

## BIOMASSES OF LARGE-CELLED PHYTOPLANKTON AND THEIR RELATION TO THE NITRICLINE AND GRAZING IN THE CALIFORNIA CURRENT SYSTEM OFF SOUTHERN CALIFORNIA, 1994–1996

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### ABSTRACT

Based on twelve quarterly cruises over three years, the relative importance and absolute biomass of phytoplankton retained on an 8  $\mu\text{m}$ -pore membrane filter increased as the depth of the nitricline decreased, even though biomass of macrozooplankton (potential grazers) also increased as the nitricline shoaled. The relative importance of  $\geq 8 \mu\text{m}$  cells was inversely related to a proxy for their biomass-specific mortality (biomass of macrozooplankton/biomass of  $\geq 8 \mu\text{m}$  cells), as was their "residual" biomass not predicted from the nitricline depth.

### INTRODUCTION

As in many other sampling programs, the biomass of phytoplankton in the region surveyed quarterly by the California Cooperative Oceanic Fisheries Investigations (CalCOFI) is assessed by determining the amount of chlorophyll retained on a GF/F glass fiber filter with nominal retention approximately 1  $\mu\text{m}$  (Venrick and Hayward 1984). This measure is well correlated with other properties of sestonic biomass (Eppley et al. 1977; Napp et al. 1988) and (when integrated through the water column) with primary production (e.g., Eppley et al. 1985; Mullin 1991; Mantyla et al. 1995).

However, biomass of large-celled phytoplankton is more variable in space and time than is that of total phytoplankton, and is relatively more important in eutrophic situations (e.g., Hopkins 1971; Furuya and Marumo 1983; Mitchell-Innes and Pitcher 1992). Further, there is evidence that some planktonic copepods are selective grazers, preferring large cells, and that their reproduction and physiology are better correlated with the biomass of large cells than with that of total chlorophyll (Runge 1985; Bellantoni and Peterson 1987; Durbin and Durbin 1989).

The purpose of this study was to determine the mesoscale spatial and temporal distribution of biomass of large-celled phytoplankton, relative to that of total phytoplankton, and to determine how the size distribution was related to that of the nutrient nitrate, and to grazing by macrozooplankton.

### METHODS

At approximately half of the locations sampled on twelve quarterly cruises by the California Cooperative Oceanic Fisheries Investigations (CalCOFI) from January 1994 through November 1996 (see, e.g., Hayward et al. 1995) samples were taken to estimate the biomass of phytoplankton  $\geq 8 \mu\text{m}$ , defined as chlorophyll retained on a membrane filter of this nominal pore diameter (filter type). On these cruises, samples were routinely taken from several depths with closing water bottles on a rosette with a CTD, and the seston from each bottle retained on a GF/F glass fiber was extracted for chlorophyll, determined fluorometrically (Venrick and Hayward 1984). From each of the shallowest ten of these water bottles (representing samples from the surface to approximately 100 m or shallower), an additional 140 ml sample was withdrawn; these were combined and filtered through the 8  $\mu\text{m}$  membrane filter, which was then extracted and analyzed as were the ten GF/F filters representing the same sampled depths.

Biomasses of chlorophyll per unit volume were then integrated to 100 m for both the total phytoplankton (GF/F filters, ten samples integrated algebraically) and the  $\geq 8 \mu\text{m}$  phytoplankton (membrane filter, one physically integrated sample) to give biomass in  $\text{mg chlorophyll} \cdot \text{m}^{-2}$ . The biomass of cells  $< 8 \mu\text{m}$  was calculated as the difference between total and  $\geq 8 \mu\text{m}$  chlorophyll, although this procedure means that  $< 8 \mu\text{m}$  chlorophyll is not an independent variable for statistical analysis. In a few cases, the measured biomass of  $\geq 8 \mu\text{m}$  cells as chlorophyll exceeded that of total chlorophyll, presumably due to subsampling or analytical variability. In these cases, the biomass of large cells was taken to be 100% that of the total. The phytoplanktonic biomass referred to as large cells would, of course, include the biomass of cells firmly attached in colonies or aggregates  $\geq 8 \mu\text{m}$  in effective size.

The concentrations of  $\text{NO}_3^-$  were determined in water samples drawn from the same bottles as the samples analyzed for biomass of chlorophyll. The vertical distribution of  $\text{NO}_3^-$  typically includes a near-surface region of concentrations  $\ll 1 \mu\text{M}$ ; the nitricline (or, in this case, nitricline), where concentrations increase rapidly with depth; and deep-water concentrations  $> 1 \mu\text{M}$ . I chose

the depth where  $[\text{NO}_3^-] = 1.0 \mu\text{M}$  as the core of the nitricline (e.g., Eppley et al. 1979), and determined this for each station by linear interpolation between the deepest depth where measured  $[\text{NO}_3^-] < 1.0 \mu\text{M}$  and the shallowest depth where measured  $[\text{NO}_3^-] \geq 1.0 \mu\text{M}$ .

At each station (weather permitting), a tow was made between the surface and 200 m or the bottom (whichever was shallower) with a 505  $\mu\text{m}$ -mesh, bridleless net equipped with a flowmeter. Each sample was preserved in formalin-seawater, and its displacement volume was measured. I multiplied data from samples taken nocturnally by 0.75 to correct for the interaction of the time of day a station was sampled and diel vertical migration (Smith 1974; Mullin 1986), thus creating a data set of "diurnal equivalent" macrozooplanktonic biomasses.

The relation between the catch of 505  $\mu\text{m}$  mesh and smaller zooplankton (passing through 505  $\mu\text{m}$  mesh, retained by 202  $\mu\text{m}$  mesh) in this region was investigated by Ohman and Wilkinson (1989). The 202–505  $\mu\text{m}$  fraction was, on average, half the  $\geq 505 \mu\text{m}$  fraction, though there was diel and onshore-offshore variability in this relation, the 202–505  $\mu\text{m}$  fraction being relatively more important by day and near shore. However, there was no relation between the size partitioning of the zooplankton and the biomass of chlorophyll. I will therefore use the biomass of  $\geq 505 \mu\text{m}$  macrozooplankton as a proxy for grazing pressure on  $\geq 8 \mu\text{m}$  cells, in the sense that variability in this proxy reflects variability in grazing, even if the magnitude of grazing by all zooplankton is underestimated.

Relations between properties are shown below as regressions of various algebraic formulations; these should be interpreted only as indicating trends, not as representing the function forms of causal mechanisms between the properties.

## RESULTS

The geographic distributions of total chlorophyll during four seasons of each year, as biomass at 10 m, are shown in Hayward et al. (1995) for January 1994–April 1995; Hayward et al. (1996) for April 1995–April 1996; and Schwing et al. (1997) for August and October 1996. These references also show the associated hydrographic properties and describe the context of each cruise relative to long-term conditions for each season.

The relative importance of  $\geq 8 \mu\text{m}$  phytoplankton tended to be greatest at nearshore locations north of the Palos Verdes Peninsula (fig. 1) and least offshore. The distribution during January 1995 (cruise 9501; fig. 1) represented the greatest departure from this generalization, when the only two stations at which  $\geq 8 \mu\text{m}$  chlorophyll exceeded 50% of the total were noncontiguous ones far offshore and southerly. Each of these stations differs so much from its immediate neighbors that the

results are suspect. Even so, the absence of large-cell-dominated stations near shore in January 1995 is notable, since a major red tide dominated by the large dinoflagellate *Gonyaulax polyedra* had begun to develop near shore (Hayward et al. 1995). This red tide, notable for its spatial extent and wintertime appearance, probably influenced the results during cruise 9504 as well, though grazing by *Noctiluca miliaris* and dispersion by storms had intervened, and abundant diatoms also contributed to unusually large chlorophyll biomasses then (Hayward et al. 1995).

An hypothesis is that large phytoplankton cells tend to form mesoscale blooms in time or space, and that these are superimposed on a "background" of relatively invariant biomasses of small cells (Hopkins 1971). That is, large cells would be disproportionately abundant in regions or times of elevated total biomass. Figure 2 shows the relation of  $\geq 8 \mu\text{m}$  chlorophyll to total chlorophyll for all 12 cruises over the 3 years (approximately 430 data points); based on the linear regression,  $\geq 8 \mu\text{m}$  chlorophyll typically ranges from approximately 3% of total chlorophyll in the most oligotrophic areas (total chlorophyll  $\approx 25 \text{ mg} \cdot \text{m}^{-2}$ ) to 67% in the most eutrophic ones (total chlorophyll  $\approx 500 \text{ mg} \cdot \text{m}^{-2}$ ). Chavez et al. (1991, their fig. 13) found similar results in a study of mesoscale circulation and phytoplankton off northern California, as did Mitchell-Innes and Pitcher (1992) in a study of temporal change off western South Africa.

As could be anticipated from the geographical distributions shown in figure 1, in each year the fraction of the total chlorophyll due to  $\geq 8 \mu\text{m}$  cells was greater where and when the nitricline was closer to the surface (fig. 3). When and where the nitricline was deeper than 75 m, large cells were  $< 25\%$  of the biomass (except for the two instances far offshore during January 1995; fig. 1). When the nitricline was shallow, large cells often dominated the biomass, although not always.

These data also imply that the biomass of large cells is more responsive to variations in the position of a shallow nitricline than is the biomass of small cells. As shown in figure 4, the decrease in  $\geq 8 \mu\text{m}$  cell biomass with respect to increasing nitricline depth, when this was  $\leq 50$  meters, was much more marked than was the decrease of  $< 8 \mu\text{m}$  cell biomass (shown by the steeper curve and larger negative exponent for the relation concerning  $\geq 8 \mu\text{m}$  biomass).

Finally, if nutrients whose distributions are unrelated to the nitricline (e.g.,  $\text{NH}_4^+$ ), and which affect large cells differentially are more important in some seasons than in others, the relation between the fraction of total phytoplanktonic biomass which is  $\geq 8 \mu\text{m}$  and the depth of the nitricline might differ between seasons. Averaged over the three years, the relative importance of large phytoplankton was greatest in the spring and least in the

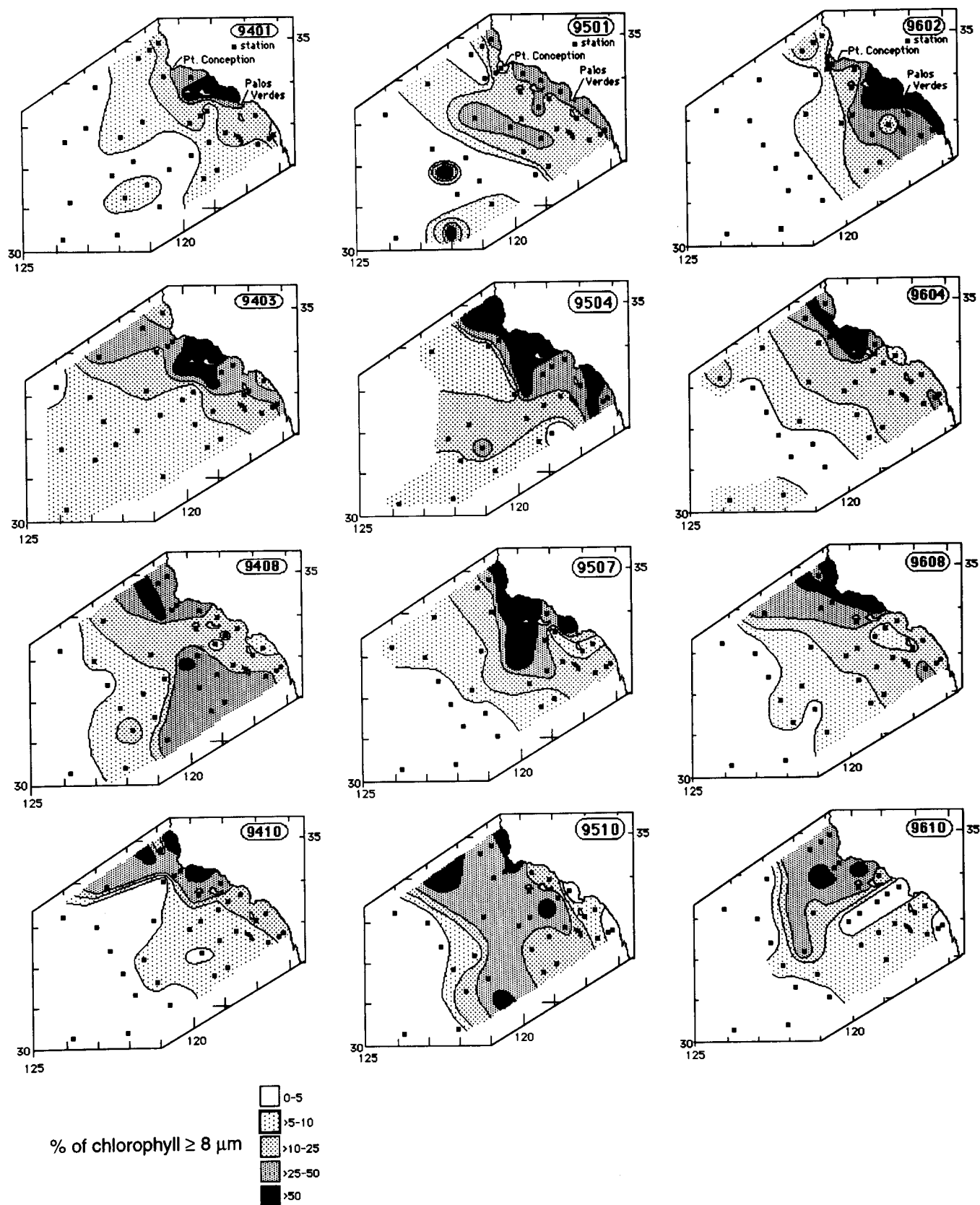


Figure 1. Distribution of the relative contribution of  $\geq 8 \mu\text{m}$  phytoplankton to total biomass of chlorophyll, 0–100 m, during 12 cruises in 1994–96 (months indicated by last two digits of cruise number). For distribution of total chlorophyll on these cruises, see Hayward et al. 1995, 1996, and Schwing et al. 1997.

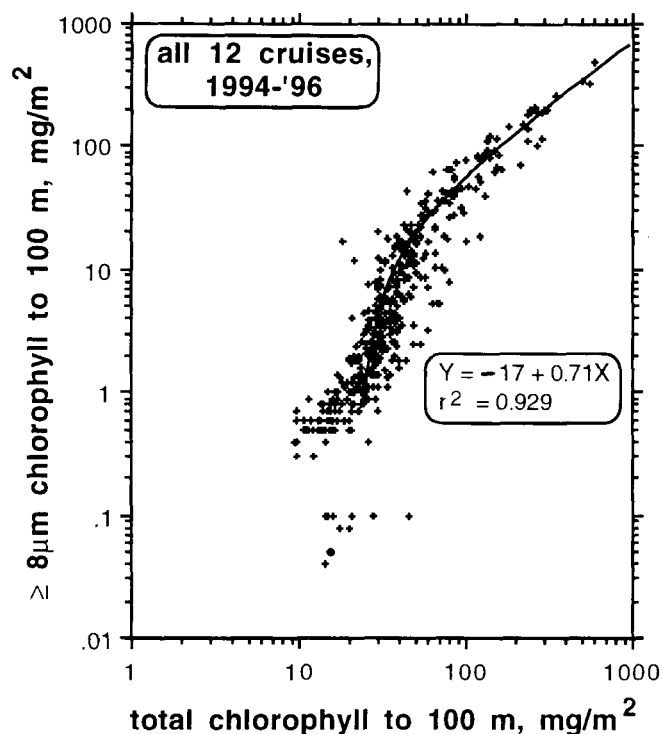


Figure 2. Biomass of chlorophyll in  $\geq 8 \mu\text{m}$  particles vs. total biomass of chlorophyll (GF/F filter) for 12 cruises over three years. On the double-log plot, the linear regression is curved.

autumn for any given depth of nitricline, though this tendency is probably not statistically significant and does not, in itself, suggest any particular cause.

In principle, grazing by macrozooplankton should reduce the biomass of large cells preferentially, but the increase in  $\geq 8 \mu\text{m}$  biomass with shoaling of the nitricline (fig. 4) occurred in spite of a similar, but less marked, increase in macrozooplanktonic biomass with a decrease in nitricline depth (compare fig. 5, top, to fig. 4). However, if macrozooplanktonic biomass  $\cdot (\geq 8 \mu\text{m} \text{ biomass})^{-1}$  is taken as a surrogate for grazing pressure per unit biomass of large cells, this biomass-specific mortality decreased as the nitricline shoaled (fig. 5, middle), and the relative importance of large cells was greatest where and when the biomass-specific grazing pressure on them was small (fig. 5, bottom).

Because grazing pressure and nitricline depth are themselves related, their relations to  $\geq 8 \mu\text{m}$  biomass of chlorophyll are convolved. However, if it can be assumed that the depth of the nitricline (presumably affecting growth) is the dominant determinant of the biomass of  $\geq 8 \mu\text{m}$  phytoplankton, it is possible to determine whether there is a detectable secondary effect of grazing pressure (affecting death). The test is whether departures or residuals of actual biomass of  $\geq 8 \mu\text{m}$  chlorophyll from the biomass predicted from the depth of the nitricline (i.e., actual data points minus values of the regression line in

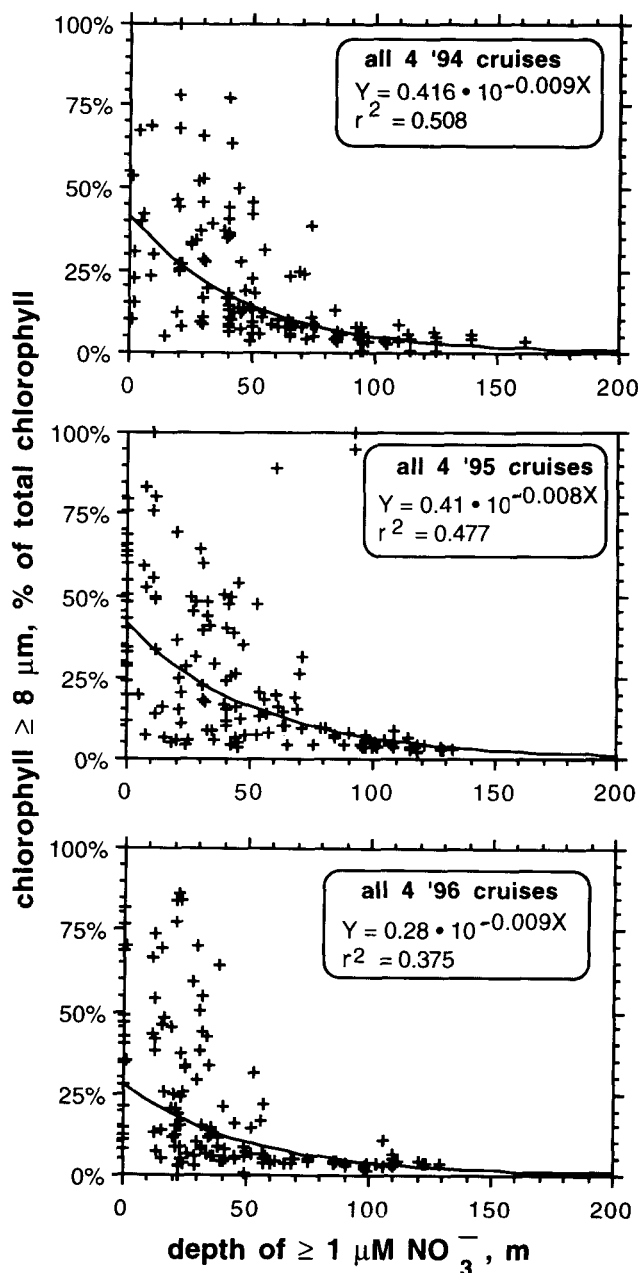


Figure 3. Relative importance of  $\geq 8 \mu\text{m}$  particles to total biomass of chlorophyll as a function of depth of the nitricline (where  $\text{NO}_3^-$  first is  $\geq 1 \mu\text{m}$ ) for 1994, 1995, and 1996.

fig. 4) are related to the surrogate for grazing pressure. As shown in figure 6, there tends to be "excess" biomass (positive residuals) where grazing pressure is low, and a "deficit" (negative residuals) where grazing pressure is high.

## DISCUSSION

The relative importance of large phytoplankton (defined here as  $\geq 8 \mu\text{m}$ —could also include aggregates of smaller cells) differed considerably in geographic pattern

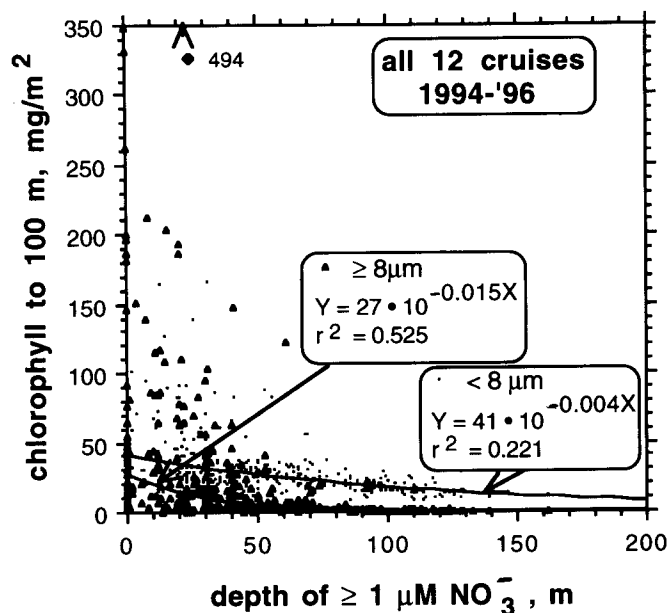


Figure 4. Biomasses of chlorophyll in  $<8$  and  $\geq 8$   $\mu\text{m}$  particles as functions of depth of the nitricline for 1994–96. Biomass  $<8$   $\mu\text{m}$  = total biomass –  $\geq 8$   $\mu\text{m}$  biomass.

over the three years studied (fig. 1), but this relative importance tended to be greater in eutrophic than in oligotrophic regions (fig. 2). Both the relative importance of large cells (fig. 3) and their absolute biomass (fig. 4) were related to the depth of the nitricline, in agreement with the conclusions of Hopkins (1971), who used a much coarser filter (22  $\mu\text{m}$  mesh) to separate “large” from “small.” This finding is consistent with, but does not prove, the hypothesis that “new” production (defined as nutrients supplied from below the euphotic zone) is more important for maintaining an elevated biomass of large cells than it is for small cells. However, Chavez (1989) reported an interesting and important example—the equatorial Pacific—in which elevated surface concentrations of nitrate were not associated with large cells.

Because other oceanographic features (e.g., turbulence) may covary with nitricline depth, other causal influences are possible. Biomass-specific grazing by macrozooplankton is one such covariable (fig. 5, middle), but there is a detectable effect of grazing pressure beyond that related to nitricline depth (fig. 6). Covariables may also have predictive utility; for example, Mitchell-Innes and Pitcher (1992) discussed the role of nitrate in affecting

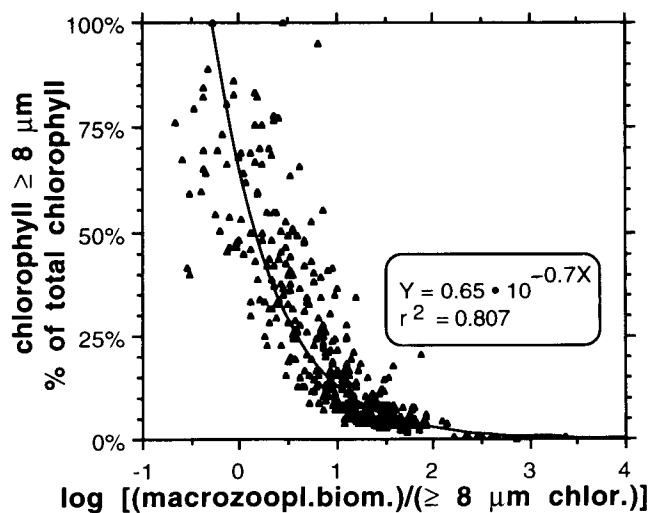
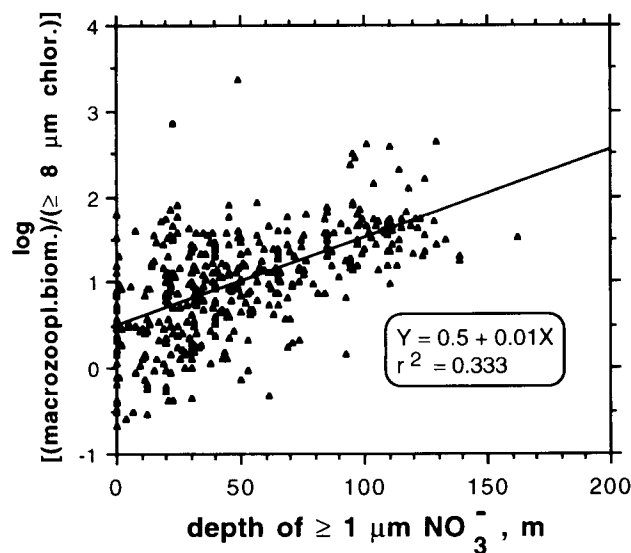
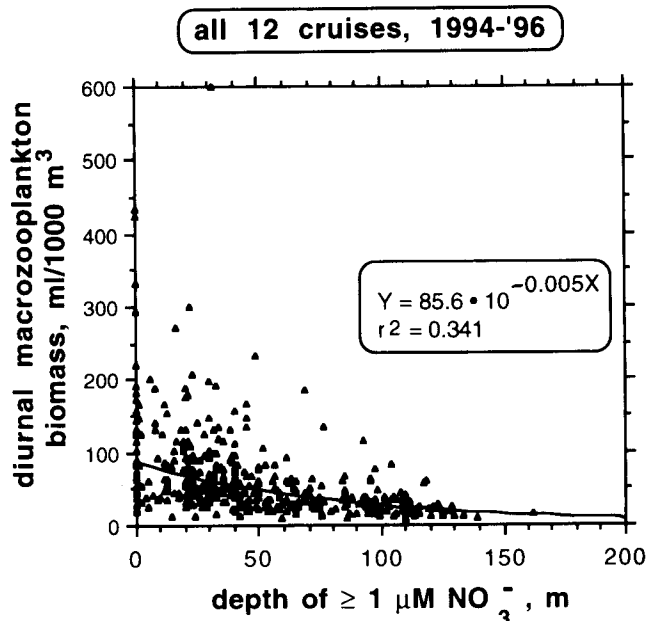


Figure 5. Relations involving macrozooplanktonic biomass, all 12 cruises. Top, Biomasses of macrozooplankton as a function of the depth of the nitricline. Middle, Proxy for biomass-specific grazing mortality of  $\geq 8$   $\mu\text{m}$  cells (macrozooplanktonic biomass  $\cdot$  ( $\geq 8$   $\mu\text{m}$  chlorophyll) $^{-1}$ ) vs. depth of the nitricline. Bottom, Biomass of  $\geq 8$   $\mu\text{m}$  cells, as a percentage of total chlorophyll biomass, vs. the proxy for biomass-specific grazing mortality.

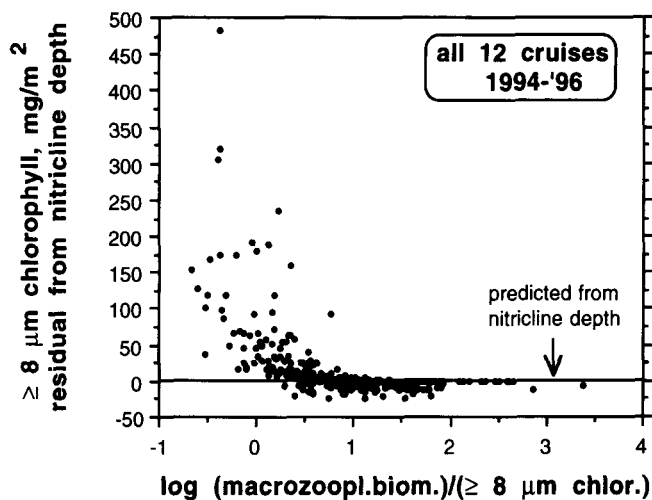


Figure 6. Residual biomasses of  $\geq 8 \mu\text{m}$  chlorophyll (actual data minus the biomass predicted from nitricline depth; see fig. 4) vs. the proxy for biomass-specific grazing mortality of  $\geq 8 \mu\text{m}$  cells.

the size distribution of phytoplankton, and therefore the suitability as food by higher trophic levels, but emphasized the use of sea-surface temperature and total biomass of chlorophyll as predictive tools, since these can be remotely sensed.

Given the paradigm that large cells participate in a "diatom-copepod-fish" food chain, while small cells are more likely to pass through a "microbial loop" or microzooplanktonic chain (e.g., Landry 1977; Beers 1986), the results of this study support the hypothesis that the production of zooplanktivorous fish will be related to nitricline depth in a nonlinear way. That is, shallow nitricline depths mean not only a greater total biomass of phytoplankton and macrozooplankton, but also that a greater proportion of this biomass will be passed to fish with relatively few "middleman" costs. This argument has been made elsewhere (e.g., Cushing 1989; Coombs et al. 1994), though definitive tests of the hypothesis are rare. Further, the hypothesis is a gross oversimplification, since the actual relation between nutrient supply and fish production also depends on other aspects, such as timing (e.g., short pulses, possibly leading to sinking of uneaten phytoplankton, vs. steady flux of nutrients), and the species and nutritional value of the phytoplankton (and zooplanktonic herbivores) which develop.

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