The Deep Chlorophyll Maximum: Comparing Vertical Profiles of Chlorophyll *a*

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The relationship between chlorophyll *a* and phytoplankton biomass (organic carbon content) is highly variable as is the yield of *in vivo* fluorescence per unit chlorophyll. Thus, vertical profiles of chlorophyll or *in vivo* fluorescence must be interpreted with caution if their ecological significance is to be established. Although the variability of carbon-to-chlorophyll ratios and fluorescence yield is large, much of it can be anticipated, corrected for, and usefully interpreted. Vertical profiles from different regions of the sea are presented: each has a deep chlorophyll maximum, but the probable mechanisms of their formation and maintenance differ widely. Most vertical distributions of chlorophyll can be explained by the interaction between hydrography and growth, behavior, or physiological adaptation of phytoplankton with no special consideration of grazing by herbivores, even though vertical distributions of epizooplankton are not uniform. The interaction between vertical profiles of zooplankton and chlorophyll will be better understood when the relationships between chlorophyll and phytoplankton biomass in those profiles is determined.

Key words: chlorophyll *a*, fluorescence, phytoplankton, vertical structure

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La relation entre la chlorophylle *a* et la biomasse phytoplanctonique (teneur en carbone organique), tout comme le rendement en fluorescence *in vivo* par unité de chlorophylle est fortement variable. C'est pourquoi il faut interpréter avec prudence les profils verticaux de chlorophylle ou de fluorescence *in vivo* quand il s'agit d'établir leur signification écologique. Bien que la variabilité des rapports carbone : chlorophylle et du rendement en fluorescence soit forte, on peut anticiper une bonne partie de cette variabilité, la corriger et l'interpréter d'une manière utile. Nous présentons des profils verticaux de différentes régions de la mer; chacun possède un maximum de chlorophylle en profondeur, mais il y a de grandes différences dans les mécanismes probables de leur formation et de leur maintien. On peut expliquer la plupart des distributions verticales de la chlorophylle par l'interaction entre les caractéristiques hydrographique croissance, le comportement ou l'adaptation physiologique du phytoplancton, sans accorder d'importance spéciale au broutage par les herbivores, même si la distribution verticale des épizooplanctontes n'est pas uniforme. On comprendra mieux l'interaction entre les profils verticaux du zooplancton et de la chlorophylle quand on aura trouvé les relations entre la chlorophylle et la biomasse phytoplanctonique dans ces profils.

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A convenient, accurate and precise measure of phytoplankton biomass is essential to most studies of biological processes in epipelagic communities. The index of choice in recent decades, the concentration of chlorophyll *a*, was supplemented by *in vivo* chlorophyll fluorescence (Lorenzen 1966). Continuous measurements of *in vivo* fluorescence at sea produced much information about the horizontal patterns of phytoplankton upon which theoretical work advanced rapidly (Herman and Platt 1980). Concurrently, more and better observations of the vertical distributions of chlorophyll *a* and *in vivo* fluorescence were collected. A feature of many profiles collected from diverse regions is a subsurface chlorophyll maximum (Anderson 1972; Venrick et al. 1973; Cullen and Eppley 1981; Ortner et al. 1980). In this commentary, it

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is shown that although deep chlorophyll maxima are common to profiles from many regions, they probably arise from several different causes. It is further shown that vertical profiles of chlorophyll or fluorescence must be interpreted with great care if their significance for the economy of the pelagic food web is to be established.

Measuring the Biomass of Phytoplankton

What is Biomass?

Biomass is defined as the amount of living material, but for practical and theoretical reasons, units have not been rigidly prescribed. Instead, "biomass' has become a catch-all term with the operational definition, "the amount of biological material that is of interest to the researcher." The word is convenient and unlikely to be abandoned, but its meaning, at least within the field of planktonic ecology, is nebulous almost to the point of uselessness. Thus, any discussion of biomass should include a specific definition and should have a justification of the choice.

The concentration of organic carbon associated with phytoplankton (usually expressed as $mg \cdot m^{-3}$) is commonly used to express the amount of phytoplankton, but phytoplankton have also been considered in terms of nitrogen (Pavoni 1969; Wroblewski 1977) or phosphorus (Perry and Eppley 1981) content. The cell volumes of phytoplankton have been calculated by different methods, and biomass has been obtained by applying conversion factors (cf. Smayda 1978). The concentration of chlorophyll *a* is often determined to estimate phytoplankton abundance, and many researchers refer to chlorophyll as an index or indicator of phytoplankton biomass. For some studies concerned primarily with photosynthesis, chlorophyll concentration *per se* is the relevant quantity upon which theoretical generalizations can be constructed (cf. Bannister and Laws 1980). For the purposes of this discussion, however, biomass will be defined as the amount of organic carbon (cf. Strickland 1965). Organic carbon concentration is a good index of the caloric content of phytoplankton and is thus an appropriate unit of biomass for studying fluxes of energy, an important step in the analysis of the dynamics of ecosystems (Platt and Irwin 1973). Also, the concentration of organic carbon associated with phytoplankton must be known to calculate growth rates from measurements of primary production.

Unfortunately, it is impossible to measure directly the organic carbon content of natural phytoplankton free of contamination from detritus and heterotrophic microplankton (Banse 1977). Indirect methods using biomass indicators or experimental manipulations must be used to estimate phytoplankton carbon in natural samples (Eppley 1968; Eppley et al. 1977; Redalje and Laws 1981).

Estimating the Biomass of Phytoplankton: Chlorophyll *a*

The concentration of chlorophyll *a* is still the best chemical indicator of phytoplankton biomass in natural samples. Quite simply, photosynthetic organisms have it, others don't. However, the interpretation of chlorophyll measurements has important limitations. Chlorophyll represents only about 1% of the dry weight of a phytoplankton cell, and the proportion can be quite variable (Strickland 1965; Shuter 1979). To those interested in chlorophyll concentration as a measure of food for herbivores, it should be clear that chlorophyll is present only in trace quantities. Zooplankters do not subsist on chlorophyll. Therefore, by themselves, distributions of chlorophyll cannot necessarily be considered as good indices of the distribution of food available to secondary producers.

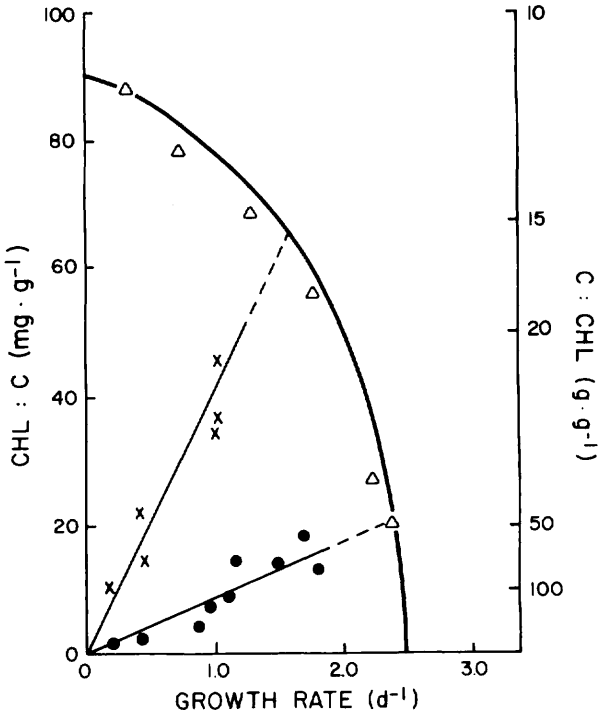

FIG. 1. The relationship between chlorophyll-to-carbon ratio (not C:Chl) and growth rate. Triangles, nutrient-saturated (light-limited) growth of *Chlorella pyrenoidosa* (Myers and Graham 1971); ×, nutrient-limited growth of *Thalassiosira pseudonana* at 0.07 $cal \cdot cm^{-2} \cdot min^{-1}$ and 12-h photoperiod (Eppley and Renger 1972; Perry 1976); circles, nitrate-limited growth of *T. pseudonana* at 0.1 $cal \cdot cm^{-2} \cdot min^{-1}$ continuous light (Caperon and Meyer 1972). In both light regimes, Chl:C is a linear function of nutrient-limited growth rate within the limits of precision, but at the lower irradiance the slope is steeper. The curve was calculated from a model presented by Bannister and Laws (1980), the source of this figure. C:Chl conversions are added for convenience.

Often, chlorophyll concentration is measured, but the desired datum is the organic carbon content of the phytoplankton. The necessary conversion is made by multiplying chlorophyll concentration by the carbon-to-chlorophyll ratio (C:Chl, $g \cdot g^{-1}$; cf. Eppley 1972; Banse 1977). Unfortunately, the ratio is by no means constant.

In laboratory experiments a wide variation of C:Chl has been demonstrated, and Shuter (1979) has modeled such changes in cellular composition. Within one strain of phytoplankton, C:Chl can vary more than fourfold as a function of nitrogen limitation (Bannister and Laws 1980; Goldman 1980). With adequate nutrients, the ratio is strongly correlated with growth irradiance (Bannister and Laws 1980) and also shows a temperature effect (Eppley 1972; Yoder 1979).

Under similar culture conditions, C:Chl for dinoflagellates is much higher than for diatoms (Chan 1980). The chlorophyll content of phytoplankton, usually measured as chlorophyll per cell, varies by about a factor of 2 with time of day (reviewed by Sournia 1974). Because carbon uptake is confined to the light period and chlorophyll synthesis may proceed in the dark, diel variation of C:Chl may be moderate to significant (Sournia 1974). Eppley et al. (1971) presented data which showed a diel variation of C:Chl of about ±25%.

The many sources of variation in C:Chl can combine to produce carbon-to-chlorophyll ratios as low as about 10 (Laws and Bannister 1980) or as high as 250 or more (Holmes et al. 1967; Sakshaug and Holm-Hansen 1977; Malone and Chervin 1979; Laws and Bannister 1980; Redalje and Laws 1981). Enough information on this variation exists to allow a mathematical description of the relationship between C:Chl and nutrient- or light-limited growth of phytoplankton (Bannister and Laws 1980; Fig. 1). There is a strong correlation between C:Chl and the relative growth rates of the algae that have been studied (Bannister and Laws 1980; Goldman 1980), and as Goldman has pointed out, the carbon-to-chlorophyll ratio is an informative index of the nutritional state of natural populations.

Because the range of possible C:Chl ratios is so large, it is not surprising that chlorophyll distributions may have patterns that are independent of the distributions of phytoplankton biomass. For instance, features of the euphotic zone in stratified water columns can influence C:Chl in such a way as to create a deep chlorophyll maximum (Steele 1964). Phytoplankton near the surface, where irradiance is high and nutrient concentrations are low, have minimal chlorophyll content. At depth (near the nitracline), decreasing irradiance and an increasing nitrate supply stimulate increases in chlorophyll relative to phytoplankton carbon, potentially by a factor of 10 or more. Temperature acts in the opposite direction, but presumably the effect is not as strong. An example will be presented in a following section.

Fluorescence *in vivo* as a Measure of Chlorophyll

Having recognized the uncertainty of the chlorophyll:phytoplankton biomass relationship, we can examine the next level of variability, fluorescence yield per chlorophyll molecule *in vivo*.

The fluorescence of chlorophyll *a in vivo* is measured by irradiating with blue light a sample of water containing phytoplankton and measuring the red light fluoresced by chlorophyll molecules. Ideally, the amount of fluorescence would be linearly related to the concentration of chlorophyll in any sample. In fact, this is not the case: fluorescence is a small and variable percentage of the light absorbed by the photosynthetic apparatus, and the capacity of the chlorophyll to absorb light is also variable (Harris 1978; Kiefer 1973b).

The variability of fluorescence yield in phytoplankton reflects the complex control of both the light absorption and of the disposition of energy in the photosynthetic apparatus (reviewed by Harris 1978; Prézelin 1982). Early studies of *in vivo* fluorescence in oceanographic contexts showed that characterization of this variability as a function of species composition, nutrition, and preconditioning could have value well beyond that of merely increasing the precision of the

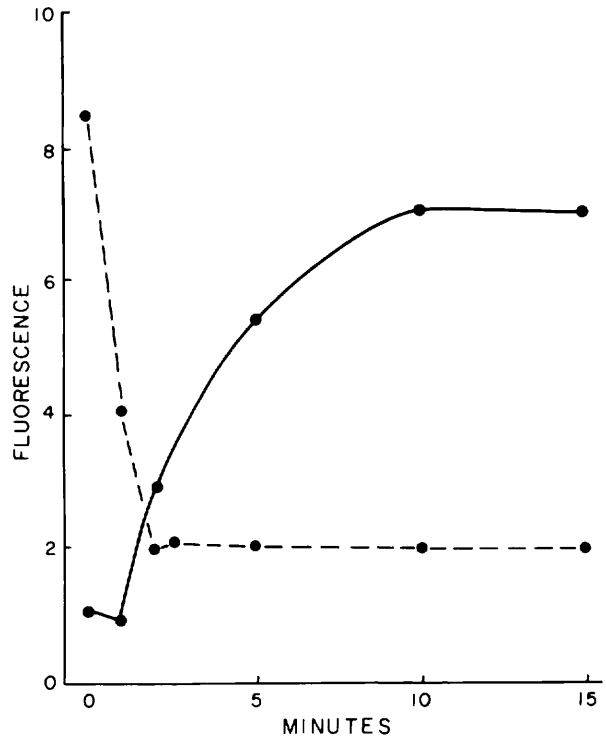

FIG. 2. Time course of fluorescence inhibition and recovery (Lake Windemere, U.K.). Fluorescence is the peak measurement from the first 5 s in the fluorometer. The solid line represents surface water exposed to dim light over 15 min. The broken line represents 5 m water exposed to bright light (1500 $\mu E \cdot m^{-2} \cdot s^{-1}$) over 15 min. From Vincent (1979).

method (Strickland 1968; Blasco 1973; Kiefer 1973a, b; Yentsch 1974a). True to these expectations, results of recent studies of *in vivo* fluorescence have been quite provocative (cf. Harris 1978; Vincent 1980; Prézelin 1982).

The ratio of fluorescence to chlorophyll *a* (R) increases with nutrient starvation of phytoplankton (Blasco 1973; Kiefer 1973b; Sakshaug and Holm-Hansen 1977) and can also show considerable variability among taxa: at least fivefold among eukaryotic microalgae grown under identical conditions (Strickland 1968). The cyanobacteria have lower fluorescence yields (Heaney 1978). Changes of R can produce easily measured, coherent patterns which can lead to inferences about processes important to primary production (Herbland and Voituriez 1977a). For instance, a transect of fluorescence and chlorophyll taken perpendicular to the Southern California coast (Kiefer 1973a) showed large differences in R between inshore and offshore water. In the latter, chlorophyll concentration is lower than, species composition is different from (Reid et al. 1978; Cullen 1980), and nutrient limitation is presumably more severe than in nearshore waters (Eppley 1968; Kiefer 1973a).

Fluorescence yield is very responsive to ambient light and can change rapidly when shifts in irradiance are experienced by phytoplankton (Heaney 1978; Harris 1978; Vincent 1979). Fluroescence can undergo changes on different time scales during measurement with a fluorometer (Kiefer

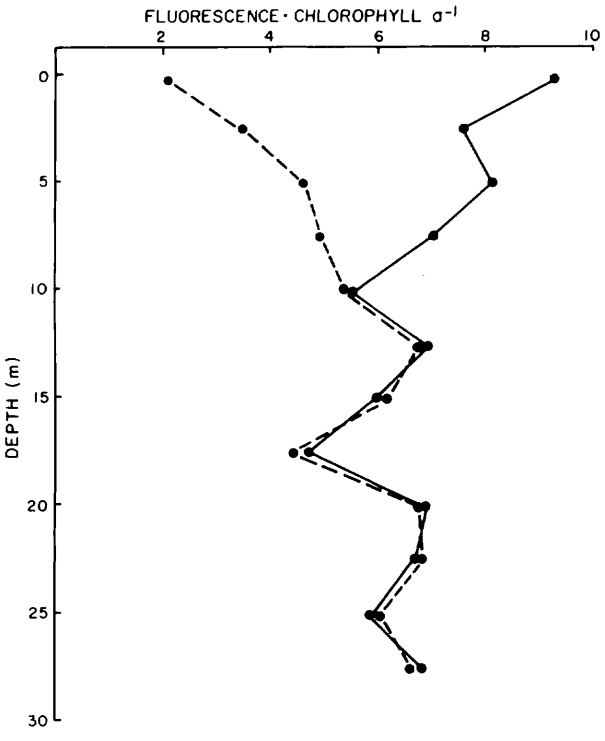

FIG. 3. Photoinhibition of fluorescence in a vertical profile (Lake Okareka, New Zealand). The broken line indicates fluorescence yield measured immediately upon collection. The solid line connects measurements made on the same samples after 2 h in complete darkness. From Vincent (1979).

1973b; Vincent 1979) and can show strong, reversible photoinhibition which is expressed on time scales of seconds to minutes (Heaney 1978, Vincent 1979; Fig. 2). Inhibition of fluorescence near the surface could possibly produce subsurface fluorescence maxima that do not represent chlorophyll maxima (Fig. 3). There are some indications that photoinhibition of fluorescence, which can decrease R by a factor of 8, is more strongly expressed among the diatoms as compared to other phytoplankton (Loftus and Seliger 1975; Harris 1978; Heaney 1978).

Diel changes in fluorescence yield have been observed in the laboratory and in the field. The dinoflagellate *Gonyaulax polyedra* grown under the relatively low-irradiance conditions of laboratory incubators has a circadian rhythm of fluorescence yield that is in phase with a rhythm of photosynthetic capacity, which is highest during the light period (Sweeney et al. 1979, see also Prézelin and Ley 1980). However, natural samples from near the sea surface may show an inverse pattern of fluorescence yield, forced by the photoinhibitory effects of bright sunlight (Kiefer 1973a; Yentsch 1974a; Loftus and Seliger 1975).

These observations make it clear that patterns of fluorescence, independent of variations in chlorophyll concentration (much less phytoplankton biomass) may be found wherever the sampling program encounters changes in light, nutrients, species composition, or time of day. Also, the type of fluorometer can determine in part the pattern observed (Vincent 1979, 1981; Harris 1980; Prézelin and Ley 1980): light histories of the phytoplankton and methods of measurement interact to produce different information from *in situ* fluorometry, continuous flow fluorometry, and dark-adapted discrete determinations of *in vivo* fluorescence.

Slovacek and Hannan (1977) suggested that addition of the photosynthetic inhibitor [3-(3,4-dichlorophenyl)-1,1-dimethylurea] (DCMU) to a sample would elevate fluorescence yield to a constant, maximal level, but subsequent studies have shown DCMU-treated fluorescence is strongly affected by light history (Harris 1980; Vincent 1980) and has a diel periodicity of greater magnitude than that of untreated *in vivo* fluorescence (Prézelin and Ley 1980).

One other aspect of uncertainty in fluorescence and chlorophyll measurements concerns the presence of chlorophyll degradation products in natural samples: these pigments may appear to be chlorophyll *in vivo* and in analysis of extracted samples. The relative contribution of these products is greater at depth, and the analysis of the full pigment fraction allows useful ecological interpretation (Gieskes et al. 1978; Jeffrey and Hallegraeff 1980).

Implications of Variability in Chlorophyll Content and Fluorescence Yield of Phytoplankton

The potential for variability of fluorescence and chlorophyll as measures of phytoplankton biomass is staggering, but the imprecision has been tolerated because the information content of fluorescence profiles is so great. I suggest that the imprecision should not be merely tolerated: it should be anticipated, recognized, corrected for, and most importantly, interpreted. Pooling data from many vertical profiles for regression analysis may be valid for some applications, but it ignores systematic variation within profiles that may have significant information content (cf. Yentsch 1974a; Eppley et al. 1977; Herbland and Voituriez 1977a; Harris 1980; Cullen and Eppley 1981).

The parameters I have been discussing are functions of light, nutrients, and species composition; frequently, all of them change sharply near the deep chlorophyll maximum. Vertical profiles should sample these variations efficaciously; therefore, to get a good picture of the important features in a vertical profile, precise measurements with high spatial resolution should be obtained, especially near the nutricline and deep chlorophyll maximum.

The Vertical Structure of Phytoplankton in Divers Environments

Just as it is misleading and unjustified to assume that fluorescence yield or C:Chl is uniform in space or time, it is also incorrect to assume that the vertical structure of marine phytoplankton is determined by the same processes in different environments. In this section I present a number of vertical profiles and will speculate on the mechanisms of their formation and maintenance.

Vertical Profiles from Relatively Stable Systems: Typical Tropical Structure

Low seasonal variation allows more temporal constancy of planktonic processes in the tropics as compared to higher latitudes (Cushing 1981) even though the effects of hydrogra-

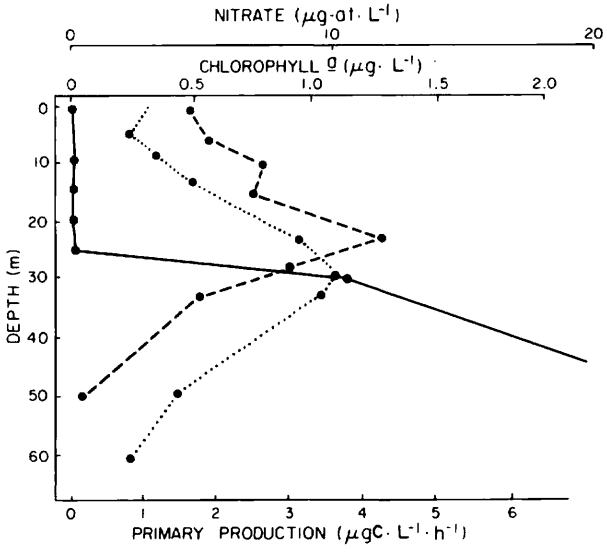

FIG. 4. Vertical profiles from the Guinea Dome, 20°50′W, 11°30′N, August 1973. Broken line, primary production; dotted line, chlorophyll *a*; solid line, nitrate. From Voituriez and Dandonneau (1974).

phy (currents, upwelling) and climate (monsoons, winds) are appreciable and seasonal (Sournia 1969; Vinogradov 1981). Because of the relatively small magnitude of fluctuations of standing stocks and the balance (*sensu* Heinrich 1962) between phytoplankton and zooplankton characteristic of unperturbed tropical regions, vertical profiles from low-latitude environments are more likely to reflect steady-state balances of fluxes which can be estimated from measurements *in situ*, rather than relicts of earlier, transient events.

The close and relatively stable coupling between physical and biological processes in the eastern tropical Atlantic Ocean has permitted the characterization of hydrographic and biological features into "typical tropical structure" (TTS; Herbland and Voituriez 1979). In a number of papers, it has been shown that TTS is a continuum of pattern, ultimately controlled by the input of nutrients from below, nutrients supplied by upwelling (Vinogradov 1981) or turbulent mixing (Kaiser and Postel 1979; Voituriez and Herbland 1979; Herbland and le Bouteiller 1982).

With the exception of "atypical" (Herbland and Voituriez 1977a) regions affected by lateral input of nutrients from nearby equatorial upwelling, most vertical profiles from the eastern tropical Atlantic Ocean have the general shape depicted in Fig. 4. The features of vertical profiles have definable relationships with the thermal structure of the water column, but from an ecological perspective, nutrient distributions are more important: the chlorophyll maximum is found near the nitracline and the peak in primary production is coincident with (according to Herbland and Voituriez 1979) or just above (Guinea Dome measurements by Voituriez and Dandonneau 1974) the chlorophyll maximum. Primary production and chlorophyll concentration in the water column are inversely related to depth of the nitracline (Herbland and Voituriez 1979); the oligotrophic extreme of TTS is characterized by a deep thermocline and nitracline, low chlorophyll concentrations, and minimal primary production; and

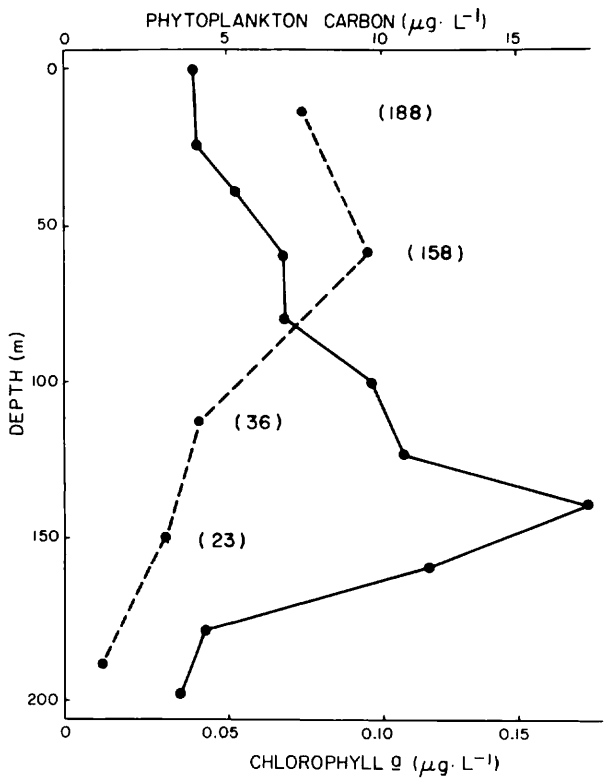

FIG. 5. Vertical profiles from the North Pacific Central Gyre, June 22, 1973. Broken line, phytoplankton carbon concentration estimated from microscopic examination of preserved samples; solid line, chlorophyll *a*. Carbon-to-chlorophyll ratios are enclosed in parentheses. From Beers et al. (1975).

hydrographic and biological features change together along the continuum, culminating in the productive extreme of TTS : shallow thermocline and nitracline, high chlorophyll and production (Herbland and Voituriez 1979). If the nutrient flux is sufficient to elevate nitrate concentrations in the surface-mixed layers, TTS breaks down.

Even if hydrographic structure changes rather abruptly (temporally or spatially) due to variations of mixing from below, TTS can be maintained, as measurements at stations affected by the meandering Lomonosov current have shown (Herbland and le Bouteiller 1982).

It appears that only one dimension (the vertical) need be considered to explain much of the variability in typical tropical structure, and indeed, profiles like Fig. 4 are similar to the later stages of time-dependent simulation models which consider only the vertical dimension (Jamart et al. 1977; Menshutkin and Finenko 1977); the subsurface chlorophyll maximum is maintained primarily as a result of enhanced primary production in a stratum.

Shoal thermoclines in the tropics are indicative of upwelling or high turbulence from below, and the negative correlation between integrated primary production and depth of the thermocline in TTS (Herbland and Voituriez 1979) is consistent with the hypothesis that vertical inputs of nutrients or energy have a dominant effect on primary production (cf.

Margalef 1978; McGowan and Hayward 1978; Eppley et al. 1979; Herbland and le Bouteiller 1982; see also an alternative explanation by Yentsch 1974b, 1981). Thus discussions of the processes important to "typical tropical structure" are probably relevant to other stable systems in higher latitudes.

A Vertical Profile of Chlorophyll that Does Not Represent Phytoplankton Biomass

Although subject to more seasonal variation of wind mixing and irradiance than the tropics, the great central gyres, and in this example, the North Pacific Central Gyre (Fig. 5), are certainly stable environments (McGowan and Walker 1979; Weiler 1980 and references within each). Chlorophyll concentrations and conventionally measured primary production rates are relatively low, and the nitracline is deeper than 100 m (Venrick 1979, and references therein). Mixing processes in this oligotropic region are not well understood (McGowan and Hayward 1978), but experimental evidence suggests that the fluxes of nutrients into the euphotic zone are probably about as low as in any oceanic environment (Eppley and Peterson 1979), and it may be proposed that a profile from a central gyre represents a situation beyond the oligotrophic extreme of "typical tropical structure."

The problem of variable chlorophyll content of phytoplankton becomes acute when profiles from the North Pacific Central Gyre are studied. If a chlorophyll profile is compared to the depth distribution of phytoplankton carbon determined by microscopic examination (Fig. 5), it becomes clear that concentration of chlorophyll is a poor indicator of phytoplankton biomass indeed (cf. Kiefer et al. 1976). The chlorophyll maximum represents a physiological adaptation to the lower irradiance and to the greater availability of nutrients in that stratum, and changes in C:Chl (Fig. 5) are entirely consistent with those measured in controlled experiments (Fig. 1). Interestingly, the ratios suggest nutrient limitation of algal growth near the surface (see McCarthy and Goldman 1979; Goldman et al. 1979; Jackson 1980; Sharp et al. 1980 for discussion of this contentious subject). As postulated by Steele (1964), this chlorophyll profile from a stable environment changes independently from phytoplankton biomass.

If the profile from the North Pacific Central Gyre (Fig. 5) represents the oligotrophic extreme of a spectrum of vertical structure, and at that end of the spectrum chlorophyll is not indicative of phytoplankton, one must address the question, at what point in the change toward eutrophy does a chlorophyll profile correspond to phytoplankton biomass? Steele's (1964) model could predict most distributions of chlorophyll in the tropics with the assumption of vertically uniform distributions of phytoplankton. However, Herbland and le Bouteiller (1982) have measured particulate phosphorus along with chlorophyll for their profiles and found similar vertical structures for each. An intermediate situation is presented by Herbland and Voituriez (1977b). (See Perry and Eppley (1981) for a discussion of particulate phosphorus as an indicator of biomass, but also Strickland (1965), Sakshaug and Holm-Hansen (1977), and Maestrini and Kossut (1981) for examples of variation of C:P in phytoplankton.) More profiles of chemical constituents and phytoplankton enumerations must be compared with chlorophyll measurements before safe generalizations can be made about the vertical distributions of phytoplankton in diverse stable environments.

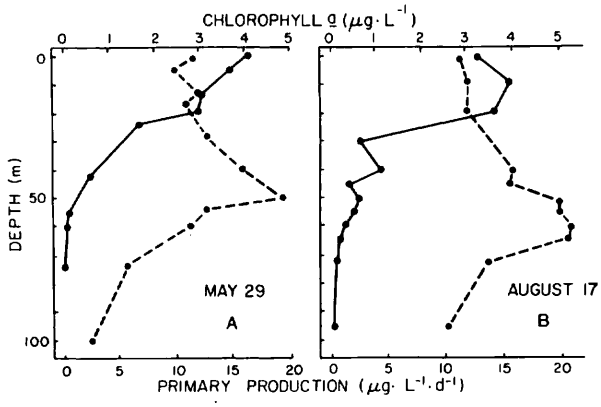

FIG. 6. Vertical profiles of *in situ* primary production (solid line) and chlorophyll *a* (broken line) at a station off the Oregon coast, 44°40'N, 127°00'W. A. May 29, 1969. B. August 17, 1969. From Anderson (1972).

Vertical Structure of Variable Environments: Transients and Relicts

In temperate latitudes, seasonal variation is expressed in irradiance, wind-induced mixing, and in some regions, upwelling. Through the seasons, then, the biomass, vertical distributions, and species composition of phytoplankton can be quite variable. Vertical profiles measured in such environments may reflect transient conditions or relict properties from prior, unobserved events.

In contrast to "typical" examples from the tropics, vertical profiles from temperate latitudes often show a near-surface peak in primary production which is to be expected during the spring bloom, but which persists through the summer, well removed from the subsurface nitracline and the chlorophyll maximum (cf. Anderson 1969; Cullen and Eppley 1981; Ortner et al. 1980; Fig. 6). Measurements have been made which confirm the inference that regeneration of nitrogenous nutrients must be higher near the surface in these environments (Harrison 1978). What process is responsible for concentrating regenerative activity near the surface, and why doesn't it act in the tropics? Perhaps the annual input of nutrients to the mixed layer each winter in temperate latitudes is retained near the surface by regenerative processes whereas deep mixing generated from above does not occur in the "typical tropical" environment, thus confining the primary production maximum to the vicinity of the nitracline. The example of the North Pacific Central Gyre (Fig. 5) is problematic, because there is little evidence that wind mixing ever reaches the nutricline (McGowan and Hayward 1978).

Significant primary production above the nitracline, which I have suggested is due to temporally distant events in temperate waters, is observed in "atypical" tropical regions and is attributed to spatially remote equatorial upwelling, which enhances production in the mixed layer by lateral transport (Herbland and Vroituriez 1977a; see also Vinogradov et al. 1971).

Just as the near-surface primary production maximum

(Fig. 6) may be a relict of nutrient input to the mixed layer months before, the chlorophyll maximum may be an accumulation of phytoplankton which was produced in overlying waters. This concept has received theoretical treatment. A term for sinking of phytoplankton was included in the mathematical model of Riley et al. (1949), and subsurface chlorophyll maxima were simulated. Jerlov (1959) suggested that physical features could dominate over biological processes in determining the vertical distributions of particles (phytoplankton): sinking particles would concentrate on density gradients. However, Steele and Yentsch (1960) presented calculations which showed that density changes in the water alone could not explain chlorophyll maxima at the foot of the euphotic zone. Steele and Yentsch suggested that physiologically induced changes in the buoyancy of phytoplankton, a response to increased nutrient supply and decreased irradiance near the bottom of the euphotic zone, could produce the observed distributions of chlorophyll.

The profiles in Fig. 6 may reflect the importance of sinking to chlorophyll profiles. The chlorophyll maximum coincides with the nitracline, exactly where one would expect to find a local maximum in primary production (Menshutkin and Finenko 1977), a decrease in C:Chl (Steele 1964), and an accumulation of sinking phytoplankton (Steele and Yentsch 1960). Anderson's (1969, 1972) papers satisfied the first two expectations, but the degree to which the chlorophyll maximum represents a decrease in the sinking rate of phytoplankton is unknown. If not supplied from above, could the chlorophyll maximum be maintained?

Vertical profiles from the Atlantic have been interpreted to suggest that chlorophyll maxima are found at depths where sinking particulate matter accumulates (Ortner et al. 1980), but falsifiable hypotheses concerning the sinking of phytoplankton and deep chlorophyll maxima have not been tested thoroughly with data from the field. Quantification of vertical fluxes is necessary (cf. Bienfang 1980).

Probably the most likely situation for chlorophyll profiles to be dominated by the effects of depth-differential sinking of phytoplankton would be after the spring bloom in temperate latitudes when sedimentation rates of phytoplankton should exceed growth rates (cf. Smetacek et al. 1978); thus subsurface chlorophyll maxima composed of diatoms could appear as transient features. An example from the western edge of the California Current (30°N, 120°W; Venrick et al. 1973), where chlorophyll profiles were collected throughout the year, is consistent with explanations invoking the sinking of phytoplankton, but species composition was not reported and definite conclusions cannot be drawn.

The Direct Influence of Density Gradients on the Vertical Distributions of Phytoplankton

On a finer vertical scale, Derenbach et al. (1979) have described chlorophyll maxima which seem to reflect an interaction between the microscale physical structure of the thermocline (cf. Woods and Wiley 1972) and the sinking of diatoms (*Skeletonema costatum*) apparently independent of physiological changes in buoyancy (Fig. 7). The interaction of horizontal shear and horizontal patchiness could also contribute to the observed pattern (G. A. Riley, Dalhousie

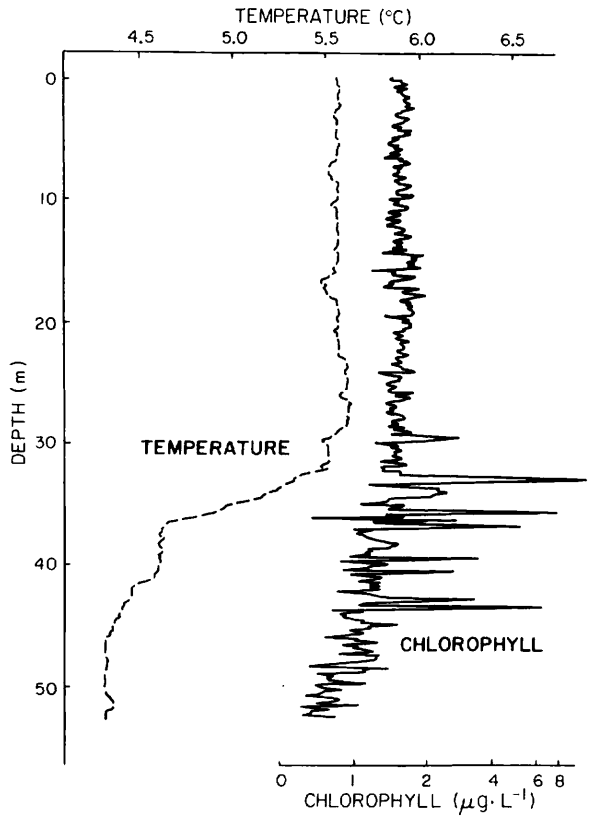

FIG. 7. Vertical profile of temperature and chlorophyll *a* (from an *in situ* fluorometer), Baltic Sea. Intense peaks of chlorophyll correspond with microscale density structure (from Derenbach et al. 1979).

University, Halifax, N.S., personal communication). The example in Fig. 7 emphasizes the utility of making high-resolution fluorescence measurements with equally good determination of physical structure. Until this is done more frequently, it will be difficult to know how commonly physical factors have overriding influence on the vertical distributions of phytoplankton. Microscale chlorophyll maxima were not found in another region of the Baltic where the thermocline was less well developed (Derenbach et al. 1979), nor have they been observed during recent cruises in the Southern California Bight (R. W. Eppley, Scripps Institution of Oceanography, La Jolla, CA 92093, USA, personal communication).

To the best of my knowledge, the exact coincidence of chlorophyll maxima and maximum density or temperature gradients in oceanic water columns has been examined explicitly with statistical methods only twice, with negative results for both the western Indian Ocean (Karabashev and Solov'yev 1978) and the Southern California Bight (Cullen and Eppley 1981). The negative results based on data with a resolution of meters do not imply that physical processes have little control over the vertical distribution of chlorophyll, nor do they say that chlorophyll maxima are not in the pycnocline, only that factors other than density structure are of greater proximate

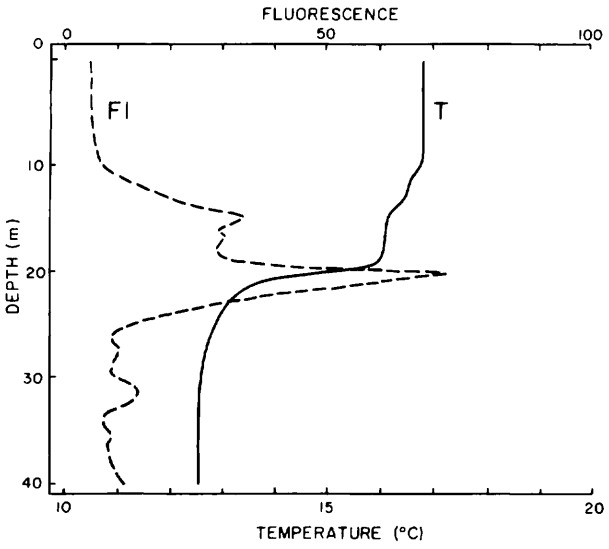

FIG. 8. Vertical profile of fluorescence (arbitrary units) and temperature from the western English Channel, 5°23'W, 49°25'N, July 1975. From Pingree et al. (1975).

importance (see a discussion on the thermocline/nitracline relationship in Herbland and Voituriez 1979).

Environments Where Density Gradients and Biological Processes Contribute to Vertical Structure

Excellent examples of the interaction between density structure and biological processes can be found near tidally influenced frontal systems. Pingree et al. (1975) have discussed the development of high concentrations of dinoflagellates within sharp density gradients near frontal boundaries and have explained the increase of phytoplankton abundance in the thermocline in terms of stability: phytoplankters above the thermocline are well mixed in a nutrient-depleted surface layer where conditions for growth are unfavorable, and those organisms below the thermocline are in a turbulent regime in which mean irradiance is too low for growth. Phytoplankton in the thermocline attain high concentrations because the characteristic mixing time of the water is considerably longer than the algal generation time, allowing growth and accumulation. Vertical profiles of fluorescence and temperature from the English Channel offer strong support for the stability–growth hypothesis (Pingree et al. 1975; Fig. 8). The extent to which the aggregation of phytoplankton in the thermocline is behaviorally determined (cf. Falkowski et al. 1980; Cullen and Horrigan 1981; Heaney and Eppley 1981) has not been assessed, although Holligan (1978) has looked for, but not found, evidence for diurnal vertical migration.

Chlorophyll Maxima and Phytoplankton Behavior

Phytoplankton can do more than grow, sink, or be consumed. Behavioral mechanisms which determine vertical position in the water column are common among unicellular

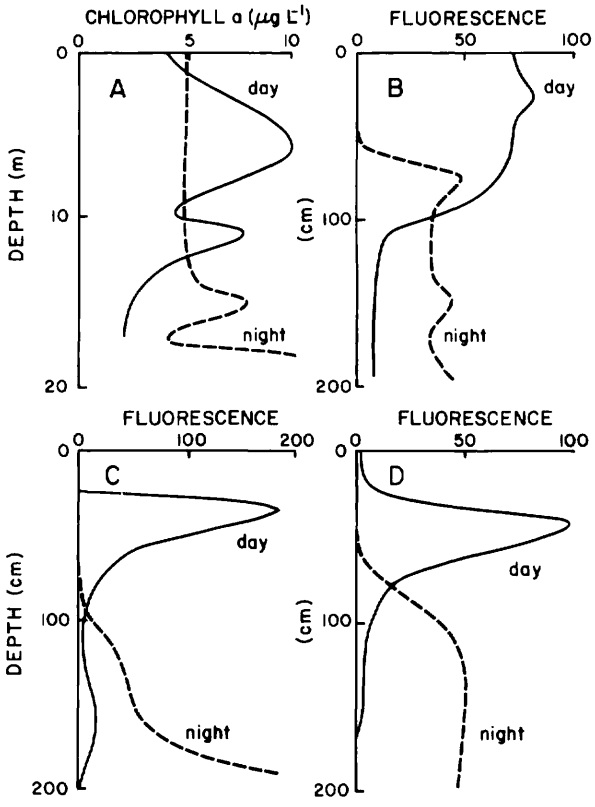

FIG. 9. Behavior of the naked dinoflagellate, *Gymnodinium sanguineum* (= *splendens*) A. Vertical profiles from "isothermal" Coyote Bay, Gulf of California (Kiefer and Lasker 1975). B–D. Vertical profiles from a 2.0-m enclosed water column in the laboratory, surface irradiance, 900 $\mu E \cdot m^{-2} \cdot s^{-1}$ on a 12-h light:12-h dark cycle: B, nitrate greater than 1 μM throughout; C, nitrate depleted throughout; D, nitrate greater than 1 μM only near the bottom of the tank. From Cullen and Horrigan (1981).

algae: motile phytoplankton can migrate vertically (Forward 1976) or aggregate in thin layers (Falkowski et al. 1980; Harris et al. 1979), blue-green algae (cyanobacteria) can move vertically by physiologically altering buoyance (Walsby and Klemer 1974), and diatoms can aggregate near a nutrient gradient by modifying their sinking rate (Steele and Yentsch 1960).

The diurnal vertical migration of dinoflagellates, classically characterized as phototactic (Hasle 1950; Forward 1976), also involves geotaxis and a diel rhythm (cf. Eppley et al. 1968; Weiler and Karl 1979; Cullen and Horrigan 1981; Kamykowski 1981). Kiefer and Lasker's (1975) measurements on a phytoplankton assemblage dominated by the dinoflagellate, *Gymnodinium sanguineum* (= *splendens*) provide an example (Fig. 9a). However, dinoflagellates are not constrained to one behavioral response: different species may have their own preferred depths during the day (Hasle 1950; Blasco 1978), and the behavioral patterns of organisms of the same species may change with nutrient availability (Eppley et al. 1968; Heaney and Eppley 1981; Cullen and Horrigan 1981; Fig. 9, B–D). Thus, behavior of phytoplankton may

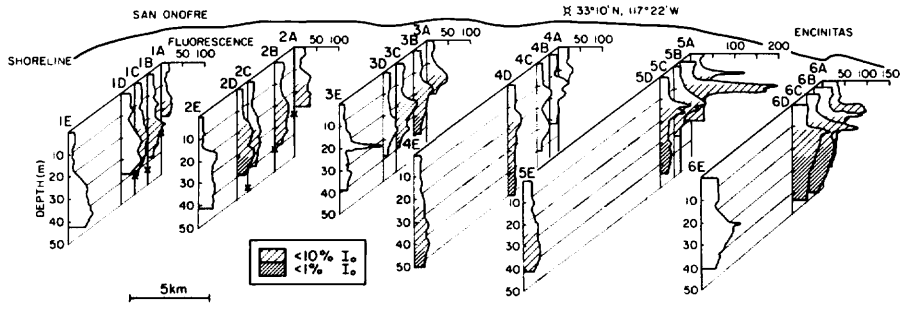

FIG. 10. Vertical profiles of fluorescence and light penetration (where measured) Southern California Bight, August 1978. Hatch marks represent percentage of surface irradiance, I_o. The 1% light level is designated by an × at those stations where it was reached. Stations are labeled 1A–E, 2A–E, etc. The letters A, B, C, D, E correspond to water depths of 30, 50, 100, 300, and 750 m, respectively. This figure shows that most of the subsurface maxima were near the 10% light level. In addition, most were near the nitracline. From Cullen (1980).

contribute significantly to a variety of vertical profiles of chlorophyll (cf. Kamykowski 1980).

CHLOROPHYLL PROFILES FROM A HORIZONTALLY HETEROGENEOUS REGION

The examples of vertical profiles given so far represent a spectrum of factors that promote formation or maintenance of deep chlorophyll maxima. In most examples, some factors are clearly more important than others. In environments with considerable horizontal heterogeneity, the situation can be much more complicated.

A 25 km × 40 km grid near the southern California Coast was sampled in 2 d for fluorescence, chlorophyll, nutrients, and phytoplankton enumeration (Cullen 1980). Inspection of the fluorescence and chlorophyll data revealed that a subsurface chlorophyll maximum was present at each station, near the nitracline and 10% light level (Fig. 10). Chlorophyll concentrations were higher and subsurface peaks more pronounced nearshore and to the south. Still, little could be inferred from the distributions of chlorophyll and fluorescence alone: the shapes of the profiles, magnitudes of the chlorophyll peaks, and relationships between chlorophyll and nutrients or light varied over a range that was similar to that encountered in the Southern California Bight over 4 yr (cf. Cullen and Eppley 1981).

Microscopic examination of preserved samples from the grid provided the information necessary to interpret the patterns observed. Phytoplankton carbon estimates from microscopic examination (Eppley et al. 1977) revealed that at 16 of the 30 stations, concentrations of phytoplankton at the surface were greater than in the chlorophyll maximum. At the 14 stations nearshore and to the south, the chlorophyll maxima were dominated by relatively large motile dinoflagellates, especially *Ceratium tripos* (cf. Falkowski et al. 1980), and had higher concentrations of phytoplankton carbon than at the surface. Even though calculating concentrations of phytoplankton carbon from examination of preserved samples has its uncertainties, the carbon-to-chlorophyll ratios from this data set were, like those from the North Pacific Central Gyre (Fig. 5), quite consistent with experimental observations: in nitrate-depleted surface waters, the ratio was 92. Where the chlorophyll maximum represented a physiological change in C:Chl, it was 25. The chlorophyll maximum layer dominated by dinoflagellates had a characteristic C:Chl of 70.

Although diatoms were not numerically important in this study, they showed a significant pattern: they were more concentrated in the chlorophyll maxima throughout the grid, consistent with other observations from temperate latitudes (Venrick et al. 1973), and this probably involved changes in sinking rate near the nitracline (cf. Steele and Yentsch 1960).

Thus, in one small sampling region, a variety of chlorophyll maximum "types" were found, each with its own ecological interpretation. Unfortunately, labor-intensive measurements were required to reveal the nature of the chlorophyll maxima. In similar studies concerned with more general questions, a few samples for phytoplankton enumeration and particle counts or analysis of particulate matter could have provided much useful information with considerably less work.

Classification of Deep Chlorophyll Maxima

The foregoing presentation has demonstrated that all subsurface chlorophyll maxima are not the same, and many can be categorized by the mechanisms of their formation and maintenance. To conclude, I will list some "types" of deep chlorophyll maxima and speculate on the implications for sampling and interpretation.

Primary production maximum and chlorophyll maximum near the nitracline, TTS — The euphotic zone is essentially a two-layer system, with a nutrient-depleted surface layer and deeper water in which light limits phytoplankton growth (Dugdale 1967). Primary production and chlorophyll concentration are maximal near the nitracline, the boundary between the two layers, where simple models of algal growth as functions of light and nutrient concentrations would predict. The chlorophyll maximum is maintained as a result of enhanced growth in a stratum. Steady-state models in the vertical dimension may be able to describe most of the chemical and biological features of typical tropical structure; input of nutrients to the euphotic zone by turbulence from below would be a very important term in any solution (cf. Margalef 1978; Kaiser and Postel 1979).

In highly structured systems such as those in the tropics, or

in temperate waters in the summer, sampling effort should be concentrated near the nitracline (chlorophyll maximum, thermocline) where parameters change most rapidly (cf. Herbland and Voituriez 1979). Especially when the relationships between phytoplankton and zooplankton profiles are being studied (cf. Mullin and Brooks 1972; Longhurst 1976; Longhurst and Herman 1981; Ortner et al. 1981) careful attention should be paid to determining the extent to which the distribution of chlorophyll reflects phytoplankton biomass (visual counts would be best, but particle counts, ATP analyses, or particulate C and N and P analyses would be useful).

Physiological adaptation of C:Chl — Some evidence indicates that C:Chl in deep chlorophyll maxima dominated by organisms other than dinoflagellates is about 25 (Eppley 1968; Beers et al. 1975; Cullen 1980), about what would be predicted from laboratory experiments. If the phytoplankton above the chlorophyll maximum is light-saturated and possibly nutrient-limited, C:Chl will be higher near the surface: about 100 in the Southern California Bight during the summer (cf. Eppley 1968; Cullen 1980; see also Steele and Baird 1962) and in the range of 150–250 in oligotrophic central gyres (Beers et al. 1975; Redalje and Laws 1981). These results strongly support the calculations of Steele (1964). Surely, when nutrient limitation is important near the surface, chlorophyll distributions can have little to do with phytoplankton biomass. Thus, attempts to relate zooplankton distributions to chlorophyll concentration may be confounded. The suggestion that zooplankton exploit preferentially the depth of maximum primary production and that chlorophyll profiles are to some extent determined by depth-differential grazing (Lorenzen 1967; Longhurst 1976; Herman et al. 1981), cannot be examined thoroughly until the proper measurements of phytoplankton biomass are made with sufficient spatial resolution, and the grazing rates of herbivores are related to the concentrations of food available to them.

Decrease in sinking rate of phytoplankton — As a purely physical process (cf. Derenbach et al. 1979), variations in sinking rate as a function of density structure may create phytoplankton patchiness that is important, or perhaps necessary (cf. Mullin and Brooks 1976) to survival of herbivores. More high-resolution measurements will tell us how common microscale chlorophyll maxima (Derenbach et al. 1979) are in nature, and what their temporal persistence is.

When a subsurface nitracline is present, sinking diatoms will aggregate on it (Steele and Yentsch 1960). If irradiance near the nitracline is conducive to growth, significant primary production will occur in that stratum (cf. Anderson 1969, 1972). To quantify important biological fluxes in a system with a "type 3" chlorophyll maximum, sinking rates above and below the maximum must be determined. Smayda (1970) has collected the best estimates, but measurements *in situ* (Bienfang 1980) would provide information directly applicable to specific profiles.

Behavioral aggregation of phytoplankton — If a chlorophyll maximum layer in stratified water is dominated by dinoflagellates or other motile phytoplankton, behavior should be considered as a mechanism of aggregation. Aggregations of dinoflagellates have been interpreted from several perspectives: Lasker (1975) suggested that a chlorophyll maximum layer dominated by *G. sanguineum* (= *splendens*) was a food resource critical to the survival of larval anchovies. P. C. Fiedler and M. Huntley (Scripps Institution of Oceanography, La Jolla, CA, personal communication) determined that herbivorous crustacean zooplankton had reduced feeding rates within a similar layer of the same organism, and stratified sampling indicated that several taxa of zooplankton avoided the layer. Fiedler and Huntley also demonstrated reduced feeding by *Calanus pacificus* on a bloom of *Gymnodinium flavum*, a dinoflagellate morphologically similar to *G. sanguineum* (= *splendens*). Resistance to grazing has likewise been suggested for the thecate dinoflagellate *Ceratium tripos* (Conover 1978; Falkowski et al. 1980). Wyatt and Horwood (1973) suggest that, independent of relative palatability, behavioral aggregation of phytoplankton will lead to reduced mortality from grazing.

Dinoflagellates grow relatively slowly (Falkowski et al. 1980; Chan 1980), so it follows that reduction of losses from both sinking and grazing would be important to their survival. Behavioral aggregation may facilitate these reductions. If herbivorous zooplankters do not exploit patches of dinoflagellates, interpretation of chlorophyll distributions is complicated further because not even phytoplankton biomass is an adequate measure of food available to herbivores. We need more determination of grazing rates on phytoplankton dominated by dinoflagellates.

Effects of Zooplankton on the Vertical Distributions of Phytoplankton

The mechanisms of chlorophyll maximum layer formation and maintenance presented so far explain vertical distributions of chlorophyll with no special consideration of grazing by herbivorous zooplankton. It would seem ludicrous to try to explain vertical distributions of phytoplankton without incorporating grazing, if it were not for the satisfactory results that have been obtained. Still, the question remains, what effect does the zooplankton have on chlorophyll profiles?

Longhurst (1976) analyzed profiles of zooplankton abundances from the eastern tropical Pacific Ocean and found that subsurface maxima coincided with the depth of maximum carbon fixation, above the chlorophyll maximum. He inferred that depth-differential grazing pressure could exist in such a stable system, and, as most of primary production is consumed by grazers (i.e. sinking is relatively unimportant), the upper boundary of the chlorophyll maximum could be maintained by herbivory. Herman et al. (1981) have made similar observations for water near the Scotian Shelf. However, as I have shown, most vertical profiles of chlorophyll can be accounted for by fairly well-understood processes without any special regard to grazing. Surely, more work is needed to help fit grazing pressure into the framework of vertical structure (e.g. Jamart et al. 1979; A. Herman and T. Platt, Bedford Institute of Oceanography, Dartmouth, N.S., personal communication). Especially useful would be detailed measurements of phytoplankton biomass to go with profiles of epiplankton abundance and chlorophyll. As soon as the true relationships between phytoplankton and zooplankton profiles are discovered and generalized, theoretical work that examines the implications of these relationships should be more

rapidly advanced.

Significant advances in the study of vertical distribution of phytoplankton (and zooplankton, nutrients, primary production) require more than just good measurement. Hypotheses must be formulated and tested (cf. Mullin and Brooks 1972; Longhurst 1976; McGowan and Walker 1979). Further, the hypotheses should reflect the state of our knowledge: it should not be assumed, *a priori*, that fluorescence represents chlorophyll, chlorophyll represents biomass, or even that biomass represents acceptable food for herbivores.

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