

STANDING CROP AND GROWTH RATES OF NET PHYTOPLANKTON AND NANOPLANKTON IN ANTARCTIC WATERS

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Abstract

The distribution of chlorophyll *a* (chl *a*) was studied over a period extending from 27th Dec. 1986 to 21st Feb. 1987, in the Antarctic ice-edge region and at 21 stations off-shore. In the ice-edge region, surface and column (0–75 m) chl *a* values averaged 1.98 mg m⁻³ and 151.50 mg m⁻² respectively and were approximately 4.5 times higher than those measured off-shore.

A conspicuous band of elevated chl *a* values was observed in the region between 64°S to 62°S. The possible mechanisms governing enhancement in phytoplankton biomass levels in the ice-edge region and between 64°S to 62°S have been discussed in the light of physical and chemical oceanographic data collected during the study.

On seven out of eight days of sampling in the ice-edge region and at 20 of 21 stations sampled off-shore, the chl *a* maxima was located at depths corresponding to 16% and 1% of the surface irradiance.

Nanoplankton (< 20 μm) constituted more than 60% of the total chl *a*. In view of their high biomass and turnover rates, the significance of nanoplankton over microplankton in the food chain dynamics of the Antarctic seas has been emphasized.

INTRODUCTION

During the last few years, our perception of the structure and function of the pelagic ecosystem has undergone a profound change. The essence of this revolution has been the increasing awareness amongst phytoplankton investigators of the importance and diversity of smaller celled (< 20 μm) phytoplankton collectively termed as nanoplankton (Pomeroy, 1974). Until recently our knowledge of the standing crop and productivity of the seas around Antarctica was based on the observations made by Hart (1934 ; 1942). On the basis of these surveys it was concluded that the Antarctic ecosystem consisted of larger than normal sized cells, with a simple progression from larger diatoms to krill and

to seals and whales. With the use of more refined techniques developed during the last few years the widespread abundance of nanoplankton and their contribution to food chain of the Antarctic marine ecosystem is quickly becoming apparent (Brockel, 1981 ; El-Sayed, 1981). The purpose of this study was i) to examine the size structure and specific growth rates of phytoplankton within the Indian sector of the Antarctic Ocean and ii) to find out to what extent the size structure in the productive ice-edge region differed from the less productive off-shore waters. Such data would help ultimately in the production of dynamic maps and models of krill circumpolar distribution (El-Sayed, 1987).

MATERIAL AND METHODS

In the ice edge-region samples were collected over a period extending between 22nd Dec. 1986 to 22nd Feb. 1987. Offshore stations were occupied on a cruise track on a more or less northward and eastward transect between Lat. 70°S to 57°S and Long. 12°E to 28°E (Fig. 1). Water samples were collected at 5 depths with 5 l PVC Niskin samplers shortly after measurements of light penetration were made and the depth of the euphotic zone was established using a Secchi disc. Water samples were drawn from a minimum of 4 depths within the euphotic zone and 1 depth below the euphotic zone which was around 75 m. Temperature was read off reversing thermometers and nutrient salts viz, nitrate, nitrite and phosphate were estimated spectrophotometrically using standard analytical methods (Strickland and Parsons, 1972). Water samples for total chl *a* estimations were filtered on to GF/C filters pretreated with 1% MgCO₃ suspension in distilled water. Chl *a* and phaeopigments were determined fluorometrically on a Turner Designs Fluorometer (Strickland & Parsons, 1972). Nanoplankton chl *a* was determined in the same way except that the water samples were pre-screened through a 20 µm nybolt screen prior to filtration on to GF/C filters. Photosynthetic rates were assessed with the ¹⁴C method (Steeman-Nielsen, 1952) as adapted by Strickland and Parsons (1972). All water samples were pre-screened through a 350 µm mesh to reduce the possibility of zooplankton grazing during incubations. Nanoplankton productivity was estimated in 20 µm pre-filtered samples. The bottles were incubated in a deck incubator maintained at ambient water temperatures. The light levels of samples drawn from the various light depths were simulated using neutral density filters (Kahlsico Co.). All samples were filtered on to 0.45 µm cellulose membrane filters. The filter papers were subjected to conc. HCl fumes to dispel any adsorbed NaH¹⁴CO₃ and transferred to vials containing 4ml of dioxane based scintillation cocktail. Radioactivity on the filters was measured on a LKB Liquid Scintillation Counter model using the channels ratio method for quench correction.

Phytoplankton growth rates were monitored in surface water samples at different locations along the ice edge whenever the ship was stationary for more than two to three days at a stretch. All water samples were pre-screened through 350 µm nybolt screen to minimise interference due to grazing by zooplankton. Nanoplankton were isolated by screening the samples through a 20 µm net. The two sets of screened samples were

transferred to semipermeable transparent membrane bags and suspended in-situ by means of a rod projecting out of the ship. Adequate care was taken to ensure that the bags were well away from the Shadow zone of the ship during incubation. Growth rates were calculated after monitoring the differences in chl a before and after the incubation period. The expression $N_t = N_0 e^{-kt}$ was used to calculate the growth rates, where 't' is the time of incubation. 'N₀' is the initial chl a concentration per unit volume, 'N_t' is the final chl a concentration at time 't' and 'k' is the relative growth constant. The mean doubling time of the population was calculated using the expression $G = 0.301/k$.

RESULTS

Hydrography and chemistry :

Temperature :

In the ice-edge region, surface temperatures varied between -1.80 to -0.50°C . The melting of sea surface ice led to a lowering of water temperatures within the first 25 m. On the cruise track there was a gradual warming of surface waters northwards away from the shelf from 0.10°C at 68°S to 1.98°C at 57°S .

Nutrients :

In the ice-edge, nutrient salts viz. NO_2 -N, NO_3 -N and PO_4 -P ranged between 2.40 and 16.90 ; 0.15 and 1.84 and 0.89 and 2.34 $\mu\text{g} \cdot \text{l}^{-1}$ respectively. Offshore NO_3 -N concentrations varied between 6.27 and 10.80 $\mu\text{g} \cdot \text{l}^{-1}$. While NO_2 -N and PO_4 -P ranged from 0.06 to 0.42 and 1.26 to 1.83 $\mu\text{g} \cdot \text{l}^{-1}$ respectively (Figs. 2a and 2b), in either region, what was noticed was that these values were well above the limiting values reported for phytoplankton photosynthesizing under such environmental conditions (Eppley *et al.*, 1979). This was true even in such instances where a decline in the quantum of these salts was noticed associated with an increase in phytoplankton biomass.

Chlorophyll a

Surface concentrations of chl a in the ice-edge region varied between 0.60 to 3.43 $\text{mg} \cdot \text{m}^{-3}$. In the water column, chl a varied between 0.51 to 4.69 $\text{mg} \cdot \text{m}^{-3}$. The chl a maxima was generally located between 10–25 m (approx. between 16 and 1% of I_0). The mean chl a value at the depth of maximum chl a works out to be 2.82 $\text{mg} \cdot \text{m}^{-3}$. Column chl a integrated for the first 75 m varied from 54.50 to 259.48 $\text{mg} \cdot \text{m}^{-2}$ (Table 1). The mean column chl a for the ice-edge region is 151.50 $\text{mg} \cdot \text{m}^{-2}$. Chl a within the nanoplankton fraction varied between 0.36 to 4.54 $\text{mg} \cdot \text{m}^{-3}$ which represents 31 to 93% of the total chl a. The contribution of nanoplankton to total phytoplankton chl a in the euphotic column varied between 36 to 93% but declined thereafter in the disphotic zone, accounting for only between 31 and 64%. The average percentage contribution of nanoplankton to total phytoplankton chl a in the euphotic zone was approx. 70% and only about 49% below the euphotic zone. Chl a concentrations along the northbound and eastbound sections ranged from 0.15 to 1.20 $\text{mg} \cdot \text{m}^{-3}$ in the water column. Integrated values of chl a (0–75 m) varied between 15.48 to 100 $\text{mg} \cdot \text{m}^{-2}$ (Figs 3a and 3b). The overall mean surface chl a value for the offshore region is 0.44 $\text{mg} \cdot \text{m}^{-3}$ whereas the

average integrated value for the first 75 m is 36.41 mg m^{-2} . A significant elevation in both surface and column values was observed in the region between 64° to 62°S . The average surface and column values for this stretch between 64° to 62°S works out to 0.81 mg m^{-3} and 74.17 mg m^{-2} respectively as compared to the average values of 0.31 mg m^{-3} and 22.12 mg m^{-2} recorded outside this region. The contribution of nanoplankton to total phytoplankton biomass varied between 27 to 100%. The average for the offshore stations is 66%. No definite trend was observed in the percentage-wise distribution of nanoplankton in the offshore stations except that higher percentages were recorded in the first 25 m in the region between 64° and 62°S .

Primary productivity :

Primary productivity in the ice-edge region varied between a wide range of 0.12 and $63.44 \text{ mg C m}^{-3} \text{ day}^{-1}$. Offshore these values ranged between 0.12 and $7.68 \text{ mg C m}^{-3} \text{ day}^{-1}$. The average column productivity values for the ice-edge region and the offshore region were 836.94 and $59.15 \text{ mg C m}^{-2} \text{ day}^{-1}$ respectively (Figs. 4a and 4b). It is amply clear from the distribution patterns of both chl *a* and primary productivity values, that the ice-edge region was more productive than the offshore waters. An elevation in productivity values was observed in the region between 64° to 62°S offshore. The average column value for the region between 64° to 62°S was $74.17 \text{ mg C m}^{-2} \text{ day}^{-1}$ as compared to $22.16 \text{ mg C m}^{-2} \text{ day}^{-1}$ recorded for the other offshore stations. Nanoplankton accounted for between 38.53 and 98.32% of the total column phytoplankton production in the ice-edge and between 35.71 and 85.50% in the offshore region. The average percentage nanoplankton primary productivity values for the ice-edge and the offshore region were approx. 69% and 62% respectively.

Phytoplankton growth rates : Values for the relative growth constants and mean doubling times for the populations of natural phytoplankton collected from different days during the study period have been shown in Table 2. In all instances the mean doubling time for the nanoplankton fraction was always lower (16.50 to 19.50 hours) as compared to 17 to 54.23 hours recorded for the net phytoplankton fraction.

DISCUSSION

Chl *a* concentrations and primary production data did serve to emphasize the large regional differences in their distribution in the Indian sector of the Antarctic Ocean. The average column chl *a* and column primary productivity in the ice-edge were 151.50 mg m^{-2} and $836.94 \text{ gC m}^{-2} \text{ day}^{-1}$ respectively as compared to the average column chl *a* and column primary production of 36.41 mg m^{-2} and $59.15 \text{ mgC m}^{-2} \text{ day}^{-1}$ for the offshore region. The difference in the ice-edge and the offshore region column values of chl *a* and primary productivity rates are almost similar which is quite usual for these waters (Pant, 1986 ; El-Sayed and Taguchi, 1978). This wide margin of difference in the standing crop of phytoplankton in the ice-edge region and offshore region can be attributed to the added presence of eponitic algae released during the melting of sea surface ice apart from the holoplanktonic forms. During this study sea-surface ice samples were collected

routinely at several points in the ice-edge region and chl *a* estimated per unit volume of melted sea ice. The mean value recorded was 86.78 mg m⁻³ of melted sea ice which would be a tremendous addition to the water column, considering a large area of sea ice approx. 17 x 10⁶ km², goes on an annual cycle of retreat during summer in the ice shelf regions of Antarctica. (Gordon, 1981). Several other investigators have drawn attention to the importance of stability of the water column in controlling production (Svedrup, 1953 & Pingree, 1978). Lutjeharms *et. al.* (1985) postulated that the melting of sea surface ice in summer resulted in density stratification and enhanced vertical stability in the upper regions of the water column near the ice-edge. As a consequence, phytoplankton were retained in the upper lighted regions of the water column and could benefit from the abundant nutrients. Conversely in the offshore regions, El-Sayed & Mandelli (1965) attributed the low productivity offshore to comparatively low stability of surface waters which he claimed prevented the organisms from remaining in the lighted zone long for enhanced production. The large differences in the productivity values in the ice-edge and offshore regions observed in these studies serve to confirm the importance of water column stability in enhancing primary productivity. A zone of elevated chl *a* and productivity values that was observed on the stretch between 64° to 62°S (the Antarctic Divergence) in the waters offshore appeared to be associated with a frontal system. These frontal systems have long been recognised as areas of high biological productivity (Pingree *et. al.*, 1982). In the Southern Ocean their location has been observed to be intermittent highly variable and geographically restricted (Lutjeharms *et. al.*, 1985). For instance, Naqvi (1986) working in an area close to this study, during the 3rd Indian Antarctic Expedition located a frontal system about 2.5 degrees south of the Antarctic Divergence. On the other hand, Rama Raju and Somayajulu (1983) located a frontal system within the region of the Antarctic Divergence, clearly depicting the large variation in the position of these frontal systems in the Southern Ocean.

The relative contribution of nanoplankton to the standing crop in the ice-edge region ranged between 29–98% $\bar{x} = 66\%$. Offshore, these percentages varied between 26–100%. These values are high in contrast to the values of 20–40% recorded by Pant (1986), but agree well with those of Brockel (1981) and Weber & El-Sayed (1987). A potentially large percentage of the ¹⁴C fixation was due to nanoplankton which accounted for an average of 69% of the total production in the ice-edge region and 62% in the offshore region offshore waters. The contribution of nanoplankton to biomass and productivity was higher in the euphotic zone as compared to the disphotic zone. Qasim *et. al.* (1974) working on phytoplankton in tropical waters noted that smaller celled phytoplankton sank far more slowly than large phytoplankton and as such could continue to remain in the euphotic column for longer periods. As the cell surface area to volume ratio in nanoplankton is quite high, nanoplankton have a distinct advantage over the large volumed cells in the utilization of light and nutrients and hence tend to grow faster than microplankton (Eppley *et. al.*, 1969). This is exemplified by the growth rates recorded for nanoplankton which are about 1.6 times higher than those recorded for the net phytoplankton fraction. The average growth rates are 1.36 for the nanoplankton

fraction as compared to 0.76 for the net phytoplankton fraction. These values are high compared to 0.33 reported for Antarctic phytoplankton by Holm Hansen *et. al.*, (1977), but compare well with the value of 0.71 reported by El-Sayed & Taguchi (1977). The measurements of Holm-Hansen *et. al.*, (1977) were based on ATP assays. Hart (1978) has pointed out that a conventional ATP, assay overestimates its concentration by 33 to 135%. The ATP assays include all organisms in the sample and leave uncertainty in their ecological application (Mayzaud and Taguchi, 1978). In this work, growth rates were calculated from measurements of biomass increase with time in incubated samples. Chl *a* was chosen as the biomass index because of its analytical convenience and its direct relationship to the autotrophic population. It is concluded thus that the measurements made in this study represent a more reliable estimate of phytoplankton growth.

The present study underscores the importance of nanoplankton over net phytoplankton in the food chain dynamics of the Antarctic seas which have traditionally highlighted the importance of larger than normal celled diatoms. Our results on the measurements of phytoplankton growth rates assume tremendous significance in that nanoplankton showed much higher growth rates than previously suspected. These conclusions have serious implications for the overall community structure and trophic organization of the Antarctic marine ecosystem. Neyer & El-Sayed, 1983 and Quetin & Ross (1985) have found that krill the major secondary consumer showed preferential feeding on larger phytoplankton than nanoplankton. On the other hand Hewes *et. al.*, (1985) observed extensive feeding of nanoplankton and picoplankton (< 1 μ m) by heterotrophic flagellates and postulated that these flagellates form a major link for the transfer of energy from the nanoplankton fraction to larger zooplankton and krill. A tightly coupled system including nano sized primary and secondary producers together with nanoplanktonic heterotrophs, microzooplankton, net zooplankton and large zooplankton and carnivores has been described as the 'emerging paradigm' of the Antarctic marine food-web (El-Sayed, 1987).

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Table 1. Temporal variations in surface water nutrient concentrations, column Chl *a* and column primary production values in the Antarctic ice-edge region.

Date	Nutrient concentrations in surface waters				Column values (integrated 0-75 m)					
	µg at l ⁻¹				mg m ⁻²		mg C m ⁻² day ⁻¹		%	
	NO ₃ -N	NO ₂ -N	PO ₄ -P	Total chl <i>a</i>	Nano-plankton chl <i>a</i>	Total prim. Prod.	Nano-plankton Prod.	% Nano-plankton chl <i>a</i>	% Nano-plankton prim. Prod.	
27 Dec '86	10.90	0.22	1.92	234.68	180.25	835.20	868.35	76.81	98.32	
28 Dec '86	15.63	1.84	2.34	154.03	138.03	3334.80	2650.20	89.61	79.47	
11 Jan '87	2.40	0.15	1.59	259.48	181.80	1970.40	1174.50	70.06	59.61	
27 Jan '87	5.07	0.21	1.17	161.30	97.15	1150.30	490.80	60.22	42.67	
3 Feb '87	4.53	0.06	0.89	92.15	64.82	1183.00	784.20	70.34	66.25	
4 Feb '87	7.76	0.23	1.22	124.33	53.12	1600.80	616.80	42.73	38.53	
16 Feb '87	8.40	0.27	1.59	131.50	49.53	38.10	29.10	37.67	76.38	
21 Feb '87	7.25	0.21	2.06	54.50	39.55	90.00	81.60	72.57	90.67	

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Table 2. Relative growth constants (k), in log₁₀ day units and specific growth rates (μ) divisions per day of natural phytoplankton populations in the Antarctic ice-edge.

Date	Samples pre-screened thro' 350 μm mesh net		Samples pre-screened thro' 20 μm mesh net Nanoplankton	
	Total k	Phyto μ	k	μ
28 Dec. 86	0.29	0.97	*	*
12 Jan. 87	0.28	0.95	0.44	1.45
27 Jan. 87	0.40	1.33	0.39	1.30
3 Feb. 87	0.18	0.62	0.40	1.32
4 Feb. 87	0.25	0.82	0.38	1.26
16 Feb. 87	0.25	0.82	0.37	1.23
17 Feb. 87	0.13	0.44	*	*

* - No Data Available

NGR - No Growth Recorded

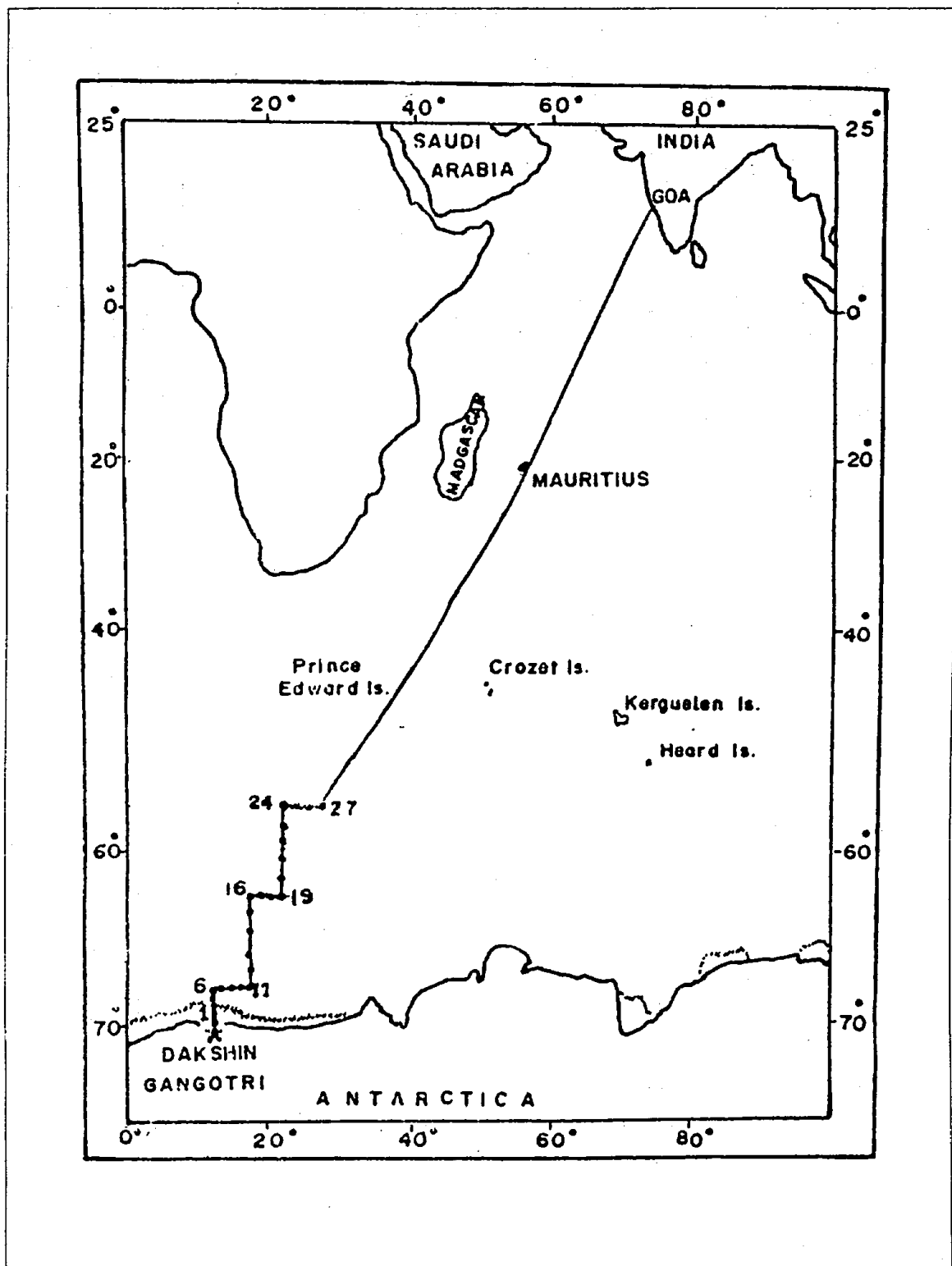


Fig. 1. Cruise track and station numbers

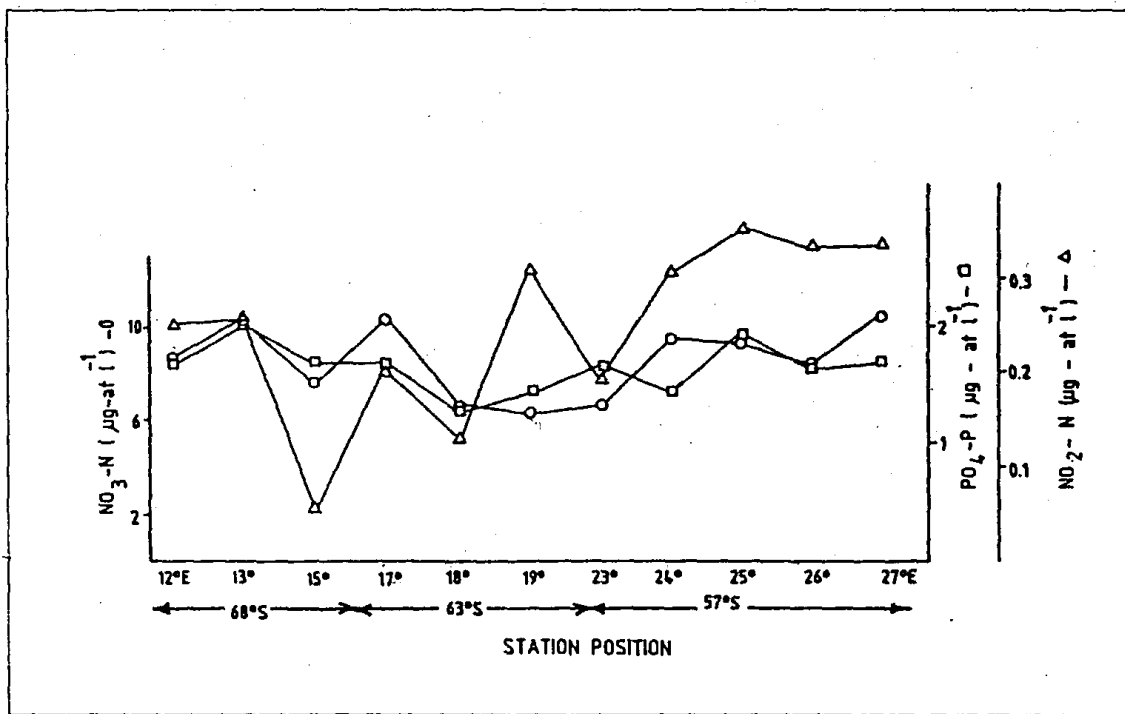


Fig. 2a. Distribution of nutrients in surface waters on the northbound transect.

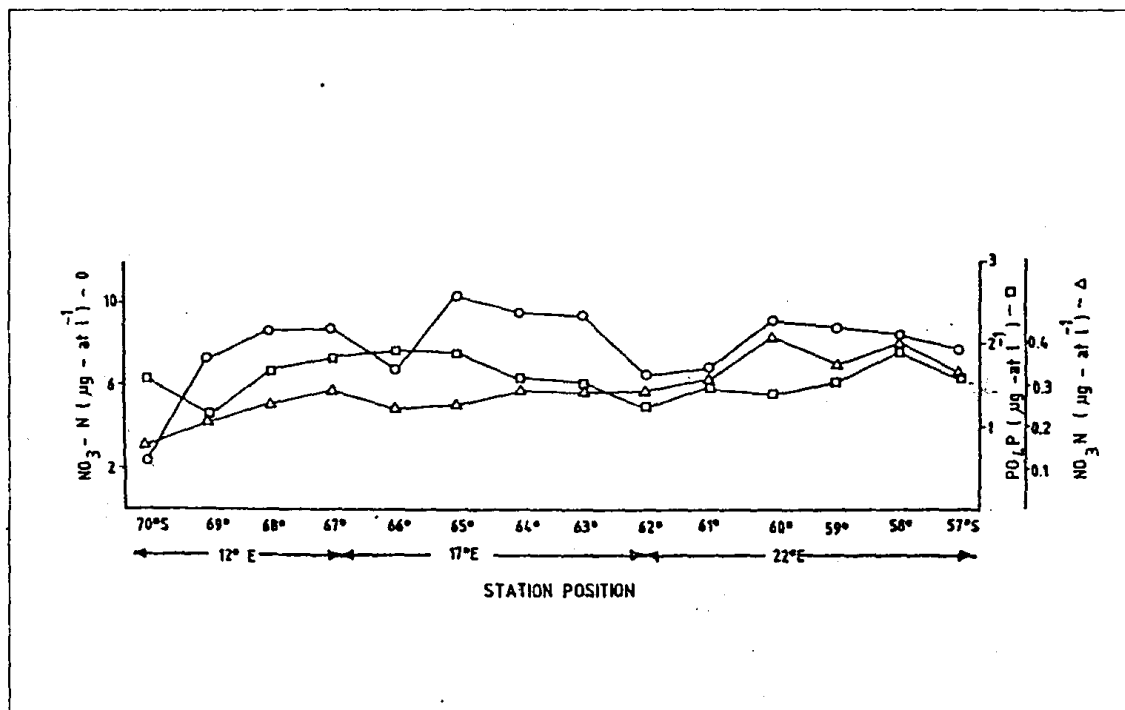


Fig. 2b. Distribution of nutrients in surface waters on eastbound transect.

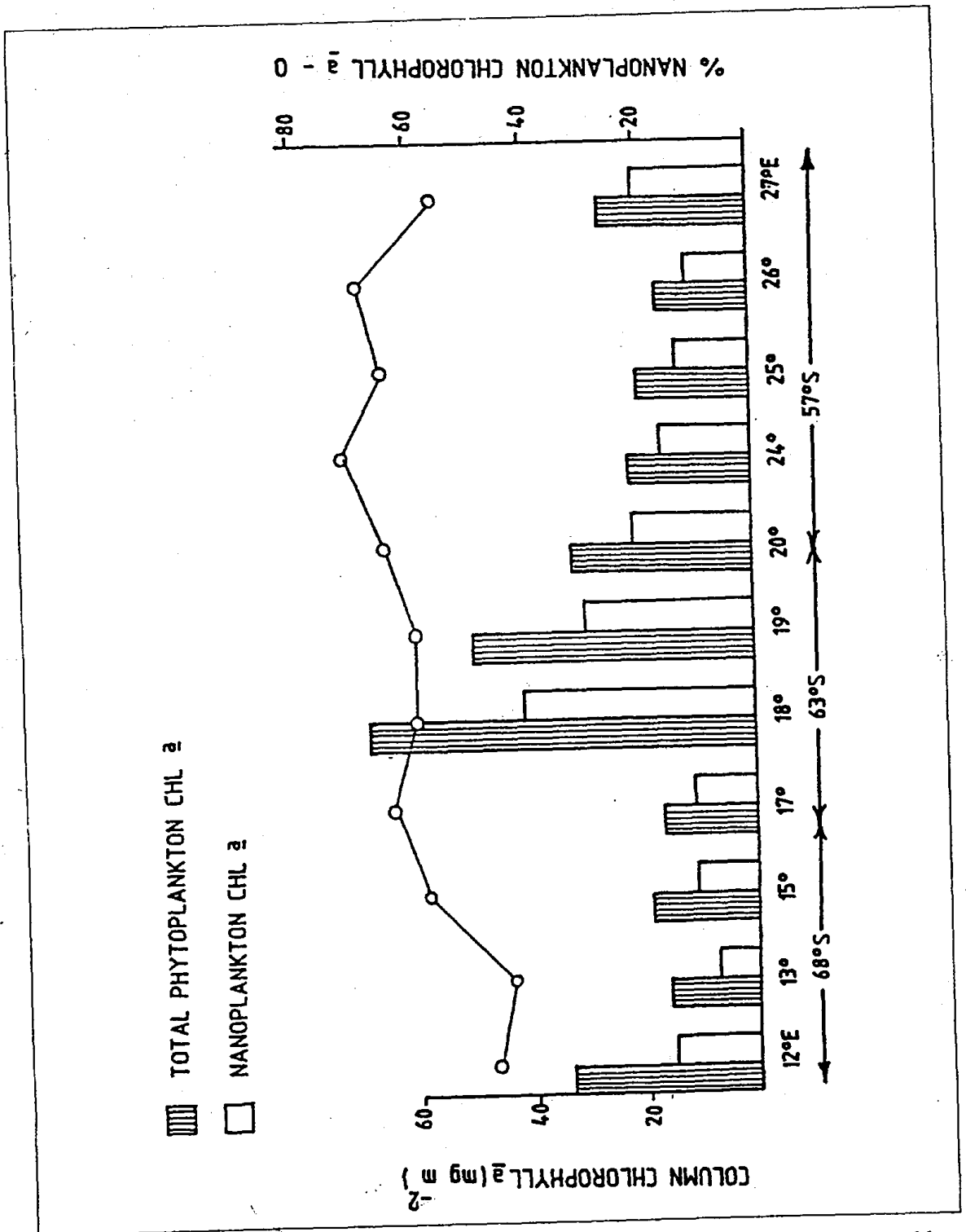


Fig. 3a. Distribution of column chl a (whole phytoplankton sample), column chl a (nanoplankton) and percentage nanoplankton chl a on the northbound transect.

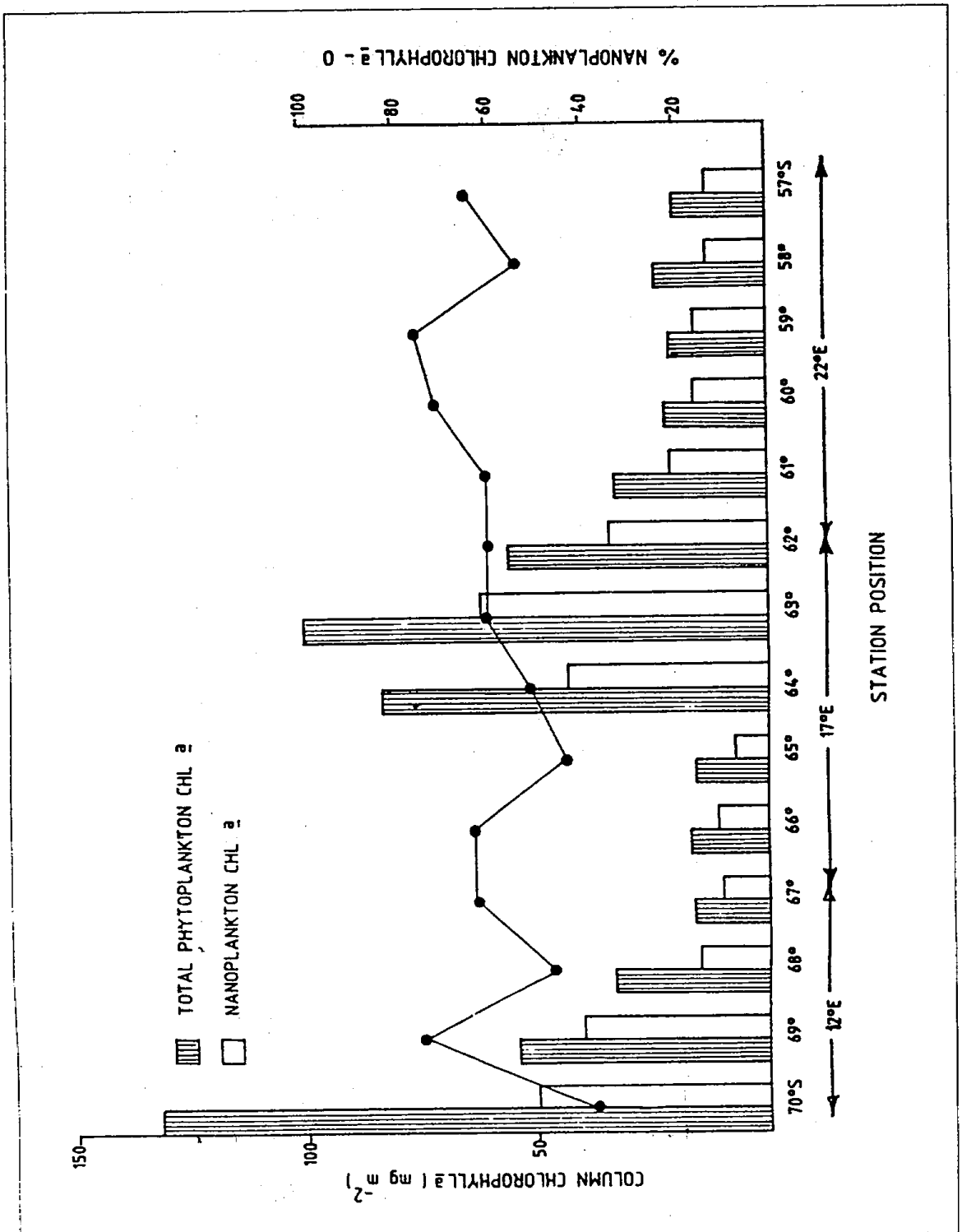


Fig. 3b. Distribution of column chl a (whole phytoplankton sample), column chl a (nanoplankton) and percentage nanoplankton chl a on the eastbound transect.

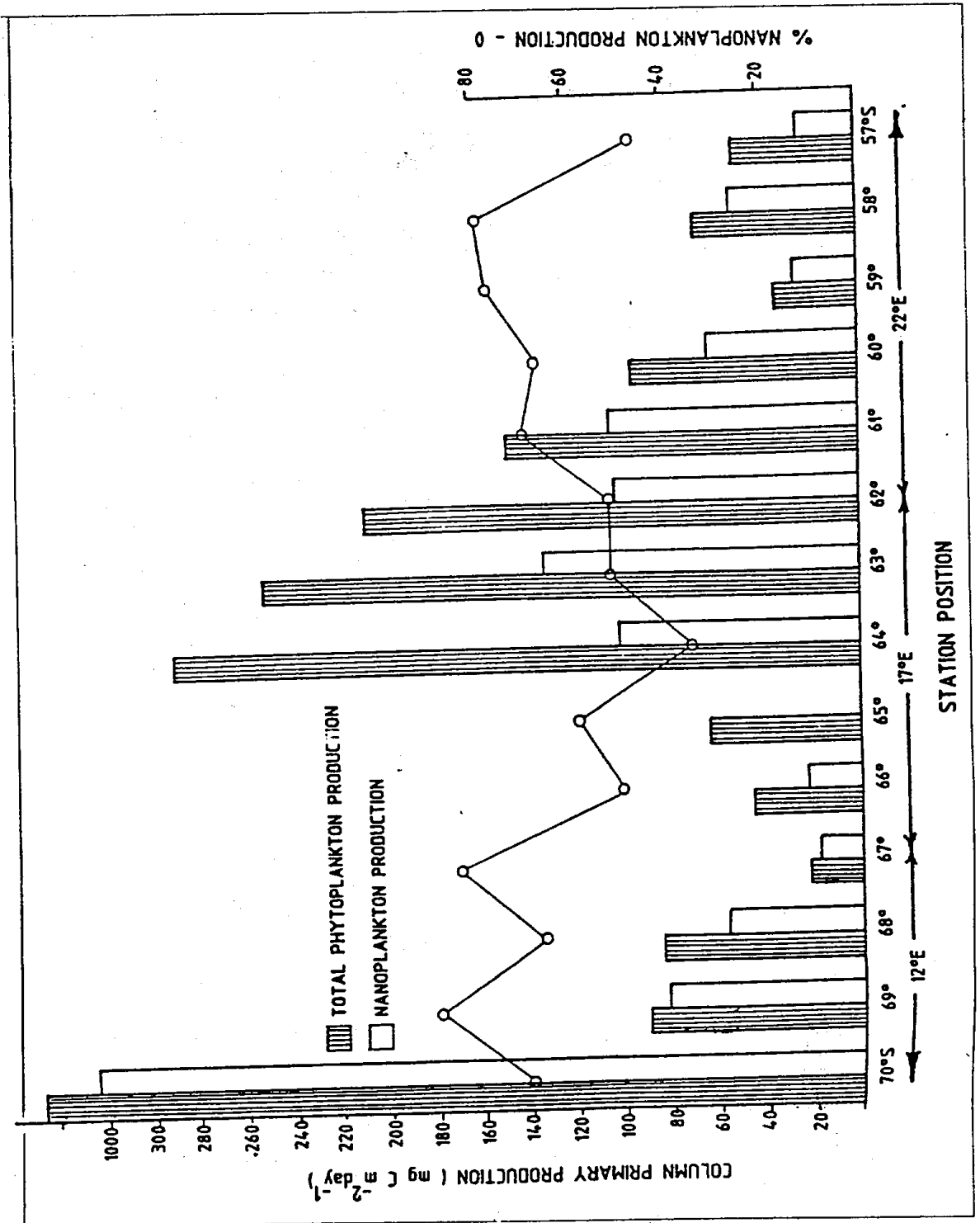


Fig. 4a. Distribution of column production (whole phytoplankton sample) column production (nanoplankton) and percentage nanoplankton production on the northbound transect.

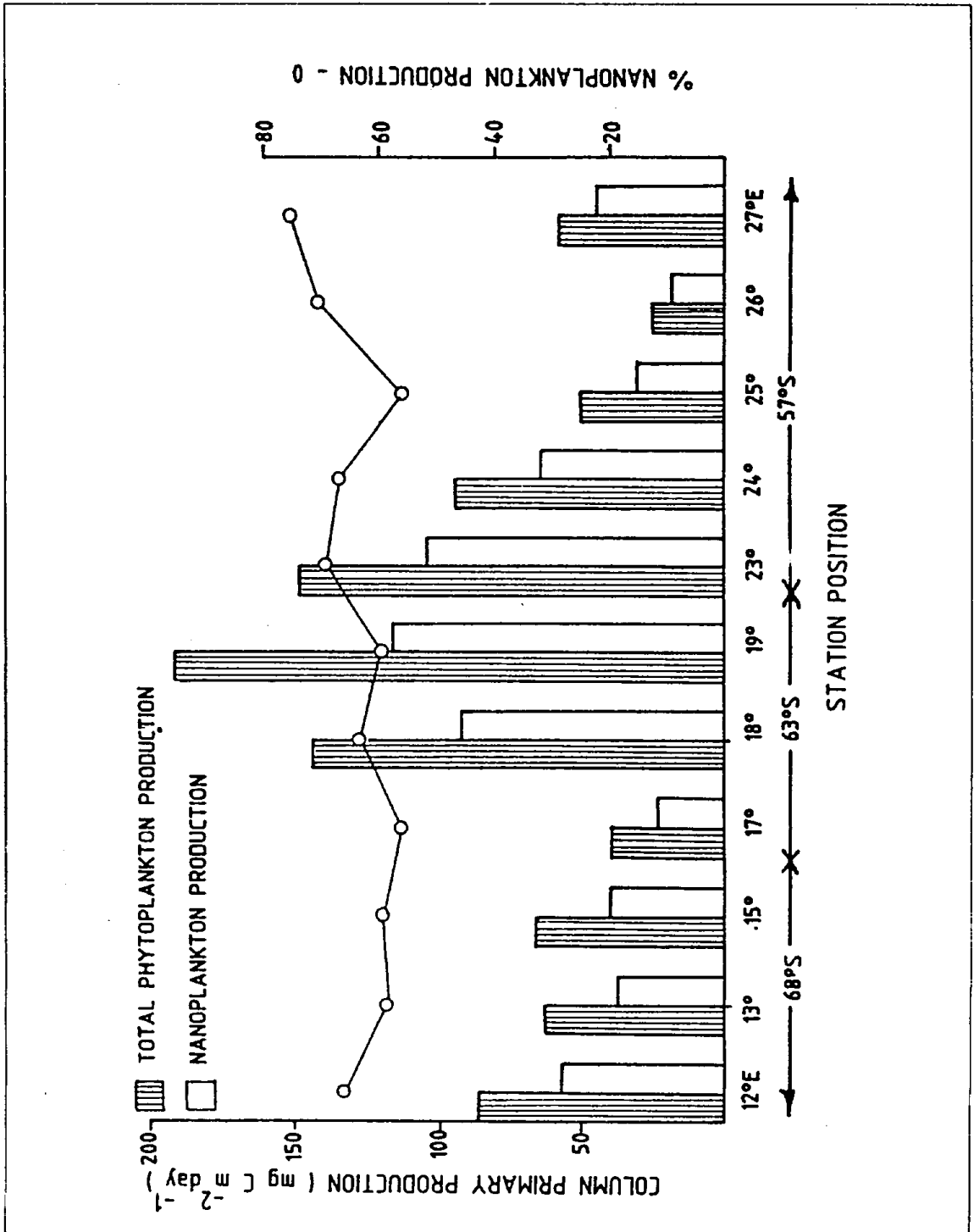


Fig. 4b. Distribution of column production (whole phytoplankton sample) column production (nanoplankton) and percentage nanoplankton production on the eastbound transect.

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