

LARGE-CELLED PHYTOPLANKTON, THE NITRICLINE, AND GRAZING DURING THE CALIFORNIA 1997–98 EL NIÑO

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ABSTRACT

During autumn 1997 and winter and spring 1998, nitriclines were deep and macrozooplankton sparse in the California Current system. However, general relations between absolute and relative biomasses of $\geq 8 \mu\text{m}$ cells and nitricline depths and grazing pressure from macrozooplankton, derived from non-El Niño years, remained valid for all but a small group of nearshore stations in winter.

INTRODUCTION

Biomass of phytoplankton is routinely measured by proxy as chlorophyll retained on a filter of 1–2 μm porosity. However, because many planktonic herbivores graze selectively on different sizes of particles, categorizing phytoplankton by size may refine the estimation of the food supply for zooplankton (e.g., Durbin and Durbin 1989). Spatial/temporal variations in the physical forces in the ocean may affect secondary production through the food web by altering total phytoplanktonic biomass, size distribution, or both.

Mullin (1998) confirmed earlier findings by Malone (1971, incorrectly cited by Mullin as Hopkins 1971) that, in the California Current system, the relative importance of large cells was greatest where and when total phytoplanktonic biomass was augmented, and that the large-cell biomass was the more responsive to physically caused variations in supply of nutrients. Malone (1971) also argued that small cells were grazed primarily by protozoans and other microzooplankton, which respond quickly to changes in food supply, while the time lags inherent in population change for macrozooplankton permit greater variability in the biomass of their large-celled food. Mullin (1998) found evidence that the residual variability of biomass of $\geq 8 \mu\text{m}$ cells (i.e., variability not related to variability in depth of the nitricline) could be related to the grazing pressure by macrozooplankton.

The vertical distributions of many properties change dramatically during a California El Niño (i.e., the manifestation of El Niño–Southern Oscillation [ENSO] in the California Current system). Generally, the nitricline

occurs deeper in the water column, but the strength of this anomaly may vary spatially, and its biological effect depends partly on whether (or where) the ratio between the depths of the nitricline and the euphotic zone is changed. The purpose of the research reported here was to determine whether the relations between biomass of large phytoplankton cells, the nitricline, and macrozooplankton were similar during the 1997–98 El Niño to those of earlier, non-El Niño years.

As in the earlier study, I will draw inferences concerning processes (acting instantaneously) from biomasses (resulting from integration of processes over time). Therefore, time lags between the acting of a process and its detectable effect on a biomass potentially confound these inferences.

The oceanographic and ecological properties of the region sampled, and relations relative to long-term mean conditions and to events in the equatorial Pacific, are reported in Lynn et al. 1998 and Hayward et al. 1999. In brief, though equatorial signs of ENSO were strong by June 1997, and southern California coastal waters were anomalously warm through much of 1997, the latter phenomenon was attributed to regional anomalies in winds during spring and summer rather than to ENSO directly. I therefore considered the California El Niño to be present in autumn 1997, though I did not use data from the spring and summer of that year to represent non-El Niño conditions.

Upwelling-favorable winds in the area studied were anomalously weak in April–June 1998, and the thermocline was anomalously deep for about one year, but the biomass of phytoplankton in the water column (as integrated chlorophyll) was normal through 1997 and 1998. However, the macrozooplankton biomasses in February and April 1998 were the smallest recorded in 50 years, and continued to be small through the year. Coastal surface waters had returned to temperatures only slightly above normal by May 1998, though positive anomalies at 50–100 m persisted until autumn.

METHODS

The biomass of large-celled phytoplankton is defined here as the chlorophyll retained on an 8 μm -porosity

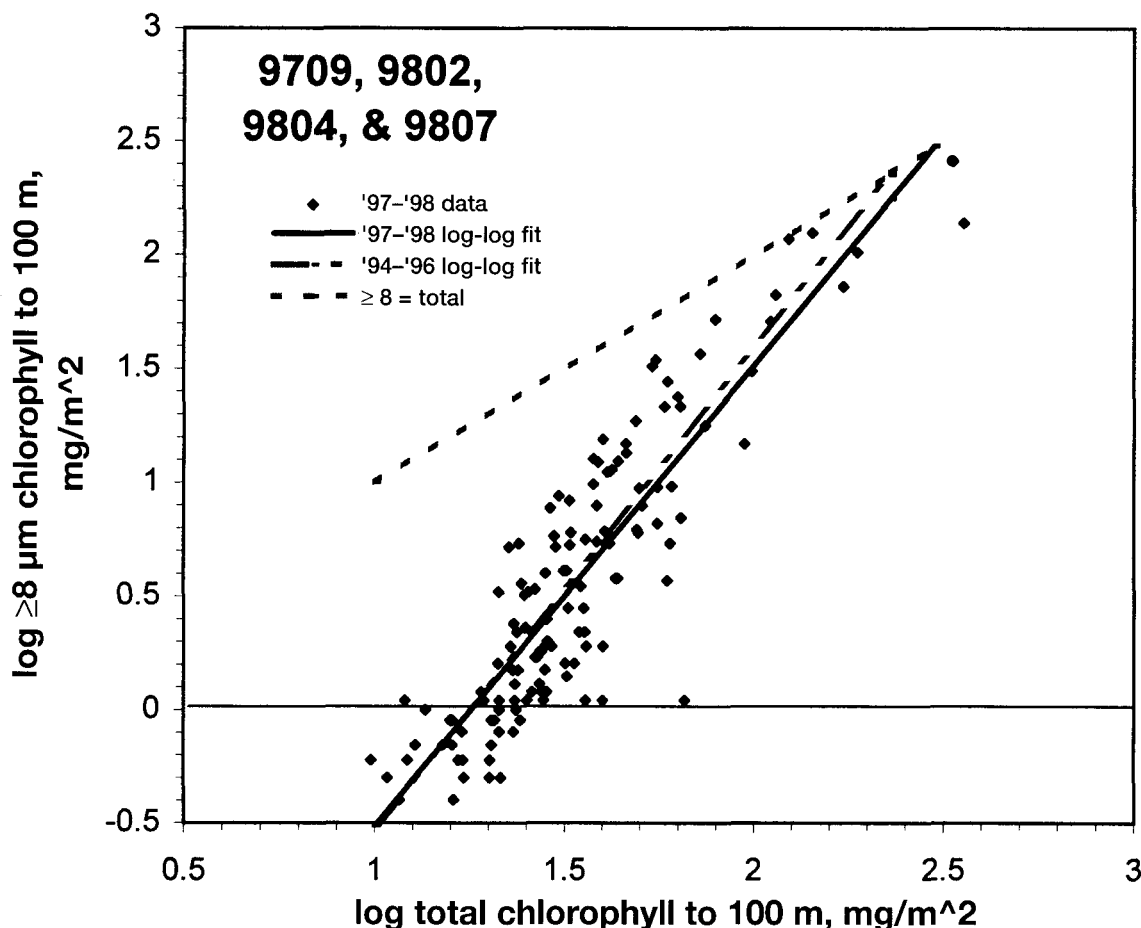


Figure 1. Log-log relation between depth-integrated biomasses of $\geq 8 \mu\text{m}$ chlorophyll and total chlorophyll during the 1977–98 El Niño: September 1997 (cruise 9709) and February, April, and July 1998 (cruises 9802, 9804, and 9807). Also shown is the linear best fit for the same relation in non-El Niño years, 1994–96, and the line representing $\geq 8 \mu\text{m}$ chlorophyll = total chlorophyll.

membrane filter from water taken at ten depths through the upper 100 m (as in Mullin 1998, where the other methods used, and locations sampled, are also given). This measure could, of course, include firmly bound aggregations of small cells. The results of the quarterly cruises in the three years (1994–96) reported in that publication are used in the present study as non-El Niño baselines. As previously, I have used negative exponential best-fit curves to describe or idealize many data sets, but a causal linkage of this mathematical form between the variables is not necessarily implied.

RESULTS

Although no stations in the present study had chlorophyll biomasses $>500 \text{ mg} \cdot \text{m}^{-2}$, the relation between $\geq 8 \mu\text{m}$ chlorophyll and total chlorophyll was similar to that found in previous years (fig. 1), the large cells becoming more important as total biomass increased. The linear fit to log-transformed data implies that $\geq 8 \mu\text{m}$ chlorophyll was $\approx 16\%$ of the total at $50 \text{ mg} \cdot \text{m}^{-2}$ and $\approx 100\%$ of the total at $300 \text{ mg} \cdot \text{m}^{-2}$.

At the subset of CalCOFI stations considered in the present study (see Mullin 1998, fig. 1), nitricline depths tended to be deeper by September 1997 than in the autumns of 1994–96, the modal decameter being displaced 20 m (fig. 2). As expected for an El Niño condition, this deepening continued in February 1998; in springs, although the frequency distributions of both 1994–96 and 1998 had several modes, arguably the 1998 nitriclines tended to be the deeper. This difference was not evident in summer (cruise 9807), and other symptoms of El Niño had waned by this time (see Introduction).

As in earlier years, there was considerable variation in the relation between the biomass of $\geq 8 \mu\text{m}$ cells (either as a fraction of the total biomass or in absolute terms) and the depth of the nitricline (fig. 3). In autumn (9709), spring (9804), and summer (9807), the general pattern can be approximated by a negative exponential curve, as in the earlier years, though when the nitricline was shallower than about 50 m in autumn and spring, the $\geq 8 \mu\text{m}$ biomasses were greater than those expected from 1994–96 relations (the solid curves in fig. 3). Table 1

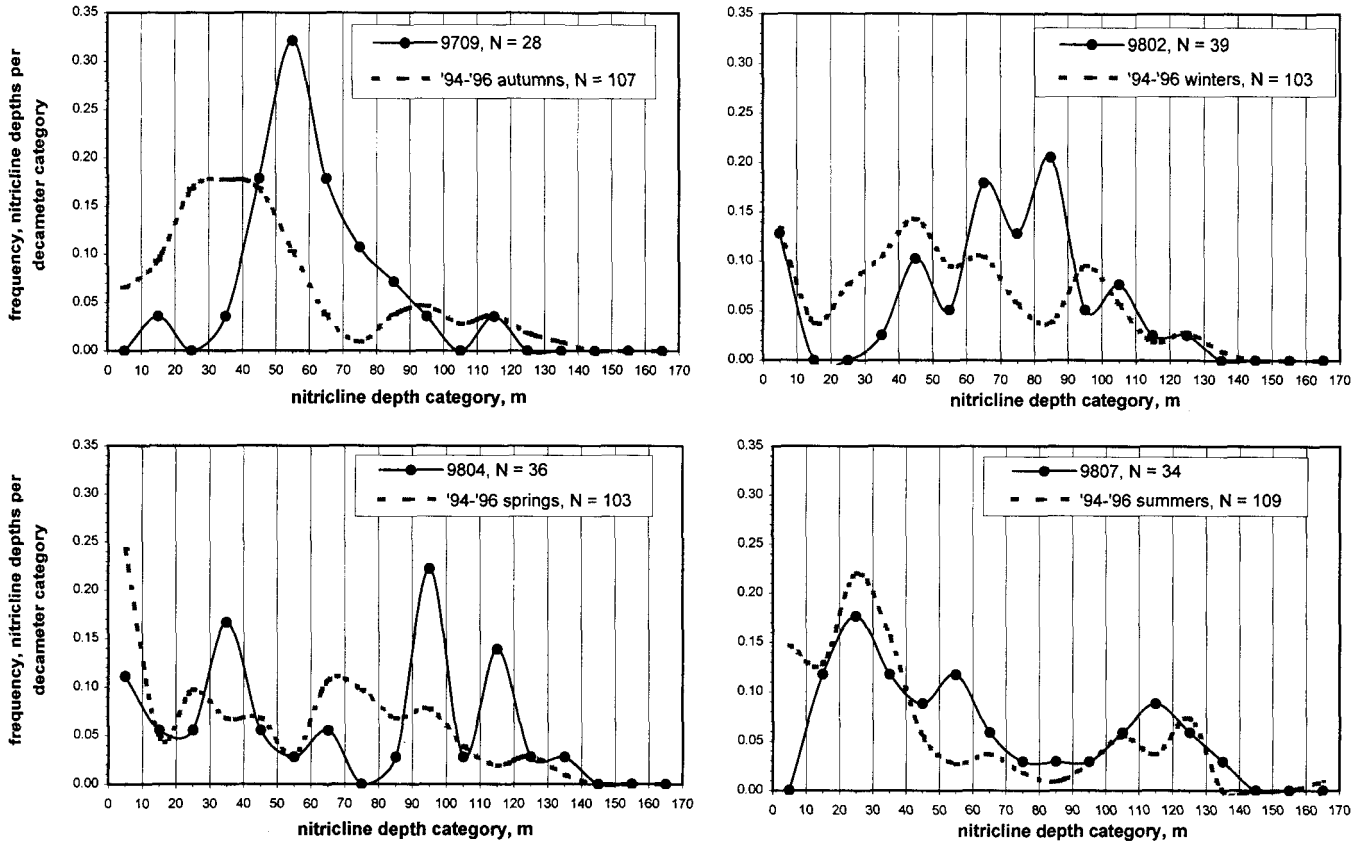


Figure 2. Frequency distributions of nitricline depths in September 1997 (cruise 9709) and February, April, and July 1998 (9802, 9804, and 9807), relative to the comparable seasons in 1994–96. Depths are categorized by decameter intervals.

illustrates this, and the normalcy of summer, by comparing the solutions for cruises 9709, 9804, and 9807 best-fit negative exponentials at three standard nitricline depths with the 1994–96 best fits for autumn, spring, and summer, respectively.

Winter 1998 (9802; fig. 3, upper right) was unusual in that there was little $\geq 8 \mu\text{m}$ chlorophyll at all five stations where the nitricline was at the surface, and a negative exponential fit is not reasonable. The five stations with unexpectedly sparse $\geq 8 \mu\text{m}$ biomass were contiguous at Point Conception and the Santa Barbara Channel. During summer (9807; fig. 3, lower right), the relations were similar to those of the previous years (see also table 1).

In 1994–96, some of the variation around the trend relating biomass of $\geq 8 \mu\text{m}$ cells to the depth of the nitricline was related to the biomass-specific grazing pressure by macrozooplankton on these large cells (Mullin 1998, fig. 6). It is thus reasonable to ask three questions about figure 3: (1) Is the variability around the negative exponential relation to nitricline depth related to grazing pressure within each cruise (9709, 9804, and 9807)? (2) Is the greater-than-expected $\geq 8 \mu\text{m}$ biomass in 9709 (relative to 1994–96 autumns) and in 9804 (relative to 1994–96 springs; table 1) related to low grazing pres-

sure? (3) Is the unexpectedly sparse $\geq 8 \mu\text{m}$ biomass where the nitricline was at the surface in February 1998 (fig. 3, upper right) due to unusually heavy grazing pressure?

An answer to question 1 is given in figure 4 (upper). The large positive residuals or anomalies (i.e., more $\geq 8 \mu\text{m}$ chlorophyll at a station than predicted from the overall relation to nitricline depth for that cruise) were dominantly at stations where the proxy for biomass-specific grazing pressure was relatively low. This is particularly evident for cruise 9804 (which also had one station with a large negative anomaly), but also true for the other two cruises. This result is similar to that for 1994–96 (Mullin 1998, fig. 6, where anomalies in both space and time were considered).

Question 2 is similarly answered in figure 4 (lower), which shows that during September 1997 (9709) and particularly April 1998 (9804), the largest excesses of observed biomasses of $\geq 8 \mu\text{m}$ cells from the biomasses expected from the biomass–nitricline–depth relations for autumns and springs of 1994–96 (fig. 3, table 1) were found where the biomass-specific grazing pressure was small. By this standard, question 2 is answered affirmatively.

While changes in the biomasses of macrozooplankton could plausibly be expected to signal a change in grazing pressure on all phytoplankton, it is less obvious

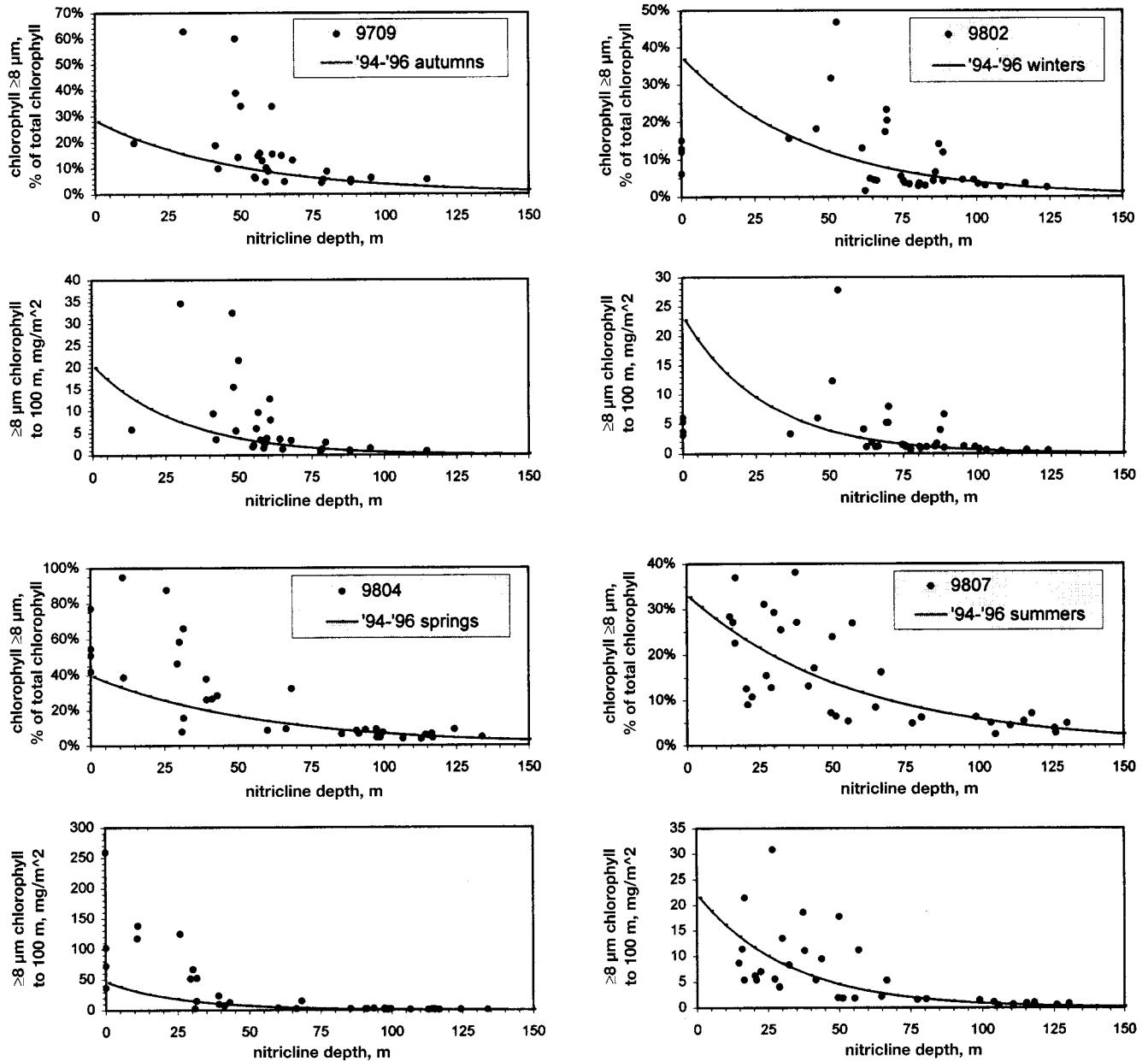


Figure 3. Chlorophyll $\geq 8 \mu\text{m}$, as a fraction of total chlorophyll (upper of each pair) or biomass per m^2 (lower of each pair), vs. depth of nitricline for September 1997 (cruise 9709), and February, April, and July 1998 (9802, 9804, and 9807). Also shown on each plot are the best-fit negative exponential relations for data from the appropriate season from 1994-96 (see Mullin 1998).

(though still plausible) that such changes would alter the size composition of the phytoplankton. If changes in grazing pressure were equally distributed over all size categories of phytoplankton, the fraction of total phytoplankton contributed by large cells should be predictable solely from depth of the nitricline, and not related to grazing. However, the anomalies in the fraction of total chlorophyll which was $\geq 8 \mu\text{m}$, relative to the seasonal mean relations to nitricline depth for the 1994-96 period, were also related to the surrogate for biomass-specific grazing pressure by macrozooplankton

(fig. 5). This finding, in turn, supports the use of the ratio macrozooplankton biomass \cdot (biomass of $\geq 8 \mu\text{m}$ chlorophyll) $^{-1}$ as a surrogate for biomass-specific grazing on the larger cells.

Finally, there is the issue of the unexpectedly small biomasses of $\geq 8 \mu\text{m}$ cells at all five stations in February 1998, where the nitricline was at the surface (fig. 3, upper right). At one of these stations, data for macrozooplanktonic biomass were not taken, but at the other four stations, the biomass-specific grazing pressures (as in the abscissae in fig. 4) were not particularly great.

TABLE 1
 Comparisons of Best-Fit Negative Exponential Relations, as Functions of Nitricline Depth, of the Relative and Absolute Biomasses of Chlorophyll $\geq 8 \mu\text{m}$ Three Standard Depths, in 1997–98 and in the Reference Years, 1994–96

| Nitricline depth (m) | % $\geq 8 \mu\text{m}$ | | mg/m ² $\geq 8 \mu\text{m}$ | |
|----------------------|------------------------|------------|--|------------|
| | Cruise 9709 | 94–96 aut. | Cruise 9709 | 94–96 aut. |
| 10 | 41% | 23% | 25 | 15 |
| 25 | 28% | 17% | 14 | 9 |
| 50 | 16% | 10% | 6 | 4 |
| | Cruise 9804 | 94–96 spr. | Cruise 9804 | 94–96 spr. |
| 10 | 50% | 33% | 66 | 32 |
| 25 | 36% | 26% | 34 | 18 |
| 50 | 21% | 17% | 12 | 7 |
| | Cruise 9807 | 94–96 sum. | Cruise 9807 | 94–96 sum. |
| 10 | 25% | 28% | 14 | 16 |
| 25 | 20% | 22% | 9 | 10 |
| 50 | 13% | 14% | 5 | 5 |

Note: The negative-exponential fit should not imply a causal mechanism, and in any case was not appropriate for February 1998 (9802).
 aut. = autumns; spr. = springs; sum. = summers.

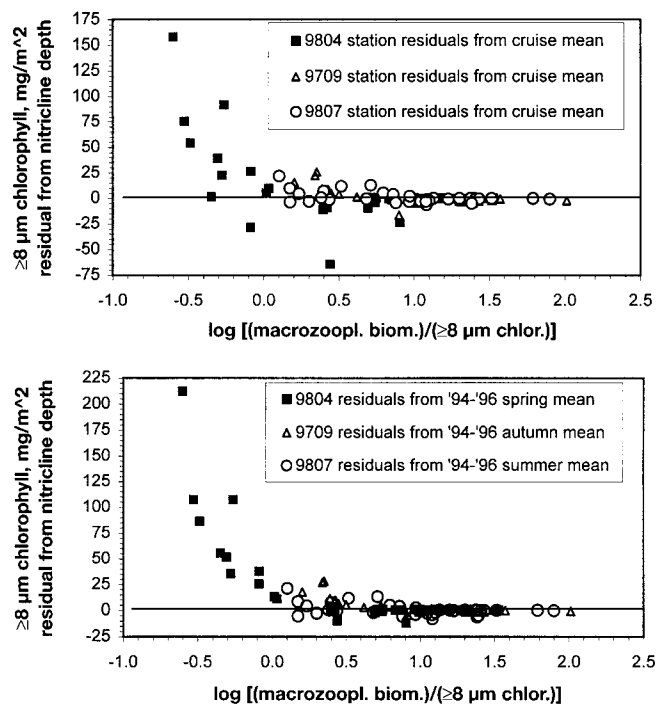


Figure 4. Anomalies in biomass of $\geq 8 \mu\text{m}$ cells, relative to a proxy for grazing pressure per unit $\geq 8 \mu\text{m}$ biomass. The horizontal line at 0 represents the $\geq 8 \mu\text{m}$ biomass predicted from an overall relation between biomass and nitricline depth; positive values indicate “excess” biomass. *Upper panel* shows anomalies for stations within each cruise relative to the overall relation for that same cruise. *Lower panel* shows anomalies for each station relative to the appropriate seasonal mean from 1994 to 1996 (cf. fig. 3, solid lines in lower panel of each pair).

Therefore, some other factor must account for the paucity of large cells, and the proximity of the stations to Point Conception–Santa Barbara suggests a topographically related cause. Very recent upwelling of subnitricline water, causing the nitricline to shoal, to which biomass of large cells had not yet responded, is plausible. This

should be indicated by a pronounced negative anomaly in temperature and positive anomaly in salinity at these particular stations, relative to other locations, but the 10 m temperature and salinity maps given in Lynn et al. 1998 provide little support for this explanation. However, the concentration of dissolved oxygen in the upper 10 m at these five stations (and at only one other on the entire cruise) was $<99\%$ of saturation, which is consistent with recent upwelling to which the phytoplankton have yet to respond with increased productivity.

DISCUSSION

The results of this study confirm the general relations between biomass of large phytoplankton, both in absolute and relative terms, and the depth of the nitricline (an indicator of supply of new NO_3^- to the euphotic zone) during the 1997–98 California El Niño, except for a small cluster of nearshore stations in winter. In this sense, the basic relations between the size composition of phytoplankton and the nutritional environment are the same during El Niño years as during other years, even though that nutritional environment changed. The implication is that the regional-scale change in the nutrient(s) or physical process(es) affecting the distribution of sizes of phytoplanktonic cells, if not NO_3^- itself, closely paralleled the change in depth of the nitricline.

Indeed, the biomass of large cells was greater than expected where the nitricline was shallow in autumn and spring of the El Niño year (cruises 9709 and 9804 in table 1). This was related to (and possibly caused by) unusually slight grazing pressure from macrozooplankton, relative to 1994–96, especially in spring (fig. 4, lower). Slight grazing pressure also meant that large cells contributed more to the total biomass of phytoplankton than would have been predicted from the relation to depths of the nitricline in 1994–96 (fig. 5). Slight grazing pres-

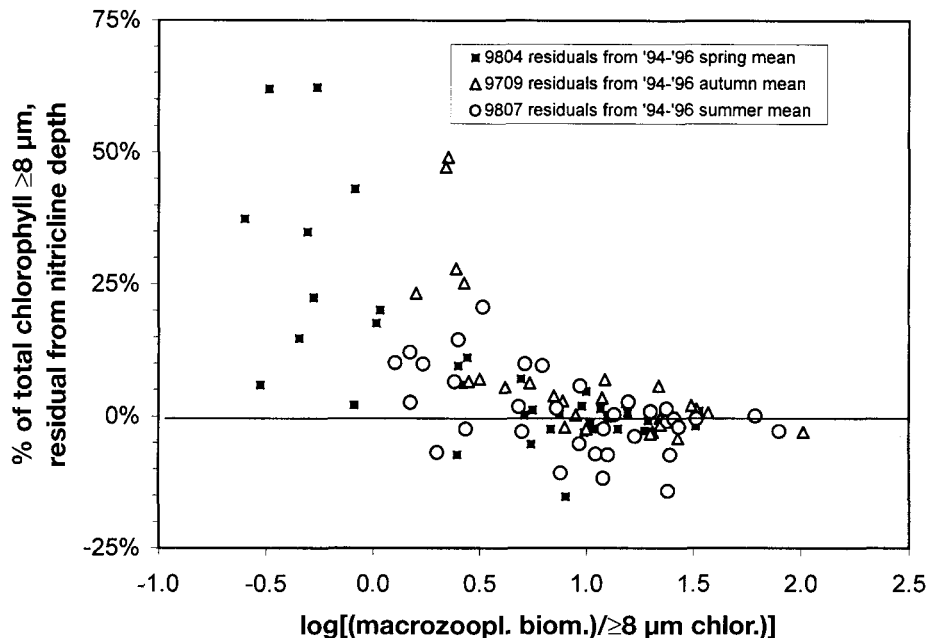


Figure 5. Anomalies in contribution of $\geq 8 \mu\text{m}$ cells to total chlorophyll, relative to a proxy for grazing pressure per unit $\geq 8 \mu\text{m}$ biomass. The horizontal line at 0 represents the percentage of total chlorophyll which is $\geq 8 \mu\text{m}$, predicted from an overall relation between this contribution and nitricline depth for springs, autumns, and summers of 1994–96 (cf. fig. 3, solid lines in upper panel of each pair); positive values indicate “excess” contribution to the total.

sure, relative to other locations on the same cruise, was also related to unusually large biomasses of large cells, compared to the overall relation to nitricline depth for that cruise (fig. 4, upper).

There remain circumstances, such as the anomalously low biomass of large cells at stations in February (fig. 3, 9802), which are not explained by the proxy variables available. In this example, spatial proximity of the anomalous stations suggests a common cause for the paucity of large cells, and some (but not all) of the evidence suggests the cause is upwelling to which the phytoplankton have not had time to respond with increased productivity and biomass.

The size distribution of phytoplankton can potentially influence sedimentation of organic matter and the structure of pelagic food webs. The results of the present study indicate that empirical relations or models developed for non-El Niño conditions in the California Current system will be useful, at least on a regional scale, during a California El Niño.

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