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SPAWNING BIOMASS OF THE CENTRAL STOCK OF NORTHERN ANCHOVY (*ENGRAULIS MORDAX*) ESTIMATED FROM THE DAILY EGG PRODUCTION METHOD OFF CALIFORNIA IN 2017

Emmanis Dorval¹, Beverly J. Macewicz, David A. Griffith, and Yuhong Gu¹

NOAA Fisheries
SWFSC Fisheries Resources Division
8901 La Jolla Shores Drive La Jolla, CA 92037

¹Oceans Associates Inc. (OAI)
Under contract with Southwest Fisheries Science Center OAI, 4007 N. Abingdon Street
Arlington, Virginia, 22207, U.S.A.

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EXECUTIVE SUMMARY

The 2017 daily egg production method (DEPM) survey for the Central Stock of northern Anchovy (CSNA, *Engraulis mordax*,) was conducted in March/April off California from about San Diego, California (32.55°N) to north of San Francisco, California (ending at 38.06°N, north of CalCOFI line 60). The survey covered a total area of 130,816.2 km². Northern anchovy spawned in waters ranging from 11° to 17°C, averaging 14.14°C. Eggs, larvae and adults were most abundant between 32.75°N and 34.04°N (San Diego, CA to Los Angeles, CA), indicating that the stock was mostly concentrated in the Southern California Bight (SCB) and spawning dynamics were similar to those observed in the 1980s. The survey area was stratified based on eggs collected from a Continuous Underway Fish Egg Sampler (CUFES) into an High and a Low Density regions, having egg density $>$ and ≤ 1 egg/min, respectively. The daily egg production in the High density area (20,675 km²) was estimated to be 19.30/0.05m² (CV = 0.23) using eggs and yolk sac larvae collected from Pairovet and Bongo nets. In the Low Density area, daily egg production was 0.45 eggs/0.05 m² (CV = 0.65) when estimated as a function of the ratio (defined as q) of egg density in the Low and High Density areas.

Adult parameters were estimated from 765 anchovies collected from 23 positive trawls during the survey. Trawling was conducted randomly, which resulted in sampling adult anchovy in both the High and the Low Density regions. Adult female parameters were analyzed from 256 mature females in 23 trawls (14 within the High Density region and 9 trawls within the Low Density region). The daily specific fecundity was 29.13 eggs/population weight (g)/day in the whole survey area, 41.54 in the High Density area, and 4.38 in the Low Density area.

The spawning biomass of the CSNA in April 2017 was estimated from the DEPM based on two methods: (1) an un-stratified method where egg production was a weighted mean of egg production estimated in the High Density area and egg production estimated in the Low Density area using the q ratio, and the adult parameters were estimated for the whole survey area; and (2) a stratified procedure where the estimate of total spawning biomass was the sum of the estimated spawning biomass in each of the two regions. Based on the un-stratified method, spawning biomass was estimated to be 308,173 mt (CV = 0.36); whereas female spawning biomass was estimated to be 171,689 (CV = 0.35) within the survey area. The estimates of spawning biomass calculated for the SCB was 152,181 mt (CV=0.43) for females and 271,752 mt (CV=0.43) for both sexes, using the stratified method. Given, the level of uncertainties associated with the computation of egg production and adult parameters in the Low Density area, biomass solely estimated in this area might be overestimated. However, egg production and stock biomass estimates from both methods were similar or within the range of estimated values for the CSNA in the 1980s, suggesting that northern anchovy may be recovering from the low period of productivity observed in the 2009-2015 period.

INTRODUCTION

Fishery independent surveys are critical for assessing and managing Coastal Pelagic Species (CPS) stocks along the North American Pacific coast. These surveys provide relative abundance indices to calibrate stock assessment and to monitor stock productivity as environmental conditions change. The Daily Egg Production method (DEPM) is a fishery-independent survey that has been used historically to assess the central stock of northern anchovy (CSNA) and the northern Pacific sardine stock in order to set harvest guidelines for annual management in the USA (Picquelle and Hewitt 1983, 1984, Hewitt 1985, Hill et al. 2016). The DEPM was originally developed by Lasker (1985) to estimate the spawning stock biomass of northern anchovy (*Engraulis mordax*) based on growth, mortality and abundance of eggs and larvae, and the adult reproductive biology of this species. The basic DEPM approach outlined by Lasker (1985) primarily consisted in: (1) calculating the daily egg production from ichthyoplankton survey data; (2) computing the reproductive parameters of females from adult fish samples; and (3) calculating the biomass of spawning adults.

The CSNA has been assumed to range from north of San Francisco Bay to Punta Baja (Figure 1) in northern Baja California (McCall and Methot 1983, Fielder et al. 1986), and to primarily spawn in the southern California Bight (SCB) in winter and spring (Fielder et al. 1986, Hedgecock et al. 1994). Throughout the 1970s and 1980s the stock supported one of the most productive fisheries off the Pacific west coast, averaging 176,272 mt in landings from 1972 to 1987 in Mexico and the USA. However, landings declined from 104,292 mt in 1987 to only 3,000 mt in 1994, mainly because anchovy were not available to the Mexican fishery and quotas for the reduction fishery in the US were set to zero starting in 1988. The CSNA was last fully assessed in 1995, when spawning biomass was estimated to be 388,000 mt based on five abundance indices, including egg production (Jacobson et al. 1995). Since the 2000s, under Amendment 8 of the CPS Fishery Management Plan (FMP) the CSNA has been managed as a monitored species, focusing mostly on monitoring fishery landings. During the last two decades off California, the DEPM was solely applied to assess the spawning stock of Pacific sardine and to tune integrated stock assessment models (Barnes et al. 1997, Lo et al. 2004, 2013, Dorval et al. 2014, 2016).

In absence of a formal DEPM survey on northern anchovy, various approaches have been developed to monitor stock productivity and estimate spawning biomass for this species. Fissel et al. (2011) used mean of egg and larval density from CalCOFI surveys to compute egg production and SSB, showing continued decline of anchovy stock off California from 1995 to 2010. McCall et al. (2016) revised Fissel et al. (2011) methods, by computing egg production based on mean egg density weighted by area, because CalCOFI inshore stations were more closely spaced and hence were effectively over-weighted in previous analyses. As a result McCall found that stock declines were more severe than predicted by Fissel et al. (2011). However, both Fissel et al. (2011) and McCall et al. (2016) computed SSB, using historical reproductive data (i.e. prior to 1995) and assuming northern anchovy daily specific fecundity has remained constant over the last two decades. This assumption may not be appropriate for estimating biomass of small pelagic species, such as anchovy, because adult reproductive parameters highly fluctuate from year to year. Indeed, extending the

McCall et al. (2016) analysis (currently known as *DEPM-light*) to CalCOFI data collected up to 2015, the SWFSC (2016) found that although trends in egg production were similar, these data were not adequate for quantifying anchovy biomass. Given uncertainties and bias associated with the “*DEPM-light*” approach, a 2016 Review Panel recommended “using year-specific” biological data, i.e. a full DEPM to estimate anchovy biomass in the future (SWFSC-PFMC 2016). The panel also noted that area-specific adult parameters might improve stock size estimates, due to current differences in fecundity at age and the ontogenetic distribution of fish at age and at size.

Sampling and statistical methods have also evolved since the last formal northern anchovy DEPM. Prior to 1996, egg production was estimated from CalCOFI Vertical Egg Tow (CalVET) plankton net samples; whereas adult fish were collected using various methods to estimate batch fecundity, spawning fraction, sex ratio, and average female fish weight (Wolf 1988a, 1988b; Scannell et al. 1996; Macewicz et al. 1996; Lo et al. 1996). Since 1996, a Pairovet net has been used to collect eggs, but using only one net during sampling and hence making this gear operate like a CalVET. In addition to Pairovet, a Continuous Underway Fish Egg Sampler (CUFES) has been used to collect CPS eggs (Checkley et al. 1997) in the upper 3 m of surface water. During the 1997 sardine DEPM survey, CUFES was used to allocate Pairovet tows in an adaptive sampling design (Hill et al. 1998, Lo et al. 2001). From 1998 to 2000, data on sardine eggs collected with both Pairovet and CUFES during each California Cooperative Oceanic Fisheries Investigations (CalCOFI) spring (April) cruise were used to estimate daily egg production (Hill et al. 1999). Starting in 2001, a cost-effective alternative was adopted to calculate the DEPM index that reduced effort in calculation and egg staging of the CUFES collections. In the new procedure, CUFES data are used for stratification and ichthyoplankton samples for egg production estimation. Since 2009, in addition to the estimates of spawning biomass based on the past procedure (i.e., where egg production was weighted by the size of each region and the adult parameters were estimated from all trawl samples in the entire survey area), an alternative estimator based on stratified sampling for each parameter was also included (Hill et al. 2009, 2010) for years when adequate adult samples were available. Finally, since 2006, an acoustic survey has been conducted simultaneously with the sardine DEPM to provide a total biomass index for CPS stock assessments (Hill et al. 2016).

The 2017 northern Anchovy DEPM survey was designed to sample from San Diego up to north of San Francisco California. Here, we describe methods of survey and data analyses, and report on the estimation of egg production, spawning biomass, female spawning biomass, and associated life history parameters. We used both the traditional method (with no stratification) and post-stratification of the sampling frame to analyze these data for a year-specific biomass estimation.

MATERIALS AND METHODS

Data

The spring 2017 CPS-Anchovy DEPM survey was conducted aboard the NOAA ship *Reuben Lasker* (March 21 – April 22). The *Lasker* covered the area off California from about San Diego, CA (32.55°N) to north of San Francisco, CA (ending at 38.06°N, north of CalCOFI line 60) (Figures 2 and 3). During the DEPM survey, Pairovet tows, Bongo tows, CUFES and surface trawls were conducted.

All ichthyoplankton tows follow specific protocols developed within the CalCOFI program and are conducted as follows: (1) Pairovet tows are fished vertically from 70 meters depth to the surface at a retrieval rate of 70 m per minute. The mesh size of the net body and the codend are 150 μm and the frame opening diameter is 25 cm. Water flow through the net opening is measured using a GO mechanical flowmeter; (2) Bongo tows consist of paired 71 cm rings connected by a central swivel. With depth permitting, the Bongo nets fish from a depth of 210 m through an oblique trajectory. The paired nets have a mesh size of 505 μm and the codends have a 333 μm mesh. The amount of water strained during a tow is measured by a GO mechanical flowmeter. For a more detailed description please refer to Smith and Richardson (1977) and McClatchie (2014).

In addition to anchovy eggs and yolk-sac larvae collected with the Pairovet net, yolk-sac larvae collected with the Bongo net were included to model the anchovy embryonic mortality curve. As in Lo (2001), CUFES data from the ichthyoplankton surveys were only used to map the spatial distribution of the anchovy spawning population and to post-stratify the survey area into high egg-density (High Density) and low egg-density (Low Density) regions. Staged eggs from Pairovet tows and yolk-sac larvae from Pairovet and Bongo tows in the High Density area were used to model embryonic mortality in the High Density area and the daily egg production, P_0 , for the whole survey area.

The survey began at the southernmost transect and effectively occupied 25 transect lines from the south to the north from March 21 to April 22. Hence, the whole DEPM survey area was located between 32.55°N (south of CalCOFI line 93) and 38.06°N (north of CalCOFI line 60) (Figures 2 and 3). The first 4 transects were spaced 10 nautical mile apart, allowing the identification of the southern boundary of the egg distribution. Once, the southern boundary was established, transect spacing was increased as much as 20 nautical miles to save time and cover a broader area of the coast. Pairovet tows were taken at 5-nm intervals on each line after the egg density from a CUFES sample met or exceeded 1 egg/min, and Pairovet tows were stopped after the egg density a CUFES sample was less than 1 egg/min. This adaptive allocation sampling was similar to that used in the 1997 sardine survey (Lo et al. 2001).

In 2017, the whole DEPM survey area (130,816.2 km²) extended from San Diego, CA (32.55°N) and to north of San Francisco, CA (38.06°N). The whole DEPM survey area was post-stratified in two regions: a High Density region and a Low Density region. The High Density area was located between 32.75°N and 34.04°N (San Diego, CA to Los

Angeles, CA), where the egg density in CUFES collections was greater than 1 egg per minute. The High Density area was estimated to be 20,675.2 km², whereas the Low Density area was estimated to be 110,141 km² (Table 1, Figure 3). The sizes of all surveyed areas were computed after a 2.5 nautical mile expansion (i.e. half of the distance between CUFES samples) from survey line or station, using the “*Projections and Transformations Tools*” of the ArcGIS software program (Version 10.4). A total of 492 CUFES samples were collected by *Lasker* over the whole survey area. CUFES sampling intervals ranged from 3 to 68 minutes with a mean of 30.50 minutes and a median of 30 minutes depending on egg densities observed onboard. The total number of Pairovet tows was 126 for the entire survey area (Table 1).

For adult samples, 2-4 trawls were conducted per night either in areas where day-time acoustic detected CPS schools or at random sites on the survey line regardless of the presence of anchovy eggs in CUFES collections. At night a Nordic 264 rope trawl with 3.0 m² foam core doors was towed for 45 minutes at the surface (0 – 11 meters). The trawl was modified for surface trawling with Polyform floats attached to the head rope and trawl wings. The trawl was modified with a marine mammal excluder device placed midsection just forward of the codend. For the whole CPS-Anchovy DEPM survey, trawling occurred from March 21 to April 21, 2017 and 23 of the 61 trawls conducted at night were positive for northern anchovy (Table 1, 2, Figure 3).

All anchovy were processed if a trawl catch contained less than 76 anchovy. Otherwise 50 anchovy were randomly sampled from each positive trawl (Table 2). After the random subsample, additional mature females were randomly processed, if necessary, from the trawl catch to obtain 25 mature females per trawl for reproductive parameters or to obtain females for use in estimating batch fecundity. Each fish was sexed, standard length (mm) and weight (g) were measured, otoliths were removed for aging, tissue was preserved in 95% ethanol for genetics, and ovaries were removed and preserved in 10% neutral buffered formalin. Each preserved ovary was blotted and weighed to the nearest milligram in the laboratory. Ovary wet weight was calculated as preserved ovary weight times 0.98 less 0.006g (Dorval et al., unpublished data). A piece of each ovary was removed and prepared as hematoxylin and eosin (H&E) histological slides. All slides were analyzed for oocyte development, atresia, and postovulatory follicle age to assign female maturity and reproductive state (Macewicz et al. 1996).

Daily egg production (P0)

The 2017 DEPM estimates were based on egg and larval data collected from March 21 to April 22 between San Diego and San Francisco, CA. These estimates were computed for the Low and High density regions. We defined the sampling unit to be a station. Anchovy eggs from Pairovet tows and anchovy yolk-sac larvae from both Pairovet and Bongo tows in the High Density region were aggregated to estimate egg production, primarily based on data from 7 transects (Figures 2 and 3). In the High Density region, 51 Pairovet and 17 Bongo samples were collected. All bongo tows were positive and only 4 Pairovet tows were negative in this region (Table 1). These eggs were examined for their developmental stages following similar methods as in Moser and Ahlstrom (1985). In the

Low Density region, 36 out of 75 Pairovet tows caught anchovy eggs.

Based on laboratory counts of anchovy eggs in CUFES samples, 156 of the 492 collections were positive for northern anchovy eggs over the survey area. In the High Density area, 109 collections were taken, including 100 positive tows. In the Low Density region, 56 of the total 383 collections were positive (Table 1).

To model the embryonic mortality curve we included yolk-sac larvae, assuming that the mortality rate of yolk-sac larvae was the same as that of eggs (Lo 1986). In this study, yolk-sac larval abundance included individuals up to the development of the functional jaw, preserved larvae ≤ 4.25 mm notochord length (Zweifel and Lasker 1976). Larval size shrinkage due to preservation was approximated to be $\leq 5\%$ (Pers. Comm. William Wastson), which would have minor effect on the size of anchovy yolk-sac larvae, and thus no correction was performed. Yolk-sac larval production was computed as the number of yolk-sac larvae per 0.05m^2 of sea surface area divided by the duration of the yolk-sac stage (number of larvae/ $0.05\text{m}^2/\text{day}$). Duration was computed using pre-hatch growth parameters estimated by Zweifel and Lasker (1976, Table 6) and in Lo (1983, Table 1) for each tow. For yolk-sac larvae caught by the Bongo net, larval abundance was further adjusted for size-specific extrusion from 0.505 mm mesh (Table 7 of Lo 1983) and for the percent of each sample that was sorted. The adjusted yolk-sac larvae/ 0.05m^2 was then computed for each tow and termed daily larval production/ 0.05m^2 .

In the whole survey area, 56 of 126 Pairovet and 45 of 76 Bongo samples had at least one yolk-sac larva. In the High Density region, 40 of 51 Pairovet tows and all 17 Bongo samples were positive for yolk-sac larvae (Figures 2, 3).

Daily egg production in the High Density region ($P_{0,1}$)

Anchovy eggs and yolk-sac larvae and their ages were used to construct an embryonic mortality curve (Lo et al. 1996). Pelagic egg samples are typically comprised of various groups of eggs of different stages representing several days of spawning, and the age to reach these developmental stages is temperature dependent (Lasker 1985, Lo et al. 1996). A data entry error was corrected in Lo et al. (1985, Table 1), because the age of stage-4 eggs at 20.8°C should have been reported as 19 h instead of 1.9 h (see Zweifel and Lasker, 1976). As result the temperature-dependent stage-to-age model (Lo et al. 1985) was updated using the equation below:

$$y_{i,t} = 13.78 \times e^{-(0.107t + 0.101i)} \times i^{1.789} \quad [1]$$

where, t is the age and i the stage of individual eggs.

Equation 1 was used to assign age to egg stages, and to compute anchovy egg density for each stage based on Pairovet samples. Anchovy eggs and estimated ages were used directly in nonlinear regression. Eggs ≤ 3 h old and eggs older than 2.5 days were excluded because of possible bias. The average sea surface temperature for all Pairovet tows collected by the *Lasker* was 14.15°C (CV = 0.09).

The anchovy embryonic mortality curve was modeled by an exponential decay curve (Lo et al. 1996):

$$P_t = P_0 \times e^{-z \times t} \quad [2]$$

where P_t is eggs/0.05m²/day from Pairovet tows or yolk-sac-larvae/0.05m²/day from Pairovet and Bongo tows, t is the age (days) of eggs or yolk-sac larvae from each tow and z is the daily instantaneous mortality rate. One tow, collected on CalCOFI line 84.1 and station 48.4, contained unusually high number of eggs ($n = 384$, including 290 stage 3 eggs). This sample was considered as an extreme outlier, as it was 6.5 times of the standard deviation (SD) of the number of eggs collected per tow in the High Density area by the Pairovet net. Therefore, this observation was dropped from the computation of egg production in the High Density area. A weighted nonlinear regression was used to estimate two parameters in equation (1), where the weights were 1/SD. After excluding the outlier, the standard deviation (SD) of eggs caught in Pairovet samples was 12.07, 18.87, and 9.42 for day-one, day-two and day-three age groups respectively. The SD for yolk-sac larvae collected in Pairovet and Bongo nets was 6.03 and 0.08, respectively.

A simulation study (Lo 2001) indicated that $P_{0,1}$ computed from a weighted nonlinear regression based on the original data points has a relative bias (RB) of -0.04 from the estimate, where $RB = (\text{mean of 1,000 estimates} - \text{true value})/\text{mean of 1,000 estimates}$. Therefore, the bias-corrected estimate of egg production in the High Density region was calculated as:

$$P_{0,1,c} = P_{0,1} \times (1 - RB) = P_{0,1} \times 1.04, \text{ and } SE(P_{0,1,c}) = SE(P_{0,1}) \times 1.04.$$

Daily egg production in the Low Density region ($P_{0,2}$)

Although 75 Pairovet samples were collected in the Low Density region (Table 1), only 36 tows had one or more anchovy eggs or yolk sac larvae (Figure 3). In this region the maximum number of eggs caught by tow was 117, whereas catches of yolk sac larvae ranged from 1 to 23 larvae per positive tow. We estimated daily egg production in the Low Density region ($P_{0,2}$) based on two methods:

(1) the product of the bias-corrected egg production in the High Density region ($P_{0,1,c}$) and q (the ratio of egg density in the Low Density region to the High Density region from CUFES samples) assuming the catch ratio of eggs/min from CUFES to eggs/tow from Pairovet was the same for the whole DEPM survey area:

$$P_{0,2,d} = P_{0,1,c} \times q \quad [3]$$

$$q = \frac{\sum_i \frac{\bar{x}_{2,i} \times m_i}{\bar{x}_{1,i}}}{\sum_i m_i} \quad [4]$$

$$var(q) = \frac{\frac{n}{n-1} \times \sum_i m_i^2 \times (q_i - q)^2}{(\sum_i m_i)^2}$$

where q is the ratio of eggs/min between the Low and High Density areas, m_i was the total CUFES time (minutes) in the i^{th} transect, $\bar{x}_{j,i}$ is mean eggs/min of the i^{th} transect in the j^{th} Region, and

$q_i = \frac{\bar{x}_{2,i}}{\bar{x}_{1,i}}$ is the catch ratio in the i^{th} transect, and d indicated that the estimate is dependent on egg production estimated in the High Density area and q . The estimates of q were computed from a total of 7 transect lines occupied by the *Lasker* in the High Density region.

(2) Eggs and larvae collected in the low density area were used to derive a separate mortality curve, upon which egg production was independently estimated from $P_{0,1}$ and labeled $P_{0,2,i}$.

Daily egg production (P_0) in the whole survey area

For the stratification method, daily egg production in the whole DEPM area (P_0) was computed as the weighted average of $P_{0,1}$ and $P_{0,2}$:

$$P_0 = \frac{P_{0,1,c} \times A_1 + P_{0,2,d} \times A_2}{A_1 + A_2} \quad [5]$$

$$= P_{0,1,c} \times w_1 + P_{0,2,d} \times w_2$$

$$= P_{0,1,c}(w_1 + q \times w_2), \text{ and}$$

$$mse(P_0) = mse(P_{0,1,c})(w_1 + w_2 q)^2 + (P_{0,1,c})^2 (w_2)^2 V(q) - mse(P_{0,1,c})(w_2)^2 V(q) \quad (\text{Goodman 1960})$$

$$\text{where } mse(P_{0,1,c}) = V(P_{0,1}) + bias^2 = V(P_{0,1}) + (P_{0,1} RB)^2, \text{ and}$$

$$w_i = \frac{A_i}{A_1 + A_2}, \text{ with } A_i \text{ equal to the area size for } i = 1 \text{ or } 2 \text{ for the DEPM survey area.}$$

The above P_0 was computed for the whole survey area between San Diego, CA (32.55°N) to North of San Francisco, California (38.06°N). The size of the survey area is 130,816.2 km². The total egg production (TEP) is the numerator of equation 5 or it is equal to $P_0 \times (A_1 + A_2)$.

Adult parameters

Four adult parameters are needed to estimate spawning biomass: (1) daily spawning fraction or the number of spawning females per the total number of mature females per day (S); (2) the average batch fecundity (F); (3) the proportion of mature female fish by weight (sex ratio, R); and (4) the average weight of mature females (g, W_f). Population values for S , R , F and W_f were estimated using the methods of Picquelle and Stauffer (1985). Daily specific fecundity (number of eggs per population weight (g) per day) is $(RSF)/W_f$. The trawls and their captured anchovy females were stratified by the Low Density and High Density regions. The parameters were estimated for each area. In addition, all females were pooled and parameter estimates were calculated for the unstratified (whole) survey DEPM area. An MS¹ Visual Basic program (Chen et al. 2003) was modified to more accurately describe batch fecundity variance and was used to summarize the trawl adult parameters, calculate adult parameter correlations and covariance, and estimate spawning biomass and its coefficient of variation.

Spawning fraction (S): In total, 256 mature female sardines were analyzed and considered to be a random sample of the population in the whole DEPM survey area. Histological criteria was used to identify spawning. Identification of postovulatory follicles aged about 20 – 30 hours old indicated spawning the night before capture, while hydrated oocytes or new (without deterioration) postovulatory follicles indicated a female spawning the night of capture. The number of females identified as having spawned the night before capture, plus the adjusted number of mature females caught in each trawl (Table 2) was used to estimate the population spawning fraction (S) and variance (Picquelle and Stauffer 1985). Estimates of females spawning the night of capture were calculated for comparisons.

Batch fecundity (F): Batch fecundity (number of oocytes per spawn) was considered to be the number of migratory-nucleus-stage oocytes or the number of hydrated oocytes in the ovary (Hunter et al., 1985). We used the gravimetric method (Hunter et al. 1985, 1992; Macewicz et al. 1996) to estimate mean batch fecundity for 13 females from the survey. The relationship of batch fecundity (F_b) to female weight (without ovary, W_{of}), as determined by simple linear regression, was:

$$F_b = -4455 + 989.4 \times W_{of} \quad [6]$$

The variance of the slope of equation 6 was 47917.21, and W_{of} ranged from 13.2 to 21.8 g (Figure 4). The intercept did not significantly differ from zero ($p = 0.23$). To compute batch fecundity for each of the 256 mature northern anchovy females that were analyzed to estimate spawning frequency, we need to account for the deviation of batch fecundity from the regression line. An error term was added to the predicted values of equation 6 by resampling the residuals, assuming they were randomly distributed with mean equal to zero.

¹ Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Female weight (W_f): The observed female weight was adjusted downward for females with hydrated ovaries, because their ovary weights were temporarily inflated. We obtained the adjusted female weight by the linear equation below:

$$W_f = -0.319 + 1.08 \times W_{of} \quad [7]$$

where W_f is wet weight and W_{of} is ovary-free wet weight based on data from non-hydrated mature females taken during the DEPM survey.

Sex ratio (R): The female proportion by weight was determined for each trawl (or each collection). The average weight of males and females (calculated from the first 10 males and 15 females) was multiplied by the number of males or females in the collection of randomly selected fish to calculate total weight by sex in each collection. Thus, the female proportion by weight in each collection (Table 2) was calculated as estimated total female weight divided by estimated total weight in the sample. The estimate of the population's sex ratio by weight was also calculated (Picquelle and Stauffer, 1985).

Spawning biomass (B_s)

The spawning biomass was computed as:

$$B_s = \frac{P_0 \times A \times C}{\frac{R \times S \times F}{W_f}} \quad [8]$$

where A is the survey area in units of 0.05m^2 , S is the fraction of mature females spawning per day, F is the batch fecundity (number of eggs per mature female released per spawning event), R is the fraction of mature female fish by weight (sex ratio), W_f is the average weight of mature females (g), and C is the conversion factor from grams (g) to metric tons (mt). P_0A is the total daily egg production in the whole DEPM survey area, and the denominator (RSF/W_f) is the daily specific fecundity (number of eggs/population weight (g)/day).

The variance of the spawning biomass estimate (\hat{B}_s) was computed using Taylor expansion and in terms of the coefficient of variation (CV) for each parameter estimate and covariance for adult parameter estimates (Parker 1985):

$$\text{VAR}(\hat{B}_s) = \hat{B}_s^2 [CV(\hat{P}_0^2) + CV(\hat{W}_f^2) + CV(\hat{S}^2) + CV(\hat{R}^2) + CV(\hat{F}^2) + 2COVS] \quad [9]$$

The last term on the right hand side of equation 9 includes the covariance term, and it is expressed as:

$$COVS = \sum_i \sum_{i < j} sign \frac{COV(x_i, x_j)}{x_i, x_j}$$

where x 's are the adult parameter estimates, and subscripts i and j represent different adult parameters, e.g., $x_i = F$ and $x_j = W_f$. The sign of any two terms is positive if they are both in the numerator of B_s or denominator of B_s (equation 8); otherwise, the sign is negative. The covariance term is:

$$COV(x_i, x_j) = \frac{n}{n-1} \times \frac{\sum_k m_k (x_{i,k} - x_i) \times g_k \times (x_{j,k} - x_j)}{(\sum_k m_k) \times (\sum_k g_k)}$$

where k refers to k^{th} tow, and $k = 1, \dots, n$. The terms of m_k and g_k are sample sizes and $x_{i,k}$ and $x_{j,k}$ are sample means from the k^{th} tow for x_i and x_j respectively.

Equation 8 can be applied to the whole survey area and/or to each of the two regions. For the female spawning biomass, the sex ratio (R) was excluded from equations (8) and (9). The stratified estimate of spawning biomass was the sum of the estimates from the Low and High Density areas. We computed stratified estimates for the whole survey area and for the SCB. The un-stratified estimate of spawning biomass used the estimated value of P_0 (equation 5) for the whole area, and all females were pooled to estimate each of the adult parameters.

RESULTS

Egg density from Pairovet

The stages of northern anchovy eggs collected from Pairovet ranged from 1 to 11 (Figure 5). Egg development stage definitions follow those described by Ahlstrom (1943) and Moser and Ahlstrom (1985): Stage 1 are newly spawned eggs with no cell divisions, and stage 11 is the final stage before hatching and is defined by a tail length greater than three-quarters of the length of the yolk sac. The distribution of mean egg density by egg developmental stage showed one major peak at stage 3. In the High Density area, the abundance of stages 1, 2, 4, 8 and 11, was low (0.1- 0.8 eggs/0.05m²), whereas catches of stages 5, 6, 7, 9, and 10 were generally moderate (2-4 eggs/0.05m²). Egg density-at-stage in the whole survey area had similar trends to the High Density region (Figure 5). The maximum number of eggs caught per Pairovet tow during the survey was 384, which was excluded from the computation of egg production below. Finally, the average sea surface temperature computed for Pairovet tows with ≥ 1 egg in the survey area was 14.14°C. This estimate was weighted by the number of eggs caught in each positive tow.

Daily egg production (P_0) for the survey area

In the High Density region, the initial daily egg production ($P_{0,1}$) estimated from the mortality curve was 18.56/0.05 m²/day (CV = 0.24). Mortality rate estimate in this area was 1.04 (CV = 0.16) (Figure 6A). After bias correction, the egg production, ($P_{0,1,c}$) was computed to be 19.30 (CV = 0.23) for an area of 20,675 km². The ratio q , the calibration factor to estimate the egg production ($P_{0,2,d}$) in the Low Density area, was 0.023 (CV = 0.62). Therefore, $P_{0,2,d}$ was estimated to be 0.45 (CV = 0.65) for the Low Density area. Egg production, P_0 , for the whole survey area was 3.43/0.05m² (CV = 0.24) for 130,816 km².

In the Low Density region, the independent estimate of egg production ($P_{0,2,i}$) was estimated to be 1.87 (CV = 0.61), but was highly not significantly different than 0 ($p = 0.10$). Mortality rate was estimated to be 1.16 (CV = 0.32) for this region (Figure 6.B). Given the level of significance of $P_{0,2,i}$, it cannot be used in the process of estimating biomass, and hence it will be dropped in any further analyses. Therefore, $P_{0,2,d}$ will be used to compute biomass for the Low Density area.

Adult parameters

In the whole DEPM survey area, northern anchovy were found in 23 tows (Figure 2, Table 1). Mature female anchovy were caught in 22 tows (Table 2). Standard length (SL) of the 765 randomly obtained sardines in each trawl ranged from 83 to 130 mm for 352 males, from 85 to 137 mm for 411 females, and was 80 and 134 mm for two fish of unknown sex (Figure 7). The smallest mature female was 89 mm SL. Since 18 immature female anchovy (size range 85 to 116 mm SL) were captured, the length at which 50% of females are mature (ML_{50}) was estimated to be 96.9 mm (Figure 8) using logistic regression (Macewicz et al. 1996, Lo et al. 2005).

Estimates of reproductive parameters of northern anchovy for the individual trawls (a maximum of 15 mature females were analyzed per trawl) are given in Table 2. The estimates of each adult parameter were stratified by the High Density and Low Density areas (Table 3). The mature female anchovy reproductive parameters in the un-stratified DEPM area, estimated from 22 positive trawls (Table 2) and 256 mature females, were F , mean batch fecundity, 10187 eggs/batch (CV = 0.08); S , fraction spawning per day, 0.082 females spawning per day (CV = 0.25); W_f , mean female fish weight, 15.9 g (CV = 0.03); and R , sex ratio of females by weight, 0.557 (CV = 0.07) (Table 3). The average interval between spawning events (spawning frequency) was about 12 days (*i.e.*, the inverse of spawning fraction), and the daily specific fecundity was 29.13 eggs/population weight (g)/day (Table 4).

Spawning biomass (B_s)

The final estimate of spawning biomass of the CSNA in 2017 using the un-stratified method (Equation 2 and 5) was 308,173 mt (CV = 0.36) for the whole DEPM survey area. Based on the stratified procedure, the estimate of the 2017 spawning biomass was

419,218 (CV = 0.70). The estimate of the female spawning biomass was 171,689 mt (CV = 0.35) and 238,877 mt (CV = 0.69) based on the un-stratified procedure and the stratified methods, respectively (Table 4). Stratified spawning biomass estimated for the SCB were 152,181 mt (CV = 0.43) for females, and 271,752 mt (CV = 0.43) for both sexes.

DISCUSSION

Egg distribution and production

The distribution of northern anchovy eggs was mostly concentrated in the SCB, between San Diego and Los Angeles (Figure 2), although low to moderate abundance of eggs were observed up to San Francisco Bay. Abundance of eggs caught in Pairovet ranged from 0 to 384 per tow, which was consistent with historical patchiness observed in anchovy egg distribution within the SCB. However, the tow with the maximum number of eggs was removed from the computation of egg production (see method section) to reduce the risk of overestimating egg production, and consequently spawning biomass. This level of egg density ($384/0.05\text{m}^2$) might have resulted from localized physical events (e.g. eddies) that could have concentrated anchovy eggs in a small area (Pers. Comm., William Watson). Therefore, it was not likely to be representative of the overall expectation of egg density in the High Density area. Anchovy eggs were also mostly distributed in nearshore waters between longitude 117.78°W and 120.46°W . The closest station sampled by the DEPM survey was 0.82 km from shore and the farthest was 152.57 km offshore. Analyses of CalCOFI survey data collected in March and April 2017 showed that only 4 CUFES samples caught eggs west of the DEPM High Density region (Appendix I). During the DEPM and CalCOFI very few CUFES samples were positive below line 92.4. These data indicated that spawning was not significant west and south of the whole DEPM survey area, and that most of the spawning stock was located off southern California.

The temperature-at-catch of Pairovet eggs indicated that anchovy spawned in waters from 11° to 17°C , with a mean of 14.14°C . In the 1980s, the northern range of anchovy spawning was found to be highly correlated with the 14.5°C isotherm, although no correlation was observed with the southern boundary of spawning (Lasker et al. 1981, Picquelle and Hewitt 1983, and Hewitt 1985). During the 2017 survey, the DEPM High Density area was mostly located between the 13° and 14°C isotherms in the north, with some spawning occurring up to the 15°C isotherm in the south (Figure 3). These results indicated that in 2017 spawning took place in closely similar environmental conditions as in the 1980s.

The daily egg production rate over the whole survey area ($3.43/0.05\text{m}^2$) was within the range of productivities ($0.14\text{-}5.42 /0.05\text{m}^2$) estimated in the SCB by Hewitt (1985), although it is difficult to statistically compare these data because different sampling coverage and post stratification methods were used in the 1980s. The 1984 survey covered areas between San Francisco and Punta Baja California, Mexico. In contrast, the 2017 did not sample Mexican waters. In addition, in 2017 survey area was post-

stratified based on adaptive allocation sampling procedure, using a threshold of 1 egg/min in CUFES samples. The CUFES sampling method was not available in the 1980s.

Adult parameters and spawning biomass

The April 2017 Anchovy DEPM survey caught anchovy adults off southern California. Trawl samples occurred in areas of high and low anchovy egg densities which is beneficial to better estimate the CSNA spawning biomass.

The fraction of females spawning per day was based on females spawning the night before capture similar to the estimation procedure in the 1980's (Picquelle and Hewitt 1984, Hewitt 1985). In the High Density area 0.12 female/day (CV = 0.20) were spawning. In the Low Density area, only one female had spawned the night before capture and resulted in a high CV (1.03). As a result, spawning biomass in the Low Density area had a very high CV (1.21). The relatively high CV estimated for spawning fraction might also have been caused by the low number of females (max = 15) analyzed in each trawl for estimating adult parameters. We recommend that effort be made to increase sample sizes in future surveys so that better precision can be achieved when estimating these parameters.

Length distribution of fish collected in spring 2017 was dominated by the 120 mm size-class. Mature females from 2017 were on average 16 mm larger than those collected during the 1984 DEPM survey (Figure 7). This difference may have resulted from environmental, density-dependent or fishing effects, but more data need to be collected to evaluate these specific effects and inter-annual variability in the size distribution of mature female anchovy.

In the 2017 DEPM survey area, the estimate of spawning biomass using the traditional method (i.e. un-stratified) was 308,173 mt and was largely distributed in the SCB. Accordingly, the biomass estimate for the SCB, using the stratified method was 271,752 mt. However, when the stratified method was applied to the whole survey area, the biomass (419,218 mt) computed was likely overestimated. This overestimation might have resulted from the lack of adult samples north of Point Conception and the level of uncertainty associated with the estimation of egg production in the Low Density area. All transects used to compute the ratio q and to infer production in this region were located in the SCB, and thus were not representative of the whole survey area. Few Paironet samples collected north of Point conception were positive and egg density was generally very low. As a result, egg production computed independently for the Low Density area was not significantly different than zero, and so could have been assumed to be null. Hence, estimates of spawning biomass using the un-stratified method for the whole survey and the stratified method for the SCB (Table 4) probably indicated the level of productivity for the CSNA in 2017. These estimates could be therefore used as relative abundance indices. Nevertheless, spawning biomass estimated over the same area for the 1984 DEPM (304,700 mt; Hewitt 1985) was closely similar to the estimate from the un-stratified. Further, northern Anchovy spawning dynamics observed in 2017 generally supported the historical stock distribution range reported by these authors.

Regardless of the methods used, the 2017 spawning stock biomass was significantly higher than recent estimates based on the *DEPM-light* method (McCall et al. 2016). From 2009 to 2011, spawning biomass was estimated below 20,000 mt by McCall et al. (2016), using egg and larval density over the CalCOFI traditional survey area. Therefore, this report shows that the CSNA may be recovering from the low period of productivity in recent years. We recommend that more annual DEPM surveys be conducted in the future, so that a new time series of spawning biomass can be constructed to monitor the overall health of the CSNA and for potential use in stock assessment of this species off California. Future time series development will also require the application of new statistical methods to better account for spatial patterns in the distribution of northern anchovy during low and high abundance years, and hence to better compute variances for both egg production and adult parameter estimates.

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REFERENCES

- Ahlstrom E. H. 1943. Studies on the Pacific pilchard or sardine (*Sardinops caerulea*). 4. Influence of temperature on the rate of development of pilchard eggs in nature. U.S. Fish. Wildl. Serv. Spec. Sci. Rep. 23, 26p.
- Barnes J. T., M. Yaremko, L. Jacobson, N.C.H. Lo, and J. Stehly. 1997. Status of the Pacific sardine (*Sardinops sagax*) resource in 1996. US Department of Commerce. NOAA Technical Memorandum NMFS-SWFSC-237.
- Checkley D. M. Jr., P. B. Ortner, L. R. Settle, and S.R. Cummings. 1997. A continuous, underway fish egg sampler. Fish. Oceanogr. 6(2):58-73.
- Chen H., N. C. H. Lo, and B. J. Macewicz. 2003. MS ACCESS programs for processing data from adult samples, estimating adult parameters and spawning biomass using daily egg production method (DEPM). Southwest Fisheries Science Center, National Marine Fisheries Service, SWFSC Admin. Rep. La Jolla, LJ-03-14.
- Dorval E., B. J. Macewicz, D. A. Griffith, N. C. H. Lo, and Y. Gu. 2014. Spawning biomass of Pacific sardine (*Sardinops sagax*) estimated from the daily egg production method off California in 2013. NOAA Technical Memorandum NMFS-SWFSC-535.
- Dorval E., B. J. Macewicz, D. A. Griffith, N. C. H. Lo, and Y. Gu. 2016. Spawning biomass of Pacific sardine (*Sardinops sagax*) estimated from the daily egg production method off California in 2015. NOAA Technical Memorandum NMFS-SWFSC-560.
- Fielder P. C., R. D. Methot, and R. P. Hewitt. 1986. Effects of California El Niño 1982-1984 on the northern anchovy. J. Mar. Res. 44, 317-338.
- Fissel B. E., N. C. H. Lo, and S. Herrick Jr. 2011. Daily egg production, spawning biomass and recruitment for the central subpopulation of northern anchovy 1981–2009. Calif. Coop. Oceanic. Invest. Rep., 52: 116-128.
- Goodman L. A. 1960. On the exact variance of products. Journal of American Statistical Association, 55(292): 708-713.
- Hedgecock D., E. S. Hutchinson, G. Li, F. L. Sly, and K. Nelson. 1994. The central stock of northern anchovy (*Engraulis mordax*) is not a randomly mating population. Calif. Coop. Oceanic. Invest. Rep., 35:121-136.
- Hewitt R. P. 1985. The 1984 spawning biomass of the northern anchovy. Calif. Coop. Oceanic. Invest. Rep., 26:17-25.
- Hill K. T., M. Yaremko, L. D. Jacobson, N. C. H. Lo, and D. A. Hanan. 1998. Stock assessment and management recommendations for Pacific sardine in 1997. California Department of Fish and Game. Marine Region, Admin. Rept 98-5.
- Hill K. T., L. D. Jacobson, N. C. H. Lo, M. Yaremko, and M. Dege. 1999. Stock assessment of Pacific sardine for 1998 with management recommendations for 1999. California Department of Fish and Game. Marine Region, Admin. Rep. 99-4.
- Hill K. T., N. C. H. Lo, B. J. Macewicz, P. R. Crone, and R. Felix-Uraga. 2009. Assessment of the Pacific sardine resource in 2009 for U.S. management in 2010. US Department of Commerce, NOAA Technical Memorandum NMFS-SWFSC-452. 182 p.
- Hill, Kevin. T, Nancy C.H. Lo, Beverly J. Macewicz, Paul R. Crone, and R. Felix-Uraga . 2010. Assessment of the Pacific sardine resource in 2010 for U.S. Management in 2011. US Department of Commerce. NOAA Technical Memorandum NMFS-SWFSC-469.

- Hill K. T., P. R. Crone, E. Dorval, and B. J. Macewicz, 2016. Assessment of the Pacific sardine resource in 2016 for U.S. management in 2016-17. US Department of Commerce. NOAA Technical Memorandum NMFS-SWFSC-562. doi.org/10.7289/V5/TM-SWFSC-562
- Hunter, J.R, Lo N.C.H, and Leong R.J.H. 1985. Batch fecundity in multiple spawning fishes. *In* An egg production method for estimating spawning biomass of pelagic fish: Application to the northern Anchovy, *Engraulis mordax* (Lasker Eds). pp: 79-94. US Department of Commerce. NOAA Technical Report NMFS 36. 99 p.
- Hunter J. R., B. J. Macewicz, N. C. H. Lo, and C. A. Kimbrell. 1992. Fecundity, spawning, and maturity of female Dover sole *Microstomus pacificus*, with an evaluation of assumptions and precision. Fish. Bull., 90:101-128.
- Jacobson L.D., N.C.H. Lo, S.F. Jr. Herrick, and T. Bishop. 1995. Spawning biomass of the northern anchovy in 1995 and status of the coastal pelagic fishery during 1994. National Marine Fisheries Service, Southwest Fisheries Science Center Admin. Rep. LJ-95-11.
- Lasker R. 1985. An egg production method for estimating spawning biomass of northern anchovy, *Engraulis mordax*. US Department of Commerce. NOAA Technical Report NMFS 36. 99 p.
- Lasker R., J. Palaez, and R.M. Laurs. 1981. The use of satellite infrared imagery for describing ocean processes in relation to spawning of the northern anchovy, *Engraulis mordax*. Rem. Sens. of Env., 11: 439-453.
- Lo N.C.H. 1983. Re-examination of three parameters associated with anchovy egg and larval abundance: temperature dependent incubation time, yolk-sac growth rate and egg and larval retention in mesh nets. US Department of Commerce. NOAA Technical Memorandum NMFS-SWFC-31.
- Lo N.C.H. 1985. A model for temperature-dependent northern anchovy egg development and an automated procedure for the assignment of age to staged eggs. *In* an egg production method for estimating spawning biomass of pelagic fish: Application to the northern Anchovy, *Engraulis mordax* (Lasker Eds). pp: 43-50. NOAA Technical Report NMFS 36. 99 p.
- Lo N.C.H. 1986. Modeling life-stage-specific instantaneous mortality rates, an application to northern anchovy, *Engraulis mordax*, eggs and larvae. Fish. Bull., 84(2):395-406
- Lo N. C. H. 2001. Daily egg production and spawning biomass of Pacific sardine (*Sardinops sagax*) off California in 2001. National Marine Fisheries Service, Southwest Fisheries Science Center Admin. Rep. La Jolla, LJ-01-08.
- Lo N. C. H., Y. A. Green Ruiz, M. J. Cervantes, H. G. Moser, and R. J. Lynn. 1996. Egg production and spawning biomass of Pacific sardine (*Sardinops sagax*) in 1994, determined by the daily egg production method. Calif. Coop. Oceanic. Invest. Rep., 37:160-174.
- Lo N.C.H., J. R. Hunter, and R. Charter. 2001. Use of a continuous egg sampler for ichthyoplankton survey: application to the estimation of daily egg production of Pacific sardine (*Sardinops sagax*) off California. Fish. Bull. 99:554-571.
- Lo N. C. H. and B. Macewicz. 2004. Spawning biomass of Pacific sardine (*Sardinops sagax*) off California in 2004 and 1995. Southwest fisheries Science Center, National Marine Fisheries Service, SWFSC Admin. Rep. La Jolla, LJ-04-08. 30 pp.

- Lo N. C. H., B. J. Macewicz, and D. A. Griffith. 2005. Spawning biomass of Pacific sardine (*Sardinops sagax*), from 1994-2004, off California. Calif. Coop. Oceanic. Invest. Rep. 46:93-112.
- Lo N. C. H., B. J. Macewicz, and D. A. Griffith. 2013. Spawning biomass of Pacific sardine (*Sardinops sagax*) off U.S. in 2012. US Department of Commerce. NOAA Technical Memorandum NMFS-SWFSC-505.
- Macewicz B. J., J. J. Castro-Gonzalez, C. E. Coterro-Altamrano, and J.R. Hunter. 1996. Adult reproductive parameters of Pacific sardine (*Sardinops sagax*) during 1994. Calif. Coop. Oceanic. Invest. Rep. 37:140-151.
- McCall A.D., and R.D. Methot. 1983. The historical spawning biomass estimates and population model in the 1983 anchovy fishery management plan. National Marine Fisheries Service. Southwest Fisheries Science Center Admin. Rep. LJ-83-17.
- McCall A. D., Sydeman, W.J., Davison, P.C., and Thayer, J.A. 2016. Recent collapse of northern anchovy biomass off California. Fisheries Research, 175: 87-94. doi.org/10.1016/j.fishres.2015.11.013
- McClatchie S. 2014. Regional fisheries oceanography of the California Current System: the CalCOFI program. Springer. 235pp. ISBN 978-94-007-7222-9
- Moser G.H., and E.H. Ahlstrom. 1985. Staging anchovy eggs. *In* An egg production method for estimating spawning biomass of pelagic fish: application to the northern anchovy, *Engraulis mordax*, R. Lasker, ed. pp. 7-16. US Department of Commerce, NOAA Tech. Rep. NMFS 36. 99 p.
- Parker K. 1985. Biomass model for egg production method. *In* An egg production method for estimating spawning biomass of pelagic fish: application to the northern anchovy, *Engraulis mordax*, R. Lasker, ed. pp. 5-6. US Department of Commerce, NOAA Tech. Rep. NMFS 36. 99 p.
- Picquelle S. J., and R. P. Hewitt. 1983. The northern anchovy spawning biomass for the 1982-1983 California fishing season. Calif. Coop. Oceanic. Invest. Rep., 24:16-28.
- Picquelle S. J., and R. P. Hewitt. 1984. The 1983 spawning biomass of the Northern anchovy. Calif. Coop. Oceanic. Invest. Rep., 25:16-27.
- Picquelle S., and G. Stauffer. 1985. Parameter estimation for an egg production method of northern anchovy biomass assessment. *In* An egg production method for estimating spawning biomass of pelagic fish: application to the northern anchovy, *Engraulis mordax*, R. Lasker, ed. US Department of Commerce. NOAA Tech. Rep. NMFS 36. 99 p.
- Scannel C. L., T. Dickerson, P. Wolf, and K. Worcester. 1996. Application of an egg production method to estimate the spawning biomass of Pacific sardines off southern California in 1986. Southwest Fisheries Science Center, National Marine Fisheries Service, SWFSC Admin. Rep. La Jolla, LJ-96-01. 37 p.
- Smith P.E. and S.L. Richardson. 1977. Standard techniques for pelagic fish egg and larva surveys. FAO Fisheries Technical Paper No. 175. 100 p.
- Wolf P. 1988a. Status of the spawning biomass of Pacific sardine, 1987-1988. Calif. Dep. Fish. Game, Mar. Res. Div., Rep. to the Legislature 9 p.
- Wolf P. 1988b. Status of the spawning biomass of Pacific sardine, 1988-1989. Calif. Dep. Fish. Game, Mar. Res. Div., Rep. to the Legislature. 8 p.
- Zweifel J. R., and R. Lasker. 1976. Prehatch and posthatch growth of fishes - a general model. Fish. Bull. 74(3):609-621.

TABLES

Table 1. Number of positive tows of northern anchovy eggs from Pairovet, yolk-sac larvae from Pairovet and Bongo, eggs from CUFES and positive anchovy trawls^a in the High Density (eggs/min > 1) and the Low Density (eggs/min ≤ 1) regions for the *Reuben Lasker* northern anchovy DEPM survey in spring 2017.

Tows and Samples	High Density Survey Area	Low Density Survey Area	Whole Survey Area
Pairovet Total tows	51	75	126
Pairovet Positive tows	47	36	83
Pairovet Total eggs	1592	249	1841
Pairovet Total larvae	374	119	493
Bongo Total tows	17	59	76
Bongo Total positive tows	17	46	63
Bongo Positive egg tows	16	15	31
Bongo Total eggs	19,875	3024	22,899
Bongo Positive larval tows	19	44	63
Bongo Total yolk sac larvae	1307	396	1703
CUFES Total samples	109	383	492
CUFES Positive samples	100	56	156
CUFES Total eggs	19,880	392	20,272
Trawl Total tows	16	45	61
Trawl Total positive tows	14	9	23
Trawl Total N. anchovy	608	215	823
Trawl Female N. anchovy	338	126	464
Area (km ²)	20,675	110,141	130,816

^a All anchovy individuals were captured at night.

^b Egg data from the Bongo net are not used in the daily egg production (P_0) estimation.

^c Total N. anchovy were those sampled and measured: including males, females, and those of unknown sex

^d Female anchovy were those sampled and measured: including mature and immature.

Table 2. Anchovy egg density region, individual trawl information, sex ratio^a, and parameters for mature female *Engraulis mordax*, used in the estimation of the March-April 2017 spawning biomass in the DEPM sampling area off California.

Area Density	Coll. No.	Month-Day	Time	Latitude °N	Longitude °W	Temp. °C	No. of fish	Sex Ratio	Mature Females N analyzed	Body weight (g) Ave.	Weight without ovary (g) Ave.	Batch Fecundity Ave.	Adj. N ^b	Number Spawning Night of capture	Number Spawning Night before capture
Low	3749	22-Mar	22:44	33.011	-117.445	16.7	3	0.417	1	17.5	16.45	10345	1	0	0
High	3754	24-Mar	20:19	32.995	-118.673	14.8	50	0.688	15	16.39	15.45	10447	8	8	1
High	3755	24-Mar	23:45	33.076	-118.692	15.7	36	0.644	15	16.36	15.49	11478	9	7	1
High	3756	25-Mar	2:38	33.123	-118.591	16	2 ^c	0	0	0	0	0	0	0	0
High	3757	25-Mar	19:24	33.423	-118.054	16.5	50	0.503	15	14.08	13.18	7646	14	1	0
High	3758	25-Mar	22:44	33.458	-117.89	16.5	3	0.6	1	15	13.81	7062	1	0	0
High	3760	26-Mar	19:58	33.199	-118.806	15.3	50	0.611	15	15.48	14.58	10086	12	4	1
High	3761	27-Mar	0:35	33.098	-118.971	15.6	50	0.391	15	16.97	15.93	10601	17	2	4
Low	3763	27-Mar	21:19	33.668	-118.71	15.9	11	0.927	9	15.83	14.81	9284	9	1	1
High	3764	28-Mar	0:18	33.542	-118.759	16.1	50	0.864	15	15.87	14.85	10073	19	0	4
Low	3765	28-Mar	3:54	33.606	-118.594	15.9	8	0.879	7	16.64	15.3	9414	7	0	0
High	3766	28-Mar	21:00	33.145	-119.661	13.6	50	0.388	15	16.13	15.28	10920	17	0	2
High	3769	29-Mar	21:24	33.398	-119.961	13.9	50	0.358	15	19.38	18.19	12748	14	3	2
High	3770	30-Mar	1:01	33.482	-119.84	14.7	50	0.45	15	17.07	16.12	11750	16	1	2
High	3771	30-Mar	3:59	33.572	-119.705	14.7	50	0.601	15	16.33	15.49	11294	16	1	2
Low	3773	31-Mar	0:11	33.947	-118.89	14.6	3	0.4	1	15	14.67	8797	1	0	0
Low	3774	31-Mar	2:32	33.924	-118.78	13.8	50	0.384	15	11.53	11.03	6430	15	0	0
High	3775	31-Mar	23:00	33.525	-120.123	13.1	50	0.664	15	18.1	17.31	12853	13	2	0
High	3776	1-Apr	1:29	33.505	-120.27	13.3	22	0.467	10	18.6	17.51	12375	9	1	0
Low	3778	1-Apr	23:02	34.258	-119.706	14.1	50	0.523	15	11.8	11.4	7133	15	0	0
Low	3779	2-Apr	1:32	34.331	-119.734	13.9	50	0.607	15	13.4	12.93	7743	15	0	0
Low	3780	2-Apr	21:15	33.82	-120.575	12.4	25	0.696	15	16.47	15.8	10398	15	0	0
Low	3082	3-Apr	21:02	34.237	-120.807	11.5	2	1	2	17.75	16.78	11563	2	0	0
All	-	-	-	-	-	-	-	-	256	-	-	-	245	31	20

^a Sex ratio, proportion of females by weight, based on average weights from subsamples and number of fish sampled in each trawl (Picquelle and Stauffer 1985).

^b Mature adjusted by the number of females spawning the night before capture

^c Only male(s) captured

Table 3. Estimated adult parameters for each area during the 2017 DEPM survey.

Area	Parameter	Mean	Variance	CV
Whole	W_f	15.91	0.2264	0.03
Whole	W_{of}	15.04	0.1925	0.03
Whole	F	10187	731573	0.08
Whole	S (night of capture)	0.121	0.0015	0.32
Whole	S (night before capture)	0.082	0.0004	0.25
Whole	R	0.557	0.0014	0.07
Whole	N trawls	22	-	-
High Density	W_f	16.66	0.1662	0.02
High Density	W_{of}	15.72	0.15089	0.02
High Density	F	10962	528468	0.07
High Density	S (night of capture)	0.17	0.0026	0.3
High Density	S (night before capture)	0.115	0.0005	0.2
High Density	R	0.548	0.0021	0.08
High Density	N trawls	13	-	-
Low Density	W_f	14.23	0.7029	0.06
Low Density	W_{of}	13.55	0.5995	0.06
Low Density	F	8483	1418251	0.14
Low Density	S (night of capture)	0.012	0.0002	1.03
Low Density	S (night before capture)	0.012	0.0002	1.03
Low Density	R	0.588	0.0037	0.1
Low Density	N trawls	9	-	-

Table 4. The 2017 spawning biomass related parameters: daily egg production/0.05m² (P_0), daily mortality rate (z), survey area (km²), daily specific fecundities: (RSF/W), and (SF/W); s. biomass, female spawning biomass, total egg production (TEP) and mean sea surface temperature for Pairovet tows.

Year	Month	Area (Density)	$P_0/0.05m^2$ (cv)	Z (CV)	RSF/W	FS/W	Area (km ²)	S. biomass (cv)	S. biomass females (cv)	Total egg production (TEP)	Temp.(°C) for positive eggs	Temp. (°C) from all
2017	Mar-Apr	¹ High	19.30(0.23)	1.04(0.16)	41.54	75.74	20675	192170(0.32)	105395(0.31)	79.8*10 ¹¹	-	-
2017	Mar-Apr	² Low _{whole}	0.45(0.65)	-	4.38	7.45	110141	227048(1.26)	133482(1.21)	9.9*10 ¹¹	-	-
2017	Mar-Apr	Stratified (Sum _{whole})	-	-	-	-	130816	419218(0.70)	238877(0.69)	89.7*10 ¹¹	-	-
2017	Mar-Apr	³ Low _{SCB}	0.45(0.65)	-	4.38	7.45	38605	79582 (1.26)	46786(1.21)	3.5*10 ¹¹	-	-
2017	Mar-Apr	Stratified (Sum _{SCB})	-	-	-	-	59280	271752(0.43)	152181(0.43)	83.3*10 ¹¹	-	-
2017	Mar-Apr	⁴ Unstratified (whole)	3.43(0.24)	-	29.13	52.28	130816	308173(0.36)	171689(0.35)	89.7*10 ¹¹	14.14	14.15

¹ High Density area is based on CUFES samples greater than 1 egg/min.

²Low_{whole} is the Low Density area for the whole survey.

³Low_{SCB} is the Low Density area for the Southern California Bight (SCB).

⁴ P_0 is the weighted average with area as the weight; and trawl samples were pooled to estimate daily specific fecundities.

FIGURES

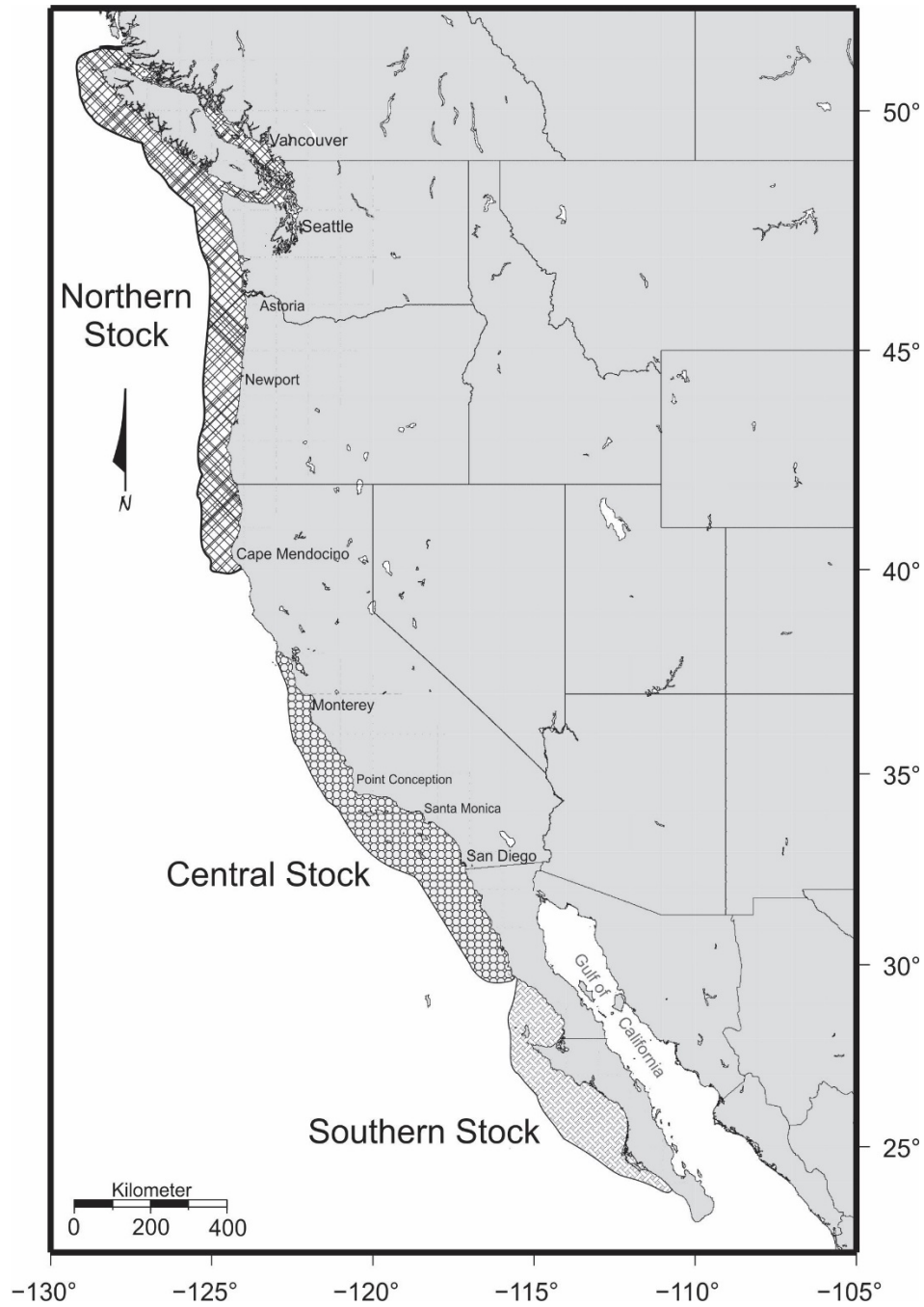


Figure 1. Map showing the approximate geographic distribution of the northern stock (crosshatched area), the central stock (opened circle area) and the southern stock (basketweave area) of northern anchovy from Baja California (Mexico) to British Columbia (Canada), as hypothesized in Fielder et al. 1986.

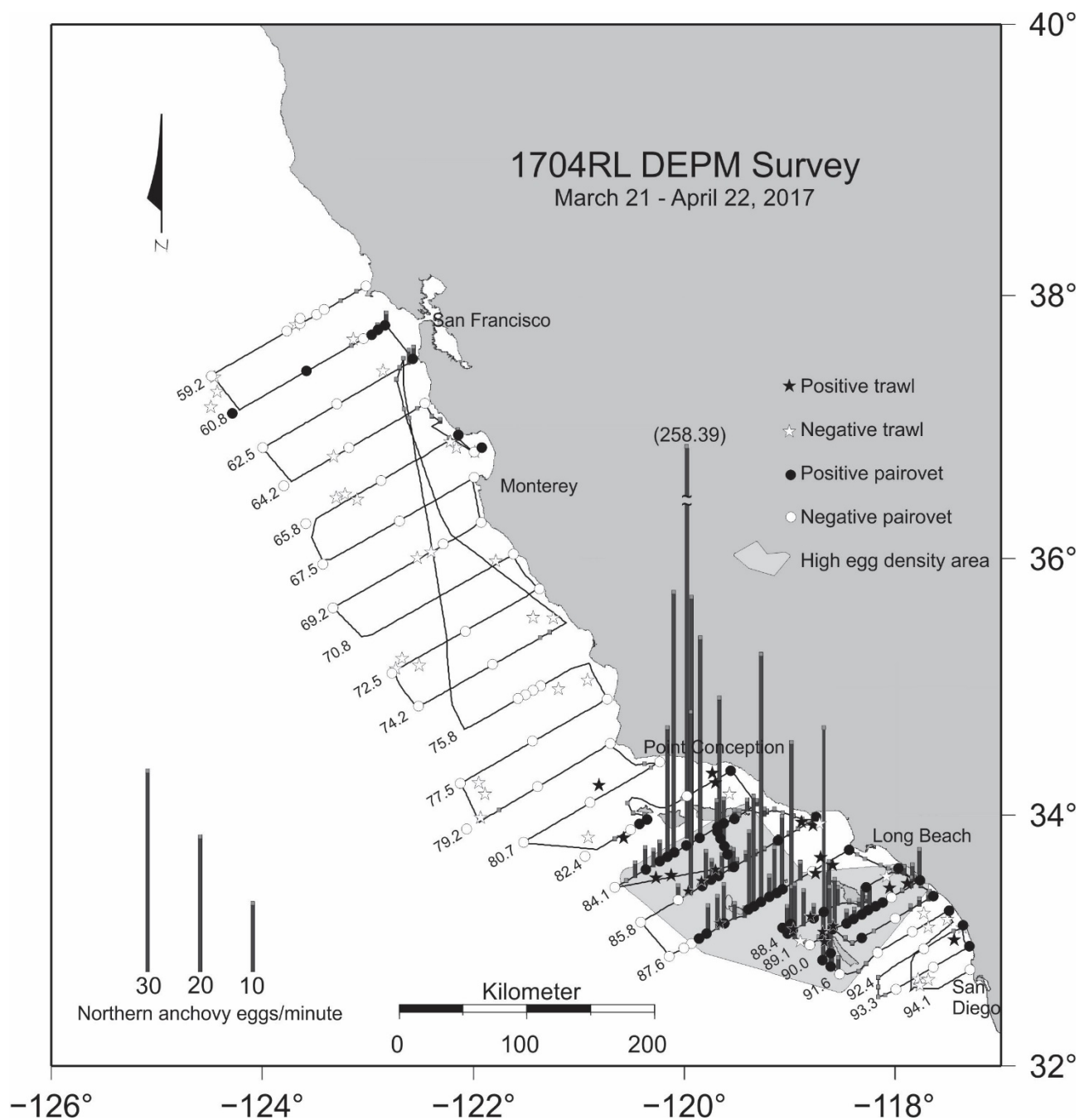


Figure 2. DEPM area and location of northern anchovy eggs collected from Pairovet (solid circle is a positive catch and open circle is zero catch) and from CUFES (Bar denotes positive collection), and trawl locations (solid star is catch with anchovy adults and open star is catch without anchovy) during the 2017 survey aboard the NOAA ship *Rueben Lasker* (solid line). Shaded area is the High Density region, and the rest of survey area is the Low Density region.

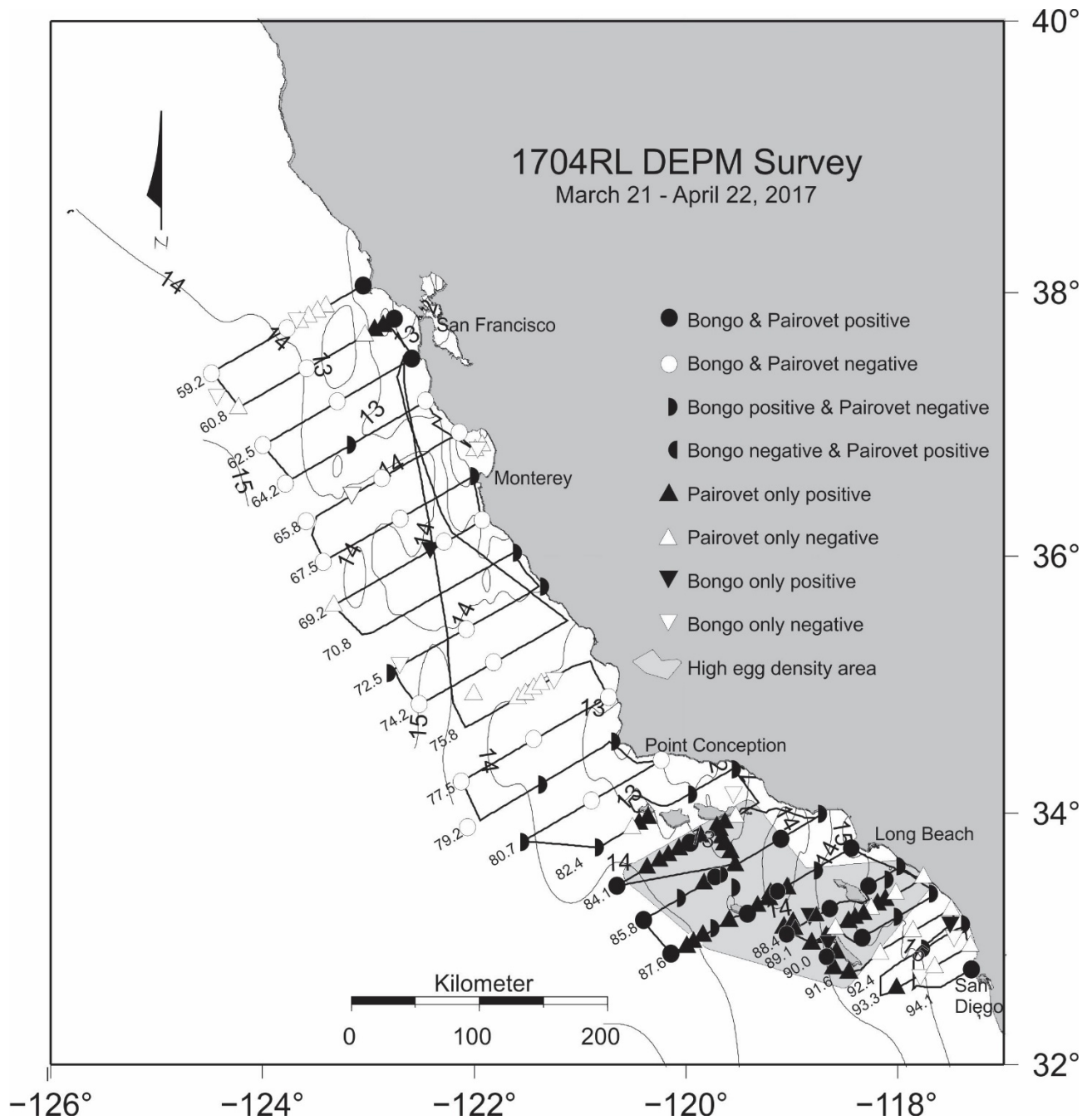


Figure 3. Location of yolk-sac larvae collected from Pairovet (circle and triangle) and from Bongo (circle and semi-circle) during the 2017 survey the NOAA ship *Rueben Lasker* (gray line). Solid symbols are positive and open symbols are zero catch. The shaded region is the High Density area and the remaining region is the Low Density area. Contour lines represent isotherms (13° to 15° C).

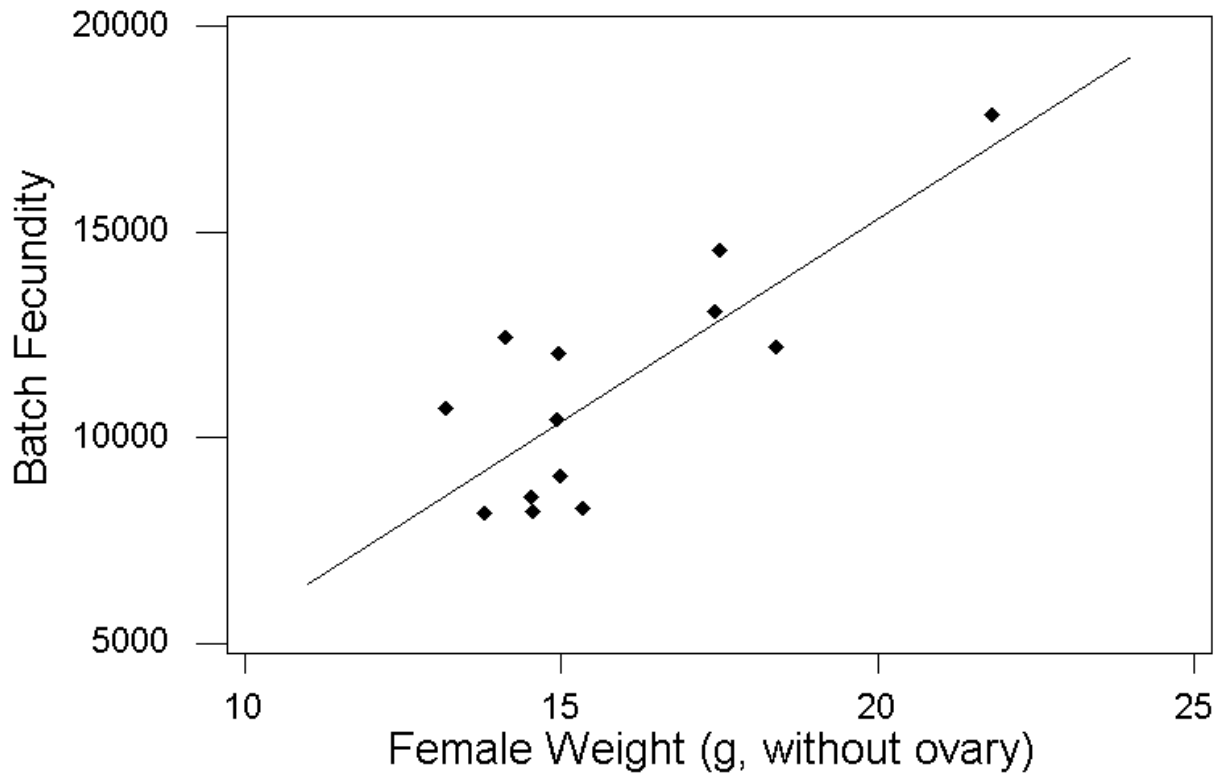


Figure 4. Batch fecundity (F_b) of northern anchovy as a function of female body weight (W_{of} , without the ovary) for a total of 13 female anchovy taken in April 2017 (solid diamond). The batch was estimated from the number of hydrated or migratory-nucleus-stage oocytes.

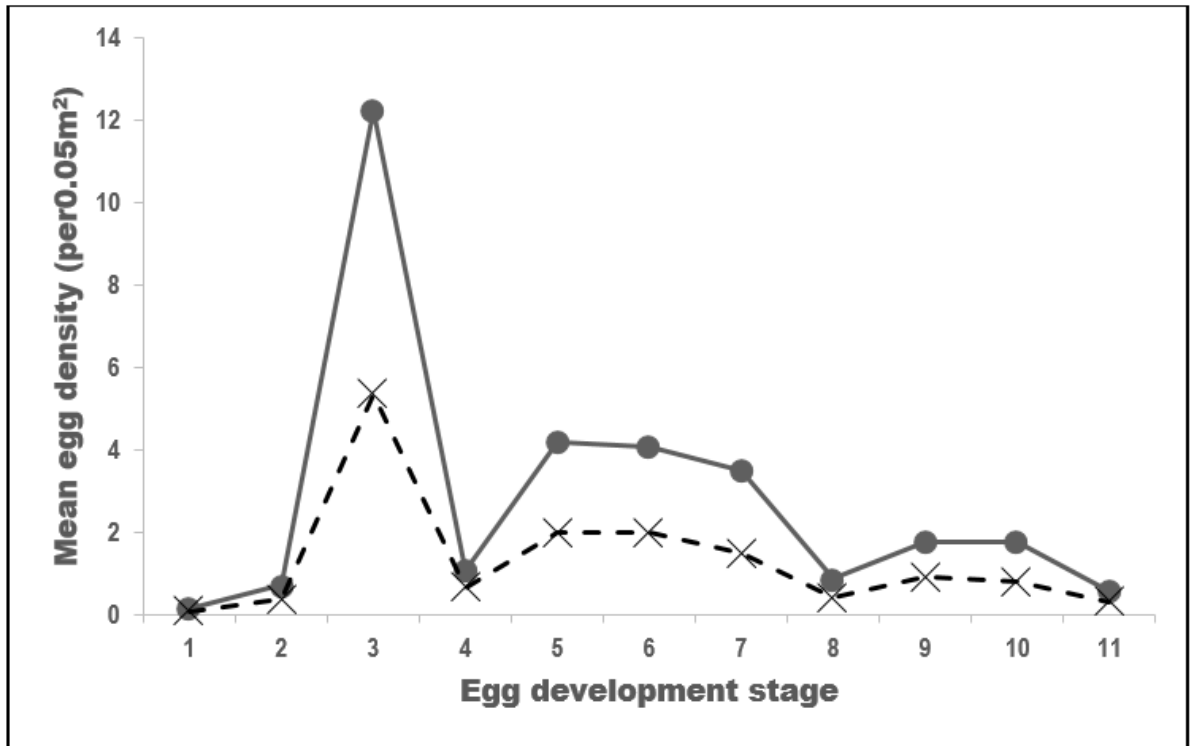


Figure 5. April 2017 mean anchovy egg density (eggs per 0.05m²) for each developmental stage within the high egg-density region (black line with solid circles) and the whole DEPM survey area (from San Diego to north of San Francisco, California; broken line with symbol X).

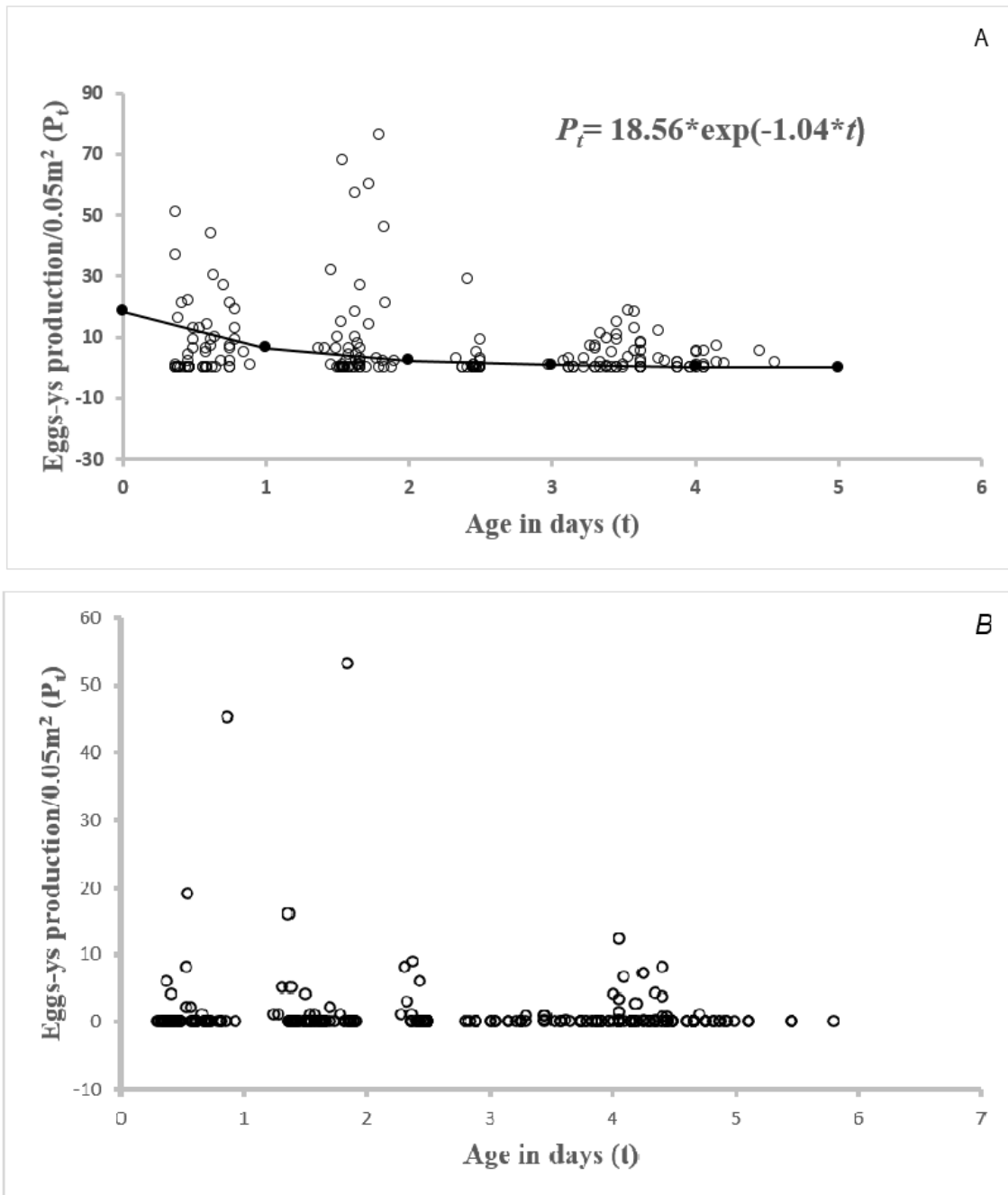


Figure 6. Embryonic mortality curve of northern anchovy in the High Density area (Panel A) and egg production at age in the Low Density (Panel B) areas. Staged egg data were from Pairovet and yolk-sac larval data were from Pairovet and Bongo during April 2017, onboard *the Rueben Lasker*. The number 18.56 in Panel-A's equation is the estimate of $P_{0,1}$ before correction for bias, and the line with solid black circles show the predicted egg production at each age from the equation. No equation and curve are shown in Panel B, as the egg production estimate was not significantly different than 0.

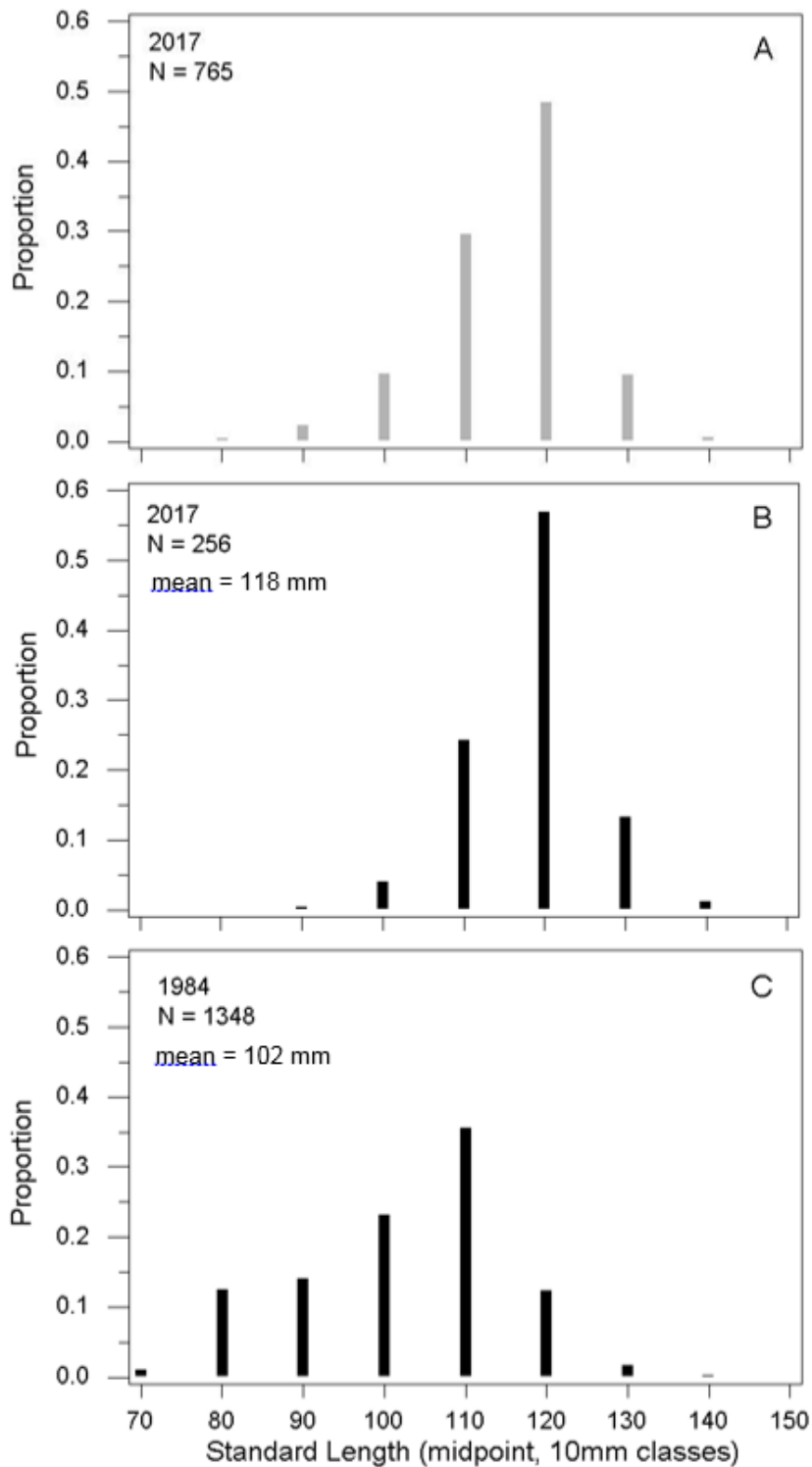


Figure 7. Length distribution of northern anchovy caught in the DEPM survey areas in 2017 (Panel A and B) and in 1984 (Panel C). Panel A includes male and female anchovy in the random samples of the trawls during 2017; whereas Panels B and C only include lengths from the mature females that were used to estimate adult parameters, respectively in 2017 and 1984.

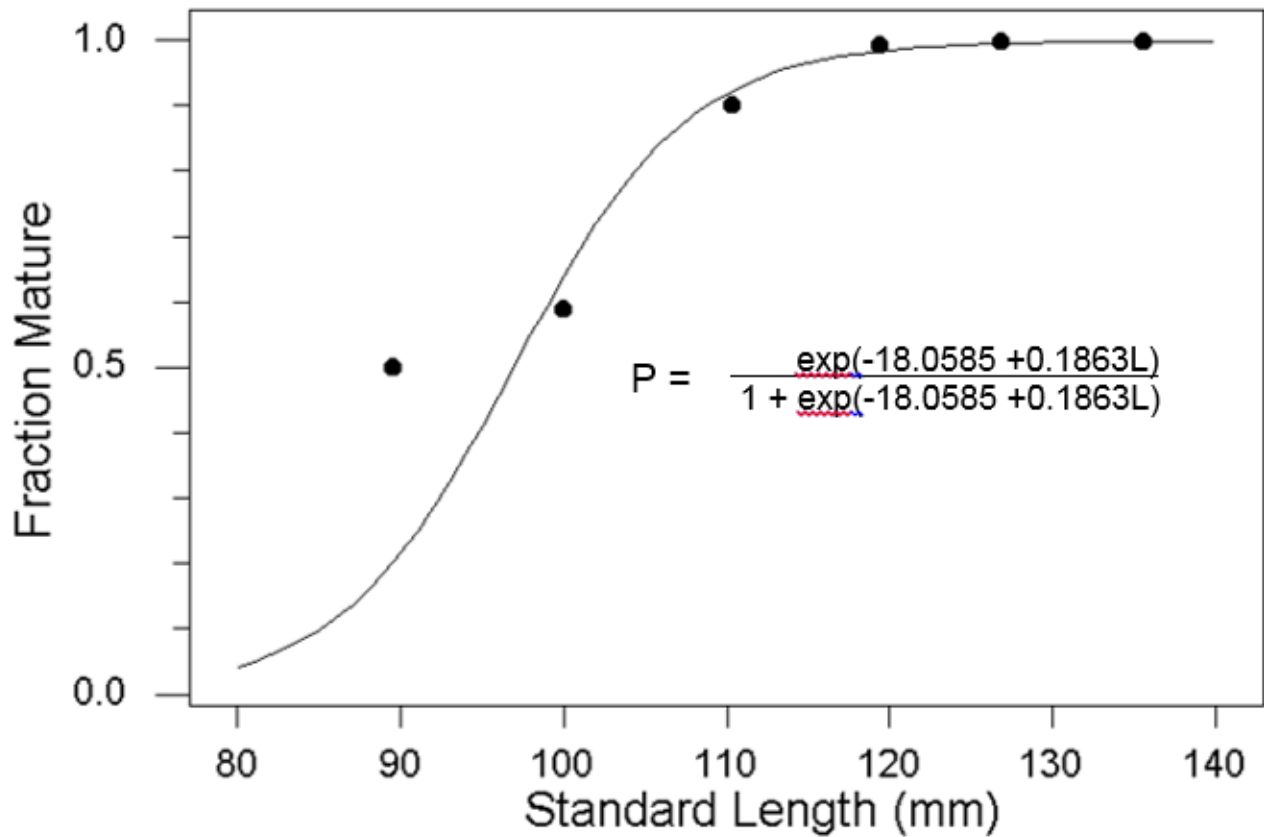
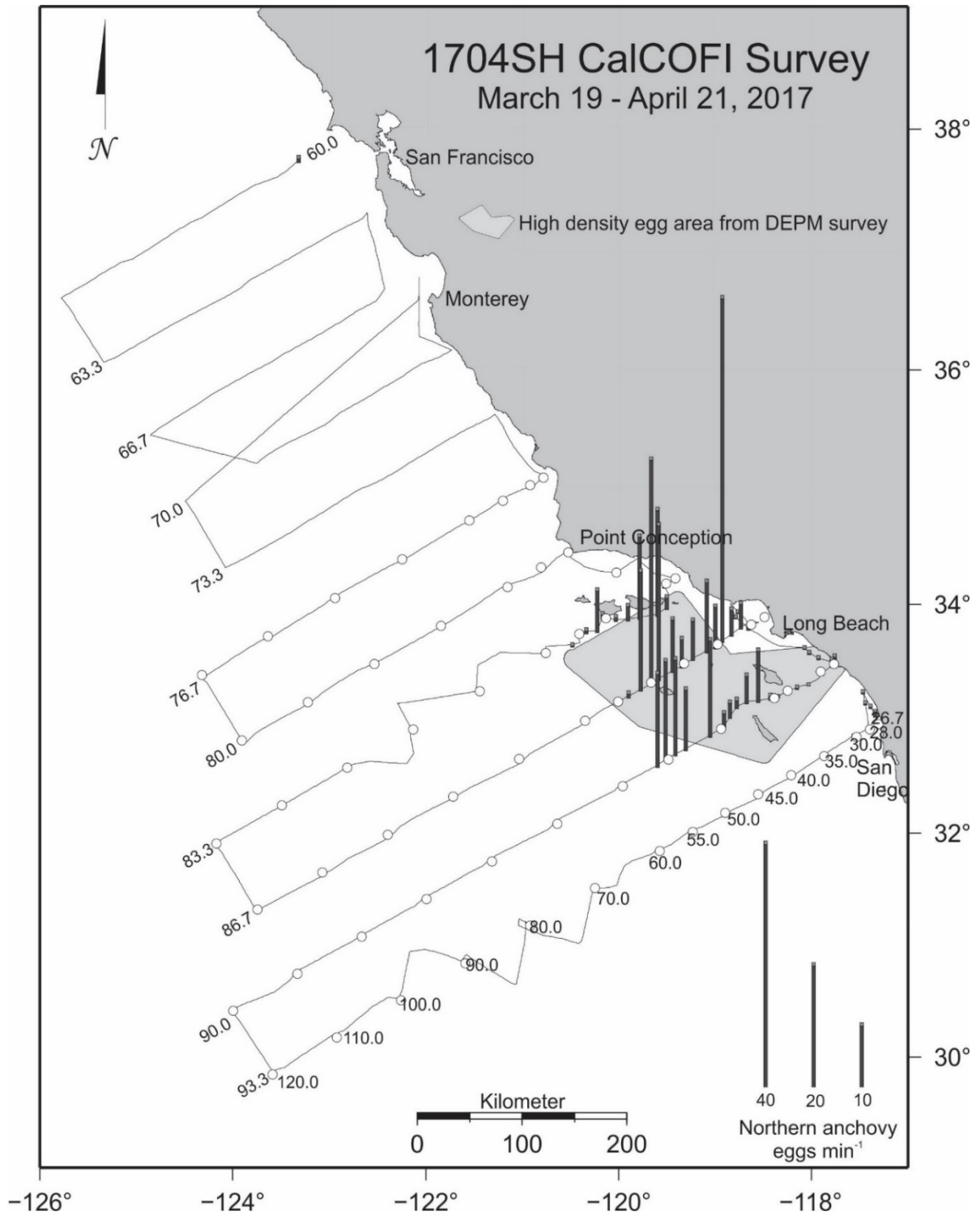


Figure 8. Fraction of northern anchovy females randomly sampled during March-April 2017 and histologically analyzed that were sexually mature as a function of standard length (L). Symbols represent actual fraction mature within 10 mm length classes. Length at 50% maturity was calculated as 96.9 mm. P is the probability of being mature during 2017.

APPENDIX



Location and abundance (black bars) of eggs collected during the CalCOFI 2017 spring survey, using the CUFES. The shaded area is the 2017 DEPM high egg-density area.