



Recent collapse of northern anchovy biomass off California



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ABSTRACT

New estimates of abundance of northern anchovy (*Engraulis mordax*) are developed from California Cooperative Oceanic Fisheries Investigations (CalCOFI) data on egg and larval densities for the period 1951–2011. Previous estimates utilizing mean density over the CalCOFI area show a hyperstability bias because of the nearshore concentration of CalCOFI stations and the tendency of the anchovy population to contract into this area when abundances are low. New abundance estimates weight sample egg and larval densities to the local area represented by that sample, and then sum contributions to obtain total abundance. We develop total egg and larval abundance estimates for January and April, form a combined index, and calibrate it to the absolute biomass estimates produced by the Daily Egg Production Method in the early 1980s. Anchovy spawning biomass was very low, 10,000–20,000 Metric Tons (MT), in the early 1950s when CalCOFI sampling began. Abundance increased and fluctuated between 0.5 and 2 million metric tons from 1960 through 1990. After 1990, spawning biomass fluctuated around 200,000 tons, briefly increased during 2005–2006, then declined substantially over four years to below 20,000 tons from 2009 to 2011. CalCOFI ichthyoplankton data collected after 2011 are not yet available for analysis, but continuous underway egg sampling conducted during CalCOFI cruises indicates continued low abundance and very limited spawning through 2015 in both southern and central California. The recent collapse of anchovy abundance occurred in the absence of a significant fishery. Present annual catches of a few thousand tons are small by historical comparison, but the exploitation rate may now be relatively high given the low stock abundance. The decline in anchovy abundance coincides with recent die-offs and reproductive failures of anchovy-dependent predators in the ecosystem (e.g., sea lions and pelicans).

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1. Introduction

The central population of northern anchovy (*Engraulis mordax*) extends from northern Baja California to northern California, is an important prey resource providing forage to many upper trophic level predators, and in the past (though not recently) supported substantial fisheries in California and Mexico. The Historical Egg Production (HEP) method developed by Lo (1985) uses egg and larval abundances at size to estimate the initial egg production rate of the spawning adult population. Abundances estimated by the HEP approach have been used extensively in previous anchovy stock assessments (MacCall, 1982; Methot, 1989; Jacobson et al., 1994, 1995; Fissel et al., 2011). The last formal stock assessment was conducted in 1995 (Jacobson et al., 1994, 1995), but recent abundance estimates were published by Fissel et al. (2011) who extended the abundance time series to 2009 for the southern California region (Pt. Conception to Mexico). Fissel et al. (2011) showed a spike in egg

production in 2005 and 2006 with estimated spawning biomass briefly exceeding a million metric tons (MT), then returning to around 150,000 MT by 2008, a decline that they attributed to recent increases in egg mortality rates. This lower level is also consistent with other analyses of anchovy productivity that show declines since the 1980s, presumably related to ocean conditions and climate (Koslow et al., 2013; Lindegren et al., 2013). Although the stock has been lightly fished in recent years, Fissel et al. (2011) voiced concern about the declining stock size and urged further investigation, but did not consider the drop in abundance from 2005 to 2008 to be a significant conservation issue.

Other lines of evidence suggest that the anchovy stock off southern California may have declined precipitously since 2008. The relative abundance of anchovy eggs and larvae in the California Cooperative Oceanic Fisheries Investigations (CalCOFI; Fig. 1) surveys declined substantially over the previous two decades, and especially in the most recent years (McClatchie et al., 2011; Leising et al., 2014). In particular, findings from the January 2008 survey were unprecedented in the history of CalCOFI, with very few anchovy eggs and no larvae at all. In more recent April surveys, egg abundances remained low, and larval abundance fell below the

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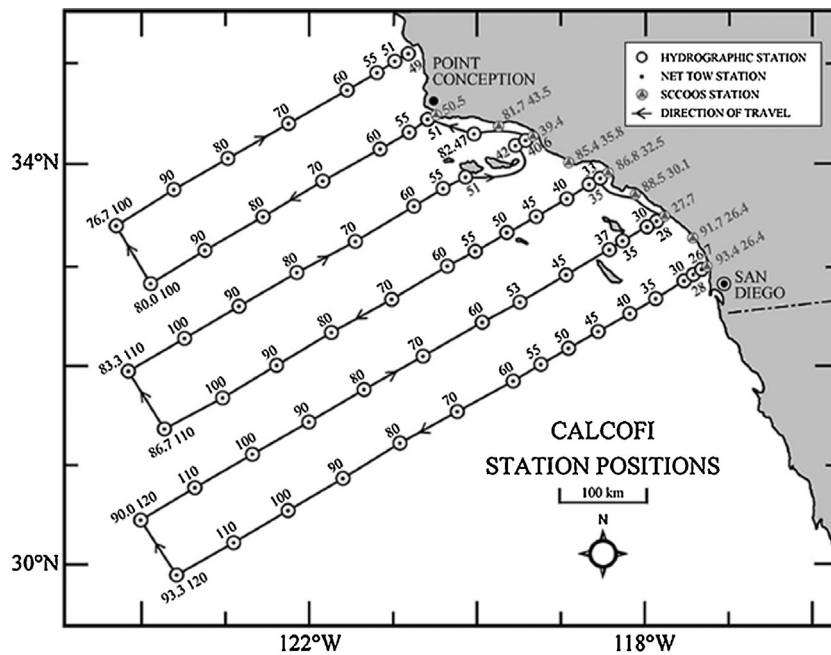


Fig. 1. Locations of core southern California CalCOFI sampling stations, showing the locations of the nine nearshore SCCOOS stations added in Fall 2004. Image web address: <http://www.calcofi.org/graphics/458-station-maps.html>.

lowest historical levels, last observed in the early 1950s. Trawl survey catch rates of adult anchovy off central California have also declined in recent years (Ralston et al., 2015), with a major decline between 2005 and 2006 and 2008–2009. Other ecological indicators such as poor breeding performance of brown pelicans off southern California (Henry, 2015), declines in seabird abundance at sea (Sydeman et al., 2015; Santora and Sydeman, 2015), unusual mortality events for California sea lions (Melin et al., 2010), and reductions of anchovy in seabird diets (e.g., Elliott et al., 2015) also suggest low availability of anchovy.

Here, we develop and calibrate a simple abundance index for the central anchovy stock, focusing on the southern California region, that revises the entire CalCOFI-based time series of anchovy abundance, as well as updating it to 2011. We also examine aspects of previous methodologies and investigate whether those biomass estimates may have been compromised by hyperstability biases (Hilborn and Walters, 1992).

2. Materials and methods

Spawning (egg production) by the central subpopulation of northern anchovy typically lasts from January to May each year, but within individual years, the monthly pattern of spawning can be irregular (Methot, 1983). Generally, average egg abundances are much higher in March/April than in January, with no trends in spawning phenology (Asch, 2015). Failure to account for seasonality is a source of imprecision, and the aliasing resulting from a systematic temporal mismatch of sampling may introduce bias at the decadal scale. These sources of imprecision and bias are difficult to eliminate. However, they can be reduced by disaggregating the data into monthly components. For these reasons, we used data from January and April separately, and estimated separate biomass scaling factors (see below).

2.1. Sampling issues

The habitat utilized by spawning anchovies expands into the offshore region in times of high abundance and contracts into

nearshore core areas when abundances are lower (MacCall, 1990; Fig. 2). This pattern of redistribution has serious consequences for abundance estimates. First, range expansion at high abundance and contraction at low abundance mean that samples from individual stations are not identically and independently distributed (*iid*). Because we cannot assume *iid*, bootstrap resampling techniques for variance calculations, cannot be justified. Second, the average density over all CalCOFI stations will not decline in proportion to the decline in population size because the CalCOFI sampling pattern has a higher density of stations in the nearshore region favored by anchovies at low population sizes, leading to “hyperstability” bias (Hilborn and Walters, 1992). Third, nine very nearshore stations were added to the CalCOFI grid by the Southern California Coastal Ocean Observing System (SCCOOS), with larval and egg sampling beginning in fall 2004 (Fig. 1). These stations are in the area occupied by anchovies when at their lowest abundances (Fig. 2) and may exhibit higher densities than are observed at an average CalCOFI station, many of which regularly have very low or zero densities. Thus, for this paper’s purpose of obtaining a consistent long-term sampling frame, adding the nearshore SCCOOS stations to the dataset has two potential detrimental effects: (1) it causes a systematic increase in the estimates of anchovy production compared to years in which these stations were not sampled, and (2) it likely increases the hyperstability bias.

We excluded the nine SCCOOS stations from our analysis to deal with these sampling issues. A statistical solution to the hyperstability issue is to expand densities separately for each CalCOFI station to obtain local population estimates, which are then summed to estimate the overall abundance in the study region. This approach is not new. Historically, this analytical technique was referred to as the “larva census” approach, described by Sette and Ahlstrom (1948). However, it is computationally complex in that it requires estimation of the area sampled by each standard station. To estimate the area sampled at each station, we calculated station-specific Thiessen polygons (Okabe et al., 2000). Thiessen polygons are a well-established technique for integrating abundance over irregularly-spaced sampling locations, and this approach is robust to the systematic abundance-related changes in spawning

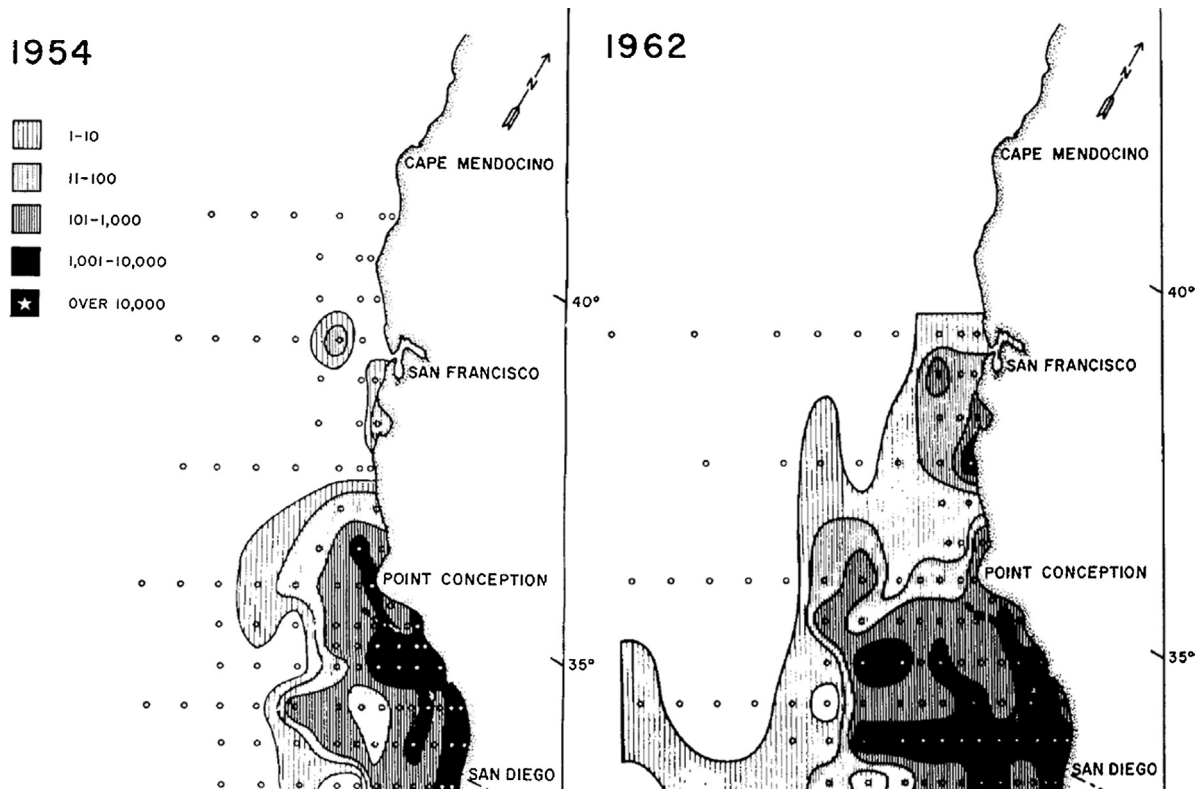


Fig. 2. Comparison of southern California anchovy larval distributions at low population size (left) and high population size (right) showing areal expansion when the stock is more abundant. Taken from Kramer and Ahlstrom (1968).

distribution described by MacCall (1990). Therefore, most geostatistical approaches (e.g., stratification and weighting) are highly questionable due to time-varying anisotropic properties of anchovy distribution. We used a jackknife resampling approach that preserves the spatial structure of sampling (see below).

2.2. Abundance indices

The most complete CalCOFI sampling for the 61-year period 1951–2011 has been in the southern California region, where we were able to develop population estimates for 51 of those years. Central California has been sampled less consistently, and we were able to develop population estimates for only 33 years, with substantial gaps in the middle of the time series; for this reason, although we present ichthyoplankton indices that include central California we do not use them to estimate biomass. Mexican waters have not been sampled by CalCOFI since the 1970s, and thus we did not attempt to estimate anchovy abundance there.

We considered two sets of CalCOFI cruises (data were obtained from <http://www.calcofi.org/>), those surveys with any portion occurring in January, and those with any portion occurring in April. For each cruise, we constructed a set of Thiessen polygons (also known as Voronoi diagrams or tessellations). Each Thiessen polygon defines an area of influence around its sample point so that any location inside the polygon is closer to that point than any of the other sample points (Fig. 3). The egg or larval population estimate (P_{ijk}) for each year (i), ichthyoplankton type ($j = \text{eggs or larvae}$) and season ($k = \text{January or April}$) is the sum of the products of station-specific (s) polygon areas (A_{iks}) and sampled density (D_{ijks}) or mean density if the station was sampled more than once:

$$P_{ijk} = \sum_s D_{ijks} A_{iks}$$

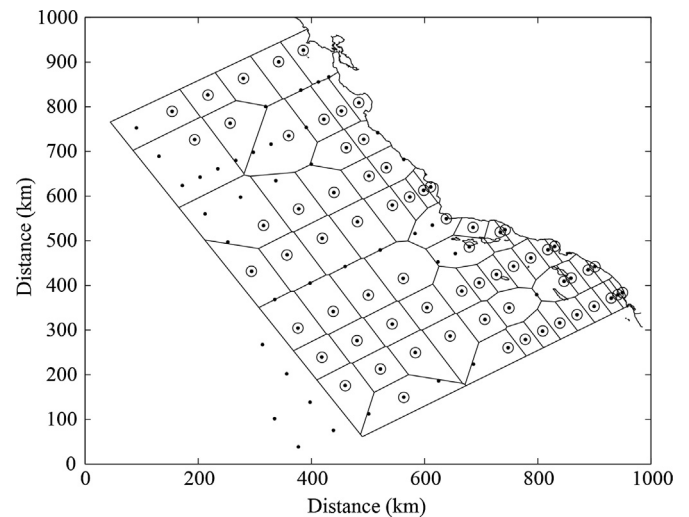


Fig. 3. Example set of Thiessen polygons for April, 2008. Dots indicate standard CalCOFI stations, and circles indicate occupied stations.

The values of A_{iks} depend on which adjacent stations were sampled in a given year and season. Samples obtained off-transect were omitted, and samples between standard stations were assumed to represent the closest standard station. If multiple samples occurred at a station, their mean density was used. We applied the tessellation approach to both the “core” 6-line southern California region and to the “full” region including central California north to San Francisco (Fig. 3 is an example of the latter). We consider egg and larval data separately, so a complete year produced four indices, two for January and two for April. In many years, only one of the two seasons (January or April) was sampled. Each of the four indices was scaled to unit mean for the period 1951–1999, and a combined

index was produced by averaging the 2–4 indices for each year. We did not use larval data after 1999 due to an apparent increase in egg or larvae mortality rates that would bias the recent larval index lower relative to the prior portions of the time series (see Section 3). We calculated arithmetic means that allowed retention of cruises with zero estimates, i.e., where either no eggs or larvae were sampled, which occurred in some of the earliest and most recent years. These instances of zero values made the use of log transformations difficult, so we did not pursue that possibility.

Precision of abundance estimates was calculated using a jackknife procedure, whereby each sample was deleted one at a time and unless multiple samples were taken (which occurred only rarely), the tessellation was recalculated so that regions of the deleted tile were reassigned to values of $A_{i,ks}$ for expanded tiles associated with adjacent samples; importantly, the total survey area remained constant for all years and all jackknife re-samplings. A new abundance estimate was obtained with each deletion, and results were combined to produce precision estimates (Efron and Stein, 1981). The jackknife procedure provided variance estimates for each of our four indices. In order to produce a variance estimate for the combined index, we first considered the survey years in which all four indices existed, and examined the matrix of correlations among the anomalies from the common mean. The largest correlation was -0.63 between January eggs and April eggs (Fig. S1), and was driven by two outliers. We therefore ignored the covariances in calculating approximate variances, simplifying calculation of the estimated variance:

$$\text{Var}(I_i) = \frac{1}{n^2} \sum_j \text{Var}(\Theta_{ij})$$

where I_i is the combined abundance index for year i , and Θ_{ij} are the two or four standardized individual indices, i.e., $j = 1, \dots, n$ and n is either 2 or 4. This approximation tends to overestimate the variance because the ignored negative covariances would be subtracted and result in a smaller estimate. Precision estimates of the combined egg and larval abundance index do not include additional uncertainty in the relationship between the combined index and the actual spawning biomass.

2.3. Calibration of abundance indices to biomass

The area-weighted combined egg and larval abundance index extends from 1951 to 2011. We calibrated this index by a least-squares fit to the daily egg production method (DEPM) biomass estimates produced from 1980 to 1985 (summarized in Jacobson et al., 1994). DEPM has been the basis of scaling for all subsequent anchovy assessments (Jacobson et al., 1994; Methot, 1989). The DEPM estimates provide the best basis for calibrating our area-weighted index, as they are not dependent on arbitrary model specifications or assumed parameter values typical of statistical population dynamics models. We have new index values for three of the DEPM years, 1981, 1982, and 1984; 1982 only has values for April, but the other two years include both January and April.

3. Results

From the 1950s through the early 1990s, larvae tended to be more abundant than eggs in January, and about equally abundant in April. Over the entire time series, April egg abundances were threefold higher than those for January, and larval abundances were higher by a ratio of 1.6. Since the mid-late 1990s, the relative abundance of larvae relative to eggs has declined by about three logarithmic units (-95% ; Fig. 4; see also Fissel et al., 2011). We applied the biomass calibration to the area-weighted combined egg and larval abundance index (excluding use of larvae after 1999) to

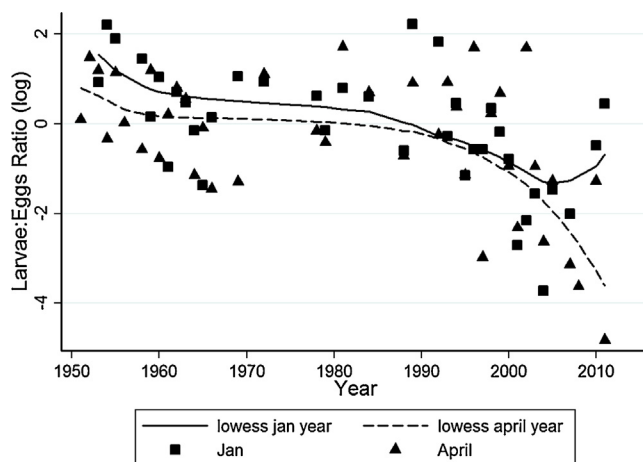


Fig. 4. Trend in abundances of larvae relative to eggs in southern California. January is solid line; April is dotted line.

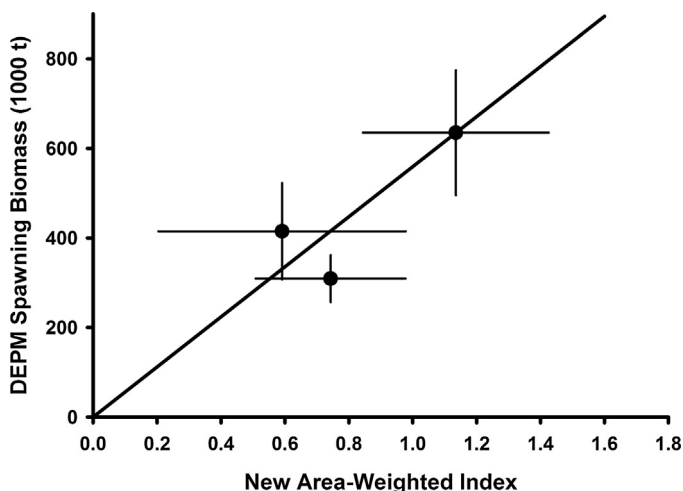


Fig. 5. Calibration of new area-weighted index based on relationship to DEPM estimates of spawning biomass (CV = 0.15). Error bars are one standard error.

derive an anchovy biomass index for the period 1951–2011. The relationship between the three area-weighted indices and the DEPM values for these three years is shown (Fig. 5). A calibration of 559,000 MT per index unit was provided by the mean of the three ratios of DEPM biomass to new index value. The CV of the three values was 0.15, and unlike previous abundance estimates, calibration variance is included in precision estimates of biomass derived from the new index. The estimated abundance in 2009–2011 is similar to the extremely low biomasses estimated for the early 1950s (Fig. 6 and Tables S1–S3). A logarithmic scale shows the magnitude of the recent decline in abundance. The new biomass estimates show higher values than those estimated by Jacobson et al. (1994) in 1957–1960, 1963–1966, 1969, and in 1986, but otherwise are in general agreement (Fig. 7). There are similar discrepancies with the time series estimated by Methot's (1989) age-structured model. The time series by Methot (1989) and by Jacobson et al. (1994) shared similar data inputs (including aerial spotter logbooks that were very sparse in the early 1960s), and are not independent of each other.

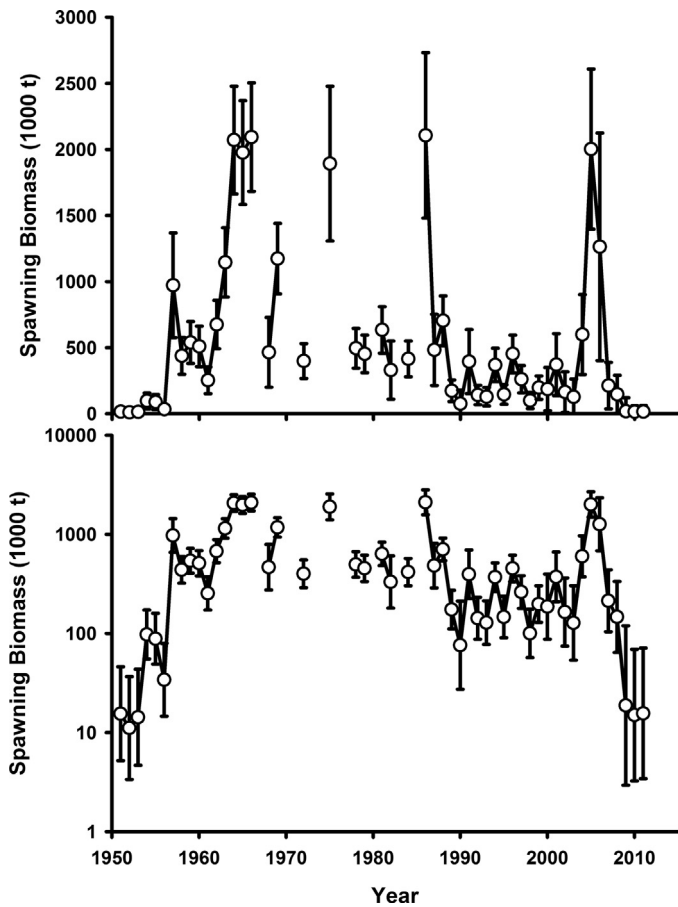


Fig. 6. Time series of anchovy biomass estimated by the area-weighted method. Error bars in upper panel are one standard error and include calibration variance. Lower panel is on logarithmic scale.

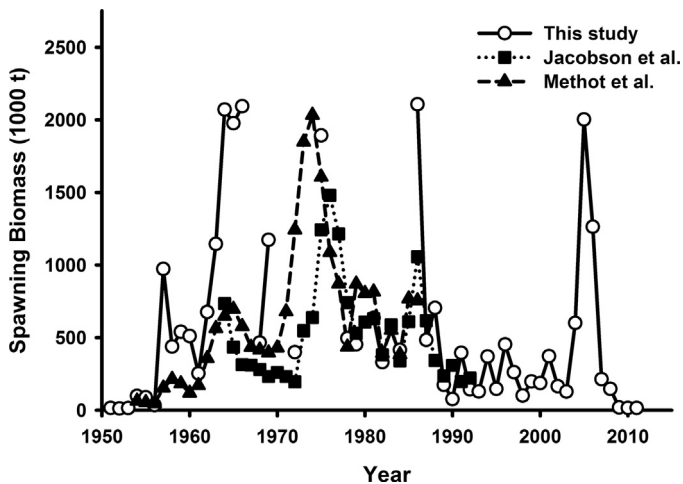


Fig. 7. Comparison of new area weighted biomass estimates (circles) and corresponding biomass estimates from Jacobson et al., (1994) (squares, solid line) and Methot, (1989) (triangles, dotted line).

3.1. Hyperstability bias

Scatterplots of egg production estimates (egg production index (EPI) and HEP) demonstrate hyperstability (Fig. 8). Power function exponents are 0.55 for EPI and 0.46 for HEP relative to area-weighted biomass estimates, thus EPI and HEP values vary approximately as the square root of stock biomass. Notably, these

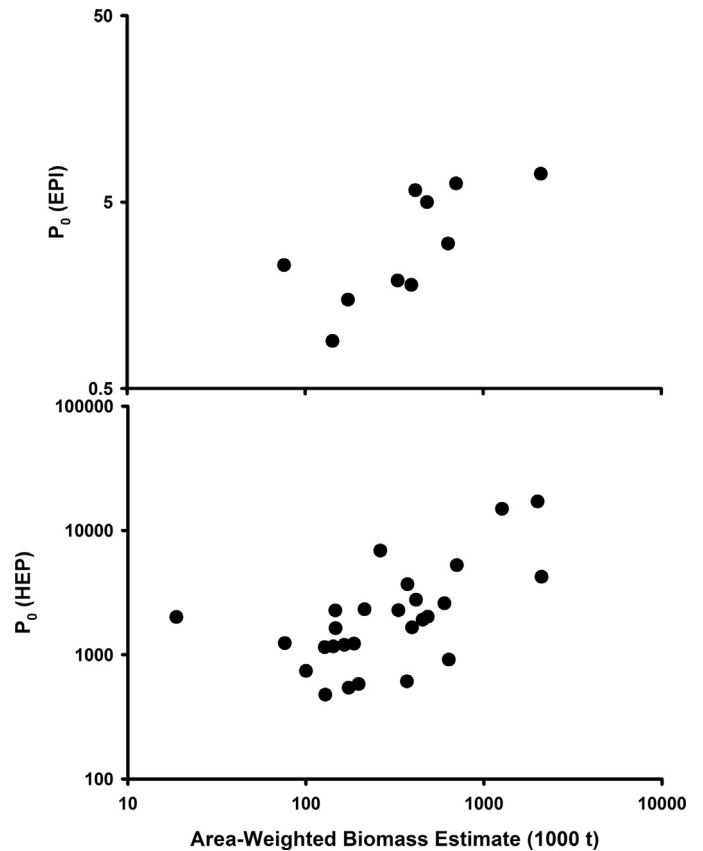


Fig. 8. Above: scatterplot of EPI estimates of daily egg production rate (P_0) with area-weighted biomass estimates (Spearman rho = 0.71), showing hyperstability (fitted power function exponent < 1). Below: scatterplot of egg production rate (P_0) estimates from Fissel et al. (2011) with area-weighted biomass estimates (Spearman rho = 0.42), also showing hyperstability.

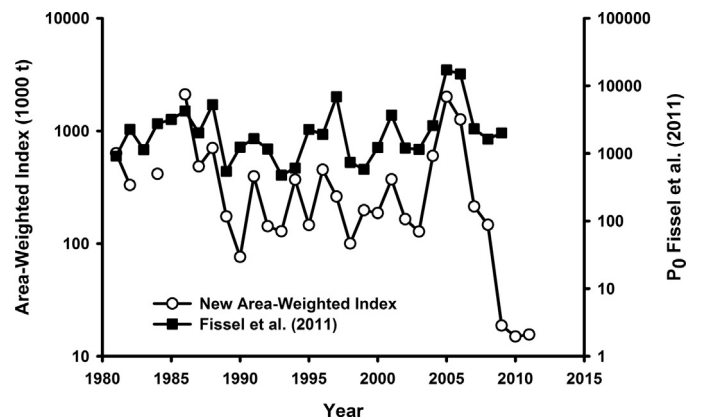


Fig. 9. Comparison of time series of egg production rate (P_0) estimates from Fissel et al. (2011) with area-weighted biomass estimates, including additional values for 2010 and 2011.

time series do not include low biomass years where hyperstability would be most apparent. The area-weighted estimates have a low correlation (rho = 0.4) with egg production indices from Fissel et al. (2011; Fig. 8). There is evidence of hyperstability in Fissel et al. (2011), especially in the 2009 estimate that appears as an outlier on the left in lower Fig. 8. When viewed as a time series (Fig. 9), the first half of the time series compares reasonably well, but an offset begins in the mid-2000s, corresponding with the change in egg-larvae ratios.

Table 1
Statistical relationship between full California estimates and southern California area-expanded population estimates.

Ratio (full/core)	January		April		All
	Eggs	Larvae	Eggs	Larvae	
N	25	25	29	29	108
Mean	1.37	1.1	1.16	1.06	1.17
Fraction above mean	0.19	0.23	0.14	0.28	0.21
Fraction at 1.0	0.44	0.24	0.52	0.48	0.43

Table 2
Ratios of full California to southern California area-expanded populations in recent years.

Year	January		April	
	Eggs	Larvae	Eggs	Larvae
2003	4.22	1.32	1	1
2004	1.18	1.39	1.01	1.12
2005	1.18	1.66	1.09	1.01
2006			1.09	1
2007	1.02	1.15	1	1.01
2008	1	1	1	1
2010	1	1.43	1	1
2011	1	1	1.28	1

3.2. Abundance estimates from Central California

Area-weighted abundance estimates of anchovy eggs and larvae for southern to central California (San Diego to San Francisco) are available in only 22 years, and very few estimates exist for the 1980s and 1990s (Table S4). Anchovy egg and larval abundances in central California are usually lower than in southern California. Relative abundance of eggs and larvae in central California tends to be somewhat higher in January than in April (Table 1). Statistical distributions are strongly skewed, with frequent near-zero abundances and rare large values in central California. Central California values were zero in 43% of the years, and contributed about 15% to the overall mean abundance estimate. Overall, the median abundance value for the full area was only 1% greater when including the central California region than that for southern California alone (Table 2). Notably, the abundance indices including central California have been low or zero since 2006, indicating that the decreased biomass off southern California is not explained by a redistribution of spawning adults to central California.

4. Discussion

The anchovy biomasses estimated from 2009 to 2011 using the area-weighted method developed here are the lowest seen in 60 years, and are matched only by similarly low values at the start of the CalCOFI sampling program in 1951–1953. Surveys of anchovy from mid-water trawls designed to survey juvenile rockfish (*Sebastes* spp.) from southern to central California corroborate this decline (Ralston et al., 2015). Although the most recent CalCOFI sample data are not yet available, the results from the Continuous Underway Fish Egg Sampler (CUFES) from recent sampling cruises have been reported by the NMFS Southwest Fisheries Science Center through 2015 (<https://swfsc.noaa.gov/textblock.aspx?Division=FRD&ParentMenuId=218&id=1340> and <https://swfsc.noaa.gov/textblock.aspx?Division=FRD&id=16135>). The published maps can be interpreted qualitatively: although anchovy eggs are usually widespread and numerous, the last substantial abundance of anchovy eggs was seen in 2008. Only a small number of anchovy eggs were encountered in 2009. No anchovy eggs were seen in 2010, 2012, and 2013, and very low numbers were observed in 2011. A slight increase in egg abundance

appeared in 2014, but only a trace appeared in 2015. We conclude that there has been no substantial recovery of the anchovy population as of 2015. The mean abundance estimated for the last three years (2009–2011) was three percent of the long-term average historical abundance estimated for 1951 through 2011 (mean = 550,000 MT), but this is very imprecise; the confidence intervals suggest that abundance was well below twenty percent of that mean.

The population was small when CalCOFI began sampling the California Current for anchovy eggs and larvae in 1951. Estimated adult biomass subsequently increased to nearly one million tons in the 1960s (MacCall, 1982). A popular explanation of the initial scarcity was that competition with sardines had held anchovies at a low abundance, and that the increase during the 1950s was associated with “competitive release” due to the decline of sardines (Murphy, 1966). However, Smith (1972) analyzed egg and larval densities from CalCOFI-like surveys conducted during 1940–1941, and concluded that anchovy abundance had been in the million-ton range then, which did not support the competition hypothesis. MacCall (1980) hypothesized that “the anchovy encountered a long series of poor recruitments during the late 1940s, and the subsequent CalCOFI records document the recovery to more normal levels of abundance”. Subsequent population modeling (MacCall, 1982), though, was unable to produce fluctuations consistent with the low levels of the early 1950s, confirming that whatever happened in the late 1940s and early 1950s was not within the range of recent “normal” population dynamics. However, the millennial-scale sedimentary deposition record from the Santa Barbara Basin clearly indicates centennial-scale episodes of disappearance or near-disappearance of anchovy and sardine, establishing that, at the longest time scales, occasional severe declines in abundance are a characteristic feature of the population residing in southern California (Baumgartner et al., 1992). While there have been recent anecdotal reports of substantial nearshore anchovy abundance¹, we hypothesize that much of the remnant population is concentrated close to shore, making them unusually visible to the public and giving a mistaken impression of abundance (hyperstability bias).

Now, 60 years after the beginning of CalCOFI egg and larval sampling, we have well-documented evidence for a sudden decline in anchovies, with probable mechanisms similar to MacCall’s (1980) hypothesis, though the explanatory details are still not clear. The anchovy population declined from at least a million tons in 2005 to about 15,000 tons estimated for 2009–2011. Remarkably, this decline occurred in the near-absence of fishing and therefore must be considered a natural phenomenon. Support for this interpretation also comes from millennial-scale records when anchovy collapses occurred in the absence of fishing. Alheit and Niquen (2004) described a similar collapse in the Peruvian anchoveta population in the early 1970s, but concluded that fisheries had undoubtedly contributed to the decline. In addition to apparent near-zero recruitment, the natural mortality rate during 2005–2009 appears to be far above normal for the central sub-population. In an assumed absence of recruitment and negligible fishing pressure, the four-year rate of decline in biomass gives an estimated natural mortality rate (M) of approximately 1.2 yr^{-1} , about twice that assumed by Jacobson et al. (1994). If recruitment was greater than zero, the observed decline in abundance would require the estimated M to be higher yet. The severe decline in anchovies is a likely factor in recent reports of reproductive failure,

¹ Herreria, C., 2014. Enormous school of anchovies makes rare appearance at Scripps Pier in San Diego. *Huffington Post*, 7/11/2014. http://www.huffingtonpost.com/2014/07/11/school-of-anchovies-san-diego_n_5572928.html. (accessed 1.06.15).

mortality, and declines of California's marine mammals (Melin et al., 2010) and seabirds (Henry, 2015; Sydeman et al., 2015). In previous historical experience, the return of viable reproductive conditions during the mid-1950s allowed rapid recovery of the anchovy population. It is reasonable to expect that abundance could recover quickly again if and when favorable conditions return. However, other factors such as predation may be currently limiting population growth. Major anchovy predators, such as California sea lions and humpback whales, have recovered from their very low abundances during the 1950s (Carretta et al., 2014; Calambokidis and Barlow, 2004), and may now be consuming a larger fraction of the anchovy population, especially under the presently low abundances and nearshore concentrations.

In addition to the ecological aspects of the anchovy decline, this study raises concerns about previous anchovy assessment methodology. In particular, previous studies that used equally-weighted average overall densities and bootstrap techniques are not appropriate for a species that contracts its range into the most densely sampled region of a study grid. Spatially-explicit methodology for area-weighting or expansion of CalCOFI samples is essential for anchovy assessments. Because the use of space by anchovy is not even, inclusion of the partial time series from SCCOOS stations is also problematic. Previous studies also used temperature corrections to estimate anchovy egg production (e.g., Lo, 1985; Fissel et al., 2011); such corrections should be retained, but need to be combined with the spatial approach we have developed here. Last, since about 2000, there has been a decrease in January egg and larval abundances relative to those seen in April. Whether this is a contraction of the spawning season or an overall shift to a later spawning season cannot presently be determined. Hunter and Leong (1981) showed that the number of spawnings during the reproductive season depends on adult anchovy feeding conditions both before and during the spawning season, so this change in spawning seasonality could be associated with poorer feeding conditions. Other changes in spawning rates are also possible and may affect our abundance estimates. We used data from January and April separately and estimated separate biomass scaling factors. In contrast, Fissel et al. (2011) combined all samples from January through April without consideration for seasonal variations in spawning nor trends in the timing of spawning.

5. Conclusion

Northern anchovy, an important component of the forage fish community of the California Current ecosystem, has declined substantially off southern California in the past decade. The estimated spawning biomass decreased by over 99% from 2005 to 2009, and merits the term “collapse”. An unknown but probably large portion of the remaining remnant population now consists of conspicuous large nearshore shoals, which are prone to hyperstability bias in interpretation, especially by members of the public. Given the limited fishing effort for this species in recent years, natural phenomena unrelated to fishing are the primary explanation for the decline. The current anchovy biomass off southern California is estimated at less than 20,000 MT (CI < 100,000 MT), similar only to the inexplicably low biomasses seen in the early 1950s. Although current annual catch levels of a few thousand tons are small by historical standards, current exploitation rates could be high given the low stock abundance, and should be taken under consideration by fishery managers.

Previous CalCOFI-based abundance estimates for anchovies have suffered from hyperstability bias due to lack of an explicitly spatial estimation method. Future assessments should include local area-expansion, seasonality, and standardization of stations included in time series analysis. Specifically, addition of nearshore

and other non-standard sampling stations may exacerbate hyperstability problems, though this is easily rectified through careful data selection procedures. The systemic causes of the recent decline in abundance are not clear, and should be a subject of future research. However, one of the proximal causes of the decline is the decrease in egg and larval survivorship during the past decade, as noted by Fissel et al. (2011). The cause of that mortality is not presently known, but the consequence was a severe reduction in the production of recruitment age fish. The decline in abundance happened faster than can be explained by poor recruitment alone, indicating that the natural mortality rate of adults also probably increased.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.fishres.2015.11.013>.

References

- Alheit, J., Niquen, M., 2004. Regime shifts in the Humboldt Current ecosystem. *Prog. Oceanogr.* 60, 201–222.
- Asch, R.G., 2015. Climate change and decadal shifts in the phenology of larval fishes in the California Current systems. *Proc. Nat. Acad. Sci.*, <http://dx.doi.org/10.1073/pnas.1421946112>.
- Baumgartner, T.R., Soutar, A., Ferreira-Bartrina, V., 1992. Reconstruction of the history of Pacific Sardine and northern anchovy populations over the past two millennia from sediments of the Santa Barbara Basin, California. *Calif. Coop. Ocean. Fish. Invest. Rep.* 33, 24–40.
- Calambokidis, J., Barlow, J., 2004. Abundance of blue and humpback whales in the eastern North Pacific estimated by capture-recapture and line-transect methods. *Mar. Mamm. Sci.* 20, 63–85.
- Carretta, J.V., Oleson, E., Weller, D.W., Lang, A.R., Forney, K.A., Baker, J., Hanson, B., Martien, K., Muto, M.M., Orr, A.J., Huber, H., Lowry, M.S., Barlow, J., Lynch, D., Carswell, L., Brownell Jr., R.L., Mattila, D.K., 2014. U.S. Pacific marine mammal stock assessments, 2013. NOAA Tech. Memo. NOAA-TM-NMFS-SWFSC-532, 414.
- Efron, B., Stein, C., 1981. The jackknife estimate of variance. *Ann. Stat.* 9, 586–596.
- Elliott, M.L., Bradley, R.W., Robinette, D.P., Jahncke, J., 2015. Changes in forage fish community indicated by the diet of the Brandt's cormorant (*Phalacrocorax penicillatus*) in the central California Current. *J. Mar. Sys.* 146, 50–58.
- Fissel, B.E., Lo, N.C.H., Herrick, S.E., 2011. Daily egg production: spawning biomass and recruitment for the central subpopulation of northern anchovy 1981–2009. *Calif. Coop. Ocean. Fish. Invest. Rep.* 52, 116–129.
- Henry, S.P., 2015. Pacific Fishery Management Council Agenda Item G.3–Anchovy Update. Agenda Item G.3. a USFWS Report. http://www.pcouncil.org/wp-content/uploads/2015/05/G3a_USFWS_Rpt_JUN2015BB.pdf. (accessed 15.06.15).
- Hilborn, R., Walters, C.J., 1992. *Quantitative Fisheries Stock Assessment: Choice, Dynamics and Uncertainty*. Chapman and Hall, New York.
- Hunter, J.R., Leong, R., 1981. The spawning energetics of female northern anchovy, *Engraulis mordax*. *Fish. Bull.* 79, 215–230.
- Jacobson, L.D., Lo, N.C.H., Barnes, J.T., 1994. A biomass-based assessment model for northern anchovy, *Engraulis mordax*. *Fish. Bull.* 92, 711–724.
- Jacobson, L.D., Lo, N.C.H., Herrick Jr., S.F., Bishop, T., 1995. Spawning stock biomass of the northern anchovy in 1995 and status of the coastal pelagic fishery during 1994. Administrative Report LJ-95-11, National Marine Fisheries Service.
- Koslow, J.A., Goericke, R., Watson, W., 2013. Fish assemblages in the Southern California Current: relationships with climate, 1951–2008. *Fish. Oceanogr.* 22, 207–219.
- Kramer, D., Ahlstrom, E., 1968. *Distributional atlas of fish larvae in the California Current region: Northern anchovy, Engraulis mordax, 1951 through 1965*. Calif. Coop. Ocean. Fish. Invest. Atlas 9, 269.
- Leising, A.W., Schroeder, I.D., Bograd, S.J., Bjorksted, E., Field, J., Sakuma, K., Abell, J., Robertson, R.R., Tyburczy, J., Peterson, W., Brodeur, R.D., Barcelo, C., Auth, T.D.,

- Daly, E.A., Campbell, G.S., Hildebrand, J.A., Suryan, R.M., Gladics, A.J., Horton, C.A., Kahru, M., Manzano-Sarabia, M., McClatchie, S., Weber, E.D., Watson, W., Santora, J.A., Sydeman, W.J., Melin, S.R., DeLong, R.L., Largier, J., Kim, S.Y., Chavez, F.P., Golightly, R.T., Schneider, S.R., Warzybok, P., Bradley, R., Jahncke, J., Fisher, J., Peterson, J., 2014. State of the California Current 2013–2014: El Niño looming. *Calif. Coop. Ocean. Fish. Invest. Rep.* 55, 51–87.
- Lindgren, M., Checkley Jr., D.M., Rouyer, T., MacCall, A.D., Stenseth, N.C., 2013. Climate, fishing, and fluctuations of sardine and anchovy in the California Current. *Proc. Nat. Acad. Sci.* 110, 13672–13677.
- Lo, N.C.H., 1985. Egg production of the central stock of northern anchovy *Engraulis mordax*, 1951–1982. *Fish. Bull.* 83, 137–150.
- MacCall, A.D., 1980. Population models for the northern anchovy (*Engraulis mordax*). *Rapp. P.-v. Reun. Cons. Int. Explor. Mer.* 177, 292–306.
- MacCall, A.D., 1982. Population model and simulations for the revised anchovy management plan. *Southwest Fish. Sci. Center Admin. Rep.* LJ-82-30, 15.
- MacCall, A.D., 1990. *Dynamic Geography of Marine Fish Populations*. University of Washington Press, Seattle, Washington.
- McClatchie, S., Brodeur, R.D., Field, J.C., Weber, E., Thompson, A.R., Emmett, R.L., Crone, P.R., Hill, K.T., Barcelo, C., Wells, B.K., 2011. *Coastal pelagics and forage fishes*. CCIEA Phase II Report 2012: Ecosystem Components, Fisheries. Southwest Fisheries Science Center, NOAA Fisheries.
- Melin, S.R., Orr, A.J., Harris, J.D., Laake, J.L., DeLong, R.L., 2010. Unprecedented mortality of California sea lion pups associated with anomalous oceanographic conditions along the central California coast in 2009. *Calif. Coop. Ocean. Fish. Invest. Rep.* 51, 182–194.
- Methot, R.D., 1983. Seasonal variation in survival of larval northern anchovy *Engraulis mordax*, estimated from the age distribution of juveniles. *Fish. Bull.* 81, 741–750.
- Methot, R.D., 1989. Synthetic estimates of historical abundance and mortality for northern anchovy. *Amer. Fish. Soc. Symp.* 6, 66–82.
- Murphy, G.I., 1966. Population biology of the Pacific sardine (*Sardinops caerulea*). *Proc. Calif. Acad. Sci. Ser.* 4 34, 1–84.
- Okabe, A., Boots, B., Sugihara, K., Chiu, S.N., 2000. *Spatial Tessellations: Concepts and Applications of Voronoi Diagrams*, second ed. John Wiley and Sons, West Sussex, England.
- Ralston, S., Field, J.C., Sakuma, K.M., 2015. Long-term variation in a central California pelagic forage assemblage. *J. Mar. Sys.* 146, 26–37.
- Santora, J.A., Sydeman, W.J., 2015. Persistence of hotspots and variability of seabird species richness and abundance in the southern California Current. *Ecosphere* 6, 214.
- Sette, O.E., Ahlstrom, E.H., 1948. Estimations of the abundance of the eggs of the Pacific pilchard (*Sardinops caerulea*) off southern California during 1940 and 1941. *J. Mar. Res.* 7, 511–542.
- Smith, P.E., 1972. The increase in spawning biomass of northern anchovy (*Engraulis mordax*). *Fish. Bull.* 70, 849–874.
- Sydeman, W.J., Thompson, S.A., Santora, J.A., Koslow, J.A., Goericke, R., Ohman, M.D., 2015. Climate-ecosystem change off southern California: Time-dependent seabird predator-prey numerical responses. *Deep-Sea Res.* 112 (Pt. II), 158–170.