positive tows (n_p), bias-corrected larvae·10 m^{-2} (density), mean temperatures(temp) and weighted temperature (wt-temp) off California and the weighted mean (larval densities·10 m^{-2}) in CalCOFI and IMECOCAL areas (wt mean)

CalCOFI area												*CalCOFI and IMECOCAL area*		
									Temperature(°C)					
Year	P_h	*CV*	α	*CV*	*n*	n_p	*Bias-corrected density <11.75 mm*	*cv*	*Temp*	*wt-temp*	*Index*[1]	*wt mean*	*CV*	*n*
1951	0.015	1.267	0.015	2.902	128	6	0.15	0.45	15.00	16.04	1	1.33	0.83	324
1952	0.023	1.000	0.013	9.462	200	7	0.26	0.48	14.50	15.76	1	0.59	0.16	550
1953	0.187	0.513	**0.327**	**0.07**	244	2	0.42	0.96	13.80	15.52	4	1.07	0.45	499
1954	1.148	0.272	0.629	0.11	200	17	2.18	0.37	14.60	17.03	1	1.84	0.52	424
1955	0.287	0.498	0.392	0.184	194	7	2.15	0.62	14.90	15.27	1	1.67	0.86	459
1956	0.113	0.513	0.342	0.284	220	5	0.26	0.52	14.40	15.10	1	1.98	1.12	489
1957	0.044	0.659	0.139	0.532	223	2	0.27	0.86	17.50	18.26	1	2.24	0.6	533
1958	0.629	0.25	0.287	0.136	257	26	2.93	0.27	16.40	17.00	1	0.99	0.28	545
1959	0.184	0.337	0.292	0.205	271	16	0.78	0.29	15.70	17.14	1	0.51	0.12	711
1960	0.585	0.528	0.338	0.257	213	6	2.33	0.63	15.40	16.76	1	1.22	0.82	528
1961	0.067	0.522	0.131	0.473	110	3	0.22	0.59	15.20	17.82	1	0.17	0.09	252
1962	0.125	1.184	**0.327**	**0.070**	78	2	0.28	0.7	15.10	13.51	4	4.80	2.83	205
1963	0.517	0.640	0.37	0.330	125	6	3.15	0.57	15.80	16.08	2	6.60	3.31	271
1964							0.00	1.00	15.17			0.46	0.21	340
1965	0.057	0.982	0.233	0.734	132	4	0.32	0.54	14.50	15.49	2	0.46	0.12	405
1966	0.381	0.756	0.336	0.452	213	7	1.38	0.52	16.10	16.57	2	0.77	0.22	562
1967							0.00	0.88	17.90			0.70	0.29	170
1968							0.00	0.00	14.52			0.00	0.00	110
1969	0.167	0.515	**0.327**	**0.070**	170	2	0.37	0.85	14.70	18.04	4	0.27	0.10	467
1972	0.246	0.512	**0.327**	**0.070**	73	1	0.58	1.00	15.50	15.70	4	0.33	0.23	176
1975							0.00	0.00	14.95			0.04	0.04	383
1978	5.436	0.304	0.28	0.132	198	34	35.73	0.3	16.00	16.00	1	9.85	2.70	468
1979							0.00	0.00	13.21			0.00	0.00	51
1980							0.00	0.00	17.40			0.00	0.00	90
1981	21.85	0.346	0.329	0.137	209	51	84.94	0.3	15.60	17.32	1	17.13	4.81	316
1982							0.00	0.00	-			0.00	0.00	11

Continue...

							CalCOFI area					*CalCOFI and IMECOCAL area*		
									Temperature(°C)					
Year	P_h	*CV*	α	*CV*	*n*	n_p	*Bias-corrected density <11.75 mm*	*cv*	*Temp*	*wt-temp*	*Index*[1]	*wt mean*	*CV*	*n*
1984	2.222	0.702	0.494	0.227	175	10	9.51	0.55	15.80	16.67	1	1.85	0.86	270
1985	0.579	0.332	0.222	0.509	53	5	2.34	0.74	14.20	14.31	3			
1986	10.97	0.24	0.519	0.522	56	15	30.59	0.38	14.70	16.07	3			
1987	46.39	0.512	0.889	0.136	66	13	83.37	0.53	15.40	14.94	2			
1988	2.876	0.335	0.157	0.618	55	13	9.83	0.59	14.40	16.07	3			
1989	1.187	0.464	0.37	0.270	123	14	4.10	0.34	16.10	17.10	1			
1990							0.00	0.00	16.56					
1991	0.848	1.268	0.009	23.220	36	4	6.37	0.88	16.70	16.10	2			
1992	0.315	1.238	0.092	1.380	132	12	1.94	0.65	16.60	16.29	3			
1993	0.643	0.367	**0.327**	**0.070**	57	2	1.62	0.72	14.80	14.66	4			
1994	0.094	4.777	**0.327**	**0.070**	91	1	0.05	1.00	15.20	15.90	4			
1995	0.758	0.322	0.221	0.190	121	11	3.21	0.35	15.60	15.80	1			
1996	7.922	0.364	0.56	0.134	60	9	13.74	0.61	15.10	15.87	1	2.13	1.31	121
1997	8.767	0.489	0.821	0.125	128	13	14.96	0.67	16.00	16.98	1			
1998	0.37	0.773	0.326	0.764	161	7	1.33	0.44	16.30	14.57	2	**4.23**	**2.48**	**301**
1999							0.00	0.00	12.80			**2.30**	**1.00**	**204**
2000							0.00	0.00	15.77			**3.87**	**1.56**	**280**
2001	0.394	0.495	0.148	2.696	132	3	1.70	0.82	15.20	14.76	1			
2002							0.00	0.00	14.89					
2003	0.333	0.841	**0.327**	**0.070**	128	1	0.76	1.00	15.60	14.80	4			
2004							0.00	0.00	16.00					
2005	0.068	0.765	0.039	1.949	190	10	2.16	0.46	15.10	15.19	1			
2006	0.103	2.961	**0.327**	**0.070**	147	1	0.25	1.00	13.40	15.10	4			
2007							0.00	0.00	13.70					
2008							0.00	0.00	13.30					
Whole	1.618	0.186	0.327	0.070										

[1] Index for nonlinear regression.
1. Weighted nls for age< = 20 d.
2. Weighted nls for age< =1 0 d.
3. Unweighted nls for age < = 20 d.
4. Equation (5) using larval production at length 2.5 mm.

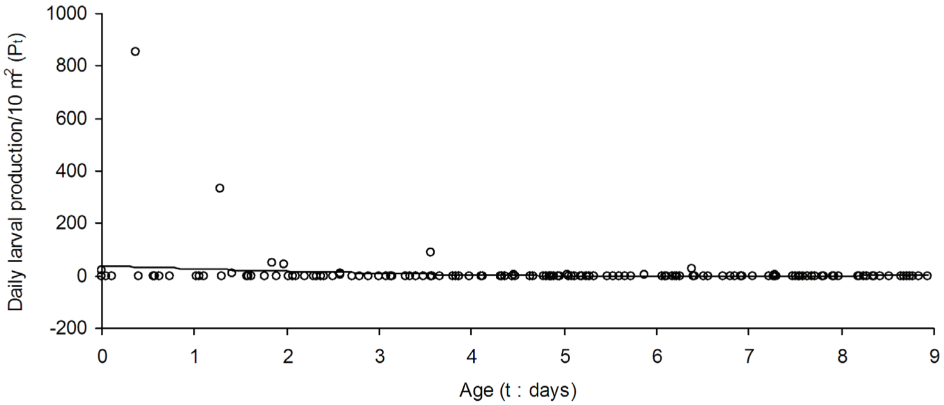

Fig. 4. Daily larval production·10 m^{-2} (P_t) and age (t) with Mortality curve ($P_t = 46.39 \exp^{(-.89t)}$) in 1987.

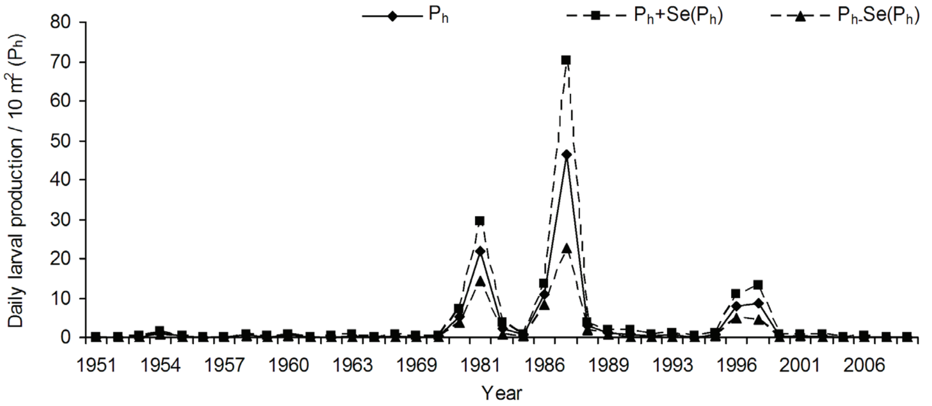

Fig. 5. Pacific mackerel larval production ·10 m^{-2} at hatching (P_h) off area from San Diego to Avila Beach, California in April-July from 1951-2008.

The correction coefficient of the two P_hs (equations 4 and 5) for years when data for larvae of all length groups were available (Table 1) was 0.82. If we exclude the high values, *i.e.* when $P_h > 20$, the coefficient was 0.6. The correlation coefficient between the logarithms of the two P_hs was 0.95. As P_h estimates from both equations were highly correlated (Fig. 6), we concluded that little or negligible bias was introduced over the whole time series by inverting the mortality curve.

Bias-corrected larval densities off Southern California in 1951-2008

The time series of larval densities for the current CalCOFI survey area, after correction for bias due to extrusion and avoidance of the net in 1951-2008 period showed two peaks, 1981 and 1987 (Fig. 7), similar to the P_h time series (Fig. 5).

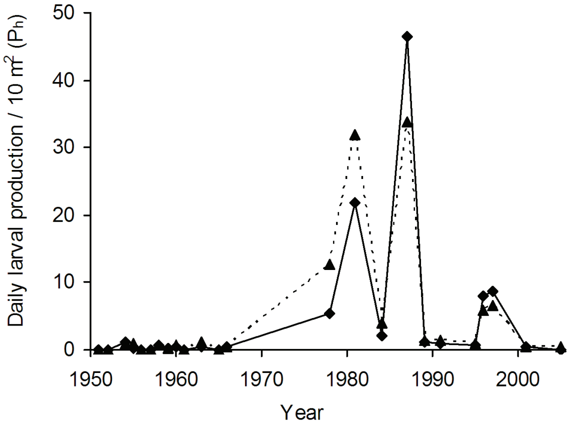

Fig. 6. Estimates of P_h from weighted nonlinear regression (solid line) and from larvae of 2.5 mm (dotted line) (equations 4 and 5) for years when larval data of all length groups were available (index 1 or 2 in Table 1).

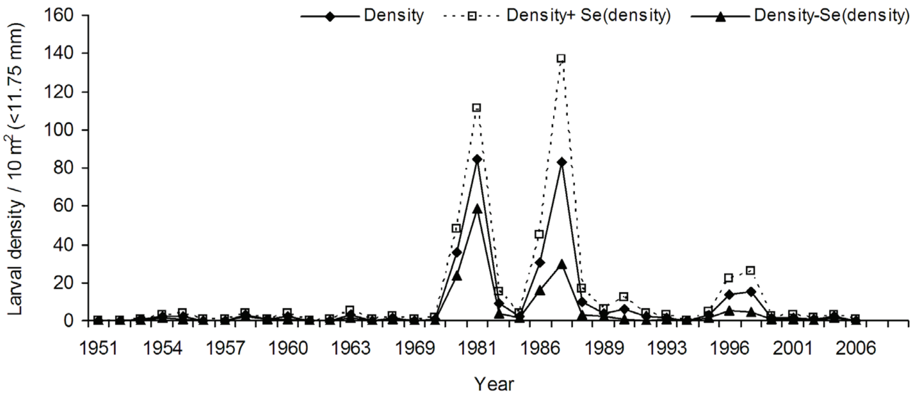

Fig. 7. The time series of larval density (larvae·10 m^{-2}) off area from San Diego to Avila Beach, near Point Conception, California in 1951-2008.

Larval densities·10 m^{-2} off California and Mexico in 1951-1984, 1996 and 1998-2000

The time series of weighted mean of larval densities derived for the periods 1951-1984, 1996 and 1998-2000 in the combined area was obtained together with the time series of simple mean larval densities in the IMECOCAL and CalCOFI survey areas respectively in 1951-2008 (Fig. 8). The time series of the weighted mean showed higher peaks during the 1980s off California and lower peaks in early 1960s (1962 and 1963) and 1998-2000 off Mexico. In 1981, larvae were most dense in California waters and although no data were available from Mexico in 1987, we assume that larval production was most concentrated in California waters in that year as well. In the late 1990s, larvae were denser in Mexican waters than that in California waters.

The correlation between the weighted mean off California and Mexico and P_h in the CalCOFI area during April–July for 1951-1984 was 0.94, excluding years when no larvae were caught (Fig. 9). The correlation (0.23) was low for years, with low densities (P_h<5). The P_h time series off California tends to capture the high peak years, but in years with low larval densities, these two time series did not match well, particularly before 1965.

Comparison between P_h and mean densities of larvae off California

For comparative purposes, we computed the mean counts of larvae per 10 m^2 with correction

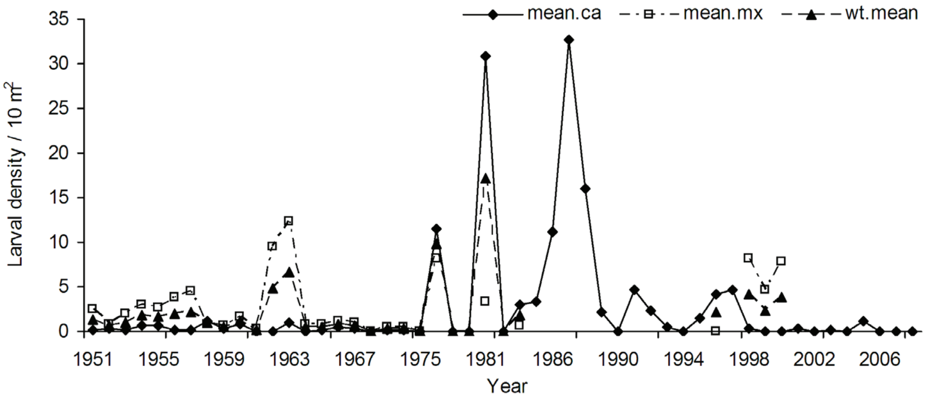

Fig. 8. Pacific mackerel larval densities·10 m^{-2} for the current CalCOFI area in April-July (diamond), for the IMECOCAL area in July-September (square) and weighted mean larval densities (triangle) of the above two series for years when both estimates were available from 1951-2008.

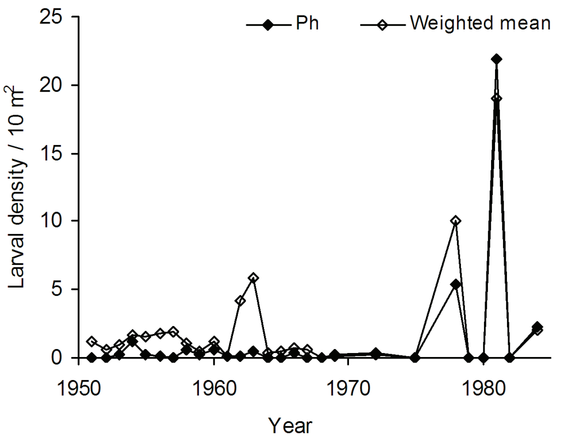

Fig. 9. Time series of Pacific mackerel larval production (P_h) from CalCOFI (solid diamond) and weighted mean (open diamond) for current survey areas of CalCOFI and IMECOCAL in 1951-1984.

for biases (Figs. 5 and 7). The time series of P_h and mean counts of larvae had similar trends but the time series of simple means was more variable than that of P_h because the mean count (the standing *stock*) is the area under the mortality curve or the integral of the mortality curve up to age from hatching (Lo, 1985). For the exponential mortality curve, the standing *stock* (x) from hatching to age *t* is equal to P_h (1-exp$^{(z * t)}$/(-z) where *z* is daily mortality rate. For example, for t = 20 d from hatching, z = 0.32, x~P_h/0.32. Nevertheless, the fluctuations in the time series of Pacific mackerel larvae are partially due to the fact that the larvae are one of the most patchily distributed pelagic species in the CalCOFI time series, and the patches can be very small although dense. We computed the index of patchiness (IP) of larval densities of Pacific mackerel, Pacific hake *Merluccius productus* and Pacific sardine *Sardinops sagax* (Jenyns, 1842) (Lloyd, 1967) as $IP = (n+[\sigma^2/n]-1)/n$ where σ^2 is the variance, and *n* is number of net tows in each year for each species in 1951-2008. The *IP* ranged from 28.1-772, 13.5-267, and 17.5-529 for Pacific mackerel, Pacific hake and Pacific sardine respectively. The *IP* of Pacific mackerel was the highest among the three.

We also compared the time series of P_h and the proportion of positive tows off California from 1951-2008 (Fig. 10). The trends were similar, and yet the time series of P_h fluctuated more than that of the proportion of positives. The proportion of positives was used as an index for the spawning biomass in the Pacific mackerel stock assessment off California from mid-90s to 2007. However, the time series did not work well for the stock assessment due to the lack of a correct error structure (Kevin Hill, *pers. comm.*[2]).

Discussion

Statistical analyses ideally should be based on larval densities corrected for all possible biases estimated from data of Pacific mackerel larvae. However, the extrusion factor was based on survey data from Jack mackerel, a species with

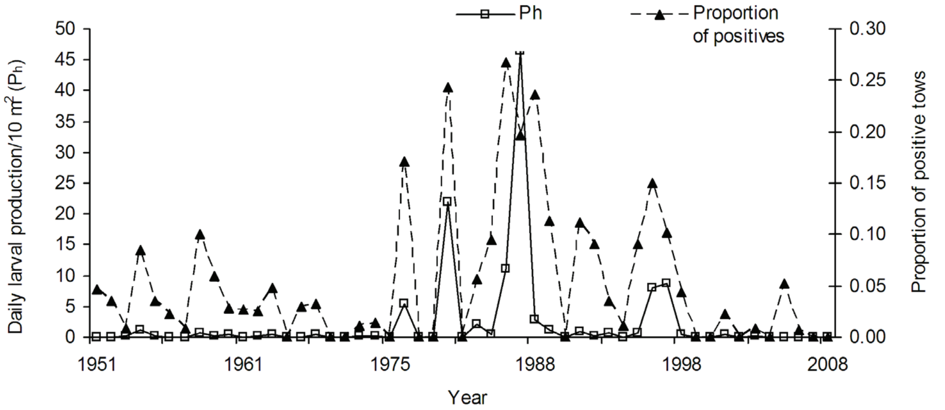

Fig. 10. Pacific mackerel larval production10 m^{-2} (P_h) (left Y-axis) and proportion of positives (right Y-axis) off California, from 1951-2008.

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[2] Kevin Hill, Southwest Fisheries Science Center, La Jolla, CA.USA.

larval morphology similar to Pacific mackerel. Therefore, in future surveys there is a need to perform direct measurements on Pacific mackerel larvae so that a more reliable extrusion factor can be used in deriving daily larval production.

The Pacific mackerel is one of the most episodic of the pelagic species sampled by CalCOFI surveys. Fishery-based information shows that high adult abundances occurred in the 1930's and again in the late 1970's through the 1980's, with the latter period also showing high abundances of larvae in the ichthyoplankton (Dorval *et al*., 2007; Crone *et al*., 2009). MacCall (1996) speculated that strong increases in Pacific mackerel abundance may characteristically precede increases in the sardine abundance, which seems to have been the case off California in the 1980's. The similar phenomenon was observed in the 1990's by comparing the Pacific mackerel daily larval production and Pacific sardine daily egg production (Fig. 11). The hypothesized mechanism is that mackerel have somewhat similar optima as sardines, but are piscivorous (anchovies are an important prey item), are more mobile and have a higher maximum reproductive potential than sardine (mackerel can spawn daily), allowing them to respond more quickly to environmental shifts from anchovy-favorable to sardine-favorable conditions. MacCall (1996) noted that a similar sequential pattern has been observed in Japanese waters where high catches of Pacific mackerel immediately preceded the rise in Japanese sardine *Sardinops melanostictus* (Temminck & Schlegel, 1846) in the early 1970's.

The mean densities of larvae off California have been decreasing since the mid-1980's and were lower than off Mexico in 1998-2000 when IMECOCAL data were available. The same trend may be continued in recent years. The shift of the peak spawning activities could be due to the migration of Pacific mackerel as result of change in oceanographic conditions. Spawning areas of Pacific mackerel have shifted between California and Mexico, exhibiting higher density off California during 1980's peak time. Because larval densities were relative low after the 1990's, data from Mexico would not have much effect on the general trend of the spawning biomass of Pacific mackerel.

Although years of high larval densities may have varied between California and Mexico, the highest larval densities in California waters were much higher than those in Mexico waters. As data from both regions were available for only three years after 1984 (1998-2000), it was not possible to construct a time series from 1951 to present. Therefore the time series of P_h from the current CalCOFI region would best serve as a conservative index of spawning stock biomass for recent years when the population has been low. Overall, the P_h time series seems to track expected biomass trends in the fishery better than the simple larval density estimates, *i.e*. when compared to past predictions from assessment models.

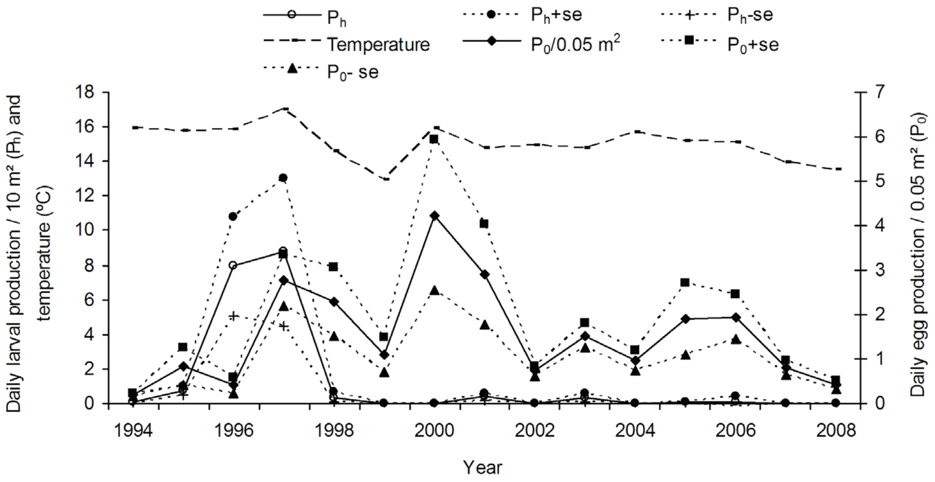

Fig. 11. Pacific mackerel larval production·$10\ m^{-2}$ (P_h) and Pacific sardine egg production·$0.05\ m^{-2}$ (P_0) (right Y-axis) with sea surface temperature (ºC) off California, from 1994-2008.

It may never be possible to obtain a single fishery-independent index for the whole eastern north Pacific stock, which ranges from Mexico to the Pacific Northwest and Canada. The omission of Mexican data in recent years probably cuts off a large segment of the population. Data collected off Mexico many years ago were under a different climate regime and the spatial distribution of the Pacific mackerel now may be different from years prior to the 1990's based on Mexico data collected in 1997-2000. For the CalCOFI area, larval densities have decreased more from 1997 whereas in the IMECOCAL area, densities seemed to be stable in 1997-2000.

In many years (*i.e.* 1964, 1967, 1968, 1975, 1979, 1980, 1982, 1990, 1999, 2000, 2007, 2008) no larval Pacific mackerel were caught during the CalCOFI survey, probably due to the coarseness of the grid and the patchiness of the larval distribution. In those years most larvae were in near shore areas, which are not covered well by the CalCOFI stations. The proportion of years with zero catches of Pacific mackerel larvae was higher than that of Pacific sardine and Northern anchovy for which additional samples were needed even for a crude index. Timing of the CalCOFI survey may not be optimal for the Pacific mackerel either, because the spring cruise typically has been a little too early and the summer too late since the 1990's, given the typical May spawning peak. Thus, among-year variation of larval index is likely driven by changes in spawning activity and survey timing rather than biomass.

Larval density estimates are potentially useful tuning indices in age-based stock assessments because unlike most surveys, their selectivity curves are objectively defined by measureable age-specific attributes such as maturity and fecundity. However, at low abundances such as have been observed recently, frequent occurrence of zero values (*i.e.,* surveys in which no larvae were observed) poses a technical problem. Standard treatment of abundance indices is to use log-transformation, and ad-hoc practices such as adding a small constant before log-transforming seldom produce satisfactory results. An alternative approach of aggregating survey years into time blocks containing non-zero abundance estimates was explored in the 2009 Pacific mackerel stock assessment[3] and the approach appears to be promising. The incomplete geographic coverage in some years, due to the transboundary distribution of the stock, is more difficult to resolve. Until an environmentally-explicit model of mackerel distribution is developed, coordination of surveys in Mexico and the United States will be necessary.

Larval density estimates are also useful to balance the effects of fishery-dependent indices in age-structured assessment models. For example, the use of the P_h index in the 2007 Pacific mackerel assessment reduced the effect of the commercial Pacific fishing vessels (CPFV) index that has driven up Spawning Stock Biomass (SSB) estimates, particularly in the most recent years of this time series (Dorval *et al*., 2007). In contrast, Crone *et al*. (2009) used only the CPFV index in their stock assessment model; hence the trajectory of their biomass estimates freely followed the trends observed in this catch-per-unit index, leading to an increase in SSB in the last three years. As the P_h index is more variable (and less consistent over time) than the CPFV data, using both indices would typically lead to more difficulty in fitting the overall stock assessment model. Therefore, until better biological and fishery data are collected in the Pacific mackerel fisheries, it would be difficult to clearly determine which strategy is the best to derive an unbiased estimate of *SSB* for this species.

Conclusions

An index based on data collected during CalCOFI and IMECOCAL surveys on a non-target species is nearly cost-free. However, a more costly Pacific mackerel-specific larval survey tailored to the timing of spawning, geographic distribution, and taking into account larval patchiness, and net avoidance, would be desirable as it would provide a less biased and more precise abundance index for the population.

Past data from many CalCOFI larval time series have shown that major trends in abundance

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[3] http://www.pcouncil.org/bb/2009/0609/H1b_ATT2_0609.pdf

are always evident despite the noise introduced by variation in reproductive effort.

The long time series of Pacific mackerel larval density, preferably the daily Pacific mackerel larval production, followed by the bias-corrected larval density, is a cost-effective fishery-independent population index obtained yearly and is beneficial to the assessment of the Pacific mackerel population and to a better understanding of its dynamics.

Acknowledgements

We thank John Hunter and Alec MacCall, Southwest Fisheries Science Center for valuable discussions during the writing of the manuscript, Richard Charter and Susan Jacobson for data processing, William Watson, Edward Weber, Akinori Takasuka and William Perrin, Southwest Fisheries Science Center for reading early draft, three anonymous reviewers for constructive comments, and Rose Sanford for organizing the manuscript.

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Recibido: 26 de febrero de 2010.
Aceptado: 22 de julio de 2010.