1 RECENT COLLAPSE OF NORTHERN ANCHOVY BIOMASS OFF CALIFORNIA

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12 **Abstract**
13   New estimates of abundance of northern anchovy (*Engraulis mordax*) are developed
14 from California Cooperative Oceanic Fisheries Investigation (CalCOFI) data on egg and larval
15 densities for the period 1951-2011. Previous estimates utilizing mean density over the CalCOFI
16 area show a hyperstability bias because of the nearshore concentration of CalCOFI stations and
17 the anchovy population tendency to contract into this area when abundances are low. New
18 abundance estimates weight sample egg and larval densities to the local area represented by that
19 sample, and then sum contributions to obtain total abundance. We develop total egg and larval
20 abundance estimates for January and April, form a combined index, and calibrate it to the
21 absolute biomass estimates produced by the Daily Egg Production Method (DEPM) in the early
22 1980s. Anchovy spawning biomass was very low, 10,000-20,000 Metric Tons (MT), in the early
23 1950s when CalCOFI sampling began. Abundance increased and fluctuated between 0.5 and 2
24 million metric tons from 1960 through 1990. After 1990, spawning biomass fluctuated around
25 200,000 tons, briefly increased in 2005-2006, then declined drastically over four years to below
26 20,000 tons from 2009-2011. CalCOFI ichthyoplankton data collected after 2011 are not yet
27 available for analysis, but continuous underway egg sampling conducted during CalCOFI cruises
28 indicates continued low abundance and very limited spawning through 2015 in both southern and
29 central California. The recent collapse of anchovy abundance occurred in the absence of a
30 significant fishery. Present annual catches of a few thousand tons are small by historical
31 comparison, but the exploitation rate may now be relatively high given the low stock abundance.
32 The decline in anchovy abundance coincides with recent die-offs and reproductive failures of
33 anchovy-dependent predators in the ecosystem (e.g., sea lions and pelicans).

34

35 **Keywords:** biomass, anchovy, hyperstability, ichthyoplankton, forage

36

37 **1. Introduction**
38   The central population of northern anchovy (*Engraulis mordax*) extends from northern
39 Baja California to northern California, is an important prey resource providing forage to many
40 upper trophic level predators, and in the past (though not recently) supported substantial fisheries
41 in California and Mexico. The Historical Egg Production (HEP) method developed by Lo
42 (1985) uses egg and larval abundances at size to estimate the initial egg production rate of the
43 spawning adult population. Abundances estimated by the HEP approach have been used
44 extensively in previous anchovy stock assessments (MacCall, 1982; Methot, 1989; Jacobson et
45 al., 1994, 1995; Fissel et al. 2011). The last formal stock assessment was conducted in 1995
46 (Jacobson et al., 1994, 1995), but recent abundance estimates were published by Fissel et al.

47 (2011) who extended the abundance time series to 2009 for the southern California region (Pt.
48 Conception to Mexico). Fissel et al. (2011) showed a spike in egg production in 2005 and 2006
49 with estimated spawning biomass briefly exceeding a million metric tons (MT), then returning to
50 around 150,000 MT by 2008, a decline which they attributed to recent increases in egg mortality
51 rates. This lower level is also consistent with other analyses of anchovy productivity showing
52 declines since the 1980s presumably related to ocean conditions and climate (Koslow et al.,
53 2013; Lindegren et al., 2013). Although the stock has been lightly fished in recent years, Fissel
54 et al. (2011) voiced concern about the declining stock size and urged further investigation but did
55 not consider the drop in abundance from 2005 to 2008 to be a significant conservation issue.
56   Other lines of evidence suggest that the anchovy stock off southern California may have
57 declined more precipitously since 2008. The relative abundance of anchovy eggs and larvae in
58 the California Cooperative Oceanic Fisheries Investigation (CalCOFI; Fig. 1) surveys declined
59 severely over the previous two decades, and especially in the most recent years (McClatchie et
60 al., 2011; Leising et al., 2014). In particular, findings from the January 2008 survey were
61 unprecedented in the history of CalCOFI, with very few anchovy eggs and no larvae at all! In
62 more recent April surveys, egg abundances remained low, and larval abundance fell below the
63 lowest historical levels, last observed in the early 1950s. Trawl survey catch rates of adult
64 anchovy off central California have also declined in recent years (Ralston et al., 2015), with a
65 major decline seen between 2005-2006 and 2008-2009. Other ecological indicators such as poor
66 breeding performance of brown pelicans off southern California (Henry, 2015), declines in
67 seabird abundance at sea (Sydeman et al., 2015; Santora and Sydeman, in press), unusual
68 mortality events for California sea lions (Melin et al., 2010), and reductions of anchovy in
69 seabird diets (e.g., Elliott et al., 2015) also suggest low availability of anchovy.
70   Here, we develop and calibrate a simple abundance index for the central anchovy stock,
71 focusing on the southern California region, that revises the entire CalCOFI-based time series of
72 anchovy abundance, as well as updating it to 2011. We also examine aspects of previous
73 methodologies and investigate whether those biomass estimates may have been compromised by
74 hyperstability biases (Hilborn and Walters, 1992).
75
76 **2. Materials and Methods**
77   Spawning (egg production) by the central subpopulation of northern anchovy typically
78 lasts from January to May each year, but within individual years, the monthly pattern of
79 spawning can be quite irregular (Methot, 1983). Generally, average egg abundances are much
80 higher in March/April than in January, with no trends in spawning phenology (Asch, 2015).
81 Failure to account for seasonality is a source of imprecision, and the aliasing resulting from a
82 systematic temporal mismatch of sampling may introduce bias at the decadal scale. Though
83 these sources of imprecision and bias are difficult to eliminate, they can be reduced by
84 disaggregating the data into monthly components. For these reasons, we used data from January
85 and April separately, and estimated separate biomass scaling factors (see below).
86
87 **2.1. Sampling Issues**
88   The habitat utilized by spawning anchovies expands into the offshore region in times of
89 high abundance and contracts into nearshore core areas when abundances are lower (MacCall,
90 1990, see Fig. 2). This pattern of redistribution has serious consequences for abundance
91 estimates. First, range expansion at high abundance and contraction at low abundance indicates
92 that samples from individual stations are not identically and independently distributed (*iid*).

93   Because we cannot assume *iid*, bootstrap resampling techniques for variance calculations cannot
94   be justified (e.g., Jacobson et al., 1994). Second, because the CalCOFI sampling pattern has a
95   higher density of stations in the nearshore region favored by anchovies at low population sizes,
96   the average density over all CalCOFI stations will not decline in proportion to the decline in
97   population size, leading to "hyperstability" bias (Hilborn and Walters, 1992). Third, nine very
98   nearshore stations were added to the CalCOFI grid by the Southern California Coastal Ocean
99   Observing System (SCCOOS), with larval and egg sampling beginning in fall 2004 (see Fig. 1).
100 These stations are in the area occupied by anchovies when at their lowest abundances (see Fig. 2)
101 and may exhibit higher densities than are observed at an average CalCOFI station, many of
102 which regularly have very low or zero densities. Thus, for this paper's purpose of obtaining a
103 consistent long-term sampling frame, adding the nearshore SCCOOS stations to the dataset has
104 two potential detrimental effects: 1) it causes a systematic increase in the estimates of anchovy
105 production compared to years in which these stations were not sampled, and 2) it likely increases
106 the hyperstability bias.
107   To deal with these major sampling issues, we excluded the nine SCCOOS stations from
108 our analysis. A statistical solution to the hyperstability issue is to expand densities separately for
109 each CalCOFI station in order to obtain local population estimates, which are then summed to
110 estimate the overall abundance in the study region. This approach is not new. Historically, this
111 analytical technique was referred to as the "larva census" approach, described by Sette and
112 Ahlstrom (1948). However, this approach is computationally complex in that it requires
113 estimation of the area sampled by each standard station. To estimate the area sampled at each
114 station, we calculated station-specific Thiessen polygons (Okabe et al., 2000).   Thiessen
115 polygons are a well-established technique for integrating abundance over irregularly-spaced
116 sampling locations, and this approach is robust to the systematic abundance-related changes in
117 spawning distribution described by MacCall (1990). Therefore, most geostatistical approaches
118 (e.g., stratification and weighting) are highly questionable due to time-varying anisotropic
119 properties of anchovy distribution. We also replaced the invalid bootstrapping approach
120 previously used by various authors with a jackknife resampling approach that preserves the
121 spatial structure of sampling (see below).
122
123 **2.2. Abundance Indices**
124   The most complete CalCOFI sampling for the 61-year period of 1951 to 2011 has been in
125 the southern California region, where we were able to develop population estimates for 51 of
126 those years. Central California has been sampled less consistently, and we were able to develop
127 population estimates for only 33 years, with substantial gaps in the middle of the time series; for
128 this reason, although we present ichthyoplankton indices that include central California we do
129 not use them to estimate biomass. Mexican waters have not been sampled by CalCOFI since the
130 1970s, and thus we did not attempt to estimate anchovy abundance there.
131   We considered two sets of CalCOFI cruises (data were obtained from
132 http://www.calcofi.org/), those surveys with any portion occurring in January, and those with any
133 portion occurring in April. For each cruise, as noted above, we constructed a set of Thiessen
134 polygons (also known as Voronoi diagrams or tessellations). Each Thiessen polygon defines an
135 area of influence around its sample point so that any location inside the polygon is closer to that
136 point than any of the other sample points (Fig. 3). The egg or larval population estimate (P_{ijk}) for
137 each year (*i*), ichthyoplankton type (*j* = eggs or larvae) and season (*k* = January or April) is the

138   sum of the products of station-specific (*s*) polygon areas (A_s) and sampled density (D_s) or mean
139   density if the station was sampled more than once:
140

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

141
142   Note that the values of A_{iks} depend on which adjacent stations were sampled in a given year and
143   season. Samples obtained off-transect were omitted, and samples between standard stations were
144   assumed to represent the closest standard station. If multiple samples occurred at a station, their
145   mean density was used. We applied the tessellation approach to both the "core" 6-line southern
146   California region and to the "full" region including central California north to San Francisco
147   (Fig. 3 is an example of the latter). We consider egg and larval populations to be separate
148   indices, so a complete year produced four indices, two for January and two for April (Tables 1
149   and 2). In many years, only one of the two seasons (January or April) was sampled. Each of the
150   four indices was scaled to unit mean for the period 1951-1999, and a combined index was
151   produced by averaging the 2-4 indices for each year. However, we did not use larval data after
152   1999 due to an apparent increase in egg or larvae mortality rates that would bias the recent larval
153   index lower relative to the prior portions of the time series (see Results). We calculated
154   arithmetic means that allowed retention of cruises with zero estimates, i.e., where either no eggs
155   or larvae were sampled, which occurred in some of the earliest and most recent years. These
156   instances of zero values made the use of log transformations difficult, so we did not pursue that
157   possibility.
158   Precision of abundance estimates was calculated by a jackknife procedure, whereby each
159   sample was deleted one at a time and unless multiple samples were taken (which occurred only
160   rarely), the tessellation was recalculated so that regions of the deleted tile were reassigned to
161   values of A_{iks} for expanded tiles associated with adjacent samples; importantly, the total survey
162   area remains constant for all years and all jackknife re-samplings. A new abundance estimate
163   was obtained with each deletion, and results were combined to produce precision estimates
164   (Efron and Stein, 1981). The jackknife procedure provided variance estimates for each of our
165   indices: January eggs, January larvae, April eggs, and April larvae. In order to produce a
166   variance estimate for the combined index, we first considered the survey years in which all four
167   indices existed, and examined the matrix of correlations among the anomalies from the common
168   mean (Table 3). The largest correlation was -0.63 between January eggs and April eggs (Fig. 5),
169   and was driven by two outliers. We therefore ignored the covariances in calculating approximate
170   variances, simplifying calculation of the estimated variance:
171

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

172
173   where I_i is the combined abundance index for year *i*, and Θ_{ij} are the two or four standardized
174   individual indices, i.e., $j = 1, \ldots, n$ and *n* is either 2 or 4. This approximation tends to
175   overestimate the variance because the ignored negative covariances would be subtracted and
176   result in a smaller estimate. Precision estimates of the combined egg and larval abundance index
177   do not include additional uncertainty in the relationship between the combined index and the
178   actual spawning biomass (see next section; Tables 1 and 2).

179
2.3.2. Calibration of Abundance Indices to Biomass
180

181   The new area-weighted combined egg and larval abundance index extends from 1951 to
182   2011. We calibrated the new index by a least-squares fit to the Daily Egg Production Method
183   (DEPM) biomass estimates produced from 1980 to 1985 (summarized in Jacobson et al., 1994).
184   DEPM has been the basis of scaling for all subsequent anchovy assessments (Jacobson et al.,
185   1994; Methot, 1989). The DEPM estimates provide the best basis for calibrating our area-
186   weighted index, as they are not dependent on arbitrary model specifications or assumed
187   parameter values typical of statistical population dynamics models. We have new index values
188   for three of the DEPM years, 1981, 1982, and 1984 (Fig. 6); 1982 only has values for April, but
189   the other two years include both January and April. The relationship between the three area-
190   weighted indices and the DEPM values for these three years is shown in Figure 6. A calibration
191   of 559,000 MT per index unit was provided by the mean of the three ratios of DEPM biomass to
192   new index value. The CV of the three values was 0.15, and unlike previous abundance
193   estimates, calibration variance is included in precision estimates of biomass derived from the
194   new index.
195

196   ## 3. Results
197   From the 1950s through the early 1990s, larvae tended to be more abundant than eggs in
198   January, and about equally abundant in April. Over the entire time series, April egg abundances
199   were threefold higher than those for January, and larval abundances were higher by a ratio of 1.6.
200   Since the mid-late 1990s, the relative abundance of larvae relative to eggs has declined by about
201   three logarithmic units (-95%; Fig. 4; see also Fissel et al., 2011). We applied the biomass
202   calibration to the area-weighted combined egg and larval abundance index (excluding use of
203   larvae after 1999) to derive an anchovy biomass index for the period 1951-2011. The estimated
204   abundance in 2009-2011 is similar to the extremely low biomasses estimated for the early 1950s
205   (Fig. 7). A logarithmic scale shows the magnitude of the recent decline in abundance. The new
206   biomass estimates show higher values than those estimated by Jacobson et al. (1994) in 1957-
207   1960, 1963-1966, 1969, and in 1986, but otherwise are in general agreement (Figs. 8 and 9).
208   There are similar discrepancies with the time series estimated by Methot's (1989) age-structured
209   model. The time series by Methot (1989) and by Jacobson et al. shared similar data inputs
210   (including aerial spotter logbooks that were very sparse in the early 1960s), and are not
211   independent of each other.
212

213   ## 3.1. Hyperstability Bias
214   Scatterplots of egg production estimates (egg production index (EPI) and HEP)
215   demonstrate hyperstability (Figs. 10 and 11). Power function exponents are 0.55 for EPI and
216   0.46 for HEP relative to area-weighted biomass estimates, thus EPI and HEP values vary
217   approximately as the square root of stock biomass. Notably, these time series do not include low
218   biomass years where hyperstability would be most apparent. The new area-weighted estimates
219   have a very low correlation with egg production indices from Fissel et al. (2011; Fig. 11). There
220   is evidence of hyperstability in Fissel et al. (2011), especially in the 2009 estimate that appears as
221   an outlier on the left in Figure 11. When viewed as a time series (Fig. 12), the first half of the
222   time series compares reasonably well, but an offset begins in the mid-2000s, corresponding with
223   the change in egg-larvae ratios.
224

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 4). 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 5). 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 6). 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 2009-2011 using the area-weighted method developed here are the lowest seen in 60 years, and are matched only by similarly low values at the beginning 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.

When CalCOFI began sampling the California Current for anchovy eggs and larvae in 1951, the population was small. 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 in 1940-41, 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

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271 early 1950s was not within the range of recent "normal" population dynamics. However, the
272 millennial-scale sedimentary deposition record from the Santa Barbara Basin clearly indicates
273 centennial-scale episodes of disappearance or near-disappearance of anchovy and sardine,
274 establishing that, at the longest time scales, occasional severe declines in abundance are a
275 characteristic feature of the population residing in southern California (Baumgartner et al.,
276 1992). While there have been recent anecdotal reports of substantial nearshore anchovy
277 abundance (Herreria, 2014), we hypothesize that much of the remnant population is concentrated
278 close to shore, making them unusually visible to the public and giving a mistaken impression of
279 abundance (hyperstability bias).
280   Now, 60 years after the beginning of CalCOFI egg and larval sampling, we have well-
281 documented evidence for a sudden decline in anchovies, with probable mechanisms similar to
282 MacCall's (1980) hypothesis, though the explanatory details are still not clear. The anchovy
283 population declined from at least a million tons in 2005 to about 15,000 tons estimated for 2009-
284 2011. Remarkably, this decline occurred in the near-absence of fishing and therefore must be
285 considered a natural phenomenon. Support for this interpretation also comes from millennial-
286 scale records when anchovy collapses occurred in the absence of fishing. Alheit and Niquen
287 (2004) described a similar collapse in the Peruvian anchoveta population in the early 1970s, but
288 concluded that fisheries had undoubtedly contributed to the decline. In addition to apparent
289 near-zero recruitment, the natural mortality rate during 2005 to 2009 appears to be far above
290 normal for the central subpopulation. In an assumed absence of recruitment and negligible
291 fishing pressure, the four-year rate of decline in biomass gives an estimated natural mortality rate
292 (M) of approximately 1.2 yr^{-1}, about twice that assumed by Jacobson et al. (1994). If recruitment
293 was greater than zero, the observed decline in abundance would require the estimated M to be
294 higher yet. The severe decline in anchovies is a likely factor in recent reports of reproductive
295 failure, mortality, and declines of California's marine mammals (Melin et al., 2010) and seabirds
296 (Henry, 2015; Sydeman et al., 2015). In previous historical experience, the return of viable
297 reproductive conditions during the mid-1950s allowed rapid recovery of the anchovy population.
298 It is reasonable to expect that abundance could recover quickly again if and when favorable
299 conditions return. However, other factors such as predation may be currently limiting population
300 growth. Major anchovy predators, such as California sea lions and humpback whales, have
301 recovered from very low abundances of the 1950s (Carretta et al., 2014; Calambokidis and
302 Barlow, 2004), and may now be consuming a larger fraction of the anchovy population,
303 especially under the presently low abundances and nearshore concentrations.
304   In addition to the ecological aspects of the anchovy decline, this study raises concerns
305 about previous anchovy assessment methodology. In particular, previous studies that used
306 equally-weighted average overall densities and bootstrap techniques are not appropriate for a
307 species that contracts its range into the most densely sampled region of a study grid. Spatially-
308 explicit methodology for area-weighting or expansion of CalCOFI samples is essential for
309 anchovy assessments. Because the use of space by anchovy is not even, inclusion of the partial
310 time series from SCCOOS stations is also problematic. Previous studies also used temperature
311 corrections to estimate anchovy egg production (e.g., Lo, 1985; Fissel et al., 2011); such
312 corrections should be retained, but need to be combined with the spatial approach we have
313 developed here. Last, since about 2000, there has been a decrease in January egg and larval
314 abundances relative to those seen in April. Whether this is a contraction of the spawning season
315 or an overall shift to a later spawning season cannot presently be determined. Hunter and Leong
316 (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 severely off southern California in the past decade.
The estimated spawning biomass decreased by over 99 percent 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 precipitous 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.

6. Acknowledgements

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475

476   Table 1. Area-expanded egg and larval population estimates (10^{10} individuals) for southern

477   California CalCOFI surveys.

| Year | January | | | | April | | | |
	Eggs	Larvae	CV Eggs	CV Larv	Eggs	Larvae	CV Eggs	CV Larv
1951	0	22.68		0.14	12.96	14.21	1.07	0.37
1952	0	14.76		0.35	3.72	16.32	1.24	1.31
1953	5.66	14.23	1.32	0.69	5.69	18.63	1.04	0.46
1954	21.4	194.61	0.61	0.18	26.43	18.87	0.92	0.36
1955	22.59	151.36	1.16	0.59	17.2	53.71	0.53	0.47
1956	0	15.68		0.48	59.11	60.27	0.49	0.47
1957					1900.99	451.15	0.62	0.32
1958	83.37	356.47	0.65	0.48	754.09	425.11	0.48	0.22
1959	171.61	202.17	0.64	0.35	355.36	1168.3	0.39	0.17
1960	8.15	23.31	0.62	0.25	1565.47	726.74	0.21	0.23
1961	10.27	3.94	0.91	0.33	470.22	577.9	0.36	0.32
1962	111.25	226.09	0.37	0.32	674.03	1499.8	0.15	0.18
1963	347.33	555.8	0.27	0.14	1165.75	2031.01	0.32	0.24
1964	1174.27	1013.98	0.26	0.4	4216.43	1342.25	0.39	0.16
1965	2506.01	643.27	0.32	0.16	1524.56	1384.61	0.46	0.2
1966	833.09	968.17	0.22	0.22	5324.92	1239.89	0.46	0.14
1967								
1968	132.1	440.52	0.29	0.26				
1969	447.11	1282.26	0.17	0.26	1770.73	485.65	0.45	0.17
1970								
1971								
1972	20.88	53.87	0.67	0.34	365.21	1096.91	0.51	0.4
1973								
1974								
1975	747.09	1574.61	0.23	0.22				
1976								
1977								
1978	208.51	389.18	0.23	0.21	594.85	506.16	0.36	0.26
1979	255.78	222.16	0.58	0.44	690.95	457.37	0.96	0.37
1980								
1981	159.69	355.27	0.42	0.29	250.4	1382.52	0.72	0.14
1982					563.51	211.35	0.39	0.18
1983								
1984	156	285.28	0.64	0.2	318.74	639.99	0.76	0.19
1985								
1986	1677.23	873.16	0.31	0.2				
1987					645.94	433.97	0.42	0.26
1988	914.82	503.37	0.33	0.2	364.68	178.97	0.82	0.27
1989	37.47	344.38	0.88	0.33	22.63	55.94	0.58	0.21
1990					91.16	75.56	0.2	0.4
1991	235.34	245.8	0.53	0.33				
1992	22.72	140.51	0.5	0.51	188.19	147.49	1.49	0.43
1993	68.97	51.9	0.61	0.33	89.9	225.44	0.84	0.33
1994	172.53	272.65	0.37	0.26	319.48	463.88	0.62	0.51

12

1995	62.54	19.7	0.93	0.65	402.63	128.9	1.09	0.42
1996	657.82	373.76	0.32	0.25	15.99	87.34	0.98	0.29
1997	200.95	113.32	0.33	0.3	642.95	32.62	1.58	0.31
1998	43.29	61.03	0.39	0.39	107.8	134.88	0.46	0.39
1999	176.11	148.04	0.41	0.83	88.28	174.21	0.61	0.45
2000	5.88	2.7	0.93	0.95	474.53	184.51	0.5	0.41
2001	119.8	7.98	0.3	0.28	710.48	69.99	0.37	0.32
2002	183.68	21.28	0.85	0.51	27.6	149.52	0.58	0.34
2003	112.17	23.57	0.63	0.27	88.19	34.04	0.67	0.79
2004	30.8	0.75	0.73	0.65	1501.73	107.87	0.73	0.69
2005	8.28	1.89	1.18	0.6	5222.7	1458.25	0.27	0.21
2006					1653.52	71.9	0.35	0.26
2007	11.96	1.61	0.81	0.55	531.78	23.09	0.45	0.33
2008	0.11	0	1.04		383.42	10.22	0.61	0.33
2009	11.18	0.07	1.8	1.54				
2010	17.62	10.86	1.39	0.52	0.59	0.16	0.8	1.3
2011	4.02	6.33	0.69	0.68	32	0.26	1.86	0.48

478

479

480

481   Table 2. Southern California indices scaled to unit mean, combined and calibrated to DEPM

482   biomass.

Year	January		April		Combined	Calibrated Biomass		
	Eggs	Larvae	Eggs	Larvae	Index	1000 t	CV	SE
1951	0	0.065	0.018	0.028	0.028	15.5	1.51	23.4
1952	0	0.042	0.005	0.032	0.02	11.1	1.78	19.8
1953	0.017	0.041	0.008	0.036	0.026	14.3	1.57	22.4
1954	0.064	0.56	0.036	0.037	0.174	97.5	0.62	60.1
1955	0.068	0.436	0.024	0.105	0.158	88.3	0.65	57.1
1956	0	0.045	0.081	0.118	0.061	34	1.02	34.9
1957			2.598	0.88	1.739	972.3	0.41	395.7
1958	0.25	1.026	1.031	0.829	0.784	438.3	0.32	139.7
1959	0.514	0.582	0.486	2.278	0.965	539.6	0.29	158.8
1960	0.024	0.067	2.139	1.417	0.912	510	0.3	153.3
1961	0.031	0.011	0.643	1.127	0.453	253.3	0.4	101.2
1962	0.333	0.651	0.921	2.925	1.207	675.2	0.27	183.2
1963	1.04	1.6	1.593	3.961	2.048	1145.4	0.23	262
1964	3.515	2.919	5.762	2.617	3.704	2070.9	0.2	407.4
1965	7.502	1.852	2.083	2.7	3.534	1976.3	0.2	392.8
1966	2.494	2.787	7.277	2.418	3.744	2093.6	0.2	410.9
1967								
1968	0.395	1.268			0.832	465.1	0.57	264.1
1969	1.338	3.692	2.42	0.947	2.099	1173.8	0.23	266.6
1970								
1971								
1972	0.063	0.155	0.499	2.139	0.714	399.2	0.33	132
1973								
1974								
1975	2.236	4.533			3.385	1892.7	0.31	585.5
1976								
1977								
1978	0.624	1.12	0.813	0.987	0.886	495.5	0.3	150.6
1979	0.766	0.64	0.944	0.892	0.81	453.1	0.31	142.5
1980								
1981	0.478	1.023	0.342	2.696	1.135	634.5	0.28	176
1982			0.77	0.412	0.591	330.5	0.67	220.4
1983								
1984	0.467	0.821	0.436	1.248	0.743	415.5	0.33	135.2
1985								
1986	5.021	2.514			3.767	2106.6	0.3	625.6
1987			0.883	0.846	0.865	483.4	0.56	269.6
1988	2.739	1.449	0.498	0.349	1.259	703.9	0.27	188.2
1989	0.112	0.991	0.031	0.109	0.311	173.9	0.47	82.1
1990			0.125	0.147	0.136	76	1.36	103.7
1991	0.704	0.708			0.706	394.8	0.61	242.1
1992	0.068	0.405	0.257	0.288	0.254	142.2	0.52	73.6
1993	0.206	0.149	0.123	0.44	0.23	128.4	0.54	69.6
1994	0.516	0.785	0.437	0.905	0.661	369.4	0.34	126.1

1995	0.187	0.057	0.55	0.251	0.261	146.2	0.51	74.7
1996	1.969	1.076	0.022	0.17	0.809	452.6	0.31	142.4
1997	0.602	0.326	0.879	0.064	0.468	261.4	0.39	103.1
1998	0.13	0.176	0.147	0.263	0.179	100	0.61	60.9
1999	0.527	0.426	0.121	0.34	0.353	197.6	0.45	88.1
2000	0.018		0.648		0.333	186.2	0.88	163.7
2001	0.359		0.971		0.665	371.7	0.63	234.5
2002	0.55		0.038		0.294	164.3	0.93	153.5
2003	0.336		0.121		0.228	127.6	1.06	134.9
2004	0.092		2.052		1.072	599.6	0.5	302.8
2005	0.025		7.137		3.581	2002.5	0.3	606.2
2006			2.26		2.26	1263.6	0.68	861.1
2007	0.036		0.727		0.381	213.2	0.82	175.5
2008	0		0.524		0.262	146.6	0.99	144.8
2009	0.033				0.033	18.7	5.47	102.3
2010	0.053		0.001		0.027	15	3.06	45.8
2011	0.012		0.044		0.028	15.6	3	46.7

483

484   Table 3. Correlations among anomalies from common annual mean (arithmetic scale).

485

	JanEggs	JanLarvae	AprEggs	AprLarvae
JanEggs	1	-0.1	-0.63	-0.47
JanLarvae		1	-0.39	0.01
AprEggs			1	-0.24
AprLarvae				1

486

487

488   Table 4. Area-expanded egg and larval population estimates (10^{10} individuals) for full California

489   CalCOFI surveys.

490

Year	January				April			
	Eggs	Larvae	CV eggs	CV larv	Eggs	Larvae	CV eggs	CV larv
1951	0	22.8		0.14	12.96	15.1	1.08	0.36
1952					3.72	16.32	1.26	1.32
1953					5.69	18.63	1.05	0.46
1954					26.48	18.96	0.93	0.36
1955								
1956					59.11	60.27	0.49	0.48
1957								
1958	105	381.03	0.61	0.44	831.13	433.17	0.44	0.22
1959	180.54	210.15	0.6	0.34	410.97	1325	0.34	0.15
1960	25.45	24.15	0.58	0.25	1586.82	749.95	0.21	0.22
1961	10.27	4.18	0.92	0.32	467.72	576.59	0.37	0.32
1962	121.74	226.47	0.35	0.32	679.5	1564.6	0.15	0.18
1963	364.99	556.55	0.26	0.14	1242.93	2172.44	0.3	0.22
1964	1177.9	1056.09	0.26	0.29	4546.55	1632.03	0.37	0.16
1965	2513.09	643.85	0.32	0.16	1535.88	1395.67	0.45	0.19
1966	834.21	1008.84	0.22	0.21	5324.92	1246.89	0.46	0.14
1967								
1968	139.53	464.88	0.28	0.25				
1969	510.84	1313.52	0.2	0.26				
1970								
1971								
1972	20.88	55.55	0.67	0.33	365.21	1096.86	0.52	0.4
1973								
1974								
1975	747.44	1581.68	0.23	0.22				
1976								
1977								
1978	362.19	399.93	0.59	0.21	717.41	550.42	0.35	0.25
1979	255.78	249.97	0.59	0.4	691.01	457.58	0.68	0.27
1980								
1981	421.34	374.12	0.88	0.28	250.4	1385.91	0.52	0.11
1982					1821.05	258.04	0.79	0.22
1983								
1984	246.84	295.23	0.53	0.2	318.72	639.97	0.77	0.19
1985								
1986								
1987								
1988								
1989								
1990								
1991								
1992								

Year								
1993								
1994								
1995								
1996								
1997								
1998					245.86	230.24	0.57	0.34
1999								
2000								
2001								
2002								
2003	473.84	31.03	0.93	0.26	88.19	34.04	0.68	0.79
2004	36.31	1.04	0.62	0.52	1510.43	121.27	0.73	0.62
2005	9.77	3.14	1.01	0.58	5684.5	1469.74	0.26	0.21
2006					1795.93	71.9	0.32	0.26
2007	12.17	1.85	0.79	0.58	531.78	23.24	0.45	0.33
2008	0.11	0	1.04		383.42	10.22	0.61	0.33
2010	17.62	15.58	1.4	0.38	0.59	0.16	0.8	1.31
2011	4.02	6.33	0.7	0.68	41.1	0.26	1.47	0.48

491

492

493   Table 5. Statistical relationship between full California estimates and southern California area-

494   expanded population estimates.

495

Ratio(Full/Core)	January		April		
	Eggs	Larvae	Eggs	Larvae	All
Ncases	25	25	29	29	108
Median	1.05	1.04	1	1.01	1.01
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 above 1.1	0.35	0.23	0.21	0.17	0.24
Fraction at 1.0	0.44	0.24	0.52	0.48	0.43

496

497

498   Table 6. Ratios of full California to southern California area-expanded populations in recent

499   years.

500

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

501

502

503   **Figures**
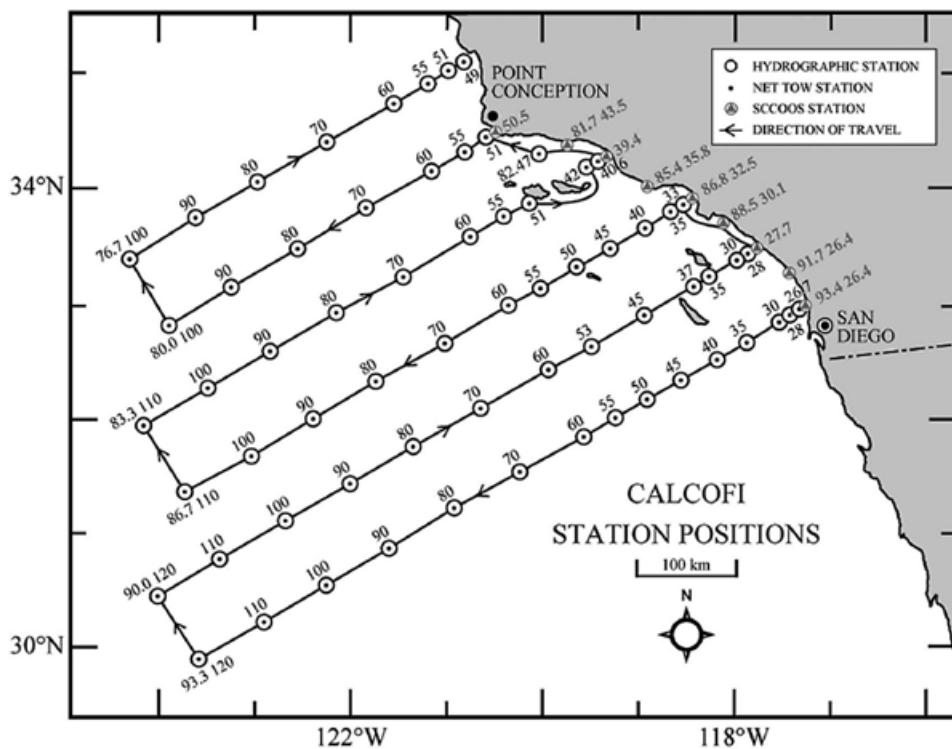
504

505   Figure 1. Locations of core southern California CalCOFI sampling stations, also showing

506   location of the nine nearshore SCCOOS stations added in Fall 2004.

507

508
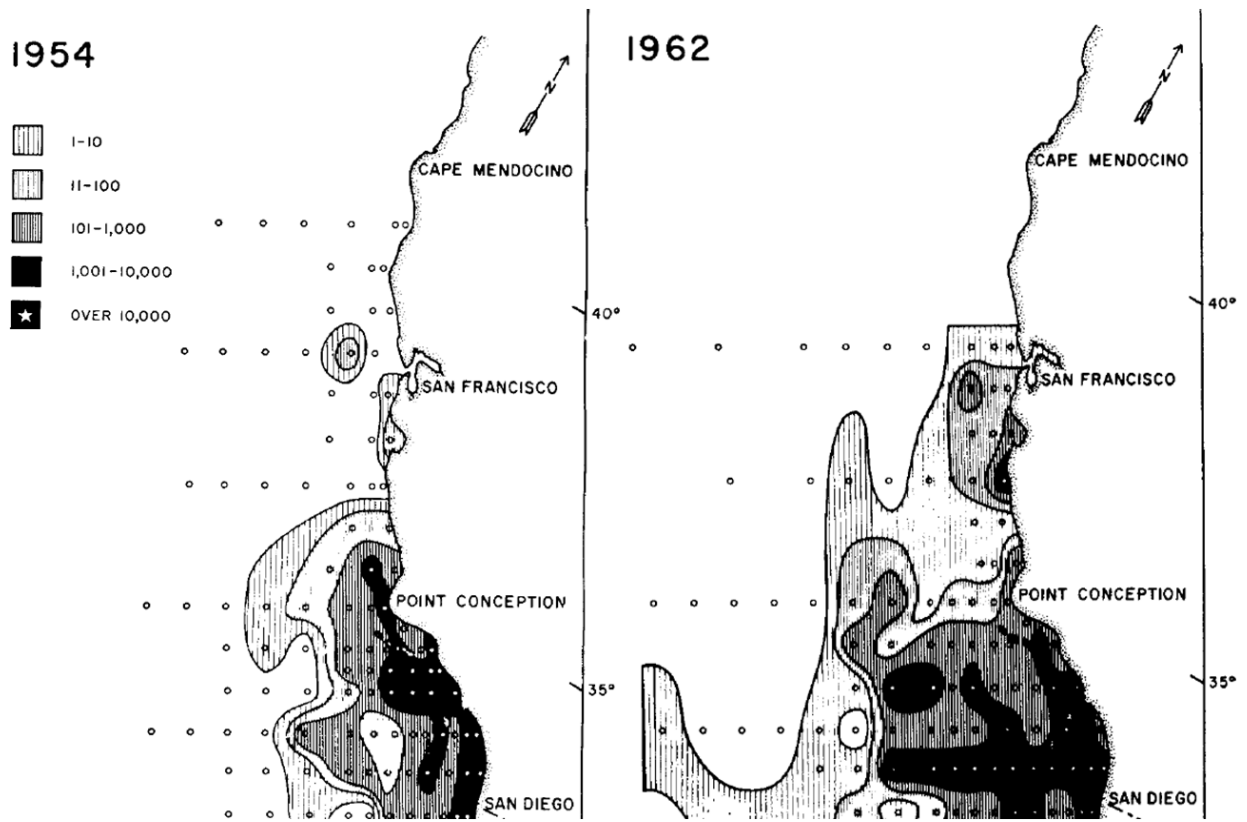
509

510   Figure 2. Comparison of southern California anchovy larval distributions at low population size

511   (left) and high population size (right) showing areal expansion when the stock is more abundant.

512   Taken from Kramer and Ahlstrom (1968).

513

514
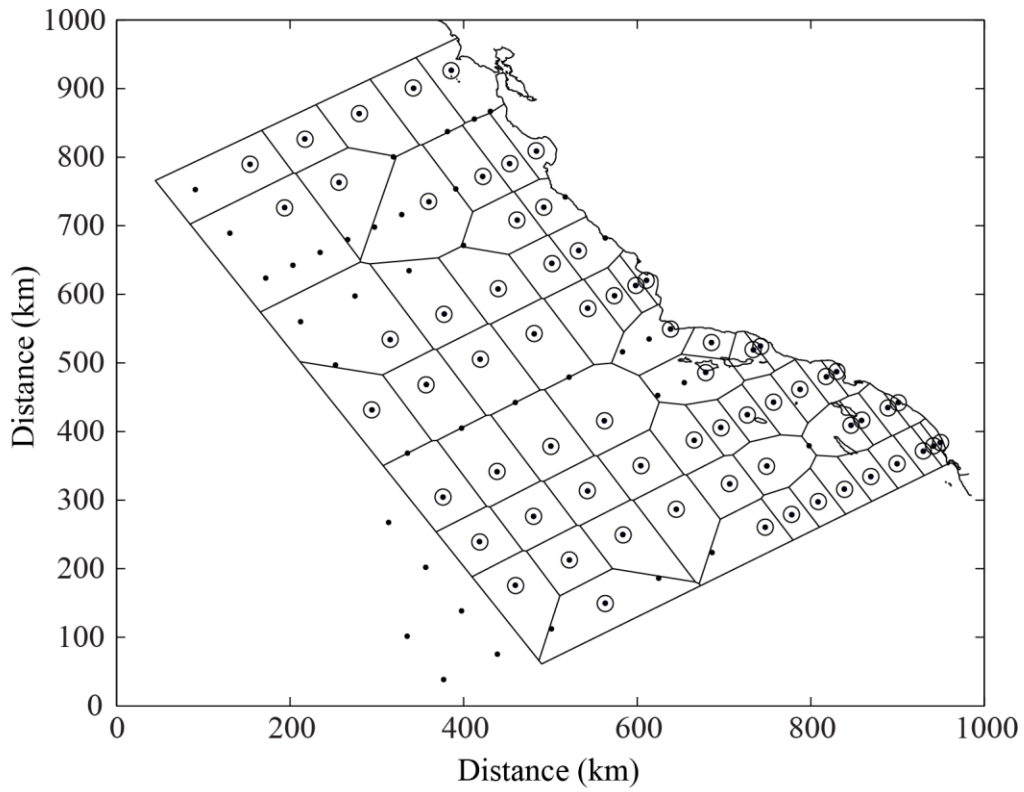
Figure 3. Example set of Thiessen polygons for April, 2008. Dots indicate standard CalCOFI stations, and circles indicate occupied stations.
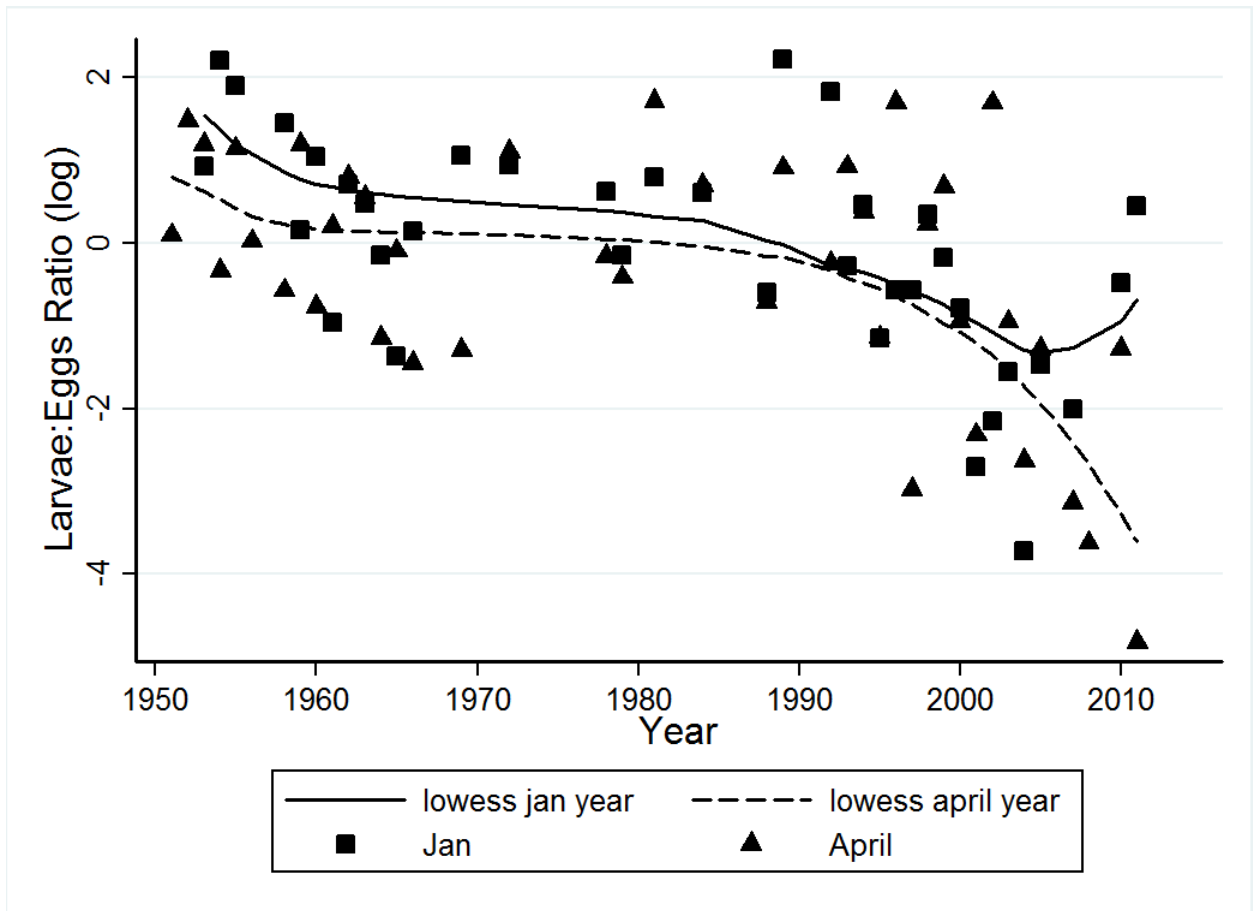
520

521   Figure 4. Trend in abundances of larvae relative to eggs in southern California. January is solid

522   line; April is dotted line.

523

524
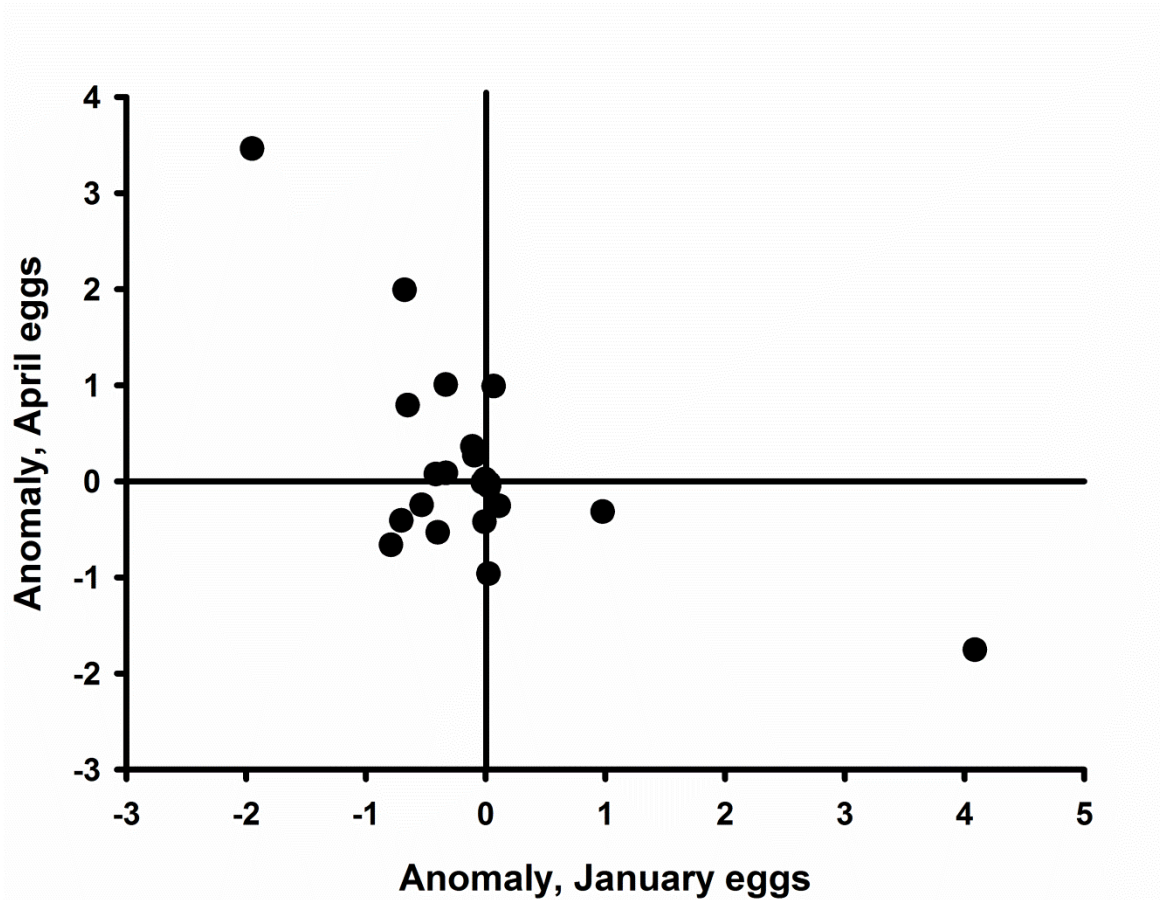
525

526   Figure 5. Scatterplot of relationship between egg abundances by season: anomalies from

527   common annual mean are shown (Spearman rho = -0.63).

528

529

530
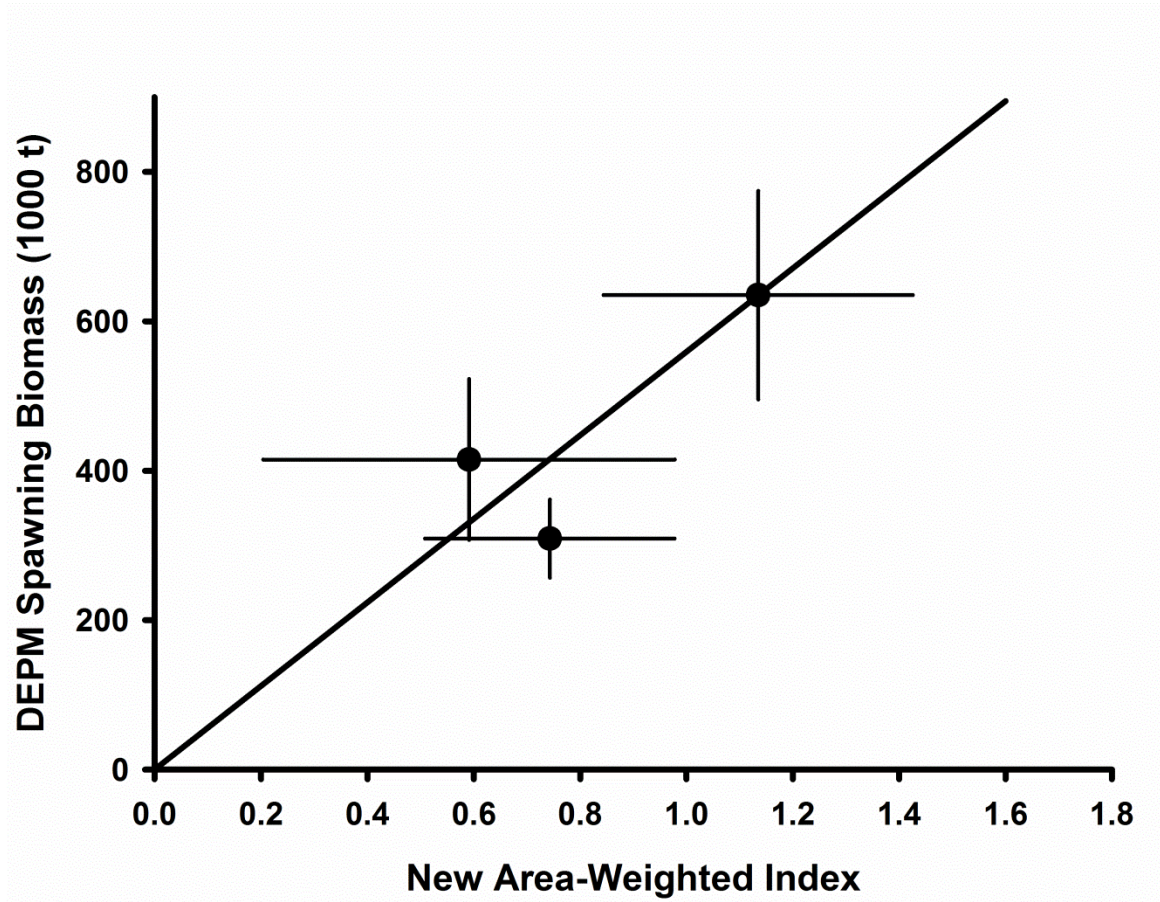
Figure 6. Calibration of new area-weighted index based on relationship to DEPM estimates of

532   spawning biomass (CV = 0.15). Error bars are one standard error.

533

534
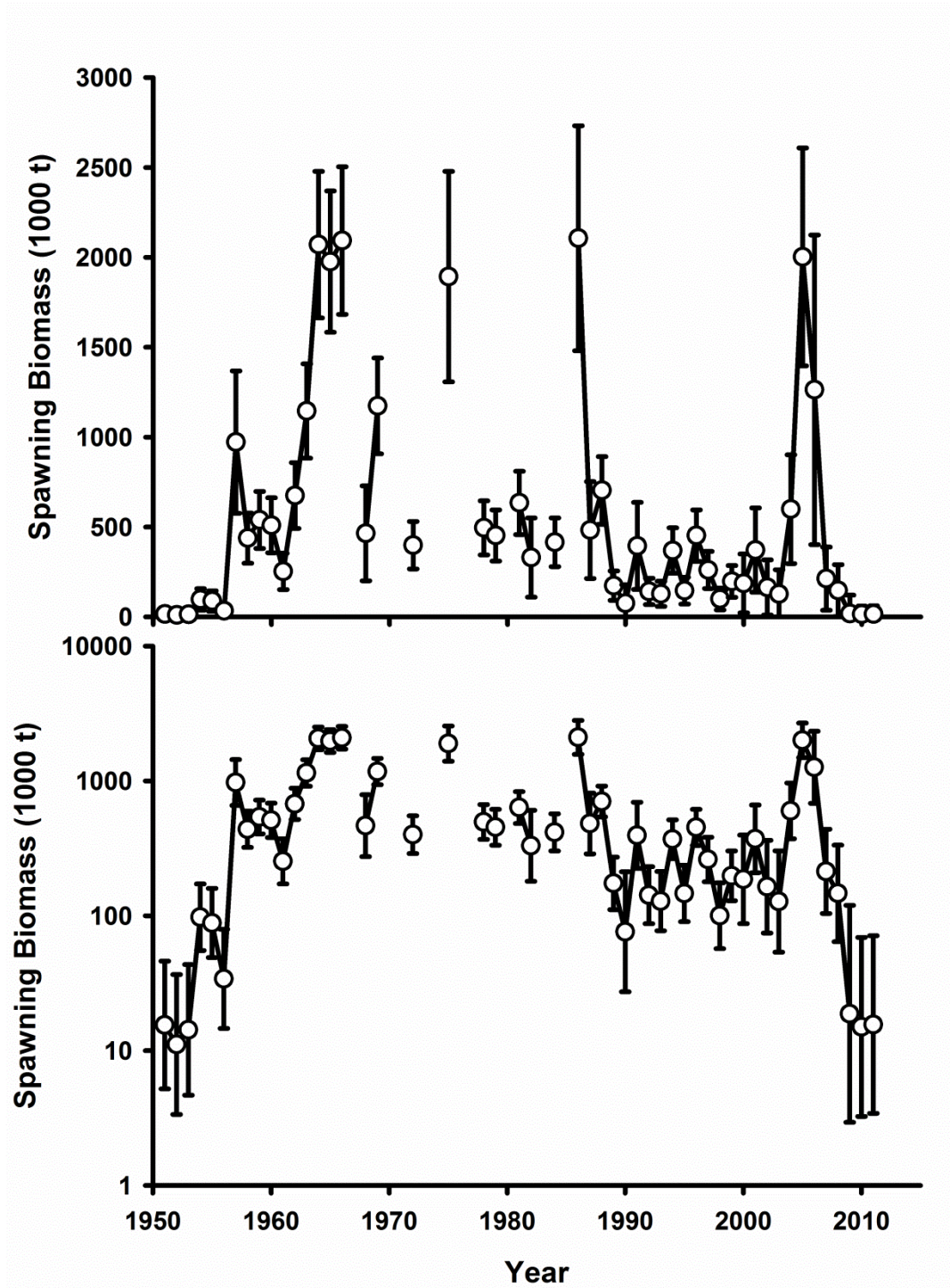
535

536   Figure 7. Time series of anchovy biomass estimated by the area-weighted method. Error bars in

537   upper panel are one standard error and include calibration variance. Lower panel is on

538   logarithmic scale.

539
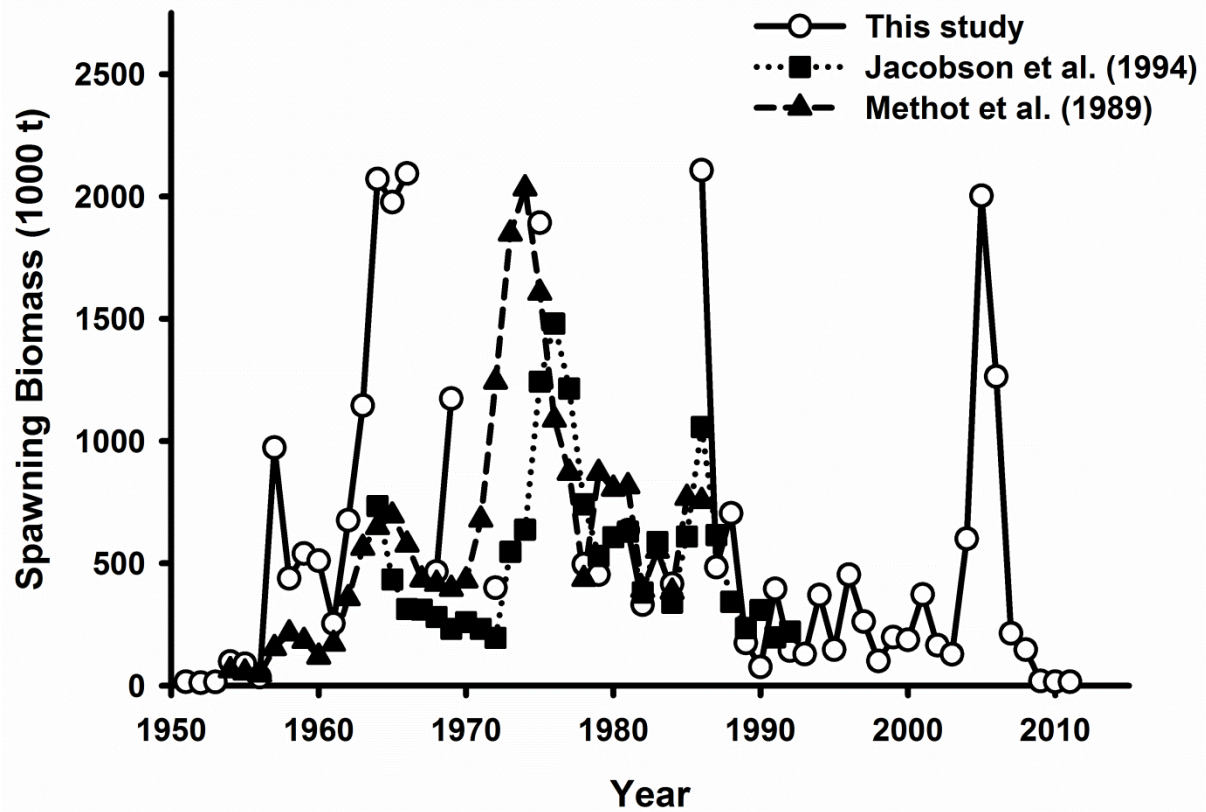
Figure 8. Comparison of new area weighted biomass estimates (circles) and corresponding

biomass estimates from Jacobson et al., (1994) (squares, solid line) and Methot, (1989)

(triangles, dotted line).

543

544

545
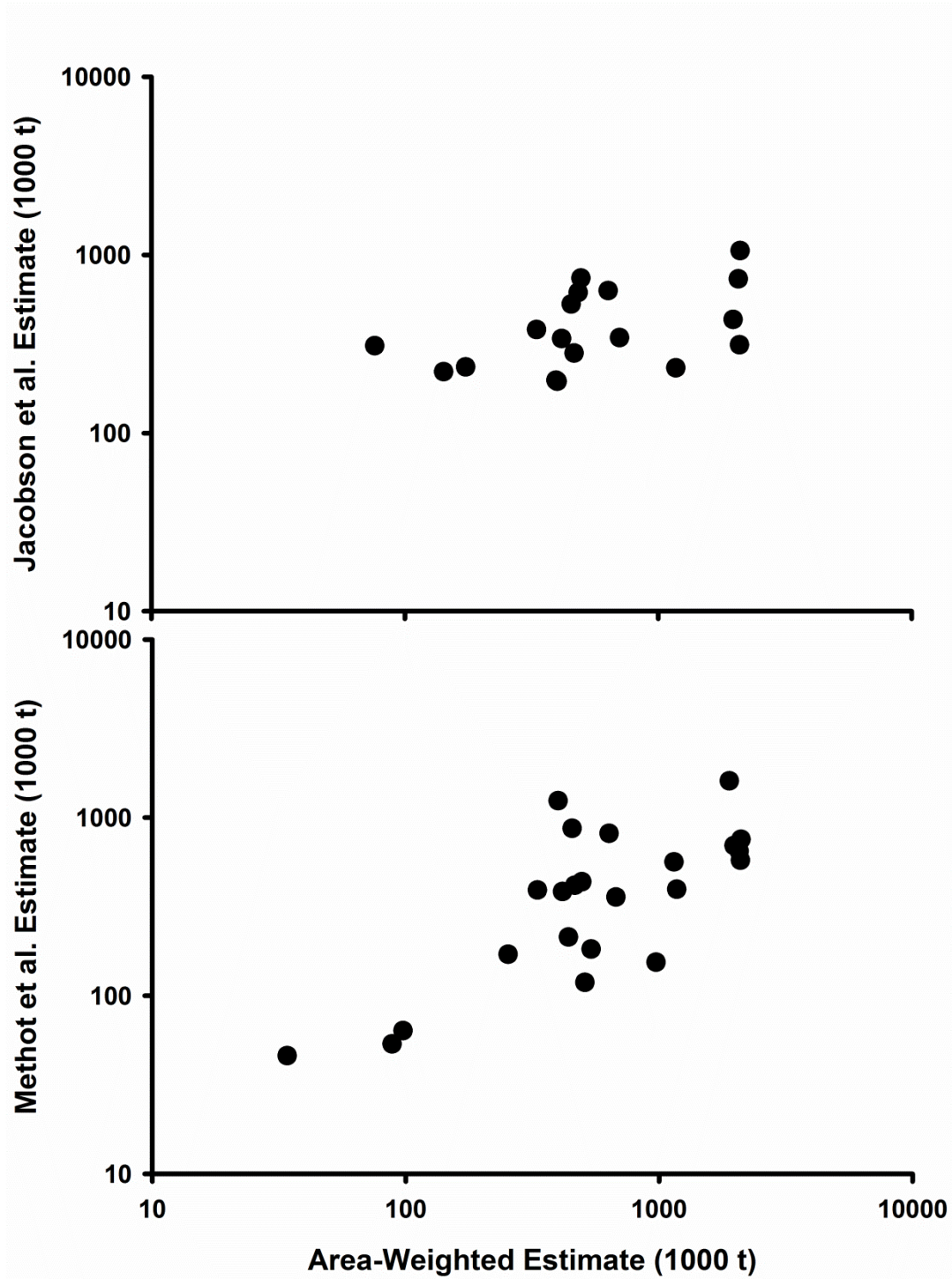
Figure 9. Scatterplots of previous biomass estimates against new area-weighted biomass

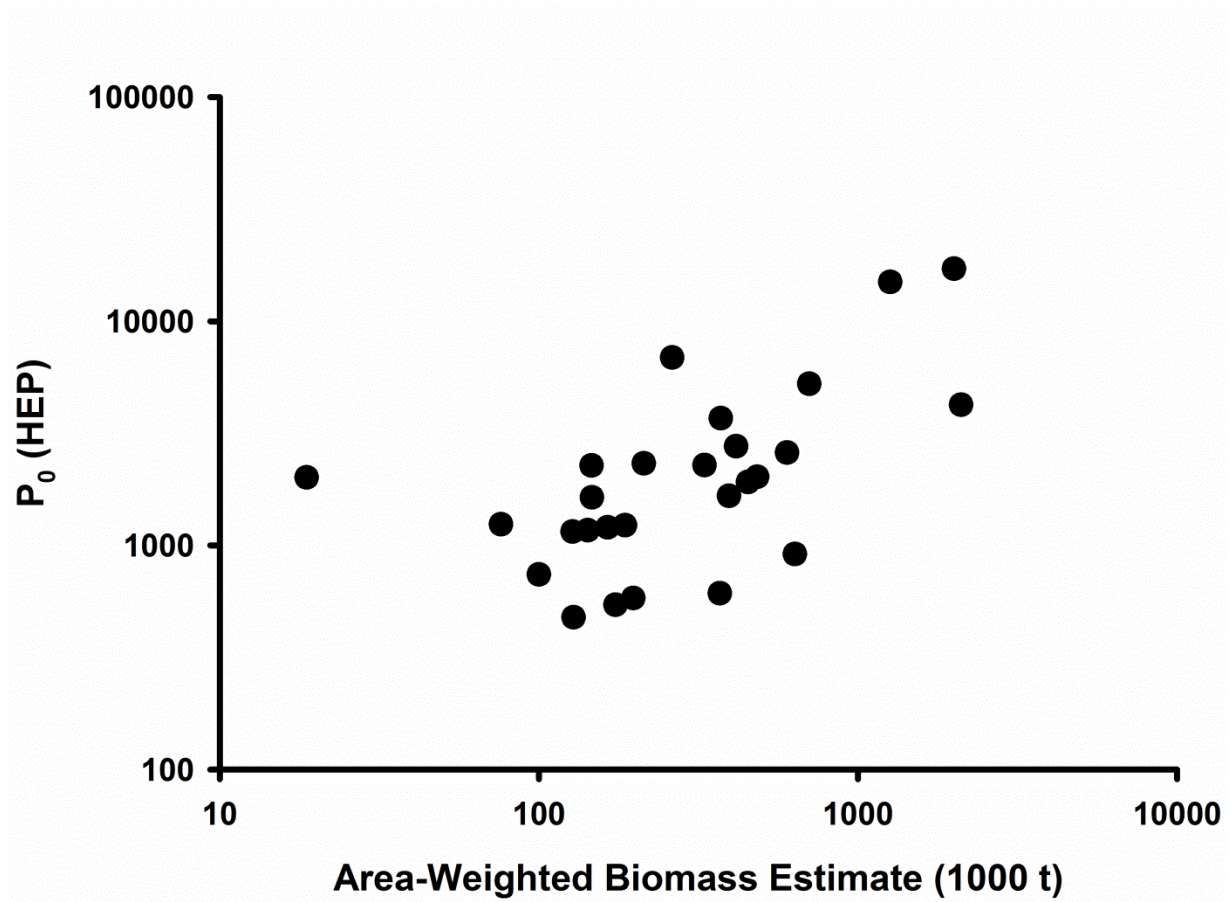estimate (log scale). Upper panel is Jacobson et al. (1994), and lower panel is Methot (1989).

548
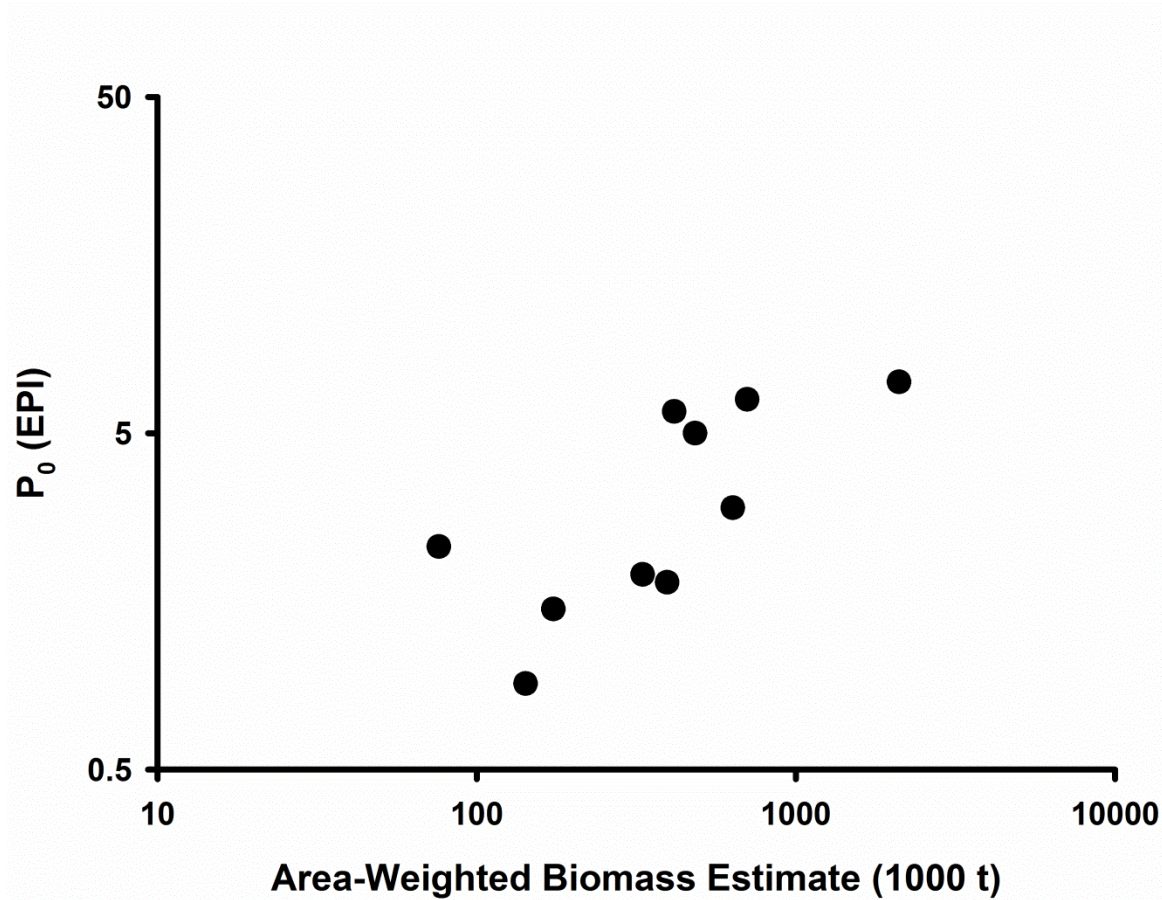
Figure 10. Scatterplot of EPI estimates of daily egg production rate (P_0) with area-weighted biomass estimates (Spearman rho = 0.71), showing hyperstability (fitted power function exponent < 1, see text).
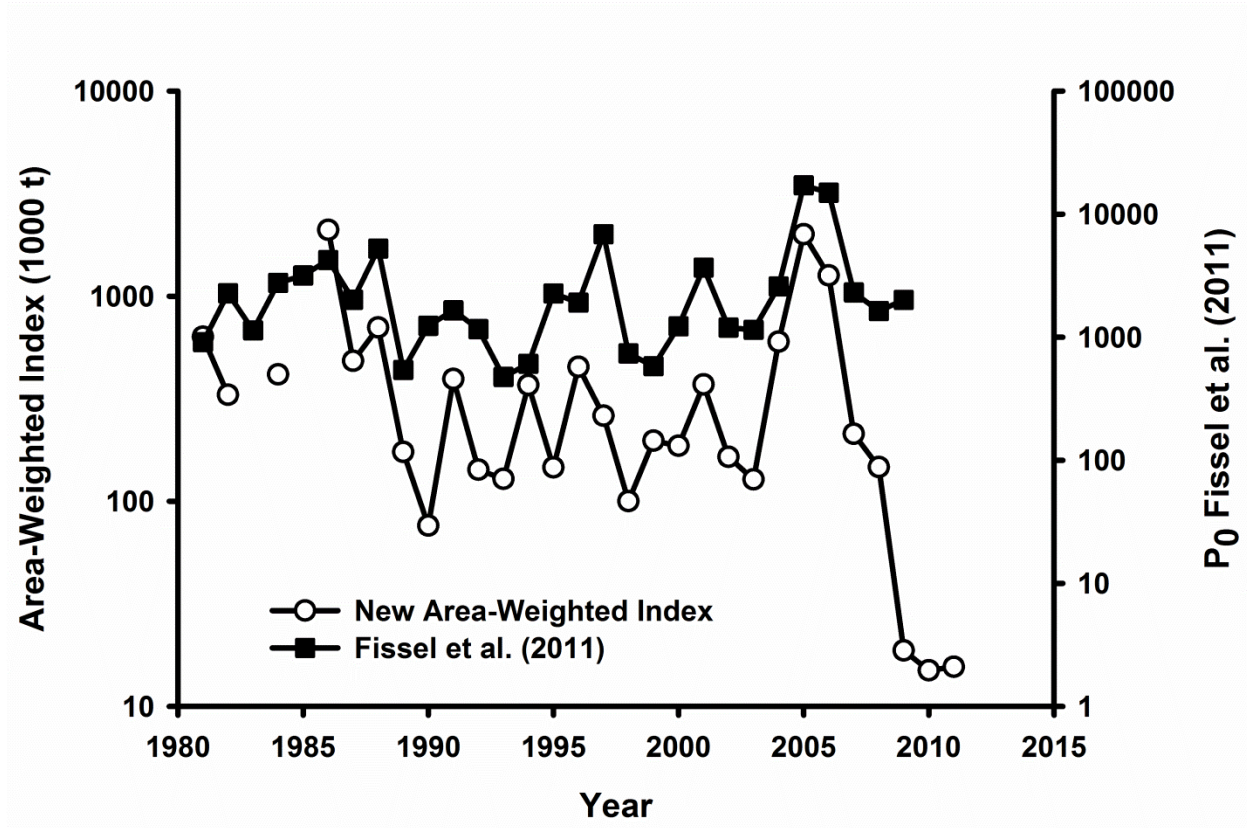
555

Figure 11. 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.

558

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561 Figure 12. Comparison of time series of egg production rate (P_0) estimates from Fissel et al.

562 (2011) with area-weighted biomass estimates, including additional values for 2010 and 2011.

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