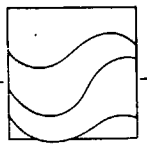

Chlorophyll
Phytoplankton
Vertical structure
Southern California Bight

Chlorophylle
Phytoplancton
Structure verticale
Southern California Bight

Chlorophyll maximum layers of the Southern California Bight and possible mechanisms of their formation and maintenance

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Received 8/5/80, in revised form 7/7/80, accepted 7/8/80.

ABSTRACT

One hundred forty-three vertical profiles of *in vivo* fluorescence taken in the Southern California Bight from 1974 through 1979 were studied in relation to other information from the same stations. Subsurface fluorescence maximum layers are usually present, and are generally located well above the 1% light level in the vicinity of the nitracline. Fluorescence maxima are usually chlorophyll maxima, and chlorophyll maxima are often biomass maxima. Chlorophyll maximum layers often contribute significantly to water column primary production, but the majority of chlorophyll maxima are not primary production maxima. Density structure of the water column does not have overriding proximate control on the position of chlorophyll maxima below the mixed layer. Although the layers are often found where light and nutrient conditions are favorable for growth, they are not maintained as the result of enhanced growth rate in that stratum. Our field observations are consistent with laboratory results which demonstrate behavioral mechanisms for subsurface accumulation of phytoplankton. These conclusions may not apply to other regions.

Oceanol. Acta, 1981, **4**, 1, 23-32.

RÉSUMÉ

Maximums de chlorophylle dans le Southern California Bight. Mécanismes possibles pour expliquer leur formation et leur persistance.

Nous avons étudié 143 profils verticaux de fluorescence *in vivo* de la chlorophylle *a*, réalisés dans le Southern California Bight de 1974 à 1979. D'autres données secondaires ont été également utilisées. Les maximums de chlorophylle subsuperficiels sont fréquents dans le Southern California Bight. Ils ont 10-15 m d'épaisseur et sont habituellement localisés bien au-dessus du niveau de lumière 1 %, au voisinage de la nitracline. La stabilité de la colonne d'eau n'est pas de la plus grande importance dans la détermination de la position des maximums. Ces maximums de chlorophylle représentent habituellement des niveaux élevés de biomasse et moins souvent des maximums de production primaire, mais ils ne sont généralement pas formés et maintenus comme des maximums de taux de croissance du phytoplancton. Nos observations sur le terrain concordent avec les résultats en laboratoire, qui démontrent le rôle de mécanismes de comportement dans l'accumulation subsuperficielle de phytoplancton.
Nos conclusions ne peuvent peut-être pas s'appliquer à d'autres régions que le Southern California Bight.

Oceanol. Acta, 1981, **4**, 1, 23-32.

INTRODUCTION

Patterns of vertical chlorophyll distribution in the upper ocean contain information on the fundamental processes which determine the vertical structure of phytoplankton abundance, and, in turn, many of the dynamic aspects of pelagic ecosystems. The study of chlorophyll distributions provides a good starting point for understanding planktonic trophodynamics. The importance of vertical heterogeneity in phytoplankton has long been recognized (cf. Herdman, 1923), and studies throughout the first half of this century showed that some phytoplankters aggregated at prefered depths (Hasle, 1950 and references therein).

Several treatments of the vertical patterns of marine phytoplankton were published before the mid-1960's. Notable were the model by Riley *et al.* (1949), which produced subsurface phytoplankton maxima, the paper by Steele and Yentsch (1960) which demonstrated a mechanism for the development of a diatom maximum on a nutrient gradient, and the observation by Steele (1964) that chlorophyll maxima need not be peaks of phytoplankton biomass, but could be due to a physiological adaptation in the ratio of cellular carbon to chlorophyll.

It was probably not until the introduction of continuous flow *in vivo* fluorometry (Lorenzen, 1966) that the features called chlorophyll maximum layers were truly appreciated. *In vivo* fluorometry made possible the observation that phytoplankton could be concentrated in thin layers easily missed by conventional sampling schemes (Strickland, 1968). Vertical movements of these layers have been observed (Eppley *et al.*, 1968; Gieskes *et al.*, 1978; Kiefer, Lasker, 1975). Recent modifications of the *in vivo* fluorometric method enabled Derenbach *et al.* (1979) to demonstrate that considerable micro-scale variability of phytoplankton can exist, with chlorophyll maximum layers tens of centimeters thick.

Several studies of the vertical distribution of phytoplankton or chlorophyll have appeared in the last decade, clearly demonstrating that the mechanisms of formation and maintenance of chlorophyll maximum layers differ by geographical location (cf. Anderson, 1972; Beers *et al.*, 1975; Dandonneau, 1977; 1979; Holligan, 1978; Kiefer, Lasker, 1975; Pingree, 1978; Venrick, McGowan, Mantyla, 1973). Jamart *et al.* (1977, 1979) presented a model that successfully simulated the development of a chlorophyll maximum layer off the northwest coast of the United States.

Although vertical profiles of chlorophyll *a* fluorescence have become routine measurements, relatively few studies have used large data sets and objective analyses to explore the observed patterns (Denman, 1977; Denman, Platt, 1978; Herbland, Voituriez, 1979; Karabashev, Solov'yev, 1978). Members of the Food Chain Research Group, Scripps Institution of Oceanography, have been taking vertical profiles of *in vivo* chlorophyll *a* fluorescence since the method was developed, and in this paper, we attempt to provide statistical descriptions of a large collection of these profiles, allowing comparison of the patterns in the Southern California Bight with those in other regions.

The Southern California Bight is an open embayment characterized by admixture of several water types and considerable horizontal variability (Jones, 1971). Upwelling has an important effect on the biota, while terrestrial runoff is insignificant (Eppley *et al.*, 1978 and references therein). Mean tidal velocities and water depths are such that tidally-induced frontal systems (Pingree, 1978) are not an important feature off the California coast.

MATERIALS AND METHODS

Sampling

Data were collected on cruises 1-14 of the Southern California Bight Study (SCBS) of the Food Chain Research Group. These cruises were conducted approximately quarterly from 1974 through 1979. Station positions are shown in Figure 1. In August, 1978 (SCBS 13, Leg 2), 33 non-standard stations were occupied. Fluorescence, temperature, irradiance and depth were measured simultaneously at these stations. Sampling at standard stations was conducted during daylight hours in a set order: secchi depth, light-temperature profile, fluorescence profile, bottle cast. The procedure normally required about one hour. In several cases, ship's drift and internal wave activity effectively shifted the position of recognizable strata. Thus, temperature, fluorescence, and bottle cast profiles are not strictly comparable at any one station. This fact was considered in our choice of analyses. Changes in vertical

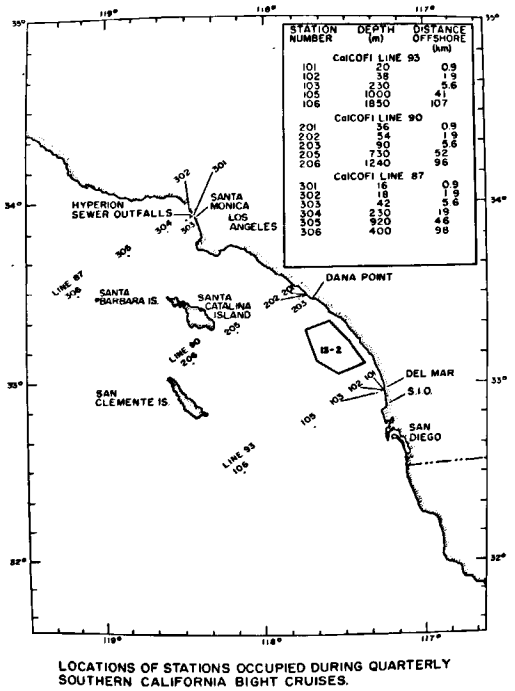

Figure 1

The location of stations occupied during the Southern California Bight cruises. Area enclosed by line represents the position of the sampling grid for SCBS 13, leg 2.

structure that occurred while we were sampling on each station have added unexplained variance to our statistical analyses, but should not have biased our results.

The fluorescence profiles were made with either a submersible or peristaltic pump, an opaque hose, and a Turner 111 or Turner Designs 10-005 fluorometer. Measurements of particulates and dissolved nutrients were as detailed in Eppley *et al.* (1978). Chlorophyll and phaeopigments were determined fluorometrically as in Strickland and Parsons (1972). Photosynthetic carbon assimilation was estimated by 24 hours simulated *in situ* deck incubations (Eppley *et al.*, 1979) from sample depths corresponding to 90, 30, 18, 12, 3, and 1 percent of surface irradiance as determined by a submersible quantum scalar irradiance meter (Booth, 1976) or by assuming that 1 percent of surface irradiance was found at three times the Secchi depth.

Fluorescence per unit chlorophyll is subject to widespread variability (Kiefer, 1973). Our fluorometers were often zeroed and calibrated, but there were not enough calibrations for us to convert all fluorescence readings to chlorophyll concentrations. Thus, we have not compared the magnitudes of fluorescence between profiles, and recognize that fluorescence is not a precise measure of chlorophyll within profiles.

Data analysis

Analog traces of fluorescence and temperature profiles were digitized and stored using a Hewlett-Packard 9845 A computer. The profiles were smoothed by using a three meter running average to obtain one value for each 2 m interval. This procedure reduced aliasing but restricted our resolution to 2 m vertical extent. Because the pump-and-hose sampling method is inappropriate for examining microscale features in fluorescence profiles (Derenbach *et al.*, 1979), our averaging was warranted.

Thickness of fluorescence maximum layers was determined by calculating the mean fluorescence of the profile, and considering segments of the profile with greater than mean fluorescence to be the maximum layers. When the bottom boundary of a layer was not reached, thickness was estimated by doubling the distance between the upper boundary and the depth of maximum fluorescence. This latter technique was used for 42 of 143 profiles. Elimination of these had a negligible effect on the dispersion statistics. When multiple peaks were encountered in a profile, the number and positions of the secondary maxima were recorded. The profiles extended to different depths; profiles were terminated when the hose reached the bottom, the base of the chlorophyll maximum layer, or the maximum reach, 40-55 m.

For most analyses pertaining to the fluorescence and/or temperature profiles, stations in very shallow water nearest to the shore (101, 201, 301) were excluded, as were those that did not reach either the depth of maximum chlorophyll from the bottle cast (11 profiles) or 50 percent of the euphotic depth (4 profiles).

Kendall's concordance analysis (Tate, Clelland, 1957) on measurements taken from bottle casts was performed using the stations for which both variables were measured at all six light levels. Concordance analyses on profile parameters versus distance offshore were done by ranking within transect lines for which measurements were available at the −01, −02, −03, −05, and −06 stations. Concordance analysis by position is the same as Friedman's test. Following the notation of Tate and Clelland, W is the coefficient of concordance, m is the number of cases, and n is the number of ranks within each case.

RESULTS AND DISCUSSION

Descriptive analysis

Choosing a parameter to describe fluorescence profiles

Fluorescence profiles from the Southern California Bight had a wide range of shapes. Our experience suggested that sharp fluorescence peaks of high magnitude were more frequently found near the coast and often represent concentrations of motile phytoplankton. Profiles with gradual changes in fluorescence were associated with intense mixing or oligotrophic conditions. To examine better these impressions, we parameterized our fluorescence profiles to reflect differences in vertical heterogeneity, keeping in mind the limitations of our data set.

A major consideration in the analysis of vertical profiles is scaling. Three chlorophyll profiles are presented as they might be found in any respectable journal (Fig. 2).

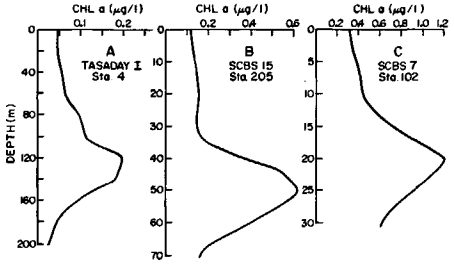

Figure 2
Three typical chlorophyll profiles: (A) North Pacific Central Gyre, near 28°N, 155°W (from Beers et al., 1975*); (B) SCBS* 15, *Sta.* 205; *(C) SCBS* 7, *Sta.* 102.

They are scaled to fill the allotted space well and look much the same. When the profiles are plotted on identical scales, differences among the profiles become apparent (Fig. 3). Objective parameters which describe vertical profiles can behave in a similar fashion. Dandonneau (1979) introduced "hardness", the ratio of maximum to mean chlorophyll in a bottle cast, to describe his profiles. This parameter treats profiles in a manner similar to Figure 2, because the depth range over which the chlorophyll increase exists is not considered.

We developed an alternative parameter for describing the pattern in fluorescence profiles, with the intention of getting a better idea of the vertical heterogeneity of the phytoplankton, reflecting the differences emphasized in

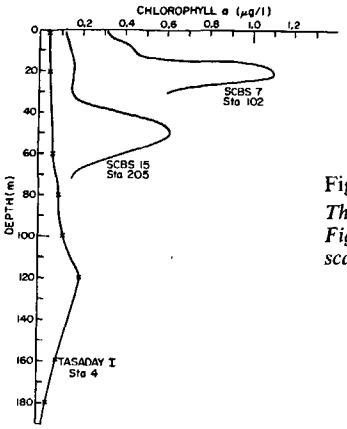

Figure 3
The same three profiles as in Figure 2 plotted on identical scales.

Figure 3. The "vertical structure index" (VSI) quantifies the depth variation of phytoplankton density (as inferred from fluorescence). The finest sampling scale was 2 m, so the index has been defined as the average percent change of fluorescence per 2 m interval over the depth range of the profile:

$$\mathrm{VSI} = \left[\frac{1}{N} \sum_{i=1}^{N} \frac{|F_{2i+1} - F_{2i-1}|}{((F_{2i+1} + F_{2i-1})/2)} \right] \times 100,$$

where N is the number of 2 m depth intervals and F_i is the fluorescence at i meters. If a profile is uniform, VSI = 0. Because the percent change is calculated in reference to the midpoint of each interval, the index converges on 200 as a profile tends toward infinite change per 2 m interval. This parameter is an approximation of $1/F(|dF/dz|)$ in percent. It reflects the abruptness of relative changes in phytoplankton abundance in profiles, independent of absolute magnitude. Also, this index measures changes in the entire profile and does not provide information specific to the fluorescence maximum. The VSI is sensitive to the depth of sampling (cf. Dandonneau, 1979). A profile which extends well below the heterogeneous layer will underestimate the VSI as compared to a profile which stops just below the fluorescence maximum layer.

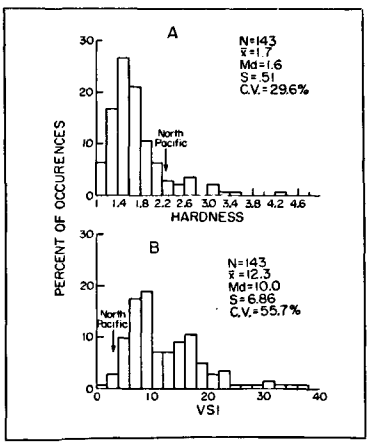

Figure 4
Frequency histograms for fluorescence profiles from the Southern California Bight. (A) "Hardness" (Dandonneau, 1979) calculated as the ratio of maximum to mean fluorescence. Mean ($\bar{x}$) = 1.7, median (Md) = 1.6, standard deviation (s) = .51, coefficient of variation (c.v.) = 29.6%, number of cases (N) = 143. (B) VSI, the vertical structure index (see text). "Hardness" and VSI of a profile from the North Pacific Central Gyre (Figure 2A) are indicated for comparison.

The frequency histogram of VSI shows that this parameter discriminates differences among the profiles better than "hardness" (Fig. 4). The coefficient of variation for VSI is 55.7%, for "hardness", 29.6%. The VSI showed a pattern with distance offshore. Concordance of VSI with distance offshore was significant for a set of 22 transects normal to the coast ($W = 0.34$, $m = 22$, $n = 5$, $p \ll .01$), and the analysis indicated that the phytoplankton showed more vertical heterogeneity nearshore except at the shallowest (−01) stations. The extinction coefficient for light increases with proximity to the coast. Concurrent with the heightening of light gradients, the phytoplankton show more relative change with depth. Only at the shallowest stations, where wind mixing affects a greater proportion of the water column and vertical exchange may be enhanced, does this trend reverse. However, when we pooled the data and plotted VSI vs. euphotic depth, no pattern was found.

"Hardness" was examined for a relationship with distance offshore, but no significant trend was present ($W = 0.10$, $m = 22$, $n = 5$, $p = .10$).

It should be remembered that neither "hardness" nor VSI is the "correct" parameter to describe vertical profiles. Depending on the question involved, it may be better to scale the distribution of phytoplankton by light level or nutrient concentration (to reflect physiological conditions), density, or characteristic mixing length (to examine interaction with physical processes; cf. Platt, 1980).

Thickness of the layers

The mean thickness of fluorescence maximum layers was 14.5 m (Fig. 5A). Concordance analysis showed that the thickness increased with distance offshore ($W = 0.49$, $m = 21$, $n = 5$, $p \ll .01$). If fluorescence maximum layers of the typical 10-20 m thickness represent phytoplankton concentrations, they should be trophodynamically important features. Pingree *et al.* (1975) and Hendricks (1979) have shown that layers of this thickness in stratified water have a characteristic vertical mixing time of at least several days, and observations of phytoplankton species assemblages in chlorophyll maximum layers of the Southern California Bight which persisted for several days (Cullen, unpubl. data; Reid, unpubl. data) to many weeks (Lasker, 1978) attest to the temporal stability of these features. Layers of increased phytoplankton with this stability would represent dependable patches (cf. Mullin, Brooks, 1976; Star, Mullin, 1979) of resource for pelagic herbivores.

The temporal scale of several days for persistence of a layer is enough for the growth rates of the phytoplankton within the layers to affect their abundance, and the vertical scale of about 10 m is typically enough for light to change fivefold and nitrate to increase from undetectable to non-limiting concentration. Given the fact that profiles are usually unimodal at the resolution of our sampling (see below), it can be inferred that phytoplankton may concentrate within certain preferred ranges of growth conditions rather than by stochastic processes.

The determination of fluorescence maximum layer thickness generated a value for the number of peaks per profile. One hundred twenty-four of the profiles had one fluorescence maximum, 17 had two, and two profiles had three peaks. Some profiles showed no strong feature that looked like a fluorescence maximum layer. Nonetheless, thickness and depth of maximum fluorescence were assigned. Defining fluorescence maximum layer as a region of fluorescence clearly above background with a recognizable inflection point, we subjectively determined that fluorescence maximum layers were encountered in ca. 90% of the profiles, similar to Lorenzen's (1976) observation that 87% of 68 stations occupied off Baja California showed a deep chlorophyll maximum.

We also examined the similarity between fluorescence profiles and chlorophyll profiles from the bottle casts, and found that in 78% of the cases, the highest chlorophyll concentration was found within 10 m of the fluorescence maximum, demonstrating that our bottle casts often sampled the fluorescence maximum layer and fluorescence maxima usually represent chlorophyll maxima.

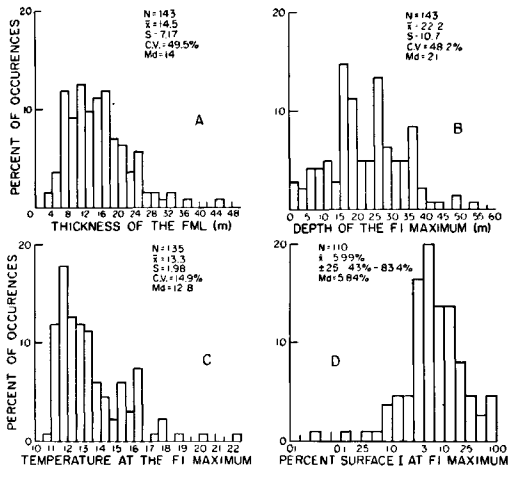

Figure 5

Frequency histograms for fluorescence profiles from the Southern California Bight. (A) Thickness of the fluorescence maximum layer. (B) Depth of maximum fluorescence. (C) Temperature at the fluorescence maximum. (D) Percent surface irradiance at the fluorescence maximum, log transformed: parameters of the distribution are expressed in original units.

Depth, temperature and light at the fluorescence maximum

A frequency distribution of the depth of maximum fluorescence shows that relatively few of the profiles had surface maxima (Fig. 5 B); these layers had measurable nitrate at the surface. Furthermore, only 4 of the 143 profiles had secondary maximum layers intercepting the surface. The mean depth of the highest fluorescence value was 22.2 m, and the depth of the fluorescence maximum increased offshore. For 23 transects normal to the coast, concordance of depth of the maximum with distance offshore was highly significant ($W=0.60$, $m=23$, $n=5$, $p \ll .01$).

The mean temperature at the depth of maximum fluorescence was 13.3°C (Fig. 5 C). This is slightly colder than the temperature at which NO_3^- is usually depleted (Strickland *et al.*, 1970). It also corresponds to the temperature at which light and nutrient-saturated growth rate on a 12 h : 12 h light : dark cycle would be approximately one doubling per day (Eppley, 1972). For the seventeen transects on which temperature at the fluorescence maximum could be determined, there was no pattern with distance offshore ($W=.02$, $m=17$, $n=5$, $p>.20$). The fluorescence maxima were not confined to isotherms on these transects, and although isotherms descended offshore, the relationships between fluorescence and temperature did not change consistently.

As shown in Figure 5 D, fluorescence maxima in the Southern California Bight are almost always found in the euphotic zone, often where light is more than adequate for growth. The geometric mean is 6% of surface irradiance. Our profiling apparatus could not reach some of the maxima and these profiles have been excluded. Only 4 of the excluded maxima were deeper than 50 m, and they would not have had a great effect on any of our results.

Chlorophyll concentration at the maximum

We have attempted to determine chlorophyll concentrations at the maximum by examining our data for chlorophyll extracted from discrete samples. The maximum chlorophyll values from bottle casts are usually between 0.5 and 3 µg/l (Fig. 6). Estimating maximum chlorophyll by multiplying the mean chlorophyll concentration at the station times the "hardness" (maximum ÷ mean) of the fluorescence profile, we obtained a similar distribution. If carbon to chlorophyll ratios are from 20 to about 100, these chlorophyll concentrations are within the dynamic range of the grazing response of herbivorous copepods (Mullin, Brooks, 1976). Consistent with this inference, Checkley (1978) found more eggs per female *Paracalanus parvus* in the chlorophyll maximum layer than elsewhere in depth profiles.

Lasker (1978, 1980) has hypothesized a link between the presence of food aggregations in chlorophyll maximum layers and the production of a good year class for anchovy. Field experiments (Lasker, 1975) demonstrated the importance of a subsurface layer of the dinoflagellate *Gymnodinium splendens* to successful first feeding for anchovy larvae. Using an estimate of 100 pg-chlorophyll *a* per cell for *Gymnodinium splendens* (Kiefer, Lasker, 1975), and observing that concentrations of 20-

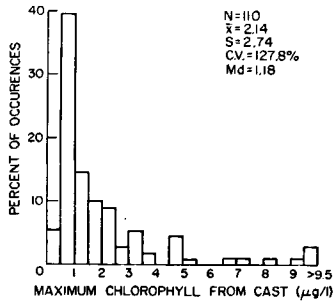

Figure 6

Frequency histogram of the maximum chlorophyll from bottle casts where fluorescence profiles were taken.

40 cells/ml supported extensive feeding of anchovy larvae, we calculated that maxima completely dominated by organisms similar in size to *G. splendens* should have chlorophyll concentrations of greater than 2 μg/l to meet Lasker's criteria. Our results (Fig. 5) show that the majority of maxima that we sampled did not meet the criteria. Within several kilometers of the coast, however, high concentrations of chlorophyll are much more common (Eppley *et al.*, 1978; Lasker, 1978).

The chlorophyll maximum as biomass maximum

Steele (1964) postulated that the chlorophyll maxima in the Gulf of Mexico were not representative of phytoplankton biomass. Venrick *et al.* (1973) demonstrated that the chlorophyll maximum in the North-Pacific Central Gyre was a peak in diatom abundance, but Beers *et al.* (1975) showed that it was not a maximum in total phytoplankton carbon. Anderson (1972) asserted that the chlorophyll maximum layers off Oregon were due, at least in part, to an elevated level of plant biomass. Given this variety of observations, it is important to determine in each study if fluorescence or chlorophyll maxima are representative of plant biomass, since chlorophyll is commonly, but cautiously, used as an indicator of food resource for pelagic herbivores (Anderson *et al.*, 1972; McGowan, Walker, 1979; Mullin, Brooks, 1972, 1976).

To determine the contribution of phytoplankton carbon to the chlorophyll maxima in the Southern California Bight, we have asked if, within profiles, two measurements tend to agree on the vertical pattern present. Our pairs of measurements were chlorophyll *a* and alternate indicators of plant carbon. We used particulate ATP, particulate organic carbon, particle volume from Coulter counts, and phytoplankton carbon from particle counts (Mullin *et al.*, 1966). None of these measurements is an accurate or precise indicator of plytoplankton biomass (Eppley *et al.*, 1977), but each should increase as a monotonic function of phytoplankton abundance with noise contributed by other components of the seston. Kendall's concordance test is the appropriate method for examining the relationship between variables within profiles, and this test has been employed previously using a variety of parameters (McGowan, Walker, 1979; Mullin, Brooks, 1972).

The analysis shows that chlorophyll *a* and each of the indicators of plant biomass are in substantial agreement (Fig. 7). Approximately half the time, the depth with the highest chlorophyll *a* appears to be a biomass maximum. In a great majority of the cases, the maximum chlorophyll bottle has levels of the biomass indicators above the median for the profile. In all cases, the concordance values are highly significant and indicate monotonic, positive, but not necessarily linear relationships between variables. However, it is clear that the chlorophyll maximum does not always represent a biomass maximum. In those cases where biomass at the chlorophyll maximum is low, the layer is probably formed by the mechanism described by Steele (1964). Exclusion of those stations at which the bottle cast did not sample within 10 m of the fluorescence maximum does not significantly change any of our concordance results.

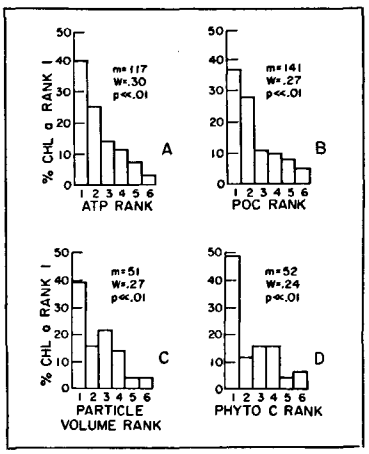

Figure 7

The relationship between chlorophyll and biomass indicators in vertical profiles. Results of the concordance analysis (Kendall's concordance, W) and histograms which show the frequency of occurrence of the number 1 *ranked chlorophyll bottle with rank of the biomass indicator. (A) Particulate ATP. (B) Phytoplankton carbon from particulate organic carbon. (C) Particle volume from an electronic counter. (D) Phytoplankton carbon estimated from electronic particle counts.*

Summarizing his findings for diverse regimes in the Western North Atlantic, Ortner (1978) stated that ATP and particulate nitrogen roughly paralleled chlorophyll in profiles and were relatively high at the chlorophyll maximum, a subjective assessment which is very consistent with our results.

Primary production at the chlorophyll maximum

To understand clearly the role of chlorophyll maximum layers in the dynamics of the euphotic zone food web, we must determine the relative contribution of the layers to total primary production. This information is necessary to assess properly their importance to herbivores because flux, not phytoplankton biomass, is the more important determinant of sustained secondary production. From the viewpoint of the phytoplankton ecologist, information on the vertical distribution of primary production in relation to plant biomass is essential in determining the means by which the vertical pattern of chlorophyll has developed.

The relationship between chlorophyll and primary production in vertical profiles is not as strong as that between chlorophyll and the biomass indicators (Fig. 8). The depth of maximum chlorophyll concentration is often the depth of highest primary production, and the

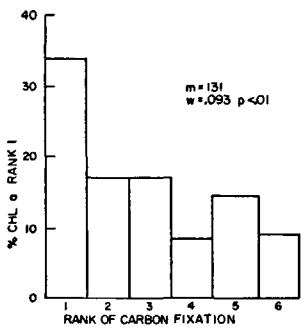

Figure 8

The relationship between chlorophyll a *and carbon fixation in vertical profiles. This histogram shows that the maximum chlorophyll bottle had the highest carbon fixation rate* 34% *of the time. The maximum chlorophyll bottle had the lowest carbon fixation rate in* 9% *of the profiles.*

Table

Observations on three typical vertical profiles. (A) North Pacific Central Gyre (Beers et al., 1975*) with ancillary information from the Food Chain Research Group (Eppley, unpubl. data). (B) Offshore Southern California Bight, SCBS* 15, *Sta.* 205. *(C) Nearshore Southern California Bight, SCBS* 7, *Sta.* 102.

Profile:	A North Pacific Central Gyre 28°N, 155°W	B SCBS 7 Station 205 52 km offshore	C SCBS 15 Station 102 2 km offshore
Euphotic depth	105 m	66 m	33 m
Integrated primary production	.054 g/m^2 – day	.162 g/m^2 – day	.516g/m^2 – day
Integrated chl *a*	18.46 mg/m^2	19.77 mg/m^2	20.22 mg/m^2
Mean chl *a*	.09 µg/l	.38 µg/l	.67 µg/l
Depth of chl *a* maximum	120 m	50 m	21 m
% surface irradiance at chl *a* maximum	0.5%	3%	12%
Temperature at chlorophyll maximum	19°C	13.2°C	14.8°C
Thickness of chlorophyll maximum layer	86 m	27 m	13 m
"Hardness"	2.22	2.18	1.78
VSI	3.56	8.51	12.95
Is the chl maximum a biomass maximum?	No	To some extent	Yes
Is the chl maximum a primary production maximum?	No	No	Yes
Depth of nitracline	150 m	45 m	15 m
% surface irradiance at nitracline	0.1%	6%	15%

concordance is highly significant, indicating a positive relationship. Nevertheless, the primary production at the depth of maximum chlorophyll is below the median 32% of the time. Comparing the depth of the maximum carbon fixation with depth of the fluorescence maximum from the continuous profiles, we found that the carbon fixation peak was shoaler than the fluorescence peak 89% of the time. Longhurst (1976) noted this previously off Baja California.

Our finding is in striking contrast to that of Herbland and Voituriez (1979), who showed that the chlorophyll maximum and primary production maximum were very highly correlated in the tropical Atlantic Ocean. Our primary production determinations were constrained to six light levels, while Herbland and Voituriez could pick their depths, improving the chances of sampling directly at the chlorophyll peak and obtaining high carbon fixation rates. Nonetheless, the Southern California Bight does not seem to fit the model of the typical tropical Atlantic (Herbland, Voituriez, 1977 *a*; 1977 *b*; 1979), with respect to the depth distribution of primary production. High production is not confined to the vicinity of the nitracline. In 50% of the 110 cases, maximum carbon fixation was at the 90 or 30% light level, commonly well above the nitracline. Also, low but measurable nitrate is often found in an irregular pattern above the nitracline. Herbland and Voituriez (1977 *b*) invoke horizontal transport to explain "atypical" features such as these near the equatorial divergence. Horizontal transport or nutrient regeneration could be responsible for the decoupling of primary production per unit volume from vertical transport of nitrate in the Southern California Bight. Spatial separation of the primary production peak from the nitracline was not predicted in the one-dimensional model of Jamart *et al.* (1977).

Trends in descriptive parameters

Our descriptive results may be applicable to the characterization of water types. The Table lists the values of several parameters for the three profiles in Figures 2 and 3. These profiles were chosen as examples of a wide range of conditions: the oligotrophic, stable (McGowan, Walker, 1979; Venrick, 1979) North-Pacific Central Gyre, an offshore station from the Southern California Bight, and a nearshore station from our study area. They are much the same as those chosen by Steele (1964) from the Atlantic for similar purposes. Patterns are readily apparent, many of which have been recognized for some time. Herbland and Voituriez (1979) present one of the best analyses of such trends. The Table is presented merely as an example. Most of the parameters show strong changes from oligotrophic to moderately eutrophic conditions, with the exception of integrated chlorophyll and "hardness", which show much less variability. These two parameters do not take into account the organization of chlorophyll in the vertical dimension, which is of prime importance to primary production (cf. Margalef, 1978).

We examined our data for many of the relationships suggested in the Table. In most cases, we found a lot of scatter, probably due to the influence of different water masses, seasonality, upwelling and the poorly quantified processes which support significant primary production well above the nitracline. Also, our study area was relatively small; thus our data reflect variability in one region more than the hydrographic differences between eutrophic and oligotrophic regions.

Mechanisms of formation and maintenance of chlorophyll maximum layers

In the descriptive analyses, we showed that chlorophyll maxima in the Southern California Bight were sometimes formed as a physiological adaptation, reflecting a change in phytoplankton carbon : chlorophyll ratios (Steele, 1964). Other mechanisms of formation or maintenance of chlorophyll maximum layers have been demonstrated or discussed. Three of these are related to physical structure, phytoplankon growth, and phytoplankton behavior, respectively.

Physical structure

Physical mechanisms produce chlorophyll maxima in the pycnocline near frontal regions in the English Channel (Pingree, 1978; Pingree *et al.*, 1975). To determine the proximate importance of physical mechanisms on formation or maintenance of chlorophyll maximum layers, we examined the relationships between fluorescence and temperature profiles. Our preliminary studies, including multiple regressions and principal component analyses, required many assumptions and led to the conclusion that there is little relationship between temperature and fluorescence profiles, except that fluorescence maxima are not found in the mixed layer.

The relationship between the depth of the thermocline (maximum 4 m temperature gradient) and depth of the fluorescence maximum is quite irregular (Fig. 9A). Vertical changes in temperature are indicative of density in nearshore waters of this region (Strickland *et al.*, 1970), so the data in Figure 9A could be used to test the null hypothesis that fluorescence maxima are confined to the maximum density gradients in profiles. The slope is significantly different than 1.0, and our rejection of the hypothesis is in agreement with Karabashev and Solov'yev (1978), who failed to find coincidence between fluorescence maxima and maximum density gradients in the Western Indian Ocean.

Derenbach *et al.* (1979) found microscale fluorescence structure associated with temperature gradients. We were not equipped to observe these features, but recent trials with an *in situ* fluorometer have not revealed this type of variation in the Southern California Bight.

Growth

We examined data from bottle casts to determine depth of the nitracline (1 μM NO_3^-) by linear interpolation at each station. The fluorescence maximum was near the nitracline in most cases (Fig. 9 B), indicating the availability of adequate nutrients and showing agreement with Herbland and Voituriez (1979). Because the layers are located in favorable light (Fig. 5D) and nutrient regimes, enhanced phytoplankton growth could be responsible for peaks in fluorescence in the Southern California Bight.

We asked if the vertical distributions of chlorophyll were in agreement with the vertical pattern of phytoplankton specific growth rate, testing the null hypothesis that the two were unrelated. Phytoplankton growth rate μ (doublings/day) was calculated as

$$\mu = \log_2 \frac{(\mathrm{PC} + \mathrm{Carbon\ uptake})}{\mathrm{PC}},$$

where phytoplankton carbon (PC) is estimated from particulate organic carbon (POC) by the equation $\mathrm{PC} = 0.158\,(\mathrm{POC}) + .0007\,(\mathrm{POC})^2$. This estimator was developed using microscopic counts of phytoplankton and chemical POC determinations (Reid *et al.*, 1970). Eppley *et al.* (1977) introduced this equation and showed it to be one of the best indicators of phytoplankton biomass available for this region.

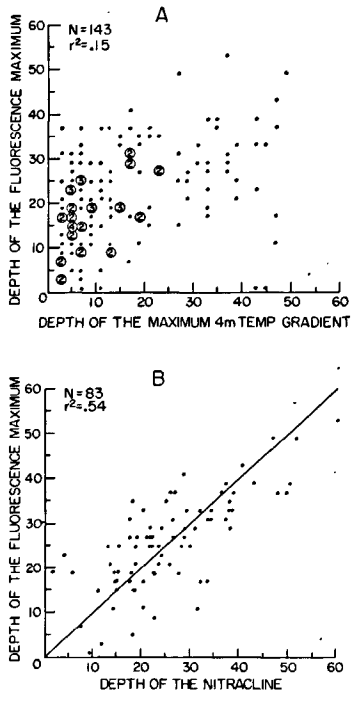

Figure 9

The relationship between features of vertical profiles. (A) Depth of the maximum 4 m temperature gradient and depth of fluorescence maximum. Coefficient of determination, $r^2 = 0.15$. The slope is significantly different than 1.0. (B) Depth of the nitracline and depth of the fluorescence maximum at those stations where a subsurface nitracline was found. The line indicates perfect correspondence and helps to demonstrate that the fluorescence maximum is usually in the vicinity of the nitracline. It is not a regression line.

Concordance analysis showed a weak but significant relationship between the variables ($W = .05$, $m = 122$, $n = 5$, $p < .01$), but not as expected if chlorophyll concentration reflected growth rate. The growth rate at the depth of maximum chlorophyll was about as likely to be below the median as above. In fact, on the average, the highest chlorophyll concentrations were found at the level where growth rate was third ranked. The mean maximal growth rate in the profiles was 0.91 ± 1.07 (2 sec.) doublings/day ($\mathrm{Md} = 0.85$ doublings/day); in the chlorophyll maximum, mean growth rate was $.53 \pm .94$ doublings/day ($\mathrm{Md} = 0.41$ doublings/day). We can reject the null hypothesis that chlorophyll shows no concordance with phytoplankton growth rate, but it is clear that chlorophyll maxima of the Southern California Bight are not, in general, the result of enhanced phytoplankton growth rate indigenous to the layer.

The effects of grazing have not been properly assessed in this analysis. Phaeopigment has been suggested as an indicator of grazing pressure (Lorenzen, 1967), but Jeffrey (1976) has shown that chlorophyll *b* interferes with fluorometric determinations of phaeopigment, and recent observations (Gieskes *et al.*, 1978) have demonstrated the importance of irradiance in determining the distribution of chlorophyll degradation products. Thus, the use of phaeopigments as an indicator of grazing must be questioned. Besides, we found no strong pattern in phaeopigment distributions. Further consideration of the depth distribution of grazing pressure (Longhurst, 1976; Lorenzen, 1967) is necessary.

Behavior

It has long been known that some phytoplankton taxa have depth preferences, and assemblages showing a preference for the chlorophyll maximum layer over surface water of the Southern California Bight have been described (Reid *et al.*, 1978). Chlorophyll maximum layers in the Southern California Bight are frequently dominated by motile phytoplankters, and occasionally pennate diatoms with relatively large vacuoles useful for buoyancy regulation (F. M. H. Reid, pers. comm.). Recent experiments in our laboratory (Cullen, Horrigan, in prep.; Heaney, Eppley, 1980) have shown that some dinoflagellates aggregate at or near a light level equivalent to 10% of surface irradiance when nitrate is depleted in the water column. Dandonneau (1977) has demonstrated regular movement of a deep chlorophyll maximum. Steele and Yentsch (1960) have shown that the behavior of diatoms can produce a chlorophyll maximum layer. In other words, some phytoplankters have control over their vertical position, and these behavioral mechanisms are common. We have found that chlorophyll maximum layers are found near the nitracline and in a physiologically important range of light levels. Thus, our field results are consistent with the inference that the behavior of phytoplankton can be important in determining the vertical pattern of chlorophyll in the Southern California Bight.

Jamart *et al.* (1979) showed that, in their model, a chlorophyll maximum layer could persist in the vicinity of the nitracline without a nutrient-dependent sinking rate for the phytoplankton. This observation weakens our argument. It should be remembered, though, that in the Southern California Bight, primary production does not always show clear peaks above the chlorophyll maximum as it does during the stratified period of the Jamart *et al.*'s model run.

CONCLUSIONS

We can conclude that no one mechanism is responsible for all the chlorophyll maxima in the Southern California Bight. Physical processes do not have the strong proximate effect that has been observed in the English Channel (Pingree, 1978) and primary production is not as well related to vertical chlorophyll distribution as in the tropical Atlantic (Herbland, Voituriez, 1979). Physiological changes of phytoplankton in response to light and nutrients certainly contribute to the chlorophyll patterns in profiles from the Southern California Bight, but not to the extent that they do in the North Pacific Central Gyre (cf. Beers *et al.*, 1975). Behavioral aggregation of phytoplankton in chlorophyll maximum layers appears to be important in our study area.

Regardless of mechanism, these layers do persist, in many cases representing a dependable food resource in an environment where malnutrition is apparently common among herbivores (Mullin, Brooks, 1976). Yet, in the Southern California Bight, these layers do not appear to be turning over rapidly. These observations lead to an intriguing question for future study: "Why don't the grazers exploit these layers to the point of depletion?". Clearly, the effects of grazing, not assessed in this study, deserve much consideration.

Acknowledgements

This work was completed with the support of DOE Contract DE-AMO3-76SF00010 and an Institute of Marine Resources assistantship for J. J. C. The authors wish to thank the members of the Food Chain Research Group, especially E. Renger, for obtaining the data for this study, E. Stewart for help with data acquisition and manipulation, and D. Osborn for typing the manuscript. K. Monan ably assisted in preliminary data analysis. G. Jackson, D. Goodman, M. Mullin and S. Horrigan commented on the manuscript.

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