

THE CALIFORNIAN EL NIÑO OF 1992 AND THE FALL OF CALANUS

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ABSTRACT

Although physical indications of the 1992 Californian El Niño were ambiguous off southern California in autumn 1991, chlorophyll and female *Calanus* were already anomalously scarce. Daily egg production in that autumn—calculated from the observed biomasses of chlorophyll, a fecundity-vs.-chlorophyll regression for autumn, and the observed abundances of female *Calanus*—was sufficiently reduced to explain the relative rarity of the next generation in winter 1992.

INTRODUCTION

The California Current system showed symptoms of an El Niño-like event during much of 1992, including anomalously high temperatures, deep mixed layers, deep nutriclines, elevated sea levels, and (for some of the year) reduced biomass of phytoplankton measured as chlorophyll (Hayward 1993). During similar past events, the biomass of zooplankton has been reduced (Chelton et al. 1982; McGowan 1985); in 1992 the reduction was superimposed on a longer-term depauperization associated with higher temperatures in the California Current system since the mid-1970s (Roemmich and McGowan 1995).

The temperature in the preceding autumn (1991), as reflected at the coast off La Jolla, California, was very near the long-term mean (the persistent positive anomaly did not begin until late December). However, sea level became anomalously high after September, and there was a strong, poleward countercurrent along the coast in October, which persisted through February 1992 (Hayward 1993). Thus some symptoms of the Californian El Niño were already present in autumn, even though some physical properties were normal.

Though the data series was too short to identify a genuine anomaly, females of the planktonic copepod *Calanus pacificus* were significantly less abundant off southern California during winter-spring of 1992 than during the comparable seasons of 1989–91. Per capita reproduction also was diminished in February 1992, in proportion to the depauperization of chlorophyll then, but the relative rarity of adult *Calanus* was much more striking than the change in fecundity (Mullin 1994). This rarity could have arisen from an excess of deaths during

the ontogeny of the adults sampled in February, reduced net immigration from populations farther north as a result of altered advection, or rarity or reduced fecundity of the preceding (autumnal) generation.

I therefore examined data and samples from the California Cooperative Oceanic Fisheries Investigations (CalCOFI) for the autumns (Oct.–Nov.) of 1988–91 to try to determine the antecedents of the biological anomalies observed in early 1992. Unfortunately, I did not measure reproduction in autumn 1991, so comparison of this demographic property with 1988 and 1989 (Mullin 1991) can be only indirect.

METHODS

The standard sampling methods used by CalCOFI, and the approaches I used for analyzing the data, have been described (Mullin 1994). Specifically, I present results for autumn 1991 as departures (anomalies) from the conditions averaged over the preceding three autumns, which for present purposes are defined as “normal.”

It may be that, because of increased depth of diel vertical migration by *Calanus* in summer and autumn (e.g., Koslow and Ota 1981), the standard 200 m CalCOFI tow is less adequate in daytime as a sampler of the total population than it is in winter and spring. Further, if a larger fraction of the population lived deeper than 200 m during 1991 than during the preceding three autumns, so that underestimation of the real population was more serious in 1991 than previously, apparent negative anomalies of abundance for 1991 would be computed even if true abundances throughout the entire water column were unaltered. If the deep-living females were permanently inactive reproductively, the effect on the subsequent generation would be the same as if they were truly absent, and the negative anomalies would still be effectively real. If the deep-living females were active, they might also be migrating at night to depths shallower than 200 m, in which case negative anomalies would be calculated exclusively or primarily at those stations sampled during daylight hours.

To examine this possibility, I recalculated anomalies in abundance for (1) only those stations sampled nocturnally on Cruise 9110 and in at least two of the preceding three autumns, using only the nocturnal data, and (2) only those stations sampled diurnally on Cruise

9110 and in at least two of the "normal" autumns, using only the diurnal data. These calculations revealed "nocturnal" and "diurnal" anomalies in abundance, and I then tested for difference in the medians. If a greater fraction of female *Calanus* migrated from below 200 m by day to shallower depths at night in autumn 1991 than in "normal" autumns, I should be able to reject the null hypothesis of equality of medians in favor of the 1-sided alternative that the median nocturnal anomaly was less than the median diurnal one.

I had measured the production of eggs by individual female *Calanus*, with and without supplemented food as cultured diatoms, in the autumns of 1988 and 1989 at a subset of the stations sampled during the CalCOFI cruises. These data, plus the concurrent CalCOFI measurements of chlorophyll biomass at those stations, resulted in regressions of per capita fecundity on chlorophyll (Mullin 1991). The mean regression was $\text{eggs} \cdot (\text{female} \cdot \text{day})^{-1} = 0.37 \cdot (\text{mg chlorophyll} \cdot \text{m}^{-2})$, for chlorophyll $\leq 100 \text{ mg} \cdot \text{m}^{-2}$.

For the present study, I used this equation, plus data on chlorophyll, to calculate per capita reproduction at all CalCOFI stations in the autumns of 1988, 1989, 1990, and 1991 (locations in figure 1). This expanded the set of stations for which reproduction could be calculated, but eliminated any variability not accounted for by the biomass of chlorophyll. I then multiplied the abundance of female *Calanus* at each station by the calculated per capita reproduction at that station to compute the population's reproduction during autumn 1991, and calculated average reproduction during the preceding three autumns similarly, in order to estimate the likely change in reproduction during 1991.

I also examined whether the mesoscale spatial distribution of *Calanus*, relative to that of chlorophyll, was any more advantageous in autumn 1991 than previously.

RESULTS

The southern California sector of the California Current system in October of 1991 (Cruise 9110) already showed some symptoms of the El Niño that was present in February 1992. Although autumnal coastal temperature was normal relative to the long-term mean, the area sampled during Cruise 9110 was anomalously warm relative to the three earlier autumns (median anomaly $+0.4^\circ\text{C}$, difference significant at $p < 0.01$ by sign test); the greatest positive anomalies were east of Point Conception in the Santa Barbara Channel and south-southeast along the Santa Rosa-Cortes Ridge (figure 1). The biomass of chlorophyll in much of the area was less than in the earlier autumns (median anomaly -16% , difference significant at $p = 0.01$ by sign test), and there was a negative relation between the two anomalies: the

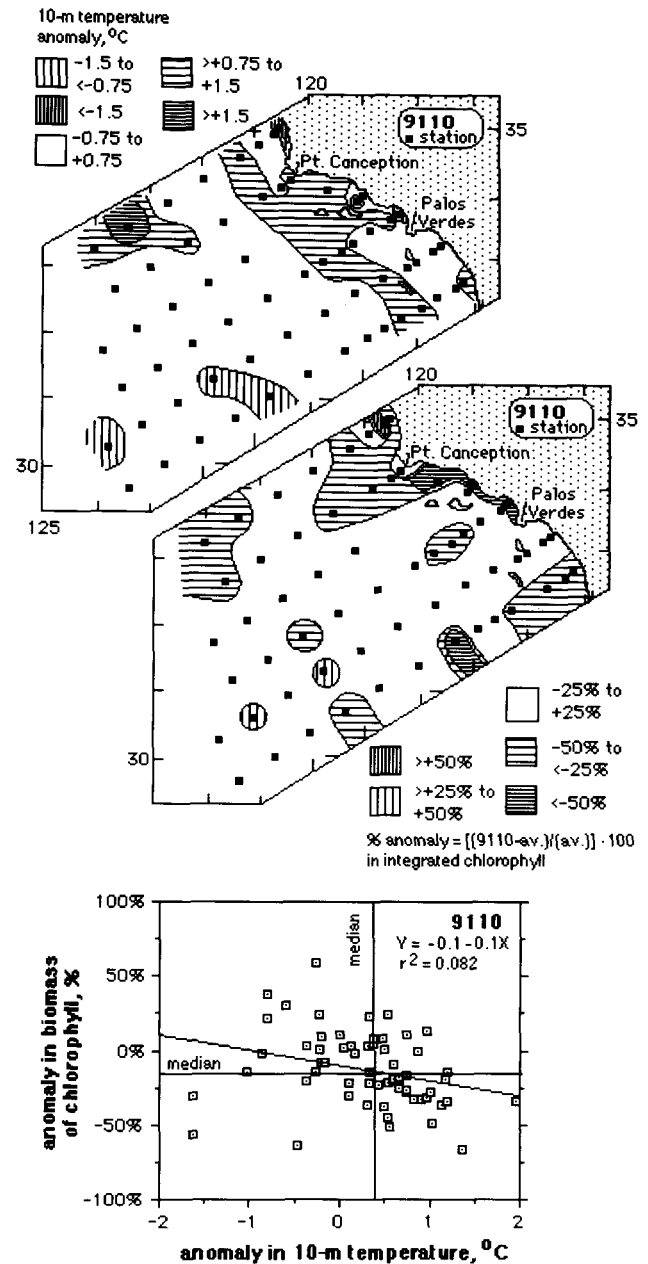


Figure 1. Anomalies in temperature at 10 m in $^\circ\text{C}$ (upper) and in biomass of chlorophyll to 100 m in percentages (middle) in October 1991 relative to conditions averaged (av.) in the previous three autumns; horizontal striping represents positive anomalies of temperature and negative anomalies of chlorophyll. Bottom, relation between the anomalies. The regression is significant ($p < 0.05$, 2-tailed).

more anomalously warm a station was, the greater the negative anomaly of chlorophyll (figure 1).

The median abundance of female *Calanus* during Cruise 9110 was significantly less than that during "normal" autumn ($p < 0.01$ by sign test). The median anomaly was -67% , and was significantly ($p < 0.05$, 2-tailed) negatively related to 10 m temperature anomaly (figure 2): the more anomalously warm a station, the more anomalously rare was *Calanus*.

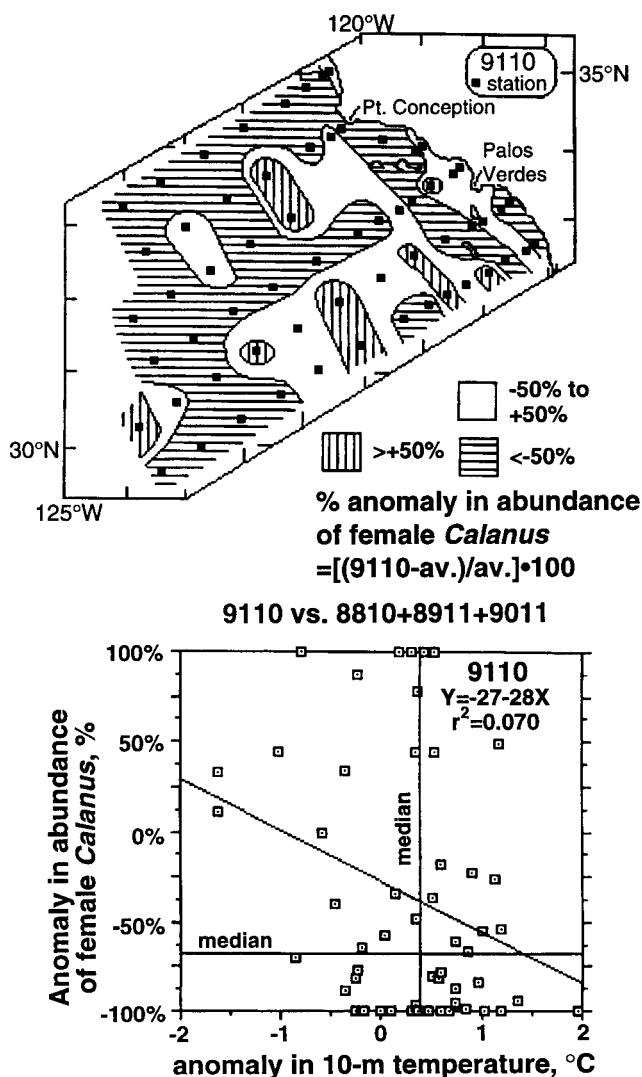


Figure 2. Upper, anomalies in abundance of female *Calanus*, as a percentage of the abundances averaged (av.) in the previous three autumns. Lower, relation of these anomalies to those of temperature. The regression is significant ($p < 0.05$, 2-tailed).

By rank sum test, the median nocturnal and diurnal anomalies in abundance did not differ significantly ($p > 0.2$, 1-tailed). This suggests that the negative anomalies shown in figure 2 were not due to increased under-sampling of females during the day in autumn 1991, although it is still possible that, if the females were non-migratory, such under-sampling occurred both night and day. As noted earlier, it is not clear that the females living permanently below the depth of sampling would contribute to the population's reproductive output.

The biomass of chlorophyll in the water column can be used, with several important qualifications, as a surrogate for the biomass of food for *Calanus*. As shown in figure 1, the median biomass was significantly reduced in autumn 1991 relative to 1988–90, and thus (since egg

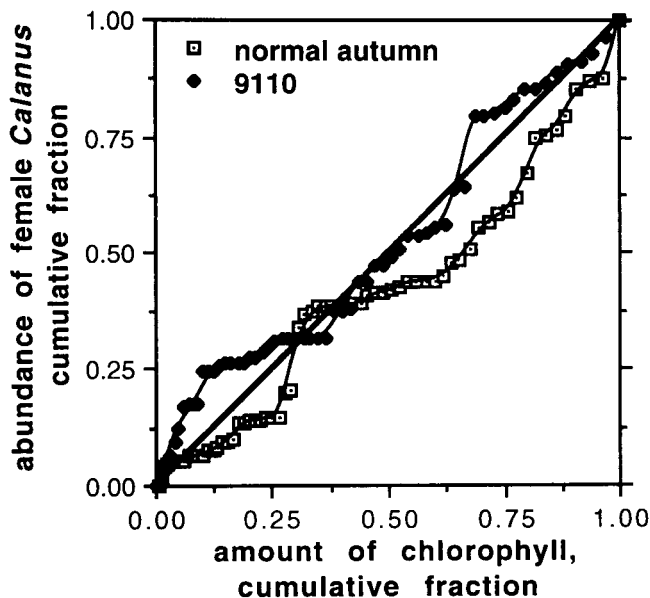


Figure 3. Relation between cumulative amount of chlorophyll and cumulative abundance of female *Calanus* in October 1991 and in the previous three, "normal," autumns. Pairs of data derived from each station (figures 1 and 2) were arranged in order of increasing biomass of chlorophyll before cumulative sums were calculated. Thus the most oligotrophic locations (with respect to chlorophyll) are to the left. The diagonal shows a "neutral" distribution for *Calanus* (see text).

production is generally food-limited in much of this region; Mullin 1991) decreased fecundity during autumn 1991 is to be expected. However, changes in the spatial distribution of *Calanus* relative to that of chlorophyll could ameliorate the general impoverishment if the female copepods became relatively more concentrated in those regions (stations or depths) where the biomasses of chlorophyll were relatively large. That is, *Calanus* could make better use of the available chlorophyll if the population's distribution changed appropriately.

To examine this question with respect to mesoscale horizontal distributions (since vertical distributions of *Calanus* were not determined), I arranged the pairs of data for amount of chlorophyll at each station (biomass times area represented by the station) and abundance of female *Calanus* in order of increasing amount of chlorophyll, then summed both and plotted the cumulative abundance of female *Calanus* against the cumulative amount of chlorophyll for autumn 1991 and for the "normal" situation represented by the three previous autumns (figure 3). Because of the way I had initially arranged the data, the diagonal on such a plot represents a distribution of *Calanus* that is nutritionally "neutral"; i.e., any given fraction of the total population of *Calanus* is spatially associated with the equivalent fraction of the available chlorophyll. Since the most oligotrophic stations with respect to chlorophyll biomass are towards the origin of the plot, points below the diagonal represent nutritionally "efficient" or "advantageous" distributions:

the fraction of *Calanus* associated with oligotrophic stations is less than the fraction of available chlorophyll these stations represent. Points above the diagonal are, by the analogous reasoning, nutritionally “inefficient” or “disadvantageous” (see Mullin 1994 for elaboration).

Figure 3 indicates that, in “normal” autumn, the horizontal distribution of female *Calanus* tended to be advantageous with respect to the food resources, whereas in autumn 1991 the distribution was essentially neutral. Thus there is no evidence of mesoscale distributional amelioration of heightened food limitation during autumn 1991.

As described in the Methods section, I estimated egg production for autumn 1991 from the biomasses of chlorophyll measured at each station and from the mean regression of individual daily egg production against biomass of chlorophyll for the autumns of 1988 and 1989 (Mullin 1991). I then multiplied these rates by the measured abundances of females and by the area represented by each station, and compared the egg production over the entire area in autumn 1991 to a similar calculation for the “normal” autumn, represented by the average of measurements in 1988–90.

I calculated that the *Calanus* population in autumn 1991 produced, over the entire area, $2.5 \cdot 10^{14} \cdot \text{eggs} \cdot \text{day}^{-1}$ [$950 \text{ eggs} \cdot (\text{m}^{-2} \cdot \text{day})^{-1}$], which is $8 \cdot 10^{14} \text{ eggs} \cdot \text{day}^{-1}$ [$3100 \text{ eggs} \cdot (\text{m}^2 \cdot \text{day})^{-1}$] fewer than normal. By this calculation, the population's daily reproduction over the entire area was only 24% that in normal autumns, which is comparable to the finding that the abundance of female *Calanus* in the subsequent, El Niño, winter (1992) was 27% that of the preceding three winters (Mullin 1994).

DISCUSSION

Although the physical characteristics of El Niño off southern California that were clear in the winter of 1992 were ambiguous in the autumn of 1991, many of the biological symptoms were already detectable, relative to the three previous autumns. These symptoms (figures 1 and 2) included inversely correlated anomalies in 10 m temperature (significantly warm overall) and depth-integrated biomass of chlorophyll (significantly depleted), and similar anomalies in abundance of female *Calanus* (significantly rare).

The reduced median amount of food in autumn 1991, represented by negative anomalies in chlorophyll, implies a potential decrease in reproduction by the *Calanus* population. In principle, this could have been offset by an improved matching between the mesoscale distributions of female *Calanus* and chlorophyll, but such improved matching did not occur (figure 3).

The most important quantitative conclusion is that the reduction in daily egg production by the *Calanus* population calculated for autumn 1991 was sufficient to explain the relative rarity of the next generation of adult females in winter 1992. This does not mean that there were no changes in the balance of immigration and emigration (vertically or horizontally), or in the survivorship of juveniles, as the El Niño condition developed. However, these factors are not required to explain the status of the adult *Calanus* population in the full-blown Californian El Niño observed in early 1992.

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