

## Primary Production System in the Southern Waters of the East Sea, Korea III. Vertical Distribution of the Phytoplankton in Relation to Chlorophyll Maximum Layer

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Vertical profiles of the chlorophyll *a*, phytoplankton abundance, nutrients and sigma-t were compared with the vertical distribution of phytoplankton species in conjunction with <sup>14</sup>C primary production in the Southern Waters of the East Sea, Korea. In the upper mixed layer the water column was only weakly stratified and ambient nitrogenic nutrient concentrations were markedly depleted. Dissolved silicate seemed to be another limiting nutrient in the surface layer. The occupation of different water depths by several dominant diatom species was well explained by the degree of silicification of each cell and the silicate concentration of ambient seawater. Subsurface chlorophyll maxima were continuously observed in the lower parts of the euphotic layer and the depth coincided with nutricline, supporting our view that chlorophyll maximum was sustained partially by enhancement of *in situ* growth of phytoplankton and partially by increase of cellular chlorophyll content. The persistence of chlorophyll maximum layer was attributed to the physiological adaptation of the phytoplankters to low light intensities and to the utilization of regenerated nutrients. Integrated water column production of organic matter by photosynthesis appeared to be better related to phytoplankton cell division than to the cell growth in terms of biosynthesis of pigments and other intracellular components.

### INTRODUCTION

Generally, the vertical distribution of chlorophyll is characterized by a subsurface maximum in the open ocean or stratified coastal waters during the summer months (Pingree *et al.*, 1978; Holligan *et al.*, 1984). The proposed mechanisms which can lead to the formation of chlorophyll maxima in the oceans include increases in cellular chlorophyll content (Cullen *et al.*, 1982), *in situ* growth (Eppley *et al.*, 1979; Lohrenz *et al.*, 1988), behavioral responses such as the active aggregation of free swimming cells (Falkowski, 1980; Villarino *et al.*, 1995), decreased sinking rates of phytoplankton cells or particles at pycnocline (Ignatiades, 1979) and depth differential grazing (Roman *et al.*, 1986). Among them, accumulation of sinking cells at density surfaces and behavioral aggregation have most often been invoked to explain that maximum. However, the coincidence often observed between the subsurface chlorophyll maximum and nutricline suggests that the phytoplankton growth by

active nutrient uptake play an important role for the maintenance and development of chlorophyll maximum (Vandeveld, 1987).

Despite a large number of field studies, the relative importance of physical and biological factors in the maintenance and development of the subsurface chlorophyll maximum remains to be ascertained (Holligan *et al.*, 1984). In addition, chlorophyll maximum in weakly stratified waters has not been thoroughly studied yet. Therefore, the first point to be examined is that the depth of maximum chlorophyll concentrations corresponds to that of maximum vertical stability.

As one of a series of studies on the primary production system in the southern waters of the East Sea, we tried to determine 1) patterns of the vertical distribution of phytoplankton in terms of chlorophyll *a* and cell number, 2) vertical community structure, 3) the possible mechanism of the subsurface chlorophyll maximum in physical, chemical and biological aspects.

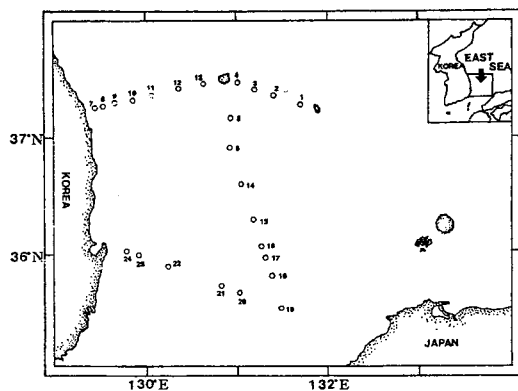


Fig. 1. A map showing the study area and 24 sampling stations.

## MATERIALS AND METHODS

### *Physical and chemical parameters*

Samples were taken at 24 stations in the southwestern part of East Sea of Korea on the training ship "Hanbada" of the Korea Maritime University from 17 to 20 May, 1988 (Fig. 1). Water temperature and salinity were measured with a Neil Brown Mark III CTD. Euphotic depth at each station was calculated from the measurement of Secchi depth. AOU, DO,  $\text{NO}_3$ ,  $\text{PO}_4$  and  $\text{SiO}_3$  were cited from Kim (1990) and  $\text{NH}_4$  and  $\text{NO}_2$ , from Ju (1990).

### *Biological parameters*

For the quantitative study of the phytoplankton, sea water was collected with Niskin samplers at each station and was subsampled into 500 ml polyethylene bottles and immediately fixed with Lugol's solution (Thronson, 1978). Aliquots of concentrated samples were subsampled into a Sedgwick-Rafter counting chamber and a Palmer-Maloney slide (McAlice, 1971). Identification and cell counting were done with a light microscope (Nikon Type 104). For chlorophyll determination, *in vivo* fluorescence of filtered sample (342  $\mu\text{m}$  mesh) was measured with a fluorometer (Turner Design III). For the calibration spectrophotometric data (SHIM-ADZU UV-180) were used. Using the  $^{14}\text{C}$  uptake method (Shim and Park, 1986) primary production

was determined at 6 stations. Water samples were collected at three depths (0 m, 15-20 m, 30-40 m) within euphotic zone and were incubated at different light intensities (100, 70, 43, 28, 6% of incident light).

### *Data processing*

The Shannon-Wiener diversity of phytoplankton community was calculated. In addition to the diversity index, Sorensen's affinity index (SAI) was calculated. This affinity index provides information on the common species in each pair of samples. SAI values range between 0 (no common species) and 1 (the composition is the same).

$$SAI = 2c : (a + b)$$

where a and b are the number of species in two samples, respectively and c is the number of common species in these two samples.

## RESULTS AND DISCUSSION

### *Physical environments*

Fig. 2 shows the vertical distribution of water temperature, salinity and density. Stability was determined by the following equation (Sverdrup *et al.*, 1942):

$$E' = 10^{-3} \frac{d \sigma_t}{dz}$$

where  $E'$  is a measure of stability. The density changes of the water column were not large, although rather high stability ranging between 0.4 and  $1 \times 10^{-4} \text{ m}^{-1}$  existed between 10 and 20 m and another one at depth greater than 50 m in some regions (Table 1). Thus, it can be described that this study area is an environment of weak stratification.

### *Chemical environment*

The dominant feature in the vertical distribution of important micronutrients, nitrate, phosphate and silicate, was the marked depletion in the upper layers. Fig. 3 shows vertical distribution of each com-

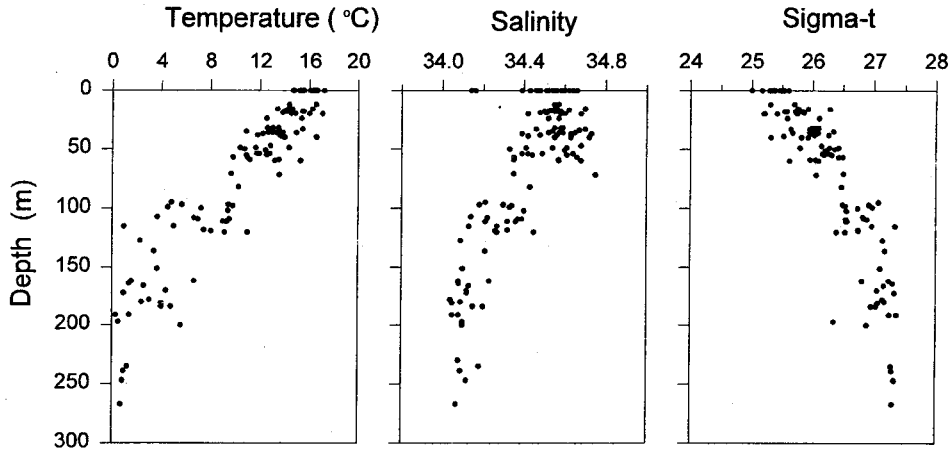


Fig. 2. Vertical distributions of temperature, salinity and sigma-t.

Table 1. The maximum stability ( $\times 10^{-4} \text{ m}^{-1}$ ) and its depth (m) in each station

Station	depth	value	Station	depth	value
1	18-20	0.545	13	6-8	0.380
2	40-42	0.460	14	14-16	0.375
3	36-38	0.535	16	16-18	0.595
4	6-8	0.615	17	14-16	0.665
5	14-16	0.680	18	6-8	0.660
6	14-16	0.480	19	38-40	0.320
7	8-10	0.430	20	18-20	0.475
9	26-28	0.555	21	24-26	0.490
10	22-24	0.405	22	28-30	0.505
11	10-12	0.510	23	16-18	0.910
12	8-10	0.770	24	16-18	1.025

ponent. AOU (Apparent Oxygen Utilization) was negative in euphotic zone with its minimum between 15 m and 25 m in depth. The AOU minimum depth was roughly corresponded to that of rather high stability. Concentration of nutrients increased at depth between 40 m and 60 m, where maximum concentration of nitrite and ammonia was found. To quantify relationships between physico-chemical parameters, a simple correlation matrix was constructed (Table 2). Positive correlations among depth,  $\sigma_t$ , AOU, silicate, phosphate and nitrate were significant with the highest correlation between silicate and nitrate.

#### Species composition and abundance

A total of 155 kinds of phytoplankton (142 species, 11 varieties and 2 forms) were identified which were composed of 104 diatoms (94 species, 7 varieties and

3 forms), 46 dinoflagellates (44 species and 2 varieties), 4 silicoflagellates (2 species and 2 varieties) and 1 euglenoid species. Diatoms outnumbered any other groups in the species number, but the composition of the major groups showed no significant changes with depth (Fig. 4).

Quantitatively, diatoms occupied 99% of total netplankton cells, and only three species occupied 88.7% within the upper 60 m layers (Shim *et al.*, 1995). Compared to previous studies, the standing stocks of netplankton were higher by orders of magnitude. Among the first five dominant species occupying 90.6% of the total cell counts, four species had occurred as dominant species in the upwelling region of Kuroshio current in Japan (Furuya *et al.*, 1986) where *Nitzschia pungens* predominated. In addition, all the groups mostly consisted of neritic and cold water species. These facts imply that there might have been plentiful nutrients through the vertical mixing of water column and concomitant spring warming of surface water might stimulate the even more enhanced production. This is well supported by the shallow depth of maximum stability and weak stratification of water column underneath (Fig. 2).

#### Depth relation of species

The vertical distribution of phytoplankton groups of net fraction was irregular. However, diatoms clearly predominated in the surface waters and

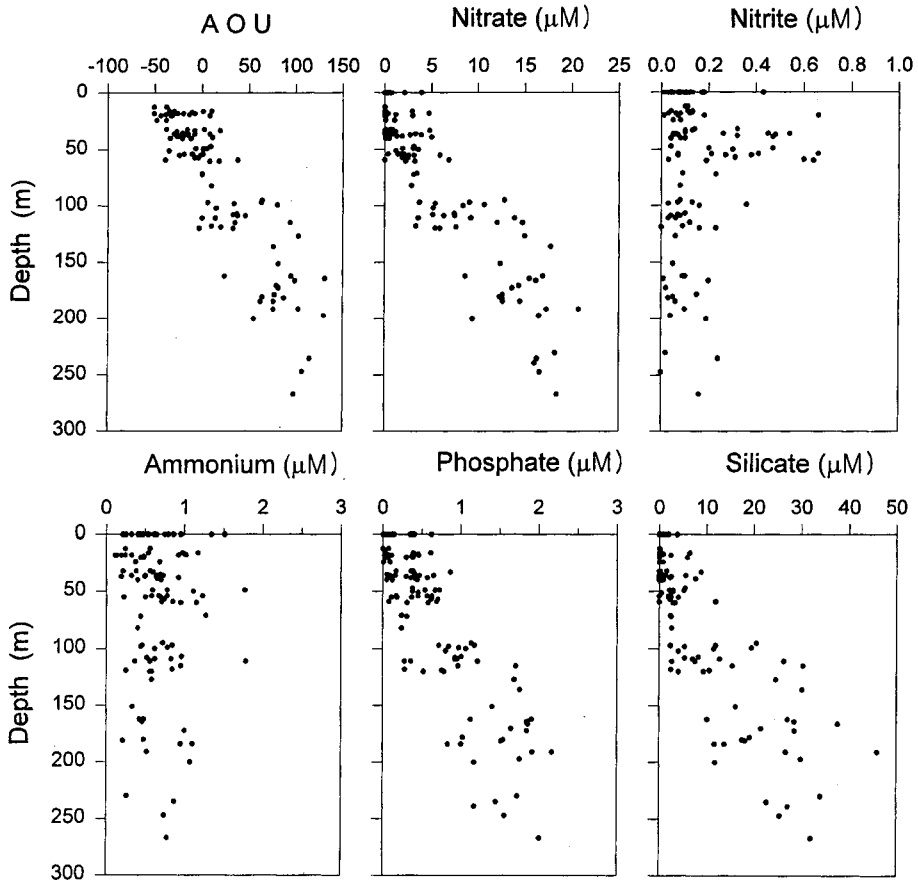


Fig. 3. Vertical distributions of AOU, nitrate, nitrite, ammonium, phosphate and silicate.

Table 2. Simple correlation matrix of parameters measured down to 200 m at all stations

	Sigma-t	AOU	SiO <sub>3</sub>	PO <sub>4</sub>	NO <sub>3</sub>	N02	NH <sub>4</sub>
Depth	0.79	0.85	0.88	0.84	0.85	0.19	0.03
Sigma-t		0.90	0.85	0.89	0.90	0.26	0.08
AOU			0.92	0.94	0.95	0.18	0.05
SiO <sub>3</sub>				0.95	0.97	0.19	0.00
PO <sub>4</sub>					0.95	0.17	0.04
NO <sub>3</sub>						0.19	0.04
N02							0.21

decreased gradually with depth (Fig. 5). This trend has been reported by many authors (Kimor *et al.*, 1987; Hernandez-Becerril, 1987). Among diatoms, centric forms were more abundant than pennate forms, and the ratio of the former to the latter forms decreased with depth. Dinoflagellates are known to be predominantly subsurface forms (Holligan and Harbour, 1977). However they appeared throughout

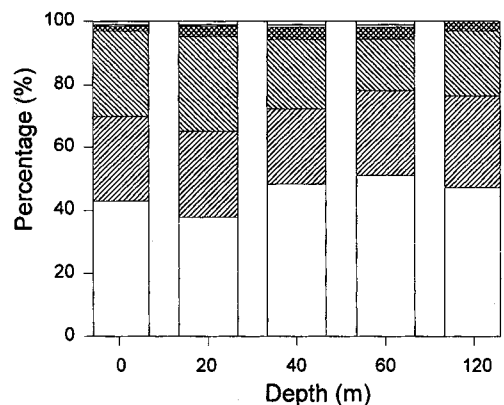


Fig. 4. Percentage compositions of the various taxonomic groups in each depth. □ centric diatoms ▨ pennate diatoms ▩ dinoflagellates ■ silicoflagellates ▨ euglenoids

the euphotic zone and moreover down to 60 m.

The predominant species, *Leptocylindrus danicus*,

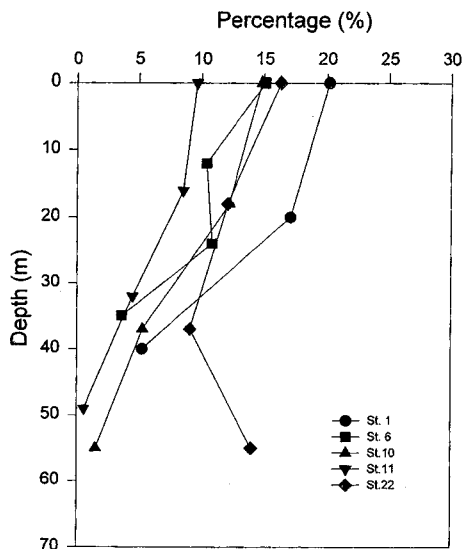


Fig. 5. The vertical distribution of quantitative percentage of diatoms to total cell count (net+nanoplankton) with depth.

was not confined to any depth, but was found at the whole euphotic zone with its maximum concentration near the surface layer.

In the Gulf of California, Gilbert and Allen (1943) reported changes in the diatom composition with depth. According to them, weakly-silicified diatom (*Chaetoceros*, *Bacteriastrum*) disappeared between 60 m and 300 m while more silicified forms (*Coscinodiscus*, *Pseudoeunotia*) were located down to 1000 m. The same trend could be seen in this study area. The weakly-silicified diatom, *Bacteriastrum delicatula*, was observed only within the euphotic zone. On rare occasions it occurred at 60 m but completely disappeared in 120 m. On the other hand, the more silicified forms belonging to genus *Coscinodiscus* occurred only at 120 m. *Leptocylindrus mediterraneus* occurred in rather deep water, 40-120 m. Silicoflagellates, such as *Dictyocha fibula* and *Distephanus speculum*, were found at cooler waters as the negative members against water temperature (Shim and Lee, 1987). They were observed mostly in 40-60 m depth where silicate concentrations began to increase. These results suggest that the vertical distribution of the silicified phytoplankton species should be influenced by degree of silicification of each cell and ambient silicate concentration.

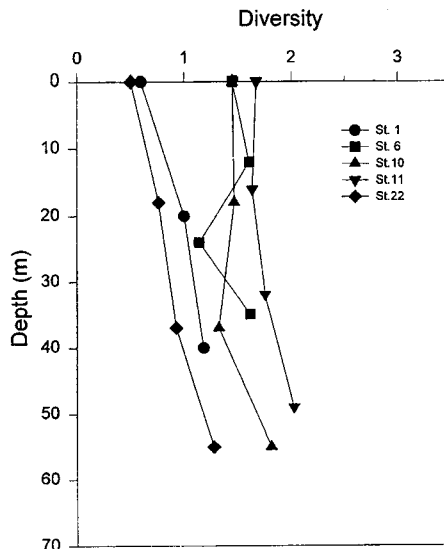


Fig. 6. The vertical distribution of diversity spectrum based on the Shannon-Wiener formula.

#### Vertical structure of phytoplankton community

The mean value of species diversity of total samples was 1.24 with the standard deviation, 0.49. This is quite a lower value than that (2.47) in May 1984 (Lee, 1986). The vertical changes of diversity exhibited slight increases showing still fairly low values in deep layer (Fig. 6). This was mainly due to increases of equitability ( $r=0.75$ ) of which average value is 0.49. Therefore, the higher values of diversity in deep layers suggest that species composition of phytoplankton change more or less evenly with depth and the community become more mature and stable in deep layer.

In order to provide more details on the vertical community structure, the ratio of number of taxa present in surface (chlorophyll maximum layer) to that within total water column (TS(TCL) : TT) was determined in each station (Table 3). Hernandez-Bercerril (1987) reported that the ratio of number of taxa throughout the euphotic zone to that in all samples (TEZ:TT) ranged 0.20-0.25 in weakly stratified or well mixed stations, and did not exceed 0.14 in the stratified station in Gulf of California. By contrast, our observation showed surprisingly high values. In all stations except st.

Table 3. The ratio number of taxa present in surface (TS) and chlorophyll maximum layer (TCl) to number of taxa within all levels to 120 m (TT) and Sorensen's affinity indices (SAI) between surface and chlorophyll maximum layers in each station

Station	TS:TT	TCl:TT	SAI	Station	TS:TT	TCl:TT	SAI
1	0.60	0.53	0.53	13	0.56	0.50	0.65
2	0.57	0.70	0.68	14	0.51	0.67	0.65
3	0.68	0.79	0.73	15	0.48	0.44	0.35
4	0.67	0.63	0.69	18	0.48	0.52	0.61
5	0.59	0.56	0.58	19	0.18	0.35	0.22
6	0.59	0.59	0.65	20	0.66	0.59	0.65
8	0.67	0.41	0.29	21	0.44	0.62	0.56
10	0.59	0.53	0.56	22	0.68	0.68	0.65
11	0.59	0.66	0.65	23	0.68	0.72	0.74
12	0.52	0.58	0.71	24	0.81	0.81	-

19, TS:TT ratios exceeded 0.48, and averaged to be 0.58. This implies that high proportion of common species occurred in surface. A similar trend was observed in CML(chlorophyll maximum layer).

Sorensen's affinity indices (SAI) between surface and CML were high averaging 0.59 (Table 3). From the high proportion of common species in both surface and CML and the high affinity between them, it could be deduced that the vertical species composition was not so variable and no distinct species groups existed in the study area.

#### Interrelations between biological parameters

In exploring the interrelationships among water column characteristics, a simple correlation matrix of water column chlorophyll, cell abundance and production parameters was constructed for all stations (Table 4). Integrated water column chlorophyll approximately to 60 m ( $\Sigma$  Chl *a*;  $\mu\text{g Chl } a \text{ l}^{-1}$ ) was estimated by the following equation:

$$\Sigma \text{Chl } a = \frac{1}{2} \sum (C_{i+1} + C_i) (D_{i+1} - D_i)$$

where  $C_i$  and  $C_{i+1}$  are the chlorophyll *a* concentration ( $\mu\text{g l}^{-1}$ ) and  $D_i$  and  $D_{i+1}$  are the depth (m) of upper and lower limit of each sampling interval. Integrated water column cell abundance ( $\Sigma$  N) was calculated by substituting cell count at each depth for chlorophyll concentration in the equation. Significant correlation between  $\Sigma$  N and  $\Sigma$  Chl *a* was observed ( $r=0.82$ ). Correlations also were signi-

Table 4. Simple correlation matrix of water column chlorophyll, cell abundance and production parameters for all stations

	$\Sigma$ N	$\Sigma$ Chl <i>a</i>	Chlorophyll maximum	
			Value	Depth
$\Sigma$ P	0.86	0.70	0.69	0.37
$\Sigma$ N		0.91	0.82	0.24
$\Sigma$ Chl <i>a</i>			0.94	0.35
Chlorophyll maximum value				0.19

ficant between depth integrated primary production ( $\Sigma$  P) and both  $\Sigma$  N and  $\Sigma$  Chl *a*, but higher correlation was observed between  $\Sigma$  P and  $\Sigma$  N. From the result, it can be said that production of organic matter by photosynthesis appeared to be better related to cell division than to cell growth in terms of biosynthesis of pigments and other intracellular components. In other words, chlorophyll *a* content in a cell was rather independent of the primary production, which could be attributed to the photo-adaptation of phytoplankton within water column.

#### Formation of chlorophyll maximum layer

Chlorophyll maximum depth corresponded roughly with the base of euphotic zone (Fig. 7, 8), either above or below the 1% surface irradiance level. The presence of CML has been reported near the study area (Shim and Park, 1986) and southwestern sea of Korea (Shim and Park, 1984).

Relationship between the vertical distribution of phytoplankton and vertical stability of sea water in the ocean has been investigated by many authors. In

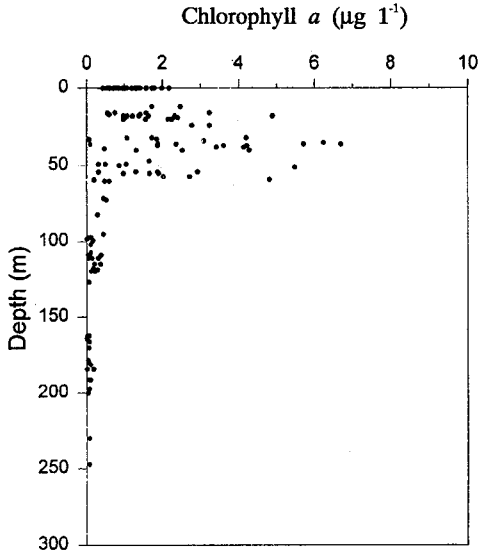


Fig. 7. The vertical distribution of chlorophyll *a* concentrations.

a stratified environment the vertical structure of the water column is characterized by strong thermo (halo)cline. In this layer of minimized turbulent diffusion, phytoplankton growth can potentially lead to the development of biomass heterogeneities (Vandevelde *et al.*, 1987). In addition, the increased density gradient can lower the sinking rate of phytoplankton cell, and thus favor their accumulation in the chlorophyll maximum (Ignatiades, 1979).

At some of the stations (sts. 2, 3 and 19), location of the chlorophyll maximum was to some extent along the isopycnal surface, consistent with the hypothesis that cells are accumulating at zone of density stratification. However, the largest vertical gradient of density in upper zone mostly occurred at 10-20 m, which was well above the chlorophyll maximum (Table 1). This suggests that the situation of the chlorophyll maximum cannot be explained solely in terms of density gradients.

The one consistent relationship was that between the nutricline and the chlorophyll maximum. Nutrient concentrations were highly depleted in the upper part of the water column (Fig. 9), which indicates that the growth of phytoplankton was limited by nutrient. The proximity of CML to nutrient supply may have resulted in active assimilation

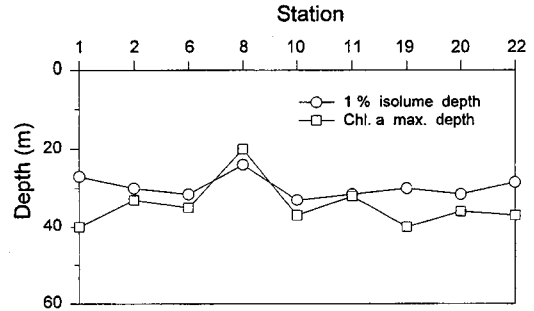


Fig. 8. The depth of 1% isolume and chlorophyll maximum at some stations.

of diffusing nutrients by phytoplankton in CML and thus enhancement of *in situ* growth of phytoplankton. However, this possibility is not fully supported by the fact that the increase of chlorophyll *a* around 35 m was accompanied by an decreasing cellular abundance. As the light conditions were unfavourable for phytoplankton to photosynthesize in CML, shade adaptation of phytoplankton to low light intensity happened through an increase of cellular chlorophyll content (Fig. 10). The unfavourable light condition in CML leads to speculation that phytoplankters may undergo loss of cell carbon. But Anderson (1969) showed that phytoplankton at depth below the 0.1% isolume could accumulate cell carbon and 15% of the total primary production lay below the euphotic depth. Therefore, it can be said that CML occurred at the intermediate depth where both light and nutrient conditions offered the best compromise for phytoplankton growth.

Hydrodynamic processes are known to act on phytoplankton production in the water column through the proximal agency of both light and nutrient (Legendre and Demers, 1984). In weakly stratified environment like this area, beginning of water column stratification caused by surface warming let phytoplankton reside in water column longer than before. Our results suggest that this might have triggered active assimilation of available ambient nutrients and rapid growth of phytoplankton. Nutricline might have been established by nutrient depletion in surface water due to photosynthetic activity and its gradient and location might depend on light

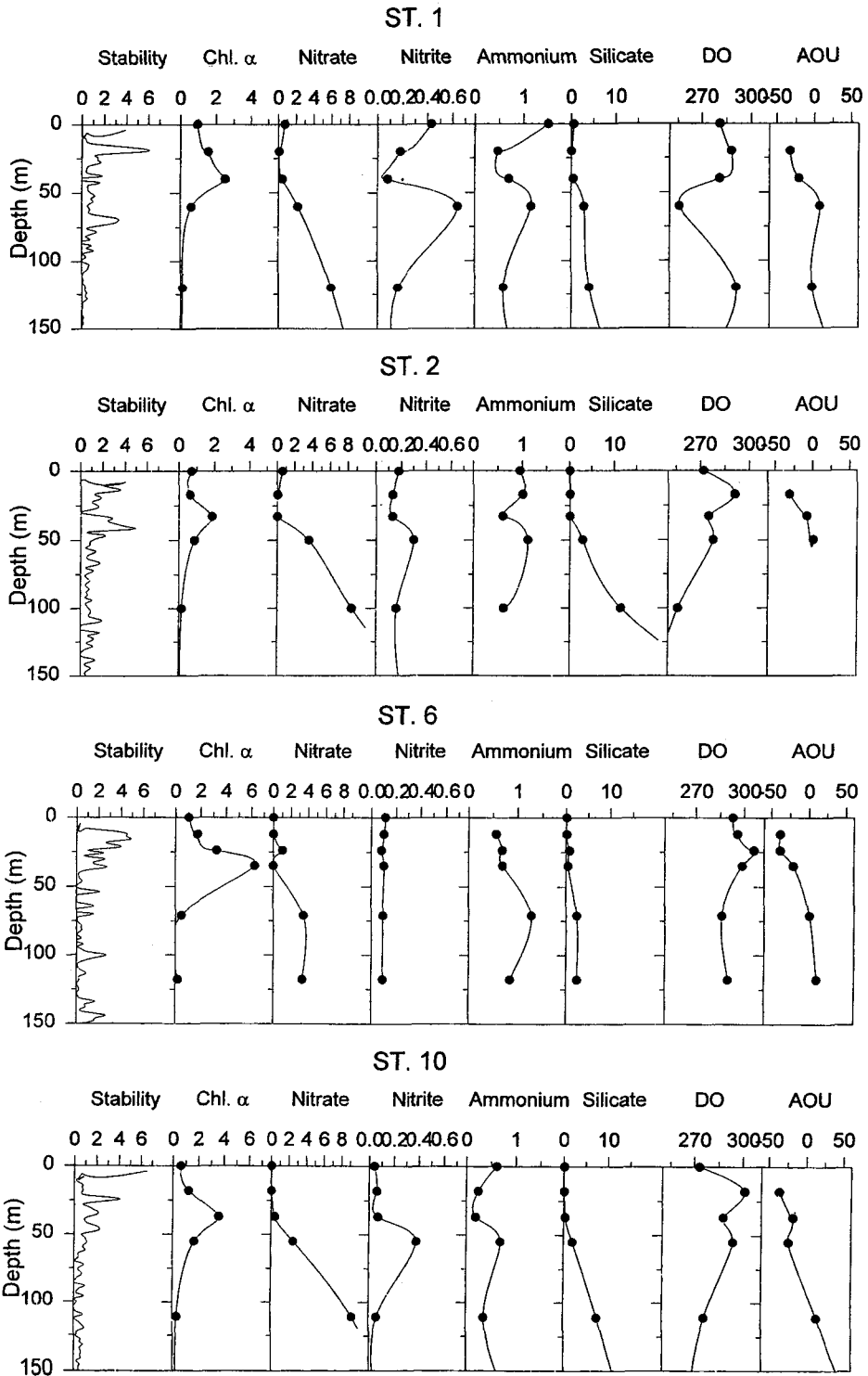


Fig. 9. The vertical distribution of chlorophyll *a* concentration with environmental factors; stability unit is  $10^5 \text{ m}^{-1}$ , nutrient  $\mu\text{M}$  and chl. *a*  $\mu\text{g l}^{-1}$ , respectively.



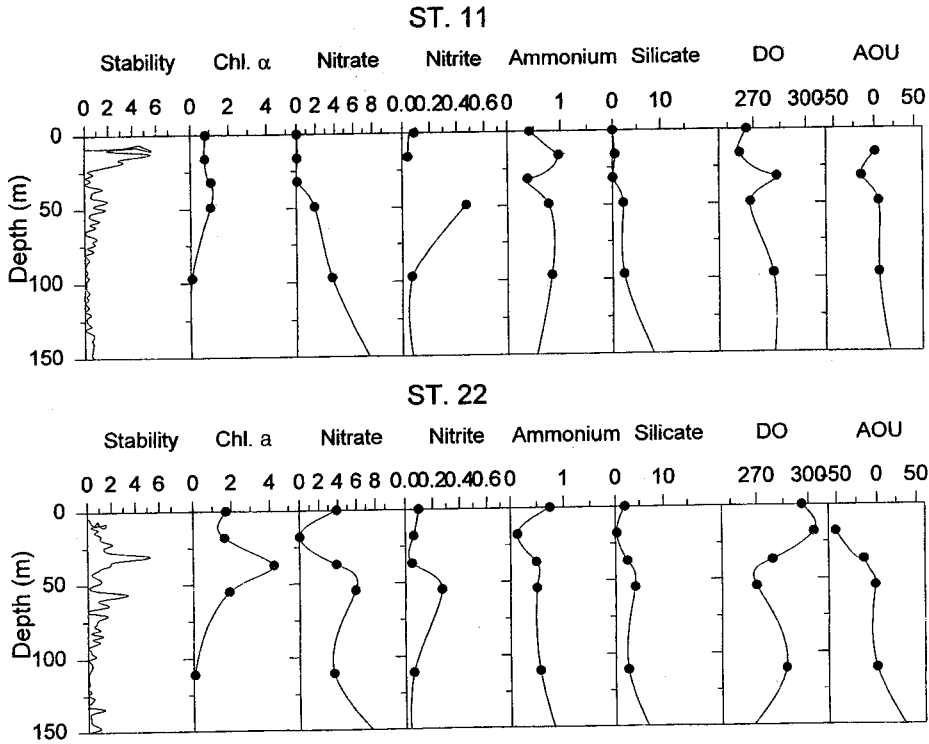


Fig. 9. continued

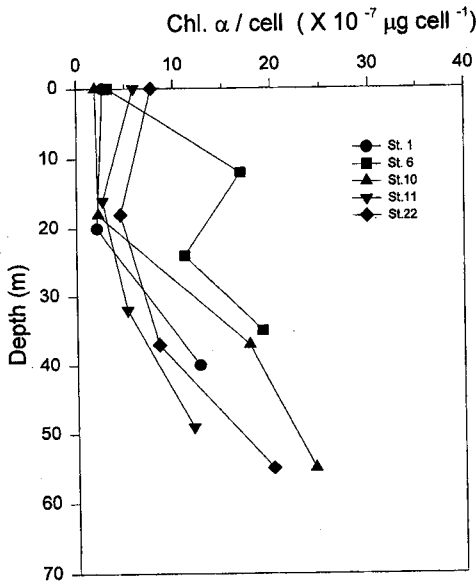


Fig. 10. The vertical distribution of cellular chlorophyll *a* content of netplankton.

conditions at maximum depth where phytoplankton could actively photosynthesize.

*Maintenance of chlorophyll maximum layer*

At our sampling stations, maximum DO was not located at the highest standing stocks, but situated just above the CML where rather high stability was detected (Fig. 9). This observation can be explained by the large respiratory demand of heterotrophs such as bacteria, microflagellates, ciliates, microzooplankton and metazoans within the CMLs and by the DO accumulation under the density cap created by the surface warming (Shulenberger and Reid, 1981).

The large respiratory demand within the CMLs could be inferred from AOU values (Fig. 9). AOU is used to obtain estimates of the amounts of the nutrients in a given water sample which are of oxidative origin. Increasing rate of AOU was the highest at the depths near the CML. This indicates that biological activity for nutrient regeneration was great near the chlorophyll maximum. The regenerated nutrients would be directly retaken up and incorporated into a variety of organic molecules to

maintain chlorophyll maximum. In this research, the effects of grazing had not been addressed, but the positioning of ammonium maxima just below or near the chlorophyll maxima showed high heterotrophic activities in the CML. The high concentration of ammonia in the CML could be favourable to nitrifying bacteria. Nitrite maximum was found to correspond to the ammonia maximum, at which layer nitrate increased rapidly. DO in the layer was not so low that bacterial denitrification could not be invoked (Fig. 9). Therefore, the nitrite maximum could be attributed partly to the extracellular release of nitrite by phytoplankton during photosynthetic nitrate reduction and partly to the bacteria oxidation of ammonia.

All the results implies that the chlorophyll maximum be supported by the physiological adaptation of phytoplankton to low light intensity and by the utilization of nutrients regenerated by the heterotrophic activity and excreted by the phytoplankton itself.

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