DEEP MAXIMA OF PHOTOSYNTHETIC CHLOROPHYLL IN THE PACIFIC OCEAN

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ABSTRACT

Data collected on several expeditions through the temperate and tropical Pacific Ocean show that during most of the year the maximum concentrations of chlorophyll occur below the surface, typically in a narrow layer near or below the depth of penetration of 1% of the surface light. The layer appears to be continuous across most of the Pacific although the depth and chlorophyll concentration vary regionally. The depth of the layer is more closely related to the depth of the nitrite maximum and to the position of the nutricline than to either light or density regimes. Productivity within the layer is low but positive, and contributes substantially to the total production of the water column. The maximum layer may be a seasonal phenomenon developing in the summer after the stabilization of the water column and mixing to the surface during the winter. Year to year fluctuations of depth and concentration of chlorophyll within the maximum layer may be related to large-scale meteorological fluctuations.

Doty and Capurro (1961) have tabulated the position, date, depth, and values of chlorophyll and productivity in the world's oceans. There are several thousands of these measurements in the Pacific. Most are in the Northern Hemisphere, and most are near land masses or islands (e.g., Hawaii, Luzon, Hokkaido, New Caledonia, New Zealand), along the equator, or north of lat 40°N. Of the values from the oceanic Pacific, between lat 50°N and 50°S, less than 10% of the chlorophyll values represent depths greater than 25 m; in the same region, over half of the productivity measurements were obtained at the sea surface. Koblenz-Mishke, Volkovinsky, and Kabanova (1970) have used these data and additional data available to them to estimate the plankton primary production of the Pacific, to construct tables and charts of its geographical variability, and to compare production in the Pacific with their estimates from other oceans. Their estimates of primary production, expressed in milligrams carbon per square meter of sea surface per day, represent production integrated through the water column. However, many of their production values are extrapolated from surface measurements, and, in large areas of the temperate gyres of the North and South Pacific, production is estimated from the available chlorophyll data, or from "oxygen or hydrogen saturation" values.

All values of total production in the water column are strongly dependent upon the assumed (usually) depth of zero productivity. This is traditionally taken to be the depth at which the light intensity has been reduced to 1% of the incident radiation, and this criterion has been used to divide the water column into a euphotic zone and an aphotic zone.

Evidence is accumulating that major concentrations of plant material in the ocean usually occur below the surface, typically within the thermocline and near the bottom of the euphotic zone. Maxima of chlorophyll or phytoplankton as deep as 100 m have been reported from the Indian Ocean (Yentsch, 1965), the Sargasso Sea (Menzel and Ryther, 1960), the Gulf of Mexico (Steele, 1964), and the Kuroshio and adjacent regions (Motoda and Marumo, 1963; Saijo, Iizuka, and Asaoka, 1969). Shallower maxima are characteristic of the California Current

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(Allen, 1939; Lorenzen, 1965, 1967). Initial results of the EASTROPAC survey (Love, 1970, 1971) indicate a chlorophyll maximum varying in depth between 50 and 100 m over large areas of the eastern tropical Pacific. Anderson (1969) has studied the chlorophyll maximum layer off the Oregon coast which is present between 50 and 75 m during the summer. The layer is continuous over a broad region in the Eastern Subarctic Pacific and maybe transpacific. Chlorophyll maxima have also been reported from the other major water masses of the Pacific (El-Sayed, 1970; Sorokin, 1970).

Different workers have attributed the existence of the maximum layer to different processes including the concentration of detrital chlorophyll in the pycnocline (Lorenzen, 1965), differential zooplankton grazing (Lorenzen, 1967), an increase in the chlorophyll/carbon ratio in plant cells, without an accumulation of cells (Steele, 1964), horizontal advection and layering of different water masses and plant populations (Sano, 1966), the sinking of active or senescent cells from shallower depth (Allen, 1932; Steele and Yentsch, 1960), and in situ production (Anderson, 1969). In short, the tendency has been to consider deep chlorophyll maximum layers as discrete and sporadic phenomena and to interpret them strictly according to local conditions.

The accuracy with which surface productivity reflects the productivity throughout the water column has been investigated by Koblenz-Mishke et al. (1970) by means of log-log scatter diagrams. There is a linear trend in their transformed data, but the spread of values around the regression line is broad. Lorenzen (1970) showed a significant linear regression, after transformation to logarithms, of total production on the concentration of surface chlorophyll. The regression, however, removes only half of the variability of the dependent variable, and the author advises that precise values of total production must depend upon direct measurements. He also cautions that extrapolations from surface values are based upon averages and will easily miss unexpected events.

There have been very few attempts to measure productivity in the deeper maximum layers. Anderson (1969) made one series of in situ measurements within the chlorophyll maximum layer off the Oregon coast. There was a peak in production within the layer and positive photosynthesis as deep as 90 m, the 0.1% light level. Implicit in most studies to date is the assumption that pigment concentrations below the level of 1% light are nonphotosynthetic and represent a loss of plant material from the "euphotic zone." The two extensive surveys from the Sargasso Sea and the eastern tropical Pacific both adjusted the depth of the lowest sample to the depth of 1% light, and rarely sampled below 100 m, even though the maximum pigment concentrations were frequently obtained from the deepest sample.

In the present paper, the authors have summarized a large amount of data accumulated over the past 8 years, all of which indicate that a deep chlorophyll maximum layer is a regular and continuous feature of much of the oceanic Pacific. It is frequently observed below the traditionally defined euphotic zone, yet it is dominated by photosynthetically active chlorophyll *a* which is present in concentrations as great as 10 times those at the surface. The development of this maximum layer appears not to be a localized process, but a widespread and regularly occurring phenomenon. Because of its limited vertical extent and great depth, the existence, extent and significance of this maximum layer has been overlooked by most previous surveys of chlorophyll and productivity. Evidence suggests that a better understanding of this layer will necessitate revision of existing estimates of total primary production in the ocean.

METHODS

Since 1964 we have been mapping and studying the subsurface chlorophyll maximum in the Pacific on a series of expeditions (Figure 1). In 1964 (URSA MAJOR Expedition: University of California, 1967) and 1966 (ZETES Expedition: University of California, 1970), chlorophyll pigments were determined with a D U Spectrophotometer; on other expeditions chlorophyll *a* and phaeophytin were assayed with a

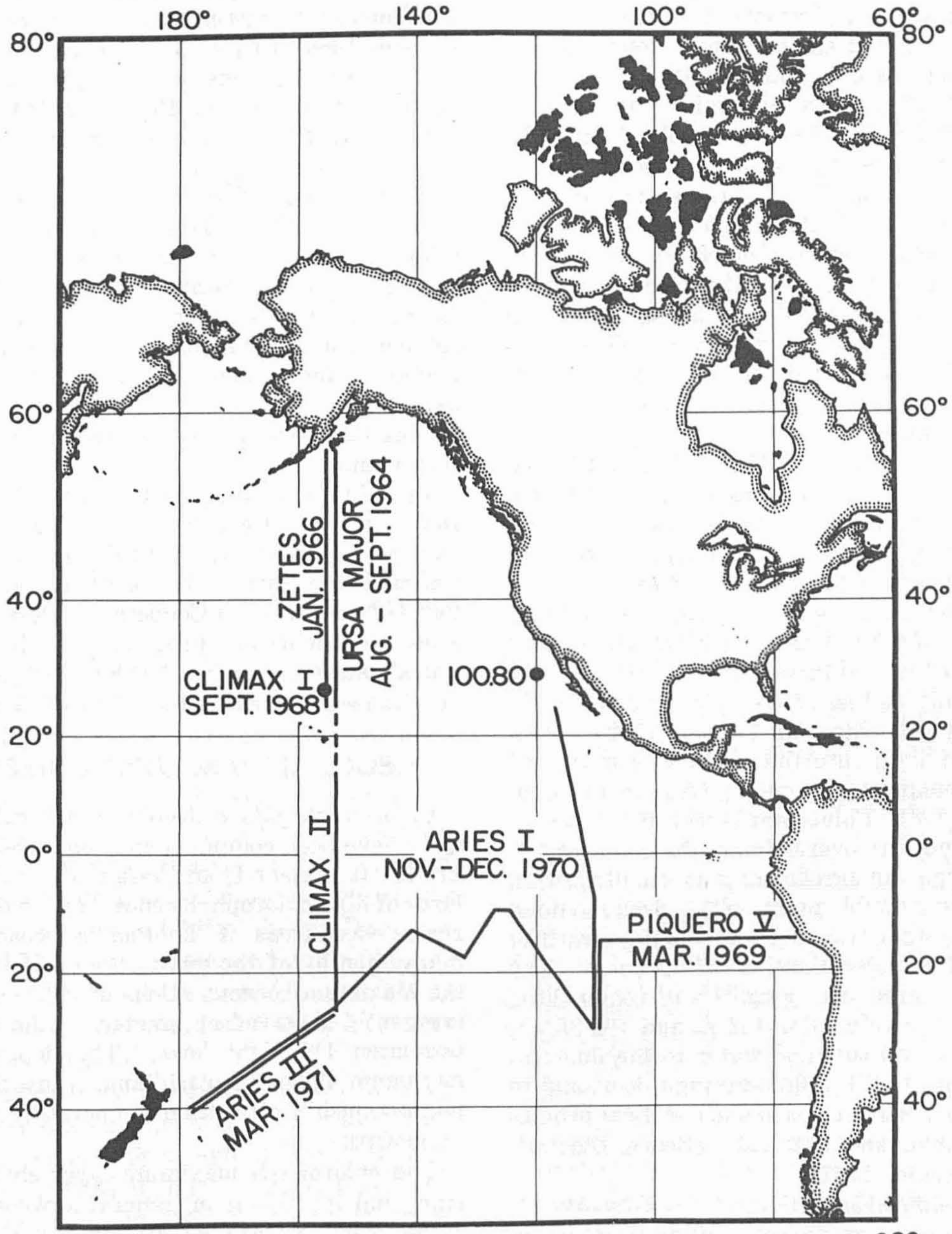

FIGURE 1.—Cruise tracks of seven expeditions from which chlorophyll data was obtained, and the location of Marine Life Research station 100.80 at which chlorophyll was sampled seasonally.

Turner Fluorometer.[2] Water samples from the same casts were preserved with neutral Formalin for subsequent phytoplankton enumeration. Additional measurements have routinely included temperature and salinity, determined with an STD; oxygen, determined by the Winkler procedure; and phosphate, silicate, nitrate, and nitrite, measured with the spectrophotometer or the autoanalyzer (Strickland and Parsons, 1968). On CLIMAX II and ARIES III ammonia was assayed (Solórzano, 1968). On stations occupied at noon, the transparency of the water was measured with a secchi disk and the compensation depth was estimated by multiplying the terminal depth by three. A wide variety of zooplankton samples were collected on all expeditions.

On the expeditions CLIMAX I, CLIMAX II, and ARIES III, observations were concentrated in two areas of the North and South Pacific, near the axes of the Central Pacific Gyres. In these regions, in addition to the above measurements, productivity was routinely measured by the uptake of C-14 by samples incubated on deck in simulated in situ incubators (Owen and Zeitzschel, 1970) and less frequently by samples incubated in situ (Steeman Nielsen, 1952). Penetration of light into the ocean was measured with a submarine photometer (Austin and Loudermilk, 1968). Coincident secchi disk determinations tended to overestimate the depth of 1% light, though the agreement was usually within 6 m. A submersible pump with a deck mounted filtering system was used to obtain stratified samples for determination of biomass (dry weight) of three size categories of zooplankton (333 μ and greater, 332-103 μ, and 102-35 μ). The same pump supplied water to the fluorometer, equipped with a flow-through door, and to the autoanalyzer for continuous vertical profiles of chlorophyll and nutrients (Beers, Stewart, and Strickland, 1967).

In September 1968 (CLIMAX I Expedition), a pair of parachute drogues, set at 10 m depth, were released at lat 27°N, long 155°W, and followed for 10 days, during which time they moved northwest approximately 150 miles. Physical, chemical, and biological properties were sampled continuously on a 24-hr schedule. In September-October 1969 (CLIMAX II Expedition), a grid of ten 24-hr stations was occupied along long 155°W between lat 27°10′ and 28°30′N, and a grid of six 24-hr stations was occupied along the same meridian between lat 24°40′ and 25°20′S. This latter pattern was repeated in March 1971 (ARIES III Expedition). The sampling routine was similar on each of these expeditions. Each 24-hr station included four casts for nutrients and chlorophyll, day and night samples for biomass of micro- and macrozooplankton, and a simulated in situ productivity experiment. In 1969 and 1971 a single in situ productivity experiment followed the routine station plan.

In addition to data collected on S.I.O. (Scripps Institution of Oceanography) expeditions, we have available data from the California Current collected by institutions participating in the CalCOFI (California Cooperative Oceanic Fisheries Investigations) program. We have made use of data from station 100.80 which is located near the western edge of the California Current.

GEOGRAPHICAL DISTRIBUTION

Chlorophyll data collected on several expeditions have been combined and contoured in Figure 2. It is clear from these that a subsurface layer of high chlorophyll concentration is present across vast areas of the Pacific Ocean during many months of the year. South of lat 46°N, the maximum concentrations of chlorophyll are frequently observed at greater depths than the estimated 1% light level. The depth of the maximum along the meridianal transects shows no relationship with either temperature, salinity, or density.

The chlorophyll maximum layer shoals near land, and in regions of general upwelling such as the North Subarctic Gyre and the Equatorial belt. It deepens near the axes of the Central Pacific Gyres. The meridianal continuity of the layer is especially remarkable considering that it passes through three major epipelagic environments: the Subarctic, where it is likely to

[2] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

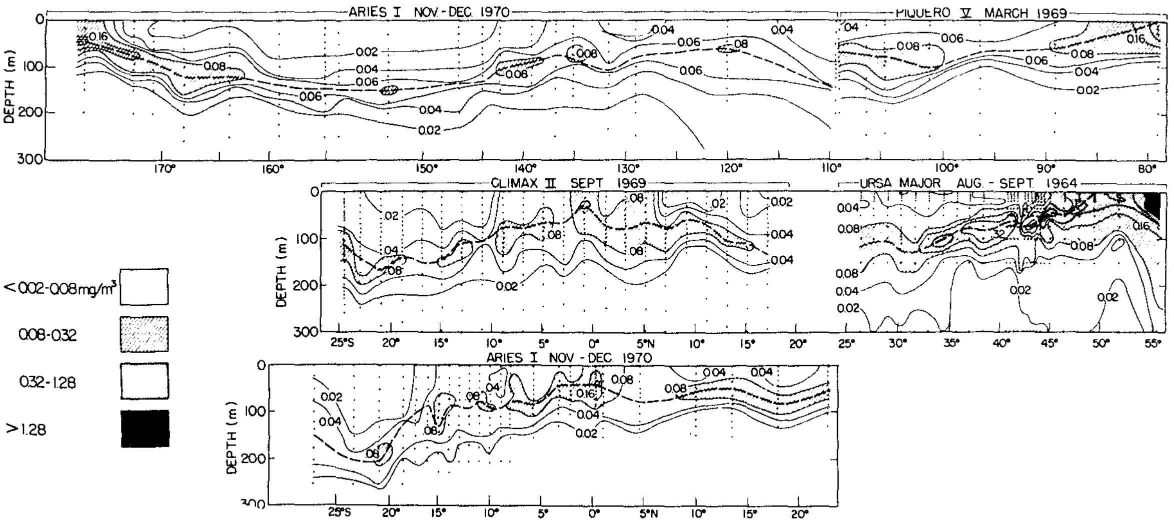

FIGURE 2.—Vertical sections of chlorophyll *a* concentrations in the Pacific Ocean; vertical exaggeration 5020.

be confluent with that discussed by Anderson (1969), the Central, and the Equatorial environments.

The east-west section indicates that the maximum layer is well developed over most of the middle latitudes of the South Pacific. The maximum layer in the South Central Gyre tends to be deeper, and the chlorophyll concentrations throughout the water column tend to be lower than in corresponding areas of the North Pacific. The greatest depth so far observed by us was at lat 20°09′S, long 118°18′W, during December (ARIES I Expedition) where a layer containing 0.05 mg/m³ occurred between 200 and 245 m depth; chlorophyll values at the surface were less than 0.01 mg/m³.

Portions of all three sections have been repeated by different expeditions. The depth and concentration of chlorophyll in the maximum layer vary somewhat, but the general features remain the same. In 1969, the Ocean Research Institute, University of Tokyo, ran a transect along long 155°W (Ocean Research Institute, University of Tokyo, 1970). The results of their chlorophyll measurements compare well with ours.

VERTICAL DISTRIBUTION

We have supplemented our discrete, quantitative chlorophyll samples with in vivo profiles of fluorescence which provide continuous, but qualitative pictures of the fine scale structure of the maximum layer (Figure 3). Although the major

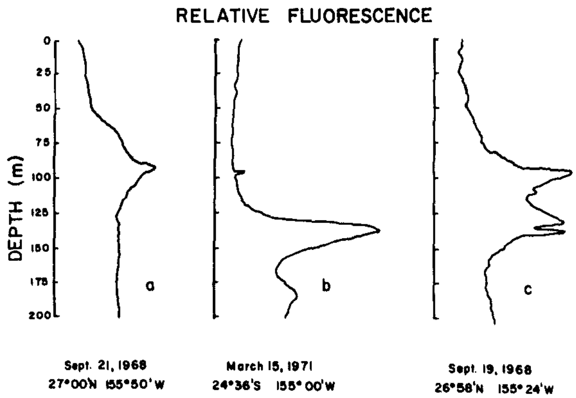

FIGURE 3.—Continuous vertical profiles of in vivo fluorescence of chlorophyll. a) a simple maximum layer in the North Central Pacific; surface chlorophyll concentration 0.02 mg/m³; b) a simple maximum layer in the South Central Pacific; surface chlorophyll concentration 0.01 mg/m³; c) a double maximum layer in the North Central Pacific; surface chlorophyll concentration 0.02 mg/m³.

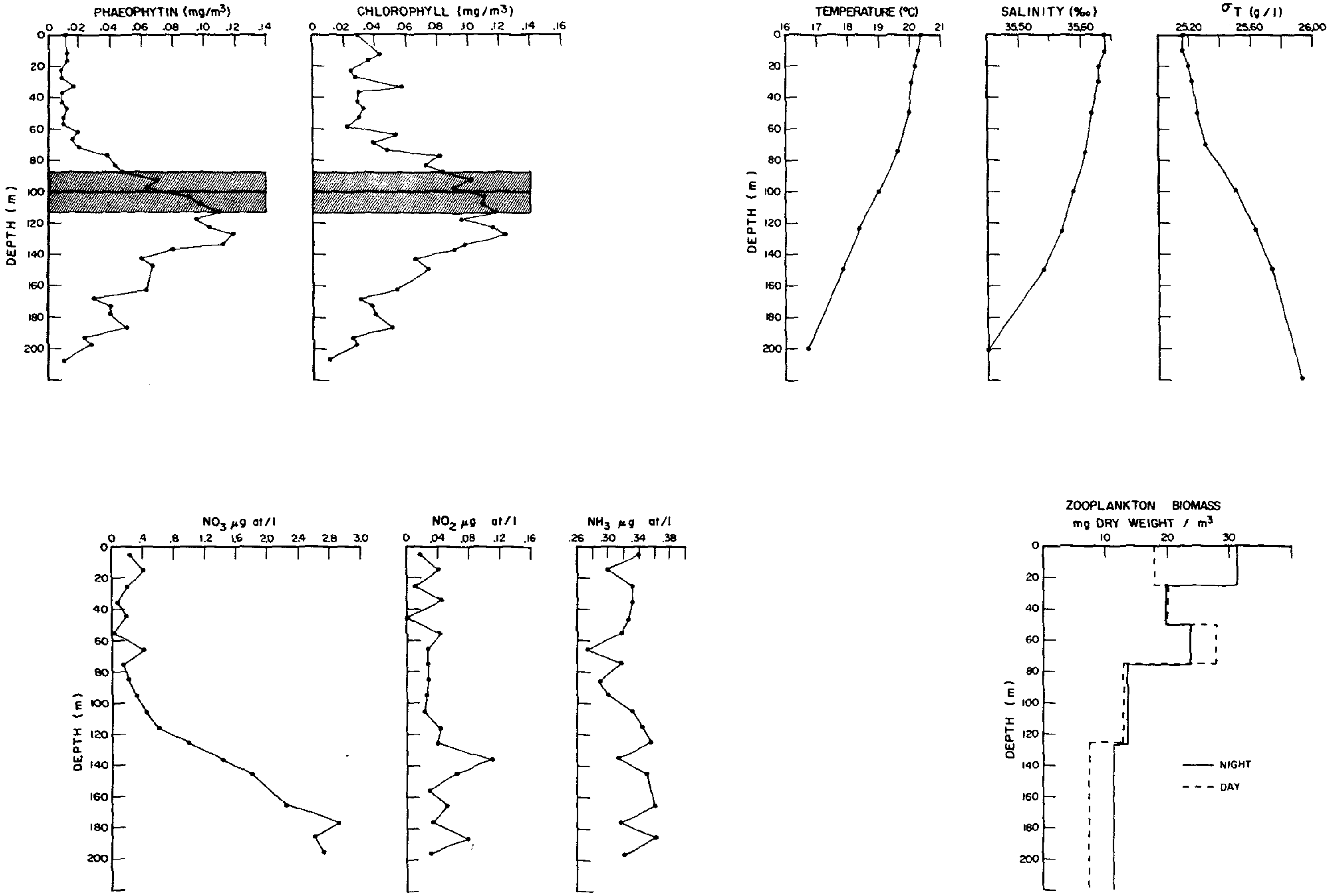

FIGURE 4.—Vertical profiles of chlorophyll, phaeophytin, and other physical, chemical, and biological properties observed in October 1969 in the vicinity of lat 25°S, long 155°W. Estimated depth of the 1% light level and 95% confidence interval indicated by horizontal bar and cross hatching.

accumulation of pigment generally occupies a layer 50-75 m thick, the core of the layer may be very abrupt. From closely spaced water samples (Table 1) we have found that the highest concentrations of chlorophyll may be contained in a layer less than 5 m thick and may exceed by 10% to 50% the concentrations in the adjacent samples. Occasionally maximum concentrations are found in more than one layer within the region of chlorophyll accumulation (Figure 3c, Table 1, 23 August 1967).

It is very difficult to sample such a narrow core with discrete water samplers. A routine cast, in which samples are usually spaced at least 15 m apart, is likely to miss the peak concentrations, and underestimate the chlorophyll content of the maximum layer. Moreover, because of the rapid vertical changes in chlorophyll concentration, slight variations in the position of the samples within the layer may appear as horizontal discontinuities of the layer. Discrete chlorophyll data, including those presented in this paper, must be interpreted accordingly.

SPECIES COMPOSITION

The numbers and species of diatoms in water samples collected on expeditions URSA MAJOR and ZETES have been enumerated (University of California, 1967, 1970; Venrick, 1969). The increase in chlorophyll concentration in the maximum layer is accompanied by a significant increase in the number of diatom cells. Furthermore, the maximum layer is composed of different assemblages of species within the Subarctic Pacific, the Transition Domain, and the Central Pacific (Venrick, 1971). In August, north of lat 40°N the species within the maximum layer were the same as those occupying the overlying water mass. South of lat 38°N, however, samples from the maximum layer were dominated by species which were not observed in shallower samples. During the winter when the maximum layer had been eroded by increased turbulence, the same species were present, but they were distributed randomly through the water column.

More recent studies were undertaken in 1968 at lat 26°57′N, long 155°10′W with a series of 19 replicate casts over a distance of 10.5 miles. Phytoplankton samples were collected from 25 m, 50 m, 75 m, and from the chlorophyll maximum layer at 125 m. A total of 80 species of diatoms were identified, of which 24, 36, and 37 were observed in the samples collected from 25 m, 50 m, and 75 m, respectively. A total of 64 spe-

TABLE 1.—Fine scale structure of the chlorophyll maximum layer.

URSA MAJOR		CLIMAX II			
2 Sept. 1964 lat 43°49′N, long 154°44′W		26 Aug. 1969 lat 27°09′N, long 155°18′W		23 Aug. 1969 lat 28°29′N, long 155°16′W	
Depth (m)	Chlorophyll *a* (mg/m³)	Depth (m)	Chlorophyll *a* (mg/m³)	Depth (m)	Chlorophyll *a* (mg/m³)
0	0.10	1	0.06	0	0.06
20	0.11	20	0.06	20	0.06
50	0.55	39	0.07	40	0.06
60	1.19	58	0.06	60	0.06
65	0.94	77	0.06	80	0.06
70	0.73	96	0.08	90	0.08
75	0.56	101	0.07	100	0.13
80	0.44	105	0.11	105	0.13
85	0.38	110	0.08	110	0.09
90	0.24	114	0.08	114	0.13
100	0.10	124	0.06	118	0.12
		141	0.02	122	0.10
				126	0.07
				130	0.07
				135	0.06
				140	0.04
				150	0.04
				165	0.03
				180	0.02
				200	0.02

cies were found at 125 m, and of these 64, 22 occurred only in samples from that depth. Thus, the chlorophyll maximum layer, which has a higher species diversity (as measured by the number of diatom species) and which may contain species not found at shallower depths appears to offer unique features as a biological habitat.

THE CENTRAL PACIFIC

Studies conducted on Expeditions CLIMAX I, CLIMAX II, and ARIES III near the axes of the North and South Central Pacific Gyres have provided us with a large amount of data concerning the vertical distribution of chlorophyll and productivity in the water column and their relationship with other physical, chemical, and biological parameters. Comparison with data collected over much wider areas on other expeditions leads us to believe that the relations observed in the Central Gyres may be pertinent to much of the oceanic Pacic.

The vertical distribution of chlorophyll and net production observed during these four studies have been summarized in Table 2. All studies show a well-defined subsurface accumulation of chlorophyll which varies in width from 50 to 75 m and contains maximum concentrations of chlorophyll in excess of 0.10 mg/m^3. The core of the layer always occurred below the depth penetrated by 1% of the surface radiation. In fact, more than half of the total chlorophyll within the water column was observed below this depth.

The rate of production per unit chlorophyll decreases with depth from a maximum at about 20 m, but this is partially offset by the increase in the amount of chlorophyll, and production rates as high as 0.13 mg $C/m^3/hr$ have been observed in the maximum layer in the South Pacific. Our in situ experiments indicate that 7% to 20% of the total production in the water column occurs below the 1% light level. These are minimum values since our in situ studies did not reach the level of no productivity. The total rate of production throughout the water column is variable on rather small spatial and temporal scales, but appears to be considerably greater than maximum estimate of 100 mg $C/m^2/day$ (8.3 mg $C/m^2/hr$) estimated by Koblentz-Mishke et al. (1970).

The vertical distribution of chlorophyll and several relevant properties are illustrated in Figure 4. Data points are mean values of observations made in replicate on six 24-hr stations in the South Central Pacific (CLIMAX II Expedition) and represent an area of 60 square miles and a time span of 6 days. Above 200 m there was an average of 12.35 mg chlorophyll per square meter sea surface. Of this, over half occurred below the estimated depth of 1% light. We estimated the light intensity at the core of the maximum layer to lie between 0.10% and 0.26% of incident radiation. The vertical distribution of phaeophytin is similar to that of chlorophyll.

The accumulation of both chlorophyll and phaeophytin occurs within the pycnocline. On a local scale, these layers may move up and down with the pycnocline, for instance in response to

TABLE 2.—Mean value and 95% confidence limits of the mean for data relative to the vertical distribution of light, chlorophyll *a*, and productivity at two stations in the North and South Central Pacific Ocean.

Position	Date	Depth of 1% light m (1)	Chlorophyll *a*: Depth of maximum m (2)	Surface concentration mg/m^3 (3)	Concentration at (2) mg/m^3 (4)	Water column total 0-200 m mg/m^2 (5)	% of (5) below (1) %	Productivity: Total above (1) mg $C/m^2/hr$	Total below (1) mg $C/m^2/hr$
Lat 27°N, long 155°W	Sept. 1968	79 ± 5	104 ± 8	0.03 ± 0.01	0.16 ± 0.03	11.92 ± 2.62	73.5 ± 8.3	16.26 ± 2.25	
	Sept. 1969	73 ± 5	111 ± 9	0.09 ± 0.03	0.11 ± 0.02	11.67 ± 1.32	53.7 ± 4.6	31.74 ± 7.35	> 2.28
Lat 25°S, long 155°W	Oct. 1969	100 ± 13	122 ± 11	0.03 ± 0.01	0.13 ± 0.02	12.35 ± 3.22	58.5 ± 6.4	12.87 ± 9.08	> 3.28
	Mar. 1971	132 ± 14	140 ± 9	0.01 ± 0.00	0.11 ± 0.05	8.13 ± 1.47	58.3 ± 9.5	11.80	> 1.20

internal waves. However, on a wider scale, there appears to be no relationship between the depth of the maximum layer and any one isoline of temperature, salinity, or density.

Plant nutrients are present in very low concentrations in the upper 100 m. Phosphate values were less than 1.5 μg at./liter in the North Central Pacific and less than 0.2 μg at./liter in the South Central Pacific. Nitrate was less than 0.6 μg at./liter in the North and less than 0.8 μg at./liter in the South, while corresponding values of silicate ranged between 1 and 7 μg at./liter in the North and between 0 and 3 μg at./liter in the South. The concentrations of these three nutrients increase systematically and significantly at, or just below, the level of the chlorophyll maximum. Concentrations of ammonia are low and irregular throughout the upper 200 m, showing no pattern with depth. In contrast, high values of nitrite in the upper 200 m (occasionally as high as 4.5 μg at./liter) were observed only within or just below the chlorophyll maximum, and may indicate recent phytoplankton assimilation of nitrate-nitrogen (Vaccaro and Ryther, 1959). In all of our studies, the relationship between the vertical distributions of chlorophyll and nutrients was far more predictable than the relationship between chlorophyll and any of the physical properties.

We have found no evidence of any accumulation of zooplankton within the chlorophyll maximum layer. Total zooplankton biomass (animals greater than 35 μ) was greatest above the maximum layer during both day and night. This appears to be true for all size categories.

THE SEASONAL CYCLE

Seasonal samples from the western edge of the California Current (station 100.80 at lat 30°00′N, long 120°07′W) during 1969 demonstrate a seasonal change in the vertical distribution of chlorophyll *a* (Figure 5). We have evidence that this maximum layer is continuous with that observed within the Central Pacific Gyre and we expect their seasonal cycles to be comparable. For a short period in February, chlorophyll is essentially homogeneous through the upper 50 m. This corresponds in time to the maximum development of the mixed layer. When the water column begins to stratify in March, chlorophyll concentrations at the surface decrease abruptly and a subsurface maximum layer develops. As the summer progresses, the maximum decreases in concentration and the layer subsidies, reaching its maximum depth just prior to the breakdown of the density stratification in December. Figure 5b illustrates the lack of temporal relationship between the depth of the chlorophyll maximum and any one isopleth of density. This would seem to preclude the formation of the maximum layer from the accumulation of cells regulated solely by their physical density.

The vertical distribution of chlorophyll during August along long 155°W is presented in Figure 2. This may be compared with the

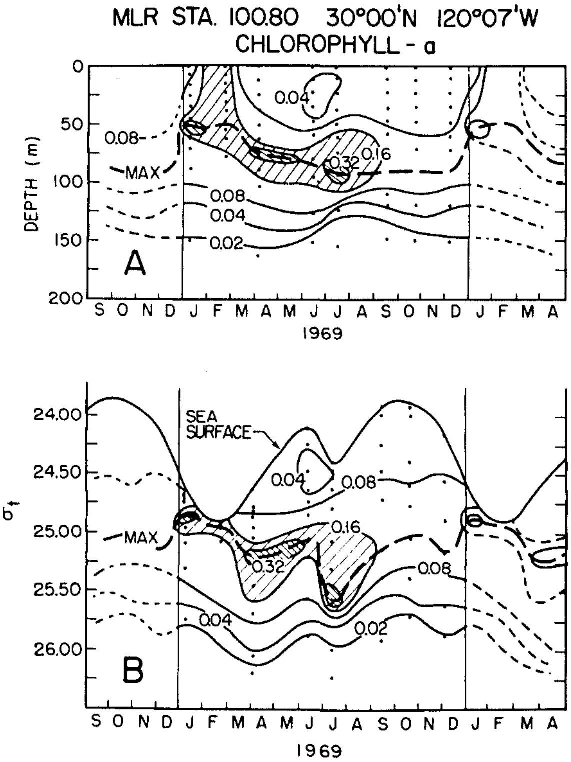

FIGURE 5.—Annual development of the subsurface chlorophyll maximum layer at lat 30°00′N, long 120°07′W. Chlorophyll *a* concentration is contoured with respect to depth (A) and density (B).

distribution along the same transect observed during January (ZETES Expedition) when a similar program of chlorophyll measurement was carried out. In January, north of lat 32°N, the mixed layer extends below 100 m. Concentrations of chlorophyll are uniform throughout this layer, decreasing abruptly below the mixed layer. Between lat 26°N and 32°N a weak chlorophyll maximum is still present near 120 m below the mixed layer which does not reach its greatest depth of 200 m until February (Robinson, 1951).

The evidence accumulated to date suggests that a subsurface concentration of plant material can persist only in the presence of a density gradient which isolates the layer from the effects of wind-driven turbulence. Thus, any seasonal fluctuations in the strength or depth of the pycnocline may be expected to affect the presence of the deep maximum layer. We can postulate with some assurance that in any environment in which the winter mixed layer regularly exceeds the depth of the chlorophyll maximum layer, the maximum layer must be a seasonal phenomenon. At any locality, the duration of the maximum layer will be determined by the duration of seasonal stratification of the water column and thus will be progressively shorter at higher latitudes.

This observation has important implications. Over most, if not all, of the ocean, the phytoplankton within the maximum layer do not represent a permanent loss to the epipelagic community. Neither need there be a balanced energy budget within the maximum layer. Sufficient energy may be produced and stored in a brief period prior to stratification of the water column or the depletion of nutrients from the surface waters to maintain the population within the maximum layer for considerable periods of time, even though photosynthesis may be depressed or absent.

LARGE-SCALE TEMPORAL FLUCTUATIONS

In the Central Gyre of the North Pacific we have recorded temporal fluctuations on a larger scale. In September 1969, the standing crop and productivity were higher and more variable throughout the water column than in the same month of the previous year. As a result, in 1969, the chlorophyll maximum layer was less sharply defined and was occasionally obscured by high chlorophyll concentrations in the overlying water. These fluctuations are of considerable interest. Namias (1971) has investigated the meteorological and oceanographic conditions accompanying a vast pool of abnormally warm water in the southern portions of the North Pacific during the summer and fall of 1968. He concludes:

> The abrupt and extensive anomalous warming of the southeastern quarter of the Pacific Ocean north of 20°N from May-June, 1968, appears to have been due largely to increased isolation and horizontal convergence of the surface layers of the sea and associated downwelling, ... These warming factors in the heat budget were associated with the development and maintenance of a strong and deep Pacific anticyclone in June which appears to have been persistently regenerated by an unusually strong mean jet around 40°N.

This period of stronger subsidence was accompanied by a clear sharpening of the maximum layer and by reduced standing crop of phytoplankton and productivity above the layer. The observations of Namias suggest that the generalized downwelling in the Central North Pacific anticyclone, which is an important factor inhibiting the vertical diffusion of nutrients into the euphotic zone, is also closely related to the depth and concentration of photosynthetic material below the mixed layer. Extrapolation leads us to expect to find similar chlorophyll maxima well developed in other large, persistent temperate gyres, such as the South Atlantic and the southern Indian Ocean.

DISCUSSION

It is evident that a deep chlorophyll maximum layer is a well-developed and consistent feature of the major gyres of both the North and South Pacific. In view of its geographic continuity, we must reevaluate the mechanisms postulated for its development, and seek a single explanation to account for the presence of a chlorophyll maximum layer in very different environmental regimes. Of the numerous hypotheses which have been put forward, several may be relevant. The increase of chlorophyll with depth corresponds to an increase in the number of phytoplankton (diatom) cells, but this may be accentuated by an increase in the amount of chlorophyll per cell. Zooplankton have been shown to be concentrated above the maximum layer and differential grazing pressure may help to maintain the abrupt gradient at the top of the maximum layer. In situ production has been demonstrated within the maximum layer at very low light intensities, and this will contribute to the formation and maintenance of the layer.

The strong development of a deep maximum within the oligotrophic environments of the Central Gyres, the effect of fluctuations of the rate of downwelling on the depth of the maximum layer and the productivity in the overlying water, and the consistent relationship between the depth of the maximum layer and the depth of the nutricline and the nitrite maximum suggest that the nutrient regime may be a critical factor in the development and maintenance of the chlorophyll maximum layer. Our observations to date support the theory of Steele and Yentsch (1960) that depletion of nutrients above the summer thermocline leads to a reduction in the buoyancy of phytoplankton, and that a subsurface maximum results from the accumulation of impoverished cells at the top of the nutricline where the absorption of nutrients decreases the sinking velocity (Eppley, Holmes, and Strickland, 1967). The maximum layer may continue to subside slowly as the nutrients at the top of the nutricline are depleted, and thus it may be that the depth of the maximum layer is ultimately determined by the nutrient regime, rather than ambient light intensity. As long as the depth does not exceed the maximum depth of the winter mixed layer the cells will be returned to higher light levels during the winter. It may be that the chlorophyll maximum layer represents a senescent stage in the annual cycle of oceanic phytoplankton which is analogous to the formation of resting spores by many neritic species.

It is evident that the chlorophyll maximum layer, which may account for a major portion of the standing crop of plant material and for a substantial portion of the primary productivity, is not restricted to the traditionally defined "euphotic" zone, the zone above the 1% light level. There is no justification for limiting samples for chlorophyll or productivity measurements to this zone. These programs must be extended below the chlorophyll maximum layer. We expect this will result in a substantial increase in the estimates of total production within the water column.

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