EGG AND LARVAL PRODUCTION OF THE CENTRAL SUBPOPULATION OF NORTHERN ANCHOVY IN THE SOUTHERN CALIFORNIA BIGHT

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Abstract

We calculated spatially weighted egg-production estimates for the central subpopulation of northern anchovy in the Southern California Bight in winter and spring for the period 1981-2015. Although there was little correspondence between the winter and spring time series, the indices indicated that anchovy abundance has been low since about 2008. Additional samples measured at a series of inshore stations for the period 2004-2015 also indicated that anchovy ichthyoplankton densities have been low since a large-production event occurred in spring 2005-2006. These data are consistent with the trends reported in previous studies. However, they are not suitable for estimating the biomass of the anchovy stock because the sampling frame of the survey is smaller than the geographic range of the stock, and fluctuations in adult spawn timing and fecundity create an unknown bias in the indices.

Introduction

The central subpopulation of northern anchovy *Engraulis mordax* (hereafter anchovy) is a coastal pelagic species that ranges from San Francisco, California to Punta Baja in northern Baja California. The stock supports a commercial purse-seine fishery and small recreational bait fishery. It is also an important forage component for many birds, mammals, and larger fish in the California current system (e.g., Glaser, 2010; Sydeman *et al.*, 2015; McClatchie *et al.*, 2016). Like many other coastal pelagic species, environmental conditions strongly affect the rate of recruitment for anchovy. High variation in the rate of recruitment causes large fluctuations in abundance over time, even in the absence of fishing (Baumgartner *et al.*, 1992). Recent ichthyoplankton surveys suggest abundance of the stock may have declined precipitously since about 2006, declining to levels not seen since the early 1950s (MacCall *et al.*, 2016).

The National Oceanic and Atmospheric Administration Southwest Fisheries Science Center is responsible for providing assessments of the status of anchovy and other coastal pelagic species in the California Current system to the Pacific Fisheries Management Council (PFMC) for management. The PFMC has allocated assessment resources to prioritize stocks with relatively large fishery catches by creating two tiers of assessment. Actively managed stocks are those that have biologically significant levels of catch. These must be assessed annually and generally require fishery-independent surveys that provide catch-per-unit-effort, age, and growth data. Monitored species are those that are not believed to require intensive harvest management. Monitored stocks are managed on the basis of landings data and available abundance indices without a formal stock assessment. A stock may have its status changed from monitored to actively managed, or vice-versa, as its population size and fishery exploitation rate changes. Anchovy have been a monitored species during all of the 2000s. The last formal stock assessment for northern anchovy occurred in 1995 (Jacobson, 1995).

Previous stock assessments for anchovy have relied heavily on the daily egg-production method (DEPM; Lasker, 1985) and related analyses. The DEPM is a method for estimating the spawning-stock size of fishes with indeterminate fecundity using survey data for ichthyoplankton and adults. The ichthyoplankton data are used to estimate production of eggs at the time of spawning. Production is calculated as the intercept of a non-linear mortality model that has been fitted to abundances of eggs and larvae by age classes. Sampling of adults is used to estimate adult size composition, female fecundity, ratio of females to males, and the proportion of females spawning at the time of the survey. Together, these data are then used to back calculate the size of the spawning stock that produced the eggs. Surveys were conducted to estimate anchovy spawning-stock biomass using the DEPM in 1979-1984 (Jacobson *et al.*, 1994).

The California Cooperative Oceanic Fisheries Investigations (CalCOFI) program has sampled ichthyoplankton in the California Current since 1951 (cf, McClatchie, 2014). Although the survey pattern has changed somewhat through time, a core set of 66 fixed stations located in the Southern California Bight have been sampled quarterly for most years in the time series (Figure 1). CalCOFI data have previously been used to create a time series of anchovy abundance for use in management by conducting an analysis known as the historical egg-production method (Lo, 1985). The historical egg-production method consists of estimating egg production similarly to the DEPM. The time series of egg production must then be scaled to estimate spawning-stock biomass because no coincident adult trawl survey data are available. Scaling is based on a regression relation obtained from years where complete DEPM estimates and historical egg-production estimates both are available. That is, adult parameters are assumed to be constant at about their means during the period when DEPM surveys occurred in the early 1980s.

Two studies have updated the time series of estimated anchovy abundance using CalCOFI data since the last stock assessment. Fissel *et al.* (2011) used the historical egg-production method to estimate anchovy abundance for the period 1981-2009. This study indicated that spawning stock biomass had declined to less than one quarter of its greatest abundance in 2005-2006 but remained near low-biomass levels that had occurred five other times during the study period. MacCall *et al.* (2016) reported pooled egg and larval abundance (rather than egg production) for the period 1951-2011. This study indicated that the anchovy population had recently declined to its smallest abundance since the early 1950s.

The MacCall *et al.* (2016) study also identified a potential bias in previous egg-production estimates of anchovy abundance that used CalCOFI data. The bias is caused by fact that CalCOFI stations have been weighted equally and treated as if they were obtained from a simple random sample in previous egg-production estimates. Stations in the CalCOFI survey are fixed and spaced more closely in the near shore portion of the sampling grid than they are offshore. This creates a "hyperstability" bias because anchovy tend to occur at greater densities near shore. Previous studies may have overestimated anchovy abundance when the population size was small and underestimated the population size when it was large.

As a result of the MacCall *et al.* (2016) study and other recent evidence that anchovy abundance may be very low (e.g., Leising *et al.*, 2015; Sydeman *et al.*, 2015), a workshop of experts on coastal pelagic species was conducted in May 2016. The purpose of the workshop was to provide recommendations for conducting stock assessments that could be used for management of coastal pelagic species for which insufficient data exist to conduct traditional stock assessments (i.e., PFMC "monitored" stocks). The workshop emphasized the central subpopulation of northern anchovy (Anonymous 2016). The workshop panel recommended development of a time series of egg and larval production based on CalCOFI data for possible use in a data-limited stock assessment of anchovy. The objective of this study was to develop a time series of anchovy abundance that included the most recent available CalCOFI data (spring 2015) and corrected for bias caused by the CalCOFI sampling pattern, and then evaluate its potential usefulness as a tool for management. This report was revised in response to a review conducted by the Coastal Pelagic Species subcommittee of the Scientific and Statistical Committee of the Pacific Fisheries Management Council on 11 October 2016.

Methods

CalCOFI Data

Ichthyoplankton data were obtained from CalCOFI cruises in the core area generally corresponding the Southern California Bight. The core area consisted of 66 stations (Figure 1) that generally have been sampled quarterly each year since 1951, except during the mid 1980s, when triennial sampling was conducted, or when logistical problems resulted in missed samples. Sampling occurred on the CalCOFI line and station coordinate system, which is a grid that is oriented -30° off of the meridian so that it is approximately normal to the west coast of North America south of Cape Mendocino. Cardinal lines are located 120 nm apart and increase in numbering by increments of 10 from northwest to southeast. The station numbering along these lines increases from northeast to southwest (i.e., inshore to offshore) and whole number increments are 4 nm apart. The rotation point is located at 34.15°N, 121.15°W which is denoted as CalCOFI line 80, station 60. The core area consists of lines 76.7, 80.0, 83.3, 86.7, 90.0, and 93.3. Sampling extends offshore to about 124°W, corresponding to stations 100, 110, or 120 depending on the line sampled.

We analyzed data for the period 1981-2015 using CalCOFI cruises in which any portion occurred in January or April. These data correspond with the spawning season for anchovy of approximately January to May (Methot, 1983). Winter and spring CalCOFI cruises generally were centered on January and April, respectively. However, cruise times varied by a few weeks among years.

We analyzed ichthyoplankton data from two types of tows at each station sampled: oblique tows that were conducted using bongo nets, and vertical tows that used CalVET or PairoVET nets (Smith and Richardson, 1977; McClatchie, 2014). Bongo nets were 0.71-m diameter paired bridleless nets with 0.505 mm square-mesh nylon. Bongo nets were towed at an angle of approximately 45° from 210 m depth to the surface. CalVET nets were 0.25-m diameter ring nets attached directly to the towing cable and towed vertically from 70 m depth to the surface. The net mesh for CalVET tows was 0.333 mm nylon in 1981 and 1982, and 0.150 mm nylon from 1983-1985. The pairoVET net replaced the CalVET net for vertical tows after 1985. PairoVET nets were 0.25-m diameter paired bridleless nets with 150-µm mesh. They also were towed vertically from 70 m depth to the surface. Oblique tows generally were more suitable for capturing larvae, and vertical tows more suitable for capturing eggs. Thus, samples from the two tow types were pooled for each station to obtain a better estimate of total combined egg and larval densities (Fissel *et al.*, 2011).

Samples from each net tow were preserved in a solution of seawater, 5% formaldehyde, and sodium borate and later sorted in the laboratory. For large samples, a subsample was sorted and identified. All eggs and larvae were counted, and larvae were measured to the nearest 0.1 mm total length.

Sea-surface temperature was measured at each station using either a bucket cast or a near-surface value (upper 5 m) from a conductivity-temperature-depth meter cast. In a few cases, sea-surface temperature data were missing due to equipment malfunction or other problems. These data were interpolated using inverse-distance weighting of data from the other stations sampled during the same cruise.

Data from nine additional stations were collected from 2004-2015 as part of the Southern California Coastal Ocean Observing System (SCCOOS; http://www.sccoos.org, accessed 9/8/2016). These data were collected and processed during CalCOFI cruises using the same procedures described above for CalCOFI data. The SCCOOS stations were located inshore in the Southern California Bight at about 30 m bottom depth (Figure 1). We summarized data from the SCCOOS stations separately from CalCOFI data to construct a shorter time series of mean egg and larval density in the near-shore area.

We defined the sampling frame of the CalCOFI area operationally to be the area from line 75 to line 95. It extended from the shore to station 105 north of line 81.67, to station 115 between lines 81.67 and 88.33, and to station 125 south of line 88.33. This area consisted of the core CalCOFI stations buffered by one half of the typical distance between stations, i.e., 1.67 units of line in the direction of northwest to southeast and 5 units of station in the direction of southwest to northeast. Samples were limited to the standard 66 core points except for the cruise conducted in April 2009. In spring 2009, the standard CalCOFI cruise was conducted entirely in March. However, an additional survey was conducted in the core CalCOFI area during April in which lines located half way between the standard CalCOFI lines were sampled (e.g., line 78.3). We used the data from the April cruise as the spring 2009 estimate to maintain consistency in survey timing with other years.

Egg and larval counts from each net tow were standardized to catch per 10 m^2 of ocean surface as follows (Kramer and Smith, 1971). Density in the sorted subsample

(d_sub_{lcti}) of each tow was estimated as:

$$1)\quad shf_{lti} = 10 * \frac{tow_{lcti}\, depth\ (m)}{volume\ of\ water\ filtered\ for\ tow_{lcti}\ (m^3)},$$

where *shf* is known as the standard haul factor, *l* = life stage (eggs or larvae), *t* = the *c* = 1-mm length class of larvae, individual tow at a station, *i* = station.

$$2)\quad d\_sub_{lcti} = count_{lcti} * shf_{ti}$$

Subsample densities were then scaled to density in the tow (d_{lcti}) as:

$$3)\quad d_{lcti} = \frac{d\_sub_{ltci}}{Proportion\ sorted_{lti}},$$

Then we averaged the sum of egg and larval densities from all tows at a station by season (winter or spring) and year to calculate station densities (d_{lci}).

$$4)\quad d_{lci} = \frac{\sum_t^{n_t} d_{lcti}}{n_t},$$

Egg and Larval Production

We estimated egg production in the core CalCOFI area by season and year using a modified historical egg-production method in which stations were weighted using the tessellation approach of MacCall *et al.* (2016). A jackknife estimator (Efron and Stein, 1981) was used in which the egg production at each station was weighted by what they termed its "area of influence." Areas of influence were determined using Voronoi tessellation of stations in each jackknife resample (Figure 2). The Voronoi tessellation was performed by constructing a polygon based on the line and station boundaries of the sampling frame described above and the shoreline based on the Global Self-consistent, Hierarchical, High-resolution Geography Database, version 2.2.0, full resolution data (Wessel and Smith, 1996). Line and station coordinates were converted to longitude and latitude using the Proj.4 cartographic projections library, version 4.9.2 (https://github.com/OSGeo/proj.4/wiki, accessed 9/15/2016). We projected the polygon to the "California Current/Albers equal area conic (WGS84) projection" (http://spatialreference.org/ref/sr-org/california-current-albers-equal-area-conic-wgs84; accessed 9/8/2016) to estimate area, also using Proj.4 with the coordinate reference system argument:

'+proj=aea +lat_1=30 +lat_2=50 +lat_0=40 +lon_0=-125 +x_0=0 +y_0=0 +ellps=WGS84 +datum=WGS84 +units=m +no_defs'.

For each jackknife resample, the areas of influence were calculated by the Voronoi tessellation using the 'dirichlet' function of the package 'spatstat', version 1.44 (Baddeley and Turner, 2005) in the R computing environment, version 3.2.3 (2015).

Egg and larval densities were corrected for several sources of bias before estimating production (Lo, 1983, 1985; Fissel *et al.*, 2011). Egg and larval counts were scaled to correct for size- and gear-dependent extrusion through the net mesh using the coefficients listed by Fissel *et al.* (2011; Appendix Table 1). Then we scaled counts of larvae captured in bongo nets to correct for net avoidance according to their size and the diel period of capture (Fissel *et al.*, 2011):

$$5)\ \ avd_{cit} = \frac{1+ e^{-0.229c}}{2} + \frac{1- e^{-0.229c}}{2}\cos\left(2\pi\frac{hr}{24}\right),$$

where *avd* = avoidance, *c* = length class, and *hr* = hour of the day, 1-24. Eight length classes were used in the analysis. The first ranged 2.5 to 3.25 mm, and the others were 1-mm classes with midpoints at 3.85 (range 3.25 to 4.25) to 9.85 mm (range 9.25 to 10.25). Larvae smaller than 2.5 mm were treated as eggs for this analysis. Larvae greater than 10.25 mm were eliminated from the analysis because they are typically able to avoid capture in ichthyoplankton tows and, thus, are only captured incidentally (Lo, 1985). Corrected counts were then standardized to densities and averaged by station similarly to the abundance data, equations 1-4, above. In Corrected numbers of eggs and larvae were calculated as (Fissel *et al.*, 2011):

$$6)\ \ m_{clti} = d_{lcit}\left(\frac{1}{avd_{cit}}\right)\left(\frac{1}{extr_c}\right)\text{' where } l = \text{larvae and tow type was bongo, or}$$

$$7)\ \ m_{cltisy} = d_{lcit}\left(\frac{1}{extr_c}\right)\text{' where } l = \text{eggs or tow type was vertical,}$$

m_{clti} = corrected number of eggs or larvae in a net tow and $extr_c$ = the extrusion coefficient for the size class.

We estimated the temperature-dependent incubation time of eggs (Lo, 1983; T_I_k) as:

$$8)\ \ t\_i_{ki} = 18.726e^{-0.125*tmp_i},$$

where *k* = sample, *tmp* = sea-surface temperature at the station.

We estimated ages of larvae using a two-stage Gompertz growth curve. First, larval lengths were corrected for shrinkage due to handling and preservation following Theilacker (1980):

$$9)\ \ log(l_{ki}) = \log(1.03 * pls_{ki}) + 0.289 * \exp\left(-0.434 * 1.03 * pls_{ki} * 15.5^{-0.68}\right),$$

where l_{ki} = estimated length of live larvae and pls_{ki} = length of preserved larvae. Equation 9 assumes that all bongo tows were 15.5 minutes in duration, as called for in the CalCOFI sampling protocol. Live lengths are 1.03 times the size of larvae after net capture and handling (Theilacker, 1980). We note the correction handling and preservation was performed after adjusting for net extrusion because the extrusion correction was based on paired samples that had been preserved at sea and then later enumerated and measured in the laboratory.

Larval ages yolk-sac larvae < 4.2 mm in length were fitted to the first stage of the Gomperz growth model as a temperature-dependent relation (Fissel *et al.*, 2011):

$$10)\, T1(l_{ki}) = \left(\frac{-1}{0.1108e^{0.1173tmp_i}}\right) log\left(\frac{\log(l_k/4.25}{\log(0.32/4.25}\right) \text{ for } l_{ki} < 4.2 \text{ mm},$$

where $T1(l_{ki})$ is the estimated age of larvae with length l_k, 4.25 is the upper bound of the growth curve, and 0.32 is the theoretical minimum size of anchovy larvae (Methot and Hewitt, 1980; Lo, 1983). The second stage of the growth curve was estimated for larvae greater than or equal to 4.2 mm as:

$$11)\, T2(l_{ki}) = \left(\frac{-1}{a^{mn}}\right) log\left(\frac{\log(l_k/27}{\log(4.1/27}\right) \text{ for } l_{ki} >= 4.2 \text{ mm},$$

where $T2(l_{ki})$ is the estimated age of larvae with length l_k, and a^{mn}= 0.046, 0.048, 0.05, or 0.052 for tows conducted during January, February, March, or April, respectively (Methot and Hewitt, 1980; Lo, 1983).

After estimating ages of larvae and stage-duration of eggs, we fit a Pareto-type mortality model to the larval data to estimate production at the time of hatching, and then assumed constant mortality for eggs to back calculate egg production at time zero. Daily larval production (dlp_{cit}) was estimated as (Fissel *et al.*, 2011):

$$12)\, dlp_{cit} = {}^{m_{cti}}/_{d_c}\,,$$

where d_c= duration – the length of time that larvae spend in length class *c* according to equations 10 or 11. Production at the time of egg hatching (*p_h*) and the larval instantaneous mortality rate (β) were estimated for each season, year, and set of stations where at least one egg or larva was captured ($dlp[m_{i.} > 0]$) by fitting a weighted least-squares regression to the function (after Fissel *et al.*, 2011):

$$13)\, log(dlp[m_{i.} > 0]) = log(p_h) - \beta\left({}^{t_{ki}}/_{t\_i_{ki}}\right) + \varepsilon,$$

where ε = the error term and the area of influence, A_i, of included stations were weights in the model. The mean value of β over estimable surveys was used for seasons where the regression could not be fit (e.g., larvae were captured at only one station).

We estimated the egg instantaneous mortality rate (α) by iteratively solving the equation:

$$14)\ \frac{m}{p\_h} = \frac{e^{\alpha t\_i}}{\alpha}$$

using the 'optimize' function in the R statistical computing environment, where t_i was the weighted mean, by A_i, of t_i_{ki}. If larvae were captured but no eggs were captured for a survey, the mean value of α over estimable surveys was used to estimate production. Daily egg production (at time zero, p_o) was then calculated as (Fissel *et al.*, 2011):

$$15)\ p_o = p_h e^{\alpha t_i}$$

Production estimates were then scaled from the area where at least one egg or larva was captured back to densities for the entire CalCOFI core area using the station areal weights described above.

Finally, we estimated the jackknife mean and variance of daily egg production for each season and year. Each jackknife replicate $\hat{p}_{0(j)}$ was estimated using the usual leave-one-out procedure (Efron and Stein, 1981) by refitting equations 4-15 leaving out one station (Figure 2). The standard error of jackknife estimates ($se(\hat{p}_0)$) was calculated as:

$$16)\ se(\hat{p}_0) = \left\{\frac{n-1}{n}\sum_{j=1}^{n}\left(\hat{p}_{0(j)} - \hat{p}_{0(.)}\right)^2\right\}^{1/2},$$

where $\hat{p}_{0(.)}$ is the mean of the jackknife replicates:

$$17)\ \hat{p}_{0(.)} = \frac{1}{n}\sum_{j=1}^{n}\hat{p}_{0(j)}$$

The mean was estimated as:

$$18)\ \hat{p}_{0_{jack}} = \hat{p}_0 - bias,$$

where $\hat{p}_0$ is the result of equations 4-15 using all stations, and

$$19)\ bias = (n-1)\left(\hat{p}_{0(.)} - \hat{p}_0\right)$$

Results

The indexes indicated a period of relatively large egg and larval production occurred in the 1980s (Figure 3; Appendix Table 2). A very large production event occurred in spring of 2005, and then production and abundance declined to very low numbers from 2008 to 2015. Estimated production and abundance reached the greatest levels measured during the last eight years in spring 2013 and 2014 but declined again in spring 2015. The winter and spring series were uncorrelated (paired Pearson correlation = -0.06).

Mean densities of anchovy eggs and larvae captured at the SCCOOS stations generally exhibited a similar pattern to that of the CalCOFI data (Figure 4; Appendix Table 3). The greatest density measured at SCCOOS stations occurred in spring 2006, a year later than the large production event in the CalCOFI core area. However, densities have remained relatively low since 2008. The greatest anchovy densities in the last eight years occurred in 2014 for both the winter and spring surveys.

A paired comparison of the SCCOOS stations to the nearest core CalCOFI station for the same survey revealed that densities tended to be greater at SCCOOS stations only when catches were relatively small. When catches were large, greater densities of anchovy were usually captured at CalCOFI stations (Figure 5).

Discussion

These results are consistent with previous literature that reported anchovy abundance has declined to very low numbers in the 2010s (e.g., Leising *et al.*, 2015; MacCall *et al.* 2015; Sydeman *et al.*, 2015). Our analysis suggests that a relatively small increase occurred in 2014 but did not recur in spring of 2015. CalCOFI surveys provide some of the only available data with which to evaluate anchovy abundance for a long time series. However, they are not suitable for estimating the biomass of the anchovy stock because the sampling frame of the survey is smaller than the geographic range of the stock, and fluctuations in adult spawn timing and fecundity create an unknown bias in the indices.

The geographic range of anchovies is larger than the CalCOFI sampling frame both in the along-shore direction and perpendicular to the shore. Some ichthyoplankton sampling has been conducted between the Southern California Bight and San Francisco in winter and spring since 2003. Most of these samples have been low or near zero since 2006 (MacCall *et al.* 2015; Leising *et al.* 2015), suggesting that a large portion of the population has not moved north out of the core CalCOFI area. However, the fishery and avian and mammalian predators that exist in Monterrey Bay underscore the fact that some unestimated component of the population resides north of the Southern California Bight. Likewise, few fishery-independent data are available that could be used to quantify the population of anchovy that reside in Mexican territorial waters or the Mexican exclusive economic zone.

The proportion of the anchovy population that occurs between the shoreline and the most inshore CalCOFI stations, and how the proportion fluctuates through time, is also unmeasured. Anchovy are most commonly captured between the shoreline and CalCOFI station 60 (Figure 2; Leising *et al.* 2015). The correspondence between the SCCOOS density series and the CalCOFI abundance indices indicates that the population inshore to about 30 m depth is trending similarly. Hewitt and Brewer (1983) also reported that production of anchovy eggs and larvae was similar between the CalCOFI core area and the inshore area of the Southern California Bight. However, the Hewitt and Brewer (1983) study indicated anchovy eggs and larvae located inshore had a more patchy distribution and may have experienced greater mortality due to predation than those in the CalCOFI survey area. These data suggest the anchovy population tends to trend similarly in the inshore to the CalCOFI survey area. Nevertheless, the population status between 0 and 30 m depth is unknown for recent years.

The historical egg-production method differs from the DEPM in two important ways: egg developmental life stages have not been determined in the laboratory (Moser and Ahlstrom, 1985), and adult parameters (size composition, female fecundity, ratio of females to males, and the proportion of females spawning at the time of the survey) have not been measured via a trawl survey. The former difference is somewhat overcome by the estimation of egg incubation time using sea-surface temperature, and then fitting a constant mortality rate during the egg stage (Lo 1983; equation 8). The latter difference potentially creates a much larger bias. The peak spawning season for anchovy typically occurs in March but considerable year-to-year variation exists (Hewitt and Brewer, 1983; Methot, 1983; Leising *et al.*, 2015). Surveys that use the DEPM do not need to coincide with the time of greatest spawning because the adult-fecundity and spawning-fraction parameters correct for the time within the spawning season in which sampling occurs. In contrast, the historical egg-production method will result in biased estimates when CalCOFI winter and spring surveys are used and majority of spawning occurs at an unusual time. This is because the spring and winter cruises bound the spawning season. If the majority of spawning occurs particularly early or late, one of the seasonal estimates will be unusually large. If the majority of spawning occurs over an unusually short period between the two surveys, the annual estimate will be under estimated. A related problem is that DEPM anchovy cruises conducted in the 1980s occurred at various times between January and May, and during a period when environmental conditions were advantageous for anchovy recruitment. Thus, using adult parameters from historical DEPM cruises to scale index estimates to biomass likely creates additional bias.

We did not produce a biomass estimate for anchovy because scaling our indices of abundance to biomass based on a relation with DEPM estimates conducted in the 1980s did not produce credible estimates for recent years. For example, MacCall *et al.* (2015) performed a similar calculation and estimated the anchovy stock size to be about 15,000 MT in 2009-2011. All of our indices of abundance indicate the population size has remained near the same level between 2009 and 2015. The California fishery harvested an average of 2,622 MT (range 1,015-5,932) between 2009 and 2014, and 17,286 MT in 2015 (http://pacfin.psmfc.org/pacfin_pub/all_species_pub/woc_r308.php, accessed 9/10/2016). The Ensenada (Baja Mexico) fishery yielded an average of 2,020 MT (range 538-3,139 MT) between 2009 and 2014 (https://www.gob.mx/conapesca/documentos/anuario-estadistico-de-acuacultura-y-pesca, accessed 9/27/2016), and more than 46,000 MT in 2015 (Concepción Enciso-Enciso, INAPESCA-Ensenada, Pers. Comm.). Predation on coastal pelagic species by marine mammals has recently been estimated to be about seven times as great as the fishery (Vetter and McClatchie; submitted). Given the additional unquantified predation by birds and piscivores, the combined removal of anchovy due to predation and fishing almost certainly exceeded 15,000 MT every year since 2008. CalCOFI data alone do not appear to be sufficient to produce an estimate of anchovy biomass, probably because of the biases described above.

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Figures

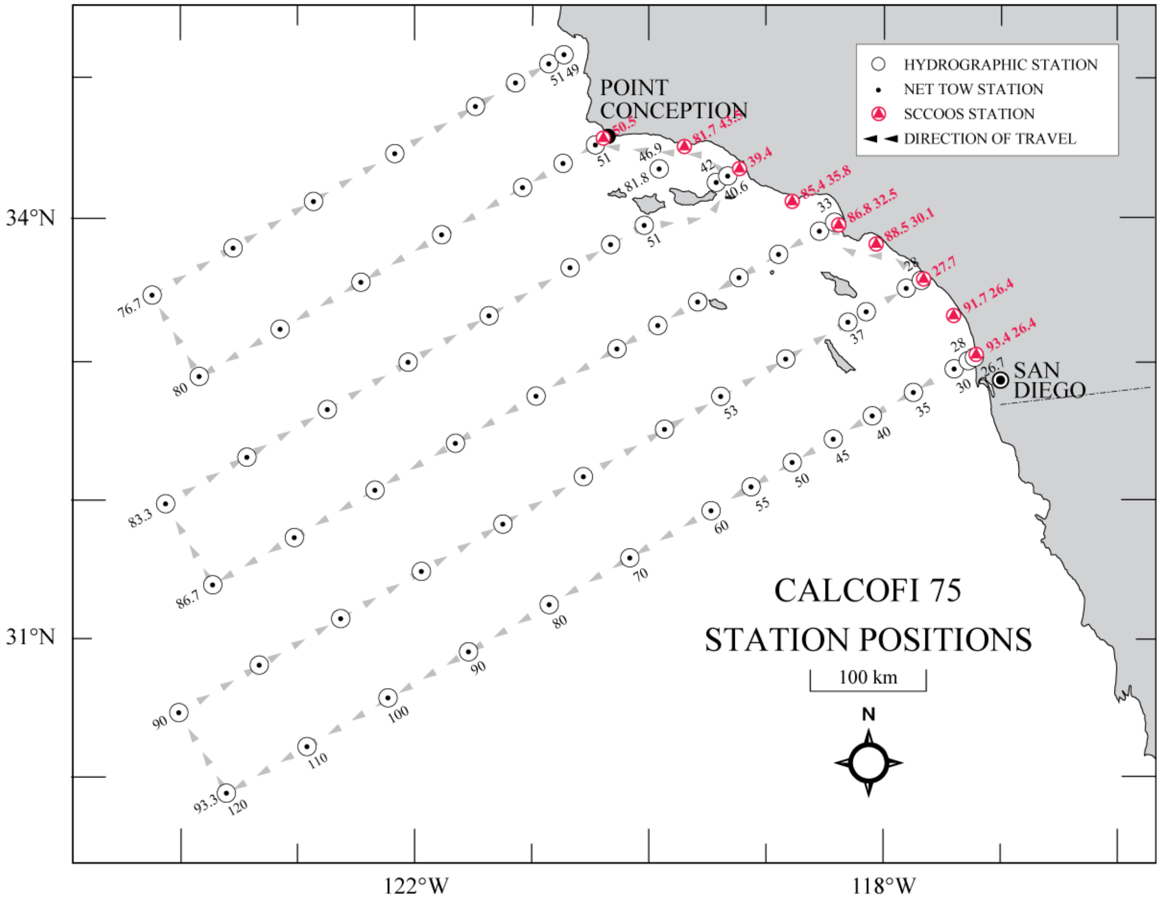


Figure 1. Core sampling pattern for the California Cooperative Oceanic Fisheries Investigations Program. Black symbols indicate 66 core stations that have been sampled consistently since 1951. Red symbols indicate inshore stations sampled as part of the Southern California Coastal Ocean Observing System since 2004. Figure from http://www.calcofi.org/field-work/station-positions/75-station-pattern.html, accessed 9/8/2016.

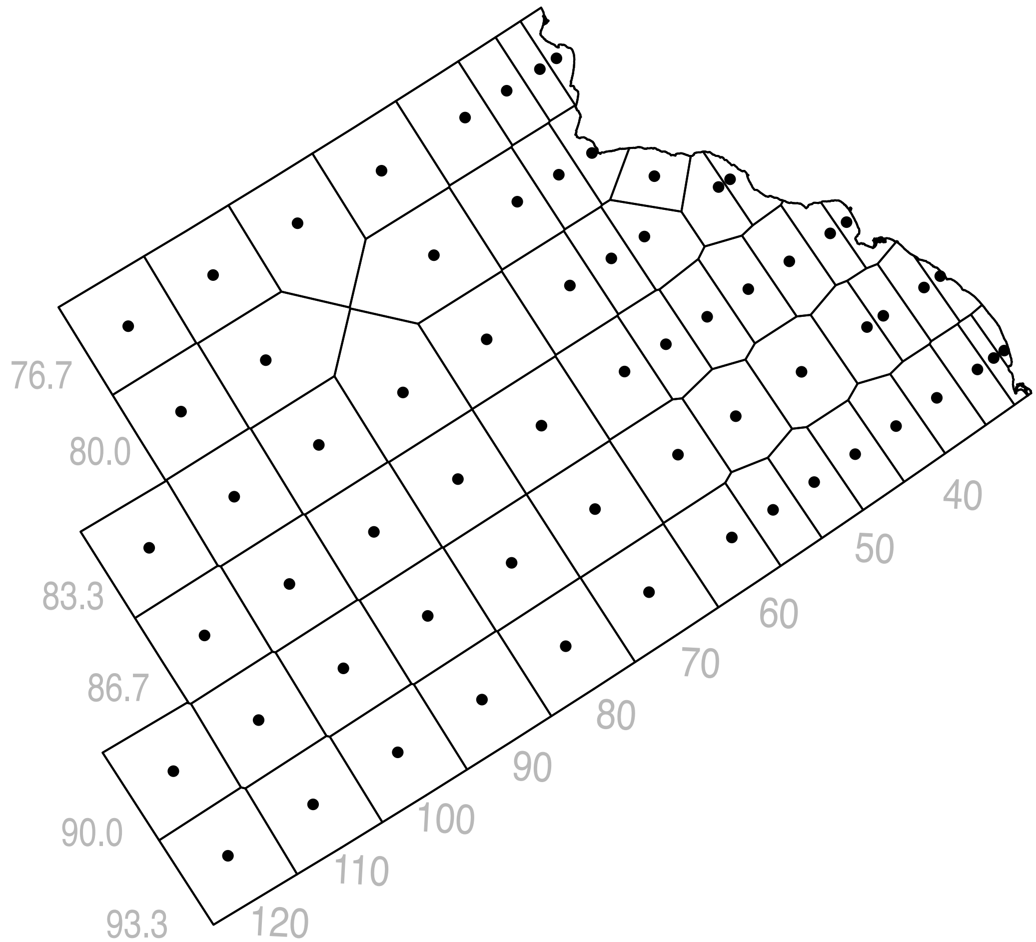


Figure 2. Example of Voronoi tessellation to determine spatial weighting of jackknife resamples. In this example, line 80, station 80 has been left out, and its area used by adjacent points.

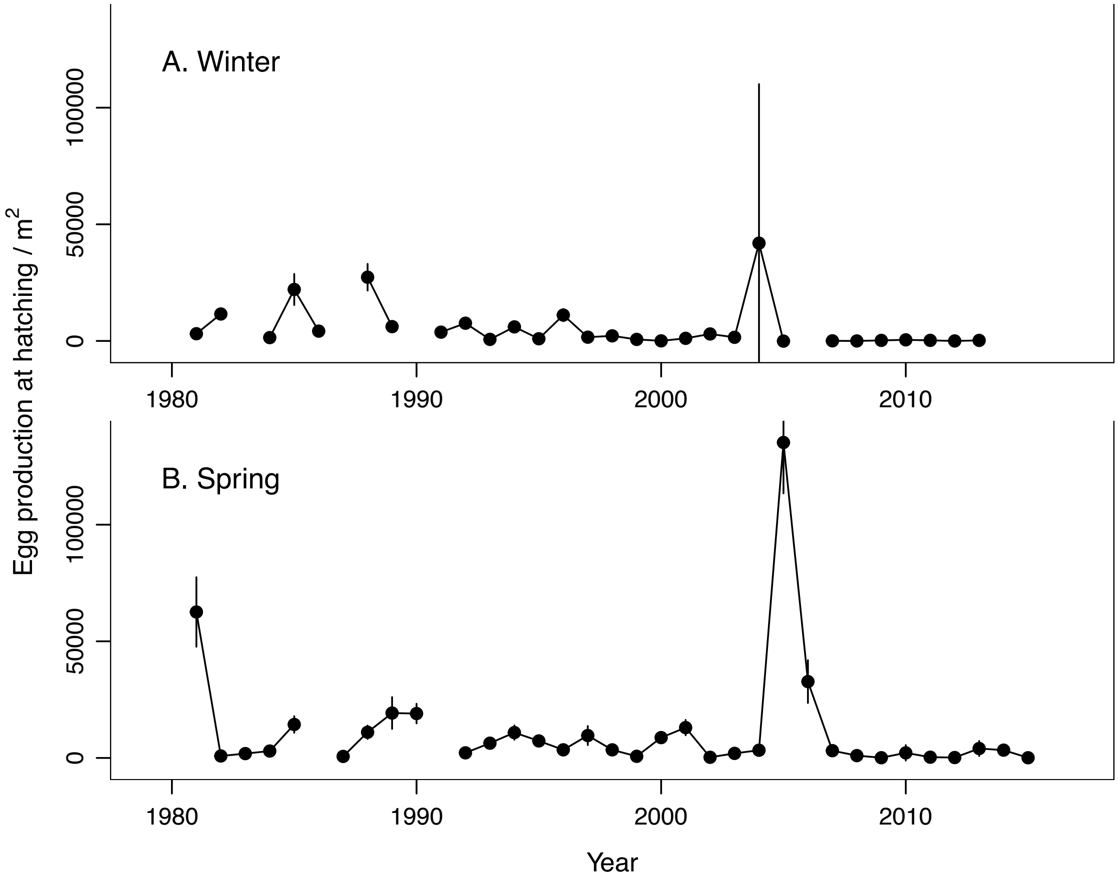


Figure 3. Estimated egg production / m^2 in the CalCOFI core sampling area, 1981-2015. Vertical bars indicate standard errors.

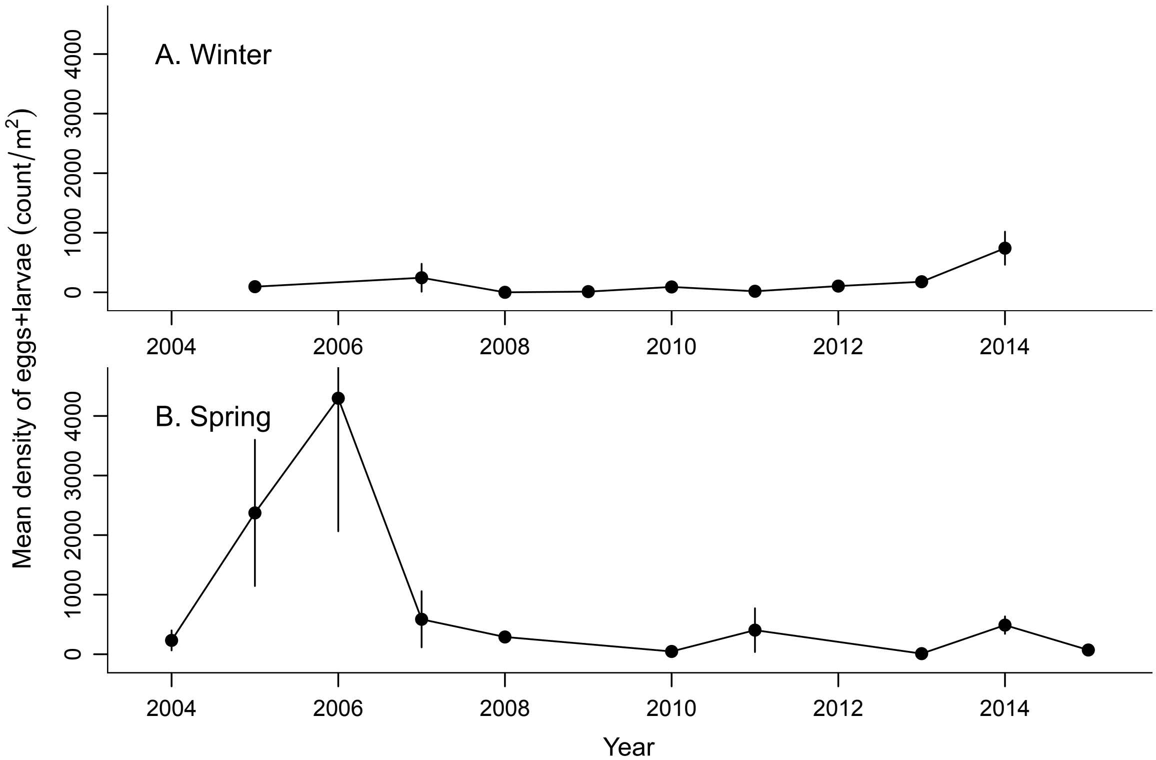
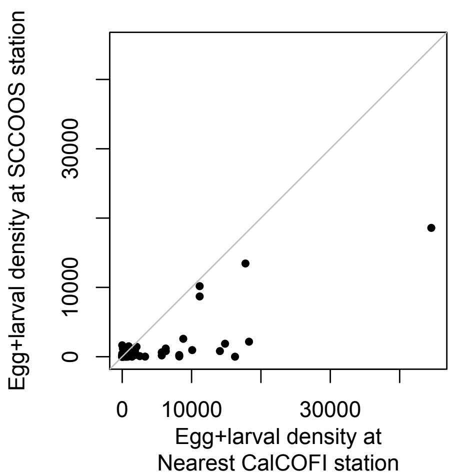


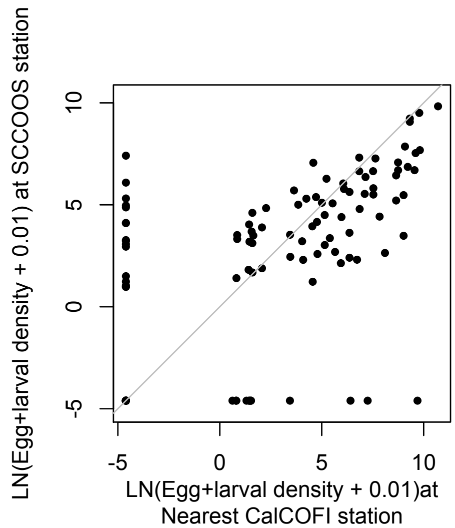
Figure 4. Mean density of anchovy total eggs and larvae at SCCOOS stations, 2004-2014. Vertical bars indicate standard errors.

Figure 5. Mean egg+larval density at SCCOOS stations plotted against mean egg and larval density at the nearest CalCOFI station for the same season and year (A). The same data are replotted on a log scale (B).

A.



B.



Appendix Table 1. Reproduction of Fissel et al. (2011) Appendix Table A1, reporting coefficients used to correct for extrusion of eggs and larvae through sampling net mesh.

TABLE A1

Larval size classes and length ranges, extrusion correction factors for bongo (CB), calvet and pairovet (CVT/PV) and growth curve coefficients.

Size Class	Range [a]	*CB*[b]	*CVT/PV*[c]	Month	a^{mn} [d]
eggs	N/A	12.76	1.10	Jan.	0.046
2.5	[2,3.25]	6.08	1.46	Feb.	0.048
3.75	[3.25,4.25]	2.58	1.37	March	0.05
4.75	[4.25,5.25]	1.62	1.30	April	0.052
5.75	[5.25,6.25]	1.24	1.25		
6.75	[6.25,7.25]	1.10	1.21		
7.75	[7.25,8.25]	1.00	1.00		
8.75	[8.25,9.25]	1.00	1.00		
9.75	[9.25,10.25]	1.00	1.00		

[a]Assignment to classes is based on preserved larval lengths (section 2.2.2). All larval sizes are measured in mm.

[b]Extrusion factors for *CB* computed directly from the logistic model of Lo (1983) equation (6), table 4.

[c]Extrusion factors for *CVT* and *PV* are fitted values of a logistic regression on the raw estimates from Lo (1983).

[d]Gompertz growth second stage parameter (Methot and Hewitt 1980).

Appendix Table 2. Egg production / m^2 estimates for the core CalCOFI area by season based on the spatially weighted historical egg-production method. Dashes indicate unsampled seasons.

	Winter		Spring	
Year	Mean	SE	Mean	SE
1981	3,097.63	1,004.41	62,584.18	14,897.10
1982	11,547.65	2,320.48	841.33	342.52
1983	-	-	1,857.58	671.97
1984	1,425.99	459.26	2,964.85	1,096.74
1985	22,068.67	6,677.42	14,348.34	3,567.80
1986	4,201.98	1,549.20	-	-
1987	-	-	660.58	369.95
1988	27,314.63	5,720.61	11,010.57	2,864.32
1989	6,140.86	1,481.08	19,247.80	6,812.42
1990	-	-	19,022.55	4,208.22
1991	3,758.06	945.40	-	-
1992	7,595.35	2,159.99	2,192.73	586.93
1993	669.37	159.32	6,328.17	2,179.51
1994	6,021.82	1,008.28	10,871.68	3,075.22
1995	936.95	336.54	7,294.18	1,908.26
1996	11,088.83	2,621.97	3,469.92	1,192.20
1997	1,608.22	362.27	9,605.08	4,088.49
1998	2,178.56	558.51	3,462.50	813.40
1999	655.57	225.30	695.82	188.27
2000	39.10	24.15	8,725.34	1,671.83
2001	1,117.77	365.75	13,002.46	3,295.84
2002	2,993.96	713.76	290.39	100.38
2003	1,558.54	359.33	1,948.15	520.22
2004	41,912.83	68,192.22	3,311.84	928.92
2005	0.01	471.21	135,245.01	21,816.99
2006	-	-	32,731.50	9,179.10
2007	42.62	20.31	3,109.85	793.61
2008	0.00	0.00	1,000.05	264.43
2009	229.54	348.38	89.24	34.82
2010	469.60	607.50	2,181.11	3,325.84
2011	246.87	126.19	317.29	227.65
2012	0.01	132.97	170.47	252.31
2013	228.20	124.04	4,039.10	3,240.75
2014	-	-	3,340.47	1,268.45
2015	-	-	76.26	27.72

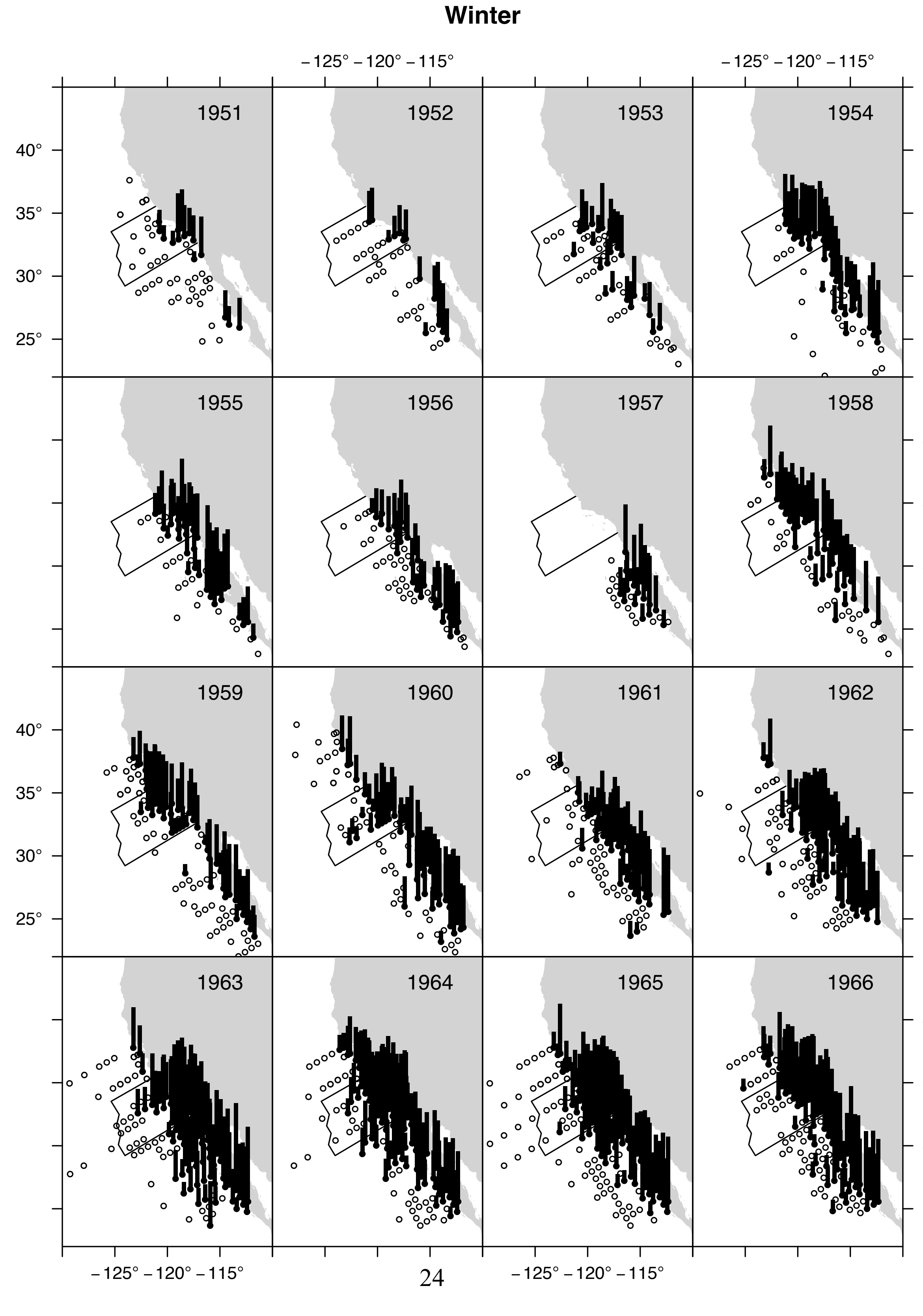
Appendix Table 3. Mean anchovy egg and larval abundance at SCCOOS stations by season and year.

	Winter		Spring	
Year	Mean	SE	Mean	SE
2004	-	-	232.16	168.34
2005	94.54	53.34	2372.48	1227.89
2006	-	-	4297.33	2233.53
2007	244.72	234.48	586.58	471.52
2008	0.00	0.00	289.78	44.56
2009	11.80	7.51	-	-
2010	90.15	88.47	46.45	28.52
2011	17.68	10.22	404.44	367.71
2012	104.69	46.17	-	-
2013	177.62	50.05	9.98	5.48
2014	740.60	278.02	488.87	146.78
2015	-	-	71.12	46.61

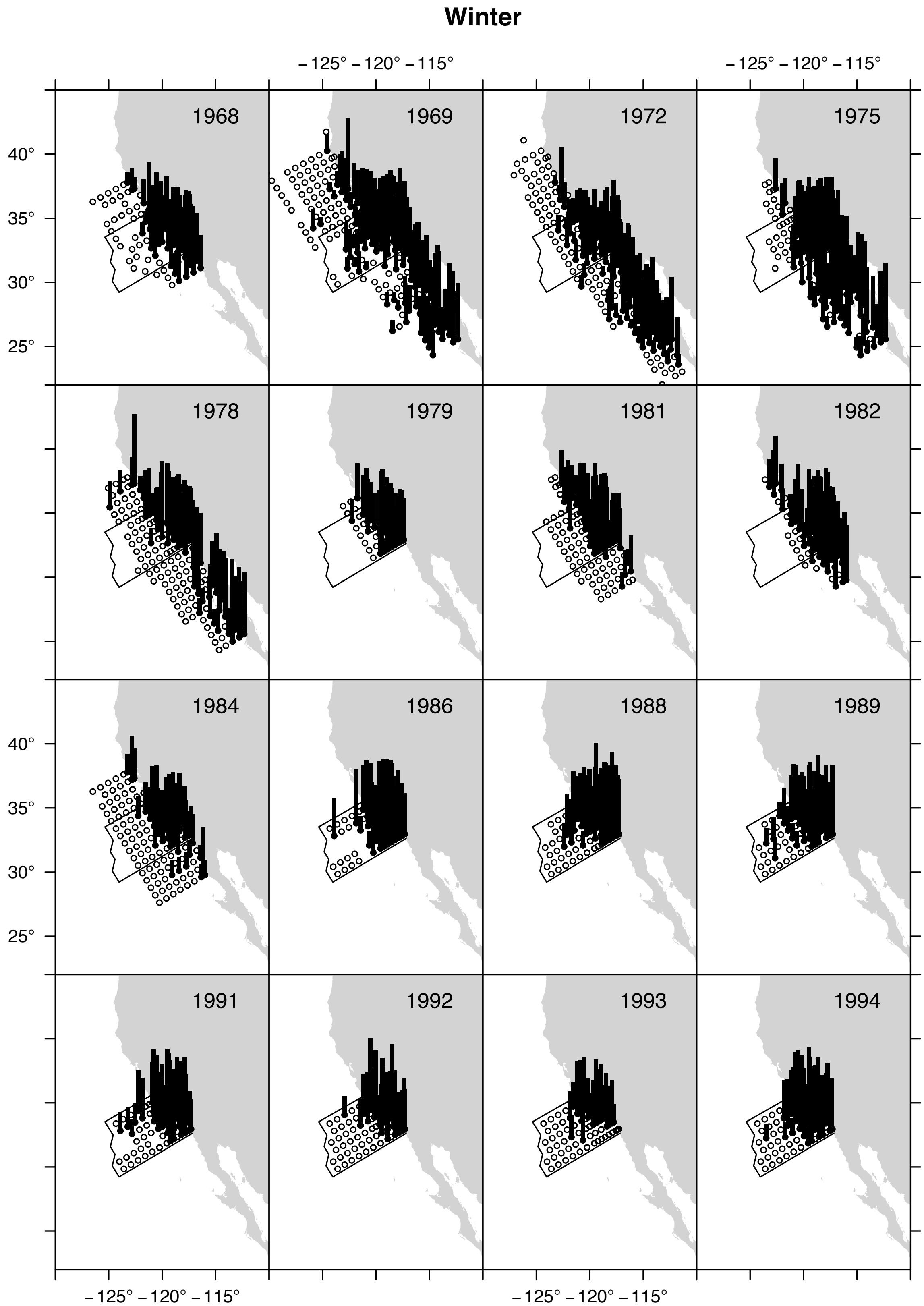
Appendix Table 4. Number of oblique (Bongo) and vertical (Pairovet or Calvet) tows conducted per station at 3,996 CalCOFI stations sampled in the study

	Number of Tows				
Tow Type	0	1	2	3	4
Oblique	90	3,696	206	2	2
Vertical	1,577	2,260	158	1	0

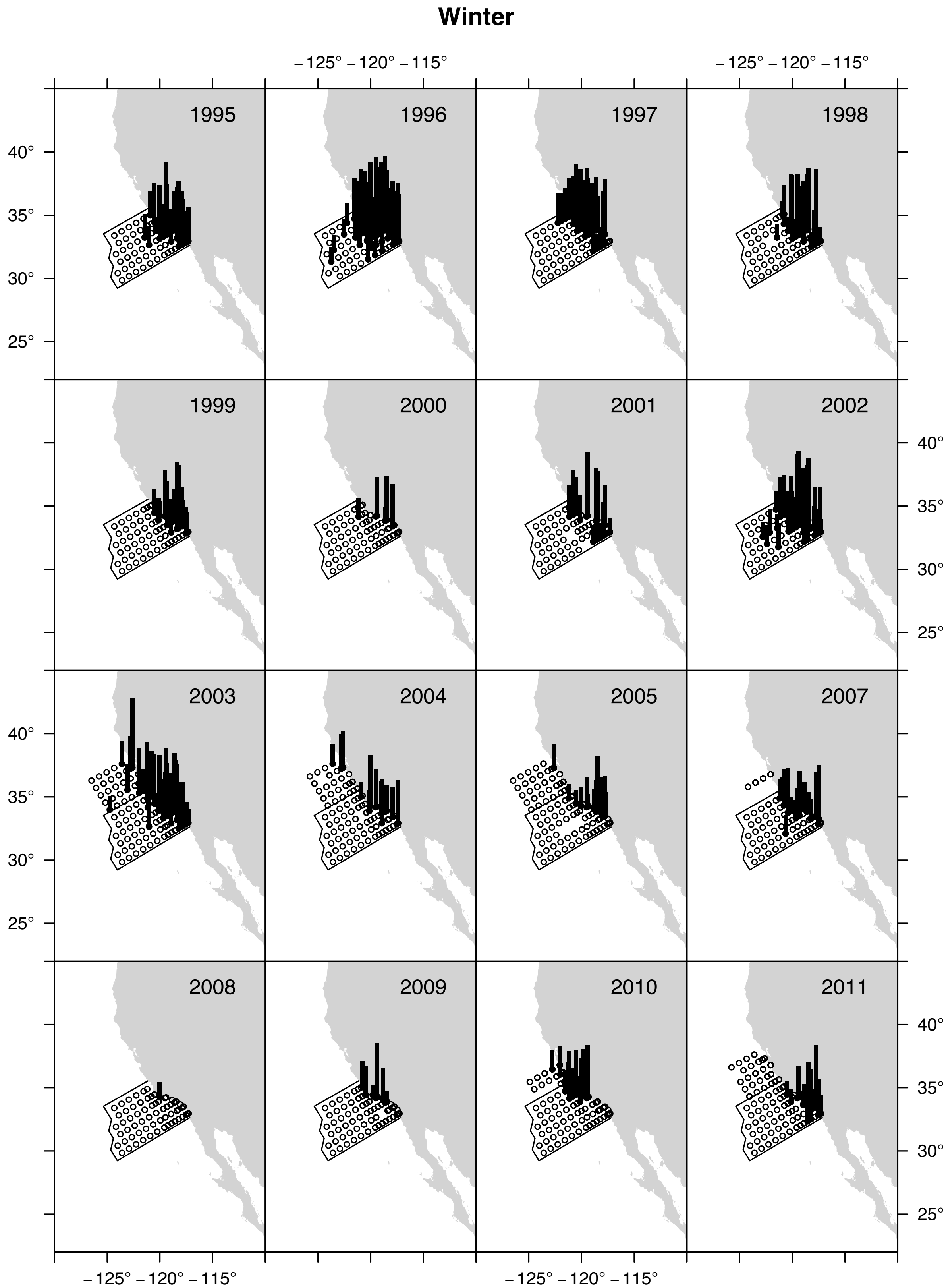
Appendix Figure 1. Winter CalCOFI stations sampled and log of corrected densities (bars) of anchovy eggs + larvae. Open circles indicate sampled stations where no anchovies were captured. Black line indicates the boundary of the core CalCOFI sampling area



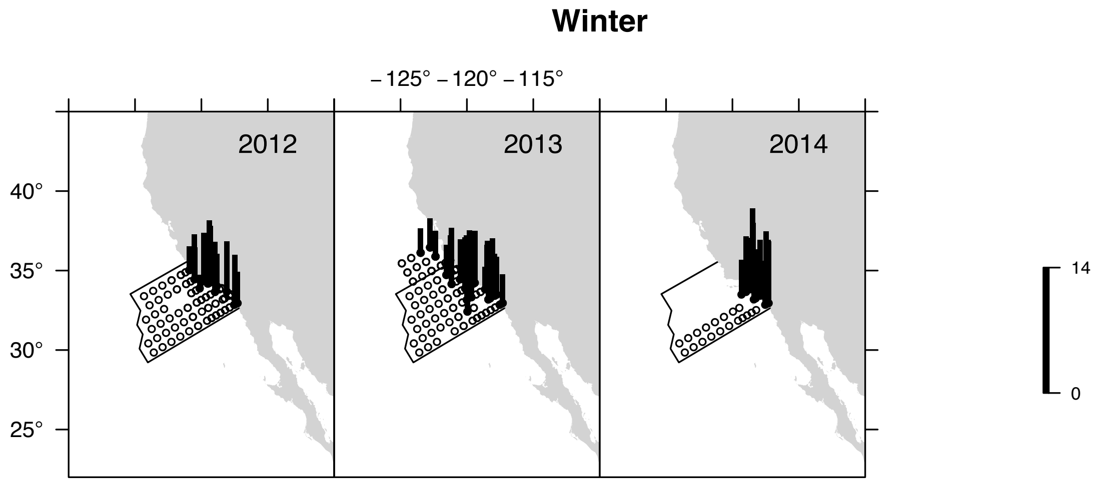
Appendix Figure 1. Continued



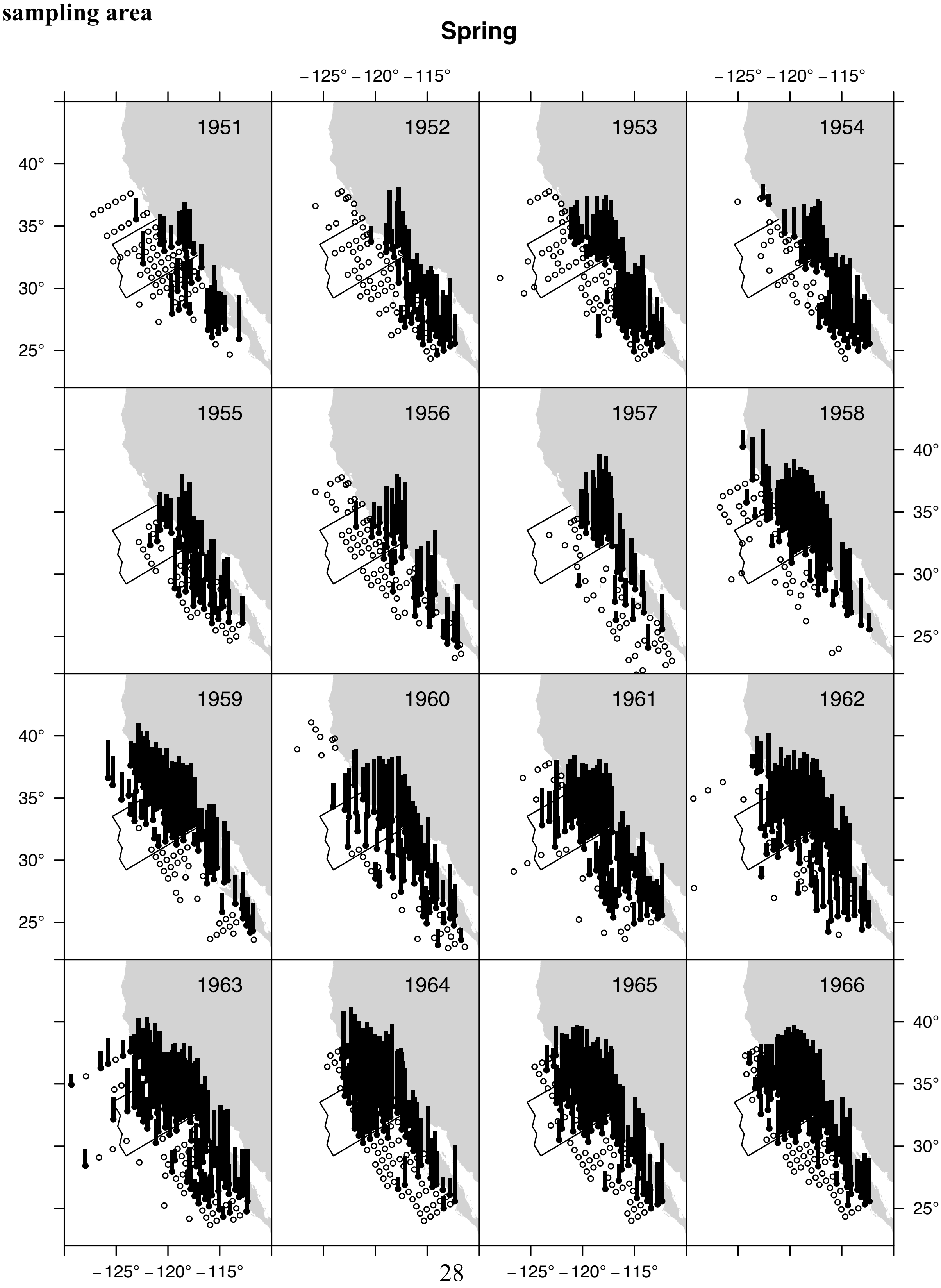
Appendix Figure 1. Continued



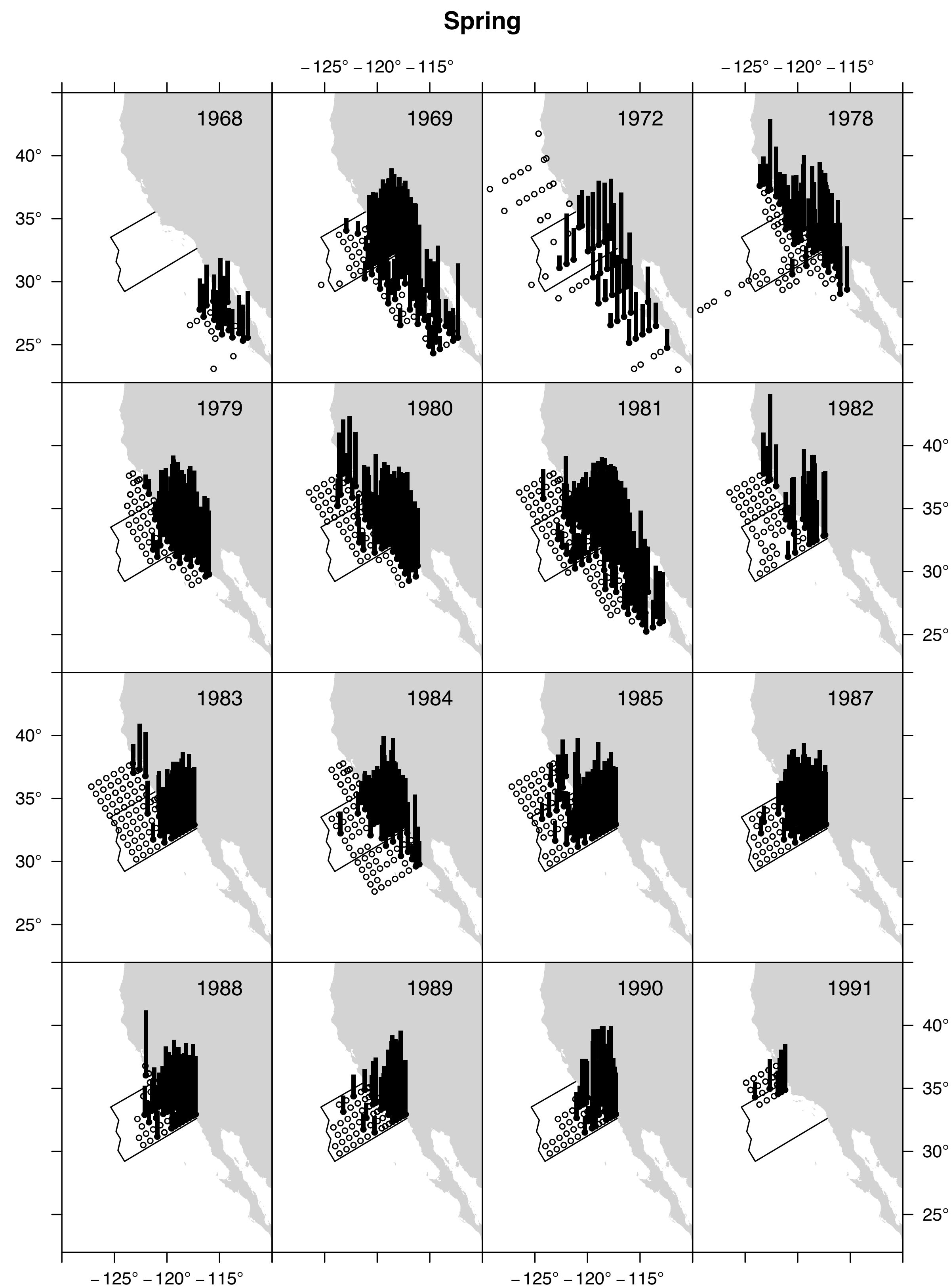
Appendix Figure 1. Continued



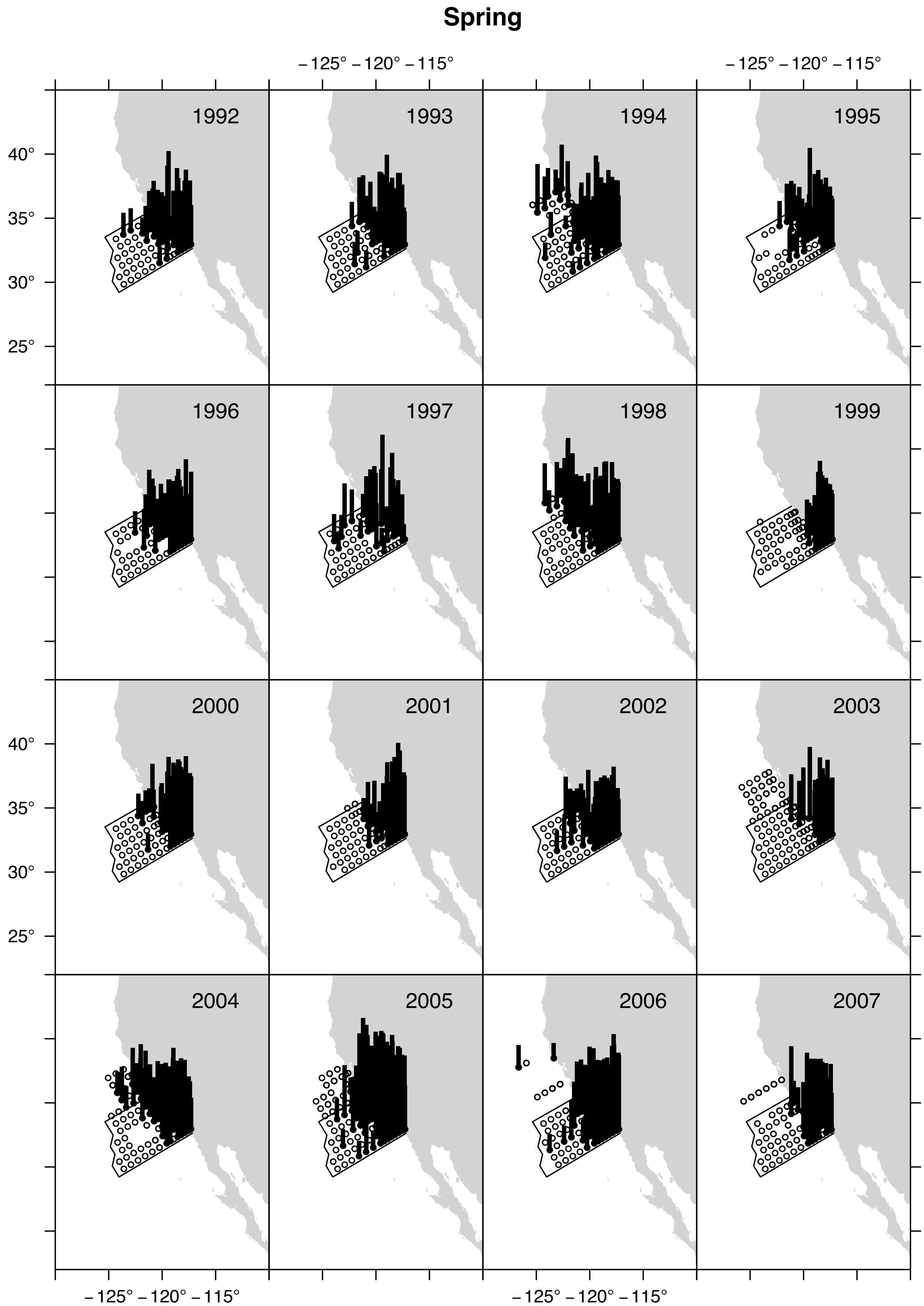
Appendix Figure 2. Spring CalCOFI stations sampled and log of corrected densities (bars) of anchovy eggs + larvae. Open circles indicate sampled stations where no anchovies were captured. Black line indicates the boundary of the core CalCOFI sampling area



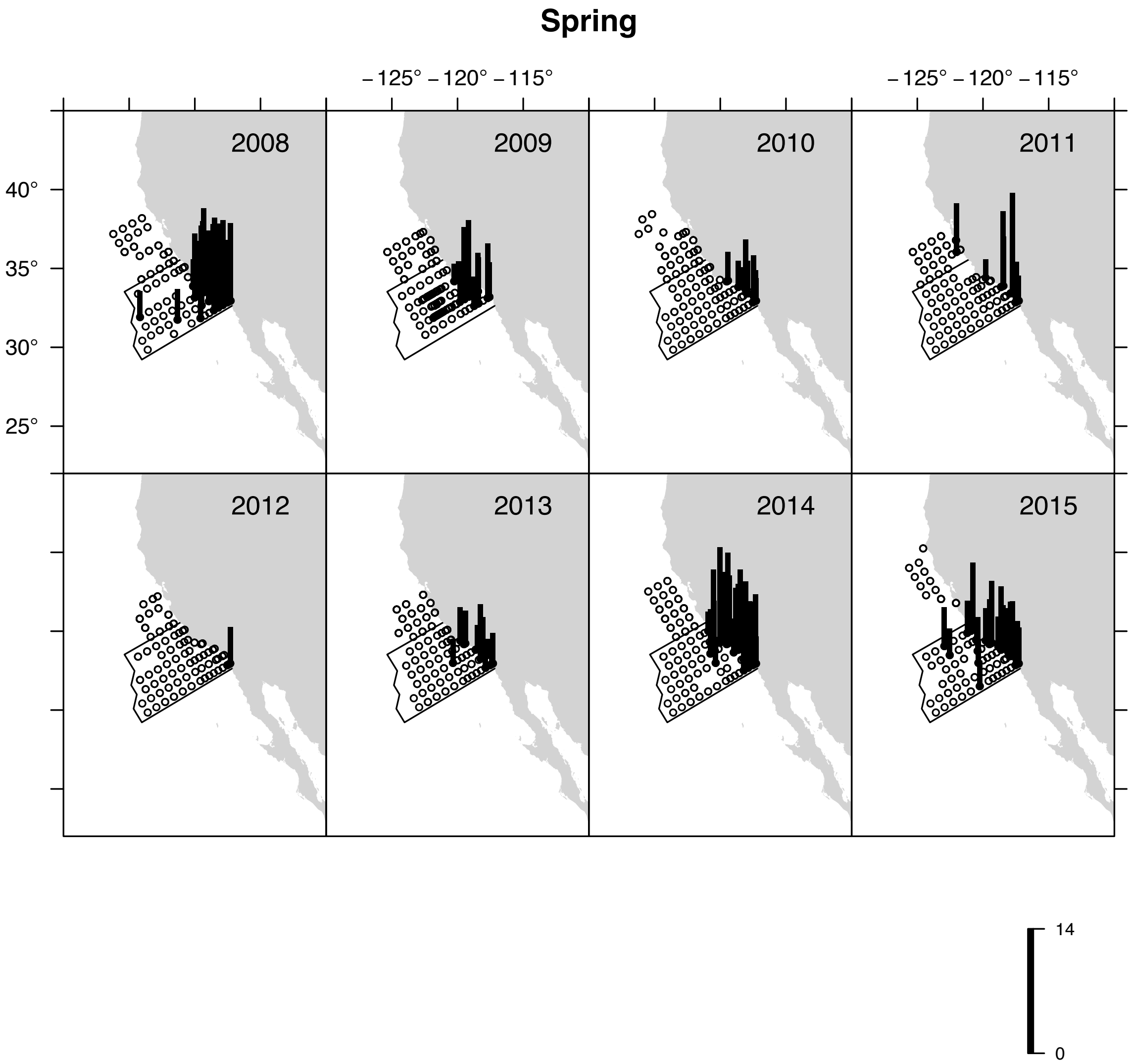
Appendix Figure 2. Continued



Appendix Figure 2. Continued



Appendix Figure 2. Continued



Appendix 1. Revisions made in response to comments made by the Coastal Pelagic Species subcommittee of the Scientific and Statistical Committee of the Pacific Fisheries Management Council

1. The historical egg-production method modified to use the spatial tessellation and jackknife variance is the preferred approach.

The other two approaches have been removed.

2. The jackknife bias-correction factor should be applied.

The correction has been applied and reported in the Methods, p. 9.

3. The annual means are unjustified.

The mean annual estimates have been removed from the manuscript.

4. If survival rates cannot be estimated for a survey because of sparse data, the mean value for surveys where they can be estimate should be used.

Mean values of egg survival (α) and larvae survival (β) have been used where needed, and this is noted in the Methods, p. 8-9.

5. There are errors in the notation for the jackknife estimate.

Corrected, equations 16-19.

6. The equation used to correct for shrinkage due to handling and preservation (Theilacker, 1980) is missing an exponent.

Corrected, equation 9.

7. The cited coefficients used to correct for extrusion of smaller larvae through the net mesh should also be reported.

Appendix Table A1 from Fissel et al. (2011) listing the extrusion coefficients has been reproduced as Appendix Table 1.

8. Recent data from 2016 are needed.

No change. Sorting and identification of 2016 samples in the laboratory has not yet been completed.

9. A comparison of egg and larval densities at SCCOOS stations with those at the inshore CalCOFI stations is needed.

Reported as Figure 6.

10. Plots are needed of the spatial sampling pattern and densities of anchovies for the CalCOFI program, including the period 1951-1984, when additional sampling outside the core area occurred.

Reported as Appendix Figures 1 and 2.

11. Explain why the extrusion correction was applied before the correction for shrinkage.

This is because the extrusion correction was developed from paired samples that were preserved and processed in the laboratory (i.e., shrinkage had already occurred). This is noted in the Methods p. 7-8.

12. The number of tows at each station should be reported.

Reported as Appendix Table 4.

13. The estimate of production at hatching is a catch curve. Its error cannot be normal.

Changed to a linear regression by taking logs, equation 13. However, the error is never used because the entire process of estimating production is refit for each jackknife resample.