ARE THERE TEMPORAL OR SPATIAL GAPS IN RECENT ESTIMATES OF ANCHOVY OFF CALIFORNIA?

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ABSTRACT

MacCall et al. (2016) recently published an estimate of the biomass of the central stock of northern anchovy (*Engraulis mordax*) off the coast of California, and found that this stock experienced a population crash from 2009–15. However, anecdotal observations concurrent to the collapse suggested that anchovy were extremely abundant. We used central and southern California data from two trawling surveys, ichthyoplankton time series, and aerial surveys to investigate whether or not any anchovy spawning was missed by MacCall et al. We found no evidence using additional and more recent data that 1) anchovy adults migrated north of the study area, 2) there was a large biomass of anchovies near shore, or 3) spawning was temporally missed by MacCall et al. Thus, we conclude that the 2009–15 population crash is real and that the anchovy population remnant contracted to extremely nearshore habitat where it appeared paradoxically abundant to observers.

INTRODUCTION

MacCall et al. (2016) recently estimated the biomass of the central stock of northern anchovy (*Engraulis mordax*) off California from the California Cooperative Oceanic Fisheries Investigations (CalCOFI) ichthyoplankton time series calibrated to past stock estimates made using the daily egg production method (Lo 1985a; Jacobson et al. 1994). MacCall et al. found that the California anchovy stock is experiencing a population crash, and that the stock size may be as low as 15,000 t (2009–11; 95% CI <100,000 t). However, recent anecdotal reports state that anchovy are abundant (Bartolone 2014; Gaura 2015). Thus, it is possible that the MacCall et al. estimate missed spawning that was inshore, north of their study area off central California, or outside of their study periods (Parrish 2015). We examine the evidence in support of and against the argument that there remains a significant anchovy stock off central and southern California that was not observed by MacCall et al.

The anchovy is a schooling coastal pelagic fish species that has undergone large oscillations in abundance for thousands of years, with periodicity of ~60 y (Baumgartner et al. 1992; MacCall 1996; Field et al. 2009). Several authors have linked population oscillations to climate influences (Lehodey et al. 2006; Lindegren et al. 2013). Indeed, the current collapse described by MacCall et al. (2016) occurred in the absence of a significant fishery, and occurred ~60 y after the last anchovy population crash in the early 1950s. Anchovy are a relatively small and short-lived species (most <16 cm in length; most fishes <5 y in age; Schwartzlose et al. 1999), with high fecundity and mortality, and are thought to do well in colder waters associated with high coastal upwelling (Rykaczewski and Checkley 2008; Lindegren et al. 2013). There are historically three population centers for anchovy on the Pacific coast of North America: a northern stock near the Columbia River mouth, a central stock concentrated in the Southern California Bight (SCB) and Monterey Bay (Schwartzlose et al. 1999; Zwolinski et al. 2012), and a southern stock off the Baja California coast.

MacCall et al. (2016) developed their anchovy biomass estimate using CalCOFI ichthyoplankton data from southern California. Although one cannot logically prove that there is no "hidden stock" of anchovies in the California Current system (CCS) that eluded the methods of MacCall et al., it is possible to test whether their conclusions are consistent with independent data and data that were excluded from their analysis. We compared egg, larval, and adult anchovy abundance and distribution in years when stock assessments were high, moderate, and low and logically tested whether the reported ichthyoplankton decline was consistent with migration of the SCB population inshore or north to central California. To address the possibility that spawning was missed temporally we looked at monthly means of CalCOFI ichthyoplankton abundance, and discuss the results in context with the phenology of anchovy in the CCS.

METHODS

We use data collected from several large-scale anchovy sampling programs operating approximately annually in the study area: CalCOFI ichthyoplankton, CalCOFI continuous underwater fish egg sampler (CUFES), the National Marine Fisheries Service (NMFS) Southwest Fisheries Science Center (SWFSC) juvenile rockfish sur-

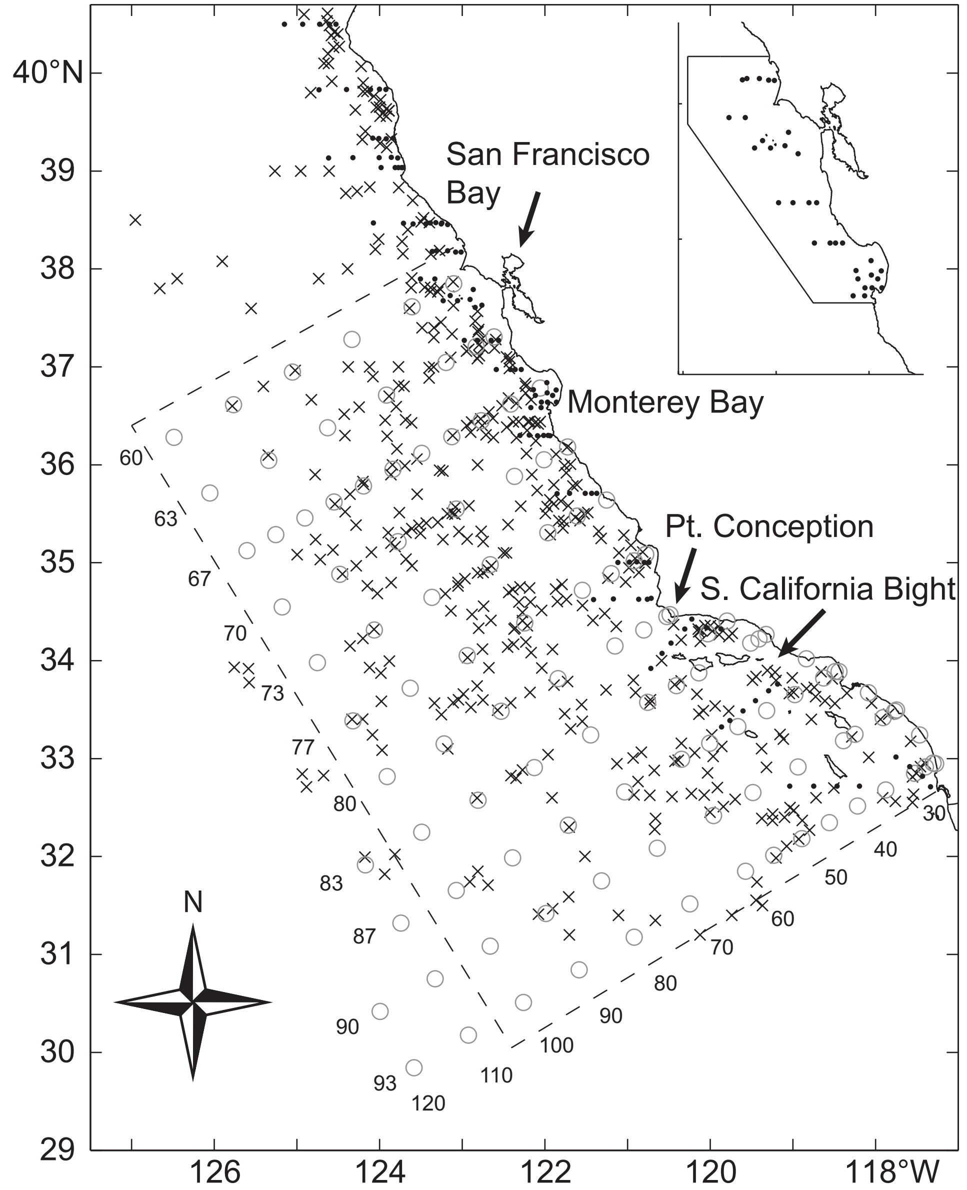


Figure 1. Central and southern California sampling. JRS stations are indicated with black dots, CalCOFI and SCCOOS stations are indicated with grey circles, CalCOFI ichthyoplankton data were used from within the dashed box, and the Spring CPS rope trawls are indicated as black crosses. The inset shows the "core" JRS region and stations. AT transects are not shown, but they generally cover the CalCOFI region and extend north of the displayed area. CalCOFI line numbers are indicated to the west of the study region, and station numbers to the south.

vey (JRS), the SWFSC Spring Coastal Pelagic Species (Spring CPS) rope trawl program, and we discuss the SWFSC acoustic trawl (AT) and California Department of Fish and Wildlife aerial surveys of coastal pelagic fishes (fig. 1). The methods for these data are presented by survey, whereas the results and discussion are organized into a comparison between central and southern California, long-term changes in abundance, abundance inshore of the standard CalCOFI stations, and seasonal patterns in anchovy abundance. Extensive time series are available for two of these surveys, the JRS and CalCOFI ichthyoplankton. We also use the underway CUFES data (2012–15) to assess the possibility that the anchovy stock has recently recovered. We compare anchovy abundance at several points in time, chosen from four published biomass estimate time series (Methot 1989; Jacobson et al. 1994; Fissel et al. 2011; MacCall et al. 2016). For "high" anchovy stock, we use 1975, for "moderate" biomass we use 1984, and for "low" biomass we use 2011 (fig. 2). We also use 2005 for an alternate period of "high" biomass, as there was a short-term recovery of the stock 2005–06 (fig. 2). We used the methods of MacCall et al. (2016)

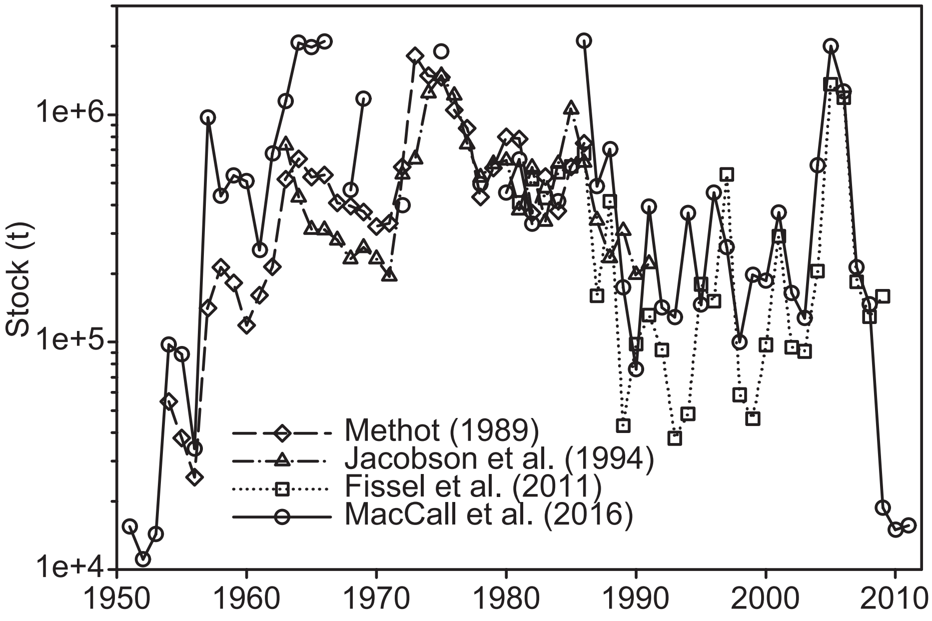


Figure 2. Published stock estimates for the central anchovy stock.

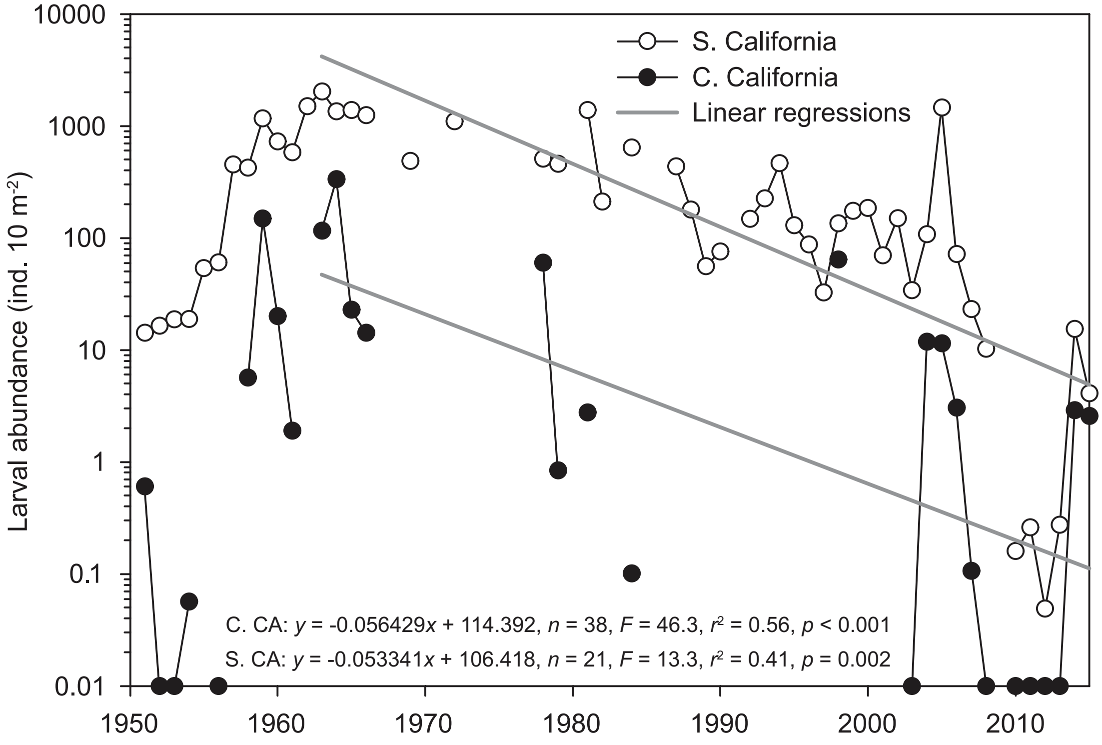


Figure 3. Spring CalCOFI mean anchovy larval abundance (ind. 10 m^{-2}) for central California (north of Pt. Conception; closed circles) and southern California (open circles). Linear regressions for 1963–2015 are shown as grey lines, neither passed the test for constant variance ($p < 0.05$).

to extend their spring larval abundance estimates to the year 2015 (fig. 3), and compared standard CalCOFI station results to those using the inshore Southern California Coastal Ocean Observing System (SCCOOS) stations for the period 2005–15.

CalCOFI

CalCOFI ichthyoplankton data were collected with plankton nets 1951–2015. During the early part of the time series, cruises were monthly, and during the later part quarterly. Between 1969 and 1981 CalCOFI cruises were made triennially. We did not group data collected in different months.

There were two major changes in sampling methods over the course of the time series; in 1969 the sampling depth was changed from 140 m to 210 m, and in 1978 the net design was changed from a 1 m ring net to a 0.7 m bongo net. The capture efficiency of the two net designs is roughly the same for the size classes of anchovy larvae that make up 90% of the catch (Hewitt 1980). For this reason, and because 100% of anchovy larvae were found shallower than 122 m (Ahlstrom 1959), the changes in sampling methods should have little effect on the abundance time series.

Anchovy abundance estimates based upon CalCOFI data are subject to spatial hyperstability bias because neither the fish nor the sampling stations are evenly distributed within the study area (MacCall et al. 2016; fig. 1). Spatial hyperstability was corrected by assigning sample locations to a 10 x 10 km grid, filling unoccupied grid elements using linear interpolation, and then averaging the entire interpolated grid. Multiple occupations of the same grid cell in the same month were averaged prior to interpolation. Only larval abundance was used, rather than larval and egg abundance, to better detect evidence of inshore spawning and to reduce any temporal mismatch between spawning and sampling. Larvae are more likely to be detected than eggs at widely spaced sampling stations and times due to advection and diffusion processes (Richardson 1981) because the egg stage is ~3 d duration in comparison to the 70–90 d spent as a larva (Hunter and Coyne 1982; Lo 1985b; Smith 1985).

We used CalCOFI station larval abundance in three ways: mean central California spring larval abundance north of Pt. Conception (lines 60–77 offshore to station 100) was compared with the southern California index of MacCall et al. (2016); we compared spring anchovy larval abundance in the SCB at the inshore SCCOOS stations to that at the inshore ends of CalCOFI lines 80–93; and we used mean monthly larval abundance data off southern California (1951–2015, all cruises, lines 77–93, stations ≤ 100) to study seasonality of spawning.

Underway anchovy egg concentration has been recorded during CalCOFI cruises using CUFES since 1996 (NOAA 2015). The CUFES device filters water pumped at ~650 $\mathrm{l\ min^{-1}}$ from an intake 3 m below the surface while the vessel is underway (Checkley et al. 1997). Fish eggs from the filtered samples were usually identified and counted every 5–30 min.

JRS

The NMFS SWFSC conducts an annual spring–summer survey in the CCS over the continental shelf and slope that is designed to collect juvenile rockfishes, although many other taxa are recorded (Ralston et al. 2015). The data used here span the years 1983–2013. Trawls made in August or later were excluded for seasonal consistency with the Spring CPS rope trawl. Marine fauna were collected at night with ~15 min tows of a modified Cobb midwater trawl with a mouth area of ~144 $\mathrm{m^2}$ and a variable mesh terminating with a cod end liner mesh of 9.5 mm. The trawl was fished at ~2 knots at a station-specific standard depth (headrope at ~10 m or ~30 m). Nonstandard tows, tows made to nonstandard depths, and tows for which an error was noted were not used. JRS cruises occupy specific stations, often more than once per cruise, and central California stations that were added or dropped mid-series were not included in this study. An exception was made for two stations, which were combined because they are only ~7 km apart and were occupied for complementary halves of the time series. The "core" region of the survey off central California as defined above then consists of 32 stations that are occupied approximately three times annually (fig. 1). We used the mean station catch per unit effort (CPUE; ind. $\mathrm{trawl^{-1}}$), and all "core" station means were then averaged to produce an annual mean. Additionally, mean station CPUE was calculated over several similar years corresponding to the "moderate" (1983–85) and "low" (2010–13) anchovy biomass periods in order to decrease trawl catch variability. JRS data north and south of the core area were available 2004–13 and processed similarly.

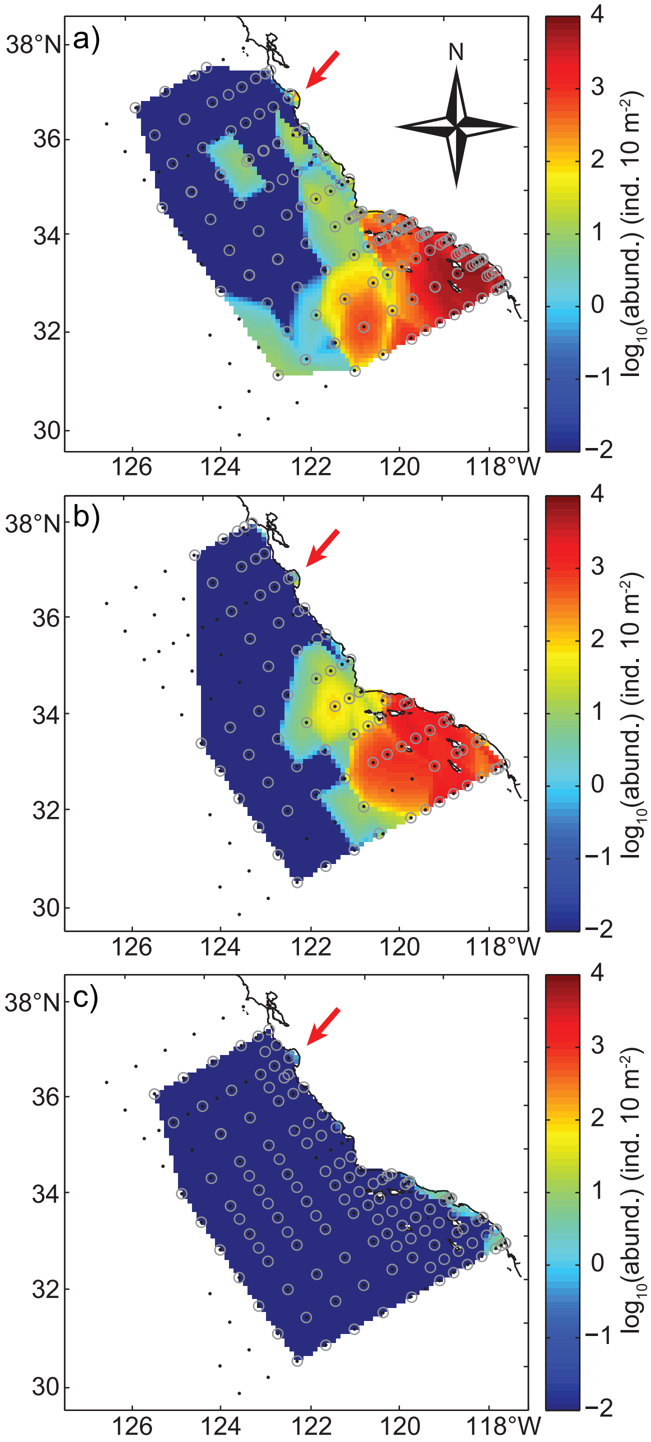
CPS

Spring CPS cruises sample pelagic nekton at night using a Nordic 264 rope trawl (Griffith 2008; Dotson et al. 2010). The rope trawl has a working mouth area of ~600 $\mathrm{m^2}$ and is fished near the surface at ~3.5 knots. It has a variable mesh concluding with 8 mm mesh in the cod end liner. Because the sampling was somewhat sparse, and because several trawls may be made within a small area in the same night, we mapped the data to a 50 x 50 km square grid to avoid spatial bias, and used the mean of samples within each grid element. Data from the entire time period (2010–13) were grouped together to reduce the inherent variability in trawl catches.

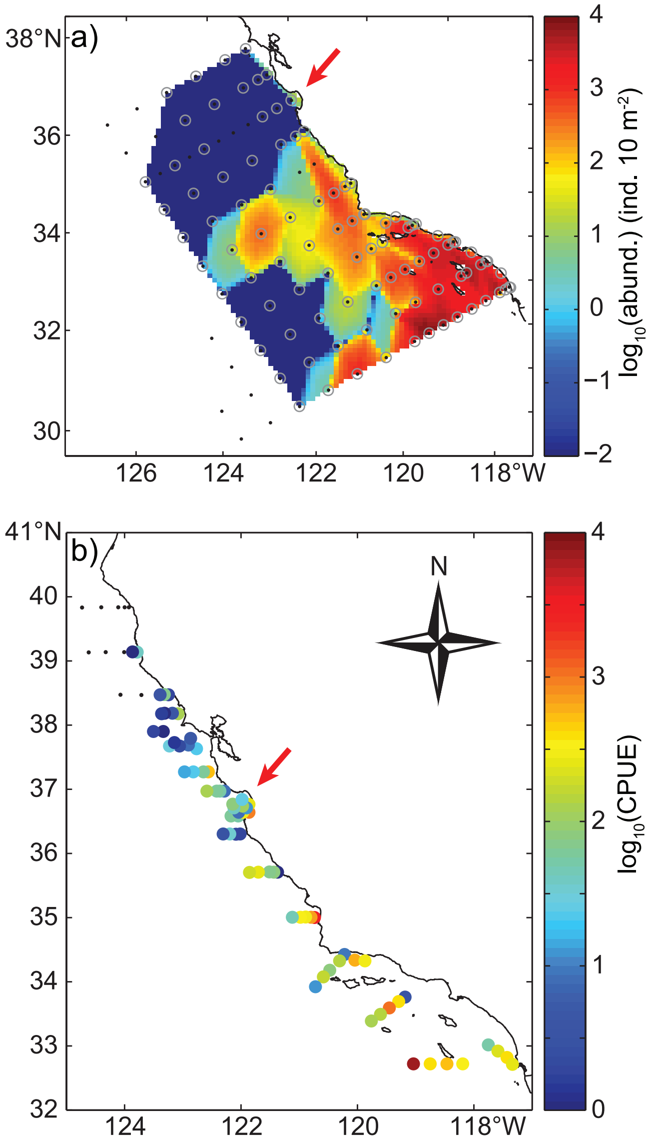
RESULTS

CalCOFI spring anchovy larval abundance in 1975, 1984, 2005, and 2011 was greatest in the SCB, with lower concentrations of larvae found north of Pt. Conception (figs. 4–5). The area of greatest larval concentration in 1975 and 1984 abutted the southern boundary of the study area.

CUFES data were not available from 1975 or 1984, but were available from the alternate "high" stock year of 2005 and the "low" years of 2010–15 (NOAA 2015). Anchovy egg distribution was predominantly in the



(Left) Figure 4. CalCOFI spring anchovy larval abundance for a) high biomass (1975), b) moderate biomass (1984), and c) low biomass (2011) years. Standard stations are indicated with black dots, and occupied stations with grey circles. The axes origin is 29.5˚N 127.5˚W. Monterey Bay is marked with a red arrow in panels a–c).



(Above) Figure 5. The short 2005–06 anchovy recovery showing a) spring 2005 CalCOFI anchovy larval abundance (standard stations are indicated with black dots, occupied stations with grey circles, and axes origin is 29.5˚N 127.5˚W), and b) 2005–06 JRS mean CPUE (stations with zero catch are shown as black dots). Monterey Bay is marked with a red arrow in both panels.

SCB in 2005, with few eggs found off central California (fig. 6). Anchovy eggs were rare and local 2010–15 off both central and southern California, with the greatest concentrations in 2014 near shore in the SCB.

The JRS anchovy CPUE off central California was greatest inshore between Pt. Conception and San Francisco Bay (figs. 5, 7). The JRS anchovy catch was not evenly distributed within the "core" area, and anchovy were significantly concentrated to the southeast (fig. 7 inset; Wilcoxon signed rank test, $n = 31$, $Z = 4.52$, $p < 0.001$). Within this subregion (1983–2013), anchovy CPUE was 196 (30% of the total nekton catch), but in the remaining portion of the "core" area anchovy CPUE was 15 (2% of the total catch).

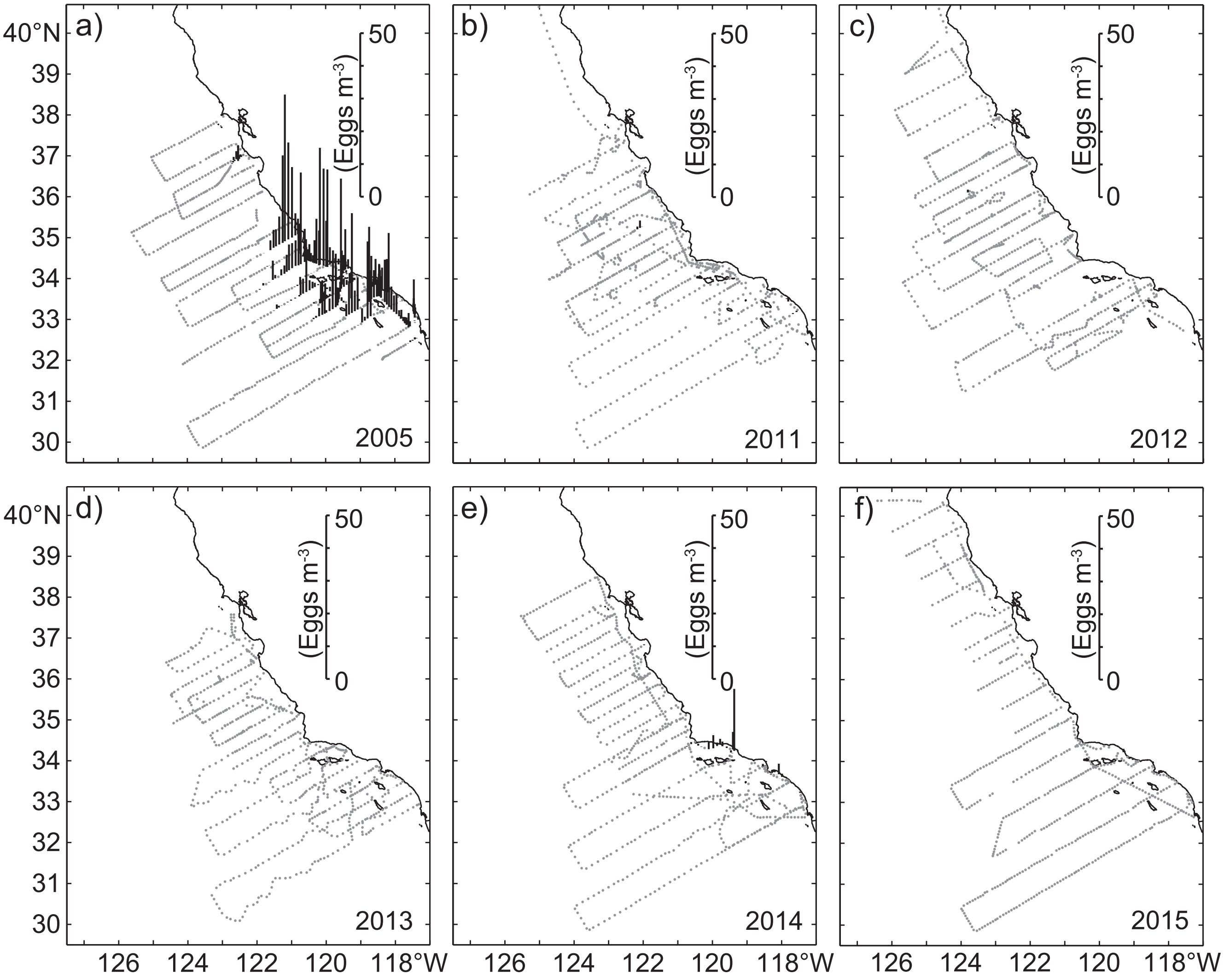


Figure 6. CalCOFI spring CUFES counts of anchovy egg density (2005, 2011–15). Zero concentration is indicated by grey dots. Data from 2015 (panel f), are preliminary and do not include seven unanalyzed stations. Data from 2010 (not shown) are similar to those from 2011–13.

A total of 524 Spring CPS rope trawl deployments were made off the entire US West Coast 2010–13 (fig. 8). Anchovy were only captured inshore in the SCB, near Pt. Conception, and off Washington State. No anchovy were collected off central California, despite the fact that it was the region of greatest effort (fig. 8).

Central and southern California anchovy abundance

April larval concentrations were compared north and south of Pt. Conception 1951–2015, with "north" defined as CalCOFI lines 60–77, north of the Pt. Conception, and "south" as the standard CalCOFI area. Larval anchovy abundance was significantly greater to the south (Wilcoxon signed rank test, $n = 26$, $Z = -4.457$, $p < 0.001$), and the north:south ratio of the mean abundance was 0.07 (fig. 3). Larval abundance was significantly greater to the south in years 1975, 1984, 2005, and 2011 (Table 1).

Only 18 of 738 CUFES samples were positive for anchovy eggs in 2011 (maximum 2.3 eggs m^{-3}), whereas in 2005, 228 of 851 samples were positive (maximum 44.9 eggs m^{-3}; fig. 6). Mean concentration was 144-fold greater in 2005 than in 2011. Egg concentrations were significantly higher to the south in 2005, but not in 2011 because there were few positive samples anywhere (table 1).

JRS anchovy CPUE was significantly greater south of Pt. Conception for both 2005–06 and 2010–13 (table 1), although in 2010–13 the median and mean were greater to the north due to the two large catches just north of Pt. Conception (fig. 7).

There was only one positive catch for anchovy off central California from the spring CPS 2010–13 (fig. 8),

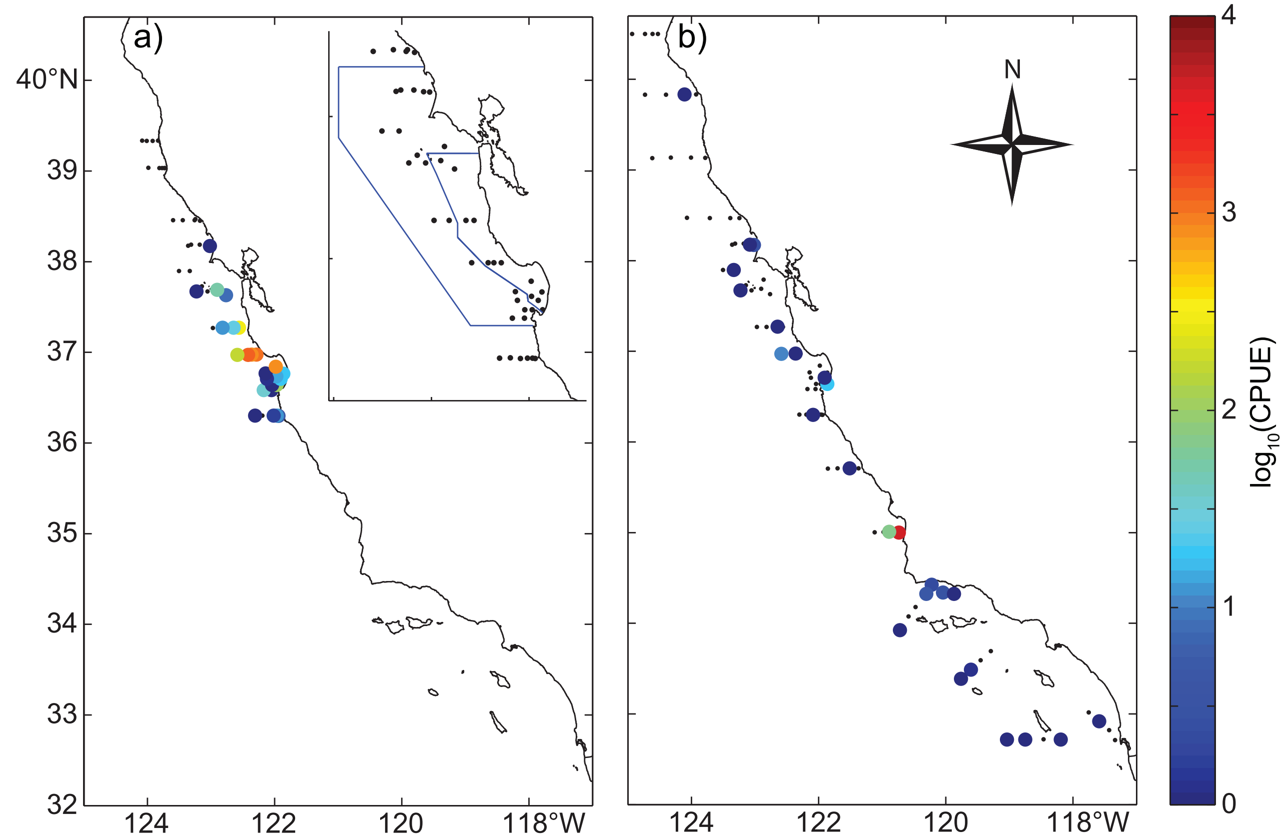


Figure 7. JRS station mean CPUE for a) moderate biomass (1983–85), and b) low biomass (2010–13) years. Stations with zero mean catch are shown as black dots. Inset in panel a) shows JRS stations off Central California as black dots. The outer blue polygon encloses the "core" stations, and the inner blue polygon encloses the region with elevated anchovy CPUE.

TABLE 1
Wilcoxon signed rank tests of anchovy abundance north (N) and south (S) of Pt. Conception.

	year	mean (N)	mean (S)	median (N)	median (S)	*n* (N)	*n* (S)	*Z*	*p*
CalCOFI larvae	1975	1.60	869.29	0	69.14	1500	1416	–36.89	<0.001
	1984	2.32	350.39	0	11.96	1198	1462	–26.96	<0.001
	2005	47.12	655.98	0	59.01	1541	1468	–22.15	<0.001
	2011	0.00	0.08	0	0	1260	1466	–4.68	<0.001
CUFES eggs	2005	0.60	1.59	0	0	325	536	–7.71	<0.001
	2011	0.01	0.01	0	0	343	415	0.89	0.375
JRS adults	2005–06	165.11	626.61	32.00	234.13	47	20	–3.45	0.001
	2010–13	103.98*	0.90	0	0.33	46	19	–2.31	0.021
CPS adults (inshore)	2010–13	0.08	53.07	0	1.05	12	8	–2.99	0.003

*Dominated by two extreme catches near Pt. Conception (fig. 7).

and southern California had significantly greater CPUE (table 1). Because there were no positive catches >50 km from shore off central or southern California, we used only the inshore grid elements between Pt. Conception and Pt. Reyes to reduce zero inflation.

Temporal patterns in abundance

The CalCOFI anchovy ichthyoplankton spring time series can be roughly divided into two temporal segments: a period of increasing abundance (1951–63), and a period of generally declining abundance (1964–2015). From 1963–2015 there is an exponential decline in anchovy larval abundance in both central and southern California (fig. 3). January–May monthly abundances all exhibit the same long-term pattern (fig. 9).

JRS pelagic trawl data off central California also suggest a long-term exponential decline in anchovy abundance 1983–2013, with a decreasing slope on a semilog scale (fig. 10). In the "moderate" biomass period (1983–85) anchovy were captured at more stations and in 1–2 orders of magnitude greater numbers than from 2010–13, even in their good habitat near Monterey Bay (fig. 7). JRS anchovy CPUE also declined over time as a fraction of nekton captured by trawls in the subregion of good

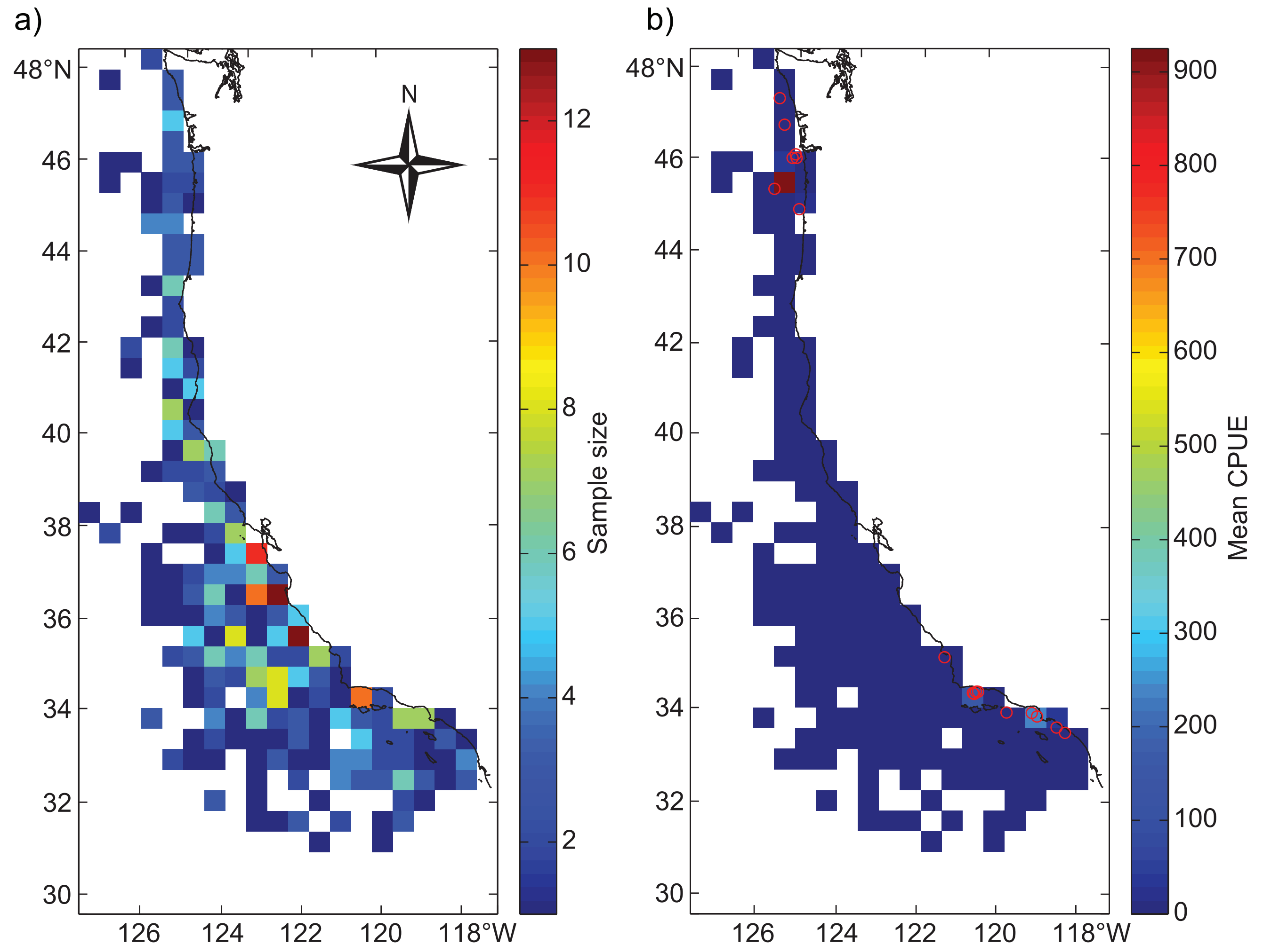


Figure 8. Spring CPS rope trawl a) spatially-averaged sample size, and b) anchovy mean CPUE (2010–13). The axes origin is 29.5°N 127.5°W, and the grid size is 50 x 50 km. Non-zero catches are marked with red circles.

habitat (fig. 7 inset). Anchovies comprised >40% of the overall CPUE in the 1980s and 1990s, 18% 2000–09, and only 0.1% 2010–13.

No CUFES data were available prior to 1996, so we used 2005 as an alternate "high" anchovy biomass year. Underway data from the CalCOFI CUFES program showed high anchovy egg abundance in 2005 throughout the SCB and north around Pt. Conception, whereas in the "low" biomass years (2010–15), few anchovy eggs were collected anywhere (fig. 6).

Undetected inshore spawning

April anchovy egg and larval abundance at nine nearshore SCCOOS stations (mean distance to shore 1.5 km) were compared to the innermost six CalCOFI stations between lines 80 and 93 (mean distance to shore 7.3 km) for the time period in which SCCOOS stations were occupied (2005–15). Neither egg nor larval abundance were significantly different between these two groups of stations (Wilcoxon signed rank test, $n = 8$; $Z = -0.14$, $p = 0.89$ for eggs; $Z = -0.84$, $p = 0.40$ for larvae). Inclusion of SCCOOS stations using the methods of MacCall et al. (2016) did not result in a significant difference in larval abundance estimates ($n = 8$, $t = -0.81$, $p = 0.45$).

Seasonal patterns in spawning

Over the course of the whole time series (1951–2015), monthly larval abundance was elevated January–May, with a peak in March (fig. 9). Egg abundance was also elevated January–May, but with peak abundance in April. January–May larval concentrations all exhibited the same long-term pattern, and (excluding April) had similar magnitudes clustering around a 1:1 ratio against April concentrations (fig. 9). Outliers from the ~1:1 ratio indicate relatively poor winter (1961, 1981, 2000–08) or spring spawning (2010–11, 2013), and most outliers were from the time period 2000–13.

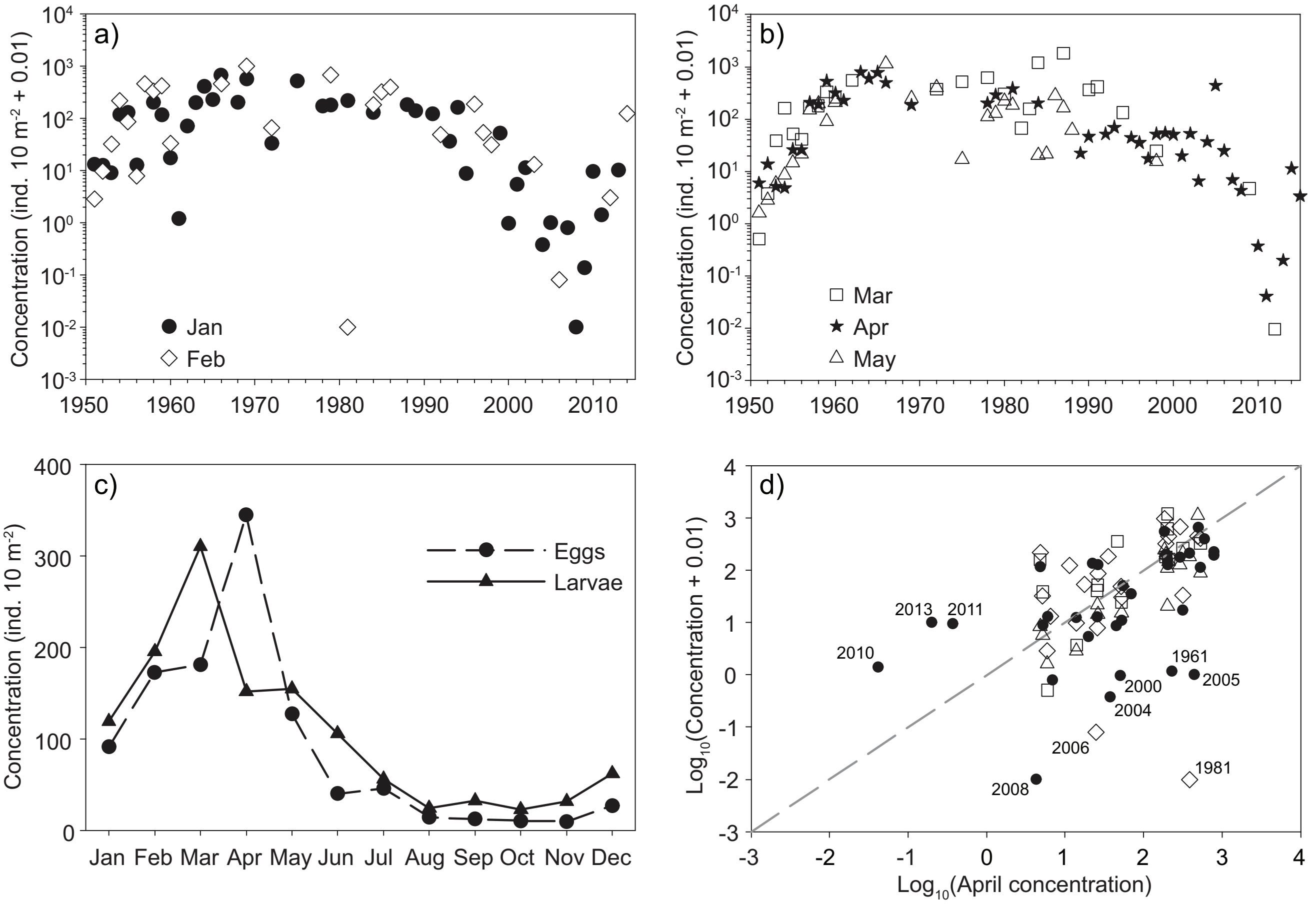


Figure 9. Southern California anchovy ichthyoplankton abundance showing a) winter larval concentration by month and year, b) spring larval concentration by month and year, c) mean concentration of larvae and eggs by month (1951–2015), and d) January–May (excluding April) monthly larval concentrations plotted against April concentration with outlier years labeled. Panel d) uses the same legend symbols as panels a) and b). The 1:1 ratio is plotted as a grey dashed line.

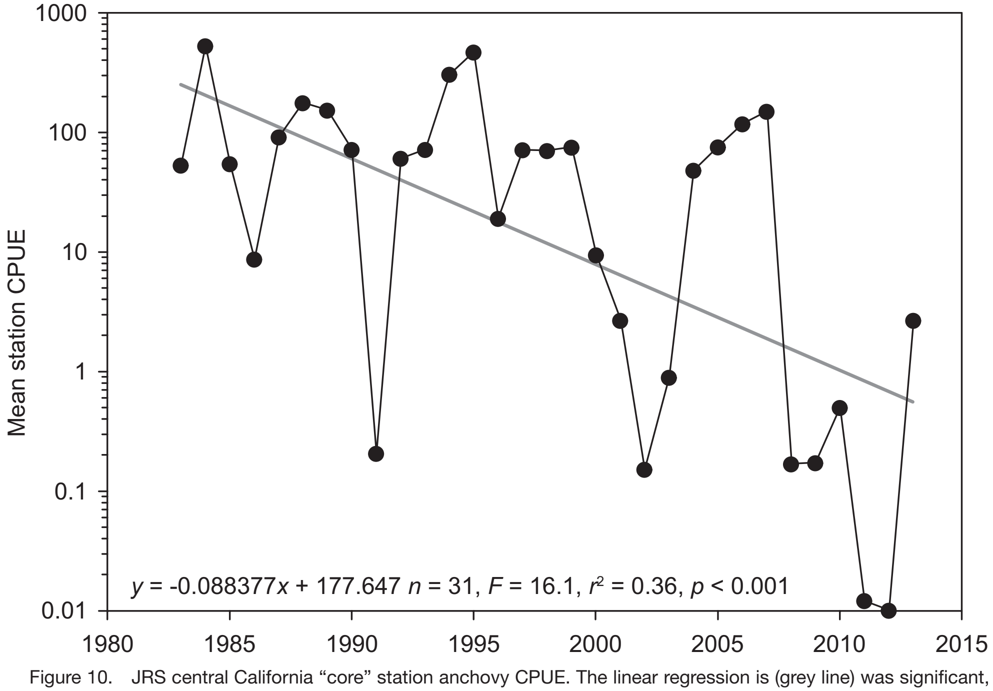


Figure 10. JRS central California "core" station anchovy CPUE. The linear regression is (grey line) was significant, but failed the constant variance assumption ($p = 0.018$).

DISCUSSION

Recent central and southern California anchovy populations

The central California coast from San Francisco Bay to Monterey Bay has been noted anecdotally and scientifically as a hotspot for anchovy and their cetacean predators (Santora et al. 2012; Drake 2013). The region of good anchovy habitat with elevated CPUE (fig. 7 inset) is relatively small, ~3,500 km^2, whereas the surface area of the SCB inside the Channel Islands is ~30,000 km^2. Larval concentrations were at least one order of magnitude lower off central California than they were in the SCB in years of high, moderate, and low biomass (1975, 1984, 2005, and 2011; figs. 3–5; table 1). Mean annual anchovy larval concentration (1951–2015) north of Pt. Conception was 7% of that to the south. Adult and egg abundance were also lower north of Pt. Conception, although from 2010–13 the data were sensitive to outliers or amounted to a comparison of zeros (figs. 6–7; table 1).

It has been known for decades that most of the central anchovy stock resides in or about the SCB (Smith 1972; MacCall and Prager 1988; Jacobson et al. 1994; Schwartzlose et al. 1999). The most important spawning habitat for anchovy is in the SCB, both in terms of larval concentrations and areal extent (figs. 3–5). The CPUE of both pelagic trawls and underway egg density sampling have consistent spatial distribution with that of larval abundance (figs. 5–6, 8). Anchovy were captured in the SCB by the Spring CPS rope trawl 2010–13, but no adult anchovy were captured off central California, despite greater effort there (fig. 8). Anchovy egg, larval, and adult abundance between Pt. Conception and Cape Mendocino was so low 2010–13 as to be inconsequential to the central stock as a whole (figs. 3–4, 6, 8). During the period of high anchovy biomass (1966–79), the fraction of total larval catch from waters north of Pt. Conception was estimated to be 0%–6% (Hewitt 1980).

Even a cursory glance at anchovy larva distribution indicates that there may be substantial spawning or advected ichthyoplankton in Mexican waters just south of San Diego (figs. 4–5). This fraction was variable and estimated to be 11%–59% of the total larval catch 1966–79 (Hewitt 1980). It is not clear whether some CalCOFI ichthyoplankton were from the southern stock. The Baja California coast has not been surveyed by CalCOFI cruises after 1981, although it has been sampled by the Mexican investigations of the California Current (IMECOCAL) program 1998–present. Thus, the current "standard" CalCOFI station pattern (lines 77–93) does not cover the full range of anchovy spawning habitat when the stock is large. If a variable amount of spawning occurs outside the standard CalCOFI station plan, this will introduce error into stock estimates based only upon US ichthyoplankton data.

Temporal patterns in abundance

The various anchovy stock estimates were in approximate agreement for the "high" (mid-1970s), and "moderate" (early 1980s) biomass periods (fig. 2). Our observation of increasing anchovy ichthyoplankton abundance 1951–63 (fig. 3) was consistent with reports of an increasing anchovy stock 1951–69 (Smith 1972). The low 2011–15 anchovy ichthyoplankton abundances (figs. 3–4, 6; MacCall et al. 2016) were consistent with catches of adults. Only two JRS net tows off southern California 2010–13 captured many anchovy (both near Pt. Conception; fig. 7), in contrast to the many trawls over a wide area that captured anchovy in a year when anchovy were abundant (fig. 5). Few anchovy off southern California and none off central California were captured by the Spring CPS rope trawl (2010–13; fig. 8). An acoustic estimate of anchovy stock size in the study area was attempted by the NMFS AT survey (2006–11), which concluded that anchovy were too low in abundance and too patchily distributed for a good estimate from 2006–10 (Zwolinski et al. 2012), and that the anchovy biomass was <10,000 t in 2011 (Demer et al. 2013).

Despite short recoveries in 1986 and 2005–06 (fig. 2), both adult and larval anchovy spring abundance have declined exponentially since the early 1960s (figs. 3, 10). Adult anchovy off central California have also declined over time as a fraction of nekton CPUE. Because both central and southern California ichthyoplankton abundances have declined together (fig. 3), few eggs have been observed between Pt. Conception and Cape Mendocino (fig. 6), and catches of adults off central California have similarly declined or are nil (figs. 7–8), there is no evidence that the anchovy stock has migrated north out of the southern California study area of MacCall et al. (2016). There is also no evidence from ichthyoplankton, trawling, or CUFES data that the stock has recovered 2012–15 after the period covered by MacCall et al. (2016).

Inshore anchovy population

The CalCOFI ichthyoplankton sampling may miss anchovy spawning close to shore. However, southerly winds in the study area advect surface water offshore, and the moving surface water can be expected to transport weakly swimming anchovy larvae. A ~5-fold inshore/offshore difference in abundance of the smallest (youngest) size classes of anchovy larvae is evidence of this larval advection offshore (Smith 1972). Prior studies of the distribution of anchovy ichthyoplankton relative to the coast found that larval abundance (ind. m^{-2}) increased with bottom depth from 8–70 m (Brewer and Smith 1982; Barnett et al. 1984), that nearshore habitat (8–36 m bottom depth) was not preferred for spawning by anchovy in comparison to the CalCOFI sampling area (Brewer and Smith 1982), and that the peak abundance of anchovy larvae was 60 km from shore (Richardson 1981). The inner stations of the five CalCOFI lines in the SCB (plus the Santa Barbara Basin station) are 2–19 km from shore at a median bottom depth of 63 m (depth range 34–578 m). The nine SCCOOS stations in the SCB are 0.1–3.7 km from shore at 20 m bottom depth, but these stations were not used by MacCall et al. (2016) because they were only occupied since 2005. There was no significant difference in larval or egg concentrations between the SCCOOS stations and the inner CalCOFI stations, or between abundance estimates made with and without SCCOOS stations, and thus there is no evidence that inshore spawning was missed by MacCall et al. (2016) in the SCB.

Egg concentrations are a more accurate index of parent stock size than larval concentration due to variable mortality rates in the egg and larval stages (MacCall et al. 2016), but are less precise due to greater patchiness. Indeed, there has been a sharp increase in anchovy egg/larva mortality in recent years (Fissel et al. 2011; MacCall et al. 2016). We used anchovy larval concentration here, rather than egg concentration, in order to reduce patchiness effects and better detect "missing" evidence of inshore spawning. The anchovy egg stage lasts 2–7 d, whereas the larval stage lasts 70–90 d (Hunter and Coyne 1982; Lo 1985b; Smith 1985). Thus, larvae are more dispersed than eggs due to movements of the water and more likely than eggs to be detected by sampling at CalCOFI stations some distance from possible close-to-shore spawning habitat (Richardson 1981).

The recent period of very low anchovy catches contrasts with newspaper reports of huge anchovy schools close to shore in Monterey Bay 2013–15 (Drake 2013; Goode 2013; Bartolone 2014; Gaura 2015) and in the SCB (Herreria 2014), and it may be argued that these fishes were missed by the mostly deeper-water CalCOFI and JRS surveys. In low biomass periods, anchovy are known to contract their range inshore (Schwartzlose et al. 1999; MacCall et al. 2016). Aerial surveys are well-suited to observe these inshore shoals. Aerial surveys of the SCB, the population center of the central anchovy stock, showed that in the "low" biomass period (2012–14) anchovy were almost entirely found <4 km from shore (Lynn et al. 2015). The maximum biomass observed aerially was 14,532 t in 2013. Thus, it is clear that even though there is a dense population of anchovy nearshore, it doesn't amount to a large biomass due to the restricted spatial distribution. Sporadic, large catches of anchovy at inshore stations by the AT survey (Zwolinski et al. 2012; Demer et al. 2013), JRS (fig. 7), and Spring CPS rope trawl (fig. 8) are consistent with a small but dense population of anchovy close to shore in low biomass years. CUFES data from 2014–15 are also consistent with a population distribution very close to shore (fig. 6). Anchovies were essentially absent from their historical offshore habitat 2009–15 (figs. 4–5), yet they paradoxically appeared unusually abundant to nearshore observers.

Seasonality of spawning

Anchovy spawn all year with a peak March–April (fig. 9; Parrish et al. 1986; MacCall and Prager 1988; Asch 2015). The use of winter and spring (January and April) anchovy ichthyoplankton abundance generally captures the peak spawning season, and the January–May monthly abundances are similar in both magnitude and long-term pattern (fig. 9). The period of steepest decline in larval abundance is characterized by relatively poor winter (2000–09) or spring abundances (2010–13), consistent with a shortening of the spawning season and perhaps match-mismatch processes (Cushing 1990).

Monthly averages of anchovy abundance (fig. 9c) were lower but otherwise similar to previously published material (Moser et al. 2001) for larvae, but differed for eggs in that February and March averages were also relatively lower in comparison to April concentrations. The overall reduced abundance is due to extension of the time series to include the recent anchovy collapse. The sharpening of the egg abundance peak resulted from our correction for spatial bias in sampling locations relative to anchovy spawning habitat (Moser et al. used an average of occupied stations).

Peak anchovy spawning in the CalCOFI area is (non-significantly) shifting –3 d $decade^{-1}$ (Asch 2015), or ~18 days across the whole CalCOFI time series. Because February larval densities were greater than those from January, May larval densities were similar to those from April, and MacCall et al. (2016) incorporated many February, March, and May cruises in their indices, the phenological shift in the timing of peak spawning would not be expected to greatly change their results. Indeed, recent CalCOFI January larval abundances would be expected to increase with such a shift relative to the early portion of the time series, producing an overestimate of the anchovy stock.

Parrish et al. (1986) found striking seasonal differences in individual anchovy fecundity from histological samples (1977–84) and the age distribution of commercial landings and scientific catches (1966–80). Therefore, Parrish (2015) argued that the use of January ichthyoplankton indices for anchovy stock assessments is difficult to justify because January egg production (1%–3%

of annual) is so small in comparison to the spring peak, and may thus be sensitive to small shifts in spawning seasonality or range. However, the great seasonal fecundity difference observed in dissected specimens (Parrish et al. 1986) is not consistent with what was observed in the water on CalCOFI cruises (fig. 9). Mean annual CalCOFI January egg concentrations were 44% of the April concentration for the period 1977–84 corresponding to Parrish et al.'s data, and 45% for all years with both January and April cruises.

Calibration

Ichthyoplankton concentration is not a direct measurement of biomass and thus requires calibration to a benchmark stock assessment in order to estimate biomass from the index. It does not matter if the index incorporates data from the time and location of maximum abundance, as long as the relationship between the benchmark and index does not change. Because the calibration stock assessments were only performed in three years overlapping with the CalCOFI ichthyoplankton surveys (MacCall et al. 2016), there is likely some error in the calibration. The accuracy of future stock estimates made from ichthyoplankton surveys will improve with additional benchmark stock assessments for calibration.

In low population years, anchovy landings may be similar to or even exceed stock assessments (Parrish 2015). Non-breeding migration of other stocks to the survey area may inflate local landings data relative to the local stock size. In addition, if the calibration stock assessment did not incorporate all anchovy habitat (e.g., extremely nearshore or waters off Mexico) then ichthyoplankton abundance is calibrated to an underestimated stock. While the calibration error may be small in years when the stock is large, it will grow in relative size as the population declines, and can lead to apparent paradoxes in low biomass years.

CONCLUSION

In regards to the question of whether or not there is an unobserved spawning population of anchovy off central California, the answer is likely "no," or at least not a big one. Both the JRS and Spring CPS rope trawl sampling programs focus their effort in central California waters (figs. 7–8). The JRS anchovy CPUE exponentially declined 1983–2013 off central California (fig. 10). The Spring CPS rope trawl captured zero anchovy off central California 2010–13 (fig. 8). Anchovy egg sampling (CUFES) observed moderate concentrations of eggs off central California in high biomass years, and few to none when the population was low (fig. 6). Larvae were present off central California in both high and low biomass years, but their concentration was not only 1–2 orders of magnitude lower than the SCB concentration but spread out over a much smaller area (figs. 3–5). Although there were anecdotal reports of large anchovy schools close to shore (Goode 2013; Herreria 2014), even if anchovy spawned there unobserved by CalCOFI ichthyoplankton sampling, underway CUFES egg sampling, JRS trawls, Spring CPS rope trawls, and the AT survey, it must have been confined to a narrow strip along the shore. A large concentration of fishes multiplied by a small surface area results in a small biomass at oceanic scales. However, there may have been substantial spawning activity in Mexican waters just south of San Diego (figs. 4–5), and it is not clear what fraction of anchovy spawning by the central stock was south of the survey area.

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