

DAILY LARVAL PRODUCTION OF PACIFIC HAKE (*MERLUCCIUS PRODUCTUS*) OFF CALIFORNIA IN 1951–2006

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ABSTRACT

Pacific hake (*Merluccius productus*) daily larval production at hatching per 10 m² from 1951–2006 was estimated based on data collected from California Cooperative Oceanic Fisheries Investigations (CalCOFI) surveys off the California coast from San Diego to San Francisco in January–April, the peak spawning time. CalCOFI cruises covered this area prior to 1985, and have covered it during January surveys since 2003 and other non-CalCOFI surveys. For some years between 1980 and 2003, the CalCOFI survey area reached only to just north of Morro Bay. For those years, the larval production at hatching was estimated using a conversion factor to scale to the entire area. The density of daily Pacific hake larval production fluctuated with major peaks in 1986 and 1987. Minor peaks were in 1952, 1958, 1972, and 1979. The density of daily larval production has been decreasing since 1987 and was particularly low in 2003–06. The decrease of Pacific hake larval production coincided with the increase of sea temperature since the 1980s. This fishery-independent time series should benefit assessments and provide a better understanding of the dynamics of the Pacific hake population.

INTRODUCTION

Pacific hake (*Merluccius productus*) is a migratory species occurring off the west coast of the North American continent, primarily from Baja California to British Columbia; its larvae live primarily below the mixed layer in colder water (Ahlstrom 1959). Adults migrate south off California and Baja California to spawn in the autumn and migrate north off Oregon and Washington to feed in the summer (Hollowed 1992) (fig. 1). Pacific hake larvae were observed in the first California Cooperative Oceanic Fisheries Investigations (CalCOFI) survey in 1949, ranked first in abundance in 1951 before the northern anchovy population began to increase, and ranked second from 1955–84 before the CalCOFI survey area was reduced to the current southern California pattern from San Diego to Point Conception (Moser et al. 1993; fig. 2). Pacific hake larvae were typically collected at temperatures above 10.5°C in the upper 150 m of the water column and have been observed as

far offshore as 200–250 miles (Ahlstrom 1959; 1968). It is believed that the spawning center moves north during warm years, and south in cool years between mid-Baja California and San Francisco (Ahlstrom 1968; Horn and Smith 1997).

The time series of Pacific hake larval abundance and distribution by month from 1951–84 were reported by Moser et al. (1993), and spatial and temporal distributions of larvae from 1961–86 were analyzed by Hollowed (1992). For most years from 1985 to 2002, the CalCOFI survey area has been reduced to cover the area in the Southern California Bight (CalCOFI line 93–line 77; figs. 3 and 4), called the southern area in this study. In 2002, the National Oceanic and Atmospheric Administration's (NOAA) Fishery and the Environment (FATE) research program recommended an expansion of the January survey to cover the distribution of hake larvae. Beginning in 2003, the January CalCOFI cruise was extended north to the vicinity of San Francisco (CalCOFI line 93–line 60; fig. 2). This extended area is defined as the larger area in this study and provides a link to the historical time series of Pacific hake larval abundance. Other surveys, like surveys for sardine during April, also cover the area from San Diego to San Francisco (Lo et al. 2005).

Ideally, methods such as the daily fecundity reduction (DFR) method for demersal fishes should be used to estimate spawning biomass of Pacific hake (Lo et al. 1993; Zeldis 1993; Moser et al. 1994). This method requires data on fish-egg stages, duration, and abundance, plus the reproductive output of adult fishes (MacGregor 1966; MacFarlane and Saunders 1997). Due to the high patchiness of Pacific hake eggs, the difficult identification of early stages of the eggs, and the fact that their eggs were consistently identified only in the last 10 years, it is not possible to carry out a DFR analysis over the whole 1951–2006 time period. Fortunately, Pacific hake larval data from CalCOFI surveys are readily available from 1951 and comprehensive correction algorithms can be applied to reduce the possible biases of measurement, such as extrusion through the net mesh, avoidance of the net, etc. It seems reasonable to consider the larval production of Pacific hake as a possible index of spawn-

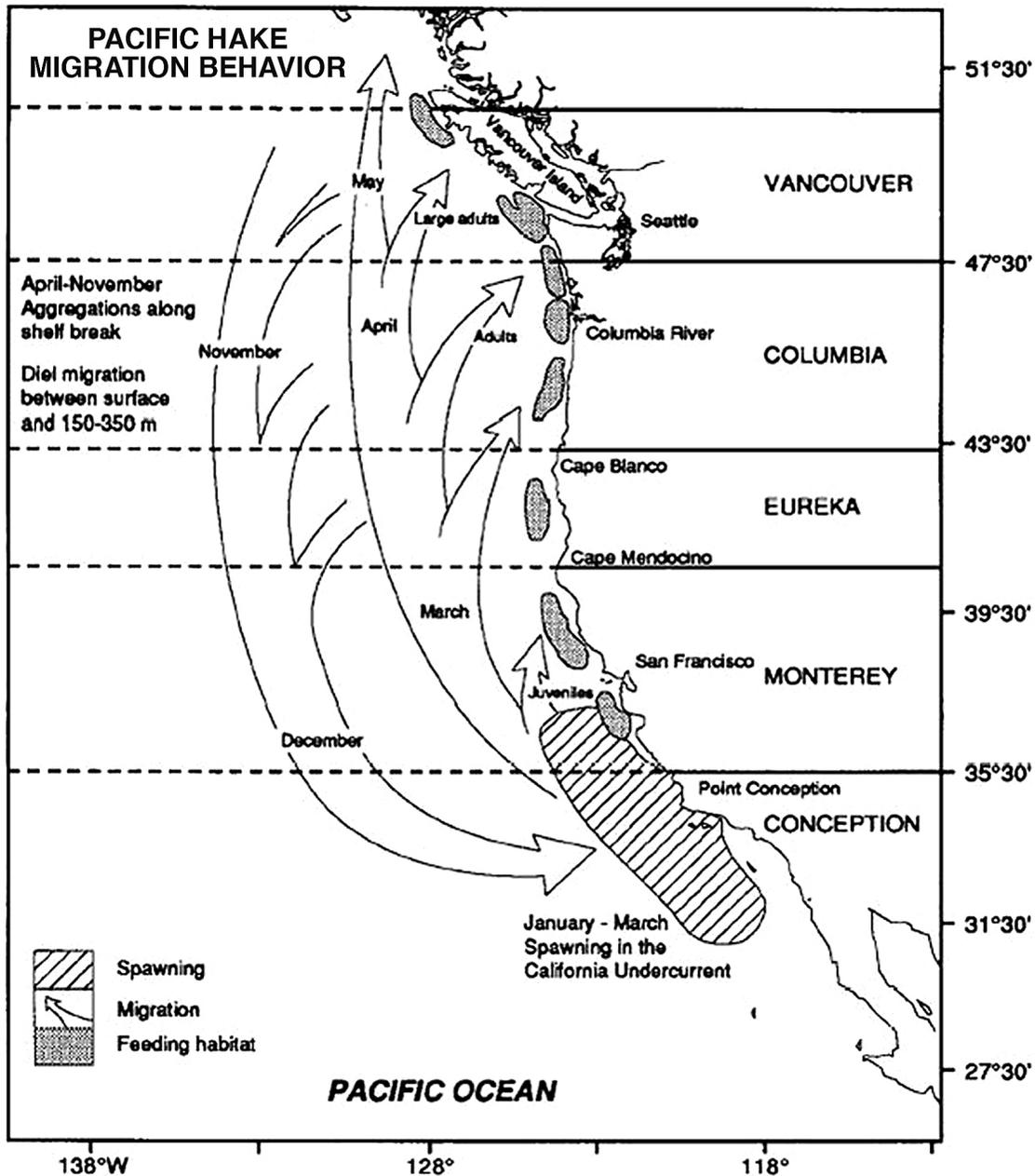


Figure 1. The general pattern of Pacific hake migratory behavior (Bailey and Stevens 1982; Dorn 1995)

ing biomass (Ahlstrom 1968) as has been done for many other fish populations (Smith 1972; Lo 1986; Lo et al. 1989). This time series can also be used to assess the role of environmental factors on the distribution and early survival rate of hake. In this paper, I analyze Pacific hake larval data from 1951–2006 for the larger area in January–April. Although this area is smaller than that of the historical CalCOFI survey (fig. 3), it encompasses the primary spawning area of Pacific hake (Moser et al. 1993) and should represent the whole Pacific hake population in most years.

MATERIALS AND METHODS

The CalCOFI survey was conducted annually from 1949–66, after which it was conducted every three years through 1984, covering the area from Baja California to the north of San Francisco (fig. 3). Starting in 1985, the survey was conducted annually but covered only the southern area from San Diego to Avila Beach, north of Point Conception. Pacific hake is a migratory species, therefore, larval data from this southern area are not enough to assess its relative population abundance. However, in some years after 1984 various non-CalCOFI

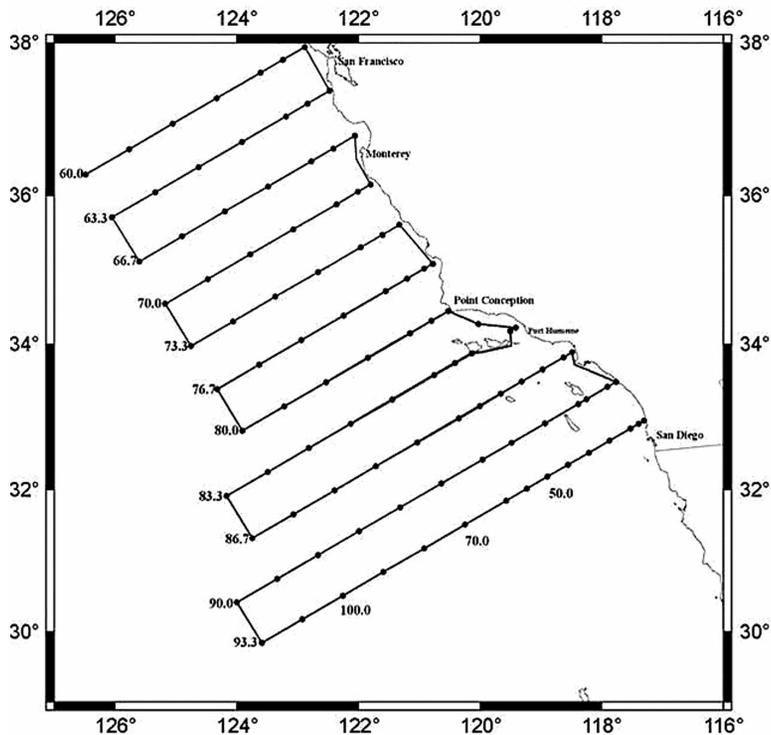


Figure 2. The larger area (CalCOFI lines 93.3–60.0) for January CalCOFI survey occupied since 2003. The southern area covers CalCOFI lines from 93.3–76.7, the regular CalCOFI Survey area since 1985. The northern area covers the path from Avila Beach to San Francisco.

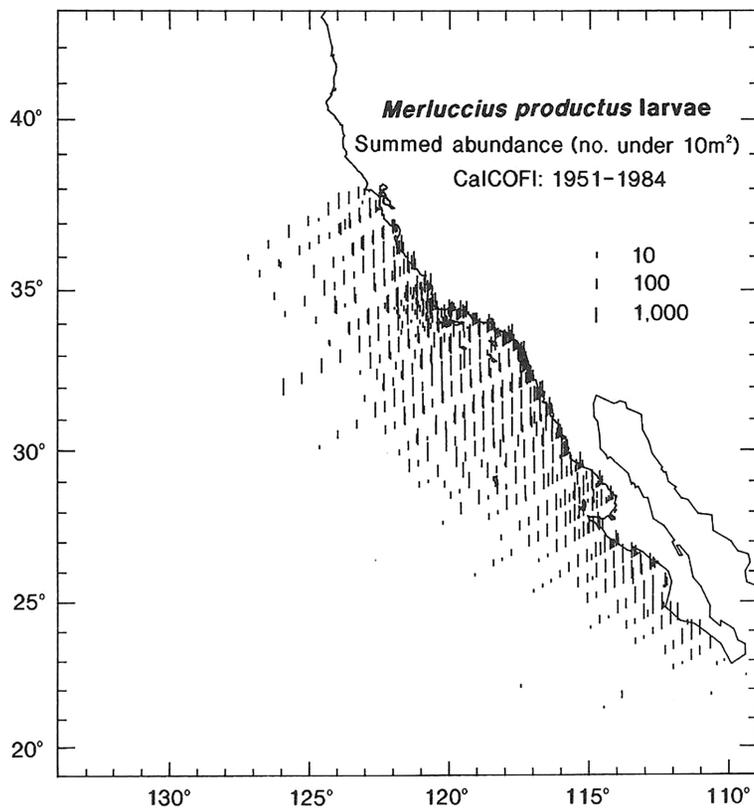


Figure 3. Pacific hake larval densities from CalCOFI surveys from 1951–84 (Moser et al. 1993).

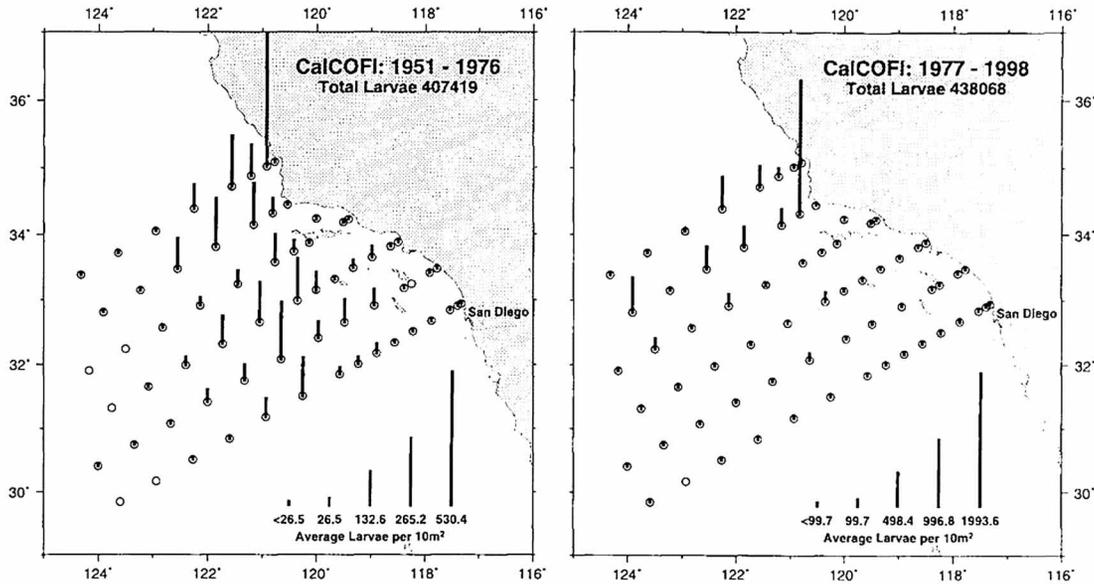


Figure 4. The mean Pacific hake larval densities in the current CalCOFI survey area from 1951–98 (Moser et al. 2001). Note the magnitudes of sticks in these two panels are different.

surveys were conducted in the area between Point Conception and San Francisco, e.g., cruises in 1987 and 1988 (Lo et al. 1993) and daily-egg-production-method anchovy or sardine surveys (Lo et al. 2005). Data from Bongo samples collected during those cruises were included in this analysis. Since 2003, the CalCOFI pattern has been expanded (figs. 2 and 5), and the survey area used in this study is this expanded area (from San Diego to San Francisco). It was reported that the spawning of Pacific hake in winter had been detected north of San Francisco between latitude 35°N–40°N in the early 1990s (Saunders and MacFarlane 1997). Therefore, the fluctuation of hake larval production in any particular area may be partially due to the expansion of the spawning area due to a regime shift, or just any recent anomalously warm temperatures.

For consistency, only January–April Pacific hake larval data from the CalCOFI database and other surveys in the same area were used in this study (Ahlstrom 1968; Moser et al. 2001). Larvae were collected by oblique tows with a 1 m ring net to 140 m from 1951–68; the depth was increased to 210 m in 1969. The 0.55 mm silk mesh net was replaced by a 0.505 mm nylon mesh net in 1969. The Bongo net replaced the 1 m ring net in 1978.

In the laboratory, samples were sorted for fish eggs and larvae. The fraction of the sample sorted depended on the amount of zooplankton: in general, if the displacement volume was less than 25 ml, the whole sample was processed. If the displacement volume was more than 25 ml, then the sample was split into 2 to 8 equal volumes for inshore stations (CalCOFI stations lower

than 80) depending on the actual volume sizes. For offshore stations, the whole volume was examined regardless of zooplankton displacement volume. All fish eggs and larvae were sorted from the processed portion of each sample. For each collection, a maximum of 100 larvae of each targeted species (e.g., Pacific hake) were measured for length in 0.5 mm increments. If more than 100 larvae were sorted from the sample, the length distribution was prorated to the entire number sorted for that species.

A standard haul factor used to compute the number of larvae per 10 m² was intended to account for variability in the volume of water filtered per unit of depth (Ahlstrom 1948; Smith and Richardson 1975). Sampling biases caused by net selectivity for small larvae and gear avoidance for larger larvae were adjusted following the method of Lo (1985). Retention rates for extrusion can be expressed as functions of larval length and mesh size (Lenarz 1972; Zweifel and Smith 1981; Lo 1983), and those for avoidance can be expressed as functions of larval length and the diurnal time of capture (Hewitt and Methot 1982). All larval abundance data were adjusted to conform to the following standard condition: no extrusion, no day–night difference in avoidance, and a constant water volume filtered per unit depth. The data were then converted to daily production per 10 m² (P_t) by dividing the corrected total number of larvae in each length group by the duration (the number of days larvae remain within each length group). Each length category was converted to age after hatching based on growth curves reported by Bailey (1982) for young larvae and by Butler and Nishimoto (1995) for older larvae,

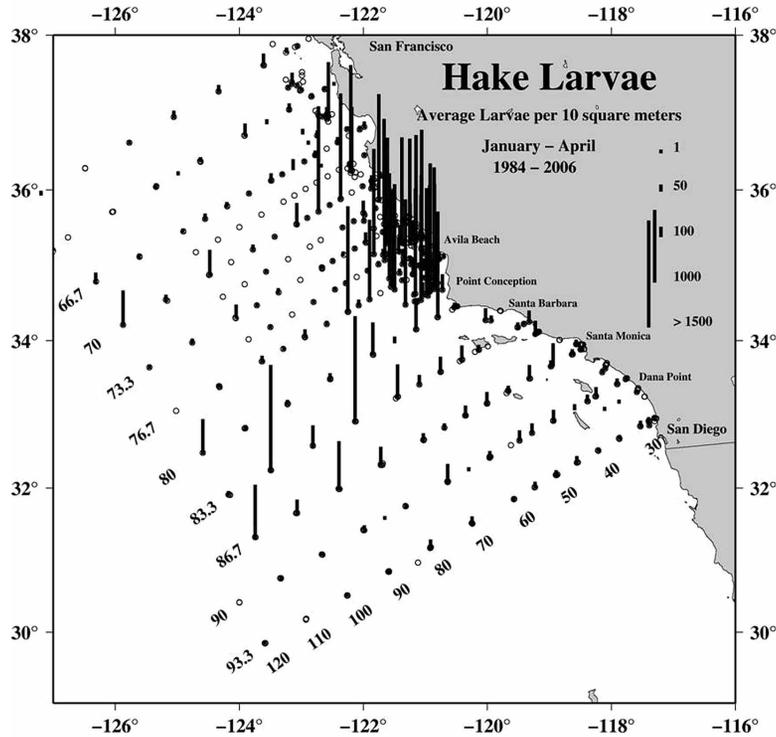


Figure 5. Pacific hake larval densities for the survey area from San Diego to San Francisco from January–April, 1984, 1985, 1987, 1988, 1991, 1994, 2003–06 where the whole area was covered. For irregular stations, data from northern area were from non-CalCOFI surveys.

after adjusting by temperature for the growth of yolk-sac larvae.

Correction Factors

Extrusion

There are no existing data on the length-specific extrusion rate for Pacific hake. Therefore, the retention coefficient of jack mackerel (*Trachurus symmetricus*) larvae due to extrusion was used as a proxy for Pacific hake. Jack mackerel larvae and Pacific hake larvae are approximately the same length at hatching and are superficially similar. Hewitt et al. (1985) reported that only the smallest size class of jack mackerel larvae (3.0 mm) was 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 $1/0.28$ or 3.571. The difference in extrusion of Pacific hake larvae between the 0.55 mm and 0.505 mm mesh nets is likely to be insignificant, as was the case for northern anchovy larvae (Lo 1983).

Avoidance/Evasion

The correction factor for avoidance/evasion was estimated using the algorithm developed for northern anchovy (Lo et al. 1989). Because larvae are able to avoid or evade the net to the same degree under sufficient light to see, and larger larvae are better able to avoid the

sampling gear, I used the Lo et al. (1989) model for the retention (or capture) coefficient of Pacific hake larvae for a specific larval length (L) and hour of the day (h): $R_{L,h}$:

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

where D_L is the noon/midnight catch ratio for length L . Data from positive tows from 1951 to 1984 in the larger area were used to model the catch ratio:

$$D_L = \frac{\bar{y}_{L,noon}}{\bar{y}_{L,night}} \quad (2)$$

The numerator is the mean catch at noon (11:00 AM–1:00 PM) of larvae size L . The denominator is the mean catch in the night (9:00 PM–3:00 AM) of larval length L . I then used an exponential curve to model the relationship between D_L and larval length, L .

Shrinkage

Bailey (1982) reported on the percent shrinkage in the standard length of first-feeding larvae due to preservation and time of handling. Shrinkage was 8.9% for formalin-preserved larvae (L) and 3.6% for ethanol-preserved larvae (L_e). Because formalin is the standard

TABLE 1

Summary of GAM for the relationship between temperature at depth and variables: line, station, month, depth and year.

Terms	Resid. Df	Resid..Dev	Test	Df	Deviance	F.Value	Pr.F.
s(line) + s(station) + s(year, df = 8) + s(month, df = 2) + s(depth)	41880.99	5606423.59	—	—	—	—	—
s(line) + s(station) + s(year, df = 8) + s(depth)	41882.99	5782190.87	-s(month, df = 2)	-1.9997	-175767.27	656.62	0
s(line) + s(station) + s(depth)	41891.00	6536134.28	-s(year, df = 8)	-8.0050	-753943.42	703.57	0
s(station) + s(depth)	41895.00	8427943.31	-s(line)	-4.0004	-1891809.03	3532.68	0
s(depth)	41899.00	11384794.73	-s(sta)	-4.0021	-2956851.42	5519.17	0
1	41903	16652776.46	—	-3.9988	-5267981.73	9841.24	0

preservative used in regular CalCOFI surveys, a correction factor is needed to convert formalin-preserved length to ethanol-preserved length in order to apply the larval Pacific hake growth curves derived by Bailey (1982) and Butler and Nishimoto (1995). The multiplier applied to larvae from 2.5–11.5 mm from CalCOFI surveys is $(1 - 0.036) / (1 - .089) = 1.058$ to convert formalin-preserved length to ethanol-preserved length, i.e., $L_e = L * 1.058$ (see later section).

Growth of Hake Larvae

Growth curves

In order to track the mortality curve of Pacific hake larvae, I first converted larval length to age, using the growth curve from Bailey (1982) for larvae < 3.16 mm (ethanol-preserved length):

$$L_e = 1.72 * \exp[3.15(1 - \exp(-0.02624t))], \quad (3)$$

for $L_e < 3.16$ mm, where t (days) is age from hatching and L_e is the length (preserved in 80% ethanol). This equation was based on data collected in 1978–79 off the California coast (Bailey 1982).

For older larvae, I used the growth curve from Butler and Nishimoto (1995):

$$L_e = 3.16 * \exp[3.64(1 - \exp(-0.0101t))], \quad (4)$$

for $3.16 \text{ mm} < L_e < 30$ mm, where t is age in days starting from length of 3.16 mm (preserved in 80% ethanol) or 3 mm (formalin-preserved length = 3.16 mm/1.058), near the size of yolk-sac absorption (Ahlstrom and Counts 1955). The age of a larva with length (L_e) = 3.16 mm would be 8.17 days after hatching, from the growth curve of Bailey (1982).

To convert length to age after hatching, I inverted the above two equations and obtained:

$$t_1 = -(1/0.02624)^* \ln\{1 - (1/3.15)^* \ln(L^*1.058/1.72)\}, \quad (5)$$

for $L < 3$ mm and:

$$t_2 = -(1/0.0101)^* \ln\{1 - (1/3.64)^* \ln(L^*1.058/3.16)\} + t_{|L=3}, \quad (6)$$

for $3 \text{ mm} \leq L < 28$ mm, where t is age after hatching and L is formalin-preserved length.

Depth Distribution of Yolk-sac Larvae and the Associated Sea Temperature

The growth of Pacific hake yolk-sac larvae ($L \leq 3.25$ mm) is temperature dependent (Bailey 1982; Zweifel and Lasker 1976). Pacific hake spawn at depths around 100 m (Ahlstrom and Counts 1955; Ahlstrom 1959; Bailey 1982; Moser et al. 1997). Estimated temperatures at the expected depth of capture in February were used in the model. Expected depth of capture was derived from a survey conducted during February 1996 in the Los Angeles Bight between 32°N–35°N and 118°W–121°W. Vertically stratified Multiple Opening/Closing Net and Environmental Sampling System (MOCNESS) samples were taken using 0.333 mm mesh nets. Based on 11 positive tows out of 25 tows, yolk-sac larvae were found between 25–100 m, with the modal depth at 50–75 m and the mean depth at 57.24 m (sd = 15 m) (Cass-Calay 2003; Cass-Calay pers. comm.). During regular CalCOFI cruises, the exact depths of yolk-sac larvae are unknown because all plankton tows are integrated tows. However, at each CalCOFI station, temperatures at depths of 20, 30, 40, 50, 75, and 100 m were recorded by hydrocast prior to 1985 and by CTD since then. I used a generalized additive model (GAM) to model the relationship of temperature and other variables: depth, CalCOFI line, station, month, and year. All factors are significant at the 5% level (tab. 1).

$$\begin{aligned} \text{Temperature} = & s(\text{line}) + s(\text{station}) \\ & + s(\text{depth}) + s(\text{Month, df} = 2) \\ & + s(\text{Year, df} = 8) \end{aligned} \quad (7)$$

I estimated the depth of yolk-sac larvae collected at a station from a random number generated from a normal distribution with mean = 57.24 m and sd = 15 m. I then used the GAM to estimate the temperature that yolk-sac larvae experienced (equation 7) based on location of the tows, month (January–June), year (1951–2006), and estimated depth of yolk-sac larvae. Due to the ran-

domly generated depths for yolk-sac larvae, the generated temperature experienced by yolk-sac larvae from each tow varies between analyses.

Temperature-dependent growth of yolk-sac larval stage

To account for the temperature-dependent growth of yolk-sac larvae (Lo 1983), I used the equation from Bailey (1982) for the relationship between the 50th percentile of time from fertilization to yolk-sac absorption (H_{temp} in hours) and depth-dependent sea temperature experienced by yolk-sac larvae ($temp$; °C):

$$H_{temp} = 1269.52 * \exp \{-108.82 * [1 - \exp(-0.0016 * temp)]\} \quad (8)$$

Because the growth curve and age conversion from length (equation 3) were based on data collected in 1978–79 and the temperatures vary among years, I could not use equation 5 directly. Instead, I first computed the 50th percentile of time to yolk absorption for the temperature experienced by yolk-sac larvae at station j (tow) for a given year i (H_{ij}) (equation 8). I then estimated the age of yolk-sac larvae (2.5 mm length group: 1.6–3.25 mm) ($t_{ij,1}$ or $t_{ij,2}$) as t_1 or t_2 (equation 5) multiplied by $H_{ij}/H_{1978-79}$, assuming that the ratio of age of yolk-sac larvae taken at any one station in any one year to that of 2.5 mm group from equation 5 ($t_{ij,1}/t_1$ or $t_{ij,2}/t_2$) is equal to $H_{ij}/H_{1978-79}$ (Bailey, 1982). For yolk-sac larvae from j th tow in year i , the temperature-adjusted age will be:

$$t_{ij,1} = t_1 * (H_{ij} / H_{1978-79}), \quad (9)$$

for $L < 3$ mm and:

$$t_{ij,2} = t_2 * (H_{ij} / H_{1978-79}), \quad (10)$$

for $3 \text{ mm} \leq L < 3.25$ mm, where $t_{ij,1}$ is the age of larvae before yolk-sac absorption and $t_{ij,2}$ is the age of larvae after yolk-sac absorption. Both t_1 and t_2 are ages computed from equation 5. H_{ij} is the 50th percentile of age of larvae at the temperature for the j th tow in year i (equation 8) and $H_{1978-79}$ was the 50th percentile at 12.55°C: the weighted temperature experienced by yolk-sac larvae (at mean depth of 57 m) with number of total larvae as the weight in January–April, 1978–79.

The larvae collected in each tow were grouped as 2.5 mm (up to 3.0 mm), 3.75 (3.5 and 4.0 mm), 4.75 (4.5 and 5.0 mm), etc. To obtain the final age of a larva, the actual length of a larva in each length group from each tow was generated by a random selection from a uniform distribution within each length category: for 2.5 mm, length was selected from 1.63–3.25 mm where 1.63 mm (L) was converted from 1.72 mm (L_c), the minimum length of larvae observed by Bailey (1982) (1.63 mm = 1.72 mm / 1.058). For 3.75 mm larvae, length was selected from 3.25–4.25 mm, etc.

Size class duration and daily larval production

The duration was estimated by the difference of the mid-ages where the mid-ages are the ages corresponding to the mid-lengths or the midpoint between two size groups. For example, the mid-length is 3.25 mm between 2.5 mm and 3.72 mm size groups. The daily larval production in each age group was the larval density in each age group divided by its duration, the time the larvae stayed in each size group.

Daily Larval Production at Hake Hatching (P_h)

The daily larval production at hatching (P_h) was estimated for each year from a larval mortality curve, similar to that of northern anchovy (Lo 1985; 1986) from 1951–2006 when the survey encompassed the survey area from CalCOFI line 93.3–60.0 (fig. 2). Hollowed (1992) reported daily mortality rates for Pacific hake larvae of different stages and found that the Pacific hake larval mortality rate decreased with age as the larvae matured through the early (<4.25 mm), intermediate (4.25–11.25 mm), and late (11.25–15.5 mm) stages. Therefore, to construct a single mortality curve for Pacific hake larvae up to 11.75 mm, an age-dependent mortality rate, such as a Pareto function, would be more appropriate than an exponential function (Lo 1985; 1986). Larvae >11.75 mm in length were excluded because they constituted less than 5% of total larvae and their degree of evasion from the net is uncertain.

The Pareto function assumes that the instantaneous mortality rate at age t from hatching (Z_t) is β/t . To account for the age zero of the youngest larvae, I chose the following form:

$$Z_t = \frac{(dP_t/dt)}{P_t} = \frac{\beta}{t+1} \quad (11)$$

and the mortality curve is:

$$P_t = P_h(t+1)^{-\beta}, \quad (12)$$

where P_t is the daily Pacific hake larval production at t days from hatching, and β is the coefficient of instantaneous mortality rate, and is actually the instantaneous mortality rate at hatching (Z_0).

I fit the curve to all individual data points of P_t and t using a weighted nonlinear regression to estimate the P_h and β where the weight is 1/standard deviation for each 10-day interval for each age group: 0–10, 10–20. Since larvae 60 days or older typically occurred in less than 10% of the tows, the mortality curve was constructed based on larvae less than or equal to 60 days old, to avoid bias.

For other years when the CalCOFI survey covered only the southern area, the P_h for the larger area was estimated from a conversion factor based on the relation-

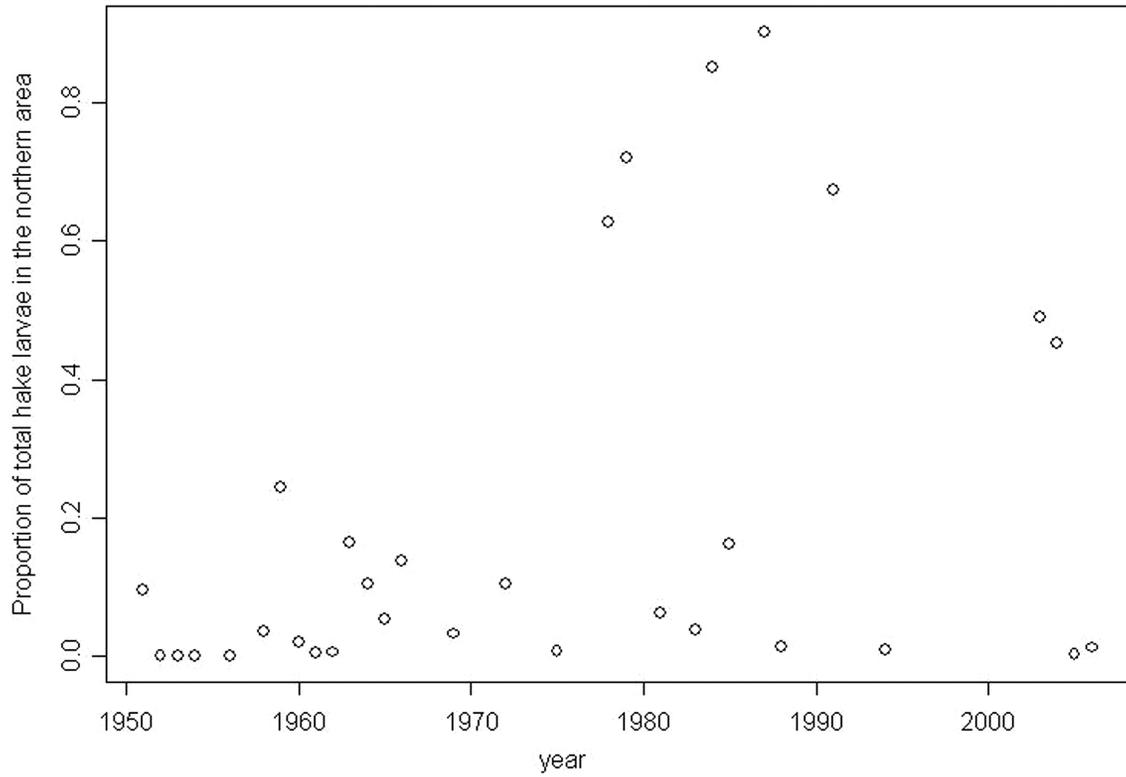


Figure 6. Percentage of Pacific hake larvae in the northern area (CalCOFI lines 76.7–60.0) from 1951–2006.

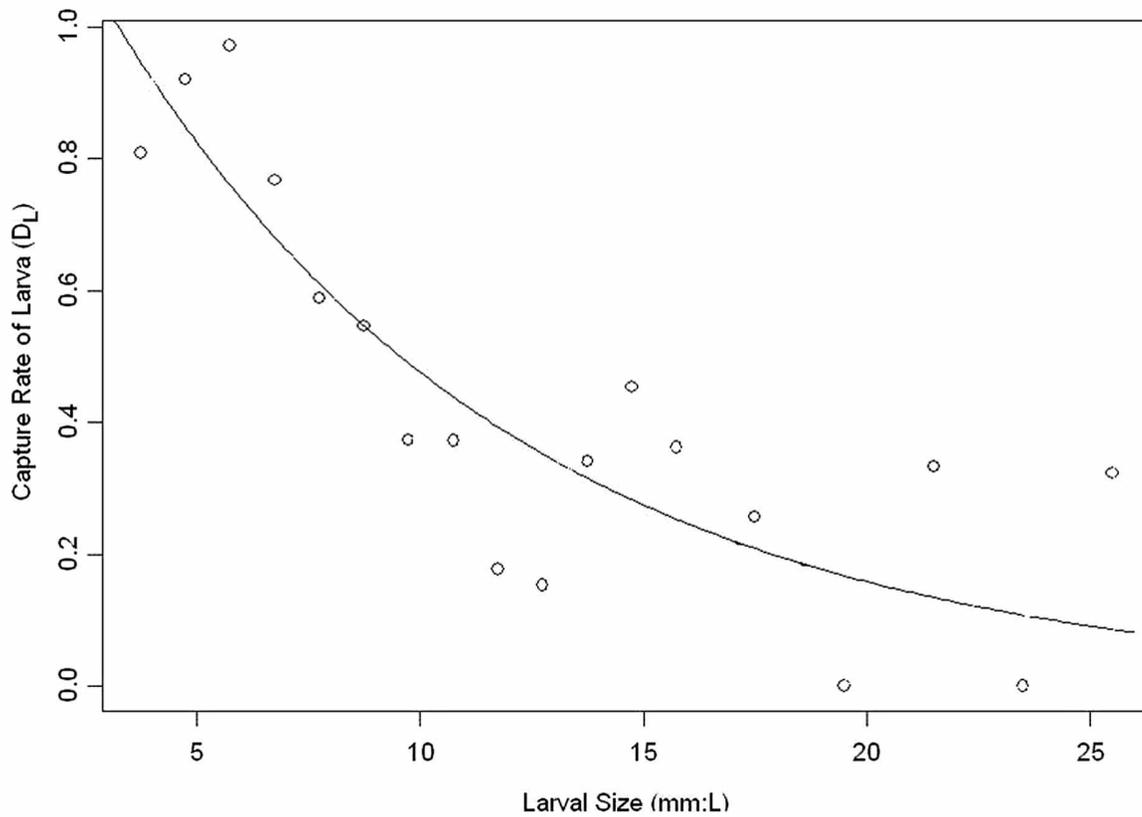


Figure 7. Capture rate of Pacific hake larvae (D_L) and larval length (mm), corrected for after avoidance.

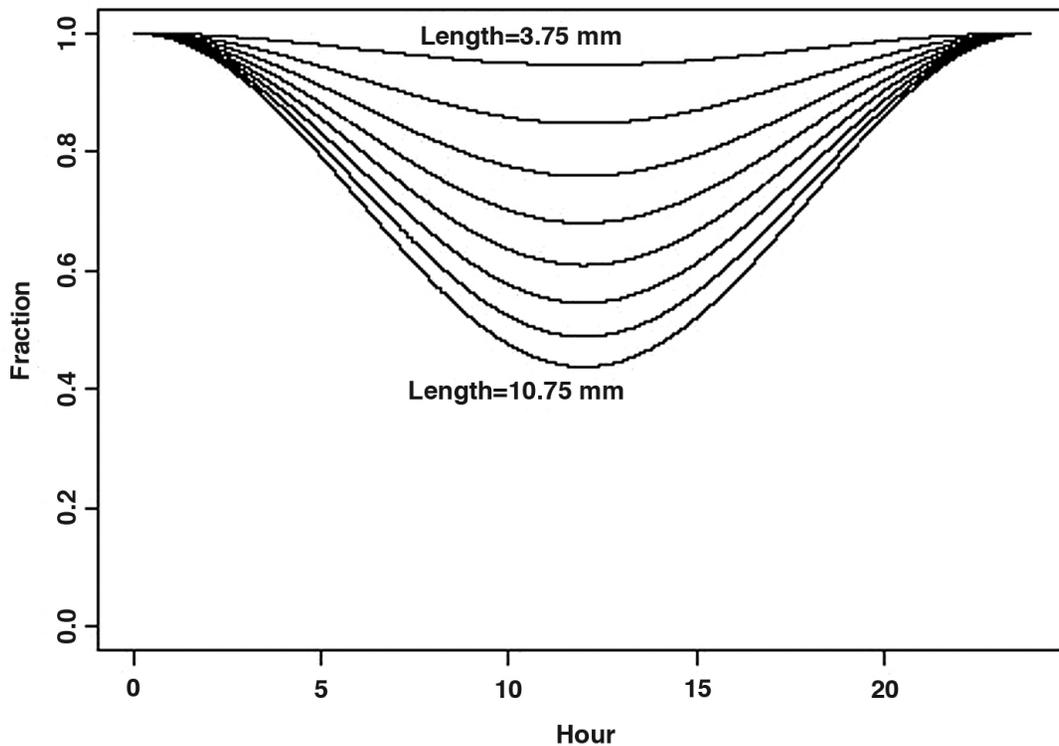


Figure 8. Fraction of Pacific hake larvae captured as a function of time of day.

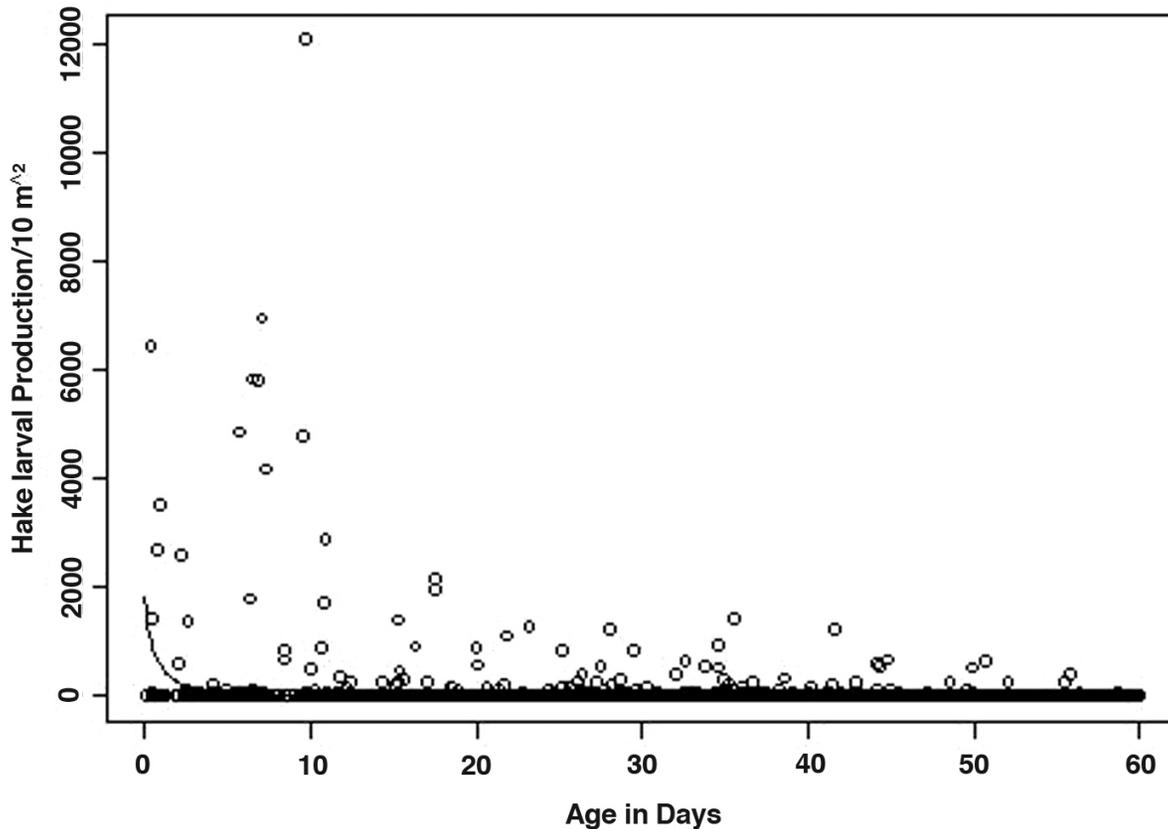


Figure 9. Daily larval production/10 m² and age with Mortality Curve ($pt = 1842 (t+1)^{-1.17}$) in 1987.

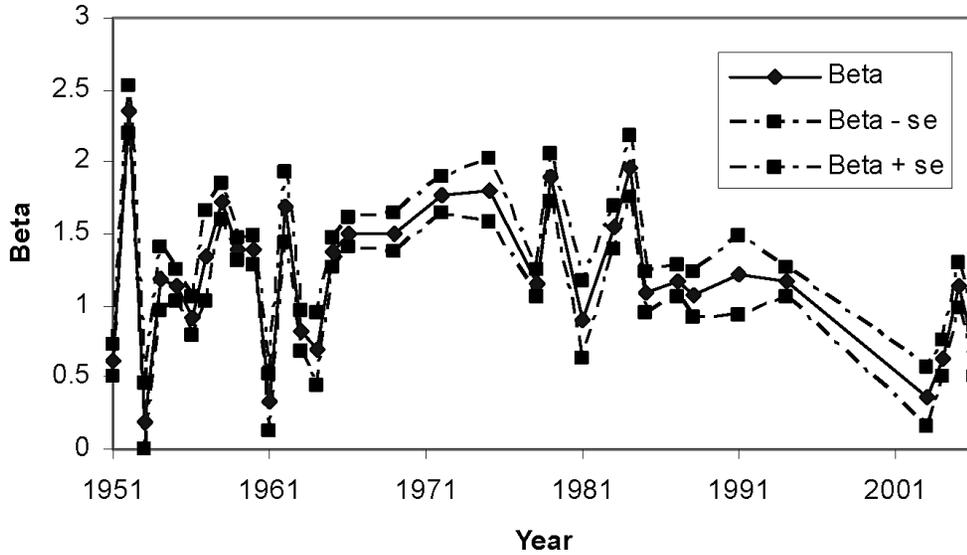


Figure 10. Time series of the estimated mortality coefficient (β or Beta) \pm Standard error.

ship between P_h of the larger area and the density of standing stock of Pacific hake larvae <11.75 mm in the southern area (\bar{x}_s), and the average temperature experienced by yolk-sac larvae (~ 57 m depth):

$$P_h = \alpha * \bar{x}_s + \eta * temp + \xi. \quad (13)$$

Although in some years more than 50% of Pacific hake larvae were found in the northern part of the study area, in most other years no more than 20% of larvae were found in the northern area (fig. 6). Moreover, the southern area is still the major spawning area (figs. 3 and 5).

RESULTS

Avoidance

The relationship between the mean noon/midnight catch ratio (D_L) and larval length (L) is:

$$D_L = 1.43 \exp(-0.11L), \quad (14)$$

where the standard errors of two coefficients are 0.23 and 0.02. (fig. 7). The estimated capture rates of larvae by length and time of day (equation 1) are shown in Figure 8.

Mortality curves

Mortality curves were constructed for each year the larger CalCOFI area was surveyed. The mortality curve and larval production with age for 1987 are provided in Figure 9. As mentioned earlier, the mortality of Pacific hake larvae is age dependent (equation 11) and the mortality coefficient, β , is also the daily instantaneous mortality rate of newly hatched larvae. The time series of β fluctuated through the years with peaks in 1952, 1958,

1972, and 1979 (fig. 10, tab. 2). I also computed the mean instantaneous mortality rates for larvae <4.25 mm (Appendix) corresponding to the early larval category of Hollowed (1992). Mortality rates ranged from 0.03 in 1953 to 0.99 in 1984 (tab. 2).

Daily larval production

For years when the CalCOFI surveys covered the larger area, the estimates of the daily larval production per 10 m² were the intercepts of the mortality curves (equation 12) (tab. 2). A comparison of the residual errors of the exponential and Pareto functions fit to observations shows that the Pareto function fit data better than the exponential function. For other years when the CalCOFI survey covered only the southern area from CalCOFI lines 76.7 through 93.3, the larval production of the larger area (P_h) was estimated from the mean number of larvae/10 m² in the southern area (x) in January–April (fig. 11), plus the error term (ξ). The temperature effect was insignificant and was excluded:

$$P_h = 0.3613 * \bar{x}_s + \xi, \quad (15)$$

where P_h is the larval production at hatching in the larger area, and \bar{x}_s is the mean larvae/10 m² in the southern area for years when the survey covered the area from San Diego to San Francisco (tab. 2) with the coefficient 0.3613 ($se = 0.0232$). The variances of the residual (ξ) around the regression increase with the mean abundance of Pacific hake larvae. The standard deviations for the residuals in three intervals with two breakpoints of larval abundance in the southern area (50 and 600/10 m²) were 2.99, 62.13, and 205.37 respectively. The error term was generated from the normal distribution, each

TABLE 2

hake larval production at hatch (P_h), the mortality coefficient (β) and their standard errors (SE), total number of tows (n), positive tows (n_p), and mean temperatures experienced by yolk-sac larvae and sea surface. For years when only southern area was surveyed where P_h was computed from equation 15 and no β was estimated.

Year	P_h	β	Average Mortality for larvae <4.25 mm	SE(P_h)	SE (β)	n	n_p	Mean Denisty (/10m ²) for larvae of length <=11.75 mm	Mean Temp for ys larvae (°C)	Wted. Temp for ys larvae (°C)	Mean Sea surface Temp (°c)	Mean Sea Surface Wted. Temp. (°c)
1951	4.83	0.61	0.143	1.74	0.11	161	83	75.56	12.02	11.76	13.91	14.09
1952	450.36	2.36	1.334	271.11	0.17	134	72	625.04	11.91	12.3	13.41	13.97
1953	0.41	0.2	0.032	0.38	0.26	185	65	107.98	11.67	11.18	13.13	13.37
1954	5.34	1.18	0.401	3.78	0.22	189	89	41.3	11.72	12.87	13.80	14.37
1955	16.57	1.14	0.378	6.65	0.11	108	73	80.95	12	12.34	13.76	13.44
1956	1.67	0.92	0.263	0.76	0.13	157	56	18.82	11.94	13.17	12.72	13.49
1957	41.86	1.34	0.509	51.03	0.32	110	74	391.96	12.34	12.38	14.26	14.53
1958	201.34	1.73	0.79	95.81	0.13	219	171	448.33	12.19	12.12	14.68	14.51
1959	50.1	1.39	0.541	14.3	0.08	253	164	144.3	12.37	11.78	14.91	14.41
1960	25.89	1.39	0.539	9.64	0.1	301	176	88.46	12.4	12.73	13.88	14.17
1961	0.55	0.32	0.063	0.4	0.2	160	69	58.17	12.36	12.27	13.66	14.23
1962	66.9	1.68	0.759	56.92	0.25	150	90	229.06	12.43	12.3	13.14	13.70
1963	4.33	0.82	0.223	2.05	0.14	187	104	40.23	12.14	11.98	13.46	13.69
1964	1.83	0.69	0.168	1.67	0.26	283	174	63.26	11.8	12.91	14.22	14.85
1965	28.97	1.37	0.52	10.49	0.1	204	119	106.59	11.87	12.16	13.58	13.24
1966	214.57	1.51	0.616	79.06	0.1	215	166	752.39	11.89	12.08	13.60	13.33
1969	125.71	1.51	0.615	63.37	0.13	288	192	373.7	11.78	11.72	13.58	13.68
1972	250.5	1.77	0.817	116.85	0.13	323	179	625.03	11.52	11.38	12.64	12.97
1975	137.83	1.8	0.843	109.85	0.22	271	140	542.63	11.78	12.6	12.38	12.91
1978	36.24	1.15	0.394	12.35	0.1	288	153	190.58	12.38	12.1	14.85	14.34
1979	303.78	1.89	0.912	7.83	0.17	249	170	721.26	12.53	12.76	13.45	12.56
1980	130.815	—	—	95.89	—	116	80	96.72	12.92	12.44	14.54	14.57
1981	9.2	0.9	0.264	8.82	0.27	316	151	120.93	12.53	13.03	14.27	14.65
1982	1.45292	—	—	16.70	—	102	31	50.14	13.08	12.87	13.56	13.20
1983	11.1588	1.54	0.638	5.47	0.15	137	46	33.87	12.66	12.6	14.97	15.23
1984	138.45	1.96	0.989	111.61	0.22	280	85	282.17	12.66	12.21	14.36	13.69
1985	39.12	1.09	0.352	19.73	0.14	201	93	194.95	12.78	12.58	13.59	12.68
1986	1082.13	—	—	97.72	—	168	69	3173.01	12.83	11.57	14.92	13.97
1987	1842.39	1.17	0.4	690.03	0.11	126	90	16445.87	12.15	11.71	14.15	13.64
1988	131.14	1.07	0.349	77.50	0.16	136	92	644.72	12.35	12.72	13.53	12.92
1989	93.78	—	—	32.66	—	127	66	347.2	12.91	12.14	14.22	12.31
1990	64.01	—	—	38.59	—	107	56	70.44	12.7	12.24	14.45	13.35
1991	34.37	1.21	0.43	34.78	0.28	202	109	202	12.59	12.7	13.91	13.72
1993	154.47	—	—	132.53	—	132	47	60.76	13.31	12.62	15.23	14.41
1994	17.69	1.16	0.41	6.69	0.11	174	95	87.78	13.04	12.56	14.99	14.85
1995	62.25	—	—	16.54	—	119	49	215.97	13.43	13.59	15.01	15.20
1996	114.75	—	—	52.17	—	123	55	173.64	13.44	12.2	15.73	14.48
1997	74.64	—	—	6.55	—	129	63	218.15	13.42	12.22	15.04	13.56
1998	5.83	—	—	2.59	—	139	34	9.01	13.37	12.28	15.72	14.15
1999	6.98	—	—	0.61	—	126	48	18.11	13.11	13	13.57	13.02
2000	8.02	—	—	2.24	—	132	58	28.16	13.07	12.81	14.58	14.66
2001	9.11	—	—	1.99	—	128	54	19.84	13	12.08	14.12	13.34
2002	120.04	—	—	14.70	—	193	149	365.49	12.77	12.79	13.89	13.41
2003	0.21	0.37	0.074	0.15	0.21	256	61	4.82	12.45	12.23	14.62	14.62
2004	1.47	0.63	0.154	0.62	0.13	282	63	16.94	12.45	11.64	14.33	12.95
2005	1.97	1.13	0.379	1.09	0.16	338	54	18.52	12.25	11.93	14.60	14.65
2006	0.74	0.68	0.163	0.45	0.18	181	48	18.201	12.4	11.97	14.17	13.83

with mean zero and the associated variance: $N(0, 2.99^2)$, $N(0, 62.13^2)$, and $N(0, 205.37^2)$ respectively.

The time series of daily larval production ($P_h/10 \text{ m}^2$) from 1951–2006 off the California coast from San Diego to San Francisco fluctuated with the highest peak of 1842 larvae/day/10 m^2 in 1987 and minor peaks in 1952, 1958, 1966, 1972, and 1979 (tab. 2 and fig. 12). The larval production has been declining with moderate fluctua-

tions since 1987 in this survey area. The mean water temperature experienced by yolk-sac larvae (~57 m depth) tended to increase from the mid-1970s to the mid-1990s and to decrease since the mid-1990's, while the sea surface temperature was more or less stable prior to 1980 and tended to increase through 2002. Both sets of temperatures have declined since 2003 (fig. 13). The larval production seems to be more related to the mean

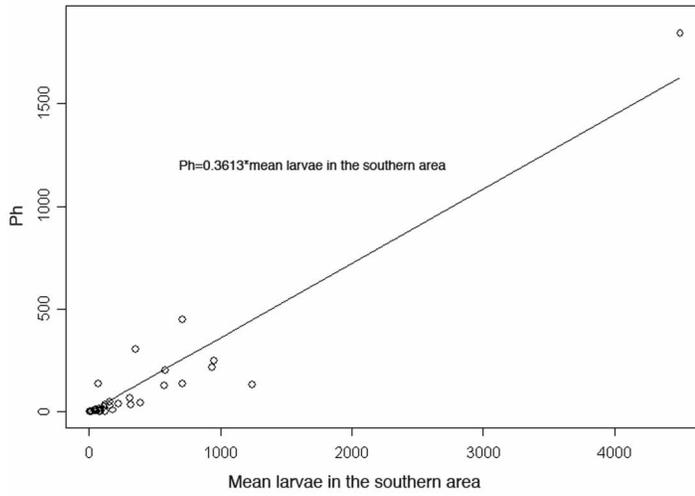


Figure 11. The relationship between P_h and the mean larval abundance in the southern area for years when the larger area was covered.

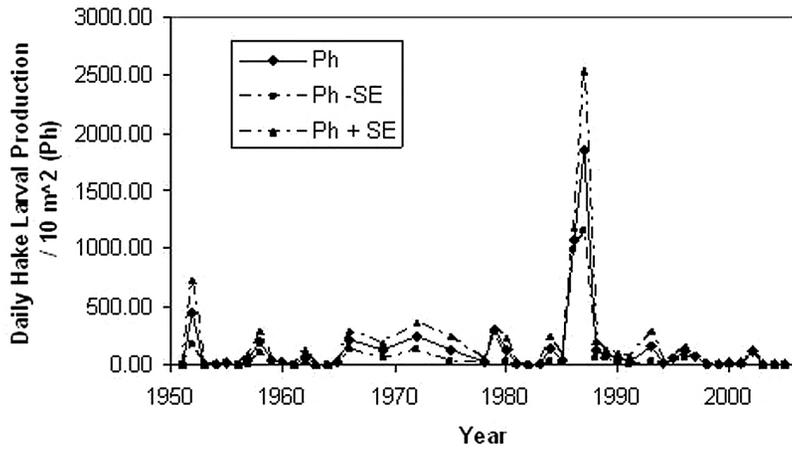


Figure 12. Pacific hake larval production/10 m² in the area from San Diego to San Francisco, in January–April from 1951–2006.

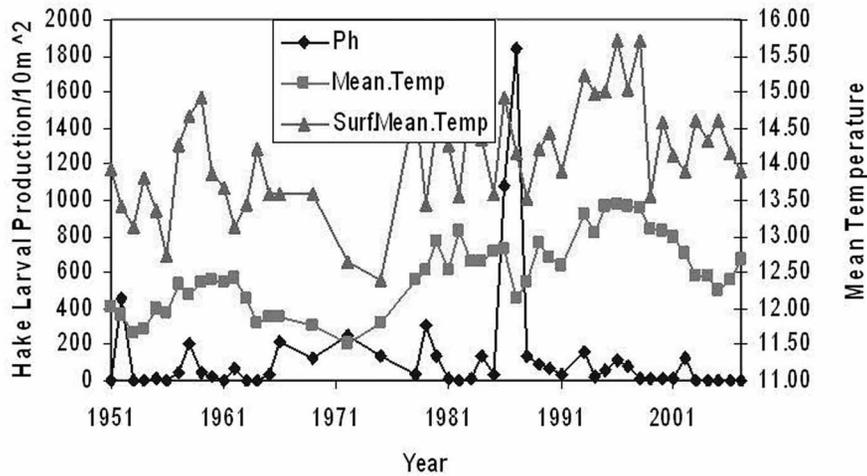


Figure 13. Pacific hake production/10 m² (diamond) and mean temperature experienced by yolk-sac larvae—57 m depth (square) and mean sea surface temperature (triangle) from 1951–2006.

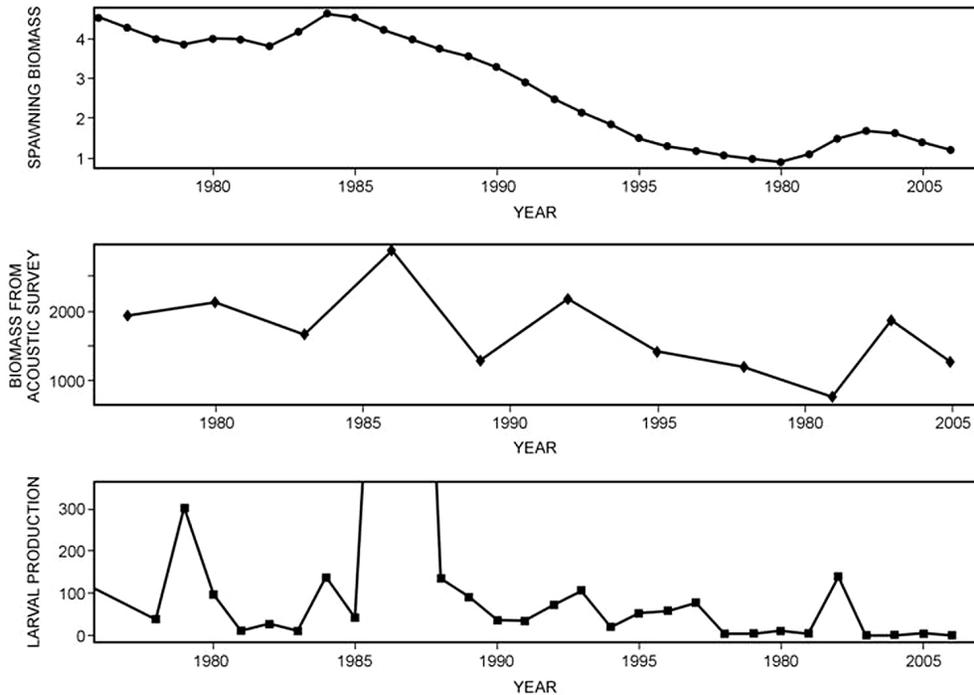


Figure 14. Time series of estimates of the spawning biomass (in million mt) from the stock assessment, biomass from the acoustic triennial survey (in thousand mt) and the larval production/10 m² for years from 1977–2006.

temperature experienced by yolk-sac larvae (~57 m depth temperature) than the sea surface temperature, with correlations of -0.26 and -0.17, respectively, although these correlations are not statistically significant. However, many of the peaks of larval production coincided with the low points of 57 m depth temperatures (tab. 2). The high larval production off central and southern California may be related to the migration of Pacific hake to California waters when the water temperature decreases (fig. 13).

DISCUSSION

This analysis provides estimates of larval production of Pacific hake from 1951–2006 for the area covered by CalCOFI lines 93.3 through 60.0 (figs. 2 and 3), an area considered favorable to the survival of the larvae (Hollowed 1992) and which has been the major spawning ground. Pacific hake larval production should be updated each year and can be used to assess the Pacific hake population because: (1) samples were collected from a broader survey area than acoustic surveys covered (Helser¹) as indicated by the observation of larvae offshore, although spawning is expected to be near-shore in most years; (2) this dataset requires nominal extra cost

to process because data are readily available for every year compared to triennial data from the acoustic-trawl survey; and (3) the larval time series is consistent with the biomass estimates from the triennial acoustic-trawl survey with a simple correlation of 0.76, significant at the 5% level ($t = 3.17$; Zar 1984) and a Spearman correlation of 0.3 based on 9 years of data (Helser¹) (fig. 14). The high peaks in 1986 for both time series indicate that Pacific hake in that year were productive. Yet, the triennial survey missed the high peak of larval production in 1987.

The estimates of P_h for years when only the southern area was sampled (tab. 2) were computed from a simple linear regression: mean densities of Pacific hake larvae in the southern area plus the error term (equation 15). Estimates may be biased for years with extreme temperatures. The mean temperature experienced by yolk-sac larvae (at ~ 57 m depth) in the southern area was included in the original analysis. However, the temperature effect was not statistically significant and was therefore excluded in the final equation (equation 15). If the temperature coefficient had been kept in the equation, it would have a minus sign indicating an inverse relationship between P_h in the survey area and temperature, a possible signor for the northern shift of the spawning center during warm years (fig. 6). More data are needed to verify the environmental effect on the migration of the Pacific hake population, and thus, the spatial distribution of its larvae.

¹ Helser, T.E., I.J. Stewart, G. W. Fleischer, and S. Martell 2006. Stock Assessment of Pacific Hake (Whiting) in U.S. and Canadian Waters in 2006. Pacific Fishery Management Council, 2130 SW Fifth Avenue, Suite 224, Portland, OR 97201. http://www.pcouncil.org/groundfish/gfsafe0406/2006_hake_assessment_FINAL_ENTIRE.pdf

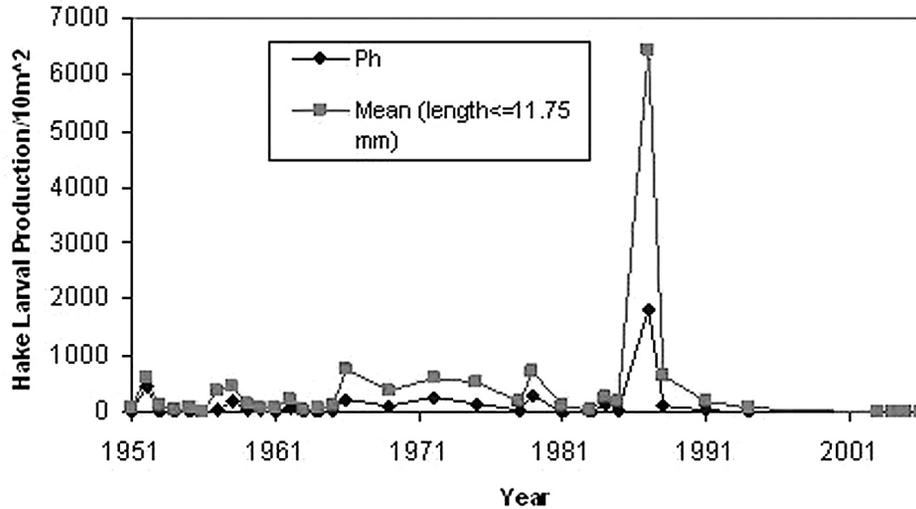


Figure 15. The time series of larval production at hatching (P_h) and the mean number of Pacific hake larvae/10 m² in the area from San Diego to San Francisco in 1951–2006. Gaps are years when only the southern area was surveyed.

For comparative purposes, I computed the mean counts of larvae <11.75 mm in length per 10 m² corrected for biases and the larval production (P_h). The time series of P_h and mean counts of larvae for years when the survey covered the area from San Diego to San Francisco had similar trends but the time series of simple means was more variable than that of P_h (fig. 15). Nevertheless, the fluctuations in the time series of Pacific hake larvae are partially due to Pacific hake being one of the most patchy pelagic species in the CalCOFI time series. The patches can be very large and dense (Horne and Smith 1997), persisting much longer in the depth range of highest larval abundance than in the mixed layer (Butler and Nishimoto 1997). On the other hand, the peaks in larval production tend to coincide with the biomass estimates from acoustic-trawl surveys (fig. 14).

Analyses in this study were based on larval abundance corrected for all likely sources of bias. The extrusion factor was based on jack mackerel larval data, therefore I recommend obtaining direct measurements and verifying if the extrusion factor based on jack mackerel larvae is reasonable to use future surveys on Pacific hake larvae. The avoidance correction factor was based on 1951–1984 data, but I do not foresee a great difference if data from later years were to be included in the analysis. The cosine function was used to model the catchability by larval length. Methods like GAM can be considered in the future to model the length-related catchability, in particular to capture the catchability during the dawn and dusk periods (Watanabe and Lo 1989). Much of the effort was made on modeling the temperature-dependent growth of yolk-sac larvae because yolk-sac larvae are the stage closest to the newly hatched larvae. The effects of temperature on the yolk-sac lar-

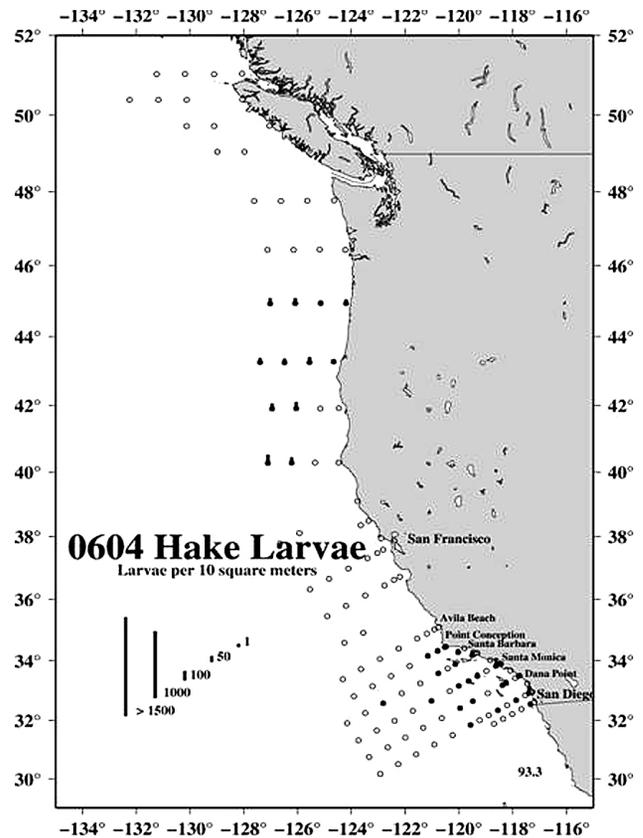


Figure 16. Pacific hake larvae density from the daily egg production method sardine coast wide survey in April–May, 2006

vae were modeled on the relationship between the 50th percentile for the time from fertilization to yolk-sac absorption and temperature (equations 8 and 9). Ideally, laboratory experiments on the growth of yolk-sac lar-

vae at different temperatures should be conducted so that a temperature-dependent growth curve of yolk-sac larvae can be derived directly from laboratory experimental data, as was done for northern anchovy (Lo 1983).

As age was derived from growth curves reported in the literature (Bailey 1982; Butler and Nishimoto 1997), the errors associated with growth curves were not readily available and thus were not incorporated in the variance of the final estimates of P_h . As a result, the variances of the estimates of P_h may be underestimated and the degree of this underestimation is unknown. It would be worthwhile to verify the applicability of any current data on the growth of Pacific hake larvae in early life stages to growth curves reported in the literature. The final estimates of larval production vary for each computation due to the randomly generated depth of yolk-sac larvae based on a mean depth of 57 m and a standard deviation of 15 m.

Hollowed (1992) computed the mortality rates for larvae that were less than 4.25 mm in length to be 0.23–0.41 for 1966–84. For comparison purposes, the mean instantaneous mortality rates for larvae less than 4.25 mm in length (Appendix) were computed (tab. 2). Estimates from this study ranged from 0.26–0.98 for 1966–84. The difference in the estimates of mortality rates between this study and that of Hollowed may be due to the theoretical mortality curves used; Hollowed (1992) used an exponential curve and I used a Pareto curve. Hollowed's estimates were based on 14°C whereas I used the temperatures found around 57 m depth, which were lower than 14°C (tab. 2).

The spawning center of Pacific hake is believed to move to the north during warm years and to the south during colder years in the area between CalCOFI lines 60.0 and 136.7 (roughly Point Reyes, California, to somewhat north of Cabo San Lazaro, Baja California Sur, Mexico) based on data of larval abundance and temperature at 100 m depth during 1951–84 (<http://test.parsus.com/noaa/hake/SummaryData.aspx>; P. Smith, pers. comm. fig. 3). In this study, most of data for the larger area came from surveys conducted in 1951–79 and direct estimates of P_h were primarily made prior to 1980. Since 1980, spawning activities have been reported north of CalCOFI line 60.0: off Oregon and Washington during the springs of 1983–84 between 40°N–48°N (Hollowed 1992) during the El Niño period, and around Cape Mendocino at 35°N–40°N in February 1990 and 1991 (Saunders and MacFarlane 1997). Pacific hake were widely distributed from 36°N to 54°N in 1998 during the summer acoustic-trawl survey (Cooke et al. 2006), and Pacific hake larvae were observed between 40°N and 45°N during a coast-wide sardine survey in April to May 2006 (fig. 16; Lo et al. 2007). Thus, estimates of P_h for the population from the current survey area

may be biased downward during the few El Niño years after 1980, e.g. P_h in 1983, 1998, and 1999 (tab. 2). For future surveys, the ichthyoplankton survey should be extended both to the north of San Francisco and to the south of San Diego during the winter-spring spawning season. This extended survey area will ensure the accuracy of the estimates of the larval production for the west coast of the North American continent and shed light on the effects of oceanographic conditions on the dynamics of Pacific hake spawning activities, and thus the spawning biomass.

A GAM was used to model the relationship between the larval production and three variables: spawning biomass from the 2006 stock assessment (Helsler¹), temperatures experienced by yolk-sac larvae close to 57 m depth, and “year”. The year effect encompassed effects of factors other than the spawning biomass and temperature on the larval production, e.g. ocean conditions. The residual plots from the GAM are the relationship between larval production and a particular variable after the effects of other variables were removed. These residual plots, although not statistically significant and all non-linear, suggested that the larval production in the survey area was inversely related to temperature (if the spawning biomass and year effects were held constant), and positively related to the spawning biomass (fig. 17A and B). If the spawning biomass and temperature were held constant, larval production in the survey area increased from the 1970s to a peak in the 1990s and decreased in recent years (fig. 17C). Therefore the decrease of larval production in the survey area during recent warm years may have resulted from the decrease of spawning biomass and/or movement of some spawning biomass to the north of this survey area (figs. 14, 17B and C).

Correlation coefficients between the P_h and recruits estimated from the stock assessment were also examined with various time lags to determine whether the specific recruitment predicts the subsequent larval production: the P_h time series. The highest correlation was for a time lag of seven years with a correlation of 0.68. The two high peaks of larval productions in 1986 and 1987 may have resulted from the high recruitment event in 1980 with an aid from 1984 (fig. 18). The correlation of 0.68 was driven primarily by the two high values of larval production and recruits and more such events are needed to ascertain the significant time lag between recruits and larval production. Overall, the high Pacific hake larval production in 1986–88 roughly corresponds to a high level of spawning biomass in 1984–86. This increase was most likely the result of two very strong year classes that occurred in 1980 and 1984, which allows for three to four years maturity, and would result in the peak in female spawning biomass (T. Helsler, pers. comm.).

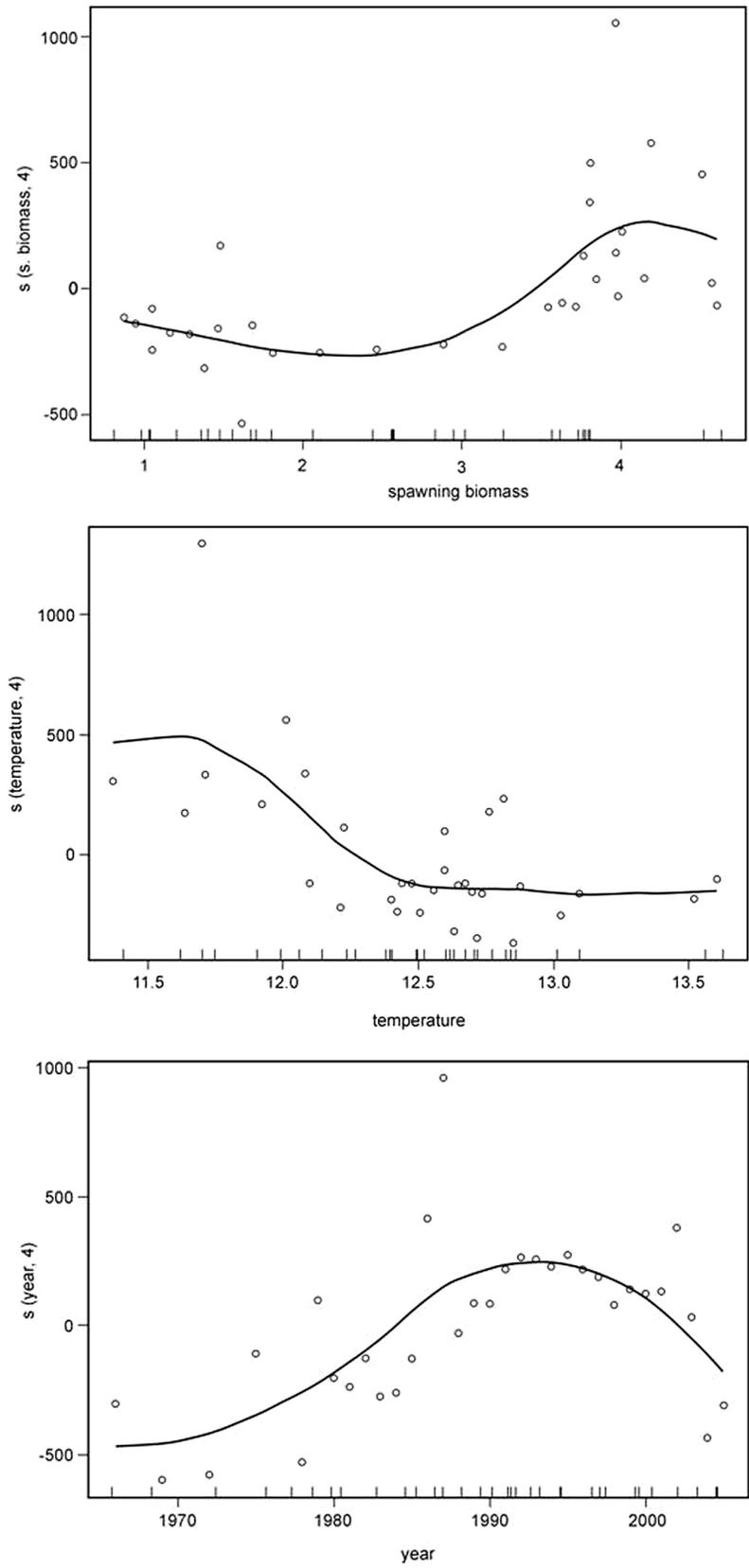


Figure 17. GAM residual of larval production as a smooth function of the spawning biomass (A) and the 57 m temperature (B) and a smooth function of year (C) for 1966–2006.

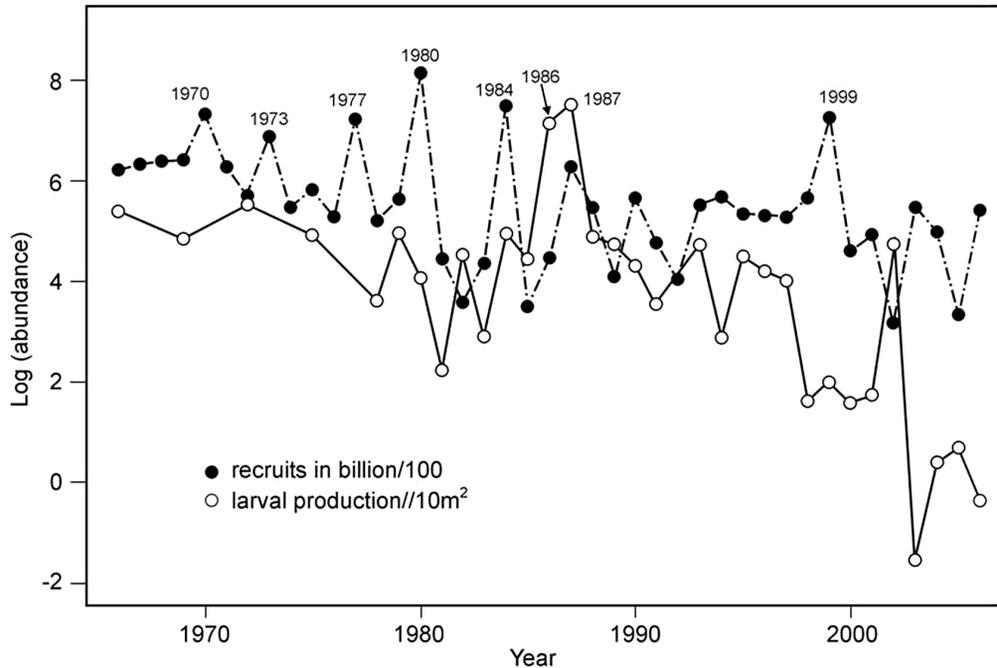


Figure 18. The time series of log (Pacific hake larval production/10 m²) (solid line) and the log(abundance of 0 age recruits from 2006 stock assessment) (dash line) in 1966–2006

The larval indices and biomass estimates from acoustic-trawl surveys, two sets of direct observations, indicate that the Pacific hake population has been declining since the mid-1980s (figs. 13–15). The long time series of daily Pacific hake larval production, a fishery-independent population index obtained yearly, benefits the final estimate of the spawning biomass derived from the stock assessment of the Pacific hake population and improves our understanding of the dynamics of the Pacific hake population (Deriso and Quinn 1998).

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APPENDIX

The average instantaneous mortality rate (equation 7) between age t_1 and t_2 :

$$Z_t = \frac{\left(\frac{dP_t}{dt}\right)}{P_t} = \frac{\beta}{t + 1}$$

$$EZ_t = \int_{t_1}^{t_2} Z_t \frac{P_1}{\int_{t_1}^{t_2} P_t dt} dt = \int_{t_1}^{t_2} Z_t \frac{Ph(t+1)^{-\beta}}{\int_{t_1}^{t_2} P_h(t+1)^{-\beta} dt} dt = \int_{t_1}^{t_2} \beta(t+1)^{-1} \frac{(1-\beta)(t+1)^{-\beta}}{(t_2+1)^{-\beta} - (t_1+1)^{-\beta}} dt$$

and

$$E(Z_t) = (\beta-1) \left[\frac{(t_2+1)^{-\beta} - (t_1+1)^{-\beta}}{(t_2+1)^{1-\beta} - (t_1+1)^{1-\beta}} \right] \quad (\text{A1})$$

Where $P_t = P_h(t+1)^{-\beta}$